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## COLONIZING PLANTS ON THE PUMICE PLAINS, MOUNT ST. HELENS, WASHINGTON<sup>1</sup>

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### ABSTRACT

Initial colonization on the devastated Pumice Plains on the northern flank of Mount St. Helens, Washington, was monitored in two large grids seven seasons after the eruptions of 1980. The Pumice Plains is composed primarily of deep pumice, but contains a few large mudflow channels and numerous small erosion gullies. Over 45% of 1,600 10 by 10 m quadrats (Willow Spring site) and over 35% of 875 quadrats (Lupine Patch site) were devoid of vascular plants. The most common species were the weedy natives, *Anaphalis margaritacea* and *Epilobium angustifolium*, as well as *Lupinus lepidus* var. *lobbii*, a native with poor dispersal usually found at subalpine elevations. The first two species invaded by long-distance dispersal; a few individuals of the latter somehow established by 1981 from surviving rootstocks or seeds, and dense populations have developed from these survivors. Other species are typically found at low densities in favorable microsites. Species richness averaged 1.03 per 100 m<sup>2</sup> at Willow Spring and 1.82 at Lupine Patch. There are 32 species at Willow Spring and 26 at Lupine Patch. Species richness was concentrated in sites with high soil moisture and where topographic irregularities permitted accumulation of seeds. Colonists are an unusual mix of natives, drawn from an array of open habitats, and introduced weeds originating in fields and clearcuts at lower elevations. Colonizing species are primarily herbaceous, perennial, and wind-dispersed, though seedlings of woody "climax" species occur. Three distributional patterns are recognized: hydrophiles, found near streams; facultative hydrophiles, concentrated in wet sites but successfully colonizing upland sites; and species distributed at random or in xeric sites. We predict that the course of succession will continue to be slow and herbs-dominated. Patches of *Lupinus lepidus* at present do not appear to facilitate colonization. Colonists will continue to be rare and be confined to favorable microsites for several years.

ONLY RARELY have terrestrial plant ecologists been able to observe the colonization of a pristine landscape. Such an opportunity was created after the 1980 eruptions of Mount St. Helens. Among the various effects of the eruptions, the most visually striking is the extensive region of pumice, deposited immediately north of the crater, aptly termed the "Pumice Plains." This 20 km<sup>2</sup> region was essentially devoid of life in 1980, in contrast to most other sites around the volcano where some plants survived the eruption (del Moral, 1983; Franklin et al., 1985). In this paper we describe the colonization of the Pumice Plains by vascular plants.

Ecologists are interested in colonization pro-

cesses for two principal reasons. First, community ecologists recognize colonization as the first stage in primary succession, which in this environment will lead eventually to a coniferous forest (Kruckeberg, 1987). At this community level, questions about the rate and direction of succession are of great interest. A better understanding of the "rules" by which individuals and species form communities should lead to a better understanding of the forces that structure mature communities. Second, population ecologists are interested in several aspects of the ecology of colonizing species, such as dispersal, demography, genetics, and ecophysiology (Baker and Stebbins, 1965; Baker, 1974, 1986; Bazzaz, 1983, 1986; Mack, 1985; Rice and Jain, 1985; Kruckeberg, 1986). In this paper we address questions relevant to both disciplines. Specifically, we ask: what life histories are represented among colonizing species on the Pumice Plains? Are colonists uniformly distributed over the landscape? If not, are there aspects of topography or life history that might explain patterns of colonization? Are species characteristic of later successional stages present among the early colonists?

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Nomenclature follows that of Hitchcock and Cronquist (1973).

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**METHODS—Study site**—Mount St. Helens, in southwestern Washington state, is at N46°12' W122°11'. A 20 km<sup>2</sup> region to the north of the crater at 1,000–1,150 m elevation received several deposits of pumice from pyroclastic flows occurring during and after the famous 18 May 1980 eruption (Lipman and Mullineaux, 1981; Peterson, 1986). These deposits, discharged in the direction of the lateral blast and collectively referred to as the Pumice Plains, range in thickness from 10–200 m (Lipman and Mullineaux, 1981), and overlay a former forest (Kruckeberg, 1987). Individual pumice particles range in size from <1 cm to >25 cm, but most are between 2 and 10 cm. Extensive channels were carved in the pumice by erosion from rainfall, melting snow, and several subsequent mudflows. The old surface has been exposed occasionally by these erosive events, permitting a few individuals to resprout, but the region was essentially barren in 1980. The Pumice Plains landscape is thus best described as a dissected plain, with extensive areas of thick pumice interrupted by a network of often deep, sometimes broad, intermittently wet gullies (Fig. 1).

