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Soil Characteristics Associated with Wild Huckleberry and Bilberry Colonies in the Northwestern United States: Implications for Managed Production and Cultivation

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Summary. With few exceptions, huckleberries and bilberries (*Vaccinium spp*.) native to western North America have not been managed in native stands or cultivated in fields. With efforts underway to produce these crops commercially under cultivated or managed conditions, more information is needed on soil requirements. Soil samples collected from naturally occurring huckleberry and bilberry colonies in Idaho, Washington, Oregon, Montana, and Wyoming were analyzed to determine physical and chemical characteristics of the soils. Soil texture and pH were the most consistent soil factors associated with the colonies. Acidic loams and sandy loams, followed by silt loams were the most common soil textures across species. *Vaccinium uliginosum* Linnaeus (alpine bilberry) and *V. membranaceum* Douglas ex Hooker (black, thin-leaf, or mountain huckleberry) were associated with wider ranges of soil textures than the other species. *Vaccinium deliciosum* Piper (Cascade huckleberry) and *V. uliginosum* were often found on seasonally wet soils adjacent to ponds, streams, and dry lakebeds. Soil pH values for individual collection sites ranged from 3.6 (*V. ovalifolium* Smith, oval-leaved bilberry or Alaska blueberry) to 6.2 (*V. membranaceum*), averaging 5.0 for all combined samples. Highly variable nutrient concentrations, even between samples from vigorous, fruitful colonies of the same species, suggest that these species tolerate relatively wide ranges of soil macro- and micronutrient concentrations. Although some of the soils were highly influenced by volcanic ash, many were not and volcanic ash does not appear to be required for survival and growth of these species. These results suggest that, with the exceptions noted above, a suitable site for cultivation or management of these crops will have a well-drained loam, sandy loam, or for *V. membranaceum* and *V. uliginosum*, silt loam soil with pH between 4.0 and 5.3.
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Despite a long history of commercial use, huckleberries and bilberries native to western North America have been harvested almost exclusively from the wild, rather than being grown in cultivation like highbush blueberries (*V. corymbosum*) and rabbiteye blueberries (*V. ashei*) or harvested from managed native stands, as for eastern lowbush blueberries (*V. angustifolium* and *V. myrtilloides*). The exception is *Vaccinium ovatum* Pursh (evergreen huckleberry), which has been cultivated on a small scale along the Pacific Coast in North America and harvested both for its fruits and ornamental foliage. At least five of the species described in this paper have long histories of domestic and/or commercial utilization and commercial demands are increasing. Recent research has also shown that some of these crops are rich sources of anthocyanins, antioxidants, and polyphenolic compounds with potential to benefit human health (Taruscio et al., 2004; Lee et al., 2004). Prospects for expanding the huckleberry and bilberry industries appear promising (Barney, 2003a).

While demands for culinary and medicinal/nutritional huckleberry and bilberry products have increased, supplies of these fruits from wild stands have dwindled (Minore, 1972). In 1994 the University of Idaho began efforts to produce these crops in cultivated fields and managed, forest colonies. Seed and in vitro propagation methodologies have been published for *V. membranaceum* (Barney, 2003b; Barney and Shafii, 2001; and Shafii and Barney, 2001) and similar trials on other species are underway. A germplasm evaluation and cultivar development program is also underway (Barney, 2004).

A critical factor in crop production is selecting a suitable site. Aside from research on *V. membranaceum* (Minore and Dubrasich, 1978; Stark and Baker, 1992), no comprehensive characterization of soil properties for these crops in western North America has been conducted. Much has been published on soil influences for highbush and lowbush blueberries in eastern North America (Kender and Eggert, 1966; Korcak, 1989; Finn et al., 1993a and 1993b), *V. myrtillus* Linnaeus (bilberry) in Europe (Ingestad, 1973), and *V. uliginosum* in Europe and Canada (Jacquemart, 1975).

Vaccinium species, like other members of the Ericaceae family, require acidic soils and are classified as calcifuges (Ingestad, 1973; Jacquemart, 1975; Korcak, 1988). According to Brown and Draper (1980) the optimum soil pH for good blueberry growth is between 4.0 and 5.2, with iron chlorosis symptoms often appearing at pH levels above 5.2. Korcak (1988) suggested a pH range of 4.5 to 5.5, with a lower limit of about 3.2. In testing 60 *V. angustifolium* soils, however, Vander Kloet (1978) observed a pH range from 2.8 to 6.6. Rorison (1986) observed that plants most capable of surviving acid soils are those with inherently slow growth rates and low nutrient requirements.

