

Insect Pest Management in Forest Ecosystems

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ABSTRACT / Understanding the role of insects in forest ecosystems is vital to the development of environmentally and economically sound pest management strategies in forestry. Most of the research on forest insects has been confined to phytophagous species associated with economically important tree species. The roles of most other insects in forest environments have generally been ignored, including the natural enemies and associates of phytophagous species identified as being important. In the past few years several in-

vestigations have begun to reevaluate the role of phytophagous species responsible for perturbation in forest ecosystems, and it appears that these species may be playing an important role in the primary productivity of those ecosystems. Also, there is an increasing awareness that forest pest managers have been treating the symptoms and not the causes of the problems in the forest. Many insect problems are associated with poor sites or sites where trees are growing poorly because of crowding. As a result, there is considerable emphasis on the hazard rating of stands of trees for their susceptibility to various phytophagous insects. The next step is to manipulate forest stands to make them less susceptible to forest pest complexes. A thinning study in California is used as an example and shows that tree mortality in ponderosa pine (*Pinus ponderosa*) attributable to the western pine beetle (*Dendroctonus brevicornis*) can be reduced by commercial thinning to reduce stocking.

In forestry, the role of insects has been largely viewed as one that competes with human needs. There is evidence, however, that net primary productivity of a forest or a stand may, in fact, be increased by the activity of phytophagous insects (Mattson and Addy 1975). Since in the past the attitude has been to view insects and other forest organisms feeding on and/or killing trees as detrimental, early efforts were concentrated on control rather than on understanding the ecological role of these organisms and their influences on forest composition and production.

There has been a tendency to use a fire-fighting approach to treat catastrophic forest insect outbreaks rather than to try to understand what complex interactions caused the outbreak. In other words, treating the symptom rather than investigating the cause of the outbreak. Outbreaks were and still are treated as single-species phenomena, but in most cases there is a complex of pests involved, including plant pathogens.

The focus on economically important species has meant that the role of insects on understory plants or on commercially unimportant trees has been largely neglected. The trend in forestry is toward more intensely managed stands, and the decision to move in this direction comes from the supposed need to produce more fiber. The dynamics of forest communities are barely understood, yet the strategies of agriculture (for example, genetically selected stock, fertilizers, single-species stands, herbicides, etc.) are being embraced by commercial forestry. The establishment of stands of trees of the same age and species on sites foreign to these species could be a serious mistake in terms of insect and disease pests. The length of time to harvest (rotation age in forestry) can be as long as 80 to 100 years and as short as 30 years. The protection and control costs could be extremely high and entire operations uneconomical. The susceptibility of these kinds of stands to insects has been pointed out by Graham (1956) and by Campbell (1966).

KEY WORDS: Phytophagous species; Forest management practices; Succession; Single-species stands; Even-age stands; Thinning

Perhaps it would be best to understand the natural system prior to changing forest management practices. If the role of insects and other organisms were understood in temperate forest ecosystem succession, then emulation of these natural systems might be a more economically and ecologically sound procedure. An overview of the many roles that insects play in forest ecosystems is available (Mattson 1977, Rafes 1966). Much remains to be done, and the landmark studies by Bormann and Likens and their many colleagues (1979) at Hubbard Brook in New Hampshire are a step in the right direction.

The vast acreage of contiguous forested land, the fact that the forest is a multiple-use resource (lumber, recreation, watershed, and domesticated animal grazing), and the great complexity, dictate a different approach to insect control as compared with agriculture. Phytophagous insects may well play positive as well as negative roles in these systems, as suggested by Mattson and Addy (1975), and a better understanding of these roles could lead to a reevaluating of insect control practices in forestry.

The major effects of insect activity in a forest stand are on stocking, density, species composition, and age composition. This, in turn, affects the productivity and succession of the plant community. As these changes take place, there are changes in the associated flora and fauna of an area. An understanding of the conditions favoring the various types of phytophagous insect populations is the basis for silvicultural control approaches as professed by S.A. Graham and others (Knight and Heikkinen 1980). The forester can determine stocking levels, age composition, and species composition in a stand. Graham (1956) states that, in theory, mixed species mixed-age stands that are not overstocked are the least subject to damage or heavy feeding by insects and other organisms. In other words, the forester can perhaps do what some insects are doing in stands such as those discussed by Mattson and Addy (1975). Thinning a stand that is overstocked, whether it is done

by a forester or an insect, will increase growth of some species on a site and therefore increase productivity. Succession on these sites is thereby influenced as well.

