

REVIEW PAPER

A critique of silvicultural approaches to managing defoliating insects in North America

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- Abstract**
- 1 A variety of silvicultural techniques have been suggested for managing forest defoliating insects. The objectives focus on minimizing defoliation or minimizing damage from defoliation.
 - 2 The theoretical foundations of many approaches have been built upon observation and correlation, and very little reliable empirical evidence exists to support the objectives of silvicultural manipulations. Existing experimental data have yielded inconsistent results.
 - 3 We review the conceptual framework and underlying assumptions of the major silvicultural approaches recommended or in use in North America.
 - 4 Well-designed, long-term studies are needed to clarify the effect of silviculture on defoliators and their effect on forests.

Keywords *Choristoneura fumiferana*, *Choristoneura occidentalis*, gypsy moth, *Lymantria dispar*, silviculture, spruce budworm, susceptibility, vulnerability.

Background

Most foliage-feeding forest insects rarely cause noticeable damage to trees and are of little concern to forest managers. However, there are notable exceptions of forest insects that occasionally reach outbreak densities, and partial, if not total, defoliation of host trees may result. Relatively few options exist for reducing the impact of defoliators. In most cases, the options consist of direct suppression of populations using insecticides, enhancing natural mortality of populations at low densities through the introduction of biological control agents, and indirect management via manipulation of the habitat in a manner that makes it less suitable for population growth of the defoliator. Given the high cost and potential for environmental damage, direct control with pesticides is increasingly unattractive. For many years, classical biological control was considered the most benign of all management actions but in recent years there has been growing concern about potentially negative effects of introduced biological control agents. Thus, manipulation of the habitat using silviculture is a potentially attractive approach to

forest pest management because it may be inexpensive, effective, long-lasting and have a low environmental impact.

The use of silviculture in forest pest management can range from an extreme of stand elimination, e.g. conversion to agriculture or a different tree species mix, to the very moderate approach of selective cutting of individual trees, and could include regeneration methods. Most uses of silviculture to influence potentially injurious factors fall within the broad category of 'improvement cuts.' Smith (1986) defines improvement cuttings in general, as those made for the purpose of improving forest composition and enhancing quality of individual trees by removing trees of undesirable form, or undesirable condition, from the main canopy. Improvement cuttings represent intermediate management. Regarding defoliator pests, they should be preliminary operations, i.e. they are designed to eliminate the threat rather than provide direct benefits. Intermediate treatments involve thinning, prescribed burning, sanitation removals, salvage, fertilization, weed control or pruning. Whereas most of these techniques serve to eliminate competition and release the desired species or individuals, thinnings have the sole purpose of enhancing the vigour of the residual stand. In thinnings, the trees targeted for removal are often obvious, i.e. undesirable species, poor bole quality,

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apparent infestation, lacking vigour. The extent of thinning is targeted to achieve an adequately stocked level, in accordance with stocking guides available for particular forests.

Regeneration systems are the other broad category of silvicultural methods, but their use is limited in managing for defoliators. With the exception of site conversion or the elimination of the mature individuals of a species that may be prone to insect problems, the intent of regeneration silviculture is to produce new growing stock of rapidly growing, vigorous trees.

The objectives of all silvicultural methods for management of defoliator impacts are any one or a combination of the following:

1. To modify the insects' habitat such that their population growth is diminished, thereby reducing the probability of reaching defoliating levels, i.e. to reduce stand 'susceptibility' to defoliation.

2. To decrease the probability of tree mortality following defoliation, i.e. to reduce stand 'vulnerability'.

3. To improve ability of the stand to regenerate following defoliation.

Susceptibility is also referred to as 'risk' and vulnerability as 'hazard'. Attempts to differentiate levels of susceptibility and vulnerability have been pursued for many types of forest insect pests, including defoliators and bark beetles. Ample evidence exists demonstrating successful use of silviculture to reduce both stand susceptibility and vulnerability to bark beetles, but that literature is reviewed elsewhere (e.g. Hedden *et al.*, 1981 and references therein). Examples demonstrating the use of silviculture to successfully mitigate the impacts of defoliating insects are more limited. The purpose of this paper is to examine the theoretical background and to review the evidence of success for use of silviculture to manage defoliators in North America.

