

# Species attributes in early primary succession on volcanoes

Tsuyuzaki, Shiro<sup>1\*</sup> & del Moral, Roger<sup>2</sup>

<sup>1</sup>Graduate School of Science and Technology, Niigata University, Niigata, 950-21, Japan; and

<sup>2</sup>Department of Botany (KB-15), University of Washington, Seattle, WA 98195, USA;

\*Author for correspondence; Fax+81 25 262 1175; E-mail TSUYU@CC.NIIGATA.U.AC.JP.

**Abstract.** We predicted that plants that can establish on volcanic soils with similar disturbance histories will have similar growth characteristics. We tested this prediction by a multivariate analysis of 27 traits of 84 species found six years after an eruption on Mount St. Helens, Washington State, USA, and Mount Usu, Hokkaido, Japan. These traits include vegetative, life-history, phenological and seed-biology characteristics. Cluster analysis revealed five species groups: annual herbs, perennial forbs, graminoids, shrubs and trees. Each group has distinct vegetative, life-history, and seed-biology traits. Except for shrubs, which were lacking on Mount Usu, both floras were well represented in each group. On intensely disturbed sites on both volcanoes, perennial forbs, whose development is dependent primarily on well-developed below-ground organs and wind-dispersal, expanded their cover more rapidly than did graminoids. These graminoids generally produce gravity-dispersed seeds and have close-set rhizomes and/or shoots. These results suggest that species that can establish during the early stages of succession on each volcano have similar vegetative, life-history, and seed-biology traits.

**Keywords:** Disturbance; Growth form; Life history; Mount St. Helens; Mount Usu.

**Nomenclature:** Hitchcock & Cronquist (1973) for Mount St. Helens and Ohwi (1975) for Mount Usu.

## Introduction

Comparisons of plant communities in different regions must depend upon life history characteristics to define plant strategy categories. Plant strategy spectra can be used to infer constraints imposed by the environment (Grime et al. 1988). To accomplish this, many ecological plant classification systems have been developed to categorize species on the basis of various attributes (e.g. Leishman & Westoby 1992; Boutin & Keddy 1993), but these systems have not been applied to harsh environments such as volcanoes.

This study examines species attributes of the vegetation on a volcano in the USA and one in Japan. While the flora of any region is biogeographically determined, disturbances such as those resulting from volcanism strongly condition initial succession patterns (del Moral

1993). Therefore, we predict that the distribution of ecologically equivalent species should be similar within similar disturbance types even on different volcanoes. To test this, we classified species found early in succession on these volcanoes into groups based on life-history and growth form traits. Second, we investigated relationships between these species groups and habitats that received different volcanic damage. Finally, we evaluated the validity of ecological species group traits.

## Methods

### Study areas

The two volcanoes are on opposite sides of the Pacific Ocean. Mount St. Helens is located in the northwestern USA (46° 12' N, 122° 11' W, peak: 2550 m) and Mount Usu is located in the northern part of Japan (42° 32' N, 140° 50' E, peak: 727 m). Precipitation patterns on the two volcanoes are distinct. While annual precipitation on Mount St. Helens is > 2000 mm, that on Mount Usu in 1984 was only 649 mm. Even though the annual precipitation is lower on Mount Usu, summer rainfall is higher. Snow-free periods are ca. 5 months on Mount St. Helens and 6 - 7 months on Mount Usu. The original floras of the two volcanoes were almost distinct. Without the eruptions, the climax vegetation on Mount St. Helens would be needle-leaved forest and alpine meadow, that on Mount Usu would be deciduous forest. On Mount St. Helens, vegetation was dominated by the conifers *Abies* spp., *Pseudotsuga menziesii* and *Pinus contorta* var. *latifolia* and subalpine meadow species such as *Lupinus lepidus*, *Polygonum newberryi*, and *Luetkea pectinata* (see also del Moral & Wood 1988). On Mount Usu broad-leaved forests dominated by *Populus maximowiczii* and *Betula platyphylla* var. *japonica* occurred (Table 1) (see also Tsuyuzaki 1987).

