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Ecological strategies of forest insects: the need for a community-level approach to reforestation

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Application. Reforestation practices, such as site preparation, seedling species, planting method, brush control and precommercial thinning, affect seedling susceptibility, attractiveness, and exposure to insects and disease. Therefore, these practices have the potential to mitigate insect and pathogen activity over long time periods, perhaps entire rotations. Effective use of these practices for forest protection requires a community-level perspective in order to anticipate potentially destructive responses by various insects and pathogens, even those not previously recognized as potential pests. This prediction will allow modification of timing or techniques, that reduce or prevent the risk of insect or pathogen population growth, in situations in which the risk of a destructive response is high.

Abstract. The traditional, single-species approach to forest pest management is considered in light of the range of ecological strategies respresented in forest arthropod communities. Insect population growth and impact depend on host variables subject to silvicultural manipulation, especially during early stages of forest development, but silvicultural practices often induce undesirable responses from non-target insect populations. A suggested approach to forest pest management involves consideration of arthropod community structure, life history traits, and interactions among arthropod and plant species in order to anticipate insect responses and refine silvicultural recommendations accordingly.

Introduction

Protection of forest resources from unacceptable levels of damage by insects and pathogens is a major goal of forest management. Damage by these organisms typically has the most serious consequences during early tree growth because damage at this time frequently affects growth rate and form (thus competitive ability) as well as survival.

Traditionally, forest protection has taken the form of remedial controls, especially pesticides, which are implemented only after some evidence of damage. Remedial options, however, are often too late to prevent serious losses, do not alter the conditions predisposing forests to insect or pathogen activity, and often disrupt the forest community in ways that promote continued pest activity. The costs of remedial options have risen with increased costs of material, labor, and litigation prompted by the biological and environmental hazards of chemical options.

These considerations have led to increased attention to silvicultural options for forest pest control. Silvicultural treatments affect tree and forest suitability for herbivorous insects (Bogenschütz and König 1976; Coulson and Witter 1984; Schowalter and others 1986a). Because silvicultural activity is concentrated in reforestation stages of management (e.g., site preparation, seedling species, planting method, brush control, precommercial thinning), these practices have the potential to mitigate insect and pathogen activity over long time periods, perhaps entire rotations. However, insects and diseases have received attention from forest managers and researchers only as individual species became economically important. Responses of non-target insects and diseases, which often respond differently to experimental treatments, have received little attention (Strong and others 1984).

The purpose of this paper is to demonstrate the need for a community-level approach to forest pest management by considering the variety of ecological strategies (i.e., behavioral responses to environmental cues) represented in forest arthropod communities. I will emphasize the variety of insect responses to given silvicultural practices and develop a protocol for using arthropod community data to anticipate and mitigate insect responses to silvicultural activities.

Factors influencing insect populations

Disturbance theory has provided a basis for understanding insect responses to silvicultural practices (Schowalter 1985). Disturbances are characterized by type, intensity, frequency, scale and reliability. Disturbance events, including climatic fluctuations, are a natural component of all ecosystems and have shaped the ecological strategies of constituent species populations (Pickett and White 1985). Forest insects show adaptive responses to disturbances as reflected in factors such as host nutritional quality, abundance, and apparency.

Host nutritional quality affects insect host choice, developmental rates, survival and reproduction. The literature on insect-plant interactions is replete with examples of the effects of nutrient (especially N, P, and K) and defensive compound (especially terpene, phenol and alkaloid) concentrations on insect feeding, growth, survival and reproduction (Harborne 1982; Hargrove and others 1984; Hedin 1983; Mattson 1980; Schowalter and others 1986a). Balances among these various nutritional factors appear to be more important to herbivory than are absolute concentrations. For example, high foliar N can compensate for high phenolic content, due to exhaustion of protein-complexing capacity (Fox and Macauley 1977). High K concentration may interfere with phenol synthesis (Király 1976). Such conditions increase host suitability for herbivorous insects.

