The Relationships Between Substrate and Ten "Western Disjunct" Plant Species in the Northern Great Lakes Region

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INTRODUCTION

Field observations of ten Western North American plant species belonging to seven families, and disjunct in the Great Lakes region were conducted during Boreal Flora class trips in the northern Great Lakes region.

Marquis and Voss (1981) stated the principal criterion to be used in considering a species to be a "western disjunct"--being a distinct discontinuity in distribution between the Great Lakes region and the west. Based on the above criterion, the species observed can be grouped into four categories following the above authors:

I. Species found in the Western United States and the Great Lakes Region
   A. without a disjunction in the Black Hills of South Dakota: Crataegus douglasii Lindley, Festuca occidentalis Hooker.
   B. with a disjunction in the Black Hills of South Dakota: Adenocaulon bicolor Nutt., Melica smithii (Gray) Vasey, Rubus parviflorus Nutt., Vaccinium membranaceum Britton.

II. Species found in the Western United States, the Great Lakes region, and the St. Lawrence area.
   A. without a disjunction in the Black Hills: Arabis holboellii Hornem., Vaccinium ovalifolium Sm.
   B.with a disjunction in the Black Hills: Goodyera oblongifolia Raf., Osmorhiza chilensis H. & A.

The purpose of this paper is to report and to discuss observations made on the relationship between substrate and the species mentioned above, as reflected by the physical characteristics of their habitat(s), their fidelity to certain habitats, their plant associates and their fidelity to some of them, and their distribution in certain habitats in the northern Great Lakes region.

Tables 1-10 list the sites and the dates on which the disjunct species were observed. Unless stated otherwise, remarks and/or discussion of the relationships between the species in question and their substrate are based on field observations and pH tests,which were conducted on soil samples taken at root level zone at ca. 2-5 cm. from the surface.

The species observed will be discussed species-by-species according to the above categories of distribution. Our observations may offer some insight into some of the phytogeographical problems these species present, and especially to previous observations (Voss and Marquis, 1981) which recorded association between the discontinuity of distribution of these species and absence of favorable conditions in some cases, and no association in other cases.

TABLES 1-10:
Sites in the Northern Great Lakes Region at which the "Western disjunct" species were observed.

Table 1: Crataegus douglasii Lindley
MI: Alger Co.: Pictured Rocks National Lakeshore, "Devil's Slide" (Log Slide), west end of Grand Sabal Dunes Complex, July 14,1988.

Table 2: Festuca occidentalis Hooker
a. MI: Emmet Co.: Wilderness State Park, Waugoshance Pt., Mt. Nebo area, June 20, 1988.
b. MI: Alger Co.: Pictured Rocks National Lakeshore, Grand Sabal Dunes Complex, west of Sabal Creek, Jack Pine woods, July 14, 1988.

Table 3: Adenocaulon bicolor Hooker
a. MI: Luce Co.: Tahquamenon River Upper Falls area, June 30, 1988.
b. MI: Alger Co.: Pictured Rocks National Lakeshore, east end of Grand Sabal Dunes Complex, July 14, 1988.

Table 4: Melica smithii (Gray) Vasey
a. MI: Luce Co.: Tahquamenon River Upper Falls area, June 30, 1988.
b. Mi: Emmet Co.: South side of Galloway Lake, ca. 1 mile N of Levering, hardwoods, July 18, 1988.

Table 5: Rubus parviflorus Nutt.
a. MI: Emmet Co.: Cecil Bay (sec. 25, Wawatam Tp.), June 20, 1988.
b. MI: Emmet Co.: ca. 1 mile W of Cross Village, deciduous forest, July 7, 1988.
c. MI: Emmet Co.: Mackinow City, Perrot St., S of west end of M.C. school yard, July 11, 1988.
d. Canada,Ontario: Algoma District: left side of Route 17 opposite Sault Ste. Marie hundred km. sign, July 25, 1988.
e. MI: Cheboygen Co.: Grass Bay, ca. 4.5 miles of E of Cheboygan, July 28, 1988.

Table 6: Vaccinium membranaceum Britton
MI: Alger Co.: Grand Sabal Lake parking lot, July 14, 1988.

