

Richard A. Gill · Jennifer A. Boie · John G. Bishop  
Lindsay Larsen · Jennifer L. Apple · R. David Evans

## Linking community and ecosystem development on Mount St. Helens

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**Abstract** In the two decades following the 1980 eruption of Mount St. Helens in Washington State, the N<sub>2</sub>-fixing colonizer *Lupinus lepidus* is associated with striking heterogeneity in plant community and soil development. We report on differences in nutrient availability and plant tissue chemistry between older, dense patches (core) of *L. lepidus* and more recently established low density patches (edge). In addition, we conducted a factorial nitrogen and phosphorus fertilization experiment in core patches to examine the degree of N and P limitation in early primary succession. We found that there were no significant differences in N or P availability between core and edge *L. lepidus* patches during the dry summer months, although nutrient availability is very low across the landscape. In the high density patches we found lower tissue N content and higher fiber content in *L. lepidus* tissue than in the younger edge patches. The addition of nutrients substantially altered plant community composition, with N addition causing an increase in other forb biomass and a corresponding competition-induced decline in *L. lepidus* biomass. The majority of the positive biomass response came from *Hypochaeris radicata*. In the second year of the fertilization experiment, the addition of N significantly increased total community biomass while *L. lepidus* biomass declined by more than 50%. The response of every species other than *L. lepidus* to N additions sug-

gests that N may be the macronutrient most limiting plant production on Mount St. Helens but that the gains in productivity were somewhat offset by a decline of the dominant species. By the third year of the experiment, *L. lepidus* began to increase in abundance with P addition. This result suggests co-limitation of the community by N and P.

**Keywords** Fertilization · *Lupinus lepidus* · Nitrogen · Phosphorus · Primary succession

### Introduction

Primary succession can be viewed as coupled de novo development of soil function and plant communities (Jenny 1941; Halvorson et al. 2005). The interaction between species-specific life history characteristics and soil development is particularly important early in primary succession when physical conditions preclude the establishment of many potential members of the plant community. For example, volcanic ash and lava flows have nearly undetectable concentrations of N (del Moral and Bliss 1993; Vitousek 1999) and the establishment and proliferation of N<sub>2</sub>-fixing species is viewed as a rate-limiting step for both community and ecosystem development in most primary successional landscapes (Vitousek and Reiners 1975; Gorham et al. 1979; Lichter 1998). Facilitation, where colonizing species ameliorate the effects of a limiting factor and thereby place themselves at a competitive disadvantage, has long been considered a major mechanism for succession (Clements 1916). While the role of facilitation has been questioned in high-resource, secondary successional environments (Connell and Slatyer 1977; Chapin et al. 1994), the severe conditions experienced on newly exposed or deposited substrate, such as tephra (del Moral and Bliss 1993), glacial outwash (Reiners et al. 1985), and dunes (Lichter 1998), more commonly requires the amelioration of low nutrient and water deficit prone conditions for the establishment of later colonists. However, facilitation

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R. A. Gill (✉) · J. A. Boie  
Program in Environmental Science and Regional Planning,  
Washington State University, Pullman, WA 99164-4430, USA  
E-mail: rgill@wsu.edu  
Tel.: +1-509-3356422

J. G. Bishop · L. Larsen · J. L. Apple  
School of Biological Sciences, Washington State University  
Vancouver, 14204 NE Salmon Creek Ave., Vancouver,  
WA 98686, USA

R. D. Evans  
School of Biological Sciences, Washington State University,  
Pullman, WA 99164, USA

alone rarely explains patterns of early succession; stochastic processes and priority effects are important (del Moral and Wood 1993), and species traits and trophic interactions must be evaluated in concert with nutrient availability to understand changes in plant communities with time (del Moral and Wood 1993; Chapin et al. 1994; Fagan and Bishop 2000). There may be strong interactions between these processes, where the stoichiometry of nutrient supply rates may strongly influence patterns of herbivory and organic matter decomposition rates which collectively control plant community structure on primary successional landscapes (Schimel et al. 1998; Leuschner and Rode 1999; Fagan et al. 2004).

On 18 May 1980, Mount St. Helens (Washington, USA) erupted violently creating approximately 60 km<sup>2</sup> of primary successional habitat (Swanson and Major 2005). A lateral blast, debris avalanche and subsequent pyroclastic flow sterilized the upper flanks of the mountain erasing all biological legacies (Swanson and Major 2005). Initial conditions on the pyroclastic flows appeared to be generally uniform, with sterile, coarse parent material with low fertility and very little structure or water holding capacity (del Moral and Bliss 1993; Halvorson et al. 2005). In 1980–1982, several individual N<sub>2</sub>-fixing lupines (*Lupinus lepidus* var. *lobbii*) colonized the north slope of Mount St. Helens, and soon began rapidly expanding outward from initial establishment sites (del Moral et al. 1995). Ten years after the eruption, lupines were found in high-density, large core areas at the sites of initial colonization with low density edges and scattered low-density patches elsewhere (del Moral and Wood 1993; Fagan and Bishop 2000). Where patches established, small-scale “islands of fertility” formed underneath individual lupine plants that included greater N concentration and larger microbial populations than in plant interspaces (Halvorson et al. 1992; Halvorson and Smith 1995).

Between 1991 and 1995, the rate of increase for newly establishing lupines was far below the remarkable rates initially noted (Fagan and Bishop 2000; Bishop et al. 2005). Because of the lupine’s pivotal role in facilitating community development (Wood and del Moral 1987; del Moral et al. 1995; Titus and del Moral 1998; del Moral and Rozzell 2005) through N-fixation and organic matter formation (Halvorson et al. 1991, 1992; Halvorson and Smith 1995), the decrease in spread of lupines likely is of major consequence for ecosystem development at Mount St. Helens. Several studies have identified herbivory as the most likely mechanism for the decreased rate of *L. lepidus* spread, although drought events as in 2003 are also important (Fagan and Bishop 2000; Bishop 2002; Bishop et al. 2005). Of considerable note are the remarkably higher herbivore loads found in low density edge areas as compared to high density core areas. This difference may be linked to higher C:N and C:P (and thus fewer nutrients) in lupine leaves from high density core areas (Fagan et al. 2004; Bishop et al. 2005; J.G. Bishop, J.L. Apple, and W.F. Fagan, unpublished manuscript). However, many questions remain un-

answered about the potential interaction between nutrient availability, plant tissue chemistry, herbivory, and succession.

Nitrogen is widely considered to be the most important macronutrient limiting plant growth early in succession because it must be obtained from atmospheric sources (Vitousek et al. 1987; Walker and del Moral 2003) while other macronutrients are present in most primary materials. However, coincident with the absence of available N in early succession is a paucity of plant-available P. For P to be available for plant uptake, it must be weathered from calcium apatite (Walker and Syers 1976; Crews et al. 1995; Raich et al. 1996), so during the initial stages of primary succession P may limit plant production for N<sub>2</sub>-fixing species and ultimately the rate of plant succession (Walker and Syers 1976; Raich et al. 1996). There is a strong potential for interactions between P and N availability because of the large phosphorus demand in legume physiology, including for N<sub>2</sub>-fixation (Vitousek et al. 2002; Schlesinger 1997).

