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DIFFERENCES AND CONSEQUENCES FOR INSECTS

Abstract

Forest insects and pathogens do not threaten forest resources unless changes in forest conditions facilitate population growth. Healthy trees in diverse forests are protected from potential pests by defensive compounds which kill or deter plant-feeding pests and by the abundance of non-hosts which increase the distance between hosts and chemically hide host trees. Forest management practices which reduce production of defensive compounds or promote the abundance and apparency of any tree species will increase the likelihood of pest problems.

Contrary to numerous assertions, old-growth forests are highly productive and remarkably resistant to potential pests. The resistance of these forests may be due largely to the diversity of plant and predator species which limit the ability of potential pests to discover and colonize suitable hosts. Consequently, herbivore populations are supported at low levels. Low levels of herbivory contribute to long-term productivity and stability by pruning healthy trees, stimulating nutrient cycling, and accelerating the decline and replacement of unhealthy trees.

By contrast, managed forests often are highly susceptible to a variety of pests. This susceptibility results from harvest and planting practices which promote the most commercially desirable tree species at the expense of pest-inhibiting diversity. Simplified tree farms also appear unable to sustain many of the generalist predators responsible for pest control in more diverse ecosystems. The situation has become critical in western Oregon and Washington where 75% of the forest landscape has been converted to Douglas-fir monoculture over the past 50 years, creating an unprecedented resource for pests such as black-stain root disease fungus and its insect vectors.

I appreciate this opportunity to participate in this conference. This programme certainly deals with a timely topic, and I'd like to commend the Students for Forestry Awareness at U. B. C. for putting this programme together.

I also welcome this opportunity to discuss insect responses to changes in forest conditions, especially those resulting from management. Insects represent at least half of the described species in forest ecosystems, but debate over the fate of old-growth forests has dealt almost exclusively with the northern spotted owl, *Strix occidentalis caurina*. Ignored in this debate has been the fate of an incredible diversity of small organisms that are neither cute nor commercially valued and which, if considered at all, are regarded in their context as pests.

Insects respond differently to intensively-managed forests compared with less intensively managed forests. I emphasize that comparison is with less intensively managed forests. Few forests remain truly wild, because fire exclusion or suppression in otherwise unmanaged forests has led to changes that promote some insects such as bark beetles and spruce budworms (Schowalter 1985).

I will cover three topics in this discussion. First, I will address factors that influence insect responses to forest management. Why would we expect insects to respond in various ways to changes in forest conditions? Second, I will discuss some examples of changes that have occurred and reasons for not ignoring these changes. Finally, I will consider some of the ways in which future forestry may be able to address or mitigate some of those changes, as we wish.

Forest conditions influence insects in at least three ways (Schowalter *et al.* 1986). Host suitability is one major factor. I note that "host" refers to both plant suitability for herbivores and prey suitability for predators, for situations where we want to consider predators of insect pests. Host suitability is essentially the nutritional quality of the host. Host abundance and apparency dictate the probability that host-seeking insects can reach and locate suitable hosts. I will discuss these three factors in detail.

As most of us know, plants need a variety of resources from the soil and atmosphere in order to grow. Plants constantly take up carbon dioxide, water, and essential mineral elements such as nitrogen, phosphorous and so on, and they budget these resources in much the same way that we budget our financial resources to mortgages, food, etc. (Fig. 1). Plants allocate their resources to a variety of metabolic pathways (Lorio 1986, Waring and Schlesinger 1985). Foliage and root tissues are high priority pathways because these are the nutrient uptake and photosynthetic machinery of the plant, and are in need of constant replacement. Storage tissues such as tubers and wood tend to be a lesser priority. If a tree doesn't put on a wood increment one year, its fitness and future survival are not necessarily threatened. Reduced wood production is a problem primarily from the standpoint of our interest in timber production. Reproduction can be a major metabolic pathway depending on the priority that reproduction may have under given circumstances. Plants also allocate resources to production of various defensive compounds, either direct toxins or feeding deterrents (Bazzaz *et al.* 1987, Harborne 1982, Lorio 1986). Many of these compounds, such as terpenes and phenols (tannins), have been studied with respect to their medical, industrial and pest management uses.

Different plants will allocate their nutrients, their resources, in various ways. Some plants require higher levels of nitrogen; others may require higher levels of phosphorous or potassium, and so on. Therefore, the balance of these nutrients in the soil is very important to the condition of the plant, as is the genetic predisposition to use these resources in various ways.

Now, if resources become limited, the plant is forced to shut down its lowest priority areas, which in many cases will be the defensive compounds. The defensive compounds produced by plants to repel insects or micro-organisms tend to be fairly complex molecules. They are expensive to produce, they take up resources that otherwise could be used to fuel other metabolic processes, and thus tend to be sacrificed under conditions of stress (Bazzaz *et al.* 1987, Lorio 1986, Waring and Schlesinger 1985).

