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Current Topics in Forest Research: Emphasis on Contributions by Women Scientists

Proceedings of a National Symposium

Gainesville, Florida

November 4-6, 1986



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Thirty-four papers are presented in nine categories: Silviculture/ Ecology, Genetics, Soils and Nutrients, Regeneration, Forest Products, Sociology, Economics, Policy, and Insects and Diseases. Also included is the Keynote Address, "Women in Natural Resources," by R. Max Peterson.

**Current Topics in Forest Research:
Emphasis on Contributions by Women Scientists**

Proceedings of a National Symposium
Gainesville, Florida
November 4-6, 1986

Compiled by
Susan V. Kossuth
and
Nancy A. Pywell

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PREFACE

The concept and objectives of this symposium were not new, only the cosponsors. The first symposium emphasizing contributions from women scientists was held in 1983. The increasing number of women in natural resources and the USDA Forest Service's commitment to promote, enhance, and endorse civil rights suggested that the timing was right for a second symposium to bring together women in natural resources research to present their research findings. This time the format was changed. An opportunity was presented to women and men to contribute oral or poster papers as well as to hear presentations from invited speakers.

To announce the symposium, information was sent to many professional journals in an effort to reach researchers in universities, government agencies, and forest industry. This was undertaken by the Program Committee, consisting of:

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We have many individuals and organizations to thank for the success of the symposium. First, special thanks to Jerry A. SESCO, Director, Southeastern Station, for creating the opportunity for the symposium, for his quiet behind-the-scenes

support and encouragement, for financial backing, and for serving as a buffer against critics by responding to their comments without bogging down the Program Committee. Thanks go to Arnett C. Mace and C.P. Pat Reid, University of Florida, School of Forest Resources and Conservation (SFRC), for their full endorsement in cosponsorship of the symposium. Thanks to Thomas F. Geary, USDA Forest Service, International Forestry, who was instrumental in announcing the symposium worldwide, resulting in the attendance of several women from foreign countries. A special thanks to Max Peterson, Chief of the Forest Service, for his positive comments in the Keynote Address. We wish to acknowledge the meticulous work of Monica Lindberg, University of Florida, SFRC, who handled registration and financial arrangements. Appreciation is extended to Jefferson-Smurfit Company for the afternoon tour "Southern Forestry in Action." Thanks also to many unnamed people in civil rights, personnel offices, and administrative positions in universities, government, and industry who supported the symposium by encouraging and supporting participants from their respective organizations. Finally, we wish to thank the speakers and participants who came and fulfilled beyond all expectations the objectives of the symposium as outlined in the opening Overview.

Papers published in this proceedings are as they were submitted by the authors--in camera-ready form. Authors are responsible for the content and accuracy of their papers. Statements by contributors outside the USDA Forest Service may not necessarily reflect Department policy.

SUSAN V. KOSSUTH
NANCY A. PYWELL

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OVERVIEW

Susan V. Kossuth

The first symposium of this kind grew out of the creative thinking of scientists at the USDA Forest Service, Northeastern Station, and developed with strong support from the enlightened management of their Director, Denver Burns. Margaret M. Harris of the Northeastern Station and Ann M. Spearing of the University of Vermont at Burlington made the concepts and ideas of the symposium a reality to me and many others in attendance at that first meeting on September 16-17, 1983. This second symposium originated in an informal discussion I had with Jerry SESCO, Director of the USDA Forest Service, Southeastern Station. He was concerned that I not feel alone and isolated as the only woman Project Leader and scientist in the Forest Service in Florida. We discussed opportunities for contact with other women scientists. I commented on the symposium held at Burlington in 1983 because there I made new friends and learned about companionship of women in research that is different from companionship of women with men in research. In the months after the first symposium I changed my whole concept of "women in forestry." The timing was right and the opportunity was created.

Many women, like me in 1983, do not even recognize that they need meetings such as this. By attending such symposia, they are working to obtain full status as professionals in natural resources. Meetings that emphasize women in natural resources raise the consciousness level that they are indeed professionals. For those of us with a Ph.D., "full status" means the "rights, privileges and prerogatives thereof"--and it must be a two-way street. We give our loyalty, time, and energies to our institutions; our employers must respond in kind. This symposium testifies to the fact that the day of the "token woman" is gone and that women indeed belong right where they are, in the jobs in natural resources that they love.

So why are we here? We are here because increasingly women are being given equal employment opportunities in the profession: women are highly competitive, they have a lot to offer the profession, and they are changing the workforce. Thus, women are making a statement. Times have changed in the United States, and the natural resources profession is out of balance in regard to the ratio of men to women. This conference represents women who are working in the profession and bringing it into balance. Women in natural resources research cover the spectrum. They graduate from universities to the Forest Service and other government employment, to industry or private enterprise, and to faculty and other research positions in universities.

There are many objectives for this symposium. The first is to focus on women scientists and their research findings. Of importance, this is to be accomplished in the same manner as it would be at national or international meetings within each discipline. The second is to establish communication links among women and men who are interested in helping women obtain and remain in employment in which to grow, to develop, to make contributions, and to advance in their careers. Some call this networking. The third major objective is to involve women graduate students so they can meet women who are already on the research career ladder. They need to know women are a positive force that is needed in this area of scientific endeavor called forestry and natural resources. This symposium is an excellent opportunity to see women as active professionals, and where graduate students may find role models or mentors. Natural resources is a satisfying profession and it needs the support of women to remain a strong, vital, and dynamic enterprise in these great United States. Each one here may add other reasons for attending and, whatever they are, we are happy you came and hope you come away with much more than you gave--the same as I did from the first symposium in Burlington, Vermont.

WOMEN IN NATURAL RESOURCES

R. Max Peterson, Chief, Forest Service
U.S. Department of Agriculture

ABSTRACT...The importance of the work being shared at this conference is not that it was produced by women, but that it is a contribution to science. Conferences that spotlight the high quality of work being done by women scientists will help breakdown stereotypes and encourage other women to pursue excellence in professions previously dominated by males. As we move closer to the goal of equal opportunity we must not lose respect for individual differences. It is the diverse backgrounds of a well-integrated society that provide unique perspectives, insights, and solutions to the challenges we face.

I am delighted to be here, and honored to be the keynote speaker at this conference. I am impressed with the depth and breadth of the papers being presented. The topics are certainly worthy of widespread review. It is both encouraging and disappointing that papers of this caliber are being presented at a conference primarily aimed at and organized by women. I look forward to the day when the number and quality of scientific contributions by women is so much a part of major scientific events that a separate seminar would simply not be considered necessary or appropriate.

This conference is encouraging because it provides a showcase for the high quality work being done by women in natural resource management and research. It also provides an opportunity to celebrate the fact that there are an increasing number of women scientists who are making significant contributions to forest science.

The history of women in science is long and illustrious, dating back at least to Madame Curie's pioneering contributions to the study of magnetism, radiation, and atomic structure and as recent as the success of Rita Levi-Montalcini (LEVI MONT-ALCHEENEE), who, along with her partner Stanley Cohen, received this year's Nobel Prize for Medicine for their work studying cell growth and the orderly development of tissue.

By the way, I think there is an interesting side note to these two examples I used. Madame Curie was educated in Poland but couldn't find work as a scientist until she moved to France and married Pierre Curie. In other words, the hurdles to overcome for a female researcher were almost insurmountable then. If her husband had not sponsored her, it is doubtful that she would have been given the opportunity to make the contributions she made.

In the more recent example, Ms. Levi-Montalcini said that she had to do most of

her early research at home. Her ethnic heritage did not allow her to take the same path to success that her research partner took.

Fortunately for all of us, despite the fact that these two great scientists did suffer discrimination, they were able to overcome adversity. That brings me to the first point I'd like to make today--a society that allows or encourages contributions from scientists from only one sex, or race, or ethnic background is doing itself a great disservice. Its progress as a society will assuredly be retarded.

We face many important challenges in the area of natural resource management. We need the best scientists, the best researchers, the best minds searching for solutions that will allow this and future generations to prosper. And we need the push for excellence that only comes from open competition to move up organizational ladders or to get financial grants, or to receive other opportunities and recognition.

That open competition has been a long time coming in professional and scientific organizations that traditionally were dominated by white males, and the Forest Service was no exception.

I promise I won't go on at length about our numerical success in providing opportunities for women--I feel that ticking off numerical strength often displays more about an organization's failure than it's success--any number that doesn't display full equality is really a reflection of how far we have yet to go! Nevertheless, for the sake of reference, I do want to provide some statistical accounting of the progress women are making in developing careers in natural resource sciences.

The first woman scientist hired by the Forest Service, Eloise Gerry, undertook wood structure research at the Forest Products Laboratory in 1910--the same year the Laboratory was established. In 1978, Susan Kossuth became the first woman to head a Forest Service research project. That was a long time coming!

It was 1932 before a woman graduated with a degree in forestry. She found employment in biology, since the notion of women actually working in forestry was still too radical to entertain.

The first woman professional forester was hired by the Forest Service in 1957--eight years after I started work in the Forest Service. That was a long time in coming too! To finish the milestones, the first female District Ranger was selected in 1979, and the first female Forest Supervisor was appointed in 1985.

How long before we have our first female Chief? Well, there's no doubt in my mind that one of my successors will be a woman.

The examples of slow progress that I've just cited all pertained to the Forest Service. However, the track record for other government agencies, universities, and private businesses could be written in the same lackluster manner.

Fortunately, women are making great strides today in the natural resource sciences and are assuming their rightful place as innovators, managers, and leaders. However, the true success story cannot be found by simply examining how many women or other minorities are entering the natural resource sciences.

That success must be measured not by how we treat everyone as equals--I see providing equality as a moral and ethical responsibility--but by how well we acknowledge and use everyone's unique talents and knowledge. For today, I'd like to focus attention on open competition, not only as a moral imperative, but as a contribution toward our social well-being.

As women, Blacks, Hispanics, Asians, Native Americans, and other minorities first started moving into the sciences, the emphasis was not on learning from them, but in fitting them into positions that were once held almost totally by white males. We often missed the boat by not taking advantage of the new resources being made available for the benefit of us all--qualified professionals with a particular perspective, with particular insights, and with unique solutions to challenges we faced.

I think the benefits to be achieved from equal opportunity are especially important in the natural resources sciences. We have a good understanding of basic scientific principles. What we don't know is who will, or how someone will, take these basic principles, rearrange them according to their unique vision, and realize a major breakthrough in solving current problems.

No one can really predict these kinds of scientific breakthroughs. No one picked Einstein out as a child who would someday provide major insights into how our world operates. Even now, no one knows what caused him to visualize the reality of $E=mc^2$, but where would the discipline of physics be today if Einstein had been prevented from working in his chosen science?

I said earlier that I was delighted to be here. The reasons transcend my position as Chief, and they transcend my career in the Forest Service. Some of those reasons can be traced to my role of father of three daughters and one son. As a parent, I felt that my children's aspirations and capabilities should not be limited or shaped by their sex. I think that's the real underlying message of this conference.

A society doesn't reach its potential until all of its members have the opportunity to reach their potential. Freedom means that a minimum of restrictions are placed on the individual. The number of women in natural resource sciences is not representative of the number of women in our society. I think this is due in part to the fact that, in the past, women were not encouraged to enter the sciences. So some of the problems we face go back to elementary and high school.

Research has shown that our expectations of others play a large role in determining behavior. For example, teachers who were told that a class they were about to start teaching was composed of very bright students tended to have a class that excelled. Similarly, if we expect that we can attract top-notch women in science, we will attract more top-notch female students.

When I was in school, relatively few women studied natural resource sciences or engineering . . . they weren't expected to! There were no women foresters, engineers, or other scientists in my graduating class. Women were in the traditional schools of journalism, nursing, education, and so on. Perhaps conferences such as this will raise all of our expectations.

Without downgrading the seriousness of the obstacles in your paths, I think some obstacles for women are self-imposed, just as they are for men. In my job, I get asked by a lot of people about career planning. I did a videotape setting out my basic advice, and it should be widely available--at least in each of the Forest Service's Regions and Stations. If you haven't seen it, I hope you'll ask to have it shown. Because my advice pertains to women as well as men, I'd like to share some of my career counseling thoughts with you.

When you're trying to build a career, I recommend you look at what the organization or field of study is likely to need in terms of future talent. For example, if an organization will be going through an expansion, it will reward those employees who are flexible and fast learners. If an organization is stable or if it is going through a period of austerity, it will seek out those employees who have built a breadth and depth of expertise that will allow jobs to be done more effectively. If an organization must deal with high priority national problems such as acid rain, it will seek out people who are adaptable and have an interest in helping provide solutions.

A second bit of advice I would pass on is that nothing succeeds like success. To find out how you can benefit your career, talk to people who have been successful. Find out the ingredients of their success. I think each successful person will tell you some of the same things, such as:

1. It's important to work as part of the team.
2. It's important to be able to communicate well, including listening. Interpersonal skills are important in every position in an organization.
3. It's important to have a positive attitude. There's an old saying, "Smile and the world smiles with you." There's a lot of truth to that. No one advocates being blind to difficulties, but successful people tend to see the difficulties as challenges to be overcome, not problems to run from. As a variation on the notion of positive thinking, I'm sure each of you has been in a situation where someone else got credit for your work, or someone else with the same qualifications got a better deal than you. It happens. Everyone gets imposed on at some time. How you handle such situations may be important to your success. Cynicism and pessimism are poisons to good ideas and good people.

Another piece of advice I pass on to people trying to build a career is that you need an orientation to the future. Traditions are important. Integrity is a must. Respect for other individuals is essential, but the one thing you can't do if you want to move forward is to live in the past. It's always a mistake to think a situation is temporary, and someday we can all go back to the "good old days." You can't. The successful people are moving toward tomorrow and helping lead the way.

A final bit of advice for people, both men and women, who are interested in building a career is that you must develop a broad orientation or perspective to your work.

Whatever your job is, it's important to understand the nature of your organization; how others fit into the picture--what their responsibilities are; and how many different jobs or tasks compose your particular field of endeavor.

There's a popular notion that if you are going to advance in your career, you must learn more and more about your particular field. That's not always true. The climb up the career ladder is not always a straight line. I think the opportunity of gaining a broader perspective is one of the side benefits to the interdisciplinary process increasingly used both in research and in operating programs. By working together, you can learn the concepts, ideas, and scientific principles of several disciplines. There is a cross-fertilization of skills and abilities. It is sometimes surprising to see the benefits of working with others.

A good example is in the field of medicine and electronics. Who would have thought years ago that someone with an M.D. degree would go back to school to study electronics, or be working closely with an electrical engineer to jointly analyze problems and seek solutions? Or, who would have thought that an electrical engineer would have to learn about how the human body functions to work effectively with a medical team? Today, the pacemaker and electronic and nuclear diagnostic equipment are just examples of the synergism of interdisciplinary approaches.

interdisciplinary approaches.

There's one other major topic I want to cover here today. That is the notion that while we strive for open competition and equality, we must not lose respect for differences. Managers have a very difficult job in this regard. They must recognize differences in a constructive way without appearing to create separate categories. There are differences between how men and women, or individuals from various ethnic backgrounds, will function on a job.

Within the last year, I was at a meeting and one of the District Rangers came to me and told me that we have another "first" in the Forest Service--our first pregnant District Ranger. She was pregnant, and she told me about some of her plans, such as working with her assistant to appoint an Acting Ranger during her maternity leave. So we had a new situation we had to deal with, and there are a lot of those that Gifford Pinchot never had to deal with. So we couldn't look at traditional approaches. This didn't mean it was a serious problem--it was merely a new one.

We have to ask what we can do so women are not forced to make a decision between having a career or having a family. Of course, when concessions are made in this direction, the question arises about the rights of men to also be given time off for paternity leave.

We have to ask what can be done to lessen the trauma of a career move in a two-career family. In this regard, we've launched a dual-career family policy which makes it possible that if one member transfers, the other is found appropriate employment in the new location. However, this presents the possibility that the dual-career family policy penalizes the single person. With the number of dual-career families at an all-time high, and with a growing number of people delaying marriage to build a career, you can see the difficulty of the questions we are facing.

I am looking forward to hearing some of the other speakers present their papers. The scope of this conference indicates that we have made good progress in achieving our goal of equal opportunity. Let me highlight some of the ideas I've presented today.

While the theme of the conference is women in science, the importance of the work being shared here is not only that it was produced by women, but that it is a contribution to science. The challenges we face in the natural resource sciences are too difficult for us to exclude any element of society from the search for solutions.

I also mentioned that in our race to achieve statistical success, we sometimes overlook a more critical value in having people with diverse backgrounds working together--that is, that diversity allows for a cross-fertilization and expansion of ideas.

I tried to offer some key points I have found useful in building a professional life, and I discussed some of the dilemmas we face as we try to find solutions that will provide equal opportunities for all.

Once again, let me congratulate all of you for putting together a very impressive conference. By spotlighting the accomplishments of some of our women scientists, you are encouraging others to follow in their footsteps.

Katherine C. Ewel²

Abstract. --Use of models for resource management is increasingly appropriate because of the growing complexity of resource management issues. Three factors limit the complexity of models that are constructed to address these issues: the amount of information necessary to construct and simulate the model; inherent error in the integration process; and the advisability of restricting the range of turnover times of the state variables that comprise the model. Models that describe only one or two basic processes in an ecosystem, such as decomposition, may be useful in spite of their simplicity. More complex models that describe entire ecosystems are often most useful if they are part of an on-going research project. Models of entire landscapes may be less complex than ecosystem models because of greater aggregation of state variables, but they are useful nonetheless for exploring management implications.

Keywords: Simulation model, non-linear differential equations, integration error, aggregation

With increased population pressure and a shrinking land base, resource management has become more dependent on active manipulation not only of ecosystems but often of entire landscapes, even for maintenance of "natural" conditions. The ability to do this, however, requires an understanding of simultaneously interacting factors such as climate variables, primary and secondary productivity, nutrient cycles, water availability, and fire frequency, as well as the perturbations introduced by management. It can be extremely difficult, however, to perform the necessary integration mentally. With increased availability and diversity of computers, the ability to conceptualize, to express mathematically, and to explore the multitude of relationships among components in managed and natural ecosystems, watersheds, and even landscapes has increased greatly.

These interactions can be explored effectively by constructing and simulating computer models. A model is an abstraction of reality: a simplification of a complex system. The mathematical models that I will discuss are sets of non-linear differential equations that express inflows and outflows from the components (state variables) that comprise a unit of the landscape, such as an ecosystem, that is assumed to be discrete. Simulation of such a model for exploring resource management practices requires estimating the magnitudes of the state variables and their flows and expressing the precise relationships among the state variables and other factors (such as climate) that govern them.

SCOPE AND USEFULNESS OF MODELS

The complexity of a model should be limited as much as possible to ensure its usefulness. Two factors set these limits. First, each interaction and/or process that is included in a model must be described in the equation, and its magnitude must be estimated. Because equations for most state variables contain at least two flows (usually more), each of which may include one or more interactions with other components, the amount of information required to support the equations mounts rapidly as the number of state variables increases. Second, there is usually no precise analytical method for solving systems of nonlinear differential equations. (The major exception is use of an analog computer, which usually limits the size and complexity of a model.) Using a digital computer is inherently inaccurate, requiring discrete time steps rather than instantaneous solutions. Although the amount of integration error can be reduced by selecting small time steps and/or sophisticated integration routines, rounding error also accumulates at each integration, at least partially offsetting any increased accuracy. Consequently, a larger model carries the potential for greater cumulative error. Because the relative importance in the model of feedback mechanisms, such as predation, and forcing functions, such as climate variables, may vary, there is no straightforward association between the accuracy of a model and its complexity. Nevertheless, it is clear that a modeler should relinquish simplicity with great reluctance.

A model should be constructed so that its state variables have turnover times that are approximately the same order of magnitude. Equations simulating the behavior of state variables with widely varying turnover times (e.g., algae and trees) are called "stiff" equations, and they may be unstable, not providing

¹Presented at the Symposium on Current Topics in Forest Research: Emphasis on Contributions by Women Scientists.

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any useful information about the real system. Two approaches for incorporating such state variables are available. A portion of a model can be excised as a subroutine and solved with a different time step, e.g., an hourly photosynthesis module in a model that includes annual changes in plant biomass. But it is then difficult to allow the simulated processes in the subroutine to interact significantly with the rest of the model, and the two become fairly independent. Moreover, the subroutine with the shorter turnover time, which is ostensibly introduced to increase accuracy, may in fact be subject to greater error because of integration error, as described above. The second approach is to incorporate state variables with short turnover times into a general, aggregated state variable (e.g., including phytoplankton and macrophytes as "plant biomass" in a lake model). The risk is in losing details that may be significant (such as the relationships between phytoplankton and consumers that may change in very short time periods). Unfortunately, there is no easy method for selecting the appropriate level of resolution; the choice must be based on the system being simulated and the issues or questions that the model is intended to address.

Lack of a data base should not deter model construction. Clearly, a strong data base and independent validation are necessary if a model is to be used to establish actual management practices. However, a model may also illustrate

the range of behavior patterns a system may follow under a variety of possible values for both state variables and processes, providing insight into the structure and function of an ecosystem as well as direction for further research efforts. Consequently, the purpose of the model should be considered before judgement is made about the extent of its data base.

Models may therefore differ in complexity, the scale of processes that are included in them, and the amount of data that support them. The strategy of determining the appropriate level of complexity, deciding on the appropriate time and geographic scales, and dealing with a large or small data base must be determined for each model. Five models that describe a broad range of complexity (1 - 21 state variables) are outlined in Table 1 and are described below to illustrate these points.

PROCESS MODELS

Although many resource management models may focus on specific ecosystems, simple models that describe important processes within an ecosystem may be of interest to resource managers. One of the first ecological models to be simulated (Olson 1963) describes the process of litter decomposition:

$$dQ/dt = -k * Q$$

Table 1. State variables included in five resource management models.

| PROCESS MODEL | ECOSYSTEM MODELS | | LANDSCAPE MODELS | |
|---------------------------------|------------------------------------|--|------------------------------|-------------------------------|
| <u>Litter Decomposition</u> | <u>Florida Pine Plantation</u> | <u>Florida Lake</u> | <u>Commercial Forest</u> | <u>Tropical Watershed</u> |
| Labile biomass | Pine foliage | Phytoplankton | Foliage | Land in forest |
| Refractory biomass | Pine stems and branches | Macrophytes | Stems and branches | Land in coffee |
| | Pine coarse roots | Macrophyte storage organs | Coarse roots | Land in pasture |
| | Shrubs | Epipelagic algae | Fine roots | Human population |
| | Herbs | Zooplankton | Litter and humus | Soil moisture |
| | Litter and humus | Benthic invertebrates | Soil organic matter | Sediments |
| | P in pine foliage | Omnivorous fish | Understory | |
| | P in pine stems and branches | Adult primary predator fish: biomass and numbers | | |
| | P in pine roots | Young primary predator fish: biomass and numbers | | |
| | P in shrubs | Adult secondary predator fish: biomass and numbers | | |
| | P in herbs | Young secondary predator fish: biomass and numbers | | |
| | P in litter | Number of white amur | | |
| | Available inorganic P | Particulate dead organic matter | | |
| | Total inorganic P | Detritus | | |
| | Soil water | P in detritus | | |
| | Deep aquifer | Inorganic P: epilimnion and hypolimnion | | |

This general model defines the decomposition constant, k , as an index of the rates at which dead organic matter (Q) decays and, indirectly, nutrients may be remineralized in the litter layer, a fairly discrete subsystem of many ecosystems. The accuracy of this model is increased by the use of two state variables rather than one (see Table 1): labile organic matter (A), which decays rapidly, and refractory organic matter (B), which consists primarily of structural material and decays more slowly:

$$dA/dt = -k_1 * A \quad dB/dt = -k_2 * B$$

This simple model was used to demonstrate the apparent impact of wastewater disposal on foliage quality as well as on decomposition rate (Dierberg and Ewel 1984). However, doubling the number of state variables also doubles the number of estimates necessary for simulation: the proportion of each of the components as well as the decay rate of each. This two-variable model has also been used to establish confidence bands for estimates of the two decay rates that describe the decomposition process (Portier and Ewel 1981).

ECOSYSTEM MODELS

Constructing and simulating a model of an entire ecosystem may serve any or all of three purposes: to test the feasibility of hypotheses about ecosystem dynamics; to determine priorities for future research by examining the behavior of the components of a model; and to predict the consequences of proposed management practices. Consequently, the data base required for a model may range from minimal to extensive based on the degree of use that the model may receive.

A model of a managed slash pine (*Pinus elliottii* Engelm.) plantation was constructed over a period of several years, as the information about magnitudes of carbon and nutrient storages and the nature of the interactions among carbon, phosphorus, and water cycles slowly increased. The earliest version of the model (Ewel et al. 1978) was developed from a very small data base and an understanding of basic ecosystem processes. Expansion of the model as the data base increased improved the resolution of this model (Table 1; Golkin and Ewel 1984), and pinpointed belowground processes as the most important target for future research. Further development has led to a partially validated, 1-yr version of the model that continues to serve as a tool for setting research priorities and may eventually become a management tool.

When data-gathering and model building are simultaneous, model development may be much more rapid, and all three goals may be realized. The carbon and phosphorus dynamics in a Florida lake that had been invaded by an exotic aquatic plant (*Hydrilla verticillata* Royle) were simulated as part of a large-scale research effort that included documentation of annual patterns in water quality and plant and animal populations. By incorporating into a single model the dynamics of major groups of plant and animal populations, dead

organic matter, and organic and inorganic forms of phosphorus (see Table 1), it was possible to demonstrate that addition of a fish that eats aquatic weeds could increase the biomass of benthic invertebrates and of game fish such as bass, increase the water quality, and increase turnover rate of carbon in spite of decreased photosynthesis rates (Ewel and Fontaine 1982, 1983). Once validated, such a model could be used to determine specific management strategies for aquatic weed control.

This model, however, contains state variables that span a wide range in turnover times: from 2 hr for carbon incorporated in phytoplankton to 29 days for carbon incorporated in omnivorous fish; turnover times for inorganic dissolved phosphorus and for detritus represent an even broader range. The combination of widely varying turnover times and the damping of programmed climate factors by the aqueous environment decrease the stability of the model, particularly when it is simulated for a long time, and therefore compromise its usefulness for exploring a broad range of potential management strategies. The pine plantation model has a greater probability of usefulness for management because the ecosystem is structurally more simple, and hence easier to express in a model, and because of the importance that climate plays in regulating inflows, outflows, and rates of processes in the structure of the model.

The usefulness of these ecosystem models is not restricted to management, however. The results also outline the general patterns and magnitudes of carbon, nutrients, and water cycles, serving as a basis for comparison not only with similar ecosystems but among ecosystem types as well. The following general carbon budgets derived from the two ecosystem models described above demonstrate the differences in magnitude and apportionment that can occur:

| Components and Processes | Florida Pine Forest | Florida Lake |
|---|---------------------|--------------|
| Live plant biomass (t/ha) | 8.0 | 0.4 |
| Gross primary productivity (t ha ⁻¹ yr ⁻¹) | 2.1 | 1.1 |
| Plant respiration (t ha ⁻¹ yr ⁻¹) | 1.2 | 0.7 |
| Increase in live biomass (t ha ⁻¹ yr ⁻¹) | 0.8 | 0 |
| Grazing (t ha ⁻¹ yr ⁻¹) | 0 | 0.1 |
| Detritus production (t ha ⁻¹ yr ⁻¹) | 0.2 | 0.4 |

LANDSCAPE MODELS

Expanding an ecosystem model to incorporate the patterns found throughout a landscape need not require increased complexity. An aggregated version of the slash pine model was constructed to explore the implications of different kinds of forest management practices on large scale carbon

storage patterns in commercial forests (Table 1). Nutrient and water cycles were omitted, replaced by factors in the carbon fixation term that account for fertilization and latitudinal changes in evapotranspiration. Simulating this relatively simple model (seven state variables and 1-yr age classes for the pines) resulted in a broad spectrum of uses, from verifying a hypothetical decomposition rate for soil organic matter (Cropper and Ewel 1983) to predicting the magnitude of decline in carbon storage patterns that could be expected if Florida plantations were intensively managed for biomass production (Cropper and Ewel in press). The model was sufficiently general to be applied to a similar analysis of the impacts of forestry practices on carbon cycling in the Pacific Northwest (Cropper and Ewel 1984). Although this general a model cannot compensate for site-to-site differences among individual forests, it expresses the general patterns that can be observed in a landscape. Its data base is stronger than the ecosystem models, in part because it is much simpler. Its breadth in geographic scope is matched by a long time-scale. Without having been validated, it has suggested potential long-term effects of resource management strategies on global carbon storage patterns.

Many processes that can be expressed in considerable detail at the ecosystem level can be aggregated at the landscape level. A model simulating population growth and related changes in land use patterns in a large tropical watershed, and their impacts on sedimentation in a proposed downstream reservoir in the Dominican Republic was constructed by assembling simple models of population growth, land use change, and water balances (Table 1; Antonini et al. 1975). This model had only six state variables. The data base was sufficient to program historic land use changes, population growth, and climate. Although it was too general to predict the specific lifetime of the reservoir, the model was useful for comparing relative impacts of a series of government policies, such as controls on forest harvesting, other land use conversions, and emigration, that would affect population and land use in the watershed. It demonstrated the importance of interactions among different components of the landscape in determining the impacts of management strategies.

CONCLUSIONS

Neither the degree of complexity nor the availability of data need define the usefulness of a model in resource management. Very complex models with only a small data base can be useful in setting research priorities; as the data base broadens they become more useful for interpreting research data. Very simple models, on the other hand, can accurately describe general behavior patterns of a portion of an ecosystem or of an entire landscape. It is also clear, however, that much of the responsibility for making best use of

a model rests on the shoulders of the modeler. A model should not be expected to be more than an abstraction of reality, but it can clearly serve as a useful tool in probing reality.

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Many silviculturalists are interested in treatments or combinations of treatments that increase production efficiency. Efficiency is improved if there is a reduction in production cost per unit of a desired quality. For a forest crop, that reduction can be measured directly in dollars. Costs associated with a silvicultural regime include the operational costs of cultural treatments, costs of installing studies to document treatment effects, costs of waiting for operational or research results, and costs of taking a wrong action. These costs make mathematical models of stand growth necessary tools for projecting probable treatment effects and resulting yields. To be useful for extrapolation, a model must reflect observed or quantified behavior of stands over the long term. This paper briefly outlines loblolly pine (*Pinus taeda* L.) stand behavior and reviews several recent advances in modeling silvicultural treatments in loblolly pine stands.

BEHAVIOR OF LOBLOLLY PINE STANDS

Much of what is known about the development of loblolly pine stands is derived from long-term observations in density-control studies installed at very early ages in natural stands and from planted spacing studies. Examination of long-term results provides much information about the effects of height growth, initial density, and the interaction of these factors in stand development.

The following are observations from loblolly pine stands of the same initial density:

- a. Stands on poor sites contain more trees per acre than stands on better sites at the same age (Figure 1);
- b. At the same mean height of dominant trees, stands on better sites contain more trees per acre than stands on poorer sites (Figure 2); and
- c. Better sites can support higher basal areas than poorer sites.

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Abstract.---Accurate prediction of stand growth and yield requires a thorough understanding of the effects that various silvicultural treatments have on stand structure and development. Tree improvement, thinning, site preparation and fertilization have been shown to change the shape and/or level of growth curves. Therefore, modeling success can be best achieved where emphasis is placed on the effect of those treatments on the basic relationships underlying stand growth and development and validation against long-term data.

Given the same site quality, basal areas and volumes produced from stands of different initial densities converge, cross over, and decline (Figure 3).

Mean annual increments of both volume and basal area culminate earlier on better sites than on poor sites and at higher initial densities than at lower initial densities. These observations and trends are apparent in the compiled information from long-term density studies (Balmer *et al.* 1975, Harms and Lloyd 1981, Gilmore and Gregory 1974, Arnold 1978, Arnold 1981, Sprinz *et al.* 1979, Hafley *et al.* 1981, Buford and Hafley 1985, Harms and Langdon 1976).

TREATMENTS

Silvicultural treatments have three classes of goals: 1) manipulating the tree directly by genetic improvement, 2) improving the competitive environment by thinning or weed control and 3) improving the chemical and physical environment by site preparation or fertilization. Advances in modeling these treatments rest on determining their effect on relationships basic to stand development.

Tree Improvement

Using long-term, block-planted genetic studies to investigate the effects of tree improvement on loblolly pine stand dynamics, Buford (1986) and Buford and Burkhart (1985) found that: 1) for seed sources and families, the shape of the height-age curve is dictated by the site, but the level of the height-age curve is dictated by the seed source or family (Fig. 4); 2) for seed sources and families, the shape of the height-diameter relationship at a given age is determined by the site and initial density, while the level of the height-diameter relationship is determined by the seed source or family and is directly related to the dominant height of the seed source or family at that age; and 3) if silvicultural treatments are the same and are equally successful, variances of height and diameter in stands originating from selected genotypes are not different from those in genetically unimproved stands. The implications for modeling growth of stands originating from selected genotypes are: 1) genetic improvement of trees affects the rate at which stands develop, but does not fundamentally alter the pattern of stand development from that of unimproved stands; 2) changes in genetic material on a given site will likely affect the level, but not the shape, of basic associations such as the height-age and height-diameter rela-

tionships; and 3) correctly characterizing the height-age profile is crucial. In general, growth of genetically improved loblolly pine can be modeled by altering the height-age curve in current growth and yield models to reflect differences in the level, or site index, attained by different sources or families (Buford and Burkhart 1986). At present, there is a major effort to identify key hypotheses about dynamics of stands of genetically improved stock and to determine the most efficient experimental means to test those hypotheses (Nance et al. 1986).

Thinning

Several diameter distribution models have been developed which include a thinning component. Thinning is accomplished by truncating the diameter distribution or by removing certain proportions of stems from specified diameter classes. Height is predicted from a height-diameter equation and is not among the thinning criteria. Examples of this type of model are given by Matney and Sullivan (1982) and Cao et al. (1982).

An individual tree model treats the stand as an aggregate of separate trees, each having specific characteristics. Such a model for loblolly pine stands was presented by Daniels and Burkhart (1975). In this model, thinning was accomplished by removing individuals meeting specified criteria from the diameter distribution. Although the individual heights are known, height was not used in thinning decisions. In the models discussed above, stand parameters are not functions of initial density or spacing, but of the number of surviving trees at any given time.

A model for thinned stands mathematically derived from a model for unthinned stands was presented by Hafley and Buford (1985). The stand is modeled as a bivariate distribution of heights and diameters with stand characteristics predicted from age, initial density, and dominant height. The model shows the convergence of basal area and volume observed in long term density studies. Thinning was accomplished by manipulating the bivariate distribution so that thinning decisions are based on height and diameter. The model was validated using data from long-term thinning studies. It closely predicted height and diameter distributions for 25 years after thinning under various regimes (Smith and Hafley 1986). Key decisions made in developing this model were that the growth of all stand characteristics, including height, is affected by initial density, that height growth effects the growth of other stand characteristics and, therefore, that height should be considered in thinning decisions.

Fertilization and Site Preparation

Recent results from the Lower Atlantic Coastal Plain indicate that both bedding and phosphorus fertilization alter the shape and level of the height growth curve on a given site. Results at ages 10 and 15 from a study in South Carolina (McKee and Wilhite 1986, Buford and McKee 1986) and at age 13 from a study in North Carolina (Gent et al. 1986) consistently show differences

of 10 feet or more in average height (at ages 10, 15 and 13) between bedded plus phosphorus and control treatments. Differences in the shape of the height-age profiles are more pronounced among treatments on the wetter sites (McKee and Wilhite 1986). Indications are that progress can be made in modeling these treatments by quantifying the effects of changes in the soil chemical and physical properties on the height growth profile.

CONCLUSIONS

This paper has presented a compilation of observations on loblolly pine stand development. Advances in modeling silvicultural treatments such as tree improvement and thinning have been made where emphasis has been placed on the effect of the treatment on basic relationships underlying stand growth and development. Progress in yield projection will continue if the emphasis in model building is placed on understanding changes in the underlying relationships of stand dynamics and validating the resulting models against long-term data.

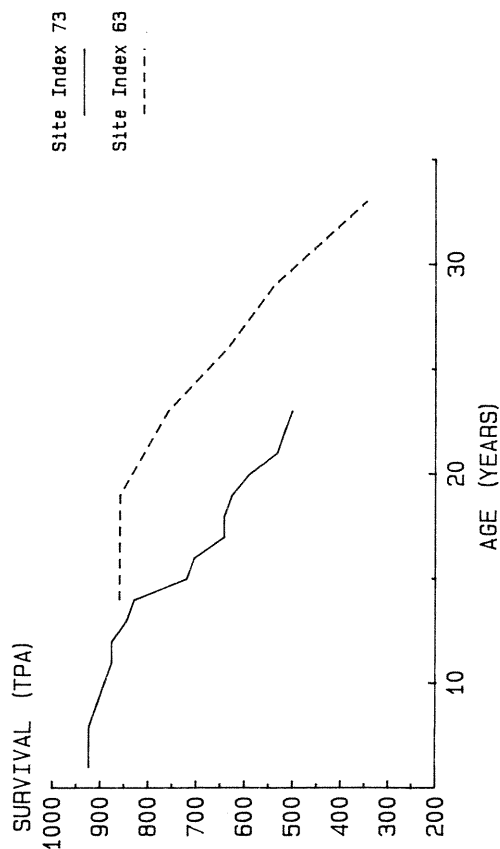


Figure 1.--Given the same initial density, stands on poorer sites contain more trees per acre than stands on better sites at the same age.

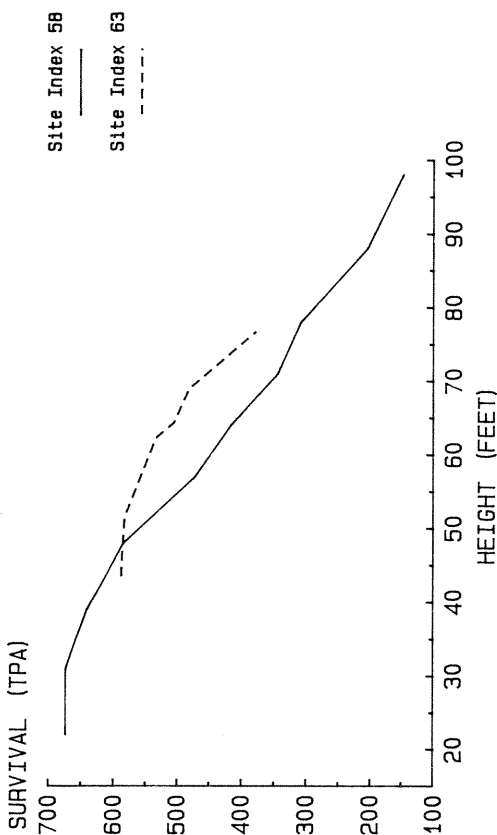


Figure 2.--Given the same initial density, stands on better sites contain more trees per acre than stands on poorer sites with the same dominant height.

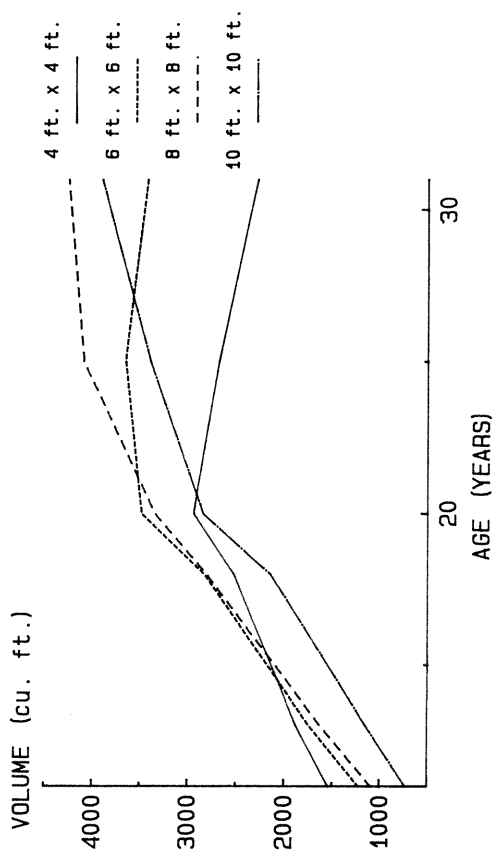


Figure 3.--Volume per acre over time for four spacings on the same site.

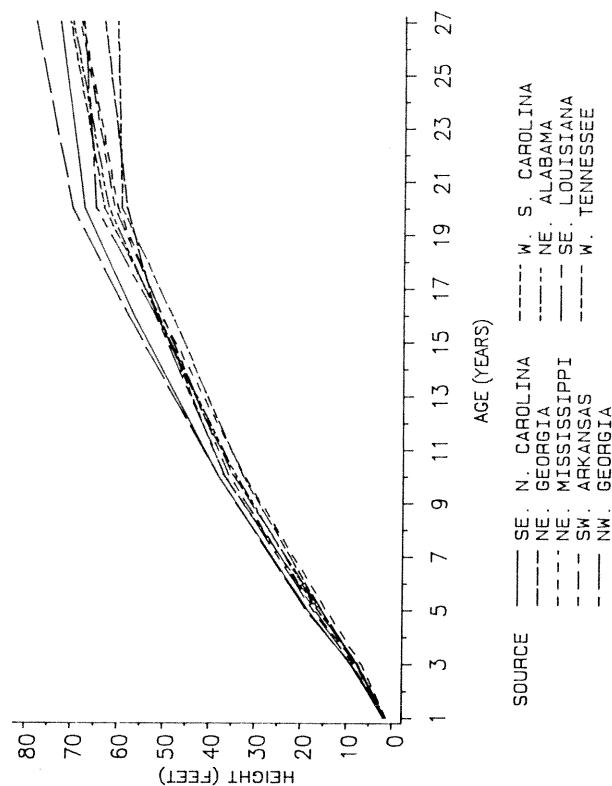


Figure 4.--Height-age profiles for sources at one location of the Southwide Pine Seed Source Study.

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Pacific Northwest forests present a fascinating paradox: low species diversity of host trees and high species diversity of fungi. It is well known that both the diversity and abundance of fleshy fungi (Basidiomycetes and Ascomycetes) are tremendous.

Why are there so many different fungal species? Is fungal taxonomic diversity related to ecophysiological diversity? For these ectomycorrhizal fungi, have they specialized in some physiological roles? Are some fungi better than others at processes which affect their host - such as enhanced nutrient uptake? Or alleviation of water stress? This paper discusses these questions and presents experimental research which answer some of these questions.

Species diversity, we suggest, is related to physiological diversity, especially fungal physiological processes which can affect the host. Historically, ectomycorrhizal fungal benefits to the host have been documented in 2 major areas: water relations and nutrition (Harley and Smith 1983, Marks and Kozlowski 1973, Alexander 1983, Reid and Bowen 1979, Parke *et al.* 1983 and many others).

Therefore, we suggest that some fungi are able to take up nutrients more rapidly than other fungi and that the host tree will benefit from this increased ability of the fungi. Similarly, some fungi may be better able to take up water from the soil and relieve plant water stress than other fungi. In the following sections, we discuss linkages between fruit bodies and fungi on tree roots, followed by a discussion of evidence that ectomycorrhizal fungi differ in their abilities to take up water and nutrients - both in pure culture and in association with tree roots.

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Abstract A fascinating paradox is the low species diversity of trees in the Pacific Northwest and the high species diversity of associated ectomycorrhizal fungi. This paradox suggests that the fungal diversity may arise from a physiological specialization for nutrient and water uptake, which will benefit the host trees. This paper describes research to support this hypothesis.

Keywords: Ectomycorrhizae, fungi, conifers, water stress, nitrogen uptake, phosphorus uptake.

LINKAGES BETWEEN FRUIT BODIES AND ROOT-ASSOCIATED FUNGI

Fruiting of Ectomycorrhizal Fungi

Fruiting Patterns

Sporocarps (fruit bodies) of ectomycorrhizal fungi are a dominant diverse feature of the forest floor and litter in many coniferous forests. An estimated 43% of the above-ground (epigeous) sporocarps in a Scots pine plantation were ectomycorrhizal; the remaining species were saprobic fungi (Richardson 1970). In Pacific silver fir stands in western Washington, USA, 50-85% of the epigeous sporocarps were ectomycorrhizal (Vogt *et al.* 1981). Observations on probable mycorrhizal fungi and lists of general occurrence have been made by numerous researchers (Trappe 1962 and papers cited therein; Ammirati *et al.* 1981; Knighton 1976; Rhoades 1972; Maas and Stuntz 1970). In some Douglas-fir forests, there may be more than 300-400 different ectomycorrhizal fungal species, but we know of no studies which have systematically surveyed these forests (Ammirati pers. comm.). In addition, hypogeous fungi are often neglected.

Importance of Hypogeous Fungi

Ectomycorrhizal fungi may fruit above-ground (epigeous) or below-ground (hypogeous, truffles) or they may not fruit at all. Hypogeous species, although they are not readily visible, are abundant and are often mycorrhizal (Fogel 1981, Vogt *et al.* 1981). The Pacific Northwest forests "harbour more known truffles species than any comparable area on earth...." (Trappe 1980).

In Oregon, 24 different below-ground species were found in a young Douglas-fir stand (Fogel 1976, 1981). Similar numbers were reported in an Italian oak stand, a German red beech forest, and a German spruce stand (Ceruti *et al.* 1967, Gross 1969). Productivity of hypogeous fungi is impressive - up to 16,700 sporocarps per hectare in a western Oregon Douglas-fir forest, with optimal production located about mid-way between any 2 tree stems (Fogel 1976).

Fruit Body-Root Connections

Thus far we have been discussing only the fruit bodies. How are fruit bodies related to ectomycorrhizal fungi on roots?

Ectomycorrhizal species are generally assumed to be functioning in a forest ecosystem if their fruit bodies are present. However, this assumption lacks supportive evidence and needs careful evaluation. "Our knowledge of most higher fungi is so very meager at the moment because our results are dependent entirely on observing fruit-bodies and these are only a small part of the actual fungus...." (Watling 1974, p. 231).

The ectomycorrhizal fungus complex consists of fruit bodies attached to hyphae in the litter/soil matrix and of fungal hyphae on the roots. The major functioning part of the complex is the ectomycorrhizal hyphae on the roots. However, most physiological studies have been conducted with fungi isolated from sporocarps.

Identification of Ectomycorrhizal Fungi

Fruit Bodies

Identification of ectomycorrhizal fungi is based entirely on the fruit body - using a variety of characters such as color of spores and the fruit body (mushroom cap and stalk), presence of gills or pores, microscopic examination of hyphal structures, etc. Even with the presence of a fruit body, often identification can be difficult (Ammirati pers. comm.).

Root-Associated Fungi

Isolation and Identification Difficulties.

Fungi are difficult to isolate from roots, in contrast to the relative ease of isolation from mushroom sporocarps (Zak 1969, 1973; Molina and Palmer 1982). Further, root-associated fungi are difficult to identify since they do not produce sporocarps in pure culture. Thus although it is important to work with ectomycorrhizal fungi known to be associated with roots, little work of this kind has been done due to difficulties of isolation, culture and identification.

Methods of Identification. By detailed morphological studies of roots ectomycorrhizal with a single, known fungal species, one can learn to identify certain fungi with reasonable success. Using characteristics of gross root morphology, degree of root branching, thickness and color of hyphal sheath, length and diameter of hyphae, etc., Last and co-workers could distinguish 3 different ectomycorrhizal types on tree roots (Last et al. 1985).

Detailed studies of ectomycorrhizal root morphology are being done by Agerer (Agerer 1987). In some cases, electron microscopy has

been used to study ectomycorrhizae (Strullu 1976). Ascomycete hyphae (simple septa) can be distinguished from Basidiomycete (dolipore septa) (Scannerini and Bonfante-Fasolo 1983). Several researchers have tried to identify fungal hyphae on the basis of species-specific monoclonal antibodies - but with limited success (Schmidt et al. 1974; Chard 1981; Wright and Morton, W. VA Univ., pers. comm.).

In our laboratory we are using DNA restriction enzyme patterns to identify these ectomycorrhizal fungi. The DNA methodology involves growing fungi in pure culture and harvesting after several weeks. We are trying several different protocols for DNA extraction which involve a CTAB extraction followed by cesium chloride density gradient centrifugations. When the DNA is sufficiently clean, restriction enzymes are used to cut the DNA, followed by Southern blots, using a yeast ribosomal probe. We have had some success with several fungal species - Boletus edulis, Laccaria laccata, and Hebeloma crustuliniforme.

Regardless of the methods chosen, it is clearly important to be able to identify fungi on roots. Then we can begin to understand fungal succession on roots and to study the different physiological functions of these fungi.

ECOPHYSIOLOGICAL DIVERSITY

Tree growth is often limited by water stress and nutrient availability, particularly phosphorus and nitrogen. Since nutrients and water enter the tree primarily through mycorrhizal roots, it is likely that these fungi can exert major controls on these processes. We know that mycorrhizae generally enhance water and nutrient uptake, but little is known about how individual fungal species differ with respect to these processes. The following sections discuss the ecophysiological diversity of ectomycorrhizal fungal species for water and nutrients.

Water Stress

Mycorrhizal associations can increase transpiration flux and the ability to tolerate water stress in their host trees. These benefits may result from several fungal effects. First, fungi explore a greater soil volume, taking up more water. Secondly, fungi improve the nutritional status of the host, thus optimizing the whole plant's physiology and its water status. Thirdly, some fungi produce rhizomorphs (root like hyphal strands) which are specialized for rapid water transfer through the hyphae. Fourth, the hyphal system has a capacitance for water storage, increasing the amount of water available to the host. What is the experimental evidence to substantiate these four suggestions?

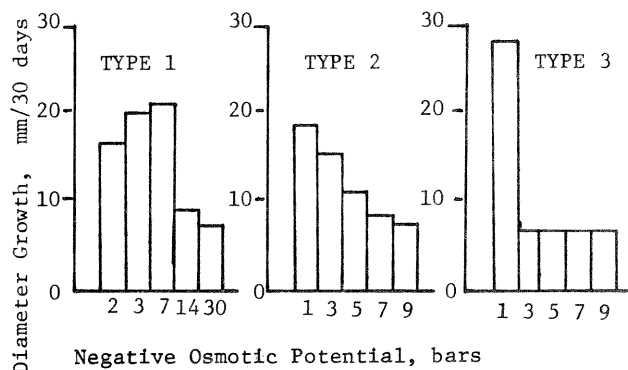
Although most work has been done with endomycorrhizae, the more limited work with

ectomycorrhizae does support the hypothesis that mycorrhizae increase water movement through the host (Ekwebelam and Reid 1983; Parke *et al.* 1983; Dixon *et al.* 1980; Reid 1979). Ectomycorrhizal roots can survive greater soil moisture depletion than nonmycorrhizal roots, perhaps due to the fungal ability to tolerate greater water stress levels than those tolerated by plant roots (Cromer 1935; Goss 1960). If fungi can influence the host water status, what ecophysiological diversity exists among different fungal strains?

In pure culture, using polyethylene glycol (PEG) to induce osmotic stress, the fungus *Cenococcum geophilum* seems to be very tolerant of low water potentials, unlike such fungi as *Suillus luteus* and *Telephora terrestris* (Mexal and Reid 1973). This fungus can survive low water potentials in the field as well (Pigott 1982). Two different fungi, *Rhizopogon vinicolor* and *Pisolithus tinctorius*, also differ in their response to PEG-imposed water stress (Dieblot and Mudge 1985).

We have collected data for a number of species and found a wide range in fungal growth response to PEG-imposed water stress in pure culture (Fig. 1). These diameter growth data represent 3 patterns of response to stress. Type 1 represents fungi which exhibits tolerance to stress, since the fungi can grow better under moderate stress (-3 or -7 bars) than under little (-2 bars) stress. Type 2 fungi have an intermediate response with progressive inhibition of growth as osmotic stress increases. Type 3 fungi show total inhibition of growth under any osmotic stress at all. In our current work, we have found another pattern, which suggests that some fungal species may be able to develop stress tolerance (M. Coleman, pers. comm.). These fungi initially grow poorly under imposed stress, but adapt over time and grow more rapidly.

Figure 1. Diameter growth in mm of 3 types of ectomycorrhizal fungi grown for 30 days in liquid culture of varying osmotic stress from -1 to -30 bars (Fig. 1)



An important step in evaluation of the range of responses of fungi to water stress is an examination of these fungi when in association with tree seedlings. We are proceeding to synthesize mycorrhizal seedlings with these osmotic-stress tolerant and intolerant seedlings to determine if the fungal attributes are passed on to the host. Similar work is being done by Mudge at Cornell NY (pers. comm.). In some other seedling work, Parke *et al.* 1983 have shown that some fungal species apparently allow seedlings to recover faster from drought stress.

Nutrient Uptake

Ectomycorrhizal fungi clearly benefit the nutrition of their hosts, particularly for nitrogen and phosphorus. We believe that some fungi are better than others at uptake of N and P. Further, this enhancement should increase nutrient levels in the tree.

Phosphorus

Fungi take up and store inorganic P (and perhaps organic P), but most fungal data in pure culture are for nonmycorrhizal fungi (Beever and Burns 1980).

In our current work, we are screening a number of different ectomycorrhizal fungi for their ability to take up inorganic phosphate. Preliminary results indicate that these fungi do differ in their phosphorus uptake rates (Brown, unpublished data).

For ectomycorrhizal roots, Langlois and Fortin (1984) reported differences in rates of P absorption between different color types of ectomycorrhizal roots. The absorption of golden ectomycorrhizal apices was much higher than that of the 3 other types throughout the season (Langlois and Fortin 1984).

There are also differences in phosphatase activities of a number of different fungi (Antibus *et al.* 1981; Ho and Zak 1979; Calleja and D'Auzac 1983). Phosphatase activity may or may not be related to P levels in the surrounding medium; data are conflicting (Calleja and D'Auzac 1983; Dighton 1983; Lacaze 1983; Doumas *et al.* 1980; Alexander and Hardy 1981). Clearly much more research on the functions of the various phosphatases is needed. In general, however, it seems likely that fungi do differ physiologically in their ability to take up phosphorus.

Nitrogen

Inorganic Nitrogen. Mycorrhizae can enhance uptake of inorganic N by trees (Bowen and Smith 1981; France and Reid 1978; Littke 1982; Rygielwicz *et al.* 1984a and 1984b). Fungal species grown in pure culture differed in their rates of ammonium uptake (Littke *et al.* 1984). The most rapid rates (*Pisolithus tinctorius*)

were 600 micromoles per gram dry weight roots per hour, 3 times greater than the lowest rates, observed in a strain of Hebeloma crustuliniforme.

The genus of the host also affected N uptake since uptake rates of Douglas-fir mycorrhizal with Hebeloma were higher than were uptake rates for western hemlock mycorrhizal with the same fungus (Rygiewicz et al. 1984a).

Mycorrhizal fungi may also be able not only to increase nitrogen uptake but also to shift the pH optimum for ammonium uptake (Rygiewicz et al. 1984a) and alter ionic balance during ammonium uptake (Bledsoe and Rygiewicz 1986).

Organic Nitrogen. Soluble organic N exists in many soils in ecologically significant concentrations. Mycorrhizal roots may be able to take up this form of N as well as the inorganic forms of ammonium and nitrate. We have studied the abilities of different ectomycorrhizal fungi to take up organic N in the form of amino acids (Bledsoe and Sangwanit, unpublished data). Our data suggest that the choice of the fungal partner can affect the amino acid uptake rate. Further, the mycorrhizal roots seem to store more amino acids in the roots, while nonmycorrhizal roots transfer more N to their shoots (Sangwanit and Bledsoe, unpublished data). All the above data support the hypothesis that there are differences in the ability of ectomycorrhizal fungal species to take up N and these differences may affect the nutrition of the host.

SUMMARY

Since mycorrhizal roots are the principal means by which trees communicate with the soil environment, understanding this linkage is necessary to the study of how forests function. We will contribute to this understanding by learning how ectomycorrhizal fungi differ functionally. This knowledge may help to explain why certain fungi do not survive when outplanted only dry, nutrient stressed sites (Bledsoe et al. 1982). In addition, identification of specialized fungal species may allow selection of fungi to enhance tree seedling growth on these stressed sites.

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Stand Dynamics and Early Growth of Yellow Birch
and Associates in the White Mountains¹

Deborah B. Hill²

Yellow birch is usually regarded as one of the more valuable commercial species of the northern hardwood forest. Today in northern New England, it still ranks third as veneer logs and fourth in sawlog value. Historically, it has averaged between 10 and 20 percent of the northern hardwood association, but in recent decades, yellow birch has been observed to be closer to the lower end of that range and its proportion in younger age classes indicates further decline in numbers.

Generally, sugar maple and beech appear to be distributed throughout old growth and second growth northern hardwood stands. Birch, on the other hand, is located primarily along streams or in other moist sites (Hoyle 1965, Kujawski and Lemon 1969). Near the periphery of its range, yellow birch is found almost exclusively on very wet sites. It is hypothesized that yellow birch is able to compete more successfully on wetter sites that are less desirable for other species, but is unable to compete aggressively with sugar maple and beech on the generally most desirable mesic sites.

Historical logging practices and silvicultural experimentation have shown that shade tolerant species, such as sugar maple and beech, regenerate cutover areas best when they occur in the understory as advance growth. Yellow birch, on the other hand, being moderately shade intolerant, regenerates best from seed on newly cut areas where there is both adequate light and disturbed seedbed conditions. Because its shade tolerance is only moderate, yellow birch does not usually regenerate successfully under a closed canopy.

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Abstract.---In the beech-birch-maple association within the northern hardwood forest type, American beech (*Fagus grandiflora* Ehrh.) and sugar maple (*Acer saccharum* Marsh.) have been observed to dominate yellow birch (*Betula alleghaniensis* Britt.) in frequency, abundance, density, and size. However, under conditions of heavy removal cutting on the typically moist but well-drained till soils of the northern hardwood type, yellow birch demonstrates aggressive growth in all these parameters in comparison with beech and sugar maple.

Keywords: Northern hardwoods, soil moisture, stand dynamics, yellow birch

The history of forest management in the White Mountains consisted primarily of logging for softwood timber in the late nineteenth and early twentieth centuries, followed within a few years by equally heavy harvesting of the more valuable hardwoods, such as the birches and sugar maple. This kind of selective cutting, otherwise known as high-grading, had a negative effect on the residual stands because they were then heavily dominated by beech of varying quality and by poor-quality specimens of a variety of other species.

The style of cutting done in the early decades of the twentieth century left many forested areas with old growth that was unmerchantable, and incoming growth of predominantly shade tolerant species. Without sufficient openings in the canopy, young yellow birch simply did not replace itself in numbers sufficient to maintain a moderate proportion in the stands. Occasionally, nearly pure yellow birch stands can be seen as the result of a major perturbation such as a hurricane blowdown or a fire. Silvicultural practices which provide larger openings than single tree removal are therefore probably more desirable for the encouragement of yellow birch proliferation in subsequent stands.

Many studies have been done to clarify the best conditions under which yellow birch will germinate and establish seedlings. The main purpose of this study was to examine the dynamics of growth between yellow birch and its competing associates in the sapling and pole-size stages of stand development. The question was whether or not yellow birch could compete aggressively with its associates, as well as what effect soil moisture had both on the development of all three species, and on their interactions.

The objectives of this study were:

First - to determine whether, under what conditions, and by what sequence of events, yellow birch might outcompete or gain ascendancy over sugar maple and beech after group selection or patch clearcutting harvesting practices.

Second - to determine the effect of soil moisture variations on the interaction between sugar maple, beech, and yellow birch, within the range of sites suitable for sugar maple and other characteristic northern hardwood species.

And finally - to determine whether or not yellow birches initiating from seed after cutting could compete successfully with advance growth seedlings or saplings of sugar maple and beech in their first decade or so of growth.

Study Area

The primary study area was located on the Bartlett Experimental Forest in Bartlett, New Hampshire just northwest of the Presidential Range of the White Mountains in the White Mountain National Forest. The Bartlett Forest has been devoted to silvicultural research since the 1930's. An experiment had been initiated there in the late 30's and early 40's to increase the proportion of yellow birch in the hardwood stands by clearcutting a series of small patches (.10-.30 ha). These thirty-odd patches were scattered over a 40-hectare area with the expectation that new areas would be opened up on a 10-year cycle, so that ultimately the entire 40 hectares would be a mosaic of small, evenaged stands. Two additional sets of clearcuts, each comprising about 10% of the area, were made in 1950 and in 1960, but no further cutting has been done since. Soils are primarily spodosols of glacial origin varying in texture. Aspects are northerly varying from ENE to WNW and elevations range from 372-492 m (m.s.l.). As a result of the northerly orientation, none of these sites were "dry" in an absolute sense: some were relatively drier than others.

Secondary study areas at the Hubbard Brook Forest in West Thornton, New Hampshire and at Sawyer River in Livermore, New Hampshire were selected because they also supported northern hardwood forest associations and had had comparable histories of logging. Hubbard Brook's second growth forests were 55 to 60 years old; Sawyer River had been cut in the 1950's and supported a 15-20 year old forest. Both sites were similar to Bartlett in slopes and elevations; Sawyer River also had a northeasterly orientation; Hubbard Brook faced south (Table 1).

Methods

To determine moisture variability on the Bartlett sites, an attempt was made to locate the water table, or at least the capillary zone, with a soil auger in each of the patches. This was successful in 12 of the 30 patches; in the remaining patches, the water table or its capillary fringe was not reached, and moisture tension was measured with a tensiometer. Where the water table had been located, narrow wells

Table 1.--Experimental plot location data

| | SITES | | |
|-------------------------|---|---|-----------------------------------|
| | Bartlett Experimental Forest Bartlett, N.H. | Hubbard Brook Experimental Forest West Thornton, N.H. | Sawyer River Livermore N.H. |
| Elevation (m) | 372-492 | 466-488 | 543-562 |
| Slope (pct) | 5-40 | 5-25 | 5-35 |
| Aspect | WNW-ENE | SW-SE | ENE |
| Area (ha) | 40.00 | 2.00 | 0.25 |
| Stand Age (\bar{x}) | 30-35 | 55-60 | 15-20 |
| No. Plots | 30 | 12 | 12 |
| Stand History | *High-grading* selection cuts, 19th century Fuelwood cuts, early 20th century Experimental small group selection cuts (.10-.30 ha) 1937-41, 1951, 1960 | Selective cuts (heavy) Softwood structural timber 1890's Valuable hardwoods, 1910-1920 | Clearcuts for timber 1950's |

were dug with a tile spade to a depth of roughly 60 cm for the purpose of monitoring the fluctuation of the water table throughout the growing season. The wells were monitored at least once a week throughout the two growing seasons of the study. Permanent 25 m² plots sites were chosen where the wells were located at Bartlett, and additional sets of 12 25 m² plots were established at the two secondary sites during the second growing season of this study. Moisture availability at the secondary sites was determined with a tensiometer calibrated according to the known moisture levels on the well sites at Bartlett.

Slope, aspect and elevation were determined for all plots. Frequency of yellow birch, beech and sugar maple was determined, as well as density, abundance, and importance value. Soils were sampled and identified. Basic weather data (max./min. temperature, rainfall) were recorded at Bartlett for both growing seasons and correlated with well data. Height and diameter measurements were taken on all experimental trees and pairs of increment cores were taken from each tree for aging.

Owing to the variability of growth parameters resulting from suppression of trees during stand development, it was decided to limit the majority of the analyses to those trees of each species which had been most successful in terms of total attained height. All tree data on each plot were scrutinized, the tallest beech, yellow birch, and sugar maple were chosen from those present, and up to three additional trees of each species were selected from a roughly comparable height class within each plot. These subsets were then utilized for the detailed data analyses. In addition, 29 dominant trees of each species, located near but not within plot boundaries at Bartlett, were harvested for stem analysis and sectioned at meter intervals. An attempt was made to select these trees from areas with varying moisture availability, but ultimately they all ended up in the wettest range as determined by tensiometer readings.

All tree data were subjected to standard statistical methods. Multiple linear regression and stepwise multiple regression analyses were run for the tallest trees of each of the three major species on all sites. Student's t tests were performed on comparison of most growth parameters between tallest trees or all trees of pairs of species on all plots.

Results

All of the observations of this study were confined to moist but well-drained glacial till soils. Within this stated range of sites, an attempt was made to include the widest possible range of soil-moisture conditions. During the course of the study it became apparent that the actual range of soil moisture was remarkably small. While soils derived from the rocky tills of the region are highly variable, the actual range of soil moisture was very small compared to that of forest soils in general.

The three areas used in this study varied primarily in age. At Bartlett, age determined from cores and discs indicated that beech and sugar maple were often present as advance growth, while yellow birch usually came in from seed after logging. The age range within the plots was narrow enough to consider them evenaged, and about 35 years old. Topography varied from knolls and slopes of varying steepness to flat or concave areas. Most of the plots were on typical moist but well-drained soils.

The site at Hubbard Brook was quite damp, with proliferation of ephemeral streams common after heavy rains. At Hubbard Brook, there were really two age classes, but most of the trees were between 55 and 70 years old. The tallest trees used for data analysis were primarily from the older age class.

At Sawyer River, information from the aging of cores and discs showed that the beeches frequently originated from advance growth; occasionally the sugar maples did also, but the majority of trees of all species at that location came in from seed or from seedling sprouts present at the time of the clearcut approximately 20 years before this study.

The original hypothesis of this study was that yellow birch was better adapted than beech or sugar maple to utilize moister sites, and was thus expected to: 1) occur with great frequency, abundance, and density; 2) be more successful in competition with sugar maple and beech; and 3) demonstrate better growth than the other two species or than itself on drier sites, as measured by parameters such as height, diameter, and volume.

Percentages of frequency, abundance and density were calculated from measurements on all trees of the three species studied on all plots. Importance value is derived from the sum of the other three parameters. Table 2 illustrates that yellow birch is often significantly greater in abundance, basal area and importance value than either or both sugar maple and beech on the wettest sites. Its dominance diminishes as the sites become relatively drier.

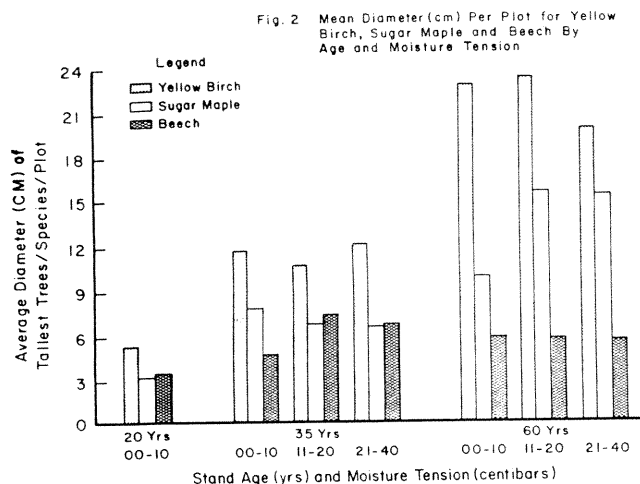
Height and diameter measurements were taken for all dominant study trees in each plot. Figures 2 and 3 illustrate that yellow birch is again greater in both height and diameter than the other two species on these characteristically damp sites. Sugar maple and beech show increases in both height and diameter with increasing dryness, but do not exceed the performance of yellow birch.

Table 2.--Frequency of occurrence, abundance, basal area (pct), and importance value of yellow birch, beech, and sugar maple by moisture tension range and stand age.

| Moisture Tension (centibars) | # Plots | Pot Frequency | | | Pot Abundance | | | Pot Basal Area | | | Importance Value | | |
|---------------------------------|---------|---------------|-----|-----|---------------|-----------------|-----------------|-------------------|-----------------|-----------------|------------------|-------------------|-------------------|
| | | YB | SM | Be | YB | SM | Be | YB | SM | Be | YB | SM | Be |
| 20 years | | | | | | | | | | | | | |
| 00-10 (wet) | 12 | 83 | 100 | 92 | 26 | 24 | 23 | 35ab ¹ | 9 | 15 ^e | 1.44 | 1.33 | 1.30 |
| 35 years | | | | | | | | | | | | | |
| 00-10 (wettest) | 18 | 100 | 83 | 86 | 36ab | 22 | 22 | 47ab | 18 ^c | 9 | 1.83ab | 1.23ab | 1.17 |
| 11-20 | 7 | 100 | 57 | 100 | 32a | 20 | 31 ^e | 34a | 16 | 23 | 1.66a | 0.93 | 1.54 ^e |
| 21-40 (driest) | 5 | 100 | 83 | 100 | 28a | 13 | 35 ^e | 32ab | 17 | 14 | 1.60ab | 0.90 | 1.49 |
| 60 years | | | | | | | | | | | | | |
| 00-10 (wettest) | 3 | 100 | 75 | 75 | 41b | 41 | 12 | 65b | 22 | 2 | 2.06b | 1.38 | 0.89 |
| 11-20 | 6 | 100 | 88 | 63 | 31 | 38 | 22 | 52b | 34 ^c | 9 | 1.83b | 1.60 | 0.94 |
| 21-40 (driest) | 2 | 100 | 100 | 100 | 25 | 37 ^d | 30 | 54b | 40 ^c | 7 | 1.79 | 1.77 ^c | 1.36 |

¹all letters indicate differences at significance levels of 90 pot or greater.

a = yellow birch > sugar maple
b = yellow birch > beech
c = sugar maple > beech
d = sugar maple > yellow birch
e = beech > sugar maple



Volume index (m^3) is a parameter derived from the product of height (m) and basal areas (m^2) of each tree within the experimental plots. Volume index values are an approximation of relative stem volume, not of actual volume (Table 3). Figure 4 shows that species other than sugar maple, beech, or yellow birch were more important components of the total volume in the younger stands, but less so in the oldest stands, particularly on the most mesic sites. Beech is a small component of all stands relative to sugar maple and yellow birch, but the three species together clearly comprise more than three-quarters of the total volume of these areas. Differences among the three species are generally most significant on the wettest sites, although on the 35-year-old stand, yellow birch dominates sugar maple significantly at all moisture levels.

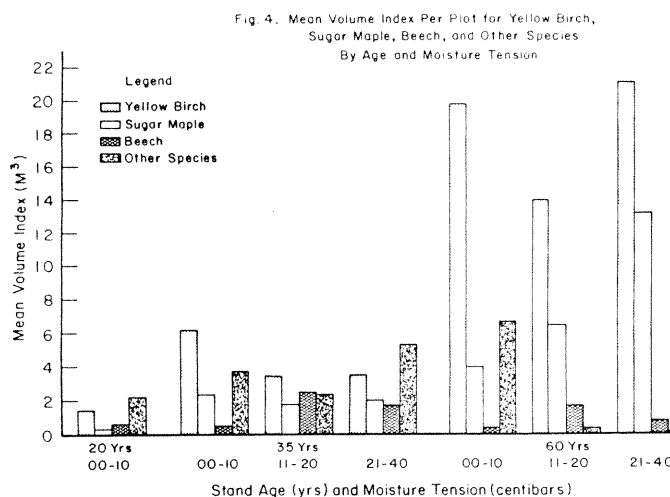
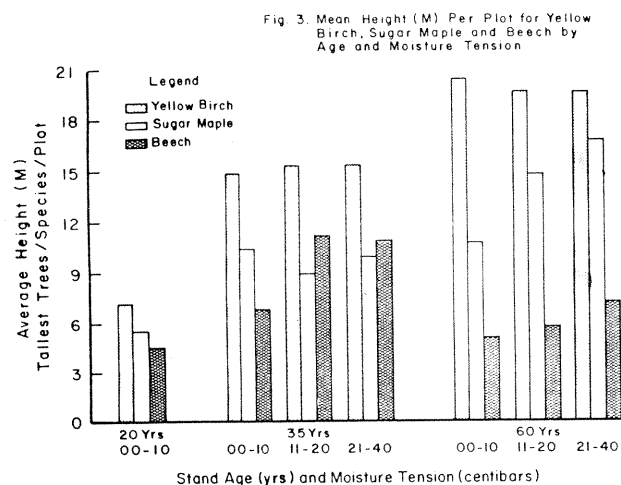


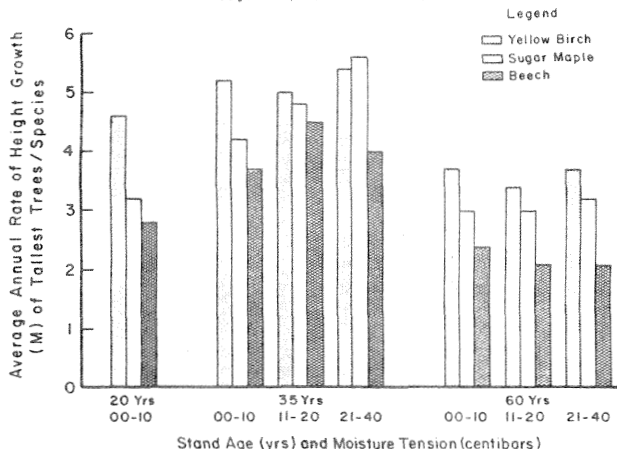
Table 3.--Mean volume index¹ and percentages per plot for yellow birch, sugar maple, beech, and all species

| Moisture Tension | # Plots | YB | SM | Be | All Species |
|------------------|---------|------------------------------|-----------------------------|---------------|-----------------|
| 20 years | | | | | |
| 00-10 (wettest) | 12 | 1.44 ^{ab} (33 pct) | 0.27 ^c (6 pct) | 0.47 (11 pct) | 4.42 (100 pct) |
| 35 years | | | | | |
| 00-10 (wettest) | 18 | 6.16 ^{ab} (48 pct) | 2.30 ^c (19 pct) | 0.52 (4 pct) | 12.74 (100 pct) |
| 11-20 | 7 | 3.52 ^a (34 pct) | 1.84 (18 pct) | 2.56 (25 pct) | 10.22 (100 pct) |
| 21-40 (driest) | 5 | 4.61 ^a (34 pct) | 2.02 (15 pct) | 1.75 (13 pct) | 13.70 (100 pct) |
| 60 years | | | | | |
| 00-10 (wettest) | 3 | 19.83 ^{ab} (64 pct) | 4.02 ^c (13 pct) | 0.39 (1 pct) | 30.87 (100 pct) |
| 11-20 | 6 | 14.01 ^{ab} (62 pct) | 6.53 ^c (29 pct) | 1.72 (8 pct) | 22.48 (100 pct) |
| 21-40 (driest) | 3 | 21.12 (60 pct) | 13.14 ^c (37 pct) | 0.85 (2 pct) | 35.12 (100 pct) |

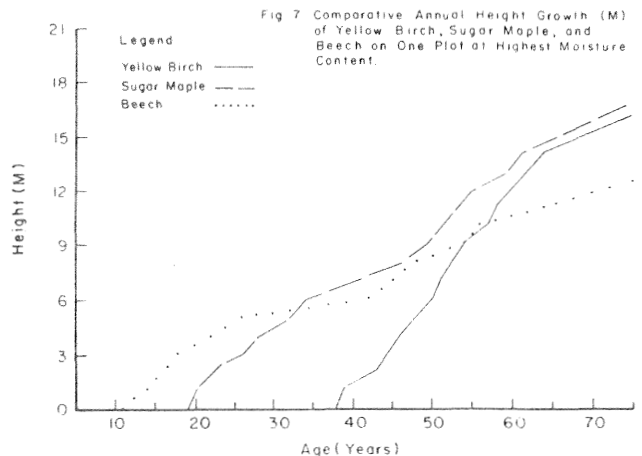
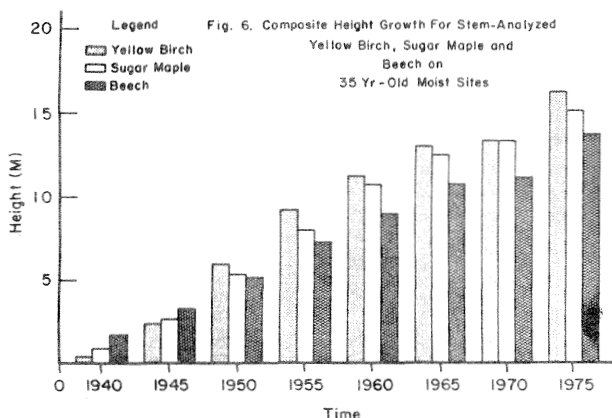
¹volume index (m^3) = basal area (m^2) x total height (m)

Rate of height growth was determined in two ways: first by dividing the height of tallest trees of each species by their ages as determined from increment cores, and second by stem analysis of the tall trees from the Bartlett plots. Data from the larger group of trees (Figure 5) show that yellow birch usually has a more rapid rate of growth than the other two species, and consistently shows a greater advantage on the wettest of the sites.

Fig. 5 Rate of Height Growth (M) for Yellow Birch, Sugar Maple, and Beech By Age and Moisture Tension



The smaller sample of 29 tall trees from Bartlett yielded results similar to those of the larger sample (Figure 6). What is most interesting in this more detailed analysis is that the yellow birches began later, and/or had achieved less height growth at the first point (1940) than the sugar maples and the beeches. But within ten years, the birches had taken dominance and maintained that dominance over the other two species for the subsequent 35 years. A measurement of the three harvested trees - one of each species - in one plot also shows the performance of yellow birch coming into the stand well after the other two species and still being able to achieve parity with, if not dominance over, the other species (Figure 7).



Data from tallest trees was analyzed by both multiple linear regression and stepwise multiple regression. All three species and experimental areas were analyzed separately. Final analysis plotted height against site factors and age but did not yield high R^2 values. The trends indicate that yellow birch height varies inversely with factors associated with reduction in moisture availability; sugar maple and beech appear to vary directly with the same site factors. Regression analysis served to corroborate that inherent differences in height growth between species were much more important than those within or between species induced by soil variables in the observed range.

DISCUSSION

Results of the various experiments performed in this study show similar patterns. In the forest, under conditions of group selection or patch clearcutting, yellow birch comes in with greater frequency, abundance, and density than either sugar maple or beech. Within the typical northern hardwood range, the wetter the cut-over sites are, the more consistently dominant yellow birch is in the stands, as measured in growth parameters such as height, diameter, and volume, and the greater ability yellow birch has to compete successfully with, and often supercede, the height growth of the other two species, regardless of the others' initial height advantage. If all three species originate simultaneously on these moist but well-drained northern hardwood sites after heavy cutting, yellow birch will probably dominate because of its rapid early height growth. If sugar maple and beech occur as advance regeneration, yellow birch still frequently can compete with, or exceed, the growth of the other two, but the probability of yellow birch dominating is less certain.

Information from statistical analyses of trees on the experimental plots, and from stem analyses of harvested trees near the

experimental plots at Bartlett, indicates that the relative rate of height growth of yellow birch, particularly in the first couple of decades of development, is significantly greater than the rates either for sugar maple or for beech.

Yellow birch thus appears to be at a selective and competitive advantage on the moister sites of the northern hardwood type range, in comparison with sugar maple and beech. The fact that yellow birch is a profligate water user with a consequent high moisture demand, compared with sugar maple and beech, may account in part for the observed differences in growth behavior among the three species on the moist sites.

CONCLUSIONS

The range of yellow birch is broad, extending from the Atlantic coasts of the United States and Canada west to the Lake States and south into Georgia along the Appalachian Mountain range. Other studies indicate that yellow birch has both genetic and morphological variability over its range (Clausen 1968, 1973; Fowells 1965; Sharik and Barnes 1979, Wearstler and Barnes, 1977). The results of this study are therefore clearly restricted to the forest types I observed - the beech-birch-maple association of northern hardwoods found on typically moist but well-drained podzolic soils, subjected to clearcutting in patches or group selection cutting. These results are probably applicable therefore only in the northeastern United States and possibly eastern Canada.