With the exception of bog-dwelling species, *Vacciniums* are usually found on moist, well-drained loamy sand or sandy loam soils that are high in organic matter and low in calcium and available nutrients (Finn et al., 1993a; Ingestad, 1973; Kender and Eggert, 1966; Korcak, 1986). Commercial highbush blueberry production, for example, is largely limited to imperfectly drained acid sand and peat soils, although rabbiteye blueberry (*V. ashei*) grows on both upland and lowland soils that range in texture from clay to sandy loams. Even with its greater soil adaptability, rabbiteye blueberry performs best on light, well-drained acidic soils with pH between 4.5 and 5.5 (Luby et al., 1990). *Vaccinium uliginosum* also requires acidic soils low in nutrients, but is typically found on moist to wet, shallow, poorly drained soils (Jacquemart, 1975).

Vaccinium adaptation to low-nutrient soils has been observed in multiple species (Ingestad, 1973; Jacquemart, 1975; Rorison, 1986). *Vaccinium* roots and rhizomes tend to be shallow and, in some cases, may lie entirely within the litter horizon. Ingestad (1973) regarded the litter horizon as the dominant nutrient source, although observing that deeper roots may be found on old rhizomes. *Vaccinium* species commonly form associations with ericoid mycorrhizae, and these associations influence uptake of plant nutrients (Haynes and Swift, 1985; Korcak, 1989; Raisa, 1999). Korcak (1989) and Raisa (1999) also concluded that soil organic matter, the presence of surface litter, and soil horizons affect mycorrhizal development and, therefore, nutrient uptake by *Vaccinium* plants. Soil pH may have implications other than direct effects on the *Vaccinium* roots and plant nutrient availability. In a greenhouse peat medium study, Haynes and Swift (1985) found the percentage of mycorrhizal infection was much greater at pH 4.5 than pH 6.5.

Vaccinium species are typically associated with organic-rich soils (Finn et al., 1993a; Jacquemart, 1975); Korcak, 1989; Luby et al., 1990). The term “rich,” however, is relative. According to Korcak (1987) the organic matter requirement for *Vaccinium* can be satisfied by as little as 2-4% organic matter. *Vaccinium* colonies can be associated with an organic surface (litter or duff) layer (Jacquemart, 1975; Korcak, 1987; Stark and Baker, 1992) that has implications for *Vaccinium* management and cultivation. Under certain conditions a thick mulch of peat, sawdust, or other organic matter is required for optimum *Vaccinium* growth and production (Korcak, 1987). Raisa (1999) concluded that *V. myrtillus* and *V. vitis-idaea* Linnaeus (lingonberry) distributions reflect the nitrogen concentrations of the humus layer.

Subsurface soil layers may also be important in *Vaccinium* distribution and productivity. Korcak (1989) noted that blueberry roots in a layered soil are concentrated in the more decomposed organic material and develop endomycorrhizal associations of the ericoid type. The more decomposed a material is, the lower it typically lies in the soil profile. Kender and Eggert (1966) observed that *V. angustifolium* plants grew more vigorously on an undisturbed, rather than a homogenized or tilled soil.

Studies with *V. globulare* (syn. *V. membranaceum*; Vander Kloet, 1988) support the general rules for *Vaccinium* soil optima. Stark and Baker (1992) concluded that suitable soils have low bulk density (< 0.8 g/cc) but high water-holding capacity (>24% w:w). Volcanic ash soils may favor huckleberry production because such soils have low bulk densities and high water-holding capacity. *Vaccinium globulare* produces shallow roots and rhizomes, and the top 10-20 cm of soil are the most important for huckleberry health. Survival and production on compacted and heavy-textured soils was observed to be poor and the best soils to have a fine, loamy texture with combined clay and silt content less than 40%. A key to productivity appeared to be high concentrations of rotten wood in and on the soil. This was determined to be especially important on heavier-textured soils, where the huckleberry roots and rhizomes may exist mostly in the surface organic layer. The best huckleberry growth occurred on soils with more than 30% organic matter. Stark and Baker concluded that, under northwestern Montana conditions, the best *V. globulare* growth and production occurs on soils with pH 4.0 to 5.5, but production is possible at pH 6.8 if the correct balance of nutrients is available. Minore and Dubrasich (1978) evaluated soil pH and other physical and biological factors related to the distribution and fruit production of *V. membranaceum* near Mt. Adams in south-central Washington. They found that soil pH correlated with abundance of *V. membranaceum* across the site. Regression analyses indicated an optimal pH of 5.5.

