A floristic and ecological analysis at the Tulameen ultramafic (serpentine) complex, southern British Columbia, Canada

Abstract

While distinct floristic and ecological patterns have been reported for ultramafic (serpentine) sites in California and Oregon, those of British Columbia are muted which is thought to be related to the moderating influence of increased precipitation, a short time since glaciation, and the presence of non-ultramafic glacial till over ultramafic sites. Despite these factors, we found clear floristic and ecological differences with respect to soil type at our study site on Grasshopper Mountain, part of the Tulameen ultramafic complex in southern British Columbia. Ultramafic soils support 28% of the local species richness and host more rare taxa than non-ultramafic soils. Many species show patterns of local restriction to or exclusion from ultramafic soil habitats. Patterns of plant family diversity also show differences between substrates.

Introduction

Ultramafic (serpentine) soils and the plants that they support have long been of interest to botanists (Whittaker 1954; Proctor and Woodell 1975; Brooks 1987). They frequently support vegetation that is distinct from surrounding areas in species composition and structure as well as high levels of plant endemism and diversity. For these reasons, and because of phenomena related to speciation and plant physiological response, Brooks (1987) and Proctor (1999) asserted that the biological importance of ultramafics far outweighs the less than one percent of the earth's surface they occupy.

The chemical and physical properties of ultramafic soils often have adverse effects on plant growth (termed the "serpentine effect"). These soils generally contain elevated concentrations of the heavy metals nickel, chromium, and cobalt, and high levels of magnesium, all potentially toxic to plants. They are generally deficient in nitrogen, phosphorus, potassium, and calcium, thereby further restricting plant growth. The reduced vegetation cover combined with rugged terrain frequently associated with ultramafic sites

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results in poorly-developed, unstable, and often dry soils. These soils also exhibit high heterogeneity, both between- and within-sites, a result of the inherent variability of ultramafic rocks and the pedological processes that weather them. Consequently, no single chemical or physical factor, nor single group of these factors can be said to be responsible for the vegetation of serpentine soils (Brooks 1987; Proctor and Nagy 1992; Roberts and Proctor 1992).

The vegetation of ultramafic soils can range in physiognomy from serpentine barrens to well-developed forests, but is usually floristically and structurally distinct from adjacent non-ultramafic soils. Some genera and families of vascular plants have shown a particular affinity or aversion to serpentine soils within certain regions (Dearden 1979; Kruckeberg 1969, 1992; Rune and Westerbergh 1992). Plant functional groups have also shown strong patterns relative to soil types. Species of dry habitats are often wellrepresented on ultramafic soils, whereas species of mesic to moist habitats are largely excluded (Kruckeberg 1979). Deciduous elements are conspicuously diminished in importance on ultramafics in Oregon (Whittaker 1954).

Kruckeberg (1979, 1992) described four categories of floristic response to serpentine: endemic, indicator, *bodenvag* (widespread), and excluded species. Serpentine endemics are those species restricted to ultramafic soils. Indicator species are those within a local or regional context that are restricted or nearly restricted to ultramafic substrates and whose presence, therefore, indicates serpentine soils. The term *bodenvag* ("soil wanderer") refers to species that are either indifferent to soil type or that have developed serpentine ecotypes or races and, thus, occur commonly on and off ultramafic sites in a given region. Excluded species are those found commonly in surrounding areas but are unable to successfully colonize ultramafic substrates.

Ultramafic soils have also been shown to host species outside of their main ranges. For example, *Polystichum kruckebergii*, a serpentine indicator fern known to also occur on non-serpentine soils (Lellinger 1985), was once thought to reach the northern limits of its range in southern British Columbia (Hitchcock and Cronquist 1973). However, it has more recently been found to track ultramafic outcrops through the interior of the province as far north as the Cassiar Mountains of northwestern British Columbia, a range extension of at least 580 km (Kruckeberg 1982; Douglas et al. 1998). Species' altitudinal

ranges are affected at ultramafic sites in the state of Washington. Several tree and shrub species occur at higher and lower elevations on serpentine than their normal elevation ranges on non-serpentine soils (Kruckeberg 1969).

Little information is available for the plant communities and vegetational responses to serpentine soils in British Columbia. There is some support for the hypothesis that the vegetational response to ultramafics is less pronounced with increasing latitude in western North America, a result of the increasing precipitation, the presence of non-ultramafic glacial till deposited *ca* 12,000 years ago, and the relatively short time available for speciation since glacial retreat (Whittaker 1954; Kruckeberg 1979, 1992; D. Lloyd, pers. comm.; R. Scagel, pers. comm.).

