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1254

ROLES OF INSECTS AND DISEASES IN SUSTAINING FORESTS[1]

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ABSTRACT: Insects and diseases only recently have been recognized as contributors to forest health and productivity. Epidemics of these organisms are triggered by factors that increase host susceptibility and availability and could be used as indicators of declining forest health and diversity. Increased productivity often follows pruning, thinning and increased soil fertility caused by insects and pathogens, compensating over time for the more conspicuous tree growth losses and mortality. Increased diversity results from modification of environmental conditions or habitat and food resources. Increased diversity inhibits continued insect and disease epidemics, increases nutrient acquisition and cycling, and stabilizes forest species interactions. Forest health and productivity may be enhanced for decades after epidemics.

INTRODUCTION

Forest insects and pathogens generally have been studied with respect to their perceived roles as pests causing reduced timber and fiber production. An alternative view recognizes the contributions of these organisms to the structure and productivity of forests valued by early settlers and resource managers. Research during the past decade has indicated that forest insects and diseases contribute substantially to forest diversity and soil fertility and to long-term forest health and productivity. As forestry becomes more broadly concerned with long-term forest health and sustainable resource production, insect and disease contributions to soil fertility and biodiversity must become better understood.

FACTORS AFFECTING INSECT AND PATHOGEN POPULATIONS

Forest insects and diseases are highly responsive to changes, especially imbalances, in forest condition. Changes in host biochemistry, density, and apparency within stands and across landscapes are particularly important factors affecting insect and pathogen epidemiology.

Host Biochemistry

Changes in host biochemical factors affect suitability for insect or pathogen growth and development. Therefore, changes in nutrient cycling processes that affect nutrient availability for plant uptake affect plant susceptibility.

Plants allocate available resources (water, carbon dioxide, nutrients) on a priority basis to various metabolic pathways (e.g., Waring and Schlesinger 1985). Foliage and root production are high priorities because these tissues are essential to resource acquisition and photosynthesis. Storage, such as in wood, is a lower priority, despite its importance to timber production, and is reduced under conditions of resource limitation. Defensive compounds, such as terpenoids and

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phenols, are expensive to synthesize in terms of both energy and resources and also may be reduced under conditions of stress or resource limitation. Consequently, because defensive compounds limit host colonization to specialized insects or pathogens capable of energy-expensive detoxification or avoidance mechanisms, unhealthy trees are more vulnerable to these organisms.

Density

Density of particular tree species affects the ability of insects and pathogens to reach suitable trees. Therefore, factors increasing the density of a particular tree species will increase the likelihood of eventual outbreaks of insects or pathogens.

Survival of dispersing insects or pathogens declines with distance from a population source, due to limited capacity for dispersal. If hosts are closely spaced, more insects or pathogens will be capable of colonizing new trees. For example, southern and mountain pine beetle infestations can be prevented by spacing pine trees at least 6 m (20 ft.) apart (Schowalter et al. 1981, Sartwell and Stevens 1975). Density of suitable stands at the landscape level has a similar effect on regional populations of forest insects and pathogens.

Apparency

Apparency is a function of chemical or other cues indicating the presence of a particular tree species and determines the ability of host-seeking insects to discriminate a host from surrounding vegetation. Factors that increase the apparency of particular host species increase the likelihood that insects will find suitable hosts.

All plant species produce a characteristic chemical "fingerprint" that is carried on the airstream. Insects orient toward hosts by following the concentration gradient in plumes of host chemicals. In forests composed of a few related species, the aerosol includes primarily plumes of host chemicals, and insects quickly perceive their hosts. In diverse forests, plumes of non-attractive or repellent chemicals produced by non-hosts mix with host chemicals downwind and disrupt insect orientation to hosts (Hunter and Aarssen 1988, Visser 1986). For example, western redcedar bark contains verbenol (an attractant) and verbenone (a repellent) that likely influence Douglas-fir beetle orientation to Douglas-fir (which does not contain either compound) in mixed conifer forests (Schowalter et al. 1991b).

