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Editors

Ecological Responses to the 1980 Eruption of Mount St. Helens

With 115 Illustrations

With a Foreword by Jerry F. Franklin

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Causes and Consequences of Herbivory on Prairie Lupine (*Lupinus lepidus*) in Early Primary Succession

John G. Bishop, William F. Fagan, John D. Schade, and Charles M. Crisafulli

11.1 Introduction

Primary succession, the formation and change of ecological communities in locations initially lacking organisms or other biological materials, has been an important research focus for at least a century (Cowles 1899; Griggs 1933; Eggler 1941; Crocker and Major 1955; Eggler 1959; Miles and Walton 1993; Walker and del Moral 2003). At approximately 60 km^2, primary successional surfaces at Mount St. Helens occupy a minor proportion of the blast area, yet they are arguably the most compelling. The cataclysmic genesis of this landscape, its utter sterilization, and the drama of its reclamation by living organisms stimulate the imagination of scientists and nonscientists alike. These primary successional surfaces are the most intensively monitored areas at Mount St. Helens because of what they may teach us about the fundamental mechanisms governing the formation and function of biological communities. At a practical level, understanding successional processes provides a conceptual basis for the restoration of devastated landscapes (Bradshaw 1993; Franklin and MacMahon 2000; Walker and del Moral 2003).

Succession is a fundamentally multitrophic process. It involves not only plants but also herbivores, predators, and decomposers. Yet, the important effects of these other trophic levels are sometimes ignored. Study of trophic interactions (i.e., interactions between consumers and resources) in primary succession can provide new insights into mechanisms of primary succession and can inform the debates surrounding what controls the level of herbivory in terrestrial ecosystems. In this chapter, we describe often-devastating attacks by insect herbivores on the prairie lupine, *Lupinus lepidus* var. *lobbii* (Dougl.), and how they have affected the (spatial) spread of this little plant, generally considered the most important colonist during the first two decades of primary succession on the Mount St. Helens Pumice Plain. We also discuss a surprising spatial pattern in the intensity of lupine herbivory on the Pumice Plain and outline two hypotheses for this pattern. One hypothesis is based on gradients in plant quality; the other is based on gradients in the density and diversity of the herbivores' natural enemies. Both hypotheses involve processes that are inherent to primary succession and that are likely relevant to systems beyond Mount St. Helens.

11.2 Herbivory in Primary Succession

Ecologists have long debated whether animal and plant populations are regulated by their consumers (so-called "top-down" forces) or by access to resources ("bottom-up" forces). Primary successional systems on land have figured little in this debate, perhaps because primary consumers (e.g., herbivores) are rarely identified as a significant factor in terrestrial primary succession. Instead, in most studies of terrestrial primary succession, the initial composition of plant communities appears to be controlled by the availability of propagules, by the ability of the plants to establish despite extreme abiotic conditions and an absence of soil resources, and by various stochastic events (Miles and Walton 1993; Walker and del Moral 2003). Subsequent changes in community composition are influenced by diverse factors, but scientists have paid the most attention to competition and facilitation among plants, which mediate resource availability, a bottom-up factor. In their classic critique of successional research, Connell and Slatyer (1977) noted that the effect of herbivores on succession had been largely ignored, essentially tacked onto a list of factors that may influence the outcome of competition or facilitation. Subsequently, potentially strong impacts from herbivores, including invertebrates, have become better incorporated into ecologists' conceptions of secondary successional change. This recognition has occurred faster in marine and freshwater systems, where consumers are ubiquitous and the importance of multitrophic interactions in succession has been recognized for decades (Lubchenco 1983; Farrell 1991; Hixon and Brostoff 1996).

Discussion of herbivore effects is nearly absent from the literature on terrestrial primary succession (Walker and Chapin 1987; Glenn-Lewin et al. 1992; Miles and Walton 1993; McCook 1994; Walker and del Moral 2003). Yet consumers do accompany most cases of primary succession. For example,

numerous vertebrate herbivores, both wild and domesticated, frequent glacier forelands (Matthews 1992, chapter 6.1), and invertebrate consumer faunas have been described in various early-successional volcanic habitats (Howarth 1987; Thornton et al. 1990; Ashmole et al. 1996; Ashmole and Ashmole 1997; Sugg and Edwards 1998; Parmenter et al., Chapter 10, this volume). At Mount St. Helens, primary and secondary arthropod consumers (i.e., herbivores and their predators) were the very first colonists of pyroclastic-flow substrates, ahead of even ruderal (i.e., highly colonizing) plants (Edwards 1986a; Sugg and Edwards 1998). The question arises as to whether consumers are truly unimportant in primary succession or whether their effects have simply been overlooked. Plant damage by herbivores, especially by invertebrate herbivores, is sometimes subtle. Damage may be readily apparent only during outbreak periods or narrow seasonal windows, and highly mobile, belowground, or endophytic herbivores may be difficult to observe. Relatively limited herbivory may have strong impacts if concentrated in portions of a patch that otherwise contribute the most to population growth and spread (Fagan and Bishop 2000). A final difficulty involves the practicalities of science itself. Elucidating the role of herbivory has taken decades, even in common and intensively studied secondary successional systems, such as old fields; large primary successional systems are infrequent and less studied.

A few studies of consumer effects in terrestrial primary succession do exist. Most exceptional is the work on floodplains of the Alaskan taiga, where primary succession on silt terraces has been intensively studied (Walker and Chapin 1986; Walker et al. 1986; Van Cleve et al. 1993). In that system, browsing by moose (*Alces alces*) accelerates replacement of willows by alders during early primary succession and affects biogeochemical processes such as nitrogen and carbon accumulation both directly through fecal deposition and indirectly through effects on nitrogen-fixing plants (Kielland and Bryant 1998). The snowshoe hare (*Lepus americanus*) also appears to accelerate change in those riparian systems from felt-leaf willow [*Salix alaxensis* (Anderss.) Coville] to alder (*Alnus* spp.) (Bryant 1987), and both types of herbivores cause a shift from nutrient-rich, early-successional shrub stages to nutrient-poor and better defended evergreens (Bryant and Chapin 1986). Fast-growing, early-successional shrubs, such as willow (*Salix* spp.) and alder, were found more palatable to herbivores than slow-growing plants, such as spruce (*Picea abies*) and labrador tea (*Ledum*, an evergreen shrub). This difference in susceptibility, attributed to the high allocation to carbon-based defenses (i.e., tannins and other phenolics) by slow-growing plants in resource-poor habitats, led in part to the landmark proposal that resource availability is a major determinant of a plant's allocation to defensive chemicals and the type produced (Bryant et al. 1983; Coley et al. 1985).

Vertebrate herbivores are common in other primary successional systems as well, but their effects are less studied (Faegri 1986; Wood and Anderson 1990; Matthews 1992). At Mount St. Helens, herds of elk (*Cervus elaphus*) are frequently observed on primary successional surfaces of the Pumice Plain and debris-avalanche deposit. Excluding elk from the latter site has led to dramatic increases in woody plants (see Dale et al., Chapter 5, this volume). In a separate study at Mount St. Helens, aster (*Aster ledophyllus*) seedlings increased by 76% in elk exclosures surrounding individual plants on the Pine Creek mudflow, suggesting that elk browsing may explain the slow rate of colonization of aster on that surface (Wood and Anderson 1990). Whether elk are as influential at Mount St. Helens as are moose in the taiga or ungulates in successional grassland ecosystems (McNaughton 1985; Ritchie and Tilman 1995; Olff and Ritchie 1998; Ritchie et al. 1998) is a critical question for understanding controls on succession at Mount St. Helens.

