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## Lupine Effects on Soil Development and Function During Early Primary Succession at Mount St. Helens

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### 17.1 Introduction

The pyroclastic flows of Mount St. Helens remain important to scientists seeking to understand the mechanisms of early succession. As in other primary-succession systems, biotic and abiotic development on these sites has been strongly influenced by legume colonists. Legumes are postulated to be critical contributors to nutrient pools during early succession, especially in infertile volcanic substrates, and are thought to facilitate colonization and growth of subsequent species that are limited by soil organic matter and by availability of critical nutrients such as nitrogen (Chapin et al. 1986; Franz 1986; Mooney et al. 1987; Vitousek et al. 1987; Chapin et al. 1994; Ritchie and Tilman 1995).

Two species of lupines, broadleaf lupine (*Lupinus latifolius*), an upright deciduous species, and prairie lupine (*Lupinus lepidus*), a prostrate wintergreen species (Braatne and Chapin 1986; Braatne and Bliss 1999), were among the initial colonists of cool mudflows (lahars) and pyroclastic deposits at Mount St. Helens. Photosynthesis, litter input, and symbiotic nitrogen fixation by lupines contributed to the formation of highly localized soil-resource islands, characterized by higher concentrations of carbon and nitrogen than in the surrounding soil, and supported larger and more diverse active populations of heterotrophic soil microorganisms in the soil (Halvorson et al. 1991b; Halvorson and Smith 1995).

Lupines growing on pyroclastic deposits have influenced revegetation of the site by other plants (Morris and Wood 1989; del Moral and Bliss 1993; del Moral and Wood 1993a,b; del Moral 1998), insect distributions (Fagan and Bishop 2000; Bishop 2002), soil resources, and microorganisms (Allen et al. 1984; Allen 1987, Carpenter et al. 1987; Halvorson et al. 1991b; Halvorson and Smith 1995; Titus and del Moral 1998b).

This chapter summarizes research about the impacts of lupines on soil that in turn influenced plant and soil microbial-community development of Mount St. Helens pyroclastic deposits. The following sections provide conceptual frameworks for viewing succession as a belowground process, describe the rationale and analytical approach of lupine-soil research at the

pyroclastic study site during the first 20 years after the eruption, summarize research findings, and suggest topics for future research.

### 17.2 Conceptual Approaches to Soil Succession

#### 17.2.1 Succession as a Belowground Process

Studies of aboveground succession often emphasize development of ecosystem form by focusing on predictable changes to the species structure of communities over time. Alternatively, studies of belowground succession of ecosystems more often focus on development of soil function because succession implies a series of changes to infertile substrates that result in increased aboveground productivity; ecosystem services; and development of traits, such as resistance and resilience to perturbations (Parr et al. 1992). This fundamental link between soil attributes and processes and ecosystem development, function, and integrity is increasingly recognized (Thompson et al. 2001). Although often viewed as an aboveground process, early succession may instead be viewed as primarily a belowground phenomenon fueled by the substantial proportion of net fixed carbon transferred through roots to heterotrophic microorganisms. Fresh photosynthates are needed by symbiotic bacteria for dinitrogen ( $N_2$ ) fixation, whereas litter inputs, carbon flow through roots (termed rhizodeposition), root sloughage, and live root material provide the carbon substrates whose supply controls microbial activity and thus nutrient cycling (Lynch and Whipps 1991). In addition to nutrient cycling, microorganisms found in the zone of soil immediately adjacent to plant roots (the rhizosphere) affect other plant–environment relationships (e.g., soil stabilization and water-holding capacity), plant–plant relationships (e.g., allelopathy and biocontrol), and plant–microbial interactions (e.g., competition, phytotoxicity, and disease) (Kennedy 1997).

Effects of disturbance and mechanisms of ecosystem response to the eruption at Mount St. Helens are discussed in

Chapter 1 in this book and elsewhere (del Moral and Bliss 1993; Dale et al. 2005) and reflect, in general, an aboveground, plant-centered perspective (see Lindahl et al. 2002). However, other approaches usually associated with soil genesis are also conceptually useful for studies of soil ecosystem development of Mount St. Helens pyroclastic-flow substrates. The state-factor approach, popularized by Jenny (1941), can be paraphrased to describe soil succession as a function of parent material being acted upon by climate and biotic activity over relief through time (Nuhn 1987). Soils undergoing primary succession are initially very similar to their parent material and are thus strongly influenced by the type and magnitude of the initial site-formation processes (Dale et al. 1998; Turner and Dale 1998). As succession proceeds, soil ecosystems are increasingly influenced by vegetation and the cumulative effects of climate. In 1986, soil textural properties on the Mount St. Helens pyroclastic-flow deposits were still largely unchanged from the initial deposit, but lupines affected the formation of an incipient A horizon and accumulations of windborne sands and other material (Nuhn 1987).

With another conceptual approach borrowed from pedology, soil-ecosystem succession can be viewed as resulting from changes in the net balance of soil additions, losses, translocations, and transformations (Simonson 1959). Physical additions and losses, resulting from mechanical processes such as deposition or erosion, and changes in soil chemistry, influenced by precipitation and leaching, may be particularly important during early succession. Important transformations or translocations during succession are often mediated by biotic activities that conduct energy through or recycle matter within system boundaries and are characterized by feedback loops and the exchange of information. For example, microbially mediated decomposition and transformation of soil organic matter are the primary driving forces in nutrient cycling, which plays a significant role in ecosystem development and functioning (Smith 1994).

### 17.2.2 Studying Succession in a Soil Ecosystem: A Problem of Integration

Measuring accumulations of individual soil properties does not equate to measuring soil succession. Although conceptually clear, the terms ecosystem and succession can be operationally difficult to characterize or monitor. No single operational definition of succession in a soil ecosystem seems entirely satisfactory, in part because the definition is context dependent, not simply related to a set of abiotic or biotic standards, such as the accumulation of nutrients, rates of energy and mass cycling, or presence of a particular species. For example, even though nitrogen fixers such as lupines are associated with primary succession, there is no clear correlation between their presence and nitrogen accumulation in soil and no consensus about their role in succession (Walker 1993). Although availability of soil nutrients seems to affect characteristics such as the growth rate of

dominant species or community richness, patterns of plant development do not appear to be closely linked to heterogeneity of nutrients in the soil (Collins and Wein 1998).

Because soil ecosystems are complex, scientists generally agree that several kinds of data, including physical, chemical, and biological properties, must be integrated to evaluate the whole (Gregorich et al. 1994; Doran and Parkin 1996). However, further work is needed to link above- and belowground processes for studies of succession. Data from plot-scale, relatively short duration studies must be scaled appropriately to be useful for understanding long-term, landscape-scale processes. The idea of studying succession from a soil perspective also implies the emergence of collective soil properties that are not predictable as a simple function of individual soil components and whose spatial and temporal patterns need not be correlated to those of any individual soil variable (Halvorson et al. 1995a, 1997). Various approaches for integration of individual soil properties have been advocated and applied to agricultural land at field scales (Halvorson et al. 1995b); to regional scales (Brejda et al. 2000a,b); and to less intensively managed landscapes, including rangeland and forestland (Herrick and Whitford 1995; Karlen et al. 1998; Burger and Kelting 1999; Herrick et al. 2002).

## 17.3 Rationale and Methods of Research

Much of the research described here was conducted on the Pumice Plain pyroclastic-flow deposits (46°12' N 122°11' W), located at an elevation of about 1160 m near Spirit Lake, where the substratum is rocky volcanic material deposited by numerous pyroclastic flows that occurred on the north face of Mount St. Helens (see Swanson et al., Chapter 3, this volume). This volcanic parent material was initially dominated by coarse (30- to 200-mm) particles, possessed little structure or organic material, and was very low in nutrients (del Moral and Clampitt 1985; Nuhn 1987; del Moral and Bliss 1993). Prairie lupine (*Lupinus lepidus*) was the predominant lupine colonist, appearing on pyroclastic-flow deposits soon after the eruption as isolated individuals and later comprising nearly monospecific patches of irregular size and distribution. More recently, individual patches have converged, and other plant species have become established (see del Moral, Chapter 7, this volume).

