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Positive plant spatial association with *Eriogonum ovalifolium* in primary succession on cinder cones: seed-trapping nurse plants

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Abstract

Cinder cones in Craters of the Moon National Monument in southcentral Idaho, USA were formed over 2200 yr B.P., but are still covered by large, relatively barren areas containing a sparse assemblage of plants. The spatial associations among 6 plant species on these sparsely vegetated areas were examined. All species were positively associated with the canopy region of *Eriogonum ovalifolium* var. *depressum*, an initial colonizer. All species were negatively associated with *Pinus flexilis*, a later-successional species.

We examined soil seed densities and N and P levels under canopies of the 6 species to develop testable explanations for positive plant associations with *E. ovalifolium*. Soil seed densities of *Phacelia hastata* and *Lewisia rediviva* were higher under canopies of *E. ovalifolium* than under 4 of the 5 other species and bare areas. Soil total N under *E. ovalifolium* canopies was also higher than under 4 of the 5 other species and bare areas. Soil seed densities and N levels were similar under *E. ovalifolium* and *Eriogonum umbellatum*, both of which had dense, prostrate canopies. Soil available P levels under *E. ovalifolium* were not significantly different than under other species or bare ground.

The positive associations of all species with *E. ovalifolium* is likely the result of seed-trapping by its prostrate canopy and more favorable establishment conditions under its canopy. The relative importance of these potential mechanisms can be tested with field experiments.

Abbreviations: EROV = *Eriogonum ovalifolium* var. *depressum*; ERUM = *Eriogonum umbellatum*; PHHA = *Phacelia hastata*; PIFL = *Pinus flexilis*; SIHY = *Sitanion hystrix*; STTH = *Stipa thurberiana*

Nomenclature: Hitchcock & Cronquist (1973). Flora of the Pacific Northwest. Univ. Wash. Press, Seattle.

Introduction

Most studies on primary successions have been done on sites having a new substrate (*sensu*

Clements 1916), as well as harsh, unfavorable conditions for plant establishment. Succession on these relatively static sites can be particularly difficult to quantify because of the large time

scales involved which often make direct observations through time inappropriate. The comparison of plant communities in chronosequences has traditionally been used to study these primary successions (Cowles 1899; Cooper 1923; Crocker & Major 1955; Olson 1958), but this approach of inferring temporal sequences from spatially distinct communities has been questioned (Drury & Nisbet 1973; Miles 1979; McIntosh 1980). Permanent plot studies of primary successions (van der Maarel *et al.* 1985; Roozen & Westhoff 1985; del Moral & Wood 1988) avoid this problem but require long-term monitoring. More recent approaches to studying primary successions have used experimental methods to investigate species interactions and various life history traits in order to explain successional patterns and mechanisms (Walker & Chapin 1986; Walker *et al.* 1986; Wood & del Moral 1987).

In this preliminary study we investigated a primary successional site on a cinder cone formed about 2200 yr B.P. (Kuntz *et al.* 1983) in Craters of the Moon National Monument, Idaho, USA. Cinder cones in the Monument are covered by extensive 'cinder gardens' or areas containing only a sparse, scattered assemblage of forbs, grasses and an occasional woody species. We used a species-region approach to analyze spatial associations among six plant species in these

cinder gardens to determine a species establishment sequence. To develop testable explanations for observed positive plant associations with *Eriogonum ovalifolium*, an initial colonizer, we examined soil seed densities and N and P levels under the canopies of the 6 species in the site.

Study area

The study area was in southcentral Idaho along the northwestern edge of the Snake River Plain in Craters of the Moon National Monument (43°28'N, 114°30'W) (Fig. 1). Climate at the Monument is typical of upper elevations of the Intermountain Sagebrush-Steppe Region (Fig. 2). Annual precipitation has a bimodal pattern with a principal peak in December in the form of snow and a smaller peak in May in the form of rain. A period of relative drought occurs from mid-June through September. Surface soil temperatures at the study site occasionally exceed 65 °C throughout the growing season.

