Potholes

SPARSE-1997

DENSE-2002

Potholes are small (typically about 12 m^2) depressions concentrated on the eastern Pumice Plain. They were sampled in 1993, 1997, and 2001-2005. In 2001, 2003 to 2005 they were located by GPS for mapping. In 2001, the vegetation in a band surrounding 50% of the sample was measured. In 2002, sites over 50 m from the nearest pothole were sampled in the same way to provide a reliable estimate of vegetation structure for comparison to the potholes. From 2001 to 2005, the same 105 potholes were sampled to determine the effects of *Lupinus lepidus*. This was undertaken because lupines expanded greatly in many potholes after 1999. I hypothesized that the continued presence and further expansion of lupines would reduce cover of other species, or at least retard its continued development.

Potholes were sampled by marking the extent of the pothole, determining the area of the pothole (calculated from distance measurements from the center to 8 points on the edge; the points being at 45 degree angles from each other), and using a quadrat frame to determine the cover of each species individually.

Border Vegetation

Methods. The pothole borders were sampled using an encircling transect of ¼ m^2 quadrats within which species cover was measured. If a pothole was small, the transect was a belt of contiguous quadrats; if it was large, 40 quadrats were sampled regularly around the periphery. Each belt was placed immediately uphill of its pothole.

In 2002, sites over 50 m from the nearest pothole were sampled in the same way to provide a reliable estimate of vegetation structure for comparison to the potholes. At each site, a central point was determined, and then a random point was determined to locate a sample point from 4 to 8 m distant. Here, species composition of each of four contiguous one-m2 quadrats was determined. The process was repeated for each of the cardinal directions, leading to a sample of 16 m^2.

Statistical analyses were conducted with these data as summarized under results. The similarity between potholes and their borders was determined by rank order correlations of the species composition. For comparison, the rank order of each border was compared to the composition of three adjacent potholes. Similarity between potholes and distant samples were calculated using Simpson's index.

Results. We compared the immediate surroundings of potholes with the potholes themselves to determine whether the vegetation of the potholes influences the vegetation of its surroundings. Since I have sampled these potholes since 1992, I know that the edges were initially barren, so that it is not the edges that have contributed to the pothole.

Table 1 summarizes several structural features of the edge vegetation compared to the paired pothole. The "Lupine" columns were calculated using all data, while "No Lup." columns were calculated after the exclusion of lupines. This was because lupines have expanded greatly in the last two years with much of the expansion occurring on the barren plains as well as within many potholes. The sample two habitats support similar vegetation in terms of species richness and cover. The diversity measures (H' is the familiar information theory statistic; Evenness is = H'/ln[richness]; D is $1\text{-}\Sigma p_i^2$, where p_i^2 is the proportion of each species) indicate that border vegetation sustains greater dominance. H' is significantly lower, and both evenness and the complement of dominance are slightly lower. These samples tend to be dominated by *Penstemon*, *Lupinus*, or mosses to a greater degree than do the potholes. Removing lupines leads to greater cover reductions in the border plots and erases any difference in richness or diversity. In short, lupines are acting to reduce the diversity of other species in the borders of potholes. This may have long-term consequences for the general vegetation of this area.

Table 1. Comparison of vegetation structure in potholes with their immediate border.

Attribute	Pothole-Lupine	Border-Lupine	Pothole-No Lup.	Border-No Lup.
Species Richness	13.6	13.2	12.7	12.3
Percent Cover	15.1	14.4	8.99	6.46*
Evenness	0.707	0.667	0.775	0.782
H'	1.834	1.703*	1.960	1.952
Simpson's D	0.749	0.696*	0.798	0.799

***** *indicates differences significant at P < 0.05 by paired t-test.***

Do the potholes influence the composition of their borders? Spearman rank correlations between all border samples and all potholes were calculated. The mean correlation between a border and its pothole was 0.704, ranging from 0.505 to 0.843. The correlation of each border to the three most proximate other potholes (determined from the map) were also calculated. The three sets of correlations were 0.495, 0.520, and 0.502, ranging collectively from 0.159 to 0.774. Analysis of variance demonstrated that these means were highly significantly different and that they formed two groups: borders with their own pothole distinct from correlations with foreign potholes. This result suggests that potholes, which I believe represent an essentially random accumulation of species, assert a strong influence on their immediate surroundings.

Pseudo-potholes

If potholes influence their surroundings, then potholes should differ in structure and cover from distant areas. We tested whether potholes represented a different subset of the general vegetation by sampling "pseudo-potholes" over 50 m distant.

Potholes were significantly more heterogeneous than were the pseudo-potholes. Potholes were divided into six spatially determined groups and the mean similarity determined within each group. These values were compared to the similarities of the pseudo-potholes. The similarity of the pothole groups (2002 data) ranged from 34.2% to 39.8%, while that of the distant sample was 49.2%. ANOVA showed that the distant sample was distinct from all the others, which formed a homogeneous group. The similarity within a pseudo-pothole sample averaged 53.9%, and the 5 groups fell into two distinct classes ($P < 0.02$), but there were no spatial trends. All potholes were less similar than all pseudo-potholes. This conclusion is strengthened when pothole groups were compared to the nearest pseudo-potholes. The two-sample t-tests, comparing the nearest pair of samples are shown in Table 2.

