The Ecology of Lupines in Crater Lake National Park, Oregon

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The ecology of two N_2-fixing legumes, Lupinus lepidus var. lobbii and L. latifolius var. latifolius, was studied in four Pinus contorta community types in Crater Lake National Park, Oregon. Soils in all four communities were low in N (<0.09%). Total carbon in the rooting zone varied from 1.35% to 3.83%. Rooting zone C:N ratios were high (45:1). Lupinus lepidus grew in the community with lowest soil nutrients. Nutrient levels tended to increase as community productivity increased in the four community types. Nutrient concentration alone, however, did not differentiate community types.

During 1984 and 1985, vegetative growth of both species began within one week after snowmelt, even though snowmelt date varied with both year and site. Maximum canopy cover was reached when flowering began, in 3-4

weeks for L. lepidus and 4-5 weeks for L. latifolius. Plants did not senesce before snowfall. Two seed morphs were produced by L. latifolius in the riparian zone. Seedling establishment was infrequent, and plants are apparently long-lived.

Lupinus lepidus plants of all sizes and ages had active N_2-fixing nodules. Lupinus latifolius plants were nodulated only when small. Nodules were rare on plants that were large enough to reproduce.

Nitrogen fixation of L. lepidus was estimated in the field by the acetylene reduction method throughout the summer of 1984. The maximum average rate of ethylene production (9.9 $\mu moles \cdot g^{-1} \cdot hr^{-1}$) occurred two weeks after snowmelt when soil temperature was 12.7^0C. No diurnal variation was found. Acetylene reduction rates declined rapidly during the remaining 13-week snow-free season. The seasonal average rate of acetylene reduction was 2.7 $\mu moles \cdot g^{-1} \cdot hr^{-1}$. The potential annual input of N by lupines was 0.04 $kg \cdot ha^{-1} \cdot yr^{-1}$. This value was very low because of the short period of high activity and low lupine cover. Although soil temperature may limit the maximum rate of N_2-fixation, it did not cause the rapid seasonal decrease. Limited water and changes in carbon allocation among nodules and storage organs may have caused the decline in nodule activity.

Greenhouse studies of lupines grown on soil from each of the four forest communities indicated that soil

type did not affect plant vigor and biomass, but did affect nodule fresh weight. All N fixed by the plants during one year in the greenhouse remained in the biomass; soil N did not increase.

In the greenhouse, Lupinus lepidus plants had higher dry weight and lower root/shoot ratios than L. latifolius. The small seed morph produced by L. latifolius in the riparian zone germinated best when fresh and did not require stratification, whereas the large seed morph germinated best after stratification. Plants from the small seed morph had lower root/shoot ratios, higher nodule fresh weight and higher biomass N concentration than plants from the large seed morph.

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THE ECOLOGY OF LUPINES IN CRATER LAKE NATIONAL PARK, OREGON

INTRODUCTION

This thesis reports a study of the ecology of *Lupinus lepidus* var. *lobii* (Gray) Hitchcock and *Lupinus latifolius* Agardh var. *latifolius* growing in four different lodgepole pine (*Pinus contorta* Dougl. ssp. *murrayana* (Balf.) Critchfield) forest communities in Crater Lake National Park, Oregon, including an assessment of nitrogen fixation by these species. Lupines are the only legumes, and apparently the only N_2-fixing higher plants, in the lodgepole pine forests that grow on pumice at high elevations in the Park (Zeigler 1978).

Although much recent literature has emphasized that biological N_2-fixation can be important, providing as much as 100 kg $N \cdot ha^{-1} \cdot yr^{-1}$ (reviewed in Evans and Barber 1977, and Sprent 1979), only a few studies have dealt with native legumes in natural forest communities (Lawrie 1981, Adams and Attiwill 1984). Even fewer have measured N_2-fixation at high elevations on very low N soils (McNabb *et al*. 1976, Wojciechowski and Heimbrook 1984).

The forests at Crater Lake National Park are of particular interest because they grow on pumice soils that initially had very little nitrogen (Youngberg and

Dyrness 1963). During the 6600 years since the soil parent material was deposited, enough N has been added to support forest vegetation. Some of this N probably came from N_2-fixation; a reasonable expectation is that lupines were major contributors. The four communities that I studied differ in productivity and may all have the potential to reach climax mountain hemlock vegetation (Franklin and Dyrness 1973). The process of succession from bare pumice without N, through lodgepole pine forests, to climax mountain hemlock is complex; I have chosen to focus on one small aspect, the role of lupines in the present forests.

The main objectives of this study were: (1) to determine current soil fertility, (2) to investigate lupine phenology and seedling biology, (3) to estimate potential input to the system by N_2-fixation, and (4) to measure growth, nodulation, and N_2 fixed by two lupine species in a greenhouse.

Data will be presented following two introductory chapters describing the physical and biological environment of the lupines. Each topic will be discussed in a separate chapter, and each chapter will have an introduction, materials and methods, results, and discussion. Finally, a general summary and conclusions chapter will summarize the ecology of the lupines.

PHYSICAL ENVIRONMENT

Crater Lake National Park is located in the Cascade Mountains in south-central Oregon at T28S to T31S, R4E to R7E, 43°05'N to 42°47'N latitude, 120°00'W to 120°20'W longitude. Study sites were located in lodgepole pine forest community types at elevations between 1650 m and 2000 m.

Information about the geologic history of Mount Mazama, the site of Crater Lake, is compiled from Williams (1942) and Harris (1980). Sixty-six hundred years ago, the final eruption and collapse of Mount Mazama formed the caldera now filled by Crater Lake. This event ended thousands of years of alternating periods of volcanism, which built the mountain, and glaciation, which gouged deep valleys into its flanks. During the final stages of the eruption, frothy pale gray and buff dacite pumice surged out of the mountain and down the slopes as a glowing avalanche, reaching as far as 56 km from the crater. Glowing avalanche deposits up to 50 m thick filled glacial valleys on the south and east sides of Mount Mazama (Kerr, Sun, and Annie Creek valleys), and covered the flatter land north of the mountain to form a broad pumice plain (the Pumice Desert and surrounding area). Because of the speed of the avalanche, there was little sorting of particles by size. This deposit consists of large sub-rounded lumps of pumice embedded in a dusty matrix. Further eruptions

deposited a layer of smoke-gray basic scoria on top of the dacite flows. Along Sand Creek, this layer is several meters thick. At the end of the eruptive phase, a thin layer of fine ash and pumice was deposited on top of the scoria layer.

Soils that developed on these pumice deposits have been described as the Steiger series (U. S. Bureau of Indian Affairs et al. 1958). These forest soils are well to excessively well drained, moderately coarse-textured Vitrandepts (Regosols). Sand-, gravel-, and cobble-sized particles of dacite pumice are mixed with fine ash. The gravel and cobble content varies from 0 to 60% and soil texture, from fine sandy loam to loamy sand. There is little horizon development. Soils typically have only A_1+AC+C, or A_1+C horizons. The Lapine series in central Oregon is similar; Lapine soils develop on transported parent material whereas Steiger soils develop in place.

At Crater Lake National Park, 70% of the annual precipitation falls as snow from November through March. Rains between June and August account for less than 6%. The nearest weather station is at 1990 m at the Park Headquarters, south of the lake. Summer temperatures rarely exceed 29°C, with July being the warmest month. Mean maximum/minimum temperatures for 1931-1961 were 15/2 in June, 21/2 in July, 21/1 in August, and 17/-1 in September. Nighttime frosts can occur in any month. Mean annual precipitation is 171 cm (Sternes 1963,

Climatological Handbook 1969). During 1984, when most of the data were collected, the summer was dry, whereas summer 1983 had been wetter than normal (Table 1). Total precipitation for January through December in 1983 was 56 cm above the 30 year average, and in 1984 was 10 cm above. Precipitation is less, and temperatures may be slightly higher in the lodgepole pine forests, which are at lower elevations than the weather station, and/or on the eastern, drier side of the Park (Froehlich et al. 1982).

Table 1. Summer and annual precipitation (cm) at Crater Lake National Park Headquarters from 1980-1985.

	Year					
Month	1980	1981	1982	1983	1984	1985
June	7.0	6.7	9.4	5.8	7.0	2.4
July	0.0	1.6	2.3	6.6	0.0	4.0
Aug.	0.0	0.0	1.8	7.7	1.5	2.9
Sept.	4.0	7.9	11.9	1.0	2.8	-
Summer	11.0	16.2	25.5	21.1	11.3	-
Annual	151	191	198	227	181	-

COMMUNITY COMPOSITION AND LUPINE SPECIES

Most of Crater Lake National Park is in the Tsuga mertensiana (mountain hemlock) Vegetation Zone of Franklin and Dyrness (1973). Persistent or climax stands of Pinus contorta occur when edaphic or topoedaphic properties limit the establishment of mountain hemlock and the Abies spp. that grow with it (Franklin and Dyrness 1973, Zeigler 1978).

Forests dominated by lodgepole pine cover 185 km^2 (26%) of the Park, at elevations from 1650 m to 2000 m. Within these lodgepole pine forests, Zeigler (1978) used floristic characters to identify four community types that contain lupines. Following Zeigler (1978), the four communities, in order of increasing productivity, are:

1. The Pinus contorta/Carex-Stipa community (PCS) occurs on flat areas with deep pumice deposits. More than 95% of the trees are P. contorta, although reproduction of Abies magnifica var. shastensis, Tsuga mertensiana, and Pinus albicaulis occasionally occurs. Common herbaceous plants are Carex pensylvanica, Stipa occidentalis, Sitanion hystrix, Lupinus lepidus var. lobbii, Eriogonum marifolium, and Spraguea umbellata. Mean herb cover is 6%. While all P. contorta communities grow on soils in the Steiger series, the soils in this community have a higher proportion of cobble- and gravel-sized particles than elsewhere. Three study sites were located in this community type, two near the Pumice

Desert and one east of the caldera rim (Figure 1a, Table 2).

2. The Pinus contorta/Carex-Lupinus community (PCL) frequently occurs on deep pumice, adjacent to community PCS, but on slightly higher ground. Over 95% of the trees are Pinus contorta. Other small conifers may also be present. Haplopappus bloomeri and Ribes cereum sometimes grow in this community, although mean shrub cover is only 2%. Herbaceous cover is much higher than in community PCS. Lupinus albicaulis, Eriogonum marifolium, Carex pensylvanica, Stipa occidentalis and Sitanion hystrix are the most common herbs. Two study areas were located in this community, 2a near the Pinnacles, where Wheeler Creek crosses the road, and 2b south of the Pumice Desert where the Pacific Crest Trail crosses the road (Figure 1b,d; Table 2).