At least eight major eruptions occurred during the last 400 years on Mount St. Helens, and seven occurred during the last 300 years on Mount Usu (Bullard 1984; Katsui 1988). The latest eruptions were recorded on May 30, 1980, on Mount St. Helens and over several

months during 1987 and 1988 on Mount Usu. These eruptions produced large quantities of ash and pumice that destroyed the vegetation on parts of both volcanoes.

After the last eruptions, re-establishment of plant communities was delayed on both volcanoes due to drought, soil instability, or isolation (Tsuyuzaki 1991; del Moral & Bliss 1993). 6 yr after the eruptions on each volcano, colonization was occurring in all habitats (del Moral & Wood 1988; Tsuyuzaki 1991). Therefore, these analyses deal with the data collected 6 yr after the eruptions, i.e., 1986 on Mount St. Helens and 1984 on Mount Usu. Five habitats were selected on Mount St. Helens and three habitats were selected on Mount Usu for study as follows (Table 1):

Mount St. Helens: Butte Camp (BC) was impacted by tephra up to 15 cm in depth. Initial mortality was moderate, but no species was lost. Pine Creek (PC) was scoured by a mud flow that removed much soil and most plants. Although conditions here are severe and the site is isolated, there is a significant legacy of survivors. Toutle Ridge (TR), on the west side of the cone, was at the edge of the lateral blast. All trees were killed, but much vegetation and soil remained. Mud flows (MF) were deposited near the BC sites. Newly deposited material was deep and there were no survivors. However, sources for colonists were near the sample points. Studebaker Ridge (SR) received the brunt of the blast, which destroyed all vegetation and removed most soil. SR is over 1 km from the nearest surviving vegetation and the environment there is harsh (del Moral & Bliss 1993).

Mount Usu: Three contrasting habitats were studied in the crater basin. Deep (1 to 3 m), stable tephra is the

dominant landform outside gullies (T). In other locations, moderate erosion formed gullies (G) with altered surface conditions, but the original soil surface had not been reached. Extreme erosion had removed large quantities of ash and exposed the original surface (E) creating a third habitat (Tsuyuzaki 1991).

In summary, on Mount St. Helens, MF and SR were the most devastated sites. There were no survivors and revegetation is completely dependent on plant immigration. BC was the least impacted site. The other habitats, PC and TR received moderate impacts permitting some survivors. On Mount Usu, T, E and G received similar damage among themselves that intensities were comparable to PC and TR. However, seedbank species appeared after the eruptions only in E.

#### Data collection

Within the five habitats on Mount St. Helens, permanent plots were spaced along transects at 100 m intervals (19 in BC, 9 in PC, 10 in TR, 7 in MF, and 10 in SR). On this volcano, circular 250 m<sup>2</sup> plots were established in treeless locations. Vegetation cover was measured in twenty-four 50 cm × 50 cm subplots per plot (del Moral & Wood 1988). On Mount Usu, 10, 8, and 4 quadrats (2 m × 5 m) were set up on T, C, and E along gullies at 50-m intervals, respectively. In each quadrat, plant cover was recorded for each species. Even though only four plots were sampled in the gully on Mount Usu, 88 % of species found in exposed sites during 1983 and 1984 were recorded here (Tsuyuzaki 1987, 1991). Therefore, all widespread species and all species with high cover were included in the comparison.

**Table 1.** Characteristics of post-eruption habitats on Mount St. Helens and Mount Usu. Location, elevation of post-eruption, and erupted periods are shown in parentheses.