Changes in nutrient balances in plant tissues can result from disturbance-induced changes in nutrient availability. Nutrients can be mobilized into soil solution or immobilized onto particle surfaces as a result of changes in precipitation pattern. Fire results in rapid mineralization of most elements and in export of volatile elements such as N and P. Changes in nutrient availability force changes in plant allocation patterns (Waring 1982). C and N allocation to defensive compounds may be governed by relative amounts of other nutrients (Mattson 1980; Schowalter 1981; Tuomi and others 1984; Waring 1982; Waring and Pitman 1983).

Resource abundance in time and space determines the probability of colonization and the extent of population growth by insects. Bark beetle outbreaks, for example, depend to a large extent on a sufficient concentration of stressed or injured trees to minimize dispersal-related mortality and permit small populations to reach numbers capable of mass attacking more resistant trees (Coulson and Witter 1984; Furniss and Carolin 1977; Schowalter 1985; Schowalter and others 1981b; Waring and Pitman 1983).

Resource apparency is a measure of perception by dispersing insects. Forest structure can mask available resources in at least three ways. First, the proximity of available resources to insect population sources determines the ability of dispersing insects to perceive and reach those resources. Apparency decreases as the distance, in time and space, between available resources and insect populations increases. Although many insects are strongly attracted to host cues, the attractiveness of these resources decreases as the time or distance between tree decline and insect dispersal increases (Furniss and Carolin 1977; Schowalter 1985; Witcosky and others 1986).

Second, the abundance of non-host trees influences the visual and chemical perception of interspersed hosts. Volatiles emanating from non-hosts may interfere with insect orientation toward sources of host cues (Courtney 1986; Schowalter and others 1986a; Visser 1986). Host-seeking insects may succumb to various mortality factors before discovering rare hosts (Courtney 1986).

Finally, forest spatial structure influences ventilation, temperature profiles and other variables critical to insect perception of host cues (Fares and others 1980; Schowalter and others 1986a). Forest edges, in particular, can disrupt host selection behavior by creating a barrier or filter to dispersing insects (Fares and others 1980; Pitman and others 1982; Schowalter and others 1986a) or can provide a focus for host-seeking insects by creating exposed resources (Schowalter 1985; Schowalter and others 1985; Witcosky and others 1986). The influence of forest structure on forest temperature, humidity and light conditions also affects insect survival and reproduction (Schowalter and others 1986a).

Forest insects show a variety of adaptive responses to changes in forest conditions. Some insects, such as aphids and adelgids, are characterized by rapid population growth and dispersal which permit a rapid response to seasonal availability of young, succulent plant tissues. Defoliators and bark beetles exploit resources available on an annual basis and show slower responses to changing conditions (Schowalter 1985). Many insects disperse randomly and rely on large numbers of dispersants to locate scattered resources whereas other species, notably wood-borers, are attracted from considerable distances to sources of smoke or host volatiles emanating from burned or injured hosts (Furniss and Carolin 1977; Mitchell and Martin 1980; Schowalter 1985; Witcosky and others 1986).

Insect responses to changes in host nutritional quality are equally varied. Although plant defenses generally have a negative effect on insect feeding, many insects appear capable of avoiding or circumventing plant defenses (Berenbaum 1980; Carroll and Hoffman 1980; Heinrich and Collins 1983). Some are able to digest plant defenses to satisfy nutritional requirements (Bernays and Woodhead 1982; Schopf and others 1982).

The results of fertilization experiments underscore the variety of insect responses to changes in nutrient regime. Most insects apparently are N-limited (Mattson 1980), but insect responses to forest fertilization have been both positive and negative. Plant allocation of subsidized nutrients among growth, storage and defensive metabolic pathways likely mediates insect responses to fertilization (Schowalter and others 1986a; Tuomi and others 1984; Waring 1982).