Table 7: Arabis holboellii Hornem.
MI: Emmet Co.: Wilderness State Park, Big Stone Bay, June 20, 1988.

Table 8: Vaccinium ovalifolium Sm.
MI: Chippewa Co.: White Fish Point, June 30, 1988.

Table 9: Goodyera oblongifolia Raf.
MI: Alger Co.: Pictured Rocks National Lakeshore, Grand Sabal Dunes complex west of Sabal Creek, Jack Pine woods, July 14, 1988.

Table 10: Osmorhiza chilensis H. & A.
a. MI: Emmet Co.: Wilderness State Park, Waugoshance Pt., Mt. Nebo area, June 20, 1988.
b. MI: Luce Co.: Tahquamenon River, Upper Falls area, June 30, 1988.
c. MI: Emmet Co.: ca. 1 mile W of Cross Village, deciduous forest, July 7, 1988.

d. MI: Alger Co.: Pictured Rocks National Lakeshore, east of Grand Sabal Dunes Complex, July 14, 1988.
e. MI: Alger Co. Pictured Rocks National Lakeshore, Grand Sabal Dunes Complex east of Sabal Creek, Jack Pine woods, July 14, 1988.
f. Canada, Ontario: Algoma District: 1.1 miles past Agawa Scenic Lookout, Awausee Lookout Trail, July 25, 1988.

OBSERVATIONS AND DISCUSSION OF THE SPECIES

Crataegus douglasii Lindley

Crataegus douglasii was observed in one site only (# 1) growing on perched sand dunes at the summit of a glacially deposited bluff above Lake Superior at the Grand Sabal Dunes Complex.

A single tall (ca. 3-4 m.) and large shurb was observed, growing at the edge of mixed woods, surrounded by Toxicodendron radicans, and large thickets of Cornus stolinifera in its vicinity (beyond a two meter radius from the species in question).

Both associates grow in a variety of habitats, including sand dunes, where the latter displays its "stoloniferous" habit by suckering from buried stem (Voss, 1985). This habit, along with our field observations, suggests that both associates may serve to stabilize the sand in the immediate vicinity of the species in question. Further observations are required in order to assess the fidelity of Crataegus douglasii to the above mentioned associates.

The Upper surface of the sandy soil at the site was dry, well penetrating, and its soil reaction was neutral (pH 7.0). It is most likely to be moister at the vicinity of the roots, above the rock bed. In addition, moisture coming from the adjacent lake may increase the actual amount of water available to the plant. The soil reaction was measured from a sample taken from the upper surface of the soil, ca. 1 m. from the plant. It does not necessarily represent the reaction at the root vicinity, which is most likely basic, since a calcareous rock bed lies underneath. The amount of nutrients available is poor in the upper surface substrate, but some may be available through underground water flow on the rock bed.

Crataegus douglasii may occur also in rocky woodlands, and in thickets on shores (Marquis & Voss, 1981, Voss 1985) in in addition to the above habitat observed.

Festuca occidentalis Hooker

Observations on this perennial species were primarily made at site # 2b. It grew close to the edge of a perched dune on glacial

deposits, facing Lake Superior southern shore, in a Jack Pine (Pinus banksiana) forest with Aralia nudicaulis, Linnaea borealis, Rubus pubescens, and Pyrola minor. The forest was rich in species (a large number of them being typical boreal forest species), which thrived in the shaded and occasionally moist conditions of the habitat, thus not necessarily being the constant associates of Festuca occidentalis. Further evidence for the variety of associates in this locality was provided in a site 'deeper' in the woods, where the latter grew under Abies balsamea with Goodyera oblongifolia, Chimaphila umbellata, Linnaea borealis, Cynoglossum boreale, and Cypripedium arietinum. Festuca occidentalis may grow on on calcareous soils with Thuja occidentalis, as was observed at site # 2a. This can be also observed along Upper Drive at UMBS. Voss (1972) noted that it may grow in open often rocky woods, wooded dunes (with pines), cedar-fir woods and thickets (often in calcareous sites), aspens, and hardwoods. Thus, capable of growing in a variety of habitats.