| Habitat   | Major disturbance | Plant survival | Major plant origin | Cover in yr 6 | Leading taxa  |
|---|-------------------|----------------|--------------------|---------------|---|
| <b>Mount St. Helens (46°12'N, 122°11'W; peak: 2550 m; erupted 1980)</b> |                   |                |                    |               |   |
| BC (1350-1680 m)  | Tephra deposits   | High           | IM + VE            | 24.9%         | <i>Agrostis diegoensis</i><br><i>Polygonum newberryi</i>    |
| PC (1380-1525 m)  | Mud scoured       | Moderate       | IM + VE            | 18.7%         | <i>Luetkea pectinata</i><br><i>Agrostis diegoensis</i>      |
| TR (1290-1430 m)  | Lateral blast     | Moderate       | IM + VE            | 9.1%          | <i>Lupinus lepidus</i><br><i>Lomatium martindalei</i>       |
| MF (1300-1360 m)  | Mudflow           | None           | IM                 | 1.5%          | <i>Polygonum newberryi</i><br><i>Abies lasiocarpa</i>       |
| SR (1150-1325 m)  | Lateral blast     | None           | IM                 | 0.3%          | <i>Lupinus lepidus</i>                                      |
| <b>Mount Usu (42°32'N, 140°50'E; peak: 727 m; erupted 1977-1978)</b>    |                   |                |                    |               |   |
| T (440-490 m)   | Tephra deposits   | Moderate       | IM + VE            | 5.2%          | <i>Petasites japonicus</i><br><i>Polygonum sachalinense</i> |
| E (440-490 m)   | Surface movements | Moderate       | IM + VE + BS       | 6.2%          | <i>Trifolium repens</i><br><i>Rumex obtusifolius</i>        |
| G (440-490 m)   | Both above        | Moderate       | IM + VE            | 4.9%          | <i>Petasites japonicus</i>                                  |

<sup>1</sup> = IM; immigrant; VE = vegetative; BS = buried seeds.

### Data analysis

Data on a range of attributes of each species were tabulated within these categories (Leishman & Westoby 1992): vegetative, life history, phenology and seed biology (see App. 1). A total of 27 attributes is used here. These include seven vegetative, five life history, nine phenology, and six seed biology traits. Clustering was accomplished with Mountford's average linkage method (Mountford 1962) to obtain species groups. Prior to clustering, the data of continuous attributes were log-transformed. A species-to-species similarity matrix based on Jaccard's similarity index ( $J = c / (a + b - c)$ ) was calculated (Jaccard 1902; Zar 1984).

To check which species groups are biased towards the respective mountains, we used a 2 (volcanoes)  $\times$  5 (numbers of groups classified by the cluster analysis) cell contingency table.  $\chi^2$  tests were used to assess the differences of the composition of each species group among eight habitats. We tested the bias of the species groups between habitat-types using one-way ANOVA on each volcano (Zar 1984).

## Results

### Characteristics of species composition

There were 46 vascular plant species in the surveyed plots of Mount St. Helens and 40 species on volcano Usu. Two species, *Anaphalis margaritacea* and *Agrostis scabra*, occurred on both. The cluster analysis shows five species groups at 41 % similarity level between the groups, based on these attributes. The species groups produced from the cluster analysis of attributes are summarized as follows.

Group 1 includes all the five annual herbs observed, of which three were forbs: *Rorippa islandica*, *Polygonum kelloggii*, and *Polygonum longisetum*, and two grasses: *Alopecurus aequalis* and *Poa annua*. Flowering occurs from middle to late season. Most of these species can develop seed banks. Seeds generally germinated from early to middle in the following season.

Group 2, perennial herbs, includes 39 forbs, 72 % of which develop long-rhizome-type below-ground systems. The other below-ground types include creeping shoots and close-set rhizomes. All nitrogen-fixing forbs known from volcanoes, i.e. *Lupinus lepidus*, *L. latifolius* and *Trifolium repens*, were in this group.

Group 3, graminoids, is characterized by gravity-dispersed seeds with close-set rhizomes or roots. It includes 18 perennial grasses, sedges and rushes and four small forbs including *Cerastium holosteoides* and *Moehringia lateriflora*. *Agrostis diegoensis*, producing

well-developed long rhizomes, was common in BC and PC on Mount St. Helens, while the other grasses failed to dominate any habitats.

Group 4, shrubs, is characterized by six species that occur on Mount St. Helens. The potential maximum height ranged from 0.2 to 4 m. Both pollination and seed dispersal types show a wide range, but do not include either wind pollination or wind-dispersed seeds. Typical of this group are *Sorbus sitchensis*, *Vaccinium membranaceum*, and *Phyllodoce empetriformis*.