Outbreak Species

The forest and its herbivores have coevolved for thousands of years. Some influences on the plant community are much more subtle than others and, as a result, are not well studied. Mattson and Addy (1975) make the point that it is normal for some grazing by herbivores to take place annually in plant communities and this may be another reason why much of the "normal" activity is ignored or not studied. Evidence for the influence of insects on forest plant communities comes from those insect species capable of becoming abundant in the dominant forest cover types. These are the species that can cause heavy defoliation and tree mortality or primary species of bark beetles that attack the boles of the trees and kill them. Outbreak species such as the spruce budworm (*Choristoneura fumiferana* Clemens), Douglas-fir tussock moth (*Orgyia pseudotsugata* McDunnough), lodgepole needleminer (*Coleotechnites milleri* (Busck)), gypsy moth (*Lymantria dispar* (L.)), and several bark beetles (*Dendroctonus* species) are capable of causing drastic changes in the plant community in a relatively short period of time.

Increasing evidence suggests that certain human activities such as logging, planting exotic species (off-site planting), and planting single-species even-aged stands create situations in which outbreaks of insects are likely to occur. There are also natural situations—such as overmature or old stands, overstocked stands, poor sites, and stands damaged by ice, snow, and wind—that are the loci of insect outbreaks. Graham viewed these situations as being unstable and conducive to insect outbreaks. Graham (1956) held that the law of natural compensations contributed to the stability of forests. Basically, this law states that, in a community of living things, compensating forces tend to keep each species in its appropriate proportion to others.

Major holocausts in forest communities, such as windstorms, snow and ice storms and, particularly, fire, tend to favor the single-species forests. Large outbreaks of insects, though they may cause considerable mortality over large areas, are somewhat different in that the feeding or the effects of feeding are more selective in terms of tree species and the mortality takes place over a longer period of time. In either case, plant succession is influenced. A recycling of the whole successional process can occur with a major holocaust such as fire. In some cases it appears that insects tend to replace fire. This may be even more prevalent now that fire prevention is such an important part of forestry.

It appears that many tree species are adapted to disturbances for their existence (McLoed 1980, Mattson and Addy 1975, Smith 1976) and therefore insects, fire, and other disturbances play important roles in the dynamics of forest communities. Foresters, on the other hand, try to protect the forest from fire, insects, or any other damaging agent and, in turn, may be working against the productivity of the forest. Logging as a disturbance could be viewed as a benefit to some sites (McLoed 1980). Smith (1976) states that any destructive agent (natural and timber cutting) operating alone seldom produces long-lasting alterations in stand composition. However, sequential combinations of destructive disturbances cause greater damage—for example, a fire following an insect outbreak, or a bark beetle (*Ips* spp.) build-up in slash following a logging or thinning operation, with the subsequent attack and top-killing of some of the remaining standing green trees.

There are a number of circumstances in the temperate forests in which the outbreak species appear to play an important role in the dynamics of a given plant community. In some cases, succession may be hastened, but in others the pioneer species may be perpetuated and succession slowed. Productivity may be reduced initially but in the long run can be increased. There are two situations in which outbreaks generally occur. The first is where the herbivores appear to be acting as scavengers. These species attack weakened trees or stands and may build up in large populations that are then capable of attacking healthy stands. These species occur on poor sites, where trees are crowded (overstocked) and are declining in vigor from competition, where species are not adapted to the site upon which they are growing, or in overmature trees that are declining from old age.

The second situation is a density-dependent phenomenon, where vast amounts of food of a similar condition and type (monocultural) are made available to the herbivores. This is the type of situation that occurs in agriculture. In some forests, trees of the same species and same age occur either naturally or by planting.