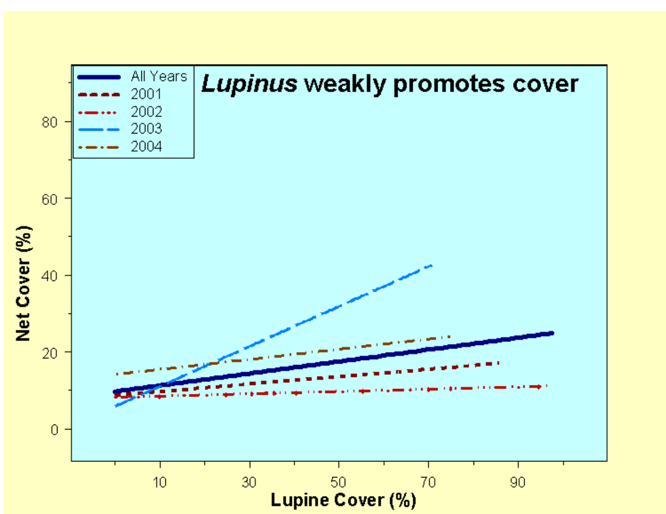
Table 2. Summary of simple t-tests of similarity among potholes and similarity among samples of the nearest sampled barren site.

Sample	Mean Similarity	Sample Size	t-value	P
Pothole A	35.2	145		
Pseudo-Pothole 1	64.6	6	4.75	0.000
Pothole B	34.2	210		
Pseudo-Pothole 2	45.2	6	3.14	0.020
Pothole C	39.8	153		
Pseudo-Pothole 3	46.6	6	1.83	N.S.
Pothole D	39.7	120		
Pseudo-Pothole 4	58.8	6	2.45	0.015
Pothole E	36.4	335		
Pseudo-Pothole 4	58.8	6	4.22	0.006
Pothole F	37.3	81		
Pseudo-Pothole 5	54.1	6	2.23	0.028

Lupine Effects on Pothole Vegetation

Structure. The regression of lupine cover to cover of other species suggested changing relationships annually from 2001 to 2004. Because lupines were almost gone in 2005, no regressions were performed. Earlier, lupines were a minor component of the potholes. I predicted that lupines would initially have a negative effect on other species, and then would promote the cover of other species. In fact, the relationship has varied to from weakly positive to insignificant (*Fig. 1),* and in the aggregate was positive (P < 0.000, r^2=0.11).

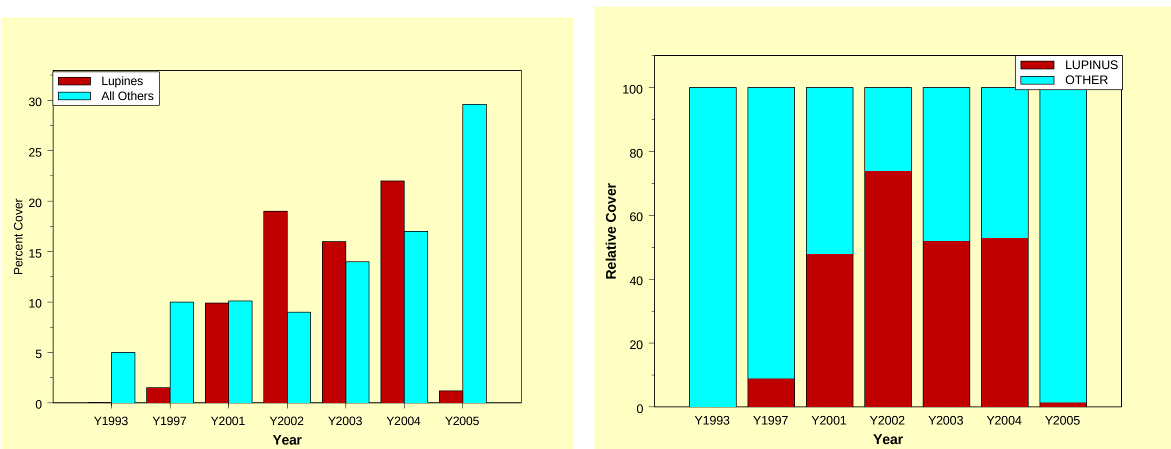
Fig. 1. Total cover partitioned between *Lupinus lepidus* and all other species in the same potholes 2001-2004. The curve is significantly positive in 2003 and overall.



In the first year (2001), the relationships of lupine cover to richness, cover of all other species, diversity (H'), and equitability (D and E measures) were not significant. In 2002, lupines began a steep increase in mean cover from 9% to 22% of a pothole. Overall cover of other species varied from 9% to 16%. However, lupine cover only significantly increased richness. In 2003, there was a positive relationship to cover, but a negative effect on other measures. In 2004, most measures were again not significantly related to lupine cover, though other cover was weakly positively affected ($P < 0.02$).