Most of the data presented in this study show that yellow birch outgrows both sugar maple and beech, and often all other species, on the experimental areas. The question arises why there is not more yellow birch in the old-growth and second-growth forests of northern New England. The answer probably lies more in the history of logging practices than in the suitability of the sites. In the undisturbed forest, the most frequent cause of openings for new growth is the demise and subsequent windthrow of individual trees. Though such relatively small openings in the canopy do provide sufficient light for the moderately shade tolerant yellow birch to germinate and grow, the small space is usually rapidly utilized by existing codominant trees or smaller growth near the opening, and by aggressive advance growth of the more shade tolerant sugar maple and beech. Only large scale natural catastrophes, such as hurricane or fire, open areas sufficiently large to encourage yellow birch regeneration. Openings larger than a hectare, particularly after fire, were more conducive to invasion by paper birch than by yellow birch, so storm-induced windthrow pockets provided the most advantageous conditions for the establishment of

yellow birch as a substantial proportion of the stand.

Early logging practices in the White Mountains of highgrading, or selecting out the best and biggest trees, were to a large extent mimicking the single tree openings in the natural forest, and as such, were more favorable to beech and maple than to yellow birch establishment. It is the more recent practices of group selection cutting (which leaves a minimal canopy), and clearcutting, either in large units or in smaller strips and patches, that have simultaneously provided the conditions of adequate light and adequate moisture, both necessary for the successful establishment of yellow birch. A side effect of clearcutting is that the water tables are higher after the transpiration pump of the forest is removed. Extensive studies (Marquis 1965a, 1965b, 1966, 1972, Hatcher 1966, Filip 1973, Erdmann et al. 1981, Roberge 1975) have shown that the strip and patch clearcutting are most advantageous to the germination, establishment, and early growth of yellow birch. The history of the three areas used in this study included periodic heavy cutting at Hubbard Brook, patch clearcutting at Bartlett, and extensive clearcutting at Sawyer River. The results of this study show that such cutting practices enhance the growth of yellow birch relative to sugar maple and beech in the sapling, pole-size, and later post-establishment stages.

The height growth of yellow birch does not vary widely throughout the range of moist sites typical of the northern hardwood forest type. The height growth of sugar maple and beech is far more sensitive to the wetter end of this range and shows increasing improvement as the sites become more mesic. Both sugar maple and yellow birch tend to dominate beech, unless beech occupied the site first as tall advance growth prior to logging. Since the wettest of the northern hardwood sites are more favorable to yellow birch than to the other two species, yellow birch can quickly gain ascendancy over the others, both in height and in numbers of trees. However, as the sites become drier, the dominance of yellow birch over sugar maple is less certain, though its dominance over beech remains fairly consistent.

The importance of certain cutting practices, such as patch clearcutting, for the success of yellow birch has been well established. The results of this study--in frequency, abundance, and density; in competitive ability; in parameters of height and diameter,--support previous work and show that yellow birch grows consistently more aggressively and successfully on those sites with abundant moisture than do either sugar maple or beech. Since soil moisture conditions can be readily ascertained, it is hoped that future yellow birch management will select areas for cutting with the moisture conditions of the regenerative site in mind.

Selecting the moister sites could insure a more vigorous and reliable crop of yellow birch than would be found on the more mesic sites of the northern hardwood type, where sugar maple and beech are likely to be more competitive.

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Effects of Mexico's Selective Cutting System on
Pine Regeneration and Growth in a Mixed Pine-Oak
(Pinus-Quercus) Forest.¹

Laura C. Snook and Patricia Negreros C.²

Abstract. Effects of the official selective harvesting system on a mixed pine-oak forest in Oaxaca were evaluated 20 years later and compared to formerly cleared forest areas and unexploited forest. Pine regeneration in selectively cut forest averaged only 5 m²/ha basal area compared to 40 m²/ha in formerly cleared areas. The correlation between pine regeneration and reconstructed residual basal area after harvest was $R = -0.82$. Pine growth increments of 4.6 m³/ha/year occurred in selectively cut areas, compared to 11.4 m³/ha/yr in formerly cleared areas. New regulations associated with the forest law of 1986 may include replacement of the official selective cutting method by an even-aged silvicultural management system. However, the lack of markets for oak wood represents an obstacle to the implementation of more intensive harvesting systems necessary to assure sustained yields of pine wood.

Keywords: natural regeneration, silviculture

INTRODUCTION

Over 80% of Mexico's industrial wood comes from pines (SARH 1978), most of which grow intermixed with oaks (Rzedowski 1978) in highland forests which cover 20 million has (SARH/SF 1984). Responsibility for silvicultural management of these and all of Mexico's forests rests entirely with the federal forest service (Ley Forestal 1960/1986). Since the 1950's, the country's forests have been exploited according to the silvicultural system known as the Metodo Mexicano de Ordenacion de Montes' (Mexican Method for Ordering Forests) (Carrillo 1955; Rodriguez 1958; Rodriguez et al 1959; Rodriguez & Rodriguez 1966). This selective cutting regime limits harvest intensity to 35% - 50% of the volume of desired (conifer) species, and at least until 1978 incorporated a diameter limit of 45 cm (Musalem 1979). In mixed forests, the application of this system often translates into selective extraction of less than 20% of total volume (FAPATUX 1980).

The Mexican method seeks to manage uneven aged stands by maintaining a balanced reverse J-shaped diameter distribution. It assumes that continuous regeneration and class-to-class recruitment will provide for sustained yields (Klepac and Mass Porras 1968). As of 1981, although a few foresters had expressed doubts about the validity of these assumptions (Musalem 1979), no field studies to confirm or modify them had been published. It was

decided to survey a pine-oak forest 20 years after exploitation to evaluate the effects of prior harvest by this method, particularly with regards to pine regeneration.

THE STUDY SITE

The study was carried out in the Zapotec community of San Pablo Macuiltianguis, in the Sierra de Juarez, Oaxaca. Their approximately 5000 ha of commercial forest is dominated by pines (Pinus patula, P. pseudostrobus, P. ayacahuite, and P. rudis) intermixed with species of oak including Quercus laurina, Q. rugosa, Q. crassifolia, Q. excelsa, Q. candicans, and Q. salicifolia. Madrone (Arbutus glandulosa), alder (Alnus acuminata), and other hardwood species occur as well (FAPATUX 1962; Perez and Perez 1984).

Forest elevations range from 2200 m to 2700 m, averaging 2450 m. Slopes average 45%, and range from 15% to more than 100%. Annual precipitation is between 1500 and 2000 mm and is strongly influenced by humid winter winds from the Gulf, known as 'nortes'. A marked dry season occurs during April and May. Average annual temperature has been estimated at 12* to 14* C (FAPATUX 1977), while a weather station at a slightly lower elevation just on the other side of the mountains registered an average temperature of 16.7* C and a precipitation of 1982 mm (Garcia 1981).

These forests were concessioned to Mexico's first newsprint paper factory, Fabricas de Papel Tuxtepec (FAPATUX), in the late 1950's, as a source of pine wood for cellulose (Diario Oficial November 12, 1956). Selective cutting of pines began about 1959, but the second cutting cycle had not yet been initiated in 1981.

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METHODS

Data Collection

A 25 km timber extraction road known as 'brecha 200', which runs through the forest from west to east, was used as a transect. At 500 m intervals, courses were run perpendicular to the road between 50m and 350 m into the forest, where sample plots were laid out. Distances from the road were selected using a random numbers table.

Among 27 plots located by this method, 4 fell in unexploited forest and one in a former clearcut where a tower had been erected to support power lines. To give statistical context to this plot, an additional plot was located in the clearcut area, and complemented with two plots located in former agricultural fields abandoned 30 years before, one in 'Agua Fria' and one behind the 'Comedor Cerro Machin'. The final data set for this study was based on 30 plots in 3 different forest types (selectively harvested, unexploited, and formerly cleared).

Four radii marked at 3 intervals were used to indicate 1000 m² circular plots with nested internal plots of 400 m² and 80 m². Trees 15 cm dbh and above were measured over the full 1000 m² while trees between 5 cm and 14.9 cm dbh were measured over 400 m². Trees 2 cm to 4.9 cm dbh were measured only within the 80 m² plot. Genus, dbh, crown class, and signs of injury were noted for each tree. Increment cores were taken of at least two small pines and at least two large pines on each plot. The former were used to determine the age and size range of post-harvest regeneration. Cores of large trees were taken to represent the range of diameter classes and provide data on increments.

Data Analysis

Measurements taken in 1982 showed the effects of past conditions on the density of pine regeneration. To relate these effects to causal factors required the reconstruction of the forest as it was just after harvest. While written records were unavailable, tree cores and information obtained by hearsay indicated that 1962 was the average year of regeneration subsequent to harvest and the clearcut for the power lines.

All trees 20 years or younger in 1982 were thus considered post-harvest regeneration. In selectively cut and unexploited forest, nearly all of these trees measured less than 15 cm dbh, but differentiation of regeneration on each plot was verified according to increments, sampled ages, and diameter distributions. To permit comparison between the 20 year old clearcut and the 30 year old abandoned fields, increments for the last ten years were subtracted from all tree diameters on the abandoned field sites.

In the case of the clearcut and the abandoned fields, it was known that residual basal area had been zero at the time of regeneration establishment. To determine residual basal area at this time in selectively harvested forest, increments since

1962 were subtracted from diameters of older trees. Average measured periodic increments of 0.44 cm/yr in pines less than 60 cm dbh and 0.36 cm/yr in pines greater than 60 cm dbh yielded respective diameter reduction factors of 8.8 cm and 7.2 cm over the 20 year post-harvest period.

Oaks were not cored, both because of physical difficulties and because it was not known whether tropical oaks have annual rings. For lack of data on Mexican oak growth, diameters were reduced to 1962 levels using the following increments, derived from an estimated volume increment of 2% a year (Mass P. 1977) and an oak volume table (FAPATUX 1977):

| Diam. class | Annual increment | 20 year reduction |
|-------------|------------------|-------------------|
| 15 - 19.9 | 0.35 cm | 7.0 cm |
| 20 - 29.9 | 0.49 cm | 9.8 cm |
| 30 - 39.9 | 0.69 cm | 13.8 cm |
| 40 - 49.9 | 0.79 cm | 15.8 cm |
| 50 - 59.9 | 0.89 cm | 17.8 cm |
| 60 and over | 1.30 cm | 26.0 cm |

Using these reduction factors, average 1962 diameters and basal areas were determined for pines and oaks in each 1982 diameter class. Diameter distribution tables for each plot were then used to determine total residual basal area (Table 1).

Table 1. Calculation of residual basal area in selectively cut forest (Site 033).

| Avg. class dbh 1982 | BA/tree 1962 | # trees | Total BA 1962 |
|---------------------|----------------------|---------|----------------------|
| <u>Pines</u> | | | |
| 17.5 | 59 cm ² | 1 | 59 cm ² |
| 25.0 | 205 cm ² | 2 | 410 cm ² |
| 35.0 | 537 cm ² | 6 | 3222 cm ² |
| 45.0 | 1027 cm ² | 1 | 1026 cm ² |
| 55.0 | 1673 cm ² | 2 | 3346 cm ² |
| <u>Oaks</u> | | | |
| 17.5 | 86 cm ² | 2 | 172 cm ² |
| 25.0 | 180 cm ² | 1 | 180 cm ² |
| 35.0 | 351 cm ² | 3 | 1053 cm ² |
| 45.0 | 579 cm ² | 2 | 1158 cm ² |
| 55.0 | 863 cm ² | 1 | 863 cm ² |

Total residual basal area: 11,491 cm²/1000 m²

To compare unexploited forest conditions with selectively cut and formerly cleared forest, a similar process of diameter reduction and transformation to basal area in 1962 was applied, using the same estimates of oak increments as in the selectively cut forest, and the following periodic pine increments measured in the plots:

| Diam. class | Annual increment | 20 year reduction |
|-------------|------------------|-------------------|
| 15 - 39.9 | 0.34 cm | 6.80 cm |
| 40 - 49.9 | 0.38 cm | 7.60 cm |
| 50 - 59.9 | 0.30 cm | 6.00 cm |
| 60 and over | 0.24 cm | 4.80 cm |

These same transformation tables were used to reconstruct the 1962 diameter distribution of each site. By combining these with a pine volume table (FAPATUX 1977), it was possible to determine 1962-1982 volume increment by forest treatment.

RESULTS AND DISCUSSION

Regeneration

As can be observed in Table 2, the average density of pine regeneration twenty years after selective cutting was 5.2 m²/ha, only 13% of the nearly 40 m²/ha on the formerly cleared sites. Regeneration establishment in unexploited forest during this period was negligible.

The residual basal area in each case followed an inverse pattern to regeneration, averaging 34 m²/ha in unexploited forest, 19.2 m² in selectively cut forest, and 0 in the clearcut and abandoned fields. A linear regression between residual basal area and basal area of regeneration yielded a correlation coefficient of $R = -0.82$, indicating that 67% of the variability in pine regeneration reflects the variation in residual basal area. This inverse relationship is no surprise since basal area is a measure of site occupation. The more growing space (light, water, nutrients) occupied by residual trees, the less is available for regeneration establishment.

Oak regeneration was insensitive to variation in residual basal area, yielding an R^2 of only 0.08. This no doubt reflects oaks' greater shade tolerance. It is notable that only in the unexploited forest, with the highest 'residual' basal area, is the average oak regeneration density approximately equal to and perhaps slightly greater than pine.

Rates of suppression amongst pines followed the same pattern as regeneration density. In formerly cleared areas, 10% of the pines were suppressed by other pines. In selectively cut and unexploited forest, 80% and 100%, respectively, of the pine regeneration was suppressed, by a mixed canopy of pines and oaks. These trees will almost certainly die before reaching commercial size.

Table 2. Pine and Oak Regeneration after 20 Years

| | Formerly Cleared | Selectively Cut | Unexploited |
|--|---------------------|--------------------|----------------|
| Residual BA 1962 m ² /ha | 0 | 19.2 \pm 1.7 | 34.1 \pm 3.0 |
| Pine regen. 1982 m ² /ha | 39.8 \pm 2.8 | 5.2 \pm 1.2 | 0.2 \pm 0.1 |
| Oak regen. 1982 m ² /ha | 6.2 \pm 2.1 | 3.6 \pm 0.7 | 0.3 \pm 0.2 |
| % pines suppressed | 10% \pm 4 | 80% \pm 4 | 100% |

Growth

Average periodic diameter increment between 1962 and 1982 differed amongst pines in different forest treatments. Combining data for available diameter classes yielded averages of 1.38 cm/yr in the formerly cleared forest, 0.45 cm/yr in selectively cut forest, and 0.35 cm/yr in unexploited forest. In the first case, rapid growth rates reflect the youth and lower range of diameters of the stands, and decreasing ring widths over the last two or 3 years indicate that these rates are slowing as competition becomes more intense.

Diameter distribution tables for 1962 and 1982 were transformed to volumes to determine the difference in volume increment/ha among forest treatments. These ranged from 4.0 m³/ha/year in the unexploited forest to 11.4 m³/ha/yr in the clearcut and abandoned fields (Table 3), comparing favorably with data for a plantation of *P. patula* in Macuilitianguis, which grew at a rate of 12 m³/ha/yr during the first 14 years after its establishment (FAPATUX 1977).

Table 3. Volume increments/ha, pine only

| | Formerly Cleared | Selectively Cut | Unexploited |
|--------------------|---------------------|--------------------|--------------------|
| Vol. pines 1962 | 0 | 125 m ³ | 460 m ³ |
| Vol. pines 1982 | 228 m ³ | 217 m ³ | 540 m ³ |
| Increment 62-82 | 228 m ³ | 92 m ³ | 80 m ³ |
| Annual incr./ha | 11.4 m ³ | 4.6 m ³ | 4.0 m ³ |

Forest dynamics

Selective cutting in the mixed forests of San Pablo Macuilitianguis, as in most of Mexico, was applied exclusively to pines. This has modified the relative dominance of pines and oaks (Table 4). While pines accounted for 64% of the total volume of the forest prior to exploitation (FAPATUX 1962), twenty years after the first selective cut they represented only 54% of the basal area. While formerly cleared sites were completely dominated by pines, only 58% of the dominant trees in selectively cut sites were pines, while 40% of the dominant trees were oaks. The intermediate pine/oak relationship demonstrated by data from the unexploited forest probably reflects the history of this particular area, which appeared to have regenerated after a fire about 40 years before.

Table 4. Forest characteristics and proportions, 1982 (adapted from Negreros & Snook 1984).

| | Formerly Cleared | Selectively Cut | Unexploited |
|-----------------|---------------------|--------------------|------------------------------------|
| Total BA | 46.0 \pm 3.8 | 47.1 \pm 2.5 | 60.1 \pm 5.4 |
| BA Pines | 39.8 \pm 2.8 | 25.4 \pm 1.8 | 45.9 \pm 7.7 |
| BA Oaks | 6.2 \pm 2.1 | 18.5 \pm 2.3 | 2.8 \pm 0.11 |
| % Pines | 87% | 54% | 70% / 64% ¹ |
| % Oaks | 13% | 39% | 5% ² / 36% ¹ |
| Pines % dom. | 100% | 58% | 84% |
| Oaks % dom. | 0 | 40% | 8% ² |

¹Data from FAPATUX (1962).

²Other hardwood species made up the missing %.

CONCLUSIONS

The low-intensity selective cutting of pines in the pine-oak forests of the Sierra de Juarez has not stimulated adequate pine regeneration to provide for the replacement of harvested trees. On the contrary, these cuttings are encouraging the successional process of replacement of pines by oaks, as has been observed in the United States by various authors, among them Christensen and Peet (1981) and reviewed by Jardel (1985).

Regeneration of pine was eight times greater in basal area (and twice as large in diameter) on sites subject to complete clearing. Growth rates followed the same pattern, annual volume increments of pine reaching levels 2.5 times greater in formerly cleared sites than in selectively cut forest. Thus it seems apparent that patch or strip clear-cutting, a close imitation of agricultural abandonment and fires which apparently maintained pine dominance in these forests in the past, would be much more effective silvicultural methods than selective cutting for ensuring and maximizing future yields of pine wood needed for cellulose and other industrial purposes.

In fact, against the backdrop of the national guidelines for low-intensity selective cutting, a movement to intensify Mexican silviculture was initiated by a small group of concerned foresters in the mid-70's, and pilot projects using a system of even-aged silvicultural management were established on 2000 ha of mixed conifer forests by the end of the decade. The silvicultural system, called the 'Metodo de Desarrollo Silvicola' (Method of Silvicultural Development) is based on the

application of seed tree regeneration cuts and periodic thinnings, and presumes to manage even-aged stands (Musalem 1979). As of 1983, 56,000 ha (less than 3% of Mexico's mixed conifer forests) were under management according to this method, and yielded 25% of the national production that year (SARH/SF 1984).

A new Mexican forestry law was signed this year, replacing the forestry law of 1960 (Diario Oficial May 30, 1986). While the associated forestry regulations will not be published until December, the appearance of the words "management plan" and "sustained yield" in the text of the new law (for the first time) may foreshadow a modification of silvicultural guidelines.

However, there are still obstacles to the implementation of a more intensive silvicultural system in Mexico's pine-oak forests. Among them is the lack of markets for oak wood. Mexico boasts over 120 recognized species of oaks (Rzedowski 1978). Neither their taxonomy nor their wood technology is well known, and there has been little use of oaks for industrial purposes.

Because loggers are paid by the cubic meter by the buyer of the wood, the lack of a demand for oaks makes it unlikely that these trees will be cut. In Macuiltanguis, an average of 140 oaks₂ occurred per hectares, representing nearly 20 m² of basal area. This density is greater than the total residual basal area which so severely inhibited pine regeneration after the selective harvest. Unless these trees are cut, adequate pine regeneration cannot be expected. Thus oak markets should be developed as part of a new silvicultural strategy to assure the future of Mexico's pine resource.

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Gains from Superior Tree Selection in Black Spruce and White Spruce¹

Katherine K. Carter²

Among the conifer species native to the forests of Maine, the spruces (*Picea* spp.) are of greatest interest to forest industry because of their superior pulping qualities and their widespread distribution throughout the state. Tree improvement programs for white spruce (*P. glauca* (Moench) Voss) and for black spruce (*P. mariana* (Mill.) BSP) have been initiated in the past decade. Research to evaluate selection methodology and to estimate potential gains has been carried out at the University of Maine in cooperation with local industry and with the U.S. Forest Service.

Results from progeny tests of superior trees selected in natural stands of white spruce and black spruce are reported here. These early results indicate that different selection methods may be preferred for each species.

WHITE SPRUCE

White spruce was one of the first species to be included in tree improvement research programs. During the 1960's, superior trees were located by field foresters in Maine and New Hampshire, and graded by Clyde Hunt of the U.S. Forest Service. A comparison-tree selection method was used, with 2 or 3 comparison trees in most stands. The parent trees ranged in age from 18 to 75 years; most were 30 to 50 years old. They averaged 9 percent greater in DBH and 8 percent greater in height than comparison trees in the same stands. A north-south range of almost 3 degrees in latitude was related to different rates of height growth: Northern parents had a mean annual increment in height of 1.3 ft/year, while southern parents averaged 1.9 ft/year.

Open-pollinated seed from 23 parents was collected to establish a half-sib progeny test. Seed was sown in the New Hampshire state nursery in 1971. In 1974, 3-0 seedlings were lifted and planted at a test site located on abandoned farm

Abstract.--Open-pollinated progeny tests were established to assess the gains attributable to plus-tree selection in black spruce and white spruce in Maine. Of 23 selected families of white spruce, all but one were taller than nursery-run checks after 11 growing seasons in the field. Height gains averaged 23 percent. Latitude of the parent tree was negatively correlated with progeny growth rates. For black spruce, progeny of plus-trees selected using the baseline method were no taller than offspring of average trees, at age 7. Heritability values for black spruce are low, indicating that family selection might be more effective than individual tree selection.

land near Moscow, Maine. Nursery-run white spruce seedlings from the New Hampshire and Maine state nurseries were included as check seedlots, as were seedlots of red spruce (*P. rubens* Sarg.) and Norway spruce (*P. abies* (L.) Karst). The experimental design is a randomized complete block with 6 replications and 10 trees per plot.

After 11 growing seasons (14 years from seed), survival averaged 71 percent. The average height for all select offspring was 9.9 ft, which represents a gain of 19 percent over the New Hampshire check and 36% over the Maine check. When northern and southern families are compared with the appropriate check lot, average height gains are 25 percent to 28 percent (Table 1). White spruce were also taller than the Norway spruce (8.7 ft) and red spruce (7.2 ft) seedlots.

Height measurements were subjected to analysis of variance to determine heritability. A heritability value of $h^2 = 0.4$ was calculated, which is close to the value of 0.35 reported by Mohn et al. (1976) in Minnesota. Height at age 14 was highly correlated with height at ages 11 and 6, and with growth of the terminal leader at age 6. Mean annual increment of the parents was correlated with progeny height at age 6 but not at later ages (Table 2).

BLACK SPRUCE

During the 1970's, interest shifted toward black spruce as a plantation species because of its rapid juvenile growth and its relative resistance to the spruce budworm. Previous work by Morgenstern (1974) had indicated little relationship between parental growth rates and juvenile growth of their progeny. In order to explore this relationship further and to test the baseline method of selection, 16 stands of black spruce throughout Maine were identified for intensive study. Five to 10 dominant or co-dominant trees in each stand were selected at random and measured to provide baseline data for mean annual height and diameter increments. "Plus" trees were then located which were 1.0 to 2.5 standard deviations above the average for that stand (Kenlan 1981). Cones were collected from plus trees and from two or more average trees (those closest to the baseline values) in each stand.

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Table 1.--Comparative heights for white spruce progenies of northern and southern select parents. Superiority of northern progeny is compared to Maine check seedlot; southern progeny is compared to New Hampshire check seedlot

| Seed source | Height (ft) | % superiority |
|-----------------------|-------------|---------------|
| Northern Trees | | |
| AC 47 | 11.2 | 53 |
| AC 21 | 10.0 | 37 |
| AC 50 | 9.7 | 33 |
| AC 31 | 9.6 | 32 |
| AC 39 | 9.0 | 23 |
| AC 54 | 9.0 | 23 |
| AC 40 | 8.9 | 22 |
| AC 78 | 8.8 | 21 |
| AC 37 | 8.3 | 14 |
| ME check | 7.3 | -- |
| | | Ave. 28 |
| Southern Trees | | |
| AC 71 | 12.0 | 45 |
| AC 55 | 11.5 | 39 |
| AC 06 | 11.4 | 37 |
| AC 83 | 11.1 | 34 |
| AC 85 | 11.0 | 33 |
| AC 16 | 10.7 | 29 |
| AC 73 | 10.5 | 27 |
| AC 02 | 10.5 | 27 |
| AC 66 | 10.2 | 23 |
| AC 67 | 9.9 | 19 |
| AC 68 | 9.6 | 16 |
| AC 72 | 9.6 | 16 |
| AC 60 | 8.5 | 2 |
| NH check | 8.3 | -- |
| AC 56 | 8.2 | -1 |
| | | Ave. 25 |

Table 2.--Correlations among parent and progeny height and growth parameters, for Spruce-Fir Committee white spruce progeny test in Moscow, Maine

| | Height 1976 | Growth 1976 | Height 1981 | Height 1984 |
|-----------------------|-------------|-------------|-------------|-------------|
| Parental height (MAI) | .64* | .58* | .37 | .34 |
| Height 1984 | .75* | .75* | .95* | -- |
| Height 1981 | .82* | .73* | -- | -- |
| Growth 1976 | .87* | -- | -- | -- |

* significant at 0.05 level.

Seedlings were grown in the nursery for 2 years and then outplanted at 3 field sites in a randomized design with 5 replications of 3-tree plots. Seedling height was measured at ages 1 and 2 (nursery), and ages 5 and 7 in the field.

At age 7, overall survival in each plantation ranges from 88 percent to 94 percent. Overall mean height varies from 3.8 ft to 4.5 ft among the plantations; within each plantation family mean heights range from approximately 80 percent to 120 percent of the plantation mean.

Measurements of seedling height in the nursery revealed a negative correlation with latitude of the parent stand, and significant differences (0.05 level) among stands. After 5 years in the field, the stand effect is still significant at 2 out of 3 plantations but the correlation with latitude has disappeared.

Examination of fifth-year data indicates that parental selection has been ineffective for improvement of juvenile growth rate. There is no significant difference in overall height between offspring of "select" and "average" parents (Table 3); nor is there a significant correlation between parental height or DBH and progeny height. There are, however, significant differences in family height when data for all 3 plantations is combined (Table 4). Based on the combined data for all 3 planting sites, individual-tree heritability is 0.19. When the 3 plantations are examined separately, however, the family effect is non-significant at 2 of the sites and heritability ranges from 0.08 to 0.27. Correlations of family height ranking across the 3 plantations are non-significant in 2 cases, and low ($r = 0.48$) in the third case.

Table 3.--Mean height of select and average black spruce progeny

| Age and Location | Progeny Height (in) | |
|------------------|---------------------|---------|
| | Select | Average |
| 1 - Nursery | 9.1 | 8.7 |
| 2 - Nursery | 10.6 | 10.7 |
| 5 - Howland | 30.0 | 31.3 |
| 5 - Demo Pond | 22.7 | 22.7 |
| 5 - Loon Lake | 30.0 | 28.7 |
| 7 - Howland | 53.5 | 53.9 |
| 7 - Demo Pond | 46.8 | 44.9 |
| 7 - Loon Lake | 51.5 | 50.8 |

Table 4.--Analysis of variance for height of black spruce families after 5 years in the field (age 7 from seed)

| Source of Variation | Degrees of Freedom | Mean Square | F |
|---------------------|--------------------|-------------|---------|
| Site | 2 | 59.7962 | 50.31** |
| Family | 67 | 3.0001 | 2.52** |
| Replication (site) | 11 | 6.8152 | 6.86** |
| Site x family | 127 | 1.1884 | 1.19 |
| Error | 1722 | 0.9996 | |

** significant at 0.01 level.

DISCUSSION

Results of these plus-tree selection and open-pollinated progeny tests indicate that different selection strategies may be desirable for white spruce and black spruce. Comparison-tree selection of superior white spruce in natural stands has resulted in substantial height gains when the progeny are compared with nursery-run check seedlings of unknown parentage. High calculated heritability values for height also indicates that comparison-tree selection would be expected to produce gains in white spruce.

Plus-tree selection was not effective in identifying black spruce parent trees that produce fast-growing progeny. The uninspiring performance of "plus-tree" progeny and the low heritability values indicate that family selection in progeny tests, rather than individual tree selection of parents, will be required to identify superior trees for inclusion in breeding programs. It also appears that black spruce field tests should include larger numbers of seedlings to provide a more reliable assessment of family performance, due to the relatively low heritability value for juvenile height in this species.

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Geographic Variation of Allozymes in Eastern
Larch (*Larix laricina* (Du Roi) K. Koch) From
Northwestern Ontario¹

Peggy H. Knowles and Dan J. Perry²

Abstract.-- Allozyme variation in eastern larch across northwestern Ontario was assessed by transplanting 20 seedlings from each of 10 populations to greenhouse conditions, rooting vegetative tissue, and subjecting root tips to electrophoretic analyses. Five loci encoded by five polymorphic enzyme systems were assayed. Allelic heterogeneity tests indicated no significant differences among populations. F statistics indicated little population differentiation with a single population indicating a heterozygote deficiency. Multi-variate analyses supported the univariate results; no statistically significant multilocus discrimination obtained among the 10 populations. However, a small amount of patchy differentiation is evidenced and may be due, in part, to inbreeding. The lack of differentiation may result from the relatively homogeneous boreal environment and the relatively short occupation since glaciation.

Isozyme analyses of natural populations of numerous plant species have indicated that forest trees are among the most genetically variable (Hamrick 1979). The majority of this diversity has been found to be distributed within populations as compared to that among populations (O'Malley and others 1979; Yeh and O'Malley 1980; Brown and Moran 1981; Yeh 1981; Guries and Ledig 1982; Wheeler and Guries 1982; Dancik and Yeh 1983; Hiebert and Hamrick 1983; Furnier and Adams 1986). Conifer species of the boreal forest generally have broad geographical distributions and have not been as thoroughly studied due to the problematic nature of rangewide access. Larch is distributed from Newfoundland west to the Mackenzie River drainage and from the northern limit of tree growth south to the central Canadian prairie provinces in the west and the northern states in the east. A disjunct portion of the range also occurs in central Alaska and the Yukon. Ecologically, larch is notable for its successful growth under extremely varied climatic and soil conditions (Fowells 1965).

The objective of this study was to assess the allozyme variation in eastern larch (*Larix laricina* (Du Roi) K. Koch) systematically across a substantial portion of its range in northwestern Ontario.

MATERIALS AND METHODS

Ten trees from each of two stands in close proximity at each of ten sites were sampled across northwestern Ontario (Figure 1). The twenty trees at each of ten sites were treated as a

single population. Sampled trees were 10 to 200 cm. in height and generally 10 meters apart with a separation of 5 meters in a minority of cases. Trees were removed from the field with balled roots, transferred to greenhouse conditions, and potted. A three month stabilization period was allowed at which time a branch end was removed from each sampled tree and vegetatively propagated. After four months growth of the rooted cuttings, one to three actively growing root tips from this clonal material were excised and ground in 2 drops of the following grinding buffer: To 0.2 g ascorbic acid, 0.095 g cysteine, 1 ml tween, 2 ml. 10% MgCl₂, 2 ml 10% CaCl₂, 17.1 g sucrose, 20 mg glutamic acid, 2 drops b-mercaptoethanol, add 0.1M tris/HCl (pH 7.5) to 100 ml volume. The grindate was then subjected to electrophoretic analysis (Table 1). Five loci encoded by five polymorphic enzyme systems (Table 1) were assayed for all individuals except for five trees that had insufficient 6pg activity. Details of the

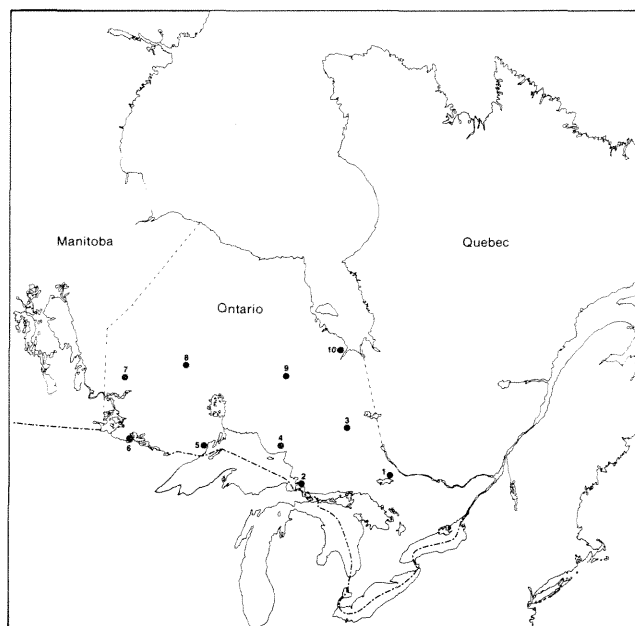


Figure 1. Map of site locations for larch samples

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TABLE 1. Enzyme systems assayed in larch root tissue.

| Locus | E.C. Number | Buffer, ¹ System |
|--|-------------|--------------------------------|
| Diaphorase (<i>Dia</i>) | 1.6.4.3 | A |
| Malate dehydrogenase (<i>Mdh-3</i>) | 1.1.1.37 | B |
| Phosphoglucose isomerase (<i>Pgi-2</i>) | 5.3.1.9 | A |
| Phosphoglucose mutase (<i>Pgm</i>) | 2.7.5.1 | B |
| 6-phosphogluconate dehydrogenase (<i>6-pg</i>) | 1.1.1.44 | B |

¹Buffer systems:

- A Tris-citrate pH 8.5 gel buffer; lithium borate pH 8.1 electrode buffer (Ridgeway *et al.*, 1970). Run at 300 volts.
- B L-histidine-tris pH 7.0 gel buffer; Tris-citrate pH 7.0 electrode buffer (Florence, 1981). Run at 200 volts.

inheritance of these allozymes are described by Cheliak and Pitel (1984).

Allelic and genotypic frequencies were tallied for each population and tested for allelic heterogeneity and deviation from Hardy-Weinberg equilibrium respectively. In both instances, the maximum likelihood G procedure was used (Sokal and Rohlf 1981). Since this procedure is not robust for small sample sizes within any row by column cell, alleles with low frequencies (less than 2) were bulked with the allele for the next lowest frequency.

A hierarchical analysis of population structure was conducted by means of F statistics (Wright 1969; Kirby 1975; Nei 1977). The statistics were calculated according to Nei's (1977) method. The average deviation of a subpopulation's genotypic proportions from Hardy-Weinberg equilibrium is measured by F_{IS} with a negative value indicating an excess of heterozygotes. Similarly, F_{IT} measures the same deviation but relative to the total population rather than the subpopulation. Finally, F_{ST} measures the extent of differentiation among subpopulations.

The pattern of multilocus variation among the 10 populations was examined by subjecting the data to principal components analysis and discriminant functions analysis. These procedures have proven useful to the understanding of genetic factors underlying geographic differentiation (Yeh and others 1985). Genotypic data were coded according to the method of Smouse and others (1982). Each genetic variable is expanded to $(n - 1)$ independent variables where n is the number of alleles at a particular locus. This scheme incorporates both gene frequency and genotypic frequency information and resulted in the construction of 10 genetic variables which were then summarized by principal components analysis into factor loadings for each individual. The principal components procedure constructs several "factors" that summarize the genetic variation and the loading for each individual is that individual's contribution to the newly constructed multidimensional "factor". Five of these summary variables or "factors" were subjected to discriminant analysis which statistically maximizes the variation among groups in order to distinguish among the 10 populations.

RESULTS

Frequencies for the most common allele at the five polymorphic loci for each of the 10 popula-

tions are listed in Table 2. Note that the common allele is actually fixed for *Pgm* and *Dia* in four and five of the 10 populations respectively. Tests for deviation from Hardy-Weinberg expectations indicated no significant departures. Similarly, no significant allelic heterogeneity was detected among the 10 populations.

TABLE 2. Frequency of most common allele.

| Site | <i>Dia</i> | <i>Mdh-3</i> | <i>Pgi-2</i> | <i>Pgm</i> | <i>6-pg</i> |
|------|------------|--------------|--------------|------------|-------------|
| 1 | .900 | .650 | .550 | .900 | .950 |
| 2 | .975 | .800 | .625 | .975 | .947 |
| 3 | 1.0 | .750 | .700 | .975 | .950 |
| 4 | 0.974 | .526 | .553 | .974 | .842 |
| 5 | 1.0 | .625 | .575 | .975 | .925 |
| 6 | 1.0 | .750 | .625 | 1.0 | .971 |
| 7 | 1.0 | .605 | .395 | 1.0 | .974 |
| 8 | .947 | .579 | .500 | 1.0 | .974 |
| 9 | .972 | .694 | .639 | 1.0 | .917 |
| 10 | 1.0 | .650 | .575 | .975 | .974 |

A summary of the F statistics is provided in Table 3. Values for F_{IS} are presented separately for each population at each locus. The average F_{IT} values over all populations for each locus and the single F_{ST} values for each locus are presented. In those populations where alleles are fixed, the F_{IS} statistics have not been calculated. Note the lack of pattern for the direction of deviation among the F_{IS} values, except for the locus *6-pg* that shows a consistent but small excess of heterozygotes over all populations. Population 1 shows the greatest value for mean F_{IS} (0.203).

TABLE 3. Values of F_{IS} for each of the ten larch populations and mean values of F_{IT} and F_{ST} for all ten populations.

| Statistic | Population | <i>Dia</i> | <i>Mdh-3</i> | <i>Pgi-2</i> | <i>Pgm</i> | <i>6-pg</i> | Mean |
|-----------|------------|-------------------|--------------|--------------|------------|-------------|-------|
| F_{IS} | 1 | -.111 | .411 | .322 | .447 | -.053 | .203 |
| | 2 | -.026 | .330 | -.325 | -.026 | -.056 | -.021 |
| | 3 | i.v. ¹ | -.029 | -.349 | -.026 | -.053 | -.114 |
| | 4 | -.027 | -.065 | .075 | -.027 | -.188 | -.046 |
| | 5 | i.v. | .208 | .079 | -.026 | -.081 | .045 |
| | 6 | i.v. | -.103 | -.282 | i.v. | -.030 | .138 |
| | 7 | i.v. | .105 | -.058 | i.v. | -.027 | .007 |
| | 8 | -.056 | -.153 | -.035 | i.v. | -.027 | -.068 |
| | 9 | -.029 | .311 | -.055 | i.v. | -.091 | .034 |
| | 10 | i.v. | -.083 | -.310 | -.026 | -.027 | -.112 |
| F_{IT} | | -.028 | .092 | -.029 | .223 | -.055 | .041 |
| F_{ST} | | .034 | .031 | .027 | .042 | .027 | .032 |

¹i.v. = insufficient variation for F_{IS} calculations.

The results of the principal components analysis indicated that each of the ten extracted factors, corresponding to the ten input genetic variables, contributed approximately equally in accounting for the existing variation. An examination of the loadings (not shown) indicated that each principal component reflected variation in very few loci, suggesting that groups of genes were not covarying in the same pattern. Individual factor loadings for the first five factors, accounting for 62% of the variation, were chosen to submit to the discriminant analysis. The first function generated by the analysis accounted for 40% of the variation but was not statistically significant indicating that there was no significant discrimination among the populations. A graphical illustration of the first and second

functions is presented in Figure 2. In combination, these two functions account for 66% of the variation existing in the factor scores. Figure 2 indicates that differentiation among populations is minimal with populations 1 and 5 showing divergence from all other populations as a group.

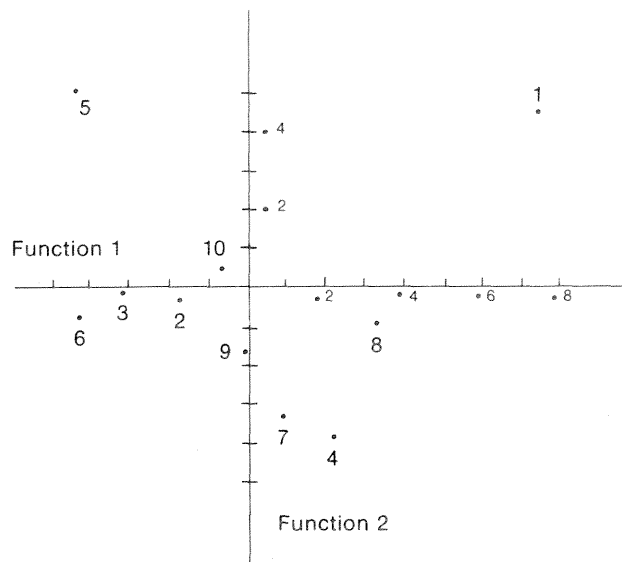


Figure 2.--Graphical plot of the centroids representing the ten eastern larch populations based on the first two functions of the discriminant analysis.

DISCUSSION

The results indicate that the isozyme structure of larch does not exhibit marked heterogeneity across the geographic area studied. Even though the sampling range extended over a 1300 km. distance in a north-south direction with a 2600 km. east-west distance, no consistent trends in isozyme variation were detected. The statistical evidence from allelic heterogeneity tests, F_{ST} statistics, and the discriminant functions procedure consistently support this general conclusion. However, the multivariate analysis does provide evidence for small but distinctive differentiation of two populations from all others as a group. Even though this differentiation does not attain statistical significance, it may represent a biologically meaningful "patchiness" of genetic structure within this portion of its range.

Deviations from Hardy-Weinberg equilibrium proportions as measured by F_{IS} warrant closer examination. Population 1 shows an excess of homozygotes. This result corresponds to a previous finding of a relatively low level of outcrossing for different trees at the same location (Knowles and others, 1986). This outcrossing study focused on seeds from samples of mature trees at locations corresponding to numbers 1, 5, 6, 7, and 9 of the present study. The multilocus outcrossing estimates, t_m (Shaw and Allard, 1982), represent the frequencies of outcrossed progeny and were calculated as .537, .735, .699, .908, and .768 for these five sites respectively. The ecological and/or genetic factors that are

encouraging this relatively high level of inbreeding at site 1 are reflected by the seedling population sampled from the same location in the present study.

The unusual genetic structure of population 1 is further emphasized by the results of the multivariate analyses. Even though the differences among the ten populations subjected to the discriminant analysis are not statistically significant, population 1 shows a substantial deviation from most other populations (see Figure 2). We interpret that this deviation results from the unusual genotypic structure of population 1 perhaps due to inbreeding at this site.

The actual level of differentiation among populations, as measured by the F_{ST} statistic, is similar to that found in several other forest tree species (Table 4). The G_{ST} statistic used for this comparison was designed by Nei (1975) and is mathematically identical to F_{ST} (Nei, 1977). Gullberg and others (1985) similarly compared population differentiation from several studies of conifer populations in the literature concluding that in areas that had been covered by ice during glaciation events, conifers had generally lower differentiation than those occupying unglaciated areas. The present findings support this conclusion with a previously undocumented species, *Larix laricina*.

TABLE 4. Population differentiation (G_{ST} , Nei, 1975) of some conifer species.

| Species | G_{ST} | Reference |
|------------------------------|----------|---------------------------|
| <i>Pinus sylvestris</i> | 0.02 | Gullberg et al. (1985) |
| <i>Pinus resinosa</i> | 0.00 | Fowler and Morris (1977) |
| <i>Pinus rigida</i> | 0.02 | Guries and Lediq (1982) |
| <i>Pinus banksiana</i> | 0.02 | Dancik and Yeh (1983) |
| <i>Pinus contorta</i> | 0.06 | Wheeler and Guries (1982) |
| <i>Pinus monticola</i> | 0.15 | Steinhoff et al. (1983) |
| <i>Pinus ponderosa</i> | 0.12 | O'Malley et al. (1979) |
| <i>Pinus radiata</i> | 0.13 | Brown and Moran (1981) |
| <i>Pinus jeffreyi</i> | 0.14 | Furnier and Adams (1986) |
| <i>Picea sitchensis</i> | 0.08 | Yeh and E)-Kassaby (1980) |
| <i>Pseudotsuga menziesii</i> | 0.03 | Yeh and O'Malley (1980) |

What accounts for the generally homogeneous genetic structure of larch across northwestern Ontario? One explanation is the lack of time for differentiation since larch has occupied the area for only about 200 to 300 generations since the last glaciation. Davis (1983) indicates that larch moved northwards and eastwards from the Great Plains reaching the present-day Canada/United States border approximately 10,000 years ago after spruces had been well established. Further, the relatively undifferentiated vegetative and topographic characteristics of the boreal region restricts selective forces to those of climatic origin. Conifers from the western part of the continent with mountainous and/or discontinuous distributions can be subject to stronger differential selection and also tend to show higher genetic differentiation (O'Malley, Allendorf and Blake 1979; Brown and Moran 1981; Steinhoff, Joyce and Fins 1983; Furnier and Adams 1986). Finally, as a wind-pollinated species in a boreal region, larch populations suffer no significant obstruction to gene flow. However,

the previously mentioned recent finding of relatively high levels of self-fertilization in larch (Knowles and others, 1986) indicates that this factor may be less important in contributing to among-population homogeneity.

In conclusion, the larch populations sampled from northwestern Ontario show no statistically significant differentiation based on isozyme variation. This is possibly due to the relatively homogeneous boreal environment and the relatively short occupation of this environment since glaciation. A small amount of patchy differentiation is evidenced and part, to inbreeding. A more complete range-wide investigation incorporating more loci and larger sample sizes would be a valuable contribution to the understanding of this boreal conifer.

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Soil and Foliage Analysis in Intensive Forest
Management¹

Sharon G. Haines and L. Wayne Haines²

Only recently have trees been considered a crop. ...foresters must know as much about how to manage crop trees as a farmer does about managing his agricultural crop.

(Haines, 1978b)

Scientists have spent over a century attempting to quantify the nutritional status of plants and the nutrient-supplying capacity of soils. Compilations by Goodall and Gregory (1947) and Chapman (1966) summarize approaches used and diagnostic criteria developed for plants and soils. When compared to most agronomic and horticultural crops, relatively little is known about nutrient requirements of forest trees. Bauer (1910) and Kubler (1912) provided most of the available nutrient data for forest trees until the 1930s.

The scarcity of data on mineral nutrition of forest trees was emphasized during a Duke University symposium in 1958 (Anonymous, 1959). Subsequently, progress on the issue of tree nutrition and modification of nutrient status via forest fertilization was summarized at a 1967 symposium at the University of Florida (Anonymous, 1968). More recent advances including use of operational fertilization in intensive forestry have also been summarized (Bengtson, 1979; Pritchett and Gooding, 1975).

The use of soil and foliage analysis in agronomy and horticulture is a rather highly

Abstract.--Forest management decisions often require knowledge of soil and foliage nutrient levels. Accurate interpretation of analytical results requires knowledge of sampling, handling, and analytical procedures, since variation in methodology can significantly alter nutrient levels measured. Inaccurate management decisions will result if analytical values obtained do not accurately reflect the nutrient status of the soil or foliage. Key aspects of soil and foliage analysis are discussed herein. Data are presented to demonstrate the impacts of variation in methodology on results obtained.

Keywords: soil nutrients, foliar nutrients, sampling procedures, analytical methods, forest trees

refined discipline. Foresters are only now beginning to tap these analyses to their maximum potential in forest management. An expansive examination of the topic is not possible in this forum; however, selected principles of soil and foliage analysis are discussed along with some factors impacting the utility of these procedures in forestry.

ANALYTICAL CYCLE

Both soil and foliage sampling have several things in common including what might be called the analytical cycle. This cycle includes accurate sampling, proper handling of samples, accurate analysis, and correct interpretation of analytical results. An error at any point within the cycle can yield inaccurate results or interpretations.

The first step in the cycle is accurately sampling the site conditions of concern. The samples collected must be representative of the situation that the sampler is interested in documenting. For example, if an area of poorly growing trees within a stand is of concern, it is imperative that the sample collected represent the portion of the stand that is unhealthy. Samples from healthy areas of the stand may also be collected for comparison; however, the identity of samples must be maintained so that correct comparisons can be made.

After collection, the samples must be properly handled until they can be analyzed. Specific details of handling are dependent upon analyses to be performed, but some general rules apply. Soil samples should be kept in a clean area away from fertilizers and other chemicals. Soil is usually air dried after collection and prior to submission to the laboratory. Foliage samples should be dried or frozen as soon after sampling as possible. If dried, the samples should be kept dry and in a clean area away from contaminating agents. If frozen, foliage should be kept totally or partially frozen until analyzed.

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The third part of the cycle involves the handling and analysis of samples once they arrive in the laboratory. Samples must be redried and ground prior to analysis. Analytical procedures should be chosen that permit the required interpretations once the analysis is completed. Both the methods and laboratory quality control standards should be well documented.

Interpretation of results obtained from the lab analyses is the final step in the cycle. Accurate interpretations are dependent upon having results available that accurately reflect nutrient status or some other characteristic. Evaluation of analytical results cannot be done without knowledge of the methods used to analyze the samples.

It is important to remember that the numbers themselves are not magical. They have no meaning in and of themselves but must be interpreted in light of research or operational results. The numbers that are ultimately interpreted can be altered by an error that occurs at any point from selecting the area to be sampled through the analysis process. Thus, it is imperative that the integrity of the analytical cycle be maintained throughout the entire process.

TYPES OF SOIL AND FOLIAGE ANALYSIS

Soil

Chemical analysis generally includes pH, organic matter (O.M.), phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), and manganese (Mn). Micro-elements determined may include aluminum (Al), boron (B), copper (Cu), iron (Fe), molybdenum (Mo), and zinc (Zn). Sulfate ($\text{SO}_4\text{-S}$), nitrate ($\text{NO}_3\text{-N}$), and ammonium ($\text{NH}_4\text{-N}$) are other nutrient levels monitored. Chemical soil analysis is used to determine the need for fertilization, rates of application of soil-active herbicides, and nutrient imbalances of trees growing on the site sampled.

Three frequently measured physical traits are particle-size analysis (texture), bulk density, and moisture-holding capacity. Other physical analyses, such as sand fractionation, are less frequently measured. Texture analysis is required to determine rates of application of soil-active herbicides. Bulk density measurements provide indications of potential rooting restrictions for new seedlings. Moisture-holding capacity can be used to characterize the moisture available on specific sites for tree growth and development.

Foliage

Chemical analysis of foliage generally includes nitrogen (N), P, K, Ca, Mg, and Mn. Micro-elements determined may include Al, B, Cu, Fe, Mo, and Zn. Sulfate is another nutrient level monitored in foliage. Chemical foliage

analysis is normally used to determine the need for fertilization (primarily with N and P in established forests) or to determine a nutrient imbalance that is causing reduced growth or unhealthy appearance of seedlings or trees.

Biochemical analyses can be performed on foliage also. These include various sugars, starches, carbohydrates, and amino acids. Rapid development of new root tissue after planting is essential for pine seedling survival, and root elongation early in the growing season is dependent upon carbohydrate reserves stored in the roots from the previous growing season (Kramer and Kozlowski, 1979). Management activities that increase levels of reserve carbohydrates in seedling root systems may provide the needed energy source for increased root elongation shortly after outplanting and thereby increase the seedling's survival potential.

FACTORS IMPACTING ANALYTICAL RESULTS

Factors that can alter analytical results include site history, map unit variability, topography, intensity of sampling, and season of the year. Factors specific to soils include the horizon or depth in the profile to be sampled. Location within the crown and the part of the leaf to be analyzed are additional factors to consider when sampling foliage. The manner in which samples are handled and analyzed can have significant effects on the results obtained in the analysis.

Site History

Results obtained cannot be interpreted properly without knowledge of the site history. Examples of site characteristics that must be documented during sampling are the site's burning and fertilization history. Soil nutrient status can be altered by these two practices for long periods. Applications of P can be monitored in many soils for years after treatment. Repeated fertilizer applications, such as are used in seed orchards, can significantly change soil chemistry (Gregory et al., 1982). Burning large amounts of surface debris can have a fertilizing effect because of the quantities of nutrients deposited in the ash. This is also true when thick organic surfaces over mineral soils are burned.

Comparisons of soil nutrient status before and after burning debris piles often reveal large differences in the levels of cations present (Table 1). A debris pile composed of approximately 60 cu m of pine stems, branches, and foliage was burned on a sandy soil (Haines, 1978a). Burning yielded increased pH as well as higher levels of P, K, Ca, and Mg, plus lower organic matter concentrations. Over a 3-month sampling period, nutrient levels in the 0-2 cm zone decreased while those in lower zones increased, indicating nutrient movement through the profile. Post-burning nutrient means were

substantially larger than those observed prior to burning.

Table 1.--Comparisons of selected nutrient concentrations at 3 depths in a soil profile before and after burning a debris pile (Haines, 1978a)^a

| Soil Depth | pH | O.M. (%) | P | K | Ca | Mg |
|------------------|-----|-------------|----|-----|-----|-----|
| -----ppm----- | | | | | | |
| <u>Pre-Burn</u> | | | | | | |
| 0-2 cm | 5.6 | 2.3 | 2 | 13 | 162 | 35 |
| 2-4 cm | 5.6 | 2.2 | 1 | 6 | 82 | 22 |
| 4-6 cm | 5.6 | 1.8 | 1 | 4 | 45 | 15 |
| <u>Post-Burn</u> | | | | | | |
| 0-2 cm | 6.9 | 1.6 | 58 | 164 | 450 | 164 |
| 2-4 cm | 6.6 | 1.3 | 31 | 119 | 167 | 81 |
| 4-6 cm | 6.5 | 1.0 | 25 | 96 | 160 | 66 |

^aMeans of 6 observations before burning and 42 observations over a 3-month period after burning.

Map Unit Variability and Topography

Map unit variability will determine the location of sample points and also, to some extent, the intensity of sampling required to obtain acceptable measures of nutrient status. Topography is also important in locating sample points since nutrient values usually vary with topographic position. For example, nutrient status on the ridgetop can be lower than that at the bottom of the slope because of topsoil erosion downslope. Samples should be collected only on those portions of the map unit or site that are of concern. Inclusions of different soil or site conditions should not be sampled. For example, small wet depressions, old home sites, old roads, or other portions of the site that are clearly different from the condition of concern should be avoided. If comparisons are needed by topographic position, samples from the ridge, sideslope, and bottom of the slope might be appropriate.

Sampling Intensity

Intensity of sampling is dependent on site variability and on the level of confidence required in the results of the analysis. Sample sizes required vary considerably depending upon characteristics of the site being sampled as well as the soil property being measured (Table 2). Five forested sites in southwest Georgia were sampled monthly for a 1-year period to determine the magnitude of variation in 16 soil properties (Haines and Cleveland, 1981). As a part of this examination, the sampling intensity required to accurately predict means

Table 2.--Sample sizes required to estimate mean values of soil properties on 2 sites within 5 percent with 95 percent confidence (Haines and Cleveland, 1981)

| Soil Property | Old Field | Pine & Hardwood |
|---------------|-----------|-----------------|
| Bulk density | 5 | 49 |
| Soil moisture | 22 | 616 |
| Surface pH | 2 | 2 |
| Surface O. M. | 52 | 205 |
| Surface P | 76 | 227 |
| Surface K | 69 | 144 |
| Surface Ca | 94 | 387 |

of soil variables was determined. Selected soil properties for two of the sites examined are included in Table 2. The old-field site is a 14-year-old slash pine (*Pinus elliottii* Engelm. var. *elliottii*) plantation on an Orangeburg soil (Typic Paleudult: fine-loamy, siliceous, thermic). The pine and hardwood site is a clearcut mixed pine-hardwood stand that had been chopped and burned. The soil is an Esto (Typic Paleudult: clayey, kaolinitic, thermic).

The differences in sampling intensities between the two contrasting sites reflect differences in site uniformity. Generally, fewer samples are needed on the old-field site with its uniform cover of pine canopy and absence of understory vegetation. Only pH can be measured at both locations with the same sampling intensity.

The variation among soil properties is caused by natural variation and by how precisely the value can be determined in the laboratory. The lowest intensity was for pH, a property that has a relatively low natural spatial variation and a simple, easily replicated analytical test. Higher sampling intensities for the other variables reflect a greater range of natural variation as well as less precise or reproducible analytical procedures.

Season of Year

Variation in foliage biochemical compounds and nutrient levels throughout the growing season has been documented (Kramer and Kozlowski, 1979; Wells and Metz, 1963). Concentration variations result with reallocation of nutrients and biochemical compounds as growth and development progress. Foliage sampling to document pine nutrition is usually conducted during the dormant season when nutrient concentrations are

most stable. However, some researchers recommend sampling during the growing season when nutrient demand is greatest.

Less attention has been given to variation in soil properties throughout the year. Haines and Cleveland (1981) measured selected chemical and physical soil properties for 12 consecutive months on five forested sites in southwest Georgia. Surface bulk density and percent moisture, O.M. and K to 20 cm, and P to 10 cm varied significantly over time at all locations. Soil pH, Ca, Mg, and cation exchange capacity to 20 cm and P at 10 to 20 cm differed significantly over time at some, but not all, sites. The authors concluded that periodic variation must be considered when effects of forest management and research treatments on soil chemical and physical properties are evaluated.

Crown Position and Leaf Portion

Nutrient composition of tree foliage is known to vary with age of foliage and position within the crown (Madgwick, 1964; Wells and Metz, 1963). Application of 198 kg-N/ha, 7 kg-P/ha, and 26 kg-K/ha over a 2-year period significantly increased loblolly pine (*Pinus taeda* L.) foliar N concentrations but not P or K (Haines and Haines, 1979). Nitrogen concentrations were significantly higher in fertilized loblolly pine foliage regardless of the portion of the crown sampled (Table 3). Rates of P and K fertilization apparently were too low to affect concentrations of those nutrients in foliage. Since operational fertilization decisions are tied to foliar N levels, sample location within the crown can determine whether or not prescriptions are accurately developed.

When determining nutrient status of broadleaf species, one must decide which portion of the leaf to analyze. Analysis of specific portions of leaves of agronomic and horticultural crops has been common for decades (Bould, 1961; Kwong and Boynton, 1959; Goodall and Gregory, 1947). Variation of nutrient concentrations by leaf portion has been documented for some forest tree species such as yellow poplar, *Liriodendron tulipefera* L. (Auchmoody, 1974; Finn, 1966), as well as sycamore maple, *Acer pseudoplatanus* L., and European horsechestnut, *Aesculus hippocastanum* L., (Guha and Mitchell, 1965).

Haines et al. (1979) compared nutrient composition of sycamore (*Platanus occidentalis* L.) blades, petioles, and whole leaves. Nitrogen was highest in the blade and lowest in the petiole; when the whole leaf was analyzed the higher concentration in the blade was diluted by lower petiole-N levels (Table 4). Petiole-P and K were both significantly higher than levels in other leaf parts; petiole-Ca was significantly lower. Given the magnitude of nutrient concentration variation, it is unlikely that one leaf portion could be selected to most accurately reflect sufficiency or deficiency for all nutrients of interest.

Table 3.--Nutrient concentrations in fertilized and unfertilized loblolly pine foliage by crown position (Haines and Haines, 1979)^a

| Crown Position | N | P | K |
|-------------------------|------------------|----------------|----------------|
| | -----pct----- | | |
| <u>Check Trees</u> | | | |
| Upper | 0.97 (0.09) | 0.13 (0.02) | 0.81 (0.07) |
| Middle | 0.78 (0.07) | 0.11 (0.03) | 0.43 (0.05) |
| Lower | 0.69 (0.09) | 0.10 (0.04) | 0.31 (0.04) |
| <u>Fertilized Trees</u> | | | |
| Upper | 1.12 (0.08)* | 0.15 (0.03) | 0.97 (0.08) |
| Middle | 0.89 (0.07)* | 0.11 (0.03) | 0.46 (0.06) |
| Lower | 0.91 (0.10)** | 0.09 (0.02) | 0.40 (0.05) |

^aMeans of 4 check and 4 fertilized trees; standard errors of the mean in parenthesis. * denotes significance at the .05 level; **, at the .01 level.

Table 4.--Nutrient concentrations in sycamore foliage by leaf part (Haines et al., 1979)^a

| Leaf Part | N | P | K | Ca |
|------------|---------------|--------|--------|--------|
| | -----pct----- | | | |
| Whole Leaf | 1.82 y | 0.12 x | 0.80 y | 0.95 y |
| Blade | 2.10 z | 0.12 x | 0.71 x | 0.96 y |
| Petiole | 0.62 x | 0.16 y | 1.22 z | 0.85 x |

^aMeans followed by different letters are significantly different at the .05 level.

Correlation of nutrient concentrations with broadleaf tree growth presents similar problems (Table 5). Haines et al. (1979) determined correlation coefficients between nutrient concentrations by leaf part and sycamore height and volume growth. Blade-N was the most highly correlated with height and volume growth of all nutrients. Blade-P and K were both more highly correlated than petiole or whole leaf concentrations. For height growth, blade-N was the best single variable predictor while blade-P was the best for volume growth.

Sample Handling

Nutrient levels in pine foliage can be used as indicators of the need for operational fertilization of established stands (Pritchett, 1979; Wells et al., 1973). When foliar nutrient levels are below established critical values, fertilization will likely result in an increase in tree growth. The analytical values obtained are dependent upon the actual nutrient content

Table 5.--Correlation coefficients between sycamore foliage nutrient concentrations and height and volume growth (Haines et al., 1979)^a

| Element/Leaf Part | Height Growth | Volume Growth |
|-------------------|---------------|---------------|
| Nitrogen | | |
| Blade | 0.86** | 0.73** |
| Petiole | 0.65** | 0.54** |
| Whole Leaf | 0.76** | 0.54** |
| Phosphorus | | |
| Blade | 0.66** | 0.76** |
| Petiole | 0.25 | 0.50** |
| Whole Leaf | 0.57** | 0.54** |
| Potassium | | |
| Blade | 0.29 | 0.48** |
| Petiole | 0.23 | 0.31 |
| Whole Leaf | 0.12 | 0.13 |

a** denotes significance at the .05 level.

and the oven-dry weight of the foliage sample. Since the results are expressed as a percentage of oven-dry weight, it is imperative that no changes occur in the weight of the sample from sampling to analysis. Weight losses can occur if respiration continues in the sample prior to oven-drying. Obviously, the situation is quite important when the foliar concentrations are close to the critical levels where a relatively small difference in the results could influence the decision to fertilize. Attempts have been made to document the kinds of changes in nutrient levels that result with different sample treatments.

In one study, the staff of the Cooperative Research in Forest Fertilization (CRIFF) program at the University of Florida tested five different handling procedures (Anonymous, 1976). Storing samples at ambient temperature at collection plus 10 days storage at room temperature resulted in increased N and K levels in slash pine foliage (Table 6). This apparently was a result of dry-weight loss from continued respiration prior to drying. Extended refrigeration following sample collection affects P levels more than other elements. The conclusion reached in this study was that the safest way to handle foliage samples after collection is to keep samples on ice or in a refrigerator until they can be dried. Drying should occur as soon after collection as possible.

Table 6.--Effects of handling procedures on slash pine foliage concentration (Anonymous, 1976)^a

| Sample Handling Treatment ^b | N | P | K |
|--|---------------|-------|------|
| | -----pct----- | | |
| Ice + Dry | 0.82 | 0.077 | 0.35 |
| Ice + Refrigerate + Dry | 0.84 | 0.078 | 0.35 |
| Ambient + Dry | 0.81 | 0.075 | 0.34 |
| Ambient + Refrigerate + Dry | 0.85 | 0.079 | 0.35 |
| Ambient + Store + Dry | 0.91 | 0.082 | 0.38 |

^aMeans of 4 observations

^bIce = 5 hrs in ice chest; dry = 24 hrs at 60° C; refrigerate = 10 days at 5° C; ambient = 5 hrs at 16° C; store = 10 days at 21° C.

Another alternative handling procedure is to freeze samples until they can be analyzed. A trial was established to determine whether or not foliage samples could be frozen prior to drying without altering nutrient concentrations obtained when the samples were analyzed. Thirty-six samples were collected and divided in half. One-half of each sample was frozen for 2 weeks after collection, thawed, dried, and ground. The other half was dried immediately after collection and then ground. All samples were analyzed at the same time. Paired t-tests indicated that N, Ca, Al, and Cu concentrations differed significantly by treatments (Table 7).

Table 7.--Comparison of effects of freezing on N, Ca, Al, and Cu concentrations in loblolly pine foliage^a

| Element | Dried | Frozen |
|----------|-----------------|-------------------|
| N (pct) | 1.15 (0.018) | 1.19 (0.016)** |
| Ca (pct) | 0.15 (0.006) | 0.14 (0.005)** |
| Al (ppm) | 404 (22) | 358 (19)** |
| Cu (ppm) | 2.0 (0.06) | 1.4 (0.09)** |

^aMeans of 36 observations; standard errors of the mean in parenthesis. ** denotes significance at the 0.01 level.

The difference in N levels had the most serious implications because decisions on

operational fertilization are made on the basis of foliar N levels. If sample handling causes N levels to be higher than they should be, stands that might respond to N fertilization would be eliminated from the program because the N concentrations are above critical levels. Similarly, if N levels are lowered by sample handling, stands might be fertilized that are not actually economically responsive.

A follow-up trial was conducted to determine if duration of freezing impacted results obtained. Samples were either oven dried only, frozen one week and oven dried, or frozen 2 weeks and oven dried. Both freezing treatments significantly altered the N, P, and Mn levels obtained (Table 8). Since freezing can alter both N and P results obtained, operational foliage samples should not be frozen. Critical levels for N and P fertilizer response were established using oven dried samples, and reliable correlations between frozen and oven dried samples have not been established.

Table 8.--Effects of freezing duration on N, P, Mn, and Zn concentrations of loblolly foliage^a

| Treatments | N -----pct----- | P -----pct----- | Mn | Zn ppm |
|-------------------|--------------------|--------------------|--------------------|------------------|
| Dried | 1.22 x (0.013) | 0.101 x (0.001) | 0.021 x (0.002) | 33.5 x (1.1) |
| Frozen 1 week | 1.17 y (0.013) | 0.095 y (0.001) | 0.024 y (0.001) | 35.9 y (1.3) |
| Frozen 2 weeks | 1.15 y (0.013) | 0.097 y (0.001) | 0.024 y (0.002) | 34.1 xy (1.2) |

^aMeans of 36 observations; standard errors of mean in parenthesis. Methods by element followed by different letters differ significantly at the 0.05 level.

Standard foliage drying procedures involve use of forced air drying ovens that are not always readily available to foresters who collect operational foliage samples. Since microwave ovens are widely available, a trial was conducted to compare nutrient concentrations obtained following conventional forced-air and microwave drying (Table 9). No significant differences in loblolly pine foliar N, P, or K concentrations were observed that would prevent use of microwave drying.

Instrumentation and Analytical Techniques

Variation in results is expected depending upon the instrumentation and the analytical technique utilized. Instruments and techniques used must be carefully documented so that the results can be interpreted correctly. Comparisons among methods of analysis have been made for some soil determinations.

Table 9.--Effect of drying method on loblolly pine nutrient concentrations^a

| Drying Method | N -----pct----- | P -----pct----- | K |
|------------------|--------------------|--------------------|-----------------|
| Forced-Air | 1.16 (0.013) | 0.096 (0.002) | 0.23 (0.014) |
| Microwave | 1.15 (0.014) | 0.095 (0.004) | 0.24 (0.008) |

^aMeans of 36 observations; standard errors of mean in parenthesis.

King and Haines (1979) examined the effects of mechanical thinning equipment on soil bulk density at 2 depths in a loamy Coastal Plain soil. Thinning had no effect on bulk density at either 5 cm or 10 cm depths (Table 10). In this same study, 2 methods of measuring bulk density (gravimetric and neutron probe) were compared. The gravimetric method requires collection of a known volume of soil, oven-drying, and calculation of the bulk density. Bulk density has traditionally been measured by the gravimetric method. The neutron probe measures density in place in the soil as a function of neutron scatter, and the value is read on the instrument.

Table 10.--Comparison of 2 methods of determining bulk density at 2 depths before and after thinning (King and Haines, 1979)^a

| Method | Before Thinning | | After Thinning | |
|------------------|-------------------------------|----------------|----------------|----------------|
| | 5 cm | 10 cm | 5 cm | 10 cm |
| | ----- g/cm ³ ----- | | | |
| Gravimetric | 1.54 (0.09) | 1.62 (0.10) | 1.50 (0.14) | 1.66 (0.08) |
| Neutron Probe | 1.21 (0.08) | 1.29 (0.06) | 1.27 (0.06) | 1.34 (0.06) |

^aMeans of 14 observations; standard deviations in parenthesis.

The neutron probe consistently underestimated density when compared to the gravimetric method. Standard deviations from the mean were greater with the gravimetric method than with the neutron probe. This is attributed to more direct measurement of density with the probe as compared to the handling, weighing, drying, and calculations required for the gravimetric method. Generally speaking, the more mechanized a method the more precise it is likely to be.

As a part of our laboratory research program, we have done extensive work comparing extractants for soil analysis across soil types on our land. Data presented (Table 11) were obtained from the A horizon of a wet, loamy sand soil in the Atlantic Coastal Plain known to be moderately responsive to P fertilization at stand establishment. Following extraction, P was determined by a modified vanadomolybdate method (Chapman and Pratt, 1961); Al and Fe were determined by atomic absorption spectrophotometry.

Table 11.--Comparison of P, Al, and Fe concentrations in the A horizon determined following five different extractions^a

| Extractant | P -----ppm----- | Al -----ppm----- | Fe -----ppm----- |
|----------------------|--------------------|---------------------|---------------------|
| Double Acid | 3.3 (0.2) | 229 (11) | 99 (6.1) |
| Mehlich I + Flourine | 4.5 (0.3) | 401 (16) | 126 (5.4) |
| Mehlich II | 4.2 (0.2) | 355 (21) | 61 (3.0) |
| Strong Bray | 39 (2.2) | 1034 (53) | 323 (18) |
| Weak Bray | 5.4 (0.3) | 473 (22) | 111 (5.8) |

^aMeans of 24 observations; standard errors of the mean in parenthesis.

The most dramatic difference is with the Strong Bray extractant that measures from 7 to 12 times as much P as the other extractants. Extractants rank the same for Al as for P, but the differences are only 2 to 4 times as large. Iron does not follow the same pattern as P and Al. Fertilizer recommendations on wet coastal plain soils are often made on the basis of soil P levels. Obviously, it is imperative to know the extractant used to obtain results being examined. More research is also needed to determine correlations of fertilizer response with results of different extractants, since response was usually correlated with only one extractant.

Attempts were made to correlate loblolly pine foliage P concentrations with soil P levels determined following the same five soil extractions. Correlation analysis was used to relate soil-P levels obtained with foliar P concentrations. Soil samples were collected from the surface, upper subsoil, and lower subsoil beneath the crown of the tree from which the foliage sample was collected. The highest correlation observed was in loblolly stands less

than 15 years old in the lower subsoil for the Mehlich I + Flourine extractant (0.523 **).

In the same study, correlations between soil Al and Fe levels and foliar P levels were examined. Both soil Al and Fe levels in the surface horizon were significantly correlated with foliar P for all five extractants. Highest correlation for soil Al was with the Mehlich I + Flourine extractant (0.649 **). The highest correlation for soil Fe was a negative one with the Weak Bray extract (-0.720 **).

MANAGEMENT IMPLICATIONS

The utility of soil and foliage analysis has been demonstrated; however, foresters still have ample opportunity to refine the use of these procedures. More in-depth knowledge of how various nutrient levels relate to site productivity and tree health and vigor is required for better utilization of the technology. Clearer understanding of the total nutrient cycle in forested ecosystems will help foresters more accurately interpret analytical results.

Standardization of collection, handling, and analytical procedures will make interpretation of results obtained more reliable. Examples presented herein have demonstrated that variation in any of the procedures can alter the results obtained. Such variation is particularly troublesome when results obtained are near critical levels that indicate nutrient sufficiency or deficiency. For example, foliage analysis results may indicate that an N or P deficiency exists and that operational fertilization can provide an economically attractive growth increase. However, if those results do not accurately reflect the nutrient status of the site in question, a bad decision will be made.

Standard procedures will also help us to develop a body of analytical knowledge that is comparable and more widely applicable in forest management. It may be too much to hope for one standard procedure to be accepted throughout the discipline, but it is a worthy goal to strive toward. At the least, researchers must become much more adept at interpreting results. Correlations among different techniques must be identified so that accurate interpretations can be made. Additionally, unless such correlations exist, we will be unable to fully utilize information that is already in the literature.

Henry George (Wahlenberg, 1960) noted, "Until there is correct thought there cannot be correct action." Correct thought is based on information. Incorrect thought stems less from a scarcity of information than from its relative inaccessibility. Information overload is often more of a problem today than a lack of data. It is imperative that pertinent information on soil and foliage analysis be readily accessible in easily understandable form for decision makers.

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Abstract.--The uncertainty about the role of tropical forests in the global cycle is due to many factors, including problems of estimating (1) forest biomass, (2) losses of soil carbon from forest clearing, and (3) rates of wood decomposition. Estimates of biomass of tropical forests based on extensive forest volume data give significantly lower values than estimates based on direct measurement methods. A major source of error in converting commercial volumes to total biomass is the high variability in the expansion factors (ratio of total biomass to commercial biomass) that suggests a need for regional estimates rather than for highly aggregated ones as has been done in the past. Loss rates of soil organic carbon upon conversion of forests to agriculture are influenced by the type of agriculture practice (small loss to small gain for pastures versus about 40 percent loss for crops), soil texture (less loss from clay soils), climate, and time. Decomposition rates of woody debris of primary forest species are slow (average decomposition coefficients of $0.02-0.07 \text{ yr}^{-1}$) and are partially regulated by the chemical characteristics of wood. These decomposition rates are slower than rates of forest regrowth and create carbon sinks in logged and natural forests. Further research is still needed to refine some of these carbon storages and fluxes to improve our understanding of the carbon cycle of tropical forests.

Keywords: Biomass, carbon cycle, soil carbon, tropical forests, wood decomposition.

Clearing of tropical forests for agriculture has the potential of producing a source of CO_2 to the atmosphere and thus exacerbating the potential "greenhouse effect". The release of CO_2 from clearing tropical forests for agriculture is due to burning and decomposition of plant material and the increased oxidation of soil organic matter. Results from models have demonstrated that land use changes in tropical forests produce a source of atmospheric CO_2 that may be as much as 20-80 percent of the amount contributed by the burning of fossil fuel (Houghton and others 1983, Detwiler 1986). These estimates of carbon flux (as CO_2) to the atmosphere are derived from models that consider rates of forest clearing, specific land uses for which an area is cleared (e.g., for permanent agriculture, shifting agriculture, pasture, or timber), and changes in biomass or carbon content of the vegetation and soil due to clearing.

There are several sources of error associated with the estimates of carbon flux from tropical forests. These errors are based mainly on

uncertainties in the value of the parameters used in models such as: the biomass or carbon content of tropical forests that are being cleared, the rates of forest clearing by forest type (i.e., low or high biomass forest), changes in soil carbon pools upon clearing, and rates of decomposition of organic material left behind on the site after clearing. The objectives of this paper are to discuss some of the sources of error associated with estimating (1) the carbon content of tropical forests, (2) changes in the carbon content of tropical soils due to forest conversion, and (3) decomposition rates of tropical woody debris.

CARBON CONTENT OF TROPICAL FOREST VEGETATION

Because of the diversity of forest types in the tropics, the problems of estimating their carbon content with any degree of precision are enormous. According to the Holdridge Life Zone system (Holdridge 1967) for classifying plant formations of the world, a system based on mean annual biotemperature and precipitation, there are 30 unique forested life zones in the tropics ranging from lowland very dry forests to montane rain forests. Each of these forested life zones potentially has a different organic carbon content because of the influence of temperature and moisture on structure and function of forests (Holdridge 1967). Brown and Lugo (1982) synthesized existing data on the carbon content of tropical forests and found that there was a highly

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significant relationship between carbon content of vegetation (expressed as biomass) and an index of life zone (ratio of temperature to precipitation; Fig. 1). Carbon content of tropical forests peaks in the moist forest life zone ($T/P=0.7-1.4 \times 10^{-2}$) with lower values in wetter ($T/P < 0.6 \times 10^{-2}$) and drier ($T/P > 2.0 \times 10^{-2}$) life zones. Thus, models of tropical forest clearing need information on the kinds of forest being cleared because their carbon content is related to the climate in which they grow. Unfortunately, this kind of information is lacking and represents a source of error in carbon flux estimates.

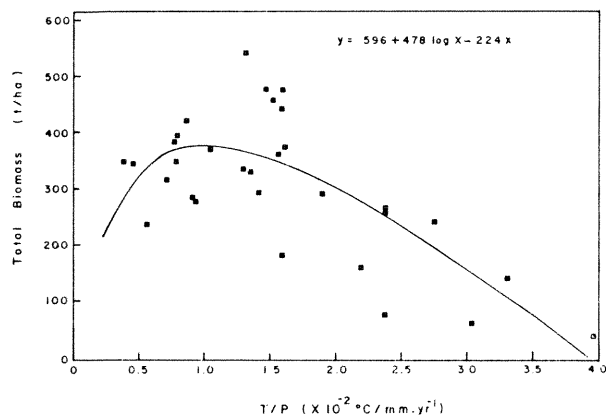


Figure 1.--Relationship between total biomass of tropical forest vegetation and the ratio of temperature to precipitation (T/P), a ratio used as an index of life zone (see text for further explanation). This relationship was determined by least squares regression analysis and is significant at $p=0.05$ with an $r^2=0.54$ (from Brown and Lugo 1982).

Another uncertainty in the data base for tropical forests is the magnitude of the carbon content of tropical forest vegetation. There have been several attempts during the last decade to both estimate the carbon pool in tropical forests and compute a weighted average carbon density (Table 1). The first four values in Table 1 are based on a summary of the published ecological literature. Variation in the estimates of the size of the carbon pool is attributed to both differences in the area of tropical lands covered by forests and differences in the carbon content of tropical forest vegetation. The changes in the amount of tropical forests used in these studies reflect improved accuracy in the area estimates by the international organizations charged with such assessments (e.g., Food and Agriculture Organization of the United Nations [FAO]) rather than a real decrease in forest area. Differences in the carbon content of forests used in the studies (Table 1) are due to (1) grouping of forests into fewer or more categories (e.g., two main types were used by Whittaker and Likens [1973] whereas six main types were used by Brown and Lugo [1982]) and (2) accessibility to a

larger data base in the later studies (e.g., many studies used by Brown and Lugo were published after 1975). It is generally agreed by those working with the global carbon cycle that the lower estimates, based on the ecological literature, of Brown and Lugo (1982) and Olson and other (1983) are more representative of the carbon content of tropical forests.