Group 5, trees, consists of ten true trees (birches, pines, willows, etc.) and two arborescent shrubs, *Salix commutata* and *S. integra*. Potential maximum height is > 3 m. These species flower early in the season, are wind pollinated and adapted to seed dispersal by wind.

### Relationship between habitats and species groups

The proportion of species in each group differed significantly between the two volcanoes (Table 2). These differences resulted primarily from differences among annuals, shrubs and trees. Annual herbs on Mount St. Helens were represented only by *Polygonum kelloggii*. On Mount Usu they were more common, particularly in exposed gullies. Shrubs were not sampled on Mount Usu, while trees were rare on Mount St. Helens, even though all plots were well below the climatic tree line.

The frequency of each species group differed significantly among habitats on each volcano (Table 2). The frequency of perennial forbs in the different habitats ranged from 31 to 60 %. Graminoid frequency ranged between 20 to 41 %. Woody species represent 20% of the species, but their abundance was highly variable, from 4 to 38 % among the habitats.

On Mount St. Helens, plant cover in 1986 was greatest at BC, where most plants survived, and moderate at PC, where the few survivors have expanded vegetatively (Table 1). Cover at TR was approximately half that of PC. Cover at both MF and SR remained very low. On Mount Usu, cover ranged from 5 to 7% in all habitats. Perennial forbs were the leading dominants in each habitat, while graminoids generally developed no more than intermediate cover in most sites.

Although graminoids, represented primarily by *A. diegoensis*, were well-established in high-cover habitats, they were sparsely represented in low-cover habitats on Mount St. Helens (Table 1). Devastated sites were dominated by species producing vigorous underground organs (e.g., *Lupinus lepidus*, *Polygonum newberryi*, *Polygonum sachalinense* and *Petasites japonicus*). Relative cover of perennial forbs was higher in low-cover habitats. On Mount Usu, the relative cover of graminoids was also lower in more intensely disturbed habitats. Therefore, perennial forbs and

**Table 2.** Number (and relative frequency) of species in each group in each habitat on the two volcanoes. A contingency table of  $2 \times 5$  cells confirms that the composition of life history groups is significantly different at  $P < 0.05$  ( $\chi^2$ -value = 9.76).  $F$ -values indicate the relative appearance frequencies of each group between the eight habitats surveyed. One-way ANOVA tests the difference of life history groups between habitats on each volcano. \* = Significantly different at  $P < 0.01$ ; NS = not different.

| Group               | Mount St. Helens |         |        |         |        |          | Mount Usu |         |        |          | Total   | $\chi^2$ -value    |
|---------------------|------------------|---------|--------|---------|--------|----------|-----------|---------|--------|----------|---------|--------------------|
|                     | BC               | PC      | TR     | MF      | SR     | Subtotal | T         | E       | G      | Subtotal |         |                    |
| Annual herbs        | 0 ( 0)           | 0 ( 0)  | 1 ( 6) | 0 ( 0)  | 0 ( 0) | 1 ( 2)   | 1 ( 3)    | 4 (16)  | 0 ( 0) | 4 ( 1)   | 5 ( 6)  | 70.2*              |
| Perennial forbs     | 17 (46)          | 11 (44) | 8 (47) | 12 (57) | 3 (60) | 21 (46)  | 12(41)    | 15 (60) | 5 (31) | 19 (48)  | 39 (46) | 14.8 <sup>NS</sup> |
| Graminoids          | 13 (35)          | 8 (32)  | 7 (41) | 5 (24)  | 1 (20) | 14 (30)  | 8(28)     | 5 (20)  | 5 (31) | 9 (23)   | 22 (26) | 13.5 <sup>NS</sup> |
| Shrubs              | 5 (14)           | 4 (15)  | 1 ( 6) | 1 ( 5)  | 0 ( 0) | 6 (13)   | 0(0)      | 0 (0)   | 0 (0)  | 0 ( 0)   | 6 ( 7)  | 58.6*              |
| Trees               | 2 ( 5)           | 2 ( 8)  | 0 ( 0) | 3 (14)  | 1 (20) | 4 (9)    | 8(28)     | 1 ( 4)  | 6 (38) | 8 (20)   | 12(14)  | 80.6*              |
| ANOVA ( $F$ -value) | 44.99*           |         |        |         |        |          | 7.26*     |         |        |          |         |                    |
| Total richness      | 37               | 25      | 17     | 21      | 5      | 46       | 29        | 25      | 16     | 40       | 84      |                    |

