1-1990

Tree Mortality Workshop

Long Term Ecological Research Network

Department of Forest Science

Oregon State University

Corvallis, Oregon 97331-5704 (503) 754-2244

January 11, 1990

Dear Workshop Participant:

Please excuse the form letter! This is a follow to our recent telephone conversation on the Tree Mortality Workshop to be held in Corvallis, Oregon April 8-10. Thanks for agreeing to participate. There are currently 25 participants, most of whom are listed on the last pages. A wide range of interests and sites is represented. If you think of someone who is not on the list, but you think would be crucial to include please contact me. We are currently at the limit for travel funds, but maybe there will be something left over.

Now on to some specifics on travel arrangements and the workshop itself.

DATE & LOCATION

Peavy Arboretum
Corvallis, Oregon
April 8-10

TRAVEL ARRANGEMENTS

In order to cover the travel of as many participants as possible we are asking that each participant cover his/her expenses while in Corvallis. We will try to reduce these expenses by offering to pick-up and deliver folks at the Eugene Airport depending upon their schedules. We are also offer to arrange your stay at a Nendell's Inn (1-800-547-0106) to get a reduced group rate if you so desire ($42/night for a single, $24/night for a double).

Airfare will be covered by the LTER intersite grant. To get the cheapest rates we ask that you arrange your travel at least 5 weeks prior to the workshop (that is the last week of February). **Please call Eric Hart of Global Express, Seattle at 1-800-448-2211 to arrange travel and reserve a room at Nendell's Inn.** The destination should be Eugene (45 minute drive) unless Portland is preferred (2 hour drive). If at all possible schedule your arrival for **Saturday April 7.** If you plan to catch the field trip to the Andrews on Tuesday, then it would probably be best to schedule your departure on **Wednesday April 10** in the morning. We should be back in Eugene by 6 PM on the 10th for those who like to fly at night.

WORKSHOP OBJECTIVES

The workshop has one general and three specific objectives:

1. Identify major hypotheses concerning tree mortality requiring intersite comparisons.

2. Assess the current status of mortality databases (concentrating primarily on permanent plots), identifying missing locations and information crucial to intersite comparisons.

3. Agree upon a set of **general** guidelines for future comparative studies that would address these hypotheses. (We do not want to get mired in discussions if tree tags should be round v. elliptical, rather we should identify which questions should be addressed using tagged trees).

4. Begin the process of intersite comparisons and synthesis with the information in hand, identifying specific topics for a potential joint journal issue.

PREPARATION PRIOR TO THE WORKSHOP

To make the workshop a success we ask that a number of steps be taken prior to your arrival.

1. Please come prepared with one major hypothesis that could be tested concerning tree mortality. If you really feel creative put down two! These hypotheses should be centered on questions that need to be answered using more than one site, so they should be oriented toward functional groups or general processes and not a particular species. Please write the hypothesis down, with a paragraph of background and send it to Harmon at least two weeks (**March 23**) before the workshop. These will be copied and sent out prior to April 7 for everyone to look over.

2. Working groups will have the responsibilities of:

   a) Assessing the state of mortality data bases. Please give some thought as to the data bases available in your region, the key players involved, the potential gaps in coverage, and the potential costs and methods to improve this data base.

b) Developing a set of guidelines for conducting mortality studies. Given your interest and hypothesis please consider what plot size, sampling interval, variables and methods that would be appropriate. Brush up on your favorite horror story illustrating what-not-to-do! If you have estimates of the time involved to sample or manage data sets that would be helpful as well.

c) Prioritizing hypotheses that could be answered using intersite mortality databases. Please think about how you would rank the hypotheses generated by the participants.

3. A major goal of the workshop is to encourage intersite comparisons and synthesis of mortality data sets. Please look over the workshop participant list and identify folks with common interests. If possible make contacts prior to the workshop to make the most of your time in Corvallis. Give serious thought to whether you would be able to generate a manuscript concerning mortality that could be included in a joint journal issue within 6 months of the workshop. Is there anyway we could help with analysis etc that would make the job more realistic for you?