The only detailed work on insect herbivory during primary succession is Catherine Bach's demonstration (Bach 1990, 1994) that brief periods of intense insect herbivory on a single, common plant species can strongly affect the rate and direction of succession on Lake Huron sand dunes. Bach experimentally excluded a specialist chrysomelid beetle (*Altica subplicata*) feeding on willow (*Salix cordata*) during a 3-year outbreak. Herbivory slowed primary succession by indirectly facilitating growth of early-successional species (Bach 1990, 1994) and affected the community trajectory (e.g., causing a decrease in monocots) (Bach 2001a). Negative effects on willows themselves were exacerbated over time because herbivore-damaged plants were more susceptible to sand accretion (Bach 2001b). Other reports also hint at an important role for arthropod consumers. On glacier forelands, spruce bark beetle (*Dendroctonus rufipennis*) damages Sitka spruce (*Picea sitchensis*) at Glacier Bay, killing forest canopy (Eglitis 1984). At Mount St. Helens, Wood and Anderson (Wood and Anderson 1990) documented insect seed predators on aster, but found no short-term effects, and Dale (1986) noted devastation of fireweed (*Chamerion angustifolium*) patches by a sphingid caterpillar. Fire tree (*Myrica faya*), an invasive nitrogen-fixing tree that severely alters successional trajectories on Hawaiian lava flows, has recently had large portions of its canopy destroyed by the introduced homopteran (leafhopper) *Sophonia*. Removal of fire tree canopy leads to dominance of nonnative grasses that take advantage of the unusually high soil nitrogen produced by fire tree (Adler et al. 1998). Although not a native system, the *Myrica–Sophonia* interaction demonstrates the potential for important top-down effects that insect consumers can have on succession when acting on keystone species (i.e., species that disproportionately affect the organization of their communities).

In what follows, we discuss the effect of insect herbivores on prairie lupine (*Lupinus lepidus* var. *lobbii*) during primary succession on the Pumice Plain of Mount St. Helens (see map, Figure 11.1). The demographic impact of herbivores on lupine is of special interest because prairie lupine acts as a keystone species in early primary succession. Consequently, what controls herbivory on lupine is also of great interest. Herbivory in this system is strikingly absent from large, high-density lupine patches, a fact that allows us to examine how top-down and

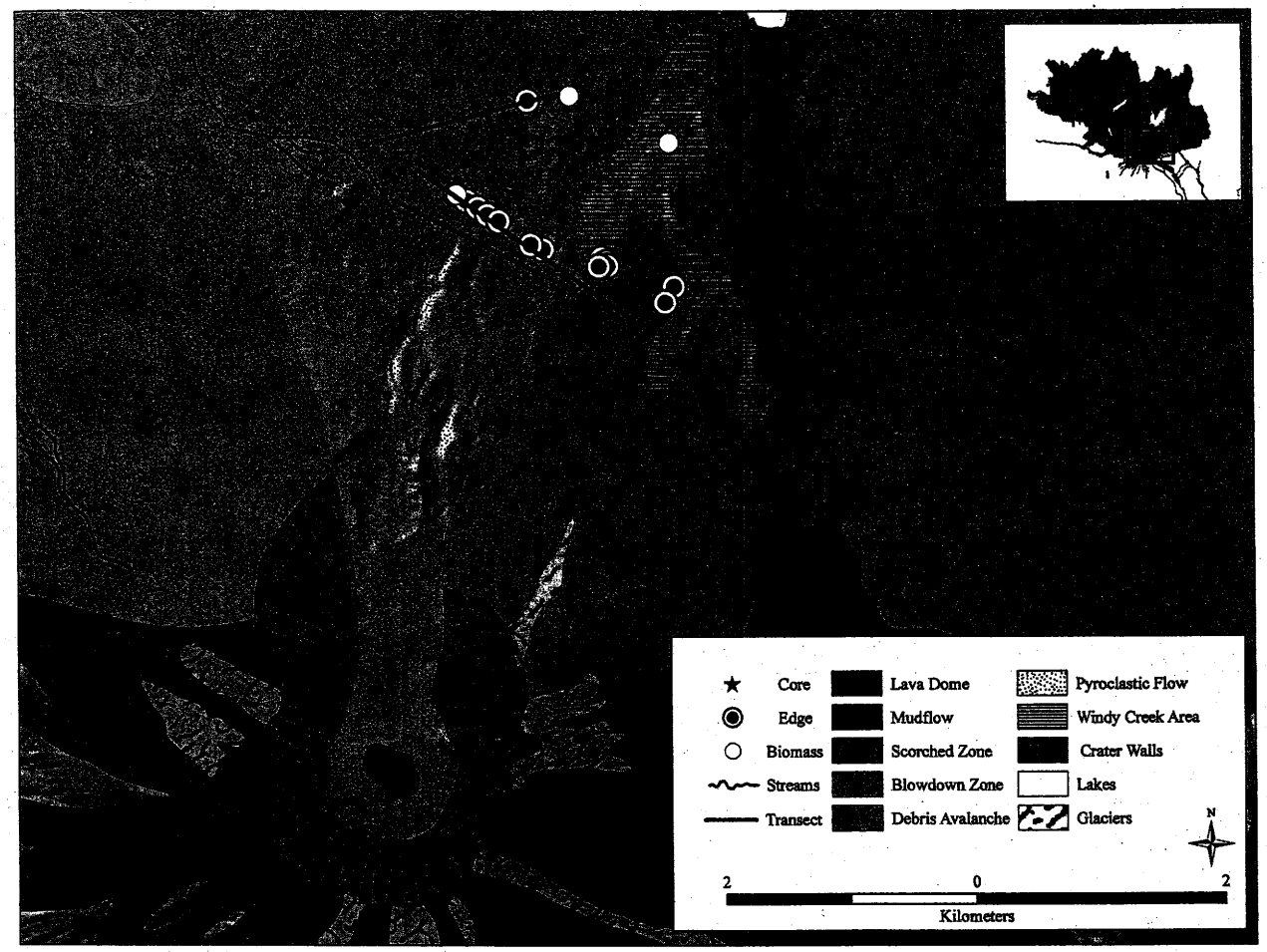

FIGURE 11.1. Map of Mount St. Helens showing the Pumice Plain, debris-avalanche deposits, and study areas.

bottom-up forces may control plant and herbivore populations during primary succession.

11.3 Lupine Effects on Succession

Prairie lupine is a nitrogen-fixing legume characteristic of alpine and subalpine pumice communities in the Washington and Oregon Cascades. Following the 1980 eruption, it was the first plant to successfully colonize pyroclastic-flow and volcanic-debris avalanche deposits on the north flank of Mount St. Helens. Isolated individuals that were discovered during reconnaissance surveys in 1981 and 1982 were of a size consistent with colonization by seed the year before. Colonization probably occurred via seeds, rather than root fragments, because root fragments might require transport by water. Initial colonists were found on uneroded pyroclastic flows several kilometers from the nearest possible source population, suggesting that water transport did not account for dispersal. The initial long-distance colonization events were greeted with surprise (del Moral and Grishin 1999) because prairie lupine seeds lack any obvious means of long-distance dispersal and are larger than those of weedy colonizers. However, prairie lupine seeds, although not abundant, were caught regularly in traps set for windblown seeds (Wood and del Moral 2000), indicating that long-distance dispersal of lupine seeds occurs frequently.