The purpose of our soil survey was to identify the soil physical and chemical characteristics associated with *Vaccinium* species over large areas of their ranges in the northwestern United States.

Materials and methods

We collected soils from colonies of *V. caespitosum* Michaux (dwarf huckleberry), *V. deliciosum*, *V. membranaceum*, *V. myrtillus*, *V. ovalifolium* (synonymous with *V. alaskaense* Howell and *V. chamissonis* Bong.; Vander Kloet, 1988), *V. ovatum*, *V. parvifolium* Smith (red huckleberry), and *V. uliginosum* in Idaho, Oregon, Washington, Montana, and Wyoming (Table 1). Because these species have shallow root systems, soil samples were collected to depths of 15 cm using a trowel after removing the surface duff layer. One sample for each site and species combination was collected from the base of a representative plant.

Soil samples were air-dried and crushed in a mortar to pass a 2-mm sieve. Particle-size distribution of bulk samples was determined by a combination of sieving and sedimentation procedures following digestion of organic matter with NaOCl (pH 9.5) and dispersion of soil particles using Na hexametaphosphate (Gee and Bauder, 1986). Chemical properties were determined using the following methods: pH (H_2O) of saturated paste (Richards, 1954); organic matter by wet digestion with $K_2Cr_2O_7$ (Sims and Haby, 1971); exchangeable cations by ammonium acetate (pH 7) extraction (Thomas, 1982); available phosphorus and potassium extracted with 0.75 N sodium acetate (Gavlak et al., 1994); ammonia and nitrate extracted with 2M KCl and analyzed by flow injection analysis (Westfall et al.,1982; 1993); sulfate-S extracted with 0.01 M calcium phosphate solution (Kalra and Maynard, 1991; Gavlak et al., 1997); micronutrients (Cu, Mn, Fe, Zn) by DTPA extraction (Lindsay and Norvell, 1978); and water soluble boron by the pouch method (McGeehan et al., 1989). The relative influence of volcanic ash was determined by NaF pH (Fieldes and Perrott, 1966). Samples with a NaF pH of 9.4 or greater were categorized as having high volcanic ash influence. General environmental observations of the plants in their respective colonies are included in this report.

Results and discussion

Particle size distribution analyses showed that loams, sandy loams, and silt loams were the most common soil textures associated with the *Vaccinium* species sampled, although *V. membranaceum* and *V. uliginosum* were collected from broader ranges of soils than the other six species (Table 2). These results are consistent with reported findings for other *Vaccinium* species, as described in the preceding section. How soil type impacts plant survival and growth is not necessarily clear, however. In his studies with *V. corymbosum* and hybrids of *V. corymbosum* with *V. angustifolium*, *V. darrowii*, *V. atrococcum*, and *V. ashei*, Korcak (1986) found that while soil type can have pronounced effects on plant growth and rooting, the growth differences were due to soil characteristics other than particle size distribution.

Vaccinium membranaceum soils ranged from loamy sands to clay loams. In the case of *V. membranaceum,* more soil samples were available than for the other species. The ability to sample from many sites may have contributed to the finding of greater soil adaptability of V. membranaceum. Luby et al. (1990), however, noted that *V. membranaceum* is, apparently, a very plastic and polymorphic derivative of several species, including *V. chamissonis*, *V. caespitosum*, *V. scoparium*, and *V. myrtillus*. Genetic differences within and between species affect plant adaptability to varying soil conditions (Brown and Draper, 1980; Finn et al., 1993b). Survival does not necessarily correlate well with productivity. Stark and Baker (1992) observed that, while *V. globulare* tolerated a range of soil textures, the best huckleberry soils were characterized by low bulk densities. *Vaccinium membranaceum* grows from Alaska through British Columbia, Alberta, south to northern California, eastern Idaho and Montana with disjunct populations in Arizona and northern Michigan (Vander Kloet, 1988). It is found on mountain slopes; on dry, open sites in coniferous forests; and is abundant in many clear cut tracts (Luby et al., 1990). Observations of field-cultivated plants and native stands (Barney, unpublished data) suggest that *V. membranaceum* is intolerant of poorly drained soils.