Insect-Forest Relationship—Case Histories

In the eastern United States, large areas of forest were cleared for agriculture. When abandoned, these sites were colonized by abnormally pure eastern white pine (*Pinus strobus* L.) stands that were commonly composed of same-aged trees (Smith 1976). In the natural condition, the pine would have been mixed with several hardwoods. However, thousands of acres of rapidly growing open-grown white pine resulted in the early 1900s. These conditions are ideal for the white pine weevil (*Pissodes strobi* Peck). This weevil attacks the tips of the

pine and kills it, causing a deformed or crooked stem and, in so doing, eventually creates an entrance court for pathogens and reduces the length of merchantable stem. In the natural forest, the white pine had little opportunity to grow in the open (Smith 1976). This is a good example of a human-created problem. There are other examples of insect and disease problems in old-field succession, as in the southern US with loblolly pine. Usually, agricultural activity results in pure stands on deteriorated sites, and these trees are susceptible to insects and diseases. The southern pine beetle (*Dendroctonus frontalis* Zimmerman), which is a tree killer, is common on these poor sites. Originally much of the land supported a mixed hardwood and pine stand.

Sometimes pure stands are created by logging, fire, clearing and planting, or by insects and disease. In some cases a plant species is perpetuated on a site, but in others succession is speeded by the disturbances and a more diverse plant community results. In Michigan, pure aspen stands resulted from logging and repeated burning (Graham 1956). In 1910, these young aspen stands were abundant in areas that were once pine-aspen-birch forests. However, a complex of insects and disease operating at each stage in the growth of these stands has reduced the aspen. In some areas conifers are returning, and in others a mixture of hardwoods is growing up. In this case, a complex of insects and diseases was responsible for a change in species composition in the community, and this is an example of hastening succession.

Almost all human attempts to establish plantations of trees have been accompanied by a series of insect and disease problems. In some cases species native to the site are planted, and in others exotic species are planted. Almost always, the plantings are of the same species and are made at approximately the same time. There is usually little consideration for local site conditions such as ridges or low wet areas, etc. As a result, some trees do well and some grow poorly on sites to which they are not adapted. In some cases, good growing species are planted on areas outside of their native range. If the stands were allowed to grow naturally, insects and diseases would cause these stands to revert to mixtures of trees. The forest manager is placed in the position of constantly working against this trend of change in species and age composition in the stand. The stands may grow well for 20 to 25 years before encountering problems. In the Great Lakes states, Jack pine and red pine stands have been attacked by a variety of insects at various stages of stand development. In the southern US, *Hylobius pales* (Herbst), a weevil, is a problem on seedlings in recently planted areas; later in stand development there are tip moths, fusiform rust (*Cronartium fusiforme*), root rots (*Fomes annosus*), and the southern pine beetle (Knight and Heikkinen 1980).

Since 1949 China has had a vigorous planting program with a variety of tree species, but primarily with two pine species. These monocultures have posed several insect problems over the years. Considerable control effort has been expended, and the Chinese are going to mixed plantations by planting other species where the original trees died (McFadden and others 1981).

The gypsy moth, *Lymantria dispar*, is a defoliator that was introduced into the United States in the mid-1800s. The larvae feed on a wide variety of tree species but prefer the oaks, particularly white oak and chestnut oak. The effect is to alter the species composition of some sites in the eastern hardwood forests by selective mortality (Campbell and Sloan 1977). As a result, subsequent outbreaks of the gypsy moth have been less damaging on those sites. The damage was most severe on weaker trees in the lower crown classes. It has also been observed that the gypsy moth is associated with disturbances and poor sites (Houston 1979, Bess and others 1947). Disturbances resulting from fire and logging activity hampered forest development and favored the preferred food of the gypsy moth. Recent outbreaks in New England have occurred in stands with low moisture availability, as on dry ridges or drained sandy soils. Trees on these sites are often the preferred hosts and usually provide refuges for pupation (Houston 1979). Stands on moist sites are fast growing and have mixtures of preferred and nonpreferred hosts. In addition, the straight trees on these sites do not provide refuges for the gypsy moth. Disturbances attributable to urbanization have created additional susceptible sites for the gypsy moth (Houston 1979). The gypsy moth generally hastens succession.

