THE HIGH ELEVATION FLORA OF MOUNT ST. HELENS, WASHINGTON

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ABSTRACT

The subalpine and alpine flora of Mount St. Helens is estimated to consist of about 95 species of vascular plants of which over 20 may have become locally extinct in 1980. In contrast, three nearby volcanoes contain two to three times as many species. The causes for this limited flora include intense and frequent volcanism that has locally extirpated some species and prevented others from reinvading. Mount St. Helens is very young and may not have existed when dispersal for alpine species was facilitated by full glacial conditions. It is isolated by 50 to 80 km of inhospitable lowlands from seed sources on other volcanoes. The area above treeline is small and lacks mesic and hydric habitats, thereby excluding many species capable of dispersing, but incapable of finding a suitable habitat. Mount St. Helens is biogeographically analogous to an oceanic island recently emerged from the sea, distant from potential seed source pools, and suffering the trauma of repeated catastrophes.

The eruptive history of Mount St. Helens is rich and well documented (Yamaguchi 1986) with at least eight major events occurring during the last 400 years. Prior to the eruption of 18 May 1980, this young volcano was the smallest and lowest (2950 m) of the volcanoes of the Pacific Northwest. The treeline of Mount St. Helens was abnormally low, ranging from about 1150 to 1350 m, depending on aspect (Lawrence 1938). Its elevation was reduced to 2550 m in 1980 by a huge debris avalanche and explosive lateral blast (see Rosenfeld 1980 for a description of events). In contrast, timberlines on neighboring volcanoes are at about 1800 m. Mount St. Helens is located at 46°12'N, 122°11'W and is 70 km north of Mount Hood (3428 m), 80 km west of Mount Adams (3752 m) and 52 km south-southwest of Mount Rainier (4393 m).

Prior to 1980, studies of subalpine vegetation on Mount St. Helens included only qualitative descriptions of xeric parkland and meadow communities developed on lava flows, pyroclastic flows, and mudflows (lahars) less than 500 years old (Crandell et al. 1975, Hoblitt et al. 1980). Unfortunately, there are no detailed floristic or vegetational studies that describe vegetation above treeline prior to the 1980 eruption.

This study evaluates what was known of the flora of Mount St.

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Helens prior to 1980, compares it to relevant floras of surrounding volcanoes, discusses reasons for its depauperate nature, and suggests that the most recent eruption has produced numerous local extinctions.

METHODS

The subalpine and alpine flora and meadow vegetation on the slopes of Mount St. Helens were poorly known prior to 1980. We used Hitchcock and Cronquist (1973) and Kruckeberg (1987) to develop an estimate of the flora prior to the massive eruptions that devastated the north flank of the volcano. The general characteristics of pre-eruption high elevation communities on Mount St. Helens can be inferred from the qualitative descriptions and checklists found in Piper (1906), St. John (1976, describing a collecting trip in 1925), and Kruckeberg (1987, describing a 3-day trip in 1979). In order to compare this subalpine flora with those of surrounding volcanoes, the following sources were consulted: for Mount Rainier, Dunwiddie (1983); for Mount Adams, Riley (1986); and for Mount Hood, Burnett (1986). Only species from these checklists likely to occur in subalpine or alpine habitats are included. Although Riley (1986) and Burnett (1986) excluded graminoids, we have included these families based on habitat descriptions in Hitchcock and Cronquist (1973) and personal observations.

Between 1980 and 1987 the first author investigated the flora above 1200 m for an average of 19 days per year. The second author averaged 21 days on the mountain each year between 1983 and 1987. Voucher specimens were prepared for all species encountered and are deposited in WTU.

Species were tabulated in several ways. All species encountered by any primary source on Mount St. Helens are listed by family. Species immigration and potential local extinction are thus indicated. Dispersal mechanisms are inferred from morphology (see Wood and del Moral 1987). Likely reasons for exclusion from the flora are estimated from knowledge of dispersal and habitat requirements.

In order to estimate the degree of disharmony in the Mount St. Helens flora, species were aggregated by plant family for each of the four volcanoes compared. Disharmony refers to an unbalanced distribution of species per family, relative to the flora of the region. A harmonious flora on Mount St. Helens would have about the same proportion of its species distributed among the families as on the other volcanoes.