'Balance of nature' and silviculture

A significant premise in many silvicultural strategies is that mimicking natural conditions will enhance resilience, i.e. the ability of a forested ecosystem to return to its previous state, or even resist perturbations. In the eastern US, attempts to change species composition to enhance resistance or resilience typically are driven by the realization that current forests most likely represent an intermediate successional stage. For example, many of the forests in eastern North America are dominated by species that are not commonly regenerating in the understory. According to classic successional theory, if forest composition and condition mirrored 'steady state', or in traditional successional terminology 'climax', insect populations and associated problems would exist at such low levels that the ecosystem functioning would absorb them, and the impact of the insect would be minimal. The notion of succession as an organized, highly predictable process has been widely questioned (see Glenn-Lewin *et al.*, 1992); nonetheless, there persist suggestions that discrete late successional communities exist for a given area. The balance of nature hypothesis suggests the existence of an equilibrium that would provide a stabilizing mechanism limiting the influence of perturbations. Under relatively steady state conditions, therefore, insects become more integral in ecosystem functioning (Mattson & Addy, 1975). Although more contemporary views of stochasticity and heterogeneity in time and space

have somewhat superseded the traditional balance of nature view (Wu & Loucks, 1995), there is still an attempt to imitate an idealized view of succession through forest management.

Management of North American forests during the last century has resulted in the dominance of species that, although competitive on a given site, are not always best suited for the site. As an example, throughout much of western North America, the dominance of *Pinus* has been maintained in certain natural forested ecosystems by periodic fire. Suppression of fires during the past century, however, has contributed to the dominance of mixed conifers (e.g. *Abies* and *Pseudotsuga*) or other tolerant conifers on sites historically dominated by intolerant *Pinus*. Contemporary mixed conifer forests are more highly favoured by the western spruce budworm (*Choristoneura occidentalis*) than pine forests, primarily because *Abies* and *Pseudotsuga* are preferred hosts and *Pinus* is not. Also, the broad expanse of mixed conifer forest blanketing the landscape creates the potential for widespread defoliation and tree mortality.

As a historic parallel, in the Lake States, forests historically dominated by pines promoted by a combination of periodic fires and low soil productivity (i.e. *Pinus strobus* and *P. resinosa*) are now dominated by oaks (*Quercus*) and aspen (*Populus*), both preferred hosts of the gypsy moth (*Lymantria dispar*). Also, extensive logging of the overstory and accompanying disturbances promoted oak regeneration at the expense of conifers (Palik & Pregitzer, 1992). High frequency fires that were once common in the prairie have also been suppressed, causing the forest to encroach into the prairie; these forests along the forest-prairie transition are dominated by oak (Abrams, 1992). Not only have such species shifts resulted in a forest more susceptible to gypsy moth, but often these species are not as well adapted to these xeric sites in which they have invaded, and tend to be less vigorous and are more likely to suffer mortality when defoliated. Although species ranges are generally unaffected, local distribution of oaks has broadened, creating a more abundant resource for the gypsy moth.

Similar increases in oak species in the eastern United States can be attributed in part to catastrophic, anthropogenic disturbances, such as logging, grazing, and changes in fire regime. The forests of the eastern United States are dominated by oak species (Abrams, 1992), in part because of the demise of the American chestnut (*Castanea dentata*) through the introduction of the pathogen, *Cryphonectria parasitica*. The potential for a theoretical 'steady state' forest is questionable when species have been extirpated.

Many of the silvicultural strategies to curtail the damage caused by the eastern spruce budworm (*Choristoneura fumiferana*) are based on the notion that current forests are susceptible to spruce budworm because logging activity has interfered with natural successional processes on a scale that creates landscapes dominated by susceptible forests. Cutting practices and fire suppression have favoured dominance of balsam fir. As supporting evidence, dendrochronological studies have shown that budworm outbreaks have been more severe, although not necessarily more frequent, during the 20th century than in previous centuries (Blais, 1983; Weber & Schweingruber, 1995). As Swetnam & Lynch (1993) and Krause (1997) point out, however, outbreaks of forest pests were common even before North America was settled by Europeans.

Table 1 Description of silvicultural activities with possible effects on forest susceptibility and vulnerability to defoliating insect pests.