Table 1.--Estimates of carbon content in tropical forest vegetation

| Area (10^6 ha) | Carbon content (t/ha) | | Carbon pool (10^{15} g) |
|----------------------|-----------------------|---------------------|----------------------------------|
| | Range | Weighted average | |
| 2450 | 160-200 | 188 | 460 ^a |
| 1480 | 115-190 | 165 | 244 ^b |
| 1838 | 40-185 | 124 | 228 ^c |
| 1510 | 70-200 | 125 | 189 ^d |
| 1930 | 12- 90 | 53 | 102 ^e |

^aWhittaker and Likens 1973

^bAjtay and other 1979

^cBrown and Lugo 1982

^dOlson and others 1983

^eBrown and Lugo 1984

Brown and Lugo (1984) made another estimate of the carbon content of tropical forests using commercial volumes. This study relied heavily on the FAO (1981) report in which average commercial volumes for eight forest types in 76 tropical countries were given. Commercial volumes were converted to total biomass of vegetation by multiplying volume by an average wood density to obtain commercial biomass and then by an expansion factor (ratio of total above and below ground biomass to commercial biomass); biomass was converted to units of carbon (assuming 1 gram of organic matter = 0.5 gram of carbon). (Details of the analysis are given in Brown and Lugo [1984].) This analysis resulted in a carbon pool and weighted carbon density of tropical forest vegetation of about one-half the values based on direct measurements given in the ecological literature (Table 1).

One of the major causes of the discrepancy between ecological-based and volume-based biomass estimates is due to sampling error. Biomass estimates derived from the ecological literature are based on direct measurements (either by harvest methods or allometry) of small areas (a total of < 30 hectares for all studies) of a few tropical forest types and extrapolated to all tropical forests. Volume-derived biomass estimates are based on large sample areas (hundreds to thousands of hectares) and tend to be a more representative sample. Selection of small sample plots for ecological studies of direct measurements may be biased towards large biomass plots

because of a preconceived notion as to what a tropical forests should look like. For example, a frequency distribution of volume-derived biomasses for tropical moist forests of the Amazon basin demonstrate that more than 50 percent of the area covered in the survey had biomass values less than 200-220 metric tonne per hectare (t/ha) (Fig. 2). Biomasses of tropical American forests obtained from destructive sampling or allometric methods ranged from 210-480 t/ha (Brown and Lugo 1982), of which 50 percent had values between 210-330 t/ha and the other 50 percent were between 370-480 t/ha, with a greater frequency at the high end of the range. These results suggest that biomasses obtained by direct measurement on a few hectares are not average for Amazonian tropical moist forests but are biased towards high biomass plots. Similar trends were obtained for forests in tropical Africa and Asia (Brown and Lugo 1984).

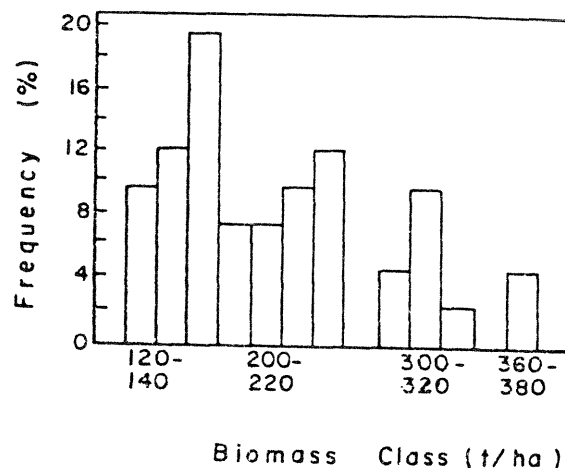


Figure 2.--Frequency distribution of volume-derived biomasses based on volume data collected from 1230 x 1 hectare plots of forests in the Amazon Basin (from Brown and Lugo 1984).

There are several potential sources of error in biomass estimates based on volume: wood densities, stand volumes, and expansion factors. Of these, the greatest error is likely to exist in the expansion factors, and the determination of new factors is the emphasis on my current research (in cooperation with Ariel Lugo). New expansion factors are being determined from detailed forest plot data which include diameters, species, and commercial volumes of individual trees in the plots and specific gravities of the species. From this information commercial biomass was calculated (sum of the product of commercial volume and specific gravity of all trees). All the available allometric data for tropical trees have been gathered (from the literature and personal records from colleagues) and allometric regression equations developed. These allometric regression equations were then used to calculate aboveground biomass of the plots for which commercial biomass was calculated. Root biomass was determined from root/shoot ratios given in Brown and Lugo (1982). Expansion factors were calculated as total biomass/commercial biomass. Results of this analysis to date are shown in Table 2 and are compared to the expansion factors used by Brown and Lugo (1984) in their earlier volume-derived biomass estimates. Differences between the earlier and present efforts are clearly evident; however, the present effort has not been completed and it remains to be seen how significant these changes will be.

In conclusion, use of forest volume data offers an advantage over ecological biomass data because larger areas of tropical forests are represented and a more realistic picture of the variability in forest biomass is provided. Revised expansion factors appear to be more variable than the previous analysis (Brown and Lugo 1984) suggested and demonstrate the need for regional biomass estimates rather than aggregated ones. A comparison of the new expansion factors (Table 1, based on the analysis to date) with those obtained by Brown and Lugo (1984) suggest that volume-derived biomass estimates of tropical forests could change by as much as plus/minus 40 percent.

Table 2.--Expansion factors for converting tropical forest volumes to total biomass

| Forest type | Expansion Factor | | Sample size |
|-------------------------------------|------------------|------|-------------|
| | Range | Mean | |
| Closed humid forests ^{a,b} | 1.3-1.8 | 1.6 | 19 |
| Open forest ^a : | 2.7-3.1 | 2.9 | 2 |
| Moist forest: | 1.0-1.7 | 1.3 | 10 |
| Wet and rain forests: | 1.9-2.4 | 2.2 | 5 |
| Dry forests: | 3.6-3.7 | 3.7 | 2 |

^aFrom Brown and Lugo 1984

^bThis category includes moist, wet, and rain forests

CHANGES IN SOIL CARBON CONTENT FROM FOREST CONVERSION

The goal of this phase of my research was to determine the changes in organic carbon content of soil due to conversion of tropical forests to agriculture. This was accomplished by sampling soil from a chronosequence of agriculture sites of known age and comparing their carbon content to that of a nearby forest site, controlling for such factors as slope, elevation, and soil texture. Sampling was accomplished in a variety of life zones in tropical America (Puerto Rico, U.S. Virgin Islands, Costa Rica, and Venezuela). Because most of the forest conversion was to pasture, sampling was concentrated in this practice,

but soils under other types of agriculture were also sampled when available. Soil samples were collected from 1 meter deep pits (1 pit/site), and from use of standard soil corers to 50 centimeters depth (where most of the carbon changes are expected to occur). Samples from the pits were used to determine both percent C and soil bulk density; core samples were used for percent C only. Carbon concentration was determined by burning the soil in an induction furnace and oxidizing the carbon in a stream of oxygen to CO₂ which was measured gravimetrically.

Some representative examples of the results are given in Fig. 3. In general, most of the soil carbon was in the top 50 centimeters of soil (about 70 percent). The absolute amount of soil organic carbon varied among the sites; higher contents were obtained for the soils in Venezuela (Fig. 3c and d) than for those of Costa Rica (Fig. 3a and b). These differences are mainly a function of soil texture; the Venezuelan soils were very high in clay content which leads to a high carbon content (Sanchez 1976). Conversion of forests to pasture appeared to result in little change in soil carbon. In some cases the pastures had more carbon in the top 50 centimeters and than the forests. The maximum decline in soil carbon on conversion to pastures appeared to be about 15 percent of the control forest sites. A compilation of literature values produced an average reduction in soil carbon under pastures of 20 percent (Detwiler 1986). Conversion of forests to annual crops resulted in greater losses of soil carbon. For example, a site in the tropical dry forest life zone cultivated with sugar and rice for 50 years or more had a soil

carbon content that was about 40 percent lower than that of the nearby forest (Fig. 3d, 50 years plot at extreme right of graph). This is equal to the value that Detwiler (1986) obtained from a synthesis of the literature.

In summary, rates of loss of soil carbon, due to conversion of tropical forests to agriculture, are influenced by the type of agriculture practice, soil texture, climate and time. The results from my research are consistent with those of Detwiler (1986), based on an analysis of many studies, and suggest that losses of soil carbon due to forest conversion to agriculture are lower than than values previously used in models (e.g., Houghton and others 1983). Use of these lower rates of soil carbon loss in models of tropical forest clearing produce a small annual release of CO₂ to the atmosphere of about 0.11-0.26 Pg (1 Pg = 10¹⁵ g) as of 1980. This is equivalent to 2-5 percent of the carbon released from the combustion of fossil fuels (Detwiler 1986).

WOOD DECOMPOSITION

Conversion of forests to agriculture (pasture and shifting cultivation), logging activities, and natural tree mortality produce woody debris in the tropical landscape. If the rates of decomposition of this woody debris are slower than rates of regrowth by the forest vegetation then these sites represent small sinks of carbon. It is often assumed that decomposition processes in the humid tropics are fast because of termite and other invertebrate activity, and the high humidity favoring microbial activity. However, many tropical woods contain high concentrations of extractives which may be toxic to fungi and invertebrates (Bultman and Southwell 1976) and inhibit decomposition. Furthermore, many tropical hardwoods are higher in lignin than temperate hardwoods. Tropical hardwoods have many chemical characteristics that are similar to temperate conifers which have slow rates of decomposition.

Rates of decomposition were determined by comparing the density of known-age and species of decomposed logs with the density of wood from live trees of the same species, and expressing the rate as the amount of mass remaining after a known time interval. This method measures only the loss of mass due to microbial processes and leaching, it does not include fragmentation processes. I have sampled wood from 20 different tropical hardwood species covering a range of diameter classes, climate types, and ages (2->20 years-old). Most of the results are still being analysed, so I will present only some preliminary findings here. Using the exponential decay model, as is typically used in such studies, I have calculated the decomposition coefficients for eight species of approximately the same age (6-6.4 years) for four different diameter classes (Table 3). These species were collected from dry forest, moist forest, and rain forest life zones and have densities of live wood ranging from 0.52-0.92 g/cm³. The decomposition coefficients decrease with increasing diameter of the debris as has been found by others for temperate wood

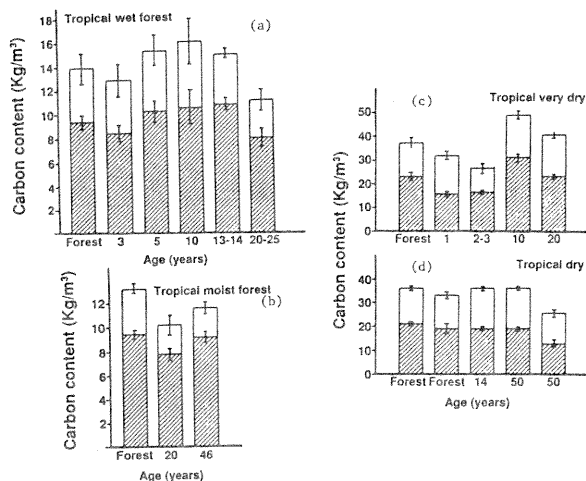


Figure 3.--Organic carbon content of some tropical forest and agriculture soils. (a) Tropical wet forest and (b) tropical moist forest life zones of Costa Rica; (c) tropical very dry forest and (d) tropical dry forest life zones of Venezuela. All agricultural sites are pastures except the right-most 50 year-old site in (d). Total height of the bar is the carbon content to 100 cm depth and the hatched portion of the bar to 50 cm depth. Each value is the mean of three samples \pm one standard error.

(Harmon and others 1986).

Other studies of wood decomposition in the tropics obtained decomposition coefficients of 0.11-0.46 year⁻¹ (Odum 1970; Kira 1978; Lang and Knight 1979), values that are about an order of magnitude greater than those that I obtained. The reasons for these differences remain to be determined. Preliminary results from the analysis of extractives, lignin, and nitrogen contents demonstrate that the slow decomposing woods have high concentrations of extractives and lignin and low nitrogen. Greater understanding of rates of wood decomposition in the tropics will be gained when the influence of wood chemistry as well as climate on this process are investigated.

Table 3.--Decomposition coefficients (yr⁻¹) for woody debris (model: $y=e^{-kt}$) of eight tropical species.

| | Size class (cm) | | | |
|-------|------------------|------------------|------------------|------------------|
| | 10-20 | 20-30 | 30-40 | >40 |
| n | 6 | 5 | 4 | 2 |
| Range | 0.006 - 0.130 | 0.016 - 0.115 | 0.004 - 0.075 | 0.012 - 0.026 |
| Mean | 0.068 | 0.058 | 0.040 | 0.019 |

CONCLUSIONS

Much of the previous understanding of the carbon cycle in tropical forests lands contained many misconceptions including: all tropical forests have high biomasses, conversion to agriculture results in high losses of soil carbon, and decomposition of all organic materials occur at fast rates. Incorporation of the results from my research and from the research of others into carbon models of tropical forests have lowered estimates of their contribution to atmospheric CO₂ from a value almost equal to that from the burning of fossil fuels (e.g., Houghton and others 1983) to a value equal to about 20 percent of that from burning fossil fuels (Detwiler 1986). Progress has clearly been made in improving our understanding of the carbon cycle in tropical forests, however results from research also demonstrate how much more there still is to learn about this cycle in the tropics.

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Abstract.--This paper reviews some of the difficulties with existing forest soil and plant chemical analytical techniques. The uses, advantages and disadvantages of the new xylem sap technology are discussed, along with results and a description of sample selection, extraction and xylem sap analysis. Xylem sap is extracted from branches or roots using a modified pressure chamber. Nutrient distribution frequencies from large areas for conifer and shrub species are needed as a reference source for routine use of the method. The newly developed portable extraction equipment is described, along with results from analysis of sap from wild huckleberry (Vaccinium globulare Rydb.) stems, alder, conifers and tropical vegetation. The potential for use of tree xylem sap technology to solve specific types of problems with insects, diseases, animal damage or growth is offered as a challenge to expand the method.

Keywords: Tree extracts, Pinus ponderosa, Pseudotsuga menziesii, Vaccinium globulare, xylem sap.

This report surveys the development of soil and plant chemical analysis for mineral nutrients and explores the potential of xylem sap analysis for problem solving in forestry.

The field of forest soil chemistry has developed slowly, drawing heavily on the methods used in agricultural soil chemistry. Scientists have acknowledged the deficiencies of agricultural methodology in handling forest soil problems. This is evident in the much more frequent use of foliage analyses rather than soil analyses (Youngberg & Davey 1968). Soil extractions require digging a soil pit, while subsamples are analyzed using artificial extraction agents. Results show what that particular extracting agent can remove from the soil, not necessarily what is available and not how much of each ion that is used by the plant.

Soil samples have to be dried, sieved, weighed, extracted and brought to volume prior to analysis. The process is time consuming and when the data are finally available, the analyst knows that the results do not directly reflect what the tree with its specific mycorrhiza is able to take up. It requires about 12 hours to collect and analyze one soil sample, not including drying time. The interpretation of forest soil chemical data is still part art, part science.

Because of the problems with using agricultural methods on forest soils (Page 1982, Walsh and

Beaton 1973) and because of the limited financial support for forest soil chemistry as a distinct science, foresters have relied heavily on foliar analyses. Foliar samples can be collected from conifers at any time of year, however, the proportions of mineral nutrients to organic compounds changes over the year, resulting in natural changes in the per gram proportions of each mineral nutrient. Thus, it is hard to compare foliar nutrient concentrations within species from spring to fall or from year to year. Annual comparisons may be confounded by differences in the absolute amount of carbon fixed because of variations in sunlight and other climatic factors. Foliar samples are not available in winter for deciduous species, many of which translocate nutrients from the leaf back into the stem before abscission occurs. The total time for sampling deciduous foliage is a few short months between the time the leaves are fully expanded and the onset of translocation prior to abscission.

In addition, foliage must be collected, cleaned, dried, ground, weighed, ashed or digested, taken up in acid and brought to volume before chemical analyses can be made. Sample collection and analysis usually takes ± 8 hours per sample, not counting drying time. The process is time-consuming and costly. Although Zinke and Stangenberger (1979) have established reference nutrient-frequency distributions for Pinus ponderosa and Pseudotsuga menziesii, these are not stratified by possible exposure to pollution or by soil types.

Another approach that has appealed to forest soil scientists is extraction of soil water using either pressure or tension (Marshall and Holmes 1979). Various lysimeters and soil water probes have been developed to collect soil water moving under the influence of gravity or tension (Hanks and Ashcroft 1980). The gravity-fed lysimeter is of

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limited value in drier climates when mobile soil water is often unavailable. Even pressure and suction devices will fail to produce water samples in dry summers. The porous cups used in soil water probes have a tendency to accumulate phosphate and other ions, making them less valuable over time.

In spite of these drawbacks, some researchers feel that soil water analysis is far superior to analyzing soil extracts made with artificial extracting agents. The main drawback is that no one has established frequency distributions for soil water ions that relate in any useful way to tree growth.

One other method, xylem sap analysis, had been explored by pomologists primarily in the laboratory to study the forms of nitrogen transport in xylem sap using suction.

In 1978, a group of scientists at the School of Forestry, University of Montana, began exploring the value of xylem sap in conifers as an indication of the water stress and nutrient stress status of trees.

The idea of xylem sap extraction was not entirely new. Bollard (1953, 1956, 1957) used tension extraction of xylem sap from apple trees to study the forms and movement of nitrogen in fruit trees. Ketchie and Lopushinsky (1981) collected natural root exudates from conifers in the field and analyzed these chemically. Scholander and co-workers (1966) used the pressure chamber in the 1960s to evaluate the degree of water stress in trees. No one had explored the possibility of field extraction of xylem sap, using the pressure chamber to collect sap for chemical analysis.

THE DEVELOPMENT OF XYLEM SAP TECHNOLOGY FOR FORESTRY

Once it was established that xylem sap could be easily obtained from roots or smaller branches with a large Scholander-type pressure chamber, and that the sap had easily measurable ion levels, it was essential to develop an understanding of the degree and sources of natural variation in xylem sap chemistry. The sources of variation that were examined were changes in ion concentration with differences in:

1. extraction pressure
2. time of day
3. time of year
4. tree to tree within species, random
5. tree to tree within species, paired trees
6. between species
7. crown aspect
8. height into the crown
9. tree age
10. trees of one species on different soils
11. flush versus hardening-off

12. insect or disease status:
 - a. infected with Endochochronartium harknesii versus uninfected
 - b. infested with Choristonera occidentalis versus uninfested (same soil)
 - c. porcupine-damaged versus undamaged
 - d. root rot-infected versus uninfected

These preliminary studies made it possible to prescribe a standard extraction procedure for conifers that can be used for making controlled comparisons of xylem sap chemistry.

The results of thousands of sap extractions are now available (Stark and Spitzner 1985a, b). These results show that the best way to obtain xylem sap from conifers is to standardize collection and analysis procedures. Trees from a stand that has growth or other problems and control or healthy trees are sampled with the following criteria, for sampling within a species:

- a. same time of day, (one branch from the test plot, followed by a branch from the control plot throughout the day)
- b. or within ten days in time of each other, with similar weather conditions (cloudy or rainy days are the best)
- c. rainy days during the pre-flush period, if the problem relates to poor branch growth.
- d. within the mid-growing season if the problem relates to radial growth.
- e. during winter if xylem sugar storage is of concern
- f. any time of year if the problem is not related to growth and if samples can be taken alternately during the day from affected and unaffected individuals.
- g. trees of ± 5 years in age
- h. trees paired within a stand or class (within affected individuals or within unaffected individuals) by similar physical appearance, size, crown form, density, color)
- i. samples from the lower one-third of the crown.
- j. on the west aspect if possible, although aspect is of minor importance
- k. within a class, all individuals should have the same apparent amount and type of disease or insect problem or be totally free of such influences depending on the objectives of the study.

Deformed individuals are sampled only when they are needed for a specific study.

Extraction Procedures

Branch ends or roots 60 cm long are cut and stripped of bark for 6 cm at the cut end. The wood is cleaned of phloem with acetone, and the pressure is increased to allow reading of the branch or root water potential. A tight-fitting Tygon tubing is placed over the cut end to contain the sap as the pressure is increased to 2.0 or 2.4 megapascals. One milliliter of xylem sap is removed from the tubing with a syringe and added

to four mls of 0.12 N nitric acid. This sample is then analyzed by inductively coupled plasma spectrometer for Al, B, Ca, Co, Cu, Fe, Mg, Mn, K, Mo, Na, P, Si and Zn. The whole process from cutting the branch to data print out takes about six to eight minutes.

A second milliliter is removed from the branch, and five microliters are injected into a nitrometer for total nitrogen analysis by chemiluminescence. The analysis takes about two minutes.

During winter, branches store small amounts of sugar in the xylem sap behind the bud. It is presumed that this material (for Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) and ponderosa pine (*Pinus ponderosa* Laws.) mostly glucose and fructose with some pinetol) will support some of the rapid new branch growth that occurs in spring during flush. If the levels of sugar storage are low, there is a possibility that the tree may be energy limited at the time of spring flush. Root sugars can also be determined through sap extraction and tissue analysis. One ml of sap extracted in winter is analyzed by the phenol-sulfuric acid sugar method (Whistler 1964).

Since results of the xylem sap research have been published (Stark and Spitzner 1985a, b), this paper will concentrate on newer work and possible uses of the method.

Xylem Sap of Wild Huckleberry

Xylem sap extractions have been successfully made from shrubs such as wild huckleberries (*Vaccinium globulare*). Shrub sap extractions are slower than conifer sap extractions because of the smaller wood volume per branch. The sap tends to bubble excessively, but collections can still be made easily by attaching a vessel to the end of the Tygon tubing.

Xylem sap was extracted from ten or more branches of *Vaccinium globulare* (wild huckleberry) growing on habitually high and low production sites in western Montana. Samples were collected under similar weather conditions within five days' time in July during fruiting. The high berry production site was significantly higher in Al, B, Fe, Mn and Na in the sap compared to the low production site. The soils from the two sites showed a pattern of significant nutrient differences (Table 1) for B, Ca, Cu, Mg and Na. Nutrient differences between xylem sap and soil agree for B and Na, but not the other nutrients. The reason for this is that the roots of this plant take considerable amounts of nutrients from the rotten wood of the O layer, with less dependence on soil nutrients than many other shrub species. Also, many of the nutrients are taken up selectively by mycorrhizal roots so that soil nutrient availability determined from artificial extracts in the laboratory would not necessarily correlate directly with the concentrations of nutrients in the xylem sap. This is a problem with most forest soil chemical data. The concentrations of nutrients in the artificial extracts do not necessarily

reflect what the plant takes up, only what is available for uptake using a specific extracting agent.

Table 1.--Mean and standard deviation of nutrient concentrations in xylem sap of *Vaccinium globulare* during July from consistently high and low productivity sites, and available soil nutrients as $\mu\text{g/g}$.

| Nutrient | good site sap | | poor site sap | |
|----------|-------------------|-----------------|---------------|-------|
| | X | SD ^d | X | SD |
| Al | 3.5 ^c | 0.4 | 0.2 | 0.03 |
| B | 0.06 ^c | 0.02 | 0.01 | 0.002 |
| Ca | 10.3 | 2.1 | 7.7 | 1.6 |
| Cu | 0.08 | 0.03 | 0.04 | 0.004 |
| Fe | 0.09 ^c | 0.02 | 0.03 | 0.002 |
| Mg | 3.7 | 0.9 | 2.6 | 0.8 |
| Mn | 2.0 ^c | 0.46 | 1.4 | 0.4 |
| Na | 0.6 ^c | 0.02 | 0.002 | 0.001 |
| P | 4.5 | 0.91 | 5.6 | 1.1 |
| Si | 0.2 | 0.02 | 0.4 | 0.1 |
| Zn | 0.2 | 0.03 | 0.2 | 0.08 |
| K | 39 | 9 | 40 | 8 |
| Total N | 24.9 | 4.1 | 13.6 | 2.3 |

| Nutrient | good site soil | | poor site soil | |
|----------|----------------|------|----------------|------|
| | X | SD | X | SD |
| Al | 1.77 | 1.4 | 15.4 | 10.9 |
| B | 0.7a | 0.16 | 0.5a | 0.2 |
| Ca | 2819a | 418 | 2243b | 658 |
| Cu | 1.4a | 0.3 | 1.0b | 0.4 |
| Fe | 62 | 0.9 | 59 | 23 |
| Mg | 203a | 24 | 168b | 39 |
| Mn | 83 | 12 | 75 | 37 |
| Na | 14a | 1.8 | 9.7b | 2.6 |
| P | 18 | 2.3 | 20 | 8 |
| Si | 64 | 6 | 54 | 22 |
| Zn | 6.6 | 1.6 | 5.3 | 2.3 |
| K | 388 | 8 | 350 | 112 |
| Total N | 396 | 11 | 336 | 112 |

a,b for soils, two means followed by different letters are significantly different at $p = < .05$.

c for sap, these values are significantly higher than those for the poor site.

d SD = standard deviation.

The importance of boron to berry production is apparent from juice, leaves, xylem sap and soils from high berry production areas compared to poor production sites. Sodium is hypothesized to be important only as a passive ion to influence the osmotic potential needed to develop large fruit size through water storage. It is not likely that Na is taken up actively so that soil Na and sap Na should correlate well.

Xylem sap analysis of wild huckleberry has provided evidence of potential control of berry productivity by nutrient availability assuming

that climatic factors are not adverse for a particular year.

Sap extraction from shrubs would be of potential value in studying shrub nutrition and in examining the influence of fire on the nutrient status of shrubs. The value of shrubs to wildlife might also be studied using xylem sap technology. An example would be the analysis of xylem sap quality of the edible branches of shrubs before and after fire.

Xylem Sap Analysis for Conifers

One important aspect of the development of sap technology is to establish what ranges of ions are likely to be found in the sap of each major conifer species relative to growth rate. This is a sizeable job, but some guidelines have already been established for Pseudotsuga menziesii (Douglas-fir), Larix occidentalis (western larch) and Pinus ponderosa (ponderosa pine) from good and poor growth sites. These data will eventually be published and will provide a frame of reference against which xylem sap from trees of these species in other areas can be compared. Such comparisons will almost certainly show significant differences in sap ion concentrations by major soil types and may also reveal ecotypes. Such broad-based sap chemistry data must be assembled and published. It will be of potential value in studying air pollution. If the crowns are weakened by air pollution or the soil ion populations are altered, the xylem sap chemistry should reflect these changes.

Xylem sap analyses of subalpine fir (Abies lasiocarpa (Hook) Nutt.) seedlings grown under the influence of alder (Alnus sinuata (Regel) Rydb.) with nitrogen-fixing symbionts and away from alders showed significantly more nitrogen in the seedlings near alder, as expected. Xylem sap analysis can be used to detect changes in plant uptake patterns, enrichment from fertilizer or changes in ion availability. Sap analyses make it possible to detect fertilizer uptake in 70 percent of the trials for nitrogen and 60 percent for other ions. The timing of sampling after fertilization is critical.

Xylem sap chemistry correlates closely with apparent radial growth rates. On sites where the soils were different (alkaline, pH 7.5 and acid, pH 5.8) but precipitation and temperature were not significantly different, Pinus ponderosa and Pseudotsuga menziesii both showed significant differences in the concentrations Ca, Mg, Mn, P and total N in the xylem sap during summer. These nutrients are now being applied as fertilizers to determine if statistical significance relates to biological significance -- i.e., radial growth.

Xylem Sap Analysis of Roots

Roots of trees may also be extracted for xylem sap but not as easily as branches. For shallow-rooted species such as lodgepole pine (Pinus contorta Dougl.) it is relatively easy to locate a secondary root near the base of a tree and pull

the root loose with gentle excavation. This method worked well with shallow-rooted tropical trees as well. Roots are extracted in the same manner as branches. A comparison between root nutrient concentrations and nutrient concentrations in the lowest live branch provides an estimate of how much nutrient is being used by the bole in radial growth.

Xylem Sap Analysis Of Tropical Species

Routine xylem sap extractions are made with equipment mounted on the tailgate of a pickup truck. This system works well wherever there are roads. In July 1986, the equipment was made more portable for use away from roads. The pressure chamber was mounted on an aluminum pack frame with short feet to allow it to stand three feet high for easier use from the ground. It is difficult to haul a large air tank over uneven trails, so the air system was modified to use a SCUBA airtank for the air supply. This required adapting a SCUBA regulator that connects to the tank to a two-stage air regulator that will control delivery pressure to the chamber by tapping into the high pressure port of the SCUBA regulator. When mounted, the system weighs about 24 Kg, plus the weight of the air tank. The SCUBA air tank weighs about the same as the pressure chamber and can be carried in a SCUBA tank harness or a standard backpack. A SCUBA tank will permit about 20-24 extractions at low pressure (150 psi). The front pouch of the backpack is useful for storing the syringe, vials, knife, tubing and other accessories needed for extraction.

The portable extraction system was used successfully in Panama at the Smithsonian Tropical Research Institute's Barro Colorado Island Preserve. Branches were extracted from Hybanthus prunifolius, Psychotria horizontalis and Psychotria furcata (all understory plants) from plots receiving supplemental irrigation during the dry season and others that were not receiving irrigation. The study is being conducted by Dr. S. Joseph Wright of the Smithsonian Institute and the author. The objective of the study is to develop an understanding of the normal functioning of this tropical ecosystem by removing one stress--dry-season water deficits--and comparing the nutrient status of the soils and vegetation with and without dry-season water stress. Results are not yet available, but there are some interesting trends in nutrient uptake that will be reported at a later date.

SUMMARY

In summary, there are many possible new and potentially valuable uses of this technique, especially now that the extraction system is portable. Problems of tree growth, disease or insect damage, animal damage and many other possible uses of the method have been tentatively explored by the author, but there are many uses yet to be discovered for this new analytical tool, all of which could help to advance the field of forest science.

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Calcium and Phosphorus Content of Oak Ectomycorrhizae from Mull and Mor Forests of Northeastern Pennsylvania¹

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Ectomycorrhizae (M), the symbiotic root-fungus associations of many tree species indigenous to temperate forests, are characterized by swollen root tips of the host species. Fungal hyphae grow as a mantle covering the root with the expanded hyphal network in the soil significantly increasing the absorptive surface of the host root (Bowen, 1973; Skinner and Bowen, 1974). In this way, M enhance the uptake of essential elements such as phosphorus (Powell, 1982). The importance of ectomycorrhizal roots has been demonstrated in nutrient poor soils (Bowen, 1973; Harley, 1969).

Numerous parameters influence ectomycorrhizal formation and function. Soil nutrient factors promoting ectomycorrhizal formation include moderate to low levels of P and N (Marx, et al., 1977; Powell, 1982). Low P levels increase phosphatase activity and P uptake (Alexander and Hardy, 1981; Bartlett and Lewis, 1973; Dighton, 1983). In acid soils essential nutrients are generally low, a situation favoring ectomycorrhizal formation and function, but heavy metal availability is enhanced (Buckman and Brady, 1969). The toxicity of heavy metals on ectomycorrhizal fungi (Thompson and Medve, 1984), root growth and biological function (Foy, et al., 1978), have been demonstrated. Our field samples have indicated heavy metal loadings in oak M from acid-mor but not from neutral-mull forests (Majumdar, et al., 1986); we have previously shown the ectomycorrhizal frequencies (MFs) of oaks in the acid-mor to be considerably lower than those in neutral-mull forests (Mineo et al., 1984). Both the diversity of mycorrhizal fungi and resultant ectomycorrhizal morphology differ in

Abstract.--Ectomycorrhizal roots of two forest-grown oak species, Quercus alba and Q. rubra, contained significantly more calcium in the neutral humus-mull than in the acidic humus-mor soils. Phosphorus content was reversed; that is, oak ectomycorrhizae contained significantly higher phosphorus levels in mor rather than mull soils. These results, obtained with x-ray microanalysis, reflected the available calcium and phosphorus content of each soil type, and on closer examination reiterated the regulatory role of ectomycorrhizae for phosphorus but suggested an additional regulatory role of ectomycorrhizae (M) for calcium. High calcium in the mull soils appeared to be excluded from M.

Keywords: Ectomycorrhizae, calcium, phosphorus, humus-mull, humus-mor, Quercus alba, Quercus rubra.

mor and mull oak forests (unpublished, Mineo, et al.). Acid environments may favor neither ectomycorrhizal formation nor function, but many interacting factors are involved in these processes.

Various physical factors encourage ectomycorrhizal formation and function such as moderate soil moisture, aeration and temperatures (Powell, 1982). Root density alone has been shown to influence solute uptake from soil (Baldwin, et al., 1972); St. John and Coleman (1983) pointed out the importance of available soil volume and community structure in the overall assessment of the biological significance of M.

Ectomycorrhizae, although influenced by the many variables of natural environments, benefit the host plants in several ways other than the increase of essential element uptake. For example, the hormonal balance of M offsets the aging of those root tips (Meyer, 1974); also the protection against certain pathogens is enhanced by the production of antimicrobial compounds and the formation of a structured rhizosphere containing other beneficial microbes (Marx, 1973). In addition, Fogel (1980) and others have pointed out the importance of M in nutrient cycling processes in natural environments. In turn, ectomycorrhizal fungi are dependent upon their hosts for both carbohydrates (Bjorkman, 1970) and other substances such as B-vitamins; photosynthesis, then, has been correlated with mycorrhizal development (Bjorkman, 1970; Marx et al., 1977), with decreased photosynthesis causing decreased MF.

The purpose of this study was to compare the P and Ca content of oak ectomycorrhizal mantles from two different forest soils with the content of those soils and to consider the influence of M on the incorporation of P and Ca into both the mantle and host fine root tissues. This attempt to understand natural processes seems appropriate considering the importance of oaks in many forest communities and the general lack of this kind of information for these species.

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METHODS

Root and Soil Samples

Beginning in the spring of 1984, oak root/soil samples were collected monthly (May-September) in both mull and mor forests using the methods of Harvey, et al. (1979). Soil and tissues were taken from within the foliar canopies of apparently healthy trees (25 to 76 centimeters diameter at breast high). The term "mull" refers to forested soils with a humus-rich layer consisting of mixed mineral and organic material that blend without an abrupt change in soil characteristics. Most feeder roots and M were located in the AH horizon which was deep (25 centimeters) and relatively stone-free. The term "mor" refers to forested soils with a distinct, unincorporated humus layer of organic material that is often matted (Armson, 1977). Most of the feeder roots and M were located in the shallow (7 centimeters) O2 horizon which was often stony. Study areas were within a 25 mile radius of each other and were chosen to exclude sloped or disturbed soils.

Soil Analyses

Composite soil samples from each forest-type were analyzed seasonally by the Soil and Environmental Chemistry Laboratories of The Pennsylvania State University. Standard methods as found in Black (1965) were used to obtain plant-available levels of elements. Potassium and calcium values were obtained from ammonium acetate extractions, while phosphorus values were obtained from ammonium fluoride extractions. The mean values of plant-available elements in the upper soil horizon of each forest (Table 1) were calculated from 5 sample sets taken over a 3-year period (1984-1986). Each sample set was comprised of 10 soil cores.

Root Analyses

Representative active ectomycorrhizal roots (swollen and light-colored) chosen from the soil/root samples were fixed in FAA (formalin, 50 percent ethyl alcohol and glacial acetic acid; 5:90:5). Soil-free M chosen at random for elemental analysis were cross-sectioned using a cryostat, dehydrated in an ethanol series and critically point dried. The roots were then carbon coated and placed on carbon microscopy stubs. Twenty-five roots from each location and for each species were analyzed for elemental content using a Princeton Gamma-Tech System III energy-dispersive spectrometer (EDS) attached to a scanning electron microscope (Figure 1). During an analysis, an electron beam focused on the sample produced an x-ray emission pattern which the EDS detected. The x-ray counts (or intensity) were displayed as a function of x-ray energy. The spectral peaks corresponded to constituent elements within the sample; continuum x-rays (background) were routinely subtracted from the characteristic x-rays (Figures 2 and 3). With this technique exact elemental concentrations cannot be directly obtained, but spectrum peak areas (or x-ray intensities) can be compared

between different samples to determine which sample has more of a particular element in question (Princeton Gamma-Tech, 1981). For example, the precise concentration of calcium within a tissue cannot be determined, but the ratio of Ca x-ray intensity/K x-ray intensity from one specimen can be compared to that of another. Ratio usage minimizes the inherent variation that occurs from sample to sample such as differences in surface roughness (and cell orientation), and in spot size, age of the filament or run time. Run time of 150 seconds, spot size which produced 200 counts per second and working distance of 23 millimeters were routinely used (Goldstein, et al., 1981). In order to normalize the spectral information for comparative purposes, potassium was chosen as the ratio denominator since chemical analyses indicated that potassium was similarly available in mull and mor soils (Table 1) and since potassium appeared to be present in the mid-range of counts on each spectrum. Actual concentrations of K, Ca and P for bulk fine root tissues were determined by the Forage Testing Laboratory of The Pennsylvania State University (Table 2) using wet ashing procedures coupled with absorption flame spectrophotometry methods (Sutcliffe and Baker, 1978).

The EDS x-ray microanalyses were performed around the outer cortex of each sample in the region of the mycorrhizal mantle. Relative x-ray intensities of elements within a given root sample were basically similar for various alternate locations on the peripheral mantle.

RESULTS AND DISCUSSION

Eastern Pennsylvania is geologically diverse; the soils of the Lehigh Valley region, where forest-mull samples were collected, were derived mainly from neutralizing carbonates of limestone and dolomite (Soil Survey, 1974), and resulted in neutral soils (pH 6.5-7.1, AH horizon) with low levels of heavy metals and 12 percent organic matter (Mineo, et al., 1984). Four mull forests were sampled; in each forest, oaks (Quercus alba and Q. rubra) predominated. The understories were comprised of Cornus florida, Viburnum spp., Rhus radicans and various herbs. The overall root densities per unit volume of soil were low. In contrast, the Pocono soils, where forest-mor samples were collected, are underlain with sandstone, shales and conglomerates and possess less buffering capacity. The resultant mor soils of the O2 horizon were acid (pH 3.8-4.7) with high levels of available heavy metals and 41-51 percent organic material (Mineo et al., 1984). Two mor forests were sampled; oaks (Quercus rubra, Q. prinus, Q. alba and Q. velutina) predominated with Acer rubrum as a common associate. The understories were comprised of Hamamelis virginiana, Rhododendron spp., Vaccinium spp., Gaylussacia spp., Gaultheria procumbens and diverse mosses. The overall root densities per unit volume of soil were high.

Although the geology, soils and community structure in each forest type differed as stated

above, the forests appeared to be similar in soil moisture, aeration and temperature. Also, all sampled oaks occupied the overstory and received direct sunlight on a sizable portion of the canopy.

Calcium and phosphorus concentrations differed in each soil type. Calcium levels were especially high in the mull soils (mean, 2,856 ppm) but lower in the mor soils (mean, 500 ppm); these mean values were significantly different from each other (ANOVA $p < 0.01$). Phosphorus levels were somewhat reversed, that is, with low-normal levels (mean, 29 ppm) in the mor soil but with low concentrations (mean, 10 ppm) in the mull soil (ANOVA $p < 0.05$) (Table 1). On the other hand, potassium levels of both soils (245 ppm mull; 230 ppm mor) were similar. The data in Table 1 represent the plant-available nutrients of the upper soil horizon, as most of the M and fine roots were found in this horizon.

Table 1. Elemental Content (ppm) of Mor and Mull Soils^{1,2}

| | P | K | Ca |
|----------------|------|-----|---------|
| Mull (neutral) | 10** | 245 | 2,856 * |
| Mor (acid) | 29 | 230 | 500 |

¹ Values, as ppm, represent the means of 5 sample sets taken over a 3-year period. Each sample set was comprised of 10 soil cores. Values are given for the A horizon only.

² Soil analyses were performed by the Soil and Environmental Testing Laboratories of The Pennsylvania State University; plant available concentrations were determined according to standard methods (Black, 1965).

* Mull, significantly different from mor ($p < 0.01$, ANOVA)

** Mull, significantly different from mor ($p < 0.05$, ANOVA)

The calcium and phosphorus content of the mycorrhizal mantles generally reflected the availability of essential nutrients in these soils. X-ray microanalysis procedures, which displayed the nascent levels of elements within this small tissue area, indicated that calcium levels were high for both oak species in the humus-mull (black bars) but low in the humus-mor (hatched bars) as shown in Figure 1. These calcium (Ca/K) values of mull M were significantly higher than calcium (Ca/K) values of mor M (ANOVA $p < 0.05$). Phosphorus levels, on the other hand, were reversed; that is, low in the humus-mull (black bars) but high in the humus-mor (hatched bars) and also significantly differed from each other (ANOVA $p < 0.05$).

Mean Levels of Calcium and Phosphorus in Mycorrhizae Relative to Potassium Levels Using X-ray Microanalysis

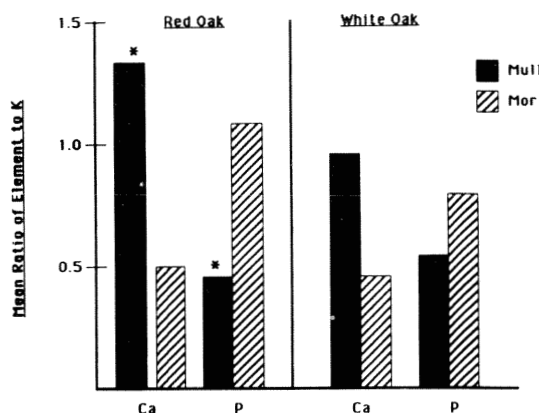


Figure 1. X-ray microanalysis data indicated that both red and white oak mycorrhizae contained higher calcium levels in mull (neutral) than in mor (acid) soils. The reverse relationship occurred for phosphorus; lower P levels were found in the mycorrhizae of mull soil than in acid soils.

* Mull, significantly different from mor ($p < 0.05$, ANOVA)

Representative x-ray microanalysis spectra (Figures 2 and 3) exemplify the results of Figure 1, namely, high calcium levels in the mycorrhizal mantles of red oak from the humus-mull soil (Figure 2) with moderate potassium and low phosphorus levels as well as low heavy metal levels. Figure 3 indicates the moderate calcium and potassium levels, but also the high phosphorus levels, in red oak mycorrhizal mantles from humus-mor soil. Enhanced heavy metal content is also visible on this spectrum. Spectra of white oak M were similar to those of red oak in each respective soil type.

A comparison of soil contents (Table 1) with relative ectomycorrhizal mantle contents (Figure 1) suggests a regulatory role for M with respect to cation inclusion especially in high Ca soils. The mull soil which was higher in [Ca] than [K] by one order of magnitude, showed only slightly more Ca included in M than K. This suggests differential incorporation of Ca and K into M; either K is excessively favored or Ca is excluded from the M. Calcium exclusion is consistent with the intricate roles of Ca in plant development (Hepler and Wayne, 1985).

A comparison of [P] in soil with that of [K] (Table 1) also demonstrates one order of magnitude difference between the availability of these two elements, but the inclusion of similar amounts of both elements in the M from mor soils (Figure 1) emphasizes the accumulation of P by M when [P] in the soil is low. The enhanced P content of the mycorrhizal mantles, over that in the surrounding soils, is consistent with the data of several other investigators for species other than oak (Alexander and Hardy, 1981; Bartlett and Lewis, 1973; Dighton, 1983; and Skinner and Bowen, 1974). Our data indicate that oak M also concentrate phosphorus.

RED OAK MYCORRHIZAL MANTLE

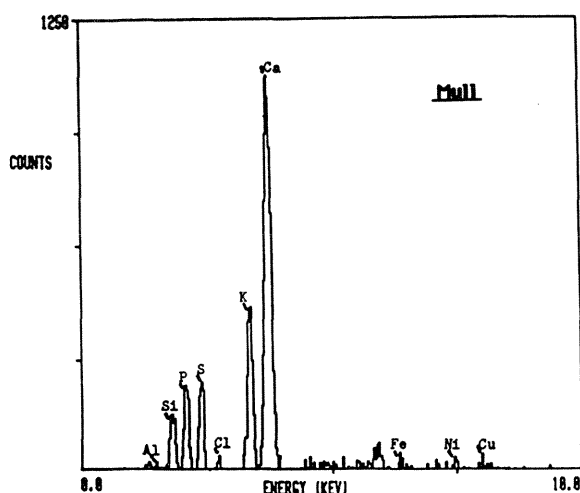


Fig 2. X-ray microanalysis spectrum (corrected for background emission) of Red oak mycorrhiza in humus-mull soil, August 1985

RED OAK MYCORRHIZAL MANTLE

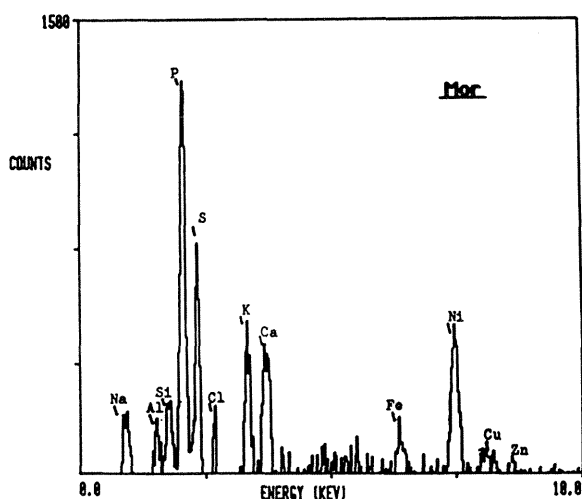


Fig 3. X-ray microanalysis spectrum (corrected for background emission) of Red oak mycorrhiza in humus-mor soil, August 1985

The differential P content of mor and mull oak M, as indicated by x-ray microanalysis, however, does not reflect the overall P content of fine root tissue (Table 2). The P content of both mor and mull M provide the same general P content to the host tissue (0.10-0.13 percent). This rather even distribution of P to fine root tissues implies a further regulatory role of M with respect to the host plant; the actual mechanism of the movement of P into host remains inconclusive (Clarkson, 1985). These data for the tissue levels of P correspond to those reported by others for oak (Fogel, 1980), for tree species other than oak (Chu-Chou, 1978) and plant tissues generally (Sutcliffe and Baker, 1978).

Table 2. Elemental Content (pct) of Bulk Fine Root Tissue^{1,2,3}

| | | P | K | Ca |
|---------|------|---------------------|---------------------|---------------------|
| Red Oak | Mull | 0.10 (0.08-0.11) | 0.91 (0.66-1.16) | 0.83 (0.55-1.27) |
| | | 0.13 (0.12-0.14) | 0.61 (0.49-0.68) | 0.50 (0.31-0.64) |
| | Mor | 0.12 (0.11-0.13) | 1.00 (0.79-1.33) | 1.18 (0.88-1.57) |
| | | 0.13 (0.11-0.16) | 0.55 (0.49-0.65) | 0.56 (0.25-0.80) |

¹ These data represent the mean value of several trees of each species in each forest location.

² The data for two successive summers were combined (1985, 1986) with the range of percentage values in parentheses.

³ Fine roots are 1.5 mm or less in diameter. (Mycorrhizae made up only a small amount of the bulk fine root samples.

The calcium and potassium content of bulk fine roots (Table 2) from mull-forests appeared to be similar in both red oak (Ca, 0.83 percent; K, 0.91 percent) and white oak (Ca, 1.15 percent; K, 1.00 percent) but were present at uniformly lower levels in the mor-forest roots (Ca, 0.50 and 0.56 percent; K, 0.61 and 0.55 percent). The high Ca levels of the mull mycorrhizal mantles, as indicated by x-ray microanalyses, were not found in the fine root tissue. Although the fine roots of the mull forest contained higher Ca levels than those of the mor forest, the proportion of Ca/K was lower than expected in the mull and higher than expected in the mor. These results suggest other differential or regulatory roles for the mycorrhizal mantle at the host-tissue interface.

The calcium levels found in fine root tissues from the mull forests (0.8-1.1 percent) were consistent with those reported for plant tissues generally (Epstein, 1972; Sutcliffe and Baker, 1978); however, the tissue-calcium levels found in the fine roots from mor forests were at the low end of the range (0.5 percent) and approached the marginal concentration supporting mitosis (Hepler and Wayne, 1985). The lower values reported for mor roots were less than those reported for river birch in acid soils with similar available [Ca⁺⁺] (Bartuska and Ungar, 1980) but were closer to those reported for *Quercus robur* as presented in the review by Fogel (1980). In an evaluation of Ca⁺⁺ in plant development, Hepler and Wayne (1985) have pointed out the paradox of intracellular Ca⁺⁺ function at sub-micromolar concentrations but an apparent requirement for Ca⁺⁺ at the millimolar level overall.

Although many factors other than M influence plant productivity (St. John and Coleman, 1983), the soil-root interface provides a significant portion of the prerequisites for potential productivity and needs to be considered as part of the total picture. A regulatory role of M has been suggested by these data for Ca as well as those proven for P; however, in the case of Ca, exclusion is suggested when soils contain high

Ca levels. Under these conditions Ca exclusion is consistent with the role of Ca in plant development.

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SOIL PHYSICAL AND CHEMICAL PROPERTIES ASSOCIATED
WITH THREE SITE PREPARATION TECHNIQUES AND THEIR
EFFECTS ON GROWTH AND SURVIVAL OF SEEDLINGS IN
NORTHERN IDAHO¹

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ABSTRACT

Survival of outplanted western white pine and Douglas-fir is often hampered by droughty soil conditions in the northern Rocky Mountains. This study was initiated to compare soil properties from three site preparation techniques and to assess the impacts on seedling survival and growth for a relatively dry planting site and a moist planting site. Surface organic matter and mineral soil were mechanically mounded to form raised planting beds on two cedar-hemlock sites in the northern Idaho panhandle region. Soil properties and seedling growth resulting from this treatment were compared with scalped and minimum scarification treatments on both sites.

Organic matter content was significantly ($P < 0.05$) altered by site preparation, as was bulk density. Nutrition in the soil was improved in the raised planting beds. An increase in volume of organic matter in raised beds acted as mulch, thus retaining subsurface moisture and moderating soil temperature. Seedling top growth was not significantly altered the first year, but nutrients in the foliage were significantly increased in the mounded treatments. Rooting depth was also greater in the mounds. Bedding the soil was most beneficial on the site with low organic matter and warm, dry soils. On the site with moderate moisture and good soil, the minimally disturbed treatment was just as productive as the raised planting bed treatment.

KEYWORDS: Site preparation, bedding, scalping, soil physical properties, soil chemical properties.

Historically, artificial regeneration in the Pacific Northwest has been unsatisfactory on sites with low soil moisture, high evaporative demand and low nutrient status (Haig and others 1941; Foiles and Curtis 1973). On such sites adequate stocking levels may be achieved through mechanical site preparation which provides favorable microsites for moisture and nutrient accumulation and reduction of vegetative competition (Wellner 1976). Use of scalping, burning, scarification or a combination of these are effective for ease of planting, but survival is often poor (Beebe 1982). Site preparation techniques that utilize mounding of surface organic and mineral soil have been effective elsewhere (Worst 1964; Wilhite and Harrington 1965; McMinn 1969; Shultz and Wilhite 1974;

Francis 1979; Frederick and others 1984). This technique concentrates limited moisture and nutrients into the planting zone for more effective seedling uptake.

In northern Idaho and the Pacific northwest in general, the growing season is characterized by harsh growing conditions, including drought and extensive heat, which can markedly reduce seedling performance especially for high value species such as Douglas-fir (*Pseudotsuga menziesii* var. *glauca* [Mirb.] Franco) and western white pine (*Pinus monticola* Dougl. ex D. Don). Mounding mineral soil and surface organic matter may alleviate much of the environmental stress imposed on seedlings in this area. This study was initiated to compare potential effectiveness of mounding to commonly used site preparation techniques which are utilized for alleviating environmental limitations to early seedling performance.

MATERIALS AND METHODS

Location

Two sites, located on the Priest River Experimental Forest near Priest River, ID, were used for this study. One site is located at an elevation of 715 m above sea level on a flat

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bench adjoining the Priest River. It is the warmer and drier of the two sites. The habitat type is classified as Abies grandis/ Symphoricarpos albus (Cooper and others in preparation) and the soil is classified as Andic Xerochrept. Annual precipitation averages 83.8 cm, with a mean annual temperature of 6.6°C (Finklin 1983).

Site 2 is at an elevation of 1 456 m above sea level. The slope angles range from 10 to 35 percent and have north-to-northeast aspects. The habitat type is classified as Tsuga heterophylla /Clintonia uniflora (Cooper and others in preparation) and the soil is classified as a Typic Cryorthent. This area is considered a productive forest site. Annual precipitation at this elevation is 92.3 cm and the mean annual temperature is 5.3°C (Finklin 1983).

Treatments

Two randomized complete block experiments were established, one on each site. At the low elevation site there were three treatments with four replications, and at the high elevation site there were three treatments replicated three times. The high elevation site was divided into three separate 1-ha areas, each was clearcut, and had approximately the same slope, aspect, soil, and habitat type. The treatments consisted of:

1. Mound--mixing the top 10 cm of mineral and organic soil into beds approximately 46 cm high and 30 m long.
2. Scalp--removal of the top 10 cm of mineral and organic soil by machine.
3. Minimal disturbance--essentially undisturbed after harvesting.

Each treatment was planted with either containerized Douglas-fir or western white pine seedlings at a 31 x 46 cm spacing with 218 trees per treatment. Trees were grown in 4 cm³ cells at the U.S.D.A. Forest Service, Coeur d'Alene Nursery, Coeur d'Alene, ID. The Douglas-fir and western white pine utilized were adapted to each of the two elevations.

Sampling

Soil samples and seedlings were collected from each treatment four times during the growing season. Soil samples were collected from 15 randomly selected microsites within each treatment, to the maximum depth of the rooting zone. These samples were categorized by soil type based on their organic/mineral composition. Temperatures were taken of each soil category under each seedling. Bulk density samples were taken at depths of 0 to 5 cm, 10 to 15 cm, and 20 to 25 cm at five random points in each treatment. Fifteen seedlings were measured for height and total rooting depth.

All soil samples used for chemical and physical analysis were passed through a 2-mm sieve. Bulk density and moisture content samples were dried at 105°C for 24 hours. Organic matter was determined by weight loss after combustion at

375°C for 16 hours. Ca, Mg, and K were extracted with 1 N ammonium acetate adjusted to pH 7.0 and determined using atomic absorption techniques (Black 1965). Soil pH was determined using 1:2 soil:water mix. Total soil nitrogen and phosphorous were determined by block digestion and analyzed using Technicon AutoAnalyzer techniques (Bremner 1965).

For Ca, Mg and K determinations, foliage was ashed and extracted using 2 N nitric acid. Analysis was performed by atomic absorption techniques. Total foliar nitrogen and phosphorous were determined after block digestion and analyzed using Technicon AutoAnalyzer techniques.

An analysis of variance was conducted on the data, utilizing a randomized complete block design. The treatment means were separated using Duncan's multiple range test.

RESULTS AND DISCUSSION

Soil Physical Properties

Mounding the organic and surface mineral soil layers had a large impact on soil physical properties. The changes that occurred were usually associated with the degree of disturbance. The mounded treatments at both sites had significantly ($P < 0.05$) more organic matter than the scalped treatment as can be seen in table 1.

The minimally disturbed treatment was not significantly different from the mounded treatment because this treatment was maintained as undisturbed as possible and much of the organic matter was left intact. The higher levels of organic matter in these two treatments are also reflected in lower bulk densities at both sites. The minimally disturbed treatment showed a slight increase in bulk density with depth because it was not layered with organic matter as was the mounded treatment (table 2). Soil density in the scalped treatment also increases significantly with depth. This is probably because organic matter was removed and soil particles were somewhat compacted. Mixing of the organic matter with the mineral soil in the mounds improved aeration of the treatment and can be seen in the lack of bulk density change throughout the profile.

Table 1.--Organic matter (%) for each elevation and treatment

| Site | Minimal disturbance | | |
|-------------------|---------------------|-------|-------|
| | Mound | Scalp | |
| -----percent----- | | | |
| Low elevation | 15.0a | 9.4b | 14.4a |
| High elevation | 27.5a | 14.5b | 29.2a |

Different letters indicate significant differences ($P < 0.05$) across treatments.

Table 2.--Bulk density (g/cc) means at three depths from both elevations

| | Mound | Scalp | Minimally disturbed |
|----------------|----------------|-------|---------------------|
| | -----g/cc----- | | |
| Low elevation | | | |
| 5 cm | 0.7a | 0.9a | 0.7a |
| 15 cm | 0.7a | 1.1b | 0.8c |
| 25 cm | 0.7a | 1.3b | 0.8c |
| High elevation | | | |
| 5 cm | 0.5a | 0.9b | 0.5a |
| 15 cm | 0.6a | 0.9b | 0.7a |
| 25 cm | 0.6a | 1.0b | 0.8a |

Different letters indicate significant differences ($P < 0.05$) across treatments.

Concentrating organic matter and surface mineral soil into mounds increased the moisture content of the soil in the rooting zone at the high elevation (table 3). This was most evident during the peak growing months of July and August. Only small differences in moisture content between treatments were detected at the low elevation site.

At the low elevation the scalped treatment had less soil moisture than the high elevation during all the sample dates except September. At the high elevation site, large soil moisture differences occurred among treatments, particularly the mounded and scalped treatments. These differences were likely caused by the increase of organic matter in the mounds, which increased moisture holding capacity by improving soil structure and porosity.

Soil temperature data were recorded throughout the growing season, however mounding had little

Table 3.--Moisture content (%) in the rooting zone for each treatment and sample date

| Sample | Mound | Scalp | Minimally Disturbed |
|----------------|-------------------|-------|---------------------|
| | -----percent----- | | |
| Low elevation | | | |
| June | 37.7b | 36.9b | 39.6a |
| July | 46.7a | 39.2b | 46.9a |
| August | 49.3a | 46.6a | 48.9a |
| September | 37.8b | 39.7b | 36.5b |
| High elevation | | | |
| June | 37.5b | 39.8a | 36.5b |
| July | 81.8a | 53.6a | 86.4a |
| August | 71.3a | 45.1b | 65.5b |
| September | 66.6a | 46.4b | 76.5a |

Different letters indicate significant differences ($P < 0.05$) across treatments.

effect on it. The temperatures at the high elevation averaged 3-4°C lower than those at the lower elevation from June to August. Lower temperatures were expected in the mounded treatments because moisture content is positively related to organic matter content and inversely related to temperature (Shultz and Wilhite 1974; Morris and Pritchett 1983). During the summer of 1983, rainfall at the low site exceeded the 75-year average by 9.8 cm and at the high site by 14.6 cm. This heavy rainfall throughout the growing season is believed to have negated any major effect of mounding on temperature or moisture content.

Soil Chemical Properties

The soil chemical properties were also affected by concentrating organic matter into mounds. However, in many cases the differences were not significant. Soil acidity differences were found between the scarified treatments and the mounds at the high elevation and could be attributed to a greater component of decayed wood. The low elevation soil generally had a higher pH than the soil at the high elevation and this difference is likely due to base cycling by grasses present at the low site. There were no significant differences between calcium, magnesium or potassium between treatments during the first growing season.

Mounding surface organic matter and mineral soil significantly changed the concentration of total nitrogen in the soil profile. At the lower elevation the highest percentage of total nitrogen was found in the mounded treatments and the lowest percentage in the scalped treatments (table 4). This was a reflection of soil organic matter content. The high elevation treatments had a greater percentage of total nitrogen than the low elevation treatments. Some of the differences may be accounted for by the large quantity of undecayed wood that was incorporated into the mounds at the high elevation.

Table 4.--Total nitrogen and total phosphorous concentrations (%) in the rooting zone as affected by site treatment (all strata types combined)

| | Mound | Scalp | Minimally disturbed |
|-------------------|-------------------|-------|---------------------|
| | -----percent----- | | |
| Low elevation | | | |
| Total Nitrogen | .27a | .12c | .18b |
| Total Phosphorous | .28a | .25b | .29a |
| High elevation | | | |
| Total Nitrogen | .31a | .34a | .28b |
| Total Phosphorous | .11a | .13a | .15a |

Different letters indicate significant differences ($P < 0.05$) across treatments.

The lowest concentrations of total phosphorous at the low elevation were in the scalped treatment and are due to the removal of organic matter (table 4). In general, higher phosphorous concentrations were present at the low elevation than at the high elevation. Since the majority of organic phosphorous compounds become available through the decay of fresh vegetation (Alexander 1977), the higher values at the low elevation can be associated with the incorporation of grasses into the mounds. At the high elevation the low soil pH values may also be limiting the release of organic phosphorous into the soil (Alexander 1977). Greater organic matter levels at the higher elevation may result in more phosphorous release, but it may be immediately tied up because of a high carbon/phosphorous ratio.

Seedling Growth Response

Rooting depth at the end of the growing season was most affected by physical changes in the soil (table 5). Douglas-fir and western white pine appeared to occupy about the same amount of below ground volume, indicating there was no species difference. However, there were treatment differences. Seedlings from the mounded treatments had the greatest rooting depth and, except for western white pine at the high elevation site, the mound seedlings had significantly deeper roots than the scalped treatment. In general, seedlings from the scarified treatment had a greater rooting depth than the seedlings from the scalped, although not significantly so. This result may have been due to less compaction in the scarified treatment and, therefore, easier root penetration.

Seedling height growth was unaffected by the site preparation techniques (table 6) largely due to the abundance of rainfall and predetermined growth from the bud. However, there were significant differences in total nitrogen at the end of the growing season in Douglas-fir foliage (table 7). Differences in total nitrogen can be attributed to

Table 5.--Total rooting depth (cm) for each treatment

| | and species at the end of the first growing season | | |
|----------------|--|-------|---------------------|
| | Mound | Scalp | Minimally disturbed |
| | -----cm----- | | |
| Low elevation | | | |
| White pine | 25.1a | 21.9b | 20.4b |
| Douglas-fir | 23.9a | 19.7b | 21.4ab |
| High elevation | | | |
| White pine | 23.9a | 20.9a | 20.8a |
| Douglas-fir | 23.9a | 18.4b | 20.3b |

Different letters indicate significant differences ($P < 0.05$) across treatments.

Table 6.--Total tree height (cm) at the end of the first growing season

| | Mound | Scalp | Minimally disturbed |
|----------------|--------------|-------|---------------------|
| | -----cm----- | | |
| Low elevation | | | |
| White pine | 7.7a | 7.4a | 7.0a |
| Douglas-fir | 15.4a | 15.9a | 15.2a |
| High elevation | | | |
| White pine | 7.6a | 6.1a | 7.6a |
| Douglas-fir | 15.7a | 15.4a | 14.6a |

better growing conditions in the mounds during 1983. This improved nutrient status should be reflected in 1984 growth. Western white pine showed no response to the treatments in terms of first year performance. This result is probably related to better adaptability of the species to harsh environments, as compared to Douglas-fir. There were no significant differences in the uptake of total phosphorous, calcium, magnesium, or potassium. There were, however, higher values for these cations at the low elevation site probably because of rapid base cycling by the grasses.

CONCLUSION

The results of mounding soil organic matter and mineral soil as a site preparation technique were varied in this experiment. As expected, organic matter levels were higher in the mounded treatment than in the scalped treatment and would lead to greater microorganism activity and, hence, increased nutrient availability.

If the weather conditions for the first year of this study had been more droughty, differences of moisture and temperature may have been more evident between the scalped, scarified, and mounded treatments. These temperature and moisture

Table 7.--Percent total nitrogen in the foliage at the end of the growing season

| | Mound | Scalp | Minimally disturbed |
|----------------|-------------------|-------|---------------------|
| | -----percent----- | | |
| Low elevation | | | |
| White pine | 1.25a | 1.22a | 1.10a |
| Douglas-fir | 1.17a | .83b | 1.12ab |
| High elevation | | | |
| White pine | 1.01a | .90a | 1.03a |
| Douglas-fir | 1.18a | .72b | 1.33a |

Different letters indicate significant differences ($P < 0.05$) across treatments.

changes would then make the differences in chemical properties and seedling growth more pronounced from the release of more nutrients from organic matter.

Based on these first year results some management strategies for the Pacific Northwest can be addressed. In areas where moisture and nutrients are not limiting, as at the high elevation site, there is no need to prepare the site intensely. Leaving the organic matter and decayed wood intact will produce favorable seedling growth. However, on droughty sites with competition problems the benefits of mounding are twofold. First, mounding creates a soil profile with lower soil density and, therefore, allows greater root penetration. Second, mounding produces a microsite of increased moisture holding capacity and nutrients for seedling growth.

This study will be continued for two more years in order to discern some of the long range effects of mounding on soil properties and tree growth. Other studies with mounding the soil mineral and organic layers will include fumigating the soil to test for beneficial organisms in the rooting zone and soil/seed manipulation to improve first year survival.

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The Use of Senescent Cultures of Postia placenta,
Gloeophyllum saepiarium, and Gloeophyllum trabeum
in the Study of Wood Decay¹

J. A. Micales and T. L. Highley²

Brown-rot decay fungi play a major role in the decomposition of wood and wood products. Unlike the white-rotting Basidiomycetes, brown-rot fungi are able to metabolize the cellulose and hemicellulose of wood but are unable to substantially metabolize lignin (Kirk and Cowling 1984). The mechanisms by which this is done are largely unknown. Brown-rot fungi produce several kinds of extracellular carbohydrate-degrading enzymes (Highley 1977; Highley and Wolter 1982; Ishihara and Shimizu 1980, 1984; Ishihara and others 1978); the role of these enzymes in the process of wood decay has not been fully explained (Kirk and Cowling 1984). A better understanding of the biochemistry of brown-rot fungi could result in the development of specific metabolic controls which could prevent or inhibit decay, thus replacing highly toxic preservatives.

One possible way to study the biochemistry of wood decay is to examine the physiology of cultures which have lost the ability to degrade wood. Most Basidiomycetes are fairly stable in culture due to their dikaryotic state. Occasionally, isolates change in culture; they become less vigorous and are unable to decay wood. Such senescence in fungi is poorly understood and has been associated with fungal

Abstract.--The brown-rot fungi Postia placenta, Gloeophyllum saepiarium, and G. trabeum are economically important decayers of wood. These organisms metabolize the cellulose and hemicellulose of woody tissues but do not substantially metabolize lignin. Senescent cultures of these species lose their ability to degrade wood and are thin and appressed compared to the more robust, floccose nonsenescent isolates. The physiology and growth habits of these senescent cultures were compared to nonsenescent isolates in order to study the biochemical mechanisms of wood decay. No significant differences were found in growth rates of senescent and nonsenescent cultures on malt-extract agar. Senescent isolates retained the ability to produce β -D-glucosidase, α - and β -D-galactosidase, xylanase, endo- β -1,4-glucanase and other cellulose-degrading enzymes. These data suggest the hypothesis that additional chemical or biochemical mechanisms besides simple enzymatic degradation are involved in wood decay by brown-rot fungi.

Keywords: Brown rot, carbohydrate-degrading enzymes, Basidiomycetes, senescence.

viruses (Day and Dodds 1979, Lemke 1977, Hammer and others 1986, Castanho and others 1978), bacteria- or mycoplasma-like organisms (Wilson and Hanton 1979), and specific chromosomes working in conjunction with plasmids (Esser and others 1984; Esser and Tudzynski 1979). A comparison of the physiology of senescent and nonsenescent cultures of brown-rot fungi should further our understanding of the decay process. The objective of this study was to determine whether certain cultural characteristics and the production of extracellular carbohydrate-degrading enzymes are related to senescence, and thus required for wood decay.

MATERIALS AND METHODS

Maintenance of Fungal Cultures

All cultures were maintained on 2.0 percent malt-extract agar (MEA) slants stored at 4 °C. Sources and dates of collection of all cultures are presented in table 1.

Identification of Senescent Cultures

Representative isolates of Postia placenta (Fr.) M. J. Larsen and Lombard [syn: Poria placenta (Fr.) Cke.], Gloeophyllum saepiarium (Wulf.: Fr.) Karst. and G. trabeum (Pers.: Fr.) Murr. were evaluated for their abilities to cause wood decay by the standard ASTM soil block method (ASTM 1971) using southern pine blocks (25.4 by 25.4 by 3.2 mm, the long axis parallel to the grain). Soil block bottles were maintained at 27 °C and 70 percent relative humidity; the percent weight loss of each block was determined after 12 weeks. Isolates which caused weight losses of less than 35 percent were considered "senescent."

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This was an arbitrary value and represents a reduction in decay capacity of about 50 percent.

Determination of Colony Morphology and Growth Rate

Senescent and nonsenescent cultures of each of the three species were grown on 2 percent MEA; gross colony morphology and light microscopy of individual hyphae were observed after 3 weeks. Growth rates were determined by inoculating 2 percent MEA with 5-mm plugs taken from the margins of 7-day-old cultures also grown on 2 percent MEA. Radial growth of each colony was measured after 2, 6, 11, and 13 days.

Growth and Enzyme Activity in Liquid Cultures

Senescent and nonsenescent isolates of each of the three species were grown in 25-ml stationary liquid cultures in 250-ml Erlenmeyer flasks with 0.5 percent cellobiose in a basal salts solution (Highley 1973) as the growth medium. In a second experiment, the fungi were grown in the same basal salts solution amended with 1 percent sweetgum sawdust with or without 0.5 percent cellobiose as a supplemental carbon source. Control flasks contained the basal salts solution alone. The liquid media were inoculated with 5-mm mycelial plugs taken from the margins of 7-day-old colonies grown on 2 percent MEA. Culture filtrates were collected by vacuum filtration and dialyzed overnight against distilled water in 12,000 to 14,000 Dalton Spectra/por dialysis tubing. Culture filtrates were then assayed for general extracellular proteins (Lowry and others 1951) using dilutions of bovine serum albumin for the standard curve.

The activities of α -D-galactosidase (E.C. 3.2.1.22), β -D-galactosidase (E.C. 3.2.1.23) and β -D-glucosidase (E.C. 3.2.1.21) were determined by the liberation of p-nitrophenol from the respective p-nitrophenol substrate (Nelson 1944). One unit of enzyme activity was defined as the amount of enzyme needed to release 1 μ M of p-nitrophenol per hour at 40 °C.

The activities of endo- β -1,4-glucanase (carboxymethylcellulase) (E.C. 3.2.1.4) and endo- β -1,4-xylanase (E.C. 3.2.1.37) were assayed by measuring the increase in reducing groups using Nelson's modification of the Somogyi method (Nelson 1944). One unit of enzyme activity was defined as the amount of enzyme needed to liberate reducing power equivalent to 1 μ M of glucose per 24 hours at 40 °C.

Cellulolytic enzyme activity was also measured by the degradation cellulose-azure as described by Highley (1983). Senescent and nonsenescent isolates of each of the three species were grown in vertical tubes of a basal salts medium (Highley 1973) on which sterilized cellulose-azure had been aseptically layered. Enzyme activity was estimated by the amount of dyed cellulose degradation products released into the agar medium. The intensity of color was estimated on a 0 to 4 scale, with 0 representing no

coloration (i.e. no cellulase activity) and 4 representing an intense blue color (i.e. high levels of cellulase activity).

Chemicals

Carboxymethylcellulose was obtained from Hercules (Wilmington, DE); all other chemicals were purchased from Sigma (St. Louis, MO).

RESULTS

Identification of Senescent Cultures

The 15, 16, and 16 isolates of *P. placenta*, *G. saepiarium*, and *G. trabeum*, respectively, were screened for their abilities to decay wood; percent weight losses of southern pine test blocks are presented in table 1. Some isolates showed decreased decay capacity. These were: *P. placenta*--ME20, ME387; *G. saepiarium*--ME517, MD483, MAD536, TA13; *G. trabeum*--MAD5096-15, MAD539s, TP356b. These cultures were termed "senescent" and were used in all subsequent tests with representative nonsenescent strains.

Determination of Colony Morphology and Growth Rate

The colony morphologies of senescent cultures differed from those of the nonsenescent isolates. Colonies produced by senescent cultures were thin and appressed compared to the more robust, floccose wild strains. Senescent isolates of *G. trabeum* and *G. saepiarium* also failed to produce the characteristic pigments found in nonsenescent cultures. Hyphae of senescent isolates were swollen and distorted.

A large degree of growth rate variation occurred among isolates of each of the three species. Growth rate was not related to senescence (figs. 1-3); certain senescent isolates (ME387, MD483) actually grew more rapidly than nonsenescent cultures of the same species.

Growth and Enzyme Production in Liquid Culture

Senescent and nonsenescent isolates of *P. placenta*, *G. saepiarium*, and *G. trabeum* were grown in a basal salt solution with 0.5 percent cellobiose as the carbon source. Culture filtrates were assayed for the presence of α - and β -D-galactosidase, β -D-glucosidase, endo- β -1,4-xylanase, and endo- β -1,4-glucanase (carboxymethylcellulase); dry weights of the mycelia and pH's of the culture filtrates were also determined (table 2). All cultures dramatically lowered the pH of the culture filtrates from an initial reading of 4.5. In most cases, the extent of this decrease was related to the dry weight of the fungus; isolates which formed the greatest amount of mycelium produced the lowest pH readings (MAD537s, MAD539s, ME20).

Total extracellular protein production appeared to be independent of dry weight and was characteristic of each species. Isolates of *G. saepiarium* formed low levels of

Table 1.--Collection data on isolates of Postia placenta, Gloeophyllum saepiarium and G. trabeum ranked by their ability to degrade southern pine as estimated by the ASTM soil-wood block assay

| Species | Isolate number | Date of collection | Source and location of collection | Weight loss |
|---|--------------------|--------------------|---|-------------|
| | | Mo/yr | | Pct |
| <u>Postia placenta</u> (Fr.) M. J. Larsen and Lombard | TRL2556 | 3/50 | Mineshaft support, Transvaal, Africa | 68.2 |
| | RLG3760R | 7/63 | <u>Betula alleghaniensis</u> Britton, Newcomb, NY | 65.9 |
| | L9138sp | 8/58 | <u>Pinus ponderosa</u> Laws., Coronado National Forest, AZ | 65.4 |
| | MD484 | -- | -- | 62.0 |
| | MAD575 = ATCC9891 | 10/20 | <u>Pseudotsuga menziesii</u> (Mirb.) Franco, Oregon | 60.8 |
| | MAD698 = ATCC11538 | 12/41 | <u>Pseudotsuga menziesii</u> , yacht "America" | 60.4 |
| | ME48 | 11/63 | <u>Pseudotsuga menziesii</u> , Clark County, WA | 60.3 |
| | ME146 | 2/62 | Telephone pole, Clark County, WA | 60.0 |
| | FP100086sp | 3/49 | Conifer sills and piles, Fairfield, OH | 59.5 |
| | MD281 | 11/57 | <u>Pseudotsuga menziesii</u> , Oregon | 59.4 |
| | BTL-V-10 | 2/52 | Philadelphia, PA | 58.3 |
| | MD506 | 4/62 | <u>Pinus</u> sp., Madison, WI | 57.2 |
| | MAD4874 | 2/50 | <u>Tsuga heterophylla</u> (Raf.) Sarg., Madison, WI | 52.5 |
| | ME387 | 9/64 | Pole, Willamette Valley, OR | 6.5 |
| | ME20 | -- | Floor planking, Pleasant Hill, CA | 5.1 |
| <u>Gloeophyllum saepiarium</u> (Wulf.: Fr.) Karst | FD18 | 1961 | <u>Pseudotsuga menziesii</u> , Elma, WA | 61.1 |
| | MAD537s | 1920 | Railway ties, Arkansas | 59.4 |
| | FP100242sp | 9/52 | <u>Picea engelmannii</u> Parry, White River National Forest, CO | 57.8 |
| | ME79 | 10/62 | <u>Tsuga heterophylla</u> , Corvallis, OR | 57.2 |
| | ME102 | 7/63 | <u>Tsuga</u> sp., Corvallis, OR | 48.3 |
| | OPSAL8691 | 6/63 | Telephone pole, South Dakota | 48.2 |
| | OKM1592-5 | 6/62 | <u>Picea engelmannii</u> or <u>Abies concolor</u> (Gord. & Glend.) Lindl., McCall, ID | 45.8 |
| | ME432 | -- | <u>Chamaecyparis lawsoniana</u> (A. Murr.) Parl. | 45.6 |
| | ME393 | 9/64 | <u>Pseudotsuga menziesii</u> , Albany, OR | 45.3 |
| | FP104089sp | 4/53 | <u>Pinus</u> sp., Gulfport, MS | 39.6 |
| | LOO13812 | 12/31 | <u>Tsuga</u> sp., Hunt County, PA | 37.9 |
| | ME637 | 7/78 | <u>Pinus contorta</u> Dougl., Gulfport, MS | 35.0 |
| | ME517 | 6/74 | <u>Picea glauca</u> var. <u>albertiana</u> (S. Brown) Sarg. | 32.9 |
| | MD483 | -- | -- | 31.3 |
| | MAD536 | 3/22 | <u>Picea</u> sp., Madison, WI | 28.7 |
| | TA13 | 7/63 | <u>Pinus</u> sp., Syracuse, NY | 14.6 |

Table 1.--Collection data on isolates of *Postia placenta*, *Gloeophyllum saepiarium* and *G. trabeum* ranked by their ability to degrade southern pine as estimated by the ASTM soil-wood block assay--con.

| Species | Isolate number | Date of collection | Source and location of collection | Weight loss |
|--|----------------|--------------------|---|-------------|
| | | Mo/yr | | Pct |
| <i>Gloeophyllum trabeum</i> (Pers.: Fr.) Murr. | ME39 | 7/61 | <i>Sequoia sempervirens</i> (D. Don) Endl., Akron, OH | 66.3 |
| | MAD SAVO IS | 11/51 | <i>Pseudotsuga menziesii</i> , "Savo Island" aircraft carrier | 63.2 |
| | DAOM-F3823 | 4/65 | Unidentified hardwood, Ottawa, Ont. | 63.0 |
| | MD76 | -- | -- | 62.1 |
| | FP125076sp | 5/62 | <i>Acer</i> sp., West Alton, NH | 62.1 |
| | MAD617 | 6/26 | <i>Thuja plicata</i> Donn, Madison, WI | 60.8 |
| | ME76 | 2/63 | Plywood flooring, Madison, WI | 59.2 |
| | MD505 | 4/62 | <i>Pinus</i> sp., Madison, WI | 51.3 |
| | 1320 | 8/64 | Unidentified hardwood, Routt County, UT | 48.1 |
| | TA-1A | 6/63 | Syracuse, NY | 48.1 |
| | MD256 | -- | -- | 43.9 |
| | ME509 | 10/72 | <i>Pseudotsuga menziesii</i> , Racine, WI | 37.1 |
| | OPSAL8601 | 6/63 | Telephone pole, South Dakota | 35.8 |
| | MAD5096-15 | -- | <i>Pinus</i> sp., Bogalusa, LA | 25.0 |
| | MAD539s | 3/24 | <i>Pinus</i> sp., Madison, WI | 3.6 |
| | TP356b | 1938 | <i>Pinus</i> sp., Spartanburg, SC | 1.2 |

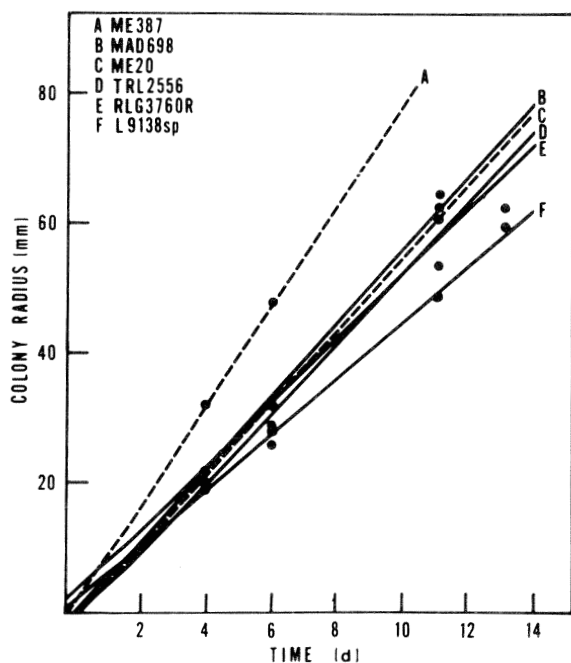


Figure 1.--Radial growth (mm/da) of senescent and nonsenescent isolates of *Postia placenta* on 2 percent malt extract agar. Solid line = nonsenescent cultures; broken line = senescent cultures. (ML86 5330)

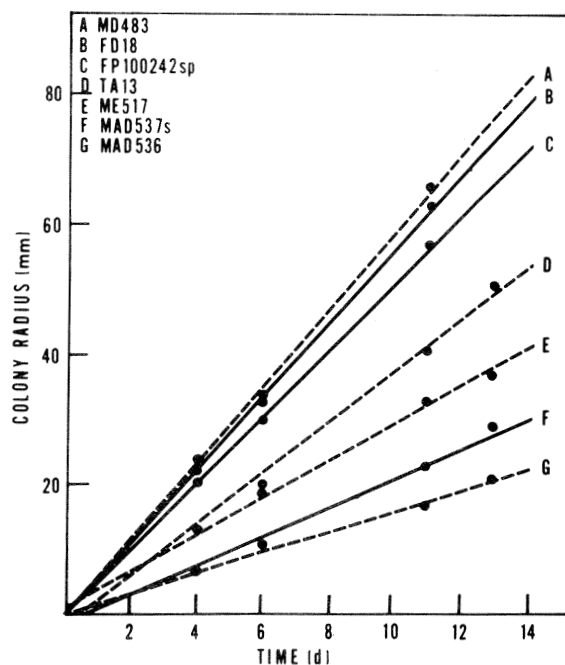


Figure 2.--Radial growth (mm/da) of senescent and nonsenescent isolates of *Gloeophyllum saepiarium* on 2 percent malt extract agar. Solid line = nonsenescent cultures; broken line = senescent cultures. (ML86 5331)

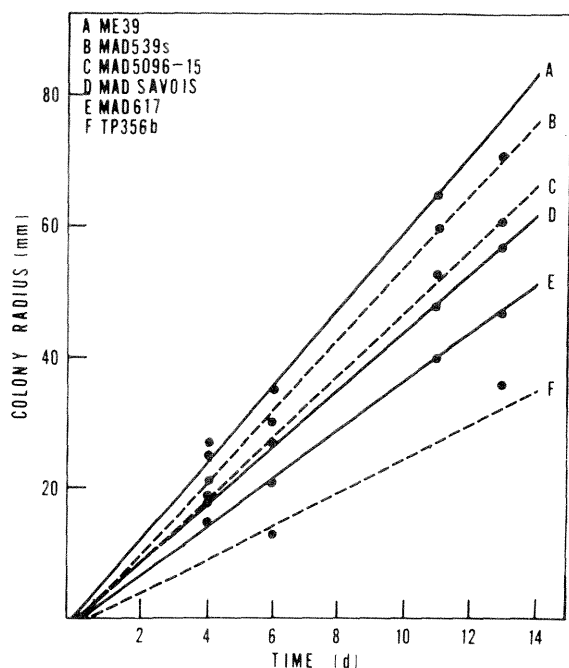


Figure 3.--Radial growth (mm/da) of senescent and nonsenescent isolates of *Gloeophyllum trabeum* on 2 percent malt extract agar. Solid line = nonsenescent cultures; broken line = senescent cultures. (ML86 5332)

extracellular proteins; enzyme production by *G. trabeum* isolates was much higher, and cultures of *P. placenta* exhibited an intermediate response. A few exceptions to this pattern were noted. Certain senescent isolates of *G. trabeum* (MAD539s and TP356b) and *P. placenta* (ME387) produced lower levels of extracellular proteins than the nonsenescent strains of each species. Another senescent isolate of *P. placenta*, ME20, produced extremely high levels of extracellular proteins.