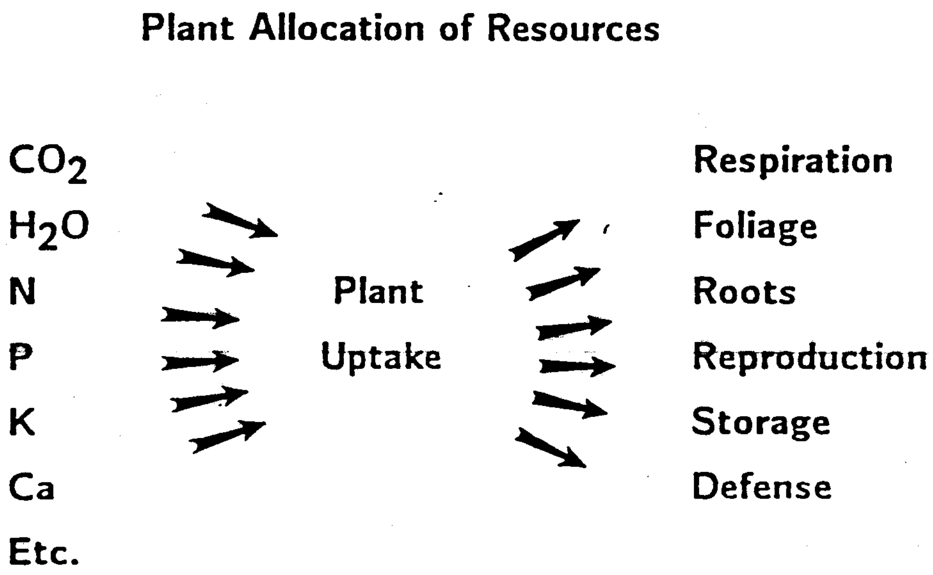

Figure 1 Plant allocation of available resources to various metabolic pathways.

A pine tree or other conifer that is growing under optimal conditions will be able to produce sufficient pitch flow, for instance, and the terpenes and phenols that are associated with pitch, to protect itself from bark beetles and associated micro-organisms, and other insects as well. If the plant becomes stressed by lightning strike, disease, nutrient imbalances and so on, then, of course, the ability to produce defensive compounds at the expense of more immediate survival needs becomes limited, and the plant may become more vulnerable to certain insects that feed on it.

A second factor that influences insects is their ability to find suitable hosts, which typically are scattered throughout a forest. The success of insects in finding a suitable host depends to a large extent on the distance between suitable hosts, usually of a particular species in a particular age class or condition which are nutritionally acceptable to the insect (Fig. 2). As that distance increases, fewer and fewer insects will be physiologically capable of reaching the second host or of discovering it (Schowalter 1985, 1986).