Parent material in the area is basaltic magma resulting from several volcanic eruptions occurring at least every 2500 yr, the most recent being about 2200 yr B.P. (Kuntz *et al.* 1983). This study focused on cinder cones (cone-like accumulations of black and black-gray cinders generally < 4 cm

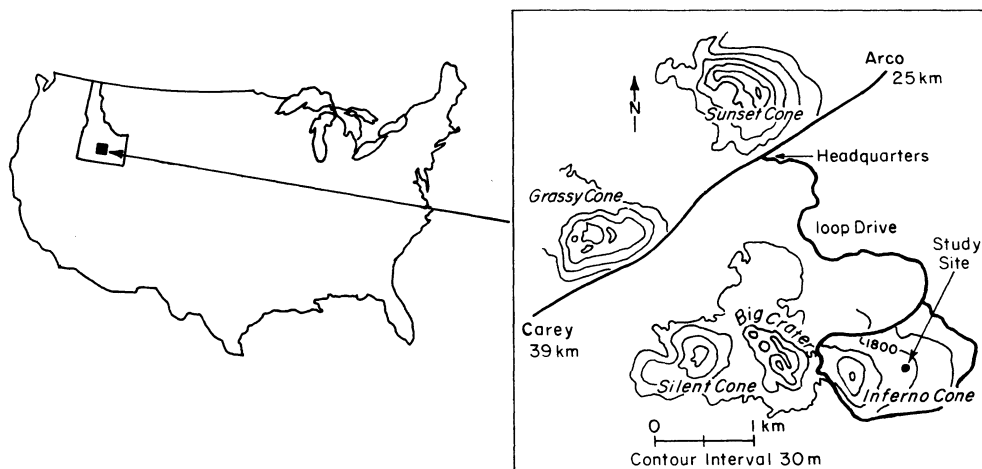


Fig. 1. Location of the study site in Craters of the Moon National Monument, Idaho, USA

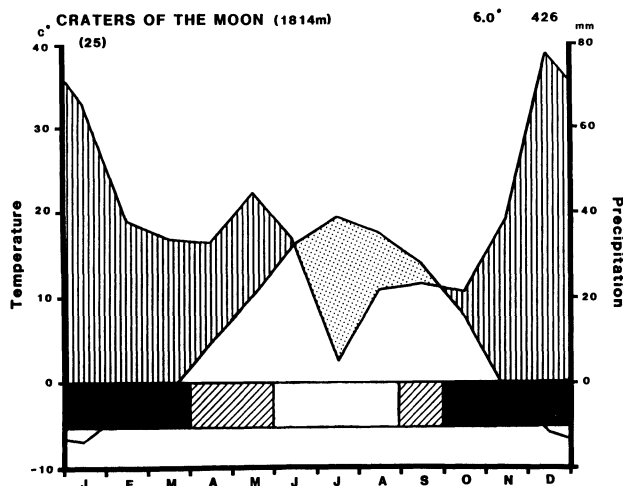


Fig. 2. Ecological climate diagram for headquarters at the Monument (3 km N of the study site) following Walter (1979). The vertically shaded area indicates the humid period; the dotted area indicates the arid period. The bar along the abscissa indicates months when the daily minimum temperature is $<0^{\circ}\text{C}$ (blackened), and months when the absolute average minimum temperature is $<0^{\circ}\text{C}$ (diagonally shaded). At the top of the diagram from left to right are the site elevation (in brackets), mean annual temperature and mean annual precipitation. The number of years of observations for this compilation is in brackets under the site name.

in diameter) which are common within the Monument. Two randomly selected study plots within 30 m of each other on Inferno Cone are reported on. Plots were at 1810 m elevation and had an east-facing aspect and 18° slope. The soil, a cindery Frigid Lithic Xerorthent, consisted of loose cinders 1-2 cm in depth overlying an A horizon of coarse-textured, black sand 12 cm thick. Beneath the A horizon was a C horizon of loose, black cinders.

Several plant communities were present on cinder cones, including cinder gardens and pine/shrub (*Pinus flexilis*/*Purshia tridentata*) dominated communities (Day & Wright 1985). The study plots were in a cinder garden which has been undergoing invasion by species of the pine/shrub community for at least 100 yr B.P., based on tree ring analysis of *Pinus* there. In early July the two typical cinder garden species, *Eriogonum ovalifolium* var. *depressum* (Polygonaceae), a persistent, mat-forming perennial, and *Phacelia*

hastata (Hydrophyllaceae), an erect perennial, were present as major species ($>5\%$ total foliar cover). 4 additional major species from the invading pine-shrub community were also present: the grasses *Sitanion hystrix* and *Stipa thurberiana*, another larger, mat-forming *Eriogonum*, *E. umbellatum*, and the first woody species to establish on this site, *Pinus flexilis*. These four species occurred in higher densities in nearby pine/shrub communities (where *E. ovalifolium* and *Phacelia* were largely absent), substantiating the interpretation that these four species are later in establishing on cinder cones.