The substrate at site # 2b was primarily well drained, nutrient poor, and dry sandy soil with moderate amounts of organic matter on the upper surface (mostly dry and undegraded). The soil reaction was neutral with a tendency to be slightly alkaline (7.0-8.0), reflecting the reaction of the upper layer, where the roots of Festuca occidentalis and its herbaceous associates are placed.

The physical appearance of the site as well as its location on the lake shore suggests that moist winds (and often fog), combined with the shade provided by the Pinus banksiana trees make the habitat moist enough for a large number of the associates, in spite of the dry and well drained substrate, which in turn, seems to be preferable by Festuca occidentalis.

Adenocaulon bicolor Hooker

Adenocaulon bicolor, a fibrous-rooted perennial, was observed growing on moist seepy slopes at two sites (# 3a & 3b) with another "western disjunct": Osmorhiza chilensis, under Acer saccharum and at site # 3b growing also with streptopus amplexifolius (which indicates presence of moisture, since it grows in dumpier sites than the ones usually occupied by the following Streptopus species), Streptopus roseus, Gymnocarpium dryopteris, and Fagus grandifolia. At both sites there were only a few individuals of the species in question, and they grew ca. 1 m from each other, whereas the abundance of Osmorhiza chilensis was prominant. The substrate in both sites was sand with rich and well mixed and degraded organic matter, which had neutral soil reaction (pH 7.0).

It appears, that Adenocaulon bicolor prefers moderately shaded woods, and moist seepy slopes, and is most likely to be found in beech-maple forests with Osmorhiza chilensis.

Marquis and Voss (1981) note that it is not rare along rocky streams, in ravines and on banks in moist hemlock-hardwood forests in the northern part of the Upper Peninsula of Michigan.

Melica smithii (Gray) Vasey

Melica smithii was observed at two sites: # 4a, and # 4b. In the former, it grew on a seepy slope above a gorge on a glacial deposit under Acer Saccharum and Fagus grandifolia: Equisetum pratense, Thelypteris noveboracensis, Osmunda claytoniana, Impatiens capensis, and Viola canadensis. At the latter it grew in hardwoods under Acer saccharum with Rubus strigosus, Allium tricoccum, and Hierchloë sp.

At both sites it was best established in moist deciduous woods, where the substrate was rich in organic matter, with a medium acid soil reaction (pH 6.0).

The above observations confirm the information in the literature about the characteristic habitat of Melica smithii, being rich beech-maple stands and wooded dunes. In addition,Voss (1972) notes that it may rarely grow under Thuja occidentalis.

Rubus parviflorus Nutt.

One of the commonest and widely distributed "western disjuncts" in the Great Lakes region (Marquis and Voss,1981) was observed at five sites. At site # 5a it grew on beach dunes on dry, nutrient poor sandy soil. Only a few plants were observed along with Campanula rotundifolia, Rosa acicularis, and Castilleja coccinea. The habitat is constantly disturbed by sand migration, and possibly by off-road vehicles.
At site # 5b it formed large thickets on a seepy bank at the edge of a mixed deciduous forest on both sides of a road close to Lake Michigan shore. It grew near Acer pensylvanicum, Acer spicatum, Acer saccharum, Betula ostrya and Corylus cornuta (which tends to grow on clearings), Equisetum pratense, Cystopteris bulbifera, Streptopus roseus, and a few (partially wilted) Osmorhiza chilensis understory plants. The substrate was mostly humus with some sand traces, and its reaction was medium alkaline (ph 8.0). The combination of dump seepy bank, roadside clearings (disturbance) and open moist woods, not far from the lakeshore, seem to be the major factor contributing to Rubus parviflorus's abundance at this site.
At site # 5c a few individual plants of the species in question grew at the edges of open woods under Betula papyrifera with Geranium bicknellii in its vicinity on a resurfaced yard of M.C. schools. The substrate was primarily dry sand with relatively low amount of organic matter (not fully degraded) which had medium alkaline soil reaction (pH 8.0). The location to the lake shore makes some additional moisture