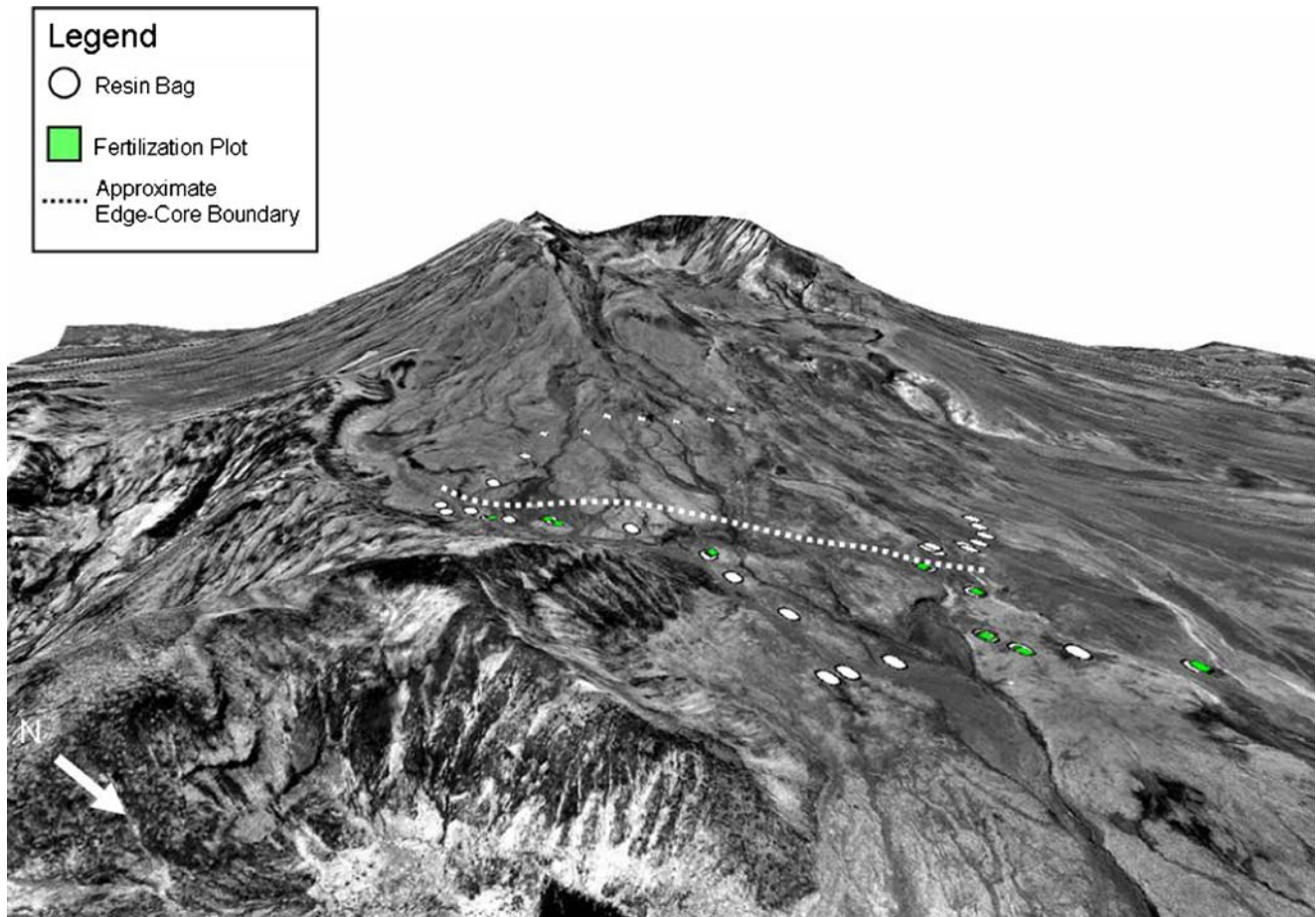
Because of the potentially strong role of plants in biological weathering of rock-derived nutrients and the accumulation of organic material in resource islands beneath individual plants, we hypothesized that there would be higher availability of inorganic nitrogen, phosphate, and base cations in the high-density core patches than in the low-density edges and unoccupied open areas. We also hypothesized that differences in nutrient supply rates would result in substantial differences in plant tissue chemistry and tissue decomposition rates. Finally, we hypothesized that nutrient availability strongly influences the abundance and distribution of the dominant pioneer plant species on Mount St. Helens. The links between these factors may elucidate the causes of the spatial distribution of herbivory in the core and edge patches and the resultant decline in lupine growth rate and expansion. Our approach in evaluating these hypotheses involved measuring plant available N, P, and base cations between core and edge areas or from between or underneath live plants, testing *L. lepidus* tissue chemistry for plants collected from core or edge patches and evaluating whether this influences rates of tissue decomposition, and finally conducting a factorial nutrient addition experiment within core patches.

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## Materials and methods

### Site description

The Spirit Lake pyroclastic flow site is located on the north slope of Mount St. Helens (46°15′N, 122°10′W, 1,160 m; Fig. 1). Mean annual temperature in 2002–2003 was 6.6°C and mean annual precipitation (1971–2004) is 224 cm, although in 2003, the second year of this study, precipitation was only 75% of the long-term mean (167 cm). In spite of high mean annual precipitation, there can be periods during the summer with severe water deficits. In 2002, there was 6 cm of precipitation



**Fig. 1** Location of the core and edge plots used to determine spatial patterns of nutrient availability and plant tissue chemistry. The nine core plots are where the factorial fertilization experiment was conducted

between 1 June and 1 September, while in 2003 there was only 1.5 cm during the same period. During summer 2004 there was 28.1 cm of precipitation.

There was a strong spatial component to the establishment of *L. lepidus* on the pyroclastic flows. Long-term research that began soon after the eruption in 1980 has established that core patches were in areas known to have had *L. lepidus* since the 1980s (Bishop 2002) and where *L. lepidus* was found in high density, while edge patches were classified based on having lower lupine density and the spatial separation from the older, core patches. Core patches are those where there has been long-term (>15 years) plant presence and plant density is high while edge plots were established more recently than core areas and plant density is lower (Fagan et al. 2004; Bishop et al. 2005). Eight core patches and eight edge patches were chosen for study during the 2002–2004 growing seasons. There are potential microclimate differences between core and edge areas since all core areas are found on the lower flanks of the mountain while the edge patches are all higher in elevation on slightly steeper slopes (Fig. 1). For all sites, aspect was similar, although there are small differences in slope.

Nevertheless, there are locations where both core and edge sites are on similar substrate and elevation indicating that differences between core and edge are not strictly due to differences in microenvironment. In addition, all of the sites we studied had poorly developed soils with little water-holding capacity, suggesting that late-growing season water deficits are a significant influence across the pyroclastic flows.

Sampling sites within each patch were randomly chosen. Each of the core patches was considered to be independent and was treated as a “core patch” replicate and each of the edge patches was treated as an “edge patch” replicate. It is unknown precisely when the edge patches were colonized, but it is likely that they were all established more than a decade after the initial colonization of the core area. The variables measured in each of the regions included membrane exchangeable nutrients, net in situ N mineralization, tissue chemistry, and tissue decomposition rate. Because of the low plant cover in edge patches, we focused on core patches for our nutrient addition experiment and we included one additional core patch for the nutrient addition experiment ( $n=9$  core patches).

## Nutrient availability

Our first objective was to determine whether there are spatial and temporal differences in soil nutrient availability based on time since pioneer plant establishment or the presence or absence of plants. We accomplished this objective using ion exchange membranes and in situ net nitrogen mineralization techniques.

### *Ion exchange membranes and resin bags*

In summer 2003, we installed cation and anion exchange membranes in the top 10 cm of the soil profile (PRS-probes, Western Ag Innovations, Saskatoon, SK, Canada) in both edge and core patches to measure relative differences in nutrient availability. These membranes provide an index rather than absolute areal amounts and are useful in gauging relative differences in nutrient availability. The permanent charge on the 17.5-cm<sup>2</sup> membranes attracts oppositely charged ions from the soil solution (Hangs et al. 2003). Based on this principle, the ions recovered from the membrane serve as a relative index of plant available nutrients. Because the membranes are sensitive to ion mobility and diffusion rates, differences in soil moisture could influence the measurement. However, this is likely also the case for root uptake and, as such, this method provides a fairly good proxy for plant available nutrients. Resin membrane data are reported in units of N cm<sup>-2</sup> 12 weeks<sup>-1</sup> (Hangs et al. 2003).