graminoids have an inverse relationship along the cover (disturbance) gradient. The establishment sites of annual herbs were restricted to exposed surfaces. Although the establishment patterns of shrubs and trees were unclear, trees did not occur at PC, TR, and shrubs did not occur at E. Neither annuals nor shrubs were common in any habitat, suggesting that their expansion was restricted even if they successfully established.

## Discussion

### *Absence of annuals - role of the seedbank*

Many approaches to forming species groups have been tried (e.g., Klinka et al. 1989; Leishman & Westoby 1992; Boutin & Keddy 1993). Annual herbs are rarely identified as a separate group, though Grime et al. (1988) note that annuals form a major component of the ruderal strategy. In forests, the annual category is often absent (Leishman & Westoby 1992). All annuals, including the graminoids *Poa annua* and *Alopecurus aequalis*, are in Group 1. There was little seedbank contribution to revegetation on less disturbed habitats, BC and PC, on Mount St. Helens. All annuals on Mount Usu originated from the seed bank in the original topsoil. However these annuals subsequently disappeared because they did not maintain their seed bank (Tsuyuzaki 1994). Without a seed bank, there would be few annuals on Mount Usu (Tsuyuzaki 1987). In addition, annual herbs are uncommon at higher elevations in the Washington Cascades and have contributed little to the revegetation on Mount St. Helens (Dale 1989; Klinka et al. 1989; Halpern et al. 1992; del Moral & Bliss 1993).

Annuals have a special role of vegetation dynamics, for example by contributing to profile stratification. Therefore, trait differences between annuals and perennials may be greater than those between forbs and graminoids. Except for the annual herb category, other

classifications (Grime et al. 1988; Leishman & Westoby 1992) are similar to ours. This suggests that the classification method described has wide applicability.

### *Perennial herbs and graminoids*

#### *- roles of seed dispersal and below-ground structures*

The pioneer stages of succession on volcanoes are often dominated by perennial herbs (Groups 2 and 3) rather than by lower plants (Yoshioka 1974; Tsuyuzaki 1987; del Moral & Bliss 1993). One cause is that seed sources for recolonization are dominated by these species. Most forbs found on the two volcanoes are wind-dispersed, even in the least disturbed habitats (Tsuyuzaki 1987; Dale 1989). In the present study, forbs in general can disperse over longer distances than can graminoids, most of which produce no special dispersal organs. Therefore, forbs invade barren sites more readily than graminoids (del Moral & Wood 1993). In less disturbed sites on Mount St. Helens, the number of seedlings of graminoids, shrubs and trees decrease with increasing distance from forest edges (Halpern & Harmon 1983).

Adaptive strategies that permit early establishment on disturbed sites differ between graminoids and forbs. On more intensely-disturbed sites, forbs are better able to expand their cover than graminoids. This capacity seems to be related to the below-ground systems of the most successful species, because long-distance clonal spreading has a significant advantage in highly disturbed habitats (Fahrig et al. 1994). Rapid colonizers usually have long rhizomes that can tolerate disturbance better and occupy soil volumes more quickly than species with close-set rhizomes (Tsuyuzaki 1989). On the floor of blast-zone forests near Mount St. Helens, cover increases initially were dominated by exotic grasses, then by colonizing forbs that show widespread recruitment and clonal expansion (Halpern et al. 1990). About 70% of perennial forbs in this flora can develop spreading underground organs. Therefore, these species

dominate more isolated sites on Mount St. Helens (Wood & del Moral 1987; del Moral & Wood 1988) and are widespread on Mount Usu (Tsuyuzaki 1991).