As nitrogen fixers and as the only successful primary producer established on pumice and other rock substrates, lupines were expected to drive the pace and pattern of early succession. Prairie lupine has met expectations in this regard. Initial substrate concentrations of organic matter and nitrogen (a nutrient that often limits plant growth) were zero (Engle 1983). Lupines accelerate soil development through direct nutrient and organic-matter input; trapping of windblown debris and propagules; attraction of insects that ultimately die in situ; and attraction of animal dispersal vectors, such as birds, elk, and mice, which transport seeds and microorganisms (Allen 1988). For example, one of us documented seven species of vascular plant (four graminoids and three herbs) and three species of fungi dispersed to a lupine patch in elk feces in 1998. Soils under lupines have much higher levels of total nitrogen, organic matter, and microbial activity than do adjacent bare areas (Halvorson et al. 1991b, 1992; Halvorson and Smith 1995;

Fagan et al. 2004). Experiments demonstrate a net positive effect of lupines on growth of such ruderal plant species as hairy cats-ear (*Hypochaeris radicata*), fireweed (*Chamerion angustifolium*), and pearly everlasting (*Anaphalis margaritacea*) (Morris and Wood 1989; Titus and del Moral 1998b), although these species may have to wait for lupines to die to take advantage of the site. In a recent survey, del Moral found that cover of other plant species is higher within lupine patches than outside them and that species composition differed substantially inside and outside patches. Some differences in plant composition are striking. For example, paintbrush (*Castilleja miniata*), which is hemiparasitic on lupine, has become abundant in many lupine patches but is rare outside them. Nutrient-responsive species, such as hairy cats-ear and bentgrass (*Agrostis pallens*), are also much more common in lupine patches. Our survey data also indicate that biomass and species richness of arthropods are much greater within large lupine patches than outside them. Later successional species, including woody plants such as willow (*Salix commutata*), Sitka alder (*Alnus viridis*), conifers, and animal-dispersed shrubs such as huckleberry (*Vaccinium* sp.), are also colonizing the Pumice Plain, and once they establish their vertical structure will dramatically alter plant and animal communities. Whether lupine facilitates establishment and growth of these species and thereby influences later stages of succession remains to be investigated. However, it is clear that any factor limiting the rate of spread of lupines, such as herbivory, may affect succession by delaying the early stages of soil formation and by changing the floristic trajectory.

Despite prairie lupine's impressive impacts on soil and community development, a number of early papers discounted lupine's facilitative effects because lupines occupied such a small portion of the primary successional landscape. This observation reflects the fact that prairie lupine failed to colonize the vast majority of available habitat during the first two decades of succession. Populations springing from the founding colonists exhibited rapid rates of growth and spread during the first few years after the 1980 eruption, but these rates were much reduced by the late 1980s (Fagan and Bishop 2000; Bishop 2002). For example, although the average rate of population increase in the patch founded in 1981 was 11.2 offspring per individual (geometric average from 1981 through 1985; Figure 11.2a), the rate of increase in similar patches founded in 1988 to 1990 averaged only 1.5 (1991 to 1995) (Fagan and Bishop 2000; Bishop 2002). Beginning from this core of initial patches, lupines rapidly colonized the 1.5-km expanse sloping down to Spirit Lake, but colonization up or across slopes (and newly created gullies) was far more circumscribed. For the sake of description, we will refer to the large, high-density patches formed during the early 1980s as "core" areas. We refer to the smaller, younger patches uphill of the core as the "edge" areas. We use these terms because the two areas loosely represent the core and edge of an invasion front. Limited dispersal ability can partially explain slow rates of spread from the core in the uphill direction. However, by 1990, a few plants located in small, isolated patches (i.e., edge

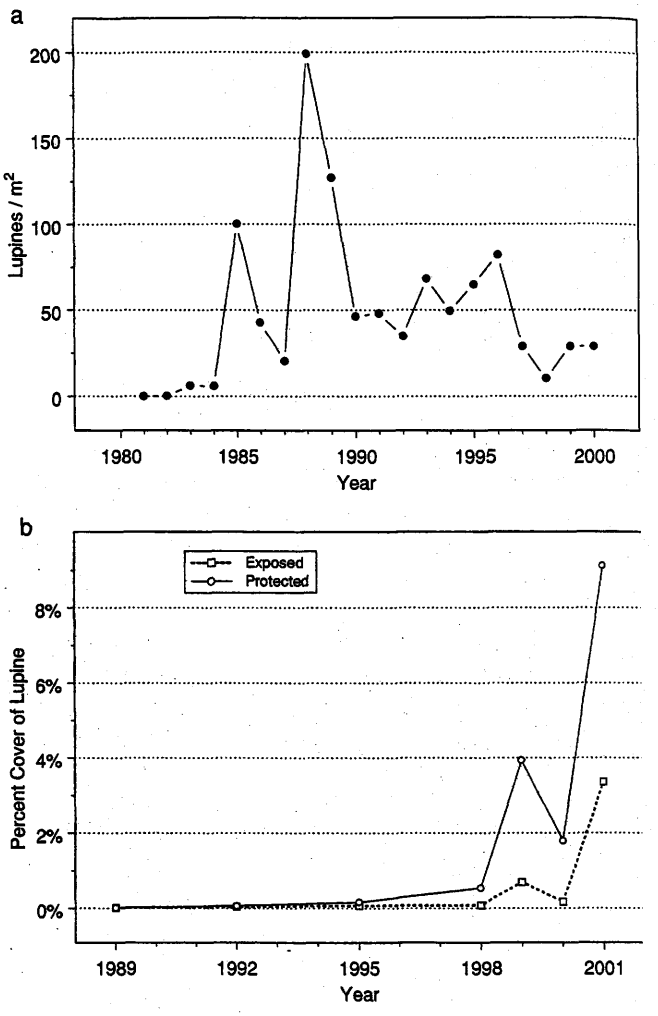

FIGURE 11.2. (a) Prairie lupine population growth in the founding cor lupine patch, 1981 to 2000. Because plants outside the 168-m² sampl grid were not counted, the data are presented as plants/m². (b) Growtl in percent cover of prairie lupine, 1989 to 2001, on a 20,000-m² gri on the east Pumice Plain. Note the abrupt increase in cover from 199 to 1999 (attributable to record snow accumulation), followed by sharp decline in 2000 (caused by tortricid root borers and noctui cutworms). Protected plots are on a north-facing slope. Data for 198 to 1999 are from del Moral and Jones (2002) and are the averag of $n = 87$ 10-m × 10-m plots in protected areas and $n = 97$ plots i exposed areas. (Data for 2000 and 2001 are courtesy of R. del Moral.

patches) were present uphill or at the same elevation as ini tial patches (Bishop 2002). Occasionally, these new edge-are patches expanded rapidly. More often, however, they expe rienced little or no population growth, despite establishmen in sites nearly identical to successful patches, suggesting tha failure to spread was not caused by an exhaustion of suitabl habitat (Bishop 2002). Even though lupine populations hav dramatically increased since 1999, large portions of availabl habitat are still only sparsely occupied. In 2002, we sample six 2.5-km transects on the Pumice Plain, stopping every 25 n to estimate lupine cover in 40-m² circular plots (thus samplin

0.12% of the survey area). We found that 24% of the plots had no live lupine and 70% of plots had less than 10% cover of lupine. Although some of these sites were unsuitable for lupine, these data indicate that, 20 years after initial colonization, relatively little of the Pumice Plain is directly affected by prairie lupine.