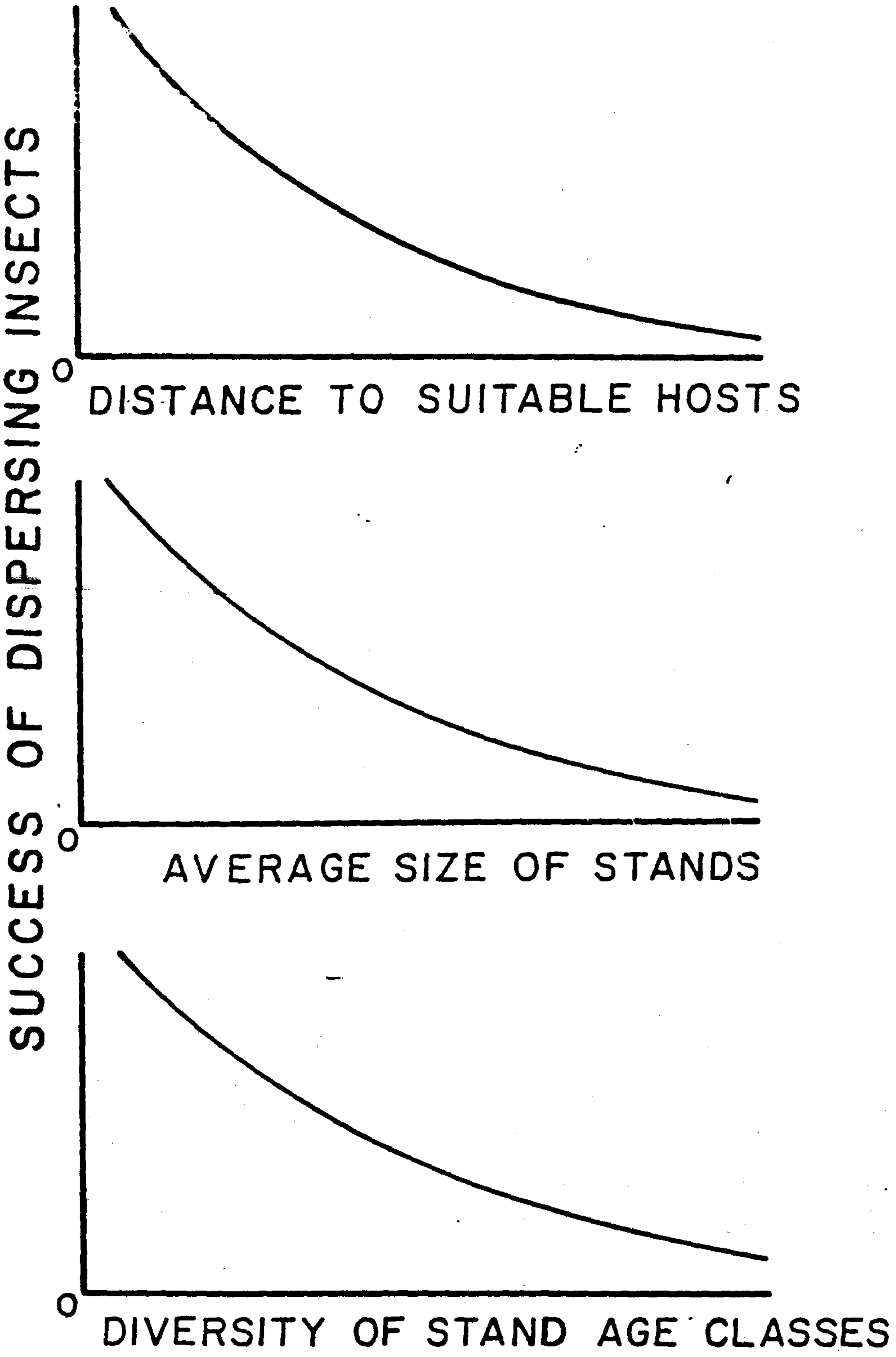

Figure 2 Relationship of insect colonization success to distance between available hosts. Average patch size and diversity of stand age classes influence distance between suitable stands on a landscape level. Used with permission of Timber Press.

Two aspects of landscape structure that can influence this distance are average patch (stand) size and diversity of patch types or ages. As average patch size increases, the size of unsuitable patches which the insect must cross becomes a limiting factor. Similarly, as the diversity of patch types or age classes increases, the proportion of the landscape occupied by unsuitable patches increases. The landscape effectively becomes a filter, so that fewer and fewer insects are able to successfully disperse and colonize new hosts.

A case in point is the way we manage pine forests and Douglas-fir forests. We plant these trees very close together, and we get very dense stands, which become bark beetle bait. There is essentially nothing in these stands or across the landscape to interrupt beetles flying from one host tree to the next.

The third aspect of forest stands that can influence insect activity is apparency. Now, insects don't view the forest the way we do, as a collection of stems and foliage with visual characteristics that allow us to recognize a tree as a Douglas-fir, a true fir, a cedar, or whatever. Rather, insects are chemotaxonomists. They recognize trees on the basis of the chemicals that the trees produce, the chemical fingerprint. Insects orient to a particular host on the basis of particular attractive compounds present in the tree or, in some cases, repellent chemicals which are absent (Visser 1986, Wood 1982). Most insects that feed on conifers can distinguish a conifer host from a hardwood, for instance, on the basis of alpha-pinene and other distinctive terpenes present in conifers but not in hardwoods. Among conifers in a mixed conifer forest, the balances of various terpenes, including alpha-pinene, beta-pinene, limonene and so on, allow insects to discriminate among hosts and non-hosts.

In a monoculture (from the insect viewpoint, a forest composed of trees producing only attractive compounds) the insect will have little difficulty finding a suitable host. All of the cues in the forest aerosol will be attractive cues, and the insect will orient upwind in the direction of higher concentration, inevitably arriving on a host. In the case of a mixed forest where we have a combination of hosts and non-hosts, the non-hosts are trees that are producing either chemicals that the insect is not attracted to or in some cases chemicals that are repellent or toxic to the insect. These chemical cues from hosts and non-hosts become mixed in the airstream until, at some point downwind, the insect is no longer capable of discriminating the host odours or orienting toward the sources of the host odours (Hunter and Aarssen 1988, Visser 1986). In this case, finding a suitable host is determined by chance, and the number of insects finding hosts will depend on the proportion of hosts relative to non-hosts.