Early studies of the impact of lupines on Mount St. Helens soil succession determined the timing and magnitude of nitrogen fixation by lupine colonists to correlate nitrogen fixation with lupine physiology and to provide data needed for constructing a nitrogen budget (Halvorson et al. 1991a, 1992). Both daily and seasonal patterns of nitrogen fixation were investigated in 1986 and 1987 by determining the activity of nitrogenase, the enzyme that fixes nitrogen, by measuring the reduction of acetylene to ethylene by nitrogen-fixing organisms found in nodules on lupine roots. Nitrogenase activity was related to nitrogen fixation in lupines more directly

by using stable-isotope (in this case, nonradioactive  $^{15}\text{N}$ ) dilution techniques (Hauch and Weaver 1986). With this approach, the amount of nitrogen fixed is determined by comparing the proportion of  $^{15}\text{N}$  in lupines to that in nonfixing plants grown in field soil with  $^{15}\text{N}$ -containing fertilizer added to it.

Studies soon shifted to understanding more about the relationship between lupines and changes in properties especially patterns of soil carbon and nitrogen and soil microbial communities. Immediately following the May 18, 1980, eruption, the pyroclastic-flow deposits seemed to be a clean slate of nearly sterile substrate with low fertility, little spatial variability or stratification of soil properties, and a high degree of homogeneity. Lupines were expected to strongly influence patterns of ecosystem development by affecting soil genesis, soil microorganisms, and subsequent plant establishment (Engle 1983; Franz 1986; Nuhn 1987; Rossi 1989; Fagan and Bishop 2000).

Lupine influence on soil pools of carbon and nitrogen and on microbial activity was evaluated by comparing lupine root-zone soil to uncolonized soil collected in 1987 from the pyroclastic-flow deposits and several other locations along a gradient of carbon and nitrogen levels related to volcanic disturbance by the 1980 eruption (Halvorson et al. 1991b). Lupine effects, it was hypothesized, would be most clearly observed in sites with low total soil carbon and nitrogen and would subsidize soil microorganisms, resulting in a larger soil microbial biomass and more rapid nutrient cycling under lupines than in uncolonized soil. Soil was again sampled in 1990 from under living and dead prairie lupine, live broadleaf lupine, and bare uncolonized soil to determine the vertical distribution of microorganisms and nutrient pools, observe the effects of additions of lupine biomass on soil microbial activity, and relate any differences in soil microbial activity to differences in lupine tissue composition (Halvorson and Smith 1995). For these studies, sieved ( $\leq 2$  mm) soils were analyzed for pH with a 1:1 deionized soil-water paste. Fresh soil was extracted with 2 N KCl for determination of inorganic nitrogen ( $\text{NH}_4$  nitrogen and  $\text{NO}_3$  nitrogen) with an autoflow colorimetric procedure. Total organic carbon was measured titrimetrically after wet oxidation, and total soil nitrogen was determined colorimetrically after Kjeldahl digestion. Microbial biomass carbon was determined with the substrate-induced respiration method (SIR-C) and product-formation equations. Soil respiration and nitrogen mineralization rates were determined from aerobic incubations.

Studies of the effects of lupines on soil development were initially limited to the analysis of relatively small numbers of samples collected beneath plants versus samples collected "away" from plants. This binary approach was sufficient to detect small-scale enriched zones in the soil under lupine plants, called resource islands and characterized by greater concentrations of soil nutrients, and larger, more active populations of soil microorganisms. This approach, however, was unable to provide detailed knowledge of the size and internal dynamics

of resource islands, important for understanding energy-flux, mass-transport, and nutrient-cycling processes at a scale beyond the individual plant. To gain more information about the spatial relationships of resources in pyroclastic soil, geostatistics were employed with samples collected in 1991.

The use of geostatistics to model the spatial variability of ecologically important soil characteristics has been well documented (Warrick et al. 1986; Robertson 1987; Rossi et al. 1992; Goovaerts 1998). In particular, geostatistics have been used to model changes in soil patterns during succession (Robertson et al. 1988; Gross et al. 1995) and relationships between individual plants and resource-island patterns in the surrounding soil (Jackson and Caldwell 1993; Halvorson et al. 1994, 1995a). In general, geostatistics characterize the similarity of samples as a function of distance or direction, termed spatial autocorrelation. The model of this relationship is then used to estimate values at unsampled locations, often applying some variation of an estimation procedure called kriging (Isaaks and Srivastava 1989).

Recently collected data have been used to place the rates of carbon and nitrogen accumulation in pyroclastic-flow deposits in historical context and to relate patterns of organic matter in pyroclastic-flow soil to the diversity and function of soil microbial communities (Frohne et al. 2001; Halvorson and Smith 2001). Samples collected in 2000 from the pyroclastic flow and other sites around Mount St. Helens were used to determine how soil properties had changed over time, the rates of carbon and nitrogen accumulation in soil, and relationships between populations of soil microorganisms and soil-carbon quantity and quality. These studies used many of the same analytical procedures as earlier work except that total soil carbon and nitrogen were determined by dry combustion, and soil enzymes, phosphatase (pNP), and dehydrogenase (TPF) were assayed with standard methods.

Recent studies have also investigated patterns of fatty-acid methyl esters (FAME) and of carbon-substrate use in pyroclastic soil (Frohne et al. 1998, 2001). FAME are derived from important membrane constituents of plants and microorganisms, called phospholipids, found in the soil and can be used to characterize both the current soil microbial community (i.e., cellular lipids) and the paleo geochemistry (i.e., the extracellular lipids) (Kennedy 1994; Buyer and Drinkwater 1997; Zelles 1999; Hill et al. 2000; Pinkart et al. 2002). Patterns of FAME have been used to distinguish soil ecosystems from one another and to measure the adaptation of soil microorganisms to changing soil conditions (Ibekwe and Kennedy 1999; Drijber et al. 2000; Mummey et al. 2002).

We extracted FAME from archived pyroclastic-flow-deposit samples from previous studies and fresh samples collected in 1997 and in 2000 to compare FAME near lupine plants to that in uncolonized soil. FAME profiles, composite information about the amount and identity of individual fatty acids in a soil sample, were summarized and compared with principal-component analysis (PCA), a statistical approach that can be used to study the correlations of large numbers of variables by

grouping them into “factors” so that the variables within each factor are more highly correlated with variables in that factor than with variables in other factors. The spatial variation of FAME profiles was also characterized with transect or gridded samples and geostatistics.

Patterns of carbon-substrate use, determined by exposing microorganisms to different carbon substrates, have also been suggested as a means for assessing the potential function of soil microbial communities or the quality of substrates in the soil available to heterotrophic soil microorganisms (Siciliano and Germida 1998; Schutter and Dick 2001; Widmer et al. 2001). Pyroclastic soil collected in 2000 was used to distinguish the metabolic characteristics of soil microorganisms in lupine-influenced soil from those in bare soil by measuring the patterns of use of 31 carbon sources with Biolog Ecoplates (Biolog, Hayward, CA, USA).

## 17.4 Summary of Results and Discussion

### 17.4.1 Nitrogen Fixation by Lupines

Nitrogenase activity in prairie lupine growing at a pyroclastic site exhibited significant diurnal trends (with lowest rates at night) apparently related to plant photosynthesis. Nitrogen-fixing activity also followed seasonal trends with high rates in June, very low levels in August, the dry and warm part of the summer season, and a partial recovery of nitrogenase activity in September after precipitation resumed. Adult lupine carbon and nitrogen composition also varied during the growing season, with trends correlated to seasonal patterns of nitrogenase activity.