available. This site demonstrates Rubus parviflorus's tendency to invade disturbed sites. This observation is enforced by the presence of Geranium bicknellii which is known to occur on disturbed sites.
At site # 5d Rubus parviflorus grew in large thickets on the border of a deciduous forest on a roadside with Acer saccharum, Acer spicatum, Abies balsamea, and albino Epilobium angustifolium (which usually invades clearings). This site is another example of a forest border habitat as well as disturbed site (road construction and vehicle fumes).
In addition, it is close to the eastern shore of Lake Superior, which suggests a source of moisture. The substrate had a medium acid soil reaction (pH 6.0)--a result which differs from results obtained at the other sites (pH 8.0). Even though it falls in the optimum pH range of Acer saccharum and Abies balsamea, according to Spurway (1941), it may indicate the reaction of the woody plant's litter (which was prominant in the soil sample) at the surface level, rather than the actual soil reaction at the root level.
At site # 5e large thickets of Rubus parviflorus dominated the understory of Acer saccharum, Acer rubrum, and Tilia americana with Cornus stolinifera, Pteridium aquilinum and young Abies balsamea growing near the edges of the Rubus parviflorus thickets. This site, a bluff of the Nipissing shore line along the trail to Grass Bay, is occupied by a fairly young forest on dune ridges.
Rubus parviflorus's preference for disturbance is reflected by the fact that an adjacent section of the forest is dominated by Betula alleghaniensis (which usually invades sites after fire), as well as clearing and traffic on the trail.

The above observations show that Rubus parviflorus is a pioneer of disturbed areas, especially along forest borders and clearings, and prefers sites not far from the Great Lakes shores. In addition, they confirm the information in the literature noting that it mainly occupies northern hardwoods, and moist mixed woods.

Vaccinium membranaceum Britton

This disjunct occurs in eastern North America only along the Michigan shore of Lake Superior (Marquis and Voss, 1981).
A few plants (some in fruit) were observed only in one site (# 6) widely spaced (more than 1 m apart) among Acer saccharum in a patch between the road leading to Sabal Lake and a parking lot at the edge of woods.

The substrate was primarily sand with dry organic matter, well mixed among the sand particles. The soil reaction was medium acid (6.0). By and large Vaccinium spp. prefer acid substrates. The reaction obtained here falls on the lower optimum pH range of Acer saccharum (6.0) according to Spurway (1941). Acer saccharum is most abundant in rich woods, especially on calcareous soils.

Gleason and Cronquist (1963) indicate that Vaccinium membranaceum occupies moist woods. Marquis and Voss (1981) indicate that it is a shrub of woods, usually coniferous, including edges on stable dunes. Although an association between Vaccinium membranaceum and conifers was not observed at the site, evidence for that may be found in the result of the soil reaction, which is the maximum pH limit to some conifers, such as Pinus banksiana. Evidence from additional sites is required in order establish this observation.

Arabis holboellii Hornem.

Marquis and Voss (1981) note that the inclusion of Arabis holboellii as a "western disjunct" is questionable since it displays less dramatic gaps in its range than most of the other disjunct species discussed by them . It is discussed here, following the above authors.

This biennial or perennial species was observed at only one site (# 7) on dry, nutrient poor sandy dunes of Lake Superior shore, primarily as individual plants greatly spaced. The species of close vicinity (in some cases placed more than 2 m. apart) were: Primula mistasinica (which is common on alkaline rocks and gravely shores, Hierodloe odorata, Schizachne purpurascens, and Lathyrus japonicus.
More information is required in order to establish correlation of association between the species observed in close vicinity and Arabis holboellii.

Voss (1985) indicates that Arabis holboellii grows ,also, on rock ledges and summits (especially in the northeastern Upper Peninsula of Michigan, and Isle Royale). This is the only species, among the "western disjunct" species observed in this study, that grows at an exposed,sunny site without woody or shrubby associates.

Vaccinium ovalifolium Sm.

Vaccinium ovalifolium was observed at only one site (# 8) occupying a hollow on sand dunes under Pinus banksiana with Ledum groenlandicum as primary associate, accompanied by Cornus canadensis and Kalmia polifolia.