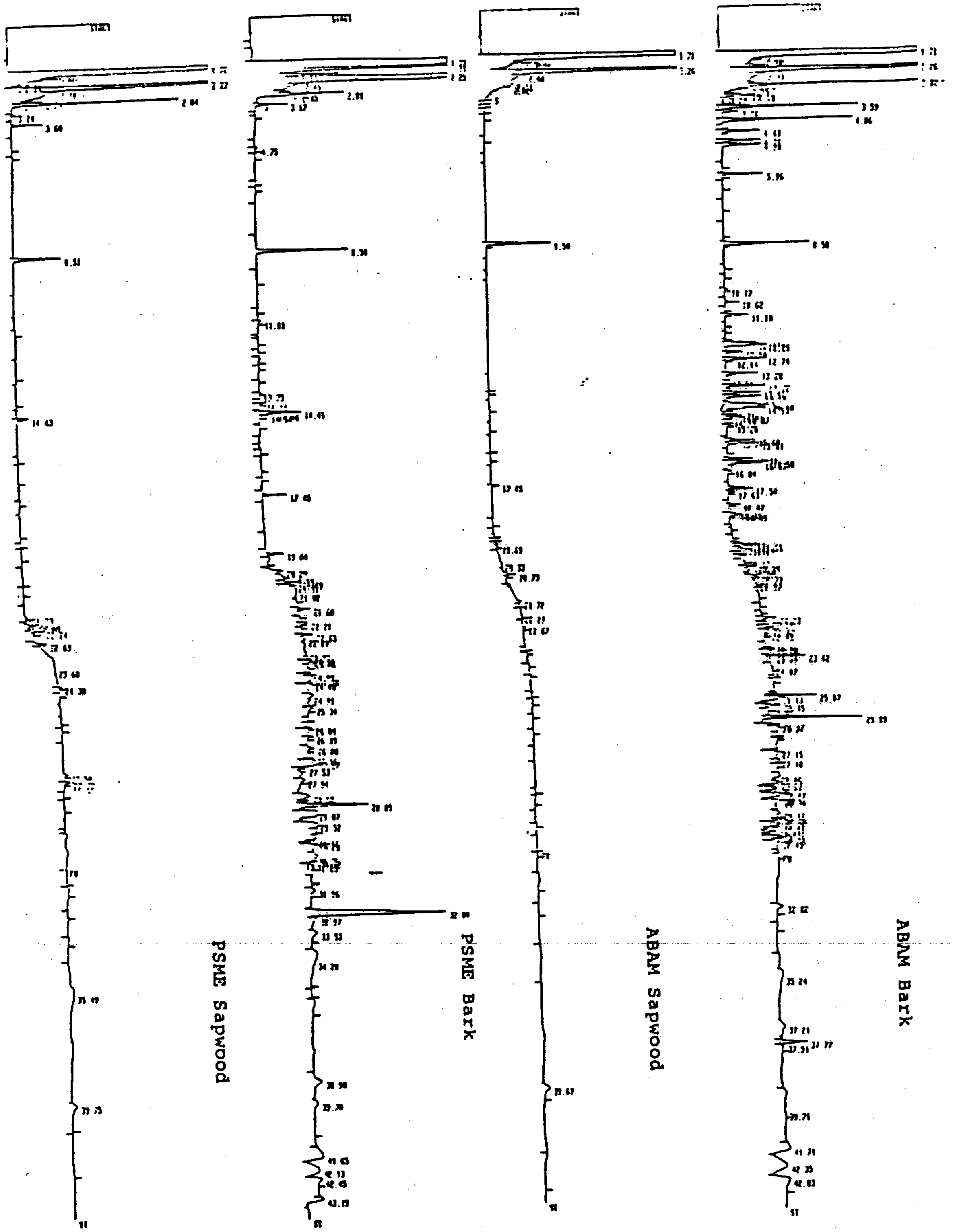

Figure 3 Terpene profiles for Pacific silver fir (ABAM) and Douglas-fir (PSME) bark and sapwood. The peaks below 2.5 min. are solvent peaks. The peak at 8.5 is a standard added to each sample.

We have some important evidence for this in mixed conifer forests. We have looked at the aromatic terpenes of Douglas-fir, Pacific silver fir and western red cedar (Fig. 3). The outer bark of these trees is a very effective chemical barrier to penetration by insects or pathogens. The bark of these trees contains a potpourri of toxic terpenes which prevents entry by most insects and pathogens. By contrast, an insect capable of reaching the sapwood finds a relatively unprotected tissue. Of course, sapwood also is not very nutritious, unless the insect carries microbial associates that can make the wood more nutritious. Because the three tree species have distinctly different chemical profiles, they host distinct communities of chemically-adapted insects and other organisms.