The  $^{15}\text{N}$  isotope-dilution technique showed nitrogenase activity to be related to seasonal nitrogen fixation in both prairie and broadleaf lupine (Halvorson et al. 1992). During one season of growth, both species fixed about 60% of their nitrogen with some evidence of preferential allocation to aboveground biomass. Prairie lupine fixed about  $18.1 \text{ mg N g}^{-1}$  biomass or an average of  $15.4 \text{ mg N}$  per plant, whereas broadleaf lupine fixed an average of  $16.3 \text{ mg N g}^{-1}$  biomass, equivalent to  $22.9 \text{ mg}$  per plant. Average net carbon fixation during the same period was 355 and 589 mg per plant for prairie and broadleaf lupine, respectively.

The potential rates of nitrogen fixation by lupines growing on the pyroclastic-flow deposits were similar to values reported for other volcanic sites (Kerle 1985). In 1986 and 1987, these nitrogen inputs were most important at the local scale with total annual fixation rates estimated to be less than  $0.05 \text{ kg N ha}^{-1}$  because prairie lupines were distributed into small patches covering less than 1% of the pyroclastic surface area. By 2000, even though lupines covered more than 50% of some parts of the pyroclastic-flow area (Bishop et al., Chapter 11, this volume), total annual symbiotic nitrogen additions may not have been the predominant source of nitrogen input (Engle 1983; Halvorson et al. 1992), a conclusion reached

in other studies (e.g., Wojciechowski and Heimbrook 1984; Holtzmann and Haselwandter 1988; Walker 1993). By comparison, atmospheric nitrogen inputs at the pyroclastic-flow site are about  $2 \text{ kg N ha}^{-1} \text{ year}^{-1}$  if similar to Oregon Cascade Range forest sites (Sollins et al. 1980; Vanderbilt et al. 2003).

### 17.4.2 The Importance of Nitrogen Fixation by Seedlings During Early Succession: Age-Specific Nutrient Cycling

The relationship between age cohort and nutrient cycling in early succession systems was postulated by Halvorson et al. (1991a), who examined the possible importance of lupine seedlings as agents of carbon and nitrogen inputs into Mount St. Helens pyroclastic deposits. Greenhouse-grown prairie and broadleaf lupine had different patterns of germination, growth, and allocation of carbon and nitrogen that were apparently related to phenology. Prairie lupine germinated rapidly and directed the majority of its resources to aboveground growth. Broadleaf lupine germinated slowly, allocating more carbon and nitrogen to belowground growth. Significant rates of nitrogenase activity were observed in both species within 2 weeks after planting, suggesting an early reliance on atmospherically derived nitrogen by young seedlings, at least those growing in infertile soil. The greatest amount of nitrogenase activity per gram of nodule occurred about 6 weeks after planting and then declined in a pattern similar to that observed for adult lupines in the field. The greatest total plant nitrogenase activity occurred after peak nodule activity because of increasing nodule biomass.

These patterns, together with estimates of seedling population density and mortality, suggest dense populations of seedlings might be significant contributors to soil nitrogen pools because they allocate a large proportion of their photosynthate to nitrogen fixation and move carbon and nitrogen into soil relatively rapidly. Seedling mortality could be particularly important during early succession because the availability of the carbon and nitrogen to other organisms would depend upon lupine decomposition. Although seedling populations and environmental conditions vary from year to year, many seedlings do not survive summer drought, insect predation, or winter conditions during the first year (Wood and del Moral 1987; Braatne 1989). Lower C:N ratios of seedling biomass compared to adult biomass (Halvorson et al. 1991a) would probably result in relatively rapid mineralization by soil microorganisms (Waksman and Tenney 1927).

Established adult lupines are more likely to withstand the prolonged periods of heat and low precipitation at Mount St. Helens that can kill up to 60% to 100% of seedlings (Braatne and Chapin 1986; Braatne 1989). Thus, adult lupines contribute proportionally smaller annual amounts of carbon and nitrogen to the ecological system over several seasons through leaf senescence, rhizodeposition, and mortality, which



are influenced by phenological characteristics (e.g., whether the plant is wintergreen or deciduous). In perennial lupine species, adult lupine carbon and nitrogen may be sequestered for several years in living material or in more decomposition-resistant forms after death. However, carbon and nitrogen sequestered in adult lupines may be released in an episodic “pulse” if mass mortality of adult lupines occurs because of factors such as insects (Bishop et al., Chapter 11, this volume).

### 17.4.3 Lupine Impacts on Soil Properties

Lupines began to influence soil development soon after colonization, and their effects are clearly evident more than 20 years after the eruption. In 1987, pyroclastic-flow deposits contained only small amounts of carbon and nitrogen, less than 5% of a minimally disturbed forest soil (Halvorson et al. 1991b). However, significantly higher pH and concentrations of carbon and nitrogen and a significantly lower average soil C:N ratio were recorded in lupine root-zone soil than in uncolonized soil (Table 17.1, 1987 data). Total inorganic-nitrogen concentrations in pyroclastic-flow deposits were small but comprised a significant proportion of the total amount of soil nitrogen, about 5% of lupine root-zone soil and 15% of uncolonized soil. In general, lupine root-zone soil contained similar amounts of  $\text{NO}_3^-$  nitrogen but significantly more  $\text{NH}_4^+$  nitrogen than did uncolonized soil. Potential nitrogen mineralization rates measured in the laboratory were of the same order of magnitude as total inorganic-nitrogen pools in the field, suggesting the transformation of nitrogen from organic material into the inorganic

forms used by plants is rapid and important in early succession within low-carbon and -nitrogen sites.

Soil pH in pyroclastic-flow deposits, first reported to be around 6.0 in 1980 and 1981 (Engle 1983; del Moral and Clappitt 1985), decreased to about 5.2 under lupines and to 5.0 in uncolonized soil by 1987. A significant drop in pH through time was thought to be the effect of acid precipitation (Nuhn 1987). Pyroclastic-flow deposits had pH values comparable to undisturbed forest sites in 1987 but had almost no detectable buffering capacity (Halvorson 1989).

Stratification of soil organic carbon is a feature in the top meter of soil under forest vegetation growing in cool, humid climates (Jobbagy and Jackson 2000), a pattern also developing under lupines. By 1990, soil under lupines contained significantly higher concentrations of total Kjeldahl nitrogen (TKN), total organic carbon (TOC), and microbial-biomass carbon near the surface (0 to 5 cm) that decreased significantly with depth. Less evidence for stratification was observed in uncolonized soil, which also contained much lower concentrations of carbon and nitrogen. Soil under the deciduous broadleaf lupine contained significantly more TKN, TOC, and water-soluble carbon than that under dead or live prairie lupine, a wintergreen species, or in uncolonized soil, showing the influence of nutrient inputs from leaf litter. Carbon in surface soil was strongly and positively linearly correlated with nitrogen (Halvorson and Smith 1995).

In 2000, the soil under prairie lupine exhibited greater electrical conductivity (EC) and higher concentrations of carbon and nitrogen than uncolonized soil at the pyroclastic-flow site (Table 17.1). When compared to other Mount St. Helens sites

TABLE 17.1. Average chemical and biological soil-quality indicators of the Mount St. Helens pyroclastic flow.