RESULTS

The flora. The high elevation flora of Mount St. Helens is extremely poor, consisting of no endemics (St. John 1976, Kruckeberg 1987) and dominated by common species found at most high ele-

vations in the Pacific Northwest. Table 1 lists species reported for the higher elevation vegetation (Piper 1906, St. John 1976, del Moral 1983, del Moral and Wood pers. obs. 1980–87, Kruckeberg 1987). Species noted by Kruckeberg and not by St. John may be species that have invaded since 1925. The flora is very poorly-represented in those families dominated by mesophytes and well-represented in taxa with good dispersal mechanisms. Nomenclature follows that of Hitchcock and Cronquist (1973).

The 23 species noted by St. John or Kruckeberg, but not by del Moral, may be species that have been eliminated as a consequence of the 1980 eruption. (Negative evidence, in this case the non-observation of species, is always problematic.) These are indicated by an asterisk in Table 1 and include *Botrychium lanceolatum, Lewisia columbiana, Caltha biflora, Trautvetteria caroliniensis, Heuchera micrantha, Saxifraga arguta, Phyllodoce glanduliflora, Dodecatheon jeffreyi, Collomia debilis, Penstemon davidsonii, Valeriana sitchensis, Aster alpigenus, Erigeron peregrinus,* and *Luzula divaricata.*

The pre-eruptive subalpine and alpine flora on Mount St. Helens was dominated by species common to other Northwest volcanoes. Dominants included *Lupinus lepidus, L. latifolius, Eriogonum pyrolifolium, Polygonum newberryi, Luetkea pectinata, Saxifraga tolmiei, Phyllodoce empetriformis, Arctostaphylos uva-ursi, Juncus parryi, Spraguea umbellata,* and *Castilleja miniata.* Today, on the southern slopes of Mount St. Helens, these species are common meadow plants.

Impoverishment and disharmony. We are unaware of any biogeographic studies of non-equilibrium conditions on terrestrial islands. Table 2 summarizes the depauperate and disharmonious nature of the Mount St. Helens flora compared to the floras of Mount Rainier, Mount Adams, and Mount Hood. Subalpine and alpine species richness is estimated to be as follows: for Mount St. Helens, 95 species (including 23 species, 24%, now possibly extinct on the cone); for Mount Hood, 185 (Burnett 1986); for Mount Adams, 198 (Riley 1986); and for Mount Rainier, 261 (Dunwiddie 1983).

Prior to 1980, Mount St. Helens' flora was only about ⅓ of that of Mount Rainier. Families with fewer than ⅓ as many species are under-represented, whereas those with more than ⅓ as many are over-represented. Based on this criterion, the following families are under-represented: Polypodiaceae, Salicaceae, Caryophyllaceae, Ranunculaceae, Brassicaceae, Saxifragaceae, Fabaceae, Onagraceae, Apiaceae, Boraginaceae, Scrophulariaceae, and Liliaceae. The Lycopodiaceae, Polygonaceae, Juncaceae, Cyperaceae, and Poaceae are over-represented.

Discussion and Conclusions

We postulate four reasons for low species richness and disharmony: 1) frequent disturbance causing relatively high local extinc-

TABLE 1. PLANT SPECIES COLLECTED OR OBSERVED ABOVE TIMBERLINE ON THE FLANKS OF MOUNT ST. HELENS. (Nomenclature has been modified to conform to Hitchcock and Cronquist, 1973. Piper's observations are from a table of "arctic-alpine species" plus higher elevation species from a table of "Hudsonian" species.) X = Species observed. * = Species not observed by authors or other field workers since 1980. [1]"Characteristic species"; Piper's list was not exhaustive. [2]Species listed by these authors that are clearly not from subalpine habitats and tree species are omitted.