**Sampling design**—In order to describe the spatial distributions of colonizing species on the Pumice Plains, we counted species and estimated abundance in two grids of contiguous 10 × 10 m quadrats established in 1986. “Willow Spring” (WS) covered an area 400 × 400 m and contained 1,600 quadrats; “Lupine Patch” (LP), beginning approximately 100 m away, covered an area 350 × 250 m with 875 quadrats. Each grid was subjectively located to encompass a heterogeneous, representative section of the Pumice Plains where colonists occurred. Colonization densities in other areas of the Pumice Plains were much lower. Permanent stakes were fixed every 50 m throughout each grid, and temporary stakes were placed every 10 m around the border of a 50 × 50 m section to be censused. This arrangement allowed us to locate accurately all plots within a section without marking each corner.

Vascular plants were censused in late August and September 1986 by walking the midline of each quadrat and recording all plants within 5 m. Abundance of a species within a plot was scored as follows: Class 0, barren; Class 1, 0–5 individuals (or ramets); Class 2, 5–20 individuals; Class 3, 20+ individuals; Class 4, 0.5% cover; Class 5, 1% cover; Class 6, 2–4% cover; Class 7, 5–9% cover; Class 8, at least 10% cover.

An importance value (IV) was computed for each species, as [relative frequency + relative

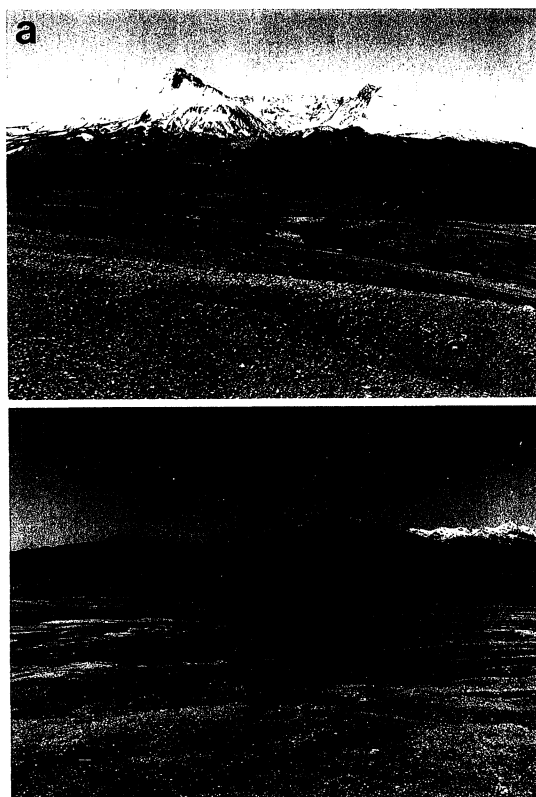


Fig. 1. The Pumice Plains landscape in early June 1986. a) Looking south at the crater; b) looking north from the same point as in (a) towards Mount Margaret; Spirit Lake is visible in the upper right-hand corner.

abundance], using the above class scores for abundance.

Statistical tests of random spatial distributions were accomplished both by variance/mean ratios and by  $\chi^2$  tests of observed frequencies with a Poisson expectation (Diggle, 1983).

**RESULTS**—Of the 1,600 quadrats in the Willow Spring (WS) grid, 45.6% were barren, and 35.5% of 875 quadrats in the Lupine Patch (LP) grid were similarly barren. Species richness averaged 1.03 per 100 m<sup>2</sup> plot at WS, and 1.82 at LP. The vast majority of colonists became established by seed via long-distance dispersal.

Table 1 gives the frequency and importance value of all species recorded. At each site the species with highest IV are, in descending order, *Anaphalis margaritacea*, *Lupinus lepidus* var. *lobbii*, and *Epilobium angustifolium*. An IV much greater than frequency indicates that the species attains high cover where found; an IV approximately equal to frequency indicates

TABLE 1. Species recorded on the Pumice Plains in 1986. F = frequency of occurrence in 1,600 plots at Willow Spring, 875 plots at Lupine Patch. IV = Importance Value (relative frequency + relative abundance)