4. Another major goal of the workshop is to perform a preliminary round of comparisons/synthesis with the data already in hand. After considerable discussion with participants, the most sensible way to proceed is for interested participants to summarize data prior to the workshop. This way we will spend less time on computer bugs and more on actual comparisons and discussion. It will, however, mean more work up front and we understand if you will not be able to generate the requested information. We are offering to perform the analysis if you can give us the data, in a ascii file on 5 1/4" disk, by the beginning of March. We need to know the formatting of the variables to proceed. It would also be helpful to know which if any biomass equations would be most appropriate for your species/site conditions. **We emphasize we are only trying to help and the data will remain under your control unless you indicate otherwise!** Table 1 lists the types of files and variables that would be helpful for most analyses. The variables for individuals that have died would be the species, DBH, the time interval between samples, whether the tree input to detrital pool as a snag or as a log (better yet what proportion?), and the cause of mortality. For a given stand we need to know the stand age, plot size, the total number of stems, the total biomass of boles, size class structure (by 10 cm classes). Background data defining the environment would be type (SAF type would be sufficient if appropriate), the mean annual temperature, the mean annual precipitation, actual evapotranspiration (if available), elevation, aspect, topographic position.

If you have any questions/problems please contact me by phone, email or letter.

Mark Harmon
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Table 1. Suggested Formats For the Mortality Files

Individual Tree Records

1) Stand/plot ID
2) species ID
3) DBH when dead or last measurement
4) date of measurement
5) interval since last measurement
6) proportion formed as snag 1.0=snag 0=log
7) cause of mortality in whatever categories you have
8) mass of individual

Stand Level Information

these data could be for the entire stand or by species and size class depending on how detailed you want the analysis. Let's try to at least have the stand level for the workshop.

1) stand/plot ID
2) Plot Area (ha would be best)
3) Date for these conditions
4) stand age
5) total number of stems (to compute overall turnover of population)
6) total biomass of boles (to compute the mass turnover)
7) species distribution (to test if some species have higher turnover than others)
8) size class structure by 10 cm classes (to test if some sizes are dying faster than others)

Environmental file

1) stand/plot id
2) stand type (whatever names you use)
3) mean annual temperature (approximate)
4) mean annual precipitation (approximate)
5) actual evapotranspiration (approximate)
6) aspect
7) topographic position (whatever classification you use)
8) elevation
9) latitude/longitude

Summary File

ideally this summarized information would be available by the time of the workshop

1) stand/plot id
2) date of measurement
3) total number of stems dying (numbers/ha/year)
4) percent stems dying
5) total bole mass dying (Megagrams/ha/year)
6) percent of bole mass dying
7) percent dying as snags
8) causes of mortality (percentage for major causes such as wind, pathogens, insects, suppression, unknown)

Preliminary Workshop Agenda

April 7 Saturday
--participants arrive throughout day

--8 PM evening mixer (no host bar)

April 8 Sunday

--8:00 AM Pick-up at Motel to workshop at Peavy Arboretum

--8:30 Introductions

--9:00 Presentations (15 minutes each)

these are intended to review interesting findings and questions in each major topical area and not to paralyze the participants

Franklin--overview
Harmon--production and nutrient cycling in PNW conifer ecosystems
Harcombe--demographic and population studies

--10:00 Coffee/Tea Break

--10:30 Presentations continued
Foster--spatial patterns
Post--modeling

--11:00 Discussion of Working Groups

--12:00 Lunch (we can order out if that's what folks want)

--1:00 PM Working Group Discussions

--3:00 Coffee Break

--3:30 Report from Working Groups on Progress/ Problems

--5:30 Miller time.

April 9 Monday

--8:00 AM Pick-up at Motel

--8:30 Review Progress Problems of Working Groups any great insights/flashes overnight?

--9:00 Working Groups reconvene to finish notes on recommendations/findings

--12:00 lunch

find JVC

--1:00 PM Break up into Synthesis Planning Groups

--3:00 coffee/tea break

--3:30 Reports of synthesis plans or outcomes of actual site comparisons?

--4:30 Synthesis Planning Groups

--5:30 Back to Motel

--8:00 Chairs of Working Groups should meet to review notes, make changes

April 10 Tuesday

--8:00 AM Pick-up at Motel

--8:30 Recap Progress/Identify Potential Problems

--10:00 Leave for Andrews/Coffee Break (this will allow you to catch a flight after 11:15 at Eugene)

--12:00 Arrive at Andrews, getting lunch along the way

--4:30 Return to Corvallis (you should be able to make a flight after 6 PM from Eugene)

--6:30 Arrive in Corvallis

April 11 Wednesday

--most participants (survivors) return home

LIST OF WORKSHOP PARTICIPANTS

April 8-10 Mortality Workshop
CORVALLIS, OREGON

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observer

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HBR

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BNZ

needs to discuss with others

~1 hour

no one from BNZ able to attend

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demographics; population/Southeast

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NC Botanical Garden

JRN

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nutrient cycling/Desert; Southwest

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demographics/Old World Tropics

Left msg. Dr. Veblen

Lauenroth - CPER

✓ Laura Huenneke JRN
El Paso

✓ Canham - Inst of Eco. Studies Millbrook

✓ Parker - Purdue

✓ Veblen a third that was approved?