The sampling within the patches was stratified, with three of each membrane type placed in plant interspaces and three membranes below plants ( $n=3$  for each microsite). Values reported for nutrients adsorbed to the membranes were averages of the three subsamples. The membranes were installed initially on 3 June 2003 and, after 6 weeks, the first set was collected and a second set installed. The second set was recovered after an additional 6 weeks. We summed the ions recovered from the membranes for the entire growing season. Because adsorption onto resins is nonlinear, with greater adsorption with fresh resins than older ones, the reported values may be greater than would be presented if single resins were used for the entire growing season (Hangs et al. 2003). We chose to replace them after 6 weeks to avoid the risk of saturating the membranes and not getting valid results.

On 24 June 2004, we placed cation–anion exchange resin (10-g) (Dowex MR-3, Dow Chemical) in nylon pouches in the top 5 cm of the soil below lupines and in plant interspaces (Fig. 1). Each of these sites was georeferenced and we recorded lupine density. On 28 August 2004, we removed these bags and transported them to Washington State University for analysis. These bags were extracted with 50 ml of 2 M KCl and we analyzed the extracts colorimetrically for NH<sub>4</sub><sup>+</sup> and NO<sub>3</sub><sup>-</sup> (Lachat Quick Chem 8000 FIA+, Lachat Instruments, Milwaukee, Wis., USA). Data are reported as the

weighted average of NH<sub>4</sub><sup>+</sup> and NO<sub>3</sub><sup>-</sup> recovered from below plants and in the interspaces.

### *Net N-mineralization*

A closed-top solid cylinder method (Hart et al. 1994) was used to determine the accumulation of inorganic N as an index of net N mineralization rates. The net N mineralization rates represent the conversion of organic N to plant-available inorganic N (Hook and Burke 1995). At each of the sites sampled, two soil cores (5-cm diam × 15-cm deep) were taken within 5 cm of each other. The first soil core was placed in a plastic bag and put on ice to transport back to the laboratory for analysis within 24 h of collection. The second soil core was placed in a plastic sleeve, capped at both ends, reinserted back into the ground and allowed to incubate between 18 July and 12 August 2002, after which it was transported to the laboratory on ice for analysis within 24 h of collection. Once in the laboratory, subsamples were sieved through a 2-mm screen to remove all rocks and roots. Inorganic N was extracted from 15 g subsamples in 40 ml of 2 M KCl by shaking on a mechanical shaker for 1 h. The suspensions were filtered through pre-washed #2 Whitman filter paper and the extracts were frozen until they were analyzed for NH<sub>4</sub><sup>+</sup> and NO<sub>3</sub><sup>-</sup>. Net rates of N mineralization were determined from the difference in soil inorganic N concentration between the final and initial soil samples (Hart et al. 1994; Hook and Burke 1995). The net rates of N mineralization were calculated as mg N (m<sup>2</sup> day<sup>-1</sup>)<sup>-1</sup>.

### *Plant tissue chemistry*

Our second objective was to determine if there were significant differences in plant tissue chemistry between core and edge areas and whether differences in tissue chemistry led to differences in decomposition rates. Several measures of tissue chemistry including leaf N, lignin, fiber, and soluble carbohydrate content have been used to examine tissue quality and susceptibility to herbivory (Melillo et al. 1982; Cotrufo et al. 1998; Gill and Burke 2002). In most plant nutrition studies the fiber fraction—consisting of hemicellulose and cellulose—and the lignin fraction are considered deterrents to herbivores because they are of little nutritional value, are difficult to digest, and bind N, while tissues high in N and soluble carbohydrates have high nutritional value and a high digestive efficiency (Meentemeyer 1978; de Lacerda et al. 1986; Gutschick 1999; Lucas et al. 2000).

Our measures of plant tissue chemistry included C/N, % nitrogen, lignin, fiber, and soluble carbohydrate content of leaf and stem tissue. *Lupinus lepidus* tissue was collected from approximately ten plants at each of nine core and nine edge sites between 21 and 22 August 2002. All *L. lepidus* tissue was prepared by drying at 55°C for 5 days, removing leaflets from the rest of the plant, and

grinding leaflets. Prepared plant tissue from each sample was sent to the Wildlife Habitat Nutrition Laboratory, Department of Natural Resources, Washington State University Pullman, for analysis by the Van Soest method to determine % acid detergent lignin, % acid detergent fiber, and % soluble carbohydrates (Van Soest 1967). Prepared plant tissue from each sample was also sent to the Soil Fertility/Nutrient Cycling and Rhizosphere Ecology Laboratory, Department of Crops and Soils, Washington State University Pullman, for analysis on a LECO CNS 2000 Dry Combustion Analyzer (LECO, St. Joseph, Mich., USA) to determine %C and %N.

Potential decomposition rates for tissue collected from core or edge areas was determined by measuring C and N mineralization from *L. lepidus* tissues in 6-week controlled laboratory incubations. Microlysimeters were constructed by placing a Whatman G/FA filter into a Nalgene analytical test filter funnel (147 series, cellulose nitrate membrane removed), then placing a small wad of glass wool over the filter. The soil, tissue, and water as described below were placed into the filter funnel and the whole apparatus was placed in a mason jar. Fifty grams of soil from a single core-area from Mount St. Helens were separately amended with 1 g of *L. lepidus* tissue (collected for biomass estimates between 21 and 22 August 2002) from each of the samples from the core and edge plots. Added to each soil and tissue amendment was 15 ml of distilled water to bring the soil to field capacity, and an additional 15 ml of water was added to the bottom of each microlysimeter to maintain moisture within the chamber. The microlysimeters containing the soil and tissue were incubated in the laboratory using methods modified from Nadelhoffer (1990) and Zibilske (1994). During incubation, the microlysimeters were loosely covered to allow oxygen to enter without losing much water. The microlysimeters were uncovered for 1 h before measurements to allow any accumulated CO<sub>2</sub> to dissipate. After the accumulated CO<sub>2</sub> had dissipated, the microlysimeters were tightly covered for 1 h to trap CO<sub>2</sub> given off by microbial respiration during the 1-h time period, after which a syringe with a stopcock was used to sample the headspace of the microlysimeter. The sample of accumulated CO<sub>2</sub> was injected into an EGM-3 Environmental Gas Monitor (P.P. Systems, Boston, Mass., USA) for measurement of CO<sub>2</sub> in ppm. The C mineralization rates were measured at 24 h, 1, 2, 4, and 6 weeks. Blanks were used to control for variable CO<sub>2</sub> concentrations in the laboratory.

Nitrogen mineralization potential of the *L. lepidus* tissue from the core and edge plots was measured by leaching of the above described microlysimeters at 2 and 6 weeks, and 100 ml of leaching solution (4 mM CaCl<sub>2</sub>•2H<sub>2</sub>O, 2 mM KH<sub>2</sub>PO<sub>4</sub>, 1 mM K<sub>2</sub>SO<sub>4</sub>, 1 mM MgSO<sub>4</sub>, 25 μM H<sub>3</sub>BO<sub>3</sub>, 2 μM MnSO<sub>4</sub>, 2 μM ZnSO<sub>4</sub>•7H<sub>2</sub>O, 0.5 μM CuSO<sub>4</sub>•5H<sub>2</sub>O, 0.5 μM Na-MoO<sub>4</sub>•2H<sub>2</sub>O) was added to the samples and left to equilibrate for 1 h. After 1 h, the solution was filtered from the samples and the sample extracts were frozen until they were analyzed for NH<sub>4</sub><sup>+</sup> and NO<sub>3</sub><sup>-</sup> on a Lachat

Quick Chem 8000 FIA+ (Lachat Instruments, Milwaukee, Wis., USA). Net N mineralization potential was calculated as the sum of soil inorganic N per g tissue.

