FEATURE

Collection of Native Strawberry Germplasm in the Pacific Northwest and Northern Rocky Mountains of the United States

James J. Luby
Department of Horticultural Science, University of Minnesota, St. Paul, MN 55108

James F. Hancock, Jr.
Department of Horticulture, Michigan State University, East Lansing, MI 48824

James R. Ballington
Department of Horticultural Science, North Carolina State University, Raleigh, NC 27695

The cultivated strawberry *(Fragaria* x *ananassa* Duch.) is an interspecific hybrid complex derived from two octoploid (2n = 56) species: *F. chiloensis* (L.) Duch., native to the Pacific coasts of North and South America, the southern Andes Mountains, and Hawaii; and *F. virginiana* Duch., found in North America from Alaska through the Sierra Nevada and Rocky Mountain ranges and throughout the eastern part of the continent (Darrow, 1966; Hancock et al,, 1990; Scott and Lawrence, 1975; Staudt, 1962). Outside of the western hemisphere and Hawaii, octoploid strawberries have been reported only on islands of the western Pacific Ocean. *Frugaria iturupensis* Staudt was described from the Kuril Islands, U.S.S.R. (Staudt, 1973), and an unassigned octoploid plant was collected from Rebun Island, Hokkaido Prefecture, Japan (Oda and Nisitani, 1989).

The evolution of strawberry at the octoploid level thus occurred largely in North America, making this continent an important source of wild germplasm. However, relatively few genotypes of *F. virginiana* have been used in developing the crop. The narrow germplasm base of North American strawberry production has recently been documented. Only 53 founding clones (Sjulin and Dale, 1987) representing 17 cytoplasm sources (Dale and Sjulin, 1990) are represented in the 134 North American cultivars introduced during the last 30 years. Furthermore, the 20 cultivars that account for most of the North American strawberry crop can be traced to 38 founding clones, of which just seven account for ≈ 50% of the genetic contribution (Galletta and Maas, 1990; Luby et al., 1991).

We collected *Fragaria* spp. in 1985 from 20 inland sites in the Pacific Northwest and, in 1989, from 53 sites in the northern Rocky Mountains (Fig. 1). The collection was made to obtain representatives of native *Fragaria* for maintenance at the U.S. Dept. of Agriculture (USDA) National Clonal Germplasm Repository (Corvallis, Ore.) and for distribution to-strawberry breeders and other researchers. Certain accessions may provide new sources of resistance to environmental and biotic stresses and improved fruit quality and productivity. Use of this material in breeding programs would broaden the strawberry germplasm base, reducing genetic vulnerability (Luby et al., 1991). The collections also provided material for specific ongoing research in *Frugaria* systematics, yield efficiency and C exchange capacity, cold hardiness, disease resistance, and fruit quality.

The germplasm collected on these expeditions was deposited at the National Clonal Germplasm Repository in Corvallis, and limited quantities of accessions are available to researchers on request '(Curator, USDA National Clonal Germplasm Repository, Corvallis, OR 97333). An import permit may be necessary for foreign deliveries. USDA phytosanitary certificates are available upon receipt of the import permit.

NATIVE STRAWBERRY GERMPLASM IN MONTANE WESTERN NORTH AMERICA

The wild octoploid strawberries of montane western North America were referred to as two subspecies in the most recent taxonomic revision by Staudt (1962), *F. virginiana* ssp. *glauca* (Wats.) Staudt and ssp. *platypetala* (Rydb.) Staudt. Only six genotypes of western *F. virginiana* (identified as *F. virginiana glauca)* are represented among the 53 founding clones traced by Sjulin and