Lupines have undergone a tremendous expansion since 1993 (Fig. 2), followed by a 2005 collapse due to adverse weather during Winter 2004-2005. In 1993, lupines were barely present (less than 0.03%), and in 1997, they represented less than 10% of the total. By 2001, they increased dramatically, both in absolute terms and as a share of the total cover. The following year, the lupine share peaked, but lupine cover continued to increase, despite a slight decline in 2003, then crashed.

Fig. 2. Total cover partitioned between *Lupinus lepidus* and all other species 1993, 1997 and in the same potholes 2001-2005 (absolute and relative terms). The two earlier samples included most of the later samples and were drawn from the same area.



Preliminary analyses indicated that *Lupinus* cover in 2004 facilitated common species in 2005. *Agrostis pallens, A. scabra, Carex mertensii, Racomitrium, Polytrichum* and these two mosses combined all were positively correlated with Lupine Cover, as was overall cover (excluding lupines). This result was not due to some potholes simply being more benign. Paired t-tests indicated that all of these species, plus *C. microptera* increased between the years.

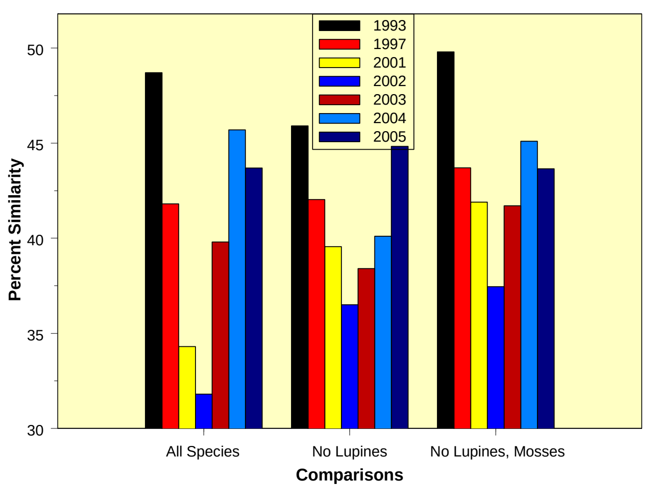
Due to the collapse of *Lupinus* cover in 2005, no correlations were expected. However, *Lupinus* cover in 2004 predicted total cover (r^2=0.23), cover without lupine (r^2=0.22) and cover without mosses or lupines (r^2=0.19) in 2005. This suggests that lupines have improved soil conditions and that when their interference is reduced, many other species can benefit.

Lupinus may initially inhibit the development of other species, but over time, it appears to produce facilitative effects. Due to herbivory and intrinsic population processes, *Lupinus* populations often crash, at which time other species, notably mosses and grasses, benefit. This prediction made in 2004 was confirmed. These results suggest that *Lupinus* can deflect trajectories, enhancing the developing vegetation mosaic by accelerating succession and by altering species composition. The spatial distribution of species in these potholes suggested that they have broad tolerances and can replace one another in a nearly random fashion. Pothole isolation suggested that early dispersal created priority effects that have enhanced the local vegetation mosaic. Whether time, species interactions or *Lupinus* will reduce this variation remains to be determined. The results from this study will be prepared for publication in 2006.

*Similarity***.** For this analysis, all plots were compared to all other plots (Fig. 3). The 1993 and 1997 samples included most, but not all of the 2001-2005 plots. In each case (all species, no lupines, no lupines or mosses), the 1993 plots had the highest similarity. This is the result of low richness and cover. The 1997 sample had lower similarity. The 2001 to 2005 samples are of the same potholes and each shows the same pattern: initial further decrease in similarity (2001), followed by increases in subsequent years (2002 to 2004), with slight declines in 2005. The increases appear to be a result of lupines decreasing the internal heterogeneity of the potholes. That is, as lupines have become increasingly abundant plots are becoming increasingly similar. Owing to larger sample sizes, nearly all differences are significantly different ($P < 0.05$, Bonferroni comparisons after ANOVA). The exceptions are 2001 with no lupines or mosses is not different from 2003, and 2001 with no lupines is not different from 2004.

Note that in 2004, similarity remains no greater than 46%, less than in 1993. The isolation of these potholes continues to suggest that initial dispersal has created priority effects that have enhanced the local vegetation mosaic. Whether time, strong species interactions or lupine dominance will smoother this variation remains to be determined.

Fig. 3. Percent similarity among pothole samples at seven sampling dates. 1993 and 1997 include most of the 105 potholes sampled from 2001 to 2005, and the entire sample is bounded geographically by the later sample. The earlier samples include 120 and 111 potholes, respectively. "No lupines" is the analysis after excluding *Lupinus lepidus*; "No lupines/Mosses" is the result of the analysis after also excluding *Racomitrium* and *Polytrichum*, both of which can be locally abundant. Within a block, means all differ significantly, except as noted in text.



Conclusion

These results indicate that lupines can have a strong effect on established vegetation. It also suggests that lupines can deflect successional trajectories and that vegetation developing with lupines will retain their distinctiveness for decades. Lupines appear to be the single plant species most responsible for both the direction and rate of succession on pumice on Mount St. Helens.