This report is part of a larger study directed to characterize the extent of the serpentine effect and to expand the knowledge of floristics and ecology of ultramafic sites in British Columbia. Through a detailed comparison of adjacent ultramafic and non-ultramafic soils, we sought to understand the uniqueness of ultramafic sites within a British Columbia context in order to help inform the decisions of conservationists and land managers.

Study Site

We compared plant communities and associated soils at Grasshopper Mountain, part of the Tulameen ultramafic complex (49° 20' N, 120° 50' W) of southern British Columbia (Figure 8). This is a relatively flat-topped mountain (elevation 1487 m) with a vertical rise of approximately 565 m. It is 6 km long and 2.5 km wide. Grasshopper Mountain was chosen because there were adjacent sections of ultramafic and non-ultramafic soils that minimized the confounding influences of aspect, topography, history, biota, and climate on the developing plant communities and permitted differences in vegetation to be directly attributed to edaphic factors.

The Tulameen ultramafic complex lies within a climatic transition zone between humid coastal British Columbia and the dry interior. The complex is overlaid by coniferous forests dominated by *Pseudostuga menziesii* (Douglasfir), *Pinus contorta* var. *latifolia* (lodgepole pine), and *P. ponderosa* (ponderosa pine) at lower elevations, and by *Pseudotsuga menziesii*, *Abies lasiocarpa* (subalpine fir), and *Picea engelmannii* (Engelmann spruce) at higher elevations. Previous studies provide information on the geology (Cook and Fletcher 1993; Fletcher et al. 1995) and pedology (Bulmer 1992; Hope 1997) of Grasshopper Mountain and limited information on the vegetation (Kruckeberg 1979; Hope 1997).

Methods

Vegetation and soils were sampled in a total of seventy-one 10-metre radius circular plots on adjacent ultramafic and non-ultramafic sections of the mountain's southern face during July and August 2002. In each section, plots were selected randomly within a stratified design based on the degree of overstorey canopy cover (open, moderate, and closed forest; Figures 9, 10, 11), slope position (top, upper, mid, lower, and toe), and elevation. The percent cover of understorey vegetation as well as forest structural data were recorded in plots. Soil chemical analyses were carried out in the laboratory of Dr Les Lavkulich, Faculty of Agricultural Sciences, University of British Columbia, for percent total C and N (Leco CN2000 Analysis), available P (Bray 1 Extraction), CEC and exchangeable K, Ca, Mg and Na (using the ammonium acetate method at pH 7.0), available Ni, Cr, Co, Mn, Al, Fe, Cu and Zn (DTPA Extraction), and pH (in 0.01 M CaCl₂).

Means of soil variables for three soil types (ultramafic, glacial till-influenced, and non-ultramafic), and means for plot-level species richness and diversity (Shannon and Simpson diversity indices) were compared using analysis of variance (ANOVA) with a post-hoc Bonferroni adjustment provided by SYSTAT 10.2 (SYSTAT 2002). Floristic observations were evaluated using summary tables, and species distributions examined in relation to the different soil types. In this fashion ultramafic indicators, excluded, and *bodenvag* species were identified. PC-Ord (McCune and Mefford 1999) was used for plot summary statistics. Taxonomic nomenclature follows Douglas et al. (1998-2002).

Results and Discussion

Soils

Soil chemical analysis indicated the occurrence of three general soil types at Grasshopper Mountain: ultramafic, non-ultramafic, and glacial tillinfluenced soils (Table 1). Ultramafic plots showed elevated levels of Mg and Ni and decreased levels of Ca and the -Ca:Mg ratio, a general index of soil nutrient favourability (Proctor and Nagy 1992), relative to non-ultramafic

plots. The values for till-influenced plots are intermediate, though only statistically so in the case of Mg. These till plots occurred in ravines and at lower elevations where non-ultramafic, glacial till accumulated through colluvial (emplaced by gravitational forces) processes over ultramafic bedrock.