Year	Surface	pH <sup>a</sup>	EC <sup>b</sup>	Total soil carbon <sup>c</sup>	Total soil nitrogen <sup>d</sup>	C:N ratio <sup>e</sup>	Soil respiration <sup>f</sup>	Net nitrogen mineralization <sup>g</sup>	Dehydrogenase <sup>h</sup>	Phosphatase <sup>h</sup>	Microbial-biomass carbon <sup>i</sup>
<b>2000</b>											
0–5 cm	Never colonized	5.05 <sup>A</sup>	76 <sup>B</sup>	1284 <sup>B</sup>	114 <sup>B</sup>	13.9 <sup>A</sup>	4.1 <sup>A</sup>	0.11 <sup>A</sup>	4 <sup>B</sup>	10 <sup>B</sup>	93 <sup>B</sup>
0–5 cm	Under live <i>Lupinus lepidus</i>	5.21 <sup>A</sup>	138 <sup>A</sup>	4604 <sup>A</sup>	384 <sup>A</sup>	12.8 <sup>A</sup>	13.6 <sup>A</sup>	0.21 <sup>A</sup>	24 <sup>A</sup>	134 <sup>A</sup>	377 <sup>A</sup>
<b>1987</b>											
0–20 cm	Never colonized	5.04 <sup>X</sup>	NM	590 <sup>X</sup>	17 <sup>X</sup>	33.5 <sup>X</sup>	1.5 <sup>X</sup>	0.32 <sup>X</sup>	NM	NM	3
0–20 cm	Under live <i>L. lepidus</i>	5.19 <sup>Y</sup>	NM	840 <sup>Y</sup>	53 <sup>Y</sup>	14.7 <sup>Y</sup>	5.9 <sup>Y</sup>	0.37 <sup>X</sup>	NM	NM	7

Data are from Halvorson (1989), Halvorson et al. (1991b), and Halvorson and Smith (2001). Significant differences between the two types of soil samples, collected under live *Lupinus lepidus* and in uncolonized areas, are indicated by different letters. For 2000, differences are based on Bonferroni adjusted tests (denoted A or B);  $p \leq 0.05$ . For 1987, differences are based on Duncan's multiple range test (denoted by X or Y).

NM, not measured.

<sup>a</sup>Determined 1:1 (soil:water).

<sup>b</sup> $\mu\text{S cm}^{-1}$ .

<sup>c</sup> $\text{mg kg}^{-1}$  soil, assayed by wet combustion 1987 and by dry combustion in 2000.

<sup>d</sup> $\text{mg kg}^{-1}$  soil, assayed as Kjeldahl nitrogen in 1987 and by dry combustion in 2000.

<sup>e</sup>Test of significance for C:N done on  $\log_{10}$ -transformed data.

<sup>f</sup> $\text{mg CO}_2$  carbon  $\text{kg}^{-1}$  soil  $\text{day}^{-1}$  after 10 (1987) or 11 (2000) days ( $n = 3$ ).

<sup>g</sup> $\text{mg N kg}^{-1}$  soil  $\text{day}^{-1}$  after 10 or 11 days ( $n = 3$ ).

<sup>h</sup> $\text{mg TPF}$  (dehydrogenase) or  $\text{pNP}$  (phosphatase)  $\text{kg}^{-1}$  soil.

<sup>i</sup>Derived from substrate-induced respiration;  $\text{mg kg}^{-1}$  soil.

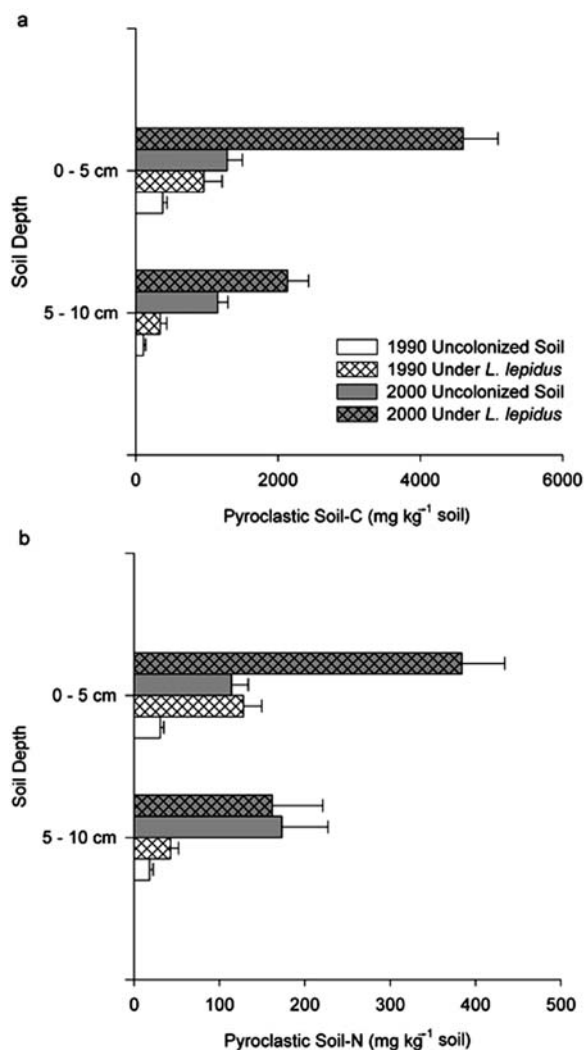


FIGURE 17.1. Vertical distribution of mean (a) soil carbon and (b) soil nitrogen in pyroclastic substrate in 1990 and 2000. Error bar is the standard error.

that received only air-fall deposits of tephra, the pyroclastic-flow site had significantly higher EC, less carbon and nitrogen, and lower C:N ratios. Samples collected in 2000 also showed the greatest concentrations of both carbon and nitrogen at the surface under prairie lupine, decreasing significantly with depth (Figure 17.1). However, no significant stratification of carbon and nitrogen was observed in uncolonized soil. Similar patterns were observed for soil enzymes, suggesting lupines are increasing both the quantity and the spatial heterogeneity of chemical and biological variables related to soil quality.

#### 17.4.4 Rates of Carbon and Nitrogen Accumulation in Soil

Soil carbon and nitrogen are increasing at the pyroclastic-flow site at rates comparable to those of other North American volcanic soils. Initial concentrations were indistinguishable from

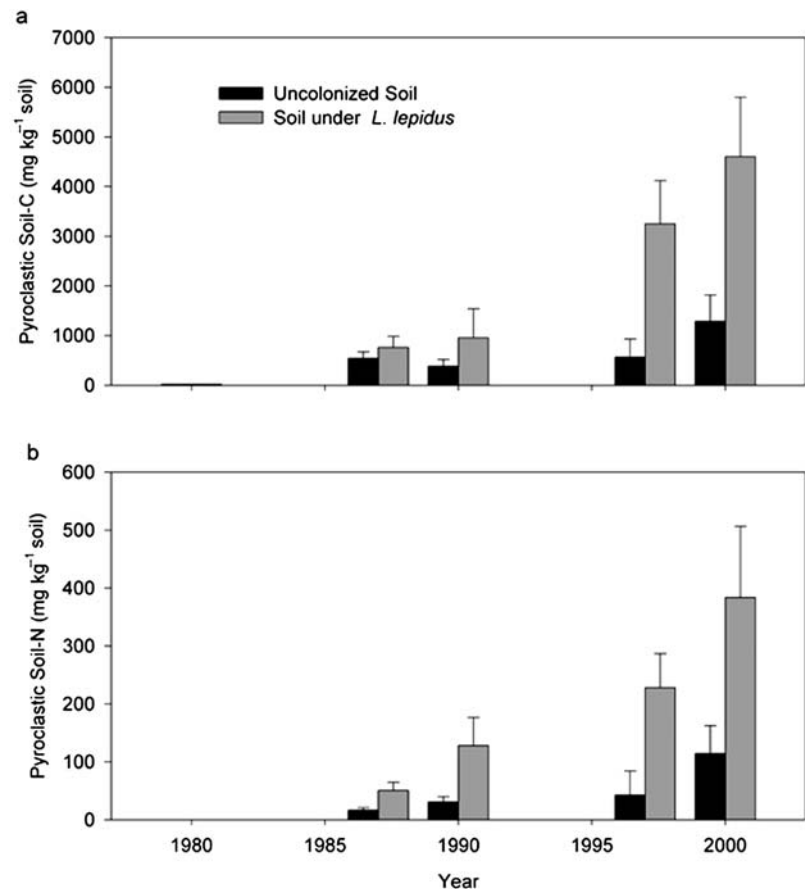
zero soon after the eruption (Engle 1983), but by 1987 total organic carbon and nitrogen had accumulated in uncolonized soil at rates of about 84 and 2.4 mg kg<sup>-1</sup> year<sup>-1</sup> and under lupines at about 120 and 7.6 mg kg<sup>-1</sup> year<sup>-1</sup> (Halvorson et al. 1991b). In comparison, Griggs (1933) observed nitrogen concentrations equivalent to accumulation rates of 3.3 mg kg<sup>-1</sup> year<sup>-1</sup> 13 years after the initial measurements of Alaskan Katmai ash deposits by Shipley (1919). Similarly, Dickson and Crocker (1953) reported nitrogen concentrations equivalent to accumulation rates of 3.5 and 8.7 mg kg<sup>-1</sup> year<sup>-1</sup> in the 0- to 12.7-cm depth of 27- and 205-year-old deposits from Mount Shasta, California. In these same deposits, they measured organic carbon concentrations equivalent to 44 mg kg<sup>-1</sup> year<sup>-1</sup> and 188 mg kg<sup>-1</sup> year<sup>-1</sup>, respectively.