3. The Abies magnifica var. shastensis-Tsuga mertensiana/Carex-Lupinus community (ACL) has abundant reproduction of A. magnifica var. shastensis and T. mertensiana. Otherwise, this community is floristically similar to community PCL. Sites of community ACL in the southwest quadrant of the Park contain hard rock gravel, probably from glacial till that mixed with the pumice. One study site was located where the Pacific Crest Trail crosses Oregon highway 62, 1.3 km west of the intersection with the main road to the lake (Figure 1c, Table 2).

Figure 1. Crater Lake National Park and study sites.

1a. NE quarter

1b. SE quarter

1c. SW quarter

1d. NW quarter

Heavy black lines enclose major stands of Pinus contorta. Study sites are indicated by community type; Pinus contorta/Carex-Stipa (PCS), Pinus contorta/Carex-Lupinus (PCL), Abies magnifica var. shastensis-Tsuga mertensiana/Carex-Lupinus (ACL), and Abies lasiocarpa/Haplopappus/Aster-Elymus (AAE). See table 2 for their physical and vegetational characteristics. Maps and limits of P. contorta stands are from Zeigler (1978).

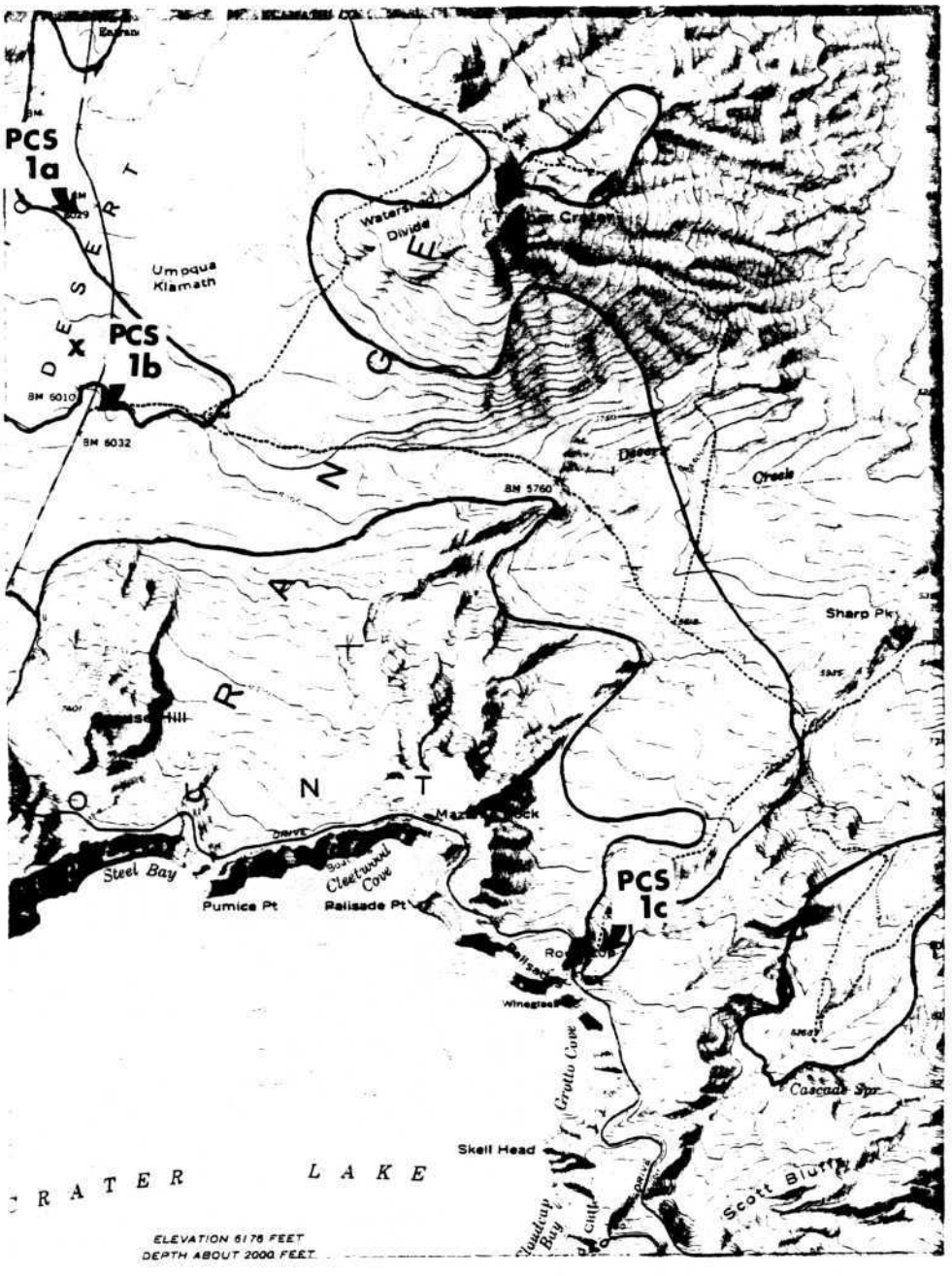

Figure 1a. Northeast quarter of Crater Lake National Park.

Figure 1b. Southeast quarter of Crater Lake National Park.

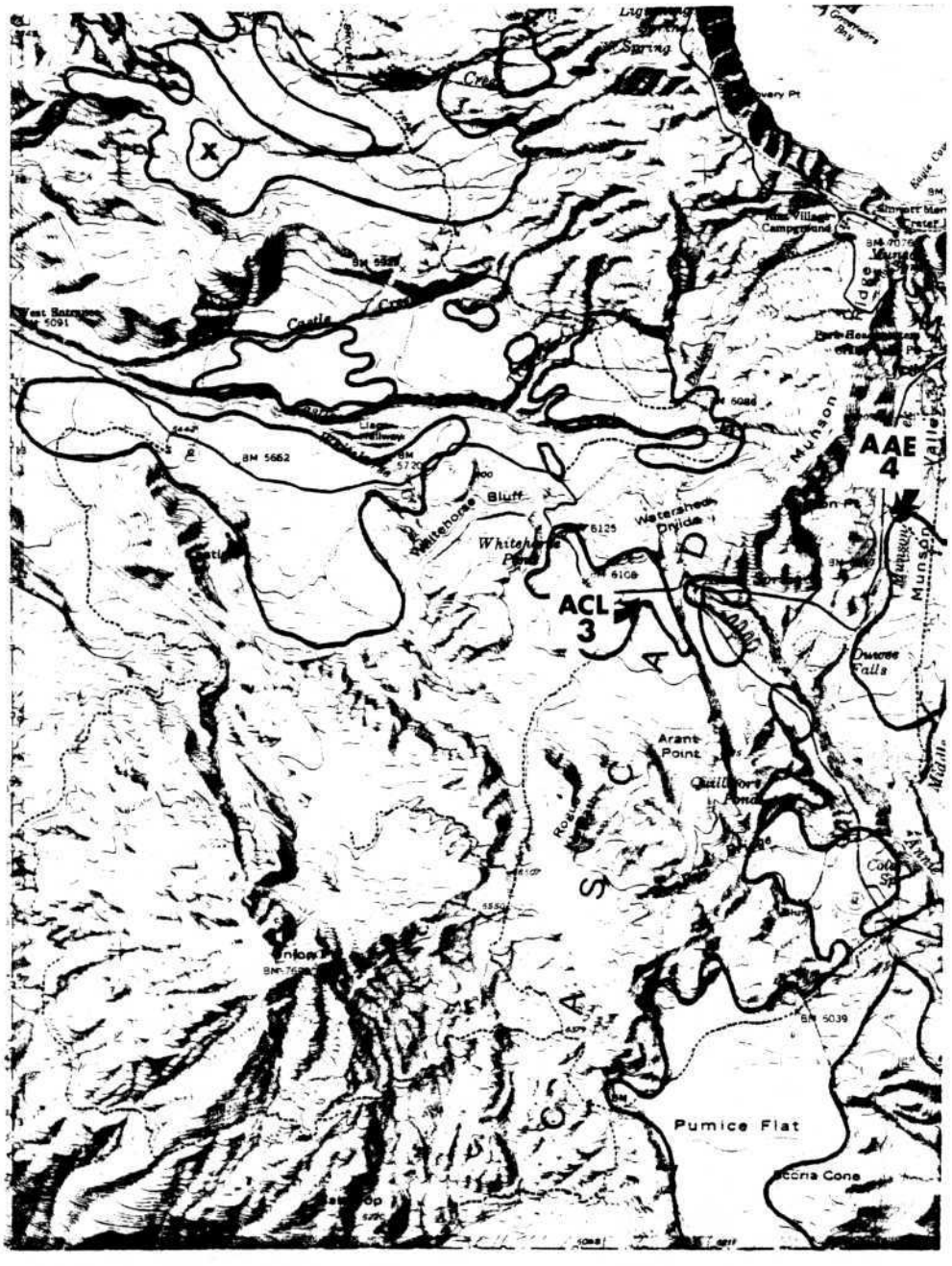

Figure 1c. Southwest quarter of Crater Lake National Park.