Silvicultural activity	Desired effect on stand susceptibility ¹	Desired effect on stand vulnerability ²
Adjustment of species composition	Reduction of amount of suitable host foliage Increased mortality during dispersal Enhancement of natural enemies	Dominance by species more appropriate to the site Lower probability of catastrophic loss (spreading the risk)
Modification of stocking level	Decreased foliage quality as a result of increased vigour Increased mortality during dispersal	Increased tree vigour/tolerance
Adjustment of age distribution	Decreased foliage quality as a result of increased vigour	Increased tree vigour/tolerance
Selective cutting of low-vigour trees	Decreased foliage quality as a result of increased vigour	Increased tree vigour/tolerance

¹Stand susceptibility is defined as potential for defoliation.

²Stand vulnerability is defined as potential for trees to die following defoliation.

Although invoking a balance of nature view and imitating purported natural processes seems attractive in that recreating pre-settlement forests may reduce pest problems, there is minimal evidence that the concept is universally applicable. A simplistic view of succession suggests that all communities have a relatively predictable endpoint, but actual patterns in nature indicate the existence of multiple successional pathways rather than predictable, deterministic endpoints and often disturbance regimes that prevent reaching a steady state of self-replication. Furthermore, in most situations, it is not possible to replicate pre-settlement communities; global change phenomena such as climate change and introductions of exotic species have contributed to modifying ecological processes and structure. Also, human population pressure may either directly (e.g. clearing land) or indirectly (management) affect habitat. Finally, although silviculture is implemented at the stand level, it is obvious from these examples that the influence of insects occurs at the landscape level.

Approaches to changing stand characteristics

We present here four silvicultural methods that are designed to reduce susceptibility to defoliation or to reduce vulnerability of trees in North America (Table 1). Other methods, e.g. fertilizer application, pruning, are not widely used in North America.

Adjustment of species composition

Modifying species composition may be the most effective means of limiting insect outbreaks. Although many forest insects are polyphagous, most foliage feeding insects are limited to feeding on a specific number of host species and, thus, replacement of these preferred hosts by non-hosts will reduce total damage. Stand characteristics can be greatly modified by removal of susceptible overstory species, an approach that represents the simplest way to reduce the potential for damage. Selective harvesting can potentially reconfigure the resource base for a pest, and hence influence susceptibility, or the likelihood that the pest will build up populations in the stand.

The simplicity of the implication that eliminating the host species will create more resistant stands belies the complexity of

species–site relationships and interference with economic values of forests. For example, although removal of the preferred hosts of gypsy moth, generally oaks, may represent a rational approach to reduce overall susceptibility of the forest, the ecological and economic consequences of removal of the dominant species in the forest may be deleterious. There is a long history of dominance by oaks in most forests in the eastern United States, although the importance of this species group is often tied to particular edaphic, climatic and disturbance regimes where it best competes with more mesic species. Furthermore, because of the prodigious volume of oak in eastern North America, the economic value of this species may far surpass other species (Barrett, 1995).

Even-aged systems of silviculture are directed toward regeneration and potentially can modify species composition drastically. Clearcutting represents the most common regeneration method and the approach could be interpreted as a mimic of widespread natural disturbance, such as catastrophic fire or severe wind. Unless artificial regeneration is used, ruderal species are likely to colonize the recently cut area, and the reduced stand-level susceptibility is a function of the susceptibility of the particular, pioneering species. Shelterwood and seed-tree methods represent two additional approaches to stand regeneration; the former favours trees that are moderately tolerant of shade, whereas the latter favours trees intolerant of shade.

Within the generalized objective of adjusting species composition resides the secondary objective of increasing plant species diversity. In particular, silvicultural practices often decrease dominance by a single species in a forest, albeit inadvertently. Forests with a mix of hosts and non-hosts are likely to have a lower probability of some catastrophic loss to defoliation. Diverse forests might also have greater variety and abundance of parasitoids and predators that serve to minimize outbreaks. Results from agricultural settings support this concept (Stamps & Linit, 1998), but evidence from forests is limited. Reeves *et al.* (1983) found greater ground beetle diversity in forests with greater tree diversity in New England forests and Crossley *et al.* (1973) found a greater number of species of arthropods in a mixed hardwood forest than a pine plantation in a given region. The significance of such findings

remains uncertain, however, as only some, if any, of the species identified in the studies may have a role in controlling pest populations.