Insect responses to silvicultural practices

The resource availability variables critical to insect populations are clearly subject to silvicultural manipulation, especially during reforestation. Practices which influence seedling condition and exposure to insects or diseases are particularly important. However, the responses of the various insect species in the community can be quite different, as shown by the following examples.

Tree species, genotype or age-class composition govern host abundance and apparency for insects. Historically, changes in forest composition to accomplish timber management objectives often predisposed forests to increased insect activity (Schowalter and others 1981a; Stoszek and others 1981). The replacement of longleaf pine (*Pinus palustris* Mill.), which is resistant to the southern pine beetle (*Dendroctonus frontalis* Zimm.), with loblolly pine (*Pine taeda* L.), which is generally less resistant to southern pine beetle, over large portions of the southern U.S. probably contributed to recent outbreaks of this insect (Schowalter and others 1981a). Similarly, the practice of growing Sitka spruce (*Picea sitchensis* (Bong.) Carr.) in open even-aged plantations (rather than under the closed canopy conditions to which spruce is adapted) provided an abundant and apparent resource for the white pine weevil (*Pissodes strobi* (Peck)) (Furniss and Carolin 1977). Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) seedlings in nurseries in western Oregon show susceptibilities to lygus bugs (*Lygus hesperus* Knight) related to seed source (genotype) and age (Schowalter and others 1986b). Trees become susceptible to different insects at different stages of development (Nielsen and Ejlersen 1977; Schowalter 1985; Schowalter and others 1986a), as a given plant passes through "windows" of susceptibility. Promotion or selection of virtually any tree species, genotype or age-class for management purposes could result in exploitation by some members of the associated fauna.

Practices which influence seedling exposure to population sources of potentially destructive insect species can significantly affect seedling growth and survival. Although nursery sites have not been selected with regard to anticipated insect activity, their location within the landscape mosaic clearly affects insect populations. Nurseries located within agricultural zones are removed from population sources of forest insects, but are vulnerable to host-switching by agricultural insects, such as lygus bugs. Nursery proximity to alfalfa fields and the timing of alfalfa harvest relative to conifer seedling growth phenology have been found to influence lygus bug (*L. hesperus*) activity in conifer nurseries in western Oregon (Schowalter and others 1986b, Schowalter and J.D. Stein unpubl. data). Although such insects have not been forest pests, the increasingly popular practice of planting clover as a forage crop in multiple-use forests in the U.S. could provide lygus with a host corridor into forested areas, thereby increasing exposure, to this insect, of seedlings in reforested sites.

Precommercial thinning is widely practiced to increase tree spacing and reduce competition at the canopy-closure stage (Witcosky and others 1986). Thinning has proven to be an effective means of managing insects sensitive to tree spacing or tree competitive stress. The southern pine beetle and the mountain pine beetle (*Dendroctonus ponderosae* Hopkins) can be controlled by spacing trees at least 6 m apart, the effective limit to pheromone communication (Larsson and others 1983; Lorio 1980; Mitchell and others 1983; Schowalter and others 1981b). Some defoliators also are sensitive to tree spacing. Host-switching by gypsy moth (*Lymantria dispar* L.) can be reduced by increased spacing between hosts (Lance 1983). Silver-spotted tiger moth (*Lophocampa argentata* (Packard)) larvae introduced onto 8- to 10-year-old Douglas-fir at the H.J. Andrews Experimental Forest in western Oregon were recovered 3-4 times more often from nearest-neighbor Douglas-fir within 3 m of the nearest source compared to nearest-neighbor Douglas-fir further than 5 m (Schowalter unpubl. data). Thinning also may influence insect survival and reproduction through changes in host condition resulting from reduced competition (Mitchell and others 1983).

However, mechanical thinning of Douglas-fir has been found to provide a source of attractive host volatiles which increases the abundance of stump- and slash-colonizing insects, including the root bark beetle *Hylastes nigrinus* (Mannerheim), a vector of black-stain root disease fungus (*Ceratocystis wageneri* Goheen and Cobb) (Witcosky and others 1986). The time of thinning influences the responses of various insects, depending on their life history characteristics (Witcosky and others 1986). Other reforestation practices, such as site preparation, planting techniques and brush control, which affect seedling condition and forest spatial structure are equally likely to induce different responses by various insect species and disease agents.

