PLANT ASSOCIATION AND SOIL FACTORS IN PRIMARY SUCCESSION ON CINDER CONES IN IDAHO

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AUTHORIZATION TO PROCEED WITH THE FINAL DRAFT

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ABSTRACT

1.) Intra- and interspecific association of major plant species in primary succession on east-facing cinder cones slopes varying in parent material age and degree of soil development were analyzed using a species-region approach.

2.) Soil parameters were measured to determine possible factors responsible for plant associations.

3.) On the least developed, most unfavorable sites the two initial colonizers, *Eriogonum ovalifolium* var. *depressum* and *Phacelia hastata*, were negatively associated with their own canopy regions.

4.) On these sites all major species were positively associated with the inner canopy of *E. ovalifolium*.

5.) Possible factors identified for these positive associations with *E. ovalifolium* were higher accumulations of seeds and fine material, and relatively high moisture, total N and available P levels in soil under the inner canopy of *E. ovalifolium*.

6.) On these sites current-year *Pinus flexilis* seedlings in the canopy region of established plants in general had lower survival rates through late-summer than seedlings not in the canopy region of any established plant. However, survival rates of seedlings in the canopy region of *E. ovalifolium* were similar to survival rates of seedlings not in the canopy region of any established plant.

7.) Clumping of *Pinus* seedlings due to animal caching of seeds was common in these sites. Survival rates among clumped seedlings and isolated seedlings were similar suggesting that intraspecific competition was not as important in establishment as other factors such as variations in climate.

8.) Both initial colonizers had higher levels of total N and available P in soils under their canopies than later-successional species on the same site.

9.) The two initial colonizers were negatively associated with the two later-successional species, *Eriogonum umbellatum* and *Pinus*, on this site.

10.) Association between species-pairs on more developed areas dominated by woody species were relatively inconsistent between sites. No consistent differences in soil parameters under different species were identified on these sites. These inconsistencies may be due to soil differences between sites (caused by buried soil horizons), past histories, chance events and reactions of plants to differences in environmental factors associated with individuals rather than species.

11.) On more developed sites species in general were most often positively associated with the outer canopy region of other species and negatively associated with the region directly outside the canopy of other species.

12.) It appears environmental conditions on the least developed sites were often below the minimum physiological tolerance levels of many later-successional species. Microenvironmental changes caused by *E. ovalifolium* appear to be one modification which improves conditions, allowing enhanced establishment of later-successional species.

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INTRODUCTION

The term plant succession refers to directional change in a plant community over time. Work by Cowles (1899) and Clements (1905, 1916, 1920, 1928) formalized successional concepts and was largely responsible for their general recognition and acceptance by the scientific community. Several of the concepts proposed by Clements have since been questioned, especially over the past 30 yr (McIntosh 1980). One controversy has revolved around the mechanisms that bring about successional change after a disturbance.

Two important distinguishing characteristics are important in determining the type of mechanisms involved in succession: first, whether the site is undergoing primary or secondary succession and secondly, whether environmental conditions at the site (excluding interaction from current plants) are unfavorable enough to prevent the establishment of species from surrounding communities. The former considers both physiological and ecological tolerances of the species while the latter considers only physiological tolerances. Physiological tolerance is the range of a species in response to the physical environment while ecological tolerance is the range of a species in response to physical environment, interactions with other species, ability to disperse into an area, and reaction to disturbance (Barbour, Burke and Pitts 1980). The two characteristics are related since the number of possible secondary successional communities at a site increases as environmental conditions become more favorable.

Primary versus Secondary Succession

Primary succession in this paper is defined as succession occurring on sites in which the plant community is in dynamic equilibrium with its environment (*e.g.* climax). Five major points characterize climax or primary successional communities (Daubenmire 1968; Mueller-Dombois and Ellenberg 1974; Barbour, Burke and Pitts 1980; Hann 1982; Hironaka, Fosberg and Winward 1983). (1) The plant community is in dynamic equilibrium with its environment. (2) Interactions between species have reached a dynamic equilibrium state. (3) No new species from the geographic area can establish in the community. (4) Competition between species is at a maximum. (5) The climax is the endpoint of secondary succession.

Without disturbance the existing plant communities in primary succession are stable and species richness changes markedly only with inherent community changes, such as soil development. In these communities most species which are capable of dispersing into the site are assumed to have done so, although many may not be able to tolerate features of the environment and therefore fail to establish. On these primary sites enough time has passed since the disturbance to allow the species which are best adapted to the long-term environmental conditions and plant interactions at the site to dominate the community.

Plant communities undergoing secondary succession are not in dynamic equilibrium with their environment. These communities can change due to inherent community changes which change primary successional communities. However, additional changes can come about in these communities since the species best suited for long-term dominance have not had enough time to express their superiority. As time since the last disturbance increases, new species will disperse into the community. Without further disturbance, the group of species best adapted to the biotic and abiotic conditions of the site will eventually dominate and the site will reach a primary successional state. The present soil in secondary successional communities is capable of supporting different plant communities through time until a community occurs that is in equilibrium with the physical environment of the site.

Generally, secondary succession occurs much more quickly than primary succession. Succession through secondary communities to an endpoint involves several pathways converging at the primary state or climax (Whittaker 1974; Huschle and Hironaka 1980). When this endpoint of secondary succession has been reached the community is in primary succession. Succession through primary states is an open-ended process which has no endpoint (Mueller- Dombois and Ellensberg 1974; Miles 1979) although the changes in environmental conditions at a site which lead to observable changes in the vegetation (and therefore succession) may take extremely long periods of time in primary succession.

In many cases it is difficult to differentiate between primary and secondary succession due to the difficulties of determining what the potential plant community or primary state of a site is.

This is due in part to the dynamic nature of natural systems caused by endless disturbances of differing magnitude and selectivity. In other cases it is apparent that a community is in a near climax or climax state (primary sucession), or at the other extreme, in an early, secondary successional state.

One complicating factor occurs in secondary successions where not only the biotic factors change, but significant community caused changes take place in the physical environment. Examples would be old-field successions where light intensity decreases with increasing plant cover. Recent work by Tilman (1984) has also shown soil nutrient micropatterns to be correlated with spatial patterns of early colonizers in old fields. In some cases, a plant community may be closer to equilibrium with environmental conditions than initially thought, but these environmental conditions may change quite quickly in early stages of succession. The plant community may be significantly changing the physical environment such as by adding organic matter to the soil, so that new species are able to physiologically tolerate the site. Therefore, the potential climax community of the area would be changing. Since the plant community in this situation may not be able to maintain equilibrium with these changing environmental conditions, it would be in secondary sucession. Most successions probably involve complex sequences of primary and secondary successional stages depending on how much the physical conditions are changing on a site during the recovery process, and how quickly the plant community is able to respond and come into equilibrium with new environmental conditions. This process is summarized in Figure 1.

Modification of the environment at a site is obviously an important component of succession. Site modification not only involves plant induced changes (autogenic succession (Barbour, Burke and Pitts 1980)), but also changes brought about by other biotic components such as animals, and abiotic components (allogenic succession (Barbour, Burke and Pitts 1980)). Site modification is generally inferred to be a positive enhancement which changes the potential plant community of the site in a progressive direction (*e.g.* allowing a greater number of species to physiologically tolerate the site). Some "modifications" are negative and change the potential plant community in a backwards direction. Negative modifications caused by plants lead to autogenic

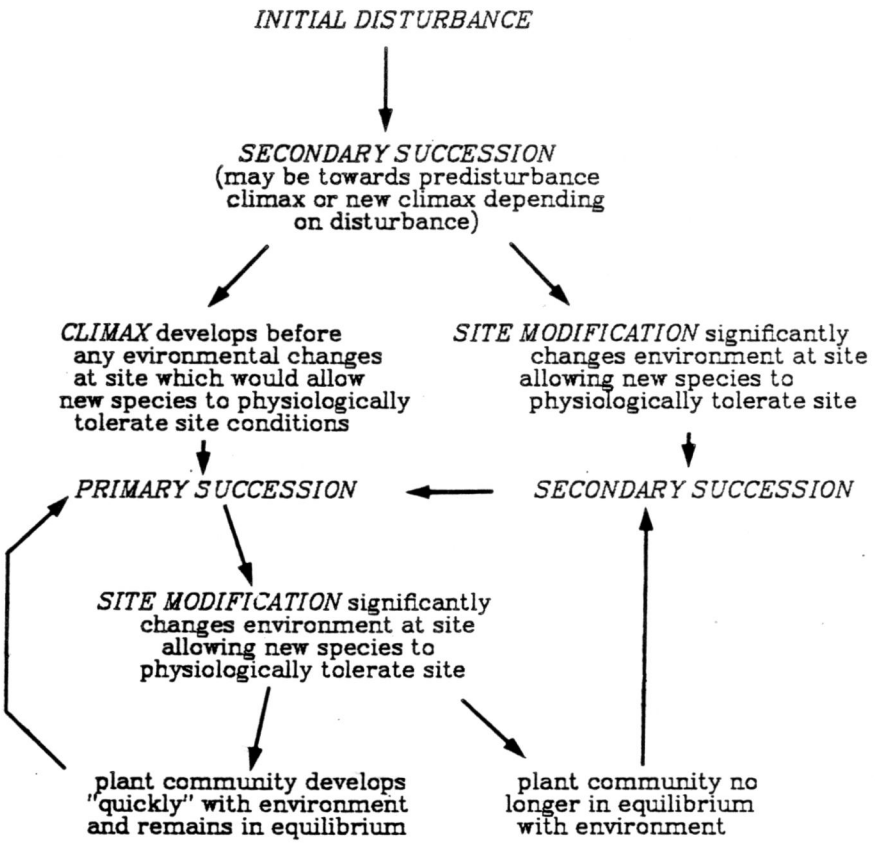


Figure 1. Relationship between primary and secondary succession (as defined in this paper). Disturbances ,other than initial, and retrogression are not considered.

retrogression (Barbour, Burke and Pitts 1980). Negative modifications brought about by other biotic factors and abiotic factors are usually termed disturbances or perturbations. Some disturbances or modifications would not be considered negative modifications in this context since they may not be dramatic enough to change the potential plant community of a site and only affect secondary succession.

Traditionally, primary succession differs from secondary succession in starting without any viable plant remains from the predisturbance community (*e.g.* on new substrates never before supporting any vegetation) (Clements 1916; Mueller-Dombois and Ellensberg 1974). This distinction may be of secondary importance relative to the physiological tolerance levels of species and the conditions at the site (Miles 1979). Cowles (1911) felt that this classification into primary and secondary succession was not of fundamental value. In a strict sense, the traditional definition can include sites which have never supported plants, but may be very favorable for growth of many species (*e.g.* superior to many secondary sites). However, it appears that primary succession is usually implied to refer only to relatively harsh sites although this is not concisely stated in its definition. Clements (1916) defined primary succession as those arising on newly formed soils or surfaces exposed for the first time which have never supported vegetation before. However, he states that these sites present extreme conditions for ecesis whereas secondary successional sites often offer optimum conditions for ecesis as a result of the action of previous succession. These two statements do not appear totally consistent since newly exposed surfaces such as mudflows, alluvium, and loess may actually be quite favorable for ecesis. How favorable a site is for ecesis is not a function of the presence or absence of viable plant remains (*e.g.* the traditional primary versus secondary distinction), but instead depends largely on the substrate's physical and chemical makeup .

Models of Successional Mechanisms

Three general models for successional mechanisms have been proposed: the facilitation model (relay floristics), and the tolerance and inhibition models (initial floristics). These models and evidence for each have been summarized by Connell and Slatyer (1977).

The facilitation model was proposed by Clements (1916) to describe primary succession. One key difference between it and the other two models is its assumption that only early-successional species can colonize a site following a disturbance. These early-successional or pioneer species modify a site making it less suitable for themselves and more suitable for later-successional species. This sequence continues with current species modifying the site so as to facilitate the invasion and establishment of new dominant species.

Evidence supporting the facilitation model comes from glacial moraines (Crocker and Major 1955; Cooper 1923, 1931; Lawrence *et al.* 1967), sand dunes (Cowles 1899; Olson 1958) and lake shores (Cooper 1913). These studies described site modification by pioneer species and the subsequent replacement of these species by new species. Analysis of the modification mechanism in these studies was relatively qualitative.

Quantitative evidence supporting the facilitation model has been limited due largely to the relatively long time scale involved in site modification processes, especially on relatively harsh, young sites which are commonly devoted to primary successional study. However, some more recent studies have provided substantial evidence for the facilitation mechanism. In primary succession on a dry lake bed Vasek and Lund (1980) found that the accumulation of soil, which was relatively high in nutrients, around plants and the redistribution of minerals by these plants permitted later-successional species to invade. One of the most thorough studies of mechanisms in primary succession was done by McCormick and his students (Sharitz and McCormick 1973; McCormick, Lugo and Sharitz 1974). A series of observational and experimental studies of succession on granite outcrops in the southeastern United States showed how changes in environmental factors allowed establishment of new species. Later-successional species were competitively superior to earlier colonizers under the higher nutrient and moisture conditions characteristic of the deeper soils associated with the establishment of pioneer species and the weathering of the granite. The pioneer species were largely responsible for site modifications which allowed for the competitive superiority of later-successional species.

The tolerance and inhibition models have been formulated largely from examples of secondary successions. In these models early-successional species also modify the site making it unsuitable for themselves. These models differ from the facilitation model in assuming that later-successional species can establish themselves along with pioneer species in early stages of succession. Thus site modification by pioneers is not a prerequisite for establishment of later-successional species. In these models the rate and pathway of succession are determined largely by the initial floristic composition of the community immediately following disturbance.