Our most interesting discovery while studying these chemical profiles is that silver fir and western red cedar bark contains significant amounts of verbenone, a repellent chemical for the Douglas-fir beetle, *Dendroctonus pseudotsugae*. We have generally believed that verbenone is a pheromone produced by bark beetles, although it has known plant origins in other taxa (*Verbena*). The pheromone is produced by colonizing bark beetles to deter excess individuals from a fully-colonized tree. Those individuals then attack neighboring hosts (Wood 1982).

Douglas-fir does not produce verbenone. Obviously, Douglas-fir beetles would not be repelled from Douglas-fir until the number of colonizing beetles became sufficient for verbenone production to deter additional beetles. However, in a mixed stand, verbenone released from the bark of true firs and red cedar could reach repellent levels. We haven't tested this hypothesis yet, but we're interested in looking at the relative susceptibility of mixed conifer stands and Douglas-fir monocultures. Are the aerosols in mixed conifer forests less conducive to Douglas-fir bark beetle colonization than are the aerosols in Douglas-fir monocultures?

Similarly, in young stands, consider a mixture of Douglas-fir seedlings growing in a sea of ceanothus, for instance. Ceanothus, as any of you who have walked through one of these regenerating forests know, is a very aromatic plant. Again, insects don't see this the way we see it. They aren't going to visually distinguish Douglas-fir and ceanothus. They are going to find the Douglas-fir as a function of their ability to distinguish the Douglas-fir aerosol from the aerosol produced by the surrounding ceanothus. Their ability to find Douglas-fir in this case may be quite different from their ability to perceive Douglas-fir in a contrasting situation in which the ceanothus has been suppressed with herbicides or dense conifer planting to provide (supposedly) better growing conditions for Douglas-fir. One of the consequences of brush control and other stand simplification practices in regenerating forests is that aphids, especially the Cooley spruce gall adelgid, *Adelges cooleyi*, and beetle vectors of black-stain root disease fungus, *Ophiostoma wageneri*, reach very high densities and become capable of causing significant foliage loss and mortality to young trees. We don't know what the long-term effects may be.

So what are we doing in managed forests that is influencing insect diversity and also the probability of pest activity? If we look at the natural process of stand succession, we see a couple of periods of very high stand diversity (Franklin *et al.* 1989). In the initial herb-shrub stage we have quite a diversity of plants which are reclaiming the site prior to conifer establishment and canopy closure. Again in the old-growth stage we have quite a diversity of plant taxa. Two contributions of these early and late successional stages are important.

First, these stages contribute to soil fertility. Old-growth and naturally regenerating stands possess the only capabilities for providing nitrogen to the soil, via nitrogen fixation in logs and canopy lichens in the old-growth and via nitrogen fixation in logs and shrubs in the regenerating stands. The intermediate Douglas-fir stage is essentially a nitrogen mining stage and eventual depletion may stress the trees and lead to their replacement. A combination of insects, including the Douglas-fir beetle and root pathogens, are involved in the transition from mature Douglas-fir forest to mixed old-growth forest.

The second benefit derived from these very diverse early and late successional stages in natural forests is the diversity that they present to potential insect and pathogen pests (Schowalter 1989). These pests are essentially filtered out of the system during successional stages in which plant diversity (the abundance of non-hosts) is high, as discussed above.

Instead of promoting this diversity in managed forests, we're trying to condense the successional sequence into primarily a Douglas-fir, or other crop species, management cycle (Franklin *et al.* 1989). We thereby remove those species and successional stages which are improving soil fertility and interrupting pest populations. Consequently, we often induce continuous pest cycles within a particular site.

We also are changing our landscape patterns, the distribution of different stand types across the landscape. If we look at the first entries into an essentially old-growth forest system (Fig. 4), we note that the distances between young stands are, at this point, relatively large. Insects are going to have some difficulty spreading across this landscape, but not as much difficulty as they might have had in the pre-management landscape. But with second and third entries, the distances between young planted monocultures become much shorter, and any insects adapted to feeding on young conifers are going to spread across this landscape very quickly. The clear-cuts from the first entry will still be supporting young trees hosting insects which can cross the short distance to fresh sources of hosts. We've removed the barriers that could interrupt accumulation of potential pests (Franklin *et al.* 1989, Schowalter 1989). Clearly, extensive monocultures created by large clearcuts and replanting have a high probability of inducing serious pest outbreaks.