#1 18-JAN-1990 14:28

From: VAX1::SMARTIN NEWMAIL
To: IN%"mharmon@lternet.washington.edu"
CC: ADUB
Subj: Final word, tree mort workshop budget

Here's the extent of the budget for your workshop out of the LTER Coordination grant in tye

ar 2:

$9,000 (Subcontract, salary)
9,000 (Participant support, travel/per diem/on-site costs)

Any participant and/or on-site costs not covered in the $9,000 will have to be absorbed by the individual sites.

This seems to meet with what you've already told people, so I don't think you need to amend your message to them (whew!). --Stephanie

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July 10, 1990

Dear Participant:

Here is my first stab at a summary of the Tree Mortality workshop that was held last April. My thanks to those who sent in summaries of the working groups, it was most helpful. Please look over the report and send me back your comments. I would like to have the finished version sent off by the end of next month, so your response will need to be fast to be included.

Where do we go from here? I have no doubt that individuals will pursue questions on their own or in small groups. I would certainly encourage each site to publish information on this subject. However, are people interested in pursuing something as a larger group effort? This could take a number of forms.

1. We could try to organize a symposium to present the major findings of the working groups. Papers that emphasize the observations at specific

sites would also be given. Since the LTER coordinating grant will no longer be supporting intersite workshops, we would need to apply to NSF to get funds for this activity. If this symposium is to be part of next year's ESA meeting we will need to have the blessing of the Long-term Ecology Section, and decide within the next month. If this is to be a separate affair then the timing is less crucial.

2. We could try to collect a common set of data that is currently not being collected. A logical area might center on identifying the causes of "background" mortality. This would cost very little to add to current efforts and would begin to quantify this important process.

3. We could try to establish a protocol for permanent plot data in general. What standards, if any, should we be shooting for? What types of data would be most useful? Are there alternative methods that would yield roughly similar data? This has probably been done before, but if not it might be a valuable contribution. This might be similar to the gap protocol published by the Pacific Northwest Research Station.

At this point I need to hear from folks about their ideas for future intersite work. I am certainly committed to helping to lead this effort, but only if this is supported by the majority of the workshop participants. So let me know! yea or nay?

Sincerely yours,

Mark

Mark E. Harmon

Research Associate

Draft Report of the Long-term Ecological Research Workshop on Tree Mortality

Department of Forest Science

Peavy Arboretum

Oregon State University

Corvallis, Oregon

April 8-10, 1990

Prepared by:

Mark E. Harmon

July 1990

INTRODUCTION

Despite the fact that forest growth has been measured for over a century, little is known about the rate of tree death or its ecological consequences (Franklin et al. 1987). This situation results, in part, from sampling strategies that are adequate to measure biomass and growth but unsuitable for mortality measurements. These strategies included the use of plots that are too small, or sampling intervals that are too short to adequately sample mortality rates. Long-term average of tree growth can be inferred from tree rings, this is much more difficult for mortality. Even when plots have been measured over lengthy periods, mortality rates are difficult to estimate unless trees dead from prior measurement periods are identified.

Lack of information on tree mortality has profound consequences on our understanding of how ecosystems behave at a number of scales:

1. Autecological. The effects of pollution and pathogens are difficult to assess unless one has information on "natural" levels of mortality. How does one judge if a pulse of mortality is unusual if you do not know what the usual is?

2. Community. Rates of species replacement are difficult to predict accurately if species mortality rates are not known. The degree species replacement is a gradual versus a sudden process depends upon temporal patterns and causes of mortality. Do early seral stands always "breakup" or is this related to the form of mortality removing trees? Much of our knowledge of successional development is based on size class analysis. Do mortality patterns actually match predictions from size class analysis? If larger early seral species have low mortality rates can they persist into stages often considered climax (e.g., eastern white pine)? If species with reverse-j shaped size distributions have high mortality rates, will they replace seral species in the canopy?