Floristic Patterns

One hundred and seventy-seven vascular plant species from 35 families were recorded on Grasshopper Mountain: 111 species in 26 plots on ultramafic soils, 70 species in 10 plots on till, and 119 species in 35 plots on non-ultramafic soils. While these differences in total species richness may be partly explained by the different sample sizes, ANOVA results indicated no significant differences (p > 0.05) among plot mean values of species richness, Shannon diversity, and Simpson diversity for the three soil types. Ultramafic studies conducted elsewhere have reported conflicting results (Wilson et al. 1990). Whereas Huston (1979) predicted decreased species diversity on sites with extreme nutrient deficiency and toxicity, and Kruckeberg (1969) and Brooks (1987) characterized species composition of ultramafic sites as depauperate, Proctor and Woodell (1975) suggested that ultramafic sites may actually have higher diversity.

Of the total species recorded, 49 (28 percent) were found solely or primarily in ultramafic plots. This finding suggests that Grasshopper Mountain, and potentially other ultramafic occurrences in BC, contribute greatly to the local, and regional, species pools. As noted by Kruckeberg (1979), the majority of this richness is derived from the presence of species common to other regions (especially the dry interior in our case) which attain a local foothold on the habitats available at ultramafic sites. The results are a flora distinct from that on adjacent non-ultramafic soils, and increased local and regional diversity.

Taking into account the differences in sample size, our study also indicated trends in the representation of families on the three soil types (Table 2). Some families are more common on the ultramafic side (e.g. Apiaceae, Asteraceae, Caryophyllaceae, Poaceae, and Pteridophytes¹), whereas others are more common on till and non-ultramafic soils (e.g. Liliaceae, Rosaceae, Ranunculaceae, Betulaceae, Caprifoliaceae, Grossulariaceae and Salicaceae). The latter four families were not observed on ultramafic soils, while representatives of two families (Juncaceae and Polygonaceae) were observed only on ultramafic soils. Gymnosperms²_and the remaining families were

similarly represented across soil types.

These patterns of restriction and exclusion indicate that there is an effect of soil type on floristics at Grasshopper Mountain. In Oregon and California the Ranunculaceae, Rosaceae, Fabaceae, Primulaceae and Scrophulariaceae are generally absent from ultramafic soils (Kruckeberg 1992), while the Caryophyllaceae have a particular affinity for ultramafics in Newfoundland (Dearden 1979) and Sweden (Rune and Westerbergh 1992). These patterns may be due to a combination of direct effects of soil chemical and physical properties on plant species and indirect effects through species interactions.

Rare Taxa

Ten rare vascular plant taxa, eight of which are provincially red- or bluelisted, were found at Grasshopper Mountain, eight from the ultramafic side and two from open, rocky cliffs on the non-ultramafic side (Table 3). The serpentine subspecies *Adiantum pedatum* subsp. *calderi* (maidenhair fern, Figure 12), is included in this list though it has not received red- or blue-listed status. *Aspidotis densa* is included because it is reported by Douglas et al. (1998-2002) to be restricted to ultramafic outcrops east of the Coast-Cascade ranges. The Tulameen ultramafic complex is the only known site in British Columbia for *Polystichum scopulinum* (Douglas et al. 1998); however, no species are currently recognized as being endemic to serpentine sites in British Columbia.

The distribution patterns of rare taxa on Grasshopper Mountain suggest that, in addition to their contribution to local and regional diversity, ultramafics may also be important to the maintenance of rare taxa in the province. Similarly, California ultramafics provide habitat for some of the last remnant patches of native California grasslands and their highly endangered flora which, on non-ultramafic soils, have been almost entirely replaced by Mediterranean grass species (Harrison 1999). At Grasshopper Mountain the rare ferns *Polystichum scopulinum*, *P. kruckebergii* (Figure 13, back cover), *Aspidotis densa* and *Adiantum aleuticum* (*A. pedatum* subsp. *calderi*) were observed only on ultramafic substrates, while *Cheilanthes gracillima* (Figure 14) was observed only on non-ultramafic rock outcrops. Similar substrate relationships for these species were observed by Kruckeberg (1964) at many sites in Washington state. The mechanisms maintaining rare taxa at Grasshopper Mountain require further study but may be related to the presence of open habitats within a forested matrix since most of the rare

species were found in open areas. Harrison (1999) has investigated two hypotheses on California serpentines that may also apply at Grasshopper Mountain: 1. that there is edaphic control of competitive dominance and 2. that there is edaphic resistance to invasion of non-native species.

