STAND AND LANDSCAPE DIVERSITY AS A MECHANISM OF FOREST RESISTANCE TO INSECTS

T. D. SCHOWALTER

Department of Entomology, Oregon State University, Corvallis, Oregon 97331-2907, USA

INTRODUCTION

Plant vulnerability to herbivorous insects depends on both suitability (determined by nutritional and defensive factors) and exposure (determined by plant location relative to herbivore population sources). The importance of plant biochemical defenses against herbivores has received much attention (Rosenthal and Janzen 1979, Cates and Alexander 1982, Harborne 1982, Coley *et al.* 1985). Herbivore populations typically are aggregated on particular trees that often differ from their neighbors in chemical composition or other factors that indicate greater susceptibility to herbivores (Alstad and Edmonds 1983, Lorio 1993). Plant compounds are important as feeding deterrents or toxins for herbivores unable to adapt appropriate avoidance or detoxification mechanisms. However, herbivores have adapted various strategies for avoiding or detoxifying the chemical defenses of their hosts (Bernays and Woodhead 1982, McCullough and Wagner 1993).

Variation in suitability among plants may be important both for reducing selection for herbivore adaptations and for minimizing host exposure to adapted herbivores. Herbivores seeking new hosts must both distinguish and be able to reach suitable hosts. Therefore, plant suitability, apparency, and distance from herbivore populations function interactively to determine colonization by herbivores (Courtney 1986, Schowalter and Stein 1987).

My objective in this paper is to evaluate plant diversity as a means of reducing host exposure to herbivores. I will consider diversity at the level of genetic variability within a particular species, and at the level of stand and landscape variability in community composition. These three levels constitute a nested hierarchy of diversity that can limit population growth of herbivores within stands and across landscapes.

Genetic Diversity Within Species

Populations of plants typically vary in genotype and susceptibility to herbivores. Herbivores usually prefer, and show highest survival and reproduction on, plants or plant species whose defenses can be tolerated or detoxified, given that these plants can be discovered (Courtney 1986). Most herbivores are specialists on relatively few (usually related) plant species, because avoidance behaviors and detoxification mechanisms require an appropriate genetic template and are energetically expensive. Insects that feed on several plant species with distinct resistance mechanisms are subject to different selective forces on each host and may develop sibling species as host-specific demes diverge (Alstad and Edmonds 1983; Via 1990, 1991; Bright 1993). Conversely, stands of plants with similar resistance mechanisms permit rapid adaptation by herbivores.

Genetic diversity within a plant species confers resistance to herbivores by presenting a matrix of susceptible and non-susceptible hosts, but genetic effects are difficult to evaluate in natural forests where genotypic effects can be confounded by plant proximity to herbivore population sources or other factors varying geographically. Conifer seed orchards and nurseries provide an opportunity to examine the importance of plant genotype independent of plant location. Herbivore impact on different genotypes replicated throughout a seed orchard or nursery can be compared to assess the extent to which injury is related to genotype.

Schowalter and Haverty (1989) examined seed losses to two insect species, *Contarinia oregonensis* and *Megastigmus spermotrophus*, in a *Pseudotsuga menziesii* clonal seed orchard and in a progeny plantation in western Oregon. The various clones or families showed different degrees of resistance to the two insects (Table 1). Resistance to one insect species was

Table 1.—Percentage seed lost to two cone and seed insect species among offspring of selected parental crosses in a *Pseudotsuga menziesii* progeny plantation in western Oregon. Means above the diagonal are seed losses to a midge, *Contarinia oregonensis*; values below the diagonal are losses to a chalcid, *Megastigmus spermotrophus*.

Parent	x Parent 1	2	3	4	5	6	7	8	9	10	11	12	Midge Mean[1]
1	—	51		43	55	56	54		68	39	43	67	53
2	8	—	58	55	84	75	62	85		76	51	59	67
3		10	—	54			61	79	65	60	59	58	62
4	13	17	6	—	59	63	57	52	75	55	52	62	57
5	6	7		11	—	69	62	55	63	68	40		62
6	10	10		24	6	—	59	56	60	58	61	67	66
7	6	6	8	7	16	6	—						59
8		4	18	13	7	10		—					65
9	5		14	13	8	14			—				66
10	2	11	6	11	4	20				—			59
11	9	12	15	16	10	22					—		51
12	6	5	2	15		19						—	63
Chalcid Mean[1]	7	9	12	14	8	14	8	10	11	9	14	9	

[1] 95% CI = 3.3-4.1 for the midge and 1.2-1.4 for the chalcid

not related to resistance to the second species. Of ten clones in the seed orchard that deviated significantly (based on 95% CI) from mean seed loss to either species, eight that were resistant to one species showed no resistance to the other. Four of these clones were highly susceptible to the second species. Only two clones were resistant or susceptible to both insects.