Species	Willow Spring		Lupine Patch	
	F	IV	F	IV
<i>Abies procera</i>	0.4	0.6	0.1	0.2
<i>Achillea millefolium</i>	0.1	0.2	0.1	0.1
<i>Agrostis</i> spp.	1.4	2.2	0.3	0.3
<i>Anaphalis margaritacea</i>	33.9	63.1	41.9	44.2
<i>Carex mertensii</i>	7.9	13.0	11.2	10.0
<i>Cinna latifolia</i>	2.4	4.7	8.3	9.1
<i>Cirsium arvense</i>	0.9	1.5	8.0	7.6
<i>Cirsium vulgare</i>	—	—	0.8	0.5
<i>Equisetum</i> spp.	0.8	0.9	1.5	1.5
<i>Epilobium angustifolium</i>	11.0	20.6	28.1	28.9
<i>Epilobium luteum</i>	0.1	0.1	—	—
<i>Epilobium watsonii</i>	4.2	8.9	13.0	14.6
<i>Hieracium albiflorum</i>	2.2	3.6	3.7	3.3
<i>Hypochaeris radicata</i>	2.4	3.9	8.7	8.0
<i>Iris</i> sp.	—	—	0.1	0.1
<i>Juncus</i> sp.	0.1	0.1	0.9	0.6
<i>Luetkea pectinata</i>	0.1	0.1	—	—
<i>Lupinus latifolius</i>	0.3	0.7	0.1	0.1
<i>Lupinus lepidus</i> var. <i>lobbii</i>	20.3	45.5	26.9	43.3
<i>Luzula</i> sp.	0.1	0.1	—	—
<i>Penstemon serrulatus</i>	2.3	3.8	0.7	0.5
<i>Petasites frigidus</i>	1.3	2.3	2.1	1.8
<i>Phacelia</i> sp. <sup>a</sup>	—	—	0.1	0.1
<i>Polygonum</i> sp.	0.1	0.1	—	—
<i>Pseudotsuga menziesii</i>	1.4	2.2	0.2	0.2
<i>Salix commutata</i>	6.6	14.6	8.8	8.8
<i>Saxifraga ferruginea</i>	0.1	0.1	0.5	0.4
<i>Senecio sylvaticus</i>	1.7	2.7	11.7	11.5
<i>Sonchus arvensis</i>	0.1	0.1	2.7	2.5
<i>Spraguea umbellata</i>	0.2	0.3	—	—
<i>Tsuga heterophylla</i>	0.8	1.2	—	—
<i>Vaccinium</i> spp.	0.1	0.1	—	—
Unknowns	0.5	0.8	1.7	1.2

<sup>a</sup> Probably *Phacelia hastata* var. *leptosepala*.

the species is sparse. For example, *Anaphalis* and *E. angustifolium* sometimes occur in dense patches at WS but not at LP, and their IVs are twice that of their frequencies at the former site. *Lupinus lepidus* occurs in high density patches at both sites. Both mean and median IV are greater at LP (7.67 vs. 6.19, and 1.65 vs. 1.05, respectively), due to a greater number of species with intermediate IVs at LP, reflecting the greater abundance of colonizers there.

Community composition of the two sites is similar (Spearman rank correlation of IVs = 0.773,  $P < 0.001$ ). The 16 ha WS has 32 species (including 2 unknown seedlings), whereas the 8.75 ha LP has 26 species (including 1 unknown). No other species was found in a much wider search of the Pumice Plains.

Species richness was significantly clumped at both sites ( $P < 0.001$ ; see Fig. 2A, 5A). High richness occurred primarily in sites of high soil moisture, due mostly to the presence of streams

or underground seeps and secondarily to such topographic features as depressions and gully slopes where high densities of seeds likely accumulate and where direct insolation is reduced.

The spatial distribution of selected species is shown in Fig. 2–5. There are three groups of species. First, species such as *Salix commutata* (Fig. 2B) and *Cirsium arvense* (Fig. 5B) occur almost exclusively near streams and may be classified as “strongly hydrophilic” in this environment. Other species included in this group are *Cinna latifolia*, *Cirsium vulgare*, *Equisetum* spp., *Epilobium luteum*, *E. watsonii*, *Juncus* spp., *Petasites frigidus*, *Saxifraga ferruginea*, *Senecio sylvaticus*, and *Sonchus arvensis*.

The second group contains *Anaphalis margaritacea* and *Epilobium angustifolium* (Fig. 3A, B), species that we classify as “facultatively hydrophilic.” These species attain their greatest cover in wet sites, but also colonize upland pumice to a significant degree. These readily dispersed rhizomatous species are among the most common colonizers on the Pumice Plains. They can attain high cover in favorable sites through clonal growth but also can reach and establish in upland sites away from gullies and streams where growing conditions are more severe.

The third group is less well defined but is comprised of species that exhibit no obvious affinity for wet sites. These species are either distributed essentially at random or are clumped in drier sites. Included here are those species that cannot attain high cover by clonal growth and thus do not exploit wet sites as fully as do species of the first two types. This third group is exemplified by *Carex mertensii* (Fig. 4A), *Hypochaeris radicata* (Fig. 4B), and *Lupinus lepidus* (Fig. 5C).

*Lupinus lepidus* is unique among the colonists on the Pumice Plains in that tremendous population increases have occurred without seed immigration from outside sources. A few (possibly fewer than 20) widely scattered individuals or seeds somehow survived the eruption and became reproductive as early as 1981 (R. Sugg, personal communication). Because lupine seeds are heavy and apparently without adaptations for long-distance dispersal, and have never been recorded in seed traps on the Pumice Plains (Wood, 1987), all of the thousands of lupines now growing on the Pumice Plains are presumably descended from these few founder individuals. In contrast, virtually all new individuals of all other species must arise from long-distance seed dispersal. The highly clumped ( $P < 0.001$ ) distribution of