Community-level approach to management

The preceding discussion illustrates the variety of insect responses to host conditions and silvicultural manipulations. The range of ecological strategies represented by the multitude of species in forest arthropod communities suggests that silvicultural practices employed to reduce populations of selected insect species will likely promote population growth of others. Silvicultural manipulation without regard to the capacity of non-target insect or diseases to respond may create a serious situation.

The concept of ecological equivalence is helpful in considering artthropod community structure. Communities characterizing different sites and biomes differ in species composition but show similar functional group (guild) structure such that community interactions and responses to forest manipulation may be widely predictable. For example, Schowalter and others (1981c) and Schowalter (unpubl. data) found similar shifts in arthopod community structure following clearcutting of southeastern mixed hardwood forests (Coweeta Hydrologic Laboratory, North Carolina) and western coniferous forests (H.J. Andrews Experimental Forest, Oregon). At both sites, functional group dominance shifted from defoliators to phloem-feeders following clearcutting and reforestation, despite differences in the plant and arthropod taxa involved. These results suggest that predictable trends in arthropod community organization occur during forest development (Schowalter 1985).

Activities of a particular functional group can predispose affected hosts to other functional groups. Elevated aphid activity appears to predispose plants eventually to increased defoliator activity which further predisposes plants to increased bark beetle activity (Schowalter 1985). Functional responses to changes in host conditions may contribute to regulation of nutrient cycling processes and to long-term site productivity (Mattson and Addy 1975; Schowalter 1981, 1985; Seastedt and Crossley 1984; Swank and others 1981; Wickman 1980; Zlotin and Khodashova 1980), further underscoring the need to manage forest insects within an ecosystem context.

Surprisingly little work has been directed toward understanding the dynamics of forest arthropod communities. Most forest entomological studies have focused on one or a few species as these became economically important (Schowalter and others 1986a; Strong and others 1984). The critical role played by the arthropod community in promoting or mitigating outbreaks of potentially destructive species (Atsatt 1981; Schowalter 1985; Tilman 1978) and the probability of induced responses of non-target insect populations to silvicultural treatments make a community-level approach to silvicultural management of forest insects imperative.

A protocol for a community-level approach to forest protection requires a thorough knowledge of arthropod community structure, life history traits, and interactions among arthropod and plant species. Such knowledge would permit anticipation of undesirable consequences of silvicultural manipulation and consideration of alternative strategies to accomplish forest management goals. For example, thinning, prescribed burning and fertilization could all contribute to the management goal of optimizing tree condition and growth but each would induce different responses from various insect species. The timing of silvicultural treatment also affects insect responses (Witcosky and others 1986).

Reforestation practices dictate the initial stand conditions which influence future insect activity and final selection of crop trees. Whether slash is burned, scattered or windrowed determines site spatial characteristics that influence subsequent plant growth, forest spatial structure, and insect activity. The tree species composition of the replanted stand influences arthropod community structure and establishes limits to the mitigation of incipient insect outbreaks through selection of crop trees during precommercial thinning. Establishment of monocultures allows no flexibility in the subsequent selection of crop trees if damage by insects or disease occurs; establishment of polycultures reduces insect population growth (Risch 1981) and increases the likelihood that some trees survive to harvest. Hence, the reforestation stage could provide a focus for management of forest insects over entire rotations.

Conclusions

Forest insect population growth and impact depend on host variables subject to silvicultural manipulation, especially during the reforestation period.

Silvicultural treatments can promote or prevent insect population growth depending on the ecological strategies represented in the forest arthropod community. Forest management or pest control strategies that fail to address underlying causes of insect population outbreaks or that fail to anticipate responses of non-target insect species will be ineffective in protecting forest resources in the long term.

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