Methods

Association analysis

Spatial association data were collected in August 1983 in the 2 10×10 m study plots. To test for interspecific plant association among major species at each plot a species-region approach (Stowe & Wade 1979; Greig-Smith 1983) similar to Hazlett & Hoffman (1975) was used. The canopy radius of each major species was recorded in each plot for calculation of their areas. The total canopy area covered by each species could be found by summing and then expressed as a percentage of total plot area.

The number of individuals of each species rooted in the canopy and outside all canopy areas was recorded and could be expressed as a percentage. If one species is spatially independent of a second species, the percentage of its individuals occurring in the canopy area of the second species would be expected to equal the percentage of the plot area covered by the second species. The expected and observed values were compared and tested for goodness of fit using the χ^2 approximation of the binomial distribution at the 5% probability level. This test assumes that individuals of the first species are spatially independent of each other. This assumption appeared to be met since the scattered individuals within a species in the plots did not appear clumped but instead tended to be randomly spaced.

Occasionally the canopy areas of two more individuals of a species overlapped each other. In these cases the distance between the centers of the two canopies was also recorded. The following formula was used to determine the area of overlap of the two canopies and could then be subtracted from their summed area to give actual combined canopy area:

$$\begin{aligned} \text{Area of overlap} = & \left(\frac{\pi r_1^2}{2} \right) - \left\{ d_1 \sqrt{r_1^2 - d_1^2} \right. \\ & \left. + r_1^2 \text{Arcsin} \left(\frac{d_1}{r_1} \right) \right\} \\ & + \left(\frac{\pi r_2^2}{2} \right) - \left\{ d_2 \sqrt{r_2^2 - d_2^2} \right. \\ & \left. + r_2^2 \text{Arcsin} \left(\frac{d_2}{r_2} \right) \right\} \end{aligned}$$

where: Arcsin is in radians

r_1 = radius of the canopy of individual A

r_2 = radius of the canopy of individual B (1)

d = distance between the centers of the canopy of individuals A and B

$$d_1 = \left(\frac{d}{2} \right) + \left\{ \frac{r_1^2 - r_2^2}{2d} \right\}$$

$$d_2 = \left(\frac{d}{2} \right) - \left\{ \frac{r_1^2 - r_2^2}{2d} \right\}$$

Since many *Pinus* individuals in the study plot were over 50 yr of age, based on tree ring analysis, current association of mature *Pinus* individuals with herbaceous species probably does not reflect conditions at the time of *Pinus* establishment. Therefore, *Pinus* seedlings (1 to ca 3 yr of age), not mature individuals, were tested for association with other species and for association with mature *Pinus* individuals.

Seed densities

To estimate soil seed densities, the upper 7 cm of soil from a 100 cm² area under the canopy of 6

E. ovalifolium individuals was collected. Samples were collected only from under isolated individuals having no other plants within 50 cm of their canopy. 6 equal-sized samples were similarly collected in an area void of plants for at least 50 cm in all directions. Samples were collected in this manner in August 1983 and June 1984. In July 1986 the soil under 9 isolated individuals of each of the 6 study species and 9 bare areas was collected. Soil samples were sieved through a 2 mm screen to remove cinders and seeds were counted. Seed viability was determined by a tetrazolium test (Colbry *et al.* 1961) which involved soaking seeds for 4 days in distilled water, splitting the seeds, applying tetrazolium solution, waiting 10 days and inspecting for reddish coloration of the embryo which designated viable seed.

Soil nutrient analysis

Five isolated individuals of each species were chosen for soil chemical analysis in early July 1985. The upper 7 cm of soil below the loose cinder of the above plants was collected. Soil samples were passed through a 2 mm screen and the fine fraction was analyzed for total N and available P. Total N was measured in the absence of an integrating measure of soil N availability. Total N was determined by Kjeldahl digestion using a block digester and a Technicon auto-analyzer. Available P was determined by extraction with NaHCO₃ following Olsen *et al.* (1954) and color was developed and read using the procedure of Murphy & Riley (1962).

We hypothesized that positive associations of other species with the canopy region of *E. ovalifolium* may be the result of differential seed dispersal patterns and/or higher nutrient levels in the canopy region of *E. ovalifolium*. A paired *t*-test was used to detect differences in seed densities in soil under *E. ovalifolium* and bare ground in 1983 and 1984. We used a one-way ANOVA and Dunnett's test (Steel & Torrie 1980) to compare the mean seed density in 1986, and soil nutrient level under each species and bare areas with the mean under *E. ovalifolium*.

Table 1. Spatial associations between the major species in plots 1 and 2. Species A is tested for positive association with the canopy region of species B.