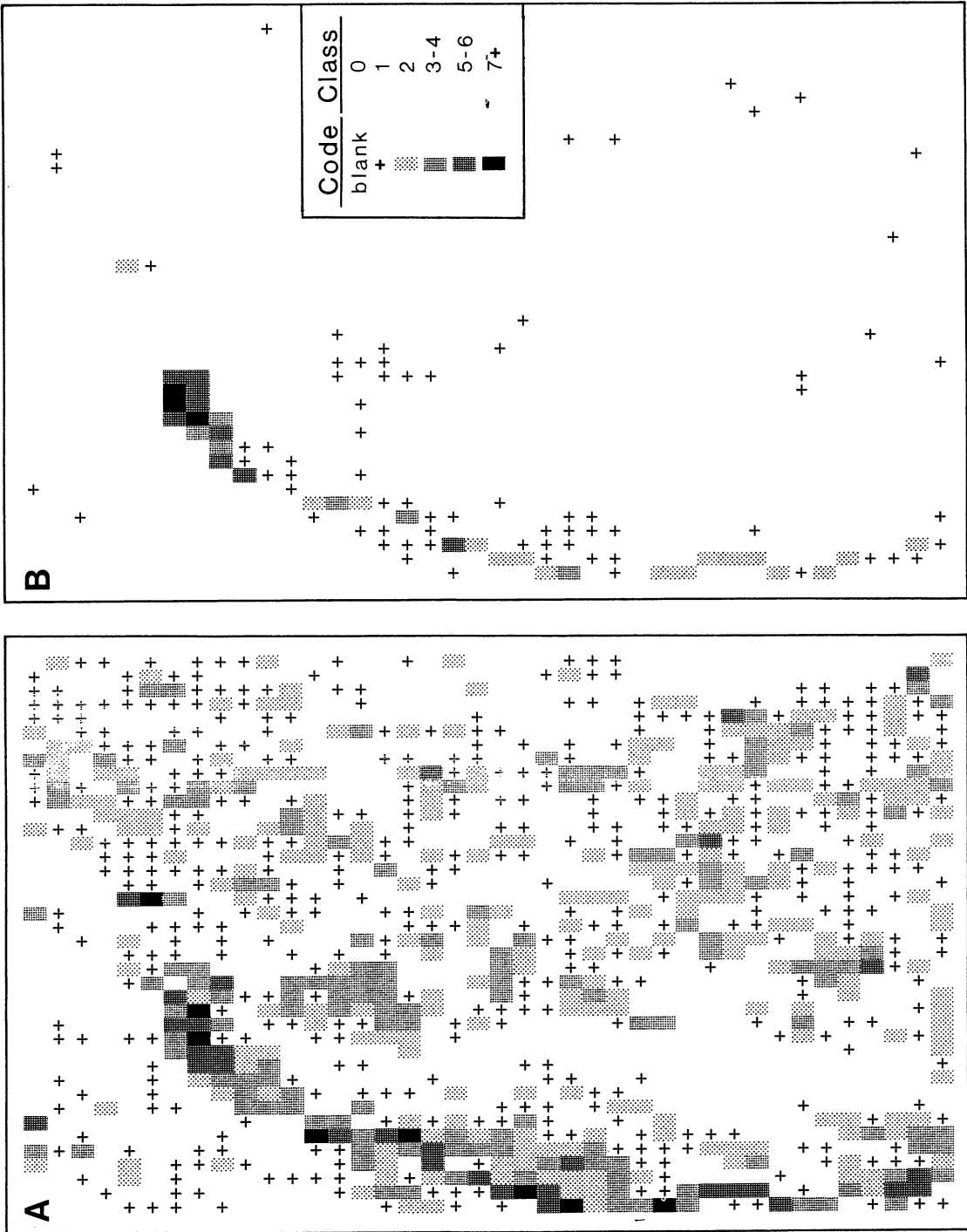


Fig. 2. Species richness and abundance of selected species at Willow Spring. Each symbol represents a value for a 10 x 10 m quadrat. A) Richness; classes refer to number of species. B) *Salix commutata*; classes refer to abundance.