Similar results were found in the progeny plantation (Schowalter and Haverty 1989). Parental crosses that were resistant to one insect generally were susceptible to the other. In this case, resistance appeared to be heritable as a dominant trait, based on the generally low seed losses for progeny of resistant and susceptible parents (Table 1).

Schowalter and Stein (1987) compared the extent of *Lygus hesperus* feeding on different seed sources (representing different genetic backgrounds) in a conifer seedling nursery. This insect is a mobile species that feeds primarily on agricultural crops in a hit-and-run manner. Results indicated significant separate and interactive effects of conifer seed source (genotype) and of proximity to *Lygus* population sources in adjacent agricultural crops. The effect of plant proximity to herbivore populations, even at this small scale for a relatively mobile herbivore, is surprising.

Data from these studies demonstrate that, within monocultures of plants, a diversity of genotypes can limit resource availability and suitability for particular herbivore species. This diversity represents a species-level defense that limits initial herbivore population growth. Genetic diversity within a monoculture is not sufficient to prevent herbivore outbreaks over long time periods, especially when conditions that stress plants and/or inhibit production of plant defenses permit herbivore population growth (Waring and Pitman 1983). When environmental conditions increase susceptibility of a given plant species, exposure to herbivores can be reduced by surrounding non-host plants and stands.

Plant Species Diversity Within Stands

Our view of plant species interactions traditionally has focused on competitive interactions. This view has supported the tree farm (monoculture) approach to forestry. Recent studies, however, are indicating that plant species interactions are more complex. Plant species often share mycorrhizae, contribute collectively to soil fertility through differential nutrient uptake and concentration in litter and rhizosphere, and increase the chemical complexity of the forest aerosol (Visser 1986, Hunter and Arssen 1988). These mutualistic aspects of plant species interactions may reduce the likelihood of plant stress and apparency to herbivores, at least for some combinations of plant species.

If genetic diversity within monocultures can affect herbivores, then a diversity of plant species within a community matrix should limit herbivory to a greater extent. Studies with several insect species in different vegetation types have demonstrated that diverse vegetation limits overall herbivory. For example, Root (1973), Kareiva (1983) and Turchin (1988) reported that intermixed crops were subjected to lower levels of herbivory by insects than were monocultures of the same crops. Examples from forests are rare, largely because manipulating tree diversity for experimental purposes is difficult, and natural variation in diversity is confounded by geographic variation in soils, aspect, and other factors that also affect herbivory (Schowalter and Filip 1993).

Gara and Coster (1968), Johnson and Coster (1978), and Schowalter *et al.* (1981b) reported that southern pine beetle, *Dendroctonus frontalis*, populations appeared to be sensitive to *Pinus* spp. density. Populations generally grew rapidly in dense pine stands and declined in sparse pine stands. However, Johnson and Coster (1978) and Schowalter *et al.* (1981b) reported that large populations (>100,000 beetles) developing under favorable conditions also were capable of sufficient aggregation to colonize sparse hosts. Thinning experiments in western North America indicated that tree spacing also is critical to mountain pine beetle, *Dendroctonus ponderosae*, populations (Sartwell and Stevens 1975, Mitchell *et al.* 1983). The effects of tree species diversity were unclear; either hardwoods compete with pines and aggravate stress-related beetle activity (Hicks 1980) or hardwoods interfere with discovery of hosts (Belanger and Malac 1980).