11.4 Herbivory on Lupines at Mount St. Helens

By 1985, insect herbivores were observed in the founding lupine patch. Their effect is illustrated in Figure 11.2. In 1984, a large seedling cohort was produced, which then experienced high mortality attributable to intraspecific competition (see Figure 11.2a). However, the continued decline in lupine density from 1986 to 1987 was caused mostly by the mortality of adult plants attacked by the root-boring larvae of two tortricid moths, *Hystricophora* spp. (near *H. roessleri*), and *Grapholita spp* (near *H. lana*). A new, even larger seedling cohort was produced in 1987, again followed by high mortality attributed to a combination of intraspecific competition and tortricid root borers. An outbreak of lupine aphids (*Macrosiphum albifrons* Essig) in 1987 likely acted synergistically with the tortricid root borers. In fact, the mortality of adult prairie lupine, the cause of which was largely underground and therefore unseen, was so striking and ubiquitous that several ecologists suggested lupines possessed a deterministic life span of 4 to 5 years. Similar die-offs have also been noted in prairie lupine populations on Mount Rainier and the Olympic Mountains in Washington State (Ola Edwards, University of Washington, Seattle, Washington; personal communication). Whatever its cause, high mortality combined with a relatively even-aged population structure causes prairie lupine populations at Mount St. Helens to undergo extreme fluctuation in numbers (del Moral 2000a,b). However, it is unlikely that this mortality is caused by a deterministic life history. A survival analysis of about 9000 individual plants that were followed for 5 to 7 years beginning in 1991 found that, although prairie lupine is short lived with only a few individuals surviving 7 years, mortality rates were relatively constant except in years with high mortality from tortricid root borers (Bishop 2002). Now we can thoroughly document an alternative cause for massive lupine die-offs: tortricid root borers [along with a more minor root borer, *Walshia* spp. (Cosmopterygidae)] "girdle" the root by eating the vascular tissue, thereby killing plants (Bishop 2002). This kind of "stand-level" mortality also occurs in bush lupine (*Lupinus arboreus*), a dominant plant of coastal prairie in Northern California, where it is killed by root-boring larvae of the moth *Hepialus californicus* (Hepialidae) (Strong et al. 1995; Maron 1998). Interestingly, whole-patch die-offs of subalpine lupine (*L. latifolius*) in the blowdown area of Mount St. Helens were documented during 1987, and there too a stem-boring lepidopteran appeared to be the cause.

Here we offer three additional examples of caterpillars affecting prairie lupine. The first is drawn from Roger del Moral's 2-ha grid, divided into 200 squares and monitored since 1989, in what we designate the edge region (del Moral and Jones 2002). Percent cover of prairie lupine on the grid increased slowly during the first 10 years of monitoring; then cover growth accelerated suddenly and dramatically in 1999, followed by an equally dramatic die-off in 2000. This die-off reduced total lupine cover by 50%, with the median 100-m^2 plot declining by 72% (see Figure 11.2b). We carefully examined plants in 11 plots on the grid and found 60% mortality of nonseedlings. Excavating the roots of dead plants revealed unequivocal evidence for massive root-borer activity, in the form of frass and galleries, in 77% of dead plants but no root-borer evidence in a sample of living plants. The remaining dead plants were too decayed to examine and may also have been killed by insects. In addition, one-third of the surviving 40% of plants had been completely defoliated by a noctuid cutworm, *Euxoa extranea*. Recovery of defoliated plants (along with the growth of the 1999 seedling cohort) accounts for the rapid recovery in 2001 (Figure 11.2b).

Decimation by tortricid root borers and noctuid cutworms not only reduced cover in edge areas in 2000 but also caused spatial contraction of some core patches. Figure 11.3 summarizes data from transects running along radii from the center point of patches to the patch margins. The 2000 growing season witnessed complete mortality of lupines on the outer one-half to two-thirds of these patches, caused primarily by tortricid root borers. In addition, noctuid cutworms heavily defoliated the few surviving plants in this area and plants at the new patch margin. By 2001, cutworm-attacked plants were mostly dead. Seedlings were abundant at the new patch margin but scarce in the region attacked by tortricid root borers. This caterpillar-induced dieback represents a 90% reduction in spatial extent of these patches. However, because lupines were at low density at the fringes of these patches, the actual proportion of plants killed in the patch was modest. Nevertheless, these losses are important because dead plants were concentrated at the margin, where they would have contributed disproportionately to future spatial spread.

Many other insects also feed on prairie lupine (Halvorson et al. 1992; Bishop and Schemske 1998; Fagan and Bishop 2000; Bishop 2002). Mortality induced by tortricid moths has provided the most dramatic herbivory, but the leaf-mining gelechiid caterpillar *Filatima* attacks more consistently. Damage by that caterpillar is conspicuous because it binds leaves into a woven yellow or white mass (Bishop 2002). Demographic surveys in 1991 and 1992 encountered no leaf-miner damage, but damage by leaf-mining gelechiid caterpillars became common in 1993 (Bishop 2002) and has continued at high levels in many areas through 2002 (Figure 11.4). Such damage is almost entirely confined to small, low-density patches and to low-density margins of large patches. For the years in which we have good sample sizes (Figure 11.4), the proportion of photosynthetic area consumed by leaf-mining gelechiid caterpillars

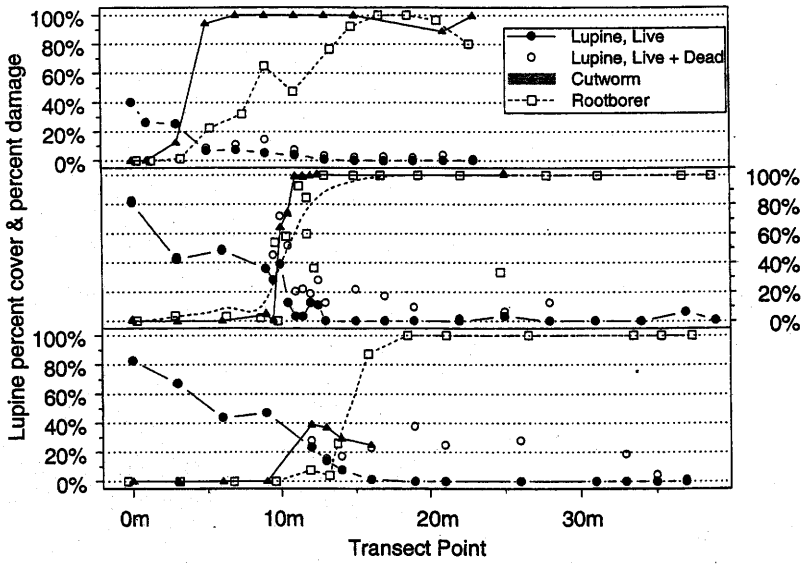

FIGURE 11.3. Herbivory along transects running fro the centers to the margins of core patches. Each pan depicts prairie lupine surface area in August 200 percent mortality caused by tortricid moth root bore from 1999 to 2000, and percent of lupine surface ar attacked by noctuid cutworms in 2000 along a tra sect. *Open circles* depict surface area of live and de lupines combined; *closed circles* are lupines alive the time of the census. At each point on the transe cover was estimated within a 0.25-m^2 frame. Sar pling at a point was repeated along a line perpendi ular to the transect until at least 200 cm^2 of lupi cover was recorded.