Species Ranges

The location of Grasshopper Mountain within the coast-interior climatic transition zone results in a mix of floristic elements with phytogeographical affinities to the coast, the interior, and the south; consequently, many species occur at the edge of their ranges (Tables 4 through 6). Several of these are species of interior BC occurring at the western edge of their ranges on the dry, ultramafic sites of Grasshopper Mountain. The presence of a few taxa, including *Pseudoroegneria spicata* subsp. *inermis* and *Eriogonum ovalifolium* var. *nivale*, may represent westward range extensions (Douglas et al. 1998-2002). Two conifers, *Pinus albicaulis* and *Pinus ponderosa*, occur at the lower and upper limits of their ranges, respectively.

Plant Species as Soil Indicators

Following the indicator classification scheme proposed by Kruckeberg (1979, 1992), the plant species of Grasshopper Mountain were grouped into local ultramafic indicator species, local ultramafic excluded species, and widespread (*bodenvag*) species (Tables 4 through 6). Within each indicator group, taxa were further subdivided into functional groups based on site moisture affinity (see Douglas et al. 1998-2002), and plant life forms that have previously been shown to respond to ultramafic soil conditions (Whittaker 1954; Kruckeberg 1979, 1992). Species occurring in less than 10% of plots on a given substrate, and species found primarily on till-influenced soils, have been omitted from this classification.

Thirty-five species are good indicators of local ultramafic conditions at Grasshopper Mountain (Table 4). However, the majority of these species are known to occur elsewhere on non-ultramafic soils. Their association with ultramafic soils at the study site may be a function of exclusion from the mostly well-developed mesic forests of the non-ultramafic side. For instance, 24 of the 35 indicator species are dry habitat associated herbs, and a number of species from other functional groups in this category are also associated with dry habitats. Similarly, Kruckeberg (1979, 1992) reported

higher richness of dry habitat associated species for ultramafic sites in British Columbia and Washington as compared with the surrounding floras.

Thirty-seven species are entirely or nearly excluded from ultramafic soils at the study site (Table 5). The main functional groups are deciduous broadleaved trees and shrubs (18 species) and mesic to moist habitat associated herbs (11 species). The exclusion of broad-leaved trees and shrubs from ultramafic soils has been previously documented (Whittaker 1954). These functional groups may be restricted to non-ultramafic substrates partly because of soil chemistry, and partly because the greater canopy cover, shade and soil moisture conditions better meet the habitat requirements of the particular species. The exclusion of dry habitat-associated herbs (six species) and the fern *Cheilanthes gracillima*, from ultramafic substrates is an interesting pattern since ample habitat appeared to be available on the ultramafic side of the mountain. These species may be directly excluded by ultramafic soil factors.

Thirty-four species representing all functional groups except ferns were widespread on all three soil types (Table 6). These *bodenvag* species may be exhibiting one of two responses to ultramafic soils: 1. they may be indifferent to the adverse chemical and physical soil environment or 2. those individuals occurring on ultramafic soils may represent edaphic races or ecotypes tolerant of soil conditions. Evidence for ecotypic differentiation has been shown for *bodenvag* species from California (Kruckeberg 1951; Rajakaruna and Bohm 1999) and the Pacific Northwest (Kruckeberg 1967). For example, Kruckeberg (1967) found strong ecotypic response in *Achillea millefolium* and *Potentilla glandulosa*, partial ecotypic response in *Antennaria racemosa*, *Juniperus communis*, *Pinus contorta*, *Pseudoroegneria spicata* and *Taxus brevifolia*. These species, therefore, may exist as ecotypic races on the different soil types. He found no ecotypic response in *Rubus parviflorus* which may simply be indifferent to ultramafic soil conditions.

We conclude that the ultramafic soils of Grasshopper Mountain exert an influence on plant growth which is similar to the vegetational response in Oregon and California. While richness and diversity levels are similar across substrates at Grasshopper Mountain, the floristics and ecological relationships are distinct. The presence of ultramafic soils within a matrix of nonultramafic soils is important for increasing local and regional diversity and for the maintenance of rare taxa. Decisions related to conservation and

management of ultramafic sites in British Columbia, as in other regions, should take into account their potential biological significance.