### Community responses to nutrient availability

Our final objective was to evaluate how sensitive plant community dynamics are to changes in nutrient availability. One motivation for doing this is to determine the extent to which the dominant pioneer plant (*L. lepidus*) is constrained by phosphorus availability and the influence of N and P availability on the other members of the plant community. We adopted a functional definition of limitation, interpreting increases in primary production or plant cover with nutrient addition as an indication of nutrient limitation. Within our eight core patches, we established a full factorial fertilization treatment (Fig. 1). Four 9-m<sup>2</sup> plots for each replicate patch were identified and randomly assigned to one of the fertilization treatments. The four treatments were: (1) control; (2) +N (7.8 g-N m<sup>-2</sup> year<sup>-1</sup> as NO<sub>3</sub>NH<sub>4</sub>); (3) +P (10 g-P m<sup>-2</sup> year<sup>-1</sup> as superphosphate); and (4) +N, +P where both nitrogen and phosphorus were added. Fertilization occurred early in the growing season in 2002, 2003, and 2004. The N addition amounts are approximately 10 times the annual input of N received through wet and dry depositions in this part of the Cascade Mountains (NADP 2004). The pH of the soils has been influenced by the highly acidic precipitation in this region and is between 5.04 and 5.19 (Ugolini et al. 1991; Halvorson and Smith 2005). Because of this, some of the fertilizer phosphate was likely complexed with iron and aluminum. In August 2002 and 2003, 0.5 m<sup>2</sup> quadrats were clipped from the interior 4 m<sup>2</sup> of the fertilized plots. Plant biomass was returned to the laboratory and dried at 55°C for 48 h. Biomass was separated based on species and weighed. In addition, we measured % cover for each species in each plot. In August 2002, we also assessed the role of nutrients in controlling the reproduction of two of the dominant non-lupine forbs, *Hypochaeris radicata* and *Hieracium albiflorum*. For these two forbs, we measured rosette size, number of reproductive stalks per plant, and the seed mass per stalk for all plants in a 1-m<sup>2</sup> quadrat in each plot. In 2004, we did not clip biomass, but rather assessed plant cover of each species within 2 m<sup>2</sup> of each treatment plot. Data for 2004 are reported as % cover rather than g-biomass m<sup>-2</sup>.

### Statistical analysis

Analysis of variance and Tukey–Kramer tests were performed in SAS (SAS, Cary, N.C., USA) to detect if there were significant differences between core and edge regions for the nutrient supply rate and tissue chemistry response variables. For the ion exchange membrane data we also determined whether there were significant

microsite differences under-plants or in plant interspaces. There were never any significant interactions between patch and microsite, so the interaction term was removed from the model. A significance level of  $P \leq 0.10$  was used due to low nutrient content and high spatial variability in the plots sampled. For the nutrient addition study, we nested the analysis of variance, using site as a random effect.

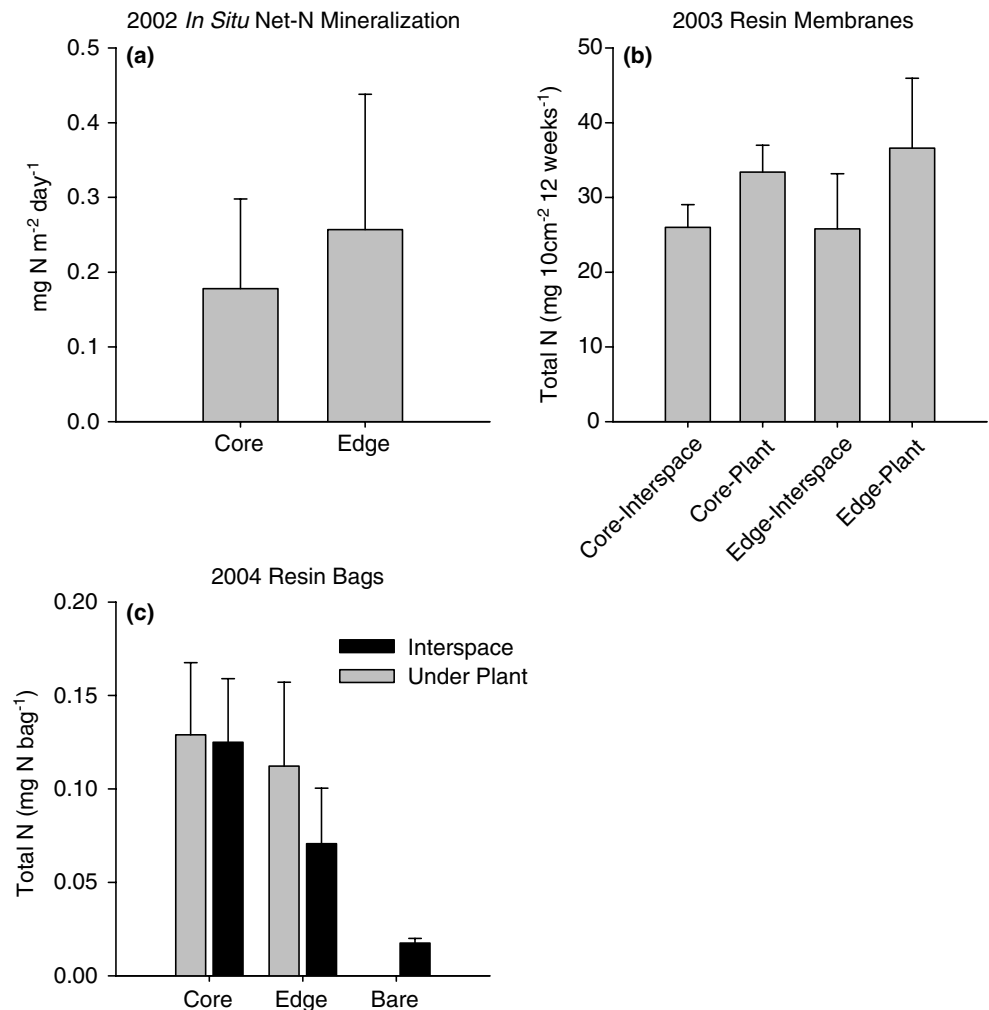
## Results

### Nutrient availability

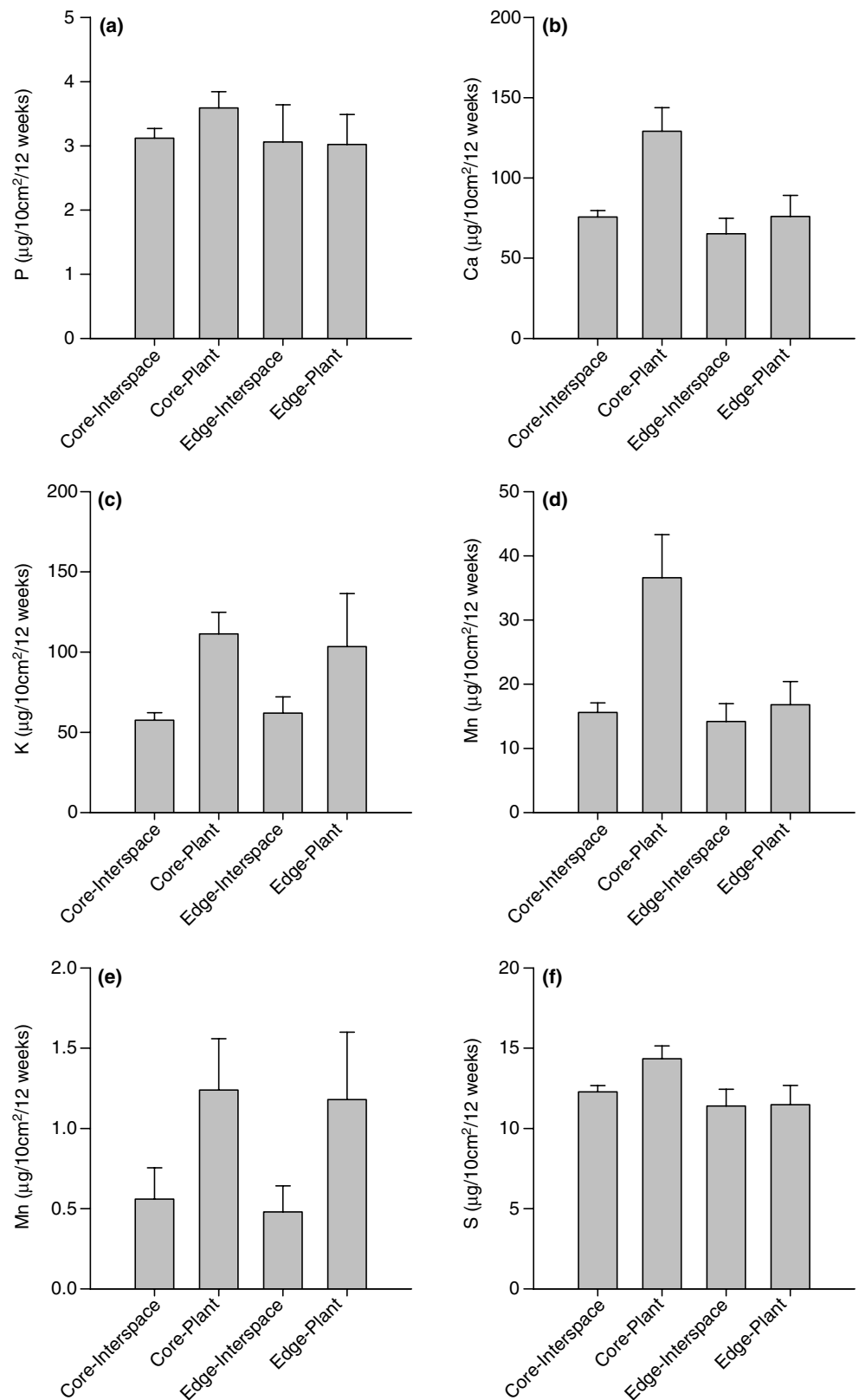
There were no significant differences between core or edge patches in resin available N or in situ net N-mineralization (Fig. 2). Mean exchangeable  $\text{NO}_3^-$  was not significantly different between patches at  $31.2$  and  $29.7 \mu\text{g NH}_4^+-\text{N } 10 \text{ cm}^{-2} 12\text{-weeks}^{-1}$  for core and edge patches respectively ( $P=0.88$ ). Although mean net N-mineralization was 1/3 higher in under-plant microsites, this difference was not significant because of the high variability in N-mineralization rates, with under-plant measures of available N of  $34.6 \mu\text{g NH}_4^+-\text{N}$