*Anomalies in tree and shrub distribution - roles of seed source and resprouting*

Any flora is determined by climatic, historical and biogeographic factors (Walter 1973), and pre-eruption vegetation is a key factor to the development of a flora (Tsuyuzaki 1991). Of course, geographically isolated floras are distinct. On Mount Usu, precipitation is concentrated during the summer, while on Mount St. Helens summer drought is common. There are subalpine coniferous forests and meadows on Mount St. Helens, and deciduous forests on Mount Usu. In this analysis, broad-leaved and coniferous trees were grouped into the same category, suggesting that these growth forms perform similar roles in their respective successions. In contrast to perennial herbs and graminoids, coniferous trees were eliminated from the devastated area on Mount St. Helens, because they were generally incapable of sprouting (Franklin et al. 1985). All tree species, which also produce wind-dispersed seeds, can reach devastated sites on Mount Usu, although their cover was restricted early in succession.

In woodlands, there are clear relationships between structural or phenological attributes and life-history attributes (Leishman & Westoby 1992). Flowering and germination times illustrate differences between groups of species. However, as the growing seasons on both volcanoes are short, phenology does not show clear relations within groups or clear differentiations between groups (del Moral & Wood 1988; Tsuyuzaki 1991).

We have detected meaningful species groups that include species from both volcanoes. The dominance hierarchies on the two volcanoes by groups are also similar. Species groups are based on the various traits that form 'syndromes' of related characteristics. Several phenological traits, except for growing season, also appear to be important characteristics of groups. Newly disturbed habitats on volcanoes on two continents impose environmental stresses that can be met only by limited suites of characteristics. Therefore, on a structural-functional basis, initial stages of succession on the two volcanoes display more similarities than differences.

**Acknowledgements.** We sincerely thank M. Haruki and D.M. Wood for their field assistance. J.H. Titus made valuable comments on the manuscript. This work was partly supported by grants from the Ministry of Education, Science, and Culture, Japan, and from U.S. National Science Foundation Grants DEB-82-21460, DEB-81-07042, BSR-84-07213, BSR-89-06544.