The tolerance model advocates that the recruitment and growth rates of typical later-successional species are neither increased or decreased by earlier colonizers. Succession in this model results in an increase in species which are able to tolerate environmental changes (such as increased shading, allelopathy, moisture stress, *etc.*) which occur through succession. In this model later-successional species can grow at lower levels of resources than pioneer species. MacArthur and Connell (1966) provide evidence for this model in forest succession. They found the canopy became thicker in each advancing sere and the less shade-tolerant species died, resulting in a climax forest composed of the most shade-tolerant species. The tolerance model has also been shown to apply to early stages of old-field successions (Keever 1979; Hils and Vankat 1982; Zimmerman and Vankat 1984).

The inhibition model proposed by Egler (1954) differs from the tolerance model in assuming that later-successional species cannot grow to maturity in the presence of earlier species. The later-successional species dominate later stages of succession because they gradually accumulate and replace shorter-lived pioneer species. Evidence supporting the early stages of the inhibition model come mainly from old-field successions where late-successional forest species may become established in recently abandoned fields (Egler 1954; Drury and Nisbet 1973). The inhibitory effect occurring in intermediate stages of the inhibition model is supported by work done by Jack McCormick (1968) who found that removal of pioneer species (annuals) resulted in faster growth and earlier flowering of later-successional species (perennials) in abandoned fields. Keever (1950) and Parenti and Rice (1969) found that early pioneer species reduced germination and growth

rates of later-successional species. Similiarly, closed canopies of shrubs have been shown to prevent the invasion of trees into seral forest areas (Niering and Egler 1955; Webb, Tracey and Williams 1972; Niering and Goodwin 1974).

OBJECTIVES

The objectives of this study were to:

1.) Develop a general chronosequence of vegetation and soils through primary succession on east-facing cinder cone slopes up to 12,600 yr of age.

2.) Analyze intra- and interspecific association of major plant species occurring on primary sites of east-facing cinder cone slopes.

3.) Determine possible causes for significant plant associations by measuring soil parameters associated with each species.

4.) Use correlations between vegetational and edaphic data to identify possible mechanisms in primary succession on these sites.

STUDY AREA

The study area is in southcentral Idaho along the northwestern edge of the Snake River Plain within Craters of the Moon National Monument (Fig. 2). The Pioneer Mountains rise abruptly from the Snake River Plain along the northern edge of the Monument. Parent material in the area is basaltic magma resulting from several volcanic eruptions occurring at least every 2500 yr, the most recent one being about 2200 yr BP (Kuntz *et al.* 1983). Volcanic activity in the area centers along the Great Rift, a narrow belt of faults, fissures, cones, craters and shield volcanoes whose vents are elongated over buried eruptive fissures (Wentworth and McDonald 1953). This study focused on cinder cones (cone-like accumulations of cinders and ash) which, although widely scattered throughout the Snake River Plain, are best developed in size, shape and number along the Great Rift within the Monument (Kuntz *et al.* 1983). Cinders on the cones are red, black or black-gray in color and generally less than 4 cm in diameter.

A general knowledge of the plant communities in the area was gained through extensive field work done on a vegetation type map of the Monument during the summer of 1982. Several plant communities are present on cinder cones, ranging from poorly developed areas lacking in any vascular plants or containing only a sparse covering of forbs (cinder gardens (Fig. 3)) to pine/shrub and shrub dominated communities. Nomenclature follows Hitchcock and Cronquist (1978), and Cronquist *et al.* (1977) where applicable. These cinder garden communities are usually dominated by ***Eriogonum ovalifolium*** var. ***depressum.*** It was suspected that the facilitation mechanism may be present in succession on the youngest, least developed sites, where harsh environmental conditions appear to limit the establishment of several later-successional species.

Reveal (1979) feels that *E. ovalifolium* along with several other species present in the cinder gardens are disjuncts from alpine and subalpine areas in the Idaho batholith to the north of the Monument. A reconnaisance trip was made to Black Cap, a large cinder cone approximately 4 km northeast of the study area, which contains cinder areas at an elevation of 2270 m. Several species present in the study area were found on this cone although no *E. ovalifolium* individuals were located. Cinder areas on Black Cap also contained species not found on cinder areas in the

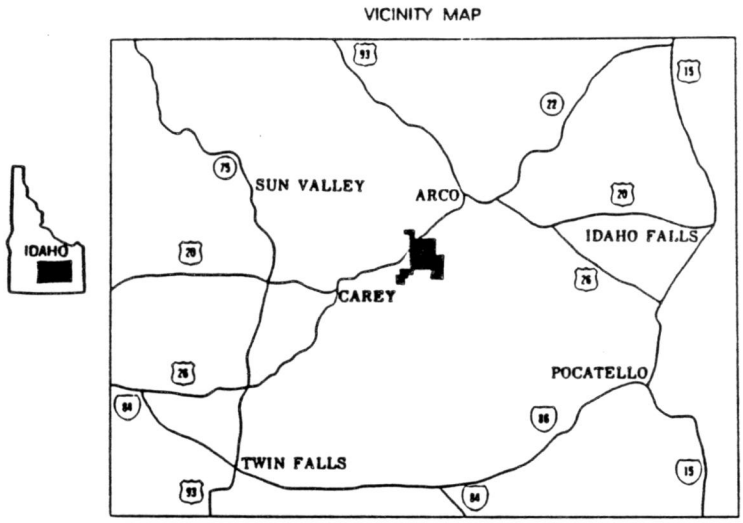


Fig. 2. Location of Craters of the Moon National Monument. The Monument is approximately 125 km west of Idaho Falls and 75 km southeast of Sun Valley.



Fig. 3. Cinder gardens on Inferno Cone in early-June, 1984. The Pioneer Mountains are in the distance.

Monument (Appendix 1). It is not clear if many of the cinder garden species and varieties in the study area are also common in alpine and subalpine areas, restricted to harsh volcanic sites or common in various types of harsh habitats throughout a wide range of elevations. Nor is it clear if plants such as *E. ovalifolium* var. ***depressum*** are true ecotypes or merely phenotypes of *E. ovalifolium.*

The pine/shrub communities are dominated by *Pinus flexilis* and *Purshia tridentata.* Two major shrub communities are present and are dominated by either *P. tridentata* or *Artemisia tridentata* ssp. ***vaseyana,*** with the latter usually dominant only on older, more edaphically developed areas.

Climate at the Monument is typical of upper elevations of the Intermountain Sagebrush-Steppe Region (Fig. 4) with 462 mm of mean annual precipitation over the past 25 yr at Monument headquarters. Annual precipitation has a bimodal pattern with a relatively high 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. Temperatures below freezing have been recorded in all months at the Monument at least once over the past 25 yr.

Strong winds blowing out of the southwest off the Snake River Plain are common, especially on relatively exposed areas such as the cinder gardens. Winds averaged 15.5 km h^{-1} at noon for June through September, 1983 at Monument headquarters. Large amounts of detached plant material were noted lodged in the canopy of ***E. ovalifolium*** individuals in cinder garden communities and it was suspected that wind-born seeds may accumulate in *E. ovalifolium* canopies.

One objective of this study was to develop a general chronosequence for vegetation and soils based on parent material age. This general approach is based on the concept that climax vegetation and soil codevelop and are a function of the same set of environmental factors: climate, topography, parent material, biota of the region, and time (Major 1951; Jenny 1958; Stevens and Walker 1970). This approach has been used by several workers in the past (Dickson and Crocker 1953, 1954; Crocker and Zinke 1955; Crocker and Major 1955). The validness of spatial inferences in developing successional models has been questioned (Drury and Nisbet 1973; Miles 1979;

McIntosh 1980), although the sites in this study had very similar slopes, aspects, and elevations and were in close proximity, making climatic differences minimal. Prevailing winds from the west and southwest during past eruptions caused greater accumulations of cinders on east and northeast sides of most cones, providing an aspect of relatively homogeneous slope on each cone.

Kuntz *et al.* (1983) summarized results of several studies which used radiocarbon and paleomagnetic methods to age lava which flowed from each cones vent , presumably during the period of cone formation. Inferno, Silent, Grassy and Sunset, the four cones on which study sites were placed, were estimated to be 2200, 6500, 7600 and 12,600 yr of age respectively. Sites on the same cinder cone, which could not be differentiated by parent material age, were to be placed on a successional gradient by their degree of soil development. Degree of soil development was based on thickness, texture and total N content of the epipedon.

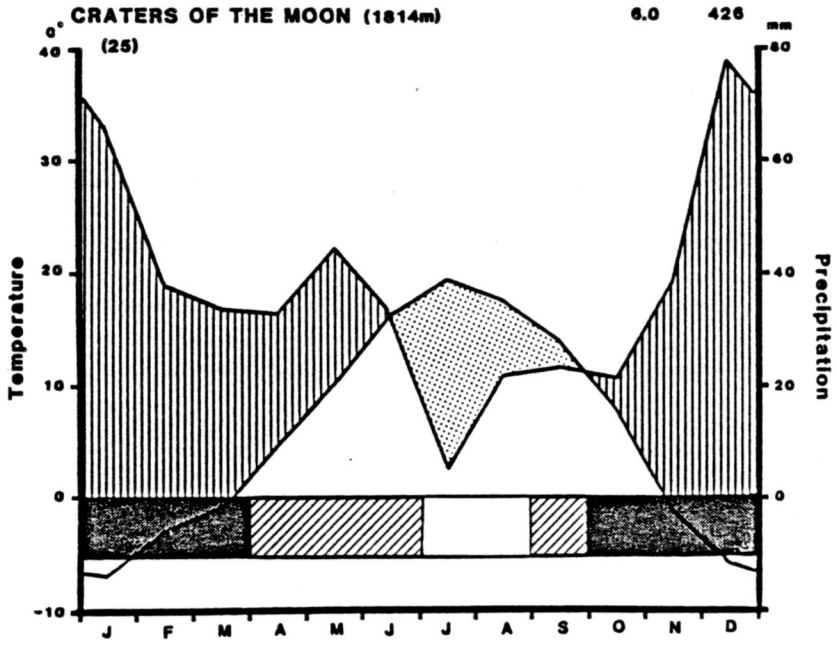


Fig. 4. Ecological climate diagram for the Monument from weather records over the past 25 yr. Format is after Walter (1979): dotted region is period of relative drought, vertically shaded region is relatively humid period, solid shaded region is months with mean daily temperature below freezing, and diagonally shaded region is months with absolute minimum temperature below freezing.

METHODS

Study Sites

A total of eleven study sites were placed on four cinder cones in the Monument (Fig. 5). Study sites were limited to east- to northeast facing aspects and slopes of 18-22° , due to the diversity of plant communitites found on cinder cones. Sites were placed well within plant community boundaries. Areas having apparent relatively non-homogenous vegetation, relatively uneven microtopography or signs of disturbance (other than volcanic) were avoided. Association of major plant species was analyzed at these sites. Soil parameters under each major species were also measured to determine possible causes for plant associations. Only primary sites were chosen since climax communities would reduce research variables associated with secondary succession (Whittaker 1974) and would show the strongest relationship with environmental factors (Major 1951; Jenny 1958). Some of the randomness which is present in communities not in dynamic equilibrium with their environment, may be avoided.

Vegetation

At each site a 10 x 20 m plot was marked and relative foliar cover of all species in mid-July 1983 was determined. Only species having greater than 10% relative foliar cover were studied and are referred to as major species at a site. Major species which had relatively large life forms in a study site were termed primary species. These species were generally longer-lived and exerted a greater influence on the environment than smaller major species (termed secondary species). In associations involving a primary and secondary species, it was more likely that the secondary species became established after the primary species. Since plant association was used in this study to determine possible establishment sequences, major species were tested only for association with each primary species. Major species were not tested for association with secondary species, although secondary species were tested for association with primary species.

The plot was divided into four 5 x 10 m subplots, two of which were randomly choosen for collection of association data. Data were collected in August 1983. To test for significant intra- and interspecific plant association among major species at each site, a species-region approach

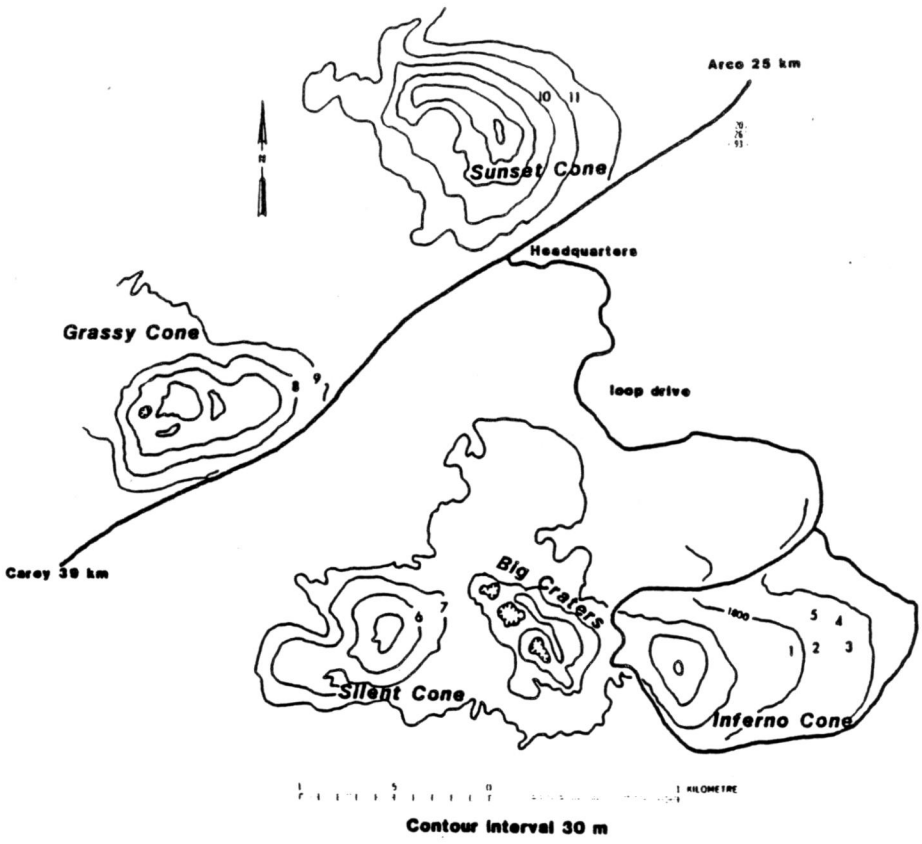


Fig. 5. The northcentral portion of the Monument showing the study area. Numbers indicate locations of the eleven study sites.