We collected *V. uliginosum* from sites with soil textures ranging from loamy sands to clay loams. *Vaccinium uliginosum* also has a complex genetic makeup that allows it to colonize sites across a great range of latitudes, elevations, and habitat types (Jacquemart, 1975; Luby et al., 1990; Young, 1970). *Vaccinium uliginosum* is a characteristic tundra shrub native to boreal, alpine, and arctic regions, extending southward into the temperate zone in coastal and mountain areas in North America, Asia, and Europe from 38^o to 80^o north latitude (Young, 1970; Vander Kloet, 1988). With the exception of one sample from an upland site in a whitebark pine forest lying above the Little Popo Agie River in Wyoming, we found *V. uliginosum* along the shores of small subalpine lakes, in boggy subalpine meadows, seasonally wet meadows, or on mountain stream banks. Our observations are consistent with other populations of *V. uliginosum* that colonize shallow, poorly-developed montane-heath soils; waterlogged podosols of upland heaths; poorly-drained podosols of birch woods; organic soils in humus and peaty bog communities; sometimes on calcareous soils of calciolus grasslands in Scandinavia and Scotland; peaty woodlands, tundra (Jacquemart, 1975); dry peaty barrens, exposed outcroppings, talus slopes, and headlands (Luby et al., 1990).

Vaccinium caespitosum and *V. deliciosum* occurred on many of our collection sites growing alongside or close to *V. uliginosum* and were abundant on some seasonally wet meadows and organic soils alongside ponds. *Vaccinium caespitosum* exhibited the greatest variety of habitats, ranging from a boggy pond bank to steep droughty hillsides. *Vaccinium deliciosum* also grew on seasonally wet soils, extending its colonization upland onto dryer soils forest. Other than one *V. caespitosum* colony on a silt-loam soil, however, both species were found on sites with underlying mineral, loam or sandy loam soils. These observations are consistent with other reports. *Vaccinium caespitosum* is widely distributed, very plastic, and polymorphic (Luby et al., 1990). It occurs from south-central Alaska through British Columbia, south in the Rocky Mountains to Arizona and south through the Cascades and Sierra Nevada, east at scattered locations from Minnesota through New York, New Hampshire, Vermont, Maine, and Labrador (Vander Kloet, 1988). In the Pacific Northwest, *V. caespitosum* ranges from sea level to 2000 m elevation and is found in wet meadows, mountain slopes, moist rocky ledges, subalpine forests, and alpine tundra (Luby et al., 1990). *Vaccinium deliciosum* is distributed from southwestern British Columbia south through the Cascade Mountains in central Oregon and also in the Olympic Mountains where it grows in open areas in subalpine forests and meadows and alpine tundra (Luby et al., 1990).

Four of the five *V. ovalifolium* collection sites were on loam soils, with one site having a sandy loam. Sites ranged from moist but reasonably well drained sites slightly upslope in riparian areas to coniferous woodlands. This finding is consistent with Luby et al. (1990) who describe *V. ovalifolium* in the northwestern United States and western Canada as typically growing on raw humus in moist coniferous forests. Vander Kloet observed that *V. ovalifolium* in western North America is native to moist or mesic coniferous woods and transitional habitats adjacent to these woods, including peaty slopes, subalpine shrubberies and ravines, and on drier and more open habitats on inland sites. *Vaccinium ovalifolium* is concentrated in the Northwestern United States northward to southern Alaska with disjunct populations in South Dakota, the Upper Great Lakes Region, and Cape Breton Island and Newfoundland in Canada (Vander Kloet, 1988). Seed collections have also been made from Japan and Sakhalin Island in the Russian Federation (U.S.D.A. 2006).