Stand level species diversity often results from forest management activity, but diversity of forest types across a landscape may also occur. Manipulation may stagger the age structure, and because of the changing dynamics of a particular stand within a forested matrix, an array of forests of varying ages can exist across the landscape. A mosaic of vegetation types, including species both resistant and susceptible to a given pest, can provide a moderating effect for outbreaks. A discontinuous resource may be one way of reducing the extent of outbreaks; however, evidence is lacking to fully support this assumption. The hypothesis that mixed forests, both in terms of species and age classes, are generally more resistant to damaging agents than monocultures and even-aged forests, has yet to be clearly demonstrated. If this supposition is accurate, increasing tree species diversity and increasing diversity across the forested landscape could lead to less frequent and less extensive insect outbreaks. It is not, however, unequivocally clear that mixed stands are much safer than pure stands in North American forests. Contrary evidence from the western United States indicates that multi-storied, uneven-aged stands (a result of selective cutting and fire suppression) has created a forest susceptible to *C. occidentalis*.

Modification of stocking level

Stocking, or stand density, typically reflects stand age, site quality and management history. Individual stem vigour also is a function of density. Overstocked stands show decreasing vigour and eventual declines in growth over time. In part, related to the dramatic changes in natural and anthropogenically influenced disturbance regimes, stocking levels throughout much of North America are not likely to be representative of pre-settlement vegetation. Reducing stocking levels may be one approach to reintroduce vigour into a stand by reducing competition. The task of attaining ideal stocking to optimize vigour presents a challenge, however. Stocking diagrams and stand simulations provide general guidelines, but these are not universally applicable nor are they site specific.

The optimal age of thinning to reduce density varies with the species and site. Competition for water can be severe, as water represents one of many factors that can limit tree growth. One of the major objectives for thinning is to minimize water deficits; therefore on dry sites, forest thinning may take place earlier in a stand rotation than in mesic sites. For shade-intolerant species, light may be the limiting factor and timing and extent of thinning as well as the species removed would correspond to opportunities to optimize light.

Adjustment of age distribution

One of the most dramatic ways to adjust the age distribution of a stand is to use even-aged management, specifically clear-cutting to regenerate the stand. This tactic would be most desirable in stands dominated by preferred hosts of a defoliator and when populations of the insect have developed to outbreak levels, or are likely to do so. This strategy has been identified with eastern

spruce budworm. Stand susceptibility to eastern spruce budworm seems to be strongly related to stand age and size of balsam fir, specifically, oldest stands are the most damaged from defoliation. Adjusting age and structure of regenerating stands has been shown to reduce the susceptibility of forests to eastern spruce budworm defoliation (Miller & Rusnock, 1993).

Site conversion drastically adjusts age distribution and may be appropriate on sites dominated by species not suited to the area. For example, in some parts of the eastern deciduous forests, more xeric sites may become dominated gradually by oak species, whereas these sites may have previously contained a mixture of pine and various hardwood species. On such sites, conversion to more suitable species, which often are less susceptible to forest defoliator pests, would be advantageous. The forests of Michigan exemplify a condition where gypsy moth-preferred species dominate and could be converted to the naturally occurring pine. In places where species shifts have occurred, selective harvesting of the less desirable species would be a way of manipulating both stand composition and age structure.

Selective removal of low vigour trees

Timber stand improvement practices aim to increase the overall vigour of a stand and of individual trees. In stands that have had no previous management, damaged, defective or low-vigour trees may be common. In a traditional sense, improvement cutting benefits the overall vigour of a stand while greatly enhancing the economic value. Improvement cuts represent one of the most common forest management practices in the United States (Smith *et al.*, 1997). A typical approach to using silviculture for managing insects is to use timber stand improvement cutting, and in many cases, judicious improvement cutting can be the best way to preclude outbreaks of bark beetles such as *Dendroctonus* species (Hedden, 1978; Nebeker *et al.*, 1985).

Salvage and pre-salvage cuttings are also common improvement techniques that relate specifically to preventing or minimizing damage from pests. Salvage thinning removes trees that have recently died or whose death is imminent (Smith *et al.*, 1997). Obviously salvage does not directly influence populations of the damaging pests, nor does it directly influence the probability of tree mortality following defoliation. Pre-salvage of individuals likely to die or vulnerable to damage has a sound economic basis as well, as low vigour or dying trees have low growth rates. Moreover, defoliated trees may deteriorate rapidly upon dying, losing economic value.