averaged 32% in edge patches but only 3% in core centers (i.e., areas with greater than 20% plant cover). Other important herbivores, such as noctuid cutworms, lupine aphids (*Macrosiphum albifrons*), and a guild of dipteran and lepidopteran predispersal seed predators, occasionally cause extreme damage in these patches, but they exhibit great spatial and year-to-year variation in their level of herbivory (Bishop 2002). As with outbreaks of tortricid root borers and leaf-mining gelechiid caterpillars, eruptions of noctuid cutworms, when they occur, also tend to be concentrated in areas of low-density lupine (see Figure 11.3).

Within the edge area, plants in the smallest patches were less likely to be attacked by tortricid root borers (Bishop 2002), suggesting that temporary escape from herbivory might be important for the establishment of new lupine patches. This kind of escape possibly underlies the explosive growth of lupine that began in 1999 (see Figure 11.2b). An extraordinarily deep snowpack in 1998–1999, with snow and cold weather lingering into July, delayed insect development. Although leaf-miner damage usually peaks in mid-August, repeated surveys in 1999 found that peak herbivory levels were postponed until September. Although lupine growth and flowering were also delayed, high soil moisture and the timing of herbivory permitted extremely high seed set.

Bishop (2002) provides extensive correlative evidence for strong demographic impacts of seed predators, leaf miners, and root borers from 1992 through 1995. These demographic impacts were largely confined to patches in the low-density edge region. In high-density core areas, seedling mortality caused by interspecific and intraspecific competition appeared to be the dominant population regulator (Bishop 2002). Experimental removal of leaf feeders and seed predators from edge patches in 1995 resulted in a 300% to 500% increase in population growth compared to control plots (Fagan and Bishop 2000). Herbivore removal in core areas resulted in higher seed production but did not lead to any increase in population growth rate (r which remained near 0. A model of spatial spread predict that herbivore effects on population growth would cause a 50 reduction in lupine's rate of advance across the Pumice Plai a delay that could diminish the effect of lupines on prima succession (Fagan and Bishop 2000).

When we carefully examine small portions of the Pumi Plain, the predicted delay in lupine advance appears qualit tively correct. Herbivory clearly reduces population grow rate, causes local spatial collapse of some patches (Figures 11.2b and 11.3), and causes a shifting mosaic of sm patches and extreme fluctuation in percent cover (del Mo 2000b).

11.5 Why Is Herbivory Spatially Structured?

The demographic impacts of lepidopteran herbivores are i pressive enough, but their spatial distribution and relationsl to lupine density are truly remarkable. For 10 consecuti years, gelechiid leaf miners have been abundant but larg confined to low-density edge patches and core margins (Figure 11.4). Although more sporadic, outbreaks of tortri moth root borers and noctuid cutworms have also been more frequent in low-density areas (see Figures 11.3, 11.4 Apparently, above a certain density of lupine, herbivores not sustained or are somehow repelled.

Negative relationships between host density and herbiv are known in other systems, but the underlying mechanis in any particular case remain obscure (Thompson and Pr 1977; Courtney and Courtney 1982; Courtney 1986; Ku 1999). The simplest, if biologically unrealistic, hypothesi that female moths disperse uniformly across the landscape

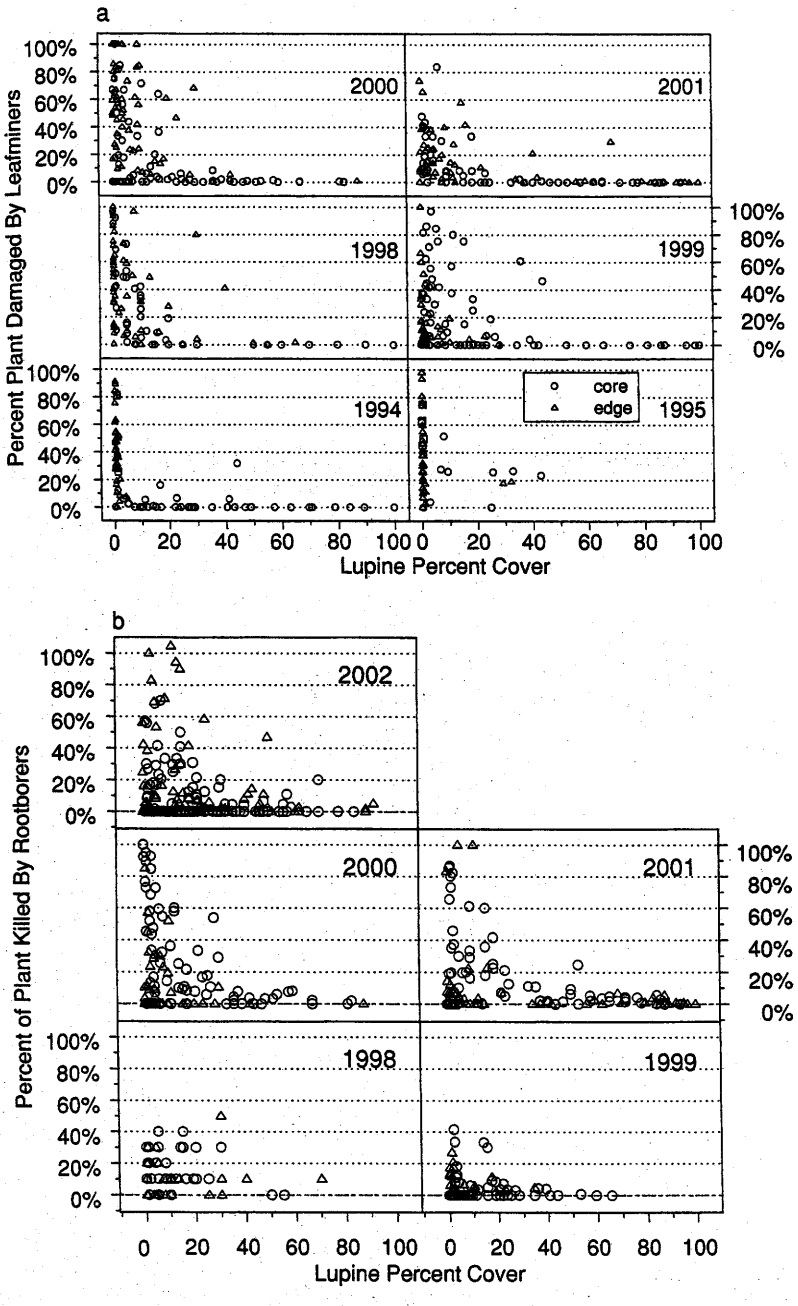

FIGURE 11.4. Relationship between lupine density and herbivore damage. (a) Leaf-miner (*Filatima* spp.) damage to prairie lupine, 1994 to 2001; (b) mortality caused by tortricid root borers (*Hystricophora* and *Grapholita* spp.), 1998 to 2002. Each point is an estimate of photosynthetic area consumed (leaf miner) or killed (root borer) in a sample. Sample area ranged from 0.25 m^2 to 315 m^2, depending on plant density. *Circles* denote core areas; *triangles* denote edge areas.