## References

- Black, C.C. & Curtis, J.T. 1976. Plant exhibiting characteristics common to Crassulacean acid metabolism. In: Burris, R.H. & Black, C.C. (eds.) *Metabolism and plant productivity*, pp. 407-426. University Park Press, Baltimore.
- Boutin, C. & Keddy, P.A. 1993. A functional classification of wetland plants. *J. Veg. Sci.* 4: 591-600.
- Bullard, F.M. 1984. *Volcanoes of the Earth*. University of Texas, Austin, TX.
- Dale, V.H. 1989. Wind dispersed seeds and plant recovery on the Mount St. Helens debris avalanche. *Can. J. Bot.* 67: 1434-1441.
- del Moral, R. 1993. Mechanisms of primary succession on volcanoes. A view from Mount St Helens. In: Miles, J. & Walton, D. (eds.) *Primary succession on Land*, pp. 79-100. Blackwell, Oxford.
- del Moral, R. & Bliss, L.C. 1993. Mechanisms of primary succession: insights resulting from the eruption of Mount St. Helens. In Begon, M. & Fitter, A.H. (eds.) *Adv. Ecol. Res.* 24: 1-66.
- del Moral, R. & Wood, D.M. 1988. Dynamics of herbaceous vegetation recovery on Mount St. Helens, Washington, USA, after a volcanic eruption. *Vegetatio* 74: 11-27.
- del Moral, R. & Wood, D.M. 1993. Early primary succession on the volcano Mount St. Helens. *J. Veg. Sci.* 4: 223-234.
- Downton, W.J.S. 1975. The occurrence of C<sub>4</sub> photosynthesis among plants. *Photosynthetica* 9: 96-105.
- Faegri, K. & van der Pijl, L. 1978. *The principles of pollination ecology (3rd ed.)*. Pergamon Press, Oxford.
- Fahrig, L., Coffin, D.P., Lauenroth, W.K. & Shugart, H.H. 1994. The advantage of long-distance clonal spreading in highly disturbed habitats. *Evol. Ecol.* 8: 172-187.
- Franklin, J.F., MacMahon, J.A., Swanson, F.J. & Sedell, J.R. 1985. Ecosystems responses to the eruption of Mount St. Helens. *Nat. Geogr. Res.* 1: 198-216.
- Grime, J.P., Hodgson, J.G. & Hunt, R. 1988. *Comparative plant ecology. A functional approach to common British species*. Unwin-Hyman, London.
- Halpern, C.B. & Harmon, M.E. 1983. Early plant succession on the Muddy River Mudflow, Mount St. Helens, Washington. *Am. Midl. Natur.* 110: 97-106.
- Halpern, C.B., Frenzen, P.M., Means, J.E. & Franklin, J.F. 1990. Plant succession in areas of scorched and blown-down forest after the 1980 eruption of Mount St. Helens, Washington. *J. Veg. Sci.* 1: 181-194.
- Hitchcock, C.L. & Cronquist, A. 1973. *Flora of the Pacific Northwest*. University of Washington Press, Seattle, WA
- Hitchcock, C.L., Cronquist, A., Ownbey, M. & Thompson, J.W. 1955-69. *Vascular plants in the Pacific Northwest I-V*. University of Washington Press, Seattle, WA.
- Katsui, Y. 1988. Usu-zan. In: Kadomura, H., Okada, H. & Araya, T. (eds.) *1977-82 volcanism and environmental hazards of Usu volcano*, pp. 226-234. Hokkaido Univ. Press, Sapporo.
- Klinka, K., Krajina, V.J., Ceska, A. & Scagel, A.M. 1989. *Indicator plants of coastal British Columbia*. University of British Columbia Press, Vancouver, B.C.
- Leishman, M.R. & Westoby, M. 1992. Classifying plants into

- groups on the basis of associations of individual traits - evidence from Australian semi-arid woodlands. *J. Ecol.* 80: 417-424.
- Miyawaki, A. 1983. *Handbook of Japanese Vegetation (rev. ed.)*. Shibundo, Tokyo.
- Mountford, M.D. 1962. An index of similarity and its application to classificatory problems. In: Murphy, P.W. (ed.) *Progress in Soil Zoology*, pp. 43-50, Butterworths, London.
- Numata, M. & Asano, S. 1969. *Biological flora of Japan. Vol. 1*. Tsukiji Shokan, Tokyo.
- Ohwi, J. 1975. *Flora of Japan (rev. ed.)*. Shibundo, Tokyo.
- Okuda, T. & Furukawa, A. 1990. Occurrence and distribution of  $C_4$  plants in Japan. *Jpn. J. Ecol.* 40: 91-121.
- Raunkiaer, C. 1934. *The life-forms of plants and statistical plant geography*. Clarendon Press, Oxford.
- Rosenfield, C.L. 1980. Observations on the Mount St. Helens eruption. *Am. Sci.* 68: 494-508.
- Tsuyuzaki, S. 1987. Origin of plants recovering on the volcano Usu, northern Japan, since the latest eruptions in 1977-78. *Vegetatio* 73: 53-58.
- Tsuyuzaki, S. 1989. Analysis of revegetation dynamics on the volcano Usu, northern Japan, deforested by 1977-78 eruptions. *Am. J. Bot.* 76: 1468-1477.
- Tsuyuzaki, S. 1991. Species turnover and diversity during early stages of vegetation recovery on the volcano Usu, northern Japan. *J. Veg. Sci.* 2: 301-306.
- Tsuyuzaki, S. 1994. Fate of plants from buried seeds on volcano Usu, Japan, after the 1977-78 eruptions. *Am. J. Bot.* 81: 395-399.
- Walter, H. 1973. *Vegetation of the earth: In relation to climate and the eco-physiological conditions*. Springer-Verlag, New York, NY.
- Wood, D.M. & del Moral, R. 1987. Mechanisms of early primary succession in subalpine habitats on Mount St. Helens. *Ecology* 68: 780-790.
- Yoshioka, K. 1974. Volcanic vegetation. In: Numata, M. (ed.) *The flora and vegetation of Japan*, pp. 237-267. Kodansha, Tokyo.
- Zar, J.M. 1984. *Biostatistical analysis (2nd. ed.)*. Prentice-Hall, Englewood Cliffs, NJ.