(Stowe and Wade 1979, Greig-Smith 1983) was used. This method involved defining the area in which an individual may influence another individual for each plant. Because an individual may influence more than just that area directly beneath its canopy, an area extending out 1.5X the canopy radius of an individual was defined as its "area of influence". Therefore an individual's area of influence would be the area of a circle, centered at the canopy center, having a radius 1.5X the individual's canopy radius.

Initially the root systems and canopy structures of each major species were looked at in an attempt to develop an equation to define each species' apparent area of influence. Several easily measured parameters of individuals of each species were observed (*e.g.* canopy diameter, canopy height and stem diameter) in attempting to develop this equation. However, the horizontal size of root systems and canopies within a species varied considerably not only due to differences between individuals, but environmental factors such as distance to other plants and soil characteristics. Therefore, for simplicity an equation of 1.5X an individual's canopy diameter was used to define the area of influence for all primary major species. The area of influence of secondary major species did not need to be defined as only density data on these species were needed in the association analysis.

The radius of the area of influence for individuals of each primary major species was recorded in the two subplots for calculation of their areas. The total area of influence each primary major species covered in each subplot could be found by summing the area of influences of all individuals of each species in the subplot. In several cases the area of influences of two or more individuals of a species overlapped each other. In these cases the distance between the centers of the two areas of influence was recorded along with the radius of each. The following formula was used to determine the area of overlap of the two areas of influence and could then be subtracted from their summed area to give the actual area of influence covered by the two individuals:

$$Area\ of\ overlap = \left(\frac{\pi r_1^2}{2}\right) - \left\{ d_1\sqrt{r_1^2 - d_1^2} + r_1^2\ Arcsin\left\{\frac{d_1}{r_1}\right\}\right\}$$

$$+\left(\frac{\pi r_2^2}{2}\right) - \left\{ d_2\sqrt{r_2^2 - d_2^2} + r_2^2\ Arcsin\left\{\frac{d_2}{r_2}\right\}\right\}$$

where: Arcsin is in radians
r_1 = radius of the area of influence of individual *A*
r_2 = radius of the area of influence of individual *B*
d = distance between the centers of the area of influences of individuals *A* and *B*

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

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

The number of individuals of each primary and secondary major species which were rooted in an area of influence and outside all areas of influence of each major species, were also recorded. Seedlings, other than those of *Pinus* in site 2, were not recorded. The results from the two randomly selected subplots could be summed and the total area of influence of each species could be expressed as a percentage of the total plot area. The percent density of each species which occurred in the area of influence of a given species could also be determined. If a species were spatially independent of a second species, the percentage of its individuals in the plot that occur in the area of influence of the second species would be expected to equal the percent area of the plot covered by the second species' area of influence.

The areas of influence of each individual were divided into three annuli or zones. These zones were defined by dividing the radius of the area of influence into three equal length segments. Zone 1, or the inner canopy, extends out from the canopy center half the distance to the canopy edge. Zone 2, or the outer canopy, extends from the outer edge of zone 1 out to the canopy edge, while zone 3 extends from the canopy edge to the outer edge of the area of influence. The number of individuals of each major species occurring in the areas of influence and the the zone in which they occurred was also recorded. This method differs from the species-region approach used by Stowe and Wade (1979) since they applied it to a contact sampling

method. Hazlett and Hoffman's (1975) method was very similiar, although they mapped individuals in plots instead of collecting radii lengths and density data.

Example of Association Analysis

An example of association analysis is shown (Fig. 6a) since this specific method has not been previously used. In this example the total area of influence of species *A* covers 20% of the total plot area while 80% of the individuals of species *B* occur in this area of influence. The expected and observed values can be compared and tested for goodness of fit using the chi-square approximation of the binomial distribution at the 5% probability level. In this example the observed and expected values vary significantly and we would conclude that species *B* is positively associated with the area of influence of species *A*. It should be noted that for simplicity in this example a small total density of species *B* is used making the validity of a chi-square approximation questionable. In actual data, if total densities in the two subplots were <20 they were analyzed using the Fisher exact test. This analysis assumes that individuals of species *B* act independently.

Figure 6b is an example of association analysis when the areas of influence are divided into three zones. The observed and expected values can be compared as in the Fig. 6a. The analysis in this latter example shows that species *B* is positively associated only with zone 3 of the area of influence of species *A*.

Soils

In one of the two subplots not being used for association analysis, one mature individual of each major species was located. Only individuals which had no other major species in the downhill half of their area of influence were selected. Soil samples were taken on the downhill side of each individual, from the center of each zone at 10 and 50 cm depths (Fig. 7). Samples were also collected at these two depths from a bare area not in the area of influence of any plants at each site. Due to relatively low numbers of major species at sites 1 and 2, samples were collected from two individuals of each major species and two bare areas.

Soil samples collected in mid-June 1983 were analyzed for moisture, texture, total N, available P and total SO_4. Samples were collected again from the same points in August 1983 but were

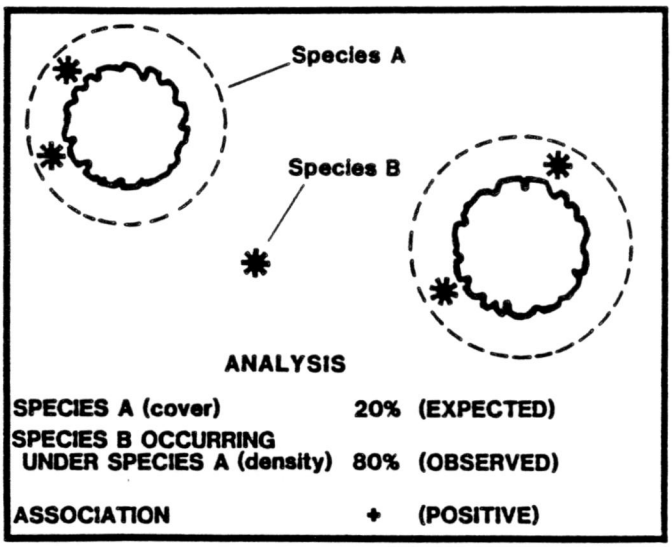


Fig. 6a. Hypothetical plot showing locations of individuals of species *A* and *B* and association analysis to determine if species *B* is significantly associated with species *A*.

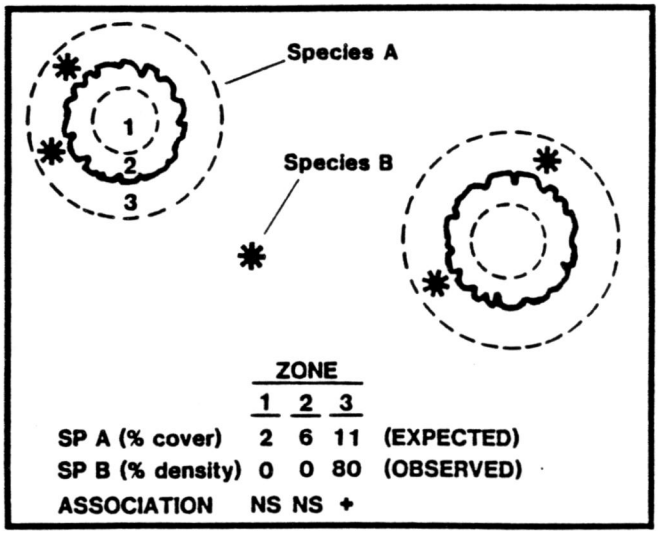


Fig. 6b. The same plot as shown in Fig. 6a. In this example the area of influences of species *A* are divided into three zones for a more informative analysis. NS denotes a nonsignificant difference between expected and observed values ($p<0.05$).

analyzed only for moisture. Moisture was determined gravimetrically from the whole substrate sample. Textural analysis was based on percentage of soil (particles <2 mm in diameter). The remaining three nutrients were analyzed by the Soil Characterization Laboratory, University of Idaho.

Amounts of these nutrients were determined on the soil fraction (<2 mm in diameter) since it was assumed any nutrients in the non-soil fraction (>2 mm in diameter) were unavailable to plants. The amount of each nutrient determined in the soil fraction was multiplied by the percent soil fraction in each substrate to express nutrients on a total substrate basis. Total N was determined by micro-Kjeldahl digestion. NH_3 was distilled into H_3BO_3 and the solution was titrated with dilute $H_2\ SO_4$. Available P was determined by $NaCH_3COO^-$ extraction and color was developed and read on a spectrophotometer. Total SO_4 was determined using the calorimetric method.

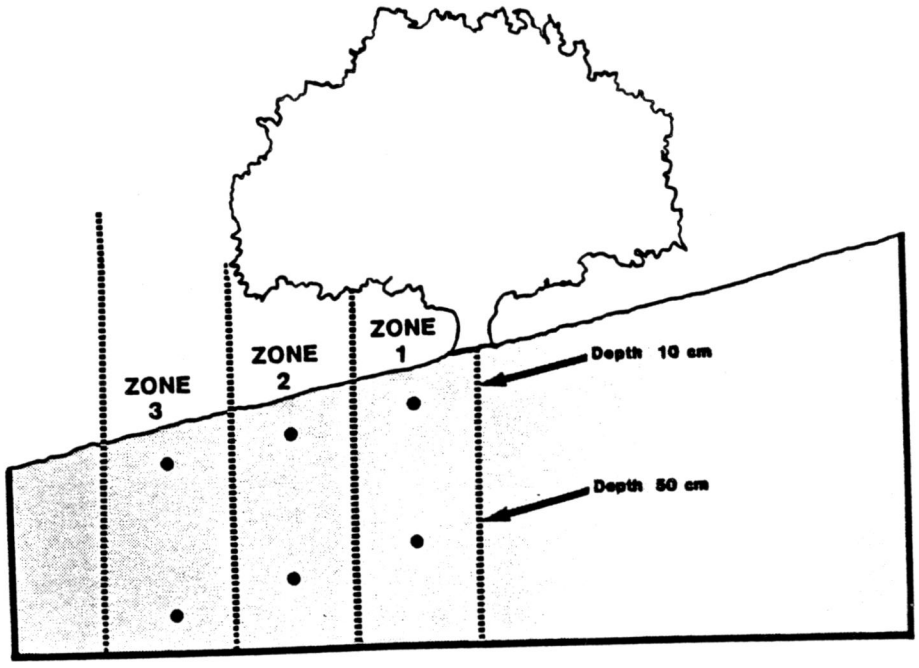


Fig. 7. Soil sampling locations under the area of influence of an individual. Samples were collected in June and August, 1984.

At each site one soil pit was also dug and the profile was photographed and described. Samples from each horizon were collected and were used in classifying each soil. Profile boxes of the soil at each site are in the museum at Monument headquarters.

Bulk density was determined at 10 and 50 cm depths using a volume displacement method. A sample was removed from each horizon and volume was determined by laying cellaphane in the hole from which the sample was taken and filling it with water. The volume of water needed to fill the hole was recorded. The soil sample was ovendried and weighed.

To examine seed densities in soil at site 1, the upper 7 cm of soil from a 100 cm^2 area within the canopy of six randomly choosen *E. ovalifolium* individuals was collected. Samples were only collected from individuals having no other plants within 50 cm of their canopy. Nearby each *E. ovalifolium* sampled, in an area void of plants for at least 50 cm in all directions, an equal size sample was collected from the upper 7 cm of soil. Six paired samples were collected in this manner in August, 1983 and June, 1984. Attempts to germinate seeds contained in the samples after stratification involving alternate freezing and thawing at weekly intervals for three months were largely unsuccessful. Soil samples were then seived to remove the non-soil fraction and seeds were counted. Seeds were deposited at the Forestry Herbarium, University of Idaho.

RESULTS

General Vegetation and Soils

The major species and soil profile at each study site are summarized in Figures 8a and 8b. All soils were cindery Frigid Lithic Xerorthents with the exception of soils at sites 8, 10 and 11. Soils at sites 8 and 11 were cindery Frigid Lithic Ultic Haploxerolls while soil at site 10 was a cindery Frigid Ultic Haploxeroll based on Soil Conservation Service guidelines (1975).