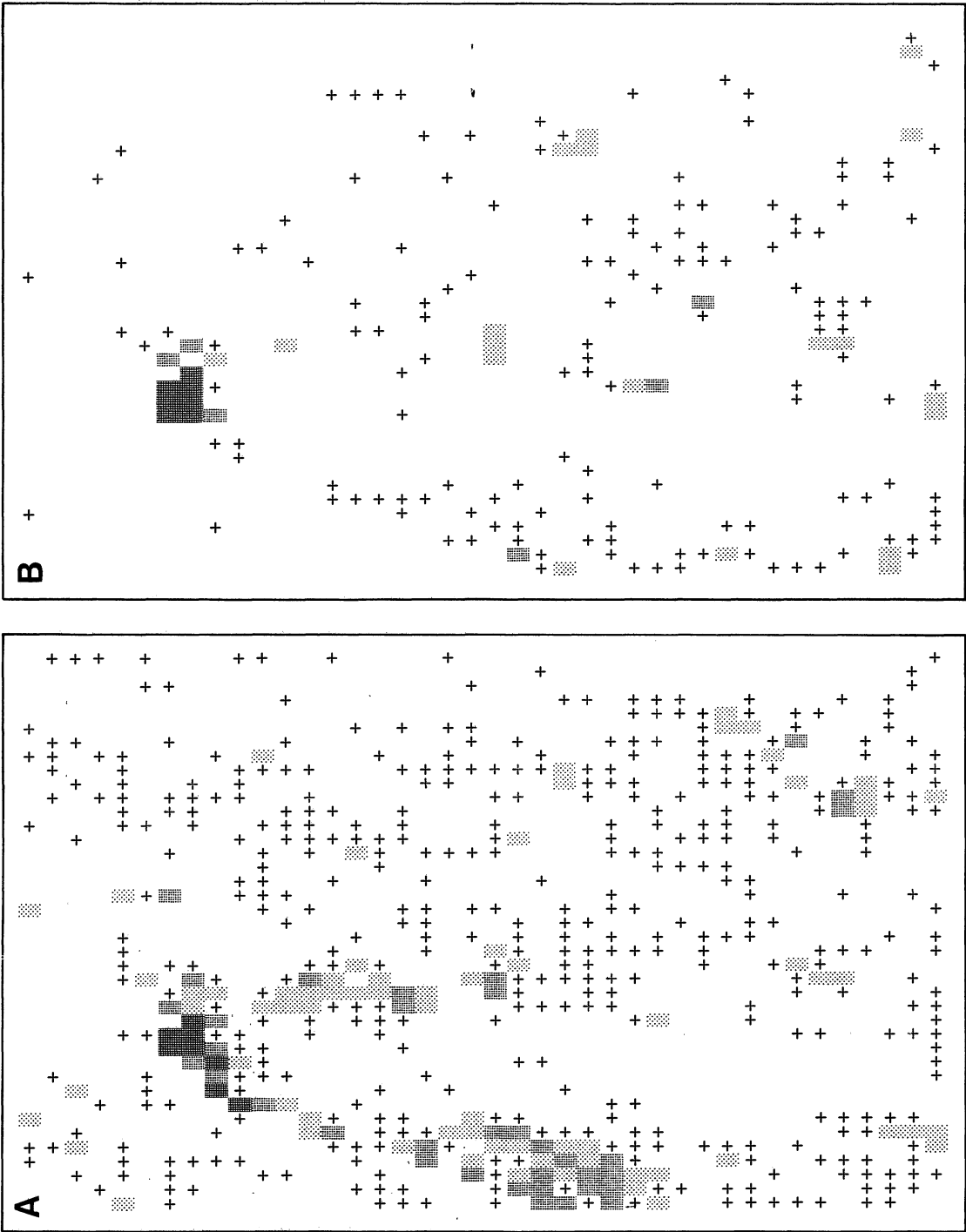


Fig. 3. Abundance of selected species at Willow Spring. A) *Anaphalis margaritacea*, B) *Epilobium angustifolium*. Symbols, codes, and classes are defined in Fig. 2.