CONTRIBUTIONS TO FOREST HEALTH AND PRODUCTIVITY

As a result of insect and pathogen responses to changes in host biochemistry, density and apparency, epidemics are most likely to occur in forests, at both stand and landscape levels, that are unhealthy, especially if tree diversity is low. Epidemics frequently reflect changes in soil conditions and vegetation diversity resulting from fire suppression or forest conversion. Consequently, these organisms can be viewed as indicators of poor health or insufficient diversity and outbreaks exploited as early warning of forest decline. However, these organisms also contribute to the remedy of these conditions through contributions to soil fertility and diversity.

Contributions to Soil Fertility

Insect herbivore and pathogen contributions to soil fertility and forest productivity have been recognized only recently, but likely are capable of alleviating stresses imposed by nutrient limitation. Mattson and Addy (1975) were among the first to propose that herbivorous insects could contribute to sustained forest productivity through stimulation of nutrient cycling. Wickman (1980) subsequently found that defoliated white fir and intermixed pines showed elevated productivity during the decades following defoliation by Douglas-fir tussock moth, compared to non-defoliated stands. The mechanisms underlying this compensatory growth were not clear, but likely included increased resource availability through nutrient cycling, and reduced competition through thinning. Alfaro and MacDonald (1988) similarly found that defoliated Douglas-fir in stands with no mortality showed compensatory growth during the subsequent fifteen years and that the increase in post-defoliation growth was positively related to the degree of defoliation. These results suggested that resources released by removal of older foliage became available for production of new tissues, i.e., a pruning effect.

Few studies have examined effects of manipulated herbivore abundances on nutrient cycling processes. Kimmins (1972) introduced sawfly larvae onto young red pine and observed a significant increase in Cs-134 flow from foliage to litter through leaching and litterfall. Seastedt et al. (1983) reported that reducing defoliation, from 4-10% to less than 2% using carbaryl, of young black locust and red maple significantly reduced leaching and litterfall contributions of potassium to forest soils, but did not affect litter decomposition or tree growth.

Schowalter et al. (1991a) designed a study to examine effects of manipulated defoliator abundance on Douglas-fir growth, nutrient turnover and litter decomposition over a three-year period in a young stand in western Oregon. Defoliators were introduced at 0 - 0.6/g foliage, causing 0 - 20% foliage removal. All other herbivores were removed manually to prevent confounding effects of insecticides on nutrient or litter dynamics. Sapling growth and foliage production were estimated from regression based on stem diameter at the root collar. Proportional collectors under each sapling intercepted 10% of the crown perimeter. Litter decomposition was measured using litterbags containing bulk senescent needles.

Precipitation volume and litterfall mass reaching the forest floor were doubled during the growing season at 20% defoliation compared to non-defoliated saplings. Inputs of nitrogen, potassium and calcium to the forest floor were increased to 15-20% of total inputs, compared to non-defoliated saplings.

Sapling growth was not affected by defoliation, indicating that resources were adequate for compensatory growth over this range of defoliation. Decomposition rate also was not significantly affected, although needles lost only 30% mass after three years.

Bark and wood boring insects and associated microorganisms (including tree pathogens) also contribute substantially to soil fertility. The nutrient-rich phloem of both conifers and hardwoods is completely mined and decayed after two years on the ground, providing inputs of potassium, phosphorus and calcium an order of magnitude higher to soil under logs compared to soil under leaf litter (Schowalter in press). Wood boring insects are instrumental in inoculating wood with a community of bacteria, yeasts, and saprophytic fungi that interact to produce vitamins and new carbohydrate resources (Blanchette and Shaw 1978, Schowalter et al. 1991b). Bark beetles also introduce nitrogen-fixing bacteria into their tunnels (Bridges 1981). Nitrogen-fixation in decomposing wood represents a substantial source of this limiting nutrient in forests (Schowalter et al. 1991b, Sylvester et al. 1982).