There was no apparent relationship between senescence and levels of glycosidase production. Enzyme levels were extremely variable among the different isolates of each species; senescent cultures typically produced equivalent or higher levels of β -D-glucosidase, α -D-galactosidase, and β -D-galactosidase than their nonsenescent counterparts. Isolate ME20, a senescent culture of *P. placenta*, produced extremely high levels of these enzymes. There did appear to be some correlation between xylanase production and senescence of *P. placenta* and *G. trabeum*; senescent isolates of these species produced aberrant levels of this enzyme. Isolates ME387, MAD5096-15, MAD539s, and TP356b produced decreased quantities of xylanase compared to the nonsenescent strains; isolate ME20 produced much higher levels of xylanase than the remaining isolates of *P. placenta*. No correlation was found between senescence and the presence of endo- β -1,4-glucanase, although senescent isolates MAD539s and TP356b (*G. trabeum*)

produced slightly lower quantities of this enzyme than the nonsenescent strains.

Senescent and nonsenescent isolates of the three species were also able to grow in a basal salt medium supplemented with 1 percent sweetgum sawdust (table 3). Fungal hyphae were observed to grow on and around the sawdust particles and gathered the sawdust into a loosely connected mat. Mycelial growth was greatly stimulated by the addition of 0.5 percent cellobiose. This increase in growth is reflected in the lower pH values and increased levels of extracellular proteins produced by most isolates in the presence of cellobiose.

As in the previous experiment, there was no correlation between levels of β -D-glucosidase, α - and β -D-galactosidase and senescence. The addition of cellobiose to the medium generally increased glycosidase production, but it is unknown whether this was due to increased amounts of mycelial growth or whether additional quantities of enzyme were induced. All isolates of *G. saepiarium* produced extremely low levels of α -D-galactosidase with or without the addition of cellobiose; this trait appears to be characteristic of the species. Certain isolates of *G. trabeum* (MAD617, MAD539s, TP356b) produced much lower levels of β -D-galactosidase in the presence of cellobiose; this phenomenon was not confined to senescent cultures.

Production of xylanase and endo- β -1,4-glucanase also appeared to be largely independent of senescence. Xylanase production by isolates of *P. placenta* generally increased with the addition of cellobiose with the exception of isolate ME387, a senescent culture. Levels of xylanase declined upon the addition of cellobiose for isolates of *G. saepiarium* and were generally unaffected for isolates of *G. trabeum*. The senescent isolates of *G. trabeum* expressed decreased levels of xylanase production with and without the addition of cellobiose. This is consistent with the results obtained in the previous experiment. Levels of endo- β -1,4-glucanase production generally increased with the addition of cellobiose for isolates of *P. placenta* and were unchanged for most isolates of *G. saepiarium* and *G. trabeum*. Certain senescent isolates of *G. saepiarium* (MAD536, TA13) and *G. trabeum* (MAD539s, TP356b) showed a decline in endo- β -1,4-glucanase production upon the addition of cellobiose.

There was no relationship between senescence and the production of cellulase as measured by the degradation of cellulose azure (table 4). The senescent isolates of *P. placenta*, ME20 and ME387, produced extremely low quantities or no detectable levels of this enzyme, but several nonsenescent isolates with good decay capacity (MAD4874, MD506, TRL2556) were also poor enzyme producers. Senescent isolates of *G. saepiarium* (TA13, MD483, ME517) and *G. trabeum* (MAD539s, TP356b) produced high levels of cellulolytic enzymes; isolates of these species which were poor cellulase producers (ME102, MAD536, 1320) exhibited little if any decreased ability to

Table 2.--Fungal mass, pH of culture filtrate, and extracellular enzyme production of senescent and nonsenescent isolates of Postia placenta, Gloeophyllum saepiarium, and G. trabeum after 4 weeks in 0.5 percent cellobiose + basal salts solution¹

| Isolate | Dry weight | pH | Protein | β -GLU ² | α -GAL ³ | β -GAL ⁴ | XYL ⁵ | CMC ⁶ |
|--------------------------------|------------|------|------------|---------------------------|----------------------------|---------------------------|------------------|------------------|
| | Mg | | μ g/ml | - - - - - | - - - - - | Units - - - - - | - - - - - | - - - - - |
| <u>POSTIA PLACENTA</u> | | | | | | | | |
| TRL2556 | 22 | 3.37 | 35 | 0.078 | 0.163 | 0.012 | 241 | 72 |
| RLG3760R | 27 | 3.02 | 34 | 0.018 | 0.040 | 0.000 | 241 | 56 |
| L9138sp | 48 | 2.98 | 42 | 0.014 | 0.140 | 0.030 | 195 | 53 |
| MAD698 | 26 | 3.27 | 47 | 0.032 | 0.048 | 0.046 | 231 | 59 |
| ME387 | 28 | 2.29 | 22 | 0.051 | 0.012 | 0.114 | 48 | 46 |
| ME20 | 30 | 2.55 | 100 | 0.534 | 0.375 | 0.595 | 341 | 63 |
| <u>GLOEOPHYLLUM SAEPIARIUM</u> | | | | | | | | |
| FD18 | 27 | 2.75 | 24 | 0.041 | <0.010 | 0.038 | 331 | 98 |
| MAD537s | 39 | 2.65 | <20 | <0.010 | <0.010 | <0.010 | 55 | 37 |
| FP100242sp | 7 | 3.46 | <20 | <0.010 | <0.010 | <0.010 | 239 | 67 |
| ME517 | 22 | 2.84 | 25 | 0.034 | <0.010 | <0.010 | 212 | 66 |
| MD483 | 18 | 2.89 | 35 | 0.131 | <0.010 | 0.016 | 325 | 60 |
| MAD536 | 7 | 4.17 | <20 | 0.055 | <0.010 | <0.010 | 122 | 36 |
| TA13 | 8 | 3.35 | <20 | 0.008 | <0.010 | <0.010 | 163 | 52 |
| <u>GLOEOPHYLLUM TRABEUM</u> | | | | | | | | |
| ME39 | 29 | 2.78 | 114 | 0.042 | 0.030 | 0.028 | 556 | 112 |
| MAD Savo Is | 27 | 2.98 | 73 | 0.030 | 0.028 | 0.009 | 516 | 80 |
| MAD617 | 14 | 3.11 | 149 | 0.592 | 0.468 | 0.362 | 557 | 104 |
| MAD5096-15 | 12 | 2.97 | 138 | 0.680 | 0.101 | 0.111 | 291 | 100 |
| MAD539s | 29 | 2.62 | 25 | 0.174 | 0.100 | <0.010 | 134 | 62 |
| TP356b | 17 | 2.86 | 28 | 0.360 | 0.134 | <0.010 | 257 | 61 |

¹All readings represent an average of 5 replications.

² β -GLU = activity of β -D-glucosidase.

³ α -GAL = activity of α -D-galactosidase.

⁴ β -GAL = activity of β -D-galactosidase.

⁵XYL = activity of endo-1,4- β -D-xylanase.

⁶CMC = activity of endo-1,4- β -D-glucanase (carboxymethylcellulase).

decay wood, with the exception of isolate MAD536. Cellulase production generally increased with time in all isolates and was not dependent on the presence of cellobiose in the medium.

DISCUSSION

A series of isolates of the brown-rot fungi P. placenta, G. saepiarium, and G. trabeum were evaluated for their ability to decay wood. There was a large variation in decay capacity; isolates which produced weight losses of less than 35 percent were considered senescent. Senescent cultures produced flattened, appressed colony morphologies; individual hyphae were often swollen and distorted. Senescence was not related to growth rate, length of time in culture, the ability of the fungus to lower the pH of liquid media, or the total production of extracellular proteins. Senescent cultures retained the ability to produce the carbohydrate-degrading enzymes β -D-glucosidase, α - and β -D-galactosidase, xylanase, endo β -1,4-glucanase,

and other cellulolytic enzymes. Xylanase production seemed to be aberrant (i.e., higher or lower than nonsenescent isolates) in senescent cultures of P. placenta and G. trabeum. Such aberrant levels of xylanase production suggests that the regulation or secretory mechanisms of these cultures may be impaired. The removal of hemicellulose occurs early in the process of wood decay (Kirk and Highley 1973, Highley and Kirk 1979); the production of xylanase is essential to this process. Further studies are needed to determine whether senescence in these species is dependent on altered xylan metabolism.

If altered xylanase levels are not the major expression of senescence, the ability to decay wood must be dependent on more than the production of extracellular carbohydrate-degrading enzymes. Senescent cultures retained the ability to produce these enzymes in response to sawdust and cellobiose; it is unknown whether the enzymes are formed in response to solid wood. A nonenzymatic mechanism, involving

Table 3.--Extracellular enzyme production and pH of culture filtrate of senescent and nonsenescent isolates of *Postia placenta*, *Gloeophyllum saepiarium*, and *G. trabeum* after 4 weeks on sweetgum sawdust (1 pct) in a basal salts solution \pm 0.5 percent cellobiose¹

| Isolate | Treatment ² | pH | Protein | β-GLU ³ | α-GAL ⁴ | β-GAL ⁵ | XYL ⁶ | CMC ⁷ |
|--------------------------------|------------------------|------|---------|--------------------|--------------------|--------------------|------------------|------------------|
| | | | μg/ml | Units | | | | |
| <u>POSTIA PLACENTA</u> | | | | | | | | |
| TRL2556 | A | 4.30 | <20 | <0.010 | 0.032 | <0.010 | 25 | 10 |
| | B | 4.41 | <20 | 0.026 | 0.245 | 0.306 | 416 | 37 |
| | C | 2.86 | 80 | 0.196 | 1.940 | 1.580 | 450 | 122 |
| RLG3760R | A | 4.44 | <20 | <0.010 | 0.060 | <0.010 | 25 | 4 |
| | B | 4.27 | 21 | 0.023 | 0.625 | 0.114 | 204 | 72 |
| | C | 2.93 | 79 | <0.010 | 0.190 | 0.010 | 342 | 107 |
| MAD698 | A | 4.45 | <20 | <0.010 | 0.018 | <0.010 | 18 | 0 |
| | B | 4.83 | <20 | 0.052 | 0.245 | 0.306 | 285 | 8 |
| | C | 3.30 | 80 | 0.196 | 1.940 | 1.580 | 460 | 78 |
| ME387 | A | 3.94 | <20 | <0.010 | <0.010 | <0.010 | 5 | 1 |
| | B | 4.02 | 20 | 0.026 | 0.216 | 0.274 | 170 | 40 |
| | C | 3.26 | 86 | 0.458 | 1.140 | 2.044 | 242 | 65 |
| ME20 | A | 4.50 | <20 | <0.010 | <0.010 | <0.010 | 5 | 0 |
| | B | 4.94 | <20 | 0.052 | 0.195 | 0.134 | 203 | 15 |
| | C | 3.54 | 100 | 0.087 | 1.260 | 0.194 | 435 | 25 |
| <u>GLOEOPHYLLUM SAEPIARIUM</u> | | | | | | | | |
| FD18 | A | 4.74 | <20 | <0.010 | <0.010 | <0.010 | 50 | 48 |
| | B | 4.60 | 24 | 0.051 | 0.020 | 0.480 | 473 | 92 |
| | C | 4.72 | 88 | 0.560 | 0.026 | 1.095 | 442 | 93 |
| MAD537s | A | 4.40 | <20 | <0.010 | <0.010 | 0.021 | 168 | 0 |
| | B | 4.90 | <20 | 0.084 | 0.012 | 0.415 | 372 | 38 |
| | C | 3.16 | 21 | 0.038 | 0.006 | 0.815 | 250 | 37 |
| FP100242sp | A | 4.51 | <20 | 0.016 | <0.010 | 0.015 | 222 | 8 |
| | B | 4.57 | <20 | 0.040 | 0.006 | 0.750 | 473 | 48 |
| | C | 4.60 | 53 | 0.088 | 0.020 | 1.000 | 355 | 43 |
| ME517 | A | 4.50 | <20 | <0.010 | <0.010 | <0.010 | 75 | 5 |
| | B | 4.40 | 21 | 0.030 | <0.010 | 0.300 | 418 | 132 |
| | C | 5.04 | 65 | 0.749 | 0.034 | 0.770 | 412 | 113 |
| MD483 | A | 4.61 | <20 | <0.010 | <0.010 | <0.010 | 10 | 2 |
| | B | 4.84 | <20 | 0.041 | <0.010 | 0.525 | 443 | 68 |
| | C | 3.27 | 51 | 0.084 | <0.010 | 0.755 | 353 | 73 |
| MAD536 | A | 4.01 | <20 | <0.010 | <0.010 | 0.030 | 48 | 0 |
| | B | 4.73 | <20 | 0.128 | 0.013 | 0.315 | 392 | 62 |
| | C | 3.07 | 35 | 0.168 | <0.010 | 0.965 | 208 | 22 |
| TA13 | A | 4.53 | <20 | 0.010 | <0.010 | <0.010 | 90 | 2 |
| | B | 4.68 | <20 | 0.080 | <0.010 | 0.390 | 438 | 108 |
| | C | 3.36 | 63 | 0.410 | 0.014 | 0.190 | 253 | 72 |
| <u>GLOEOPHYLLUM TRABEUM</u> | | | | | | | | |
| ME39 | A | 4.42 | <20 | <0.010 | <0.010 | <0.010 | 28 | 0 |
| | B | 3.96 | <20 | <0.010 | 0.030 | 0.200 | 557 | 113 |
| | C | 4.45 | 68 | 0.936 | 0.400 | 0.635 | 592 | 130 |
| MAD Savo Is | A | 4.28 | <20 | <0.010 | <0.010 | <0.010 | 12 | 0 |
| | B | 4.57 | 21 | 0.034 | 0.215 | 0.215 | 553 | 85 |
| | C | 3.84 | 65 | 1.455 | 0.425 | 0.585 | 508 | 70 |
| MAD617 | A | 4.37 | <20 | 0.019 | <0.010 | <0.010 | 75 | 15 |
| | B | 4.32 | 27 | 0.079 | 0.305 | 0.635 | 568 | 132 |
| | C | 4.25 | 114 | 1.765 | 0.615 | 0.208 | 583 | 128 |
| MAD5096-15 | A | 4.50 | <20 | 0.026 | <0.010 | <0.010 | 18 | 0 |
| | B | 4.45 | 24 | 0.072 | 0.105 | 0.800 | 442 | 73 |
| | C | 4.75 | 130 | 1.985 | 0.720 | 1.445 | 498 | 78 |

Table 3.--Extracellular enzyme production and pH of culture filtrate of senescent and nonsenescent isolates of *Postia placenta*, *Gloeophyllum saepiarium*, and *G. trabeum* after 4 weeks on sweetgum sawdust (1 pct) in a basal salts solution \pm 0.5 percent cellobiose¹--con.

| Isolate | Treatment ² | pH | Protein | β-GLU ³ | α-GAL ⁴ | β-GAL ⁵ | XYL ⁶ | CMC ⁷ |
|---|------------------------|------|--------------|--------------------|--------------------|--------------------|------------------|------------------|
| | | | <u>μg/ml</u> | <u>Units</u> | | | | |
| <u>GLOEOPHYLLUM</u> <u>TRABEUM</u> --con. | | | | | | | | |
| MAD539s | A | 4.52 | <20 | 0.154 | <0.010 | 0.117 | 35 | 5 |
| | B | 5.04 | <20 | 0.226 | 0.192 | 0.870 | 447 | 145 |
| | C | 3.51 | 42 | 0.920 | 0.388 | 0.185 | 143 | 70 |
| TP356b | A | 4.63 | <20 | 0.039 | <0.010 | <0.010 | 18 | 0 |
| | B | 4.79 | <20 | 0.395 | 0.770 | 0.515 | 442 | 75 |
| | C | 3.42 | 58 | 1.895 | 0.640 | 0.140 | 285 | 58 |

¹Each reading represents an average of 3 replications.

²Treatment A = Basal salts solution, B = Basal salts solution + 1 percent sweetgum sawdust, C = Basal salts solution + 1 percent sweetgum sawdust + 0.5 percent cellobiose.

³ β -GLU = activity of β -D-glucosidase.

⁴ α -GAL = activity of α -D-galactosidase.

⁵ β -GAL = activity of β -D-galactosidase.

⁶XYL = activity of endo-1,4- β -D-xylanase.

⁷CMC = activity of endo-1,4- β -D-glucanase (carboxymethylcellulase).

hydrogen peroxide and ferrous ions, has been proposed to explain the rapid depolymerization of cellulose which occurs during brown rot (Koenigs 1972, Koenigs 1974a and b, Kirk and Cowling 1984); this proposal has not been proven (Highley 1982, Highley and Murmanis 1985). The loss of such a nonenzymatic mechanism would explain why senescent cultures are unable to decay wood despite the production of carbohydrate-degrading enzymes.

The debilitating agent associated with the senescence of these cultures has not been identified but appears to be transmissible (Highley, unpublished data). The distorted hyphae of these senescent cultures resemble those of strains of *Leucostoma cincta*

(Hammar and others 1986) and *Rhizoctonia solani* (Castanho and Butler 1978) which contain dsRNA, the genetic material of fungal viruses. Experiments are currently underway to screen the isolates used in this study for dsRNA. The potential use of senescent cultures for the biological control of wood decay, as hypovirulent strains of *Cryphonectria parasitica* (Murr.) Barr are used in the control of the chestnut blight fungus (Anagnostakis 1982), needs to be explored.

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Table 4.--Breakdown of cellulose-azure^{1,2} by brown-rot fungi having different capacities to decay wood

| Isolate | Cellulase activity | | | | | | | | | |
|--------------------------------|--------------------|-----|-----|-----|-----|-----|-----|-----|-----|-----|
| | Time (days) | | | | | | | | | |
| | 7 | | 14 | | 21 | | 28 | | 42 | |
| | -C | +C | -C | +C | -C | +C | -C | +C | -C | +C |
| <u>POSTIA PLACENTA</u> | | | | | | | | | | |
| TRL2556 | 1.0 | 1.0 | 1.5 | 1.5 | 2.0 | 1.5 | 2.0 | 1.5 | 2.0 | 2.0 |
| RLG3760R | 2.0 | 2.5 | 2.5 | 2.5 | 3.0 | 3.0 | 3.0 | 3.0 | 4.0 | 4.0 |
| L9138sp | 1.0 | 1.0 | 1.5 | 2.0 | 2.0 | 2.5 | 2.5 | 3.0 | 2.5 | 4.0 |
| MD484 | 2.0 | 1.0 | 2.0 | 1.0 | 3.0 | 1.0 | 3.0 | 1.5 | 4.0 | 2.5 |
| MAD575 | 1.0 | 1.0 | 1.5 | 1.5 | 2.0 | 1.5 | 2.0 | 2.0 | 2.5 | 3.0 |
| MAD698 | 1.0 | 1.0 | 1.5 | 1.5 | 2.0 | 2.0 | 3.0 | 3.0 | 3.0 | 3.5 |
| ME48 | 2.0 | 2.0 | 3.0 | 2.5 | 3.5 | 2.5 | 3.5 | 3.5 | 4.0 | 3.5 |
| ME146 | 2.0 | 2.0 | 3.0 | 3.0 | 3.5 | 3.5 | 4.0 | 4.0 | 4.0 | 4.0 |
| FP100086sp | 1.0 | 1.0 | 1.5 | 1.5 | 2.0 | 2.0 | 3.0 | 3.0 | 3.5 | 3.5 |
| MD281 | 2.0 | 2.0 | 3.0 | 3.0 | 3.5 | 3.0 | 4.0 | 4.0 | 4.0 | 4.0 |
| BTL-V-10 | 2.0 | 2.0 | 3.0 | 2.5 | 3.0 | 2.5 | 3.0 | 3.0 | 3.0 | 3.5 |
| MD506 | 1.0 | 1.0 | 1.5 | 1.0 | 2.0 | 1.0 | 2.5 | 1.5 | 2.5 | 2.5 |
| MAD4874 | 1.0 | 1.0 | 1.0 | 1.0 | 1.5 | 1.0 | 1.5 | 1.5 | 1.5 | 1.5 |
| ME387 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| ME20 | 0.0 | 1.0 | 0.0 | 1.0 | 0.0 | 1.0 | 0.0 | 2.0 | 0.0 | 1.5 |
| <u>GLOEOPHYLLUM SAEPIARIUM</u> | | | | | | | | | | |
| FD18 | 2.0 | 3.0 | 3.0 | 3.5 | 3.5 | 3.5 | 4.0 | 4.0 | 4.0 | 4.0 |
| MAD537s | 2.0 | 0.0 | 2.5 | 1.0 | 3.0 | 1.0 | 2.5 | 1.5 | 3.0 | 1.5 |
| FP100242sp | 2.0 | 0.0 | 4.0 | 1.5 | 3.5 | 3.0 | 4.0 | 3.5 | 4.0 | 4.0 |
| ME79 | 3.0 | 3.0 | 3.5 | 3.5 | 4.0 | 4.0 | 4.0 | 4.0 | 4.0 | 4.0 |
| ME102 | 1.0 | 1.0 | 1.5 | 1.5 | 1.5 | 1.5 | 1.5 | 1.5 | 2.0 | 2.0 |
| OPSAL8691 | 2.5 | 2.0 | 4.0 | 3.0 | 4.0 | 3.0 | 4.0 | 3.5 | 4.0 | 3.5 |
| OKM1592-5 | 2.5 | 2.5 | 3.0 | 3.0 | 3.5 | 3.0 | 4.0 | 3.5 | 4.0 | 3.5 |
| ME432 | 2.0 | 2.0 | 2.0 | 2.0 | 2.0 | 2.0 | 2.0 | 3.0 | 2.5 | 3.0 |
| ME393 | 2.0 | 2.0 | 2.0 | 2.0 | 2.0 | 2.0 | 3.0 | 3.0 | 3.0 | 3.0 |
| FP104089sp | 2.0 | 3.0 | 4.0 | 0.5 | 3.5 | 2.0 | 4.0 | 3.5 | 4.0 | 4.0 |
| L0013812 | 2.0 | 2.0 | 3.5 | 3.0 | 3.0 | 3.0 | 3.5 | 3.5 | 3.5 | 3.5 |
| ME637 | 2.0 | 2.0 | 2.5 | 2.5 | 2.5 | 3.0 | 3.0 | 3.5 | 3.0 | 3.5 |
| ME517 | 2.0 | 2.5 | 3.0 | 3.5 | 3.0 | 4.0 | 4.0 | 4.0 | 4.0 | 4.0 |
| MD483 | 1.0 | 2.0 | 2.0 | 2.5 | 2.0 | 2.5 | 2.0 | 3.0 | 2.0 | 3.0 |
| MAD536 | 1.0 | 1.0 | 1.0 | 1.5 | 1.0 | 1.0 | 1.5 | 1.0 | 2.0 | 2.0 |
| TA13 | 2.0 | 0.5 | 3.0 | 1.5 | 4.0 | 2.0 | 4.0 | 3.0 | 4.0 | 4.0 |
| <u>GLOEOPHYLLUM TRABEUM</u> | | | | | | | | | | |
| ME39 | 3.0 | 3.0 | 3.0 | 4.0 | 3.0 | 4.0 | 3.0 | 4.0 | 3.0 | 3.0 |
| MAD Savo Is | 3.0 | 2.5 | 4.0 | 3.0 | 4.0 | 3.5 | 4.0 | 3.5 | 4.0 | 4.0 |
| DAOM-F3823 | 3.0 | 2.0 | 4.0 | 3.0 | 4.0 | 3.0 | 4.0 | 4.0 | 4.0 | 4.0 |
| MD76 | 2.0 | 1.0 | 2.5 | 1.5 | 3.0 | 2.5 | 3.5 | 2.0 | 4.0 | 3.5 |

Table 4.--Breakdown of cellulose-azure^{1,2} by brown-rot fungi having different capacities to decay wood--con.

| Isolate | Cellulase activity | | | | | | | | | |
|----------------------------|--------------------|-----|-----|-----|-----|-----|-----|-----|-----|-----|
| | Time (days) | | | | | | | | | |
| | 7 | | 14 | | 21 | | 28 | | 42 | |
| | -C | +C | -C | +C | -C | +C | -C | +C | -C | +C |
| GLOEOPHYLLUM TRABEUM--con. | | | | | | | | | | |
| FP125076sp | 2.5 | 2.0 | 4.0 | 2.5 | 4.0 | 3.0 | 4.0 | 3.0 | 4.0 | 3.5 |
| MAD617 | 3.0 | 2.5 | 4.0 | 3.0 | 4.0 | 3.5 | 4.0 | 3.5 | 4.0 | 4.0 |
| ME76 | 2.5 | 3.0 | 3.0 | 3.0 | 3.0 | 3.0 | 2.5 | 3.0 | 3.0 | 2.5 |
| MD505 | 2.5 | 3.0 | 3.0 | 3.5 | 3.0 | 3.5 | 3.0 | 4.0 | 3.0 | 3.0 |
| 1320 | 1.0 | 2.0 | 1.0 | 2.0 | 1.0 | 2.0 | 1.0 | 1.5 | 1.0 | 1.0 |
| TA1A | 3.0 | 3.0 | 4.0 | 4.0 | 4.0 | 4.0 | 4.0 | 4.0 | 4.0 | 4.0 |
| MD256 | 3.0 | 3.5 | 3.5 | 4.0 | 3.5 | 4.0 | 3.5 | 4.0 | 4.0 | 3.5 |
| ME509 | 2.5 | 2.0 | 3.0 | 2.5 | 3.0 | 3.0 | 3.0 | 3.0 | 3.0 | 3.0 |
| OPSAL8601 | 2.0 | 2.0 | 2.5 | 3.5 | 3.0 | 4.0 | 3.0 | 4.0 | 3.0 | 4.0 |
| MAD5096-15 | 3.0 | 2.0 | 4.0 | 3.0 | 4.0 | 3.0 | 4.0 | 3.0 | 4.0 | 3.0 |
| MAD539s | 2.0 | 1.0 | 3.5 | 2.5 | 4.0 | 3.0 | 4.0 | 3.5 | 4.0 | 4.0 |
| TP356b | 2.0 | 1.0 | 3.5 | 2.0 | 4.0 | 3.0 | 4.0 | 3.5 | 4.0 | 4.0 |

¹0 = no dye released.

1 = very slight color visible

2 = slight color visible.

3 = moderate color visible.

4 = deep color visible.

²-C = no cellobiose in medium.

+C = 0.1 pct cellobiose in medium.

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A Consideration of Factors Affecting the
Development and Physiology of Tissue-
Cultured
Plants¹

Hazel Y. Wetzstein²

The applications of tissue culture are numerous and include rapid clonal propagation, the production of disease free plants, isolation of genetically unique lines, germplasm storage, chemical screening, and plant breeding applications. The number of *in vitro* culture protocols for tree species is increasing. Yet, protocols with efficiencies suitable for commercial production are much less frequent, and are commonly restricted to horticulturally oriented ornamental and fruit tree species. The advent of biotechnological procedures has the potential of accelerating tree improvement through methods such as genetic engineering, somatic hybridization and somaclonal screening. However, the future prospects for the clonal production of many hardwood species, except as a research tool are limited by economics (Sommer and Wetzstein 1984). Particularly for forest tree species, the current high costs associated with tissue culture production greatly limit its application for mass propagation.

Attempts at increasing the efficiency of tissue culture systems are most often approached through the optimization of media components. Protocol development is often centered around regeneration or multiplication rates, with little consideration given towards evaluating plantlet form and structure.

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Abstract.--In the development of tissue culture protocols, it is suggested that in addition to regeneration rates, consideration be given to plantlet structure and form. Tissue-cultured plants have been described to have an atypical anatomy and physiology. The modification of the culture environment (e.g., light, medium matrix, gas environment) may be a means of increasing the efficiency of culture systems and of producing more competent plants. Some results of studies using Liquidambar styraciflua are described.

Plants developed in culture often exhibit unusual anatomical and physiological features which may contribute to survival difficulty after transfer to greenhouse or field conditions (Wetzstein and Sommer 1982; 1983) and to early depressed field performance (Frampton and Isik 1986). These characteristics include altered leaf anatomy, poor vascular development, root system abnormalities and depressed photosynthesis.

Many of these tendencies are a result of the peculiar conditions associated with culture systems, some of which may potentially be modified to elicit more "normal" plant development. Developmental aspects should be an important consideration in tissue culture methods. For this reason, we have been studying environmental and media factors and their role on plantlet development at the University of Georgia. The rationale has been to understand how specific factors affect plantlet development, toward the modification of these factors to produce more competent plantlets with greater efficiency.

PLANTS REGENERATED IN CULTURE

Plantlets developed in culture have been described to have an atypical form. We have been interested in the tissue culture of sweetgum, Liquidambar styraciflua L., an important hardwood species in the Southeastern U.S. Initial evaluations of regenerated plantlets originated in an attempt to explain the stress and desiccation exhibited by cultured plants upon transfer to *ex vitro* conditions (Wetzstein and Sommer 1982; 1983). Stress and mortality of cultured plantlets appears to be due, in part, to water deficits as a result of reduced cuticle and wax development, increased stomatal densities, nonfunctional stomata, and extensive intercellular and substomatal

air spaces. Similar observations have been described in other plants regenerated in culture (e.g., Brainerd et al 1981; Donnelly and Vidaver 1984a; Grout and Aston 1978).

Environment has been shown to have a pronounced effect on plant morphology and physiology (Esau 1965; Fitter and Hay 1981). The evaluation and manipulation of conditions *in vitro* hold promise for improved developmental patterns.

FACTORS AFFECTING DEVELOPMENT

Environmental and substrate effects can influence growth and development of plants in culture. Some of these factors can potentially be manipulated. This paper will describe conditions which we have been evaluating using Liquidambar as a model. These include light effects, medium matrix, and gas environment factors.

Light Effects

Plants in culture are usually placed under low light conditions. A carbohydrate source is present in the medium of most culture systems, thus high light for extensive photosynthesis may not be necessary in a heterotrophic situation. However, the lack of a functional autotrophic system may be a major problem in transplant vulnerability when plantlets are taken from culture to field.

Low photosynthetic rates have been measured in some culture systems (e.g., Donnelly and Vidaver 1984b; Smith, Palta and McCown 1986). However, under our culture conditions for Liquidambar, lack of photosynthetic capacity is not a limiting characteristic in plantlet acclimatization and transplant growth (Lee, Wetzstein and Sommer 1985). Plantlets exhibited higher rates of photosynthesis compared to noncultured plants grown under similar light conditions (Table 1).

Table 1.--Net photosynthesis of sweetgum seedlings and plantlets at light intensities of 315 (high), 155 (medium) and 50 (low) $\mu\text{Es}^{-1}\text{m}^{-2}$.

| Light Intensity | Photosynthesis ($\text{mgCO}_2\text{dm}^{-2}\text{h}^{-1}$) | |
|-----------------|---|-----------|
| | Seedlings | Plantlets |
| High | 6.4 | 12.1 |
| Medium | 4.7 | 13.6 |
| Low | 2.7 | 11.4 |

As in manipulations for the production of autotrophic suspension cultures, it appears that plants in culture can be conditioned to undergo active photosynthesis. The development of full photosynthetic capacity should be a consideration.

The effect of light on development is also an important factor. Light intensity effects on leaf anatomy were evaluated in sweetgum in an effort to induce a more normal leaf morphology. A comparison was made of cultured and noncultured plants at different light levels. Leaves developed under higher light levels were thicker, had a more differentiated palisade, fewer intercellular spaces, and greater cuticle development compared to low light leaves. However, when *in vitro* and *ex vitro* leaves developed under similar light levels were compared, cultured leaves were generally smaller, thinner and had more extensive intercellular spaces.

Stomatal morphology was less affected by light levels, but varied greatly between cultured versus noncultured plants. All leaves *in vitro* had large, open and raised stomata (Figure 1). Leaves developed *ex vitro* had small, sunken stomata with ellipsoid guard cells (Figure 2).

Some of the divergent leaf characteristics commonly described in tissue culture systems can be diminished by the use of higher light intensities. Thicker, more differentiated leaves with more developed cuticles form under higher light. However, factors other than low light are responsible for other characteristics such as raised, nonfunctional stomata with higher densities.

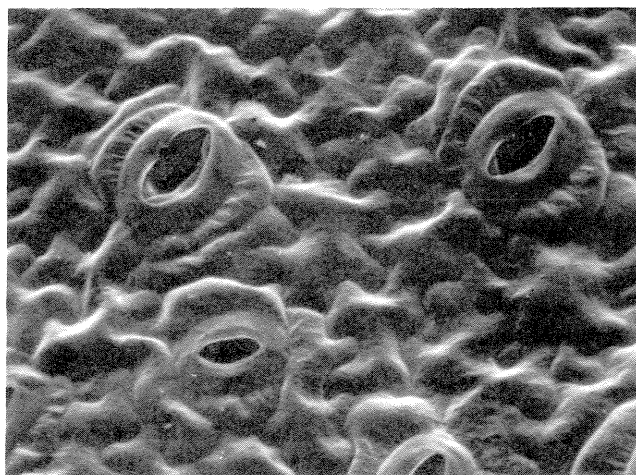


Figure 1.--Surface of leaf developed in culture. Note raised, open stomata. X 750.

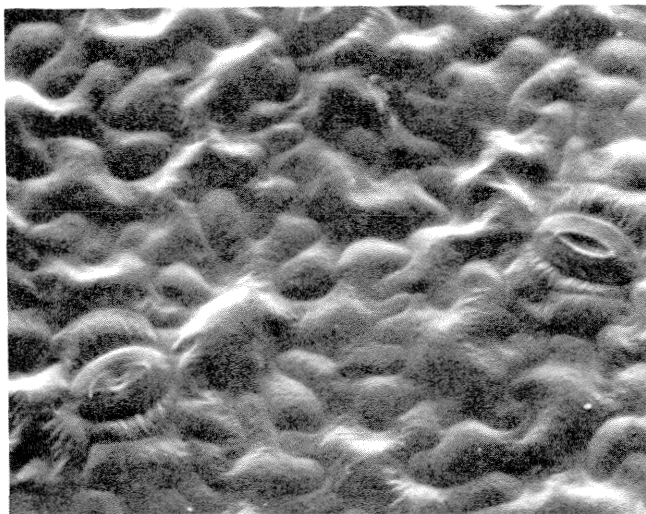


Figure 2.--Surface of noncultured leaf grown under the same light conditions as Figure 1. X 750.

Medium Matrix

Culture growth and development can be influenced by the physical nature of the medium. A solidified medium is frequently used as a support and to obtain orderly, oriented growth. In contrast, faster growth rates have been reported in liquid or low-agar medium, but with vitrescence symptoms occurring in some species.

In a study comparing medium matrix and culture growth, we found greater shoot growth, root growth, and rooting percentages in liquid versus agar (0.8% Phytager) cultures of Liquidambar (Lee, Wetzstein and Sommer 1986). Shoot-root ratios were greater for liquid than agar-grown plantlets (0.75 versus 0.18, respectively). Further studies are underway to evaluate osmotic and matrix potential effects, availability and diffusion of nutrients, and cell differentiation differences as a result of medium matrix changes.

In studies with sweetgum, trends of less negative leaf water potential and more negative leaf osmotic potential are observed in liquid versus agar medium cultures over time. Turgor pressure is greater in liquid versus agar leaves. The processes of cell growth and enlargement are extremely sensitive to water deficit conditions. Water potential and specifically turgor pressure may be directly affecting cellular expansion and division. Differences in the degree of

cortical and vascular tissue development of sweetgum shoots are also observed in liquid versus agar cultures. More extensive cell division is exhibited in liquid versus agar cultures.

Plantlet nutrient uptake appears to be facilitated in liquid versus agar culture medium in our sweetgum system. Significantly higher levels of some nutrients on a per plantlet basis were observed in plants on liquid medium. Agar has been shown to have a restrictive effect on the diffusion of some molecules (Patil, Adhyapak and Joshi 1985). Uptake differences may also be a reflection of root developmental differences. Roots initiated on liquid medium were more numerous, of larger diameter and with more lateral branching and root hair development compared to agar medium cultures.

Gas Environment

The gas environment within the culture vessel can affect plant development *in vitro*, yet is given relatively little consideration in culture protocol development. A variety of vessels and enclosure types is available with varying permeability values to water vapor and other gases.

A lack of adequate gas exchange could lead to variations in CO₂, O₂, ethylene, acetaldehyde and other compounds at accumulation or deficit levels. For example, ethylene has been shown to accumulate in culture systems (e.g. Garinlertvatana et al. 1982; LaRue and Gamborg 1971). Also of question, is if CO₂ levels in culture are adequate for photosynthesis. Container size has been shown to influence growth and morphogenesis in culture. This effect may, in fact, be due to gaseous environment modification.

We found that Liquidambar cultures are capable of high rates of photosynthesis (Lee, Wetzstein and Sommer 1985). Yet in culture, plantlets displayed comparably lower growth vigor than noncultured plants. It is possible that restricted gas exchange (i.e., ethylene accumulation or limiting CO₂) may be a factor. An area of current study is the evaluation of different film enclosures on gas permeability, and plant growth and morphogenesis. Information such as this may contribute to the attainment of full photosynthetic potential and more rapid, efficient growth in culture.

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An Exceptional Case of Natural Regeneration
of White Spruce in Interior Alaska¹

Tricia L. Wurtz and John C. Zasada²

The distribution of the boreal forest is circumpolar, ranging between the latitudes of 50 and 68 degrees north. In North America, the most economically important boreal species is white spruce (*Picea glauca* Moench Voss); it is the cornerstone of the forest products industry in western Canada. In Alaska, it is estimated that there are 12.8 million acres (4.8 million ha) of commercial white spruce forest land (Hutchison 1968). The most significant exploitation of Alaska's forests occurred during the gold rush period at the turn of the century, when large quantities of white spruce were used for a variety of purposes. Since then, white spruce has been harvested in interior Alaska mostly for local use, with small quantities exported to Pacific Rim countries.

Based on research and operational experience in Canada, white spruce is a difficult species to regenerate (see Zasada and Gregory 1969, and Dobbs 1972 for reviews). Attempts at natural regeneration have often been particularly unsuccessful, in part because good seed crops are sporadic and as yet, unpredictable. The vast majority of Canadian studies have found that a mineral soil seedbed provides the best conditions for seed germination and early seedling development. Such a seedbed is usually provided by removing the surface organic layer by mechanical means, fire, or a combination of the two.

While a mineral soil seedbed is ideal for the establishment of white spruce, it is also well suited to the regeneration by seed of spruce's woody competitors (mainly *Betula papyrifera* Marsh and *Alnus* spp. in Alaska). Moreover, these hardwood species exhibit a period of rapid juvenile growth, which allows them a head start over the slow-growing spruce.

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Abstract.--Traditionally, successful natural regeneration of white spruce (*Picea glauca* Moench Voss) requires a mineral soil seedbed for germination and establishment. Such a seedbed is usually provided in managed systems by scarification. This study suggests that if a large seed crop is imminent, and if the dimensions of the harvested area are small, scarification may not be necessary for sufficient stocking. In such a case, scarification may result in such dense stands that it is detrimental to seedling growth.

METHODS

This study was begun in 1971, and was conducted at Bonanza Creek Experimental Forest, about 25 km southwest of Fairbanks, AK (65°N, 148°W). In the Fairbanks area, in 1985, there were 107 frost-free days (May 21 - September 5). The mean annual temperature was 28°F (-2.2°C), and the total annual precipitation was 12.9 inches (33 cm) (NOAA 1985). The site was a 160 to 180 year-old white spruce stand on a gentle southwest-facing slope. The experiment consisted of three clear-cut units of 2.5 - 3.8 acres (1.0 - 1.5 ha) each, and three shelterwood units of 5.7 acres (2.3 ha) each, each with a residual stand of about 33 trees per acre (80 trees/ha). The residual stand accounted for 35 - 45 square feet of basal area per acre, out of the 80 - 120 square feet per acre of the original stand. The units were roughly square in shape. The harvesting was done in August and September of 1972. Eleven thousand board feet per acre was removed from the shelterwoods, and 17,000 board feet per acre was removed from the clearcuts.

The site was scarified immediately following logging using a tractor and standard straight-edged blade. Scarification was done in 6 foot (1.8 m) wide strips, paralleling the contour of the hillside. Within the strips, 6- to 10-foot-long (1.8- to 3-meter-long) scarified patches alternated with unscarified patches. During the month that scarification was completed and in the following months, a large seed crop fell, measured in an undisturbed stand nearby at 500 filled seeds per square meter.

The next spring, forty square-meter plots were established in each of the six units, twenty on scarified surfaces and twenty on unscarified surfaces. These plots were surveyed after the first five growing seasons, and again after the thirteenth growing season, in 1985. In spring, 1986, fifteen 1 milacre (4 square-meter) plots were established in the dense stands that now occupy surfaces that were scarified in 1972. Ten dominant spruce seedlings were selected in each plot, and all other woody vegetation was cut at the ground and removed. The basal diameters of the seedlings in the cleaned and thinned plots were measured at the beginning and the end of the 1986 growing season. Seedlings growing in fifteen unthinned control plots were also measured.

A two-way analysis of variance was done on the seedling density data, while the first season thinning study results were subjected to a one-way anova (Sokal and Rohlf 1981).

RESULTS

Based on the survey conducted in 1985, thirteen years after harvesting, no difference was found between clearcut and shelterwood silvicultural systems in the density of spruce stems per square meter. However, there was a highly significant difference ($p < 0.001$) between scarified and unscarified surfaces. No interaction between silvicultural treatment and scarification treatment was observed. These results were not only true for spruce densities, but also for birch and alder densities (Table 1).

Table 1.--Number of seedlings per square meter by treatment type, 1985 survey (Mean \pm 1 SE, $n = 60$)

| Treatment | Spruce | Birch | Alder |
|--------------------|-------------|-------------|------------|
| <u>Scarified</u> | | | |
| Clearcut | 35.2 (2.15) | 28.1 (2.29) | 2.5 (0.72) |
| Shelterwood | 35.8 (2.03) | 29.9 (2.09) | 3.6 (0.53) |
| <u>Unscarified</u> | | | |
| Clearcut | 2.9 (0.60) | 1.3 (0.49) | 0.4 (0.33) |
| Shelterwood | 2.9 (0.60) | 0.7 (0.25) | 0.0 (0.02) |

Spruce, birch and alder frequencies are shown in table 2. Frequency is defined as the percent of square-meter plots with at least one seedling of a given species.

Table 2.--Percent frequency of seedlings in square-meter plots ($n = 60$ per treatment)

| Treatment | Spruce | Birch | Alder |
|--------------------|--------|-------|-------|
| <u>Scarified</u> | | | |
| Clearcut | 100 | 100 | 46 |
| Shelterwood | 98 | 98 | 78 |
| <u>Unscarified</u> | | | |
| Clearcut | 68 | 32 | 5 |
| Shelterwood | 63 | 19 | 3 |

The spruce seedlings ranged in height in 1985 from 11 to 64 inches (0.3 - 1.6 m) on scarified surfaces, and from 5 to 72 inches (0.13 - 1.8 m) on unscarified surfaces.

The seedlings that were released in the spring of 1986 showed significantly more diameter growth ($p < 0.001$) in a single growing season than

seedlings growing in unthinned control areas:

| | <u>control</u> | <u>thinned</u> |
|--------------------------|----------------|----------------|
| Diameter growth (mm) | | |
| in 3 units (Mean \pm) | 0.90 (0.10) | 1.89 (0.12) |
| 1 SE, $n = 50$ for | 0.72 (0.06) | 1.41 (0.12) |
| each value) | 0.67 (0.08) | 1.00 (0.09) |

DISCUSSION

Scarification significantly increased white spruce seedling density and frequency in this study. An unexpected result was that spruce establishment was good even on unscarified surfaces. If 60 percent milacre stocking is the criterion for acceptable stocking, stands on both scarified and unscarified surfaces were more than sufficiently stocked. This is most likely due to the combination of two factors: the small dimensions of the harvested units, and the large seedcrop that fell in the months after scarification was complete. One way to look at the importance of small harvesting unit dimensions is to consider the number of seeds required by each seedbed type to produce one established seedling. A mineral soil seedbed may need only 5 or 10 seeds per established seedling, while a seedbed on unscarified forest floor may require 100 or even 1000 seeds to produce a single established seedling. To maximize the chance that unscarified surfaces throughout the entire cutting unit receive enough seed, units should be laid out so that no point is more than 200 to 300 feet (60 - 90 m) from a seed source. It has been recommended that clearcuts be no more than 400 feet (120 m) wide if natural regeneration is to be relied upon (Zasada 1972).

Seed regeneration of the competing species, birch and alder, is also favored by the same cultural practices associated with the successful regeneration of white spruce. In this case, scarification improved conditions for birch establishment even more than it did for spruce. Scarification increased spruce frequency by 50 percent, while it led birch frequency to increase by 300 percent in clearcuts and by 500 percent in shelterwoods. Other scarification methods, such as removing only part of the organic layer, or tilling the substrate to make a seedbed of mixed organic and mineral soil, may provide conditions that give spruce seedlings the advantage over birch. Various new scarification systems are being tested now in Alaska with just that goal in mind. Alternately, one can attempt to control the competing species' seed source. As yet, this technique has not been tried in Alaska.

This study produced excellent spruce regeneration on both scarified and unscarified surfaces. The scarified areas, though, are severely crowded with a combined spruce and birch density of 60 seedlings per square meter. A low-level management plan would allow the crowded seedlings to self-thin, with the dominant seedlings gradually establishing themselves as the dominant trees. A more intensive management plan would seek to

ensure that each dominant spruce seedling was free to grow. Such a plan might call for cleaning out the competing vegetation and thinning the spruce seedlings. The results from the first season cleaning and thinning study demonstrate that overcrowded spruce seedlings respond rapidly to being released. The utilization of interior Alaska's forests is not yet intensive enough, however, to warrant such intermediate treatments on a large scale.

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A System Approach to Structural Design of Roof Assemblies¹

Monica McCarthy and Ronald Wolfe²

Abstract.--Current design procedures for light-frame residential roof assemblies do not encourage the most efficient or innovative use of material. These procedures are based on properties of each individual member without concern for interactions between members. At the Forest Products Laboratory we are developing analytical structural models that will eventually lead to system oriented design. We tested four full-scale roof assemblies to failure to verify these roof assembly models.

These structural models will be useful to those involved in developing design recommendations. The models will help evaluate the effects of factors such as lumber strength and stiffness, roof pitch, truss configuration, span, sheathing properties, and connector properties on roof assembly performance. Significant improvements in material utilization could result from design changes based on this sensitivity analysis.

Keywords: Structural methods, wood, roof assemblies.

Communication between forest researchers and wood products researchers is extremely important. There are many areas where wood products research overlaps forestry research. Conservation of resources can be enhanced by more efficient design and use of material. The development of reconstituted wood products (small pieces of wood held together by adhesives) allows for use of timber previously considered waste, and permits use of smaller diameter trees. Use of hardwoods is another area of interest to both foresters and forest products researchers. There is a great deal of potential for exciting and creative research developments, especially when communication across disciplines is encouraged. At the Forest Products Laboratory, in the structural research area, we are investigating ways to use wood more efficiently and innovatively for structural purposes.

There have been many barriers to using wood in highly engineered structures. The main barriers have been concern about decay, insect damage, and fire resistance. Other barriers include its variability and size limitations. The size of a piece of lumber has traditionally been limited by the height and width of the tree from which it is cut. Knots and other irregularities (grain orientation, varying growth rates) make the performance of an individual piece of lumber variable, which necessitates conservative approaches in design.

There are also factors which speak in favor of wood. It is by its nature a structural material, because it must support itself as it grows vertically. It has a high strength to weight ratio relative to other materials such as steel. It is very easy to work with, and in many cases large wood timbers are actually more fire resistant than steel. The development of preservative and fire resistant treatments for wood has reduced difficulties with decay, insect damage, and fire resistance.

The development of plywood, glulam beams, and other wood products which combine several pieces of lumber with the use of adhesives has revolutionized the wood products industry and opened the door to seemingly unlimited potential for engineered use of timber. Not only are the size limitations overcome, but with the dispersion of characteristics such as knots, the variability problem can be greatly reduced. There are areas now in the commercial market where engineered wood products are or could be competitive with steel and concrete.

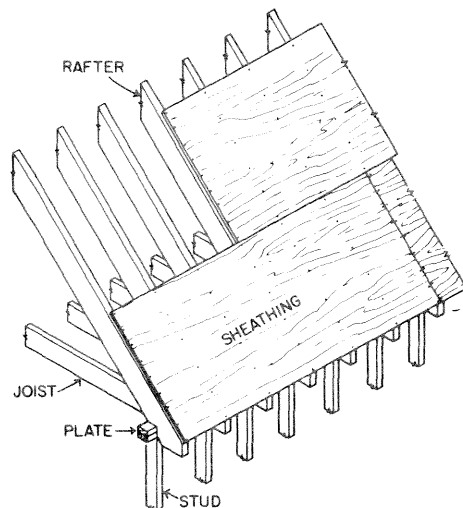
Even with the performance of single members more reliable and predictable, understanding and predicting the performance of full structures is another step. As a start in that area, we are looking into the performance of light-frame residential structures. We, in cooperation with others, are developing structural models for light-frame residential floors, walls, and roofs. The purpose of these models is to improve our understanding of the performance of these systems which will eventually lead to more efficient structural design, as well as innovations in designs and types of materials used.

Because wood has been seen as having limited potential for sophisticated engineering design, much of present residential wood design is based

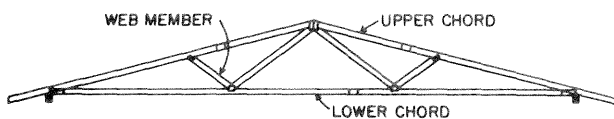
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on tradition. The evolution of wood structures over the past 200 years has been guided by those innovations which reduce construction labor costs rather than those which improve structural efficiency. Roughly 150 years ago, the introduction of mass produced steel nails led to the shift from heavy timber, post, and beam construction to light-frame platform construction. This was a major change to construction methods, but not necessarily an improvement to structural performance. The popular residential building form used today remains the same as it was in the early 1800's. More recently, the replacement of board sheathing with wood-based panels, and the use of light-frame trusses to replace solid-sawn lumber rafters and joists (fig. 1) were also changes adopted primarily for labor saving purposes. Because there has been a plentiful supply of timber at a relatively low cost, by comparison to other materials, there has been little need to improve the material efficiency of wood structures.



(a) RAFTER ROOF ASSEMBLY



(b) PREFABRICATED TRUSS WITH METAL PLATES

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Figure 1.--Typical roof configurations. (a) Rafter roof assembly; (b) prefabricated truss with metal plates.

CURRENT DESIGN PROCEDURES

Current design procedures consider each element of a structural assembly to be acting independently. For example, each rafter of a roof assembly is expected to support an equal share of a uniformly distributed load. Little recognition is given to the possibility that loads may be distributed away from a weak member within

the assembly. In addition, when one considers an entire structural system, assembly interactions (floor, wall, roof) may also affect load distribution. For example, a limber wall may create roof problems if the roof is allowed to spread apart too easily at the ends.

Because of its high degree of variability, and the assumption that members act independently, current design methods assume that each member has a near minimum strength for its grade. This is an example of the built-in conservatism in current design, which also allows for a comfortable margin of error.

Currently accepted design methods discourage the development of innovative systems. If someone wants to design an innovative system that relies on assembly interactions to provide the safety margins required by current design codes, they have the option of building and testing the system to demonstrate its load capacity. Such tests are prohibitively expensive and rarely used for large systems.

ROOF ASSEMBLY TESTS

In order to learn more about system performance and to provide a data base for validation of computer models, we built and tested two rafter roof assemblies and two trussed roof assemblies (fig. 1). Rafter assemblies are an older form of roof construction where ceiling joists (the bottom horizontal pieces) are nailed to rafters (the top pieces to which plywood roof sheathing is attached) at the construction site. Trussed roof assemblies are made from prefabricated trusses held together with metal truss plates. In this report we will discuss the test results of the trussed roof assemblies.

The two trussed roof assemblies were similar except for their pitch--one had a 3/12 pitch (3 in. of rise for every 12 in. horizontally) and the other had a 6/12 pitch. Each roof assembly was built with nine trusses (fig. 2). Trusses were fabricated so that some were intentionally made from low stiffness material, some

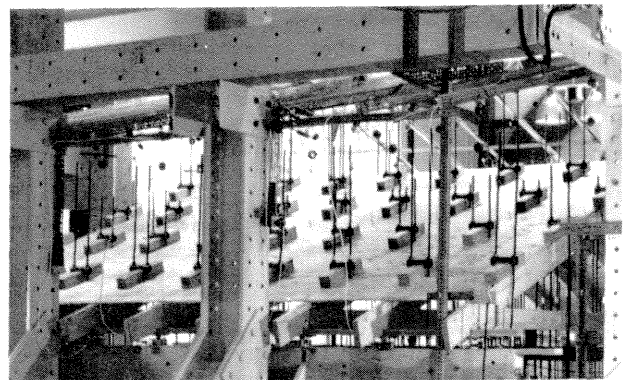


Figure 2.--Test setup for roof assembly tests.

from medium stiffness material, and some from high stiffness material. The purpose of this was to exaggerate stiffness variability to evaluate its effect on assembly performance.

We measured loads, deflections, and sheathing nail slips, a total of 96 data values for each load increment, as we loaded the trusses to their design load. Before assembling the roof, each truss was loaded individually outside the assembly. This simulates the performance that is assumed in current design procedures. Once the roof was constructed, trusses were loaded individually in the assembly. This type of load would occur in real life when, for example, bundles of shingles are piled on the roof or a person is walking on the roof. Finally, we loaded all the trusses in the assembly simultaneously. This simulates a snow load on the roof.

Figure 3 shows how the trusses deflected at design load for the three types of loadings. Trusses appeared stiffer when loaded individually in the assembly than when they were loaded individually outside the assembly. This was due to the stiffening effect of the plywood and load distribution. Each truss loaded individually in the assembly actually carried only 40 to 60 percent of the applied load. The end trusses

deflected more because load could only be distributed in one direction (toward the inner trusses), and so they carried a higher proportion of the applied load. When the full assembly was loaded, trusses deflected more than they did when loaded individually in the assembly, because all trusses were loaded and less load could be distributed to adjacent trusses. In both loadings within the assembly, the variability in deflections among trusses decreased. This means that the more limber trusses carried less load than the stiffer trusses. Thus, provided that stiffer trusses are also stronger, roof assemblies have some built-in safety valves.

We also learned that the end wall stiffness is very important. This is an indication of interaction between subsystems (how wall performance affects roof performance).

MODEL DEVELOPMENT

These tests provided useful and interesting information, but they were very specific to the particular roof assembly design and loading conditions used. In cooperation with the Forintek Corp. of Canada we are developing computer models that will simulate roof assembly performance. Once these models are validated with experimental tests they can be used to model many different roof assemblies, and to evaluate effects of factors such as lumber strength and stiffness, roof pitch, truss configuration, span (length), sheathing properties (e.g. plywood thickness), and connector properties (e.g. nail diameter, truss plate area).

As new materials and designs are developed, an initial determination of their viability can be made with a computer model rather than an expensive structural test. For example, structural models may facilitate the development of reconstituted structural wood products made from hardwoods.

SUMMARY

In wood roof systems, interactions exist which are not accounted for in current design methods. Development of structural models will enable us to quantify and learn more about these interactions, thus promoting more knowledgeable and efficient design of wood structures as well as providing potential for innovative design.

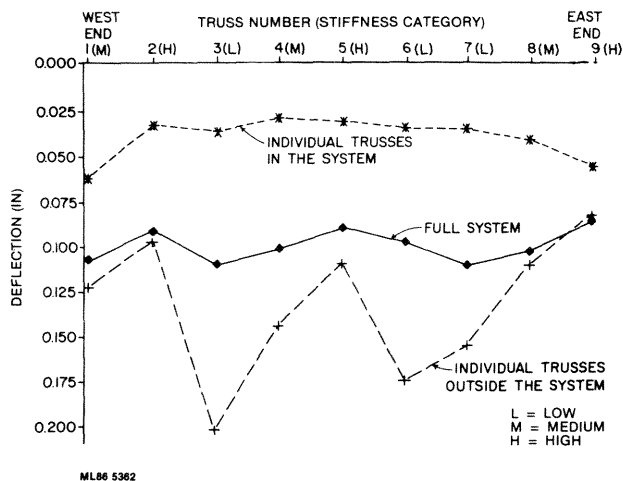


Figure 3.--Deflections for the 6/12 roof system at 33 pounds per square foot design load.

Strength of Mechanically Fastened

Wood Connections¹

Marcia Patton-Mallory²

Abstract.--Some of the most highly stressed areas of a wood structure are in the vicinity of mechanical fasteners. Consequently, the majority of structural failures initiate at the fastener or in the connection areas. The focus of the ongoing, and most recently completed, research at the USDA Forest Products Laboratory in the Engineering Design Criteria Research Work Unit is to understand the strength of mechanically fastened wood connections. The analysis methods used included a European based "Yield Theory" which describes mechanisms of failure for bolts, nails, and lag screws considering fastener yield strength, wood crushing strength, and connection geometry. Additionally, fracture mechanics analyses are being used to predict connection failures where crack propagation is the primary mode of failure. This analysis is used where fastener end-distances and spacing control connection strength. The results of this research are used as a basis for wood connection design criteria, published by the National Forest Products Association, which are subsequently incorporated in the Uniform Building Code and local building codes.

Keywords: Wood connection, mechanical fastener, nail, bolt, design criteria, wood joint, timber construction.

Mechanical fasteners used in wood construction are familiar to any person who has ever driven a nail to connect two pieces of wood, used screws or bolts, or seen the toothed steel plates commonly used to connect members of wood trusses. Because of our familiarity with these fasteners we often take their behavior for granted.

What is the significance of mechanical fasteners, and why do scientists study their behavior? The history of mechanical fasteners use in connecting wooden members dates back to ancient Egypt and Rome where wood building connectors were iron, copper, or bronze nails. Viking ships were built using copper nails. Fastening of wood has been indispensable since the earliest times of civilization. Even today our industrial progress depends upon our ability to fasten things together. Like the principle of a chain being no stronger than its weakest link, an item made of wood is no stronger than the connections holding it together. In fact, it is my intention to help you realize that connections in wood structures many times do, in fact, limit the strength of the structure.

The concept of fastening wood using mechanical fasteners is a simple one, however, the behavior

of the fastener in a wood connection is extremely complex. Despite this complex behavior, simplified design guidelines exist for designing wood connections utilizing mechanical fasteners. The current design information is based on laboratory tests of ideal connections. For the most part, wood connection performance has been satisfactory. However, according to forensic engineers who investigate failure of wood buildings, over 90 percent of failures occur in the vicinity of the connections.

WHY DO WOOD CONNECTIONS FAIL?

There are many reasons why the connection has a higher failure rate. First, the connection is an area of high stresses. When most mechanical fasteners are installed, part of the wood member is removed and the metal fastener transmits load by interacting with only a small area of the wood cross section. Fasteners which are installed by driving, such as nails and truss plates, initiate small splits in the wood which also create areas of stress concentration.

Second, tensile strength of wood in the direction perpendicular to the grain severely limit the strength of many connections. The detailing of connections during design and installation can have significant strength-reducing implications.

Finally, but not least important, is the lack of basic understanding of how the large number of in-service factors interact to increase the nominal connection stresses. For example, shrinkage perpendicular to the grain in multiple fastener connections can cause shrinkage stresses

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which result in connection failure at loads well below the design load. Slight eccentricities in a group of fasteners can cause the connection to perform as a semi-rigid connection (a connection that transmits moment) which can cause stresses perpendicular to the grain to exceed perpendicular-to-grain strength, failing the connection. Connection spacing and end distance requirements assume that sound wood exists near the end of the member. However, in-service drying can cause significant end splits to develop. Also, wood contains numerous knots and other naturally occurring defects which are also areas of high stress. The probability of these factors occurring simultaneously, and their synergistic effects are important real life design concerns.

WHAT IS THE FOCUS OF FPL RESEARCH ON CONNECTING WOOD?

Research relating to connecting wood is primarily spread among three research work units (RWU's). These are (1) Engineering Design Criteria, (2) Engineered Wood Products and Structures, and (3) Improved Adhesive Systems. The majority of the mechanical fastener research in the Engineering Design Criteria RWU is on the common fasteners: bolts, nails, and lag screws. The Engineered Wood Products and Structures RWU conducts a limited amount of research on behavior of truss plated connections. Their research on truss plated connections is usually limited to the necessary testing of specific connections for input into floor and roof analysis computer programs. Truss plates are proprietary products, therefore, their design information is supplied by the plate manufacturers.

Timber connectors such as split rings and shear plates are used in some timber structures. However, there has been less demand for information on these types of wood connectors compared to information on design criteria for the common fasteners.

Wood joinery was used commonly in early wood construction, but is seen most commonly now in furniture. These connections include the mortise and tenon, dove-tail, and finger joint. Only the finger joint has been studied as an engineered wood connection during recent times at FPL.

The Improved Adhesives Systems RWU conducts research on performance of adhesive connections, and with the Engineering Design Criteria RWU, has conducted isolated studies combining adhesives with mechanical fasteners.

WHAT INFORMATION IS NECESSARY TO DESIGN A WOOD CONNECTION?

There are three levels of complexity in designing an adequate wood connection. The three research work units at FPL which are involved in Wood Engineering Research have vital and distinct roles in understanding connection performance.

On the most basic level are the material properties which ultimately limit the connection capacity. Basic material properties and factors which affect these properties are primarily the responsibility of the Engineered Properties of Wood RWU. As mentioned earlier, low tension perpendicular-to-the-grain strength is a major material property limiting connection performance. Wood compression strength parallel and perpendicular to the grain significantly affect connection strength and stiffness behavior.

A second level of complexity exists by considering the way the fastener transfers loads between members of the connection. Geometric variables include spacing, end distance, bolt bearing area, size and alignment of bolt holes, and the relationship between loading stresses and grain orientation. Engineering Design Criteria RWU considers these variables by considering the connection as a single entity. How does a bolt fail? How do the stresses in the vicinity of the fastener hole combine to cause failure? What kinds of deformations can be expected from a typical connection type in different species of wood? How much do connections creep under load, and is the "load duration" effect the same for connections as is used for solid wood members? When small flaws exist in the vicinity of a mechanical fastener, at what stress does the flaw grow to a significant crack causing fracture of the wood and failure of the connection? These are the questions we seek to answer.

There is a third level of complexity which considers the connection as one type of member in a structure made of many types of members. Research in the Engineered Wood Products and Structures RWU evaluates the performance of wood structures using information about the way each part of the structure interacts and performs. For the adequate design of a wood structure, the connection must transfer loads between members and eventually to the foundation. This research combines beam, column, sheathing, and connection performance to model complete roof, floor, and wall systems.

For example, strength and stiffness of the fasteners between sheathing and the wood frame of a shear wall are critical to wall performance. The consequences of inadequate shear walls are critical considerations during earthquakes and high winds. As part of my graduate research I tested shear wall panels to evaluate shear stiffness and shear strength of the wall as a function of sheathing and fastener type. (Patton-Mallory and others 1984 and 1985). Subsequently, we verified a shear wall stiffness model using the same wall test data (Patton-Mallory and McCutcheon 1986). The stiffness model can evaluate shear wall performance for walls with two different sheathing types, e.g. plywood on the exterior and gypsum on the interior surface. The results of the shear wall research can be used by building code officials and others to evaluate sheathing required to achieve acceptable shear performance in the walls of a structure.

THE EUROPEAN "YIELD THEORY" RESEARCH EFFORT

The bulk of our current fastening research in the Engineering Design Criteria RWU is to develop adequate computer models to predict how connections deform and fail when loaded. Eventually, we will be able to conduct the majority of connection tests using the computer, saving laboratory testing for model development and verification.

One research effort is to put all dowel-type fasteners on a common analytical basis. The European community has been using a "Yield Theory" to describe the performance of dowel-type connections. In the term dowel-type connection they include nails, bolts and lag screws. Briefly, the Yield Theory evaluates fastener yield using the yield strength of the metal fastener and the bearing strength of the wood. Yield strength is the load beyond the linear elastic connection performance, and can be considered maximum fastener load for most practical purposes. A visiting scientist from Norway, Professor Petter Aune, studied the applicability of the Yield Theory to typical connections in U.S. construction (Aune and Patton-Mallory 1986a,b).

The Yield Theory explains some of the empirical adjustment factors that we currently use for connection design. For example, when designing a bolted joint with steel side plates, the deformation in the connection occurs primarily in the wood main member, and is significantly less than the deformation seen in a bolted joint made entirely of wood. The Yield Theory predicts a 25 percent increase in yield load when wood bearing is the primary mode of failure. When bolt bending is the primary failure mode, a much smaller increase is justifiable (Soltis and Wilkinson 1986). By using analytical models rather than relying on experimental data, we can better understand which factors influence connection performance, and properly account for these factors in our design criteria. The most significant impact from adopting the Yield Theory is to bring all similar type fasteners together with a common analytical basis. This should result in more uniform reliability of connection design criteria.

A second research effort involves using fracture mechanics to predict connection failure due to propagating cracks. In this research I evaluate critical end distances and spacing of bolted connections. The model is being developed cooperatively with Professors Steve Cramer and Bob Rowlands at the University of Wisconsin. Fracture mechanics is an area of engineering analysis that evaluates how small flaws grow to critical cracks, and lead to eventual structural failure. Applications of fracture mechanics to the performance of wood products have existed in the literature for many years (Patton-Mallory

and Cramer 1986), but have not had significant effect on how we design wood structures. The intent of our cooperative effort is to use fracture mechanics principles and wood material properties to better understand stress concentrations and failure process in the vicinity of mechanical fasteners.

Complimentary to the spacing and end distance research is the need to predict load distribution among fasteners in a multiple fastener connection. This research also involves developing a computer model to describe the distribution of load among fasteners in a multiple fastener connection as a function of material properties and connection geometry. Historically, the majority of research has been conducted on single fasteners. The single fastener data are used to design connections containing multiple fasteners. Simply derived modification factors account for multiple fastener connection strength being less than the sum of individual fastener strengths. However, significant fabrication effects exist in multiple fastener connections. Most bolt holes are oversized to allow easy installation of bolts, and to account for small misalignments. When the connection is loaded, the oversized holes cause fasteners to come into bearing at different loads, resulting in one or two bolts carrying the load in a connection designed for 4 bolts. This causes the loaded bolts to exceed their design load. This phenomenon is thought to be the cause of recent building failures which involved large wood beams with multiple bolt connections. Our future research will investigate ways to minimize this problem.

FROM RESEARCH TO DESIGN CRITERIA

How does the research we conduct on mechanical fasteners find its way into the handbooks and building codes which are used by building designers? The building designer relies primarily on a local building code. Local codes rely on wood design information from the "National Design Specification for Wood Construction" published by the National Forest Products Association (NFPA). NFPA uses results from research conducted at the Forest Products Laboratory, as well as research from universities and other sources, to specify design criteria for wood connections.

To summarize, the research on mechanical fasteners at the Forest Products Laboratory involves the expertise of many people. My contributions are primarily in the area of spacing and end distance effects, including applications of fracture mechanics to predict failure, load distribution and strength of multiple fastener connections, and applications of the European Yield Theory as a common method to predict yield loads of all dowel-type fasteners.

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Modeling the Effect of Moisture Content
on the Flexural Properties of
Dimension Lumber¹

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Abstract.--Moisture content of a piece of lumber affects its flexural properties. Until recently, the only procedures available to adjust flexural property values of dimension lumber to some common moisture content were based on data from small, clear pieces of wood or mean values of small lumber samples. Currently, these procedures adjust property values by a fixed percentage regardless of the piece's quality. Given actual data from dimension lumber, this paper discusses the modeling of the effect of moisture content on flexural properties of southern pine and how one might judge the adequacy of a model. Traditional models were inappropriate for strength properties.

Keywords: Analytical models, bending, mechanical properties, moisture content, lumber.

This paper reports on the process of modeling flexural properties of dimension lumber as a function of moisture content. The modeling was done with published data on southern pine (McLain and others 1984) and resulted in recommendation of models for use in various situations (Green and others 1986). A similar study was done on Douglas Fir (Aplin and others 1986), resulting in recommendation of models for use with that species.³ The recommended models are being combined to produce a procedure which is species independent.⁴ These moisture content studies were initiated for two reasons:

--Concern about procedures currently used to adjust flexural properties for moisture content. The current procedure (ASTM D 245, 1986) is based on mean properties of small samples of lumber (Green 1980) and is independent of lumber quality. A procedure accurate over the entire distribution and based on larger samples would be preferable. In addition, some studies (Gerhards 1968, 1970; Hoffmeyer 1978; Madsen 1975, 1980) have indicated that an adjustment factor should be dependent upon lumber quality--as was, in fact, the case from 1930 to 1964 under the so-called "25 percent rule."

--The need of a reliable adjustment procedure for data from the In-Grade program. The In-Grade program is a large-scale lumber-testing program being carried out in the United States and Canada.

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Because of the scope of the In-Grade program, some of the testing is carried out in the field, on lumber which vary in moisture content from one piece to another. These data will not be useful without a procedure to adjust the flexural property values to a common moisture content.

The procedures described in this report were developed for four properties, using three sizes of southern pine lumber in three grades at four target moisture contents:

| <u>Grades</u> | <u>Sizes</u> |
|-------------------|--------------|
| Select Structural | 2 by 4 |
| No. 2 | 2 by 6 |
| No. 3 | 2 by 8 |

| <u>Moisture contents</u> | <u>Properties</u> |
|--------------------------|-----------------------|
| Green | Modulus of rupture |
| 20 percent | Modulus of elasticity |
| 15 percent | Flexural stiffness |
| 10 percent | Moment capacity |

Coefficients for adjustment procedures for all properties, sizes, and grades are given in Green and others (1986). Further details of the procedures used in gathering and drying the lumber are given in McLain and others (1984). This paper is designed to cover the modeling process used in developing the procedures. For simplicity, the discussion in this paper deals only with one property (modulus of rupture (MOR)), one grade (Select Structural), and one size (2 by 4). In the overall study described in Green and others (1986) for all flexural properties, models were first derived from data for each of the nine grade/size combinations. Then models were derived from all the data sets simultaneously.

The final section of this paper shows how to assess the accuracy of these models.

THE MODELS

Several analytical models were tested for their ability to predict the effect of moisture content on flexural properties:

- (1) A zero adjustment model.
- (2) Constant percentage models.
- (3) Strength ratio models.
- (4) Weibull models.
- (5) Surface models.

All modeling was based on the assumption that given percentiles of the property distributions at one moisture content are adjusted to the corresponding percentile of the property distribution at another moisture content. Each type of model contains a value of moisture content above which the flexural properties do not change, known as the intersection moisture content, M_p . Traditionally this value has been 21 percent for southern pine, although Wilson (1932) shows that this value varies with property for clear wood. Given the models considered in this paper, we found no reason to change this value (Green and others 1986).

Zero Adjustment Model

This is the simplest of all the models; no adjustment for moisture content is taken. Although not an appropriate model for our purposes, it serves as a baseline against which other models can be compared.

Constant Percentage Models

Constant percentage models do adjust for moisture content, but the adjustment factor is the same, regardless of the quality or size of the lumber. All current standard adjustment procedures for dimension lumber and for clear wood are of this type. An example is the model developed by Wilson (1932) and given in the Wood Handbook (1974) for small clears. This model for longleaf pine is shown as the solid line in figure 1. The ASTM D 245-81 (1986) adjustment factor for all species of lumber is shown as the dashed line. Each of these lines starts at 8,500 pounds per square inch (lb/in.^2), the value given for green (21 percent moisture content) longleaf pine in the Wood Handbook. Note that the adjustment for small clears is much larger than the adjustment for lumber. To adjust a value of 8,500 lb/in.^2 for a green piece, i.e. a moisture content of 21 percent, to 15 percent, one would follow the plotted lines and read off adjusted values of 12,000 lb/in.^2 for the small clears and 9,500 lb/in.^2 for the ASTM lumber.

The form of the constant percent models is $P_2 = F \cdot P_1$ where P_i is the property value at moisture content i , $i = 1, 2$, and F is the moisture content adjustment factor. F is a function only of the two moisture content levels, M_1 and

M_2 . One could obtain lines to adjust other values by using the same constant percent, F , and varying the initial property P_1 . This yields a set of fanning lines. One of these sets of lines for the ASTM lumber adjustment procedure is shown in figure 2. Think of these lines as a set of contours. When you wish to adjust a property P_1 at moisture content M_1 to the corresponding property at moisture content M_2 , you need to find a contour which intersects the point (M_1, P_1) . Following this contour along to M_2 you are then able to read off the corresponding property value at the point (M_2, P_2) .

To determine the moisture content adjustment factor, F , for constant percentage models, one fits a regression to all pairs of property value and moisture content values (M, P) . M and P without subscripts denote general pairs of data points. The moisture content of the green samples is replaced by M_p . Three different types of regression models were used:

| | |
|-------------|-----------------------------------|
| Linear | $P = a + b \cdot M$ |
| Exponential | $P = \exp(a + b \cdot M)$ |
| Quadratic | $P = a + b \cdot M + c \cdot M^2$ |

The moisture content adjustment factor F to adjust properties from moisture content M_1 to M_2 is $F = P_2/P_1$, where P_i is the value from the equation at M_i , $i = 1, 2$. The linear model will give a set of linear contours (like the ASTM lumber model), the exponential model will give a set of concave contours (like the clear wood model), and the quadratic model will yield a set of convex contours if the value of c is less than zero, which was the case in this study. These models fit the average trend of the data. The Select Structural 2 by 4 data plus the three fitted lines are shown in figure 3. Data points with moisture content values larger than 21 percent are plotted at 21 percent, which is the value of M_p . The linear model is shown as the solid line, the exponential model as the short dashed lines, and the quadratic model is shown as the long dashed line. These three lines do not differ by much, so they will yield similar adjustment procedures. To obtain a model independent of grade and size, one must fit the three regression models to all the data, instead of just a selected grade and size.