then oviposit on the nearest lupine. If the number of females per square meter is the same everywhere on the landscape, lupines in low-density areas would receive more eggs per plant than those in high-density areas because each low-density lupine draws moths from a greater area. We tested this null model for gelechiid leaf miners in 2001 by comparing caterpillars per square meter in high- and low-density areas. The data were obtained by harvesting all plants from four 0.64-m^2 plots in the core and two 100-m^2 plots in the edge, then carefully quantifying the number of caterpillars on each plant. Contrary to what the uniform distribution null model would predict, the number of caterpillars per square meter of land surface was four times higher in the core area than in the edge area (Table 11.1). Furthermore, we found 70 times more caterpillars per plant and 13 times more caterpillars per square meter of lupine surface in the edge plots than in the core plots, contrary to expectations based on the distribution of caterpillars per square meter in core and edge areas (Table 11.1). A second hypothesis is that greater diversity in core patches makes finding a host more difficult for caterpillars or adults. This concept also seems unlikely because prairie lupines are far more abundant in the core than in the edge. In core patches, cover of potential hosts is often greater than 60%, and host plants form a contiguous "canopy" (Fagan and Bishop 2000; Bishop 2002).

Succession itself suggests two additional explanations for the observed distribution of herbivory. First, by virtue of their

	N	Surface area sampled (m^2)	Number of plants sampled	Leaf area sampled (m^2)	Plants/m^2	Percent cover	Caterpillars/m^2 surface area	Caterpillars/m^2 lupine	Caterpill per plan
Core	4	0.64[a]	88.3	0.62	137.9[a]	96.3[a]	5.47[a]	9.5[a]	0.04[a]
Edge	2	100	60.0	0.95	0.6	0.95	1.23	128	2.77

[a]Denotes significant difference between core and edge ($p < 0.05$, t test).

longer existence, larger size, or other properties, core patches may have accumulated a greater abundance and diversity of arthropod and vertebrate predators (e.g., spiders, insects, and birds), which may, in turn, suppress or eradicate herbivores. Second, successional changes in soil development and fertility or increased intra- and interspecific competition may result in lower-quality lupine tissue in core areas, mediated by increased concentration of defensive chemicals, decreased nutrient concentration, or unfavorable nutrient ratios. These general explanations correspond to top-down and bottom-up controls, respectively, on herbivore populations.

11.5.1 Top-Down Explanations

Patch age alone might predict more predators in core areas because the probability that a population of predators will discover a patch increases with time. In addition, core plant communities are larger, denser, more diverse, and probably more productive. Accompanying these changes are increased habitat complexity and physical structure. The biomass of soil microbes is also greater in core plant communities (Halvorson and Smith 1995). Any of these conditions could lead to a larger and more diverse prey base that might sustain larger predator populations. For example, colonies of ants, such as *Formica lasioides* and *F. pacifica*, are commonly found in core areas but only rarely in edge areas, perhaps because minimum resource requirements for colonies are not met in edge areas. Throughout the summer, it is not uncommon to see these ants dragging noctuid cutworm caterpillars across the pumice.

In August 1995, we censused, by visual inspection, predators on and under lupine plants in edge and core areas. We found the density of predatory spiders, beetles, and true bugs to be four times higher per plant on core plants than on edge plants (Fagan and Bishop 2000). In 1999, we further characterized the distribution of arthropods using pitfall traps. We placed 53 traps in edge patches and along transects running from the centers to the margins of core patches. Traps were sampled every 10 days for 90 days from July to September (a total of 4770 trap-days). (The deep snowpack of 1999 prevented us from reaching the Pumice Plain until July 1, about 1 month later than usual.) Of the many arthropods caught in these traps, we discuss here the relative abundance of moths, several predatory beetles in the family Carabidae, and parasitoid flies (family Tachinidae, some of which attack larger caterpillars, such as noctuids). We focus on three beetle taxa: tiger beetles (*Cicindela oregona*), a large and highly mobile predator; *Cal soma* spp., one of the largest ground beetles whose commc name, "caterpillar hunter," reflects active predatory behavi and a predilection for caterpillars; and *Nebria* spp., which a nocturnal predators. Many small moths could not be identifie so we have lumped them as "microlepidoptera." This categor includes the tortricid moths *Hystricophora* and *Grapholita*, th gelechiid *Filatima*, and several other taxa.

The distribution of adult microlepidoptera was quite sin ilar to the pattern of herbivory; they were more than thre times as frequent in edge traps as in core traps (Table 11.2a In contrast, the larger-bodied noctuid moths, the three predz tory beetles, and parasitoid flies were all more common i core patches (Table 11.2a). The distribution of insects withi core patches, along transects running from center to margin, i instructive. The frequency of beetles, tachinid flies, noctuid and microlepidopterans along the transect all increased as tot plant cover decreased (Figure 11.5). However, in many case the distribution of predator taxa was better predicted by th presence of food items than by plant cover (see Table 11.2b) For example, *Calasoma* beetles (the caterpillar hunters) ar strongly predicted by the distribution of tachinid flies, noc tuid cutworm moths, and microlepidoptera but not by plan cover (Table 11.2b). The tachinid *Peleteria* was closely asso ciated with its putative host, noctuid moths. In fact, four of si predators and parasitoid taxa showed strong association wit noctuid cutworms. In contrast, the catch density of the tige beetle *Cicindela* is predicted strongly by low plant cover, b noctuid cutworms, and by *Nebria* but not by microlepidopter or by tachinids. *Nebria* was predicted only by plant cover (no shown). Overall, the pitfall data confirm that core patches hav a greater abundance and diversity of predators. However, man of these predators reside in the lower-density margins of cor patches, where lepidopteran prey is most abundant.

The distributions of predators and both larval and adult lep idopterans in core patches suggest that these predators are no responsible for the absence of herbivores at core centers. Other wise, both moths and predators would occur in our center trap at some point in the season. Other predators not sampled b these traps or not yet analyzed, such as birds, spiders, or ants could be responsible for the lack of herbivores at core cen ters, but this hypothesis would require that these other preda tors discover moths, including night-flying noctuids, so effi ciently that moths have no opportunity to die in traps. We have observed that some core patches in some years sustain

	Noctuidae*	Micro**	*Cicindela***	*Calasoma****	Nebria	Tachinidae*
Edge	1.3 (61)	10.7 (257)	3.3 (78)	0.0 (0)	5.4 (130)	4.1 (99)
Core	3.4 (215)	3.0 (86)	8.4 (245)	6.7 (194)	8.7 (252)	7.5 (218)

One-tailed Wilcoxon-signed rank test: * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$.

a. Comparison of herbivore and predator abundance in core and edge areas: number of individuals/trap (total individuals) for 29 core traps and 24 edge traps.