3. Ecosystem Processes. Wood is perhaps one of the most abundant natural organic materials on earth, yet we have little idea what at what rate it is added to detrital pools or what happens to dead wood in natural ecosystems. In fact, amounts of dead wood are rarely quantified in ecosystem inventories and rates of mortality are rarely considered in production and nutrient cycling budgets. Does this mean the process is

unimportant or simply unmeasured? To what degree has the global detrital pool been underestimated because this process has been ignored?

To begin answering some of these questions, a two day workshop was held in Corvallis, Oregon on 8-9 April 1990. While many sites have ongoing projects concerning tree mortality, the emphasis of discussions centered on intersite studies that would lead to dramatic improvements in our understanding of ecosystem behavior. In some topical areas, such as the turnover rate of trees, data was not as limiting as originally thought. The number of studies based on new and old permanent plots has increased dramatically in the past few years. Rather the problem lies in access to data that is diffusely spread among a large number of investigators, most of whom have collected data at great personal cost. In other topical areas, such as mortality causes, most of the existing data is qualitative, correlative, and of little predictive value.

WORKSHOP OBJECTIVES

The Tree Mortality Workshop had four specific objectives:

1. Identify major questions concerning tree mortality requiring intersite comparisons.

2. Assess the current status of mortality databases, identifying missing locations and information crucial to intersite comparisons.

3. Agree upon a set of general guidelines for future comparative studies that would address these hypotheses.

4. Begin the process of intersite comparisons and synthesis with the current data base.

WORKING GROUPS

Working groups in major subject areas including causes of mortality, spatial patterns, large-scale events, population processes, and ecosystem processes were established. Each working group was responsible for identifying the major questions in each topical area, and assessing the degree current data sets could serve to test hypotheses. For those topic areas where current data was suitable, an outline of a comparative, intersite paper was prepared. The following sections briefly summarize the findings of the working groups.

Causes of Mortality

Although this is an important subject and very relevant to issues such as ecosystem response to global change, pollution, and exotic pests/pathogens, there is very little information on why trees in natural forests die. Past research has focused on specific pathogens and insects or on large scale disturbances such as fire. In contrast, there are very few studies that describe the causes of "background" mortality. Consequently, unless a episode of mortality is very large and has an obvious causal factor it is difficult to assess whether the response is normal or abnormal. A perfect example might be the "die-off" associated with acid rain. Can we really prove which trees died because of acid rain related problems with our current level of information?

A number of steps could be taken to increase our knowledge concerning the factors responsible for tree death:

1. An assessment of the different causes of tree death using current databases.

2. Development of new measures and approaches that would permit identification of mortality causes.

3. Linking population focused studies with ecophysiological and pathological studies.

Causes of mortality can be divided into classes based on their difficulty of identification. Direct physical causes (e.g., fire, wind damage) are often noted in mortality studies and are easy to identify as they leave distinct symptoms. A large fraction of trees, however, appear to die of indirect causes. This includes insects, root rots, competition (suppression), physical damage, drought stress, and air pollution. If we are to understand the role that indirect causes play in controlling mortality rates, the linkage between the proximate and ultimate causes must be identified. Even for direct physical causes it is useful to identify, if possible, the factors predisposing trees to that form of mortality. For example, a root rot may predispose a tree to windthrow. This type of analysis leads to the concept of a mortality spiral--a series of events which ultimately leads to tree death. In some cases a strong physical force, such as wind, kills a perfectly healthy individual. In many cases, however, a series of events predisposes the tree to mortality. A number of important questions need to be answered before the mortality spiral concept can be used. How many steps can one really identify in an ecological type survey? How long is evidence observable? What is the temporal relationship between a stress and mortality causes?. How long does a stress predispose trees to an elevated mortality risk?

Although the current database will identify some of the major physical causes, the number of ecosystems represented is scant. A more systematic, intersite effort would confirm if some biomes or seral stages are more prone to physical damage than others. We know, for example, there are gradients within the Pacific Northwest in physical damage, with coastal forests having much higher wind-related mortality than interior forests. Moreover, wind related damage increases greatly in coastal systems with forest age. Are these general trends? While identification of physical versus other forms of mortality may seem trivial, it has number of important implications for nutrient cycling, carbon stores, and wildlife habitat. It would also be the first step to quantify the number of trees dying of unknown causes. A reasonable starting point would be to adopt a system similar to that currently being used at the Andrews for a number of other sites. Whatever system is used, it is important that the symptoms as well as the causes of mortality be noted. It is also important that investigators with experience identifying pathogens in the field be involved in at least defining the symptoms most useful to record.

