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Plant Succession Following the Mount St. Helens Volcanic Eruption: Facilitation by a Burrowing Rodent, Thomomys talpoides

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ABSTRACT: The 18 May 1980 eruption of Mount St. Helens in the Cascade Range (USA) initiated plant succession over a broad region. Northern pocket gophers *Thomomys talpoides* survived in widespread subalpine and montane sites where up to 25 cm of tephra had buried dormant or only recently snow-free vegetation. Burrowing and consequent construction of mounds by this herbivorous rodent has both modified the physical structure of the tephra and led to the placement of pre-eruption soil material on the tephra surface. We compared the composition of the plant community and the pattern of seedling establishment on and off gopher mounds.

More plant species and individuals survived burial on mounds than at off-mound sites. Seedlings are also most diverse on mounds. We conclude that pocket gophers, through their soil-disturbing activities, can strongly affect plant population dynamics in volcanically disturbed areas, and thus may be an important agent in determining the pathway of succession. Limited observations suggest that differential herbivory may further affect plant community composition. Possible mechanisms that enhance plant survivorship and seedling establishment on mounds are discussed.

INTRODUCTION

Secondary plant succession is a process in which pattern and pace are determined, in part, by differential tolerance of plant species to disturbance, and by their differential capabilities for dispersal and ecesis (Clements, 1916). Because animals can disturb a site, disperse plant propagules, and both directly and indirectly affect plant survivorship, they have the potential to alter the pathway of succession (Andersen *et al.*, 1980; MacMahon, 1981). In many cases, especially among terrestrial mammals, animal influences on succession result from their disturbing the soil. Modification of the soil through trampling (Laycock and Conrad, 1967; Lock, 1972) and digging (Abaturov, 1972; Hansen and Morris, 1968; Goszczynska and Goszczynski, 1977; Grant *et al.*, 1980; Grant and McBrayer, 1981) is well-documented, and direct effects of such modification on plant populations has been described (Laycock, 1958; McDonough, 1974; Platt, 1975; Tevis, 1956). Nevertheless, the qualitative and quantitative relationships between particular animal species and successional processes remain largely unknown.

The continuing eruptions of Mount St. Helens in the Cascade Range of Washington State and the associated deposition of tephra over previously vegetated landscapes have initiated plant succession over a large area. In particular, the 18 May 1980 eruption involved first a lateral, northerly directed explosive blast and then a northeasterly deposition of cool, windborne tephra that together affected more than 500 km². The effects of the windborne tephra on plant communities vary with both thickness and composition of the deposit, which in turn varies spatially on both a local and regional scale (Mack, 1981).

Despite the apparent intensity of the disturbance, numerous organisms and propagules survived the eruption and became participants in the secondary successional process. Among these "residual" organisms was the Northern pocket gopher, *Thomomys talpoides*, an herbivorous rodent that burrows to obtain both food and shelter. These animals are found naturally in openings in subalpine forest in the Cascade Range (Dalquest, 1948) and readily occupy accessible lower elevation sites where timber harvest has promoted herbaceous plant productivity.

Soil mounds created by gophers subsequent to the 18 May eruption were observed at numerous and widespread sites, both inside the area affected by the lateral blast and in the zone that received windborne tephra (Andersen, 1982). Wherever activity was noted, material excavated from the loamy upper portion of the pre-eruption soil profile had been deposited on the surface of the 10-25 cm of overlying tephra. In some areas, gopher activities had covered up to 2% of the ground surface with pre-eruption soil (hereafter, "old-soil") during the 4 months following the eruption (Andersen, 1982).

The mixing of tephra and old-soil by *Thomomys talpoides* can modify the substrate physically, chemically and biologically—any of which could influence plant population processes. Further, herbivory by gophers could directly affect populations of established and/or colonizing plant species. As part of a study examining the role of animals in reforestation of the volcanically altered region, we here test the null hypothesis that no difference exists in plant species composition and pattern of seedling establishment on and off gopher-created old-soil mounds.

METHODS

The study site is a 19-year-old clear-cut, elevation 1300 m, on National Forest lands∿20 km NE of Mount St. Helens (Snyder Pasture No. 4; 46°16'N, 121°53'E). The area was not affected by the 18 May 1980 lateral blast, but received windborne tephra that averaged 12 cm thick 4 months after deposition. The deposit consists primarily of loose pumice, sand, and gravel, but it is capped with a 6-10 mm layer of compact silt that is very hard when dry (Waitt and Dzurisin, 1981). The clear-cut, which has a westerly aspect and ∿10% slope, is in the transition between the *Abies amabilis* and *Tsuga mertensiana* zones described by Franklin and Dyrness (1973).