By 2000, carbon and nitrogen had increased in uncolonized soil at an average annual rate of about 64 and 5.7 mg kg<sup>-1</sup> soil, respectively, compared to 230 and 19.2 mg kg<sup>-1</sup> soil in lupine-colonized soil (Figure 17.2). These concentrations are equivalent to net increases of about 42 kg C ha<sup>-1</sup> year<sup>-1</sup> and 3.7 kg N ha<sup>-1</sup> year<sup>-1</sup> for uncolonized soil and about 150 kg C ha<sup>-1</sup> year<sup>-1</sup> and 12.5 kg N ha<sup>-1</sup> year<sup>-1</sup> for lupine-colonized soil in the surface 5 cm, assuming a bulk density of 1.3. Significant ( $p > 0.05$ ) quadratic orthogonal contrasts indicate that rates of accumulation are increasing. Between 1997 and 2000, carbon and nitrogen increased in uncolonized soil by an average of 128 and 168% (241 and 24 mg kg<sup>-1</sup> soil year<sup>-1</sup>) and under lupines by 42% and 68% (452 and 52 mg kg<sup>-1</sup> soil year<sup>-1</sup>). Increasing rates of accumulation after an initial period of quiescence have also been reported for other locations undergoing primary (Chapin et al. 1994) and secondary (Zak et al. 1990) succession.

#### 17.4.5 Lupine Effects on Soil Microbial Carbon and Activity

Within 18 months after the 1980 eruption, pyroclastic-flow substrates were dominated by bacteria but exhibited low respiration rates (Engle 1983). Similarly, Halvorson et al. (1991b) reported very low amounts of active soil-microbial-biomass carbon and cumulative respiration in pyroclastic-flow soil in 1987. However, overall microbial activity was correlated with soil carbon and nitrogen and was significantly higher in prairie lupine root zones than in uncolonized soil. The average soil-microbial-biomass carbon to soil carbon ratio was less than 1% in uncolonized soil and under lupines, indicating very low substrate availability. However, this result may also be an artifact of analytical difficulties encountered in measuring very low values for microbial and total soil carbon. Adding glucose, a carbon substrate easily used by soil microorganisms, to soil collected from several sites along a volcanic disturbance gradient increased respiration in all soils tested. The greatest relative responses were observed in pyroclastic-flow soil at the low end of the carbon and nitrogen gradient. Respiration responses in pyroclastic soil occurred only after a relatively long lag time compared to other soils, indicating a small soil

FIGURE 17.2. Change in concentration of (a) soil carbon, and (b) soil nitrogen in Mount St. Helens pyroclastic deposits after the May 18, 1980 eruption.



microbial population size and low in situ resource availability to microorganisms.

Samples of pyroclastic soil collected in 1990 were also used to detect patterns of soil-microbial-biomass carbon and carbon and nitrogen mineralization from lupine biomass-amended and nonamended soils (Halvorson and Smith 1995). Similar to TOC and TKN, surface soil under broadleaf lupine contained the most microbial carbon, followed by dead and live prairie lupine and uncolonized soil, respectively. The average soil-microbial-biomass carbon to soil carbon ratio in the 0- to 5-cm depth under lupines was about 24%, and in uncolonized soil 10%, higher than in samples collected only 3 years earlier. These ratios, also higher than the 2% to 3% common to equilibrium agricultural systems reported by Anderson and Domsch (1989), infer a carbon-limited soil ecosystem, but one in which much of the carbon input from lupines or other sources is available for microbial use (i.e., it is not recalcitrant or occluded). Rather than accumulating as soil organic matter, this carbon is incorporated into soil microbial biomass. In addition, carbon inputs might be rapidly metabolized by soil microorganisms, and the apparently high soil-microbial-biomass carbon to soil carbon ratios might be the result of a priming effect (Kuzuyakov et al. 2000), where soil respiratory activity (used to calculate the microbial biomass carbon values) is dispro-

portionately stimulated by very small inputs of carbon or nitrogen in “trigger solutions” (De Nobili et al. 2001). Evidence for priming effects associated with carbon inputs by Mount St. Helens lupines was also observed in the soil of relatively undisturbed sites (Halvorson et al. 1991b) and in pyroclastic-flow soil, where the relationship between SIR-C and both TKN and TOC was curvilinear (Figure 17.3) (Halvorson and Smith 1995).

The rates at which microbial processes can proceed are governed by the characteristics of microbial populations, by the environment, and by the quantity and bioavailability of carbon substrates and nutrients. Carbon mineralization potentials (the initial amount of decomposable carbon substrate in the soil,  $C_0$ ) and carbon mineralization rate constants (the speed at which it decomposes,  $k$ ) were estimated for surface soil (0 to 5 cm), collected in 1990, with a nonlinear least-squares approach described by Smith et al. (1980) with 20-day aerobic incubation data. Bare, uncolonized soil contained significantly smaller pools of readily mineralizable carbon and thus had a lower average mineralization potential ( $C_0 = 10$  ppm) than did soil under live prairie lupine ( $C_0 = 67$  ppm), which, in turn, had mineralization potentials significantly lower than those of soils under dead prairie lupine ( $C_0 = 114$  ppm). Conversely, mineralization rate constants were significantly higher for bare

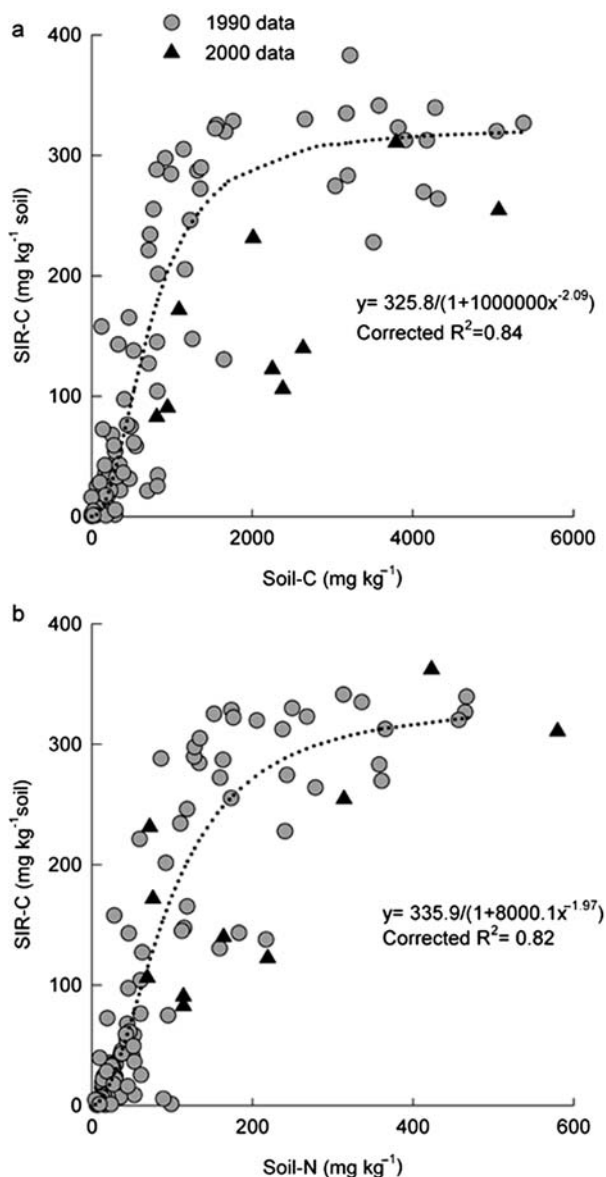


FIGURE 17.3. Relationship between microbial-biomass carbon (substrate-induced respiration method, SIR-C) and (a) soil carbon or (b) soil nitrogen observed in pyroclastic deposits (0–5 cm) for 1990 and 2000.