Strength Ratio Models

Strength ratio models assume that the moisture adjustment factor, F , depends on the strength ratio of the lumber. The strength ratio is a function of lumber quality. The "25 percent rule" (fig. 4) is such model. The strength ratio of a piece of lumber varies from 0 to 100 percent and is an estimate of the strength of the piece in

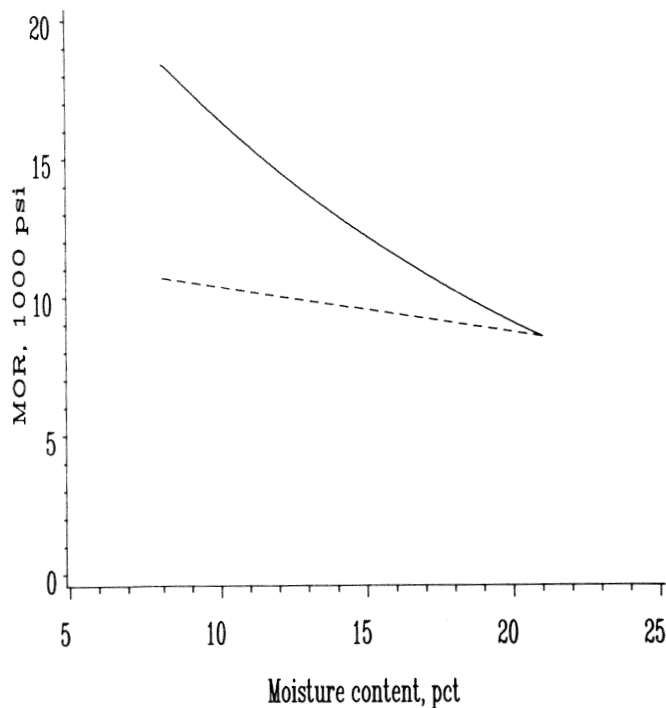


Figure 1.--Current moisture content adjustment procedures for MOR: solid line = small clears, dashed line = lumber. These procedures are similar to the constant percentage models used in this study. (ML86 5340)

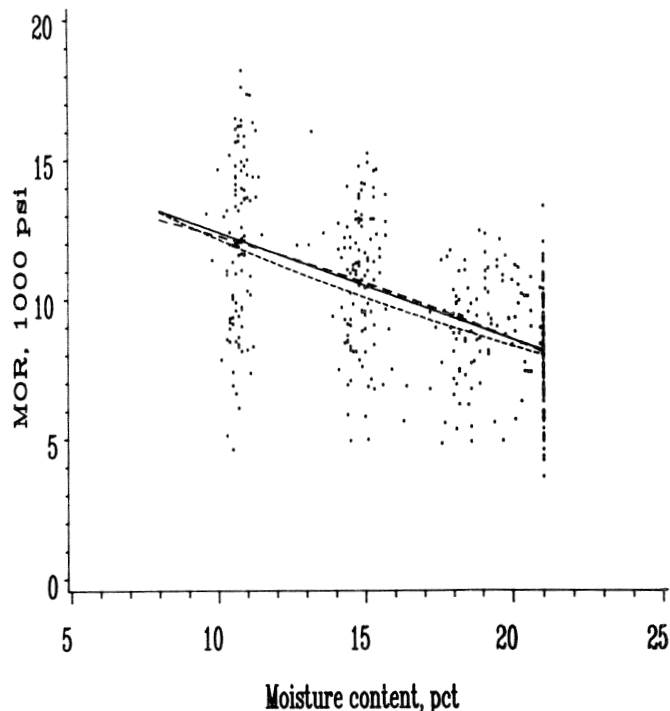


Figure 3.--Select Structural 2 by 4 MOR data. Pieces with moisture contents above 21 percent are plotted at 21 percent: solid line = linear fit, short dashes = exponential fit, long dashes = quadratic fit. These lines are used to construct constant percentage models. (ML86 5342)

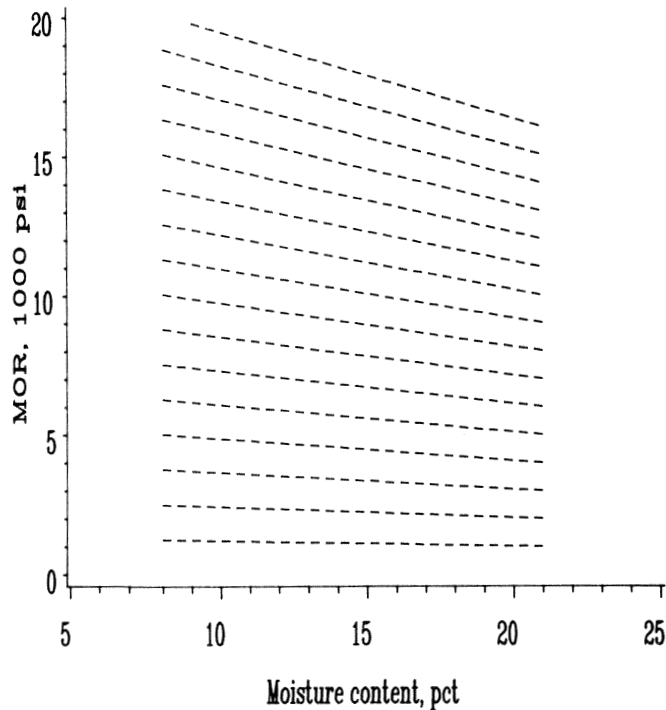


Figure 2.--A set of contours for ASTM D 245 moisture content for MOR of lumber. The procedure was a constant percentage model. (ML86 5341)

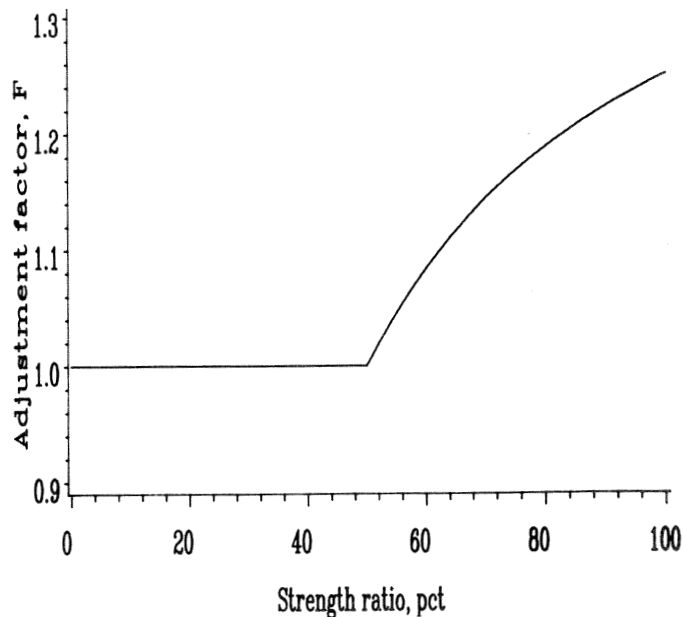


Figure 4.--Moisture content adjustment factor, F (from green to 15 pct): 25 percent rule, as a function of strength ratio. This procedure is a strength ratio model. (ML86 5343)

comparison to one with no strength-reducing defects such as slope of grain or knots. To be graded as Select Structural, No. 2, or No. 3, the strength ratio of a piece of lumber must be greater than or equal to 65 (67 for 2 by 4s), 45, and 26 percent, respectively. If the strength ratio is below some cutoff value, y_0 , here 50 percent, then $F = 1$, i.e. no adjustment is taken. The maximum adjustment, F^* , occurs for pieces with strength ratio of 100 percent, here $F^* = 1.25$, i.e. a 25 percent increase from green to 15 percent moisture content.

The southern pine data set gives us little information from which to choose a form for an adjustment factor dependent upon strength ratio, because 55 percent of the data had strength ratios above 90 percent (even though only approximately one-third of the data is Select Structural with the other two-thirds being No. 2 or No. 3). Therefore we assumed that F had a value equal to one below some cutoff, y_0 , then curvilinear (like the 25 pct rule) or linear until it reached a value of F^* at 100 percent strength ratio. The cutoff values chosen were 0, 26, 45, and 50 percent. The values of 26 and 45 percent correspond to the minimum acceptable strength ratio values for No. 3 and No. 2 grades of structural lumber, respectively. The value of 0 percent gives a nonzero adjustment factor for every piece, and the 50 percent value corresponds to the value used in the 25 percent rule.

Given the assumed form of the strength ratio models, all that was left to model was F^* as a function of moisture content. To do this, pieces with strength ratios of 100 percent were selected. As with the constant percent models, the property values were modeled as a function of moisture content by using either the linear or exponential model. Because grade is assumed not to be a factor (having already been taken care of with strength ratio), the models of F^* were done by size or with all the data. As an example, the MOR of the 2 by 4 data with strength ratios of 100 percent are plotted in figure 5 against moisture content with the fitted linear (solid line) and exponential (short dashed line) models. Again either the linear or exponential MOR/moisture content relationship will give similar moisture content adjustment models. A quadratic model could have been used, but the results would not differ significantly from the exponential or linear model. The value of F^* going from green to any other moisture content is plotted in figure 6 for the exponential model. At 15 percent moisture content this mean value is 1.23 which compares favorably with the value of 1.25 from the 25 percent rule. To obtain a model independent of size, one must fit the models of F^* , using all the pieces with 100 percent strength ratio instead of just one size.

Weibull Models

This type of model is obtained by first fitting a two-parameter Weibull distribution to each of the 36 grade/size/moisture groups. The distributional parameters are given in McLain and others (1984).

The fitted two-parameter Weibull distribution is plotted with the data for Select Structural 2 by 4, 20 percent moisture content group in figure 7. The two parameters of the Weibull distribution are known as the shape and scale parameters. The shape and scale parameters were then modeled as a quadratic function of moisture content. The shape and scale parameters for the Select Structural 2 by 4 data and fitted quadratic curves are given in figure 8. Then the property value, P_2 , at moisture content M_2 , given the property value, P_1 , at moisture content M_1 is:

$$P_2 = a_2 \left((P_1/a_1)^{(b_1/b_2)} \right)$$

where a_i is the estimated scale parameter and b_i is the estimated shape parameter at moisture content i , $i = 1, 2$. Weibull models fit to each grade/size combination contained six coefficients each (two parameters, shape and scale, each modeled by a quadratic equation which has three coefficients). Therefore, there are 54 coefficients when considering all the data (9 separate grade/size combinations). Using analysis of variance, we were able to reduce this number of parameters to 19, but the resulting model is still dependent upon grade and size. To use a Weibull model for grades and sizes which were not tested requires some assumption of how the coefficients vary across grades and sizes. Sizes could be modeled using nominal values--3.5, 5.5, and 7.25--but there is no clear numerical conversion for grade.

Surface Models

A surface model is obtained by fitting a surface to the relationship between MOR and moisture content. In these models, we attempted to find contours that were similar to how the underlying data behaved. For example, a visual summary of the Select Structural 2 by 4 data is given in figure 9. For each of the four groups of data (target moisture contents of 10, 15, 20 pct and green), 21 percentiles (2nd, 5th, 10th, ..., 90th, 95th, and 98th) are plotted versus the average moisture content for that group. The green group is plotted at 21 percent moisture content. Now if we join like percentiles, this forms a target of what our contours should look like with perhaps some smoothing. Some of these contours look as if they could be fitted with a straight line; others look as if a quadratic equation would be necessary. So we fitted linear and quadratic surface models, depending on whether the fitted contours appear in a linear or a quadratic format. In this paper, only the quadratic surface models will be discussed.

A quadratic model was fitted to each of the 21 percentile sets, each consisting of 4 pairs of points, mentioned above. Next, the coefficients of the quadratic and linear terms were plotted versus the predicted MOR values at 15 percent moisture content using the quadratic equations (figs. 10 and 11). Some baseline moisture content must be chosen, but the choice

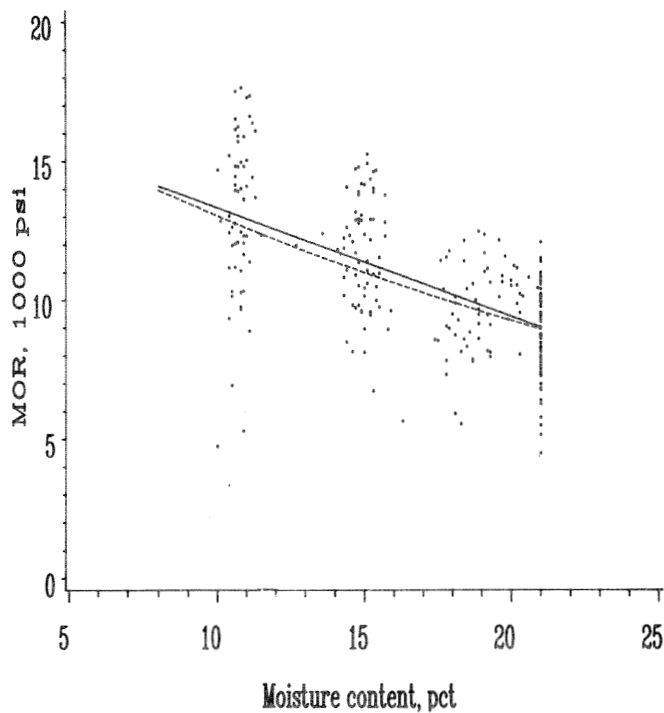


Figure 5.--MOR data for 2 by 4's with 100 percent strength ratio. Pieces with moisture contents above 21 percent are plotted at 21 percent: solid line = linear fit, short dashes = exponential fit. (ML86 5344)

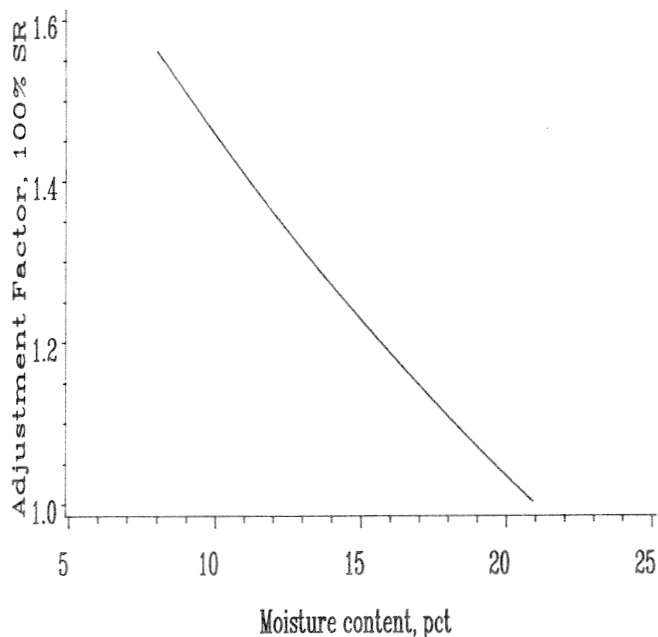


Figure 6.-- F^* , Moisture content adjustment factor at 100 percent strength ratio (from green to another moisture content). (ML86 5345)

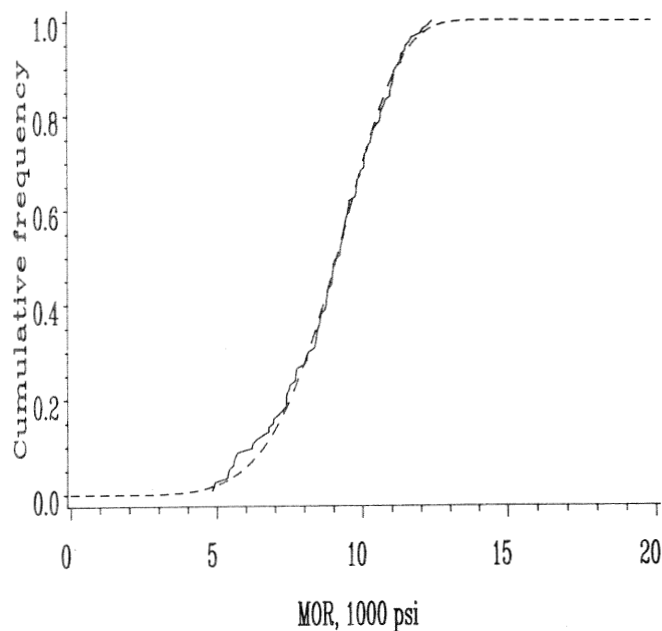


Figure 7.--Select Structural 2 by 4 MOR, 20 percent moisture content group: data = solid line, fitted two-parameter Weibull distribution = dashed line. (ML86 5346)

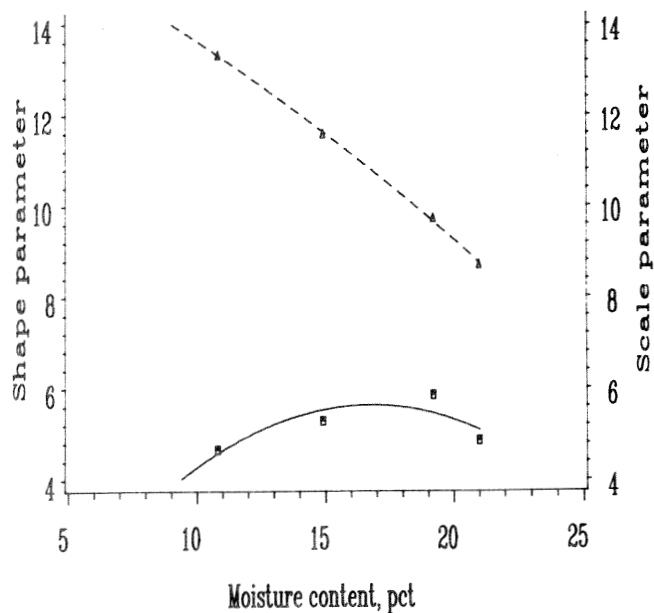


Figure 8.--The Weibull distribution's shape parameter (squares) and scale parameter (triangles) data for Select Structural MOR with fitted quadratic curves: Weibull shape = solid line, scale = dashed line. (ML86 5347)

of 15 percent was arbitrary. Now a cubic function was fitted to these points. Contours using these fitted coefficients are shown in figure 12. Contours for small values of MOR do not behave nicely because there is no Select Structural 2 by 4 data in this region. Given any property value P_1 at moisture content M_1 , one needs to find a contour that goes through the point M_1, P_1 .

The property value at M_2 is then read off of this same contour. In practice, these contours start behaving badly near the extremes of MOR. Therefore, the contours above and below the data were bounded (fig. 13). (The bounding for higher MOR values would be more apparent for lower grades of lumber because for those grades there would be no data in that region.) The lower contours were not allowed to be concave, and the upper contours are parallel to the contour going through the predicted MOR value at 15 percent moisture content of 14,000 lb/in.² (essentially the upper bound of the data). To fit surface models which are independent of grade and size, coefficients were fit to 189 sets of quadratic and linear terms (9 grade/size combinations each with 21 sets of percentiles) instead of just 21 sets for each grade/size combination.

ASSESSING THE MODELS

If no adjustment for moisture content is made, the curves of the MOR distributions for the four moisture contents (green, 20, 15, and 10 pct) are quite different (fig. 14). However, if each of the four distributions were adjusted by a perfect procedure to a common moisture content, the four adjusted distributions would have exactly the same curve. The similarity between the curves of adjusted distributions would reflect the ability of the procedure to model the effect of moisture content.

As mentioned, models were first derived using only a single grade/size combination and then using all nine grade/size combinations. For simplicity, this report contains graphs only of models derived from Select Structural 2 by 4 data (see figs. 15 and 16). These models are then compared with those derived from all nine grade/size groups (see table 1). When each of the four data sets for Select Structural 2 by 4s are adjusted to a moisture content of 21 percent (green) using the quadratic surface model for Select Structural 2 by 4s, the cumulative distribution functions appear to be quite similar (fig. 15). Although the distribution functions are not identical, we did not find other models that gave curves that were more similar. Using the data from Select Structural 2 by 4s with the quadratic constant percent model for Select Structural 2 by 4s yields a set of cumulative distribution functions that are slightly more discrepant, especially at upper end (fig. 16), but much better than no adjustment. Strength ratio models were worse than any constant percent models. Weibull models worked as well as the quadratic surface models but were not independent of grade and size.

Another way to characterize how well a model does is to look at the maximum absolute differences at selected percentiles between the four

data sets adjusted to the same moisture content. Table 1 shows the maximum absolute differences in MOR at the 5th, 50th, and 95th percentile between the four moisture content groups of Select Structural 2 by 4s when those data were unadjusted and when adjusted by two of the types of models considered in this study. The absolute differences for the two model types are shown both for models derived only from Select Structural 2 by 4 data and for models derived from the data of all nine grade/size groups (models independent of size and grade). Similar results are found when adjusting the data to another moisture content.

Table 1.--Maximum absolute differences (lb/in.²) for Select Structural 2 by 4 adjusted to green (21 pct moisture content)

| Model | 5th percentile | Median | 95th percentile |
|-----------------------------|----------------|--------|-----------------|
| No adjustment | 2,210 | 4,150 | 5,590 |
| Constant percent, quadratic | | | |
| Select Structural 2 by 4 | 530 | 310 | 750 |
| All nine grade/size | 640 | 930 | 1,370 |
| Surface, quadratic | | | |
| Select Structural 2 by 4 | 560 | 230 | 450 |
| All nine grade/size | 690 | 220 | 610 |

Some loss in precision occurs when going from an individual grade/size model to an overall model which is independent of grade and size. However, one would prefer a model independent of grade and size, so that data from sizes and grades which were not part of this study could be adjusted. A model independent of grade and size would not have to be changed if grading rules or standard dimensions changed. Also, models specific to one grade and size may overfit some of the peculiarities of the given sets of data. This is why one might use the quadratic surface model independent of grade and size to adjust lumber property data. It adjusts all parts of the property distributions almost as well as a model dependent upon grade and size.

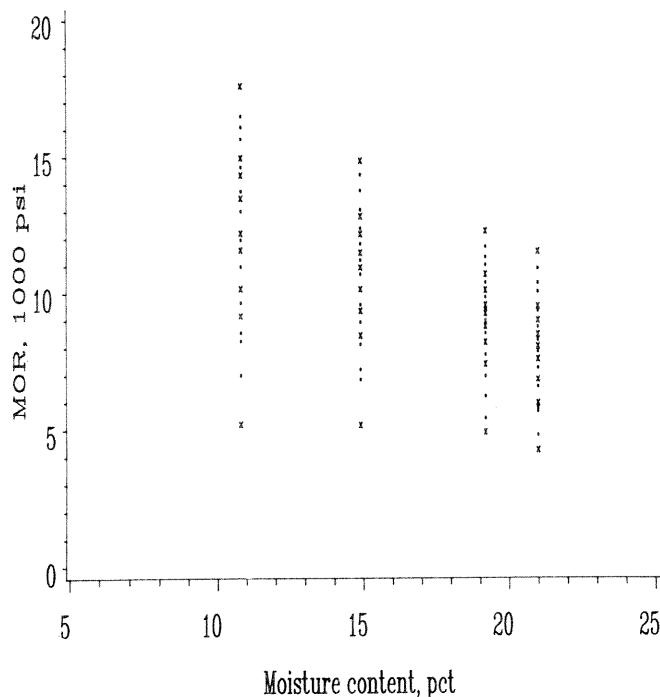


Figure 9.--Select Structural 2 by 4 MOR data, selected percentiles (2nd, 5th, 10th, ..., 90th, 95th, 98th) plotted at group average moisture content (21 pct for green group). The 2nd, 20th, 40th, 60th, 80th, and 98th percentiles are represented by Xs. (ML86 5348)

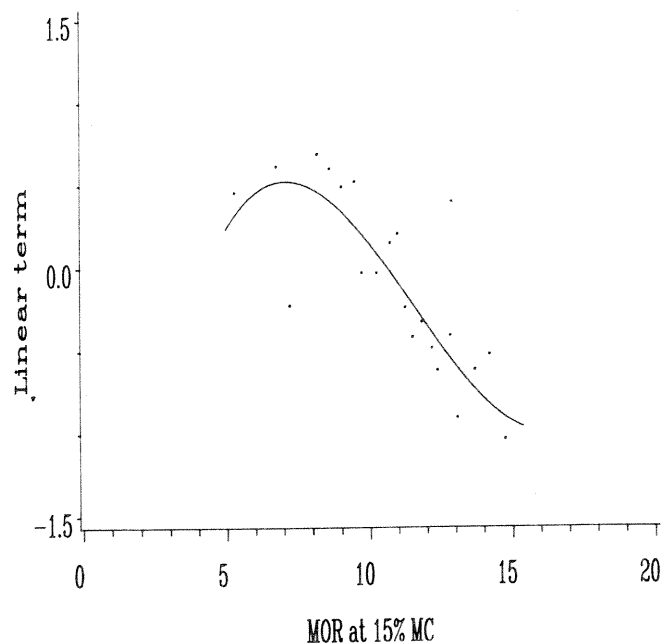


Figure 10.--Linear coefficients for the surface model versus predicted MOR at 15 percent moisture content plus fitted cubic equation. (ML86 5349)

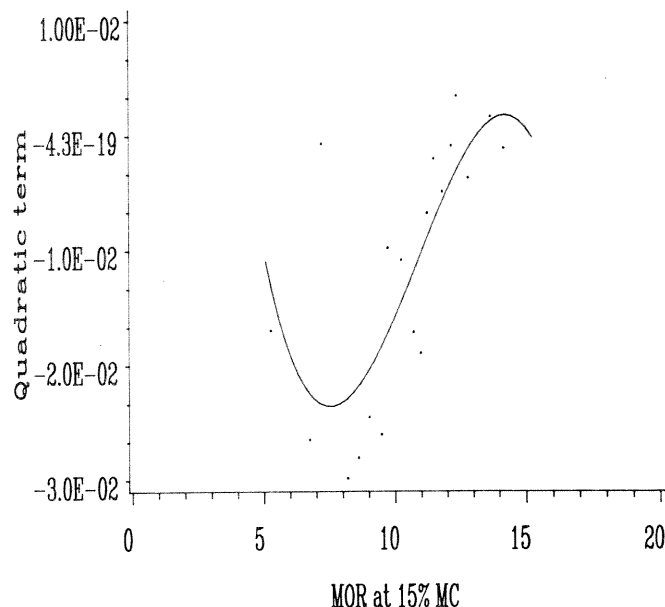


Figure 11.--Quadratic coefficients for the surface model versus predicted MOR at 15 percent moisture content plus fitted cubic equation. (ML86 5350)

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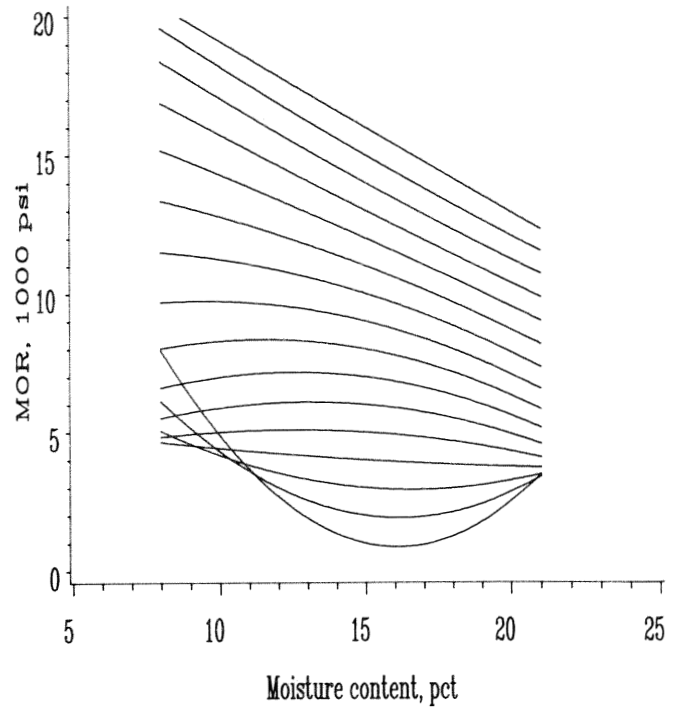


Figure 12.--Unmodified quadratic surface model contours for Select Structural 2 by 4 MOR. (ML86 5351)

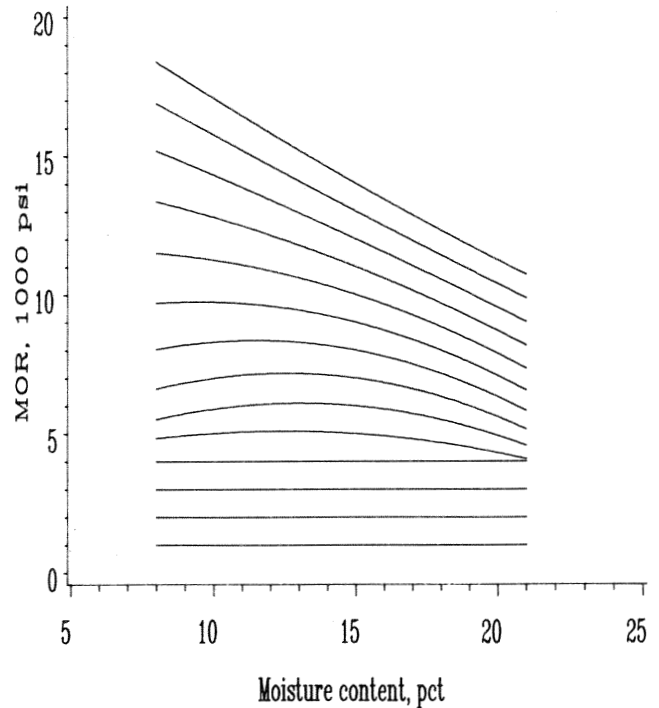


Figure 13.--Modified quadratic surface model contours for Select Structural 2 by 4 MOR: bounded moisture content adjustment for small and large values of MOR. (ML86 5352)

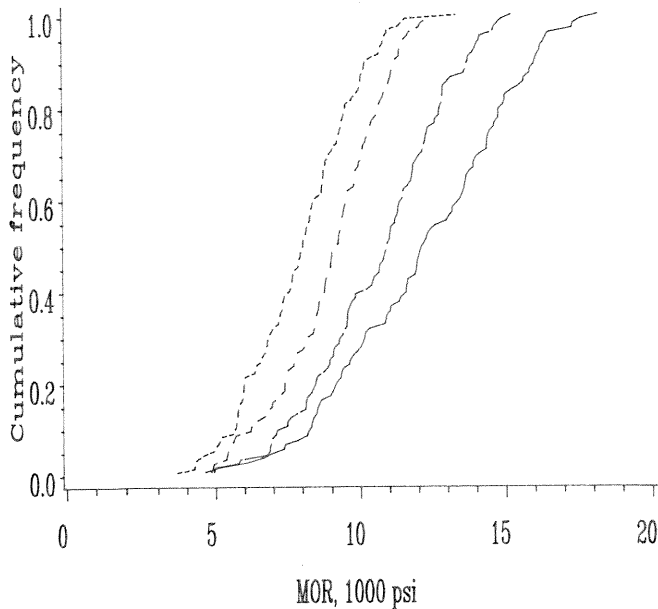


Figure 14.--Cumulative distribution functions for Select Structural 2 by 4 MOR data with no adjustment for moisture content: solid line = green group, long dash = 20 percent group, medium dash = 15 percent group, short dash = 10 percent group. (ML86 5353)

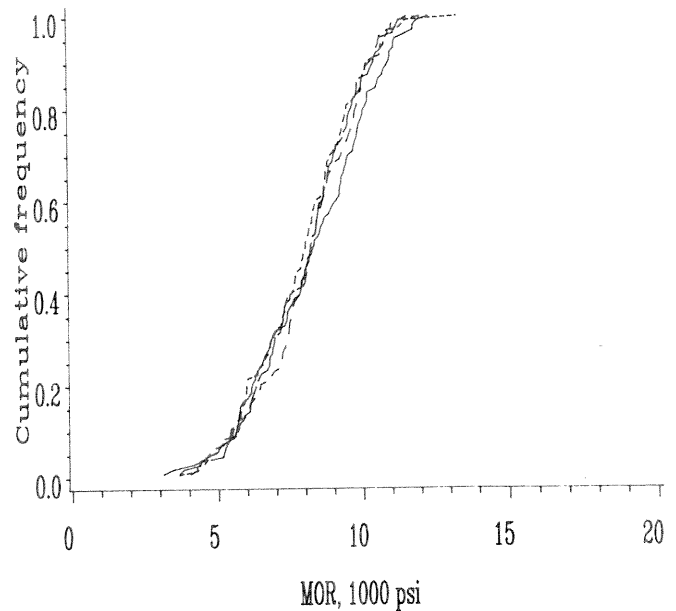


Figure 16.--Cumulative distribution functions for Select Structural 2 by 4 MOR data after adjusting data to green (21 pct moisture content) by the Select Structural 2 by 4 quadratic constant percent model: solid line = green group, long dash = 20 percent group, medium dash = 15 percent group, short dash = 10 percent group. (ML86 5355)

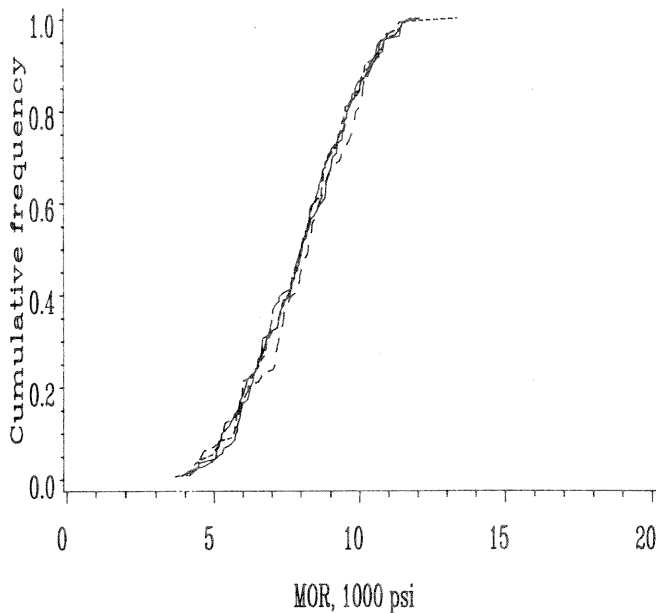


Figure 15.--Cumulative distribution functions for Select Structural 2 by 4 MOR data after adjusting data to green (21 pct moisture content) by the Select Structural 2 by 4 quadratic surface model: solid line = green group, long dash = 20 percent group, medium dash = 15 percent group, short dash = 10 percent group. (ML86 5354)

THE IMPORTANCE OF ARCHEOLOGICAL SITES RELATED TO THE
NAVAL STORES INDUSTRY IN FLORIDA¹

Sandra Jo Forney²

The production of naval stores was the first major industry of the southern pine forests. The industry extracted resin from pine trees and distilled it to produce rosin, turpentine, pitch, tar and other products. Over the past three centuries, naval stores have been used in the construction of ships, paper sizing, perfumes, adhesives, pharmaceutical supplies, plastics and paints.

Like other forest products, the naval stores industry provided employment for Blacks leaving the plantation system during the Reconstruction Era. Archeological investigations in other areas of the Southeast have provided glimpses of the social and economic nature of the plantation system (Otto 1975, 1977, 1980; Singleton 1980).

Since the lumber and turpentine industry was essentially an extension of the plantation system (Shofner 1974, 1981a, 1981b) relationships similar to those among the plantation owner, the overseer and slave or indentured servant and later share-cropper may be expected among the workers of a naval stores operation. The following discussion, adapted from historical research of primary and secondary sources, forms the basis for establishing the potential significance of archeological sites related to the naval stores industry in Florida.

Over the years the turpentiners evolved a distinct society due to their usual isolation (Hickman 1962). During the latter 19th and early 20th centuries, naval stores was an industry with a routine of labor, language and life that was distinct and often viewed as picturesque. A typical day's work for a turpentiner was from "kin to kant" (dawn to dark). He would rise about 4:30 a.m., eat a quick meal prepared the night before, and head into the woods at first light. Between 8:00 and 9:00 a.m. the turpentiners ate a light meal which also was prepared and packed the night before. They worked until nearly sundown, then walked back to their quarters for supper and home chores. This ritual was performed five or six days per week depending on how fast

each got the prescribed job done (Schultz 1981:38).

As in the plantation system, naval stores operations also had an overseer or foreman. This individual, who made his rounds on horseback, was called a "woods rider." Woodsriders were generally Caucasian and their duties were to inspect and supervise the work at a turpentine stand. The Black workers were under the complete control of the woods rider. In fact, it was said that a woods rider, sporting a pistol and whip, was the law in those isolated areas.

The workers usually received company scrip or metal tokens as wages. These were only redeemable at the operator's commissary which was usually located at the turpentine distillery. Other forms of money could be acquired by trading scrip at a discount, however, for most workers, access to areas outside the turpentine camp or distillery was forbidden. Saturday was generally payday at the turpentine camp. Male workers were paid about \$10 per month, while female workers, naturally, received \$2 less. The woods rider, however, received around \$30 per month, which was usually paid in currency rather than scrip.

Goods were usually purchased on credit from the commissary whose keeper affixed a high interest charge. Thus, the workers were usually indebted to the company store, making their ability to leave the turpentine camps for other employment even less likely. The commodities supplied by the commissary system suggest that most meals of the workers probably consisted of cornbread, bacon, black coffee and an occasional treat of baking powder biscuits (Pridgen 1962:150). Berries, grapes, persimmons, nuts and other edible wild plant foods were probably also gathered in season.

Housing and water were furnished as part of the workers' compensation. Because the trees began to lose their productivity after several years, turpentine camps were occupied temporarily, usually for a period of five years. Most of the early trees were worked near rivers for easy shipment. Side camps and distilleries, where the resin was processed into turpentine, began moving into the interior portions of the forest when railroad lines were completed in the late 19th century.

Most turpentine workers lived in shacks or quarters grouped closely together or in rows to prevent the social isolation inherent in living

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alone in the woods, and to provide a better means of overseeing and controlling workers activities. These rough lumber shanties, occupied by both workers and the woods rider, were located at side camps and at the distillery.

Early shanties for the workers were often one-room pole structures with no floor or windows. If a worker's family was large, a lean-to was often added along one wall for additional sleeping space. Each shanty occupant or family probably had a small garden of vegetables to supplement their diet.

Data compiled during a land acquisition appraisal of a Liberty County turpentine camp in the 1930's, provides an indication of status differentiation in the camp (USDA 1934). In addition to 27 box and frame quarters to house 157 occupants and their families, the camp, encompassing 640 acres, included a combination church and school, commissary and cemetery.

The workers' shanties, valued at \$10 each, were 22'x24' wood frame structures with at least two rooms. Housing for the foreman, however, consisted of a six-room dwelling measuring 22'x40', and was valued at \$50. The appraised value of the stable, shed and garage was equal to that of the workers' shanties in the camp.

With few exceptions, archeological remains from occupational areas of the side camp differ little from those of the distillery site, since most commodities at both types of sites were purchased at the company commissary. Glass and ceramic remains constitute the majority of the utilitarian materials associated with these sites. Kerosene lantern gloves and bases, beverage and medicinal bottles, and ornate cut glass dinnerware are the most common types of glass reflecting life at the turpentine site. The greatest percentage of utilitarian ceramics collected from these sites is ironstone, with other types in lesser frequencies. The material remains associated with a turpentine stand include isolated objects such as beverage bottles, cups, tools, and other equipment used during the operation of gum collection, as well as an occasional domestic item.

The socio-economic conditions of turpentine workers remained constant, despite a number of technological advances which improved harvesting and processing techniques. One of the major developments which drastically changed the industry was the introduction of the clay collecting cup.

Initially, the gum or resin was collected in "boxes" or collecting basins chopped into the bases of trees with a broadaxe. A "streak" or wedge-shaped groove was then cut into the face of the tree above the box to allow gum to flow. Each week a new streak was cut to increase this flow. The box cavity was found to weaken the tree at the base, leaving it vulnerable to disease, wind, and fire and to lessen the value of the tree as timber for lumber.

Although the boxing method remained in common use until about 1915, Charles Herty's 1904

invention of the clay cup, initiated a new method for collecting pine resin. A streak was made in the tree and then an incision was cut into the face where a gutter was fastened to direct the flow of resin into the collecting cup which hung by a single nail below. The use of clay increased the quality of resin by avoiding impurities which tended to collect in the open box cavity.

Stylistic changes in turpentine collecting cups are a major source for determining the chronology of a naval stores related site in Florida. Distinctions in the physical characteristics of collecting cups may be due to functional, temporal or spatial considerations. The relative dates and possible ranges for the manufacture and use of these cups were derived from a number of sources, particularly previous research conducted by Ralph Clements at the Olustee Forest Experiment Station.

Turpentine cups now in the Museum of Florida History collection in Tallahassee beautifully illustrate variations in 20th century clay and metal cups. Because they were much cheaper to purchase than metal, clay cups were almost exclusively used in Florida, except in the northern part of the state where clay cups could easily break during a freeze.

The Herty cup was the most common style on the market. Established in 1904, the Herty Turpentine Cup Company of Daisy, Tennessee, produced at least 60,000 cups per day until about 1914, when the advent of galvanized iron cups forced a decrease in the demand for ceramic cups. These cups were marketed exclusively in Alabama, Georgia and Florida (Smith and Rogers 1979).

Major ownership in the Herty Cup Company was with the Consolidated Naval Stores Company of Jacksonville from 1910 until 1942 when the company was voluntarily dissolved. These dates correspond nicely with the major era of naval stores production in the State, particularly in the Jacksonville area.

Another variety of clay collecting cup was connected to the tree by a metal fastener at the rim instead of being hung by a nail. The exact purpose of this unique attachment is not currently known. These cups were probably used in Florida between 1910 and 1925. Reminiscent of the Herty cup, due to its fluted exterior and similar red paste, this cup may also have been made at the Tennessee plant.

The clay Pringle cup, curved to fit the shape of the pine tree, was also on the market during the first quarter of the 20th century. Although the location of manufacture is presently unknown, a patent date of July 10, 1910 is indicated on the bases of these cups.

Several varieties of yellow clay cups were apparently being made and used almost exclusively in the Escambia County, Florida area during the early 1930's. Although their paste was consistent, shapes and sizes varied greatly suggesting temporal distinctions in the styles or perhaps different manufacturers.

An unnamed Jacksonville company, possibly associated with Charles Hertty's business, manufactured a cement cup in the mid-1930's. Experimental glass cups were also made in Jacksonville during the late 1930's.

As early as 1914, galvanized iron cups were on the market. Styles included the flower pot shaped Birdeye cup, the trapezoid shaped Buzzard wing cup, and a variety of metal oblong boxes. During the 1920's and '30's an array of tin, galvanized iron and aluminum cups were being manufactured for use in collecting pine resin.

In a final attempt to produce quality resin free of leaf litter and other debris, steel oblong boxes with a fired enamel finish were used during the waning years of the industry.

Another source of data for establishing a chronology of the naval stores industry in Florida is the development of specialized tools used in chipping and dipping the pine gum. Five technological innovations occurred in the industry's peak years between 1900 and 1935 were in collecting cups. During the latter 50 years of the industry at least 38 new tools, equipment and extraction methods were adopted and accepted, over half of which occurred between 1942 and 1958.

The common chipping tool known as a hack replaced axes and single bevel hatchets in the first half of the 19th century. Further advancements were made in design during the early 20th century with the introduction of the No. 2 hack in 1900, the No. 0 hack in 1910, and the detachable blade hack in 1915. These early hacks, which were attached to a handle and weight, continued in use throughout the course of the industry.

To accompany the new extraction methods, a broadaxe for mauling the incision into the streak was introduced in 1908 to replace the boxing axe in use since 1700. A puller, invented in 1865 to chip high streaks, was still in use in at least the late 1930's.

In 1918, the hogal was invented to smooth the bark for gutter insertion and chip subsequent streaks. Chipping paddles to prevent chips from falling into the cup were introduced during the late 1920's. Two styles of specialized buckets and dip paddles were invented in the 1930's to replace the dip spoon previously in use since 1750.

It is apparent from the preceding discussion that historic archeological sites related to the naval stores industry provide a potentially important source of data for the study of status differentiation and the evolution and geographical distribution of harvesting technology. Unfortunately, a review of the results of cultural resources inventory and assessment surveys conducted during the past several years indicates that sites associated with the naval stores industry, with few exceptions, have been "written off" as an insignificant cultural resource. It is urged that future investigations conducted in Florida and other states make every

effort to more appropriately consider and evaluate this valuable historic resource during the inventory compliance and preservation process.

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Community Forestry in Mexico's Natural Forests:

The Case of San Pablo Macuiltianguis¹

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Abstract. Seven years after Mexico's National Institute for Research on Biotic Resources (INIREB) initiated a community forest industry project for rural development in a Zapotec village in the mixed pine-oak forests of highland Oaxaca, the results and the process are evaluated. In addition to problems of inadequate technology and technology transfer, social factors including the emigration of local people to urban areas for work and education has created a labor shortage which has affected the forest industries. It is suggested that demographic dynamics like these may impose unexpected obstacles to the Mexican policy of encouraging community-owned small-scale forest industries.

Keywords: Emigration, rural development, social forestry, technology transfer.

Seventy percent of Mexico's 40 million ha of forests are in the hands of nearly 8000 'ejidos',³ and indigenous (Indian) communities whose communal rights to the land cannot be bought or sold (SEP 1981; SARH/SF 1984). Further, the approximately 10 million peasants who live in Mexico's forested areas are among the poorest people in the country (de la Madrid 1983). Therefore, Mexico's national forestry policy seeks to achieve the double objective of stimulating forestry sector production at the national level and providing a basis for socio-economic development of forest communities, by organizing forest landowners and integrating them into forest harvesting and transformation activities (SFF 1981; de la Madrid 1983; Castanos 1984; Ley Forestal 1960;1986).

However, while a number of community forestry projects have been initiated in different parts of the country (SARH/SF 1984), the process of developing, implementing, and evaluating the methods for achieving forestry and rural development objectives among Mexico's peasant communities is just beginning. It is hoped that this review of seven years of experience in the community of San Pablo Macuiltianguis on the part of INIREB (Mexico's National Institute for Research on Biotic Resources) will contribute to this process.

BACKGROUND AND SETTING

San Pablo Macuiltianguis is an indigenous Zapotec community of about 1600 people, located in the highlands of the Sierra de Juarez, in the state of Oaxaca, Mexico. Their communal property includes approximately 5000 ha of commercial temperate forest at an average elevation of 2400 m, mostly dominated by pines (*Pinus patula*, *P. pseudostrobus*, *P. rudis*, *P. ayacahuite*) and oaks (*Quercus laurina*, *Q. rugosa*, *Q. crassifolia*, *Q. excelsa*, *Q. candicans*, and *Q. salicifolia*) (FAPATUX 1962; Perez & Perez 1984).

Until 1959, San Pablo Macuiltianguis was not accessible by road, and the community lived off of subsistence agriculture and peddling goods among the highland villages and between these villages and the cities of Tuxtepec and Oaxaca, three days walk away down the mountains (Garcia 1972; AMETICAL 1980; Perez & Perez 1984). All this began to change when the forests of San Pablo Macuiltianguis and other communities of the Sierra de Juarez were concessioned to the first newsprint paper mill in the country, Fabricas de Papel Tuxtepec (FAPATUX), as its source of pine wood for cellulose (Diario Oficial November 12, 1956). A highway and a web of lumber extraction roads were built through the Sierra and its forests in 1959, and the economy of San Pablo Macuiltianguis began to shift towards forestry.

Under the terms of the concession, the community had no right to sell their wood to buyers other than the paper company, nor could they transform it themselves. However, community members worked as loggers, paid by the m³ for pine bolts cut and delivered to roadside for the paper company. The company also paid forest use payments known as 'derecho de monte' to the community as a whole, most of it deposited directly into a trust fund for community development.

During the first few years of the concession, as many as 80 men from Macuiltianguis worked as loggers, cutting up to 12,000 m³/year (AMETICAL 1980) or more (Carlos Ruiz, pers. com.) of their

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³The 'ejido' is a communal land grant made to peasants as part of Mexico's Agrarian Reform.

allowable annual cut of 25,000 m³/pine (FAPATUX 1977). Subsequently, conflicts between the community and the paper company over the price paid for their wood (or labor) and the difficult working conditions in the forest, led to a work stoppage between 1968 and 1972.

During this period, the men of San Pablo Macuiltianguis did no logging. To compensate for the loss of their principal source of income, many emigrated to distant cities and the United States (Garcia 1972). When forestry activities were reinitiated in 1972, under a more favorable agreement with the paper company, fewer men than before worked in the forest, delivering an average of only 5000 m³/year, only one fifth of the annual allowable cut, or even less (community archives).

The community of Macuiltianguis felt their relationship with the paper company was unfair. Conscious now that their forest represented "green gold", they began to look for ways to obtain greater benefits from the exploitation of this community resource.

THE ESTABLISHMENT OF A COMMUNAL FOREST INDUSTRY

In 1977, four years before the end of the FAPATUX concession, the community of San Pablo Macuiltianguis made contact with INIREB, and requested their support in establishing a forest industry in the community. INIREB, in particular their Laboratory for Wood Science and Technology (LACITEMA) was interested in evaluating the process of technology transfer to determine how their scientific knowledge about natural resources could be integrated into the production process. "We did not want to collect information and make conjectures about what the community could do with their resources, but to initiate a process, a dynamic, and to learn about it by evaluating not only the difficulties that came up, but also the community's capacity to overcome the difficulties generated during this process" (AMETICAL 1980).

Both the community and INIREB had hopes that by providing opportunities for stable employment in local forest industries the rate of emigration from San Pablo Macuiltianguis could be slowed. During the work stoppage, 56% of the economically active population had emigrated (Garcia 1972), and since then about 30% of the population was living outside the community at any given time (AMETICAL 1980; Perez & Perez 1984).

"We expected that a peasant industry would encourage the forest owners to stay and work in their communities; and that a community industry would produce economic resources which would be reinvested directly into the community...a communal industry would serve as a lever, with multiplier effects, to stimulate the development of communities which were stagnating, slipping backwards, or had a slow or erratic development dynamic" (AMETICAL 1980).

While the community of San Pablo Macuiltianguis wanted to establish a pine sawmill, the terms of the concession and the interests of the paper

company did not permit them to use the pines in their forest. As a consequence, and to achieve a greater degree of transformation, more value added, and more potential for local employment, the Institute suggested that the community invest instead in a small factory to produce tool handles from the unexploited oaks in the forest (AMETICAL 1980).

In 1978, permission was obtained from FAPATUX to use the oaks, and with \$700,000 pesos (\$30,000 US at that time) which had accumulated in their trust account of forest use payments, and a bank loan for \$1,000,000 pesos (\$44,000 US), the community invested in a flatbed truck, a building, and the simple lathes and sanders necessary. INIREB helped them with the complicated paperwork and other efforts necessary to achieve this, and to obtain the electrical connection to power the factory. The oak was cut and split by community members during "tequios", unremunerated communal labor sessions, and in 1980 the tool handle factory began functioning, staffed by 16 members of the community (Perez & Perez 1984).

There were still many problems ahead. Among others, thousands of hammer handles were refused by the buyer because they did not meet quality control standards. Problems with maintenance, due in part to the poor state of the machinery when it was bought second hand, and in part to the lack of training of personnel in this field, led to low rates of production. Problems in personnel management derived from the form of payment (which was changed from an hourly to a piece rate with incentives) and absenteeism due to agricultural labors. This made it very difficult to achieve a continuous rate of production and integrate the factory's output into a supply system for potential buyers.

By this time, INIREB had been participating alongside the community for nearly three years. They felt that many of the problems which were impeding the development of the industry should be resolved by the communal assembly, autonomously. They did not want to find themselves taking over the process and interfering with the development of a sense of responsibility and duty on the part of the community, so they withdrew (AMETICAL 1980).

THE END OF THE CONCESSION AND THE INSTALLATION OF THE SAWMILL

At the end of 1981, the paper company's 25 year concession over the forests of the Sierra de Juarez ended. The community authorities decided to install, at last, the pine sawmill that the community had always wanted. Using an advance paid by the paper company for 5000 m³ of pine wood, the community bought a new sawmill, and installed it in 1982, with the technical assistance of FAPATUX.

By the end of 1982, San Pablo Macuiltianguis boasted the complete infrastructure necessary for an integral forest utilization system. They had a forest with an allowable annual cut of 25,000 m³

of pine and 20,000 m³ of oak, a complete network of extraction roads, a market for cellulose products, a pine sawmill, a factory for oak tool handles, and a carpentry shop; all belonging to the community as a whole. The harvesting, transportation and transformation activities provided employment for approximately 100 people.

However, the tool handle industry had shut down due to problems with the machinery, lack of raw materials (oak was more difficult to fell and buck than pine, and then had to be split to be processed), lack of labor, and administrative problems. The sawmill which began working in November was closed down by the end of the year for lack of wood. The timber harvesting activities were paralyzed due to lack of manpower in the forest, reflecting in part a lack of working capital to pay them with.

In early 1983 the authorities of San Pablo Macuilianguis returned to INIREB to request counsel and support. The Institute agreed to analyze the forestry situation in the community as soon as funds could be obtained to support the necessary research. Before these arrived, a major forest fire swept through the forest, affecting about 3000 ha in May 1983 (Quintero, Servicio Forestal Oaxaca, pers. com.).

Conscious of the importance of cutting the damaged trees before they rotted, and their inability as a community to cut such a volume (estimated at 80,000 m³, Quintero pers. com.), the authorities of San Pablo Macuilianguis contracted with the paper company to extract most of the burned trees. The logs cut at 2.62 m would be delivered to the community sawmill and the bolts (1.25 m) would be sold to the paper company for cellulose. Timber extraction began in August 1983 and the sawmill began to function again (largely with workers from neighboring communities) until the director (a member of the community) resigned at the end of the year, in protest to the heavy time demands and his low salary.

INIREB'S EVALUATION

In April of 1984, the yard of the sawmill was full of logs, and the salvage cutting continued. A new director for the sawmill was named by the community assembly, and sawing activities resumed. It was during this month that the author, with a grant from CONACyT (Mexico's National Council for Science and Technology), returned to San Pablo Macuilianguis with a team of researchers (Masters students in Ecology and Biotic Resources at INIREB), and three outside consultants, to evaluate community forestry activities and advise how their problems might be resolved. Seven separate studies were carried out and their results delivered to the community in June 1984. This paper draws on several of them.

The major obstacles to the development of the forest industries in San Pablo Macuilianguis were: 1) problems with raw materials supply; 2) an insufficient labor force; and 3) a lack of administrative and technical capacity. Therefore, in

addition to evaluating the productive forestry activities per se (forest harvesting, the sawmill, and the tool handle industry), a socioeconomic survey was made of the community.

The communal forest industries of San Pablo Macuilianguis have been shut down periodically for lack of wood supply. This results from both technical and social factors. The sawmill requires 8400 m³ of pine roundwood/year to produce 8000 board feet/day during 222 working days a year. This volume represents just over a third of the allowable annual cut of pine. However, between August 1983 and April 1984, of 16,000 m³ of pine harvested, only twenty percent was cut as sawlogs, a proportion which would provide less than half of the sawmill's annual needs (J. Mayoral, R. Perez, pers. com.). This despite the fact that the forest study indicated that half of the standing volume was of adequate size and quality for sawlogs (FAPATUX 1977).

In part, this proportion reflected the paper mill's interest in supplying its own needs for cellulose over community needs for sawlogs, during their post-fire salvage contract, but previous and simultaneous harvests carried out by the community itself also cut big trees to bolt size. This has occurred largely as a result of the selective cutting regime applied to the forest, combined with inadequate extraction technology.

Although mechanical winches have been used on occasion to haul logs uphill to the road, most of the wood cut in San Pablo Macuilianguis is rolled downhill manually to the extraction roads (the average slope is nearly 0 percent). Since the official silvicultural system limits extractions to 30 to 40 percent of the pine volume (15 to 25 percent of total volume), the density of residual trees is very high (see Snook & Negreros 1986). As a result, the rolling of large logs among the trees which are left is difficult, and loggers generally buck all logs to 1.25 m bolt length if they are located more than 50 m from the road, regardless of their diameters (which may reach 80 cm or more) and optimum use.

A more intensive silvicultural system (which would also improve regeneration and growth, see Negreros and Snook 1984; Snook and Negreros 1986), combined with improved extraction methods, would permit the extraction of large logs at sawlog length, thus assuring sufficient raw material supply to the community sawmill, and additional income to the community.

A more complex aspect of the raw materials supply problem for the community forestry industries of San Pablo Macuilianguis is the labor supply. Since the beginning of the concession, there has been insufficient labor to extract the annual cut of pine, much less the oak, in San Pablo Macuilianguis. In 1984, despite a call for workers in neighboring communities, only 12 teams of loggers were available, of the 25 or more necessary to cut their 25,000 m³ annual cut of pine during 37 working weeks a year.

Only the forest fire of 1983, and the

resulting community contract with the paper factory to extract the damaged trees, has assured the supply of raw materials to the sawmill. However, this contract has a fixed time limit. Unless it is continuously renewed, the problem of raw materials supply will reappear.

The lack of manpower available to cut wood is in part a function of the technological problems of extraction which reduce the productivity and thus the earnings of loggers, who are paid according to the volume of logs delivered to roadside. A time and motion study revealed that a pair of loggers spent nearly 60 percent of their time moving logs with a pevee and debarking bolts for cellulose by hand with axes. In addition, by producing mostly boltwood for cellulose, loggers earned 40% less per m³ than they would have had they produced sawlogs.

If boltwood for cellulose were sold with bark, and if the time spent moving logs by hand to roadside could be cut in half by modifications in silviculture and improved extraction technology,³ loggers could produce 36 m³/week instead of 26 m³/week, and fewer loggers would be necessary to cut the same volume of wood. If they also produced 35% of their total volume as sawlogs, they could not only assure the supply of wood to the sawmill, but would also earn almost 50% more than at present. Such modifications would contribute to the resolution of the raw materials supply problem in two ways: by increasing productivity and by providing greater incentives and rewards for logging.

The problem of insufficient labor supply affects the wood transformation industries as well. In 1984, only 7 percent of the economically active men in Macuiltianguis were working in the forest industries, while 60% of the workers came from neighboring communities. This reflected in part the low salaries which Macuiltianguis citizens considered inadequate. But while the maximum earnings of a logger result from the value of a m³ of wood and his own productivity, the salaries of the forest industry workers are low because the communal assembly fixed them that way.

While it is desirable that forest industries belong to the communities which own the rights to the forest land, this has implications which can in fact create obstacles to their own industrial development. In San Pablo Macuiltianguis, where the forest and the industry belong to the community as a whole, every member of the community has an equal right to share in the profits of the forestry activities. Since only 13% of the members work in forest-related activities, the majority of the community wants the industry to produce a high profit margin rather than paying good salaries. In 1984, most workers felt that their wages were inadequate, yet sawmill earnings were scheduled to be invested in additional infrastructure (including vehicles), or applied to profits.

The repeated suspension of production for lack of labor or raw materials, or subsequent to the

resignation of the different directors of the forest industries, has occurred partially because of this conflict between allocation to profits and allocation to salaries. With an increasing proportion of forest workers from other communities, one would expect this conflict to worsen.

Emigration also affects the availability of workers in the forestry activities of the community. In 1984, 60% of the men between 16 and 35 years of age were living outside the community, half of them working (many in the US), and half studying. This demographic dynamic could be significant for the future of the forest industries in San Pablo Macuiltianguis, and may be indicative of a pattern echoed in other forest communities in Mexico.

The emigration of economically active citizens from San Pablo Macuiltianguis began during the second World War, when American agriculturalists came to Mexico to hire 'braceros' to work in the American fields. A number of men went from San Pablo Macuiltianguis. Nearly 25 years later, during the work stoppage protest against the paper factory, more than half of the economically active population emigrated, both to Mexico City (75%), and to the United States (15%) (Garcia 1972), sending money back to support their families.

This pattern of emigration from San Pablo Macuiltianguis may reflect the traditional mobility of the Tzapotecs. Before the forest concession, most of the members of the community were peddlars (Garcia 1972), and the goods they sold were not, for the most part, products of their own fields or labors, but coffee, avocados, and other products from the neighboring villages of the Chinantecs. Because they derived their income principally from long-distance trading rather than the production of goods from a fixed point, perhaps the Macuiltecos are not particularly attracted to the idea of becoming industrial workers with fixed places and times of work. In fact, 11 percent of the families of San Pablo Macuiltianguis are merchants today, maintaining 20 stores in the community.

The multiple devaluations of the peso during the past 5 years (from \$23/dollar in June 1981 to \$800/dollar in November 1986) have provided an additional incentive to emigrate to the United States. Accumulating savings is important to citizens of San Pablo Macuiltianguis for several reasons. One of them is the community tradition of unremunerated citizen participation in the community government. Some of these jobs, for example, the committee responsible for communal natural resources, including the forest, now require full-time dedication. A serving citizen may have to maintain his family with no income for as long as three years. There are so many community responsibilities, that an average citizen of San Pablo Macuiltianguis is involved in one or another during 7 to 10 years of his life. (If a citizen does not serve, when named by the Assembly, he loses his rights as a member of the community, and forfeits all property).

Another demographic phenomenon which affects the labor supply for forest industries in San

Pablo Macuiltianguis, is the emigration of young people from the community to study. After graduating from secondary school in the community, 30 percent of the young people go to the cities to study in technical schools or high schools. Some of them continue through university. These young people with their technical diplomas or professional degrees are unlikely to return to the community because the available employment does not require or remunerate this level of preparation, and life in a small mountain village does not offer the stimulation of a city. While a number of young people from San Pablo Macuiltianguis have studied forestry, in 1984 only one of them was working in the communal forest industries. (To work in forestry per se, forestry graduates must obtain government employment, since by law only the forest service can carry out management responsibilities, regardless of the ownership of the forest land).

Community interest in advanced education has other implications for the local forest industries. Sixty percent of the parents in San Pablo Macuiltianguis consider expenses associated with the education of their children to be among the most significant of the family expenditures. In 1984, 39% of the families were maintaining one or two children in some city, to study. The cost of maintaining a child in a provincial city was \$5000 to \$10,000 pesos a month, and up to \$15,000 pesos a month in Mexico City. The salaries paid in the communal forest industries were about \$15,000 pesos/month at that time, clearly inadequate for providing for the educational goals of many families. (In June, 1984, the peso/dollar exchange was \$191/1.00).

The problems of raw materials supply and labor availability were observed to be complex, involving the interaction of sociological, cultural, economic, technological, and even legal factors. Some of these reflect the very processes of socioeconomic development, and changing expectations. Many are linked to structural features external to the community. For example, the selective extraction regime applied to Macuiltianguis' forests is the official silvicultural system defined by federal forest service guidelines, and applied to all Mexican forests (see Snook & Negreros 1986, in this volume). By the same token, it has been paper company policy to buy debarked logs. The peso to dollar exchange rate, in part a function of international oil prices, has probably affected the community's labor supply by encouraging emigration to the United States.

Yet many operational problems within the forest industries were perceived as a function of insufficient technical and administrative capacity within the community, or inadequate technology transfer. In fact, the inexperience of community leaders, who named by the community assembly, gamely undertook to manage the fledgling forest industry complex (first the oak tool handle factory, then the sawmill and timber extraction activities), were hampered in these undertaking by their lack of training and skills. Maintenance and marketing problems have already been mentioned. Startup of the sawmill was delayed nearly a year after it was

installed, because no working capital had been budgeted to pay workers or loggers. The lack of accounting skills on the part of the communal committee which had been named by the assembly to direct the forestry activities, led to accusations of fraud, and community doubts about the economic potential of the oak tool handle led to its virtual abandonment. Nor had an evaluation of future raw materials supply in light of the fire damage been programmed with the responsible forest service personnel.

INIREB had offered courses in machinery maintenance and administration for Macuiltianguis even before the tool handle factory was installed, but the community did not send their personnel, perhaps because there were to take place at Institute headquarters, a full day away by bus. Other short courses, on tree felling and accounting, had been offered at the paper company's nearby forestry camp in the Sierra, but only one community member had gone in each case.

However, the community had arranged for a few of their workers to spend a few weeks training in another sawmill, and had hired a technician to help them start up their own sawmill. They had also requested that the paper company send one of their accountants to help them organize their books. Community leaders had come twice to INIREB to request help, first in setting up and then in diagnosing their forest industry. And while it was not easy to arrange working sessions with community leaders to deliver and discuss the results of those evaluations, they may have been taken into account, and acted upon, since then. (The results of the analysis described in Snook & Negreros 1986, in this volume, which had been presented to the assembly in 1983, were found later to have been used to define terms for the salvage cutting contract signed with the paper company after the forest fire). Meanwhile, the sawmill seems to continue to function.

CONCLUSIONS

This overview of the San Pablo Macuiltianguis experience in forestry development has been far from exhaustive, yet certain observations can be made. To begin with, a dynamic process was initiated when the forests of San Pablo Macuiltianguis were recognized as a resource, and the community has been an active protagonist, particularly since the work stoppage of 1968. While they requested INIREB's advice on establishing a community forestry industry in 1977, the community responded to the end of the forest concession in 1981 by abandoning the oak tool handle factory and established the pine sawmill on their own initiative.

There have certainly been weaknesses in the process of technology transfer, which have led to inefficiency, problems, shutdowns, and a potential for continuing or worse difficulties in the future. In part, these may have reflected the very dynamism of the community, which has been more adaptive than persistent in its response to

obstacles. The difference in perceptions between INIREB and the community about the best solution may also have impeded adequate follow-through. For example, the oak tool handle factory does seem like the optimal forest industry to improve forest utilization and silviculture (see Negreros & Snook 1986, in this volume), and maximize employment and profit per unit volume of wood. Yet the community perceived the sawmill, probably a simpler operation and less difficult to supply and maintain, as more desirable.

Among the most important lessons from the San Pablo Macuilianguis experience, however, is the demonstration that certain key assumptions about the community forestry development process were not borne out. For one, emigration was not slowed by the creation of jobs in the community -- rather, the industry suffered from insufficient labor supply. In this case, the seeming anomaly may reflect traditional cultural values, changing expectations, or international financial relationships, but apparently this assumption has been shown not to hold in other rural development experiences as well (Rhoda 1979).

An implicit hope of the Mexican community forestry development policy has been to increase the level of timber harvesting, and thus reduce the severe shortfall of cellulose, which is currently met by imports. Yet it appears that the rhythm of extraction in San Pablo macuilianguis dropped to levels inadequate even to supply their own community industries, until the forest fire and subsequent salvage contract. Part of this may reflect other forestry policies (for example the official silvicultural system) whose effects may indirectly discourage community participation in forestry. It would appear that specific strategies and tactics should be developed to provide incentives and means for increased levels of harvesting.

Finally, it is humbling to acknowledge that the process of forestry development, even in a seemingly isolated mountain village, is so complex, and subject to so many unexpected and constantly changing factors, many seemingly unrelated to forestry. One wonders what responses might be expected in connection with the new Mexican forestry law of 1986, the new US immigration law, or the increasing unemployment of Mexican university graduates resulting from the country's deepening economic crisis and cutbacks in government spending. What does seem clear among the mind-boggling linkages and uncertainties of this community forestry development dynamic, is that the success of Mexico's forestry policy depends largely on the understanding of sociological processes.

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Diffusion of Innovations: A Sociological Approach
to the Nonindustrial Private Forests Challenge¹

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Abstract.--Methodology based on diffusion of innovations research was developed to identify nonindustrial private forestland owners who are opinion leaders and investigate their traits, attitudes and values. The sample was composed of sixty-four respondents who live in the South Carolina Piedmont region. They were verified as "early adopters." More than one-half of the sample valued lifestyle enhancement benefits of their forestland more than timber production/economic benefits. This preliminary study lends credence to the theory that an interdisciplinary approach, similar to that successfully applied to farmers, is appropriate to improve technology transfer to nonindustrial private forestland owners.

Keywords: Change agent, early adopter, information source, lifestyle enhancement, opinion leader, technology transfer.

This paper presents results of a study designed to develop methodology to identify opinion leaders who own nonindustrial private forestland and to search for common traits, attitudes and values. Understanding the attitudes and values of opinion leaders can enhance technology transfer programs to improve forest management on private forestland.³

Numerous studies have been made of the private forestland owner. In general, the intent of technology transfer efforts has been to increase wood production on private land in a manner similar to wood-using industry land management practices. However, the goals and attitudes of private owners differ from those of the wood-using industry. Lip service has been given to private owner objectives, but successful technology transfer programs must be designed to satisfy these goals. Technology transfer between professional foresters and private landowners may be expedited by an interdisciplinary approach combining social science--the study of people--with forestry.

SOCIOLOGICAL BACKGROUND

Rural sociologists have used diffusion of innovations research to improve technology transfer to farmers by defining their attitudes toward their land, their enterprises (e.g., crops, livestock) and new farm practices. Diffusion is that type of communication by which an innovation

spreads among members of a social system (Zaltman et al. 1973). An innovation, in sociological terms, is any idea perceived as new by the receiver. This study was designed to test the applicability of some diffusion of innovations methodology to private forestland owners.

Rogers and Shoemaker (1971) defined adopters of innovations in five groups as innovators, early adopters, early majority, late majority and laggards or late adopters. Innovators are the first 2.5 percent to adopt a new idea, followed by early adopters (13.5 percent), early majority (34 percent), late majority (34 percent) and laggards (16 percent). Muth and Hendee (1980) suggested the five categories are appropriate for describing forestland owners. Baird (personal communication 1982) wrote in a problem analysis that the results of numerous surveys "indicate forestland owners follow a decision-making process that is one of the most well-established phenomena in sociology--the innovation-decision process." Applying diffusion of innovations research methods to categorize forestland owners will allow foresters to recognize the early adopter groups and direct information transfer programs to them. The early adopter category, more so than any of the other four, exhibits the highest degree of opinion leadership and, therefore, is the key target audience for change agents (Rogers 1983).

METHODS

Preliminary Work

One hundred and forty scientists in the fields of rural sociology, forestry and natural resources were contacted by mail. The study design was based on suggestions of the fifty-nine respondents and of other personal contacts. Following pilot interviews with research scientists and investigation of questionnaires used in other studies, the final 12-page questionnaire and interviewing techniques were developed and field tests were conducted.

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³In this paper, private forestland refers to nonindustrial private forestland.

Selection of Study Areas

Eight counties were selected based on statistical data and discussions with the county agents in all eighteen counties in the South Carolina Piedmont region. First-stage selection was based on three factors used to create a composite ranking: (1) income from forest products as a percentage of total land-derived income in the county, (2) the percentage of county commercial forestland owned by private forestland owners, and (3) the number of acres of private forestland in each county. Data used are available for all South Carolina counties, as well as generally throughout the United States. Final selection was based on four factors: (1) the counties were among the top ranked according to the composite ranking scheme, (2) the percentage of national forestland within the county was low (less than 20% of the total commercial forestland), (3) no major urban areas occurred in the county, and (4) the county agent was willing to cooperate and relatively enthusiastic about the project.

Identification of Opinion Leaders

Opinion leaders were identified by requesting a list from three people in each county who were familiar with the county residents. County Extension Service agents, South Carolina Forestry Commission foresters, and one other local resource person provided lists which were prepared independently.

Sixty-four of the one hundred and ninety-six nominees were selected for interviews based on the following criteria:

1. All opinion leaders named by more than one informant were asked to participate in the study (except those eliminated by Item 2).
2. The county agent or commission forester (primary informant) was consulted to screen the list of nominees. Professional foresters, landowners employing full-time foresters, additional members of the same family owning forestland mutually, and those persons judged as likely to be uncooperative or unknown by the primary informant were deleted from the lists. The remaining opinion leaders were ranked by the primary informant in each county and interviewees were chosen according to this order.

3. A minimum of seven and a maximum of fifteen opinion leaders were interviewed in each of the eight counties.

Interview Process

All subjects were personally interviewed by the author. Each interview was tape-recorded and lasted about two hours. Short answers to specific questions were written on questionnaire forms during the interview. Other responses were transferred from the tape to the forms after the interviews were completed. The primary goal was to establish an atmosphere conducive to

conversational responses rather than restricting replies to forced-choice lists.

RESULTS AND DISCUSSION

Evaluation of Informants

The ability of the county agent and the county forester to name opinion leaders was compared by developing a "success indicator" based on identical nominations. The test revealed the amount of cross-over between informants, taking into account the differences in numbers of names submitted by the three informants in each county. A score of 1.00 would indicate complete agreement. Although differences occurred between counties, and between agent and forester in the same county, the average success indicator was essentially the same: agent .32, forester .33. The two types of change agents exhibited approximately the same informant ability. It is important to recognize a limitation to this success indicator test: it assumes the agent, the forester, and the third resource person had equal facility for recalling names of opinion leaders and recognizing opinion leadership qualities of nominees based on the written descriptive characteristics provided by the author and enumerated below:

1. Not the first, but one of the first, to try a new idea.
2. Having more education than the average, but not the most.
3. A leader in community organizations, but not usually state or national ones.
4. Respected by neighbors as a "good manager" of his land.
5. Owning a moderate area of farm/forestland but not the largest amount.
6. Getting most of his information about new farm/forestry practices from county agents, extension bulletins, newspapers, and magazines.
7. Progressive in his thinking but not radically different from most other people.

Verification of Opinion Leaders

The self-designating method (Rogers 1983) was used to verify that the opinion leaders could be categorized as early adopters. Combined responses to the seven questions on a self-judgment test developed by the author indicated 81 percent of the opinion leaders considered themselves early adopters and 16 percent considered themselves early majority. One person thought he was an innovator and one a late majority adopter.

Majority Traits, Attitudes and Values

A diverse population was deliberately selected to include a variety of people with regard to age,

race, religion, sex, occupation and other characteristics. The only common attribute required for nomination was opinion leadership. Nevertheless, many attitudes and traits were shared by a majority of the opinion leaders.

Personal Characteristics

Most of the opinion leaders sampled were over 50 years old, male, a farmer, or a businessman. Most spouses never worked outside the home or were retired. The respondents had two or three children and considered the family upper-middle class or upper class socially and economically. The family's annual income was over \$20,000 with nearly equal numbers earning \$20-30,000, \$30-40,000, \$40-50,000 and over \$50,000. Few reported incomes of less than \$20,000. Most opinion leaders believed that their family could not get by on less income, although 44 percent indicated they could.

Cultural Characteristics

The typical opinion leader was of Scotch-Irish descent and spent his childhood on a farm. He went on a vacation sometime during the past 12 months, either traveling or to the beach. He liked music, was more likely to read magazines than books, and watched television more than he listened to the radio. He had no desire for more leisure time. Many were retired and others preferred working to relaxing. Hunting, reading and fishing were favorite pastimes when participating in leisure activities.

Over 90 percent of the opinion leaders reported reading magazines regularly. The most popular was "Progressive Farmer." Only 11 percent of the opinion leaders read forestry-related magazines. Opinion leaders enjoyed a wide variety of music including opera, classical, religious, and swing, but "country" music was the most popular. Nearly one-half of the respondents listed news as their favorite television, followed by sports. As was the case with magazines and music, a wide variety of preferences was given.

Institutional Characteristics

A typical opinion leader was married and living with his spouse. He characterized himself as a political conservative; only one was a liberal. Seventy percent of the respondents had at least some college; 53 percent had a degree. He was a member of a Protestant church, usually Methodist, Presbyterian, or Baptist, and often one or two other social groups and one or more civic, government, farm or professional organizations, but he did not belong to a hobby group. The Farm Bureau and Cattleman's Association were the two farm, business or professional organizations in which opinion leaders were most active. Many were members of several other dairy, beef or other livestock organizations. About one-third of the respondents did not belong to any farm, business or professional organization. However, nearly one-half of these opinion leaders belonged to a

forestry-oriented organization or served on a forestry advisory committee.

Twenty-two percent of the respondents did not participate in civic or government organizations. Those who were active in such groups participated in twenty-six different organizations, with the Soil Conservation Service and Lions Club ranking first and second. Participation in organized groups was usually restricted to the local level, not state or national. This was one characteristic which distinguished these opinion leaders as early adopters instead of innovators.

Information Sources

One of the key variables in technology transfer is information sources. Diffusion of innovations research indicates that early adopters get most of their information from local change agents, farm magazines and extension bulletins. This was true of the people in this study. The percentage of opinion leaders using each source was:

| Information Source | Percent |
|------------------------------|---------|
| County forester | 85 |
| SCS or ASCS | 74 |
| County agent | 68 |
| Farm/forestry magazines | 66 |
| Industry forester | 58 |
| Extension/research bulletins | 56 |
| Forestry organizations | 47 |
| Family traditions | 47 |
| Paid forestry consultant | 45 |

More than 65 percent of those evaluating information sources rated the above sources as "good." Other sources rated good by 50 percent or fewer were a logger or buyer (50), friends and neighbors (42), newspapers (40), television (38), other forest landowners (37), and radio (31).

In discussions with the landowners, it became clear that newspapers, radio, and television are good sources of farm technology information but little forestry information is received via these mass media. Apparently, forestry technology transfer programs are not fully utilizing these communication channels. It should be noted that diffusion research has shown that mass media has been most useful for creating awareness, not persuasion.

Forestland Ownership

The typical opinion leader had lived on or near his forestland more than 20 years, many all of their lives. Approximately one-third of the respondents bought all of their forestland, one-third inherited it and one-third owned some land that was bought and some that was inherited.

The total number of acres of rural property reported by these individuals ranged from 85 to 12,000. Those reporting acres by forest type owned between 30 and 5,400 acres of forestland. The median size was 300 acres. Sixty-seven percent of their rural property was in forestland.

Most of the forestland was in natural pine or mixed pine-hardwood. Only 16 percent was in planted pine and 8 percent in hardwoods.

Most opinion leaders had sold pine and hardwood pulpwood and sawtimber and cut their own Christmas trees, fenceposts and firewood. Only two people reported no sales. One-half of the respondents reported making a sale of forest products within 10 years after acquiring the land. Income from past sales had been used for farm, business or living expenses; to reinvest in other areas; or to pay for the land from which the timber was harvested. Only four respondents had used timber sales income for reforestation of their land and only five planned to use future timber sales income for this purpose.

Nearly 80 percent of those interviewed said: "I wish I had invested some money or more money to improve my forestland." They were aware of the increase in prices for timber and, in retrospect, thought investing more money in improving their forestland for timber production would have been a good investment. However, many believed that the time for profitable investment had passed, prices would not continue to increase, and they did not intend to invest money in forestry.

Reasons for Valuing Forestland

Opinion leaders gained satisfaction from owning their forestland for several reasons other than, or in addition to, income production from timber sales. Some of the most frequently given reasons were not related to timber production or economics but were categorized as lifestyle enhancement values. More than 80 percent of these owners said:

I'm proud of it.
It protects the environment.
It is satisfying just to own it.
Birds and animals live in my forest.
It's like money in the bank.
Wildlife is important to me.
I like to walk in the woods.
We cut firewood from our forest.
It will help finance my retirement.

When asked specifically about wildlife, 78 percent of the respondents had hunted game animals, but more had enjoyed the following activities:

Appreciated fall leaf colors.
Gathered wildflowers, nuts, or berries.
Watched migratory birds.
Observed birds and animals.
Provided food for wild animals.
Observed flowering plants.

Forty-eight percent of these owners valued their forestland primarily for timber production (11 percent) or economic reasons (37 percent). More than one-half of them (52 percent) gave lifestyle enhancement values as the primary

reasons. Since this was the case, effective change programs must be designed to encompass noncommodity lifestyle enhancement goals which are clearly unrelated to economics or timber production. Chi-square tests indicated that the respondent's age, income, education, retirement status, and size of his forestland holdings were not related to his primary reason for valuing his forestland, but his occupation was related to his perceived benefits.

| Independent Variable | Chi-square | p-value |
|--|--------------------|---------|
| Age: < 50, = or > 50 | 0.938 | 0.33 |
| < 60, = or > 60 | 0.382 | 0.54 |
| Income: < \$30,000, = or > \$30,000 | 0.543 | 0.46 |
| Education: college degree, no degree | 0.963 | 0.33 |
| Occupation: farmer, businessman | 6.313 ^a | 0.01 |
| Retirement: yes, no | 1.666 | 0.20 |
| Size of forestland ownership: < 300 acres, = or > 300 acres | 0.087 | 0.77 |

^a A Chi-square of 6.31 with a p-value of 0.01 indicates nonhomogeneity.

Those owners whose primary source of income was farming gave reasons related to timber production or economics, and businessmen gave reasons related to lifestyle enhancement values.

CONCLUSIONS AND QUESTIONS

Three conclusions of the study lend credence to the use of an interdisciplinary approach combining forestry and sociology to improve technology transfer to private forestland owners:

1. Opinion leaders who own nonindustrial private forestland can be identified equally well by county agents and county foresters.
2. These opinion leaders can be categorized as early adopters.
3. More than one-half of the opinion leaders placed more importance on lifestyle enhancement benefits of their forestland than on timber production/economic benefits.

This preliminary study has explored the applicability of some diffusion of innovations research methodology to the nonindustrial private forestland owners social system. The findings are presumed applicable in rural counties of the South Carolina Piedmont, but not necessarily elsewhere. Much work remains to be done. Two important questions are:

1. Do the findings apply to other nonindustrial private forestland owners (a) who are not living on their land? (b) who live in other geographic locations?

2. Do silvicultural practices spread through the nonindustrial private forestland owners social system in a manner similar to diffusion of innovations in other social systems?