Timber stand improvement often involves the removal of trees in suppressed or intermediate crown classes that might die from inferior ability to compete for resources such as light or moisture, rather than injurious agents. In such cases, the procedure is simply a thinning rather than a salvage. Nonetheless, the overall effect is likely to increase the vigour of remaining trees, even if the objective does not emphasize reducing the impacts of damaging agents.

Sanitation harvests are a particular type of thinning used as an early response to potential pest and disease problems, and the objective is to remove low vigour, low quality trees. Unlike pre-salvage, however, the intent of sanitation cutting is to remove those trees that may cause the build-up of insect populations,

such as trees that may have been attacked. The most successful sanitation cuttings are those that either interrupt the life cycle of an organism such that pest spread is limited, or those that remove host species such that the susceptibility of a stand is lowered. Although this concept is viable for control of bark beetle damage when trees containing live broods are removed, there has been no demonstration of applicability for controlling defoliator outbreaks.

Rationale and consequences of silvicultural approaches

Reduce the probability of tree mortality from defoliation, i.e. reduce vulnerability

Insect defoliation represents an inciting stress, *sensu* Manion (1981), that has a significant impact on the physiological functioning of the tree and negatively influences tree vigour. Defoliation alone typically does not kill trees directly, but represents one of many factors affecting tree vigour. Studies have determined that tree mortality often represents a multi-decadal process and that losses in tree vigour may be evident long before an insect defoliation episode (LeBlanc, 1998; Pedersen, 1998). It therefore becomes difficult to predict which individual trees will die from insect defoliation, given simple defoliation estimates or vigour estimates at a particular point in time. The lack of predictive ability represents a substantial impediment when attempting to pre-empt mortality.

Changing vulnerability, i.e. the likelihood that trees will die, can be accomplished by either pre-salvage cuttings or conventional thinnings. In many cases, salvage cutting removes trees that have already been killed, and the objective of pre-salvage is to remove trees that are likely to die immediately following defoliation. Basing the criteria for tree removal on obvious signs of reduced vigour may be the only way to determine which trees to cut. However, as pointed out above, trees likely to die may not demonstrate any external loss of vigour. Although pre-defoliation crown condition has been cited as a significant variable to determine tree mortality from gypsy moth (Herrick & Gansner, 1987), effective use of vigour classifications for determining potential mortality has not been demonstrated with defoliators. The most successful use of vigour classes for pre-salvage thinning evaluation has used ponderosa pine prone to *Dendroctonus* bark beetle attacks. Decisions about tree removal are made by evaluating the risk that trees remaining after a cutting cycle will be attacked.

Salvage operations are directed simply by economic, rather than ecological objectives. In salvage operations, economic gain is made from the value of recently killed trees. Salvage operations obviously do little to control or influence populations of defoliators, but have been successful for controlling bark beetles because salvage can remove brood trees that may recruit pest populations via attraction or reproduction. In pre-salvage cutting, trees are harvested before mortality, but the trees removed are those that are likely to die. In white fir forests defoliated by Douglas-fir tussock moth, *Orgyia pseudotsugata*, pre-salvage thinning increased the growth of the survivors compared to survivors in a forest that was not thinned (Wickman, 1988). The effect on survival of trees was not clear, however.

Piene (1989) determined that survival of balsam fir after spruce budworm defoliation was related to the ability of a tree to rapidly increase foliage biomass. Epicormic shoot growth accelerates foliage area and is enhanced by thinning forests.

Reduce the probability of outbreaks and defoliation

Empirical evidence

All defoliators have finite limits to their distribution, determined by host availability, and therefore insects can be managed in part by removal of their preferred species. Indeed, the universal approach to managing forest insects is first to evaluate susceptibility and work toward creating a more 'resistant' forest. Actual empirical evidence to suggest that management aimed at changing species composition could be used to successfully control defoliators is scant. Using aerial photography, Van Raalte (1972) compared a forest over a 24-year span and found that the forest was equally susceptible to spruce budworm defoliation 24 years after initial survey, despite an attempt at reducing susceptibility through cutting. The silvicultural approach emphasized a reduction in the most susceptible species, fir. Kemp (1980) pointed out that despite the publications of several guidelines outlining recommended silvicultural methods for reducing spruce budworm defoliation susceptibility, studies testing the efficacy of these recommendations did not exist.