$10 \text{ cm}^{-2} 12\text{-weeks}^{-1}$  and plant interspaces having  $25.7 \mu\text{g NH}_4^+-\text{N } 10 \text{ cm}^{-2} 12\text{-weeks}^{-1}$  ( $P=0.16$ ). In only one location was there  $\text{NO}_3^-$  recovered above minimum detection limits. Results from our paired-core in situ net N mineralization were not significantly different between patch-types, averaging  $0.23 \text{ mg N m}^{-2} \text{ day}^{-1}$ . We did not stratify our N-mineralization analyses so we cannot determine whether there are differences between microsites based on this method. Ion exchange techniques and net N-mineralization are not directly comparable, but they both provide an index of N-availability. In 2004, again there were no significant differences between edge and core plot N-availability measured using ion-exchange resin bags ( $P=0.25$ ; Fig. 2c). The consistency between ion exchange membranes and in situ net N mineralization rates suggest that N availability is not significantly different between core and edge patches. For phosphorus, there were no significant differences between patch type and microsite, with an average recovery from the anion exchange resin of  $3.2 \mu\text{g PO}_4^--\text{P } 10 \text{ cm}^{-2} 12\text{-weeks}^{-1}$  (Fig. 3a). One important implication of these results is that during the summer when soil water potentials are low, supply rates of N and P from soil pools are quite variable across the pyroclastic flows,

**Fig. 2** Indices of available N (2002–2004). **a** In situ N-mineralization in 2002. **b** Inorganic N recovered from ion exchange membranes in 2003 that were placed in core patches either under plants (*C-P*) or in plant interspaces (*C-I*) or in edge patches under plants (*E-P*) or in plant interspaces (*E-I*). **c** Inorganic N recovered from ion exchange resin bags in 2004 from either under plants or in plant interspaces for core or edge patches or areas that are not currently colonized (*bare*)



**Fig. 3** Nutrients recovered from ion exchange membranes that were placed in core patches either under plants (*C-P*) or in plant interspaces (*C-I*) or in edge patches under plants (*E-P*) or in plant interspaces (*E-I*). Measurements were made during 12 weeks during the 2003 growing season. **a**  $\text{NH}_4^+$  and  $\text{NO}_3^-$  recovered, with nearly the entire recoverable inorganic N found as  $\text{NH}_4^+$ ; **b**  $\text{PO}_4^{2-}\text{-P}$ ; **c**  $\text{K}^+$ ; **d**  $\text{Ca}^{2+}$ ; **e**  $\text{Mg}^{2+}$ ; **f**  $\text{Mn}^{2+}$ . For inorganic N,  $\text{K}^+$ , and  $\text{Mn}^{2+}$ , nutrient availability was significantly greater under plants than in interspaces. For  $\text{PO}_4^{2-}$ ,  $\text{Ca}^{2+}$ , and  $\text{Mg}^{2+}$ , there was significantly greater ions recovered from the core areas than edge patches. Error bars are one standard error



although not consistent with current patterns of plant density. In the older, high density core areas where the number of individual plants and total plant biomass is higher, the nutrient availability per individual is much

lower than in the low-density edge patches, but in both cases tends to be very low.

We found significant differences in nutrient availability between both core and edge patches and between

microsites for several rock-derived micronutrients. There was significantly more  $\text{Ca}^{2+}$ ,  $\text{Mg}^{2+}$ , and S under plants in core patches than in interspaces or in edge patches (Fig. 3). For nearly all of these cations, concentrations increased by nearly 100% in core patches. Plant presence also significantly increased membrane extractable for  $\text{K}^+$  and  $\text{Mn}^{2+}$  and significantly decreased  $\text{Cu}^{2+}$  (data not shown) (Fig. 3).

#### Plant tissue chemistry

*Lupinus lepidus* leaf chemistry was significantly different between the core and the edge regions for several variables (Table 1), despite no measured significant difference in potential C mineralization between the core and edge region tissues (Table 2). Tissues of *L. lepidus* from core patches had lower N content ( $P=0.0616$ ), and higher C:N ( $P=0.0126$ ) and fiber content ( $P<0.0001$ ) (Table 1). Fiber content in *L. lepidus* leaf tissue was negatively correlated with *L. lepidus* leaf N content ( $P=0.001$ ) (Fig. 4) suggesting that N limitation in the core due to increased competition for P and N may be contributing to high fiber and low N content in *L. lepidus* tissues from the core. In addition to higher N content, tissues of *L. lepidus* from edge patches also had significantly higher soluble carbohydrate content ( $P=0.0002$ ) and a significant positive correlation ( $P=0.001$ ) between the two variables was found.

Potential net N mineralization of *L. lepidus* tissue was significantly higher in the edge region than the core region ( $P=0.0175$ ) (Table 2) and was positively correlated with N content of *L. lepidus* tissue ( $P=0.015$ ) and soluble carbohydrate content of tissue ( $P=0.002$ ). The higher N and soluble carbohydrate content in edge tissues along with a positive correlation ( $P=0.014$ ) between in situ soil net N mineralization and tissue net