Plant family Species	Piper[1], ca. 1900	St. John[2], 1925	Krucke-berg[2], 1979	del Moral, 1980–1986
		PTERIDOPHYTES		
Lycopodiaceae				
Lycopodium sitchense	X	X	X	X
L. annotinum	–	X	–	*
Ophioglossaceae				
Botrychium lanceolatum	–	X	X	*
Polypodiaceae				
Cryptogramma crispa	–	X	X	X
Selaginellaceae				
Selaginella wallacei	–	X	–	*
		GYMNOSPERMS		
Cupressaceae				
Juniperus communis	X	X	X	X
		ANGIOSPERMS–DICOTS		
Apiaceae				
Lomatium martindalei	X	X	X	X
Asteraceae				
Achillea millefolium	–	X	X	X
Agoseris aurantiaca	X	X	–	X
A. glauca	–	–	–	X
Anaphalis margaritacea	–	X	X	X
Antennaria microphylla	X	X	X	X
A. lanata	–	–	X	X
Arnica latifolia	X	X	X	X
A. cordifolia	–	–	–	X
Aster alpigenus	X	X	–	*
A. ledophyllus	X	X	X	X
Erigeron peregrinus	–	X	–	*
Eriophyllum lanatum	–	X	–	X
Hieracium albiflorum	–	X	X	X
H. gracile	–	–	X	X
Luina hypoleuca	–	X	X	X
Microseris alpestris	X	X	X	X
Campanulaceae				
Campanula rotundifolia	–	X	–	X
Caryophyllaceae				
Silene parryi	–	X	–	X

TABLE 1. CONTINUED.

Plant family Species	Piper[1], ca. 1900	St. John[2], 1925	Krucke-berg[2], 1979	del Moral, 1980–1986
Crassulaceae				
Sedum oreganum	–	X	–	*
Ericaceae				
Arctostaphylos uva-ursi	–	X	X	X
Phyllodoce empetriformis	X	X	X	X
Phyllodoce glanduliflora	X	X	X	*
Vaccinium scoparium	X	X	–	X
Vaccinium membranaceum	–	–	–	X
Fabaceae				
Lupinus latifolius	–	X	X	X
L. lepidus var. *lobbii*	X	X	X	X
Gentianaceae				
Gentiana calycosa	–	–	–	X
Hydrophyllaceae				
Phacelia hastata	–	X	X	*
Onagraceae				
Epilobium angustifolium	–	X	X	X
E. alpinum	–	X	–	X
Polemoniaceae				
Collomia debilis	–	X	–	*
Linanthastrum nuttallii	–	–	–	X
Phlox diffusa	X	X	X	X
Polygonaceae				
Eriogonum pyrolifolium	X	X	X	X
E. ovalifolium nivale	–	–	–	X
Polygonum newberryi	X	X	X	X
P. minimum	–	X	–	X
Portulacaceae				
Lewisia columbiana	X	X	–	*
Spraguea umbellata	X	X	X	X
Primulaceae				
Dodecatheon jeffreyi	–	X	–	*
Ranunculaceae				
Aquilegia formosa	–	X	–	X
Caltha biflora	X	X	–	*
Trautvetteria caroliniensis	–	–	X	*
Rosaceae				
Fragaria virginiana	–	X	X	X
Luetkea pectinata	–	X	X	X
Potentilla arguta	–	–	–	X
Rubus lasiococcus	X	X	X	X
Sibbaldia procumbens	–	X	X	X
Sorbus sitchensis	X	X	X	X
Spiraea densiflora	X	X	X	X

TABLE 1. CONTINUED.

Plant family Species	Piper[1], ca. 1900	St. John[2], 1925	Krucke-berg[2], 1979	del Moral, 1980–1986
Salicaceae				
Salix barclayi	–	X	X	X
Saxifragaceae				
Heuchera micrantha	X	X	X	*
Saxifraga arguta	–	X	–	*
S. tolmiei	X	X	X	X
Scrophulariaceae				
Castilleja miniata	–	X	X	X
Penstemon cardwellii	–	–	X	X
P. confertus	–	X	–	X
P. davidsonii var. *menziesii*	X	–	–	*
P. serrulatus	–	X	–	*
Valerianaceae				
Valeriana sitchensis	X	X	X	*
Violaceae				
Viola adunca	–	–	–	X
ANGIOSPERMS—MONOCOTS				
Cyperaceae				
Carex mertensii	–	X	–	X
C. pachystachya	–	–	–	X
C. phaeocephala	–	X	–	X
C. rossii	–	X	X	X
C. spectabilis	X	X	X	X
Juncaceae				
Juncus parryi	–	X	X	X
J. drummondii	–	–	–	X
Luzula divaricata	X	X	–	*
L. piperi	–	–	X	X
Liliaceae				
Smilacina racemosa	–	X	X	X
S. stellata	–	X	X	X
Xerophyllum tenax	–	X	–	X
Poaceae				
Agrostis diegoensis	–	–	X	X
A. exarata	–	X	–	X
A. variabilis	–	X	–	*
Bromus carinatus	–	–	–	X
Calamagrostis sesquiflora	–	X	–	*
Danthonia intermedia	–	X	X	X
D. spicata	–	X	–	*
Festuca occidentalis	X	X	–	X
Festuca viridula	–	–	X	*
Phleum alpinum	–	X	X	X
Poa incurva	–	X	–	X
Sitanion hystrix	–	X	X	X
S. jubatum	–	–	X	X
Stipa occidentalis	–	X	–	X
Trisetum spicatum	X	X	–	X