soil ( $k = 0.16$  per day) than either live or dead prairie lupine,  $k = 0.10$  or  $0.09$  per day, respectively. Assuming that the carbon mineralization rate is proportional to the amount of carbon substrate remaining in the soil (i.e., first-order kinetics), these data indicate the average residence time for soil carbon in pyroclastic-flow soil was extremely short, less than 2 weeks, and thus biologically active (Paul and Clark 1989; Herrick and Wander 1997). This analysis, together with observations of low amounts of TOC, TKN, and soluble carbon in soil and zero net nitrogen mineralization in some lupine-biomass-amended soils, indicates that much of the carbon in early Mount St. Helens pyroclastic-flow substrates was contained in microbial

biomass and also that microbial populations were nitrogen limited. Competition for inorganic nitrogen between microorganisms and plants may be an important mechanism for controlling early succession.

Lupines continued to augment biological indicators of soil quality in 2000 (Table 17.1). Soil collected under lupines contained significantly more microbial-biomass carbon than did uncolonized soil, a value about two orders of magnitude greater than in 1987 and about a 67% increase from 1990. Compared to 1990, ratios of soil-microbial-biomass carbon to soil carbon declined under lupines to about 8% but remained nearly unchanged in uncolonized soil, about 7%. This pattern indicates that soil organic matter is accumulating or that microbial populations are being limited in part by some other nutrient, such as nitrogen (see Figure 17.3 and following discussion). Development of larger or more active microbial populations under lupines was also reflected in significantly more soil dehydrogenase and phosphatase, important enzymes that affect biological oxidation of soil organic matter and plant nutrition (Tabatabai 1994), and in a higher metabolic quotient ( $qCO_2$ ), the amount of basal respiration per unit of soil microbial biomass. Greater microbial-biomass-carbon and enzyme activity under lupines implies an increased biological potential to mineralize soil carbon, nitrogen, and phosphorus.

Patterns of  $qCO_2$  reflect how soil microorganisms and the average quality of carbon and nitrogen substrates are closely related (Smith 1994) and may indicate a shift from a carbon-limited to a nitrogen-limited soil ecosystem (Smith 2002). Comparatively high values of  $qCO_2$  have been attributed to low microbial efficiency in disturbed, stressed, or developing ecosystems or in systems with relatively poor carbon-substrate quality. Several studies have shown that average  $qCO_2$  decreases with the age of the ecosystem and is higher in soils without vegetation or in monocropped agroecosystems (Smith 2002). However, other studies suggest  $qCO_2$  may be insensitive to disturbance and ecosystem development and unable to distinguish between the effects of disturbance and stress (Wardle and Ghani 1995). Various estimates of  $qCO_2$  derived from 1987 data previously reported by Halvorson et al. (1991b) show little difference between uncolonized and lupine soil but indicate that  $qCO_2$  for pyroclastic-flow substrates was higher than that for other, less-disturbed, Mount St. Helens sites (Wardle and Ghani 1995; Smith 2002).

More recent comparisons suggest average  $qCO_2$  in the 0- to 5-cm soil under prairie lupines is higher than in uncolonized soil. Metabolic quotients under lupines doubled between 1990 and 2000 from about 30 to 58  $\mu g CO_2$  carbon per  $\mu g$  SIR-C  $g^{-1}$  soil  $day^{-1} \times 10^3$ . In contrast,  $qCO_2$  in uncolonized soil declined from about 18 to 9  $\mu g CO_2$  carbon per  $\mu g$  SIR-C  $g^{-1}$  soil  $day^{-1} \times 10^3$  (Halvorson and Smith 1995). The increasing  $qCO_2$  observed under lupines suggests that the activity, number, or type of soil microorganisms is increased by the quantity or quality of carbon and nitrogen inputs by plants.

In 2000, average rates of soil respiration from aerobic laboratory incubations were more than 2 times higher than in



1987 (see Table 17.1). In contrast, net nitrogen mineralization rates in 2000 were lower than in 1987 and accounted for a smaller proportion of total soil nitrogen, a pattern of succession suggested by Vitousek et al. (1989). Soil respiration and net nitrogen mineralization were higher under lupines than in uncolonized soil in 1987 and 2000.

Soil microbial biomass remains significantly and positively correlated to concentrations of soil carbon and nitrogen ( $p < 0.05$ ) (see Figure 17.3). Data for samples collected in 2000 compare well with models developed in 1990 by Halvorson and Smith (1995) that predict a saturation or carrying capacity of about 330 mg biomass C kg<sup>-1</sup> soil or about 430 kg microbial biomass C ha<sup>-1</sup> in the surface 10 cm. However, soil-microbial-biomass-carbon data observed in 2000 were somewhat below model predictions in relation to soil carbon. This relationship could occur if average carbon-substrate availability is decreasing as the recalcitrant forms of soil carbon continue to accumulate in the soil or if soil microbial populations are increasingly limited by the supply of nitrogen in the soil because of greater competition for nitrogen by plants.

#### 17.4.6 Fatty-Acid Methyl Ester Profiles

Lupines have influenced the quantity and quality of fatty acids in pyroclastic-flow soil over time in comparison to uncolonized sites (Frohne et al. 1998, 2001). Soil collected in 1988 under live and dead lupines and stored air dried contained significantly greater proportions of those fatty acids associated with bacteria (15:0), gram-negative bacteria (16:1 $\omega$ 7c), and fungi or plants (18:1 $\omega$ 9c; 18:2 $\omega$ 6c) than did bare soil. Similarly, samples collected in 1997 and analyzed while still fresh showed higher proportions of fatty acids associated with gram-positive bacteria (16:0 iso); fungi or plants (18:1 $\omega$ 9c; 18:2 $\omega$ 6c); eukaryotes, mosses, and higher plants (23:0); and protozoa (20:4 $\omega$ 6c) under live and dead prairie lupine than in uncolonized bare soil (Vestal and White 1989; Findlay 1996; Sundh et al. 1997; Frohne et al. 1998; Zelles 1999; Pinkart et al. 2002). In comparison, very little fatty-acid material was recovered from either stored or fresh uncolonized soil, confirming the extremely low fertility of pyroclastic-flow material and the continuing direct link between carbon inputs by plants and development of more active and diverse soil ecosystems during succession.

Principal-component analyses of fatty-acid profiles extracted from archived samples of uncolonized soil collected from 1981 to 1988 showed that samples collected in the 1980s were less variable and distinct than were samples collected in 1997. The latter samples were likely influenced by the presence of fatty acids often found in higher plants, mosses, and eukaryotes. The presence of these fatty acids in samples of uncolonized soil collected in 1997 might be attributed to cryptogamic crust growing on the pyroclastic surface and present on about 50% of the samples, changes in the archived samples related to storage (Petersen and Klug 1994), or the influence of plant roots from nearby lupines.

Spatial analysis fatty-acid profiles collected in 1997 showed that the influence of lupine plants extends beyond the plant surface cover (Frohne et al. 1998). Although fatty-acid profiles for soil collected from directly under lupine plants were distinct and more variable than those from uncolonized soil, profiles from uncolonized locations within 0.5 m of a plant were more similar to those under lupine plants than were profiles from farther away.