Schowalter and Turchin (1993) conducted a relatively unique experiment to test effects of *Pinus* spp. density and stand diversity on *D. frontalis* populations. They manipulated pine and hardwood basal areas in a 2 x 2 factorial experiment and introduced equivalent *D. frontalis* populations into replicated plots to prevent confounding effects of plot proximity to beetle population sources. Infestations subsequently developed only in the dense pure pine stands and achieved infestation sizes (>10 dead trees) sufficient to warrant suppression in this treatment (Fig. 1). Infestations did not develop in dense pine stands where hardwoods were present or in low density stands, indicating that tree spacing and stand diversity both function to reduce insect population growth.
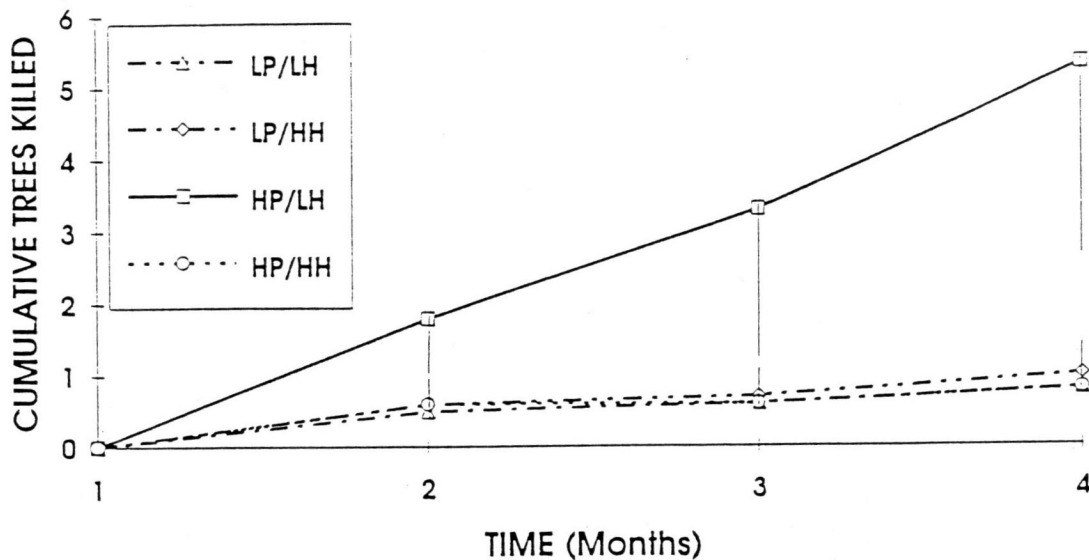
Figure 1.—Cumulative pine mortality to *Dendroctonus frontalis* by pine and hardwood basal area treatments in Mississippi and Louisiana during 1989 and 1990. Vertical lines represent 1 SEM. Low pine (LP) = 11-14 m²/ha ba; high pine (HP) = 23-29 ba; low hardwood (LH) = 0-4 ba; high hardwood (HH) = 9-14 ba. Two infested trees were introduced into each experimental stand at the beginning of study. N=8.

Schowalter (unpubl. data) compared arthropod abundances among replicated and intermixed plots representing young Douglas-fir, *Pseudotsuga menziesii*, plantations (10-15 years old), mature natural *P. menziesii* monocultures (100-150 years old), intact old-growth *P. menziesii/Tsuga heterophylla* (450 years. old) and old-growth *P. menziesii* shelterwood (450 years old) treatments in western Oregon. Western spruce budworm, *Choristoneura occidentalis*, was significantly more abundant and caused twofold more defoliation in the mature monoculture than in other treatments. This difference also could reflect the greater predator diversity and abundance in old-growth stands (Perry 1988, Schowalter 1989, Torgersen *et al.* 1990), or unmeasured differences in mutualistic endophyte diversity or foliage quality among age classes (McCutcheon and Carroll 1993).

Stand Diversity Across Landscapes

Diversity at the landscape level augments diversity at the stand level. As the diversity of stands representing different species composition or age classes increases, the distance between stands containing suitable resources increases (Perry 1988, Schowalter 1989). Although herbivores are capable of dispersing over considerable distances, several factors reduce the likelihood of distant hosts being discovered or colonized. First, insect ability to perceive hosts over long distances is limited for most species. Plant cues or other factors conveying host location become dissipated in the forest aerosol, making distant hosts and hosts in diverse stands less apparent (Visser 1986). Second, survival decreases with distance as a result of longer exposure to mortality agents and exhaustion of energy reserves, reducing insect ability to reach distant hosts. Therefore, diverse landscapes should prevent localized outbreaks from spreading to distant hosts.