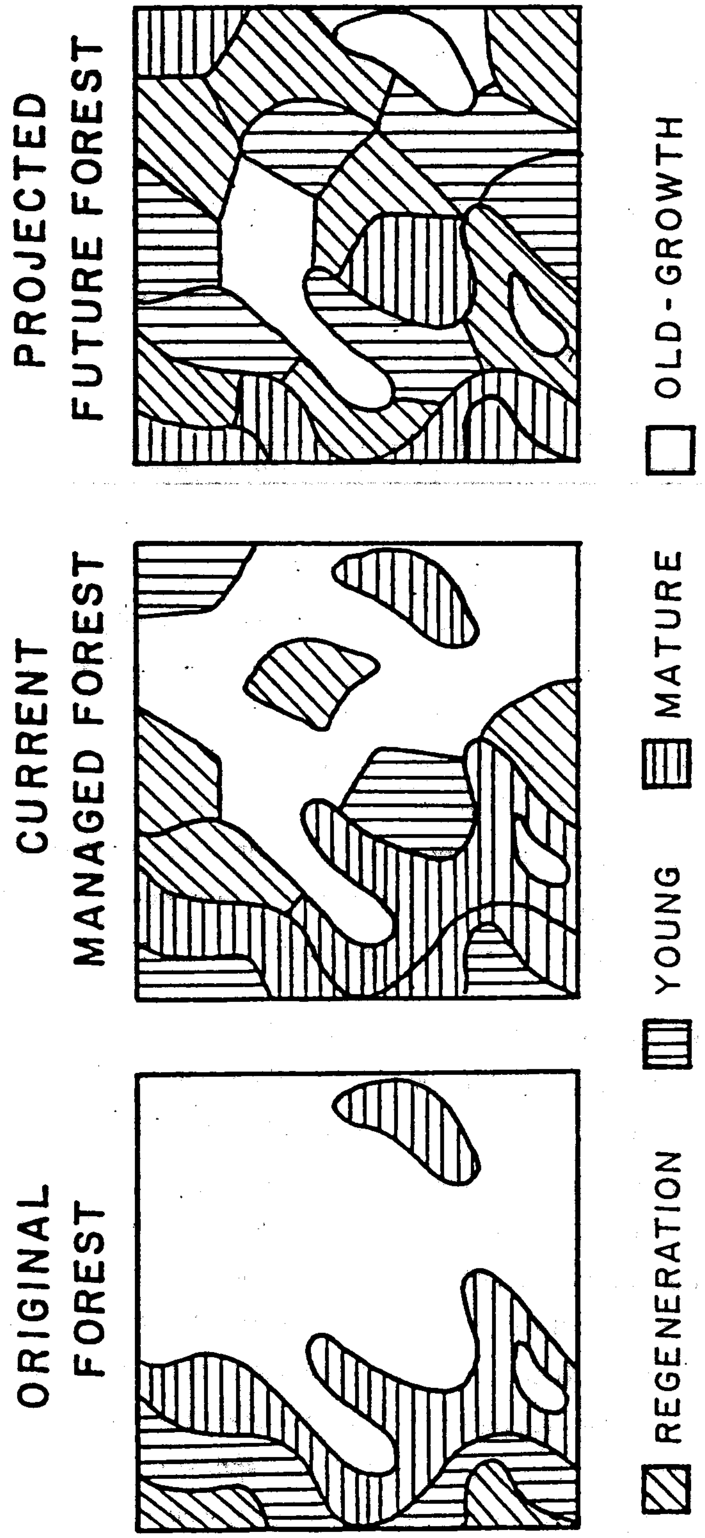

Figure 4 Changes in stand accessibility to dispersing insects following forest fragmentation. Repeated entries over relatively short time periods reduce average patch size and diversity of stand age classes, making stands more accessible to pest populations. Used with permission of Timber Press.

This is aggravated by the fact that we're also, in conjunction with our harvesting practices, establishing a road network which provides access to virtually all sites for pests that may be associated with roads. There's quite an array of insect, pathogen, and weed pests that we know to spread along roads. Black-stain root disease, Port Orford cedar root rot (*Phytophthora cinnamoni*), gypsy moth (*Lymantria dispar*), and spotted knapweed (*Centaurea maculosa*) are among a few of the pests that we now find spreading rampantly through forests along road systems, as a result of disturbed roadsides or of hitchhiking on recreational and commercial vehicles.

What are some of the differences in insect communities that we see between managed and unmanaged stands? What are some of the consequences of the changes occurring in managed forests?

It's very difficult to study ~~insect communities in old-growth~~ forests. I guess I don't need to point out that just getting up into the canopy to see what's up there entails some logistic problems as well as some serious safety concerns. As Mike Amaranthus has indicated, too, the difficulties of going down into the soil are also formidable. The distributions of organisms associated with roots and rhizospheres under the forest floor are probably even less well known than the canopy fauna.