**Table 1** Mean, standard error, and  $P$  value for tissue chemistry variables

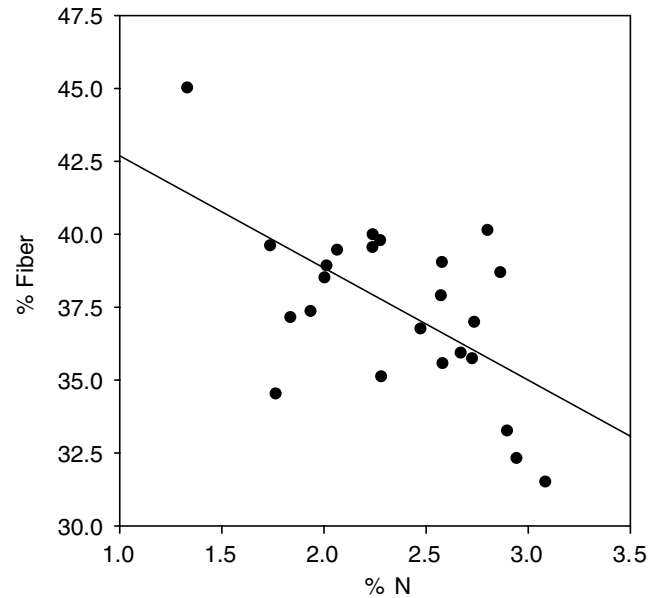
| Variable                | Core                      | Edge                      | $P$ -value |
|-------------------------|---------------------------|---------------------------|------------|
| % C                     | 46.55 (0.09) <sup>a</sup> | 44.59 (1.43) <sup>a</sup> | 0.1051     |
| % N                     | 2.25 (0.13) <sup>a</sup>  | 2.61 (0.12) <sup>b</sup>  | 0.0616     |
| C:N                     | 21.69 (1.31) <sup>a</sup> | 17.20 (0.46) <sup>b</sup> | 0.0126     |
| % Fiber                 | 39.38 (0.50) <sup>a</sup> | 34.78 (0.59) <sup>b</sup> | <0.0001    |
| % Soluble carbohydrates | 52.85 (0.53) <sup>a</sup> | 56.73 (0.70) <sup>b</sup> | 0.0002     |
| % Lignin                | 6.52 (0.16) <sup>a</sup>  | 6.67 (0.18) <sup>a</sup>  | 0.5120     |
| Lignin:N                | 3.12 (0.20) <sup>a</sup>  | 2.63 (0.20) <sup>a</sup>  | 0.1073     |

Differing letters indicate significant differences ( $P<0.10$ ) between the means of core and edge regions

**Table 2** Mean and standard error for tissue decomposition variables

| Variable  | Core                        | Edge                        |
|---|-----------------------------|-----------------------------|
| Carbon mineralization [ $\text{mg CO}_2$ ( $\text{g tissue}^{-1}$ )]                            | 538.3 (19.701) <sup>a</sup> | 549.3 (11.458) <sup>a</sup> |
| Tissue net nitrogen mineralization [ $\text{mg N}$ ( $\text{g tissue}^{-1} \text{ day}^{-1}$ )] | 0.007 (0.004) <sup>a</sup>  | 0.026 (0.007) <sup>b</sup>  |

Differing uppercase letters indicate significant differences ( $P<0.10$ ) between the means of core and edge regions



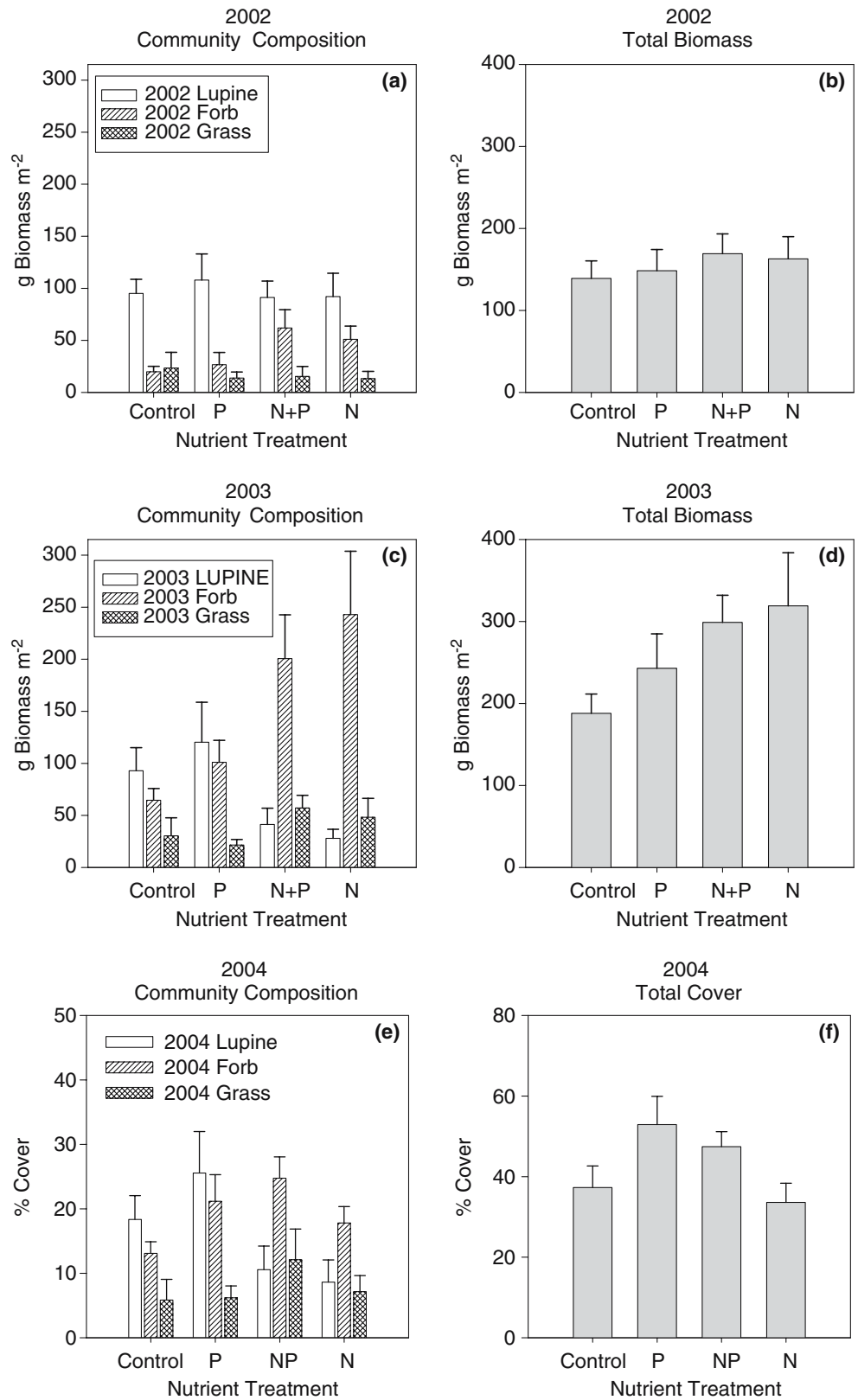
**Fig. 4** Negative correlation between tissue N and fiber content ( $P<0.002$ ;  $R = -0.59$ )

N mineralization potential suggest that decreased competition resulting in higher P and N availability in edge patches could be linked to higher tissue palatability by herbivores and greater nutrient turnover in edge plots.

#### Community responses to nutrient availability

During the first year after fertilization, there were no significant changes in *L. lepidus* or grass biomass ( $P>0.10$ ; Fig. 5a, b). However, forb biomass increased significantly with N addition ( $P<0.01$ ) and, as a result, there was significantly higher total biomass with N additions ( $P=0.08$ ). Mean forb biomass increased from  $19.9 \text{ g m}^{-2}$  in the control plots to  $51.0$  and  $61.9 \text{ g m}^{-2}$  in the +N and +NP treatments. The most substantial changes in community structure happened in the second year of the experiment (Fig. 5c, d). During 2003, *L. lepidus* declined by more than 50% with N addition but increased by 30% with P addition, although the effect of P was not statistically significant (paired- $t$ :  $P>0.36$ ). The proportion of healthy (i.e., non-aborted) seeds in *L. lepidus* was 28% greater in P addition ( $F_{1,45} = 5.2$ ,  $P=0.027$ ) and 26% less with N addition ( $F_{1,45} = 7.9$ ,  $P=0.007$ ). There was no significant interaction between N and P addition ( $P>0.7$ ), showing that