A close relative of the gypsy moth, the Douglas-fir tussock moth, *Orgyia pseudotsugata*, occurs in the western United States and Canada. The larvae are defoliators of Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco, and true firs, *Abies* spp., depending on location. For example, in California the larvae feed almost exclusively on white fir, *Abies concolor* (Gord. and Glend.) Lindl., except at high populations, when larvae will feed on almost any plant. Outbreaks occur every 9 to 10 years, and considerable effort has been expended to explain these outbreaks and to characterize the plant communities where defoliation was greatest. In northern Idaho, defoliation of grand fir, *Abies grandis* (Dougl.) Lindl., was greatest on upper slope and ridgetop sites and in the older stands of grand fir and Douglas-fir (Stoszek and others 1981). The percentage of grand fir in the stand was important, as were stocking levels. The higher the site occupancy or stocking, the greater the damage. The results indicate that there is a density-dependent relationship between the insect and grand fir in northern Idaho (Stoszek and others 1981). Tussock moth-caused tree mortality would mean changes in stocking levels, species composition,

and age composition on these sites. In California, the results of another study were similar, except that the greatest damage was in relatively open-grown white fir stands (Williams and others 1979). These stands were predominantly white fir, even though the stocking levels were low. In another California study it was found that white fir growth actually increased for years after an outbreak of the tussock moth, suggesting a role in primary production on these sites (Wickman 1980).

From many viewpoints, the spruce budworm is probably the most important forest insect in North America (Jennings and others 1979). The spruce budworm periodically defoliates millions of acres of the spruce-fir forest in eastern North America. The ecological implications are, indeed, interesting, since it appears that the spruce budworm is important in the maintenance of the spruce-fir type and the perpetuation of balsam fir, *Abies balsamea* Mill., in these stands. Balsam fir is fire-susceptible and does not invade well after fire, but it does well if openings are made without undue disturbance to the soil (McLoed 1980). The disturbance created by the spruce budworm is similar to that created by wind damage, but over much larger areas. Rather than occurring in patches, the balsam fir is regenerated over extensive areas. It is speculated that the heavy use of insecticides in eastern Canada since the 1950s has prolonged the outbreaks of spruce budworm and has shortened the time between outbreaks (Blais 1974). Those stands with a high percentage of mature balsam fir are the most susceptible to the spruce budworm. This appears to be a highly coevolved system between an insect and a plant.

There are other insect-tree interactions in which the insect appears to be perpetuating a species on-site and, in a sense, slowing succession by benefiting the pioneer species by opening a stand. The opening of a stand by tree killing or defoliation permits more light to get to the vegetation beneath. The opening of a stand tends to allow more precipitation to reach the soil, and this increases runoff and silting in streams. More light reaches the trees in the understory, and this delays natural thinning since they would eventually be shaded out.

The lodgepole needleminer in Yosemite National Park in California seems to play an important role in maintaining lodgepole pine stands. The needleminer weakens trees and is capable of killing them, but often the mountain pine beetle, *Dendroctonus ponderosae* Hopkins, will kill already-weakened trees. The role of needleminer is thought to be similar to fire in stand establishment (Telford 1961, Fowells 1965).

Bark Beetles

Bark beetles' (Family Scolytidae) relationship to trees or stands has been studied extensively. Most of the species in the family are essentially secondaries, decomposers, or recyclers of nutrients in a plant community. There are a few tropical

ambrosia beetles that can be considered primaries—that is, they attack standing healthy green trees (Rudinsky 1962). Some of the most interesting bark beetles are secondaries that attack standing green trees that are weakened and predisposed in some way. These beetles, such as many species in the genera *Dendroctonus*, *Ips*, *Scolytus*, and *Pseudohylesinus* have a tremendous impact on plant communities in terms of stocking levels, species composition, and age composition. As a result of this relationship, forest entomologists have worked on hazard rating systems (Salman and Bongberg 1942, Ferrell 1980, Schmid and Freye 1976). It appears in most cases that these insects play a role that, on a longer-term basis, benefits the community. Since these beetles are responding to host trees that are in some way weakened, there is a relationship between the availability of suitable host material and the population density of the beetles. Further, it is well known that in some situations, when beetle populations are high, apparently healthy green trees are killed. These epidemics have been of great concern to foresters in Europe and North America.