Obvious conflicts arise when elimination of the susceptible species contradicts economic or management goals of a forest. For example, highly valued oak species dominate the eastern deciduous forest, and any attempt to eliminate the species would be both economically and ecologically disruptive. These species, however, are the primary host of gypsy moth, the major defoliator in eastern north America. Losses of oak in the eastern United States have resulted in increases in species such as maple (*Acer*), which are less susceptible to gypsy moth defoliation. Superficially, it seems likely that forests may become more resistant over time, but the persistence of the species composition and mixture in contemporary North American forests is uncertain. Conversion from oak forests to species that may be more suitable for a given site, e.g. establishment of pine on xeric sites as recommended by Gottschalk (1993), remains a possibility for gypsy moth susceptible forests.

The aim of traditional sanitation thinning is to reduce the spread of particularly damaging agents. Although it may be possible to reduce the extent of defoliation by reducing the dominance of hosts, it is not possible to reduce the actual spread of defoliating insect populations. Sanitation has been invoked in managing defoliators (e.g. Gottschalk, 1993). However, the appropriateness of the technique, if not the name, is questionable.

On an experimental scale Muzika *et al.* (1998) examined the value of imposing thinning on highly susceptible forests in advance of gypsy moth defoliation. During 2 years of severe (> 60% of the canopy) defoliation, results on three pairs of stands (one thinned and one unthinned) varied. Defoliation was identical for one pair of stands; in another pair, the thinned stand had greater defoliation than the unthinned, and on the third pair, the unthinned stand had greater defoliation than the thinned stand.

Mechanistic basis

Influence the quantity and quality of foliage. Despite considerable research on the effect of foliage quality, there is little evidence that variation in foliage quality has an important influence on the dynamics of actual defoliator populations. The dynamics of most defoliator populations appear to be driven by an array of complex interactions among predators, parasitoids and diseases. It is likely that foliage quality is involved in these complex interactions, but the ultimate effect of foliage quality on population dynamics remains obscure. This lack of a clear understanding of the role of foliage quality prevents any manipulation of it as a means to affect outbreaks.

Several silvicultural recommendations for western spruce budworm management have stated that manipulations should promote tree vigour because fast growing, vigorous trees do not provide favourable habitat for the budworm as do stagnated trees (Carlson *et al.*, 1985; Carlson & Wulf, 1989). This conjecture is related to the broader issue known as the 'plant stress hypothesis', which hypothesizes that insect performance and population growth are inversely related to host plant vigour. This hypothesis continues to be a matter of debate and to date this relationship seems to hold true more regularly for bark beetles than for foliage-feeding insects (Berryman, 1972; Mattson & Haack, 1987; Herms & Mattson, 1992). Applying the plant stress hypothesis to western spruce budworm, Wulf & Cates (1987) and Cates *et al.* (1983) concluded that drought and other agents of stress caused an increase in foliage quality and promoted outbreak development. These authors also concluded that, based on these relationships, silvicultural practices that increase tree growth and vigour would reduce forest susceptibility to the western spruce budworm.

Most of the conclusions about the plant stress hypothesis and host suitability are based on studies where the relationship between insect performance and tree stress was inferred from correlation. Experimental work has not consistently supported this conclusion. In studies where tree vigour was manipulated through fertilization and watering, insect performance was lower on the stressed trees, the opposite of what would be expected from the plant stress hypothesis (Clancy *et al.*, 1993, 1995). With fertilizer application on a large scale, Mason *et al.* (1992) found that western spruce budworm was more successful, in terms of biomass, pupal weight, larval densities and egg mass density in fertilized forests. Moreover, the various putative defensive compounds that may have an influence on insect success respond to fertilizer application in very different ways (Muzika, 1993; Kytö *et al.*, 1996; Bjorkman *et al.*, 1998).

There seems to be no scientific basis for the conclusion that silvicultural practices that promote tree growth and vigour will reduce susceptibility to defoliators. In some cases there is evidence that lowering stand density and subsequent increases in growth and vigour may ultimately result in decreased susceptibility. However, there is no evidence that the mechanism behind this relationship is at all related to changes in foliage quality relative to insect growth and development.