Due to the presence of buried soil horizons at many of the sites (Fig. 9), it was apparent that the original cones have been overlaid with cinders from more recent eruptions. Buried horizons appear to be A horizons with the exception of obvious buried cinder C horizons beneath these A horizons. Lack of any second or buried B horizon between buried A and C horizons seems to confirm this. Nearly all buried A horizons were relatively fine textured (*e.g.* loams) and red-brown in color. These were originally thought to be buried B horizons, since present epipedons in the area are brown to black in color. The red-brown color of these buried horizons may be due to burning of their organic matter caused by high temperatures of overlain cinders at the time of fallout. Leaching from cinders above may also be a factor as evidenced by a thin layer of gray, relatively highly weathered cinders directly above these red-brown horizons. These highly decomposed cinders may be remnants of an original cinder pavement, which is found above present A horizons at all sites.

The presence of a black, relatively coarse-textured, buried A horizon at site 2 may be due to relatively low organic matter content of this horizon at the time it was overlain by cinders. This buried horizon is similiar in color and texture to the A horizon currently at this site, which is very low in total N, and therefore organic matter .. The buried A horizons which are red-brown loams probably had higher levels of organic matter which facilitated burning when they were overlain with cinders.

The red-brown horizons contained virtually no volcanic glass from identified events of the Cascade volcanic complex. Transported igneous minerals, such as quartz and feldspars which would be expected in loess deposits, were absent or present only in trace amounts ($<1\%$ volume).

INFERNO CONE

Study Site 1

Eriogonum ovalifolium (5.8)
Phacelia hastata (7.9)

Study Site 2

Eriogonum ovalifolium (26.7)
Phacelia hastata (6.1)
Sitanion hystrix
Stipa thurberiana
Eriogonum umbellatum (6.9)
Pinus flexilis (25.2)

Study Site 3

Purshia tridentata (84.4)
Chrysothamnus nauseosus (15.9)
Ribes cereum (49.9)
Stipa thurberiana

Study Site 4

Pinus flexilis (33.8)
Purshia tridentata (53.6)
Chrysothamnus nauseosus (38.1)
Ribes cereum (38.1)
Sitanion hystrix
Poa secunda

Study Site 5

Pinus flexilis (58.9)
Purshia tridentata (25.7)
Ribes cereum (18.3)
Artemisia tridentata (61.0)
Sitanion hystrix
Stipa thurberiana
Poa secunda

SILENT CONE

Study Site 6

Purshia tridentata (75.5)
Eriogonum ovalifolium
Eriogonum umbellatum
Agropyon spicatum

Study Site 7

Purshia tridentata (58.7)
Artemisia tridentata (34.2)
Eriogonum umbellatum
Cymopterus terebinthinus
Agropyron spicatum

GRASSY CONE

Study Site 8

Purshia tridentata (41.4)
Chrysothamnus nauseosus (10.0)
Symphoricarpos oreophilus (5.9)
Eriogonum umbellatum
Cymopterus terebinthinus
Balsamorhiza sagittata (12.0)
Agropyron spicatum

Study Site 9

Purshia tridentata (48.7)
Artemisia tridentata (60.5)
Eriogonum umbellatum
Cymopterus terebinthinus
Poa secunda
Agropyron spicatum

SUNSET CONE

Study Site 11

Purshia tridentata (57.5)
Artemisia tridentata (20.9)
Eriogonum heracleoides (17.5)
Cymopterus terebinthinus
Poa secunda
Agropyron spicatum

Study Site 10

Purshia tridentata (63.2)
Eriogonum heracleoides (44.9)
Cymopterus terebinthinus
Balsamorhiza sagittata (32.4)
Poa secunda
Agropyron spicatum

Fig. 8a. Major species listed by study site. Primary major species are followed by their mean total foliar cover at the study site.

INFERNO CONE

Study Site 1	Study Site 2	Study Site 3	Study Site 4	Study Site 5
0-2 CP	0-2 CP	0-1 CP	0-0.5 CP	0-2 CP
2-8 A	2-13 A	1-23 A	0.5-4 O	2-16 A
8-8 C	13-20 A/C	23-28 A/C1	4-16 A	16-46 C
8-62 A/C	20-71 C	28-41 C1	16-34 C	46-60 2Cb
62-64 2Ab	71-86 2Ab/2Cb	41+ C2	34-38 2Ab/2Cb	60-74 3Cb
64+ 2Cb	86+ 2Cb		38-110 2Cb	74-80 4Ab
			110-119 3Cb	80-115 4Ab/4Cb
			119-126 3Cb/3Ab	115+ 4Cb
			126+ 4Cb	

SILENT CONE

Study Site 6	Study Site 7
0-2 CP	0-2 CP
2-10 A	2-12 A
10-16 A/C1	12-14 A/C1
16-37 C1	14-20 C1
37+ C2	20-60 C2
	60+ C3

GRASSY CONE

Study Site 8	Study Site 9
0-1 CP	0-1 CP
1-23 A	1-6 A
23-29 A/C1	6-10 C
29-40 A/C2	10-17 2Ab
40-72 C3	17-20 2Ab/2Cb
72-75 C4	20-33 2Cb
75+ C5	33-36 2Cb/3Ab
	36-40 3C1b
	40+ 3C2b

SUNSET CONE

Study Site 10	Study Site 11
0-2 CP	0-1 CP
2-5 A	1-5 A
5-40 C1	5-29 B
40-62 C2	29-32 B/C1
62-72 C2/2Ab	32-42 C1
72+ 2Cb	42+ C2

Fig. 8b. Soil profiles at each study site. The first column refers to horizon depth while the second column refers to horizon type. Horizon symbols follow Soil Conservation Service (1975) guidelines. CP refers to loose, cinder pavement.

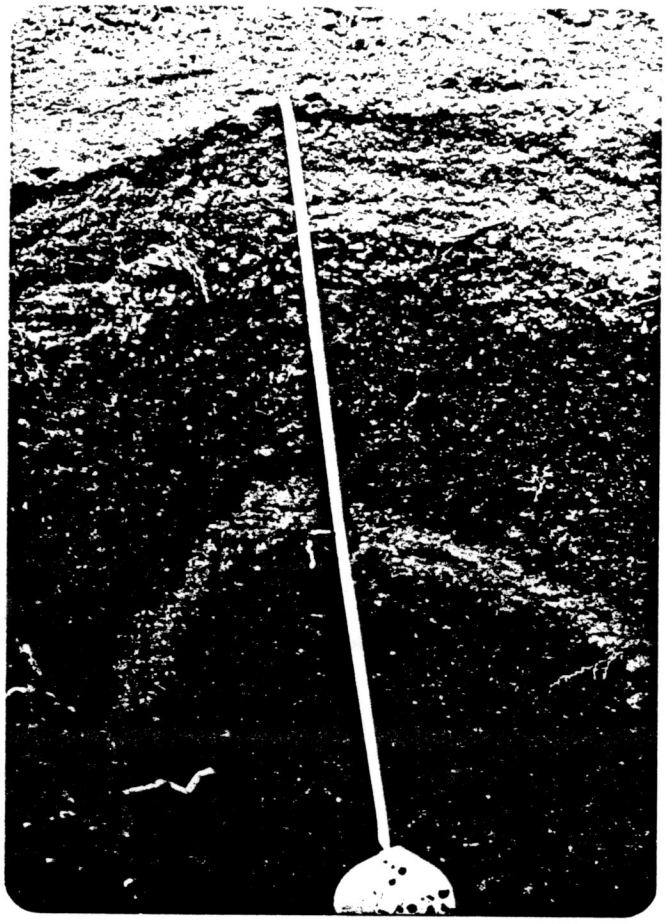


Fig. 9. Soil profile at study site 9 on Grassy Cone. The buried, red-brown horizons were apparently past A horizons.

The absence of loess deposits on these relatively young volcanic deposits is consistent with the findings of Lewis *et al.* (1975). It appears all buried horizons are the result of cinder decomposition and inputs from biotic components.

The presence of these buried horizons makes a chronosequence analysis very questionable since the parent material and time factors (Jenny 1958; Major 1951) are difficult to interpret. The assumption that all sites are on the same successional pathway may not be valid. However, from field observations a general vegetation sequence of cinder garden to pine/shrub to shrub community still seems valid on east-facing cinder cone slopes. It is not inferred that these communities are discrete stages nor that one community is always a prerequisite for the following successional community.

When a buried loam horizon was within 1 m of the surface, pine/shrub or shrub communities were usually present and usually contained *Artemisia tridentata* ssp. *vaseyana*. Woody species utilized this horizon as witnessed by the relatively high numbers of their roots in these buried horizons where overlain cinders were not too deep.

Sites

Sites 1 and 2 were cinder garden communitites characterized by low vegetational cover and large areas of bare cinders. Site 1 was the youngest of all sites in terms of soil development, total vegetational cover and species richness. From mid-May through early-July several species were common here, including the perennials *Allium simillimum* and *Lewisia rediviva* and the annuals *Mimulus nanus* and *M. suksdorfii*. By mid-July these species were largely absent aboveground and only two major species were present: *Eriogonum ovalifolium* var. *depressum*, a non-deciduous, mat-forming perennial and *Phacelia hastata*, an erect perennial which was apparent most of the year only as a small rosette (Fig. 10). *Cryptantha interrupta* and *Aster canescens* were active at this site in mid-July but were not present in large enough amounts to meet the requirements for major species.

Soil consisted of a loose cinder pavement 1-2 cm in depth overlying an A horizon of coarse-textured, black sand (Fig. 11). Beneath the A horizon was a C horizon of loose, black cinders

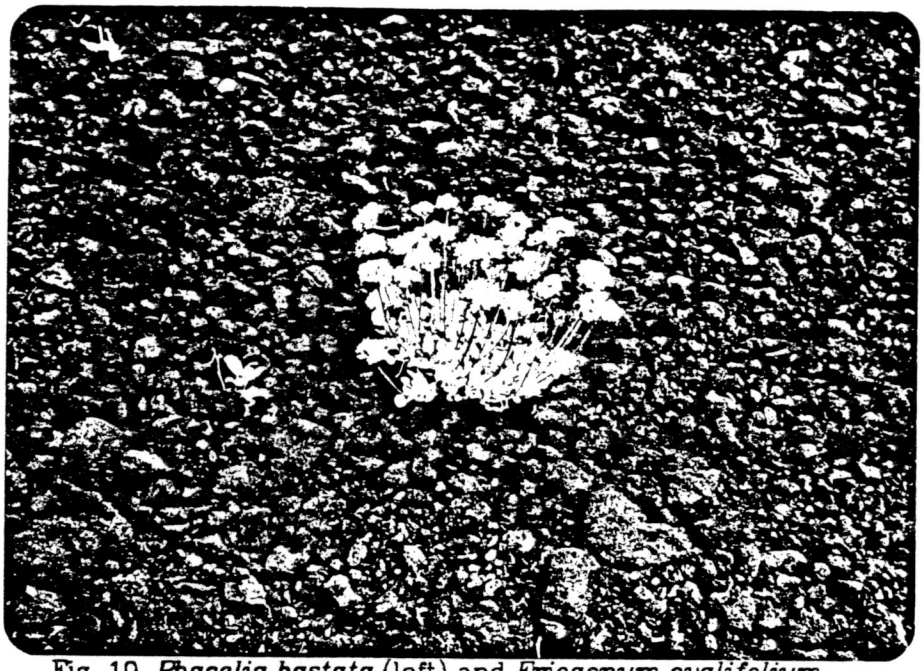


Fig. 10. *Phacelia hastata* (left) and *Eriogonum ovalifolium* var. *depressum* (right) in cinder gardens on Big Craters in mid-June, 1984.

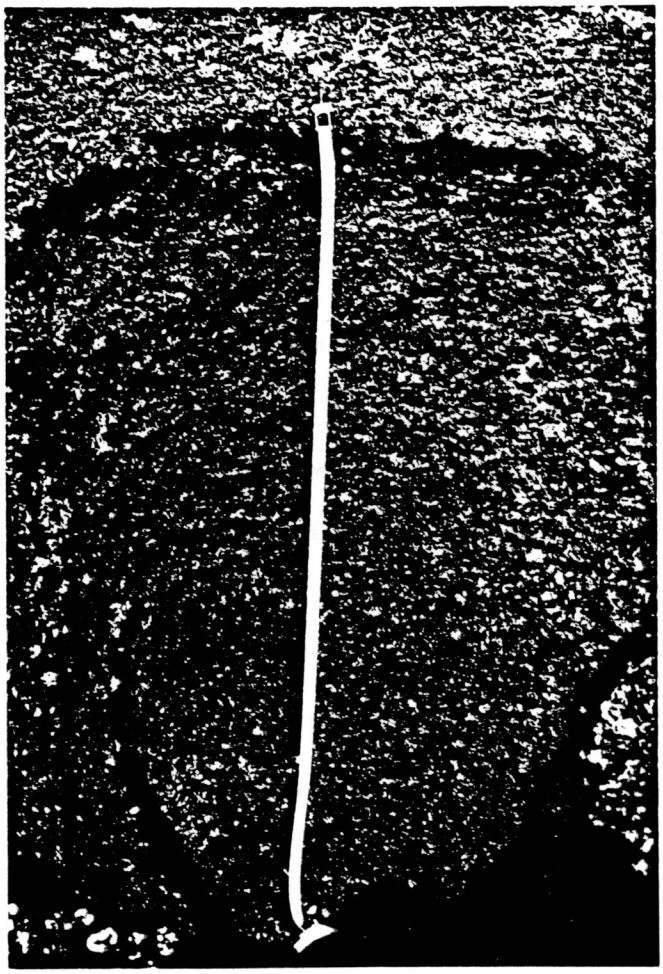


Fig. 11. Profile of poorly developed soil at study site 1 on Inferno Cone.

which were laid down from an eruption approximately 2200 yr BP at Big Craters (Kuntz *et al.* 1983). Due to the underlying cinders, this A horizon will hold more water at field-capacity than a similiar textured sand not underlain by a coarse- textured layer (Alway and McDole 1917; Miller 1969). Daytime soil surface temperatures at this site were found to exceed 50° C in July. Eggler (1941) found the range of daily soil temperature at the 7.6 cm depth to exceed that of air temperature and that the time lag between the two was suprisingly small.