Conversely, herbivore populations are promoted in landscapes that provide greater homogeneity of resources and few barriers to population spread. Major outbreaks typically occur in relatively homogeneous landscapes.

Declining forest health in eastern Oregon and Washington is largely the result of change in landscape diversity. Forests in this region originally were a diverse matrix in which stands of shade-tolerant mixed-conifer *Pseudotsuga/Abies/ Pinus* forest in moist sites at higher elevations, north aspects, and riparian areas were embedded within an arid landscape dominated by sparse fire-tolerant *Pinus/Larix* forest and savannah. Fir defoliators such as *C. occidentalis* occurred as local populations forced to search for hosts aggregated within a largely inhospitable landscape. As a result of fire suppression and selective logging of *Pinus* and *Larix* over the past century, the fir forest spread across this landscape. The landscape is now relatively homogeneous, dominated by forests of dense *P. menziesii* and *Abies* spp. Drought stress of these mesic species in addition to resource concentration has permitted *C. occidentalis* to reach epidemic population levels over most of this large area (Hadfield 1988).

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In contrast to the situation in eastern Oregon and Washington, *C. occidentalis* historically has occurred at innocuous population levels in western Oregon and Washington, although localized outbreaks have occurred. Recent (and past) activity of *C. occidentalis* in western Oregon is concentrated around a major pass through the Cascade Range. This area has been affected by years of drought but also was accessible to epidemic *C. occidentalis* populations spilling over the pass from eastern Oregon (pers. obs.). Nevertheless, Schowalter (1989 and unpubl. data) found that, near this area, *C. occidentalis* was rare or absent in diverse old-growth forests but was abundant and causing measurable defoliation in mid-successional *P. menziesii* monocultures. Perry and Pitman (1983) compared suitability of *P. menziesii* foliage from eastern and western Oregon for *C. occidentalis*. They found that foliage from western Oregon was more susceptible to budworm feeding and suggested that the greater diversity of trees, predators, and parasites in western Oregon has limited budworm populations and minimized selection for resistance to this insect. If diversity has been a major factor preventing budworm defoliation in western Oregon and Washington, then widespread commercial production of mid-successional *P. menziesii* forests may result in increasing *C. occidentalis* activity in this region.

Outbreaks of *D. frontalis* in the southeastern U.S. also result from change in landscape diversity. Most of the land area in this region originally was vegetated by sparse woodlands and savannahs dominated by *Pinus palustris*, a species tolerant of the frequent fires and drought of this region and relatively resistant to bark beetles (Schowalter *et al.* 1981a). Mesic riparian and bottomland forests included a diverse assemblage of intolerant species, including *Pinus taeda* and hardwoods. Bark beetles in this landscape would have been restricted primarily to scattered injured or diseased trees. Land conversion followed by eventual abandonment and reforestation led to establishment of dense stands of rapidly growing and commercially valuable *P. taeda* over most of this region. This species is susceptible to *D. frontalis*, resulting in devastating outbreaks across the region (Schowalter *et al.* 1981a, Schowalter and Turchin 1993).

These observations indicate that diversity can be effective in limiting herbivore epidemiology. However, diversity may not provide protection when herbivores reach large population size in a sufficient proportion of the surrounding landscape.

SUMMARY

Plant vulnerability to herbivores is a function of both biochemical suitability and exposure to herbivore populations. Plant exposure to herbivores can be minimized by plant diversity. Plant diversity at genotypic, species, and landscape levels presents herbivores with a mosaic of suitable and non-suitable hosts and non-hosts. This increases the distance herbivores must travel to reach new hosts and increases the difficulty of discovering suitable hosts hidden by non-hosts in diverse stands and landscapes. By contrast, limited genetic diversity within monocultures of commercially valuable trees provides a concentrated resource for adapted herbivores. This resource inevitably will become more vulnerable to herbivores, especially during adverse conditions that stress plants and/or limit defensive capability. Localized outbreaks occur where isolated stands become vulnerable. These outbreaks can be restricted to isolated vulnerable stands in a diverse landscape that provides barriers to herbivore population spread. Regionwide outbreaks occur where a sufficient proportion of the landscape is occupied by suitable hosts. Large populations can expand into otherwise resistant stands and affect resistant or sparsely distributed hosts.

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