Species B	Plot	Total canopy area %	Species A						PIFL seedlings % density assoc. in canopy	SIHY % density assoc. in canopy	STTH % density assoc. in canopy
			EROV	PHHA	ERUM	PIFL seedlings	SIHY	STTH			
			% density assoc. in canopy	% density assoc. in canopy	% density assoc. in canopy	% density assoc. in canopy	% density assoc. in canopy	% density assoc. in canopy			
EROV	1	10.9		42	29	61	39	39	+	+	+
	2	12.7		27	20	19	35	30	+	+	+
PHHA	1	5.9	21		0	0	13	7	NS	NS	NS
	2	6.2	10	NS	10	0	7	39	NS	NS	+
ERUM	1	5.3	16	+		0	12	0	NS	NS	NS
	2	8.5	2	-		0	33	10	+	+	NS
PIFL	1	16.2	6	-	10	24	5	2	-	-	-
	2	34.2	7	-	14	28	7	5	-	-	-
SIHY	1	6.6	18	+	10	0		0			-
	2	6.0	23	+	7	10		9			NS
STTH	1	6.1	22	+	6	9	0				
	2	7.3	20	+	24	0	6	NS			

+ denotes significant positive association with species B ($P < 0.05$).

- denotes significant negative association with species B ($P < 0.05$).

NS denotes not significantly associated with species B ($P > 0.05$).

Results

Plant spatial association

Association analysis showed that all 5 species were positively associated with *E. ovalifolium* in plot 1 (Table 1). The same was true in plot 2 with the exception of *E. umbellatum* and *Pinus* seedlings. The other consistent trend was the negative association of all species, with the exception of *E. umbellatum* in plot 1 and *Pinus* seedlings, with the canopy region of *Pinus* trees (Table 1). The positive association of *Pinus* seedlings with mature *Pinus* (all of which bore cones) probably resulted from large seed size which decreased dispersal distance from parent plants.

Seed densities

The only species present in high enough seed densities to allow statistical analysis were *Phacelia* and *Lewisia rediviva* (Portulacaceae), a perennial forb present aboveground only until mid-June to

early-July on these sites. Viable seed densities of both species in August 1983 and June 1984 were significantly higher in soil under the canopy of *E. ovalifolium* than in soil under bare areas (Table 2). In July 1986 viable seed densities of *Lewisia* under *E. ovalifolium* were significantly higher than under bare areas and under all species, except *E. umbellatum*. In the case of *Phacelia*, seed densities were higher under *E. ovalifolium* and *E. umbellatum*, as well as under *Phacelia* canopies. The high *Phacelia* seed densities under *Phacelia* canopies probably reflects the close proximity between the sampling location and the parent plant.

Soil nutrients

Soil total N under the canopy of *E. ovalifolium* was significantly higher ($P < 0.05$) than under bare areas and other species, with the exception of *E. umbellatum*. Soil available P levels under *E. ovalifolium* were not significantly different ($P > 0.05$) than levels under bare areas or other

Table 2. Soil viable seed densities of *Phacelia* and *Lewisia* under bare areas and canopies of study species. Values are means (1 SD).

Date	Seed	Soil seed density (seeds/m ²)						
	Species	EROV	Bare	PHHA	ERUM	PIFL	SIHY	STTH
Aug 1983	<i>Phacelia</i>	833 (121)	183* (160)					
	<i>Lewisia</i>	567 (137)	83* (75)					
June 1984	<i>Phacelia</i>	2283 (421)	383* (172)					
	<i>Lewisia</i>	633 (216)	33* (52)					
July 1986	<i>Phacelia</i>	1856 (456)	78* (109)	656 (459)	600 (300)	133* (141)	200* (150)	189* (154)
	<i>Lewisia</i>	1322 (380)	44* (73)	78* (109)	311 (176)	89* (136)	144* (142)	178* (156)

* (1983 and 1984) $P < 0.05$ that difference in means of EROV and bare ground equals zero, using paired t -test.
* (1986) $P < 0.05$ that there was no difference from EROV mean using one-way ANOVA and Dunnett's test.

Table 3. Soil nutrient levels under each species and bare areas. Values are means (1 SD).