The substrate consisted primarily of dry, well-drained sandy soil with some organic matter (leaves and stems). The soil reaction was strongly acid (pH 4.0)--a preferable pH for Ericaceous species. Although the upper surface of the substrate was dry, the occurrence of Cornus canadensis, a typical boreal species, as well as the topography of the habitat, and the shade provided by Pinus banksiana indicate the availability of water or moisture. Marquis and Voss (1981) indicate that Vaccinium ovalifolium grows in habitats of steep wooded slopes, hemlock hardwoods, and wooded, sometimes open dunes

(the latter corresponds to our observations).

Goodyera oblongifolia Raf.

This orchid was observed only in one locality (# 9) in a Jack Pine (Pinus banksiana) forest on perched dunes on a glacial deposit above Lake Superior. Five sites were observed within the forest and at its edges.
At the first site a few plants of Goodyera oblongifolia grew under Abies balsamea with Chimaphila umbellata, Linnaea borealis, Festuca occidentalis (another "western disjunct"), Cynoglossum boreale, and Cypripedium arietinum. The site was well shaded, and the substrate consisted of dry sandy soil covered by a layer of ca. 3 cm. of organic matter (primarily conifer litter). The soil reaction was strongly acid (pH 5.0), suggesting a strong influence of the conifer associate.
At the second site, a single plant of the species in question grew on a moss mat under Abies balsamea with Chimaphila umbellata, Linnaea borealis, and Aralia naudicaulis. This site was also shady and the sandy substrate was covered mostly by conifer and some organic matter. The soil reaction was medium acid (pH 6.0).
At the third site a single plant of Goodyera oblongifolia grew under Abies balsamea with Linnaea borealis, Chimaphila umbellata, and a few Acer seedlings on dry sandy soil covered by a thin layer of dry organic matter and conifer litter. As at the previous site the soil reaction was medium acid.
At the forth site, a single plant of Goodyera oblongifolia grew under Pinus banksiana in a half sunny barren opening at the edge of the forest with Chimaphila umbellata and Rosa sp.--growing ca. 1 m. beside Goodyera oblongifolia. The latter was smaller in size compared to plants observed at the other sites. This site was drier and most likely poor in nutrients compared to the other sites. Soil sample was not taken from this site, but the presence of Pinus banksiana suggests a strongly acid to medium acid reaction.
At the fifth site, a single plant grew with Acer saccharum and Clintonia borealis near a stream at the border between the Jack Pine forest and deciduous woods. The substrate was rich sandy soil with more moisture compared to the other sites at which Goodyera oblongifolia was observed.

The above observations suggest that Goodyera oblongifolia prefers coniferous mixed woods and medium acid sandy soils, with a limited amount of nutrients. The result of the soil reaction obtained at the first site may indicate capability for more acid substrates, most likely being the minimum pH limit. In addition, it may grow in deciduous woods on rich sandy soils.
Case (1987) notes that it grows most abundantly in dry Cedar-Spruce woods in immediate vicinity of the upper Great Lakes shores, and may occasionally grow on margins of wooded bogs and swamps.

Osmorhiza chilensis H. & A.

Osmorhiza chilensis was observed in six different sites (observations were conducted at sites # 10 b-f).
At site # 10b a few Osmorhiza chilensis plants grew among Rubus parviflorus at the edge of deciduous woods on a seepy bank along roadside close to Lake Michigan. The woody associates were: Acer saccharum, Fagus grandifolia, and Betula ostrya. The substrate was dry degraded organic matter with some sand traces. The soil reaction was medium alkaline (pH 8.0).
At site # 10c Osmorhiza chilensis was very abundant (ca. 5 plants per square meter), and grew in deciduous moist woods under Acer saccharum and Acer pensylvanicum with Botrychium virginianum, Equisetum sylvaticum, Milium effusum and Clintonia borealis. The substrate was moist sandy soil (sand dunes above glacial deposits) with well mixed humus, which had a neutral soil reaction (pH 7.0).
At a second site in the same forest a large thicket of Osmorhiza chilensis grew under Acer saccharum with Smilacina stellata on moist slopes above a gorge.
A few Osmorhiza chilensis plants--smaller and less vigorous --grew at a drier and more open site at the edges of the previous one with Abies balsamea, Picea glauca, and Botrychium virginianum. These associates are capable of growing at drier habitats.
At site # 10d Osmorhiza chilensis grew in Jack Pine (Pinus banksiana) forest on perched dunes on a glacial deposit above Lake Superior. Three partially wilted plants grew at the edge of the forest (facing the dunes) under Pinus banksiana with Linnaea borealis and Abies balsamea. The substrate was dry, nutrient poor sandy soil with a neutral soil reaction (pH 7.0). At a second site (in the same locality) at the edge of the bluff above the Lake shore, larger and healthier Osmorhiza chilensis plants grew under Pinus banksiana with Abies balsamea (as a low shrub), Streptopus amplexifolius, Rubus pubescens, Aralia nudicaulis and a few seedlings of Acer and Fagus. The substrate was mostly well drained, dry sandy soil with some dry organic matter, and neutral soil reaction (pH 7.0). As indicated previously, this site was characterized by richness in species thriving under the shade and moisture.
At site # 10f Osmorhiza chilensis grew in rich and mixed deciduous forest under Acer saccharum and Acer spicatum with Streptopus roseus, Thelypteris dryopteris, and Viola spp. on a rich and moist soil placed on a rock bed. The substrate had a neutral soil reaction (pH 7.0). This site was characterized by transition of species with a change of altitude. Osmorhiza chilensis became absent in higher altitudes, as soon as Acer spp. were replaced by other woody plants.