Identifying the indirect causes of mortality will take some new approaches and fields of study such as physiology and pathology. Initial progress could be made by identifying factors predisposing trees to mortality. Examples include, crown form, relative height, position and diameter, growth rate, leaf area (or some proxy like sapwood thickness), and evidence of past physical damage. To be most useful this type of information should be collected on dead as well as living trees. Factors showing the highest correlation to mortality would then give some insight into the cause of mortality. For example, small trees with slow growth rates that die standing probably died from competition effects. Variations in mortality between years might give insight into the relationship between mortality and drought stress, air pollution, and climate change.

Many causes or series of events leading to mortality will not be identified until an experimental approach that incorporates ecophysiology and pathology is used. While we know that certain factors increase the likelihood of mortality, our understanding of the degree this risk is increased is very poor. For example, does defoliation increase susceptibility to beetle attack to a certainty or by 5%? An example of experiments that quantify the importance of predisposing factors might be the work of Mitchell et al. (1983) on bark beetles. They manipulated the vigor or individual trees using thinning, fertilization, and watering and observed the response to beetle attack. Other factors that might be manipulated drought stress, degree of physical damage (partial or complete girdling), and defoliation. In some areas these experiments may have already been conducted; a review on past experiments would be extremely valuable and timely.

Large Scale Events

Mortality occurs on a number of spatial and temporal scales depending upon the cause or disturbance. To some degree there is an inverse correlation between the size of a disturbance and the frequency of the disturbance. Thus tree fall gaps occur annually on the scale one hectare, whereas fires occur decades to centuries on many hectares. Causes of mortality that kill trees annually on the scale of a hectare can be considered as "background" mortality. Causes that kill many individuals over an entire stand or landscape on the time interval of decades to centuries can be considered "episodic" mortality.

The importance of mortality to ecosystem change depends upon the scale the cause operates on. The simultaneous sudden death of a large number of individuals dramatically resets the system and its trajectory. Traditionally, sudden death has been viewed as setting succession back to earlier stages. However, given climate change, sudden death may be the way that ecosystems adjust to that change. Background mortality, on the other hand, may be the mechanism by which species diversity (both of plants and animals) is maintained within an established forest. This might be achieved by making resources such as light available or by increasing small scale heterogeneity.

The inverse relation between size and frequency implies that measurements on the scale of a hectare or less will not reliably detect episodic mortality. Therefore measurement in permanent plots over periods of a few decades is unlikely to adequately record large-scale infrequent events. To measure these events, it is important to obtain data at a broader spatial scale in conjunction with a permanent plot system. Although the temporal resolution of large-scale events is often coarser than permanent plots, this information is essential for evaluating the relative importance of smaller frequent versus larger infrequent events.

A number of methods have been used in the past to document large-scale patterns of mortality. However, not enough has been done to compare biomes in terms of complete disturbance regimes. Given the possibility of global climate change, it is crucial that past, present, and future changes of episodic mortality be understood in a wide range of biomes. While most effort has been placed on understanding the gradual response of ecosystems to global change, it is more than likely that changes in the disturbance regime will cause just as large a change in ecosystem behavior.

In order to advance our knowledge of mortality on the largest scales we need to know the limitations to gathering information by the following methods:

1. Large-scale monitoring of plot networks such as the continuous forest inventory system of the US Forest Service.

2. Remote sensing at a number of scales from areal photography to satellite imagery.

3. Dendrochronological methods to cross-date time of tree death and infer mortality from release of survivors.

4. Inference of date of death from decay classes.

5. Use of historical land survey data.

6. Repeat photography of forest stands.

7. Fossil pollen and stratigraphic methods which would indicate the rate species are lost given climate change or pathogen outbreaks.

For each method the efficiency, spatial and temporal resolution, availability of past data, length of record, and cost should be assessed.

Quantifying the disturbance regime is a core area of research within LTER and many other sites with long-term studies. It might be useful at this time to assess the degree to which intersite comparisons could be made with the current data, and map out a strategy to improve this database for future efforts. This process was started during the 1983 Disturbance Regime Workshop organized by Fred Swanson and Nel Caine, but this effort only involved nine sites. Another workshop including all the current LTER sites and other research sites would make an important contribution.