At site 2, both *E. ovalifolium* var. *depressum* and *Phacelia hastata* were again major species but four additional major species were present: the grasses *Sitanion hystrix* and *Stipa thurberiana*, another mat-forming *Eriogonum* which is slightly larger than *E. ovalifolium*, *E. umbellatum*, and the first woody species to establish on these cinder areas, *Pinus flexilis* (Fig. 12). These latter two species were present as scattered individuals of relatively low densities although their relative cover in the plot was as high as other major species due to their relatively large size. The fact that these two species occurred in low densities on this site , while having higher densities in pine/shrub communities (where species such as *E. ovalifolium* and *Phacelia hastata* were generally absent) substantiates the idea that these are the last of the major species at this site to establish here.

Pinus flexilis is extremely slow growing on site 2 and current association of mature *Pinus* individuals with other plants probably does not reflect conditions at the time of *Pinus* establishment. Therefore, the association of mature *Pinus* individuals with herbaceous species was not analyzed, although the converse (association of herbaceous species with mature *Pinus* individuals) was determined. To gain information on *Pinus* establishment, *Pinus* seedlings were tested for association with other species as well as mature *Pinus* individuals. Due to relatively high densities of these seedlings, survival was monitored at site 2 from June through August, 1983.

Soils were slightly more developed here than in the previous site, with an A horizon 12 cm thick, and higher levels of total N and finer texture at the 10 and 50 cm depths (Fig 13). A 2 cm thick buried A horizon was present at the 62 cm depth. Below this was a buried C horizon of cinders similiar to the non-buried C horizon.



Fig. 12. Study site 2, containing the initial colonizers and the grasses *Sitanion hystrix* and *Stipa thurberiana*, as well as scattered individuals of *Eriogonum umbellatum* and *Pinus flexilis*. The pine/shrub community is in the background.

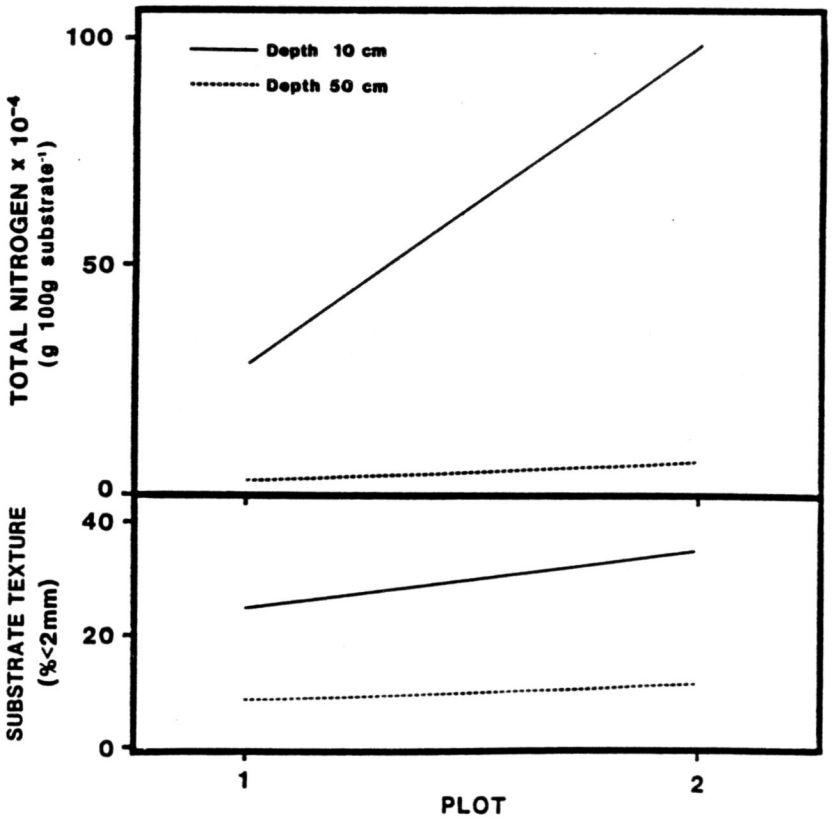


Fig. 13. Total N levels and substrate texture under bare areas at 10 and 50 cm depths at study sites 1 and 2.

The remaining nine sites were in pine/shrub or shrub dominated communities. These sites will not be described in depth here for reasons to be discussed in later parts of this paper.

Intra- and Interspecific Plant Associations

Site 1

Vegetation analysis from site 1 showed that *Phacelia* was positively associated with the inner canopy (zone 1) of *Eriogonum ovalifolium* (Table 1). Both these initial colonizers were negatively associated with their own canopy regions (zones 1 and 2).

Site 2

At site 2, not only *Phacelia* but all other major species were positively associated with the inner canopy of *E. ovalifolium* (Table 1). *Pinus* seedlings, but not mature individuals, were tested for association with *E. ovalifolium.* Of 39 isolated individuals or clumps of current-year seedlings found at this site, 21 (54%) were within the area of influence of an established plant (any species). (Clumps are seedlings rooted within 2 cm of each other.) Most of these isolated individuals or clumps were within the area of influence of a species other than mature *Pinus flexilis.* The average number of seedlings in each clump in June was similiar for clumps within an area of influence (2.6 individuals clump^{-1}) and those outside any area of influence (2.8 individuals clump^{-1}).

A significantly lower percentage of seedlings within an area of influence of any plant survived until late-August (56%), compared to seedlings outside any area of influence (73%) ($p<0.05$). However, seedlings within the area of influence of *E. ovalifolium* had a 69% survival rate over this period, which is similiar to that of seedlings in bare areas. Survival rate among lone seedlings and clumped seedlings was not significantly different ($p<0.05$).

As in site 1, *E. ovalifolium* and *Phacelia* were negatively associated with their own canopy region. *Eriogonum umbellatum* appears to be the last of the herbaceous species studied at this site to establish in these cinder areas. Both the initial colonizers, *E. ovalifolium* and *Phacelia*, were negatively associated with the inner canopy of *E. umbellatum* (Table 2).

Site	Species	Total	Zone		
			1	2	3
1	*Phacelia*		+		-
1	*E. ovalifolium*		-	-	
2	*Phacelia*		+		
2	*E. ovalifolium*		-	-	
2	*Sitanion*		+		
2	*Stipa*	+	+		
2	*E. umbellatum*		+		
2	*Pinus* (seedlings)		+		

Table 1. Significant associations with the total area of influence and separate zones of *Eriogonum ovalifolium* at study sites 1 and 2. Positive and negative signs indicate significant positive and negative associations respectively ($p<0.05$).

Site	Species	Total	Zone		
			1	2	3
2	*Phacelia*	-	-		
2	*E. ovalifolium*	-	-		
2	*Sitanion*				
2	*Stipa*		+		
2	*Pinus* (seedlings)		+		

Table 2. Significant associations with the total area of influence and separate zones of *Eriogonum umbellatum* at study site 2. Positive and negative signs indicate positive and negative associations respectively ($p<0.05$).

Site	Species	Total	Zone		
			1	2	3
2	*Phacelia*	-	-	-	-
2	*E. ovalifolium*	-	-	-	-
2	*Sitanion*	-	-		
2	*Stipa*	-	-		
2	*E. umbellatum*		-		
2	*Pinus* (seedlings)	+	+	+	+

Table 3. Significant associations with the total area of influence and separate zones of *Pinus flexilis* at study site 2. Positive and negative signs indicate significant positive and negative associations respectively ($p<0.05$).

At site 2 all other species except *E. umbellatum* were negatively associated with the total area of influence of mature *Pinus* individuals (Table 3). The two initial colonizers, *E. ovalifolium* and *Phacelia*, were negatively associated with all zones of *Pinus*. *Eriogonum umbellatum* was negatively associated only with the inner canopy of *Pinus*. *Pinus* seedlings were positively associated with all zones of mature *Pinus* individuals.

Sites 3 through 11

On the remaining nine, more developed sites, association between the same species-pair were often inconsistent between sites, making generalizations difficult. Results of association analysis for sites dominated by woody species are given in Appendix 2. Association results between subplots at the same site were also found to be highly variable for each species-pair tested. When associations were analyzed seperately for the two subplots at each site (instead of summing these data for a sample of the site) many species-pairs showed a positive association in one subplot and a negative association in the second subplot. The number of these conflicting associations between the subplots at each site are summarized in Table 4. No conflicting associations were found in the two early-successional, cinder garden communities while all sites dominated by woody species, with the exception of sites on Silent Cone, contained conflicting associations. However, these comparisions should be interpreted cautiously since the higher number of inconsistencies may be due to the larger size of the species on the more developed sites which in some cases resulted in smaller numbers of individuals in each subplot. These smaller sample sizes may not include enough individuals in a subplot sample for significant associations to express themselves.

Although specific species-pairs results are difficult to interpret, species in general were found to be most often associated with zone 2 (Table 5). A greater or equal percentage of species-pairs showed a significant negative association with zone 3 than with other zones.

Possible Factors

Site 1

Two possible factors were identified for *Phacelia*'s positive association with the inner canopy of *E. ovalifolium*. One factor was relatively high soil moisture levels under the inner canopy of

Sites	Cinder Cone	Dominant Life form	Inconsistent Species-pairs (%)
1,2	Inferno	herbaceous	0.0
3,4,5	Inferno	woody	10.7
6,7	Silent	woody	0.0
8,9	Grassy	woody	5.5
10,11	Sunset	woody	10.0

Table 4. Percentage of species-pair associations inconsistent (p,0.05) between subplots within a site for cinder gardens sites (1 and 2) and woody species dominated sites on each cinder cone.

Site	Total Number of Species-pairs	Positive Species-pairs (%)			Negative Species-pairs (%)		
		Zone			Zone		
		1	2	3	1	2	3
3	9	22	33	22	11	11	0
4	20	10	20	10	0	5	10
5	28	14	21	4	0	0	32
6	4	0	50	0	0	0	25
7	8	13	62	13	0	0	13
8	24	29	33	21	0	0	0
9	12	0	58	0	33	0	50
10	15	20	87	7	13	0	13
11	15	13	93	33	27	0	20

Table 5. Percentage of species-pairs associations at each study site which were significantly positive or negative, by zone (p<0.05).

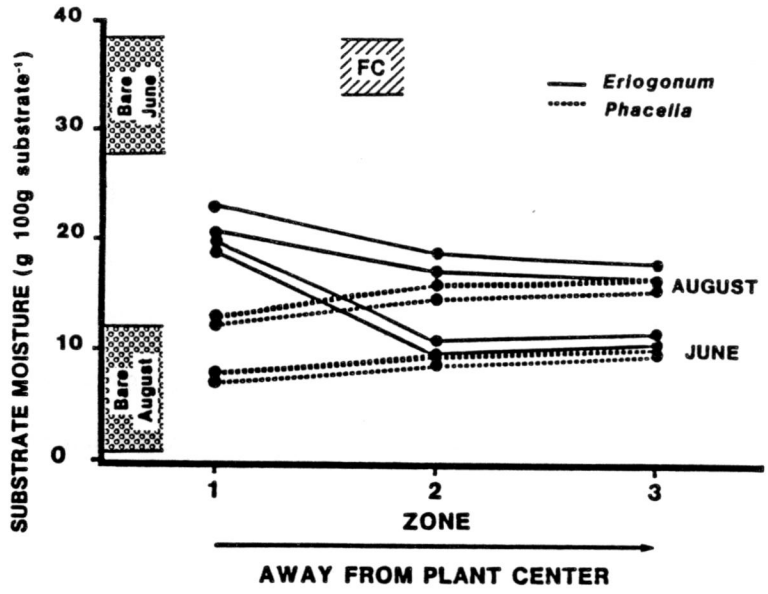


Fig. 14. Substrate moisture under zones of *Eriogonum ovalifolium* var. *depressum* and *Phacelia hastata*, and under bare areas at the 10 cm depth at study site 1. FC denotes profile-drained field-capacity range of bare area samples.