The site has variably wet cool winters and dry mild summers. Winter precipitation in the form of rain and snow is heavy; late winter snowpack depth is quite variable, but depths >3.0 m are common. The winter of 1979-1980 was relatively mild, with the study site partially snow-free at the time of the 18 May eruption (Andersen, 1982). The winter of 1980-1981 was similar, with the site largely snow-free by 20 May (pers. observ.). In contrast, the winter of 1981-1982 produced a heavier snowpack and the site remained snow-covered well into June.

No quantitative information is available on plant community composition within the clear-cut prior to the 18 May eruption. Present composition suggests the pre-eruption community was dominated by a combination of shrubs (*Vaccinium* spp., *Menziesia ferruginea, Rhododendron albiflorum*), with herbaceous species represented by *Carex subfusca, Epilobium angustifolium, Anaphalis margaritacea* and other early successional perennials. Total plant cover in September 1980 (based on a 200-m line transect) was 32%, with tephra covering 58% of the ground surface. Woody debris from timber harvest covered the remainder. Similarly aged but volcanically undisturbed clear-cuts have plant cover on open soil approaching 100% (Dyrness, 1973).

Fifty-four gopher-created soil mounds were permanently marked in September 1980 with wood stakes placed 0.5 m N of the mound perimeter. The composition of the mound material varied, but old-soil material, easily distinguished from the fresh tephra on the basis of texture and color, was usually dominant. Mound diameter averaged 28.0 cm (Andersen, 1982). These mounds were revisited during the following three summers (except where precluded by loss of stakes) and plant community composition noted qualitatively and/or quantitatively.

Plants associated with mounds and off-mound sites were quantitatively sampled using paired 0.20 x 0.50 m quadrats centered either on mounds or 0.75 m upslope from the mound perimeter, respectively. In both locations, the long axis of the frame was oriented perpendicular to the contour line. If the off-mound location contained evidence of gopher activity, or if >50% of the frame fell under the canopy of a conifer sapling, the frame was shifted 0.5 m along the contour. We note that our off-mound quadrat sites do not represent a true random sampling of the off-mound area within the study site. We assume, however, that no biases in off-mound plant composition or survivorship data result from our placement of off-mound quadrats adjacent to mounds.

All plants within the quadrats were classified, counted and identified to species where possible. A plant was classified as "seedling" if it was considered to have originated on or in the mound or tephra, without regard to the origin of the propagule from which it developed. Seedlings on mounds could have originated from young (posteruption) seed that reached the site from either a local or distant source, or from pre-eruption, residual seed present in soil brought to the surface by gophers. No seedlings observed in off-mound quadrats in 1981 are likely to have originated from residual propagules. For 1982 data, we assume the same relationship; however, erosional downcutting of tephra and an inability to destructively sample preclude certainty as to origin. Some plants, which we here term "established residual" (ER), appeared to have grown up through the mound or tephra, with roots originating in the tephra-covered pre-eruption soil. Clumps or bunches of sedges and grasses were counted as individual ERs, while relatively widely spaced, small graminoids having only a few leaves were considered to be individual seedlings. Stems of dicots were counted at the soil surface and individual stems classified by relative size. Most dicot seedlings were rosettes only a few mm across and identification to species was either not possible or is based on subsequent identification of similar-looking tagged seedlings. The data presented here are based primarily on the annual qualitative examinations and on the 1982 census, which took place 20-27 July 1982, when mounds were 21-23 months old.

Vegetative plants on and off of mounds were tagged in summer 1982 with 8 x 9 mm paper tags attached to a loop of thread around the plant on the ground surface. The tag was somewhat protected from weather and disturbance by partial concealment under a pumice gravel.

Pocket gopher herbivory on common residual plants was qualitatively examined by placing several animals inside each of three 12 x 12 m hardware cloth enclosures located within the blast and tephrafall areas. These enclosures contained the herbaceous *Epilobium angustifolium* and *Lupinus latifolius,* the shrub *Vaccinium parviflorum,* and other species. Feeding trials were also conducted to ascertain the palatability of the very abundant *E. angustifolium.* Two captive animals were fed fresh *E. angustifolium* shoots and roots, while two other animals were offered carrot and laboratory chow, a diet known to be adequate for long-term maintenance of captive gophers. The animals were caged individually within the same room, and provided with food and water ad lib.

RESULTS

Mounds showed major changes in physical appearance between 1980 and 1983. Most obvious was a reduction in height and in the apparent contribution of old-soil to the mound, undoubtedly due to both downslope erosion of the relatively fine old-soil material and its movement into the underlying, very porous tephra. A few mounds were buried under reworked tephra.