Enhance natural enemies/increase naturally occurring insect mortality. Most forest insect pests are characterized by a temporal sequence of several years of low insect abundance interspersed with episodes of high population levels (Berryman,

1987; Myers, 1993; Shepherd, 1977). For many species, there is some uncertainty about exactly what factors maintain populations at sub-outbreak levels for many years but natural enemies, including predators, parasitoids and disease, are considered to be critical to governing low density populations (Varley *et al.*, 1974; Myers, 1993; Berryman, 1995; Royama, 1997).

Many authors have advocated silvicultural procedures that might increase natural enemy abundance and/or activity. The logic behind these recommendations is easy to understand but, as illustrated by the examples given below, the evidence supporting these mechanisms is characteristically scant. The basis for many of these recommendations are studies that find correlations between stand characteristics and the abundance or intensity of a pest mortality agent. Recommendations are then formed by extrapolating these findings to conclude that modification of a stand's characteristics will function to increase this mortality and thereby decrease the frequency of pest outbreaks. However, the population processes that determine the abundance of a pest species tend to be complex and it is probably overly simplistic to conclude that correlation implies causation. It is difficult or impossible to predict how modification of one portion of a complex food-web will affect the dynamics of another part of that web.

The largest source of mortality affecting low-density gypsy moth populations in North America is predation, mostly caused by small mammal predators (Bess *et al.*, 1947; Campbell *et al.*, 1977; Elkinton *et al.*, 1996; Grushecky *et al.*, 1998; Jones *et al.*, 1998). Variation in predation rates is closely tied to temporal and spatial patterns of gypsy moth abundance. Declines in predator abundance and predation intensity are associated with the temporal release of gypsy moth populations from low to high densities (Elkinton *et al.*, 1996; Jones *et al.*, 1998). Gypsy moth outbreaks are most common in forest stands where small mammal abundance is comparatively low (Bess *et al.*, 1947; Smith, 1985; Yahner & Smith, 1991; Liebhold *et al.*, 1998a). North American gypsy moth larvae feed during the night and seek resting sites, such as bark crevices, during the day. These resting sites may function as refuges where larvae escape predation, and several authors have found that gypsy moth outbreaks are more common in forest stands where these refuges are most common (Campbell *et al.*, 1975; Valentine & Houston, 1979).

Several authors have advocated silvicultural practices that promote predation of gypsy moths by small mammals. Many of these recommendations have focused on the removal of large trees with deep bark fissures and dead branches which serve as refugia from predators (Bess *et al.*, 1947; Gottschalk, 1993). One element of these recommendations is that by removing trees containing many resting sites in the overstory, larvae seeking resting sites will be forced to rest low on tree boles or in the forest litter, where predation rates are likely to be higher. This reduction in refugia can be accomplished by removal of trees with poor crown conditions during sanitation thinnings (Gottschalk, 1993).

Although the logic behind these recommendations is understandable, the available evidence testing these activities does not appear to support its application. Grushecky *et al.* (1998) found no difference in predation levels between stands where a sanitation thinning was performed and predation in nearby unthinned stands. Liebhold *et al.* (1998b) collected partial life-

table data in these same stands and reported no significant differences in generational survival or mortality caused by parasitoids and disease in thinned vs. unthinned stands. Although there were some decreases in gypsy moth densities in thinned vs. unthinned stands, these differences appeared most likely to be due to simply a reduction in available foliage caused by the thinning rather than any enhancement of natural enemy abundance or activity.

Predation by ants and birds is a major source of mortality in low-density western spruce budworm populations (Campbell *et al.*, 1983). Carlson & Wulf (1989) advocated the use of even-aged silvicultural methods (i.e. clearcut, seed-tree and shelterwood regeneration cuts) as a method of reducing forest susceptibility to the western spruce budworm, in part because the result is a young forest in which the foliage is closer to the ground where they believe predation by vertebrate predators would be greater. We are aware of no studies indicating that predation on pupae is greater for individuals located near the ground and/or indicating that predation is greater on populations in young trees. Thus, there seems to be no evidence supporting the claim that thinning can enhance predator activity. Although Garton & Langelier (1985) found that foliage gleaning birds were most abundant in early successional stands in the mixed conifer forests of Washington State, and suggested that the potential for avian predation of western spruce budworm was greatest in these stands, no measurement of avian predation was made.