We collected *V. myrtillus*, *V. parvifolium* and *V. ovatum* from forest sites on well drained loam and/or sandy loam soils. *Vaccinium parvifolium* was approximately equally distributed between the loam and sandy loam soils. *Vaccinium parvifolium* is fairly widespread at low to intermediate elevations on the west slopes of the coastal ranges from Alaska to northern California and occurs inland to southeastern British Columbia Luby et al., 1990).

Unfortunately, as we were limited to single samples of *V. myrtillus* and *V. ovatum*, we can draw no conclusions as to optimal soil textures for these species. *Vaccinium myrtillus* is widely distributed in northern Europe and Asia where it occurs in lowland to alpine open pine or spruce forests, mostly on moist, humus, or peaty soils. In the northwestern United States and Rocky mountains, *V. myrtillus* grows in moist, open sites in montane or subalpine communities, often in clear cut areas or regenerating pine or spruce/fir forests. The species is native from Alaska and Alberta to New Mexico, west to British Columbia, south through the Cascade Mountains to central Oregon. *Vaccinium myrtillus* appears much less frequently through this range than other *Vaccinium* species (Luby et al., 1990). *Vaccinium ovatum* is native only along the Pacific coast from southern California to central British Columbia (Vander Kloet, 1988).

All soils we sampled were acidic, ranging from pH 3.6 to 6.2 and averaging pH 5.0 across species and sites (Table 3). This finding is consistent with published reports for *Vaccinium* species generally (Korcak, 1988; Luby et al., 1990), European and Canadian populations of *V. uliginosum* (Jacquemart, 1975), European populations of *V. myrtillus* (Ingestad, 1973), and *V. membranaceum* (*globulare*) growing in Montana and Washington State (Minore and Dubrasich, 1978; Stark and Baker, 1992).

Soil organic matter concentrations were highly variable, ranging from 1% to 60% (Table 3). Soil samples exhibiting organic-rich, poorly drained, wetland (histic) properties were associated with 80% of the *V. deliciosum,* 50% of the *V. uliginosum*, and 40% of the *V. ovalifolium* sites. Although we did not sample the litter or duff layers, virtually all sample sites in this survey had surface layers of intact to partially decomposed forest or wetland organic matter. Decomposing wood on the soil surface and within the soil profile was abundant on many of the collection sites, and we frequently observed roots and rhizomes from *Vaccinium* species colonizing the duff layer or penetrating into decomposed stumps and fallen trunks. Our observations are consistent with those made by other investigators (Jacquemart, 1975; Korcak, 1987; Stark and Baker, 1992). These observations suggest that maintenance of forest litter in managed forest stands or organic mulches in field cultivation of western *Vaccinium* species may be beneficial.

Macro- and micronutrient concentrations (Tables 3 and 4) varied widely, even within species. Ammonium-nitrogen concentrations averaged higher than nitrate-nitrogen concentrations for all species. Relatively high concentrations of both ammonium- and nitrate-nitrogen are likely due to two factors. First of all, average organic matter contents of the soils are relatively high, reflecting the poorly drained or higher-elevation environments. Secondly, because we were unable to air-dry samples immediately, there was considerable mineralization of organic nitrogen following sample collection. It is clear, however, that many of the *Vaccinium* soils are characterized by relatively large quantities of organic matter and mineralizable nitrogen.

The wide variations seen in soil nutrient concentrations are consistent with observations reported by Raisa (1999) who found no differences in optima for *V. myrtillus* and *V. vitis-idaea* along nutrient gradients. Raisa suggested that light and moisture may be more important factors determining site dominance of these species, although it seems clear from the present and other studies that soil pH is also a critical factor affecting *Vaccinium* distribution. Western *Vaccinium* species' tolerance of wide ranges of soil nutrient profiles is also consistent with observations that *Vaccinium* species, in general, are adapted to nutrient-poor soils (Ingestad, 1973; Jacquemart, 1975; Rorison, 1986).

Of the 56 soil samples analyzed, 48% were categorized as high volcanic ash influenced soils. It is clear that volcanic ash-influenced soils are not required for *Vaccinium* growth. However, there does appear to be considerable overlap between the environments in which volcanic ash is found and those that support many of western North America's *Vaccinium* species.