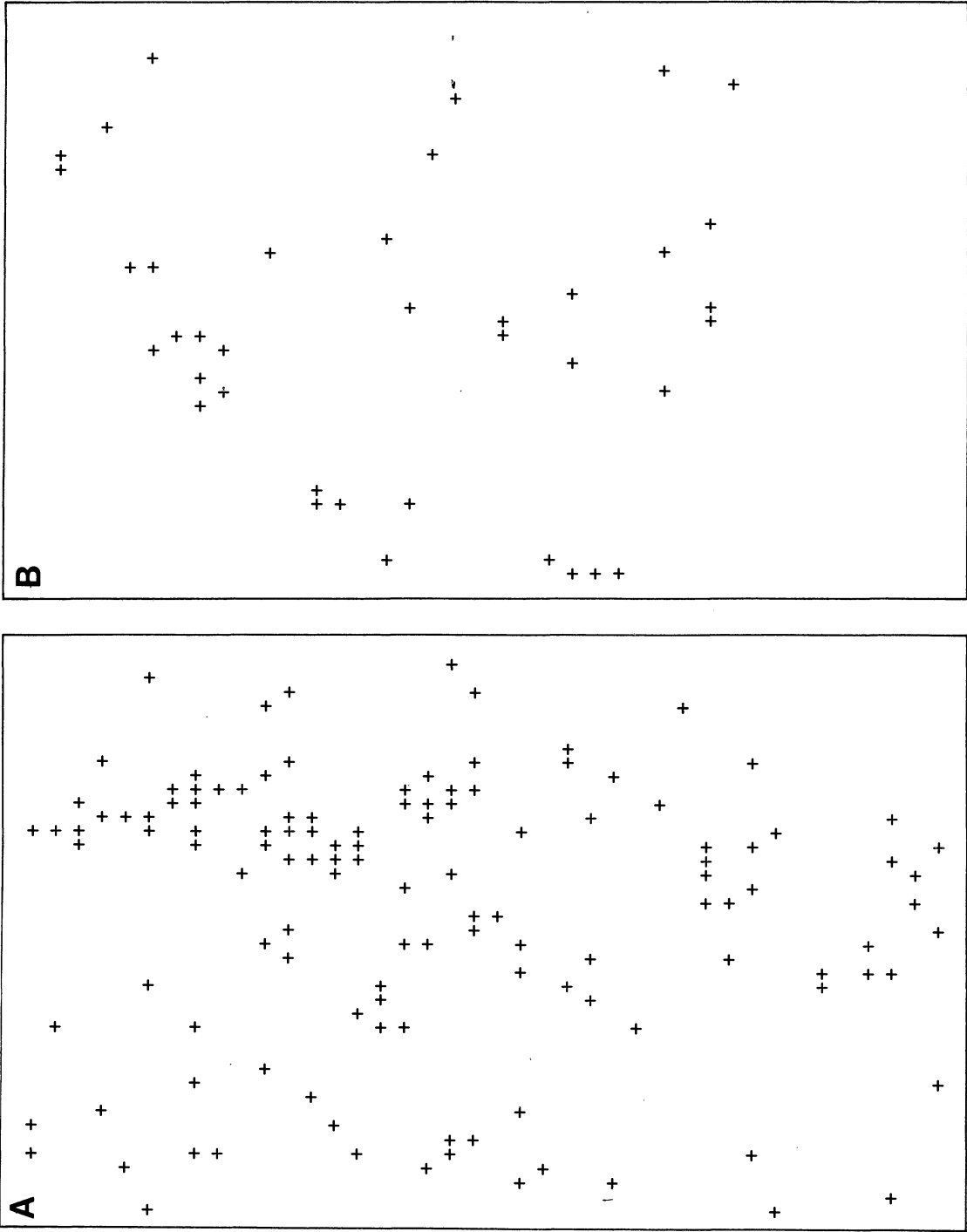


Fig. 4. Abundance of selected species at Willow Spring. A) *Carex mertensii*, B) *Hypochaeris radicata*. Symbols, codes, and classes are defined in Fig. 2.