Soil nutrient	Soil location						
	EROV	Bare	PHHA	ERUM	PIFL	SIHY	STTH
Total N (%)	.054 (.005)	.032 (.004)	.031* (.003)	.035 (.019)	.027* (.006)	.034* (.003)	.029* (.006)
Available P ($\mu\text{g/g}$)	3.6 (0.9)	2.5 (0.6)	2.9 (0.6)	2.3 (0.9)	3.4 (1.6)	2.4 (0.5)	2.4 (0.4)
N:P	172.0 (40.2)	118.9 (20.7)	120.8 (18.0)	132.8 (42.9)	77.9 (27.8)	147.8 (8.5)	117.9 (15.8)

* $P < 0.05$ that there was no difference from EROV mean using one-way ANOVA and Dunnett's test.

species (Table 3). Since Tilman (1982) proposed that plant distributions may be correlated with ratios of resources or nutrients, rather than specific nutrients, we calculated the ratio of total N to available P. Total N:available P under *E. ovalifolium* was not significantly different ($P > 0.05$) than ratios under bare areas or other species (Table 3).

Discussion

The positive plant associations with *E. ovalifolium* suggest a facilitation mechanism (Connel & Slatyer 1977) or nucleation process (Yarranton & Morrison 1974). This may result from (1) higher accumulation of seeds, and/or (2) more favorable conditions for germination and establishment under *E. ovalifolium*'s canopy relative to other species.

Since seed densities were determined from soil collected under isolated individuals (no other plants within 50 cm) it is unlikely that higher seed densities under *E. ovalifolium* and *E. umbellatum* resulted from their closer proximity to seed sources or parent plants. It appears the prostrate canopies of these species acted as traps for wind dispersed seeds. Wood & del Moral (1987) have similarly found that seed trapping by nurse plants is an important mechanism in primary succession on Mount St. Helens, Washington State, USA. Although statistically higher seed densities were only found for *Phacelia* and *Lewisia*, all other

study species, except *Pinus*, have small seeds which are wind dispersed over cinders and could be expected to accumulate under *Eriogonum* canopies. Seeds of all forb study species are < 2.5 mm in length and weigh < 5 mg. Both grass study species (*Sitanion* and *Stipa*) have awned florets < 1 cm in length and < 2.5 mg in weight. Seeds often remain intact in the detached inflorescences in these forbs (as well as in *Sitanion*) and these dried inflorescences were commonly observed lodged in the mat-forming canopies of *Eriogonum*.

In seed bank studies, the high spatial variability in seed densities often prevents statistical conclusions (Thompson 1986; Bigwood & Inouye 1988). The clustered spatial pattern of seeds causing this variability appears to be more prevalent in open habitats (Kellman 1978; Schenkeveld & Verkaar 1984) such as cinder gardens. In our study, one cause of clustered seed distributions appeared to be seed trapping by prostrate *Eriogonum* canopies.

Pinus seedlings were positively associated with *E. ovalifolium*, but trapping of wind blown *Pinus* seeds does not appear consistent with dominant dispersal mechanisms in this *Pinus*. *Pinus flexilis* seeds are 1-1.5 cm in length, wingless and weigh > 90 mg. These large seeds are commonly dispersed by Clark's nutcrackers and red squirrels (Lanner & Vander Wall 1980; Benkman *et al.* 1984). Both these dispersers are common in the pine/shrub community adjacent to the study site. This suggests that other factors, in addition to

seed trapping, are needed to explain positive associations with *E. ovalifolium*.

The positive associations of *Pinus*, as well as other species, with *E. ovalifolium* may result from more favorable germination and establishment conditions under *E. ovalifolium*. Total soil N was higher under *E. ovalifolium* than under bare areas and most other species (although we should note that total N may not necessarily reflect inorganic N available for plant uptake). Hirose & Tatenos (1984) also found relatively high soil N levels under a mat-forming colonizer in a volcanic primary succession. Similarly, higher soil N levels under shrub canopies relative to levels under interstices between shrubs have been found by several workers in arid and semi-arid sites (Garcia-Moya & McKell 1970; Charley & West 1975; Vasek & Lund 1980). We found soil N levels under both *E. ovalifolium* and *E. umbellatum* to be similar. Retention of litter as well as wind-blown organic matter accumulation in the dense, prostrate canopies of these forbs may be responsible for higher soil N levels under their canopies.

Although both *Eriogonum* species had relatively high seed densities and soil N levels under their canopies, plants were positively associated only with *E. ovalifolium*, the initial colonizer. Soil seed densities and N levels tended to be higher under *E. ovalifolium* than *E. umbellatum*, but these differences were not statistically significant. Larger sample sizes may have allowed us to detect significant differences in seed densities and N levels under these two species. Future experiments on nutrient and moisture availability patterns and plant response can be used to test potential mechanisms that may explain the observed positive associations with *E. ovalifolium*.

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