Received 12 August 1994;

Final revision received 6 March 1995;

Accepted 16 March 1995.

**App. 1.** Attributes noted for species of two volcanoes. Class type and number indicate how each attribute is coded for analysis. Attributes are grouped into four main categories: vegetative, life history, phenology and seed biology. Class types: B = binary (presence/absence); NM = nominal multistate; OM = ordered multistate; C = continuous.

| Attribute  | Class type |
|--|------------|
| <b>Vegetative</b>  |            |
| Growth form <sup>1</sup>   | NM7        |
| evergreen tree • broad-leaved tree • evergreen shrub • deciduous shrub • fern • graminoid • forb                 |            |
| Height <sup>2</sup> (maximum height)   | C          |
| Leaf area <sup>2</sup> (length/2 × breadth/2 × π)  | C          |
| Leaf shape (leaf length / leaf breadth)  | C          |
| Leaf texture <sup>2</sup>  | NM3        |
| soft • hard • thick-leathery   |            |
| Leaf hairness  | NM4        |
| no hairs • some hairs • variable • very hairy  |            |
| Root system <sup>3</sup>   | NM5        |
| abundant roots • close-set rhizomes and/or shoots • creeping shoots • long rhizomes and/or shoots • annual roots |            |
| Storage organ <sup>2</sup>   | B          |
| <b>Life history</b>  |            |
| Dormancy form <sup>2,4</sup>   | NM5        |
| phanerophyte • chamaephyte • geophyte • hemicryptophyte • therophyte •   |            |
| Longevity <sup>3</sup>   | NM4        |
| tree • shrub • perennial • annual  |            |
| Photosynthesis <sup>5</sup>  | NM2        |
| $C_3$ • $C_4$  |            |
| Nitrogen fixation  | B          |
| Pollinator <sup>6</sup>  | NM4        |
| bee • moth/butterfly • insect • wind   |            |
| <b>Phenology<sup>2,7</sup></b>   |            |
| Growth in early season   | B          |
| Growth in middle season  | B          |
| Growth in late season  | B          |
| Flowering in early season  | B          |
| Flowering in middle season   | B          |
| Flowering in late season   | B          |
| Seed release in early season   | B          |
| Seed release in middle season  | B          |
| Seed release in late season  | B          |
| <b>Seed biology</b>  |            |
| Germination in early season  | B          |
| Germination in middle season   | B          |
| Germination in late season   | B          |
| Seed volume <sup>2</sup> (long axis/2 × short axis/2 × length/2) (mm <sup>3</sup> )                              | C          |
| Dispersal mode <sup>8</sup>  | NM4        |
| gravity • self • animal • wind   |            |
| Seed dormancy  | OM3        |
| no • short • long dormancy   |            |

<sup>1</sup>Based on Klinka et al. (1989) classes; <sup>2</sup>Determined from Hitchcock et al. (1955-1969), Ohwi (1975) and Miyawaki (1983); <sup>3</sup>Based on Tsuyuzaki's (1989) classes; longevity order is referred to Leishman & Westoby (1992); <sup>4</sup>Based on Raunkiaer's (1934) classes; <sup>5</sup>Information from Downton (1975), Black & Curtis (1976) and Okuda & Furukawa (1990); <sup>6</sup>Flower classes are based on those of Faegri & van der Pijl (1978); Flower morphology and likely pollinator are classification keys; <sup>7</sup>Early: before late June; middle: during early and late seasons; late: after late August; <sup>8</sup>Based on classes by Numata & Asano (1969).