**Fig. 5** Changes in plant biomass within the core region after nutrient additions in 2002 and 2003. **a** Distribution of biomass between the dominant N<sub>2</sub>-fixing forb (*L. lepidus*, open bar), non-lupine forbs (striped bar), and grasses (hatched bar). There was a significant increase in forb biomass ( $P < 0.05$ ) with N addition. **b** Changes in total biomass in 2002. **c** 2003 biomass for *L. lepidus*, non-lupine forbs, and grasses. There was a significant decline in *L. lepidus* biomass with N addition with a concomitant increase in non-lupine forb biomass. **d** There was a significant nitrogen effect on total plant biomass in 2003, while P had no significant effect



the negative effect of nitrogen addition on *L. lepidus* is not offset by the addition of P. However, the decline in *L. lepidus* biomass was offset by the accumulation of forb and grass biomass. There was 3–4 times more forb

biomass in the plots receiving nitrogen additions (+N and +NP treatments) than in the control plots ( $P < 0.01$ ). Nearly all of this increase in forb biomass is accounted for by an increase in *H. radicata*, a non-native

species (Table 3). The addition of P had no significant effect on forb or grass biomass. In both 2002 and 2003, there was greater plant biomass in plots receiving N addition than in control or +P plots ( $P=0.08$ , 2002;  $P<0.001$ , 2003). In 2004, we analyzed plant cover rather than biomass. We found that, in 2004 after 3 years of fertilization, both N and P additions increased forb biomass (phosphorus  $P<0.001$ ; nitrogen  $P=0.03$ ), had no significant effect on grass cover, and lupine biomass significantly decreased with N addition ( $P<0.0001$ ) and significantly increased with P addition ( $P=0.064$ ). The interaction between N and P was never significant for these analyses.

Nutrient addition significantly altered reproduction for both *H. radicata* and *H. albiflorum* in 2002, which could potentially explain the substantial increase in these species in 2003 (Fig. 6). We found that for *H. radicata* N addition significantly increased reproductive output ( $P<0.02$ ). While seed mass per flowering stalk was not significantly different between nutrient addition treatments, there were significantly more flowering stalks per plant with N addition ( $P<0.001$ ), which translated into a 530% increase in seed mass  $\text{cm}^{-2}$  rosette. There was also a significant increase in seed mass produced by *Hieracium* with N addition ( $P<0.05$ ). Phosphorus addition did not significantly alter any of these parameters, nor were there any interactions between P and N additions. However, there was a significant interaction between N and P for rosette size ( $P<0.07$ ).

## Discussion

### Spatial distribution in nutrient availability

We initially predicted that regions that had been occupied by *L. lepidus* for a longer period (core regions) would have more N available for plant uptake than more recently established regions (edge regions). This hypothesis was developed based on research by Halvorson et al. (1991, 1992) and Halvorson and Smith (2005) that indicates that *L. lepidus* locally contributes significant amounts of N to the soil as sites develop with longer periods of occupation. Contrary to what was anticipated, N availability, measured using ion exchange

membranes, resin bags, and in situ net N mineralization, was similar in the edge and core regions. Gross N fluxes could be higher in the core region, but increased uptake and immobilization cause no difference in the variable measured here. This result is contrary to other work that has previously been reported from this same region on Mount St. Helens (Fagan et al. 2004; Halvorson and Smith 2006; J.H. Titus, unpublished data), but may demonstrate the high spatial variability of N availability in the area broadly classified as “edge”. There are small, older patches of lupine within the edge region where N availability is as high as in the larger core areas, while a small number of measurements in areas that have never been occupied appear to have appreciably lower N than in either occupied core or edge patches (data not shown). This may be a consequence of the extremely low N availability across the landscape at Mount St. Helens and the sensitivity of the measurements that we made. Despite similar N availability in both regions, competition for nutrients is likely much higher in the core regions than the edge regions. The higher density of plants in the core results in many more plants in the core competing for the same amount of N as is available in the edge where plant density and biomass  $\text{m}^{-2}$  and density is significantly less (Bishop et al. 2005).

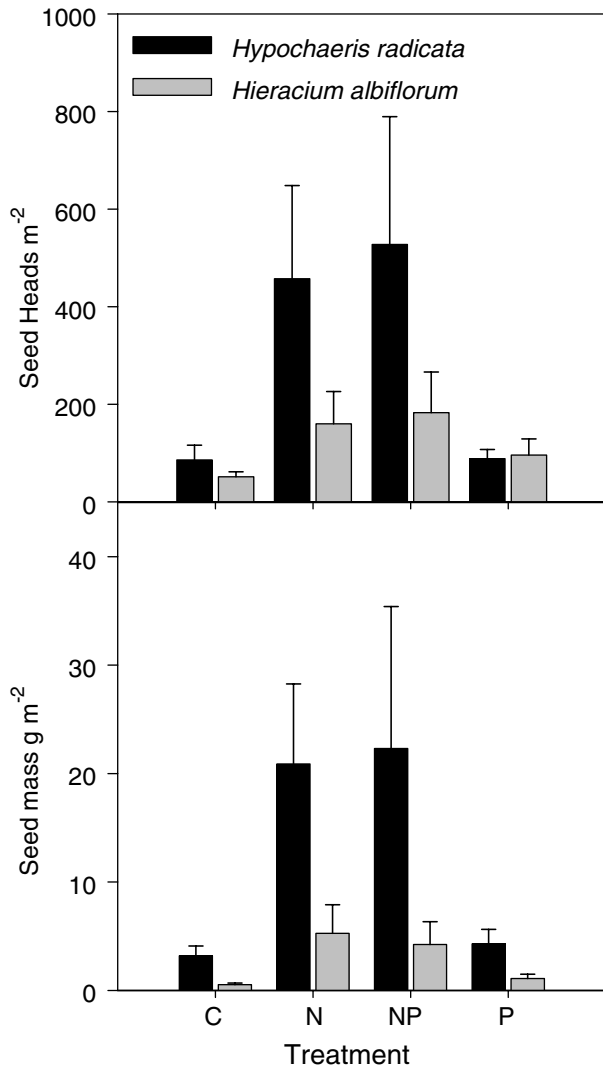
The role of plant presence in determining nutrient availability is clearly seen in all of the rock-derived nutrients. For some of these, namely  $\text{K}^+$  and  $\text{Mn}^{2+}$ , the creation of islands of fertility occurs very rapidly since we are able to see increases in membrane exchangeable cations under plants in both edge and core patches. For others, including  $\text{Ca}^{2+}$ ,  $\text{PO}_4^{3-}$ , and  $\text{Mg}^{2+}$ , the only differences we observed between plant interspaces and plants were seen in the core region. There are two plausible explanations for these patterns. First, the underlying mineralogy of the volcanic deposits is heterogeneous and may differ systematically between core and edge areas, resulting in different stoichiometry of the rock derived nutrients. Alternatively, there surely are differences in susceptibility of weathering of the various minerals in the rocks that could influence the rate of accumulation of the various rock-derived nutrients.

Significantly higher standing biomass and density in the core patches than the edge patches results in higher total N demand  $\text{m}^{-2}$  in the core. The biological demand