ACKNOWLEDGMENT

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A Comparison of Profitability for Agricultural and Forestry Production on Southern Marginal Cropland¹

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Land is the fundamental production resource for agriculture and forestry. For the past two decades the U.S. has been burdened with declining agricultural commodity prices, excess crop production, and most recently, increasing acreage being cropped for agriculture. Fedkiw et al. (1983) estimated that there are 2 to 7 million acres of crop and pastureland in the Southern States of North Carolina, South Carolina, Florida, Georgia, Alabama, Mississippi, Louisiana, Arkansas, Tennessee, and Texas which would produce a greater net return from forestry than from existing agricultural crops. Vasievich estimated that there are close to nine million acres of highly erodible agricultural low productive cropland in these ten Southern States. Converting marginal cropland to forest would reduce excess crop production and increase agricultural commodity prices, thus providing a higher rate of return on investments to those who remain in agriculture. Higher commodity prices could also reduce the cost of farm crop subsidy programs.

Timber is unique among marketable commodities in that its prices over the long term have been increasing in relation to the prices of other goods. Adams and Haynes (1980), in what is probably the best known forest econometric model, project a continuation of this trend of increasing prices. If the demand for timber continues to increase as expected through 2030, further real price increases are likely for southern timber. This outlook exist in part because of inadequate regeneration of pine after harvest and loss of forest acres to other land uses.

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Abstract.--An analysis is underway to compare returns from crop and pine timber production on marginal cropland in 10 Southern States. Marginal, highly erodible cropland has much lower yields than most other farmland producing the same crops in the same regions. Low yields retard earnings, no matter what the product price. Much of this marginal cropland may be highly productive for pine culture.

Not surprisingly, we have found very low returns from corn, wheat, and soybean production on such land. Although the analysis is incomplete, we believe that returns from pine culture will be higher than that from crops, even when 10-year Conservation Reserve payments are ignored.

Keywords: Marginal cropland, returns, production alternatives, crop conversion.

This paper describes progress in an effort to compare the net returns of investment alternatives in agriculture and forestry for owners of southern marginal cropland. The analysis is confined to sites within the 10 states on which low agriculture productivity and high erosion potential. Marginal cropland, as used in this paper, is defined as land presently in agricultural crops that does not generate returns sufficient to cover the cost of production and that has an erosion factor of at least 3T (three times the Soil Conservation Service acceptable soil loss tolerance).

Marginal cropland in the South is identified by using Major Land Resource Areas (MLRA). MLRA's are major geographic land resource units that are characterized by a particular pattern of soil climate, water resources and land uses. In the South 30 different MLRA's contain marginal cropland.

Land Use in the South

In a thorough discussion on southern land use, Healy (1985) reported that 56.5 percent of southern land is forested. The Coastal Plain tends to be pine country, the Piedmont a mixture of pines and hardwoods with the upland forest consisting of a few local softwood stands, but containing predominantly hardwoods.

Agriculture, ranked second, occupying 17.6 percent of the total land area of the 12 Southern States examined by Healy. By acreage, the South's principal crops are soybeans (over 25 million acres) wheat, corn, hay, cotton, rice, and peanuts. The highest value crop is soybeans with tobacco a close second. Healy found that grazing is the third most important use of southern land. Approximately 41 million acres, 12.5 percent of the South's land are used exclusively or primarily for pasture and rangeland. The fourth most important land use category Healy discussed was called the "built-up area," which accounts for 6.4 percent of the South's land.

Flexibility of land use has always been an important asset in America. National Resources Inventory (NRI) of the Soil Conservation Service (SCS) indicates that between 1967 and 1975 approximately 80 million acres of land has shifted between agriculture and forestry.

During that period, there was a net loss of approximately 30 million acres of forestland (Alig 1983). Many acres lost to forestry were gained by agriculture as agricultural prices increased in the 70's.

Analysis of competitive land uses is complicated by the different time patterns of income flows from various uses (Alig 1986). All else being equal, landowners may prefer (or require) the annual returns of agriculture, to the less frequent returns from forestry. Land use comparisons also involve "expected" net incomes. Alig raises an additional complication because little is presently known about how landowners estimate future prices and cost associated with alternative uses. In this paper, we present expected incomes for agriculture and explain how forestry incomes are to be calculated in hopes of reducing complications and providing landowners and policy-makers with relevant information.

Government Programs

Recent concern within and outside the USDA has focused on consistency of some USDA programs designed to influence land use decisions. Specifically, programs to reduce excess production of agricultural commodities, to support commodity prices conflicting effects and income and to promote conservation have inconsistent and conflicting effects.

Commodity price and income support programs are designed to improve prices and raise farm income (Osteen, 1984). Higher, more certain income leads to increased investment in crop production, including bringing marginal cropland under cultivation. When a commodity program is instituted, it is to the land-owner's advantage to maximize the use of the area under cultivation. By doing so the landowner minimizes the impact of withdrawing a part of the land from production and maximizes the acreage base from which payments computed.

If future prices are uncertain, landowners are less inclined to commit to long term investments. Higher, more stable prices encourage the development of more marginal land, and discourage the conversion of cropland to forest. Hence, if marginal cropland is erodible, some commodity programs tend to encourage the use of erodible land, while soil conservation programs hope to discourage such use.

Empirical Viewpoint

Some research indicates that the price increases associated with commodity programs benefit as much or more nonparticipants than participants. Johnson and Short (1983) indicated

that 70 percent of indirect (price improvement) benefits of the 1978 corn acreage reduction program in selected Southern States were received by those who did not participate in the program. Gardner (1981) estimates that farm programs increased prices received by farmers by 6 percent in 1978-79. Participants and nonparticipants alike benefit from these price effects. Participants also receive direct payments, but they give up income on land temporarily idled to comply with program requirement.

Reichelderfer (1984, 1985) studied farms in highly erodible areas of the U.S., including the Southern Piedmont, the Southern Coastal Plain, and the Southern Mississippi Valley. Erosion was measured at 2,800 sample points in 68 counties. The characteristics of the operators who managed the land at each point were then tallied and analyzed. One of the major goals of this effort was to identify relationships between USDA program participation and erosion. The results show that those participating only in commodity programs had a higher percentage of their land eroding at greater than 5 tons per acre per year than did nonparticipants and those participating in both conservation and commodity programs. Nevertheless, she found that participants in the USDA programs show some contribution to soil erosion.

Reichelderfer (1984) found that 50 to 75 million acres (41 to 18 percent of the U.S. cropland) losing more than 5 tons per acre per year to erosion were operated by participants in USDA commodity and/or conservation programs. However, 70 to 95 million acres of all cropland eroding at similar rates were operated by those who did not participate in USDA programs. USDA program participants farmed 30 to 70 million acres in such a way that erosion was at or below 5 tons per acre per year.

Conservation Reserve

The developers of the Conservation Reserve that is included in the Conservation Title of the 1985 Farm Bill estimate that over 70 million acres nationally and 5 million in the South will be eligible for the reserve in SCS capability classes six to eight or two to five. These classes have an average soil loss greater than 3T per acre per year in their present agricultural crops (Neal, 1986). These figures include wetlands as well as highly erodible land. The program is structured so that conversion from agriculture to permanent grasses or forestry will be gradual. One-sixth of all land in the reserve is targeted to be planted to trees.

Conservation Title of the 1985 Farm Bill

Clearing for agriculture in the past has been a major cause for declining forest acreage. Since 1960, 6 percent of the nation's forest land has been lost to agriculture (Fedkiw et al., 1983). Many of the gained acres by agriculture have been marginal cropland. For one or more physical reasons, this land is not as productive as the average quality farmland.

For the past 30 years the USDA farm programs have encouraged conversion of some agricultural land to forest. In the mid 1950's the Soil Bank Program was initiated with the primary purpose of diverting land from the production of farm crops, but also to establish conservation practices. This program led to the development of numerous pine plantations scattered throughout the South. Between 1957-1961 nearly 2 million acres of trees were planted in the South (Alig, Mills and Shackelford, 1982). Many of these pine plantations now contains pulpwood, small sawlogs, and other forest products. The reserve program is similar to The Soil Bank except that conservation is the major concern of the newer program.

The 1985 Conservation Reserve Program (CRP) has four parts each having its own objective:

Conservation Reserve: Provide annual rental payments for 10 years to take out of production cropland that has the highest erosion levels. Also provide half of the cost to establish a conservation cover on converted land.

Swampbuster: Discourage conversion of additional wetlands to agriculture by making landowners that do so ineligible for many government benefits.

Sodbuster: Discourage the breaking of new highly erodible land into agriculture and encourage the use of adequate conservation practice if crops are planted.

Conservation Compliance: Encourage widespread use of conservation practices on highly erodible land by tying compliance to government program benefits.

The CRP will attach permanent land use restrictions on 45 million acres over the next 15 years. Financial incentives are offered to encourage landowners to take advantage of alternative production activities. Land qualifies for the program if it is susceptible to annual erosion greater than 3T per acre per year. Neither land subject to potential wind erosion nor highly erodible land not presently being cropped for agriculture is eligible for the program.

Landowners wishing to participate are accepted in a first come first served voluntary bidding system. There is a maximum annual number of acres per county accepted into the program (25

percent of cropland in any one county). After bids are accepted, the landowner must grow either trees or grasses on the bidden land area for 10 years without harvesting or selling whatever is grown on the land. In return, the federal government will pay 50 percent of the cost of conversion plus an annual payment for the first 10 years. The Cross-Compliance program in the CRP will penalize landowners that farm highly erodible cropland after 1990 without an approved conservation plan by making them ineligible for many government programs. This program is an example of how the government is trying to improve and implement its existing programs.

Fedkiw et al. (1983) reported a possible long-run economic gain for owners of marginal cropland in the South who convert to loblolly pine (*Pinus taeda* L.) plantations. Conversion to forest crops from agriculture could decrease farm surpluses, increase the nation's long term timber supplies, dampen the expected strong upward trend in softwood timber prices, and provide an economically efficient and competitive return on forest investment while reducing soil erosion and stream sedimentation and improving wildlife habitats.

Investment decisions for land are usually constrained by capital limitations, lack of relevant information, owner objectives, market expectations (short and long term), and future technological developments. The investment alternatives for marginal cropland were analyzed here according to the profit maximization criterion. Different profit maximization criteria are discussed by Hirshleifer (1984) and Henderson and Quandt (1968). These criteria include unit cost, present value of net returns, present value of benefits and cost, internal rate of return, and pay-off period. In this analysis, the present value of net returns before taxes is used to determine the profitability of each production venture.

Agriculture

In analyzing the profitability of agriculture and forestry, it is assumed that only three crops, soybeans, corn, and wheat are grown on southern marginal cropland and that only southern pine will be grown on converted marginal cropland. These crops and tree species were selected because they are the most prevalent crops and trees grown commercially in the South. Others (Hardie 1983; Eason and Flinchum 1984, and Fedkiw et al. 1983) have in some way compared agricultural production to forestry production using land rents or returns per acre. Here the production of three agricultural crops is compared with to southern pine production on southern marginal cropland. The income landowners receive from USDA agricultural and forestry income and support programs is also considered.

Agricultural Crops

The per acre yields for each crop are the result of the best two out of three years 1982 to 1985 on the selected MLRA by state from SCS crop budget data. The annual national average yield for corn is 110 bu/acre, but on southern marginal cropland the highest average yield for the specified period is 80.7 bu/acre. The highest annual average yield for soybeans on marginal cropland is 27 bu/acre in Louisiana compared to the annual national average of 75 bu/acre. The national average annual yield for wheat is 70 bu/acre, while on marginal cropland the top yield is in Mississippi at 41 bu/acre.

The estimated costs per acre for producing acre of corn, soybeans, and wheat on southern marginal cropland were taken from budget data of the SCS of the USDA (Tables 1, 2, and 3). Total costs per acre ranged from \$77 to \$179 for corn; \$81 to \$243 for soybeans, and wheat from \$63 to \$160. These total costs included both variable costs and land ownership cost, cost differentials are assumed due to regional land characteristics.

TABLE 1. ANNUAL AVERAGE NET RETURNS BEFORE TAXES FOR WHEAT GROWN ON SOUTHERN MARGINAL CROPLAND

| STATE | AYIELD | PRICE | TOT COST | GROSS RET | NET RETURN |
|----------------|----------|--------|----------|-----------|------------|
| | BU./ACRE | \$/BU. | | \$/YIELD | |
| ALABAMA | 38 | 3.12 | 85 | 119 | 34 |
| ARKANSAS | 38.4 | 3.23 | 97 | 112 | 15 |
| FLORIDA | 35.7 | 3.24 | 148 | 119 | -29 |
| GEORGIA | 35.4 | 3.11 | 62 | 113 | 51 |
| MISSISSIPPI | 40.5 | 3.28 | 119 | 133 | 14 |
| NORTH CAROLINA | 37.4 | 3.10 | 124 | 110 | -14 |
| SOUTH CAROLINA | 35.7 | 3.11 | 122 | 115 | -8 |
| TENNESSEE | 38 | 3.16 | 95 | 120 | 25 |
| TEXAS | 39.1 | 3.49 | 115 | 136 | 21 |

^aBEST TWO OUT OF THREE YEARS

SOURCE: Derived from unpublished data provided by USDA Soil Conservation Service, Washington, DC. 1986.

Total costs (variable cost and land ownership cost), yields (per bushel per acre), and current normalized prices data for 1985 were extracted from the SCS data files and used to calculate net returns (before taxes) for each crop by state on MLRA's classified as marginal southern cropland. Established yields were multiplied by the current normalized price per crop to obtain the gross returns. Total cost was then subtracted to get net return before taxes.

Net returns per acre before taxes for wheat varied from -\$52 to \$75; corn returns per acre ranged from \$105 to \$65; and soybeans the lowest of the three crops -\$155 to \$25. Unfortunately, it was not possible to obtain data on the amount of income support and commodity monies provided

TABLE 2. ANNUAL AVERAGE NET RETURNS BEFORE TAXES FOR SOYBEANS GROWN ON SOUTHERN MARGINAL CROPLAND

| STATE | AYIELD | PRICE | TOT COST | GROSS RET | NET RETURN |
|----------------|----------|--------|----------|-----------|------------|
| | BU./ACRE | \$/BU. | | \$/YIELD | |
| ALABAMA | 21.4 | 4.98 | 115 | 106 | -9 |
| ARKANSAS | 20.4 | 5.08 | 108 | 108 | 0 |
| FLORIDA | 25.8 | 5.11 | 163 | 132 | -41 |
| LOUISIANA | 26.8 | 5.03 | 126 | 118 | -8 |
| MISSISSIPPI | 25.7 | 5.10 | 121 | 131 | 10 |
| NORTH CAROLINA | 22.98 | 5.02 | 131 | 103 | -28 |
| SOUTH CAROLINA | 21.19 | 5.08 | 131 | 99 | -32 |
| TENNESSEE | 23 | 5.05 | 145 | 116 | -29 |
| TEXAS | 23.7 | 4.80 | 93 | 96 | 3 |

^aBEST TWO OUT OF THREE YEARS

SOURCE: Derived from unpublished data provided by USDA Soil Conservation Service, Washington, DC. 1986.

TABLE 3. ANNUAL AVERAGE NET RETURNS BEFORE TAXES FOR CORN GROWN ON SOUTHERN MARGINAL CROPLAND

| STATE | AYIELD | PRICE | TOT COST | GROSS RET | NET RETURN |
|----------------|----------|--------|----------|-----------|------------|
| | BU./ACRE | \$/BU. | | \$/YIELD | |
| ALABAMA | 47.1 | 2.72 | 132 | 128 | -4 |
| ARKANSAS | 59.8 | 2.66 | 123 | 159 | 36 |
| FLORIDA | 80.7 | 2.74 | 154 | 221 | 67 |
| GEORGIA | 53.7 | 2.74 | 168 | 147 | -21 |
| MISSISSIPPI | 60.8 | 2.88 | 162 | 175 | 13 |
| NORTH CAROLINA | 62.5 | 2.62 | 147 | 184 | 37 |
| SOUTH CAROLINA | 58 | 2.73 | 151 | 158 | 7 |
| TENNESSEE | 80.2 | 2.74 | 164 | 219 | 55 |
| TEXAS | 56.7 | 2.87 | 112 | 163 | 51 |

^aBEST TWO OUT OF THREE YEARS

SOURCE: Derived from unpublished data provided by USDA Soil Conservation Service, Washington, DC. 1986.

to individual landowners growing crops in the specified MLRA's. Plans later are to determine cash amounts by state, crop and production region for marginal land to see if there is a significant difference between the expected income and the actual income received.

Net returns before taxes with average yield and normalized prices are shown in Tables 1, 2, and 3. For example corn grown in Arkansas on MLRA 1170 with a yield of 54.1 bushels per acre netted \$17 per acre before taxes at a price of \$2.66 per bushel. Corn grown in Florida on MLRA 1561 had a yield of only 35.9 average bushels per acre and priced at \$2.74 a bushel netted -\$65 per acre. To break even or to cover cost the Florida yield must be at least 60 bushels per acre at the current price. Yields do have a direct relationship to income earned. Since the yields per acre for each crop on marginal cropland are far below the national average, net returns before taxes for the crops in most of the specified acres with in each state produce low to negative returns per acre.

Forestry

A Forest Service analysis of the timber situation in the U.S. projects significant increases in the demand for southern pine because of economic growth and the South's improving position relative to the Pacific Northwest. The timberland base is expected to continue to decrease, and future growth on some land may be lower than originally anticipated (Haynes and Adams, 1980). Continued increase in demand with a relatively stable supply suggest that real softwood prices will rise over time.

Historical land use patterns support the assumption that the land used for timber growing is that left over from most other uses. From 1952 to 1977, real prices of southern softwood stumpage increased from an index value of 57.8 to 138.9 (1967=100). Despite the real price rise for timber and timber products, private nonindustrial timberland holdings decreased from 143 to 134.1 million acres. In that same time period, holdings of forest industries increased from 32.1 to 36.2 million acres (Hardie, 1984). The Conservation Title of the 1985 Farm Bill provides an incentive to the nonindustrial landowner to convert from agricultural crops on erodible land. Vasievich³ calculated that there are 8.8 million acres of highly erodible cropland are suitable for growing trees (Table 4).

Analysis of forestry investments is not yet complete. Some cost analysis has been done, but other analysis is just underway. Forestry returns will be calculated by Timber Mart South's production regions for each state for high, medium and low quality tree sites.

Cost Assumption

Management cost (cost of production) and establishment cost are the only cost associated with growing pine. The establishment cost is a fixed one-time expenditure per rotation, while management cost is the continuing cost of maintaining and managing a pine stand throughout its production period.

The major expense in establishing pine plantations are site preparation, seeds or seedlings and planting. Since the land under investigation is presently in crops, site preparation cost are assumed to be close to zero. Variables for this analysis include total cost, which is the sum of conversion cost (cost of transferring production from crops to trees), establishment cost, management cost, and landownership cost (excluding land purchasing cost). Vasievich has estimated total planting cost of producing pine on highly erodible to be 63 per acre.

³Unpublished USDA Forest Service, Southern Timber Supply Study, Provided by Dr. J. Michael Vasievich, East Lansing, MI. October, 1986.

Growth and Yield

Timber yield at the end of a given cropping period or rotation. The annual incremental growth depends upon species, site condition, management practices. Since we are interested only in southern pine, it is assumed that all owners use the same management practices, and thus that yield depends only on site quality. The productive capacity of a forested area is often expressed in terms of as site index (SI). The height of dominant trees at a certain age. Loblolly pine was selected because it will produce the height yields on highly erodible Southern soils. SCS data on soil type/site and site index for marginal cropland in the South was averaged for a 25 year rotation. Land with low agricultural productivity is not necessarily poor for tree growing. Although thinning schedules could have been calculated using mean annual growth, site quality, and typographic region thinning possibilities were ignored in the analysis. The estimated average volume for marginal highly erodible cropland, according to Vasievich,⁴ is 108 cubic feet per acre per year.

Stumpage Price

Stumpage price is the price paid for trees as they stand in the forest. Stumpage prices vary considerably with tree quality, and location, but these factors were all assumed to be equal for each set of calculations. Past and current stumpage prices for timber were taken from Timber Mart South (various volumes).

Government Cost-Share Programs

Several existing federal and state programs help offset the cost of starting a forest. The two major existing programs are the Forestry Incentive Program (FIP) and the CRP. The Forestry Incentive Program, administered through the Agricultural Stabilization and Conservation Service (ASCS), may reimburse landowners up to 68% of stand establishment cost not to exceed some maximum amount per acre.

For all eligible landowners who have acceptable bids, the CRP pays 50% of establishment cost and an annual incentive payment for 10 years in exchange for growing permanent cover (trees or grass) on the contracted acres. For those who participate, stand establishment cost are minimal. The 10 year income support also makes growing trees more attractive to some farmers, who are concerned about cash flow, but willing to convert to trees.

Calculating Forestry Returns

There are many variables that affect the economics of forestry in contrast to annual crop production. Agricultural crops are harvested annually or semiannually, but trees are grown for

⁴Ibid.

much longer periods of time and for uses other than timber sales. This study is concerned only with income received from tree sales.

Using the production regions of Timber Mart South and adjusting acreage three different net returns for each state were computed on the basis of site quality. The rotation length is to be 25 years. Site qualities are defined as:

- (1) high site - annual mean growth per acre of 85 cubic feet or more,
- (2) medium site - annual mean growth per acre of 50 to 85 cubic feet,
- (3) low site - annual mean growth per acre of 49 cubic feet or less.

It is also assumed that there will be no opportunity cost occurring for any other land uses other than the crops presently grown on the land and southern pine. For each state and each site type from all previously mentioned data Present Net Worth (PNW) for forestry will be calculated.

Return Comparison

The most appropriate criterion for comparing returns from crops and forestry is an annualized version of present net worth.⁵ The recommended 4 percent real discount rate (i)⁵ can be multiplied by the PNW to get net annual equivalent value by state and site quality. The net annual equivalent value of revenue due to timber sales permits comparison of a series of annual crop returns with one future return for each site quality from timber.

Landowners who participate in CRP and convert to trees are eligible for an annual incentive payment averaging \$40 an acre for 10 years. Participation; therefore, reduce the burden of lost cash flow. For example, net return before taxes for corn in North Carolina is \$7 per acre, net returns for CRP participants is approximately \$40 per acre for the first 10 years. After cost for labor and management are deducted, income per acre of agricultural crops is no where near that of tree cover under the CRP.

⁵ Four percent is the real discount rate used by the Forest Service for evaluating long-term investments in resource management which includes estimate for long-term measures of the opportunity cost of capital in the private sector.

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Determinants of Hardwood Lumber Price¹

Jennifer M. Jacobsen and William G. Luppold

The erratic movement of hardwood lumber prices over the last 15 years has been a source of aggravation to producers and buyers of hardwood lumber (fig. 1). In this paper, we isolate and measure the factors that determine overall hardwood lumber price and the price of the predominate domestic hardwood species--oak. By analyzing overall hardwood lumber and oak lumber price, we can compare and contrast price formation of hardwood lumber in general to price formation of our most important species of hardwood lumber.

Hardwood lumber price, as used in this paper, is the average price of more than 30 domestic hardwood species, and oak lumber price refers to grade No. 1 Common (medium grade) red and white oak. Discussion of the determination of these prices is presented in five sections. The first section discusses theoretical factors influencing price and how these principles apply to hardwood and oak lumber price formation. This discussion is followed by discussions on model development, data base, and empirical results. The final section presents an analysis of the empirical model and conclusions.

THEORETICAL CONSIDERATIONS

In most elementary textbooks, price is shown as a function of supply and demand. These relationships usually are shown via linear demand and supply curves intersecting at some market price. If demand increases relative to supply, then price goes up; conversely, when supply increases relative to demand, price goes down. In the real world, price determination cannot always be fully explained this way because there may be large amounts of inventory on hand, or more than one demand interacting with a common supply. Such is the case of the hardwood lumber market.

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Abstract.--Increased export activity in the hardwood and oak lumber markets coincided with rising prices of these commodities, which also coincided with an increase in the overall price level of all commodities. To determine the effect that domestic and international demands have on the prices of hardwood and oak lumber, relative price models were developed to remove the effects of inflation. The models indicated that exports to Europe have had and will have an influence on hardwood lumber price and oak price seems to be more sensitive to changes in exports than overall hardwood lumber price. The main determinants of hardwood lumber and oak lumber prices were found to be domestic demand and millstock levels.

Keywords: Oak, demand, exports.

As indicated, price is mainly the result of supply and demand forces. However, in any given year, as much as 20 percent of the hardwood lumber produced is held in inventory in the form of millstocks (lumber on hand at sawmills). Furthermore, hardwood millstocks can vary by as much as 20 percent from one year to the next. The volatility of millstocks results from the yearly differences in lumber production versus lumber demand and, therefore, affects hardwood lumber price.

Domestically produced hardwood lumber is demanded by both domestic and foreign buyers. The domestic market for hardwood lumber is nearly 20 times the size of the export market. Almost 50 percent of the lumber demanded domestically is oak. Although the export market for hardwood lumber is relatively small, the level of exports seems to affect lumber prices significantly. Again oak is the major exported species accounting for 50 percent of the exports.

MODEL DEVELOPMENT

Luppold (1982) developed an equation for nominal hardwood lumber price as part of a system of equations depicting hardwood lumber demand, supply, and price. The price equation was a multiplicative form and was estimated using ordinary least squares (OLS) procedures. The specification of Luppold's price equation is presented in equation 1 and includes variables representing past lumber price, quantity of lumber demanded domestically, quantity of lumber exported, and millstocks.

$$[1] \quad P = b_0 \text{EXP}^{b_1} \text{QD}^{b_2} \text{QE}^{b_3} \text{MS}^{b_4}$$

where b_0 , b_1 , b_2 , b_3 , and b_4 are estimated parameters and:

P = Current price of hardwood lumber
 EXP = Average price of hardwood lumber over the past 3 years
 QD = Quantity of hardwood lumber demanded
 QE = Quantity of hardwood lumber exported
 MS = Level of millstocks

The weakness in Luppold's specification is that inflation, exports, and expectations of inflation all followed similar paths during the last 15

years. Therefore, the influence of exports could have been over- or underestimated. A real-price (inflation adjusted) model or its operational proxy, a relative price model, would resolve this problem. The difference between relative price movement versus nominal (actual) price movement

can be seen by comparing figures 1 and 2. The models to be presented in this paper are relative price models. Since price expectation in the hardwood lumber market tends to be related to inflationary expectations, the current specification excludes past lumber prices.

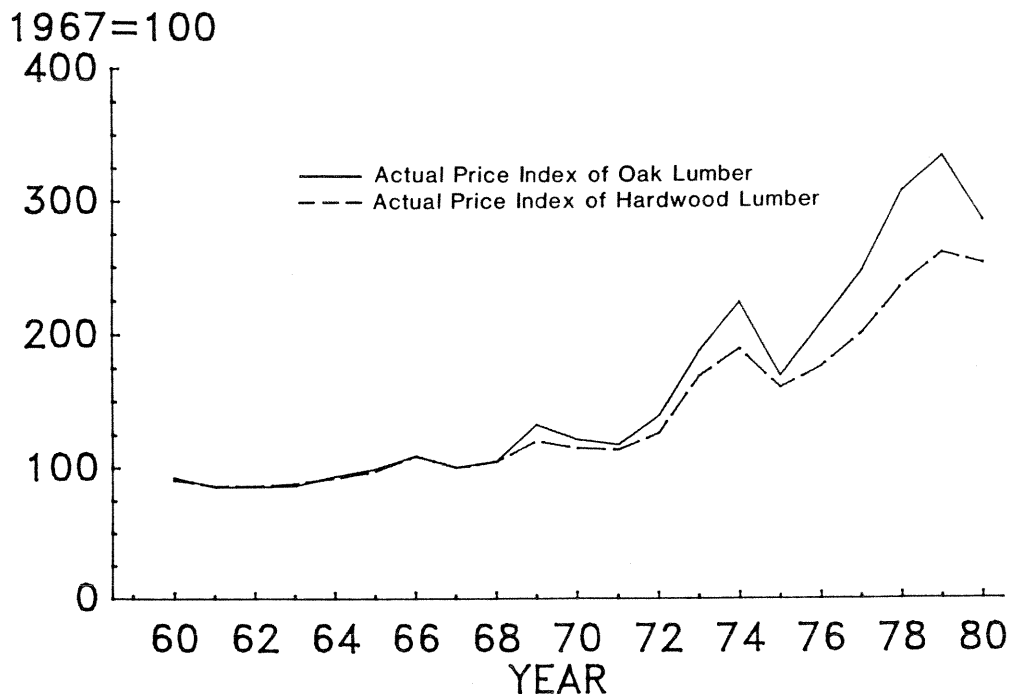


Figure 1.--Indexes of actual oak and hardwood lumber prices.

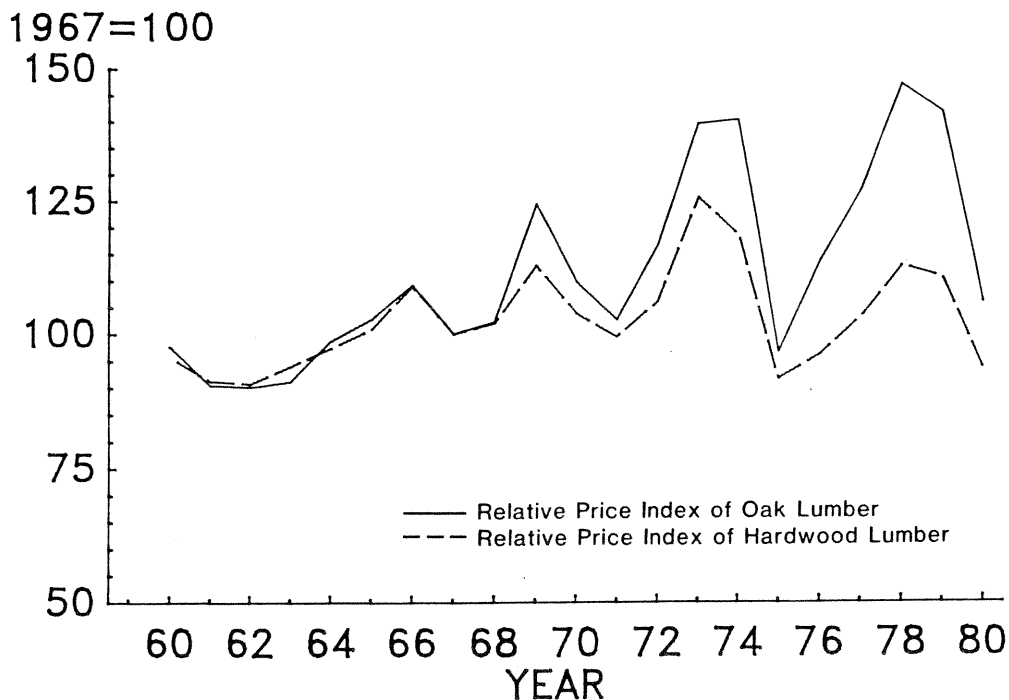


Figure 2.--Indexes of relative prices of oak and hardwood lumber (relative to the price index for all commodities).

Another difference between the specification of the current price equations and Luppold's (1982) specification is that European and non-European exports are represented by separate variables. This allows us to separate the effects of European exports from those of exports in general and to test whether European exports affect domestic lumber price differently from non-European exports. The specific definition of the variable to be included in the hardwood lumber and oak lumber relative price equations is outlined in Table 1.

DATA BASE

The data base used in the estimation of the hardwood lumber price equations and the oak lumber price equation extended from 1960 through 1980. All data were obtained or derived from secondary sources.

Indexes for hardwood lumber price, oak lumber price, and the producer price index of all commodities were obtained from U.S. Department of Labor (1961-80) Producer Price and Price Indexes. Since no aggregate oak price representing all grades and species was available for the study period, the price of No. 1 Common red oak was used as the dependent variable in the oak price equation.

Quantities of hardwood lumber and oak lumber exported were obtained from U.S. Exports, Schedule B. Commodity by Country (U.S. Department of Commerce 1961-79). Millstock and lumber production figures were obtained from U.S. Department of Commerce (1961-80) Current Industrial Reports: Lumber Production and Mill Stocks. Quantity of hardwood lumber demanded domestically was derived by subtracting exports and changes in millstocks from production figures.

The quantity of oak lumber demanded and the millstocks of oak lumber were estimated by multiplying the proportion of oak lumber produced by domestic quantity demanded and by millstocks, respectively. The proportion of oak lumber produced was calculated by dividing oak lumber production by total hardwood lumber production.

MODEL ESTIMATION

The statistically estimated parameters of the hardwood lumber and oak lumber price equations are presented in Table 2. Both equations fitted the data relatively well, as indicated by the R^2 's and the "t" statistics. The nonintercept variables representing exports to Europe, millstocks, and domestic demand were significant at the 0.10 level or better. The variable representing non-European exports was insignificant in both equations. Although the Durbin Watson (DW) statistics are reported for both equations, they are not strictly interpretable because of the inclusion of a lagged dependent variable in the model specification.

The price equations were estimated in multiplicative form by taking the natural logarithms of all variables before estimating the relationships through OLS procedures. Because the equations are in multiplicative form, the resulting parameters are measurements of the percentage change in price resulting from a 1-percent change in the respective independent variable. Such measurements are termed flexibilities (Tomek and Robinson 1972). Because the non-European export coefficient is not statistically significant, future use of the term "price flexibility of export" refers to exports to Western Europe.

ANALYSIS

The estimated price flexibilities indicate that oak lumber price is affected by changes in domestic demand, millstocks, and exports to a greater degree than hardwood lumber price. This finding may explain why oak price tended to fluctuate more than hardwood lumber price even during the pre-1973 period when exports were a minor part of the market. The increased divergence between oak lumber and hardwood lumber price fluctuations since 1973 (figs. 1 and 2) probably results because (1) changes in oak exports affect oak price more than changes in hardwood exports affect hardwood price, and (2) changes in oak exports to Europe have been greater than changes in total hardwood lumber exports to Europe.

Table 1.--Dependent variables for the hardwood lumber and oak lumber price equations

| Variable | Actual variable used in hardwood lumber price model | Actual variable used in oak lumber price model |
|--------------------------------------|---|---|
| Quantity demanded domestically | Quantity of hardwood lumber domestically consumed in current year | Quantity of hardwood lumber domestically consumed multiplied by the proportion of oak lumber produced |
| Exports to Western Europe | Quantity of hardwood lumber exported to Western European countries | Quantity of oak lumber exported to Western European countries |
| Exports outside of Western Europe | Quantity of hardwood lumber exported to other than Western European countries | Quantity of oak lumber exported to other than Western European countries |
| Millstocks (inventories) | Average level of millstocks of hardwood lumber at end of current year and past year | Average level of millstocks of hardwood lumber multiplied by the proportion of oak lumber produced in current year and past year |

Table 2.--Ordinary least squares estimates for hardwood and oak lumber price equations (t statistics in parentheses)

| Item | Hardwood lumber | Oak lumber |
|--------------------------------------|---------------------|---------------------|
| Intercept | 4.06** (2.32) | -0.066 (0.141) |
| Quantity demanded domestically | 0.610*** (3.50) | 1.44* (2.51) |
| Exports to Western Europe | 0.017** (1.52) | 0.074*** (3.41) |
| Exports outside of Western Europe | -0.046 (0.815) | -0.119 (0.942) |
| Millstocks | -0.662*** (6.47) | -0.931*** (4.78) |
| R ² | 0.822 | 0.819 |
| DW | 1.31 | 0.90 |

*** = Significant at the 0.01 level.

** = Significant at the 0.05 level.

* = Significant at the 0.10 level.

Another fact demonstrated by the estimated price flexibilities is that a 1-percent change in domestic demand or millstocks has a much larger influence on hardwood lumber and oak lumber prices than a 1-percent change in exports. In the case of oak lumber price, exports would have to increase by 19.5 percent to have the same impact as a 1-percent change in domestic demand and by 12.6 percent to have the same impact as a 1-percent change in millstocks. However, to fully understand the causes of price variation, the relative impacts of changes in the independent variables that are represented by the flexibilities must be coupled with the actual changes in these independent variables.

From 1972-80, yearly changes in domestic demand averaged 6 percent, millstocks averaged 12 percent, and exports averaged 50 percent. Analysis based on these 1972-80 average yearly changes shows that changes in domestic demand affected oak lumber price 2.3 times as much as changes in exports, and changes in millstocks affected oak lumber price 3 times as much as changes in exports. Similarly, changes in domestic demand affected hardwood lumber price 5.2 times as much as changes in exports, and changes in millstocks affected price 10.1 times as much as changes in exports. In the late 1970's, when domestic demand was increasing and millstocks were decreasing, increased levels of exports helped push lumber prices up even further. On the other hand, during 1979 and 1980, when domestic demand was decreasing and

inventories were increasing, increases in exports helped moderate the drops in hardwood lumber and oak lumber prices. However, since 1980, changes in export demand have moderated; therefore, the effect of exports on hardwood lumber prices has become almost nonexistent.

CONCLUSIONS

The primary factors influencing hardwood lumber and oak lumber prices are price expectations, domestic demand, exports, and level of millstocks. The results of model estimation indicate that the coefficients associated with these variables are higher in the oak lumber equation than in the overall hardwood lumber equation. This explains why there is a greater variation in oak lumber price than in overall hardwood lumber price. The results also indicate that while changes in domestic demand have the greatest relative influence on hardwood lumber and oak lumber price, large swings in level of exports over the last several years have contributed to the large swings in price.

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An Economic and Ecological Perspective on the Renewability of Forest Ecosystems¹

Judith Maxwell²

Abstract.--The role of economic factors in forest management is evaluated from the standpoint of ecological considerations. An alternative approach, which recognizes a forest as a technology in itself, is used to discuss the role of induced technical and institutional innovation in the development and adoption of management techniques which are more consistent with ecological processes.

Keywords: forest management economics, technical choice.

Man and forests have co-evolved in response to each other. Historically, the onus was on man to adapt by devising types of shelter and methods of hunting and gathering which increased the probability of survival. Only very recently, from the standpoint of evolutionary time, have forests become the adapters. This change can be attributed to the emergence of the modern economic state with the primacy it places on human goals and technical advance as a means for overcoming resource scarcity. Forests are primarily viewed as a system for producing market-oriented outputs, such as timber, as opposed to such nonmonetary products as recreation and aesthetics. Furthermore, the failure of market prices to reflect the values associated with the assimilative and regenerative capacities of forest ecosystems have resulted in the choice of "economic" management techniques which ignore impacts on the long-term renewability of forest ecosystems.

RECENT TRENDS IN FORESTRY: SOME OBSERVATIONS

Population pressure, fuelwood demand, and the willingness of governments to liquidate natural resources for foreign exchange have resulted in a loss of two-thirds of Southeast Asian rainforests and one-half of Africa's tropical forests, while more than one-third of Amazonian forests have been cut over (Spears and Ayensu, 1985). Accelerating rates of tropical deforestation have been one factor leading to several alarming projections of species extinctions (Myers, 1979; Ehrlich and Ehrlich, 1981; Soule and Wilcox, 1980). However, even though these ecosystems are extraordinarily vulnerable, little is known about the correlation between the disappearance of tropical forests and species extinction (Harrington and Fisher, 1982).

In contrast, the area of temperate forests has remained relatively stable in recent years; standing timber inventories have actually increased in the U.S. However, the quality of regional forest resources in the U.S. has been questioned (Birch, 1986; McLintock, 1983; Marty, 1983). Also, while there is a general commitment to reforestation in

many countries in the temperate zone, this has frequently meant the establishment of monocultures of *Pinus spp.* resulting in declines in species diversity similar to those associated with agriculture. For mixed temperate hardwood forests, logging practices have negatively impacted natural regeneration causing soil erosion and stream siltation. Selection cutting (high grading) of the hardwood forests in the eastern U.S., by concentrating on the harvest of commercially preferred species and log sizes, has resulted in increasing acreages of poor quality and largely suppressed individuals of less desired species (Barrett, 1980; Seymour, Hannah, et al, 1986). McConnell (1980) suggests that high grading has degraded loblolly pine in the eastern U.S. Ledig (1986) discusses the correlation between the dysgenic effect of certain forestry practices on genetic resources and the potential for diminished resilience of future forests.

Of all the natural resources examined by Manthy (1978), wood was the only commodity that has experienced a continuous long-term upward trend in its real price in the U.S. Such increases in real price are considered to be indicative of "economic" scarcity. Starting in 1979, however, the real prices for standing timber and finished products plunged and have since become so volatile as to be useless in determining scarcity. Brown (1981) argues that a preferred measure of resource scarcity includes some concept of carrying capacity such as the ratio of production to population and points out that the world production of wood on a per capita basis actually declined over the period 1964 to 1980. However, production is a function of demand and the availability of substitutes and, as such, is a very imprecise measure of scarcity.

Hannon (1986) contends that there exist finite limits to the capacity of technical change to mitigate the effects of increasing resource scarcity. Evidence of this limit is the substitution of low-wage for high-wage labor and low-return capital for high-return capital as already witnessed in the shift of extractive resource industries, such as forestry, from developed to developing countries. If we also account for the effects of resource use on the environment, it becomes apparent that resource scarcity reduces both long-term material wealth and environmental quality. We are increasingly confronted with the difficult choice between environmental quality and commercial goods and services. However, where consumers and producers are geographically separated, it is in the consumers' best interest to

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avoid this choice. This factor, in part, has led to a ban on log exports by several southeast Asian nations.

The scarcity of wood in some regions and for particular end-uses has resulted in an increasing trend to plantation forestry. Forestry is undergoing a transition similar to that experienced by agriculture. Some believe that agriculture, by habitat modification, is threatening the very basis of its resounding success—the availability of natural environments which provide an inventory of new genetic strains.³ However, ex situ preservation of genetic capital for agricultural crops far exceeds that for tree species, and given the difficulty in maintaining genetic integrity in storage, in situ preservation is preferred (Ledig, 1986). Jasso (1970) has documented the effects of the expansion of agriculture on the genetic diversity of several species of *Pinus* as remnant stands are increasingly confined to poor sites.

In the case of northern hardwood forests, it is not the lack of genetic capital in a regional sense that is at issue, but the lack of productive use of this capital in individual management decisions. In the northern U.S., plantation forestry has the potential to increase both genetic and species diversity and to create a more diverse regional habitat, as did agriculture initially. However, the correlation between the supply of genetic capital and the extent of diverse, natural forests must be considered whenever habitat is modified or converted.

Duerr (1986) argues that while forests are biologically renewable, what really counts is their social renewability, noting that the ragged condition of many nonindustrial private timber holdings is a social decision. However, our ability to increase the efficiency of extraction and to develop highly productive monocultures in response to economic factors has far outstripped the ability of our social and political institutions to respond to resultant negative impacts on environmental quality. This is due to missing markets for many forest ecosystem benefits and the absence of data on ecosystem processes.

My own research is directed toward explaining technical choice in the management of mixed hardwood forests of the eastern U.S. in terms of the absence of markets for certain forest outputs and to clarify the role of political and social institutions in influencing the development and adoption of techniques which account for environmental impacts. This paper explores some of the

the economic and ecological issues which are relevant to the proposed research.

COMMERCIAL VALUES AND THE VALUE OF FOREST ECOSYSTEMS

The fact that nature's values are seldom economic values is exemplified by the rapid invasion of abandoned farmland by weedy, shade intolerant. And, even though trees provide the major commercial value for forests, characteristics such as immobility, low dispersibility, small number of progeny, and long life spans cause trees to be more susceptible to habitat modification, pollutants and pests than such generalist species as annual plants.

The dichotomy of views is apparent in what many ecologists and economists measure to determine the productivity and stability of natural ecosystems. For ecologists the focus is on ecosystem resilience and the production of biomass, as opposed to economists' preoccupation with the sustained yield of a particular species or log size. The latter concept is epitomized in plantation forestry which maintains an ecosystem in its most highly productive phase (albeit a phase characterized by very low species diversity) through reliance on fertilizers, pesticides, and energy inputs.

The nature of constraints used also shows fundamental differences between the two disciplines. Ecology emphasizes the conservation laws of energy, carrying capacity, and the determination of a stress threshold for ecosystem resiliency. Economics rarely emphasizes physical constraints, except when signaled by prices, concentrating on financial constraints such as interest rates and institutional constraints on investment strategy.

The temporal and spatial treatment of these constraints also differs. For temperate hardwood forests, a time frame of 300 or 400 years is consistent with successional processes well in excess of human planning horizons. The result is that the high discount rates used by private owners to assure short-term profit maximization can cause overexploitation and eventual exhaustion of renewable resources such as forests (Clark, 1973). Even if the discount rate were zero, meaning that future dollars equal current dollars, the relatively short lifespan of humans will still result, for many owners, in forest management practices aimed at keeping a forest in its short-term productive phase even if this undermines long-term health and productivity.

In ecological analysis the choice of boundary (spatial) conditions will focus on the area within which material and energy flows take place and are determined by whether the analysis concerns a species or some higher order process. In economics, borders tend to be political or managerial or may be defined by an economic relationship such as a trade pattern.

One of the major failings of economics, from the standpoint of ecologists, is its preoccupation with human values and the underlying premise that

³It is important to distinguish between species and genetic diversity. Tree improvement programs can provide for more genetic diversity in monocultures than can be obtained in nature where parents are widely separated and the radius of seed dispersal is relatively limited. The concern here is for the loss of genetic capital as habitat is converted to monoculture production not the lack of species diversity in the monoculture itself.

monetary units can be used to value the non-monetary aspects of natural resources. The observed increasing dependence of man-made ecosystems on energy inputs led to the study of energy flows in natural systems, with one objective being to draw attention to the finite limits to development imposed by energy but not made apparent by economic measures. Lave (1986) contends that the major difficulty in estimating the benefits and costs of changes in environmental quality lies in the quantification of these effects in physical terms rather than in evaluation via monetary reductionism which tends to divert attention away from the important issues. However, do energy units do a better job?

ECONOMICS AND ECOLOGY: THE INTERFACE

In spite of obvious differences, there is enough common ground between the two disciplines to support a combined economic and ecologic paradigm for forest management. The short-sightedness of traditional human "use" values, which change too unpredictably over time to be of use in evaluating long-term returns to forest management (such as lumber prices and timber utilization standards), has resulted in a proliferation of new resource value concepts. Economics can take the longer view. In particular, option value, quasi-option value, and bequest value refer to concern over the availability of future uses; the loss of future valuable uses, yet unknown, to habitat modification; and to the altruistic desire to preserve availability for future generations, respectively. These are examples of economists' attempts to find alternative measures of the benefits of natural ecosystems and to incorporate some metric of risk when there exists a potential for catastrophic costs when our current state of knowledge regarding the response of ecosystems to stress is limited.

In practice, the measurement of these value concepts has remained difficult and largely limited to the valuation of individual species and aesthetic and recreation benefits which directly benefit humans. Ehrlich and Ehrlich (1981) differentiate between the direct and indirect benefits of species preservation, defining the latter to consist of the largely free services of ecosystems and the processes which support them. These include the maintenance of atmospheric and aquatic quality, the amelioration and control of climate, flood control, the maintenance of a genetic library, and the supportive role of food webs and nutrient cycling.

The overall deficiencies in the data regarding ecosystem benefits led S.V. Ciriacy-Wantrup (1968) to suggest the Safe Minimum Standard Approach (SMS) which is defined as the minimum level of preservation which ensures survival. This approach has been promoted by Bishop (1978) to argue for the preservation of species. While avoiding quantification of benefits, Bishop takes the continued discovery of valuable uses for species as an indication of their high and rising value. Given that the survival of species is

dependent on preservation of its habitat, and that this habitat is dependent on the ability of its ecosystem(s) to withstand perturbation, suggests the usefulness of the SMS approach in arguing for the preservation of whole ecosystems or even larger areas.

Norton's (1986) concept of contributory value would assign value to species, not due to their direct value to humans, but according to their role in maintaining and accentuating ecosystem processes which provide indirect benefits to man. Contributory value recognizes both the long time frames involved in many ecological processes and the synergism which can result from the interaction of two or more species creating benefits of which none is individually capable. Though empirically elusive, this value concept does provide a useful focus for conceptualizing how forest ecosystems might be evaluated.

Before evaluation can be achieved, some method needs to be devised for monitoring the integrity of forested landscapes over time. The concept of total diversity, developed by Whittaker (1960) and MacArthur (1965) and extended by Norton (forthcoming), offers a more simple spatial framework for evaluating economic and ecologic implications of the diversity-stability hypothesis. Norton argues that it is total diversity, not within habitat diversity, that correlates with stability. Whereas within habitat stability refers to the number of species and frequency and complexity of interactions within a closed ecosystem, total diversity is solely a function of the total number of species in a given geographic area that consists of multiple ecosystems in various successional stages.

As such, the concept of total diversity implicitly recognizes the importance of underlying ecosystem processes by assuming that these processes and/or interdependencies are the result of non-random organization over evolutionary time. Stability is positively related to species count for a geographic area; the more numerous and varied are invading species, the more rapidly and fully will systems develop defenses against similar invasions following future disturbances. Systems which evolve in an environment of high total diversity also exhibit more complex specializations and interdependencies. This view is consistent with the observed changes in diversity within an ecosystem due to successional processes and explains the stability of less diverse, mature ecosystems such as the redwood forests.

The total diversity-stability correlation also explains the fragility of very diverse systems such as tropical forests. The substantial total diversity of the tropics meant that individual ecosystems had to develop mechanisms to withstand the intense, albeit normal, competition or else remain unstable. The effectiveness of these systems in dampening out "standard" disturbances actually increases susceptibility to new, more intense or more pervasive disturbances. Thus, greater local stability may result in diminished global stability.

For northern mixed hardwood forests, which also exhibit a high degree of ecosystem diversity, this may mean that forest management practices which continually diverge from natural successional processes, even if with-in habitat diversity is increased, may not produce greater stability. This also does not suggest that management should be directed at minimizing perturbation *per se*. In his study of forest community development in Wisconsin, Loucks (1970) observed that periodic disturbance resulted in alternating high productivity phases with high diversity phases and concluded that the ability of a forest ecosystem to rejuvenate itself is dependent on the natural tendency to alternate between the two phases.

As a forest economist, I am not able to evaluate the usefulness of the total diversity concept for monitoring the effects of forest management practices, pollution and natural disturbances on mixed hardwood forests. However, it does seem to square with observations. In particular, the concept of total diversity provides a more satisfying answer to the question, "What is forest productivity?" by refuting the traditional notion that practices that increase diversity enhance stability and that local stability is concomitant with global instability.

THE ROLE OF INDUCED INNOVATION AND INSTITUTIONAL CHANGE

Given that diverse forest ecosystems provide substantial benefits to humans, it still remains that these benefits are difficult to quantify relative to those resulting from highly productive monocultures. The fact that many silviculturists agree that historic management practices in northern hardwood forests have negatively impacted productivity, even when the traditional "preferred species/log size" measure of productivity is used provides a strong basis for considering alternative management techniques. However, the absence of a market for most benefits from forests indicates that the development and adoption of appropriate techniques will require institutional innovation.

Binswanger, Ruttan and others (1986) have clearly shown that technological change is sensitive to economic factors such as input and product prices. Ruttan (1971) and Runge (1986) argue that the absence of markets, for both the assimilative capacities and the environmental amenities of ecosystems, has resulted in their overuse or abuse, leading to a demand for an institutional mechanism, such as legislation, to ameliorate negative impacts. This explains the rapid increase in environmental agencies and regulations over the past 15 years.

This high and rising demand for environmental quality is largely limited to upper income countries such as the U.S., where per capita consumption of most forest products has declined since the turn of the century (Duerr, 1986) as has the conversion of forestland to agricultural uses. However, who can blame the poorer countries for the low value placed on environmental quality when

the primary concern is sustenance? The solution to declining environmental quality in less developed countries is likely to require both an increase in and a redistribution of income.

In the U.S., the environmental risk associated with the degradation of forest ecosystems is likely to be less susceptible to control through existing legal and regulatory institutions, due to some of the characteristics discussed by Page (1978) and adapted here to consider forests. First, while there exists a potential for catastrophic loss (that is, a forest ecosystem is stressed beyond some threshold and collapses, thereby imposing high costs to society in terms of altered climatic patterns or loss of potentially valuable genetic strains), the probability of such a catastrophe is very low. Secondly, most of the current environmental legislation is geared to address immediate, acute and visible problems, while the decline in a forest ecosystem may extend over so many years that changes are imperceptible and even masked by other factors. These two characteristics, combined with our ignorance concerning the interactive mechanisms both in forests and between pollutants, disease and pests, make it very difficult to impose corrective measures.

However, the fourth characteristic, the irreversibility of an ecosystem collapse, makes public action necessary. Irreversibility is defined by both economics and time. Once a stress threshold has been crossed ecosystem decline becomes irreversible due to either the long time required for rejuvenation or prohibitive economic costs. Until we recognize the asymmetry which exists between the very modest benefits to individual owners who use dysgenic forest practices and the potential for very high societal costs, we will continue to underinvest in the development of new technological and institutional innovations which will result in the management of forests which is more consistent with ecosystem processes.

Fifth, our traditional definitions of forest productivity fail to recognize that a forest ecosystem and its subcomponents are technologies in themselves. These "ecotechnologies" (Jorgensen and Mitsch, forthcoming) offer strategies for enhancing the productivity of both natural and man-made systems by management (manipulation) of species or higher order processes within an ecosystem. Examples include the management of forests to provide: 1) *in situ* gene banks which protect both genetic capital and the site specific characteristics which are the inputs in the production of this capital; 2) forest islands which are repositories of locally adapted species for colonization when adjacent land is abandoned; 3) forest islands and corridors which serve as oases and passageways for migratory animals; and, 4) forest/wetland and complexes to control acid mine seepage or other point source pollutants.

Sixth, the common property nature of many of the outputs of these ecotechnologies indicates that government or other public institutions must be involved in both the development and the adoption of these ecotechnologies. We have long been aware of the disincentive to the development of a new

technology that cannot be embodied in a product that has a market value or when the benefits of an innovation are rapidly diffused, as in biotechnologies such as high yielding crop varieties. This resulted in an institutional innovation, in the form of government and other publicly funded research institutions, that provides incentives to innovators through direct compensation. The major difference, then, between ecotechnologies and most biotechnologies produced in public institutions is that the latter have relatively well-defined markets. However, while ecotechnologies may provide substantial benefits to society, the individual consumer would be unwilling to pay for a good or service from which other users cannot be excluded. Therefore, public agencies will also be instrumental either in the direct utilization of these ecotechnologies or in providing incentives to individual landowners.

All of these characteristics, I believe, indicate a diminished capacity to provide a timely response to concerns over the renewability of forests. Given the probability of ecosystem collapse, albeit small, and the increase in types and intensities of disturbances to which our forests are subjected, I do not think that we can rely on the usual endogenous pressures which induce technical and institutional change in response to typical problems of environmental quality. However, the theory of induced innovation does provide a basis for determining appropriate responses. In particular, we need to examine how the specific environmental benefits provided by forests are impacted by forest management techniques, and to assess the efficiency and equity of more environmentally benign techniques. We need to do this even though standing inventories are high and the real prices for many forest products remain low because these measures do not adequately reflect the value of many of the indirect benefits provided by forest which are negatively impacted by management practices.

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Forestry Research Evaluation: Why and How¹

Pamela J. Jakes and David N. Bengston²

Abstract.--Recent trends in federal research allocations and increasing scrutiny of research by the public have resulted in a growing interest in forestry research evaluation among forestry research decisionmakers. Current research in this field concentrates on adapting and developing methods for evaluating the impact of forestry research.

Keywords: Research management, program evaluation, forest policy.

Forestry research evaluation is not a new idea or activity. We have traced the first forestry research evaluation to Bernard Fernow. In 1893, Fernow estimated potential increases in timber value from research on the physical characteristics of various timber species in an effort to justify an annual investment of \$40,000 (USDA 1893).

Although research evaluation is not new, interest in developing rigorous methods to evaluate the impacts of forestry research is new. Early forestry research evaluations used relatively informal, nonquantitative techniques to evaluate the general effectiveness of forestry research programs. Recent evaluations of forestry research have concentrated on identifying the specific impacts of new knowledge--knowledge embodied in new production techniques, more effective and useful products, or more refined management practices. Because of this focus, these evaluations have concentrated on applied, not on basic research.

Recently public forestry agencies in the U.S. and Canada have initiated programs to develop methods and frameworks for evaluating forestry research, with a major objective of identifying and quantifying its impacts on the economy, the environment, and society. Why is this activity receiving increasing attention? How should or can we go about evaluating the impact of forestry research? Some answers to these questions are offered below.

WHY EVALUATE FORESTRY RESEARCH

Several major trends contribute to the growing interest in forestry research evaluation.

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First, the level of funding for forestry research has been declining. The magnitude of the decline becomes apparent when we compare recent federal funding of forestry research in the U.S. to funding of agricultural research (fig. 1). One explanation offered for the gap between the funding level for forestry research and that for agricultural research is agriculture's long tradition of research evaluation. Agricultural research evaluations carried out over the past two or three decades have consistently shown high rates of return to agricultural research (Evenson et al. 1979). This has resulted in the widespread perception that investment in agricultural research benefits society. Although we may feel that forestry research produces similar high payoffs, we have lacked, until quite recently, empirical evidence supporting this hypothesis.

A second trend relating to budgets is the "militarization" of research. Significant shifts in research priorities in recent years have resulted in more of the research budget going to national defense (fig. 2). In 1985, 72 cents out of every federal research dollar went to defense programs (Norman 1985). This shift has resulted in increased competition among non-military research programs for the remaining federal research funds.

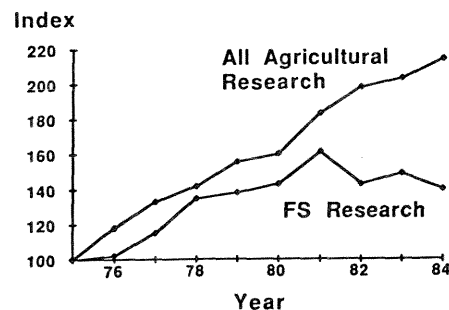


Figure 1.--Growth in U.S. agricultural and forestry research budgets, 1975-1984 (Gregersen and Olmstead 1986).

The third trend is increasing public participation in science and technology decisionmaking. In forestry this trend has been most evident in discussions on the use of pesticides and herbicides in forestry management. In agriculture, we have a striking example of how the public can have a major impact on research programs in the recent legal battle in which the University of California was sued for the allegedly harmful social impact of its agricultural mechanization research (Martin and Olmstead 1985). There may be an important lesson for the forestry research community in this action, as agricultural research decision makers have been widely criticized for not giving enough attention to the social consequences of their research.

Why evaluate research? Because research evaluation can help policy and decision makers meet the demands or opportunities resulting from these trends. John Fedkiw, Associate Director, Office of Budget and Program Analysis, USDA, has been quoted as saying "Evaluation results can be a powerful tool for research managers because such results provide a basis for disinterested judgment in allocating revenues to enhance national welfare or State welfare" (Fedkiw 1985). And Robert Buckman, former Forest Service Deputy Chief for Research, has stated that, "Evaluation activities...give a legitimacy and a credibility to research" (Buckman 1985).

HOW DO WE EVALUATE FORESTRY RESEARCH

Research evaluations can be divided into two categories: impact evaluations and process evaluations (fig. 3). Impact evaluations focus on the impact of research innovations that have been adopted and put into practice. They analyze research inputs and outputs while treating the research process itself as a black box. Process evaluations peek inside the black box to analyze the process by which research inputs are transformed into outputs. Process

evaluations focus on the effectiveness or efficiency of decisionmaking, resource allocation, planning, and other research activities.

The current research in forestry research evaluation focuses on impact evaluations. The research evaluations conducted in agriculture have provided a valuable starting point for research on forestry research evaluation. Research to date has illustrated that methods developed for agricultural research evaluation may be used to evaluate some forestry research efforts.

For example, using an economic surplus approach common in agriculture, Bengston (1984) evaluated returns to research resulting in the development of structural particleboard. He calculated average internal rates of return ranging from 19 to 22 percent. Somewhat surprisingly, a sensitivity analysis indicated that the rates of return were very insensitive to estimates of research costs. Marginal rates of return ranged from 27 to 35 percent, suggesting that further investment in this type of research would produce attractive rates of return.

Westgate (1985) applied the method developed by Bengston to evaluate the impact of containerized forest tree seedling research. He calculated internal rates of return ranging from 37 to 111 percent, depending on (1) the quantity of containerized seedlings produced in the future, (2) estimates of research costs, and (3) the price discount of containerized seedlings. The internal rate of return was very sensitive to assumptions made for the latter two factors.

Although agricultural research evaluation methods are applicable in some forestry cases, we've identified five characteristics of forestry research that make it necessary to develop evaluation methods.

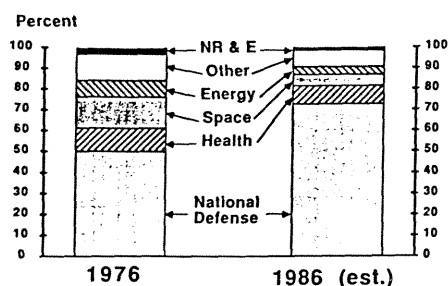


Figure 2.--Percent of U.S. federal budget by budget function, 1976 and 1986 (estimated) (National Science Foundation 1985).

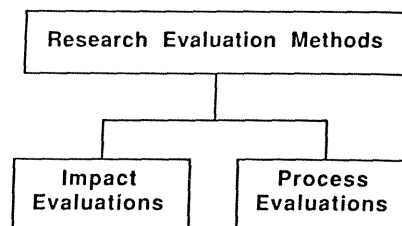


Figure 3.--Impact and process evaluations in the context of the research process.

First, agricultural research evaluations have focused almost exclusively on commodity research. Early forestry research evaluations have also concentrated on commodity research by evaluating research efforts in forest products and utilization and timber management. This early emphasis in forestry is understandable--it is relatively easy to identify the research inputs and outputs for these areas of forestry research, there is a market for the outputs that helps establish research benefits, data required for evaluations are available, and agricultural methods can be adapted for the evaluation. However, commodity research is only a small portion of the total forestry research effort. Other areas of research, particularly those for which research benefits are not easily measured or valued, can not be evaluated using existing methods. We need to develop methods for evaluating commodity as well as non-commodity research.

Second, methods currently available for research evaluation are useful primarily for case studies of specific projects or innovations. However, narrowly focused case study evaluations have been criticized for only considering highly successful research efforts, thus casting doubt on the representativeness of the evaluation results for a given field or industry. We need methods that will enable us to conduct more aggregate level evaluations of forestry research. Aggregate level research evaluations avoid the "success story" criticism by ignoring individual innovations and by instead examining the relationship between research in a broad area and the growth or productivity in an entire industry or sector of the economy. Policy implications are also more credible from this type of evaluation.

In one of the few aggregate research evaluations conducted, Gregersen et al. (1983) evaluated returns to investments in all forest products utilization research. Even with a conservative estimate of benefits and an extremely liberal estimate of costs, the calculated rate of return on the public investment in forest products utilization research was about 20 percent. At the University of Georgia, Fred Cabbage and Don Hodges are developing methods that will allow them to perform an aggregate-level analysis of the impact of public investments in forest management research.

Third, most of the evaluation methods used to date have generated a single measure of worth related to economic efficiency. In forestry, we have found average rates of return ranging from 9 percent for forest fertilization research in the Pacific Northwest (Bare 1985) to more than 400 percent for research leading to the development of the softwood plywood industry (Seldon 1985). For decision makers, economic impacts are seldom the primary

criteria in determining policy or research program direction; therefore we need to develop multiple measures of the worth of a project. We need to develop methods for evaluating the impact of forestry research on society and the environment, as well as the economy.

In an effort to provide broader economic measures of research impacts, David Lewis and his students at Oklahoma State University are evaluating the usefulness of macro-economic statistics, such as employment and income data, in research evaluation. These statistics can tell us more about impacts on society than the traditional measures of economic efficiency.

Fourth, agricultural and forestry research evaluations have been almost exclusively ex post evaluations, analyzing the benefits and costs of past research. It is difficult to make decisions on current or future research programs using studies of past efforts. If evaluations are to be useful in research planning, management, and policymaking, ex ante evaluation methods are needed. Ex ante evaluations analyze the anticipated impacts of research in progress or proposed for future funding. The development of methods for conducting ex ante evaluations of forestry research is critical to the growth of forestry research evaluation as a vital segment of the broader discipline of evaluation research.

Finally, evaluation methods cannot be developed in isolation from the intended users of evaluations. We must understand how evaluations are used and by whom in order to produce useful, relevant evaluation methods. Most of the agricultural and forestry research evaluations have been oriented primarily towards education--that is, increasing knowledge in evaluation research. The challenge is to adapt and expand our effort to ensure that it meets the needs of individuals involved in forestry research resource allocation and policy formation.

How do we evaluate forestry research? Although there are methods available to evaluate some of the impacts of applied forestry research, the answer to this question must be provided by the client (decision maker, policy maker, legislator, citizen) conducting or requesting the evaluation. The issues important to that individual or group determine the impacts evaluated. Clients should be aware that methods are available for evaluating the economic impact of individual technologies. Additional methods for evaluating economic impacts are being developed as well as methods for evaluating social and environmental impacts. We will probably never be able to evaluate all impacts on equal terms, but we must recognize that a variety of impacts are possible and that all must be considered in a thorough evaluation.

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The Forest Products Laboratory (FPL) of the USDA Forest Service has gained international recognition as a leader in wood utilization research. Since its establishment in 1910 on the campus of the University of Wisconsin, FPL has grown to the point where it now employs about 300 scientists, professionals, technicians, administrative, and other staff. In addition to addressing research needs of the forest products sector in the United States, a part of FPL's mission is to "provide worldwide expertise on the technical aspects of wood." Thus, among FPL's technology transfer activities is the distribution of technical articles, features, and written materials to more than 2,000 foreign addresses. Additionally, FPL regularly schedules tours, programs, and technical conferences and meetings for special groups, including a large number of foreign visitors and scientists.

This paper assesses the sources, growth and subject matter of foreign (non-US) requests for information and services provided by FPL over States for information and services provided by FPL, uses this classification to catalog FPL's

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Abstract

In the period 1955-84 the USDA Forest Service's Forest Products Laboratory (FPL) received approximately 3,000 requests for information and services from foreign (non-US) sources. Requests from outside of the United States have grown from fewer than 50 per year in 1955-70 to more than 10 times that number in 1984. Approximately two-thirds of the requests have originated in industrialized countries. More than three-fourths are from private firms and individuals, together with research and educational organizations. The most frequent form of technology transfer is through direct visits to FPL in Madison, WI. Foreign requests for FPL's services have ranged broadly across a number of technical fields: economics and utilization, manufactured boards, protection and preservation, pulp and paper production, wood properties, and wood energy. Requests by technical fields have been largely similar when comparing industrialized with non-industrialized

Keywords: technology transfer, forest products, international.

records of requests for such foreign-oriented information and services, and describes the major and minor lines of FPL's foreign-oriented technical assistance.

ANALYSIS

Description of Data

Data for this study were obtained from FPL's general correspondence files in Madison. All correspondence to FPL during the 30-year period 1955-1984 was surveyed. Recording forms were used to document requests for services, information, materials, etc., from foreign sources according to the following format: (1) country and year of request, (2) type of institution represented by the request, (3) type of information or service required; (4) technical subject of and requests are defined and discussed individually in the following sections.

Region and Time Period

FPL's requests from foreign sources were documented by country and year. These data were then aggregated according to nine geopolitical regions and three 10-year time periods. The results are shown in Table 1.

Of the nearly 3,000 requests reported here, those from mainly industrialized regions outnumbered those from mainly non-industrialized regions by a ratio of 2:1. Only in the first sub-period (1955-64) did non-industrialized regions dominate. For the past three decades as a whole, foreign requests for FPL's services were led by Europe, Asia, and Canada, respectively.

Table 1. FPL's foreign requests, by world region.

| World Region | 1955-64 | 1965-74 | 1975-84* | Total |
|-----------------------------|---------|---------|----------|-------|
| ----- No. of requests ----- | | | | |
| <u>Industrialized</u> | | | | |
| Australia & New Zealand | 17 | 78 | 209 | 304 |
| Canada | 28 | 67 | 295 | 390 |
| Europe and USSR | 87 | 230 | 809 | 1126 |
| Japan | 12 | 37 | 117 | 166 |
| <u>Subtotal</u> | 144 | 412 | 1430 | 1986 |
| <u>Non-industrialized</u> | | | | |
| Africa | 10 | 27 | 122 | 159 |
| Asia (ex. Japan) | 100 | 123 | 273 | 496 |
| Latin America & Caribbean | 69 | 29 | 187 | 285 |
| Middle East | 9 | 8 | 23 | 40 |
| Oceania (ex. Aust. & N.Z.) | 0 | 0 | 12 | 12 |
| <u>Subtotal</u> | 188 | 187 | 617 | 992 |
| <u>All regions (Totals)</u> | 332 | 599 | 2047 | 2978 |

*Data are not complete for years 1977-79.

In some regions the bulk of foreign requests originated from just a single country. For example, India and the Republic of South Africa accounted for more than half of FPL's requests from Asia (excluding Japan) and Africa, respectively.

Figure 1 shows the annual numbers of foreign requests during the study period. Because of missing data, numbers of requests are not shown for the years 1977-1979. The time trends of requests from industrialized and non-industrialized regions move in roughly parallel fashion. Requests increased dramatically after 1971, and again after 1982.

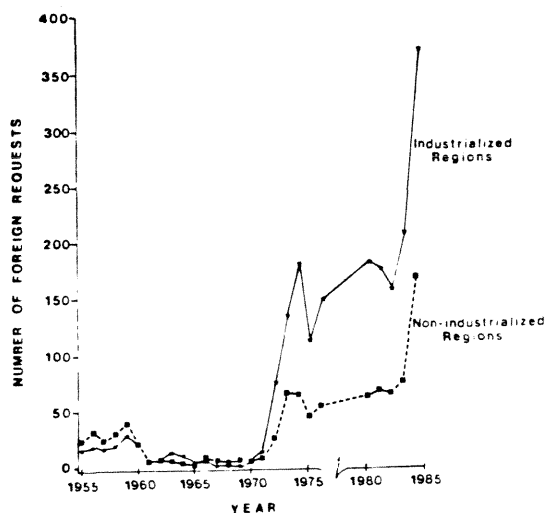


Figure 1. FPL's Foreign Requests, by Year.

Because of missing data, numbers for 1977-79 are not plotted.

Types of Institutions

The requests for technical information and services were classified by the type of institutions represented: private, governmental, educational international agency, or research. The classification was based entirely on information contained in the letterheads and correspondence. Thus assignment to one category or another is inherently affected by a high degree of researcher subjectivity. A part of this problem arises because the categories are overlapping and not always separable. For example, universities, government laboratories, and private firms often engage in research and are considered research institutions themselves.

Subject to these limitations, Table 2 shows that requests have been dominated by private organizations and individuals, research organizations and educational institutions (mainly universities). For the 30-year study period, these three types of institutions accounted for more than three-fourths of FPL's requests from outside of the United States.

Table 2. FPL's foreign requests, by type of institution making the request.

| Type of Institution | 1955-64 | 1965-74 | 1975-84* | Total |
|-------------------------------|---------|---------|----------|-------|
| ----- (No. of requests) ----- | | | | |
| Private | 103 | 125 | 582 | 810 |
| Research | 38 | 191 | 527 | 756 |
| Educational/University | 20 | 82 | 523 | 625 |
| Governmental | 53 | 123 | 216 | 392 |
| International agency | 24 | 5 | 63 | 92 |
| (Not defined) | (9) | (47) | (79) | (135) |
| <u>Total</u> | 247 | 573 | 1990 | 2810 |

*Data are not complete for years 1977-79.

Types of Information and Services

The requests were classified according to the types of information and services asked of FPL. The categories of requests were: visits to FPL's facilities in Madison, professional advice on technical procedures and research analysis, publications and research materials (e.g., wood samples, chemical compounds), services to be performed (e.g., testing and operational), FPL scientists to participate in international conferences and, through cooperative agreements between FPL and foreign institutions, to provide study, training, and research experiences for foreign students and scientists in the United States.

Table 3 indicates that, since the late 1960s, the most numerous requests concerned visits to FPL's facilities in Madison. Requests to visit FPL, requests for professional advice, and requests for publications and materials accounted for four-fifths of all foreign inquiries during the last two subperiods.

Table 3. FPL's foreign requests, by type of information or service requested.

| Type of information or service requested | 1955-64 | 1965-74 | 1975-84* | Total |
|---|------------|------------|-------------|-------------|
| ----- (No. of requests) ----- | | | | |
| Visits to FPL | 14 | 206 | 616 | 836 |
| Professional advice | 86 | 147 | 490 | 723 |
| Publications & materials | 19 | 92 | 477 | 588 |
| Technical services | 8 | 46 | 188 | 242 |
| Participation in international conference | 10 | 11 | 104 | 125 |
| Cooperative agreement | 191 | 80 | 30 | 301 |
| ICA | 159 | 2 | 1 | 162 |
| PL-480 | 6 | 74 | 16 | 96 |
| Other | 26 | 4 | 13 | 43 |
| <u>Totals</u> | <u>326</u> | <u>582</u> | <u>1905</u> | <u>2815</u> |

*Data are not complete for years 1977-79.

But during the first subperiod 1955-64, more than half of the requests originated through cooperative agreements. Most of these agreements were administered through the International Cooperation Administration (ICA), predecessor of the Agency for International Development (AID). The ICA provided funds for training and study by foreign individuals at the Madison facility, often in conjunction with the University of Wisconsin. By 1965 the ICA support had essentially disappeared, and a reduced level of foreign contact with FPL was maintained through the funds of Public Law 480 (often called the "Food for Peace" program). For the 30-year period, approximately two-thirds of FPL's foreign requests under these cooperative agreements originated in non-industrialized countries.

Technical Subjects

The requests were distributed over a wide variety of technical specialties in forest products technology. The survey recognized the following seven categories: wood properties, wood protection and preservation, manufactured boards, pulp and paper production, economics and utilization, wood energy, and other. Often a single request or contact, such as a visit to FPL, was motivated by interests in more than one subject. In these cases, all of the different subject areas were recorded separately. Additionally, some inquiries were directed towards broad research programs at FPL, and these requests were classified as "general".

Figure 2 shows the distribution of requests by technical subjects for the industrialized and non-industrialized regions separately. These distributions were highly similar. For both industrialized and non-industrialized regions, requests were spread quite evenly across protection and preservation, economics and utilization, pulp and paper production, and wood properties. Manufactured boards and wood energy were relatively less important, despite the popularity of wood energy issues during the past few years.

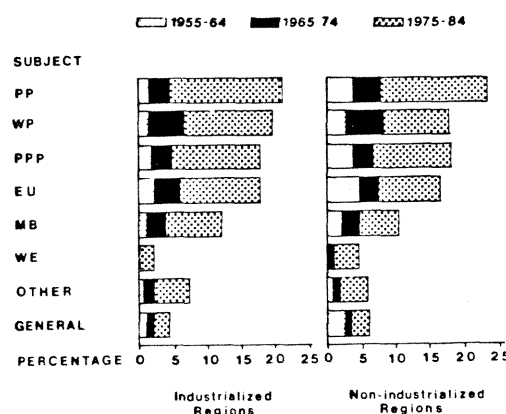


Figure 2. FPL's Foreign Requests, by Technical Subject.

Percentages are for protection and preservation (PP), wood properties (WP), economics and utilization (EU), pulp and paper production (PPP), manufactured boards (MB), wood energy (WE), OTHER and GENERAL.

DISCUSSION

The data and observations presented here attest to the international stature of FPL, and the remarkable growth in its service to the world's forest products industries. This growth is inferred from FPL's correspondence files alone, which is only one indicator of FPL's contacts and technical exchanges at the international level. Travel and communication in a "global village" make FPL accessible to increasing numbers of scientists everywhere. We do not claim that the data presented are highly accurate. A survey of government files spanning three decades is bound to contain inconsistencies and incompatibilities from year to year. The period is sufficiently long that many countries changed political boundaries and names, and many new developments occurred in forest products technologies. Hence, readers should regard these survey data as broadly indicative, not quantitatively precise.

There are many policy questions which come to mind when reviewing technology transfer activities within an organization. Can and should FPL include technology transfer objectives for international clientele? If so, what is the optimal mix of domestic U.S. international service for public agencies? The pattern of requests by technical subjects is broadly similar when comparing the non-industrialized and industrialized regions. Is this an accurate reflection of reality? What are the implications for the issue of "appropriate technology"? The answers to these and other policy questions can only be addressed by the analysts and decision-makers of the USDA Forest Service and FPL. Today's complex market for international goods and services and the growing competition by non-industrialized countries in these markets require close attention by policy makers to the issue of technology transfer.

State Forest Practice Regulation --
The Massachusetts and California Cases¹

Terry K. Haines and William C. Siegel²

Abstract.--The current status and legal background of forest practice regulation in the United States is briefly discussed. The California and Massachusetts statutes, the most comprehensive in their respective regions, are examined in more detail. For both States, historic perspectives are analyzed; important statutory and regulatory provisions discussed and compared; and proposed legislative changes and current administrative trends identified. State forest regulatory trends within the context of using public regulation as a policy tool to control forest landowner activities are briefly examined.

Keywords: Forest policy, forestry practices, public regulation, forest protection, private landowners.

A major component of public forest policy in the United States concerns the appropriate role of government in the management of private forest lands. This question has been widely debated in America for more than a half century. Presently governments at all levels influence private forestry practices through such policy tools as taxation, direct and indirect subsidies, and formal regulation. Historically, regulatory control has been the most controversial of these influences.

HISTORICAL BACKGROUND

Public regulation of private forest lands was first introduced in North America in the early 17th century when the Plymouth Colony passed a law that prohibited the cutting of trees without official permission (Siegel and Cubbage 1985, Huffman 1978). A number of other regulatory laws controlling timber cutting were later passed in many of the colonies (Kawashima and Tone 1983).

After the Declaration of Independence, however, public regulation of private forestry practices received scant attention which resulted in widespread timber exploitation and waste that continued unabated for more than 100 years. Public concern finally led to federal legislation in the late 19th and early 20th centuries that authorized set-aside of public lands and federal purchase of private lands for forest preserves--later designated as national forests. Regulation was not seriously considered at that time.

Extensive debate over public regulation of private forestry in the United States did not begin until about 1917 and continued through the

mid-1920's (Siegel and Cubbage 1985). In 1919, both the U.S. Forest Service and the Society of American Foresters began campaigning for federal regulatory legislation. Even though these attempts resulted in legislation actually being introduced in Congress, all failed.

The debate began once again in the late 1930's (Siegel and Cubbage 1985). Fearing that an onerous federal regulatory law would be enacted if they failed to respond at the State level, 15 States (10 in the East and 5 in the West) passed legislation between 1937 and 1949 for the control of forestry practices on private woodlands (Cubbage and Ellefson 1980). The primary purpose of these laws was to counter the threat of timber shortages by requiring adequate regeneration after harvest--usually in the form of a seed tree requirement. Enforcement was generally mild in the East and strict in the West. The call for further regulation largely disappeared during the 1950's and 1960's, with only one additional state forest practice act being passed.