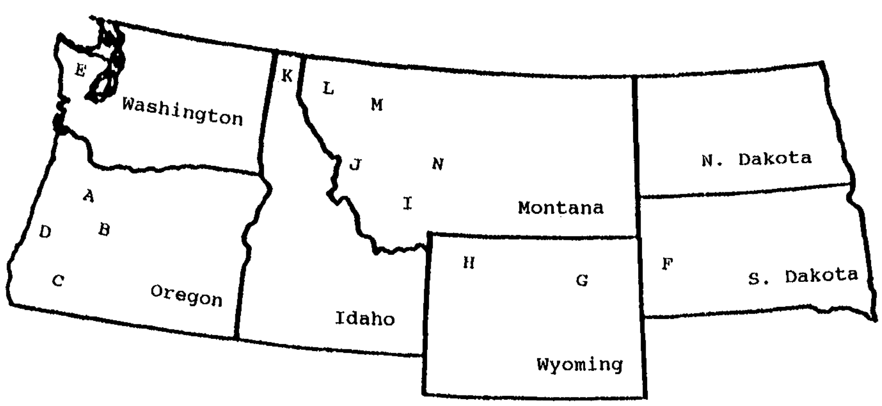

Fig. 1. Map of the western United States showing target regions for *Fragaria* germplasm collections in 1985 and 1989: A, Cascade Mountains (west slope); B, Cascade Mountains (east slope); C, Siskiyou Mountains; D, Coast Range; E, Olympic Mountains; F, Black Hills; G, Bighorn Mountains; H, Absoroka Range and Yellowstone Plateau; I, Madison, Tobacco Root, and Pioneer Mountains; J, Bitteroot Range; K, Cabinet and Selkirk Ranges; L, Flathead and Whitefish Ranges; M, Lewis Range; N, Big Belt, Little Belt, and Crazy Mountains.

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Dale (1987). However, the utility of *F. virginiana* ssp. *glauca* for improvement of several important traits in the cultivated strawberry has been well documented. Hildreth and Powers (1941) and Powers (1944, 1945, 1954) observed that genotypes from the Rocky Mountains contributed considerable winter hardiness, tolerance of blossoms to frost, early maturity, and good fruit quality. Darrow (1966) indicated that it was also a potential source of drought tolerance and resistance to powdery mildew [*Sphaerotheca macularis* (Tul.) Lindau], red-stele root rot *(Phytophthora fragariae* Hickman), and root knot nematode *(Maloidogyne hapla* Chitwood). Newton and Van Adrichem (1958) found that some genotypes were resistant to verticillium wilt *(Verticillium albo-atrum* Reinke and Berth). The important everbearing and day-neutral flowering characteristics were also derived from this species (Ahmadi et al., 1990; Bringhurst and Voth, 1984; Ourecky and Slate, 1968; Powers, 1954; Scott, 1959).

Hildreth and Powers (1941) collected and evaluated some 42,000 genotypes of *F. virginiana* ssp. glauca from 1100 sites in the Rocky Mountains in the 1930s and 1940s. While some of this germplasm was used in further breeding to produce cultivars (Darrow, 1966; Scott and Lawrence, 1975) still grown on a limited basis, this massive collection was lost with the closing of the USDA small fruit research program at Cheyenne, Wyo. More recently, *F. virginiana* ssp. *glauca* germplasm from two sites in the Sierra Nevada in California was collected and evaluated by Hancock and Bringhurst (1979, 1988).

Fragaria vesca L., a diploid, is the only native North American strawberry in addition to the octoploids (Darrow, 1966; Scott and Lawrence, 1975; Staudt, 1962). It is also widespread in Europe and Asia. All other diploid, tetraploid, and hexaploid species occur only in Asia and Europe (Darrow, 1966).

Little is known about the potential germplasm value of Pacific Northwest or Rocky Mountain populations of *F. vesca,* but data from other montane populations suggest they may possess useful genetic variability. Collections from high elevations in California had cold tolerance and earliness, and produced a high flowers : runners ratio (Hancock, 1977; Hancock and Bringhurst, 1978). This germplasm also was frost resistant and had reduced susceptibility to root rot. One population from Hecker Pass, Calif., had an unusually high reproductive effort in terms of flowers per plant and mean fruit weight (Hancock and Bringhurst, 1988). Genes for these traits could be transferred to octoploids through synthetic polyploids (Bringhurst and Voth, 1984).

COLLECTION EXPEDITIONS

A primary objective of the expeditions was to collect seeds, clones, and herbarium specimens of *F. virginiana* and *F. vesca.* Material of other local native fruit species (Rubus, *Vaccinium, Ribes, Vitis, Prunus, Malus, Sorbus,* and *Sambucus)* was also collected where available and as time permitted (Ballington et al., 1988; Luby and Hancock, 1991). In 1985, collections were made between 21 July and 13 Aug. The Coast Range of Oregon, the Siskiyou Mountains (Oregon), the southern Cascade Mountains (Oregon and Washington), and the Olympic Mountains (Washington) were the target areas for the 1985 expedition (Fig. 1). In 1989, collections were made between 31 July and 19 Aug. The Black Hills (South Dakota), and the Bighorn (Wyoming), Absoroka (Wyoming and Montana), Madison (Montana), Tobacco Root (Montana), Pioneer (Montana), Bitteroot (Montana and Idaho), Selkirk (Idaho), Cabinet (Montana), Whitefish (Montana), Crazy (Montana), Big Belt (Montana), and Little Belt (Montana) ranges of the Rocky Mountains were the target areas for the 1989 expedition (Fig. 1). All collection sites were in National Forests except for one site each in Yellowstone and Glacier National Parks. U.S. Forest Service maps were used to locate and identify most sites.