TABLE 2. NUMBER OF SPECIES IN PLANT FAMILIES ON FOUR VOLCANOES: MOUNT ST. HELENS, MOUNT RAINIER (Dunwiddie 1983), MOUNT ADAMS (Riley 1986), AND MOUNT HOOD (Burnett 1986). Parenthetical values are post-1980 estimates, where different. [1]Lycopodiaceae and Selaginellaceae. [2]Ophioglossaceae and Polypodiaceae.

Family	Mount St. Helens	Mount Rainier	Mount Adams	Mount Hood
Fern allies[1]	3 (2)	4	3	3
Ferns[2]	2 (1)	6	5	3
Cupressaceae	1	1	1	1
	ANGIOSPERMS—DICOTS			
Apiaceae	1	5	5	6
Asteraceae	16 (14)	50	35	27
Boraginaceae	0	2	0	2
Brassicaceae	0	14	8	5
Campanulaceae	1	1	1	1
Caryophyllaceae	1	9	5	4
Crassulaceae	1 (0)	3	2	1
Droseraceae	0	1	1	1
Ericaceae	5 (4)	11	9	7
Fabaceae	2	7	4	5
Gentianaceae	1	1	1	1
Hippuridaceae	0	1	0	0
Hydrophyllaceae	1 (0)	3	2	2
Hypericaceae	0	1	1	1
Onagraceae	2	11	6	8
Polemoniaceae	3 (2)	9	7	7
Polygonaceae	4	9	7	8
Portulacaceae	2 (1)	5	3	2
Primulaceae	1 (0)	3	2	2
Ranunculaceae	3 (2)	13	8	9
Rosaceae	7	15	12	10
Salicaceae	1	4	2	3
Saxifragaceae	3 (1)	15	9	8
Scrophulariaceae	5 (3)	20	18	17
Valerianaceae	1 (0)	1	1	1
Violaceae	1	1	1	1
	ANGIOSPERMS—MONOCOTS			
Cyperaceae	5	13	10	9
Juncaceae	4 (3)	6	4	3
Liliaceae	3	9	5	7
Poaceae	15 (11)	20	19	19
Orchidaceae	0	2	1	1
Totals	95 (72)	276	198	185

tion rates; 2) low immigration rates due to isolation and ineffective dispersal mechanisms (e.g., mammals, ants, water, and gravity); 3) the immaturity of the volcano resulting in poor soils; and 4) a lack of mesic and hydric habitats.

The flora may have increased during the interval between major eruptions (1852 to 1980). For example, Piper (1906) listed only 45 species for the upper slopes of Mount St. Helens. Lawrence (1938,

1939) found 80 vascular plant species on pumice between 1200 and 2200 m. Lawrence stated that at least some were recent immigrants and that new species should be expected to invade each year. Kruckeberg (1987) stated that 70 vascular plants species common in other subalpine and alpine regions of the Cascades do not occur on Mount St. Helens. In contrast, species in groups with effective long-distance dispersal mechanisms, such as lycopods, composites, grasses, sedges and rushes, are well represented. The vegetation of subalpine meadows on Mount St. Helens is characterized by widely distributed species common to Northwestern volcanoes, whereas many other common species are lacking.