Conclusions

From the perspective of selecting a growing site or expanding a native stand, soil texture and pH were the most consistent soil factors associated with naturally occurring western huckleberry and bilberry colonies during our survey. Well-drained, acidic loams and sandy loams appear suitable for cultivating all of the species surveyed. Well-drained silt loams also appear suitable for *V. membranaceum*, as do loamy sands, provided adequate irrigation is available. *Vaccinium uliginosum* is also adapted to silt loams, loamy sands, and organic, peat soils. *Vaccinium uliginosum* and *V. deliciosum* tolerate seasonally wet soils, as well as drier, upland soils, although the effects of poor soil drainage on fruit production remain to be determined. As all of these species have been successfully grown in container culture in peat-moss or bark-based potting soils, production on organic, peat soils may be feasible if appropriate pH and water drainage are provided.

Soil pH values between 4.0 and 5.3 appear suitable for all surveyed species. Production on soils up to pH 6.2 seems possible for *V. membranaceum*, given that other soil and environmental conditions are favorable. Highly variable nutrient concentrations, even between vigorous, fruitful colonies of the same species, suggest that naturally-occurring colonies of western huckleberries and bilberries tolerate relatively wide ranges of soil macro- and micronutrient concentrations. Likewise, high concentrations of soil organic material or high volcanic ash influence do not appear to be necessary for plant vigor and berry production. For managed production and cultivation, a target of 4% or greater organic matter would seem appropriate. Application of an organic mulch or maintenance of natural forest litter may be beneficial to plant survival and productivity.

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Table 1. Collection sites for huckleberry and bilberry soils.

National Forest	Species [z]							
	CP	DE	ME	MS	OF	OV	PA	UG
Idaho								
Boise N.F.	1	0	1	0	0	0	0	1
Clearwater N.F.	0	0	0	0	0	0	0	0
Kaniksu N.F.	1	0	2	0	1	0	0	0
Nez Perce N.F.	0	0	1	0	0	0	0	0
St Joe N.F.	0	0	1	0	0	0	0	0
Targhee N.F.	0	0	2	0	0	0	0	0
Montana								
Beaverhead-Deer Lodge N.F.	0	0	0	0	0	0	0	1
Bitterroot N.F.	0	0	1	0	0	0	0	0
Flathead N.F.	1	0	2	0	0	0	0	0
Gallatin N.F.	0	0	1	0	0	0	0	0
Lolo N.F.	1	0	2	0	0	0	0	0
Oregon								
Deschutes N.F.	1	0	0	0	0	0	0	1
Mount Hood N.F.	0	1	1	0	2	0	2	2
Willamette N.F.	0	1	2	1	0	0	0	1
Washington								
Colville N.F.	1	0	0	0	0	0	0	0
Gifford Pinchot N.F.	1	1	3	0	0	0	1	0
Mt. Baker-Snoqualmie N.F.	0	0	1	0	0	0	0	0
Okanogan N.F.	0	0	1	0	0	0	0	0
Olympic N.F.	0	0	0	0	3	1	5	0
Wenatchee N.F.	0	2	1	0	1	0	0	0
Wyoming								
Shoshone N.F.	0	0	1	0	0	0	0	1

[z] CP = *V. caespitosum*, DE = *V. deliciosum*, ME = *V. membranaceum*, MS = *V. myrtillus*, OF = *V. ovalifolium*, OV = *V. ovatum*, PA = *V. parvifolium*, UG = *V. uliginosum*

Table 2. Physical characteristics of native huckleberry and bilberry soils. Columns show the number and percentage of samples falling within each textural class and high volcanic ash concentration designations.

Species	Clay Loam	Silty Clay Loam	Silt Loam	Loam	Sandy Loam	Loamy Sand	High Volcanic Ash Soils
V. caespitosum	0	0	1 (14%)	3 (43%)	3 (43%)	0	3 (43%)
V. deliciosum	0	0	0	2 (50%)	2 (50%)	0	2 (40%)
V. membranaceum	1 (4%)	1 (4%)	6 (25%)	7 (29%)	5 (21%)	4 (17%)	12 (52%)
V. myrtillus	0	0	0	1 (100%)	0	0	1 (100%)
V. ovalifolium	0	0	0	4 (80%)	1 (20%)	0	2 (29%)
V. ovatum	0	0	0	0	1 (100%)	0	1 (100%)
V. parvifolium	0	0	0	4 (57%)	3 (43%)	0	5 (63%)
V. uliginosum	2 (29%)	0	1 (14%)	1 (14%)	2 (29%)	1 (14%)	3 (38%)
Totals	3 (5%)	1 (2%)	8 (14%)	22 (39%)	17 (30%)	5 (9%)	29 (48%)

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Table 3. Mean pH, organic mater, and micronutrient concentrations in native huckleberry and bilberry soils with ranges in parentheses.