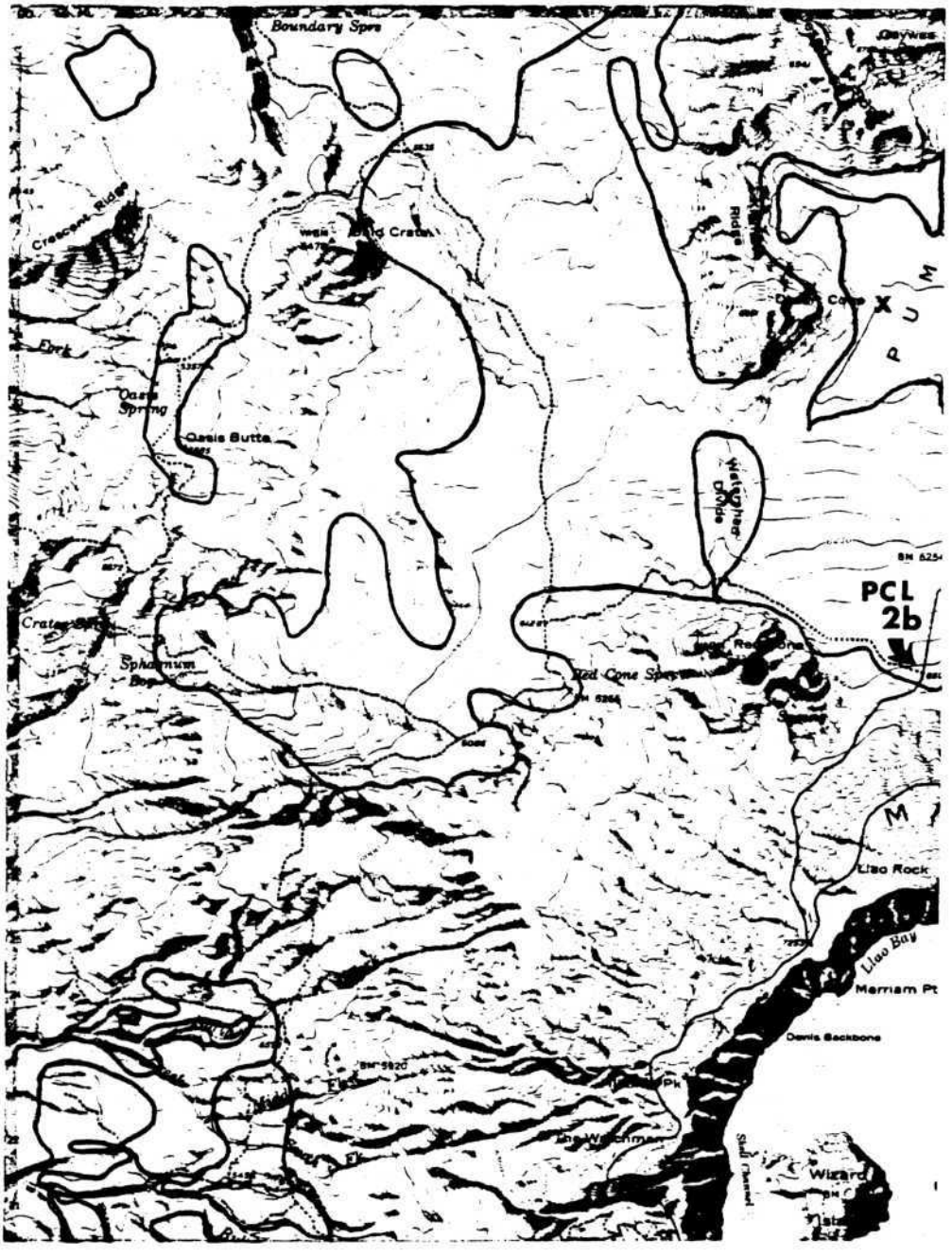

Figure 1d. Northwest quarter of Crater Lake National Park.

Table 2. Physical and vegetational characteristics of study sites in Crater Lake National Park. Types of data collected at each site during the summers of 1984 and 1985 are denoted by X.

	Community type[1]						
	PCS			PCL		ACL	AAE
# trees/ha[2]	4680			4200		5900	5660
% lupine cover[2]	0.1			2.6		5.3	11.0
% herbaceous cover[2]	6			25		24	50
Site identification	1a	1b	1c	2a	2b	3	4
Elevation (m)	1845	1830	2000	1700	1980	1890	1900
Slope and aspect	0	0	10% ENE	14% NE	0	0	2% ESE
Type of data							
N_2-fixation estimates	X	X		X	X		X
Phenology		X	X	X			X
Soil analysis	X	X	X	X	X		X
Soil collected for greenhouse		X		X		X	X

[1] See Figure 1 for key to abbreviations for community types.

[2] Data from Zeigler (1978).

4. The Abies lasiocarpa/Haplopappus/Aster-Elymus community (AAE) is a forest-meadow mosaic. Pinus contorta is the dominant tree (61%), but there is abundant reproduction of A. lasiocarpa, A. magnifica var. shastensis, T. mertensiana and P. contorta. Shrub cover of Haplopappus bloomeri is 9% and herbaceous cover is 50%. The most common herbs are Lupinus latifolius, Aster ledophyllous, Carex pensylvanica, Stipa occidentalis and Sitanion hystrix. The study site was located in Munson Valley along a service road (Figure 1c, Table 2).

In community types PCL, ACL, and AAE, I selected sites with relatively high L. latifolius cover. Although L. lepidus is present in these community types (Zeigler 1978), there were no individuals in my study sites.

Species Studied

Lupinus lepidus var. lobbii is a perennial species found in open subalpine forests from British Columbia to southern California. Lupinus latifolius var. latifolius grows from the Cascade Mountains west to the coast at all elevations from southern British Columbia to California. Lupinus albicaulis Doug. ex Hook. grows from the lowlands of the Puget trough on the west slopes of the Cascades south into California and western Nevada, at increasing elevations toward the southern portion of its range (Hitchcock et al. 1961). These species are perennials,

with large underground structures, a taproot in L. lepidus and a caudex in L. latifolius and L. albicaulis.

Lupinus latifolius and L. albicaulis are closely related, and often intergrade, especially from the southern Cascades into the Sierra Nevada of California (Hitchcock et al. 1961). According to Zeigler (1978), Lupinus latifolius and L. albicaulis distinctly segregated among communities, L. latifolius in community AAE and L. albicaulis in communities PCL and ACL. However, I could not differentiate between the two species, and found more morphological variation within the lupine populations in each community than among communities. The key characters of the plants in Crater Lake National Park are intermediate between the two typical species as described in Hitchcock et al. (1961). I decided to treat all lupines in these three communities as L. latifolius because most specimens were more similar in morphology and in habitat to that taxon.

SOIL FERTILITY

Introduction

Soils in central Oregon that have developed on pumice are low in most major plant nutrients. Bioassays indicate that plants respond primarily to added N, but also to P and S amendments (Youngberg and Dyrness 1965). Soil from the Pumice Desert in Crater Lake National Park has even lower amounts of N, C, and P than pumice soil from lower elevations in central Oregon (Horn 1968). Differences in plant productivity and cover suggest that the four community types differ in soil fertility, especially N and organic matter content (Zeigler 1978).

Materials and Methods

Soils were sampled at depths of 0-5, 5-25, and 25-35 cm, which are above, within and below the rooting zone of lupines, respectively, in communities PCS, PCL, and AAE in August 1984 or in July 1985. Depth of the litter layer was measured at site 1b, community type PCS. Available ammonium-N and nitrate-N were extracted from fresh samples with KCl (Keeney and Nelson 1982), then measured using an autoanalyzer. Total N and P were measured using an autoanalyzer after Kjeldahl digestion (Bremner 1965). Total C was determined by the Leco dry combustion method (Nelson and Sommers 1982).

Significance of results was tested using analysis of variance.

Results

The litter layer in site 1b of community type PCS was 2 cm of lodgepole pine needles. Available ammonium-N and nitrate-N were less than 0.001% in all communities and at all sampling depths. Total N and C were highest in the surface 0-5 cm and decreased with depth at all sites (Table 3), except for a low surface N value in site 2b, which was probably caused by a sample size of 1. The C:N ratio in the rooting zone ranged from 34:1 to 62:1, community PCS having both the highest and lowest values. Average C:N was 45:1.

Site 1, community PCS, had the lowest total N and C, although nitrogen in the rooting zone did not differ significantly between communities PCS and site 2a of community PCL, or between site 2b of community PCL and community AAE (site 4). The difference between sites was significant in the PCL community type and between PCS and AAE ($p=0.05$) (Table 3). There were not enough data to determine the significance of differences at other depths. Carbon in the rooting zone was lowest in community PCS, but there were not enough samples to test the significance of this difference.

Total P in all soils ranged from 400 to 600 ppm, and did not differ among sites or with depth. These values are in the same ranges as P in other Oregon forest soils.

Table 3. Total nitrogen and carbon concentrations (%) at 3 depths in soils from 4 sites in 3 different communities. Community types and sites are defined in Table 2, page 14. The rooting depth of the lupine species is 5-25 cm. Sample size in each class varied from 1 to 5. Means followed by the same lower case letters are not significantly different at the 0.05 level. There were not enough data to determine significance at other depths. The limit of detection for N is 0.001%. Depths where samples were not collected are designated by NA.

	% Nitrogen				% Carbon			
	site				site			
	PCS	PCL		AAE	PCS	PCL		AAE
Depth (cm)	1	2a	2b	4	1	2a	2b	4
0-5	0.038	0.140	0.055	0.205	1.86	2.47	4.79	5.52
5-25	0.032a	0.045a	0.085b	0.084b	1.35	NA	3.83	3.62
25-35	0.000	0.028	NA	NA	0.34	1.71	NA	NA

Discussion

Young, relatively unweathered pumice soils, including those at Crater Lake, are on the low end of the normal range for soil N (Youngberg and Dyrness 1965). Fresh pumice tephra from Mount St. Helens contains 0.006% N (Radwan and Campbell 1981). Total nitrogen in temperate mineral soils ranges from 0.02-0.50%, and carbon from 0.2-5.9% (Brady 1974). A Douglas-fir forest on well-developed non-pumice soils in the western Cascades of Oregon had 0.14% N in the rooting zone (Spycher et al. 1983). In the unforested Pumice Desert, near my sites 1a and 1b, carbon varied from 0.18-2.5% (mean=0.90%), and total N from 0.05-0.50% (mean=0.25%) (Horn 1968). A sample from the desert-forest ecotone had the lowest N and the highest C. Excluding ecotone samples, carbon was 0.18-0.82%. In my PCS forest sites, total N is lower and C is higher than in the Pumice Desert. In the forest, N may be located more in the vegetation. Carbon may be higher in the forest soil because of greater biomass and litter production.

In the lodgepole pine forests in Crater Lake National Park, the rooting zone is enriched in N and C relative to the subsoil. Even so, rooting zone concentrations of N are probably low enough to limit the growth of many species. Soils with less than 0.07% N are considered too infertile to use as nursery soil for

anything except pioneer pines with low nutrient requirements (Wilde 1958).

The 45:1 C:N ratio in pumice soils at Crater Lake is high compared with agricultural soils (11:1, Brady 1974) and western Oregon forest soils (17:1, Spycher et al. 1983). Carbon levels in my samples are comparable with carbon in other forest soils, but N levels are much lower compared with other forest soils.

Although soil nutrients may be an important factor determining which community develops, measurement of soil nutrients is not enough to identify the habitat of these lodgepole pine community types. While there was a trend of increasing N and C consistent with increasing community productivity, the differences between PCS-PCL and PCL-AAE were not statistically significant (least significant difference, $p=0.05$). The effects of many environmental factors, including precipitation, snowpack, soil and air temperature, and drainage are probably important.

PHENOLOGY AND SEEDLING ESTABLISHMENT

Introduction

The growing season for plants in the Park is short. Snow generally remains in my study areas until mid- to late June. In 1984, the snow-free season was 13 to 15 weeks long. One might expect plants in this environment to grow rapidly after snowmelt, to reproduce quickly, and to store large reserves of carbohydrates both for maintenance respiration and also for rapid growth following snowmelt (Bliss 1971). Individual plants were followed for two years to document the annual cycle of growth and reproduction.

Materials and Methods

Ten plants were measured and tagged in sites 1c, 2b, and 4 in communities PCS, PCL, and AAE, respectively, at the end of the 1983 growing season (Figure 1a,b,c). Every two weeks during the summers of 1984 and 1985, measurements were made of height to the top of the highest inflorescence, canopy cover by vertical projection of the foliage (Daubenmire 1968), and floral stage of each plant. Each inflorescence was classed as in bud, flowering, fruit swelling, or seeds dispersed, based on the condition of 50% of the flowers in the inflorescence. Because of poor growth and high mortality of the initial sample plants in community PCS during

1984, an additional 20 plants in that community were tagged at site 1b early in 1985 and followed for one season.