Species strangely absent from Mount St. Helens are noted in Table 3, along with potential reasons for their absence, related to those factors stated above. In addition, several species may have succumbed to the most recent disturbance. The list is meant to illustrate reasons potentially excluding a species from a habitat and should not be construed as definitive. Species from the list of Kruckeberg (1987) (except for three known to exist in 1979) have been categorized as follows: 18 of 67 species appear to be absent primarily because their dispersal mechanisms are effective for only short distances. The bulk of the species (27 of 67) appear limited both by inefficient dispersal and the absence or small size of suitable habitats. The true alpine zone is small on this volcano, especially since 1980. Lush meadow habitats, such as the extensive meadows near Paradise on Mount Rainier, have never been common and today are virtually absent. Glaciers that existed on steep slopes were nearly completely removed. Their remnants apparently did not support any distinct wetland vegetation. Bogs do not exist on or near the cone. Therefore lush meadow species (*Anemone occidentalis*) and bog dwellers (*Kalmia microphylla*) do not occur. A few species, such as *Allium cernuum,* may tolerate drought, but require better developed soils than occur. Twenty species have effective dispersal mechanisms, but are absent primarily for reasons related to their special habitat requirements. The lack of a sizable, stable alpine habitat may exclude genera like *Empetrum* and *Dryas.* Wet meadow species are absent because of insufficient moisture. The absence of stable, dry soil and very acid soils may limit other species. Species such as *Vaccinium deliciosum* are expected; their absence may be due only to chance. Species other than those mentioned by Kruckeberg (1987) might be expected, but are lacking for one or more of the reasons discussed below.

Although none of the studies cited above is complete, each implies a depauperate flora. Incomplete collecting may account for some gaps in earlier studies since these concentrated on the north slopes. However, species confined to the north slope may indeed now be absent from the volcano.

It is likely that low richness and disharmony of the flora above

TABLE 3. SUMMARY OF PROBABLE CAUSES FOR THE ABSENCE OF COMMON SPECIES FROM MOUNT ST. HELENS VOLCANO.

Reason	Total	Examples
Primarily dispersal	18	
No special mechanism	12	*Arabis* spp., *Draba aureola, Arenaria* spp., *Saxifraga* spp., *Smelowskia* spp., *Thlaspi fendleri, Phacelia sericea, Polemonium elegans*
Mammals	6	*Agropyron* spp., *Deschampsia atropurpurea, Erigeron* spp.
Dispersal and habitat	27	
Lack of alpine habitat	1	*Oxyria digyna*
Too dry	24	*Anemone* spp., *Kalmia microphylla, Erythronium montanum, Ranunculus* spp., *Dodecatheon jeffreyi, Douglasia laevigata, Solidago multiradiata, Veronica cusickii, Silene* spp., *Thalictrum* spp.
Lack of suitable soil	2	*Allum cernuum, Spiraea betulifolia*
Primarily habitat	20	
Lack of alpine habitat	6	*Artemisia norvegica, Silene acaulis, Salix* spp., *Dryas octopetala, Empetrum nigrum*
Too dry	10	*Epilobium latifolium, Polypodium hesperium, Habenaria dilatata, Aster alpigenus, Pedicularis* spp., *Senecio triangularis, Saussurea americana*
Lack of suitable soil	4	*Sedum* spp., *Cheilanthes gracillima, Cassiope mertensiana*
Chance	2	*Vaccinium deliciosum, Haplopappus lyallii*

timberline on Mount St. Helens result from a combination of several factors. Frequent eruptive disturbances probably caused the local extinction of many species. *Caltha biflora, Dodecatheon jeffreyi,* and *Festuca viridula* are among species probably extirpated from the cone in 1980. These are species not known from the south half of the cone, and they generally occur in mesic habitats.

The youth and small size of the volcano have several important consequences. Some species may have reached other alpine areas during glacial maxima at a time when Mount St. Helens either did not exist or lacked high elevation habitats. Poorly developed substrates preclude the development of habitats for mesophytic species. Over time, soil development will occur so that species common, for example, at Sunrise on Mount Rainier, may be able to grow. Such species include *Potentilla flabellifolia* and *Veronica cusickii.* Many families under-represented on Mount St. Helens are primarily mesophytes.