Species	pH	Organic Matter (%)	Boron (ppm)	Copper (ppm)	Iron (ppm)	Manganese (ppm)	Zinc (ppm)
V. caespitosum	5.1	6.5	0.25	0.51	136.1	70	4.1
	(4.3-5.4)	(3.4-9.5)	(<0.1-0.6)	(0.3-0.8)	(81-200)	(5.0-240)	(0.3-16)
V. deliciosum	4.9	25.8	0.7	1.0	582.5	13.4	4.8
	(3.9-5.6)	(13.0-55)	(0.5-1.2)	(0.2-1.7)	(180-1100)	(1.3-23)	(0.3-14)
V. membranaceum	5.2	10.1	0.4	0.9	165.0	71.0	4.0
	(3.7-6.2)	(1.1-52)	(<0.1-1.5)	(0.2-2.3)	(40-510)	(2.3-330)	(0.2-20)
V. myrtillus	5.2	16.0	0.1	0.5	140.0	110.0	0.9
V. ovalifolium	4.5	22.8	0.7	1.4	438.6	89.9	6.5
	(3.6-5.3)	(6.5-59)	(<0.1-1.6)	(0.2-3.5)	(110-1100)	(7.1-500)	(0.4-20)
V. ovatum	5.2	13.0	0.2	1.7	180.0	71.0	1.4
V. parvifolium	4.9	16.9	0.5	1.5	431.3	46.8	5.6
	(3.9-5.6)	(4.0-60)	(<0.1-1.6)	(0.4-4.4)	(130-2000)	(14.0-150)	(0.3-32)
V. uliginosum	5.1	21.9	0.4	2.5	310.5	19.6	2.0
	(4.3-5.7)	(5.3-56)	(0.1-0.9)	(0.2-14)	(72-770)	(0.6-75)	(0.2-5.8)

Table 4. Macronutrient characteristics of native huckleberry and bilberry soils. Columns show averages with value ranges in parentheses.

Species	NO_3-N (ppm)	NH_4-N (ppm)	Phosphorus (ppm)	Potassium (ppm)	SO_4-S (ppm)	Calcium (cmolc/kg)	Magnesium (cmolc/kg)
V. caespitosum	14.9	25.2	5.2	110.6	6.0	3.9	0.8
	(<0.8-80)	(4.1-96)	(2.2-16)	(60-180)	(3.6-12)	(1.4-5.9)	(0.3-1.2)
V. deliciosum	62.9	510.2	4.0	236	42.4	4.9	1.4
	(<0.8-170)	(31-1200)	(1.5-8.4)	(110-360)	(8.7-110)	(2.5-8.1)	(0.7-2.0)
V. membranaceum	13.0	64.4	9.9	198.3	11.4	6.1	1.5
	(<0.8-120)	(2.0-640)	(1.0-79)	(33-810)	(2.3-27)	(0.7-21)	(0.1-7.4)
V. myrtillus	1.2	60.0	2.9	100.0	4.5	3.6	0.7
V. ovalifolium	40.4	157.5	9.9	160.1	17.0	4.1	1.6
	(<0.8-130)	(6.7-740)	(<1.0-45)	(60-470)	(5.8-39)	(0.6-11)	(0.1-4.3)
V. ovatum	1.5	24.0	3.4	77.0	7.7	4.3	1.3
V. parvifolium	130.9	180.4	5.5	136.8	22.4	5.3	1.8
	(<0.8-820)	(8.8-1200)	(2.0-11)	(50-410)	(5.8-110)	(0.7-17)	(<0.02-7.6)
V. uliginosum	61.9	320.4	16.7	223.4	35.0	7.7	2.3
	(1.0-190)	(2.7-800)	(<1.0-120)	(54-660)	(5.8-100)	(2.3-24)	(0.6-7.3)