THE LEGAL FRAMEWORK OF PUBLIC REGULATION

A firm legal basis for public regulation of private forestry practices has existed for many years (Cubbage and Siegel 1985). The courts have unanimously ruled that such regulation is constitutional if enacted to protect the public health, safety, morals, or general welfare. Use of the state's police power to restrict landowner activities in this regard is discussed in Carmichael (1975). Forest practice laws have usually been challenged in court on the basis of the 5th Amendment's taking clause which prohibits the public taking of private property without just compensation. This constitutional provision is generally applied to the individual States through the due process and equal protection clause of the 14th Amendment (Paster 1983). In that respect, the courts have held that forest practice regulation is an appropriate exercise of police power if it does not discriminate among and applies equally to all forest owners.

State v. Dexter (32 Wash. 2d 551, 202 P. 2d 906, 70 S. Ct. 147 [1947]) is the landmark decision

¹ Paper presented at National Symposium of Current Topics in Forest Research: Emphasis on Contributions by Women Scientists, November 4-6, 1986, Gainesville, Florida.

² Forester and Project Leader, respectively, Law and Economics, Southern Forest Experiment Station, U.S.D.A. Forest Service, New Orleans, Louisiana.

involving State forest practice legislation. The only such case to reach the U.S. Supreme Court, it concerned a violation of the Washington state forest practice statute. The defendant maintained that the requirements specifying that trees below a certain diameter could not be cut, and that a cutting permit had to be obtained before logging, was the equivalent of taking private property rights without compensation and due process (Siegel 1974). The trial court ruled for Dexter, but the Washington State Supreme Court reversed and held the law to be constitutional. Its decision was upheld by the U.S. Supreme Court. The Dexter decision has been frequently used in subsequent years to support the enactment of forest practice regulatory statutes.

CURRENT FOREST PRACTICE LAWS

After a relatively quiet period during the 1950's and 1960's, attention was once again focused on State forest practice legislation during the 1970's and 1980's.

Since 1970 a number of States have enacted comprehensive legislation to regulate forest operations on private, and in some instances, public, forest land. The older laws passed prior to the 1970's emphasized timber production and reforestation (Siegel and Cabbage 1984). The modern laws, however, set standards for a variety of forest management activities that include timber harvesting, regeneration, road construction, and slash disposal. They also attempt to protect a wide range of other forest resources such as water quality, soil productivity, fish and wildlife, air quality, and in some cases, aesthetics. These statutes are a response, in part, to the environmental movement of the 1960's and 1970's. The Western States, in particular, have many forested areas on steep slopes with highly erodible soils and near streams. These sites are very sensitive to forest operations. Another force behind enactment of the newer laws has been the Federal Water Pollution Control Act Amendments of 1972. This legislation requires the individual States to develop water quality management plans for the control of nonpoint source water pollution, including that emanating from silvicultural activities.

Enhancement of forest productivity is in the best interest of many western states. Because forest industry is very important to their economies, six Western States--Alaska, California, Idaho, Nevada, Oregon and Washington--currently have a forest practice law enacted or revised during the 1970's. In addition, New Mexico has an older forest conservation law that is rather narrow in scope. It sets standards for tree utilization, slash disposal and fire control measures. Massachusetts is the only State in the East with a comprehensive modern law. However, a number of other Eastern States have legislation affecting forest practices. Maine regulates forest operations through a zoning law that primarily restricts forest activities in the environmentally sensitive area of the unincorporated townships of

the State. Approximately 28 percent of the forest land in these townships is subject to the law.

New Hampshire and Vermont have piece-meal systems of forest practice regulation. Each has several laws to regulate specific forest activities.

Florida, Maryland, Missouri, New York and Virginia have regulatory legislation originally adopted in the 1940's or 1950's--although some have been amended in recent years. Maryland also has a separate seed tree law adopted in 1977. The statutes of Maryland, Virginia, and Florida are primarily concerned with ensuring proper reforestation of cutover sites. Those of New York and Missouri address a broader range of activities, but compliance with them is strictly voluntary in return for forest management assistance from the State. Missouri also grants a tax subsidy to those who follow its rules.

Although forest practice regulation in the East has not been as comprehensive or severe at the State level as in the West, in recent years there has been a proliferation of local ordinances in several Eastern States. In some cases, these have been very restrictive or even prohibitive to timber operations. For example, among the 567 municipalities in New Jersey, about 100 have established ordinances restricting timber operations (Hogan 1984).

Modern forest practice legislation in the United States has significant implications for the Nation's forest resources. An examination of the history, development, and major provisions of these statutes indicates that they have indeed been a major component of forest policy during the last several decades. The California and Massachusetts laws, as the most comprehensive of their respective regions, provide excellent illustrations of the developing role of regulation in forest policy and how the approach has differed in the West as compared to the East. As Western States without regulatory legislation consider enactment of such statutes, they will certainly examine closely the regulatory experience in California. Similarly, the proliferation of local laws in the East may prompt many States in that region to consider State legislation similar to that of Massachusetts. For these reasons, we have examined and compared the California and Massachusetts laws in terms of major provisions, costs, effectiveness, and implications for other States. Conclusions will follow.

THE CALIFORNIA AND MASSACHUSETTS STATUTES

The Forest Practice Act of 1945, adopted primarily to control destructive harvesting practices associated with meeting World War II wood needs and to defuse threatened federal legislation, was the first California law to regulate forest practices. This statute regulated harvesting practices to insure reforestation and protection of residual stands but was declared unconstitutional in 1971. The court found

(Bayside Timber Co. v. Board of Supervisors of San Mateo County, 97 Cal. Rptr. 431) that the members of the Board of Forestry and the District Committees, who were responsible for preparation and adoption of rules, had a pecuniary interest in the regulation of forest practices. It also objected to the provision of the law that required approval of two-thirds of the owners of private timberland prior to adoption of forest practice rules. The 1945 law was replaced in 1973 by the Z'berg-Nejedly Forest Practice Act which stipulates that the membership of the Board and District Committees shall include five members from the general public. These members, who constitute a majority, may have no direct financial interest in timberland. Furthermore, the provision requiring the approval of forest landowners was removed from the Act. The current law has been modified extensively since its original enactment, by both legislative amendment and the courts.

In contrast to California, forest practice legislation in Massachusetts has been subject to little or no litigation. The current law regulating forest practices is the 1983 Forest Practices Cutting Act. An earlier Cutting Practices Act had been passed in 1943 in response to the forest devastation resulting from a 1938 hurricane. That law required, as a minimum, that seed trees be left after harvesting to insure regeneration. Landowners were also required to give notice of their intent to cut and the State was charged with preparing a cutting plan. Over the years it became too much of a burden for the State to prepare all the required plans and to administer the Act effectively. As a result, in 1977 the Governor's Committee on Policy called for radical revision of the law. This played a major role in adoption of the 1983 statute. Two other factors also influenced its enactment.

First, compliance with provisions of the State's Wetlands Protection Act was impeding logging operations and creating costly delays in harvesting of up to 45 days.³ The new law is coordinated with the Wetlands Act, and an administrative agreement with the Department of Environmental Quality and Engineering has eliminated many of the delays. The third factor in the adoption of the current law was the rapid proliferation of local ordinances regulating forest operations, some of which have been highly restrictive.

General Provisions

The stated intent of both the Massachusetts and California laws is basically the same--to maximize the timber resource while at the same time protecting all other forest resources. The Massachusetts law regulates activities on all public and private forest land. The California statute, by contrast, is applicable to all nonfederal public and private woodland.

Certain activities are exempt from regulation in both States. In Massachusetts these activities include cutting for right-of-ways, small commercial harvests of up to 25,000 board feet or 50 cords, and clearing for conversions to other land uses. California exempts operations on parcels of land 3 acres or less in size, removal of dead or dying trees, and cutting of fuelwood. Exemptions in California, however, only apply to certain administrative filing requirements. The operations must still comply with all other rules and regulations of the Act.

The California Forest Practices Act of 1973 did not initially preempt county rule enactment and local ordinances stricter than their State counterparts were adopted. However, a 1981 amendment removed this county authority. The amendment gave the Board of Forestry the authority to issue, at its option, county specific rules upon recommendation of the county. To date this has been done for five counties.

The Massachusetts Act does not currently limit the authority of local governments to promulgate rules. Although the state law to date has satisfied the regulatory needs of most local governments, an amendment to control enactment of local ordinances is being considered.

Administrative Rule Establishment

The two laws also differ in their method of establishing administrative regulations. The Massachusetts forest practice law directs the Division of Forest and Parks to adopt one set of rules that apply to operations in the entire State. To insure protection of nontimber resources, the rules must also be approved by the Department of Environmental Management. The California law, however, directs the Board of Forestry to divide the State into at least three districts. Each district has a separate set of rules promulgated by an appointed committee. To achieve a balance between timber and nontimber interests in the rule-making process, the Board must maximize cooperation and input from other State resource agencies in the rule making process. Both laws provide for public input in the rule-making process by requiring that public hearings be held prior to adoption or revision.

The rule-making bodies in California are each composed of nine members, five of whom may have no financial interest in timberlands. This membership composition provides points of view that may not be present on the Massachusetts forestry rule-making committee. The latter is composed by law of eight members, four of whom by definition have a financial interest in forestry. The eight-member committee must include a forest landowner, a representative from the primary wood-using industries, a licensed timber harvester, a consulting forester, three representatives of other resource interests, and one person representing the general public. This appears to give a fairly balanced membership, but close examination of the current board reveals a preponderance of interests in

³Telephone interview with Thomas Quink, Chief Forester, Massachusetts Division of Forests and Parks, Boston, July 1986.

timber. Currently, the public member is a Massachusetts tree farmer and at least one member representing other resource interests is involved in forestry and the Tree Farm Program. Thus, at present, 6 of the 8 committee members have a financial interest in forestry. The requirement that rules prepared by the Massachusetts Committee be approved by the Department of Environmental Quality before final promulgation appears to provide for further review of the rules and their impact on forest resources. However, this may not be the case. The Commissioner of Environmental Management is also the State Forester and his approval is generally a mere formality.

Practices Addressed By Regulation

Rules in both States require timber operators to be licensed. The rules also address harvesting systems to be used, regeneration methods, logging practices, road construction, and slash disposal.

Clearcut size and the use of shelterwood and seed tree cuts are included in the regulations. Massachusetts limits clearcut size to 10 acres. Larger areas may be allowed if approved by the State in the cutting plan. In California, the maximum allowable clearcut is dependent on the site's erosion potential. The size may range from 80 acres for a site with a low erosion potential to 20 acres in areas with an extremely high potential.

Both States require minimum stocking standards to be met after harvest. The Massachusetts law mandates establishment of 1,000 seedlings per acre within 2 years of harvest. In California, the number of seedlings required varies depending on the productivity of the site. Regeneration standards must be met within 5 years of harvest.

Both the Massachusetts and California rules require that care be taken when conducting forest operations such as tree felling, use of logging equipment, yarding, and construction of roads and skid trails. However, the regulations in California are considerably more detailed and prescriptive than those in Massachusetts. For example, they include specific rules concerning the proper installation of drainage structures, the allowable distance between water bars, treatment of fill and surfacing materials, and maintenance requirements. The Massachusetts regulations require only that adequate ditches, culverts and water bars be provided.

Each State's law gives special attention to operations in wet areas, on steep slopes, and in the vicinity of lakes and streams. In addition, Massachusetts requires that specialized harvesting and road construction practices be used in aesthetically sensitive areas.

Administrative Procedures

Detailed administrative procedures are required in both States for conducting forest operations. However, filing requirements of the California act are more complex and numerous than those in Massachusetts.

Massachusetts requires a notice of intent/forest cutting plan, notice to abutters if cutting will occur within 200 feet of another's property, and a notice of completion. An additional form is required for operating in a wetland or on steep slopes. The notice of intent/forest cutting plan is a check off/fill-in-the-blank type of form. It addresses silvicultural methods, method of designating trees to be cut, estimated volume of species on the site, logging and erosion control measures, special procedures in buffer strips, and measures to control mud on highways. Both a detailed map of the operation site and a locus map outlining the cutting area on a U.S. Geological Survey topographic map are required. Cutting plans are subject to review and approval by the Division of Forest and Parks. Although plan requirements are complex, the law does not require that they be completed by a forester as in California.

Currently, all operations in Massachusetts are inspected prior to, during, and upon completion of logging. Proposed harvesting in wetlands is always inspected prior to harvesting plan approval. Decisions of the Division may be appealed by the operator or landowner to the Director of Forests and Parks and ultimately to the Superior Court.

The sites associated with approximately 80 percent of all California harvesting plans submitted are inspected prior to plan approval. Selection of sites is an administrative decision. Furthermore, all operations are inspected at commencement, during operations, and upon completion.

The California Act requires preparation of a timber harvesting plan by a licensed forester; the plan is then submitted to the Department of Forestry for approval. Several legislative modifications have been made over the years to render harvesting plans the functional equivalent of the State environmental impact reports. These changes were made in response to Natural Resources Defense Council v. Arcata National Corp. (1 Civ. No. 37555, Cal. Ct. App. 10th Dist. [July 8, 1976]) where the court ruled that timber harvesting plan approval was subject to the environmental review requirements of the State's Environmental Quality Act. As a result, the forester must conduct a feasibility analysis to evaluate possible activities that might be conducted to lessen adverse environmental effects. In addition, the soil erosion hazard rating of each site must be determined.

The timber harvesting plan in California is also a check off/fill-in-the-blank form that addresses silvicultural methods, harvesting and erosion control practices, road and landing construction, special operations near water, and hazard reduction. As in Massachusetts, the owner or operator must also submit a detailed map of the operation site. Harvesting plans are subject to review by the California Department of Fish and Game, the State Water Quality Control Board, and district interdisciplinary teams.

Landowners in California are required to supply the Department of Forestry with the names and

addresses of adjoining property owners within 300 feet of the cutting boundaries. The Department then notifies abutters of the proposed operations. The landowner must also notify the Department when operations are completed. Periodic stocking status reports are then required until stocking meets minimum standards.

If California owners sell their property during harvesting, they must inform the purchaser of the forest practice regulations regarding stocking standards after harvesting. Otherwise, the prior owner may be held responsible for reforestation costs.

Timberland conversions in California require a permit and may be denied if the state determines that the site would be better left in timber production. In contrast, conversions in Massachusetts require no approval.

Enforcement

Tools for enforcing forest practice rules are provided in the laws of both States. Legal actions are avoided if possible. Agency personnel prefer to achieve compliance by providing the operator and/or owner with educational or technical assistance.

When necessary, each State may issue stopwork orders. In Massachusetts the order remains in effect until deficiencies are corrected or until a hearing is held. In 1984, 1,059 harvesting plans were submitted with only 25 stopwork orders being issued -- either for failure to submit a cutting plan or for failure to follow practices approved in the plan. No violations of the Act have resulted in judicial action to date. In addition to stopwork orders, the Superior Court may levy a fine of up to \$100 per acre for failure to make the necessary administrative filings and for violating rules. Failure to obtain an operator's license is subject to a fine of up to \$1,000 per violation. Thus far, no fines have been imposed nor licenses revoked for violation of the Forest Practice Act (Henly and Ellefson 1986).

In California, a forest practice inspector may issue a temporary stopwork order that is effective for up to 7 days. If the infractions are not corrected, court action may be sought. The courts can order that immediate corrective measures be taken by the responsible party. If repairs are not made, the courts may authorize the Department of Forestry to take corrective action itself at the expense of the responsible party. Expenses incurred may result in a lien on the property involved.

Violations of the California Act are punishable by a \$1,000 fine and/or 6 months in jail. Each day of a violation is considered a separate offense. In 1984, 964 of the 1,260 timber harvesting plans submitted were found in violation of the law. Of these, 40 resulted in enforcement actions but only in one instance was of an operator's license suspended.

The California forest practice law requires numerous and more detailed administrative filings than does the Massachusetts statute. The California law is also more explicit regarding actions that should be taken to achieve a particular performance standard. In Massachusetts, owners or operators have more discretion in selecting specific practices to achieve compliance with the standards.

Economic and Cost Considerations

The laws of both States, although differing in a number of respects, have been moderately to highly effective in protecting and enhancing both timber productivity and nontimber resources (Henly and Ellefson 1986).

Estimates of the cost of compliance with the California Act range from \$25 to \$80 per thousand board feet (Henly and Ellefson 1986). A major cost is for preparation of the timber harvesting plan; this averages \$1,000⁴. Complex plans, however, may cost as much as several thousand dollars. The expenses incurred by small landowners may be proportionally much higher than those of a large landowner for similar plans. The costs of complying with other requirements are more difficult to quantify. However, the Act has resulted in an annual state-wide increase in reforestation expenditures of \$2 to \$3 million (Vaux 1983).

There has been some speculation that the California Law would have an overall negative impact on forest investment in the State. For example, the increased cost of compliance may have been a factor in the divestment of California holdings by both Weyerhaeuser and International Paper companies (Henly and Ellefson 1986). Although a decrease in timber production was anticipated, two recent studies found no evidence that the level of timber produced in California has changed since passage of the Forest Practice Act (Green and others 1981, Henly and Ellefson 1986).

It is too early to determine in a meaningful way the economic implications of the Massachusetts Act. At least several more years experience will be needed.

Conclusions

Regulation of forest practices and enforcement of the rules in California are generally much stricter than in Massachusetts. Certainly one factor responsible for the difference is the greater potential for damage to the environment in California, with its steep slopes and fragile soils, as compared to Massachusetts. Since both States are well known for their active environmental groups, that alone would not necessarily be expected to result in greater regulation in

⁴Vaux, Henry J. Private forest regulation: Current issues and future trends. Paper presented at the Western Forest Economists Meeting, Wemme, Oregon. May 8, 1985.

California. Another explanation for the disparity in the two states' forest practice legislation may be related to the extent of federal land holdings. The West Coast States have experienced extensive public ownership and public involvement in forest resources since 1900. This history has probably facilitated stricter state regulation of private forestry in the West than in the East since strict regulation is perceived as less onerous than public ownership. The debates during the 1960's over forest management on private land also no doubt helped set the stage for greater public regulation in the West (Salazar 1985).

On the other hand, the major force behind enactment of the Massachusetts Forest Cutting Practices Act was the profusion of local ordinances restricting forestry operations. The same force will probably result in the enactment of similar laws in other Eastern States. Furthermore, the Massachusetts law has been largely successful thus far and is generally supported by environmental organizations, forest industry, local governments, and private landowners (Henly and Ellefson 1986). It therefore provides a viable model for other States in the region. Connecticut, Maine, New Jersey, Maryland, and Pennsylvania have all considered enactment of new or revised State forest practice legislation during the last few years.

In the West, additional states may follow the lead of Alaska, California, Oregon, Washington, and Idaho in passing a comprehensive statute. Forest practice legislation was seriously considered by the Montana Legislature in 1985.

Additionally, since the regulatory environment is a dynamic one, current laws will be revised periodically as society's goals for the management of forest resources change.

The often opposing interests of environmental groups, forest industry, landowners and local governments are certain to result in conflicts as regulatory programs evolve or are revised. Hopefully, the outcome will be positive: well balanced laws which are technically strong and which require environmentally sound methods of harvesting and stand management at a cost which is not prohibitive for either forest landowners or the public.

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A Cone and Seed Disease of Southern Pines Caused
by the Pitch Canker Fungus¹

Jane Barrows-Broadus²

Abstract.--The pitch canker fungus, Fusarium moniliforme var. subglutinans (FMS), causes serious damage in pine seed orchards in the southeastern United States. These orchards supply the genetically improved seeds required for replanting harvested forest lands in this region. The same pathotypes of FMS that cause symptoms of pitch canker on main stems, branches, and shoots of southern pines also cause mortality of reproductive structures on loblolly (Pinus taeda) and slash (P. elliottii var. elliottii) pines, the two most economically important southern pine species. The pattern of fungus isolation and histological data indicates that outbreaks of shoot dieback and cone deterioration can occur independently in loblolly pine seed orchards. During the approximate 19-month period between production of female strobili and maturation of fully developed pine seed, there are potentially numerous opportunities for the causal pathogen to reduce seed yields. At this time, determination of a complete disease cycle on pine reproductive structures awaits further investigation.

Keywords: Shoot dieback, seed orchard management, histopathology.

In the southeastern United States, the bulk of seedlings for reforestation plantings by private industry and public forestry organizations come from seed orchards. At least 65 percent of the 915 million seedlings produced annually in this region are from genetically improved pines grown on 9,800 acres of seed orchards. Pitch canker, caused by Fusarium moniliforme Sheld. var. subglutinans Wollenw. & Reink. (FMS), is one of the diseases that is rapidly increasing in importance in seed orchards across the Southeast. Although seed orchard managers have noticed the disease for at least 25 years, the perceived insignificance of past outbreaks limited attempts to determine the causal agent. In 1975, however, the disease suddenly became severe in two loblolly (Pinus taeda L.) seed orchards in separate regions of the South. Since then the pitch canker disease has been confirmed in more than 40 seed orchards (Dwinell and others, 1985; Kuhlman and others, 1978).

SYMPTOMS

The two primary symptoms on vegetative structures are pitch canker and shoot dieback. Pitch cankers are characterized by a bleeding, resinous

canker on the trunk or large branches of a tree. The canker is usually sunken and the bark is retained, while the wood beneath the canker is deeply pitch-soaked. Pitch-soaking of the underlying wood and the absence of swelling or callus help separate pitch canker from the other canker diseases of pine.

The other symptom is shoot dieback in the upper crown. Lesions form on the late-summer flushes of growth; in autumn, fully developed needles turn yellow to reddish brown (fig. 1). In the spring, new shoots may expand before they are killed by girdling of the older tissue. Witches' broom develops in some trees when adventitious buds form in response to repeated infection and dieback.

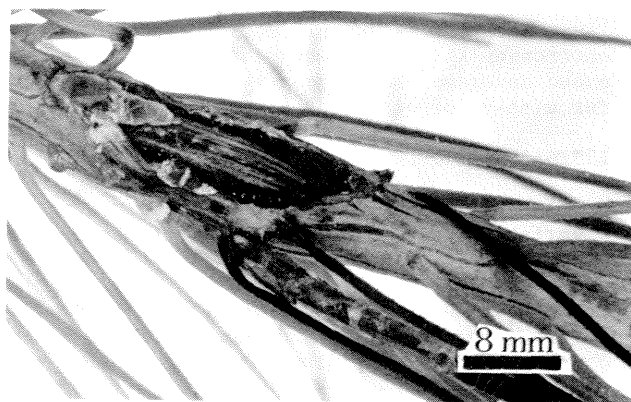


Figure 1.--Canker formation on lateral shoots in the upper crown is a symptom of shoot dieback.

¹Presented at the Symposium "Current Topics in Forest Research: Emphasis on Contributions by Women Scientists"; November 4-6, 1986. University of Florida, Gainesville, FL 32611.

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Several symptoms of FMS infection are observed on the pine reproductive structures. FMS causes the mortality of female flowers and mature cones. FMS-infected loblolly pine cones tend to be misshapen and smaller than normal, and scales on green cones at harvest time are resinous with purple discoloration. Mycelia of FMS are often present on outer surfaces of badly deteriorated loblolly pine cones. Some infected cones have a necrotic tip characterized by internal pitch pockets. External resinous lesions colonized by FMS are also observed on some loblolly pine cones (fig. 2).

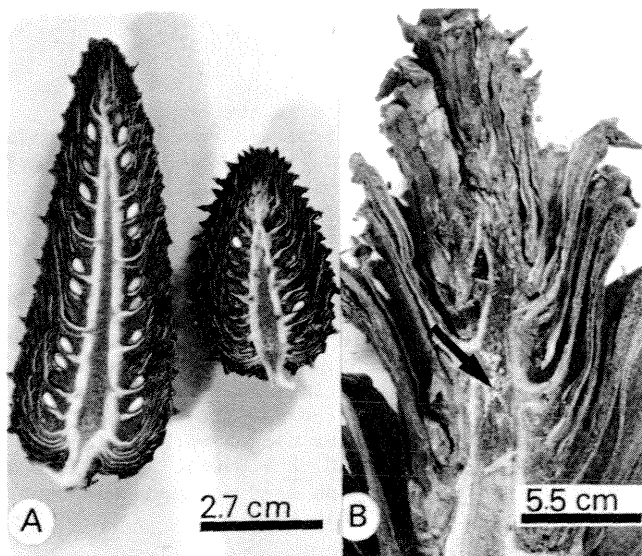


Figure 2.--(A) Loblolly pine cone infected with *Fusarium moniliforme* var. *subglutinans* (right) is smaller and has fewer viable seeds than healthy cone (left). (B) Another symptom of infection is a terminal necrosis characterized by internal resin pockets (arrow).

Preliminary observations on slash pine (*P. elliottii* Engelm. var. *elliottii*) indicate that the amount of infection in a given seed lot may vary from 0 to 98 percent. Internal loblolly pine seed tissues infected with FMS range from potentially sound (based on radiography) to mummified. Radiographs (fig. 3) of many infected seeds show the gametophyte shrunk from the seed coat and slight deterioration of the embryo. Other symptoms detected by radiography are dark circular areas in the seed tissues. Microscopic examination reveals a lack of cellular organization of the tissue and the presence of hyphae throughout the seed (Barrows-Broadbuss and Dwinell, 1985; Miller and Bramlett, 1978).

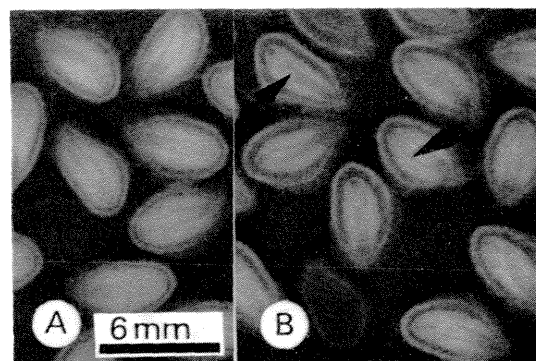


Figure 3.--(A) Radiograph of noninfected seeds with gametophyte and embryos intact. (B) Radiograph of infected seeds. Gametophyte tissue is shrunk from the seed coat and embryo (arrows) appears slightly faded.

CONE HARVESTING WOUNDS

Most canker-producing organisms, including FMS, require a wound as an infection court. Most cone-harvesting practices result in wounds to the trees. Subsequent pitch canker symptomatology reflects the different harvesting practices required by different pine species. For example, in loblolly pine seed orchards cones are usually harvested by tearing them off the branches. Shoot dieback symptomatology is most commonly observed in this species. Wounds in the upper crown caused by cone harvest may therefore exacerbate outbreaks of shoot dieback.

Although loblolly pines generally recover from outbreaks of shoot dieback, at the height of an epidemic considerable loss of the cone crop may occur. The impact of disease on cone yield, however, varies from orchard to orchard. For example, most of an 85 percent decline in cone yield in one loblolly pine orchard was attributed to shoot dieback, whereas in another loblolly pine orchard, cones initiated during an epidemic resulted in a record cone and seed crop. Damage assessment of shoot dieback should therefore include the relative susceptibilities of individual clones and their cone production histories, since both vary by genotype (Barrows-Broadbuss and Dwinell, 1985; Kuhlman and others, 1982).

In slash pine seed orchards, bole cankers often develop through injuries caused by mechanical shakers used in cone collection. The most obvious damage caused by tree shakers is the actual removal of bark at the point where the pads grasp the bole. Cankers may also develop at grasp sites where there is no obvious bark removal. Pitch cankers frequently develop on the upper portion of the bole where the vibration (or whiplash) of the main stem is most vigorous. Some seed orchards have considered harvesting with nets as an alternative to harvest with tree shakers (Dwinell and Barrows-Broadbuss, 1981).

OTHER WOUNDS

Any wound, regardless of cause or location, provides an infection court for the pathogen. In addition to cone harvest, routine seed orchard management practices such as branch pruning and mowing create wounds for the pathogen to invade. Weather-related injuries such as those from wind and hail may also serve as entry points. Hurricanes, tornadoes, and ice storms in recent years have caused intensification of pitch canker in at least two seed orchards.

An array of insects feed on female strobili throughout their growth and maturation period, and possibly create infection courts for the pathogen. These insects may also transmit the pathogen into the cones. The deodar weevil (*Pissodes nemorensis* Germar) and the pine tip moth (*Rhyacionia* spp.) create wounds on shoots that may become infected by airborne spores of the pathogen. Deodar weevils, their associated galleries, and chip cocoons are frequently contaminated by FMS (Bramlett and others, 1977; Blakeslee and others, 1978).

INOCULUM SOURCES

Sporodochia of FMS occur routinely on infected, small-diameter branches. These fruiting bodies are found during all seasons of the year and are most frequently located in fascicular scars. Sporodochia range from 1 to 3 mm in diameter and are a light salmon-orange color (*sensu* Ridgeway) (Blakeslee and others, 1978). Except for supporting conidiophores, the sporodochia normally contain only conidia (fig. 4).

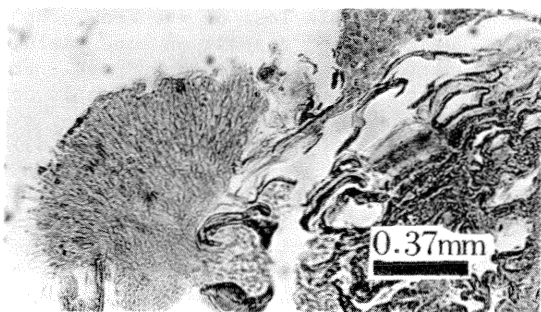


Figure 4.--Sporodochium of *Fusarium moniliforme* var. *subglutinans*.

Conidia of FMS are airborne, and maximum dispersal occurs during precipitation with turbulent air. The conidia are present throughout the year and can be recovered from dead branches in the crown, rainwater falling through infected trees, and from the air. FMS is also isolated from forest soils, surfaces of pine needles, branches, boles, and from bark and debris adhering to tree-shaker pads. Pathogenicity tests of these

isolates on slash and loblolly pines indicate that FMS occurs naturally in mixed populations of pathogenic and saprophytic strains.

RELATIONSHIP BETWEEN SHOOT DIEBACK AND CONE INFECTION

Barrows-Broadus and Dwinell (1985) studied an outbreak of shoot dieback in a loblolly pine seed orchard in South Carolina to determine the effect of shoot dieback on the conelets, cones, and seeds.

Disease Surveys

In March 1983, ramets in the orchard were surveyed for shoot dieback and rated for disease severity by using the Kelley and Williams (1982) rating system. Twelve clones ranging from low (<1 percent) to high (>50 percent) disease incidence, were selected for sampling branches, conelets, and cones. In December 1983, another disease survey was conducted, and the 12 clones selected from the previous survey were rated again, based on new infections since March 1983 (table 1). The second survey in December 1983 indicated that disease incidence declined for 7 of the 12 clones, but the severity ratings for new infections among the clones matched those made in March ($r = 0.80$, $P = 0.01$). This disease pattern in loblolly pine seed orchards has been observed by other researchers.

Recovery of FMS from Samples

In September 1983, 24 branches bearing 5-month-old conelets were randomly collected from each clone. In October 1983, 12 mature 19-month-old cones were randomly collected from each clone and subjected to standard cone analysis techniques (Bramlett and others, 1977). All samples including the seeds and scales from mature cones were cultured on *Fusarium*-selective media (Agrawal and others, 1973) and prepared for histological examination (Johansen, 1940).

FMS was recovered from branches and conelets collected in September 1983 (table 2). Recovery of FMS from conelets in some clones was not correlated with recovery from the branches. Clone C-1-515, for example, averaged 16.7 percent branches infected and 45.5 percent conelets infected with FMS. Conversely, 25 percent of the branches sampled from clone G-1-575 were colonized by FMS, but FMS was not recovered from the conelets.

Table 1.--Average disease severity ratings of shoot mortality caused by *Fusarium moniliforme* var. *subglutinans* on clones of loblolly pine in a seed orchard^a

| Clone | Ramets (No.) | March rating ^b | December rating ^c |
|----------|-----------------|------------------------------|---------------------------------|
| M-3-6 | 8 | 4.5 a | 4.0 a |
| N-3-43 | 26 | 3.6 b | 1.9 b |
| O-1-576 | 15 | 3.2 b | 1.3 c |
| B-1-561 | 26 | 3.0 b | 2.0 b |
| P-1-581 | 16 | 2.3 c | 1.1 c |
| C-1-515 | 24 | 2.3 c | 2.3 b |
| A-1-521 | 34 | 1.8 cd | 1.1 c |
| D-1-513 | 24 | 1.6 cde | 1.2 c |
| L-1-575 | 25 | 1.0 e | 1.1 c |
| H-18-3 | 14 | 1.0 e | 1.0 c |
| G-1-573 | 19 | 1.0 e | 1.1 c |
| K-18-106 | 17 | 1.0 e | 1.0 c |

^aFive-point scale after Kelley and Williams (1982): 0 = no disease, 1 = <1 percent exhibiting dieback, 2 = 1-10 percent; 3 = 11-20 percent; 4 = 21-50 percent; and 5 = >50 percent. Within columns, means not followed by the same letter are significantly different ($P = 0.01$) according to Kramer's (1956) extension of Duncan's multiple range test to group means with unequal numbers of replications (ramets).

^bFirst survey in March 1983; all current infections (wilted shoots with red needles) were counted.

^cSecond survey in December 1983; new infections since March were counted (needles on old infections had turned gray). Disease severity ratings were correlated with the March ratings ($r = 0.80$, $P = 0.01$).

Table 2.--Recovery of *Fusarium moniliforme* var. *subglutinans* from branches and 5-mo-old conelets in 12 clones of loblolly pine grown in a seed orchard^a

| Clone | Branches infected (avg %) | Conelets/ branch (No.) | Conelets (No.) | Conelets infected (avg %) |
|----------|---------------------------------|------------------------------|-------------------|---------------------------------|
| B-1-561 | 66.7 a | 0 | 0 | 0 |
| M-3-6 | 65.8 | 0.21 | 5 | 100 |
| O-1-576 | 58.3 ab | 0 | 0 | 0 |
| P-1-581 | 45.8 abc | 0 | 0 | 0 |
| N-3-43 | 33.3 bcd | 1.12 | 19 | 31.5 |
| G-1-575 | 25.0 cde | 1.75 | 28 | 0 |
| C-1-515 | 16.7 de | 0.96 | 22 | 45.4 |
| D-1-513 | 12.5 de | 0.71 | 16 | 6.3 |
| A-1-521 | 4.2 e | 1.92 | 36 | 5.5 |
| H-18-3 | 0 e | 1.04 | 22 | 0 |
| K-18-106 | 0 e | 1.21 | 24 | 0 |
| L-1-575 | 0 e | 1.07 | 22 | 4.5 |

^aBased on 24 branches (replications) per clone. Means not followed by the same letter are significantly different ($P = 0.05$) according to Duncan's multiple range test.

Histology of natural infections on branches looked similar to those previously described by Barrows-Broadbush and Dwinell (1983) on loblolly pine seedlings artificially inoculated with the pitch canker fungus. Conelets attached to infected branches became infected when the parenchyma connecting the conelet to the branch was colonized by the pathogen. The tissues of mature seeds colonized by FMS lacked cellular organization compared with tissues in noninfected seeds. Hyphae were observed in the embryo cavity and between the gametophyte and the integument.

Results of this study demonstrated that outbreaks of shoot dieback may directly affect the developing cones. There was evidence, however, that conelet deterioration could occur independently of shoot dieback.

CONTROL STRATEGIES

Because the pathogen requires a wound as an infection court, control recommendations in seed orchards concentrate on altering management practices to reduce wounding, especially during periods of high disease risk, primarily in the fall and winter. The use of tree shakers for cone harvest is discouraged; otherwise use trained personnel to properly adjust and operate them. Clip rather than tear loblolly pine cones to reduce stripping of the bark. Avoid mower damage to the tree stem and anchor roots.

After cone harvest, if abnormal cones are not culled before seed extraction, it may be difficult later to separate infected seeds from noninfected seeds. Identification and culling of fungus-damaged cones during harvesting operations could increase the percentage of seed germination.

At this time, control measures are not available to prevent seed destruction by the pathogen. Progress has been made at the Forestry Sciences Laboratory at Athens, GA, in identifying peak periods of susceptibility for developing cones. Determination of a complete disease cycle, however, awaits further investigation.

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The Great Plains occupies approximately one-fourth of the continental United States land mass and extends from the Canadian prairie provinces to the Texas panhandle, and from the eastern Forests to the Rocky Mountains. It spans 1700 miles north to south and about 500 to 800 miles east to west. The Great Plains is a major agricultural region, yet it is characterized by harsh, variable climatic conditions. Favorable conditions may be followed by intense heat, cold, drought, or hail. Temperatures in many areas range from below 0°F to over 100°F. At most locations, the wind seldom stops blowing (Griffith 1976).

Until settlers arrived over a century ago, only Indians and a few trappers roamed the Great Plains. Today, nearly 94 percent of the land is occupied, with 33 percent agricultural crops; 56 percent grasslands, range, and pastures; and less than 2 percent in trees (Griffith 1976).

Before the arrival of the settlers, prairie fires, insufficient water, adverse weather conditions, extremely alkaline soils, and grazing by herbivores excluded most tree growth. Native grasses such as big bluestem, little bluestem, and buffalograss were the climax type of vegetation. Trees grew successfully only on sites with high water tables or on rocky slopes protected from the wind--river bottoms, woody draws, and sides of protected hills or buttes (Girard and others 1983; Tolstead 1947).

The predominant native trees in the western Great Plains are species found in the western forests, such as Rocky Mountain juniper and

Abstract.--Windbreaks are planted in the Great Plains to protect soil from wind and water erosion, to protect crops and livestock, to beautify and conserve energy on rural farmsteads, and to improve wildlife habitat. Although over 200 species of insects can damage trees in windbreaks, only a few species damage trees severely and adversely affect windbreak function. This review of forest entomology research in the Great Plains includes recent research accomplishments of the USDA Forest Service for several of the more destructive insect species.

Keywords: Shelterbelt, borer, defoliator, tip moth, seed-damaging insect, cankerworm, carpenterworm, metallic pitch nodule moth, ash seed weevil, seedbugs, coneworms, Zimmerman pine moth.

ponderosa and lodgepole pines. Similarly, the predominant native trees on the eastern and northern edges of the Great Plains are hardwood species native to the eastern and boreal forests, respectively.

The early settlers recognized the importance of trees in protecting humans, animals, and crops. As early as 1865 some states offered 5 cents per year and later \$2 per year for each acre planted to trees. The Timber Culture Act of 1873 enabled homesteaders to obtain 160 acres of land by planting 40 acres of trees. Between 1935 and 1942, over 200 million trees and shrubs in 18,600 miles of windbreaks were planted on 30,000 farms in the Great Plains as part of the USDA Forest Service's Prairie States Forestry Project. These trees were planted to reduce wind erosion and desiccation and to provide relief jobs for the drought-stricken population. The federal government furnished and planted the trees; the owners cultivated and protected them. In 1942 windbreak tree planting became the responsibility of the USDA Soil Conservation Service. Trees were planted on farms cooperating in a complete soil conservation program (Read 1958). Tree planting and maintenance costs were shared with the farmer. Some windbreaks planted since 1930 have been removed because of deterioration or conflicts with farm mechanization and central-pivot irrigation systems, higher land values, taxation, and improved crop varieties (Griffith 1976).

Currently, federal and state governments are actively promoting the renovation of existing windbreaks and the establishment of trees in farm, field, energy, and noise abatement plantings and as living snow fences. In 1985 the Conservation Reserve Program was established by the U.S. Congress to promote soil conservation on highly erodible lands by planting trees and grass.

Many tree species planted in the Great Plains performed poorly or failed because they were not

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adapted to the adverse climatic and site conditions, or because they were damaged by insects or diseases (Bruner 1890; Dahl 1940; Read 1958; Wilson 1962). Over 200 species of insects damage trees in the northern Great Plains (Stein and Kennedy 1972); additional species are common to the central and southern Great Plains. Most tree species planted in the Great Plains are susceptible to one or more serious insect pests; but, these insect pests usually are present in low numbers, do not kill the tree, and are not limiting factors to its survival. However, insect damage may reduce the protective value of trees. Wind protection to field crops, livestock, and homes can be reduced by defoliation or death of part of or an entire tree. In those areas of a planting where one or more trees are killed or damaged, wind velocities may be significantly higher than in surrounding undamaged areas.

The role of insects in the failure of trees planted in Nebraska was recognized as early as 1890 (Bruner 1890). Between 1910 and 1940 forest entomology investigations in the Great Plains were conducted either by entomologists working for the USDA Bureau of Entomology or at the State Agricultural Experiment Stations. These investigations were limited to identification of insect pests and to life cycles and control studies on tip moths (*Rhyacionia* spp.) (Baumhofer 1932; Swenk 1927; Wygant 1936), carpenterworms (*Prionoxystus robiniae* (Peck)) (Munro 1939; Munro and Fox 1934; Scholz 1935), spring cankerworms (*Paleacrita vernata* Peck) (Dean 1915), and several other insects that damaged trees in the Forest Service's Bessey Nursery near Halsey, NE, (Baumhofer 1932; Wygant 1936) or in tree plantings (Munro 1939; Scholz 1935; Severin 1947, 1948; Ware 1936; Wygant 1938). During the 1950's and early 1960's the Lakes States Forest Experiment Station was responsible for identifying species of tree insect pests in the Dakotas and for learning more about their biologies (Kennedy 1968; Kennedy and Wilson 1969; Wilson 1962). In 1966 this responsibility was transferred to the Rocky Mountain Forest and Range Experiment Station, with research centered at Bottineau, ND. Responsibility was transferred to the Forestry Sciences Laboratory, Lincoln, NE, in 1981.

During the 1960's and early 1970's tree insect pests and their natural enemies were identified (McKnight and Aahrus 1973b; Stein and Kennedy 1972; Stein and Tagestad 1976) and biologies of major pest species such as elm sawflies (*Cimbex americana* Leach) (Stein 1974b), carpenterworms (*P. robiniae*) (McKnight 1973; McKnight and Tunnock 1973; Peterson 1964, 1971), lilac borers (*Podosesia syringae* (Harris)) (Dix and others 1978; McKnight 1973; McKnight and Tunnock 1973; Peterson 1971), cankerworms (Geometridae) (Stein 1974a, 1974c, 1974d), and ash bark beetles (*Lignyodes* spp.) (McKnight and Aahrus 1973a) were documented. Methods of sampling cankerworms, tip moths, and hardwood borers were developed, and insecticides were tested for control of cankerworms (Frye and others 1976; Stein 1969; Stein and Doran 1975), carpenterworms (Dix and

Kovner 1979; Dix and others 1979; Flavell and others 1978; McKnight and Tunnock 1973), lilac borers (Dix and Kovner 1979; Dix and others 1979; Flavell and others 1978; McKnight and Tunnock 1973), and tip moths (Dix and Jennings 1982; Van Haverbeke and others 1971). Since 1975 the Forest Service has continued to document the biologies of major insect pests, and has developed techniques for the early detection, evaluation, and reduction of damage. Recent Forest Service research in the Great Plains has focused on the spring cankerworm (*P. vernata* Peck (Lepidoptera:Geometridae)), the metallic pitch nodule moth (*Retinia metallica* (Busck) (Lepidoptera:Tortricidae)), the carpenterworm (*P. robiniae* (Lepidoptera:Cossidae)), the western pine tip moth (*Rhyacionia bushnelli* (Busck) (Lepidoptera:Tortricidae)), and the Zimmerman pine moth complex (*Dioryctria* spp. (Lepidoptera:Pyralidae)), and seed-damaging insects.

SPRING CANKERWORM.--Siberian elm (*Ulmus pumila* L.) is one of the few tree species that can survive the harsh environmental conditions of the northern Great Plains. This fast-growing, alkaline-tolerant, drought-resistant, cold-hardy tree is commonly planted in field windbreaks and urban plantings. However, cankerworm larvae can severely defoliate these trees in the spring (Frye and others 1976). Damaged trees are unsightly and less vigorous than healthy trees.³ High winds may severely damage crops in fields adjacent to defoliated windbreaks.⁴

Spring cankerworms have a 1-year life cycle. Moths emerge and mate as soon as the soil thaws in March, April, or May. Females crawl up tree trunks and lay eggs under bark scales or in bark fissures. During May and June the eggs hatch and larvae feed on young leaves for about 3 to 6 weeks before dropping to the ground where pupation and overwintering occur in the soil (Hildahl and Peterson 1974; Stein 1974a).

Cankerworm damage can be reduced by spraying *Bacillus thuringiensis* (B.t.), carbaryl, or other insecticides on the leaves of elms infested with second instar larvae (Thompson 1962; Frye and others 1976; Hard and others 1979). Damage levels will remain low for at least 2 years after a single application of B.t. (Hard 1979). Although these insecticides are effective in reducing infestation levels, they are not used frequently in the northern plains because 1) they must be applied in the spring when farmers are busy planting, cultivating, and spraying crops; 2) aerial application is costly; and 3) at the time of

³Dix, M.E.; Frank, A. Effects of artificial defoliation on growth and carbohydrate storage of Siberian elm. (Manuscript in preparation).

application aerial applicators are busy spraying field crops. The planting of Siberian elm sources that are less preferred by cankerworms would provide an alternative method for minimizing damage (Dix and Cunningham 1984).

During the late 1970's, 160 Siberian elm trees that were less preferred by spring cankerworms, had superior morphological characteristics, or were disease resistant were identified in field windbreaks. A laboratory technique for evaluating cankerworm preference for clones of these trees has been developed, and five nonpreferred clones were identified with this technique.⁵ These clones were less preferred probably because of chemical or morphological characteristics of the leaves. Cankerworm preferences also will be evaluated in field plantings. Nonpreferred clones will be incorporated into a breeding program designed to produce genetically superior elm trees for planting in the northern plains.

Several clones that were preferred by cankerworm larvae in laboratory trials escaped defoliation in windbreaks. These elms leafed out either earlier or later than most other elms. Leaves of trees that flush early are probably tougher and less palatable by the time newly hatched larvae begin feeding than those of other trees. Conversely, when egg hatch precedes bud break by several days, larvae must migrate to trees with leaves or risk starvation (Cunningham and Dix 1983).

CARPENTERWORM.--Larvae of carpenterworms tunnel into sapwood of hardwood trees throughout most of North America (Drooz 1985). In a survey of green ash (*Fraxinus pennsylvanica* Marsh) in North Dakota windbreaks in 1972, 28 percent of plantings and 7 percent of the trees were damaged by carpenterworms (McKnight and Tunnock 1973). Detection and assessment of infestations is difficult and time consuming because the larvae tunnel into trees immediately after hatching. They feed and extend their tunnels within trees for 2 to 4 years before pupating in the tunnel. Several insecticides that are registered for control of carpenterworms kill young larvae before they mine into trees. However, timing of application is difficult, because the initiation and duration of moth flight and egg hatch, which are dependent upon seasonal temperature can vary by as much as 4 to 6 weeks (Dix and Kovner 1979; McKnight and Tunnock 1973). For these reasons, a method of detecting and assessing infestations with attractants was developed.

The male attractant (Z,E)-3,5-tetradecadienyl acetate (Z3,E5-14:AC) was isolated and partially characterized by Solomon and others (1972) and Doolittle and others (1976). A trapping technique using this attractant was developed by evaluating the effect of trap design,

attractant dispenser, attractant release rate, isomer ratio, and trap placement on catches of carpenterworms in native stands and plantings. Traps with Conrel⁶ hollow fiber dispensers releasing 36, 54, or 72 µg of Z3,E5-14:AC per day caught more males for a significantly longer period of time than traps with wick dispensers baited with 36 µg of attractant. Traps with septa dispensers caught males for the entire moth flight. Addition of antioxidants to extend the length of attraction increased the efficacy of wick dispensers, but not the efficacy of fiber or septa dispensers. Metal-cylinder, milk-carton, and cardboard-cylinder type traps all caught large numbers of males; however, the cardboard-cylinder traps were the most economical to construct, least messy to handle, and the easiest to store. The largest number of males were caught in traps hung between 1.5 m and 6 m high and at sites with moderate or light undergrowth (Doolittle and others 1976; Solomon and others 1978; Dix and others 1979, 1984, 1987; Dix and Doolittle 1984). Hollow fiber dispensers baited with the Z3,E5-14:AC are now commercially available.

METALLIC PITCH NODULE MOTHS.--Larvae of metallic pitch nodule moths mine the buds and growing tips of pines, especially ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.). Infested branches are stunted, and branch tips are frequently killed (Van Deusen and Dix 1980). Metallic pitch nodule moths prefer pine sources from the northern and central Great Plains and northern Rocky Mountains that are taller than 1.5 m (Van Deusen and Dix 1980). During the past 10 years the number of windbreaks in the northern and central Great Plains infested with the moth and the number of infestations within a windbreak have been increasing. This corresponds with the increased use of ponderosa pine in windbreaks and subsequent growth of these pines.⁷

Metallic pitch nodule moths have a 1-year life cycle. In Nebraska, moths usually emerge during early May and lay eggs on the new growth. The solitary larva tunnels into new growth and buds during summer. During July a pitch nodule or round pinkish mass composed of pitch, sawdust, and insect excrement is formed over the initial point of attack. The larva overwinters within its tunnel and pupates in early spring (Dix 1985; Dix and others 1987). Biological data needed to develop and validate a simple life cycle model for the moth are being researched by Dix.

One spring application of carbaryl, applied immediately after moth flight and before larvae tunnel into stems, can reduce the proportion of ponderosa pine branches that become infested and also the number of infestations per branch.

⁵Dix, M.E., USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Lincoln, NE.; and Cunningham, R., USDA Agricultural Research Service, Northern Great Plains Research Center, Mandan, ND. (Unpublished data).

⁶Mention of proprietary product or service does not constitute an endorsement by the U.S. Department of Agriculture.

⁷Dix, M.E. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Lincoln, NE. (Personal observation).

Timing of the insecticide application is crucial, because carbaryl is ineffective if it is applied early in moth flight or during peak flight (Dix 1985).

Synthetic attractants of male moths can be used to successfully time insecticide applications and to detect infestations. When responses of male moths to traps baited with a series of known synthetic attractants of male tortricids and related compounds were compared, several compounds appeared promising, but an attractant could not be positively identified because male response varied with site and year (Dix and Jacobson, in press; Dix and others 1984). For this reason, Dix and Underhill used electroantennography to identify an attractant. This attractant has been successfully field tested in Nebraska.⁸

WESTERN PINE TIP MOTH.--This insect has caused extensive damage to young pine trees in the central and northern Great Plains since it was first observed at Bessey Nursery in 1909. Larvae mine into young needles and buds, causing reduction in growth and deformation of branches and leaders. Young trees may die following repeated severe infestations.

Both systemic and contact insecticides are registered for control of moths. Application of contact insecticides must be timed to coincide with egg hatch, and early application is critical. The insecticides must kill the larvae before they bore into the bud where they are protected. Seasonal variations in the rate of development of the pine tip moth make a fixed application schedule ineffective. Methods of timing insecticide applications from plant phenology observations and degree-day accumulations currently are under study.⁹

ZIMMERMAN PINE MOTH COMPLEX.--Larvae of ponderosa twig moths (*Dioryctria ponderosae* Dyar), *D. tumicolella* Mutuura Monroe and Ross, and Zimmerman pine moths (*D. zimmermani* (Grote)) mine under the bark of ponderosa (*P. ponderosae*), Austrian (*Pinus nigra* Arnold), and Scotch pines (*P. sylvestris* L.), girdling branches and trunks. Infested branches often bend downward or break off at the main stem, especially after heavy snow or during high winds (Harrell 1984). Ponderosa twig moths and *D. tumicolella* damage trees throughout Nebraska, while Zimmerman pine moths are found only in extreme eastern Nebraska. The life cycle of ponderosa twig moths takes 14 to 24 months to complete, while those of *D. tumicolella* and Zimmerman pine moths last approximately 1 year (Harrell 1984, 1986a). *D. tumicolella* damage can be reduced by applying acephate as a stem or

trunk implant, dimethoate as a stem drench, or disulfoton as a soil drench, in early April before first instar larvae bore into the trunk. The number of first instar ponderosa twig moth larvae and older *D. tumicolella* larvae can be reduced by applying acephate or dimethoate at 2-week intervals in mid-summer (Harrell 1986b, 1986c).

SEED-DAMAGING INSECTS.--Insect damage to seeds of conifers and hardwoods in the Great Plains is a major concern in seed production areas, in genetically superior stock, and in research programs to improve trees. The western conifer seedbug (*Leptoglossus occidentalis* Heideman) can destroy up to 80 percent of the seed of ponderosa and Scotch pines; ash seed weevils (*Lignyodes* spp.) can destroy up to 90 percent of the green ash and lilac seed (Dix 1986).

Forest Service entomologists have identified insect species that damage ponderosa pine, Scotch pine, and green ash, and some insect species that damage other conifer and hardwood trees. Dix (1986) determined that lilac is an alternative host for the ash seed weevil. Detailed information on life cycles and impact of damage on seed yield is available for only a few of these species. Aspects of the life cycle, behavior, and seasonal abundance of the western conifer seedbug and the ponderosa pine coneworm (*Dioryctria auranticella* Groté), and the effect of insect damage on seed yield are being studied.⁹ Effective techniques for control of most seed-damaging insects in the Great Plains are not available. Laboratory analyses of acephate in Scotch pine cones indicate that acephate residues should kill webbing coneworm (*D. disclusa* Heinrich) larvae for 10-15 days after spraying (Dix and others 1981), but this needs to be verified in the field. Carbofuran, an insecticide used to control seed-damaging insects in the south, was ineffective in reducing webbing coneworm and western conifer seedbug damage to Scotch pine seeds in Nebraska and North Dakota (Dix and Van Deusen 1983).

SUMMARY.--In summary, trees growing in windbreaks and native stands are essential components of the Great Plains environment. However, many trees perform poorly or die because of adverse climatic and site conditions and damage from insects and diseases. Forest Service research is improving tree performance by selecting and breeding genetically improved sources of trees and developing methods of reducing insect injury to trees. Entomology research has collected biological information and developed techniques for detecting, evaluating, and reducing damage for some of the most destructive insect species. Further research should refine these techniques, develop new techniques, and obtain the biological data needed to effectively manage infestations of and damage by several important seed-damaging insects and tip borers. In addition, insects that damage the seeds of spruce, honeylocust, and pines need to be identified and their effect on seed production assessed. The most destructive of these seed-damaging insects can then be targeted for additional research. This

⁸Dix, M.E.; Underhill, E.W. Sex attractant of *Retinia metallica* (Busck) (Lepidoptera:Tortricidae): Identification and field studies. (Manuscript in preparation).

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research should result in additional guidelines for reducing insect damage to trees that can be integrated into managements plans for future plantings in the Great Plains.

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HORMONAL REGULATION OF MYCORRHIZA¹

Nada Gogala²

The laboratory of plant physiology at the University of Ljubljana is mainly devoted to the investigation of hormonal regulation in mycorrhiza.

It was determined that fungi influence with growth substances the development of the root system and growth of green plants on degraded soil. On the other hand, the tree with its growth substances in the root and in the exudate influences the growth and metabolism of the mycelium.

In the root exudate of the scotch pine *Pinus sylvestris* we found all growth stimulators--auxins, gibberellins and cytokinins and the inhibitor abscisic acid (ABA). Cytokinins at concentration of about 10^{-7} g/ml are stimulators of fungal growth, while at supraoptimal higher concentrations inhibit it (Fig. 1).

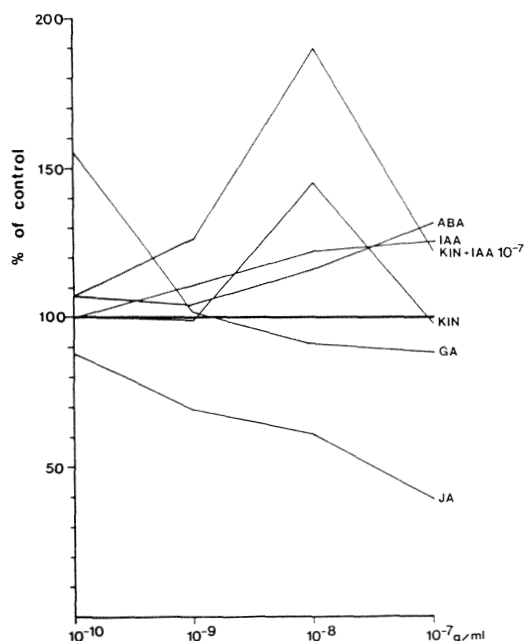


Figure 1.--Influence of various growth substances on growth rate of the fungus *Suillus variegatus*. Fresh weight of mycelium after 2 weeks of growth,

expressed in percentage of control values (100%) at different concentrations of growth substances in medium.

Gibberellins inhibit growth, indole acetic acid (IAA) does not have a significant influence, but together with cytokinins work synergistically. ABA is without effect, while JA (jasmonic acid) is a very strong inhibitor. We think that the relation of the growth substances in the exudate and in the roots is very important for normal growth of the mycelium around the roots and between the cells of rhizodermis.

We also investigated the influence of some environmental factors on the exudation of cytokinins and gibberellins from pine trees. Young seedlings of *Pinus sylvestris* were cultivated in bidistilled water in growth chambers at different photoperiods, different light intensities and three different temperatures. After 6 days of treatment cytokinins and gibberellins were extracted and analyzed by paper and column chromatography and tested with bioassays. According to our results we can claim that the amount of cytokinins and gibberellins increases with increasing length of the daylight phase. Light intensity does not affect the exudation of gibberellins, but the effect on the exudation of cytokinins is obvious. There were more cytokinins in the exudate at higher light intensities (Fig. 2).

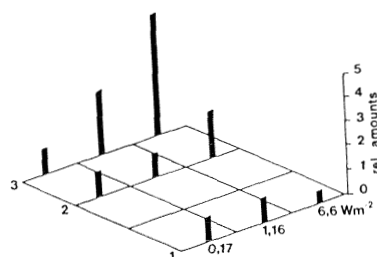


Figure 2.--Influence of light intensity on the exudation of cytokinins and gibberellins from red pine seedlings. 1: relative amounts of gibberellins at different light intensities, detected with the endosperm bioassay, 2: relative amounts of cytokinins in the water phase, and 3: the same in a butanol phase, detected with the radish cotyledon bioassay.

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Similarly temperature did not influence gibberellin exudation and the optimal temperature for the exudation of cytokinins was 22° C. (Figs. 3 and 4.)

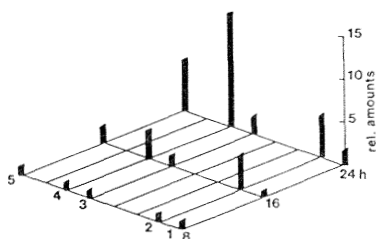


Figure 3.--Influence of photoperiod on the exudation of phytohormones. 1,2: relative amounts of gibberellins at different day-length, detected with the endosperm bioassay. Exudates from pine seedlings of two provenances. 3: relative amounts of cytokinins in the water phase and 4: the same in the buthanol phase, detected with the tobacco tissue assay. 5: Cytokinins, detected by Amaranthus hypocotyl assay.

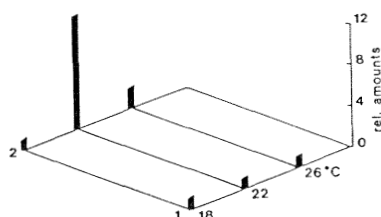


Figure 4.--Influence of temperature on the exudation of phytohormones. 1: relative amounts of gibberellins at different temperatures, detected with endosperm bioassay. 2: Cytokinins detected with Amaranthus hypocotyl assay.

Our conclusion is that only certain combinations of environmental conditions such as a long day regime, higher light intensities and optimal temperature bring about such a combination of hormones in a rhizosphere, which promotes mycelium growth and the formation of mycorrhiza.

Plant hormones, mainly cytokinins in the exudate influence the uptake of ions, e. g. sodium, calcium, potassium and phosphorus, into the mycelium. During the first days after inoculation cytokinins are responsible for a decreasing content of elements in the mycelium but later, after 15 days of growth, there is an evident increase in uptake.

On the basis of this and previous papers we can generalize that cytokinins from the root exudate of higher plants may influence the growth of fungi and regulate the uptake and distribution of important elements in the mycelium of mycorrhizal fungi (Fig. 5). It is still unclear how cytokinins influence the cell membrane. To clarify this question EPR (electron paramagnetic resonance) was used to measure the fluidity of the membranes with and without the

cytokinins (Fig. 6). Mycelium was grown in the standard medium. During growth zeatin was added to the medium. After 14 days the mycelium was spin labeled with a nitroxide derivative of palmitic acid methylester (MeFASL). The results show that zeatin at concentrations of 10^{-6} mol/l produces a slight decrease in membrane fluidity, but at a concentration of approximately 10^{-3} mol/l the fluidity of the membranes increases.

The observed changes in membrane fluidity might be connected with changes in ion transport mechanisms and/or binding properties of the membranes.

The influence of cytokinins on the growth of fungi is connected with the concentration of minerals in the medium. In a medium poor in minerals the effect of cytokinins is more pronounced.

On the other hand, we are also investigating the influence of hormones from the mycelium on the growth of trees and their roots. Auxins are very important for the formation of mycorrhizal roots. We found IAA and TR (tryptophan) as its precursor in all mycorrhizal fungi, but not at the same concentrations. We therefore decided to extract these auxins from the fungus, and to treat tree cuttings with them in order to improve rooting. Good results were obtained when Acer pseudoplatanus was treated with auxins from Lycoperdon species.

With increasing air and soil pollution, investigation of mycorrhiza becomes more and more important in forestry. Mycorrhizal fungi accumulate heavy metals. Various species of fungi do not accumulate the same metals and not in the same concentrations. We can therefore find more Cd in the mycelium of Suillus variegatus as in Amanita muscaria or Boletus edulis. The growth of mycorrhizal fungi is inhibited by heavy metals as, for example, Zn, Cd, and others.

For practical purposes we are also investigating the effects of fungicides and herbicides used in nurseries. The use of these chemicals at too high concentrations in agriculture and forestry is problematic, since it influences not only parasitic fungi and weed plants, but they also inhibit the growth of symbiotic microorganisms. Herbicides in general are strong inhibitors of growth of the mycorrhizal fungi Boletus bovinus and Suillus variegatus (Fig. 7). At the concentrations used in nurseries they completely inhibit the growth of the mycelium. We tested "Roundup," "Gramoxone," and "Basamid." The fungicides "Benomil," "Captan," and "Cuprablau" also inhibit fungal growth (Fig.8).

With the use of tissue culture we are able to investigate the influence of mycorrhizal relationships in vitro. We tried to stimulate with fungal metabolites the axillary buds of the seedlings of Pinus sylvestris and adventive buds from embryos in vitro. Some influence on the axillary buds was observed, but we think that

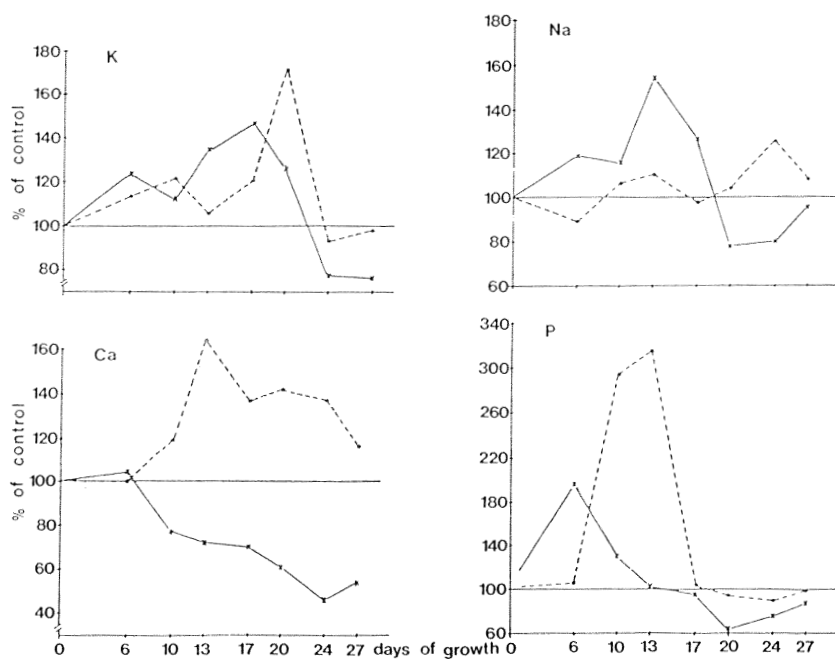


Figure 5.--The influence of zeatin (10^{-5} mol/l) on the ion transport into and through mycelium of *Suillus variegatus*. x—x: Concentration of ions in mycelium, o—o: concentrations of ions in medium.

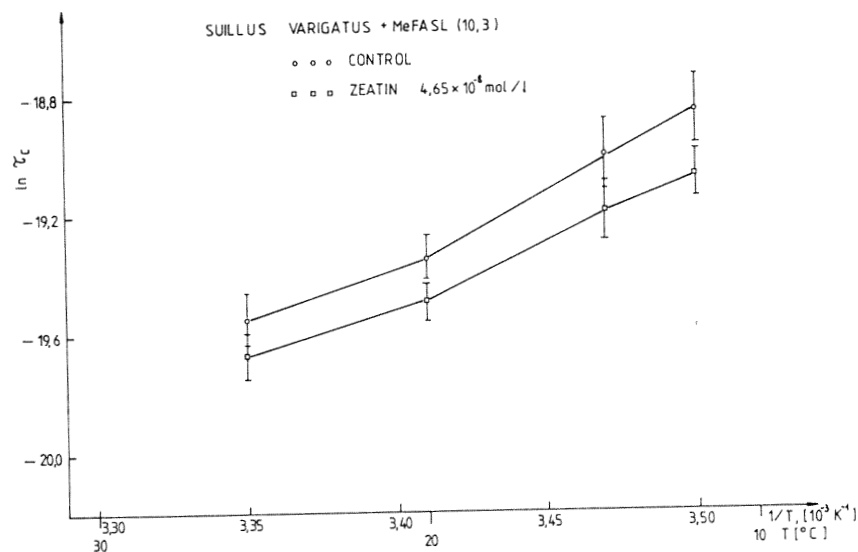


Figure 6.--The change of membrane fluidity of fungal hyphae after treatment with zeatin, measured as correlation time of MeFASL at different temperatures.

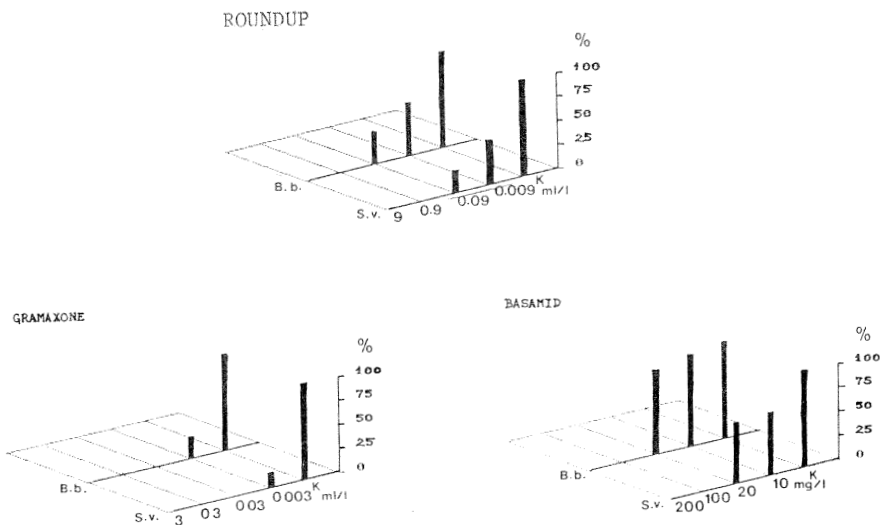


Figure 7.--Fresh weight of mycelium of *Suillus variegatus* (S.V.) and *Boletus bovinus* (B.b.) cultivated in medium at various concentrations of fungicides and herbicides Roundup, Gramaxone, and Basamid.

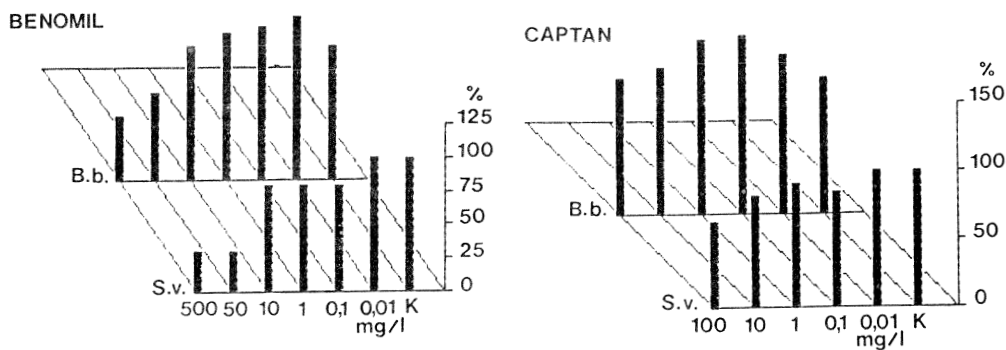


Figure 8.--Fresh weight of mycelium of *Suillus variegatus* (S.v.) and *Boletus bovinus* (B.b.) cultivated in medium at various concentrations of the fungicides Benomil and Captan.

other species should be tested with higher concentrations of natural growth substances.

BAP (benzyl-amino-purine) gave us the best results. The best initiation of buds was obtained with seedling apices soaked in BAP for 3 hours. Buds longer than 1 mm were separated and elongated by far-red light. Elongated buds and shoots were treated again with BAP which resulted in the initiation of secondary buds or were rooted with NAA (naphthalene acetic acid), IAA or IBA (indole butyric acid).

The highest rooting percent (64%) was obtained with treatment with 54 μ m NAA. Rooted shoots and plantlets were placed in a substrate with or without the mycelium of *Pisolithus tinctorius*. After two months the stimulative effect of the mycelium was evident (Fig. 9).

We hope that in the next months the formation of mycorrhiza will occur. In such a way we could like to get the mycorrhizal trees for afforestation on nutrient depleted or eroded land.

An interesting new approach is the stimulation of mycelia with weak DC electric currents, similar to those, normally produced by both fungal hyphae and plant roots. Significant differences in fresh and dry weight (85% and 50%, respectively), reflect a drastic growth rate enhancement of the stimulated mycelia. The effect was observed regardless of whether chloridised silver or stainless steel electrodes were used. Changes in the pattern of ion accumulation were found, with increases in calcium and potassium content and decreases in sodium and phosphorus content.



Figure 9.--Plantlets of Pinus sylvestris two months after planting in substrate with mycelium of Pisolithus tinctorius (above) or without it (below).

In conclusion, our work is aimed at elucidating various aspects of mycorrhizal relationships and

the importance of this form of symbiosis for forest ecosystems.

Pauline C. Spaine²

Abstract.--The enzyme-linked immunosorbent assay (ELISA) is a immunochemical test that can be designed to both detect and relatively quantify the amount of mycelium in a host plant. ELISA is therefore a rapid and sensitive procedure for detecting plant pathogens. Two procedures, the indirect and indirect preabsorption ELISA were used to detect Cronartium quercuum f. sp. fusiforme (Cqf) in Pinus taeda seedlings. Detection of Cqf homogenates with the indirect ELISA was possible with fungal fresh weights as low as 20 µg/ml. However, when the indirect ELISA was applied to detect Cqf homogenates mixed with healthy tissue (simulating an infection situation), binding efficiency was decreased and detection levels were lowered. For further testing of Cqf-infected P. taeda seedlings, the indirect preabsorption ELISA was designed to eliminate the interference from healthy plant homogenates in binding to the ELISA plates. This assay eliminated the interference from healthy plant homogenates and maintained a high sensitivity for Cqf detection.

Keywords: ELISA, Cronartium, fusiform rust, resistance screening.

HISTORY OF THE DISEASE AND DISEASE RESISTANCE SCREENING EFFORTS

Fusiform rust, caused by the fungal pathogen Cronartium quercuum (Berk.) Miyabe ex Shirai f. sp. fusiforme (Cqf), is the most economically destructive disease in pine plantations in the Southeastern U.S. Annual losses to the disease exceed 130 million dollars annually (Anderson and others, 1982). The disease causes tremendous losses in nurseries, young plantations and seed orchards. The highest percentage of mortality from the disease occurs in seedlings and young trees less than 8 years old (Agrios 1978; Czabator 1971).

Control of fusiform rust in forest tree nurseries relies primarily on fungicide spraying of the seedlings in nursery beds (Schmidt and others, 1981). The most economical and long-term control of fusiform rust in field plantings is to increase the level of resistance to Cqf in the pine population through breeding and selection (Czabator 1971; Dinus and others, 1976; Jewell 1960).

Screening for disease resistance in the field depends upon an assessment of both the incidence and severity of the disease. These field tests, however, require a minimum of 4 to 5 years for

evaluation of new plantings. Greenhouse screening of Pinus elliotii Engelm. var. elliottii seedlings at the USDA Forest Service Resistance Screening Center maintained by Forest Pest Management in Asheville NC, can provide resistance ratings as early as 6 to 7 months after inoculation with Cqf basidiospores. Screening center ratings based on gall and infection characteristics of greenhouse inoculated seedlings are closely correlated with field resistance.

Early infection of P. elliotii tissues by Cqf in some cases produced necrotic responses that were thought to limit fungal growth, and were observed to occur with increased frequency in a resistant family line (Miller and others, 1976). Using light and transmission electron microscopy, Gray and Amerson (1983) observed several responses of P. taeda L. to Cqf infection as early as 36 hours after in vitro inoculation with Cqf basidiospores. In three P. taeda families examined, all displayed a necrotic response, but, the resistant family developed cell and tissue necrosis more rapidly than families rated as susceptible or intermediate in disease resistance. Frampton and others (1983), working with 24 full-sib families of P. taeda seedlings inoculated in vitro with Cqf, observed various characteristics of two phenotypic responses. These responses, a rapid necrosis and the appearance of a dark staining substance seen 7 days after inoculation, were highly correlated with families having low disease resistance ratings in the field.

Most in vitro studies examining early rust resistance have been done via microscopy. These assays are tedious, and assessment and grading scales may differ subjectively from one lab to the next. During the last 5 years, however, sensitive serological techniques such as enzyme-

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linked immunosorbent assays (ELISA) have made it possible to detect pathogens in plants in nanogram and picogram quantities (Van Regenmortel, 1982; Yolken, 1978). ELISA is an objective and quantitative method that allows large numbers of specimens to be examined rapidly. Recently investigators have used ELISA to detect fungal pathogens such as *Verticillium lecanii* in wheat (Casper and others, 1979) and *Epichloe typhina* in tall fescue (Johnson and others, 1982). ELISA has also been used for the quantification of enzymes in fungi (Martin and others, 1983). In the area of forest pathology, Gooding and Powers (1965) using serological techniques, were able to differentiate between 3 closely related tree rusts (*Cronartium*).

This paper will describe two versions of an ELISA for the detection of fusiform rust. These assays were compared for the detection of *Cqf* from axenic cultures, and secondly for the detection of *Cqf* mycelial growth in *P. taeda* seedlings.

ELISA

Enzyme-linked immunosorbent assay (ELISA) is a diagnostic technique which has emerged over the last decade, and is based upon immunological principles. Immunoassays such as ELISA rely on the specific binding that can occur between antigens (foreign substances) and antibodies made against those antigens (Cunningham, 1978). Experimental observations made in 1971 recognized that when an antigen or antibody is chemically (covalently) linked to an enzyme, the resulting conjugate retains both its immunological and enzymatic activity (Koenig and Paul, 1982; Yolken, 1978). Antibodies or antigens labeled with various markers have been found to be particularly useful for assays of biological substances (Savage and Sall, 1981; Voller and others, 1980) as in an ELISA. The label can be an isotope (radioimmunoassay), a fluorescent molecule (fluoroimmunoassay) or an enzyme (ELISA) giving increased sensitivity in detecting the antigen-antibody reaction (Voller and others, 1980).

There are numerous versions of ELISA (Koenig and Paul, 1982; Van Regenmortel, 1982), each being modified slightly for the system to which it is applied. Illustrated here are the two versions of ELISA discussed in this paper (Figures 1 and 2).

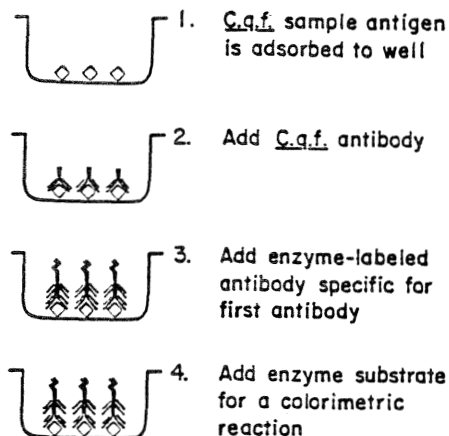


Figure 1. The Indirect ELISA

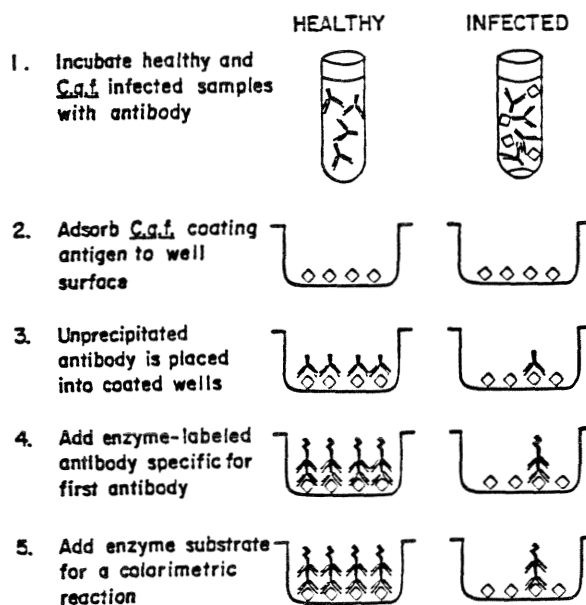


FIGURE 2. The Indirect Preabsorption ELISA

In the indirect ELISA (ID) (Figure 1), the antigen (pathogen) is coupled to the plate, then the antibody that was produced against the antigen (primary antibody) is added. In the next step, after incubation and washing, a secondary antibody (goat anti-rabbit), that has been commercially conjugated to an enzyme is added to the plate.

In the indirect preabsorption ELISA (IPA), the inoculated and healthy samples are incubated with primary antibody in separate tubes before adding them to the ELISA plate (Figure 2). Subsequent steps follow as in the indirect ELISA.

The final step in the above ELISAs is the addition of substrate. The enzyme label conjugated to the antibodies will catalyze the reaction of substrate to product, yielding a colorimetric reaction. The amount of colorimetric product is dependent on the quantity of antigen that was originally present in the test sample.

MATERIAL AND METHODS

Pinus Taeda Inoculations

Basidiospore inoculum was collected according to method II (Amerson and others, 1985). Leaves of Quercus rubra L. bearing telia were suspended in a moist chamber over sterile acidified distilled water (pH=2.2) for 36 hours. The water was collected and the basidiospores were concentrated on a 5 µm millipore filter. Spores were resuspended in distilled water (pH=5.5), and the concentration of spores was adjusted to approximately 2000 spores/µl with a Coulter counter (Coulter Electronics Inc., Hialeah, Florida). A Hamilton syringe and repeating dispenser were used to deliver 1 µl droplets to embryo hypocotyls.

Before they were germinated P. taeda seeds were nicked at the micropylar end and incubated 4 to 5 days in 1% hydrogen peroxide at 28 to 30°C. Seedcoats were removed and the seeds were surface sterilized in 15% Chlorox for 5 minutes, then rinsed twice in distilled water. Embryos were aseptically excised from gametophytic tissues and grown on a Greshoff and Doy x ½ medium (Mott and others, 1981) for 1 week before inoculation. After inoculation, seedlings were maintained at 23°C in the dark for 3 days, then transferred to a mixed incandescent/florescent light environment. Seedlings were evaluated from 3 to 8 weeks after inoculation, along with uninoculated control seedlings of equivalent age from the same families.