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Mean and Standard Errors for Selected Soil Variables for Ultramafic, Till-influenced and Non-Ultramafic Plots

Soil Variables	Soil Type					
	Ultramafic		Till		Non- Ultramafic	
	n = 26		n = 10		n = 35	
Ca meq/100g	4.045 +/- 0.415	а	4.633 +/- 0.962	а	10.126 +/- 0.926	b
Mg meq/100g	8.204 +/- 0.656	а	3.502 +/- 1.012	b	1.102 +/- 0.099	с
Ca:Mg	0.502 +/- 0.031	а	1.887 +/- 0.432	а	9.583 +/- 0.395	b
Ni ppm in soil	20.819 +/- 2.622	а	2.585 +/- 0.716	b	0.569 +/- 0.097	b

Table 1: Means and standard errors for selected soil variables for ultramafic, tillinfluenced and non-ultramafic plots. Shared letters denote a non-significant difference (p > 0.05) based on ANOVA results and the post-hoc Bonferroni adjustment.

Rare Taxa Found on Grasshopper Mountain Including Their Provincial Ranking and the Soil Type on Which They Occurred

Species	Ranking	Soil Type
Adiantum aleuticum (A. pedatum subsp. calderi)	_	Ultramafic
Aspidotis densa	—	Ultramafic
Arabis holboellii var. pinetorum	blue	Ultramafic
Cheilanthes gracillima	blue	Non-Ultramafic
Crepis atrabarba subsp. atrabarba	red	Primarily Ultramafic
Lupinus arbustus subsp. pseudoparviflorus	red	Ultramafic
Melica bulbosa var. bulbosa	blue	Ultramafic
Polemonium elegans	blue	Non-Ultramafic
Polystichum kruckebergii	blue	Ultramafic
Polystichum scopulinum	red	Ultramafic

Table 2: Rare taxa found on Grasshopper Mountain including their provincial ranking and the soil type on which they occurred. Rare vascular plant taxa have been defined through the work of the BC Conservation Data Centre and are summarized in Douglas et al. (1998). Red-listed species are taxa considered "candidates for legal designation as endangered or threatened species." Blue-listed species are "vulnerable rare taxa that could become candidates for the Red List in the foreseeable future."

Total Number of Species per Family for Ultramafic, Till and Non-
Ultramafic Plots

Family	Ultramafic	Till	Non- Ultramafic	Total
Apiaceae	5	1	2	5
Asteraceae	11	5	6	14
Betulaceae	0	2	3	3
Caprifoliaceae	0	1	2	2
Caryophyllaceae	3	1	1	3
Ericaceae	2	2	1	3
Fabaceae	2	1	2	2
Grossulariaceae	0	1	2	2
Gymnosperms	8	5	7	10
Hydrophyllaceae	1	0	1	1
Juncaceae	1	0	0	1
Liliaceae	4	5	7	7
Onagraceae	2	0	1	2
Orchidaceae	2	2	2	2
Poaceae	7	2	4	8
Polygonaceae	4	0	0	4
Pteridophytes	4	1	1	4
Pyrolaceae	1	1	1	2
Ranunculaceae	1	0	3	3
Rosaceae	5	5	11	12
Salicaceae	0	0	3	3
Saxifragaceae	1	0	1	2
Scrophulariaceae	3	1	4	5
Other	5	5	9	9

Table 3: Total number of species per family for ultramafic, till, and non-ultramafic plots, and total across all three soil types. The gymnosperms, pteridophytes, and "other" are represented by three, two and 13 families, respectively.

Local Ultramafic Indicator Species: Species Restricted to or Found Primarily on Ultramafic Soils at Grasshopper Mountain

Functional Group	Species
Deciduous broad-leaved shrubs and trees	Rosa nutkana
Evergreen coniferous shrubs and trees	Juniperus communis var. montana Pinus albicaulis * Taxus brevifolia †
Evergreen broad-leaved shrubs	Arctostaphylos uva-ursi
Mesic to moist habitat-associated herbs	Cirsium edule ‡ Lupinus arcticus subsp. subalpinus
Dry habitat-associated herbs	Achillea millefolium var. Ianulosa Antennaria racemosa ‡ Arenaria capillaris subsp. americana ‡ Astragalus miser var. serotinus ‡ Bromus carinatus Castilleja hispida var. hispida (yellow form) Cirsium hookerianum ‡ Crepis atrabarba subsp. atrabarba ‡ Epilobium minutum Eriogonum heracleoides var. angustifolium ‡ Eriogonum ovalifolium var. nivale ‡ Eriogonum umbellatum ‡ Koeleria macrantha ‡ Lomatium macrocarpum‡ Luzula multiflora subsp. multiflora Melica subulata Phacelia hastata var. hastata ‡ Pseudoroegneria spicata subsp. inermis ‡ Senecio canus ‡ Senecio integerrimus var. exaltatus ‡ Silene parryi
Ferns	Adiantum aleuticum (A. pedatum subsp. calderi) Aspidotis densa Polystichum kruckebergii Polystichum scopulinum
Total Number of Indicator Species	35