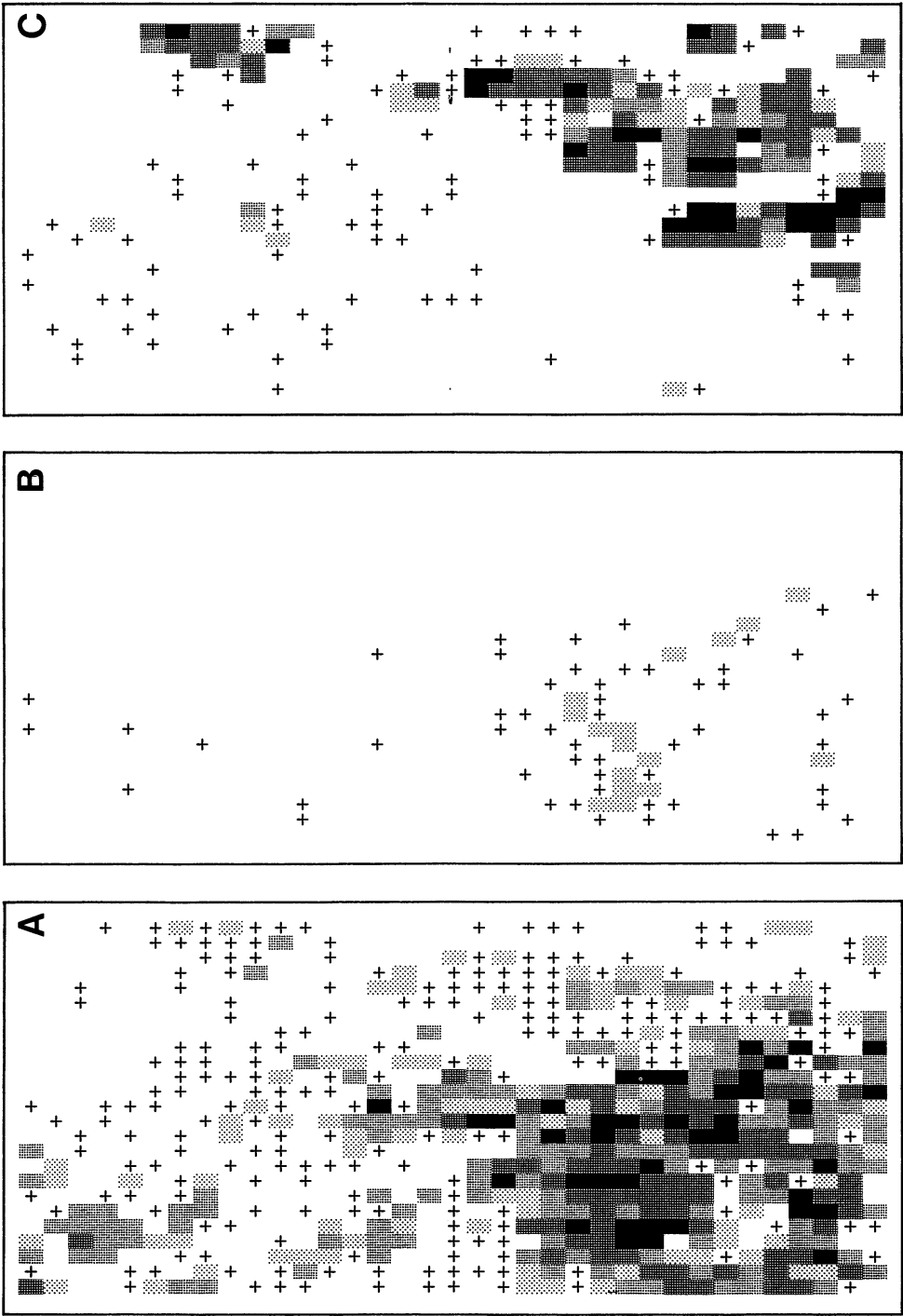


Fig. 5. Species richness and abundance of selected species at Lupine Patch. A) richness; B) *Cirsium arvense*; C) *Lupinus lepidus*. Symbols, codes, and classes are defined in Fig. 2.



lupine (which is not clonal) arises from local or “neighborhood” recruitment about parental plants. This phenomenon frequently results in locally dense populations comprised of hundreds of individuals, often attaining 100% cover in portions of a 10 × 10 m quadrat.

*Carex mertensii*, *Hypochaeris radicata* (Fig. 4A, B), *Hieracium albiflorum*, *Penstemon ser-rulatus*, and *Pseudotsuga menziesii* are all distributed essentially at random and occur almost exclusively as isolated individuals. This random pattern is most pronounced at WS, because LP contains a greater concentration of wet areas and thus promotes more uneven abundance distributions. With the exception of *Penstemon*, which is a mat-forming species, none of these latter species are clonal.

**DISCUSSION**—A landscape essentially devoid of plants in 1980 is very gradually beginning to be filled with plants, although at an average density of only 1 to 2 species per 100 m<sup>2</sup>. This contrasts sharply with species densities where even a few plants survived the eruption (del Moral and Wood 1986, 1988). The rapidity of vegetation recovery in these latter areas is due largely to the growth of species rooted in pre-eruption soil, and illustrates the importance of any “biological legacy” (Franklin et al., 1985) in accelerating the recovery process.

**Floristics**—The 32 identified species are an unusual mix of two basic floristic types: a native, upland element, and a lowland weedy element comprised largely of introduced European species. The native group is typified by *Carex mertensii*, *Epilobium watsonii*, *Lupinus lepidus*, *Salix commutata*, and *Spraguea umbellata*. All are common and widespread in the western Cascades (Hitchcock and Cronquist, 1973), and *Lupinus* and *Spraguea* are also common at high elevations. The weedy group is typified by *Cirsium arvense*, *Hieracium albiflorum*, *Hypochaeris radicata*, *Senecio sylvaticus*, and *Sonchus arvensis*. These latter species (all Asteraceae) are typically found in low elevation disturbed sites, have exceptional wind dispersal capabilities, and, with the exception of *Hieracium*, are all introduced. The natives *Anaphalis margaritacea* and *Epilobium angustifolium* could also be placed in this latter group, as they exhibit many weedy tendencies, but they attain greater prominence in montane floras than do the other species.

We know of no analog for this particular floristic assemblage combining lowland weedy species with montane and high elevation species, although on Isla Fernandina in the Galápagos, Hendrix (1981) reported “weedy

composites” to be among the first colonists of deep tephra deposits. Colonists on Japanese volcanoes at comparable elevations are primarily native species and are dominated by willows and alder (Riviere, 1982; Ohsawa, 1984). Early colonization on Hawaiian ash-falls was rapid and dominated by cryptogams, followed by woody species. Grasses and forbs were infrequent and exotic species were rare (Smathers and Mueller-Dombois, 1974).

We suspect that members of the lowland flora are successful colonists because the Pumice Plains is functionally equivalent to a habitat 300–400 m lower in elevation. This is because the lack of sheltering trees results in an abnormally early date of snowmelt for this altitude. The Pumice Plains is usually snow-free by late March or early April, whereas forested areas at similar elevations typically retain snow until mid-May. Thus the environment on the Pumice Plains closely approximates the longer, spring-wet summer-dry growing conditions of lower elevations.

**Life histories**—Colonizing species are primarily perennial, herbaceous, and wind-dispersed with light, usually plumed seeds. Of the woody species, only the shrubby willow (*Salix*) is at all common. However, scattered seedlings of Douglas fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), and noble fir (*Abies procera*) do occur. These species will be dominants in later successional stages on the Pumice Plains; their presence in the early stages of primary succession suggests that habitat conditions even now do not preclude their establishment. However, these individuals are sufficiently rare and immature as to render premature any conclusions about rate or direction of succession at this time.

Species that employ animal dispersal are conspicuously rare. Until vegetation develops on the Pumice Plains, we suspect that animal-dispersed species will continue to be rare, since there is now little cause for animals, particularly birds, to visit the area. Only ravens and killdeer are consistently observed on the Pumice Plains (D. M. Wood, personal observation).