Antigen Preparation

Northern red oak (Quercus rubra) leaves bearing telia columns of C. quercuum f. sp. fusiforme were obtained from the USDA Forest Service Resistance Screening Center in Asheville, NC. Telial columns were removed and individually rolled on 1.5% water agar to remove urediospores. Columns were gathered into groups of five and suspended

over a modified Greshoff and Doy medium plus 1 gm/l yeast extract and 1 gm/l peptone (Amerson and others, 1978). Basidiospores were discharged from the telia onto the medium to produce axenic colonies. Mycelium used for antigen preparation was subcultured from these plates and grown in darkness at 24°C in a liquid Greshoff and Doy medium with 1% bovine serum albumin. Eight-week-old Cqf mycelial cultures were collected in a Buchner funnel (Whatman #1 filter paper), washed several times with phosphate buffered saline (PBS) (pH=7.4) and ground in a glass mortar with motorized pestle.

The homogenate was centrifuged twice (10,000 g, 10 minutes), and the pellets were combined. The pellets were resuspended in a volume of PBS equal to three times the pellet weight and stored at -4°C. For immunization of the rabbits, the fungal homogenate was diluted to 0.003 gm/ml and a 0.03 ml aliquot was emulsified in 2 ml PBS and 1.7 ml Freund's incomplete adjuvant. Two New Zealand white rabbits were injected weekly for 4 months with 2 ml of emulsified suspended given intramuscularly and subcutaneously. After 1 month of immunization, the rabbits were bled weekly from the marginal ear vein. Reactivity of the blood serum was tested by an agar double immunodiffusion test (Ouchterlony, 1958) and was seen as a visible precipitation band.

Immunoglobulin Preparation

The immunoglobulin (Ig) fraction from the anti-serum was purified by precipitation with an equal volume of 36% saturated sodium sulfate. The Ig precipitate was collected by centrifugation at 650 g for 15 minutes and the pellet washed twice with 18% sodium sulfate. The Ig was resuspended in 2 ml of half-strength PBS and dialyzed exhaustively against half-strength PBS at 4°C. The Ig fraction was adjusted with 0.02% Na₃ to inhibit microbial activity. The purified Ig fraction was stored at 4°C.

Indirect ELISA (ID)

Test samples were ground in a tissue homogenizer with virus buffer (PBS + 0.05% Tween-20 + 2.0% polyvinyl-pyrrolidone [Sigma]). Samples were serially diluted in coating buffer (Na₂CO₃ 0.15M; NaHCO₃ 0.035M [pH=9.8]) and 200 µl were added to the Immulon II ELISA plates (Dynatech Laboratories, Inc., Alexandria, VA 22314) for 3 hours at 36°C in triplicate wells. Plates were washed by flooding wells with PBS + 0.05% Tween-20 + 0.5% egg albumin. Additional washings between incubation steps were done with PBS + 0.05% Tween-20. After incubation and washing, 200 µl of purified Ig were added per well, and the plate was incubated overnight at 4°C. After three washes, 200 µl of goat anti-rabbit alkaline phosphatase conjugated Ig (1:1000) were added to each well. Plates were incubated for 2 hours at 37°C and washed three times. Ninety minutes after the addition of substrate (p-nitrophenol phosphate [1.0mg/ml in

10% diethanolamine (pH=9.8]), absorbance values (405 nm) were determined by a Titertek Multiskan photometer (Flow Laboratories, McLean VA 22104).

The sensitivity of the ID ELISA was tested using dilutions from 5000 at 20 $\mu\text{g/ml}$ of a 1:10 Cqf mycelial homogenate. These fungal concentrations were tested at 1:700, 1:800, and 1:1200 dilutions of antibody followed by 1:1000 dilution of goat anti-rabbit conjugate. To test for binding interference between fungal mycelium and plant extracts on the ELISA plate, 100 mg/ml of healthy plant homogenate were mixed with each dilution of Cqf mycelium so that equal healthy plant concentrations were maintained at each dilution.

Indirect Preabsorption ELISA (IPA)

Wells of an ELISA plate were coated with 200 μl of a 1.0 mg/ml Cqf mycelial homogenate and incubated for 3 hours at 36°C. Plates were washed with PBS + 0.05% Tween-20 + 0.05% egg albumin. In a separate test tube, plant and/or fungal dilutions were mixed with an equal volume of Ig at 1:800 and incubated for 4 hours at 4°C. Following incubation, samples were centrifuged at 7000 g for 10 min. The supernatant containing unprecipitated antibody was removed from each sample, and placed in the previously coated wells of the ELISA plate followed by incubation overnight at 4°C. After incubation, plates were washed (PBS-Tween) and goat anti-rabbit alkaline phosphatase conjugate at 1:1000 dilution was added at 200 $\mu\text{l/well}$. Development of the plates was as described in the ID ELISA.

RESULTS AND DISCUSSION

To determine the sensitivity of detection of Cqf antisera to Cqf mycelial homogenates, three homogenate dilutions at 10, 0.1 and 0.001 mg/ml were tested over a range of antibody dilutions (data not shown). A 1:600 to 1:800 dilution of antibody detected a 0.1 mg/ml dilution of Cqf. had a small standard deviation and maintained large difference in absorbance from healthy plant controls. At a 0.1 mg/ml dilution of Cqf a 1:600 antibody dilution had an average absorbance of 0.153 ± 0.034 and a 1:800 antibody dilution had 0.135 ± 0.011 absorbance. Healthy plant homogenates (100 mg/ml) tested at antibody concentrations of 1:400 and 1:1000 had an absorbance of 0.045 ± 0.026 and 0.035 ± 0.009 , respectively. An ID ELISA standard curve for the detection of Cqf mycelial homogenates (Figure 3) indicated that each of three dilutions of the antibody (1:700, 1:800, and 1:1200) could detect Cqf homogenate down to 20 $\mu\text{g/ml}$ dilution at which point healthy plant absorbance began to interfere. In the ID ELISA, absorbance from healthy plant homogenate remained uniform at all concentrations tested with a 1:700 antibody dilution, indicating little specificity for the antibody. Part of this constant absorbance may be due to nonspecific binding of secondary antibody (goat anti-rabbit)

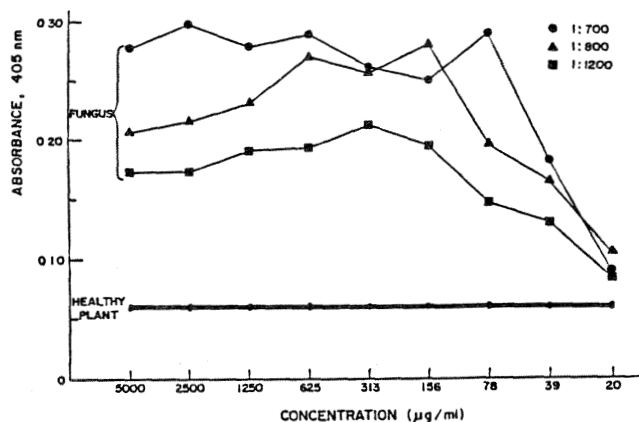


FIGURE 3. Indirect ELISA for Cqf at 3 antibody concentrations.

(Van Regenmortel 1982). Conjugate alone had a mean absorbance of 0.021.

In the ID ELISA, when Cqf and plant homogenates were mixed, detection of Cqf was severely inhibited. Healthy plant homogenates may have non-specifically adhered to the polystyrene plate, thereby interfering with Cqf binding. This interference limited Cqf detection levels in infected plant samples and led to the adoption of an indirect preabsorption ELISA (IPA). This procedure circumvents nonspecific binding by healthy plant homogenates by allowing dilutions of plant, fungus and antibodies to preincubate together in a tube before being put on the ELISA plate (Figure 2). The IPA ELISAs detection of Cqf mycelial homogenates alone or mixed with healthy plant homogenates was possible at less than 10 $\mu\text{g/ml}$ fungal fresh weight. Detection of Cqf mycelial homogenate alone and mixed with healthy plant were similar, thus indicating little or no healthy plant interference.

Detection of Cqf in Pinus Taeda

Cqf mycelium was detected in all inoculated P. taeda seedlings tested 3 to 8 weeks after inoculation with Cqf basidiospores (Figure 4). Healthy plant controls were significantly different ($P=0.05$) from Cqf inoculated plants at every week tested. Levels of the fungus appeared to decrease over time as more plant material was incorporated into the assay each week (Figure 4). This decrease may have been due to a resistance mechanism in families such as 7-56, which is rated as field resistant ($P.L. = 65$). More likely, the growth of the seedling relative to the infection site was not taken into consideration in these preliminary assays. It is important to note however, that the antibody to axenic hyphae and this same antibody was then able to detect Cqf infection from basidiospore infections. The growth differential and an earlier sampling time after inoculation will be taken into account in future assays before quantitative evaluations can be made.

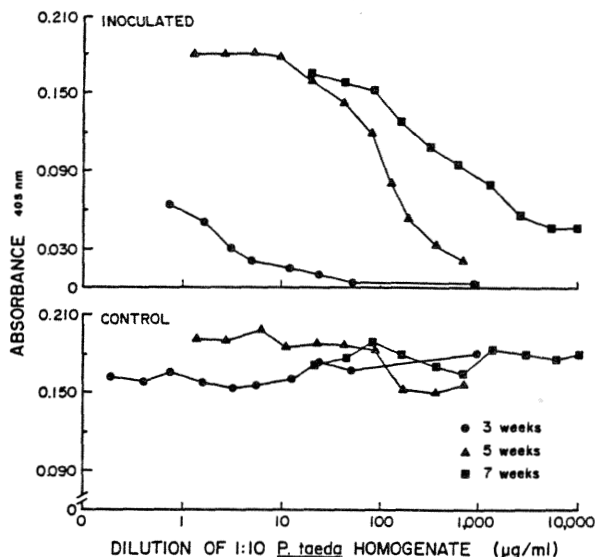


FIGURE 4. Indirect Preabsorption ELISA of *P. taeda* seedlings 3, 5 and 7 weeks after inoculation with *Cqf* basidiospores and control seedlings of equivalent age.

In conclusion, a sensitive ELISA immunoassay for the detection of *Cqf* mycelium in inoculated *P. taeda* seedlings has been developed. ELISA is a sensitive tool capable of examining host-pathogen relationships and can be used in combination with tissue culture to study different environmental and nutritional settings. Once the growth dynamics of the fungus and the host are better understood, we can begin to use the ELISA for the quantitative evaluation of *Cqf* infection in genotypically different *P. taeda* lines.

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THE BIOLOGY OF LEUCOLOPSIS PULVERULENTA DOGNIN

(LEPIDOPTERA, GEOMETRIDAE)¹

Joy Woolfson de Noboa²

Since immemorable times, even before the Spanish colonization of Ecuador, the forest resources of the country were exploited without any kind of protectional policies. By the beginning of this century the highlands called "La Sierra" were almost completely deforested.

Because of this reason, some fast growing trees like Pinus and Eucalyptus were brought to reforest the highlands. But with the introduction of these exotic species and the forming of monospecies woods ecological changes happened, bringing with them some problems such as the adaptation of native species of insects to these trees.

This is the case of the defoliator Leucolopsis pulverulenta, a white moth known only from Colombia and Ecuador that has changed her food preferences from native shrubs like Lupinus sp. and Hypericum laricifolium to the now more abundant Pinus radiata in some areas of the highlands. Cyclically it can become a pest that delays the natural growing rate of the groves and sometimes kills the trees.

This work is about the biology of the White Moth. It is supported by an agreement between the United States Agency for International Development, the Ministry of Agriculture of Ecuador and the Pontificia Universidad Catolica del Ecuador. It is divided in two parts. In the first part the life cycle of the moth is studied under laboratory conditions. In the second part, a census was made to determine the annual population variations of the moth in nature.

MATERIALS AND METHODS

The laboratory colony was established from eggs, larvae, pupae and adults collected during periodical visits to the Parque Nacional Cotopaxi, a paramo park located from 3500 to 5897m over sea level, one hour south from Quito; that was reforested with some species of the genus Pinus, mainly with P. radiata.

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The eggs were kept in plastic boxes with filter paper and moisture, until hatching. After that the larvae were separated. The larvae were reared at room temperature (10 - 20 degrees centigrade), each one in a plastic transparent round box 4cm x 1.5cm with filter paper at the bottom moistened with a 0.04% formaldehyde solution and fresh, young pine needles that were changed every other day. At the same time, the boxes were monitored for the presence of molts. The pupae were sexed and placed in soap-boxes 9 x 6 x 2.5 cm with filter paper and the same moistening solution. All the boxes were sterilized with a 2% formaldehyde solution before using.

For reproduction, a newly emerged male and female were placed together in a transparent plastic bag, with filter paper, moistening solution and a small cotton ball soaked in sugar solution. The bags were checked daily for eggs.

To make the adult population census, a square meter was marked on the wall of a house at the Parque Nacional Cotopaxi. Each month since March 1986, on the night of a new moon, a light trap was used to attract the moths that were collected and counted each hour for three hours.

DESCRIPTION OF THE INSECT

The adult is a white brilliant moth, with little silver spots on the anterior wings; wingspread measures 20 to 40 mm, being the males generally bigger than the females, the head is orange; the female has filiform antennae and the male plumose.

The eggs are light green, oval and their size is approximately 0.75 x 0.5mm. When they are close to hatching the color changes to purple.

The first instar larva is greenish with two yellowish dorsal lines and a black cephalic capsule. From the second instar the larva is greenish-yellowish with a black dorsal stripe and two black lines on each side; the cephalic capsule, the feet and the prolegs are orange.

The pupa is greenish with black spots on the abdomen and black lines on the wing area.

RESULTS

The duration of each stage is indicated in Table 1 together with the mode which serves to make a representative life cycle of the moth. The sizes of the cephalic capsules can help to determine the instars of the larvae in the field.

TABLE 1

| STAGE | RANGE | MODE' | SIZE | SIZE OF CEPHALIC CAP. | SURVIVAL |
|-------------|-------|-------|-------|--------------------------|----------|
| | days | days | mm | mm | % |
| Egg | 7-23 | 11 | 0.75 | --- | 100 |
| 1st. instar | 6-30 | 14 | 3-5 | 0.3 -0.5 | 61.9 |
| 2nd. instar | 6-26 | 11 | 5-11 | 0.5 -0.75 | 8.6 |
| 3rd. instar | 5-26 | 7 | 10-13 | 0.75-1.1 | 2.9 |
| 4th. instar | 5-21 | 7 | 13-15 | 1.1 -1.5 | 2.3 |
| 5th. instar | 4-23 | 7 | 15-21 | 1.5 -2.0 | 2.0 |
| 6th. instar | 7-22 | 14 | 21-30 | 2.0 -3.0 | 1.6 |
| Prepupa'' | 1- 5 | 2 | | | |
| Pupa | 11-28 | 21 | 10-15 | | 1.4 |
| Adult | 2-15 | 15 | 20-40 | | 1.3 |

' Mode.- Is the most repeated number inside the range.

'' Prepupa.- This stage is already counted in the sixth instar.

The cycle begins with the oviposition, in nature the eggs are laid in two or three columns on the pine needles, in the laboratory the eggs are laid uneven in the bags where the females have been placed.

After hatching, the larvae leave the corion almost complete. These first instar caterpillars are very active. They go towards the light and hang from silk threads. Maybe this is their dispersal mode.

As the percentage of survival indicates in Table 1, the first and second instar larvae are the most delicate. They can be affected by viruses, fungi or bacterial diseases and changes in the environmental humidity and food deficiency. Of course, these factors also affect the older larvae, but as they grow they get stronger.

In their sixth instar, the larvae enters the prepupal stage that takes the last two days. The larvae stop eating, their color turns greener and they make a very light silk web.

The adults have nocturnal habits, the mating and laying of eggs occurs during the night. A female can lay 20 to 200 eggs in a time of 1 to 6 days. The sex ratio male to female is 1.1 to 0.9.

Figure 1 represents the life cycle of the moth which lasts approximately three and a half months under laboratory conditions; the larval period which causes the damage to the trees takes 56% of the cycle.

Analyzing Figure 2, the time between the peaks, May through October, represents the field life cycle which is slightly longer than the one in the laboratory. This can be explained because the laboratory conditions of humidity are relatively stable, but in the field, the insect has to go through the dry season estivating.

The population of this moth is now controlled naturally by the pathogens named before and by two microhymenoptera parasites, one, a Scelionidae, of the eggs and the other, Casinarina cavigena, an ichneumonid of the larvae.

FIGURE 1: The life cycle

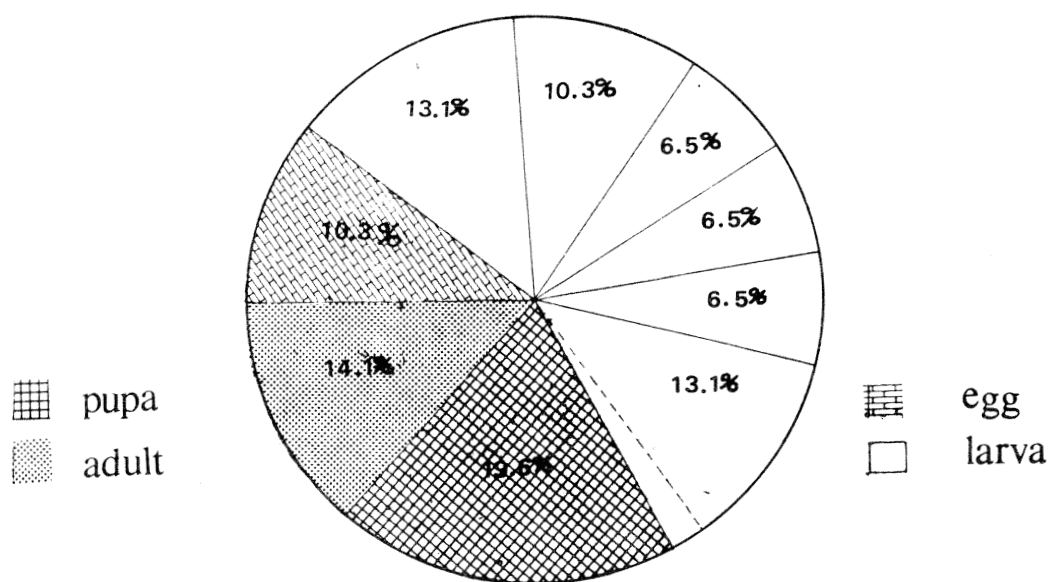
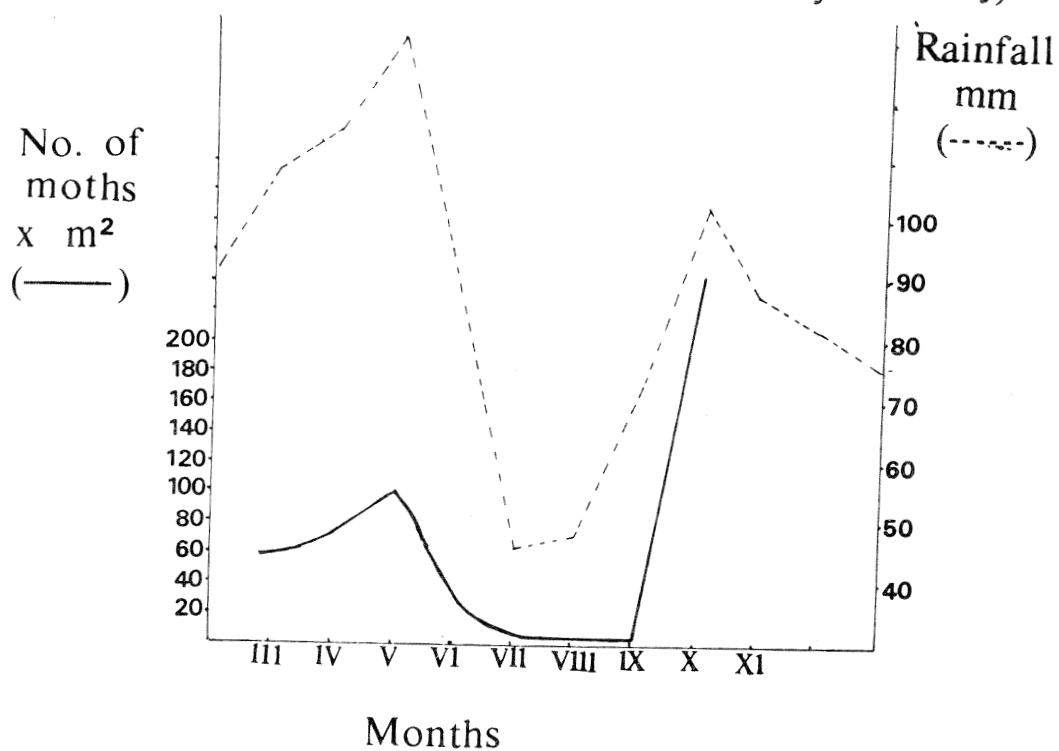


FIGURE 2: Relation cycle- seasons (dry or rainy)



Soil Solar Heating for Pest Control at Colorado
and Nebraska Forest Tree Nurseries¹

Diane M. Hildebrand²

Forest tree nurseries produce a valuable crop-- tree seedlings for reforestation, afforestation, and shelterbelts, as well as for ornamental plantings. In 1985, state and Federal forest nurseries produced about 850 million seedlings for forest and shelterbelt plantings on 140,000 ha (345,000 acres) across the United States (Forest Service, 1986). In 1985 in the Rocky Mountain Region of the USDA Forest Service (Colorado, Wyoming, South Dakota, Nebraska, and Kansas), trees were planted on 2,600 ha (6,400 acres) on Federal lands alone (Forest Service, 1986). Tree seedlings are a high value crop; conifer stock at the U. S. Forest Service Nursery in Nebraska is worth over \$90,000 per 0.4 ha (1 acre).

Soil-borne nursery pests including weeds and plant pathogens affect the production of tree seedlings. The primary impact of weeds is reduction in crop yield due to competition for light, water, space, and nutrients. Because conifer seedlings grow slower than most weed species, nursery weeds can greatly reduce the yield and quality of the crop (Owston and Abrahamson, 1984). Weed control in bare root nurseries usually includes fumigation before sowing, applications of herbicides, and weeding by hand. Not all of the weeds are controlled in one herbicide application, and repeated applications may be necessary. Often more than one kind of herbicide must be used, because no single herbicide is both safe for growing tree seedlings as well as effective against all weed species. Nearly all herbicides used sometimes cause phytotoxicity in the tree crop (Owston and Abrahamson, 1984). Weeding by hand is usually necessary and is very expensive.

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Abstract.--Solar heating by covering soil with thin clear polyethylene sheeting for several weeks during summer significantly reduced populations of weeds and damping-off fungi at the Colorado State Forest Service Nursery and the USDA Forest Service Bessey Nursery (Nebraska). Daily high temperatures achieved under the polyethylene averaged 8.5°C higher than in uncovered control plots. The maximum temperature recorded in solar-heated plots exceeded 46°C at 8 cm depth. Seasonal fluctuations in mineral ions in the soil solution were greater than differences due to solar heating. Oats planted immediately after solar heating exhibited an increased growth response in the solar-heated plots. However, lodgepole pine sown the following spring did not show a similar response.

Keywords: *Pythium* spp., *Fusarium* spp., soil chemistry, weeds, *Pinus contorta*, solar pasteurization.

Among the most widespread and destructive diseases of nursery tree seedlings is damping-off, which kills the seedlings either before (pre-emergence) or immediately after (post-emergence) they break through the soil (Sutherland and Van Eerden, 1980). Several fungi can cause this disease, but the most common in the Rocky Mountain Region are species of *Fusarium* and *Pythium*. Only very young seedlings are affected, and these soil-borne fungi directly invade the radicle and/or the hypocotyl at the ground line. After the seedling develops woody tissue, in four to six weeks, they are no longer susceptible to damping-off. Damping-off pathogens survive saprophytically or as various types of thick-walled spores in the soil between crops (Sutherland and Van Eerden, 1980).

Fumigation

Soil fumigation is widely used today in bare-root nurseries because soil-borne pathogens and weeds are controlled in a single application (Cooley, 1985). The most commonly used fumigant, 67% methyl bromide with 33% chloropicrin (trichloronitromethane), is injected into the soil several inches below the surface, and the soil is immediately covered with polyethylene sheeting. The polyethylene is removed after a few days, and the soil is allowed to aerate before planting. Fumigation by commercial contractors costs approximately \$1,100 per 0.4 ha, but is cost-effective considering the reduction in costs required for hand-weeding alone (Boyd, 1971; Landis et al., 1976).

Although widely used, chemical fumigation has several drawbacks. Fumigation is not always effective due to problems in even distribution of the fumigant. Fumigation inefficiencies are often not detected until the tree seedlings emerge and damping-off or weeds become evident. In addition to soil-borne pathogens and weeds, many kinds of desirable organisms are also destroyed by chemical fumigation. Populations of decomposers, detritivores, and mycorrhizal fungi are decimated. Endomycorrhizal fungi are more sensitive than

damping-off fungi, and ectomycorrhizal fungi are also destroyed (Munnecke and Van Gundy, 1979). In addition, fumigation chemicals are hazardous to apply and require special handling. Fumigant vapors may damage nearby vegetation. Recent restrictions in the use of fumigants related to methyl bromide indicate a need for alternative chemical and cultural practices. Alternative chemical fumigants include forms of biodegradable methyl isothiocyanate, e.g. Basamid granular.

Solar Heating

Solar heating of soil is a cultural practice that is less expensive and less hazardous than fumigation, and destroys fewer beneficial organisms. Solar heating (solar pasteurization, soil solarization) consists of covering moist soil with clear polyethylene sheeting for several weeks during the hottest months to reduce population levels of soil-borne pathogens and weeds (Katan et al., 1976).

Solar heating has been effective against a variety of weeds and soil-borne pathogens, especially for agricultural crops in warm climates such as Israel and California (Grinstein et al., 1979; Jacobsohn et al., 1980; Ashworth and Gaona, 1982). Studies also showed that disease reduction was still evident the second growing season after solar heating (Katan et al., 1983; Pullman et al., 1981b).

In some climates, solar radiation can increase soil temperatures to over 40°C at a depth of 30 cm under polyethylene sheeting (Pullman et al., 1981b), chiefly by preventing evaporation and partly by the greenhouse effect (Mahrer, 1979). Continuous or repeated sub-lethal temperatures under moist conditions over long periods either kill pathogenic fungi directly or weaken them so they cannot compete effectively with saprophytes. In laboratory tests, 90% of the propagules of *Verticillium dahliae* Kleb. died after two hours at 45°C or after seven days at 38.5°C in natural field soil. In pure culture at 45°C, seven hours were required for 90% mortality (Pullman et al., 1981a). Plant pathogens are apparently more sensitive to elevated temperatures than are saprophytes. Mycorrhizal fungi such as *Glomus fasciculatus* (Thaxter) Gerd. & Trappe can survive solar heating and colonize crop roots (Pullman et al., 1981b).

Besides the direct effects of elevated temperature during solar heating, toxic effects of released volatiles from soil organic matter may contribute to pest control. Zakaria et al. (1980) found that volatile degradation products of oilseed meal amendments reduced populations of *Fusarium* spp. in closed containers.

Horowitz et al. (1983) found that foliar scorching and decreased emergence were the main effects of solar heating on weeds. In their study the lowest damaging temperature for weed seeds was 45°C, and moisture was found to sensitize seeds and other weed propagules to damage by heat.

Solar heating may affect soil chemistry. For example, a few studies have reported increases in nitrate and ammonium nitrogen, potassium, calcium magnesium, chloride, and phosphate in the soil solution due to solar heating (Stapleton et al., 1983; Chen and Katan, 1980). In addition to disease reduction, this increase in soluble mineral nutrients may contribute to the increased growth response observed in crops grown in solar-heated soil (Stapleton et al., 1983).

Solar heating of soil for conifer nurseries has been evaluated recently in a few areas of the United States. Results at the Iowa State Nursery at Ames indicated reduced populations of weeds from solar heating but no significant decreases in populations of *Fusarium* spp. (Croghan et al., 1984). In trials at the Bend Nursery in eastern Oregon, Cooley (1983) found that populations of *Fusarium* spp. were significantly reduced by solar heating, but tree seedling survival after ten weeks was similar in control and solar-heated plots. Results at the J. Herbert Stone Nursery, Medford, Oregon (Cooley, 1985) indicated significant reductions in populations of *Fusarium* spp. due to solar heating, but again seedling survival was not improved.

Nursery managers in Colorado and Nebraska were interested in alternatives to methyl bromide for controlling weeds and damping-off fungi. This study was undertaken to evaluate solar heating for reductions in pest populations and to measure changes in the soil solution and any growth response in a conifer crop. This study showed some significant reductions of *Pythium* spp., *Fusarium* spp., and weeds by solar heating in Colorado and Nebraska, but no beneficial effects in lodgepole pine sown the following spring.

MATERIALS AND METHODS

Study Area Locations

Solar heating trials were conducted at two nurseries in the Rocky Mountain Region. The Colorado State Forest Service (CSFS) Nursery is located on the western edge of Fort Collins, Larimer County, Colorado, at 1560 m (5120 ft) elevation. The soil in the study area was mainly Kim Loam with areas of Altvan Sandy Clay Loam (Moreland, 1980). Tree seedling production began at the nursery in the middle 1960's. Study plots were located in a nursery block in which an entire spruce planting had been recently plowed under due to excessive losses to damping-off. The nursery block was 91 m by 61 m (300 ft by 200 ft), sloped gently (1-3%) to the southeast, and had never been fumigated.

The USDA Forest Service Bessey Tree Nursery is located on the north edge of the Nebraska National Forest, Bessey Division, 3 km west of Halsey, Thomas County, Nebraska, at 840 m elevation. The soil in the study area was Meadin loamy sand of the Dunday-Loup association in the Middle Loup River Valley (Sherfey et al., 1965). Damping-off (Hunt, 1965) and nematode damage (Peterson, 1962) are recurring problems at Bessey Nursery, and

methyl bromide fumigation before sowing is standard procedure.

Soil Treatments

At each nursery, six treatment plots (3.7 m x 61 m at CSFS, and 3.2 m x 15.2 m at Bessey) were arranged at least 1.2 m apart in a randomized block design parallel with nursery beds during the summer (1982 at CSFS and 1983 at Bessey). After irrigation to field capacity, three plots were covered with thin (0.05 mm at CSFS, and 0.038 mm at Bessey) clear polyethylene for eight weeks for solar heating, and three plots were left uncovered as controls.

Before polyethylene placement, six Ryan model J thermographs (Ryan Instruments, Inc., Kirkland, WA 98033) were buried to record range and duration of temperatures. At CSFS, one thermograph was buried at 8 cm and one at 15 cm depth along the center of each of two solar plots and one control plot at a random distance from the ends. At Bessey, three thermographs were buried 1.5 to 2 m apart near the center of one control and one solar plot, one each at 8 cm, 15 cm, and 30 cm depths.

Soil Assay

Soil samples for laboratory assay of populations of species of *Pythium*, *Fusarium*, and viable weeds were taken in June before polyethylene placement, in late August after polyethylene was removed, and the following spring before sowing.

For assay of damping-off fungi four soil samples--composites of several cores taken to a depth of 15 cm with a soil probe within a 30 cm radius--were collected at regular intervals along the center of each of the six plots, the first sample location chosen at random. Assay for species of *Pythium* and *Fusarium* were similar to procedures used by Johnson and Zak (1977), except three instead of five plates of selective media were used per sample.

For comparison purposes, population levels of *Pythium* spp. of less than 15 propagules per gram of soil (PPG) were considered low, 15 to 25 PPG moderate, and over 25 PPG high. Population levels of *Fusarium* of less than 1000 PPG were considered low, 1000 to 1500 PPG moderate, and over 1500 PPG high. These levels correspond to levels of damage observed in nursery soils³.

Soil for weed assay was collected from the top 2.5 cm of soil from within a 929 cm² (1 square foot) frame for each sample, with four samples taken per treatment plot. Each soil sample was poured into an aluminum foil pan, watered as needed and kept in a Scherer Environmental Chamber with 12 hours light at 25°C and 12 hours dark at

18°C. After two weeks weed seedlings were counted. This germination test estimated the number of weeds expected to develop if a crop were planted.

The significance of treatment effects on populations of species of *Pythium*, *Fusarium*, and weeds was determined by two-way analysis of variance where homogeneity of variances could be achieved by data transformation. Otherwise, the more conservative "test for equality of means whose variances are assumed to be unequal" (Sokal and Rohlf, 1981) was used. Post-treatment values were compared with the pretreatment values and then with the values for the spring after treatment.

Soil samples were collected from Bessey Nursery for analyses of minerals in the soil solution and other properties. These samples were composites of nine probe cores taken 6 m from the ends of one solar and one control plot. The two sample locations were less than 4.6 m apart, on either side of an irrigation line. Soil was sampled before polyethylene placement in June 1983, after polyethylene removal in August 1983, and the following spring 1984. These samples were analyzed by the Colorado State University (CSU) Soils Testing Laboratory for texture, bulk density, organic matter, and for the following minerals from soil paste (1:1 soil and water for sandy soil): pH, calcium, magnesium, potassium, sodium, nitrate, ammonium, and chloride.

Tree Seedling Survival

A crop of lodgepole pine (*Pinus contorta* Dougl.) was sown in May 1984 at Bessey to evaluate solar heating treatment effects on seedling survival. Five subplots (30 cm along the bed x 76 cm across the bed, encompassing 4 rows) were monitored in each of the six treatment plots (3 check, 3 solar). The number of surviving seedlings were counted beginning two weeks after sowing on May 25, 1984, and then approximately every two weeks through July 17. A final count was made on October 1, 1984.

RESULTS

Soil Temperature

At the CSFS Nursery, highest temperatures averaged 9.5°C higher in the solar plots than in the control plot. Average temperatures recorded by the thermographs at 8 cm were usually much higher than those at 15 cm, especially in solar plots (fig. 1). Due to equipment malfunction, the 8 cm thermograph for the control plot was not buried until July 12, and the temperature record for one of the 15 cm thermographs buried in a solar plot was lost after July 24. Because the recording range of the thermographs used at CSFS was 10-40°C, temperatures above 41°C were off-scale. The average high temperatures are under-estimated for the solar plots, because the highest value used in the computation was 41°C. At CSFS the temperature exceeded 41°C on 45 days at 8 cm, and four days

³ Russell, Kenelm W. 1986. Data presented at the Nursery Pathologists Workshop, Feb. 19-20, Westwater Inn, Olympia, WA. (Forest Pathologist, Washington State Dept. Natural Resources, Olympia 98504).

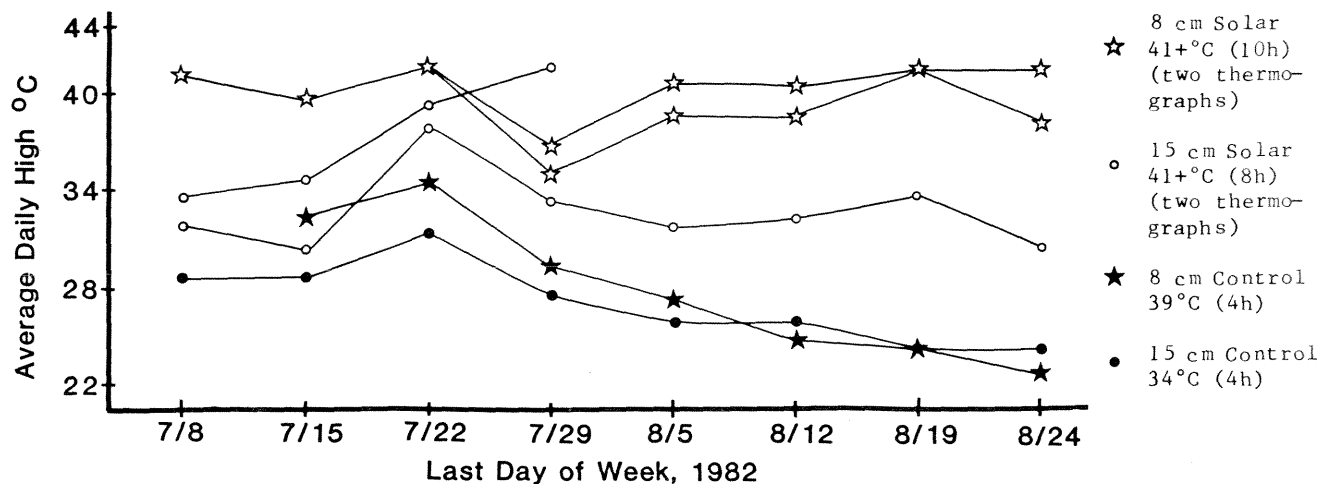


Figure 1. Weekly averages of daily high temperatures recorded by thermographs buried at 8 and 15 cm in two solar and one control plot at the Colorado State Forest Service Nursery, 1982. Highest temperature achieved and the duration in hours (h) that the temperature remained within 1°C of the high is given for each thermograph.

at 15 cm in the solar-heated plots, with an average duration of six hours. Temperatures in control plots steadily decreased due to shading by weeds.

At Bessey Nursery highest temperatures averaged 8°C higher in solar than in control plots. Average high temperatures recorded at 30 cm were much lower than near the surface (8 cm), but temperatures remained within 1°C of the daily highs much longer at greater depth (fig. 2). The temperature achieved at 8 cm in the solar plot exceeded 46°C (the limit of the recording capability of the thermographs used at Bessey) several times. At these times, the temperature remained above 45°C for two to six hours, with an average of 4.1 hours. While the temperature was off-scale (46+°C) on August 2 at 8 cm in the solar-heated plot, the chart tore and the subsequent record was lost. Weed growth was kept to a minimum in control plots by periodic light cultivation.

Pythium Populations

At the CSFS Nursery solar heating resulted in significant ($P < 0.05$) decreases in population levels of *Pythium* spp. (Table 1). Population levels of *Pythium* spp. decreased over the winter in all plots. Population levels in control plots decreased from high to moderate, while levels in solar-heated plots decreased from moderate to low.

At Bessey Nursery the population levels of *Pythium* spp. were initially different between control and solar plots before polyethylene placement in June 1983 (Table 1). By August 1983 the solar heating treatment significantly reduced population levels in solar plots, while those in control plots remained similar to June 1983 levels. By the following spring, population levels of *Pythium* spp. had returned to or exceeded pretreatment levels, probably due to the influence of the winter cover crop.

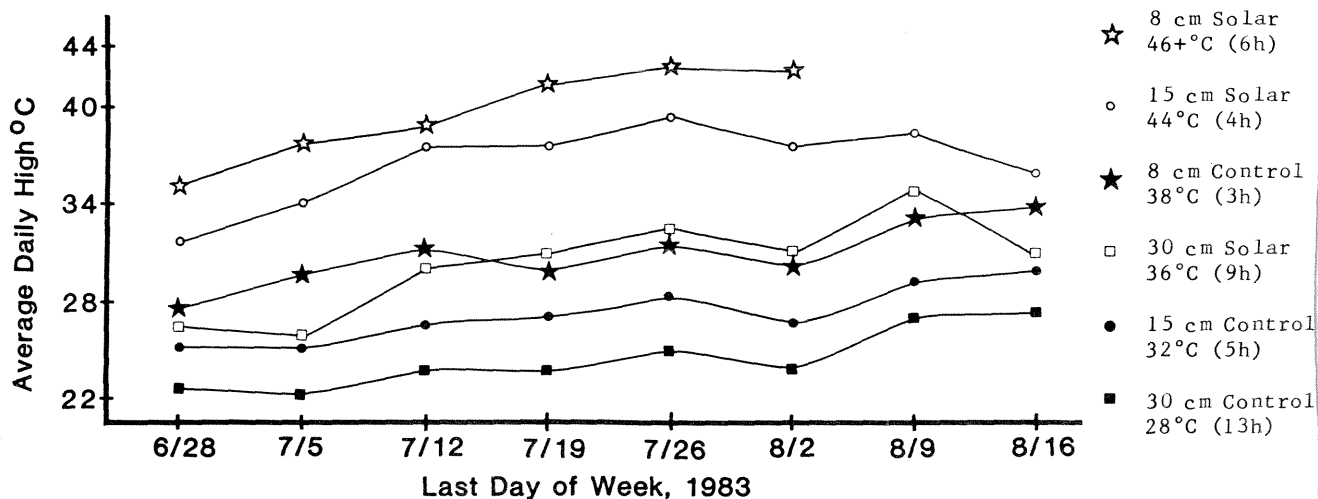


Figure 2. Weekly averages of daily high temperatures recorded by thermographs buried at 8, 15, and 30 cm in one solar and one control plot at Bessey Nursery, 1983. Highest temperature achieved and the duration in hours (h) that the temperature remained within 1°C of the high is given for each thermograph.

Table 1. Coefficients of variation, means, and their significance for population levels of *Pythium* spp. (propagules per gram of oven-dried soil) in control and solar-heated plots before and after treatment, and the following spring at the Colorado State Forest Service Nursery (A) and at Bessey Nursery (B).

| Sampling Time | Treatment | Coefficient of Variation (Percent) | Mean ^a | Population ^b Level | Coefficient of Variation (Percent) | Mean ^a | Population ^b Level |
|---------------|-----------|------------------------------------|-------------------|-------------------------------|------------------------------------|-------------------|-------------------------------|
| A. CSFS | | | | | B. Bessey | | |
| Before | Control | 88.07 | 63.8 c | High | 103.07 | 42.2 cde | High |
| | Solar | 87.52 | 55.8 c | High | 113.00 | 7.3 b | Low |
| After | Control | 58.83 | 58.2 c | High | 55.63 | 30.4 cd | High |
| | Solar | 55.78 | 22.1 b | Moderate | 124.72 | 0.3 a | Low |
| Spring | Control | 54.19 | 18.7 b | Moderate | 52.33 | 49.9 de | High |
| | Solar | 136.78 | 7.3 a | Low | 44.69 | 54.8 e | High |

^a Means followed by the same letter are not significantly different at $P < 0.05$, as determined separately for each nursery by the test for equality of means.

^b Based on data by K. W. Russell.

Fusarium Populations

At the CSFS Nursery solar heating resulted in significant ($P < 0.05$) decreases in population levels of *Fusarium* spp. as determined by two-way analysis of variance. Homogeneity of variances was achieved by transforming data by $Y' = \sqrt{Y + 3/8}$, in order to use analysis of variance. The interaction between treatment and time of sampling was significant, showing that population changes over time in the solar plots differed from population changes over time in the control plots. This indicates a significant treatment effect (Green, 1979, p. 62). After solar heating, population levels of *Fusarium* remained high in control plots, but decreased from high to low in solar plots (Table 2). Over the winter, population levels

of *Fusarium* spp. greatly increased in control plots, while those in solar plots remained low.

At Bessey Nursery, population levels of *Fusarium* spp. were initially low in all plots and remained low (Table 2). Homogeneity of variances was again achieved by transforming data by $Y' = \sqrt{Y + 3/8}$, in order to use analysis of variance. Two-way analysis of variance showed only that population levels of *Fusarium* spp. were different between control and solar plots both before and after solar heating. The interaction between treatment and time of sampling was not significant, indicating no treatment effect.

Table 2. Means of population levels of *Fusarium* spp. (propagules per gram of air-dried soil) compared for control and solar-heated plots before treatment, after treatment, and the following spring, at the Colorado State Forest Service Nursery (A), and at Bessey Nursery (B).

| Sampling Time | Treatment | Coefficient of Variation (Percent) | Mean | Population ^a Level | Coefficient of Variation (Percent) | Mean | Population ^a Level |
|---------------|-----------|------------------------------------|-------|-------------------------------|------------------------------------|-------|-------------------------------|
| A. CSFS | | | | | B. Bessey | | |
| Before | Control | 45.12 | 2233 | High | 39.10 | 444 | Low |
| | Solar | 32.60 | 3122 | High | 92.11 | 200 | Low |
| After | Control | 68.18 | 1900 | High | 78.40 | 467 | Low |
| | Solar | 102.10 | 822 * | Low | 170.31 | 78 ns | Low |
| Spring | Control | 10.38 | 9745 | High | 125.10 | 178 | Low |
| | Solar | 45.36 | 656 | Low | 189.70 | 100 | Low |

^a Based on data by K. W. Russell.

ns = No significant interaction, no treatment effect.

* Significant at $P < 0.05$ indicated by significant interaction between treatment and sampling time in two-way analysis of variance.

Table 3. Coefficients of variation, means, and their significance for weed populations (number per 929 cm²) in control and solar-heated plots before treatment, after treatment, and the following spring at Colorado State Forest Nursery (A), and at Bessey Nursery (B).

| Sampling Time | Treatment | Coefficient of Variation (Percent) | Mean * | Coefficient of Variation (Percent) | Mean * |
|---------------|-----------|------------------------------------|---------|------------------------------------|--------|
| A. CSFS | | | | B. Bessey | |
| Before | Control | 80.03 | 13.3 c | 195.03 | 5.0 b |
| | Solar | 94.97 | 24.7 c | 167.71 | 0.4 b |
| After | Control | 128.00 | 3.8 b | 119.47 | 9.9 c |
| | Solar | 384.42 | 0.3 a | 0.00 | 0.0 a |
| Spring | Control | 112.01 | 211.4 d | 180.99 | 4.3 b |
| | Solar | 164.96 | 30.3 c | 163.30 | 0.3 b |

* Means followed by the same letter are not significantly different at $P < 0.05$, as determined by test for equality of means.

Weeds

At the Colorado State Forest Service Nursery, populations of weeds were significantly reduced by solar heating (Table 3). By August most of the weed seeds in the control plots had germinated and the resulting plants matured, and a new crop of weed seeds was accumulating on the ground. The major weed species growing in the control plots and adjacent areas were *Portulaca oleracea* L., *Physalis heterophylla* Nees., and *Amaranthus retroflexus* L. Very little weed growth occurred under the polyethylene in solar plots although some *P. oleracea* was growing slowly in spots. Some dead weed seedlings were observed when the polyethylene was removed. By the spring following solar heating, weed populations increased to levels greater than pretreatment levels in control plots and returned to pretreatment levels in solar-heated plots, probably due to intense seed production in control plots and adjacent areas. Solar heating greatly reduced weed cover compared with control plots. Solar-heated plots had fewer and smaller weeds than control plots.

At Bessey Nursery, solar heating significantly reduced weed populations while weeds increased in control plots (Table 3). By the spring following solar heating, weed populations had returned to pretreatment levels, probably due to weed seeds blown in from other areas. A variety of weeds occurred in the treatment area, including volunteer oats (*Avena fatua* L. var. *sativa* (L.) Hausskn. and chokecherry (*Prunus virginiana* L.) from previous crops. The weeds included *Trifolium* spp., *Mollugo verticillata* L., *Capsella bursa-pastoris* L., *Bromus tectorum* L., and *Medicago* spp.

Soil Properties

Soil from the study area at Bessey Nursery was loamy sand with 1% organic matter, bulk density of 1.6 g/cm³, and pH about 5.5. If one looked only at the differences between the control and solar plot results for August (after treatment), increases would be evident in calcium (Ca),

magnesium (Mg), sodium (Na), potassium (K), chloride (Cl), ammonium nitrogen (NH₄-N), nitrate nitrogen (NO₃-N), and pH (Table 4). However, considering the pretreatment values, slight seasonal increases between June and August were evident for ions of Ca, Mg, Na, K, NH₄-nitrogen, and NO₃-nitrogen. Increases due to solar heating over and above summer increases were shown for Ca and NH₄-nitrogen. Large increases over the winter, however, were measured in May for Ca, Mg, and NH₄ nitrogen in the control sample. These winter fluctuations were greater than any increases due to solar heating the previous summer.

Tree Seedling Survival

In all plots and treatments, most of the lodgepole pine mortality at Bessey occurred at the beginning of the growing season. Seedlings continued to die at a slow rate through October 1984. By the end of the growing season, control plots yielded 14.3 seedlings/929 cm² (ft²) and solar heated plots 12.4 seedlings/929 cm². Due to the high variability within treatments, analysis of variance indicated no significant effects on seedling survival between the treatments. Seedlings in solar-heated plots were not noticeably larger than seedlings in control plots. By October 1, 1984, losses in solar-heated plots were 31% and in check plots 27% of the number of live seedlings on May 25. Although lodgepole pine sown in the study area the spring following solar heating showed no beneficial effects, the oat cover crop was darker green and more lush in the solar heated plots compared with that in the surrounding control area in November 1983.

DISCUSSION

The highest temperature recorded under the polyethylene was over 46°C at a depth of 8 cm. Since the thermographs could not record above 46°C, the actual highest temperature achieved is unknown. In other studies conducted in warmer soils, temperatures of 50°C at a depth of 15 cm

Table 4. Soil chemical analyses (measured in soil paste, 1:1 soil to water) for samples taken in control and solar-heated plots in June (before treatment) and August 1983 (after treatment) and the following May 1984 at Bessey Nursery.

| | Ca ⁺⁺ mg/l | | Mg ⁺⁺ mg/l | | Na ⁺ mg/l | | K ⁺ mg/l | |
|------|-----------------------|-------|-----------------------|-------|----------------------|-------|---------------------|-------|
| | Control | Solar | Control | Solar | Control | Solar | Control | Solar |
| June | 7.7 | 8.6 | 1.8 | 2.4 | 2.0 | 2.4 | 5.4 | 7.3 |
| Aug. | 12 | 26 | 3 | 4 | 3 | 5 | 8 | 11 |
| May | 51 | 47 | 12 | 11 | - | - | 6 | 6 |

| | NH ₄ ⁺ -N mg/l | | NO ₃ ⁻ -N mg/l | | Cl ⁻ mg/l | | pH | |
|------|--------------------------------------|-------|--------------------------------------|-------|----------------------|-------|---------|-------|
| | Control | Solar | Control | Solar | Control | Solar | Control | Solar |
| June | 0.4 | 0.7 | 1.9 | 3.5 | 6 | 5 | 5.7 | 5.7 |
| Aug. | 0.6 | 2.4 | 7 | 12 | 4 | 5 | 5.3 | 5.8 |
| May | 6 | 3 | 8 | 6 | 6 | 4 | 5.5 | 5.2 |

and 60°C at 5 cm were reported (Pullman et al., 1981b). In the Rocky Mountain Region, nighttime cooling by re-radiation may be an important factor in prevention of higher soil temperatures under the polyethylene.

Some studies have linked increased crop growth with increases in minerals in the soil solution due to solar heating (Katan, 1984). In contrast to reports in the literature, in this study soil samples from control and solar-heated plots were analyzed before, immediately after, and the spring following solar heating. Information from the additional sampling times helped separate seasonal fluctuations and measuring error from solar-heating effects. In this study, solar heating resulted in measurable increases in Ca and NH₄-N, but seasonal fluctuations over the winter were greater than solar heating effects. Measuring error probably accounts for the fluctuations in pH, and a portion of the fluctuations in the ions.

These results underscore the danger of taking only post-treatment samples as done by previous workers. Because a statistical sample is not taken for chemical analysis of soil, more than one set of samples (e.g. pre-treatment and post-treatment for both control and treatment) must be taken. Seasonal variation may exceed any apparent change due to treatment, or the soil in the sampling areas may have differed before treatment.

Population levels of *Pythium* spp. were significantly reduced by solar heating at both nurseries but returned to pretreatment levels over the winter at Bessey, possibly due to the influence of the oat cover crop. There was no winter cover crop planted at CSFS. Reduction in population of *Fusarium* spp. were statistically significant only at CSFS. Weed populations were also significantly reduced by solar heating at both nurseries, but returned to pretreatment levels

by spring, probably from blown-in seed. In addition, germination of weed seeds in the spring may have been higher than in August because any cold requirement to break seed dormancy would have been satisfied by spring.

Population levels of *Pythium* spp. were high and of *Fusarium* spp. and weeds were relatively low at the spring sowing of lodgepole pine at Bessey. The lodgepole pine showed no beneficial effects due to solar heating. Reductions in populations of *Fusarium* spp. by solar heating have not been accompanied by improved survival of conifer seedlings sown the following spring in other studies (Cooley 1983, Cooley 1985). The winter cover crop sown immediately after solar heating at Bessey did show an increased growth response in the solar heated plots compared with that in the surrounding control area in November 1983. Fall-planted crops would benefit the most from the control of weeds and soil-borne plant pathogens by solar heating.

Solar Heating in Practice

Both fumigation and solar heating require the use of tractors, personnel, and polyethylene sheeting; however, with solar heating the health hazards and cost of handling the toxic fumigant are eliminated. Even partial reduction in the annual cost of herbicides and labor for weeding makes the solar heating technique attractive. A disadvantage of solar heating is that the area being treated must be out of production for six to eight weeks during the summer preceding planting. Keeping the polyethylene intact and in place for that length of time also constitutes an operational difficulty due to wind.

Solar heating effects on a fall-sown eastern redcedar crop are being investigated at Bessey Nursery.

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MANAGING INSECTS AFFECTING OAK REGENERATION
BY PRESCRIBED BURNING^{1/}

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Abstract--The lack of oak regeneration in many areas of the eastern U.S. has generated interest in prescribed burning as a forest management tool to improve the natural regeneration of oak stands. Researchers are studying the role of insects as a factor in the oak regeneration problem. Recently they found that a complex of insects play a detrimental role in all aspects of oak regeneration. It is conceivable that burning under the right conditions and at appropriate times in the life cycle of these insect pests could reduce the numbers of insects and eliminate breeding habitats, or both.

Our data indicate that burning may reduce the populations of several insect pests of oak regeneration, including the acorn weevil, Conotrachelus posticatus (Boheman) and the sap beetle, Stelidota octomaculata (Say). The intensity of the burn seems to be critical in reducing insect populations.

Oaks are the most important hardwood trees in the eastern U.S. The establishment and survival of oak as a major stand component are serious problems in the Central and Mid-Atlantic States. Forest managers in these states are having difficulty reestablishing oak on the good sites that have in the past produced high-quality timber. What factors have changed in the last 50 to 100 years that could account for changes in the regeneration of oak forests? One explanation is that the exclusion of wildfire has altered the ecology of these stands to the detriment of oak regeneration (McGee 1979). Research has shown that fire was a natural component of many plant communities (Heinselman 1978), but effective fire suppression since the early 1900's has altered the structure and composition of many of these communities.

Previous research indicates that fire can augment oak regeneration, though the mechanisms for this are not well understood. Teuke and Van Lear (1982) reported that burning increased the proportion of oak in the advance regeneration pool as well as improved the form of the seedlings. Keetch (1944) also reported that an intense spring fire in a 25-year-old mixed hardwood stand resulted in a coppice stand of 85% oak. Carvel and Maxey (1969) found that an intense fire in a young mixed-hardwood stand converted it to a predominantly oak stand.

Carvel and Tryon (1961) studied the correlation between site factors and the amount of oak regeneration in a stand. They found that the stand history, or the degree of disturbance during the past 20 years, was very closely correlated with the amount of oak regeneration. They found that grazed, burned, or thinned stands possessed a greater reservoir of advanced oak regeneration than undisturbed stands.

Another poorly understood factor in the oak regeneration problem is the role of insects. Researchers are now aware of a complex of insects that have a detrimental effect on all aspects of oak regeneration. Insects of the genus Curculio have been reported by various authors (Dorsey et al. 1962; Gibson 1972, 1982) to infest large percentages of acorns. Other insect groups reported to infest acorns include moths (Gibson 1972, 1982), gall-forming wasps, and flies (Gibson 1972). Insects associated with acorns are a significant factor in acorn viability and subsequent oak seedling establishment. Scientists at the USDA Forestry Sciences Laboratory in Delaware, Ohio, have identified several insect pests of germinating acorns and young seedlings, in addition to those listed above. The total impact of these insects on oak regeneration is believed to be significant.

Research on the control of acorn pests is scarce. Dorsey et al. (1962) found that a granular application of insecticide distributed around the base of oak trees significantly reduced infestations of acorns by Curculio spp. This is an impractical control method for wide-scale use and would control only a few of the insect pests of oak regeneration.

Prescribed burning has been used as an insect control technique for several pest species. In 1912, Webster promoted burning alfalfa fields

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after harvesting for control of the alfalfa weevil, Hypera postica (Gyllenhal) (Komarek 1970). Simmons et al. (1977) reported an 87.5% mortality in populations of the maple leaf cutter, Paraclemensia acerifoliella (Fitch), after the leaf litter was burned in a maple-beech forest prior to spring emergence of the adult moths. Miller (1978) found that prescribed burning was a promising tool for controlling the red pine cone beetle, Conophthorus resinosae Hopkins, and for protecting cone crops in seed production areas. Research by Williams et al. (1980) demonstrated that the exclusion of fire increased the extent of Douglas-fir tussock moth [Orgyia pseudotsugata McDunnough] outbreaks, and they further suggested that prescribed fire represents a biologically sound tool to control the extent of future outbreaks.

While these studies have evaluated prescribed burning as a control technique for a specific insect pest, other studies have looked at insect populations following prescribed burning. Metz and Farrier (1973) found that annual burning in loblolly pine stands in South Carolina resulted in significantly lower mesofaunal insect populations. Harris and Whitcomb (1974) reported that fire seemed to have altered populations of some ground beetles, decreasing the abundance of some species while increasing the abundance of others. In a longleaf pine forest, Fellin and Kennedy (1972) observed that the number of insects decreased each year during 3 years of prescribed burning.

Because of the biology and behavior of many of the insect pests of oak regeneration, it is conceivable that prescribed burning would have a significant effect in limiting these insect populations. For instance, the acorn weevil, Conotrachelus posticus (Boheman), which feeds and breeds in germinating acorns, spends a major portion of its life on the forest floor. This insect is found as an adult in both the spring and the fall (Gibson 1964), periods when prescribed burning is most feasible in eastern hardwood forests. The acorn moth, Melissopus latiferreanus (Walsingham), is present in the duff as a larva or pupa for much of the same time period (Murtfeldt 1894) and would also be susceptible to burning. While the biology of some of the lesser known pests of oak regeneration is not yet fully understood, it is believed that many of these insects do spend all or part of their lives on the forest floor and would, therefore, be affected by a prescribed burn. Included in this group are a sap beetle, Stelidota octomaculata (Say), and another acorn moth, Valentinia glanduella (Riley), both of which have been reported to be primary pests of sprouting acorns (Galford 1986a). Insect pests of oak seedlings, such as the weevil Barypeithes pellucidus (Boheman), that feed on the leaves, stems, and roots of young oaks (Galford 1986b) may also be affected by fire. These insects

spend much of their lives on or in oak seedlings and would be eliminated when fire destroys the aboveground parts of the seedlings. The oaks would resprout, but theoretically the insects would be killed.

The studies presented here are a preliminary evaluation of the effect of prescribed burning on insect pests affecting oak regeneration.

MATERIALS AND METHODS

These studies were conducted in conjunction with two prescribed burns conducted on the Athens Ranger District of the Wayne Hoosier National Forest in Hocking County, Ohio, in April 1984 and April 1985.

Prescribed Burns

The 1984 burn involved 48 acres (19.4 ha) of well-stocked oak-hickory forest. The silvicultural objectives of the burn were to reduce understory competition and increase the proportion of advanced oak reproduction. To meet these objectives, a slow, low- to moderate-intensity fire was planned. In general, the average rate of spread was 5 chains/hr (ca 100 m/hr), and the average flame length was 2.5 ft (0.76 m). However, fire behavior was inconsistent in some areas because of variations in fuel and litter in the burned area and the changes in the weather that occurred during the 3-hr burn. With this particular burn, fire intensities were great in several areas and extreme scorch heights occurred.

In 1985, 12 acres (4.9 ha) of similar forest land were burned with the same objectives as those for the 1984 burn. Although weather conditions were identical for both burns (average temperature 22°C and 52% RH), fuel moisture was much higher in 1985 than in 1984. This resulted in a slow, low-intensity fire. The rate of spread of the fire was 3 chains/hr (ca 60 m/hr) and the average flame length was 1.5 ft (ca 0.46 m).

Unburned areas adjacent to the burned areas served as controls in these studies. These areas were selected because of similar forest type, ground cover, slope, and aspect.

Sampling Techniques

Two techniques were used to sample populations of known insect pests affecting oak regeneration: the baited pitfall trap and the collection of leaf litter. The baited pitfall trap (Harris and Whitcomb 1971, 1974; Rickard 1970) was designed to capture the acorn weevil, C. posticus. Metal coffee cans, 10 cm in diameter and 13 cm deep, containing acorns of

either bur oak (Quercus macrocarpa Michx) or northern red oak (Q. rubra L.) were buried so that the open end of the can was level with the ground. Each can had a hardware-cloth lid wired to the top. Our previous studies had shown that C. posticatus is attracted to acorns and will walk or fall into the cans.

In 1985, the trap was modified, and each can was fitted with a screen funnel. The funnel had a 2-cm flange along the outside circumference of the can. This change was made to assure that no weevils could leave the cans by crawling up the sides. Also, the bottom of the can was removed and replaced with screen to allow water to drain.

In both years, the pitfall traps were located ca 4 m from the base of oak trees throughout the burned and adjacent unburned areas. Eleven pairs of pitfall traps were placed throughout the area that was burned in 1984, and an equal number of traps was placed in the adjacent unburned area. Trap pairs were 1 m apart. The spacing between trap sites was at least 25 m.

In each location, one of the traps of each pair contained ca six red oak acorns; the other can contained ca six bur oak acorns as the attractant source. In the study area that was burned in 1985, 25 single pitfall traps were located (at least 10 m apart) throughout the burned area, and 16 traps were located in an adjacent unburned area; all traps were baited with bur oak acorns.

Pitfall trap sites were monitored from April through October during 1984 and 1985, and only during the months of April and October during 1986. At weekly intervals during 1984 and biweekly intervals during 1985 and 1986, we visited all of the trap sites and removed and counted any C. posticatus in the cans. We also added a fresh acorn to each can and removed any that were obviously rotten.

The second sampling technique involved the collection of leaf litter from the forest floor (Fellin and Kennedy 1972) to sample populations of ground-dwelling insects, including C. posticatus.

Samples of litter were removed periodically from beneath oak trees (several species) throughout the burned and unburned study areas. Each sample, which included the litter, fermentation, and humus layers (Hoover and Lunt 1952) of the forest floor, was placed in a plastic bag and labeled by sample site. Four transects of 10 samples each were taken in both the burned and unburned area in 1984. The distance between samples was 5 to 10 m, and the transects were at least 30 m apart. Two transects of 10 samples each were taken in both the burned and unburned area in 1985. As in 1984, the sample sites were at least 5 m apart and the transects at least 30 m apart. Every

4-6 weeks, a sample 75 cm in diameter was taken 2-3 m from the base of an oak tree, and as the study period progressed, each subsequent sample was taken around the base of the same trees in a clockwise manner. Succeeding samples were at least 1 m apart.

Following collections in the field, samples were returned to the lab and placed in cold storage (5°C) until the insects could be reared from the sample. After removal from cold storage, each sample was placed in a fiberboard rearing drum. As the litter inside the drum dried, the insects dropped or crawled through the bottom opening of the drum and were collected weekly. Also collected weekly were those insects that crawled into a polyethylene bottle located near the top on the side of the drum. The litter samples were left in the drums 4-6 weeks depending on the dryness of the sample and the presence of emerging insects. Emerging insects were collected and stored in alcohol and eventually identified as to family. Insects of special interest, such as C. posticatus and M. latiferreanus, were identified and counted individually.

Release-Recapture Studies

As part of the 1985 burn, we conducted a marked release-recapture study of the immediate effect of burning on C. posticatus. One hundred and fifty lab-reared weevils were marked with Tech-Pen Ink ^{3/} (Wineriter and Walker 1984) and held for 24 hr on acorns until 1 hr before the burn. The weevils were divided into three groups of 50 each, and each group was released on the ground ca 10 m from a pitfall trap site. The weevils were then covered loosely with leaves and other debris from the forest floor. The ground where C. posticatus was released was marked with metal flags so that it would be possible after the burn to find the exact location where the release occurred.

RESULTS AND DISCUSSION

1984 Burn

Pitfall traps--In the first two collection periods following the 1984 burn (April 25 and May 2), fewer C. posticatus were captured from the pitfall traps in the burned area than in the unburned area (fig. 1A). This may indicate that the burn immediately lowered the number of weevils in the burned area. Although

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differences were not significant (t-test; $P \leq 0.05$), we feel that the lack of significance was the result of too few samples being taken during this collection period. Limited samples were taken because the contents of all but two of the pitfall traps in the burned areas were destroyed by mammals.

Again during each of the weekly collection periods in August, September, and October 1984, fewer weevils were captured in the burned area than in the unburned area. However, only the collections of August 22-30 were significantly different (t-test; $P \leq 0.05$). This reduction of the weevil population several months after the burn was not exclusively the result of a direct kill of the insects by the fire since most of the weevils present in the fall were newly emerged and were present as larvae underground when the burn occurred. Rather it may be due in part to the destruction by fire of acorns that would have been breeding habitat for the weevils present in the spring. Also, the fire destroyed much of the leaf litter, and this reduction in soil cover could have made the soil surface less hospitable to weevils during the hot and dry summer months.

These pitfall traps were again monitored throughout 1985 and during April of 1986 to determine if the prescribed burn had any effect on weevil populations in subsequent years. Very few weevils were collected in 1985 from any of the pitfall traps, either in the burned or unburned areas (fig. 1B). These reduced catches may be indicative of an overall decrease in the indigenous C. posticus population, which may have been the result of a poor acorn crop in 1984. These numbers seem to indicate that the 1984 burn had limited impact on C. posticus populations in the following year. However, the extremely low catches and lack of any clear trends (fig. 1B) make it difficult to arrive at any definite conclusions.

The number of weevils collected in the pitfall traps during April of 1986 was also low (avg. 3.2 weevils/trap in control area vs 1.9 weevils/trap in burned area). These differences were significant (t-test; $P \leq 0.05$) and may indicate that 2 years after the burn, fewer C. posticus were present in the burned area compared to the unburned area.

S. octomaculata, another pest affecting oak regeneration, is attracted to acorns and was collected in the pitfall traps in April of 1986. Significantly more (t-test; $P \leq 0.05$) S. octomaculata were collected from pitfall traps in the unburned area than the burned area (223 vs 112 individuals, respectively). Previous opportunities to collect this sap beetle had been missed in 1984 and 1985 because it was not yet recognized as a significant pest of germinating acorns.

Litter samples--The number of C. posticus collected in the litter samples is shown in figures 2A and 2B. The results were similar to those for pitfall traps. More weevils were captured in the unburned area than in the burned area immediately following the burn in 1984 (April 19 collection) (fig. 2A). The same results were observed in late summer and fall. These differences between the burned and unburned areas were significant for the late summer (August 6) and fall (September 13 and November 7) collections (t-test; $P \leq 0.10$).

Litter samples were again collected throughout 1985 and in April of 1986 from the same sites as in 1984. More C. posticus were reared from litter sampled in the unburned area than in the burned area throughout spring and summer of 1985. The differences were significant in the April, July, and August collections (fig. 2B).

There are apparent discrepancies between data from the pitfall trapping and from litter sampling when results for 1984 and 1985 are compared. On one hand, litter collected in the unburned area contained more C. posticus than the burned area during the spring and summer months. Further, the results from litter samples indicate that the 1984 prescribed burn may have affected the spring population of C. posticus 1 year after the burn occurred. But there seems to be no difference between burned and unburned areas in catches at pitfall traps during the second year following the burn.

One possible explanation may be that pitfall traps measure activity as well as density of insect populations. In an inhospitable area, such as one that has been burned or one that has few acorns, the weevils may wander more widely in search of places to feed or breed, increasing the likelihood of being trapped, and thus leading to the erroneous impression that the population density is greater. Also, the number of C. posticus collected from the pitfall traps was lower in 1985 than in 1984 in both the burned and unburned areas, but comparable numbers of C. posticus emerged from the litter samples in each of the 2 years.

These differences seem to indicate that the pitfall traps may have been less efficient in 1985 and 1986 than in 1984 in terms of capturing C. posticus. Minor changes in the trapping system between 1984 and 1985, such as the addition of the funnel insert did not seem to affect trap catches. However, we conducted a biweekly collection schedule in 1985 instead of a weekly schedule as in 1984. This change may have resulted in suboptimum conditions for the acorns that were used as the attractant source. The biweekly collection schedule, possibly along with other climatic factors that affected the decomposition of the acorns in the traps, may be

the cause of the apparent discrepancies in trap catches between 1984 and 1985.

Collection of other insects from litter samples--Several thousand individuals, representing 146 families from 14 orders, were reared from the litter samples collected before and after the 1984 prescribed burn. The general trend is a decrease in the number of individuals in all families of insects in the burned area compared to the unburned area. Thirteen families that were apparently most affected by the burn, along with the number of individuals collected in the unburned and burned areas, are listed in Table 1. In litter collections taken after the burn (collection periods 2, 3, and 4), the number of listed individuals collected in the burned area was less than the number in the unburned area.

The Curculionidae family includes C. posticatus and other weevil pests of acorns. The family Nitidulidae includes the species S. octomaculata, which has been discovered to be a pest on germinating acorns (Galford, in press). The Cynipidae include gall-forming wasps. This family includes several species that damage developing acorns in the crown of oak trees (Gibson 1972, 1982). The gall-forming flies of the family Cecidomyiidae may also include species of insects that form galls in developing acorns.

Phasmidae and Buprestidae are two other families of insects not listed in Table 1 that are known pests affecting oak regeneration that also appear to be affected by the burn.

Phasmidae (walking sticks) defoliate trees and can be especially serious on young seedlings (11 individuals collected from the control area following the burn vs 4 individuals in the burned area). The Buprestidae (flat-headed borers) family includes at least one species of insect in the genus Agilus that bores through the stems of young seedlings (2 individuals collected from the control area vs 0 from the burned area).

Although it is apparent from this generalized information that burning did have an effect on insect populations in general, information on specific known pests is not available (with the exception of C. posticatus) because of the lack of suitable sampling procedures.

1985 Burn

Pitfall trapping and litter sampling conducted before the April 12, 1985, burn indicated that fewer C. posticatus were present in both the burned and unburned areas in 1985 than in 1984.

After the prescribed burn, results from the pitfall trap sampling showed no change between the populations of C. posticatus in the burned

and unburned areas. However, more weevils were found in the burned area than in the unburned area during each of the collection periods throughout the spring and fall.

Unlike the results of pitfall trapping, there were significantly fewer C. posticatus collected in the litter samples from the burned area than from the unburned area (6 weevils vs. 11 from the 15 April collection and 8 weevils vs. 17 from the 29 May collection).

In our release-recapture study, we returned 1 hour after the burn to the three locations where marked C. posticatus were released before the burn. Upon close examination of the area, we found numerous live weevils beneath the scorched litter, apparently unharmed by the fire. No dead weevils were observed at any of the locations, and no marked weevils were collected in subsequent litter collections or pitfall trap collections in the area. The 1985 sampling data, along with the finding that marked C. posticatus survived the burn, led us to believe that the 1985 burn had very little effect on C. posticatus populations. These findings seem to demonstrate that for a prescribed burn to be effective in reducing populations of C. posticatus in an area, the intensity of the fire must be moderate to high, and most of the litter must be destroyed in the process.

SUMMARY AND CONCLUSIONS

I have attempted to evaluate the impact of prescribed burning on C. posticatus and other litter-inhabiting insects by measuring the relative abundance of insects in burned and unburned areas. I hoped to determine if fire would effectively reduce insect numbers by examining absolute numbers of insects present in the burned area and in an unburned control area.

In studies of this type, we must realize that the heat of the fire may be less important than later ecological and other changes that may ultimately reduce, or in some other way, affect insect populations. Many insects lack the ability to adapt to the xeric conditions on the forest floor following a fire. Also, insects may not be able to withstand the lack of food or breeding material, or the greater temperature fluctuations on the forest floor after a fire (Ahlgren 1974). This may be the case when fire destroys acorns on the ground that serve as the breeding habitat for C. posticatus and other insects. In addition, fire destroys the litter where these insects seek refuge, thus making burned areas inhospitable until litter levels return to normal depths. These types of ecological changes would be difficult, if not impossible, to measure in short-term experiments.

The role of insects in the oak regeneration problem is a complex one and any control technique developed to limit their impact needs to be broad. Fire is a natural environmental regulator of animal populations, particularly insects (Komarek 1970). The preliminary evidence presented here indicates that prescribed burning may have potential as a silviculturally acceptable procedure to manage some insect pests of oak regeneration.

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Figure 1A- *Conotrachelus posticus* collected from pitfall traps

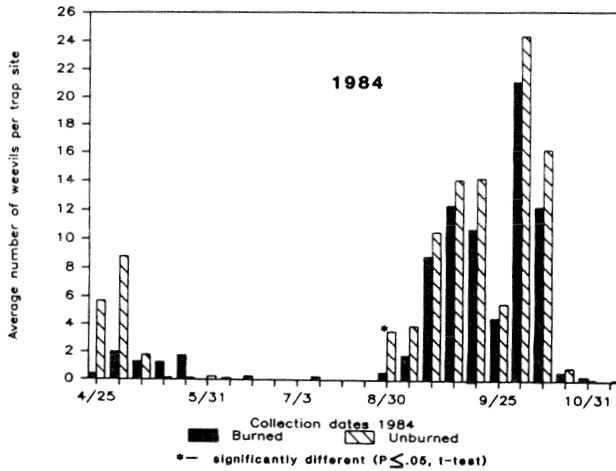


Figure 1B- *Conotrachelus posticus* collected from pitfall traps

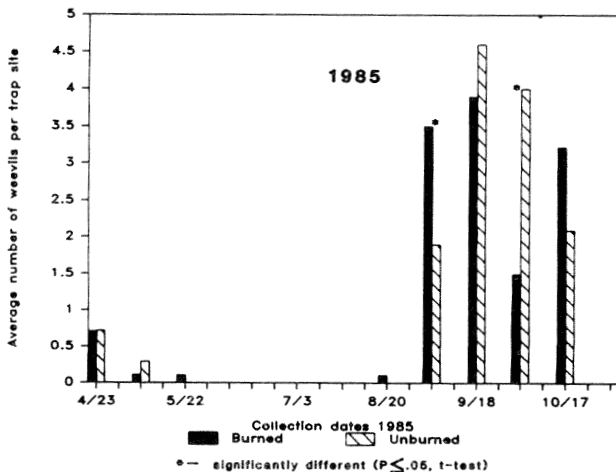


Figure 2B- *Conotrachelus posticus* collected in litter samples

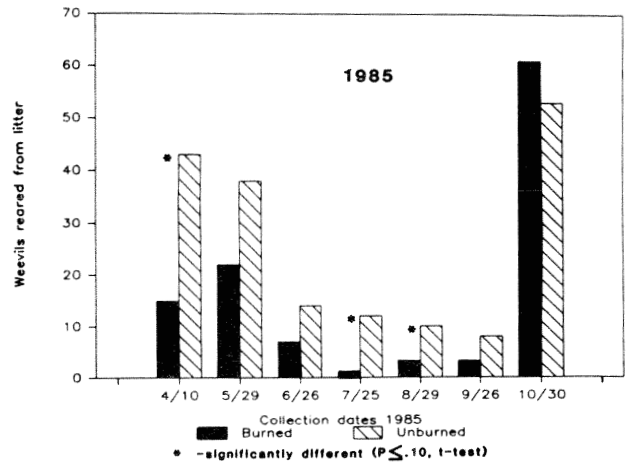


Figure 2A- *Conotrachelus posticus* collected in litter samples

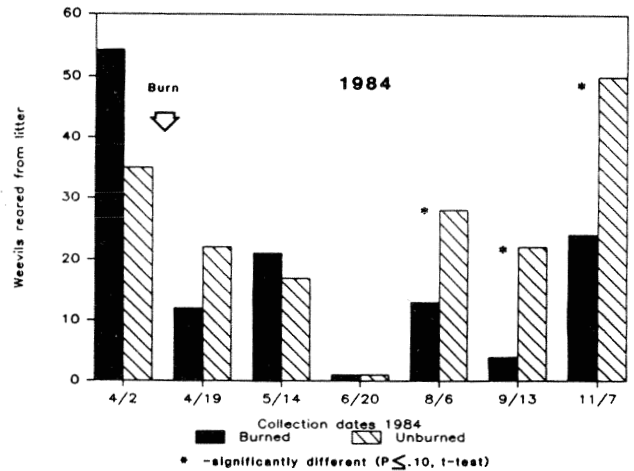


TABLE 1. --NUMBER OF INSECTS COLLECTED IN BURNED AND UNBURNED AREAS IN HOCKING CO., OHIO, 2 APRIL-7 NOVEMBER 1984, BY ORDER AND FAMILY

| ORDER | FAMILY | BEFORE BURN | | AFTER BURN | | | | | |
|-------------|--------------------------|-------------------------|-------------------------|---------------------|---------------------|---------------------|---------------------|---------------------|---------------------|
| | | 1A/ CONTROL PRE-BURN | 1B/ CONTROL PRE-BURN | 2 CONTROL BURNED | 3 CONTROL BURNED | 4 CONTROL BURNED | 5 CONTROL BURNED | 6 CONTROL BURNED | 7 CONTROL BURNED |
| COLLEMBOLA | PODURIDAE | 19 | 15 | 15 | 2 | 6 | 0 | 11 | 0 |
| | ENTOMOBRYIDAE | 15 | 14 | 15 | 1 | 0 | 0 | 11 | 0 |
| COLEOPTERA | MITIDULIDAE | 79 | 95 | 52 | 12 | 3 | 1 | 55 | 1 |
| | CURCULIONIDAE | 35 | 54 | 22 | 12 | 18 | 21 | 100 | 41 |
| | (CONOTRACHELUS POSTICUS) | | | | | | | | |
| DIPTERA | CECIDOMYIDAE | 324 | 436 | 190 | 236 | 160 | 6 | 558 | 19 |
| | CHIRONOMIDAE | 48 | 159 | 74 | 28 | 34 | 0 | 0 | 0 |
| | HYCETOPHILIDAE | 32 | 48 | 21 | 28 | 18 | 0 | 82 | 3 |
| | SCIARIDAE | 41 | 48 | 55 | 25 | 41 | 0 | 219 | 5 |
| HYMENOPTERA | CYNIPIDAE | 44 | 34 | 21 | 5 | 1 | 1 | 13 | 1 |
| | EULOPHIDAE | 40 | 22 | 22 | 12 | 0 | 0 | 42 | 0 |
| | FORMICIDAE | 50 | 37 | 257 | 19 | 32 | 8 | 257 | 11 |
| | PLATYGASTERIDAE | 7 | 8 | 10 | 7 | 2 | 0 | 34 | 0 |
| | PTEROMALIDAE | 27 | 13 | 13 | 7 | 7 | 0 | 11 | 0 |

A/ PRESCRIBED BURN EXECUTED ON 12 APRIL 1984

B/ DATES OF LITTER COLLECTION: 1 - 2 APRIL 1984 (PRE-BURN, 1 COLLECTION)
2 - 19 APRIL (IMMEDIATE POST-BURN, 1 COLLECTION)
3 - 19 MAY AND 21 JUNE (POST-BURN, 2 COLLECTIONS)
4 - 9 AUGUST, 12 SEPTEMBER, AND 7 NOVEMBER (POST-BURN, 3 COLLECTIONS)

SYMPOSIUM ON CURRENT TOPICS IN FOREST RESEARCH:
EMPHASIS ON CONTRIBUTIONS BY WOMEN SCIENTISTS
Gainesville, Florida
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