We can use mountain climbing techniques to get limited data on the diversity and abundances of insects in old-growth forest canopies. Young stands can be sampled relatively easily from the ground for comparison. Table 1 presents data from a comparison of six old-growth and six adjacent regenerating stands replicated across the Andrews Forest in western Oregon (Schowalter 1989). Several points can be made from these data.

First, we have quite a balance in the biomass of different functional groups of arthropods in the old-growth forest as contrasted with the young forest where virtually all the biomass is tied up in sucking herbivores, particularly the Cooley spruce gall adelgid. Second, I want to point out that this biomass in the old-growth forest is distributed within about 10,000 kilograms of foliage per hectare, contrasted with the biomass in the young stands which is distributed within only about 1,400 kilograms of foliage per hectare. The potential impact of the herbivores in the young trees is quite a bit greater than the impact of the herbivores in the old-growth forest. Third, despite claims that complex old-growth forests or wilderness areas are going to be sources of insect outbreaks, in fact most of the data indicate that managed monocultures are more likely to generate insect outbreaks. In these data, the very high densities of Cooley spruce gall adelgids in the young stands may actually pose a threat to surrounding older stands which otherwise would not be exposed to these very high populations. Fourth, in the old-growth system, the biomass of predators is balanced against the biomass of herbivores, indicating that predators are quite capable of controlling herbivore populations. In the regenerating stands the predators are obviously playing catch-up; the very large adelgid population is clearly out of control. Finally, note the diversity of species in the two systems. Remember that these data are just for foliage species and represent essentially the resident fauna. I wasn't trying to sample all the insects that might fly into conifer canopies, but rather those insects that would be consistently associated with the conifer canopy. Species number and the balance among species are much higher in the old-growth than in the regenerating stands, even though the clearcuts were adjacent to old-growth.

Table 1. Arthropod biomasses and numbers of species in canopies of old-growth (>400 yr old) and regenerating (10 yr old) conifer forests at the H. J. Andrews Experimental Forest in western Oregon during 1986. Adapted from Schowalter (1989).

	Old-growth		Regenerating	
	Biomass (g/ha)	Number of Species	Biomass (g/ha)	Number of Species
Herbivores				
Defoliators	180	6	0	0
Sap-suckers	10	7	370	3
Predators				
Generalists	150	30	45	7
Specialists	14	10	4	3
Others	30	21	1	2

What are the consequences of species reduction if some species are not capable of persisting in young managed stands? One is the loss of chemical resources that are represented by these various invertebrate species. Although plants are being increasingly examined for sources of medically or industrially useful compounds, few invertebrates have been examined. We know from the few species that have been examined (primarily from a pest management standpoint) that there is quite an array of complex chemicals with potential application. Examination of just a few of the chemical structures produced by beetles, ants and termites, for instance, illustrates the diversity of compounds which have not yet been synthesized (Blum 1980, Harborne 1982, Wood 1982). What little research has been done on potential uses of these chemical resources indicates that some of these have medical uses (wasp and ant venoms and beetle secretions, for example). Other chemicals have been used industrially, as in the case of shellacs and lacquers originally made from scale insect secretions. Some of the chemicals used by insects for protection have been used to derive insecticides, fungicides and insect repellents.

Many of the predators present in old-growth do not occur in young monocultures (Schowalter 1989). Their absence may be due to loss of habitat resources, such as cavity trees, which often are not retained in managed forests; to loss of necessary alternate prey species during different seasons, as found for some generalist predators (those predators that feed on a variety of prey species); or to extreme temperature fluctuations beyond the tolerances of many species. Regardless of the reason, if predators disappear in managed forests, their ability to control pest populations is sharply reduced.

Finally, we don't understand the complex roles of many species in forest ecosystems. We've always assumed that the organisms we call "pests" are primarily destructive to plants, but some recent research indicates that even pests may make significant positive contributions to soil fertility and site productivity in forest ecosystems.

Many plant-feeding organisms function as natural thinning agents. As a result of their selective feeding on stressed, injured, or non-adapted plants, they accelerate ecological succession, the decline and replacement of these plants by plants better adapted to the site conditions (Schowalter 1985, Schowalter *et al.* 1986). The removal of unhealthy plants also releases captured nutrients to the soil and reduces future competition for resources. Because stressed hosts are replaced by healthier hosts and non-hosts, pest outbreaks increase forest health and diversity, thereby mitigating the conditions that promoted the outbreak.