Samples collected in 2000 revealed that lupines are associated with greater quantities and a more diverse array of fatty acids in relation to their inputs of carbon and nitrogen into pyroclastic soil. As in previous studies, Frohne et al. (2001) reported significantly higher concentrations of soil carbon inside lupine patches (about 4000 mg kg<sup>-1</sup>), more than five and seven times greater, respectively, than at the patch edge (about 800 mg kg<sup>-1</sup>) or in uncolonized soil (550 mg kg<sup>-1</sup>). In correlation to soil carbon, they identified at least 61 fatty acids in the soil under prairie lupine, significantly more than the 21 found in soil at the edge of the lupine patch or the 16 identified in uncolonized soil. Both the amount of soil carbon and the number of fatty acids were observed to change dramatically over short distances, increasing significantly within 50 cm along a transect extending from areas with little plant growth into zones of relatively dense plant cover.

The number of identified fatty acids was significantly, but nonlinearly, related to concentrations of soil carbon (Figure 17.4). At low concentrations of soil carbon (0% to 0.25%), the number of fatty acids was strongly related to soil carbon, but at higher concentrations the incremental increase in the number of fatty acids per unit of soil carbon decreased.

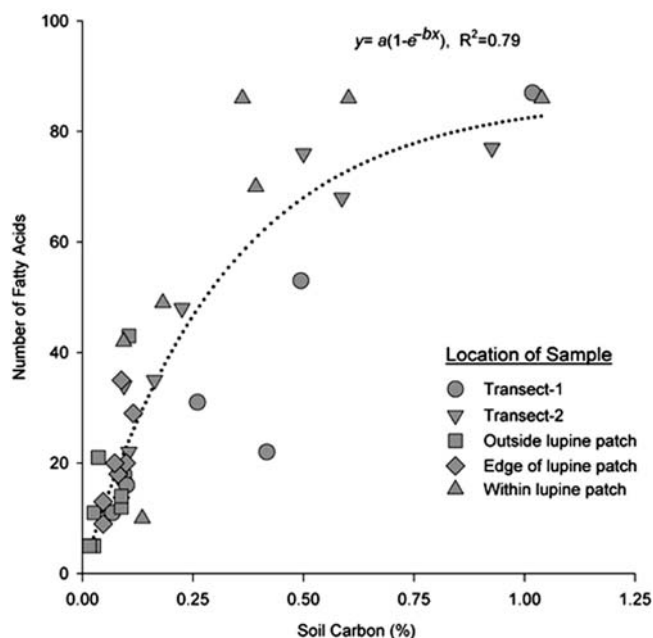


FIGURE 17.4. Relationship between pyroclastic soil carbon (0–5 cm) and the number of identified fatty acids. Samples were collected in July 2000.

Low concentrations of soil carbon were most often associated with uncolonized locations, where carbon and nitrogen accumulate more slowly in the soil from a relatively diverse variety of sources, transported by mechanisms such as animal feces, carcasses, seed rain, water, or wind deposition. There, establishment and composition of soil microbial communities would be conditioned by chance encounters between opportunistic microorganisms and unpredictable supplies of resources. Hence, fatty-acid profiles in uncolonized pyroclastic soils, influenced by both substrate and microbial diversity, would be controlled by microscale versions of low-probability stochastic events thought to be important for determining early development of devastated landscapes (del Moral and Bliss 1993; Turner et al. 1998). The number of fatty acids (i.e., substrate diversity) is thus strongly linked to the quantity of soil carbon in uncolonized locations. Conversely, at locations with more soil carbon, relatively large inputs of carbon from a few predominant plant sources (e.g., lupines) may disproportionately increase the amount of the soil-carbon pool size relative to the variety of fatty acids.

Uncoupling of the relationship between the quantity of inputs and substrate diversity may favor the development of larger but relatively less diverse microbial communities because of microbial competition and specialization. However, in carbon- and nitrogen-limited pyroclastic soil, lupine inputs appear to increase the complexity of fatty-acid profiles and support larger, more active microbial populations. Principal components of the fatty-acid profiles under lupines were distinguishable and more variable than those in uncolonized soil or at the edge of a lupine patch in 2000 (Figure 17.5a). Similar to total soil carbon and the number of fatty acids, principal-component data varied over distances of less than 1 m, as revealed by changes in the first principal component observed at the boundary between uncolonized soil and lupine patch (Figure 17.5b).

More diverse numbers of fatty acids observed under lupines were reflected in substrate-utilization patterns. Microorganisms from samples of uncolonized and patch-edge soil were able to utilize only a few of the substrates offered to them, and not every sample replicate responded the same way, suggesting highly variable and very small population numbers. Microorganisms from samples collected beneath lupine plants were able to utilize more than half of the substrate types offered to them and did so comparatively rapidly (Frohne et al. 2001). Relatively rapid response to a greater variety of substrate types and less variable patterns of substrate utilization provide further evidence for the presence of larger or more active soil microbial communities with the capability to metabolize many kinds of substrates in the soil under lupines.

#### 17.4.7 Lupine Effects on Spatial Patterns

The first studies of the Mount St. Helens pyroclastic-flow deposits using geostatistics detected spatial autocorrelation for surface characteristics such as soil moisture, temperature, and

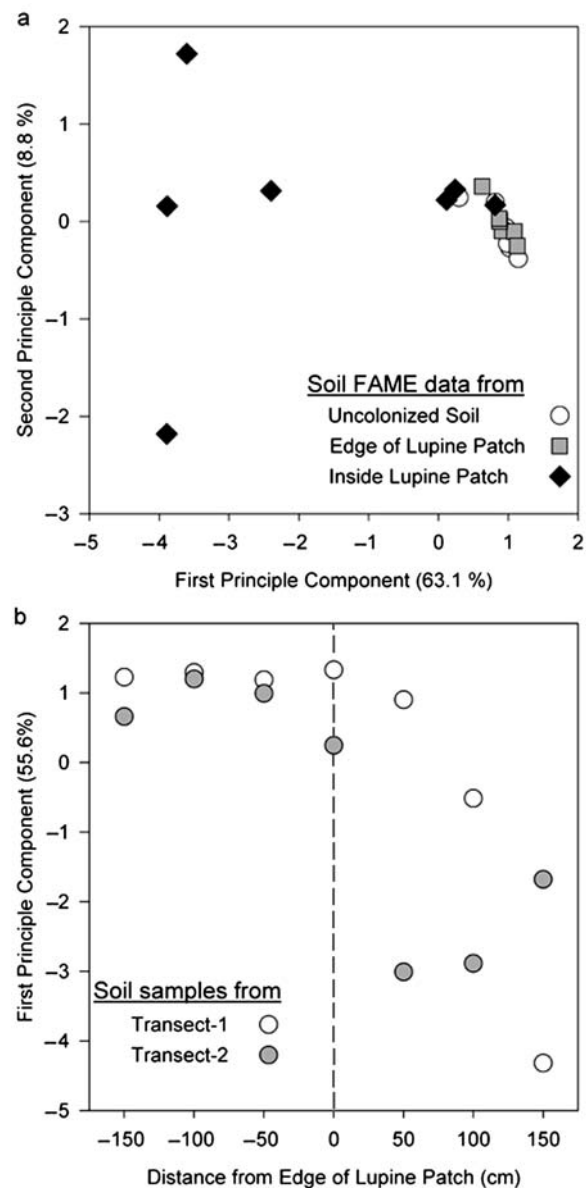


FIGURE 17.5. Plots of (a) the first two principal components calculated for soil fatty-acid methyl ester (FAME) data from samples collected in 2000 and (b) the first principal component for surface soil samples (0–5 cm) collected at 50-cm spacing along transects across lupine patch boundaries.

pH at scales of less than a meter, probably influenced most by microtopography and microclimate (Rossi 1989). Concentrations of soil carbon and nitrogen in uncolonized pyroclastic deposits were too low for reliable spatial comparisons whereas plant distribution, probably also influenced by microtopography and microclimate, exhibited only slight, small-scale spatial autocorrelation and evidence of some spatial aggregation.