Western spruce budworm disperses during three distinct periods each generation: first instars disperse following egg hatch, second instars hatch following emergence from overwintering sites in the spring, and adult females disperse. Mortality during spring dispersal appears to be the greatest and most variable of the three dispersal phases (Campbell, 1987). Dispersal losses are thought to be greatest in sparsely stocked stands because randomly dispersing individuals are less likely to land on hosts and are more likely to fall to the forest floor where mortality may be intense (Beckwith & Burnell, 1982). Based upon this relationship, reduction in stand density through forest thinning is often recommended as a silvicultural treatment to reduce susceptibility to western spruce budworm (Carlson *et al.*, 1985; Schmidt, 1986; Carlson & Wulf, 1989). However, there is little or no evidence actually supporting the relationship between stand density and spring dispersal mortality for the western spruce budworm. Instead these conclusions are based upon early work with the eastern spruce budworm, *C. fumiferana*, in which Mott (1963) found mortality of dispersing second instars to be related to stand density. Jennings *et al.* (1986) also observed this inverse correlation between stand density and dispersal-related mortality of *C. fumiferana*, but they concluded that it was a small effect and '... such losses may be insignificant in terms of overall generation survival.' Thus, there is little evidence for a strong relationship between stand density and dispersal mortality for *C. fumiferana* and no evidence for *C. occidentalis*. Despite this lack of evidence, the recommendation to reduce stand density as a means of lowering forest susceptibility to western spruce budworm may be legitimate, based upon empirical observation of decreased defoliation as a result of thinning (Carlson & Wulf, 1989). However, there is no scientific basis from which to conclude that the mechanism behind this effect is reduction of dispersal mortality.

The evidence supporting the use of silviculture to promote naturally occurring mortality of defoliator populations is sparse or lacking. Even though there may be observations that outbreak frequency is related to the abundance of a specific natural enemy or some other characteristic of a stand, this does not necessarily mean that stand manipulations to increase this mortality will necessarily reduce the outbreak frequency in that stand. Most defoliator species exist in a highly complex trophic web with their hosts and natural enemies. As a result of this complexity, manipulation of the habitat to enhance a single part of this food web may not always result in the expected outcome. In one large-scale experiment, Mason *et al.* (1992) examined mortality of western spruce budworm from parasitoids and found that parasitism of both larvae and pupae was reduced when an *Abies* dominated forest was fertilized in an attempt to invigorate the stand. However, thinning the stand did not influence parasitism (Mason *et al.*, 1992).

Conclusions

Opportunities exist for indirectly influencing the effects of defoliators by ecologically based silvicultural activity, but influencing actual populations of defoliators appears less likely. Within silvicultural guidelines, specific objectives to reduce vulnerability or susceptibility may represent appropriate approaches, but must conform to broader objectives that also include economic and social considerations. In particular, the financial considerations of intermediate treatments, which constitute the majority of silvicultural applications to managing defoliators, represent a significant factor in decision making.

The following considerations must be acknowledged when attempting to use silviculture to either influence populations of defoliators or moderate the potential effects of the defoliators:

1. Silviculture may be used to affect vulnerability via removal of the least vigorous trees. However, this may be impractical owing to the difficulty of identifying trees most likely to die.

2. There is little or no evidence that silviculture can be used for altering susceptibility other than by eliminating host species. In some cases, this approach represents an ecological and economic dilemma.

3. Relationships between defoliator populations and natural enemies and habitat are complex and difficult to predict. Relationships that are inferred from correlative studies cannot be used to predict outcomes of manipulations.

4. The use of silviculture to restore forests to overstorey composition representative of pre-settlement forests may not always result in lowering the impact of defoliators. The balance of nature hypothesis may represent a simplistic approach of limited value in managing forest defoliators.

5. Attempts to use plant stress hypothesis, tree vigour or similar approaches for managing forest defoliators based on foliage quality are inappropriate guides. Susceptibility to defoliation seems unchanged or, at best, unpredictable in light of these characteristics, and has not been shown to influence insect populations.

Most silvicultural prescriptions for control of defoliators and their damage appear to be based on correlations of likely effects of thinning, rather than experimental manipulation. For most defoliating insects, it is possible to identify stand characteristics

that are correlated with defoliation frequency or intensity. Recommendations based on such characteristics may be flawed, however, in many cases, primarily because the correlation between stand characteristics and defoliation may not be the result of direct causal relationships. Clearly, there is a need to apply experimental manipulation as a way to develop and test silvicultural methods.

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