About 70 seedpods of L. latifolius were spread on the ground in each of the four communities in September 1983 to estimate the germination rate of seeds. Each pod probably had an average of 2 viable seeds, accounting for those that would have been eaten by insects or were too immature to germinate. Seedlings that germinated were followed during the 1984 season.

Germination and establishment of natural seedlings was noted, but no seedlings were marked.

Results and Discussion

Vegetative growth of L. lepidus at site 1b began within 2 days after snowmelt in late June and maximum cover was reached within 4 weeks (Figure 2). At snowmelt, matted green leaves from the previous growing season were on the soil surface. These old leaves remained green for about 2 weeks, until replaced by new vegetation. In 1984, when snowmelt was around June 26, lupines bloomed from July 21 through September 1. Seeds matured about 30 days after anthesis. Individual plants often had two crops of seed during 1984, flowering a second time shortly after the first crop matured. During 1985, mortality in the population of 20 marked plants at site 1b was 20%.

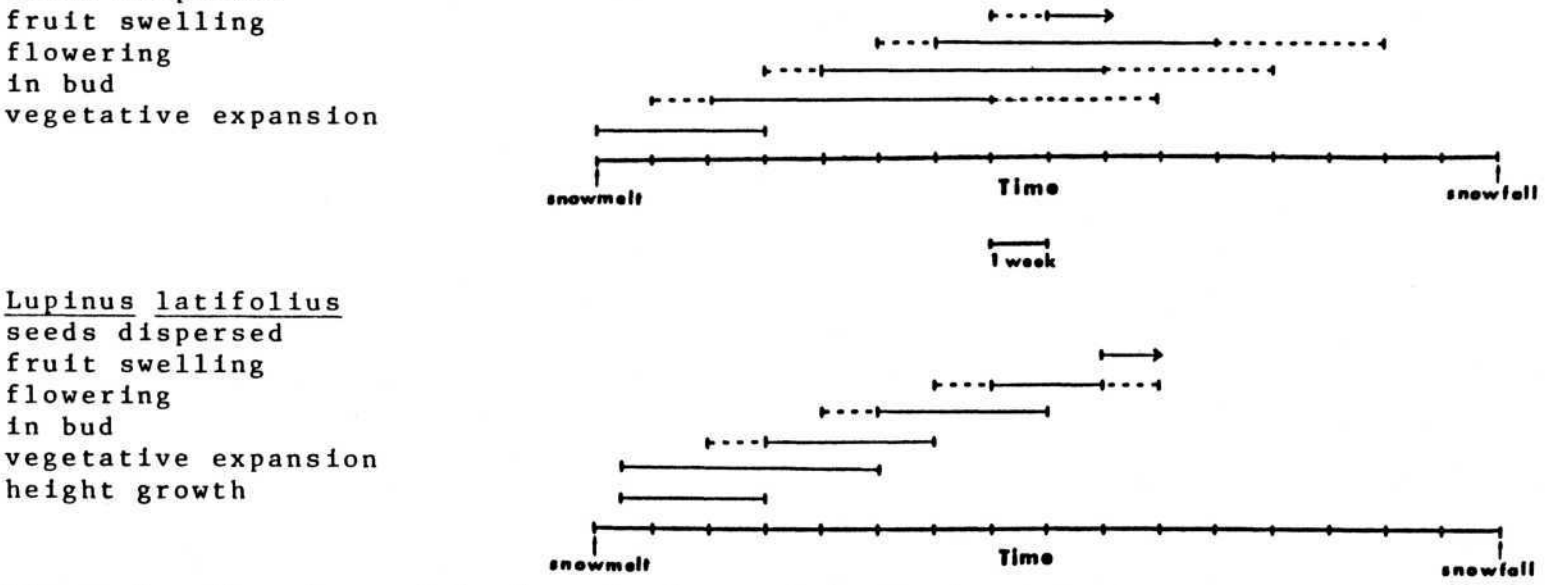

Figure 2. Phenology of lupines in Crater Lake National Park. Lupinus lepidus data were compiled from general observations of the population in 1984 and marked plants at site PCS 1b (Figure 1) in 1985. Lupinus latifolius 1984 and 1985 data from marked plants in sites PCL 2a and AAE 4 (Figure 1) were pooled to indicate maximum length of phenological stages. Snowmelt was about 6/23/84 and 6/10/85 (site PCS 1b), 6/23/84 and 6/10/85 (site PCL 2a), and 7/7/84 and 6/14/85 (site AAE 4). Snowfall was 10/13/84 at all sites. Key: solid line-at least 50% of the population is in that stage, dashed line-25 to 50% of the population in that stage. One division = 1 week.

Lupinus lepidus plants labeled at site 1c in 1983 grew poorly in 1984. After snowmelt, the plants increased in size for about four weeks; then most of the plants noticeably decreased in size and leaf number. At the end of 1984, the sample population had average canopy cover of 2 cm^2 compared with 1983 average cover of 110 cm^2. Mortality was 30% per year in both 1984 and 1985. Only one plant bloomed in 1984, whereas eight had bloomed in 1983. The poor growth in 1984 did not appear to be a result of either disease or insect damage. This population also grew poorly in 1985.

There appears to be little herbivory on L. lepidus. Occasionally, a leaf gall is formed around an insect larva.

Lupinus latifolius had similar phenology in both communities PCL and AAE. Shoots emerged within one week after snowmelt, and maximum size was reached within 5 weeks (Figure 2). Some plants continued to increase in cover gradually through September, but I believe this increase was caused by a bending and spreading of mature stems. The peak of bloom was in early August, 1984, after vegetative expansion has ceased and about 5-6 weeks after snowmelt. After the seeds matured, the lowest leaves usually became yellow and started to senesce by mid- to late September. However, plants remained green

until snowfall, which was during the second week of October, 1984.

I was not able to determine plant age, except in a general way, and therefore cannot describe long-term growth patterns. The general pattern, however, is for L. latifolius to grow for at least two years (perhaps longer) with a single stem, to blossom in the third year, and then slowly increase in size and number of stems and inflorescences. Lupinus arboreus also does not bloom during its first year (Sprent and Silvester 1973).

Year to year variation in growth can be dramatic. In 1985, growth and seed set was poor compared with 1983 and 1984. All size measurements were comparable between 1983 and 1984, but in 1985, plants at the Wheeler Creek site (community PCL, site 2a) were an average of 60% shorter and 80% smaller in cover. The average number of stems per plant was 3.5 in 1983, 4.5 in 1984, and 2.8 in 1985. At the Munson Valley site (community AAE), height growth and cover were similar in all three years, but the average number of stems was 8.9 in 1983 and 1984, compared with 5.7 in 1985. Both populations bloomed about one month earlier in 1985 than in 1984, because snowmelt was 2-3 weeks earlier in 1985. Few flowers were pollinated and seed set was poor at both sites 2a and 4 in 1985. Average mortality of the marked plants at both sites was 5% per year.

In 1983, two seed-pod and seed morphs were observed on L. latifolius plants in the riparian zone of Wheeler Creek (community PCL, site 2b). Seeds from the top of the inflorescence were larger (4.6 x 4.2 mm) and medium brown in color. Seeds from pods lower in the inflorescence were smaller (3.6 x 2.4 mm) and black with yellow spots. This difference in size of both dimensions is significant at the .05 level (t-test, n=20). The large brown seeds germinated best after stratification (83% stratified vs. 20% unstratified). One month after seed maturation, 80% of a sample of the small yellow-spotted seeds germinated within one week without stratification, compared to 3% with stratification. Viability of the small seed morph declined quickly. Three months after maturation the small seeds had only 10% germination in 3 weeks without stratification, and 30% germination in 4 weeks after stratification. The large and small seed types produced morphologically different plants in the greenhouse (see chapter 9). Seed dimorphism within the same inflorescence has been reported in many legumes (McDonough 1977). Seed morphs often differ in germination requirements, especially dormancy, stratification, and viability. Seedlings from two seed morphs of the perennial legume Alysicarpus monilifera differ in root growth, shoot spread, and total dry weight (Maurya and Ambasht 1973).

Several insect species live on Lupinus latifolius. An unidentified white larva ate seeds in 30 to 40% of the pods in 1983. Seeds that had been partially consumed did not germinate in a laboratory trial. In September 1984, aphids covered all inflorescences and seedpods at the Wheeler Creek site. Aphids and ants were found on plants throughout the summer of 1985, and leaves of plants at this site had necrotic spots, as if some sucking insect had attacked expanding leaves.

From the L. latifolius seed spread in the field in September, 1983, only two or three seedlings germinated at each site. Cotyledons on all seedlings were partially eaten. The remaining cotyledons yellowed and senesced by late July. Seedlings grew until they had about three small true leaves per plant, and then all shrivelled and died by mid-August. In 1985, there were no seedlings at the sites where seed had been spread. I believe that insufficient moisture caused mortality.

For the perennial lupines at Crater Lake, natural seedling establishment is infrequent. Few seeds of L. lepidus germinated in community PCS in either 1984 or 1985. Lupinus latifolius seeds germinated and seedlings were abundant at the Wheeler Creek site (community PCL, site 2a) in both 1984 and 1985. Most of the 1984 seedlings died before the end of the season. Establishment at this site was better in 1985, perhaps because of 4.6 cm of rain in late July and early August.

In community AAE, site 4, L. latifolius germination was poor and no seedlings were found.

In community AAE, site 4, L. latifolius germination was poor and no seedlings were found.

NITROGEN FIXATION BY LUPINES

Introduction

The parent material of the lodgepole pine forest soils in Crater Lake National Park contained little nitrogen when it was deposited 6600 years ago. Enough N has been added to the system to meet the requirements of the current forest vegetation. Lupines, the only N_2-fixing higher plants in high elevation lodgepole pine forests of the Park, are potential contributors to the N pool. Nitrogen may also enter the system by atmospheric deposition or from free-living N_2-fixing bacteria. Estimates of atmospheric inputs in western Oregon range from 0.5 to 2 $kg \cdot ha^{-1} \cdot yr^{-1}$ (Sollins et al. 1980).

Nitrogen may be lost from a system by denitrification, leaching, or volatilization during fires. Losses were not measured, but should not exceed 1 $kg \cdot ha^{-1} \cdot yr^{-1}$ (K. Cromack, Oregon State University, personal communication, May 1985).

The amount of N fixed by lupines is determined by both nitrogenase activity and nodule biomass. Nitrogenase activity is regulated by photosynthate supply, available water, and soil temperature (Sprent 1979). The relatively harsh environment and low lupine cover suggest that N_2-fixation in these forests is probably low.