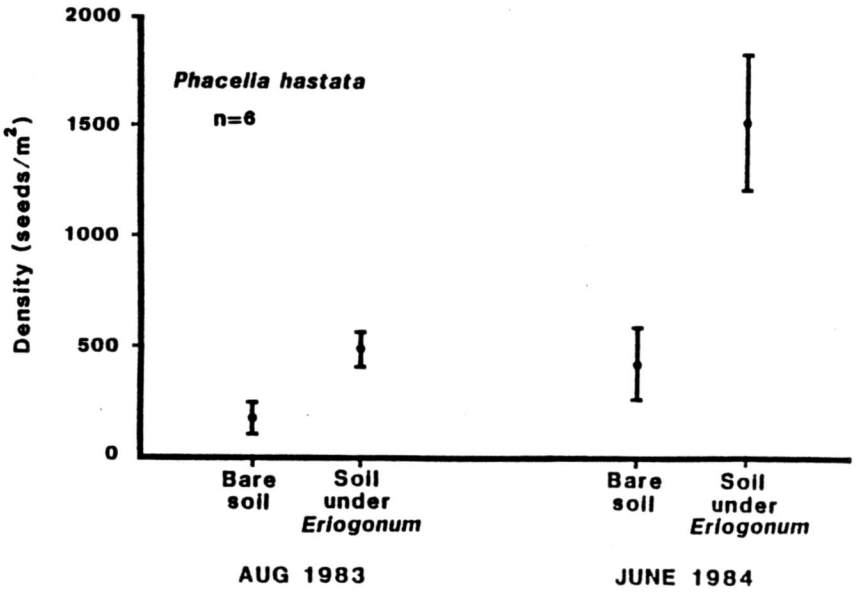


Fig. 15. Seed density of *Phacelia hastata* in the upper 7 cm of soil under bare areas and *Eriogonum ovalifolium* var. *depressum* in August 1983 and June 1984. Points indicate the mean (n=6) and lines indicate ±*SE*.

E. ovalifolium (Fig 14). In both June and August, moisture levels under the area of influences of the isolated *E. ovalifolium* individuals sampled were highest under zone 1. Moisture levels under the isolated *Phacelia* individuals sampled were lowest under zone 1. In June, moisture levels under both species were lower than levels in bare areas at this site. In August, levels under these two species were equal or higher than levels at bare areas.

Total N and available P levels at the 10 cm depth were similiar under both species. Moisture, total N and available P levels at the 50 cm depth were lower than those at the 10 cm depth but did not show any consistent differences between zones or species. Analysis of total SO_4 was not possible for several sampling points in sites 1, as well as site 2, due to inadequate soil sample size. Due to these missing values a comparision of total SO_4 levels with vegetation data was not feasible.

The second possible factor responsible for the higher than expected occurrence of *Phacelia* individuals in the inner canopy of *E. ovalifolium* was seed dispersal patterns of *Phacelia*. Results show that seed densities of *Phacelia* were significantly higher ($p<0.05$) in soil under *E. ovalifolium* canopies than in soil of nearby bare areas (Fig 15). The only other seeds found in high enough densities to allow statistical analysis in these samples were those of *Lewisia rediviva*, which is present aboveground only until late-June to early-July on these sites. Seed densities of this species were also significantly higher ($p<0.05$) in soils collected under *E. ovalifolium* compared to soils of nearby bare areas.

Site 2

At site 2 *E. ovalifolium* also had higher moisture levels under its inner canopy but was not unique in this respect at this site. A second possible factor for the interspecific positive associations with *E. ovalifolium*'s inner canopy was higher total N and availabe P levels under this species (Fig. 16). Both these nutrients were at higher levels under all three zones of not only *E. ovalifolium*, but also the other initial colonizer, *Phacelia*, when compared to soils under *E. umbellatum* and *Pinus flexilis*, the two other species sampled at this site. Nutrient levels under these two later-successional species were similiar to levels from bare areas not within the area of

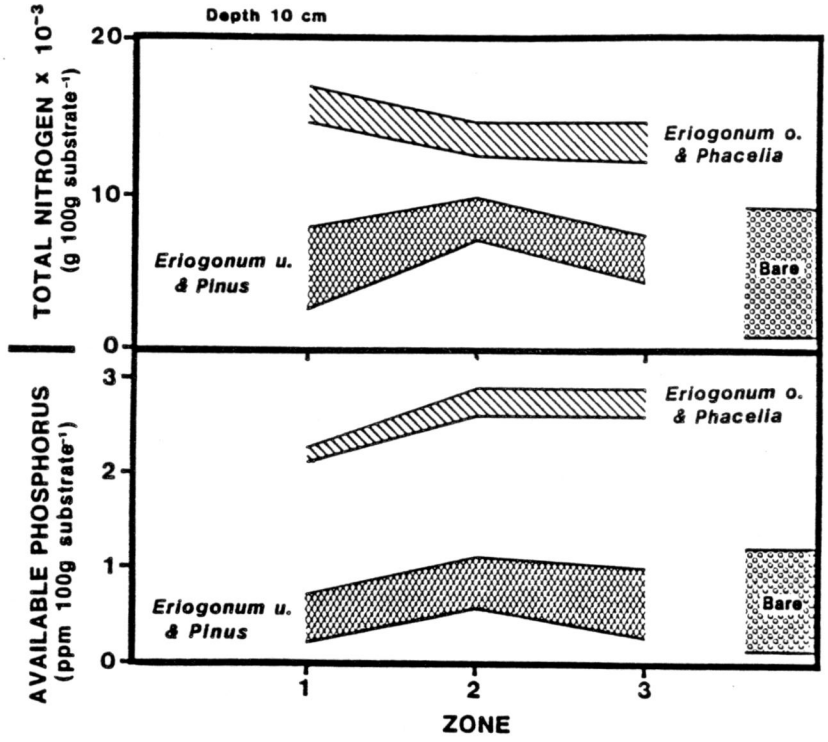


Fig. 16. Soil total N and available P levels under zones of species and bare areas at the 10 cm depth at site 2. Shaded areas show nutrient ranges and not neccessarily trends of a species.

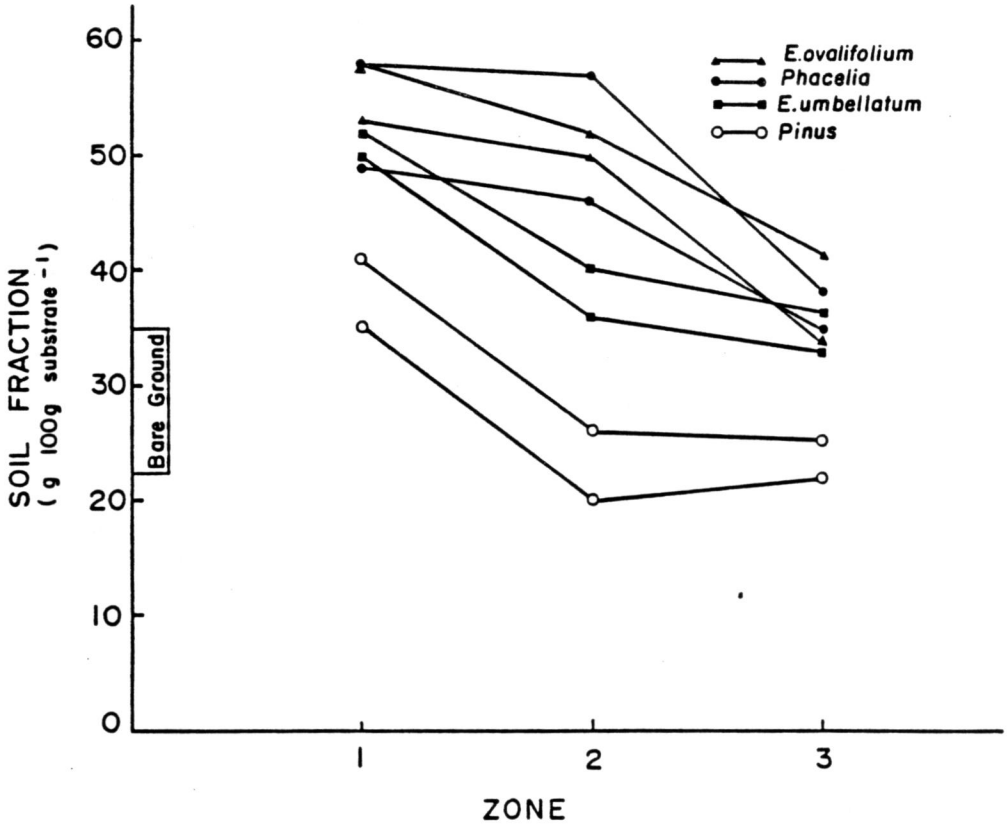


Fig. 17. Soil fraction in the substrate at the 10 cm depth under the four major species at study site 2.

influence of any species. *Eriogonum ovalifolium*, *E. umbellatum* and *Phacelia* had higher percentages of soil in the substrate under their canopies than the substrates under bare areas at this site (Fig. 17).

Sites 3 through 11

Data on soil moisture in the remaining nine, more developed sites failed to identify interpretable differences in moisture levels between species. In some cases a species did show higher moisture levels than other species at a site, but these high levels were not found at other sites. In the vast majority of cases, moisture patterns between the zones of a species changed from June to August, 1983. Levels of other nutrients examined showed similiar variability, with either no apparent difference between levels under different species, or lack of any consistently high or low levels under a species from one site to the next. The range of total N was much greater on these more developed, woody species dominated sites than in sites 1 and 2 (Fig. 18).

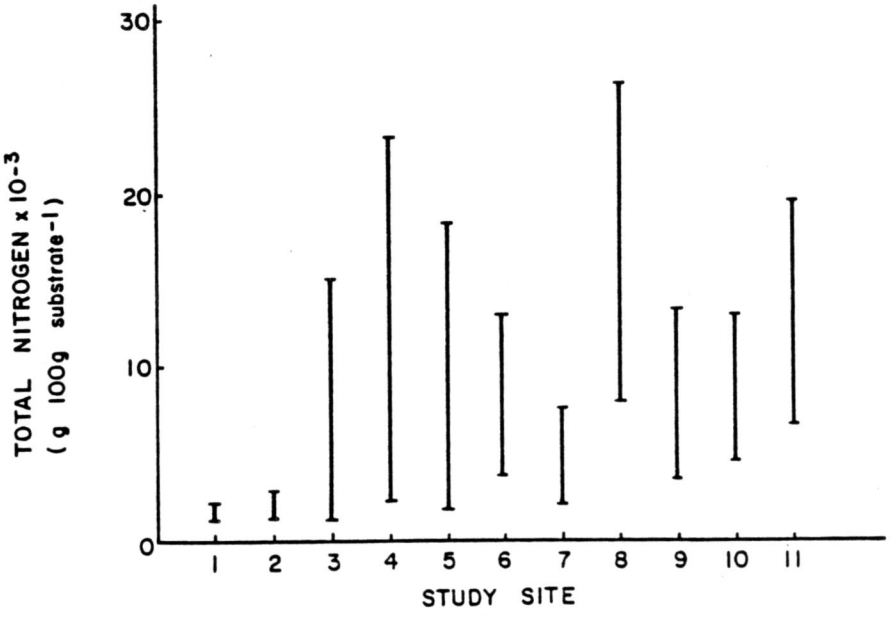


Fig. 18. Range of total N in the soil at the 10 cm depth at the eleven study sites.

DISCUSSION

A specific chronosequence of vegetation and soils was not developed in this study due to overlain cinders at most sites. These made determinations of parent material age and development of a soil chronosequence infeasible. Each overlain cinder horizon attests to a major volcanic disturbance after the cone was originally formed and colonized. Buried soil horizons undoubtably affect successional processes on these sites after cinder fallout. Even if the age of the last cinder fallout on an area could be estimated, differences in the presence, thickness and physical and chemical composition between buried horizons makes inferences of specific successional pathways between some sites risky. However, a general successional pathway starting with a pure, bare cinder substrate going through cinder garden and pine/shrub communities to shrub dominated communities still seems valid and is supported by Eggler (1941).

On poorly developed sites, where ***Eriogonum ovalifolium*** is a dominant, all other species studied were found to be positively associated with the inner canopy of *E. ovalifolium*. In the least developed areas of cinder cones such as site 1, ***Phacelia hastata*** is the only other major species. Two possible reasons for ***Phacelia***'s positive association with the inner canopy region of *E. ovalifolium* were higher moisture levels under *E. ovalifolium*, and its ability to act as a wind break, thereby accumulating wind-blown seeds of *Phacelia*.

The positive association of desert annuals with herbaceous perennials and shrubs has sometimes been inferred to be due to enhanced water availability under the later plants. Muller (1953), and Muller and Muller (1956) felt that accumulation of wind-blown material increased organic matter and fine particulate matter in the soil under the canopies of these plants leading to greater soil water-holding capacities.

In June when growing conditions were most favorable, moisture levels under both species were lower than that of bare soil at the site. By August, the moisture levels under both species were greater than moisture levels under bare soil due to plant use. By late-July the two species were less active and their leaves began graying. At this time moisture uptake probably decreased and resulted in higher moisture moisture levels under both species relative to moisture levels in

bare areas. The high moisture levels under the inner canopy of *E. ovalifolium* in August were probably also due to shading by its canopy. Dew appears to be uncommon on this sites and what does occur is probably not in high enough amounts to runoff plants into the soil. It is not known if aboveground absorption of dew by plants is significant on these sites.

The statistically significant difference in *Phacelia* seed densities between soil under *E. ovalifolium* and soil of bare areas appears to be unique in seed density studies on natural vegetation. Major and Pyott (1966) reviewed the difficulties in obtaining statistically valid estimates of seed densities and Whipple (1978) concluded that all seed density estimates from natural vegetation were made from too few samples. In this study the objective was to determine only whether seed densities were statistically different in two types of soil (not estimate actual seed densities). Another probable factor responsible for statistically significant results was the relatively sterile soils of the cinder gardens. Apparently no quantitative studies have been done demonstrating higher seed accumulations around plant bases. However, Viereck (1966) felt that mat-forming pioneer species were important in accumulating seeds and other fine wind-blown material in primary succession on gravel outwash.