1982 census data. — There was no significant difference in the frequency of occurrence of live vegetation in quadrats between mound and off-mound sites: 29 (59%) of the 49 off-mound quadrats examined contained ≥ 1 plant, while 40 (82%) of the 49 mound quadrats contained plants ($\chi^2 = 1.75$, $p > 0.1$).

Differences between mound and off-mound sites were noted in species richness, the numbers of individual plants represented within quadrats, and the number of seedling vs. residual plants represented within the quadrats (Table 1). Ten species grew on or through mounds, compared to six at off-mound sites. The most frequently encountered residual plant growing within mound quadrats was *Carex subfusca,* while *Epilobium angustifolium* was most common in off-mound sites (Table 1). *Carex* seedlings were high in both frequency of occurrence and abundance on mounds; only one off-mound quadrat

contained *Carex* seedlings
On-mound seedlings
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TABLE 1. — Plant
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seed on or in the

Species
Epilobium angustifolium
Carex spp.[1]
Vaccinium spp.[2]
Lupinus latifolius
Rubus lasiococcus
Unidentified seedlings
Other species[3]

[1]Primarily *C.*
[2]Shrubs
[3]Includes the
and the woody

contained *Carex* seedlings.

On-mound seedlings and plant survivorship.—A series of 21 individually tagged mound seedlings provided data on seedling growth rates, despite a high incidence (86%) of tag loss (*cf.*, *Off-mound seedlings* below) and/or plant disappearance. For example, an *Anaphalis margaritacea* rosette, 2 mm in diam and of negligible height when tagged in late July 1982, was 1.5 cm tall in September 1983; a nonreproductive sedge, 5 cm tall, was 7 cm tall with one flowering stem a year later.

A sequential examination of individual mounds over the 3-year period indicated that *Carex* (probably *subfusca*) and *Anaphalis margaritacea* were dominant contributors to mound seedling flora. Further, such an analysis shows that some of these seedlings survived between years. For example, in July 1981 Mound 18 had three forb seedling rosettes, each a few millimeters in diameter, and several hundred very small graminoid seedlings on it. In July 1982, the mound held ∿70 *Carex* 2-4 cm tall, in all likelihood the survivors of the 1981 cohort. The mound also held ∿50 *Carex* <2 cm, probably repre-

TABLE 1.—Plant species found within 49 paired quadrats placed on and adjacent to 2-year-old gopher mounds. "N" refers to the number of quadrats in which the species/class combination was present. "Abundance" refers to the average (± SE) number of plants per occupied quadrat (0.10 m²). Established residuals (ER) are plants considered to be growing out of old soil underlying tephra, as opposed to seedlings (S) which are considered to have originated from seed on or in the mound or tephra

Species	Class	Location: Mound N	Mound Abundance	Off-mound N	Off-mound Abundance
Epilobium angustifolium	ER	4	8.3 ± 5.71	6	3.2 ± 1.22
	S	—		1	1.0
Carex spp.[1]	ER	17	6.8 ± 2.07	2	1.5
	S	23	11.6 ± 2.98	1	2
Vaccinium spp.[2]	ER	4	8.5 ± 3.23	4	4.5 ± 2.06
	S	—		—	
Lupinus latifolius	ER	3	1.3 ± 0.33	—	
	S	3	1.0 ± 0.0	4	1.25 ± 0.25
Rubus lasiococcus	ER	4	1.8 ± 0.48	7	2.00 ± 0.84
	S	—		1	3
Unidentified seedlings	S	17	6.7 ± 2.20	1	∿200
Other species[3]	ER	6	3.5 ± 0.89	2	2.5 ± 1.5
	S	1	1.0	—	

[1]Primarily *C. subfusca*, with a few *C. mertensii* likely and also grasses within seedling category
[2]Shrubs
[3]Includes the herbaceous perennials, *Mitella breweri*, *Gayophytum humile*, *Anaphalis margaritacea* and the woody *Rubus parviflorus*

senting the 1982 cohort, and ∿50 unidentified tiny forb seedlings much like those noted in 1981. By September 1983, Mound 18 contained seven *Carex* clumps ranging up to 3 cm in diam, and 13 *Anaphalis* plants 1-3 cm tall, which presumably represented the 1982 forb cohort because only seedling rosettes were noted in 1982. *Lupinus latifolius* and *Epilobium angustifolium* also contributed small numbers to the population of mound plants >1 year old on the basis of this form of analysis.