Cool summer temperatures may directly reduce nitrogenase activity. N_2-fixation can occur at low temperatures (Englund and Meyerson 1974, Vessey and Patriquin 1984); however, field and laboratory studies demonstrate higher rates with increasing temperatures (Schwintzer 1979, Wheeler et al. 1979), with an optimum range of 10 to 15 degrees over which activity changes little. Soil temperatures in the lodgepole pine forests at Crater Lake are below reported optima of 15°C to 30°C for alder (McNiel and Carpenter 1980), and annual lupines and acacia trees in Australia (Trinick et al. 1976, Lawrie 1981).

Short, cool, dry growing seasons at Crater Lake National Park may indirectly limit N_2-fixation by limiting photosynthesis. N_2-fixation is an energy-requiring process: nodules need adequate photosynthate for the respiratory production of ATP. Fixed carbon is allocated to vegetative growth, reproduction, nodules, and storage. In subalpine lupines, carbohydrate storage in underground plant parts is probably a priority, both for respiration during the 9 month dormant season and also to facilitate rapid vegetative growth at the start of the next growing season (Mooney and Billings 1960).

Water stress reduces N_2-fixation both directly and indirectly. At low water potentials, nodule growth rate is slower (Gallacher and Sprent 1978), nodule respiration is decreased (Pankhurst and Sprent 1975), and

translocation of fixed N out of nodules is slower (Minchin and Pate 1975). Soybeans grown under low soil water potentials show reduced N_2-fixation from both reduced photosynthesis and reduced translocation of carbon to nodules (Kuo and Boersma 1971).

The amount of N fixed per unit land area depends on the active nodule biomass. Low lupine cover at my sites, and therefore low nodule biomass, will limit N_2-fixation per hectare. The amount of active nodule biomass also changes during the year in response to both phenological events and patterns of rainfall and temperature (Adams and Attiwill 1984, Wheeler et al. 1979).

Materials and Methods

Nodulation

To assess N_2-fixation by lupines, I excavated root systems of both species in all communities and recorded the presence or absence of nodules. Nodules were sliced open; if they were red inside, I assumed that leghemoglobin was present.

Nitrogenase Activity

The acetylene reduction assay (Stewart et al. 1967) was used to estimate nitrogenase activity. Six vigorous plants, average in size and with their phenology representative of the population, were chosen for each trial. Nodules attached to 2- to 3-cm of root were

placed in Cryovac bags and sealed with rubber bands around a rubber septum. These bags are gas-tight (W. C. Denison, Oregon State University, personal communication, August 1985). Each bag was evacuated with a syringe, and 45 ml of air plus 5 ml of acetylene were injected to start the assay. Acetylene was generated using a miner's lamp immediately before the assay. Samples were buried in the soil at nodule depth for 60 minutes; then replicate gas samples were transferred to 10 ml vacutainer evacuated blood-sampling tubes (McNabb and Geist 1979). Disposable 1-ml syringes were used to transfer 0.5 ml gas samples from vacutainers to a Hewlett-Packard 5830A gas chromatograph for quantitative analysis of ethylene. The column was 183 cm X 1.65 mm ID, filled with 80-100 mesh Poropak R, and the oven temperature was 55^{o}C. Rate of ethylene production was calculated per gram fresh weight of nodule.

On July 21, assays were run at 2 hour intervals from 7 am until 6 pm to establish if nitrogenase activity varies during the day. Samples of soil from around roots, but without any roots or nodules, were also assayed to establish the presence of non-symbiotic N_2-fixers in the soil. All other experiments were run between 11 am and 3 pm at approximately 2-week intervals throughout the summer.

Soil rooting zone (10 cm) and shaded air temperatures (10 cm) were measured using a thermistor

thermometer. Barometric pressure was taken while samples were incubated to correct for molar gas volume differences between the field and the laboratory. Midday water potential of two or three leaves from plants near those assayed by acetylene reduction was measured in the field using a multiple-sample thermocouple psychrometer (Operator's manual, Decagon Devices, no date) on four of the assay dates. The thermocouple psychrometer was calibrated concurrently, using sucrose solutions. Predawn and midday leaf water potentials of both lodgepole pines and lupines were measured with a pressure chamber at site 1b (community PCS) on August 9, 1985. Soil water content (%) was measured on August 18, 1984.

Canopy cover (cm^2), nodule fresh and dry weights, and above-ground dry weight after drying for 24 hours at 80^oC were determined for all plants used for acetylene reduction. Average cover of L. lepidus in the stand was measured by the line intercept method (Canfield 1941). Five 100-m transects were placed parallel to each other and 50 m apart at sites 1a, 1b, and 100 m east of site 1a in the Pumice Desert study area.

I used simple linear regressions to relate acetylene reduction to time, soil temperature, leaf water potential, plant biomass, and nodule biomass. Community-level rates of N_2-fixation were estimated by combining canopy cover in the study area with a conversion factor relating nodule biomass to canopy cover that was

calculated from the plants used for acetylene reduction assays. The maximum N that could be fixed per gram fresh weight of nodule in one year was estimated by integrating seasonal activity, and by assuming: 1- nitrogenase activity was 0 at snowmelt, June 24, and rose linearly to the rate measured 2 weeks later, 2- no diurnal variation, and 3- nighttime activity equal to midday activity (Silvester et al. 1979). A conversion factor of 3 for moles of acetylene reduced per mole of N fixed was used (Hardy et al. 1973).

Results

Nodulation of Lupinus lepidus

Nodules were absent from only one plant of more than 100 of all sizes and ages. The one plant without nodules was a large, probably old, specimen. First year seedlings were nodulated by the 4th week after germination. Nodules were always at depths between 5 and 20 cm. Some plants had a few large, many-lobed nodules on the main root; some had many small nodules on side roots. Nodules were firmly attached to the root. The cortex of nodules was red, indicating the presence of leghemoglobin, throughout the season from shortly after snowmelt until snowfall, even after acetylene reduction activity was too low to measure late in the season.

Nodulation of *Lupinus latifolius*

Nodules were only occasionally found on *L. latifolius*. Plants appeared to be nodulated only until they were old enough or large enough to bloom. Plants with only one vegetative stem were likely to have nodules at 5-30 cm deep, whereas plants with more than one vegetative stem were seldom nodulated. Plants probably have two stems and bloom in their third or fourth year. The nodules on older plants were loosely attached to the main root at 30 cm. Although *L. lepidus* nodules did not resemble roots at all, nodules on *L. latifolius* sometimes look like 3-5 mm young root primordia. I may have missed nodules on *L. latifolius*, expecting them to resemble *L. lepidus* nodules.

Seasonal and Diurnal Acetylene Reduction Rates

The maximum average rate of ethylene production by *L. lepidus* (9.9 μmoles$\cdot g^{-1} \cdot hr^{-1}$) occurred on July 7, my first measurement, two weeks after snowmelt. Acetylene reduction declined during the season (Figure 3). Within 2 weeks, the average rate had fallen to 3.2, 30% of the maximum. From six weeks after the maximum until snowfall, the rate varied around 1 μmole$\cdot g^{-1} \cdot hr^{-1}$. There was large variation in acetylene reduction rates among individual plants (Figure 3).

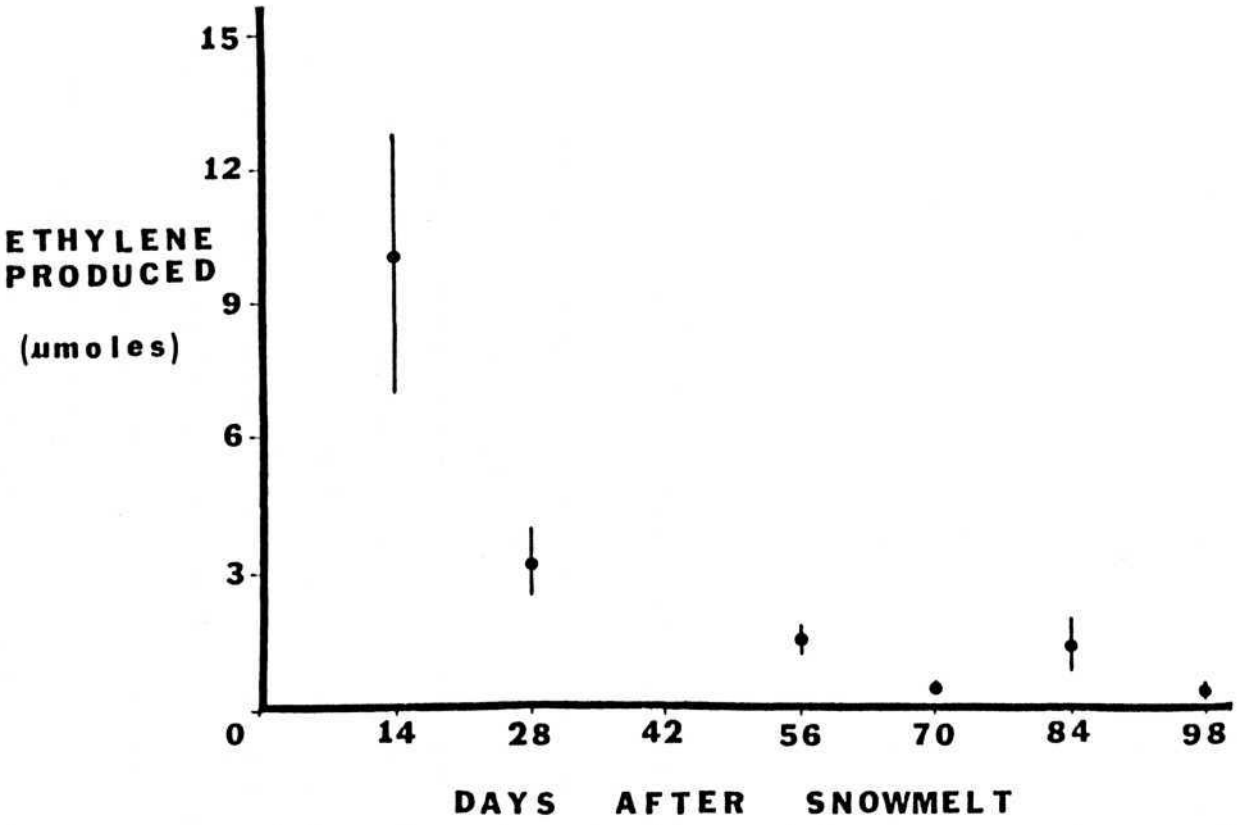

Figure 3. Nitrogenase activity of Lupinus lepidus nodules, expressed as µmoles of ethylene produced per gram of nodule fresh weight per hour (mean ± SE) during the 1984 growing season. Each mean represents 6 measurements. Snowmelt was about June 24.

The acetylene reduction assay was run on five samples of L. latifolius nodules on September 2, 1984. The rate per gram of nodule was 6.9 μmoles·g^{-1}·hr^{-1}. This value is within the range of rates found for L. lepidus, but is substantially higher than comparable late-season rates of L. lepidus.

There was no diurnal pattern in acetylene reduction rate (Table 4). Differences among times were not significant (least significant difference test).

In the absence of nodules, soil samples did not reduce acetylene.