Some bark beetles will breed in slash (downed residue from logging operations) or in trees downed from windstorms or snow breakage. In the Scandinavian countries, *Ips typographus* L. on Norway spruce, *Picea excelsa* Link, and *Tomicus piniperda* (L.) on Scots pine (*Pinus sylvestris* L.), cause major damage after wind and snow damage but are also troublesome as an aftermath of logging practices where too much breeding material is left (Nilsson 1976). The effect on the community is similar to other perturbations, but in those cases the insects are acting in concert with a physical factor. The result is a revitalization of a community that has reached a stage where it is susceptible to the physical factor. The downed material provides a breeding site for the insect and the end result is an effect, over a much larger area, that lags because of the breeding time of the beetles. Other *Ips* species and *D. pseudotsugae* Hopkins are known to behave similarly in the western United States. The 1962 Columbus Day windstorm in California produced many bark beetle problems because of a build-up of beetle populations in damaged or weakened trees. In some cases the *Ips* species and *Scolytus ventralis* LeConte built up in the downed material and then top-killed large standing green trees, which were later attacked by the western pine beetle and mountain pine beetle in the case of pine or filled in by fir engraver in the case of true firs.

Other bark beetles attack trees that have been predisposed or weakened by some factor such as drought, flooding, root diseases, smog injury, crowding, or competition. Most often this occurs at some point in the development of the community, and the beetles act as thinning agents by removing or killing the trees. The beetles hasten mortality that would otherwise occur as a result of the predisposing agent or some other mortality

factor (insect or disease). These bark beetles are somewhere between the primary and secondary beetles and tend to hasten the successional process or perpetuate the pioneer species (slow succession).

There are several interactions between bark beetle species and major timber types that are of interest. Spruce beetle, *Dendroctonus rufipennis* (Kirby), infestations commonly develop in windthrown trees, but then the beetles spread to dominant and codominant standing green Engelmann spruce, *Picea engelmannii* Parry, and kill them (Schmid and Freye 1976). The result is a change in species composition where subalpine fir (*Abies lasiocarpa* (Hooker) Nuttall) is a component or a perpetuation of Engelmann spruce by the release of suppressed trees in the understory. The last major outbreak of the spruce beetle occurred between 1940 and 1952, when more than 5 billion board feet of Engelmann spruce were killed (Massey and Wygant 1954). Outbreaks of the spruce beetle have occurred at intervals of approximately 50 years, and the beetles appear to be important in maintaining Englemann spruce stands (Miller 1970).

Dominant, overmature trees are more susceptible to bark beetle attack. These old trees are often attacked by a complex of organisms, but the bark beetles are responsible for hastening the mortality. The risk of a mature ponderosa pine or Jeffrey pine dying because of *Dendroctonus* attack has been calculated using a risk-rating system. In California this system was found to work only in the mature pure pine stands of northeastern California (Salman and Bongberg 1942). Recently a risk-rating system has been developed for the true firs (Ferrell 1980). There, a beetle, *Scolytus ventralis*, is one of the major mortality factors of mature overstory true firs (*Abies concolor* and *A. magnifica* A. Murr.). There are other examples of bark beetles removing overmature trees from communities, too, and the primary effect is to alter the age structure of the stand.

The mountain pine beetle attacks several species of pine. In some cases the trees are overmature, in others the stand is overstocked for the site, or the trees are predisposed by some other factor. Oftentimes, trees over vast acreages are killed. In many of the interior areas of the western United States, the mountain pine beetle is the most important tree killer of ponderosa pine (Sartwell and Stevens 1975). Most of the tree mortality in second growth stands occurs in stands that are very dense, with the trees not growing well because of competition. With some of the other *Dendroctonus* and *Ips* species, the presence of logging slash or trees damaged naturally by storms provides breeding material that starts the outbreak. With the mountain pine beetle in the inland ponderosa pine, it was found that certain stand conditions were associated with the outbreaks (Sartwell and Stevens 1975). The stands were essentially even-aged, pure or nearly pure ponderosa pine,

between 50 and 100 years old. The outbreaks usually occur earlier in a stand developing on a good site rather than on a poor site. The basal area is usually 150 ft²/acre or higher. The logical procedure would be to thin these stands before the beetles do.