The above observations suggest that Osmorhiza chilensis prefers most woods (beech-maple), but may grow also in dry open deciduous woods, and occasionally on dunes and sandy bluffs (Marquis and Voss, 1981) provided with some moisture and shade.

The substrate may range from rich to relatively poor nutrient content, with a typical neutral soil reaction.

CONCLUSIONS

Most of the "western disjunct" species observed during this study have one habitat which they are most likely to occupy. However, each one has a range of physical characteristics of the habitat which expands its ability to occupy more than one type of habitat. For example: Osmorhiza chilensis commonly grows in moist woods (beech-maple), but may grow, also, in open deciduous woods, and occasionally on dunes and sandy bluffs.

The substrate requirements of the species range from dry, well drained and nutrient poor sandy soil to moist, nutrient rich sandy soil with a large amount of humus. All the species were observed on sandy soil, and they differed in their requirements of pH, amount of nutrients and organic matter available, texture, and amount of moisture. In addition, each species has a specific and preferred combination of other physical characteristics of the habitat, such as topography, and amount of light/shade. Two species were noted for having special requirements, i.e. Rubus parviflorus (clearings and disturbed areas), and Arabis holboellii (exposed, sunny habitats on sandy dunes and rocks).

All the species fail to inhibit such habitats as heavily shaded deciduous woods, bogs, and fens (except for Goodyera oblongifolia which may occupy the margins of wooded bogs and swamps, according to the literature).

The species in each distribution group have, by and large, some common substrate and habitat requirements, but there are exceptions, such as Vaccinium membranaceum in group I.B.

Among the observed species there are three pairs of species, belonging to the families: Ericaceae, Rosaceae, and Poaceae. Vaccinium ovalifolium and Vaccinium membranaceum grow basically on the same substrate: dry sandy soil, but they differ in pH requirements, amount of moisture in the soil, and associates. Crataegus douglasii and Rubus parviflorus grow on the same type of soil, but occupy different habitats, and differ in their special requirements. Festuca occidentalis and Melica smithii also differ in their special requirements of substrate and habitat.

Some of the observed species occured in certain habitats together. Adenocaulon bicolor grew, at both sites it was observed with Osmorhiza chilensis, but did not occur at all sites where the latter occur--suggesting that Adenocaulon bicolor is more specific in its requirements (which may be the amount of moisture or a specific nutrient requirement).

Festuca occidentalis occurred with Goodyera oblongifolia at site # 2b/9 because the habitat had a combination of conditions favorable to both species, but do not occur together in all the habitats occupied by Festuca occidentalis. Osmorhiza chilensis occured at site # 10b with Rubus parviflorus, since the habitat was a moist seepy bank. The most abundant species observed in a number of sites were: Osmorhiza chilensis and Rubus parviflorus.

The group of ten "western disjunct" species observed, may be tied together on the basis of their distribution across the continent, but they differ in their substrate and habitat requirements, and may be tied together on the basis of the latter criteria only if broad generalizations are made.

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