On site 2, where other major species were present, all species were positively associated with *E. ovalifolium*'s inner canopy (Fig. 19). In this area, *E. ovalifolium* was unique in having the combination of relatively high levels of moisture, total N and available P under its inner canopy. In the case of *Pinus*, only seedlings were tested for this association. *Pinus* seedlings not only tended to occur near *E. ovalifolium* (as shown by their positive association), but also had relatively high survival rates near *E. ovalifolium*, at least through late-August.

Higher concentrations of N in soil under plant canopies relative to soil in interspaces between plants have been found by several workers (Rixon 1970; Garcia-Moya and McKell 1970; Charley 1972; Tiedeman and Klemmedson 1973; Wallace and Romney 1972; Nishita and Huag 1973; Charley and West 1975; Barth and Klemmedson 1978; Vasek and Lund 1980; Lajtha and Schlesinger 1984). Hirose and Tateno (1984) found soil organic nitrogen and ammonium nitrogen increased as distance toward colonizers decreased on volcanic sites. Due to the large number of

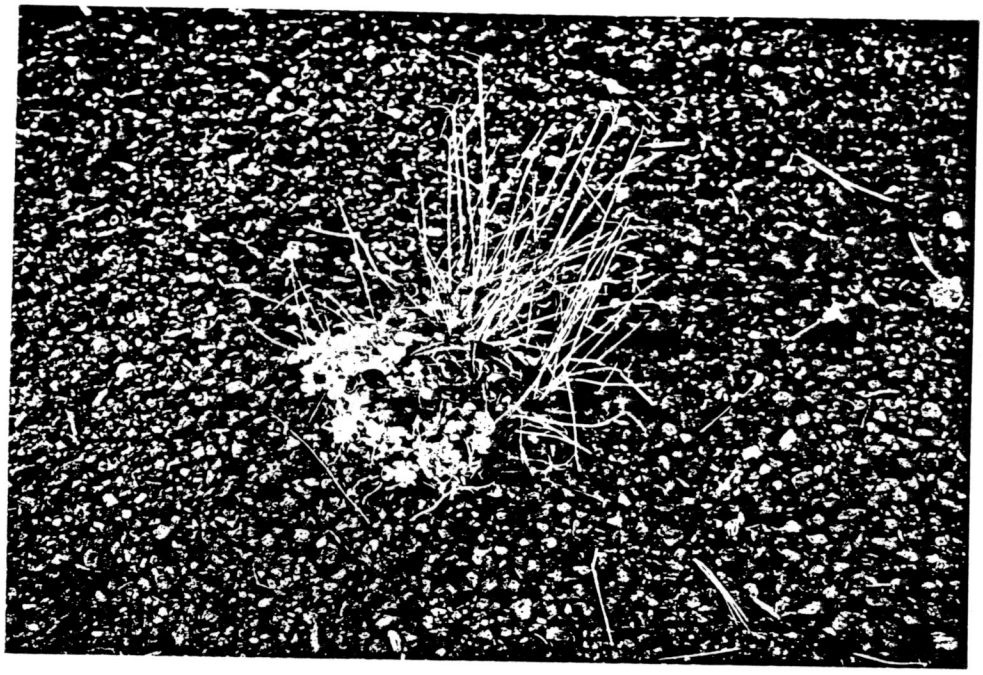


Fig. 19. Apparent facilitation of *Eriogonum umbellatum* and and *Sitanion hystrix* by *Eriogonum ovalifolium* var. *depressum* at study site 2 on Inferno Cone.

documented cases of relatively high N levels under desert shrubs, it appears to be a general phenomenon occurring in several ecosystems (Charley and West 1977). A similiar spatial gradient from plant canopies to interspaces has been observed for available P (Ebersohn and Lucas 1965). Higher fertility under plants in these studies was contributed to soil protection against wind erosion, accumulation of wind-blown soil and litter, protection of understory vegetation, and the plants serving as reservoirs of essential elements.

Soils under *Phacelia* also contained relatively high levels of total N and available P. Levels of these nutrients in soil under bare areas were similiar to levels under the two later-successional species, *E. umbellatum* and *Pinus*. It is assumed the high soil nutrient levels under initial colonizers were not present before these plants established. Instead, it appears these two nutrients accumulated under *E. ovalifolium* and *Phacelia*. Both these species had relatively high root:shoot ratios, and their own litter as well as wind-blown material tended to accumulate in the canopy of *E. ovalifolium* as shown by seed density data. *Eriogonum umbellatum* and *Pinus* also had relatively large root systems and wind-blown material probably accumulated in the canopy of the former species, which is very similiar in growth form to *E. ovalifolium*. Accumulation of litter and wind-blown material would increase the percent soil fraction under canopies of these species. Substrates under canopies of all major species were found to have higher soil fractions than nearby bare areas (Fig. 17). Percent soil fraction was highest under herbacous species, especially the two initial colonizers. A decrease in soil bulk density and an increase in soil moisture content from bare ground to colonized sites has been observed on volcanic primary sites (Hirose and Tateno 1984).

The higher nutrient levels under the two initial colonizers could be due to three major factors. (1) The initial colonizers accumulated more material under their canopies than later-successional species. (2) The initial colonizers had lower nutrient absorption rates than later-successional species. (3) In the case of total N levels, differences in the species and numbers of soil microbes under the initial colonizers versus later-successional species may also be a factor.

The initial colonizers did tend to accumulate more fine material in substrates under their area of influence than *Pinus*, but not neccessarily more than *E. umbellatum* (Fig. 17). Substrate texture under zone 1 of the latter was similiar to substrate texture under the two initial colonizers. Therefore, higher accumulations of fine material under the initial colonizers appears to be partially, but not totally, responsible for higher nutrient levels under these two species.

Higher nutrient levels observed under the initial colonizers in this study may also have been due to different levels of uptake and storage of nutrients by these species relative to later-successional species. Several researchers (Bradshaw *et al.* 1960; Snaydon and Bradshaw 1962; Clarkson 1967; Rorison 1968; White 1972; Christie and Moorby 1975; Ingestad 1976; Mahmoud and Grime 1976; Blair and Cordero 1978) have found slowly growing species typical of infertile sites to have low nutrient absorption rates and show a small increase in this rate with increasing nutrient levels. These early-colonizing species absorb less nutrients under higher nutrient conditions than later-successional species typical of sites having these higher nutrient levels (Chapin 1980). *Eriogonum ovalifolium* and *Phacelia* were probably less efficient in absorption of accumulated nutrients, while uptake in *E. umbellatum* and *Pinus* decreased accumulated soil nutrients to levels comparible to bare areas. Species typical of infertile habitats often have higher tissue concentrations (lower efficiency) of a limiting nutrient relative to species of fertile habitats, when grown under the same conditons (Chapin 1980). This higher nutrient concentration may in turn lead to litter of higher nutrient content, although translocation of these nutrients may counteract this affect.

Higher microbial populations under later-successional species could lead to a higher rate of mineralization of organic N into inorganic N (*e. g.* ammonium and nitrate) which plants are able to utilize. This would lead to lower levels of total N in soil under these species. Unfortunately, no data on microbial populations or organic versus inorganic N levels were collected in this study. In conclusion, higher nutrient levels under the initial colonizers were most likely due to a combination of higher accumulations of fine material and lower nutrient absorption rates by these species relative to later-successional species, and possibly differences in microbial populations

under these two groups of plants.

Seed dispersal patterns were undoubtably an important factor in this site as in site 1. Not only *Phacelia*, but *E. umbellatum*, *Stipa* and *Sitanion* all had relatively small seeds which were easily transported by wind. It is not known if wind is an important dispersal mechanism of the large seeds of *Pinus flexilis* here. *Pinus flexilis* posesses both wind- and animal-dispersed characteristics (Smith and Balda 1979). Dispersal of these seeds by animal caching is probably significant as was suggested by Eggler (1941). Golden-mantled ground squirrels (*Spermophilus lateralis*), Clark's Nutcrackers (*Nucifraga columbiana*) and red squirrels (*Tamiasciurus hudsonicus*) were common in these areas. The latter two have been found to be important seed predators and dispersers of *Pinus flexilis* , respectively (Lanner and Van DerWall 1980; Benkman, Balda and Smith 1984). Clumped seedlings in bare areas were probably due to animal caching. In herbaceous, mat-forming canopies, clumped seedlings may be due to wind dispersal, although the average number of seedlings per clump in bare areas and canopies were very similiar. This suggests that animal caching may be the dominant dispersal mechanism in both cases. Strong winds in these areas were undoubtably capable of moving *Pinus* seeds, but it is unlikely that wind would consistently deposit several seeds in tight clumps ($<$ 2 cm in diameter).

Survival rates were not lower for seedlings in clumps compared to lone seedlings. This suggests that intraspecific competition was not very intense between *Pinus* seedlings, at least through late-summer. Established *Pinus* in this area commonly was made up of several closely clumped individuals (Fig. 20) and suggests that intraspecific competetion among clump members may be less of a factor in establishment than variations in environmental conditions, *etc.*. Stem clumping among *Pinus flexilis* individuals resulting from clumped seedlings is common in this species (Lanner and Van DerWall 1980).

The initial colonizers were negatively associated with both later-successional species (*Eriogonum umbellatum* and *Pinus*) in these sites. Environmental correlations with these data are difficult to interpret, since information on tolerance levels and competitive ability of these species is lacking. The data do show a gradient in the strength of the negative associations with *Pinus*.



Fig. 20. Young *Pinus flexilis* in the cinder gardens near study site 2. This clump contains six individuals.

The two initial colonizers were negatively associated with all zones of *Pinus*, while *E. umbellatum*, the last herbaceous colonizer, was negatively associated only with the inner canopy region of *Pinus*.

On more developed sites, dominated by woody species, the vegetation showed a relatively high degree of spatial heterogeneity, with associations often inconsistent between subplots within a site. Associations between the same species-pair were also inconsistent from site to site. Environmental factors measured at these more developed sites did not correlate well with vegetation data, at least at this level of sampling. Lack of consistent nutrient levels under a species may have been due to general soil differences (*e.g.* buried horizons) between sites. Correlations with vegetation data may have been identified if a more intensive sampling scheme had been used, but the results suggest that nutrient levels were not consistently different under different species.

The lack of correlations between vegetation and soil data may have been due to the use of a species-centered approach. An organism-centered approach may have identified more correlations, since plants are probably reacting to environmental factors which are unique to microsites associated with individuals rather than species.

On younger sites, differences in nutrient levels of species, as well as plausible correlations with vegetation results, were identified. On the youngest sites, few physiologically acceptable niches are available for the vast majority of species in the area. These harsher sites had a smaller range of physical conditions and lower minimum levels of nutrients. It appears that the critical levels required by most species in the area were somewhere within this range of physical conditions on these harsh sites. Microsites in the canopy of *Eriogonum ovalifolium* appear to be one of the few acceptable niches which other species can physiologically tolerate. On sites dominated by woody species the physical conditions were probably above the critical levels required for many species. With more favorable conditons on more developed sites, past history (such as past spatial patterns of individuals) and chance events (scramble competition, *etc.*) are probably more important factors in the establishment process.

On more developed sites, species in general were most often positively associated with the outer canopy region of other species and negatively associated with the region directly outside the canopy of other species. In general, the outer canopy region of plants (zone 2) was probably more favorable for establishment since it tended to have higher accumulations of litter (*e.g.* more nutrients) and lower air and soil temperatures than zone 3, while having more physical space and less intense root competition than zone 1.

Successional Theory

Although the correlations between the vegetation and environmental data presented here have not been experimentally proven as valid cause and effect relationships, they do provide a logical basis for development of hypotheses. It appears that *E. ovalifolium* enhances the establishment of all other major species on harsh sites, as proposed by the facilitation model. This mechanism is probably not the sole method by which later-successional species establish on these sites. Site modification by animals which enhances establishment of plants is also apparent on these sites. Initial colonizers are common in depressions in mule deer (*Odocoileus hemionus*) tracks in cinder garden communities (Fig. 21). This apparent enhanced establishment may be due to increased moisture conditions and seed and organic matter accumulation in these depressions.

With the establishment of *E. umbellatum* and *Pinus*, which are facilitated by *E. ovalifolium*, conditions become unfavorable for the herbaceous pioneers. Therefore, the initial colonizer *E. ovalifolium* appears to modify the environment making it less suitable for itself, as well as *Phacelia*. This mechanism is proposed in all three models of successional mechanisms.

The traditional differentiation between secondary and primary succession is based upon the presence or absence of viable plant remains from predisturbance. Under the unfavorable physical conditions at sites 1 and 2 in this study, the presence of viable propagules is of secondary importance , since most species do not appear able to physiologically tolerate physical conditions at these sites. Due to this relatively unimportant distinction and the predominance of other poorly-defined, inconcise or inconsistently used traditional terminology used in classifying and conceptualizing successions (Miles 1979; McIntosh 1980), a general classification of succession based on



Fig. 21. "Line" of *Phacelia hastata* individuals which have apparently established in depressions caused by mule deer tracks in cinder gardens on Inferno Cone.

these traditional terms has been bypassed in several population-level approaches to successional theory (Drury and Nisbet 1973; Horn 1975, 1976, 1981; Grime 1977, 1979; Noble and Slatyer 1980).

Although a population-level or organism-centered approach seems vital in understanding succession, a classification of the site in which a succession is taking place may also be valuable in terms of developing general concepts. A more preliminary classification of succession would be based on environmental conditions at a site relative to the physiological tolerance of the species in the area (*e.g.* how many species are thought to be absent due to abiotic factors), and whether or not the vegetation at the site is in dynamic equilibrium with environmental conditions. A classification of succession based on these two points would help clarify interpretations of successional mechanism models (Connell and Slatyer 1977) as well as general successional concepts such as those proposed by Odum (1969), Margalef (1968) and Whittaker (1970), which have been largely rejected by several workers (Drury and Nisbet 1973; Peet and Christensen 1980; McIntosh 1981).