Restricted habitats subject the flora to several processes likely to reduce richness. 1) Disturbances may totally eliminate certain habitats; 2) existing habitats are smaller and less diverse and therefore less likely to have as many species due to simple species-area effects;

3) populations of rare species will be small and of limited distribution and therefore more susceptible to elimination; and 4) small habitats are less likely to intercept invading seeds than large habitats. In addition, species unable to withstand burial by tephra and other mild impacts may succumb whereas more tolerant species survive. Long distances from seed sources also contribute to limited recolonization from surrounding areas, despite the 123-year dormant period preceding the 1980 eruption. Nearby subalpine and alpine communities on the Old Cascades nonvolcanic landscape, notably on Mount Margaret and Strawberry Mountain, probably were depauperate because they were decimated by thick tephra deposited in A.D. 1480 (Yamaguchi 1986). As a result, many seed sources of the pre-1980 landscape may have been as distant as the nearest volcanoes.

The frequency of major disturbances on Mount St. Helens is such that the flora appears to be far below its equilibrium richness (see Malanson 1984). Studies of isolated young woodlands (less than 350 years old) in Britain (Peterken and Game 1984) suggest first that such woodlands are depauperate and disharmonious and second that they acquire most of their species within 20 years. Even minor isolation serves to restrict colonization rates dramatically.

The balance between frequent episodic local extinction and presumably gradual colonization on Mount St. Helens, combined with small area and an immature landscape, has produced a monotonous flora remarkably limited in richness. The 1980 eruptions may have contributed to this impoverishment, with as many as 23 of 95 species being eliminated in 1980.

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Literature Cited

Burnett, R. E. 1986. Flowering plants of the Mt. Hood Area. Mazama 67:1–12.

Crandell, D. R., D. R. Mullineaux, and R. Meyer. 1975. Mount St. Helens volcano; recent and future behavior. Science 187:438–441.

del Moral, R. 1983. Initial recovery of subalpine vegetation on Mount St. Helens, Washington. Amer. Midl. Naturalist 109:72–80.

——— and D. M. Wood. 1988. Dynamics of herbaceous vegetation recovery on Mount St. Helens. Vegetatio 74:11–27.

Dunwiddie, P. W. 1983. Checklist of vascular plants: Mount Rainier National Park, PNW Nat. Parks & Forests Association.

HITCHCOCK, C. L. and A. CRONQUIST. 1973. Flora of the Pacific Northwest. Univ. Washington Press, Seattle.

HOBLITT, R. P., D. R. CRANDELL, and D. R. MULLINEAUX. 1980. Mount St. Helens eruptive behavior during the past 1500 years. Geol. Mag. 8:555–560.

KRUCKEBERG, A. R. 1987. Plant life on Mount St. Helens before 1980. *In* D. E. Bilderback, ed., Mount St. Helens 1980, botanical consequences of the explosive eruptions, p. 3–21. Univ. California Press, Berkeley.

LAWRENCE, D. B. 1938. Trees on the march. Mazama 20:49–54.

———. 1939. Continuing research on the flora of Mount St. Helens. Mazama 21(12):56–60.

MALANSON, G. P. 1984. Intensity as a third factor of disturbance regime and its effect on species diversity. Oikos 43:411–413.

PETERKEN, G. F. and M. GAME. 1984. Historical factors affecting the number and distribution of vascular plant species in the woodlands of central Lincolnshire. J. Ecol. 72:155–182.

PIPER, C. V. 1906. Flora of the state of Washington. Contr. U.S. Nat. Herb. Govt. Printing Office, Washington, D.C.

RILEY, J. 1986. Mount Adams Wilderness plant list. Mimeographed report, U.S. Forest Service.

ROSENFELD, C. L. 1980. Observations on the Mount St. Helens eruption. Amer. Sci. 68:494–509.

ST. JOHN, H. 1976. The flora of Mt. St. Helens, Washington. The Mountaineer 70(7):65–77.

WOOD, D. M. and R. DEL MORAL. 1987. Mechanisms of early primary succession in subalpine habitats on Mount St. Helens. Ecology 68:780–790.

YAMAGUCHI, D. K. 1986. The development of old-growth Douglas-fir forests Northeast of Mount St. Helens, Washington, following an A.D. 1480 eruption. Ph.D. dissertation, Univ. Washington, Seattle.

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