Plant-feeding insects also contribute directly to soil fertility. In one study (Schowalter *et al.* in press) we looked at through-fall and litter-fall across experimental defoliation levels from zero to

20 percent. We found that 20 percent defoliation nearly doubled the amount of water and litter-fall reaching the forest floor during the growing season. That translated into significant contributions of nitrogen, potassium and calcium to the forest floor. Three oribatid mites were significantly more abundant in litterbags under defoliated trees than under non-defoliated trees. These effects help explain evidence of long-term enhancement of increment growth following defoliation (Alfaro and MacDonald 1988, Wickman 1980). Although we see the expected declines in wood increment during periods of defoliation and immediately following defoliation, we see a reversal of this trend 7-10 years after defoliation. The most defoliated trees showed the greatest compensatory growth, perhaps fueled by increased soil fertility, nutrient cycling, and allocation of resources to younger, more efficient foliage.

We obviously don't have enough information about the long-term consequences of so-called "pest" activity. We need to understand the roles of these species, particularly their potential contributions to long-term soil fertility and forest productivity. If trees or stands can compensate for losses to some pests through increased growth resulting from increased resource availability, then we may, over sufficient time periods, recover lost timber production by the time of harvest. Evidence of positive roles for some pests suggests that pest control often may be unwarranted, but also underscores the importance of retaining all species within managed ecosystems as insurance against loss of critical species with unrecognized roles.

A major role of pests may be the diversification of simplified ecosystems. Forest management which focuses on production of timber species has triggered innumerable pest outbreaks. Many of the budworms, bud moths, and bark beetles are associated primarily with areas of extensive second-growth timber production. Dense stands of Douglas-fir and grand fir have been established in interior B.C. and the U.S. during this century as a result of fire suppression and selective logging of fire-maintained ponderosa pine and western larch. These management practices provided the necessary conditions of stress and abundance that have promoted continuous defoliation by the western spruce budworm, *Orgyia pseudotsugata*. Current U.S. Forest Service recommendation for alleviating this situation is replacement of fir stands as they are harvested with open-canopy pine/larch stands. Similarly, current practices for alleviating southern pine beetle, *Dendroctonus frontalis*, depredation in the southern U.S. involve replacement of commercially-favored but susceptible loblolly pine stands with the pre-settlement dominant and resistant longleaf pine.

In coastal B.C. and the U.S., black-stain root disease has become a serious problem in regenerating stands. Several root feeding bark beetles are known to vector this disease (Witcosky *et al.* 1986). These root beetles emerge from decaying roots on cutover sites and girdle and kill numerous planted seedlings. They also bore into root systems of crop trees as well as stumps in pre-commercially thinned stands. We don't understand the reason for boring in living trees, whether this represents attempted reproduction or feeding to obtain necessary nutrients. The pathogen can be introduced into crop trees directly through this feeding or indirectly through establishment and growth within stumps. We also know that these beetles and the fungus are significantly associated with both roads and pre-commercial thinning (Hansen *et al.* 1988, Witcosky *et al.* 1986). The beetles carry fungus spores at a small but growing frequency. Fewer than five percent of beetles carry the fungus at this point, but as more and more stands become infected, more and more beetles will come into contact with infected trees and the transmission rate may increase.

With over 75% of forest lands in western Washington and Oregon harvested and replanted to Douglas-fir monoculture in the past 50 years, we have an unprecedented potential for spread of insects and pathogens of Douglas-fir. Few young stands in western Oregon and Washington are neither infected nor within walking distance of the insects that vector the black-stain fungus spores (Hansen *et al.* 1988). Again, the current U.S. Forest Service recommendation for alleviating this situation is to avoid monocultures, especially on high-risk sites, and instead plant mixed-conifer stands that interrupt disease transmission.

A consistent theme throughout this conference is the value of maintaining diversity in our managed forests. Diversity provides strong protection against pest outbreaks, as well as insuring protection of key ecological processes. Of course, as Hamish Kimmins notes, monocultures do occur naturally. However, they tend to be rare, compared with more diverse ecosystems, and they persist only where soil conditions and/or fire have maintained open savannah conditions which limit insect populations or where outbreaks have not occurred for strictly random reasons. Fire suppression or climatic change which increase tree stress and/or density, such as in the lodgepole pine forests of interior B.C. and the U.S., often results in nearly continuous insect outbreaks if non-hosts do not become established and interrupt the pest cycle.

In conclusion, do we want to continue to manage forests as we have been, as extensive monocultures of economically important crop species, under density conditions that make them extremely vulnerable to insect and pathogen pests? Are we willing to accept the increasing risk of pest depredation and cost of suppression? Or will we rather promote the diversity of species and structures which mitigate pest activity and promote productivity in natural forests? Diversity is a key difference between wild and managed forests and a major factor promoting pest outbreaks. The more diversity that we can reintroduce into our managed forests, at both stand and landscape levels, the less vulnerable our forests should be to insect and pathogen pests.

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