In the lodgepole pine stands of western Canada and the United States, it was found that the situation was somewhat similar to that found in ponderosa pine (Safranyik and others 1974, Amman 1977). Generally, the beetles prefer the larger-diameter trees growing on the better sites. The management alternatives to avoid epidemics of this beetle are to harvest stands before they reach the susceptible age class and diameter and to create mixed species stands or stands with a mosaic of even-aged trees of different age classes (Safranyik and others 1974). The role of the beetle on any particular site depends on whether lodgepole pine is seral or is the persistent or climax type. In seral stands the continued role of the beetle depends upon fire, as lodgepole pine is perpetuated by periodic fires on these sites (Amman 1977). The mountain pine beetle plays an important beneficial role in this system since the trees are killed at an age so that the vigor of the stand is maintained and the stand is kept at maximum productivity.

In California's westside Sierra Nevada mixed conifer forest, both the mountain pine beetle and the western pine beetle, *D. brevicornis* LeConte, kill weakened ponderosa pine. In some situations, trees are weakened by root disease, particularly the black stain root disease, *Verticicladiella wageneri* Kendrick. The disease seems to occur in pockets, and these areas are called disease centers. Beetle activity is common in these centers (Goheen and Cobb 1980). Ponderosa pine susceptibility to beetle attack has also been associated with photochemical oxidant injury in southern California (Cobb and others 1968). The beetles are active on poor sites where ponderosa pine is not growing well. Drought also predisposes trees to bark beetles, but particularly on poor sites. There was a drought in California for two years (1976-77) from which considerable tree mortality resulted. Several species of trees died, including ponderosa pine. Most of the mortality was concentrated at the lower elevations, on poor sites, or where trees were crowded or overstocked. From observation it appears that *Ips* spp. are more prevalent during the drought periods. These beetles kill smaller pines but also top-kill larger trees, leaving the lower part of the bole to be infested by the *Dendroctonus* spp.

Blodgett Forest Thinning Study

Most studies on the relationship of insects to forest stands have been concerned with the development of stand-hazard rating systems. Attempts have been made to identify the stand conditions in which insects cause the most damage, and these determinations have been made for a number of those insects

Table 1 Mean volume of ponderosa pine per plot in thinned and unthinned units at Blodgett Forest, El Dorado County, California, 1978 to 1981.

	Control	Block	Individual
Number of plots	17	17	15
Mean original volume, ft ³	1237 (35.1 m ³)	932 (26.4 m ³)	1240 (35.1 m ³)
Mean remaining volume, ft ³ after cutting	1237 (35.1 m ³)	602 (17.1 m ³)	656 (18.6 m ³)
Mean cut volume, ft ³	0	330 (9.4 m ³)	584 (16.5 m ³)
Mean killed volume (to 1981), ft ³	135 (3.8 m ³)	78 (2.2 m ³)	58 (1.6 m ³)
Mean cut and killed volume, ft ³	135 (3.8 m ³)	408 (11.6 m ³)	641 (18.2 m ³)

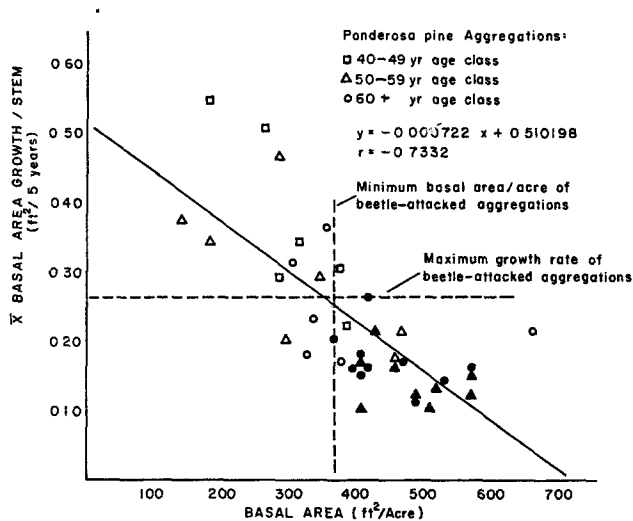


Figure 1. Growth rates and basal areas of 38 ponderosa pine aggregations at Blodgett Forest Research Station, El Dorado County, California. Solid symbols indicate past or present bark beetle activity (from Lang and others 1978).

discussed above (Hedden and others 1981). The next step is to develop silvicultural prescriptions for these stands based on the research results of various experimental management procedures. There have been relatively few of these controlled studies on the silvicultural control of forest insects.