Also conspicuously lacking are species from the dry grassland communities typically found at higher elevations on the volcano (del Moral, 1983; del Moral and Wood, 1986). We suspect that lack of immigrant seeds limits the establishment of these species (Wood, 1987).

**Species richness**—Moisture is the most significant factor promoting local species richness on the Pumice Plains. Up to twelve species may occur per 100 m<sup>2</sup> in sites with streams or

seeps, compared to an overall mean of 1.03 or 1.83 per 100 m<sup>2</sup> for WS and LP, respectively. High richness results from the "strongly hydrophilic" group of species that occurs almost exclusively and with high fidelity in wet sites: *Cinna*, *Cirsium*, *Equisetum*, *Epilobium watsonii*, *Juncus*, *Petasites*, *Salix*, *Saxifraga*, and *Senecio*. For example, mean richness is 3.76 ( $N = 130$ ,  $SD = 1.81$ ) in the subset of plots at WS that contain either *Salix commutata* or *Epilobium watsonii*, both good indicator species for moisture (Hitchcock and Cronquist, 1973, and personal observation). At LP, mean richness in this same subset is 5.24 ( $N = 149$ ,  $SD = 1.90$ ). Colonizing species such as these hydrophiles must possess good dispersal capabilities, but presumably must "pay" for this capability by sacrificing some life history trait, such as seed mass and consequent seedling vigor. Thus it is logical that seedling establishment will be enhanced in sites where abiotic stresses are reduced.

Moisture promotes richness for two principal reasons. First, high soil moisture reduces drought stress as a significant cause of mortality. This may be especially important for seedlings, because summer surface temperatures on dry sites on the Pumice Plains can exceed 50 C (value recorded at a meteorological station in WS; Reynolds and Bliss, 1986, and personal communication). Since moist substrates are cooler, potential damage to stems and prostrate leaves is reduced. Thus, species otherwise susceptible to drought or heat stress may encounter favorable conditions for germination and growth only in wet sites. Second, high richness may simply be due to a greater concentration of seeds in sites of high moisture. Streambeds and gullies can act as sinks to trap wind-blown seeds, thereby concentrating rare species and raising the probability of a species occurrence. Very likely there is an interaction between these two factors; mere entrapment of seeds is insufficient to promote establishment without concomitant favorable growing conditions, and favorable conditions are likely to occur only in wet sites. It is also possible that streams supply wet sites with higher nutrient concentrations, but we have no data to support this hypothesis.

*Lupines*—The spatial distribution of *Lupinus lepidus* is strikingly different from that of any other species. Lupine, a nitrogen-fixing plant, attains its highest cover and density where richness is low, i.e., primarily on upland pumice away from wet areas. Monospecific populations comprising several hundred lupine individuals in a 100 m<sup>2</sup> area are not uncommon.

Lupine's distribution pattern accords with its habitat preference elsewhere on Mount St. Helens and in the Cascades, where it typically occurs at middle to high elevations on exposed south-facing slopes of low cover, often on unstable soils. The only other species with similar habitat preferences are uncommon on the Pumice Plains (*Penstemon serrulatus* and *Spraguea umbellata*)—both are typically found at higher elevations.

*Predictions*—1) There will be a steady but slow rate of increase in species richness, since the high degree of habitat isolation effectively prevents establishment of species with less-than-exceptional dispersal capabilities (cf. Rejmanek, Haagerova, and Haager, 1982). Most species possessing such capabilities are already present. 2) Woody taxa, especially trees, will continue to be rare. As compared to herbaceous taxa, trees have a long juvenile period and thus most population growth in the near future must occur from long-distance seed immigration. When tree seedlings now present on the Pumice Plains attain reproductive maturity, then rate of population growth should increase markedly. The timing of this switch among species from outside or "donor-control" to "local control" of population growth will be an important aspect of succession in this landscape. For example, *Lupinus lepidus* has always exhibited local control and populations are growing rapidly; *Anaphalis margaritacea* and *Salix commutata* are just beginning the switch as individuals attain reproductive maturity; most other species retain donor control. 3) Since *Lupinus lepidus* is actively fixing nitrogen on the Pumice Plains (plants are heavily nodulated), and since nitrogen levels in pumice are quite low (del Moral and Clappitt, 1983; W. Nuhn, personal communication), with time this species will act to facilitate the invasion of other colonizers intolerant of low soil nitrogen. This has not yet occurred to any significant degree, as lupine's spatial pattern does not match that of any other species. It is possible that lupine densities within patches may be so high that any effects of habitat amelioration are outweighed by competitive inhibition, e.g., for water. For example, on Kilauea Volcano in Hawaii, *Myrica faya*, an introduced nitrogen-fixing tree, contributes 15–20 kg/ha/yr of nitrogen to volcanic soils (Vitousek et al., 1987) but is rapidly attaining dominance due to its aggressive growth rate (Walker, Vitousek, and Whiteaker, 1987). However, we predict that the disparity in pattern of colonization between lupine and other species on the Pumice Plains will become less

strong as nitrogen levels increase and colonizers exploit this resource.

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