Contributions to Forest Diversity

Insects and pathogens also contribute to forest diversity in a variety of ways. The importance of maintaining diversity often is not appreciated, especially where maximization of commercial resources is a goal, but if even pest species can contribute to soil fertility and long-term forest health, we can only speculate on the contributions of the myriad of unstudied species to forest health. Furthermore, diversity at both stand and landscape levels results from insect and pathogen outbreaks and provides biological barriers to continued development and spread of insect and pathogen epidemics.

Forest insects and pathogens typically are restricted to scattered injured and stressed hosts susceptible to colonization by these organisms. Selective consumption, death and decomposition of these trees opens the canopy and provides space, light, nutrients and germination sites for a variety of other plant species. Such canopy gaps and/or log substrates provide light and nutrient resources essential for the development of some plant species, including hemlocks. Different tree species also contribute differently to light penetration and soil fertility. Because various plant species intercept light or use nutrients differently, trees of different species compete less intensely for these resources than do conspecific trees. Furthermore, some plants concentrate specific nutrients in their litter, e.g., alders have nitrogen-rich leaf litter; western redcedar has calcium-rich leaf litter (Kiilsgaard et al. 1987). Consequently, diverse forests have richer, less acidic, and more biologically-active soils than do pine or Douglas-fir monocultures.

Dead or dying trees, and the insects and fungi they harbor, provide necessary food and habitat resources for a variety of wildlife species. Schowalter and Sabin (1991) found that three litter arthropod species were significantly more abundant under defoliated Douglas-fir saplings compared to undefoliated saplings. The factors responsible for this response were not clear but included altered environmental conditions, resulting from increased light and water, and nutrient resources in litter, defoliator feces and tissues. Because of the importance of litter arthropods to decomposition processes, community responses to defoliation likely influence the rate of mineralization.

Insect and pathogen epidemics, or subsequent fire, in dense, unhealthy forests create extensive areas of tree mortality and increase landscape-level stand diversity. Such areas regenerate trees in the seed shadows of surviving trees and provide resources for early successional herbs, shrubs, trees, and associated animals, increasing stand-level diversity. In fact, the interactions between forest insects, pathogens, and fire were responsible for the structure and functional integrity of forests prior to management. Periodic fire favored fire-tolerant species and ensured mineralization of litter, especially decay-resistant pine and Douglas-fir litter. Manipulation of species composition and fire, and resulting imbalances in resource supply and demand, may be largely responsible for chronic insect and pathogen outbreaks in western forests.

Increased stand and landscape diversity inhibits continued insect and pathogen spread, as discussed above. Similarly, epidemics of conifer insects or pathogens are inhibited by natural succession. For example, Pacific Northwest forests are susceptible only during the mid-successional stage when Douglas-fir becomes dominant; outbreaks would be ended naturally by the declining host availability in more diverse old-growth (>250 year old) and regenerating forests. By contrast, the virtual elimination of early and late successional stages, as well as non-commercial species, in managed forests harvested every 50 - 80 years has led to continuous epidemics of bark beetles, western spruce budworm, black-stain root disease and root rots (Franklin et al. 1989, Hansen et al. 1988). Stopping these pest cycles requires disruption of this continuous supply of hosts, i.e., reestablishment of the natural barriers provided by diversity at both stand and landscape levels.

CONCLUSIONS

Despite limited study of the contributions of insects and pathogens to forest health and long-term productivity, accumulating evidence suggests that these organisms respond to declining forest health and diversity and function to increase soil fertility and diversity. Although growth reduction and tree mortality are conspicuous results of insect and disease epidemics, contributions to soil fertility and species diversity have been shown to increase productivity and stabilize species interactions for decades following outbreaks of these organisms. These roles likely minimize forest stagnation by providing for constant tree and species turnover and rejuvenation, thereby buffering forests from effects of environmental change. Current models for predicting impacts of insects and diseases on forest resources do not address these positive roles. Further study of insect and pathogen contributions to forest health and long-term productivity is essential if we are to achieve sustainable forestry goals.

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