Small-scale spatial patterns were again observed at the pyroclastic-flow site in June 1991 during a study to determine

the relationship between the pattern of soil variables and plant locations. Samples ( $n = 97$ ) of surface soil (0 to 5 cm) were collected in a small, modified grid pattern ( $3 \times 3$  m) and analyzed for several soil properties, including moisture content, pH, electrical conductivity, inorganic nitrogen, net nitrogen mineralization, microbial-biomass carbon, and carbon mineralization (respiration) rate. Spatial autocorrelation was characterized with variography (nonergodic correlograms) and spatially interpolated with kriging.

Spatial patterns were most apparent for soil variables associated with carbon but not for variables related to nitrogen because concentrations of nitrogen in pyroclastic-flow substrates were so low that they affected the reliability of measurements. Concentrations of inorganic nitrogen were less than  $2 \text{ mg kg}^{-1}$  with only slight autocorrelation and little apparent relationship to lupine plant location. Similarly, during a 10-day aerobic incubation, net nitrogen mineralization rates revealed little spatial autocorrelation, and maps produced by kriging indicated a random distribution across the sampling grid. Conversely, those soil variables influenced by carbon inputs from lupines, such as microbial-biomass carbon and soil respiration, showed significant spatial autocorrelation made even more evident after accounting for the confounding effects of spatial outliers. Kriged maps of the distribution of the carbon-related variables in the sample grid showed several discrete biological hotspots associated with plant location. These locations supported up to 40 times more microbial-biomass carbon and respiration rates more than an order of magnitude greater than the surrounding uncolonized substrate.

Another modified grid design ( $4 \times 4$  m) was again employed in 1997 to examine the spatial distribution of surface-soil (0 to 5 cm) properties in an area of transition between uncolonized soil and a lupine patch (Frohne et al. 1998). Lupines appeared to influence the pattern of soil moisture, with spatial autocorrelation accounting for about 75% of the total variability. Geostatistics indicated less spatial autocorrelation for pH in samples separated by very small distances (about 25 cm) than for samples separated by about 50 cm, indicative of a patchy distribution of pH, perhaps related to the location of lupine plants. Geostatistics explained more than 70% of the overall plot variation for electrical conductivity but suggested patterns larger than the extent of the sampling plot. Kriged maps indicated that concentrations of soil variables (such as soil carbon and nitrogen, pH, and electrical conductivity) and biological properties (such as microbial-biomass carbon and fatty-acid profiles) were not randomly distributed. Instead, they were often higher inside the lupine patch than they were in nearby uncolonized soil, with relatively sharp transition boundaries.

When contrasted against the background of uncolonized deposits, soil patterns related to lupines were distinct and easily measured at the pyroclastic-flow site shortly after the eruption. Patterns were often observed over short distances for those variables influenced by randomly distributed carbon and nitrogen inputs, such as single-plant colonists or animal droppings,

or for those influenced by microclimate or microtopography. Soil variables exhibiting larger-scale patterns were associated with patterns in the deposition of the pyroclastic material, topography, and the flow of water.

#### 17.4.8 Important Patterns for Succession: Abundance or Availability?

The importance of the carbon and nitrogen inputs by lupines, especially during the earliest stages of succession, may lie not in landscape-scale estimates of the rate of nitrogen inputs but rather in the temporal and spatial context of those inputs. The first lupines colonized extremely infertile pyroclastic-flow substrates, and under such conditions the ability to fix nitrogen proved to be an important advantage that allowed lupines to establish and persist. Individual lupines were an early creator of small-scale soil patterns and a direct linkage between above- and belowground processes, serving as a conduit for inputs of carbon and nitrogen into the soil. These early inputs were disproportionately important for the development of soil organic matter and the microbial communities responsible for nutrient retention and cycling and for increasing the availability of nitrogen pools in the soil, which is needed for the subsequent success of other plant species.

Patches of lupines can be thought of as resource islands that are composed of ensembles of covarying soil properties correlated spatially within the landscape. They are associated with living plants but also reinforce patterns of predecessors (i.e., areas of previous plant mortality), creating a historical context of nutrient availability. Understanding the importance of resource islands to other organisms, especially in studies of nutrient-limited ecosystems like Mount St. Helens, requires information about both abundance and availability of resources. Emphasizing the likelihood of encountering “enough” resources, at the “right” time, rather than focusing only on the locations of highest concentrations or rates of accumulation, may change the way we define resource islands or evaluate ecosystem development.

Lupines influence the average probability of subsequent plant colonists or soil microorganisms encountering resources in nonlimiting quantities and/or quality (Halvorson et al. 1995a). Aboveground, lupine plants ameliorate the local microclimate, provide cover and food for invertebrates and vertebrates, promote aeolian deposition of fine soil particles, and trap windborne seeds. Belowground, the nutrient inputs from lupine colonists create distinct zones of relative nutrient abundance. The likelihood of a particular seed or microorganism encountering those resources is affected by its proximity to the lupine and by dispersal patterns, a function of time, distance, propagule abundance, transport mechanisms, and random events. Locally dispersed lupine seeds and microorganisms in the lupine rhizosphere have the highest chance for encountering nutrients, followed by seeds that are preferentially transported to the lupine vicinity by biotic vectors, such as

small vertebrates or windborne seeds trapped by lupine plants themselves. These patterns indicate a reinforcing feedback between lupine colonists and other resource-island-promoting mechanisms, such as the growth of other plants or heterotrophic microorganisms. Propagules separated from lupine resource islands by greater distance or those affected mostly by random dispersal processes have the lowest spatial probability of encountering resource islands.

In addition to spatial uncertainty, low substrate availability to heterotrophic soil microorganisms and competition for resources between lupines and microorganisms may decrease the temporal probability of encountering resources by other plant species. On extremely infertile sites, both plants and heterotrophic microorganisms are limited by the quantity of soil nitrogen. Generally, carbon inputs from plants drive microbially mediated activities, such as nitrogen fixation and decomposition, thereby increasing the availability of nitrogen to plants in a cooperative or facilitatory manner (see Connell and Slatyer 1977). However, data from pyroclastic deposits suggest soil microorganisms may actively compete with plants for nitrogen during early succession, when quantities are limiting. During such times, plant-microbial interactions might be competitive or antagonistic (Smith 1994; Lindahl et al. 2002). Competition for nitrogen by soil microorganisms, fueled with carbon substrates supplied by lupines, would limit its availability to nonlegume plants and reinforce the advantage of nitrogen fixation for lupine colonists. Mineralization would become a significant source of nitrogen to plant colonists only at times when the amount of nitrogen available in the soil exceeded the needs of soil microorganisms (Halvorson and Smith 1995). However, as soil nutrient pools increase, so does the likelihood of encountering them. Consequently, the importance of incremental carbon and nitrogen inputs by

lupines will diminish together with the spatial and temporal uncertainty of encountering them. In addition to providing a simple source of carbon substrates for heterotrophic microorganisms, other plant inputs, such as polyphenolic compounds and organic acids, may increase in importance for influencing the activity of soil microorganisms, nutrient nitrogen and phosphorus availability, and tolerance of low-pH soil conditions (Jones 1998; Hättenschwiler and Vitousek 2000; Hocking 2001).

## 17.5 Future Research Needs

Pyroclastic deposits at Mount St. Helens provide a unique opportunity to investigate the impacts of legumes (lupines) on ecosystem development and to come to a more complete understanding of how the aboveground processes associated with succession relate to and are affected by changes in belowground resource pools and processes. However, more information is needed about how the quantity and quality of plant inputs, soil microorganisms, and nutrient cycling change as soils develop. Important temporal and spatial patterns of belowground succession need to be identified together with appropriate scales of measurement. Appropriate experimental designs are needed that can translate small-scale, short-term spatial and temporal patterns of microbial processes, such as nitrogen mineralization, nitrification, and denitrification, into longer-term landscape-scale patterns of carbon and nitrogen cycling. This achievement will require determining which soil and microbial variables are most important at different spatial and temporal scales, what measurements should be taken and when, and what complex interactions among soil variables should be taken into consideration (Halvorson et al. 1997).