**Table 3** Mean biomass for the dominant plants found in nutrient addition plots for 2002 and 2003

| Forb biomass                | Biomass ( $\text{g m}^{-2}$ ) 2002 |                     |                     |                     | Biomass ( $\text{g m}^{-2}$ ) 2003 |                     |                     |                     |   |
|-----------------------------|------------------------------------|---------------------|---------------------|---------------------|------------------------------------|---------------------|---------------------|---------------------|---|
|                             | Control                            | +P                  | +NP                 | +N                  | Control                            | +P                  | +NP                 | +N                  |   |
| Species                     | Mean (STE) <i>n</i>                | Mean (STE) <i>n</i> | Mean (STE) <i>n</i> | Mean (STE) <i>n</i> | Mean (STE) <i>n</i>                | Mean (STE) <i>n</i> | Mean (STE) <i>n</i> | Mean (STE) <i>n</i> |   |
| <i>Lupinus lepidus</i>      | 95 (13.5)                          | 9108 (25.0)         | 991 (15.8)          | 992.2 (22.3)        | 993 (22.2)                         | 9120 (38.4)         | 941.3 (15.6)        | 828.0 (8.8)         | 8 |
| <i>Hypochaeris radicata</i> | 12.9 (3.8)                         | 913.8 (8.8)         | 847.6 (15.2)        | 831.5 (8.3)         | 842.4 (11.4)                       | 966.0 (17.2)        | 8127.4 (34.8)       | 9166.2 (60.0)       | 9 |
| <i>Hieracium alba</i>       | 0.4                                | 11.8 (0.8)          | 22.9 (1.0)          | 35.3 (2.4)          | 34.5 (1.6)                         | 75.6 (2.7)          | 724.0 (16.4)        | 514.8 (7.1)         | 5 |
| <i>Penstemon cardwellii</i> | 0.4 (0.29)                         | 20.8 (0.38)         | 33.5 (2.93)         | 42.5 (1.29)         | 43.4 (1.94)                        | 48.9 (5.5)          | 69.1 (7.0)          | 424.9 (15.2)        | 4 |
| <i>Achillea millefolium</i> | 4.4 (3.9)                          | 41.7 (1.6)          | 43.5 (2.1)          | 41.8 (1.2)          | 35.7 (3.7)                         | 35.3 (2.7)          | 316.2 (8.8)         | 47.0 (5.7)          | 3 |

Mean values are in  $\text{g m}^{-2}$ . The *n* column reflects the number of plots from the nine sites where the individual species were found. Other forbs (found at fewer than two plots): *Castilleja miniata*; *Phacelia hastata*; *Epilobium angustifolium*



**Fig. 6** Influence of nutrient addition on reproductive output of *Hypochaeris radicata* (solid black bars) and *Hieracium albiflorum* (solid gray bars) measured at the end of the growing season 2002. The addition of N significantly increased the production of seed heads and total seed mass for both forbs. Error bars are one standard error

rather than the nutrient supply rate may be a critical control over feedbacks between nutrients and plant tissue chemistry. Changes in plant tissue quality are likely a consequence of lower nutrient availability per individual. We observed that core plants had significantly more tissue fiber and less nitrogen than edge plants, both of which could influence nutrient supply rates and rates of herbivory. Several studies have concluded that the observed spatial differences in herbivory on Mount St. Helens is at least partially linked to *L. lepidus* tissue nutritional quality (Fagan et al. 2005; Bishop et al. 2005; J.L. Apple and J.G. Bishop, unpublished data). Our data suggest that *L. lepidus* tissues in the core regions should potentially be less susceptible to herbivory than edge regions due to lower tissue P, because of greater plant demand for the same P supply rate. One unanswered question that remains is the degree to which there

are differences in the availability of dissolved organic nitrogen and the capacity of various plant species to actively compete with microbes for this uncharacterized source of nitrogen (Schimel and Bennett 2004).

#### Tissue chemistry and decomposition

Net N mineralization potential of *L. lepidus* tissue was positively correlated with N content and soluble carbohydrate content of *L. lepidus* tissue, and thus was found to be significantly higher in the edge region than the core region. The positive correlation between in situ net N availability and net N mineralization potential of edge tissues supports the hypothesis that higher N availability may be linked to higher tissue palatability for herbivores and possibly greater nutrient turnover in edge plots. Research by Belovsky and Slade (2000) supports the hypothesis that insect herbivory may accelerate nutrient cycling. Greater nutrient turnover in edge plots could reinforce the higher N and P content of edge tissues and higher susceptibility to herbivory. These feedbacks may serve to limit expansion rates of *L. lepidus* into new habitats on Mount St. Helens while allowing older core patches to persist. We have already demonstrated that spatially structured herbivory controls rates of *L. lepidus* expansion on Mount St. Helens (Fagan and Bishop 2000; Fagan et al. 2005; Bishop 2002) and that tissue stoichiometry is the likely underlying mechanism controlling herbivory (Fagan et al. 2004; Bishop et al. 2005; J.L. Apple et al., in review). A positive feedback between nutrient availability, herbivory, and decomposition rates could substantially alter patterns of persistence for primary successional species on the pyroclastic flows.

#### Community responses to nutrient additions

Walker and Syers (1976) proposed a theory of soil development where in most cases nitrogen should be the macronutrient that is most limiting to primary production. However, so long as there are N<sub>2</sub>-fixing species in the flora, P should become limiting after sufficient time as it is weathered out of primary minerals and potentially lost from the ecosystem or occluded into biologically inaccessible forms. However, Raich et al. (1996) found that plant communities on young (140 years) lava flows in Hawaii were co-limited by P and N. Plant production in the Raich et al. (1996) experiment responded most to N, but also demonstrated a significant increase in productivity with P addition. In a number of other cases production on young primary successional landscapes have been limited strictly by N (Miles and Waldon 1993; Vitousek et al. 1993). Raich et al. (1996) postulated that the difference between young ecosystems limited by N and those that are limited by both N and P is controlled by the texture of the parent material. Tephra is much finer textured than lava flows and would

likely weather more rapidly than lava, increasing P availability early in succession. In addition, competitive interactions may mask species-specific nutrient limitations. While the community failed to respond significantly to P additions on Mount St. Helens, S. Wills and J.G. Bishop (unpublished data) found that in plots where *H. radicata* and other competitors had been removed *L. lepidus* increased dramatically with P additions relative to control plots. Those data, in concert with our nutrient addition experiment, suggest an interesting dynamic. The community is N-limited while the pioneering N<sub>2</sub>-fixing lupine is constrained by P availability. However, so long as there is competition between *L. lepidus* and the other forbs, particularly the non-native *H. radicata*, *L. lepidus* may be unable to capitalize on additional P. However, lupins did respond reproductively to P addition even with competition (proportion of non-aborted seeds was higher in 2002) and, by 2004, data indicate an eventual increase in both lupin and N responsive forbs. This result suggests co-limitation of the community by N and P.

Identifying individual factors that limit production or influence susceptibility to herbivory on Mount St. Helens is difficult. A number of studies have demonstrated that lupine species are remarkably plastic in their strategies to overcome P deficiencies. Unlike *L. lepidus*, *Lupinus albus*, a crop plant in Australia, can develop proteoid roots under conditions of low P availability and may secrete citric acid to solubilize occluded P (Gardner et al. 1983). However, root architecture may alter a plants susceptibility to root boring insects, increasing or decreasing the likelihood of mortality due to herbivory or water stress (Lynch and Ho 2004). In addition, plant uptake rates of available nutrients may be sensitive to growing season precipitation, and it is likely that there are periods in late summer where soil water potential is extremely low. In addition, topographic and parent material differences further complicate our ability to isolate individual factors that may influence succession at Mount St. Helens.

The processes controlling changes in species composition over time within ecological systems has been a major theme of ecological research for well over 100 years (Cowles 1899; Clements 1904, 1916). Platt and Connell (2003) illustrate the complex processes that determine whether species replacement will be directional or random based on the nature of the disturbance and the life history characteristics of the pioneering species. Their model predicts that catastrophic disturbances, such as Mount St. Helens, should produce directional change in species based on colonization ability of early species. Our results contribute to this discussion by identifying how interactions between species-specific responses to nutrient availability and climate contributed to a drastic change in plant community composition. In control and +P plots in 2002, *L. lepidus* accounted for 70% of the aboveground biomass and averaged approximately 100 g m<sup>-2</sup>. By 2003 in the +N plots *L. lepidus* con-

tributed only 13% to aboveground biomass and averaged less than 35 g m<sup>-2</sup>. These data suggest that species-level nutrient limitations manifest themselves very differently than total ecosystem nutrient limitation. The response of all species other than *L. lepidus* suggest that N is the macronutrient most limiting to plant production on the pyroclastic flows of Mount St. Helens and that N addition altered competitive dynamics sufficiently that there was nearly a complete loss of the dominant plant from the community in the 3 years of this experiment. However, there is a delayed response where *L. lepidus* can increase with P addition. It is unclear what would occur in the absence of a massive response by the non-native ruderal *H. radicata*.

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