Spatial Patterns

While there are many important questions concerning spatial patterns of mortality, there is very little current information to test hypotheses or even look for patterns. A major contribution studies on this topic could make involves the question of spatial scale. How does one take plot level data and expand it to a larger scale? What are the key variables needed to stratify a landscape to estimate mortality? Scaling questions would be answered as we understand the relative importance of background versus episodic mortality. Insight into variables useful for sample stratification could be identified by comparing communities and seral stages within a region. There are, however, a number of questions which deal specifically with spatial patterns at number of scales which are important.

<u>Stand Level Patterns</u>. The response of the community to mortality depends upon whether it is aggregated. In other words, are single or multiple tree gaps formed? It is also important to know whether aggregated mortality is simultaneous and if the cause will persist to inhibit future regeneration. The answer to these questions depends strongly upon the mortality cause. Root rots, for example, tend to be aggregated and can inhibit regeneration of some species. In contrast, competition caused mortality might be more regular in spatial arrangement and not inhibit future regeneration.

Unfortunately permanent plots, even those as large as 1 ha, were thought by the participants to be too small to provide an adequate statistical sample unless the record was extremely long. Alternatively one could compare spatial patterns of live versus dead trees. An example of this type of study was recently reported by Kenkel (1988). This type of analysis could be improved greatly if physical causes such as wind could be separated from other causes. By including regeneration, the degree past mortality controls present structure of trees and regeneration could be tested.

Landscape Level Patterns. Pattern analysis on this scale needs to consider the variation in rates among patch types as well as the interaction between patch types. On the former level of variation, considerable progress could be made by comparing rates between community types, seral stages, and levels of productivity. Evidence from the Pacific Northwest would indicate that seral stage and the level of site productivity have far larger influence than community type. Is this true for biomes that have a greater number of species and physionomic types?

The interaction of patch types is of great importance for understanding the future impacts of large-scale disturbances as well as predicting the fate of biological reserves. A major question to be answered is whether the original disturbance patch will expand in the future. Even a small increase in linear dimensions can greatly increase the area impacted (e.g., increasing the linear dimensions of a circular disturbance patch by 10% will increase the area 20%). There is actually considerable information on these interactions, although most of it has not been placed in a GIS format. For example, it is known that bark beetles will often kill surrounding trees after a fire or windthrow. Windthrows will migrate through a landscape opened up by fire, wind, or clear-cutting. What factors control whether the originally disturbed patch will expand? This probably varies with the cause. Wind related expansion may be strongly influenced by spatial arrangements, whereas bark beetle attack may be controlled by the vigor of surrounding trees the year after the original disturbance. The main future challenge will be to move from a largely anecdotal to a predictive/probabilistic database.

Regional Level Patterns. Given the possibility of global climate change it is important to begin to understand how mortality rates vary over the range of a species. Obviously mortality rates are higher on the edge of ranges, but is this true for seedlings, saplings, or all size classes? If the rate of mortality is only elevated for seedlings this implies that climate change may not result in wholesale mortality of established trees. Rather, disturbances such as fire may be required to remove these species. On the other hand, the mortality rate of mature trees may also increase near range boundaries if decreased vigor predisposes individuals to increased pathogen/insect attack. It is therefore important to consider the regional pattern of mortality causes to get some insight into the response of species to a changing climate. Potential exists to compare rates of mortality on the scale of a biome for some common species, but will need to assemble many separate data sets. Alternatively, regional data bases such as the Forest

Service Continuous Forest Inventory might reveal large scale patterns.

Population Dynamics

Tree mortality, along with regeneration, is a basic population process. Yet, most population research has traditionally focused on regeneration, in part, because the long life-span of trees would indicate meaningful mortality studies could not be conducted. Those mortality studies that have been conducted, however, reveal that forests are exceedingly dynamic with tree half-life as short as 35 years (Lieberman and Lieberman 1985). In fact, studies of 5 to 10 year duration over a suitable area can yield highly reliable estimates of background mortality rates.

Tree mortality has a number of important implications for understanding population processes and community structure. To predict future changes in community composition it is important to know not only the establishment rate, but the mortality rate. Unfortunately the static size class analysis used in past studies focuses on the establishment process and the relative tolerance of small individuals. It does not logically follow that a high establishment rate as saplings will lead to a high density in the canopy. High establishment rates, for example, could be offset by a high mortality rate. It may be that a species with less abundant seedlings and a low mortality rate will dominate the future canopy layer.