Acetylene Reduction and Environmental Variables

Soil temperature rose for 4 weeks after snowmelt to a maximum of 13.7°C, and then declined during the rest of the summer (Table 5). For the entire summer, the correlation coefficient between soil temperature and log μmoles of acetylene reduced was significant ($r=0.67$, $n=48$). Both nitrogenase activity and soil temperature rose after snowmelt, peaked, and then declined. The peak acetylene reduction rate occurred two weeks before the maximum soil temperature (Table 5).

Leaf water potential decreased during the dry period between snowmelt and August 30 (Table 5). The correlation coefficient between water potential and acetylene reduction was not significant. Between July 7 and August 18, however, both leaf water potential and

Table 4. Average acetylene reduction rate of *Lupinus lepidus* nodules in Crater Lake National Park at 5 times during the day on July 21, 1984. Sample size = 6 for each time.

Time	Mean acetylene reduction rate ($\mu moles \cdot g^{-1} \cdot hr^{-1}$)	SE
730	2.0	0.5
1000	0.6	0.2
1230	4.1	1.2
1500	5.2	2.8
1815	3.8	1.1

Table 5. Soil temperature at nodule depth (10 cm), midday leaf water potential, and average acetylene reduction by nodules of Lupinus lepidus in Crater Lake National Park during the 1984 growing season.

Date	Soil temperature (^{0}C)	Leaf Ψ_l (MPa)[1]	Acetylene reduction (μmoles$\cdot g^{-1} \cdot hr^{-1}$)
7/7	12.7	-1.2 to -3.0	9.9
7/21	13.7	ND	3.2
8/18	10.7	-3.4 to -4.6	1.5
9/1	6.9	-1.6 to -2.3	0.4
9/16	7.8	-1.5 to -1.9	1.3
9/29	5.1	ND	0.3

[1] ND: Data for leaf water potential were not collected on these dates.

nitrogenase activity declined. After a rain on August 30-31, leaf water potential increased and soil temperature decreased simultaneously. In mid-August, soil water content was 5.4%.

In August 1985, 10 days after 4.5 cm of rain, predawn xylem potentials at site 1b were between -0.2 MPa and -0.3 MPa for both lodgepole pine and L. lepidus. By midday, lodgepole pine potentials had fallen to -0.35 MPa and lupines to -1.0 MPa in the sun and -0.75 MPa in the shade.

Canopy Cover of Lupinus lepidus and Nodule Biomass

Log transformed nitrogenase activity was significantly correlated with aboveground biomass ($r=0.67$, $n=48$), but not with nodule biomass ($r=-0.2$, $n=48$) or with nodule number per plant ($r=-0.1$, $n=48$). Lupinus lepidus cover was patchy and low (48 $m^2 \cdot ha^{-1}$, SE=15). The ratio of nodule fresh weight to average lupine cover was 25 $g \cdot m^{-2}$ (SE=6).

Potential N_2 Fixed

Annual nitrogen input from L. lepidus was estimated to be 30 mg per gram fresh weight of nodule. Seasonal N_2-fixation potential is therefore 0.75 $g \cdot m^{-2}$ of canopy cover. Given 48 $m^2 \cdot ha^{-1}$ of actual lupine cover, I estimate a total of 0.036 kg N fixed per hectare in the study area in 1984.

Discussion

Nodulation of Lupines

Lupinus lepidus plants of all sizes and ages did have active nodules. Lupinus latifolius, however, appears to form nodules in the seedling stage, fix nitrogen for only a few years while the plant is growing rapidly and forming its large perennial underground caudex and root system, and then cease N_2-fixation, slough its nodules and fail to produce new ones. Nodulation and N_2-fixation are inhibited when there is sufficient N in the soil for plant growth (Gibson and Jordan 1983). For long-lived perennial lupines with a large root system, the growth increment in each year may be so small (see Phenology chapter) that there is enough N in the plant or the soil for maintenance and growth without additional N from N_2-fixation.

Nitrogen Fixation and Environmental Variables

The seasonal pattern of nitrogenase activity (Figure 3) may represent the interaction of several causal factors. Temperature probably limits the absolute maximum rate of N_2-fixation in this system, where soil temperatures never exceeded 14°C. Even though nitrogenase is active at low temperatures, maximum rates have never been reported below 15°C. Nitrogenase in subalpine lupines is probably adapted to low

temperatures, but activity should increase at higher temperatures, if other conditions are favorable.

As acetylene reduction rates dropped after the maximum on July 14, there was a concomitant decrease in leaf water potential, which may have contributed to the lower nitrogenase activity. Low midday leaf water potentials can be caused by either a cumulative seasonal drought, or diurnal cycles of midday low water potentials and nightly recharge.

Most summers at Crater Lake National Park are dry, the major source of water being snowmelt. Cumulative depletion of soil water may occur during the summer. In mid-August, the soil water content was 5.4%, which is below the permanent wilting percentage in pumice soils (7.7%) (Youngberg and Dyrness 1963). N_2-fixation in four pasture legumes stops when soil water content approaches the permanent wilting percentage (Holter 1978).

Other evidence, however, suggests that sites where lodgepole pine grows are not droughty. Lodgepole pine is found in moderately mesic environments, and this species is sensitive to low moisture (Lotan and Perry 1983). In the southern extension of Crater Lake National Park, white fir saplings in stands on pumice that contained lodgepole pine had higher predawn xylem potentials than in adjacent stands on alluvium that did not contain lodgepole (-0.7 MPa vs. -1.8 MPa) (McNeil and Zobel 1980). In several lodgepole pine stands in central

Oregon, predawn xylem potentials never dropped below -1.1 MPa during the summers of 1969 and 1970 (Mason and Tigner 1972). Lupines, however, may not be as efficient as lodgepole pines in either obtaining water from the soil or controlling water loss from leaves. Lupinus lepidus at site 1b had greater diurnal variation in leaf water potential than lodgepole pines at the same site.

Low midday water potentials may develop on pumice soils even though they have high water-holding capacity (Youngberg and Dyrness 1963, Flint and Childs 1984), because of low conductivity of unsaturated pumice soils (Horn 1968). D. Chapin (University of Washington, personal communication, June 1985) measured diurnal stress in Polygonum newberryi and Eriogonum pyrolifolium in tephra at Mount St. Helens. During the dry summer of 1984, however, all plants recovered during the night and a cumulative seasonal decline in water potential was not observed. Low midday water potentials may temporarily inhibit photosynthesis in L. lepidus, and this may reduce midday N_2-fixation rates.

The seasonal pattern of nitrogenase activity is probably also determined by carbon allocation. Relative allocation of photosynthate to growth, nodules, reproduction, and storage may change during the summer. I hypothesize that nitrogenase activity is high early in the summer because carbon is allocated to nodules. In mid-summer, some carbon is allocated to reproduction.

Late in the summer, storage organs--such as the thick taproot--receive a high proportion of the photosynthate. Consequently, nodules receive less carbon in mid- to late summer, and nitrogenase activity is low.

In summary, early in the season I expect soil water is available and carbon is allocated to nodules, and temperature probably limits the maximum rate of N_2-fixation. Later in the season, carbon allocation patterns and low midday water potentials probably both contribute to the decline in and low level of nitrogenase activity.

The rate for the one assay of L. latifolius was higher than the rate for L. lepidus on the same date. All the L. latifolius plants were young, and had small nodules that probably had a high ratio of active/senesced tissue. Nodules on smaller, perhaps younger, L. lepidus plants tended to have higher rates than nodules on larger plants, but there were not enough data to calculate a meaningful correlation coefficient.

Potential N_2 Fixed

On a community level, L. lepidus appears to contribute little N to the soil. My estimate of 0.04 $kg \cdot ha^{-1} \cdot yr^{-1}$ is only a few percent of the estimated rainfall input (Sollins et al. 1980). Around individual lupine plants, however, the amount of N fixed may be significant. In an area with complete lupine cover, a

value of 7.5 $kg \cdot ha^{-1}$ annually would accumulate into a significant amount over the lifetime of a lupine.

In the estimate of potential N fixed by L. lepidus, the magnitude of the variance in the data was so great that little significance can be attached to the actual numbers. The greatest sources of error were predicting nodule biomass from plant cover, and the natural variation in acetylene reduction rate among plants. Other authors who have presented potential N accretion values have not reported the variance of their data (Adams and Attiwill 1984, Lawrie 1981, Schwintzer 1979). Even with the high variance, it is clear that the contribution of N by lupines in this system is small.

GREENHOUSE STUDY

Introduction

Seeds of lupines collected in three of the lodgepole pine community types at Crater Lake were germinated and grown for one year on five different soils in a greenhouse in Corvallis, Oregon. The purposes of the greenhouse study were to: (1) compare the growth and nodulation of different seed-sources on a variety of soils in a common environment, and (2) quantify the amount of N_2 fixed during a year by each species of lupine and determine to what degree it is released into the soil and held in the plant.

Materials and Methods

Pumice soil was collected from each of the four lodgepole pine community types in the Park in September 1983. Washed beach sand from Florence, Oregon was used as a no-N control soil. The soils were sieved through a 1.5 cm mesh to remove large roots and wood fragments.

Lupinus lepidus seeds were collected from sites 1a and 1b in community PCS (seed type 1); L. latifolius seeds were collected from site 2a in community PCL (seed type 2) and from site 4 in community AAE (seed type 4). There were two seed morphs from the population at site 2a, and these were separated as 2S (small black and yellow seeds) and 2L (large brown seeds).

The experimental design was a 4x5 factorial with two replications. Pots were randomized within each replicate.

Seed types 1 and 2S were planted without stratification. Large brown seeds (2L and 4) were stratified at 4^0C for 14 days to encourage germination. In early February, 1984, 8 to 16 seeds were planted in each pot. As seedlings emerged, pots were thinned to 2 plants each. Pots were watered to saturation and allowed to drain to field capacity 2 times per week for 2 months, then once per week for 11 more months. The greenhouse was ventilated in the summer and heated in the winter.

General growth and vigor were recorded for all plants for one year.

In March, 1985, plants were harvested, separated into shoots, roots, and nodules, dried for 24 hours at 80^0C, and weighed. Nitrogen concentration in the soil and plants from each pot was determined by the Kjeldahl method (Bremner 1965).

Data were analyzed by two-way analysis of variance to determine to what degree soil type or seed type is related to variation in: 1-plant dry weight, 2-root/shoot ratio, 3-nodule fresh weight, 4- final soil N concentration, and 5- plant N concentration.

Results

Germination

Within one month after planting, 56% of the seeds that eventually germinated had done so. By two months, 85% of the seeds that were going to grow had germinated. Germination of the small, black and yellow seeds (2S) was less than the other seed types (Table 6).