	Plant cover	*Calasoma*	*Nebria*	*Arctophyto*	Tachinidae	Micro	*Euxoa*	*Schinia*	R^2
Calasoma					0.67***	0.67*	0.52*		0.54
Cicindela	−8.6*		0.22**				0.42**		0.66
Peleteria							0.20*	0.46***	0.54
Arctophyto		0.28***							0.40
Linnaemyia				0.26***			0.06**		0.79

b. Linear-regression results for five predator and parasitoid taxa in core traps. Dependent variables are in the left-most column. No transformation resulted in a significant coefficient for plant cover when insects were in the model, except in the case of *Cicindela* and *Nebria* (not shown). For *Calasoma*, the predictor variables microlepidoptera and *Euxoa* were collinear. Table entries for these two variables are from two separate regressions. *Peleteria* spp., *Arctophyto* spp., and *Linnaemyia comta* are tachinid taxa; Tachinidae denotes total tachinids, Micro denotes total microlepidoptera.

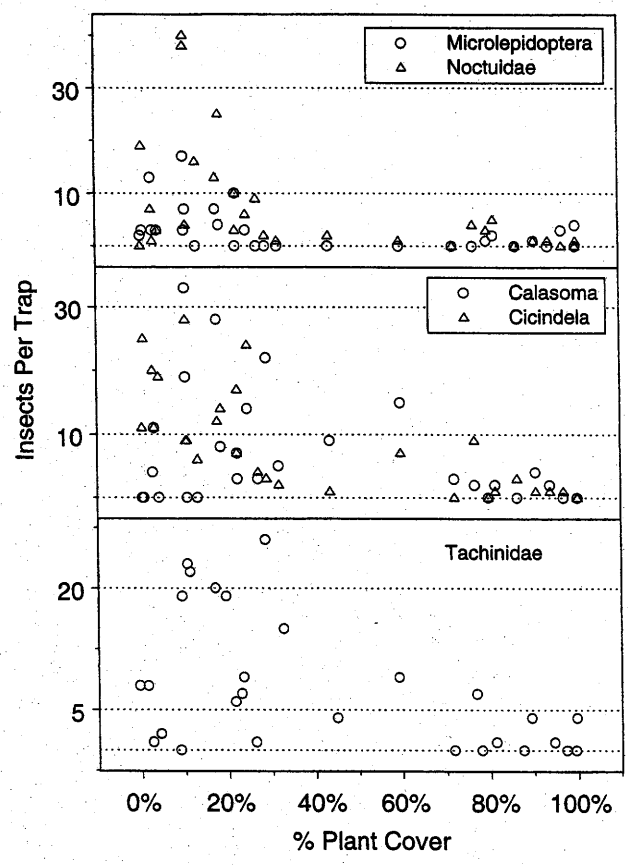

FIGURE 11.5. Distribution of moths, predatory beetles, and parasitoid flies in core patches in pitfall traps in 1999. Note that all predator taxa are more common at patch margins.

very little herbivore damage, even in low-density margins. In these cases, the pitfall data suggest that depletion of herbivores by predators is highly plausible.

11.5.2 Bottom-Up Explanations: Plant Quality

Specialist herbivores routinely identify and prefer their host taxa for purposes of oviposition as well as for feeding. Moreover, ovipositing females are known to discriminate among different-quality plants within a single host species (Bernays and Chapman 1994; Renwick and Chew 1994), suggesting that variation in lupine tissue quality could drive the negative correlation between plant density and herbivory. This discrimination might occur if core plants are either more effectively defended or are nutrient poor relative to edge plants. In fact, in preliminary experiments, we found that edge plants are indeed a higher-quality resource: caterpillars of gelechiid leaf miners exhibited a significantly reduced relative growth rate when fed leaves of core plants than when fed leaves of edge plants (Fagan et al. 2004).

Many studies conclude that nitrogen is a limiting nutrient for insect herbivores (McNeill and Southwood 1978; Mattson 1980; White 1993). On the other hand, recent comparative analyses of carbon, nitrogen, and phosphorus in plants and their insect herbivores conclude that phosphorus may be limiting more often than realized (Markow et al. 1999; Elser et al. 2000). These latter studies use elemental ratios (i.e., stoichiometry) to develop a common scale from which to gauge nutrient limitation. For example, most consumers are far more nutrient rich (i.e., lower C:N and C:P ratios) than their food. Likewise, if there is a cost to overconsuming one nutrient to obtain another, comparing N:P ratios between a consumer and its food can identify when phosphorus is more limiting than nitrogen.

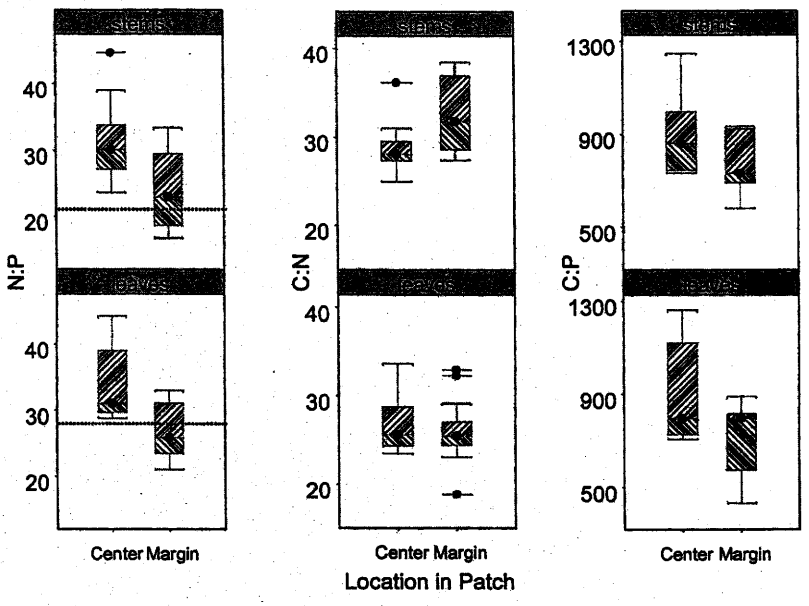

FIGURE 11.6. Elemental nutrient ratios from inner and outer portions of the transects depicted in Figure 11.3. *Shaded boxes* comprise the upper and lower quartiles around the median (*horizontal line*); *connected fences* and *unconnected dots with horizontal lines* indicate the extents of data and outliers, respectively. The *dotted horizontal line* shows N:P for *Hystricophora* root borers (stems/roots) and gelechiid leaf miners (leaves). Herbivore C:N and C:P ratios are lower than the graph minimum. Methods and the full data set are given in Fagan et al. (2004).