A knowledge of tree mortality is also important to understand the species, rate, and location of tree regeneration. Obviously, tree gap formation is related to the tree mortality rate (although not all trees form large gaps when they die), but few gap studies have actually used mortality measurements to calculate gap formation. Rather a static approach using maximum tree age or short-term observations has been used. To what degree do these estimates correspond to long-term records of tree mortality? What are the characteristics of dying trees that favor regeneration? To what degree does the past pattern of mortality effect the present pattern of regeneration?

The workshop participants outlined a number of important questions concerning the factors controlling tree mortality:

1. To what degree are mortality rates associated with taxonomic level? This question is especially crucial for extrapolating results in regions, such as the tropics, with high species diversity. However, it could be generalized to ask to what degree is there a genetic versus environmental control of mortality rates.

2. How does one construct guilds of species with similar mortality rates? Again this is crucial for extrapolation of results to larger scale and for model construction. Should these guilds be based on physiological traits, successional position, recruitment strategy, or maximum longevity?

3. To what degree is mortality a function of size? How does this effect the competitive ability of species? Are smaller trees always at higher risk to mortality or does this change with successional status or stand age?

4. To what degree is mortality controlled by site productivity? Does a higher rate of growth also lead to a higher rate of mortality?

Ecosystem Level Processes

Wood is one of the most abundant organic substances on earth, yet the rate it is transferred to detritus or how long it persists once it is dead is not know for most ecosystems. This lack of knowledge has its roots in a number of sources. On the applied research front, foresters assumed silvicultural practices would reduce mortality to insignificant levels and that dead trees would be utilized. From a basic research front, ecologists did not measure dead wood mass because of low nutrient concentration (although this can be offset by a large mass), and mortality rates (estimated from short-term, small plots) were exceedingly low compared to fine litterfall. This has resulted in a persistent and incorrect notion that dead trees need not be considered in ecosystem level studies.

Probably the most important ecosystem level area that tree mortality information could contribute would be the global carbon budget. This information would indicate the degree that global detrital production and detrital stores have been underestimated. Our current estimate is that above ground litter production and total detritus both have been systematically underestimated by 10%. Although this may seem like a trivial amount, varying production by only a few percent could make the biota a net sink on carbon. In regions where dead wood is the major fuel, tree mortality rates would allow an estimation of carbon added to the atmosphere via wood burning. As the mortality rate appears to increase during succession, this information would give more realistic predictions of the amount carbon lost as old-growth or primary forest ecosystems are harvested.

Review of the database currently available indicated, that it is not extensive, but represented most forested biomes. The strategy developed at the workshop would be to use to current mortality data to derive correlations between living woody biomass, forest age, productivity, and climatic data. These correlations would then be coupled with more extensive databases on climate or live biomass to provide biome and global estimates of woody litterfall. These estimates would then be compared to previous estimates of global litterfall production and detrital stores.

The data required to estimate the contribution of tree mortality to detrital production would be diameter distribution of dying trees of each major genus or species in a community. As a minimum sample, 5 hectare-years was suggested as the minimum for reliable estimates. A similar size distribution for living trees would also be needed to compute the living biomass. Size distribution data could be converted to mass using published biomass regression equations. Average nutrient contents of wood/bark would be used to approximate the nutrients returned to the forest floor via mortality. Given wide size range in woody plants and varying lower cut-off for coarse wood, it was decided to include all woody tissues in the input (above and below ground).

CONTINUED EFFORTS

As stated above, the Corvallis workshop was only a beginning. It is important that progress continue on this and related fronts, if major contributions are to be made. A number of possibilities exist to continue these efforts:

1. A symposium could be held to report on site specific and intersite findings. This would encourage the workshop participants to summarize ongoing studies. A joint publication of the symposium would most desirable.

2. Communication between all interested investigators could be enhanced by newletters and frequent use of electronic mail.

3. A catalog of all permanent plot vegetation data currently being collected in North America would be useful for encouraging more intersite comparison and less duplication of effort. Although this is currently being undertaken in LTER, there are many other important sites that are not considered in this network.

4. A joint intersite project could be started on tree mortality. Initially this should be a simple, inexpensive project that will yield significant results. A suggested project would be to quantify the cause of mortality over a 5 year period.

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