Off-mound seedlings and plant survivorship. — Seedlings off mounds were extremely rare throughout the study area in 1981. Although more common in 1982, seedlings were patchy in distribution and areas of concentration differed substantially from areas in which our off-mound quadrats were located. For example, *Lupinus latifolius* seedling densities locally exceeded 20 m^{-2} on tephra overlying a haul road. The road bed supported many established residual *L. latifolius,* which served as seed sources. A series of these seedlings, tagged in the same manner as the mound plants described above, provided a minimum estimate of 70% survivorship ($N_o = 44$) between late July 1982 and late June 1983. This contrasts with the low apparent survivorship of seedlings of species noted within off-mound quadrats. Seedlings were present, albeit rare, in off-mound quadrats in 1982 (Table 1), yet none of the 44 off-mound quadrat sites re-examined in 1983 contained plants unambiguously assignable to the 1982 cohort on the basis of size (*e.g.,* growth observed in the tagged *Anaphalis* and *Lupinus,* or the *Carex* on Mound 18). Twenty-one of the 44 off-mound quadrats contained seedlings (1983 cohort), but most represented two kinds, *Carex* sp. and a fir (*Abies* sp.) (Table 2). Only four off-mound quadrats contained seedlings in 1982, and while each contained *Lupinus,* no lupine was present in the two quadrats that could be found and were examined in 1983. The site at which the group of ∿200 seedlings was noted in 1982 could not be found due to trampling damage by wapiti (*Cervus elaphus*).

Herbivory on residual plants. — Pocket gophers in enclosures readily consumed foliage of residual *Lupinus latifolius* and presumably roots as well. Old-soil mounds were constructed at the bases of these plants, but excavation may have started at the tephra surface, rather than as a continuation of an existing tunnel as would normally occur in foraging situations. Neither the woody *Vaccinium* nor *Epilobium angustifolium* were used to any extent for food. The latter was noted to have been nibbled at and then ignored in one enclosure, suggesting the plant is unpalatable. The feeding trials support this inference: the two animals offered only *E. angustifolium* died within 4-5 days while the control animals fed carrot and lab chow remained healthy.

TABLE 2. — Seedlings present within off-mound quadrats, July 1982 (N = 49) and August 1983 (N = 44)

Species	1982 Numbers of quadrats	1982 Average abundance	1983 Number of quadrats	1983 Average abundance	(Range)
Anaphalis margaritacea	1[a]	—	2	1.5	
Carex spp.	1[b]	2	11	5.4	(1-20)
Epilobium angustifolium	1	1	2	1.5	
Lupinus latifolius	4	1.25	0	—	
Unidentified	1	∿200	2	4.5	(1-8)
Abies sp.	0	—	13	1.0	

[a] 1982 *Anaphalis* presence based on assumption that some of the "unidentified seedlings" were that species

[b] This category may include some grass seedlings

DISCUSSION

On the basis of the data presented, we reject the null hypothesis and accept the alternative that mound-constructing activities of *Thomomys talpoides* lead to changes in local plant community composition and dynamics. Gopher-created mounds have a richer residual plant community, and support more seedlings than comparable areas of undisturbed tephra. Further, seedlings on mounds are surviving and appear likely to eventually contribute to local population growth through their own reproduction.

Residual plant diversity differs between mound and off-mound sites in part because of interspecific and intraspecific differences in ability to survive burial under tephra. This follows from differences in both stored nutrient reserves and the ability of shoots to mechanically penetrate the tephra. Mounds locally increase the depth of overburden, but in constructing them, pocket gophers break up the hard crust that forms on the dry tephra surface. Such modifications could increase either mortality or survivorship of buried plants, depending on the species and individual involved.

We suggest *Carex subfusca* individuals benefited from pocket gopher disturbances. We removed tephra from several 2 x 2 m sites apparently free of plants and exposed *Carex* that appeared to have initiated shoot growth but that died prior to breaching the tephra surface. Further, on the basis of plants exposed in trenches dug in 1980, del Moral (1983) independently concluded that graminoids suffer disproportionately when buried by tephra. Yet *Carex subfusca* is common on mounds (Table 1). There is no evidence to suggest *Carex* is eaten by *Thomomys talpoides,* and thus a reasonable hypothesis is that disturbance of the tephra crust by gophers increases the probability that buried *Carex* will reach the surface.

In contrast, *Epilobium angustifolium,* which also is not eaten, is capable of penetrating up to 15 cm of the undisturbed tephra gravels and the dry overlying crust (pers. observ.). Assuming that the plant does not act as a repellent, we expect residual *E. angustifolium* to be equally frequent and occur in equal abundance on and off mounds, which in fact is the case (Table 1). A similar independence from the influence of gopher activity may explain the pattern for *Rubus lasiococcus,* which has a stoloniferous growth habit. It apparently can breach unmodified tephra at the study site (perhaps relying on periods when the crust is moist). The palatability of *R. lasiococcus* to pocket gophers is unknown.