Vigor and Growth Habit

There were no apparent differences due to soil type in seedling growth and vigor for a given seed type, except that most seedlings in sand were mildly chlorotic, especially during the first two months of growth. Lupinus lepidus (seed type 1) resembled plants in the field. Although all plants of L. lepidus bloomed between June 30 and August 15, there was no seed set, probably because there were no pollinators in the greenhouse. Lupinus latifolius plants from small seeds (2S) developed a rosette of 4 to 6 leaves in the greenhouse, a growth form never seen in the field. Lupinus latifolius plants from large seeds (2L and 4) were morphologically similar to each other and to field plants. These plants produced leaves on an upright stem. After growing for 4 months, the aboveground stems of about 50% of these plants died back to soil level. By 7 months, all plants that had died back had produced a second aerial stem. In the

Table 6. Greenhouse germination percentage of seed types collected in September 1983 from three sites in Crater Lake National Park. Value is mean of 10 pots.

Seed source[1]	Germination (%)
1	84
2S	36
2L	80
4	68

[1] Seed source:

1-Lupinus lepidus seed, community PCS, sites 1a, 1b.

2S-L. latifolius small seed, community PCL, site 2a.

2L-L. latifolius large seed, community PCL, site 2a.

4-L. latifolius large seed, community AAE, site 4.

field, only one aerial stem is produced during the first growing season.

Plant Dry Weight

Lupinus lepidus had greater biomass than plants from any seed type of L.latifolius (Table 7). There were no significant differences in final dry weight among the three seed types of L. latifolius. Soil type was not a significant factor determining dry weight (Table 8).

Root/Shoot Ratios

Root/shoot dry weight ratios (Table 9) varied between 0.3 and 25. Seed type was a significant factor accounting for variation in the ratio (Table 8). The average root/shoot ratio of L. lepidus was less than 1.0, substantially lower than the root/shoot ratios of L. latifolius. Small black and yellow seeds (2S) had lower ratios than large brown seeds (2L and 4). Soil type was not significant (Table 8).

Nodule Fresh Weight and Relative Dry Weight

Seedlings on all soil types, including sand, were nodulated within two months after germination. At harvest, I found nodules in all pots, except for one replicate of large brown L. latifolius seeds in soil from site 3. Nodule fresh weights ranged from less than

Table 7. Mean final dry weights (g per pot, n=2) of two species of lupines grown from 4 seed types on 5 soil types for 13 months in the greenhouse. Seed and soil were collected in September 1983 in Crater Lake National Park.

	Seed source[1]				
Soil type[2]	1	2S	2L	4	$\bar{X}$
1	5.98	2.71	3.32	2.07	3.5
2	12.69	7.28	3.79	2.41	6.5
3	6.44	2.70	2.99	1.75	3.5
4	10.74	6.15	4.78	3.00	6.1
5	13.43	6.96	7.21	1.92	7.4
$\bar{X}$	9.8	5.2	4.4	2.2	

1 Seed source:

1-*Lupinus lepidus* seed, community PCS, sites 1a, 1b.

2S-*L. latifolius* small seed, community PCL, site 2a.

2L-*L. latifolius* large seed, community PCL, site 2a.

4-*L. latifolius* large seed, community AAE, site 4.

2 Soil types:

Rooting zone soils from community PCS (1), PCL (2), ACL (3), and AAE (4), and dune sand from Florence, Oregon (5).

Table 8. Analysis of variance summary for dry weight, root/shoot ratios, nodule fresh weight, relative fresh weight, soil N and plant N of greenhouse grown lupines.

Analysis	SSE[1]	df	MSE	Source	F-value[2]
Dry weight	305.35	19	16.07	block	0.78
				seed	8.09 **
				soil	1.62
				seed x soil	0.30
Root/shoot	321.74	19	16.93	block	5.60 *
				seed	6.17 **
				soil	1.26
				seed x soil	0.61
Nodule fresh weight	4.36	19	0.229	block	5.04 *
				seed	2.96
				soil	4.35 *
				seed x soil	1.11
Relative nodule weight	0.057	19	0.0030	block	9.03 **
				seed	2.39
				soil	3.20 *
				seed x soil	1.26
Soil nitrogen	0.003	19	0.00015	block	0.03
				seed	1.11
				soil	168.52 **
				seed x soil	0.43
Plant nitrogen	3.91	19	0.206	block	0.01
				seed	5.43 **
				soil	2.21
				seed x soil	1.68

[1] SSE=error sum of squares for the analysis, df=residual degrees of freedom, MSE=mean square error.

[2] *,** significant F ratio at the 0.05 and 0.01 levels, respectively.

Table 9. Mean root/shoot ratios (n=2) of two species of lupines grown from 4 seed types on 5 soil types for 13 months in the greenhouse. Seed and soil were collected in September 1983 in Crater Lake National Park.

	Seed source[1]				
Soil type[2]	1	2S	2L	4	$\bar{X}$
1	0.84	3.2	9.7	13.8	6.9
2	0.70	2.7	6.5	10.8	5.2
3	0.61	2.8	3.6	3.3	2.6
4	0.77	3.8	7.5	4.6	4.2
5	0.58	2.3	7.1	4.9	3.7
$\bar{X}$	0.70	3.0	6.9	7.5	

[1] Seed source:

1-Lupinus lepidus seed, community PCS, sites 1a, 1b.

2S-L. latifolius small seed, community PCL, site 2a.

2L-L. latifolius large seed, community PCL, site 2a.

4-L. latifolius large seed, community AAE, site 4.

[2] Soil types:

Rooting zone soils from community PCS (1), PCL (2), ACL (3), and AAE (4), and dune sand from Florence, Oregon (5).

0.01 g to 1.4 g per pot (2 plants per pot) (Table 10). Soil type was a significant factor explaining variability in nodule weight (Table 8). Lupinus lepidus and L. latifolius plants from small black and yellow seeds had higher nodule fresh weights than L. latifolius from large brown seeds, but the difference was not significant. The greatest nodule fresh weight was in sand, and the lowest in soil from site 3, which had the highest initial soil N concentration.

Soil type was a significant factor influencing relative nodule weight (nodule fresh weight/plant dry weight) (Table 8). Plants in soil from community type ACL (soil 3) had the lowest relative nodule biomass (Table 11). Lupinus latifolius plants from small black and yellow seeds had the highest relative nodule biomass (11%), compared to 5 to 8% for plants from the other three seed types, although the data were too variable for the difference to be significant.

Soil Nitrogen Concentration

Soil N was lowest in sand and highest in soil from site 3 (Table 12). Control pots of pumice soil without plants contained from 0.55 g N (soil type 2) to 2.42 g N (soil type 3). Seed type had no significant effect on final soil N concentration, and there was no difference

Table 10. Mean nodule fresh weights (g per pot, n=2) of two species of lupines grown from 4 seed types on 5 soil types for 13 months in the greenhouse. Seed and soil were collected in September 1983 in Crater Lake National Park.

	Seed source[1]				
Soil type[2]	1	2S	2L	4	$\bar{X}$
1	0.32	0.30	0.08	0.04	0.19
2	0.65	1.43	0.20	0.09	0.65
3	0.19	0.11	0.01	0.03	0.09
4	0.62	0.61	0.45	0.32	0.40
5	1.90	0.69	0.49	0.24	0.83
$\bar{X}$	0.74	0.63	0.25	0.14	

1 Seed source:

1-Lupinus lepidus seed, community PCS, sites 1a, 1b.

2S-L. latifolius small seed, community PCL, site 2a.

2L-L. latifolius large seed, community PCL, site 2a.

4-L. latifolius large seed, community AAE, site 4.

2 Soil types:

Rooting zone soils from community PCS (1), PCL (2), ACL (3), and AAE (4), and dune sand from Florence, Oregon (5).

Table 11. Mean relative nodule fresh weights (nodule fresh weight/plant dry weight, %, n=2) of two species of lupines from 4 seed types grown on 5 soil types for 13 months in the greenhouse. Seed and soil were collected in September 1983 in Crater Lake National Park.

	Seed source[1]				
Soil type[2]	1	2S	2L	4	$\bar{X}$
1	5.7	14.9	3.3	2.4	6.6
2	6.7	20.7	5.2	5.0	9.4
3	2.9	4.3	0.2	3.1	2.6
4	6.6	10.7	10.4	14.9	10.7
5	13.4	8.7	8.1	13.1	10.8
$\bar{X}$	7.5	11.4	5.4	7.7	

1 Seed source:

1-Lupinus lepidus seed, community PCS, sites 1a, 1b.

2S-L. latifolius small seed, community PCL, site 2a.

2L-L. latifolius large seed, community PCL, site 2a.

4-L. latifolius large seed, community AAE, site 4.

2 Soil types:

Rooting zone soils from community PCS (1), PCL (2), ACL (3), and AAE (4), and dune sand from Florence, Oregon (5).

Table 12. Mean soil nitrogen concentration (%, n=2) in containers of greenhouse-grown lupines. Seed and soil were collected in September 1983 in Crater Lake National Park.

	Seed source[1]					
Soil type[2]	empty[3]	1	2S	2L	4	$\bar{X}$
1	0.035	0.028	0.027	0.021	0.030	0.028
2	0.031	0.044	0.034	0.026	0.039	0.036
3	0.14	0.14	0.15	0.14	0.15	0.14
4	0.095	0.081	0.064	0.067	0.086	0.078
5	0.00	0.00	0.00	0.00	0.00	0.00
$\bar{X}$	0.061	0.061	0.058	0.056	0.051	

1 Seed source:

1-*Lupinus lepidus* seed, community PCS, sites 1a, 1b.

2S-*L. latifolius* small seed, community PCL, site 2a.

2L-*L. latifolius* large seed, community PCL, site 2a.

4-*L. latifolius* large seed, community AAE, site 4.

2 Soil types:

Rooting zone soils from community PCS (1), PCL (2), ACL (3), and AAE (4), and dune sand from Florence, Oregon (5).

3 Nitrogen concentration (%) of control pots that were not planted, but were watered.

in N concentration between pots in which plants had grown for a year and control pots without plants.

Plant Nitrogen Concentration

Whole plant N concentration was between 1.0 and 2.8% (Table 13). Seed type was a significant factor explaining variation in plant N concentration (Table 8). The highest N concentration was in L. latifolius plants from small seeds and in plants on soil from communities ACL and AAE (types 3 and 4). The lowest N concentration was in plants on sand and on soil from community PCS (type 1). Total N content (%N times dry weight) in plants varied from 7 mg in a pot where no nodules were found to 410 mg. There were seed-type differences (not significant) in mean total N per pot (2 plants), but there was also a lot of variation within a seed type (Table 14). Lupinus lepidus averaged slightly higher than L. latifolius from 2S seeds. Lupinus latifolius from large seeds had the lowest mean N accumulation.

Table 13. Mean plant nitrogen concentration (%, n=2) of two species of lupines from 4 seed types grown on 5 soil types for 13 months in the greenhouse. Seed and soil were collected in September 1983 in Crater Lake National Park.