It appears that site modification must be present as a mechanism in succession on sites where plant communities are currently in a primary state (*e.g.* in dynamic equilibrium with their environment) and in which abiotic, environmental conditons do not allow most species of surrounding areas to establish, if these new species are to establish. Environmental conditions at the site must improve so as to exceed the minimum physiological tolerance levels of these species. Modifications can come about through several factors such as plants, animals and weathering of parent material. Positive site modification by plants (the facilitation mechanism) appears to be present on sites in this study. *Eriogonum ovalifolium* modifies microsites and thereby enhances establishment of later-successional species. This is undoubtably not the only site modification which allows these later-successional species to establish (as shown by mule deer tracks), nor is the facilitation mechanism in general felt to be the only plant mechanism in succession on these sites. Succession most likely involves all three general models (facilitation, tolerance and inhibition) as well as other non-plant biotic, and abiotic factors.

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Appendix 1. List of species found in cinder gardens on Black Cap in June 1984.

Species

Lesquerella occidentalis

Mentzelia laevicaulis

Arenaria nuttallii

Cryptantha interrupta *

Phacelia hastata *

Allium simillimum *

Cymopterus terebinthinus **

* denotes present in cinder gardens of study area

** denotes present in shrub communities of study area

Appendix 2. Significant associations between species for the total area of influence and seperate zones. Species B is tested for association with species A. Positive and negative signs indicate positive and negative associations respectively ($p<0.05$).

Site	Species A	Species B	Total	Zone		
				1	2	3
1	*Eriogonum ovalifolium*	*Phacelia hastata*		+		-
1	*Eriogonum ovalifolium*	*Eriogonum ovalifolium*		-	-	
1	*Phacelia hastata*	*Phacelia hastata*	-	-		-
2	*Eriogonum ovalifolium*	*Phacelia hastata*		+		
2	*Eriogonum ovalifolium*	*Eriogonum ovalifolium*		-	-	
2	*Eriogonum ovalifolium*	*Sitanion*		+		
2	*Eriogonum ovalifolium*	*Stipa thurberiana*	+	+		
2	*Eriogonum ovalifolium*	*Pinus* (seedlings)		+		
2	*Phacelia hastata*	*Sitanion*		-	-	
2	*Phacelia hastata*	*Stipa thurberiana*		-		
2	*Phacelia hastata*	*Pinus* (seedlings)				
2	*Eriogonum umbellatum*	*Eriogonum ovalifolium*	-	-		
2	*Eriogonum umbellatum*	*Phacelia hastata*	-	-		
2	*Eriogonum umbellatum*	*Sitanion*			+	
2	*Eriogonum umbellatum*	*Stipa thurberiana*				
2	*Eriogonum umbellatum*	*Pinus* (seedlings)			+	
2	*Pinus*	*Eriogonum ovalifolium*	-	-	-	-
2	*Pinus*	*Phacelia hastata*	-	-	-	-
2	*Pinus*	*Sitanion*	-	-		
2	*Pinus*	*Stipa thurberiana*	-	-		
2	*Pinus*	*Pinus* (seedlings)	+	+	+	+
3	*Purshia tridentata*	*Chrysothamnus nauseosus*	+		+	
3	*Purshia tridentata*	*Ribes cereum*		+		
3	*Purshia tridentata*	*Stipa thurberiana*	-	-	-	+
3	*Chrysothamnus nauseosus*	*Purshia tridentata*				
3	*Chrysothamnus nauseosus*	*Ribes cereum*				
3	*Chrysothamnus nauseosus*	*Stipa thurberiana*	+	+	+	
3	*Ribes cereum*	*Chrysothamnus nauseosus*		+		
3	*Ribes cereum*	*Purshia tridentata*	+			+
3	*Ribes cereum*	*Stipa thurberiana*				
4	*Pinus*	*Chrysothamnus nauseosus*			+	
4	*Pinus*	*Purshia tridentata*	+		+	+
4	*Pinus*	*Ribes cereum*	+	+		
4	*Pinus*	*Sitanion*				
4	*Pinus*	*Poa sandbergii*				
4	*Purshia tridentata*	*Chrysothamnus nauseosus*				
4	*Purshia tridentata*	*Pinus*				
4	*Purshia tridentata*	*Ribes cereum*	+		+	
4	*Purshia tridentata*	*Sitanion*				
4	*Purshia tridentata*	*Poa sandbergii*	-			-
4	*Chrysothamnus nauseosus*	*Pinus*				
4	*Chrysothamnus nauseosus*	*Purshia tridentata*	+	+		
4	*Chrysothamnus nauseosus*	*Ribes cereum*				+
4	*Chrysothamnus nauseosus*	*Sitanion*				
4	*Chrysothamnus nauseosus*	*Poa sandbergii*	-		-	-
4	*Ribes cereum*	*Chrysothamnus nauseosus*				
4	*Ribes cereum*	*Pinus*				
4	*Ribes cereum*	*Purshia tridentata*	+		+	
4	*Ribes cereum*	*Sitanion*				
4	*Ribes cereum*	*Poa sandbergii*				

Appendix 2. (continued).

Site	Species A	Species B	Total	Zone		
				1	2	3
5	*Pinus*	*Artemisia tridentata*	-			-
5	*Pinus*	*Chrysothamnus nauseosus*	-			-
5	*Pinus*	*Purshia tridentata*	+	+		
5	*Pinus*	*Ribes cereum*			+	-
5	*Pinus*	*Sitanion*	-		+	-
5	*Pinus*	*Stipa thurberiana*	-		-	-
5	*Pinus*	*Poa sandbergii*	-		+	-
5	*Purshia tridentata*	*Pinus*			+	
5	*Purshia tridentata*	*Artemisia tridentata*	-			
5	*Purshia tridentata*	*Chrysothamnus nauseosus*	-			-
5	*Purshia tridentata*	*Ribes cereum*		+		
5	*Purshia tridentata*	*Sitanion*				
5	*Purshia tridentata*	*Stipa thurberiana*				
5	*Purshia tridentata*	*Poa sandbergii*	-			-
5	*Ribes cereum*	*Pinus*	+			+
5	*Ribes cereum*	*Chrysothamnus nauseosus*				
5	*Ribes cereum*	*Purshia tridentata*	+	+		
5	*Ribes cereum*	*Artemisia tridentata*				
5	*Ribes cereum*	*Sitanion*				
5	*Ribes cereum*	*Stipa thurberiana*				
5	*Ribes cereum*	*Poa sandbergii*	-			
5	*Artemisia tridentata*	*Pinus*				
5	*Artemisia tridentata*	*Chrysothamnus nauseosus*				
5	*Artemisia tridentata*	*Purshia tridentata*			+	
5	*Artemisia tridentata*	*Ribes cereum*		+		
5	*Artemisia tridentata*	*Sitanion*			+	
5	*Artemisia tridentata*	*Stipa thurberiana*				
5	*Artemisia tridentata*	*Poa sandbergii*	-			-
6	*Purshia tridentata*	*Agropyron spicatum*	+		+	-
6	*Purshia tridentata*	*Eriogonum ovalifolium*	-			
6	*Purshia tridentata*	*Eriogonum umbellatum*		+		
7	*Purshia tridentata*	*Artemisia tridentata*	+		+	+
7	*Purshia tridentata*	*Agropyron spicatum*	+		+	
7	*Purshia tridentata*	*Cymopterus terebinthinus*	+		+	
7	*Purshia tridentata*	*Eriogonum umbellatum*	+	+		
7	*Artemisia tridentata*	*Purshia tridentata*	+		+	
7	*Artemisia tridentata*	*Agropyron spicatum*	-			-
7	*Artemisia tridentata*	*Cymopterus terebinthinus*	+		+	
7	*Artemisia tridentata*	*Eriogonum umbellatum*				

Appendix 2. (continued).

Site	Species A	Species B	Total	Zone		
				1	2	3
8	*Purshia tridentata*	*Chrysothamnus nauseosus*				
8	*Purshia tridentata*	*Symphoricarpos oreophilus*				
8	*Purshia tridentata*	*Balsamorhiza sagittata*				
8	*Purshia tridentata*	*Agropyron spicatum*	+		+	+
8	*Purshia tridentata*	*Cymopterus terebinthinus*	+		+	+
8	*Purshia tridentata*	*Eriogonum umbellatum*				
8	*Chrysothamnus nauseosus*	*Purshia tridentata*				
8	*Chrysothamnus nauseosus*	*Symphoricarpos oreophilus*				
8	*Chrysothamnus nauseosus*	*Balsamorhiza sagittata*				
8	*Chrysothamnus nauseosus*	*Agropyron spicatum*	+	+	+	
8	*Chrysothamnus nauseosus*	*Cymopterus terebinthinus*	+	+	+	+
8	*Chrysothamnus nauseosus*	*Eriogonum umbellatum*	+	+	+	
8	*Symphoricarpos oreophilus*	*Chrysothamnus nauseosus*				
8	*Symphoricarpos oreophilus*	*Purshia tridentata*				+
8	*Symphoricarpos oreophilus*	*Balsamorhiza sagittata*				
8	*Symphoricarpos oreophilus*	*Agropyron spicatum*		+	+	
8	*Symphoricarpos oreophilus*	*Cymopterus terebinthinus*	+	+		+
8	*Symphoricarpos oreophilus*	*Eriogonum umbellatum*				
8	*Balsamorhiza sagittata*	*Chrysothamnus nauseosus*				
8	*Balsamorhiza sagittata*	*Purshia tridentata*	-			
8	*Balsamorhiza sagittata*	*Symphoricarpos oreophilus*		+		
8	*Balsamorhiza sagittata*	*Agropyron spicatum*	+		+	
8	*Balsamorhiza sagittata*	*Cymopterus terebinthinus*	+		+	+
8	*Balsamorhiza sagittata*	*Eriogonum umbellatum*				
9	*Purshia tridentata*	*Artemisia tridentata*	-			-
9	*Purshia tridentata*	*Symphoricarpos oreophilus*				
9	*Purshia tridentata*	*Agropyron spicatum*	+	-	+	
9	*Purshia tridentata*	*Poa sandbergii*	-	-		
9	*Purshia tridentata*	*Cymopterus terebinthinus*	+	-	+	-
9	*Purshia tridentata*	*Eriogonum umbellatum*				-
9	*Artemisia tridentata*	*Purshia tridentata*	+		+	
9	*Artemisia tridentata*	*Symphoricarpos oreophilus*				
9	*Artemisia tridentata*	*Agropyron spicatum*	+		+	
9	*Artemisia tridentata*	*Poa sandbergii*	+		+	-
9	*Artemisia tridentata*	*Cymopterus terebinthinus*	-	-	+	-
9	*Artemisia tridentata*	*Eriogonum umbellatum*	+		+	-

Appendix 2. (continued).

Site	Species A	Species B	Total	Zone		
				1	2	3
10	*Purshia tridentata*	*Eriogonum heracleoides*	+		+	
10	*Purshia tridentata*	*Balsamorhiza sagittata*			+	
10	*Purshia tridentata*	*Agropyron spicatum*	+		+	
10	*Purshia tridentata*	*Poa sandbergii*	+		+	
10	*Purshia tridentata*	*Cymopterus terebinthinus*	+	+	+	-
10	*Eriogonum heracleoides*	*Purshia tridentata*				
10	*Eriogonum heracleoides*	*Balsamorhiza sagittata*	-			
10	*Eriogonum heracleoides*	*Agropyron spicatum*	+	-	+	
10	*Eriogonum heracleoides*	*Poa sandbergii*			+	
10	*Eriogonum heracleoides*	*Cymopterus terebinthinus*	+	+	+	+
10	*Balsamorhiza sagittata*	*Purshia tridentata*	+		+	
10	*Balsamorhiza sagittata*	*Eriogonum umbellatum*	+	+	+	
10	*Balsamorhiza sagittata*	*Agropyron spicatum*	+		+	
10	*Balsamorhiza sagittata*	*Poa sandbergii*			+	
10	*Balsamorhiza sagittata*	*Cymopterus terebinthinus*		-	+	-
11	*Purshia tridentata*	*Artemisia tridentata*			+	
11	*Purshia tridentata*	*Eriogonum heracleoides*	+		+	
11	*Purshia tridentata*	*Agropyron spicatum*		-	+	-
11	*Purshia tridentata*	*Poa sandbergii*	+	-	+	-
11	*Purshia tridentata*	*Cymopterus terebinthinus*	+	-	+	-
11	*Artemisia tridentata*	*Purshia tridentata*			+	
11	*Artemisia tridentata*	*Eriogonum heracleoides*	+		+	
11	*Artemisia tridentata*	*Agropyron spicatum*		-	+	
11	*Artemisia tridentata*	*Poa sandbergii*	+	+	+	
11	*Artemisia tridentata*	*Cymopterus terebinthinus*	+		+	
11	*Eriogonum heracleoides*	*Purshia tridentata*	+			+
11	*Eriogonum heracleoides*	*Artemisia tridentata*	+		+	+
11	*Eriogonum heracleoides*	*Agropyron spicatum*	+		+	+
11	*Eriogonum heracleoides*	*Poa sandbergii*	+		+	+
11	*Eriogonum heracleoides*	*Cymopterus terebinthinus*	+	+	+	+