Survivorship of residuals could also be influenced by herbivory associated with mound construction, although our data on this point are contradictory. It is known that *Thomomys talpoides* removes above- and belowground parts of plants at sites where it breaches the soil surface (*see* Andersen and MacMahon, 1981). Our data for residual *Lupinus latifolius* (Table 1) are opposite to those expected if herbivory sharply decreases survivorship. Mounds are often associated with palatable plants, and the association of lupine with mounds may reflect the attraction of gophers to these food plants. We infer presence of these ERs to be a consequence of incomplete consumption, rather than any positive plant response to substrate disturbance.

Seed germination and seedling establishment may be enhanced on gopher mounds due to more favorable soil moisture, temperature or nutrient conditions. Both a higher organic matter content (4% vs. 0.2%) and smaller pore size of old-soil material would increase water-holding capacity of mound substrate compared to tephra (MacMahon and Warner, 1984). Immature surface soils derived from pumice have both low thermal conductivity and volumetric heat capacity relative to clay or sand soils (Cochran, 1969). Assuming comparable differences between fresh tephra and old soil, the tephra would feature greater temperature extremes at its surface and reduced heat transfer into deeper portions of the profile. The darker old-soil surface could also modify absorptance of solar radiation. The old-soil has greater amounts of important inorganic nutrients (*e.g.,* ppm NO_3:10.9 vs. 0.9) and a higher cation exchange capacity (10.4 vs. 1.7 meq/100 g: MacMahon and Warner, 1984). Further, old-soil may be the only source of inocula necessary to establish mycorrhizal relations that are beneficial to ∿90% of plant species. Both infection frequencies and Endogonaceae spore counts per g soil of soils and rhizospheres were greater for *Lupinus latifolius* and *Anaphalis margaritacea* growing in gopher mounds than in adjacent tephra (Allen *et al.*, 1984). The paucity of seedlings on tephra substrate has been noted elsewhere in the Mount St. Helens region (Halpern and Harmon, 1983; del Moral, 1983).

Soil mounds created by burrowing mammals can be important sites for establishment of particular plant species. Tevis (1956) found them to be the only locations suitable for germination of *Abies magnifica* within grassland, and numerous studies have shown that the persistence of annuals and other fugitive species is linked to continued soil disturbance (Laycock, 1958; Platt, 1975; McDonough, 1974). At Mount St. Helens, it appears that disturbance of tephra and the mixing of old soil with overlying tephra may independently influence the plant community, the former via effects on established residuals, the latter via effects on colonists derived from residual or immigrant seeds. This suggests the particular kinds of animals present in various areas may be a critical determinant of early successional patterns because tephra disturbance, *i.e.*, the breaking up of the surface crust, is accomplished by a variety of processes and organisms, such as hooves of ungulates and gravity-induced mass movement, while mixing and upward displacement of old soil is only accomplished by gophers and a few other burrowing animals.

The xeric-adapted *Lupinus lepidus* has established viable populations in areas of pure tephra, devoid of gophers, and without the mycorrhizae whose linkage to gopher-disturbance we allude to above. We also note that effects resulting from gopher soil-mixing activities may be manifested after the animals themselves have disappeared from a locality, and thus their impacts may be more widespread than would be realized from an analysis of current distribution (*cf.*, Andersen, 1982, Table 1). We are currently undertaking field experiments designed to establish whether the relative abundance in residual and seedling numbers here associated with gopher-disturbed sites constitutes a cause-and-effect relationship. The long-term consequences of pocket gophers and their disturbances on successional patterns is also being investigated.

Pocket gopher populations tend to be clumped (Andersen, 1982; Andersen and MacMahon, 1981). Further, the past clear-cutting operations in the volcanically altered region have created a mosaic of habitats suitable for, but of varying accessibility to, pocket gophers. Antos and Zobel (1982) found that remnants of winter snowpack in stands of mature timber strongly influenced the effect of tephra from the 18 May eruption on survivorship of small trees, shrubs and evergreen forest floor herbs. Such variation in snowpack depth would undoubtedly have also occurred in open habitats suitable for pocket gophers, and perhaps had similar effects on plants there. The timing of the eruption, coupled with the particular 1980 spring snow conditions, has likely produced a complex spatial mosaic in terms of the impact of the event on plant populations. The animal influences on plant successional processes that we document here, coupled with *Thomomys'* spatial patchiness, will foster further vegetational heterogeneity.

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