The western pine beetle seems to play an important role in the succession of the mixed westside Sierra forest. Ponderosa pine is a shade-intolerant species and the pioneer species, whereas white fir, Douglas-fir, sugar pine, incense cedar, and black oak are all shade-tolerant to some degree. Ponderosa pine invades open sites after fire or logging or both. The pine stands are nearly pure for several years until a canopy is formed and gradually the shade-tolerant species become established in the understory. As the crowded pine stands become older, they are gradually removed by root disease, and the western pine beetle and the shade-tolerant species are released. After a number of years and with the aid of ground fires, an open mixed stand of very large trees results. The bark beetles and root disease

obviously play an important role in hastening succession in this serc.

In 1978, a long-term study was established to examine the relationship of stocking levels in ponderosa pine to bark beetle-caused tree mortality. Preliminary studies had shown that at Blodgett Forest, California, bark beetle mortality was concentrated in pine aggregations with a basal area of 350 ft²/acre (80.4 m²/ha) and a mean basal area growth rate of less than 0.26 ft³ (.024 m³)/5 yr (Figure 1).

Blodgett Forest is on the western side of the central Sierra Nevada mountains and is a mixed coniferous forest consisting of five conifer and one hardwood species. However, ponderosa pine occurs in single-species groups or aggregations throughout the forest. The hypothesis was that stand susceptibility to beetle attack is related to this aggregation as a collective unit rather than to growth rate of individual trees.

Fifty pine aggregations were located on the 40-acre (16 ha) study area and grouped into 15 geographical blocks. There were five replications of three adjacent blocks, as follows: 1) no treatment, 2) thinning of individual aggregations only, and 3) thinning of an entire block that included individual aggregations of pines. The goal of the thinning was to reduce basal area to approximately 200 ft²/acre (45.9 m²/ha). The plots have been sampled annually for ponderosa pine mortality since 1979.

Table 1 gives mean volumes of pine per plot for the control and two treatments. The cut volume was summed with the volume of trees killed by beetles in the post-treatment period to 1981 to give total volume removed from the original stands. To study the effects of the treatments over this period, analyses were made on the proportion of original volume killed by beetles, the proportion of remaining volume (after cutting) killed by beetles, and the proportion of total volume removed (killed plus cut) of the original volume. These proportions were calculated for each plot, and for statistical analysis were converted to radians with the arcsine-square root conversion to reduce dependence of variances on means. A two-way analysis of variance by treatment and group was calculated for each converted proportion. The only significant differences found

Table 2. Proportions of volume killed and cut in treatments and control plots from 1978 to 1981 at Blodgett Forest, El Dorado County, California.

Proportions	Control	Block	Individual	F-test significance
Beetle-killed volume to original volume (1978)	0.50 ^a (11%) ^b	0.37 (8%)	0.19 (4%)	0.14
Beetle-killed volume to volume after cutting	0.50 (11%)	0.46 (12%)	0.35 (10%)	0.73
Beetle-killed and cut volume to original volume (1978)	0.50 ^c (11%)	1.36 (40%)	1.50 (46%)	0.001

^aArcsin-square root converted proportion.

^bActual mean percentage.

^cSignificantly different from two treatments using Duncan's multiple range test, $p = 0.05$.

were between the proportion of original volume cut and killed for control compared with the two treatments. Means of converted proportions and actual percentages were calculated for all five groups combined (Table 2) because groups were found to be not significantly different. The proportions of remaining volume killed (Table 2) indicate that beetles are taking about the same proportion of trees in each treatment, but the actual volume killed is higher in the control plots, since they have about twice the volume remaining as the block and individual treatment plots. The significantly lower proportion killed or cut in the control plots indicates that three years of beetle activity have not had the same proportional effect on reducing volume as the cutting treatments. However, it is anticipated that in the long run, because of tree competition, significantly more trees will die from bark beetle attack in the control plot. By sampling tree mortality in these plots on an annual basis the critical stand reentry time can be determined. After many years of observation this study should determine if thinning is an economically feasible method of bark beetle control.

Conclusion

The Blodgett Forest study demonstrates one method for understanding the relationships between phytophagous insects and their hosts. In the future, forest pest managers must develop a better understanding of forest ecosystems and the role that insects play in them in order to develop ecologically and economically sound pest control strategies.

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