	Seed source[1]				
Soil type[2]	1	2S	2L	4	$\bar{X}$
1	1.61	2.70	1.67	0.64	1.6
2	2.07	2.54	1.90	1.40	1.9
3	1.88	2.24	1.97	2.30	2.2
4	1.61	2.45	2.22	2.59	2.1
5	1.67	2.12	1.79	1.38	1.7
$\bar{X}$	1.7	2.4	1.9	1.7	

1 Seed source:

1-Lupinus lepidus seed, community PCS, sites 1a, 1b.

2S-L. latifolius small seed, community PCL, site 2a.

2L-L. latifolius large seed, community PCL, site 2a.

4-L. latifolius large seed, community AAE, site 4.

2 Soil types:

Rooting zone soils from community PCS (1), PCL (2), ACL (3), and AAE (4), and dune sand from Florence, Oregon (5).

Table 14. Mean total nitrogen content of biomass from each seed type. Each mean is the total for 2 plants in a pot, and 2 pots for each soil type in the greenhouse. Seed was collected in September 1983 in Crater Lake National Park.

Seed type[1]	$\bar{X}$ (mg)	range
1	172	20-290
2S	124	30-250
2L	82	10-220
4	36	7-110

[1] Seed type:

1-*Lupinus lepidus* seed, community PCS, sites 1a, 1b.

2S-*L. latifolius* small seed, community PCL, site 2a.

2L-*L. latifolius* large seed, community PCL, site 2a.

4-*L. latifolius* large seed, community AAE, site 4.

Discussion

Growth habit, vigor, biomass, root/shoot ratio, and relative nodule fresh weight were affected by seed type, but not by soil type in this greenhouse experiment. *Lupinus lepidus* seedlings had the highest dry weight and lowest root/shoot ratio. This species also had higher nodule fresh weight than *L. latifolius* plants from large seed (seed source 2L and 4). During the first year, *L. lepidus* seems to have the greatest capacity for high rates of N_2-fixation, as it had high nodule biomass, and the greatest accumulation of biomass N.

The two populations of *L. latifolius* from large brown seeds (2L and 4) could not be distinguished from each other by the criteria I used to quantify growth. Plants from these two seed types had the highest root/shoot ratios, lowest nodule fresh weight, and least biomass accumulation during the year. In the greenhouse, these plants allocated relatively more energy to roots than did *L. lepidus*.

Lupinus latifolius plants from small seeds (2S) differed from *L. latifolius* from large seeds in all the seedling performance measurements. Compared with plants from large seeds of this species, plants from 2S seeds had lower root/shoot ratios, higher nodule fresh weight, and higher whole plant N accumulation. This seed source also produced plants with the highest N concentration and relative nodule fresh weight of all 4 seed types. Plants

from 2S seeds are similar to L. lepidus in allocating carbon to shoot growth and nodules.

Lupinus lepidus plants were vigorous in the greenhouse and, superficially, looked like wild populations. Lupinus latifolius plants, in contrast, were not vigorous, had periodic shoot dieback, and produced few leaves. The poor growth and vigor of L. latifolius may have been caused by warmer temperatures in the greenhouse than in the field, by restricted rooting volume, or unfavorable moisture conditions.

Soil type affected only nodule fresh weight and plant N concentration, of the measurements made. Initial soil N may be an important variable controlling these characteristics, because the highest nodule fresh weight was in the soil with lowest N and the highest plant N concentrations were in the two highest N soils.

I determined N concentration of the total plant, without separating aboveground (high N) tissue from belowground (lower N) tissue. Lupinus arboreus seedling leaf litter contains 4.8% N, whole seedlings 1.1% N (Silvester et al. 1979). Since whole plant N in the greenhouse lupines ranged from 1.7-2.4%, foliar N was probably at least 4.8% N, which is high compared with 1-4% in deciduous tree foliage and herbaceous plants (Larcher 1980).

Growth of plants for one year in pots in the greenhouse had no effect on soil N concentration. All

fixed N was apparently held in the biomass. In the field, N may gradually be released as leaves, fine roots, and nodules senesce. Pulses of N may be released to the soil when plants die. Some N is released from seedlings of L. arboreus by seedling exudates, litter, and possibly foliar leaching (Gadgil 1971a). Larger amounts of N are released when roots die as a result of shading or mechanical damage (Gadgil 1971b). If N was exuded belowground in my pots, it either may have been too little to be detected by my methods, or may have been taken up again by active roots, or by bryophytes on the soil surface.

SUMMARY AND CONCLUSIONS

Phenology, Seeds and Seedlings, and Species Distribution

Lupinus lepidus and *L. latifolius* have similar phenologies. Shoots emerge within a few days after snowmelt and early growth is rapid. Maximum canopy cover of both species is reached by the time flowering begins. *Lupinus lepidus* starts blooming 3-4 weeks after snowmelt, and seeds mature 30 days later. In some years, some *L. lepidus* plants have two seed crops, blooming a second time shortly after the first crop matures. *Lupinus latifolius* plants bloom once during the summer, starting 4-5 weeks after snowmelt.

Although seed crops were plentiful and laboratory germination of *L. lepidus* was high, I saw no seedlings during the 3 summers of data collection. There may be seed predation by insects or rodents, or the litter layer on the soil surface may hinder germination. This species might require a mineral soil seedbed, and a particularly moist season for establishment.

Seedling establishment of *L. latifolius* varied among sites and from year to year. Seedling germination at site 2a, community PCL, was abundant in both 1984 and 1985, but establishment percentage seemed higher in 1985, when there was rain during the growing season. Midsummer precipitation is probably critical to the establishment of seedlings. I observed no seedlings at site AAE 4.

The different behavior of the two seed morphs from the riparian population of L. latifolius in community PCL may be of ecological significance. Fresh small seeds had high germination rates, and did not require stratification. After aging, germination rates were much lower. In the field, seeds may germinate late in summer, after rains begin. Fall establishment may increase the growth rate during their first full growing season, so seedlings can compete for light with neighboring vegetation. Plants from small seeds have the potential to contribute a significant amount of high N leaf litter to the soil, if growth habit and allocation patterns of wild plants are similar to greenhouse plants. Greenhouse plants from small seeds had higher plant N concentrations, higher relative nodule fresh weight, and lower root/shoot ratios compared with plants from large seeds. Greater allocation of carbon to shoot growth may be an advantage in the riparian zone where root growth is less critical because moisture is abundant, and neighboring vegetation limits light penetration to the understory.

Although both L. lepidus and L. latifolius can grow on soil from any of the four communities in a common greenhouse, they do not grow together in the field. The PCS community type is an unfavorable environment for many species, as indicated by low species richness, cover, soil C, and productivity, yet L. lepidus is abundant and

vigorous. The greenhouse growth characteristics of this species (high biomass, nodule weight, and total N accumulation) may lead to its success in this community type. Lupinus latifolius and conifers other than lodgepole pine may be excluded by a combination of factors, including local climate, and physical, chemical, and biological soil properties. The PCS community type tends to occur in slight depressions where cold air drainage or cold, wet soil after snowmelt might inhibit seedling establishment (Zeigler 1978).

Community types PCL, ACL, and AAE are more productive, perhaps because of a more favorable environment. Lupinus lepidus, which seems to grow only beneath openings in the forest canopy, may have a higher light requirement than L. latifolius. Establishment may require a mineral soil seedbed beneath a canopy opening. Lupines are strongly light-demanding (Silvester et al. 1979). Lupinus latifolius, which grows taller than L. lepidus, should compete better with neighboring vegetation for light in the more productive community types. Organic matter was higher in community types PCL and AAE than in community type PCS. This would improve soil structure, microbial activity, and water-holding capacity (Brady 1974), which may be necessary for growth of L. latifolius. These effects of organic matter would not have been apparent in the greenhouse because I sieved the soil and watered regularly.

Nitrogen Fixation and Accretion

Nitrogenase activity may be controlled by many factors, the relative importance of which varies during the season (Sprent 1979). Nitrogen fixation by L. lepidus is probably influenced by phenology. Maximum rates of acetylene reduction occurred during the period of vegetative expansion. During flowering, rates declined rapidly and remained low for the rest of the summer. Seasonal acetylene reduction patterns may also be caused by shifts in carbon allocation from vegetative growth and N_2-fixation to reproduction and storage. Environmental factors unrelated to phenology may be equally important in controlling the rate. Sprent and Silvester (1973) observed a decrease in N_2-fixation when fruits of Lupinus arboreus began to swell, and leaves and nodules were senescing. They attributed the reduction in nitrogenase activity to diversion of nutrients to pods, but also noted that the reduction in activity could have been caused by a drought at the same time. In clover, acetylene reduction rates declined after the onset of flowering, but this decline was also associated with a dry period (Vessey and Patriquin 1984).

Little N has accumulated in the soil of the lodgepole pine communities during 6600 years. Total N in the soil is only 10% of the estimated cumulative input from precipitation. Lupines have either contributed

little N to the system, or volatilization and leaching losses are very large. Nitrogen accretion due to lupines is small on a community level because of low nodule biomass and low annual rates of N_2-fixation. Low, patchy cover of L. lepidus leads to low nodule biomass in the PCS community type. Lupine cover (L. latifolius) is higher in community types PCL, ACL, and AAE, but nodule biomass is low because only young plants of this species are nodulated.

Lupines may, however, contribute significant N on a smaller scale. The maximum acetylene reduction rate of 9.9 μmoles$\cdot g^{-1} \cdot hr^{-1}$ for L. lepidus is comparable to rates of acetylene reduction in crop legumes (Hardy et al. 1973). In a particularly favorable year, this high rate may continue for several weeks, significantly increasing the amount of N fixed. Acetylene reduction rates per gram of nodule were much higher in L. latifolius than in L. lepidus in late summer, so the seasonal cumulative amount may be higher for nodulated L. latifolius.

Greenhouse studies indicated that fixed N is held in the plant rather than released into the soil, at least during the first growing season. Senescence of leaves, fine roots or nodules, and plant mortality creates a high concentration of N in the immediate neighborhood of lupines. In a subalpine meadow in Washington, soil from the microsite directly beneath L. latifolius had 40% more N than soil from between plants (Belsky and del Moral

1982). In community type PCS, the most intensively-sampled community, there was large within-site variation in soil nutrients. One sample in particular had 2-3 times the N concentration of the three other samples, and may have been taken from a spot where a lupine had recently grown.

Higher concentrations of N must stimulate microbial activity. When a L. lepidus plant dies during the summer, all traces of leaf litter are gone within 3 weeks. These spots could be important microsites for the establishment of seedlings. Seedling establishment of all species in this community was poor, so I cannot draw conclusions on this point.

Other Ecological Roles

Lupines in Crater Lake National Park add N and C to the system, serve as food for insects and occasionally deer, and increase nutrient conservation and cycling. The presence of lupines may also increase soil calcium, phosphorus, and pH, and contribute to the development of mull humus in the neighborhood of plants (Rehfuess 1979).

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