To examine whether nutrient concentration might explain herbivory patterns, we measured tissue concentration of carbon, nitrogen, and phosphorus in the year 2000 from undamaged or slightly damaged lupines at both ends of the transects shown in Figure 11.3 and in gelechiid leaf miners and tortricid root-borer larvae. We divided tissue into "root" parts fed upon by tortricid moths (mainly the upper root and caudex) and leaves (eaten by gelechiid leaf miners). Plants at the margin are somewhat more phosphorus rich (i.e., they have a lower C:P) for both tissue types than are plants at the core, and stems were nitrogen poor, but these differences were not statistically significant (Figure 11.6). Both herbivores were extremely nitrogen and phosphorus rich compared to the tissue they feed upon. However, plants from low-density margins were 23% more phosphorus rich per unit of nitrogen than were core plants. Whether this difference matters may depend on the N:P of the herbivores, illustrated in Figure 11.6 by dotted lines. In fact, herbivore N:P closely matches that of margin plants but is phosphorus rich compared to plants near the center of the core patches. Because herbivore C:N and C:P ratios do not change greatly in response to host-plant nutrient content (Elser et al. 2000), these results suggest that both herbivores could be phosphorus limited on center plants. Although reports of phosphorus limitation in insect herbivores are rare, Schade et al. (2003) recently showed that soil phosphorus availability affected abundance of a curculionid weevil by influencing the C:P ratio of its nitrogen-fixing host, mesquite (*Prosopis*). Such an effect at Mount St. Helens could be exacerbated by other factors. For example, because accumulated thermal units can limit larval growth rates, in montane environments (where thermal units may be marginal) more nutritious host plants may be required (Scriber and Lederhouse 1992; Hunter and McNeil 1997).

Nutrient availability may also be affected by differences in plant defensive chemistry. Like many plants, lupines produce an array of secondary chemicals that assist in the defense against herbivore attack (Wink et al. 1982; Johnson and Bentley 1988; Adler et al. 1998). Chief among these are quinolizidine alkaloids (QA), which may constitute as much as 5% of foliar nitrogen (Johnson et al. 1987, 1989) and which exhibit intraspecific variation (Carey and Wink 1994; Wink and Carey 1994; Wink et al. 1995). We have not yet assessed the content of QA or other defensive chemicals in prairie lupine. Whether center or margin plants are likely to be better defended is difficult to predict, as are the precise effects of QA. QA concentration is correlated with tissue nitrogen concentration in bigleaf lupine (*Lupinus succulentus*) and yellow bush lupine (*L. arboreus*), and QA content initially increases in response to herbivore damage (Johnson and Bentley 1988; Johnson et al. 1989; Bentley and Johnson 1994), both of which observations suggest that margin plants should produce more QA. QA and other defensive chemicals are often more effective against generalist herbivores, such as noctuid cutworms, than they are against specialists, such as gelechiid leaf miners and tortricid root borers (Smith 1966; Stermitz et al. 1989; Montllor et al. 1990; Bennett and Wallsgrove 1994), and even QA deterrence of generalists can be mitigated by increased tissue nitrogen (Johnson and Bentley 1988). Thus, it would be somewhat surprising if QA governed host use for all three herbivore species. Nevertheless, investigating lupine secondary chemistry is a critical component of future research.

11.6 Conclusions

Insect herbivores have strongly affected population dynamics of the prairie lupine on the Pumice Plain, but herbivores have not prevented the lupine population from growing to an enormous size and becoming the dominant plant on the landscape. Nevertheless, areas of intense herbivory still cause substantial

local reductions in lupine patch size and spread rate, and a large proportion of the landscape has yet to be occupied. Prairie lupine would undoubtedly have achieved landscape-dominant status sooner and to a greater degree in the absence of herbivory. Remarkably, the activities of at least three different herbivore species are more or less confined to low-density areas of lupine. This distribution is counterintuitive, because the high-density areas offer much greater biomass of lupine. Although more plant species are present in these high-density patches, they often contain an interconnected carpet of lupine constituting a more continuous resource than in low-density areas. Our current research is focused on uncovering the reasons for this surprising spatial pattern. Our observations of herbivore and predator distributions indicate that suppression of herbivores by predators and parasitoids in core areas provides one plausible explanation. On the other hand, variation in plant quality is also consistent with observed patterns of herbivory. As is the case with many other successional processes, revealing the mechanisms that underlie observed patterns of herbivory requires experimental manipulation.

Although we have focused much of our efforts on understanding why herbivory is so strongly concentrated in edge areas, it is also important to recognize that the near absence of herbivory from core areas may be critically important to successional processes. Large mats of lupines trap seeds and detritus blowing across the landscape and change soil chemistry, facilitating subsequent colonists (Morris and Wood 1989; Titus and del Moral 1998b; del Moral et al., Chapter 7, this volume). Long-established core patches harbor numerous species that are rare or absent in nearby bare areas, including orchids (*Spiranthes* spp.), paintbrush (*Castilleja miniata*), several grasses, and numerous fungi (Allen et al., Chapter 15, this volume). As shrubs and trees continue to colonize and grow in lupine-prepared areas, core patches may provide habitat for birds, rodents, and other species that add to the diversity of these areas. Thus, areas in which herbivores are only weakly affecting lupines may become foci of colonization for other taxa.

Dichotomous views have dominated the ecological literature regarding the prevalence of population control by top-down processes (i.e., control by consumers) versus bottom-up processes (resource limitation). Recently, a more synthetic view has emerged that holds that both forces will interact to determine population size and density of primary consumers, with bottom-up forces providing a resource template upon which top-down forces can act (Hunter and Price 1992; Price 1992). In this view, environmental variation will determine plant quality and, hence, the bottom-up template. Important predictions to test include these:

- Do higher trophic levels increase in importance with increasing primary productivity (Oksanen 1990)?
- Does variation in plant quality caused by successional processes cascade up to affect higher trophic levels?
- And, most importantly, under what combinations of soil development, plant-community structure, and abiotic conditions do natural enemies dominate trophic interactions during succession?

Lupine patches on the Pumice Plain comprise a suitable system for examining the interaction of top-down and bottom-up factors because patchy colonization and accelerated soil development create sharp resource gradients on a relatively uniform environmental background. Spatial spread of nascent patches, both through wavelike expansion from initial patches and by creation of new foci through jump-dispersal, replicate and recreate earlier stages of the resource gradient. Superimposed on these resource gradients are temporal changes stemming from successional processes, especially the addition of higher trophic levels. However, while the recovering landscape is suffused with scientific opportunity, the complexity of patch types and the dynamic nature of succession also present challenges. Drawing generalizations can be difficult if only a few patches are studied in only a few years, and opportunities to test for successional mechanisms can be fleeting. Twenty-five years after the volcano's cataclysmic eruption, there remain exciting prospects for new studies and experiments into the effects of food web dynamics on the recovery of Mount St. Helens.

In summary, although population size and the area occupied by lupine have expanded dramatically in recent years, our 2002 survey showed that even after the recent explosive growth, prairie lupine is still absent, or present only at very low density, on most (70%) of the Pumice Plain. In light of our work, it seems likely that the continued absence of lupines, along with high rates of patch turnover, is explained in part by herbivory and in part by physical factors. Herbivory by several lepidopteran larvae, each with different modes of feeding, is strikingly elevated in low-density areas of lupine. Thus far, patterns of nitrogen and phosphorus availability appear to explain this pattern of herbivory better than suppression of herbivore populations by predators. Given the known effects of prairie lupine on soil and community development on the Pumice Plain, herbivory on prairie lupine has likely altered the pace and pattern of succession.

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