Table 4: Local ultramafic indicator species: species restricted to or found primarily on ultramafic soils at Grasshopper Mountain. ‡ denotes an interior species occurring at the western edge of its range. † denotes a coastal species occurring at the eastern edge of its range. * denotes a species occurring at the lower limits of its altitudinal range.

Local Ultramafic Excluded Species: Species Restricted to or Found Primarily on Non-Ultramafic Soils at Grasshopper Mountain

Functional Group	Species
Deciduous broad-leaved shrubs and trees	Acer glabrum var. douglasii Alnus viridis subsp. sinuata Betula papyrifera var. papyrifera Holodiscus discolor Lonicera involucrata Lonicera utahensis Philadelphus lewisii Populus tremuloides Prunus virginiana Ribes lacustre Ribes viscosissimum ‡ Rosa gymnocarpa Salix spp approximately 3 species Shepherdia canadensis ‡ Spiraea betulifolia subsp. lucida ‡ Symphoricarpos albus
Evergreen broad-leaved shrubs	Ceanothus velutinus var. velutinus ‡ Penstemon fruticosus ‡
Mesic to moist habitat-associated herbs	Actaea rubra Arnica cordifolia ‡ Aster conspicuus ‡ Clintonia uniflora Fragaria vesca var. americana Fragaria virginiana var. platypetala Orthilia secunda var. secunda Pedicularis bracteosa var. latifolia Prosartes hookeri var. oregana Thalictrum occidentale Valeriana sitchensis
Dry habitat-associated herbs	Allium cernuum var. cernuum Antennaria rosea Arabis exilis ‡ Arabis holboellii Artemisia michauxiana ‡ Heuchera cylindrica ‡
Ferns	Cheilanthes gracillima +
Total Number of Excluded Species	37

Table 5: Local ultramafic excluded species: species restricted to or found primarily on non-ultramafic soils at Grasshopper Mountain. [‡] denotes an interior species occurring at the western edge of its range. ⁺ denotes a southerly species occurring at the northern edge of its range.

Widespread (*Bodenvag*) Species: Species Found Commonly on All Soil Types at Grasshopper Mountain

Functional Group	Species
Deciduous broad-leaved shrubs and trees	Amelanchier alnifolia Prunus emarginata Rubus parviflorus Vaccinium membranaceum
Evergreen coniferous shrubs and trees	Abies lasiocarpa var. lasiocarpa ‡ Pinus contorta var. latifolia Pinus monticola Pinus ponderosa ‡# Picea engelmannii ‡ Pseudostuga menziesii var. ? (study site on border of varietal ranges) ‡†
Evergreen broad-leaved shrubs	Mahonia aquifolium Pachistima myrsinites
Mesic to moist habitat-associated herbs	Angelica arguta Aquilegia formosa subsp. formosa Aster engelmannii ‡ Bromus vulgaris Epilobium angustifolium subsp. angustifolium Erythronium grandiflorum subsp. grandiflorum Goodyera oblongifolia Lilium columbianum Maianthemum racemosum subsp. amplexicaule Osmorhiza sp. Viola glabella
Dry habitat-associated herbs	Agoseris aurantiaca subsp. aurantiaca Calamagrostis rubescens ‡ Carex rossii Fritillaria affinis var. affinis Hieracium scouleri var. griseum ‡ Lomatium dissectum var. multifidum ‡ Pedicularis racemosa Piperia unalascensis Sedum lanceolatum var. lanceolatum
Dry to moist habitat associated herbs	Castilleja miniata (orange form) Moehringia macrophylla +
Total Number of Bodenvag Species	34

Table 6: Widespread (*bodenvag*) species: species found commonly on all soil types at Grasshopper Mountain. [‡] denotes an interior species occurring at the western edge of its range. [†] denotes a coastal species occurring at the eastern edge of its range. ⁺ denotes a southerly species occurring at the northern edge of its range. [#] denotes a species occurring at the upper limits of its altitudinal range.