The elevation of collection sites was determined by altimeter and was accurate within 30 m based on calibrations at reference points where the elevation had been determined by the U.S. Geological Survey. Slope and aspect were determined by planeometer and compass, respectively. Associated flora were noted at each site and used to assign the sites to plant communities described by Daubenmire (1943), Munz and Keck (1959), and Peet (1988).

At each site, seed was collected if available. Where seed was not available, we attempted to collect clonal samples from ≈ 20 genotypes. Representative herbarium samples were gathered and pressed at most sites. Fruit and clonal specimens were placed in plastic bags and packed in ice chests while in transit. Fruit samples were sent to the National Clonal Germplasm Repository (Corvallis) for seed extraction. Clonal material was shipped to the Germplasm Repository, Univ. of Minnesota, or Michigan State Univ. for rooting. Seeds were regenerated from *F. virginiana* clonal material in a greenhouse at Michigan State Univ. in Spring 1990 by random pollination among genotypes collected from within each site. This seed was shared with the Germplasm Repository. Herbarium specimens have been deposited at the Germplasm Repository, North Carolina State Univ., and Michigan State Univ.

On the 1989 expedition, a composite soil sample was collected at each site by taking a 2-cm-diameter core to a depth of 20 cm adjacent to each collected *Fragaria* plant. Concentrations of K (ammonium acetate extractable), P (Bray Pl or Olsen test for soils with pH >7.2), pH [l soil : 1 water (w/v)], and organic matter content (wet digestion) were determined for each sample (Rehm et al., 1985).

DESCRIPTION OF COLLECTIONS

Collections and site characteristics are summarized in Tables 1 and 2. In the Pacific Northwest, a total of 23 accessions were collected from 18 sites including 17 seed samples. Fruits were unripe or unavailable at 41 additional locations where species or species hybrids were observed. The Rocky Mountain collections in 1989 included > 800 clonal specimens and nine seed samples from 45 sites. The individual sites and accessions are described in more detail by Ballington et al. (1988) and Luby and Hancock (1991).

Collection sites included several distinct habitats and were widespread in latitude and altitude. *Fragaria virginiana* generally occurred in disturbed or open areas such as roadsides or roadbanks, recent clearcuts, gravelly slopes, open woods, and meadows. Several genera that were nearly always associated in the understory of plant communities containing *F. virginiana were* herbaceous *Potentilla* spp., *Berberis aquifolium* Pursh, *Physocarpus malvaceus* (Greene) Kuntz, *Holodiscus discolor* (Pursh) Maxim., *Symphoricarpus oreophilus* Gray, *Menziesia ferruginea* Smith, *Ribes* spp., *Lonicera* spp., and *Spiraea* spp. In the Pacific Northwest, elevations of collection sites ranged from 800 to 2100 m in Oregon and 400 to 1400 m in Washington. In the eastern Rocky Mountains, *F. virginiana* occurred mainly in the spruce-fir [*Picea englemannii* Parry - *Abies Lasiocarpa* (Hook.) Nutt.] and Douglas fir [*Pseudotsuga menziesii* (Mirb.) France] zones in sites with moderate moisture and limited competition. Collection from high elevation sites (> 1500 m) was emphasized. In western Montana and Idaho, collection sites were often at elevations < 1500 m in the drier Ponderosa pine *(Pinus ponderosa* Dougl.) and Douglas fir zones. Above this elevation, precipitation was high, and tree and shrub growth was so lush that ground cover species such as *Fragaria* were apparently quickly shaded in openings where they might otherwise have become established.

The diversity of habitats where *F. virginiana* was collected, ranging from dry *Pinus ponderosa* forests to wet meadows, suggests that valuable traits in certain accessions could include resistance to drought or to conditions associated with saturated soils (anaerobiosis, low nutrient availability, root rot pathogens). Sites having elevation, aspect, soil texture, and soil profile that might contribute to drought or heat stress include LH 4, LH 10, LH 11, LH 22, LH 28, and LH 38 (Table 1). Sites with conditions promoting prolonged soil saturation included BL 27, BL 30, LH 6, LH 29, LH 34, and LH 35 (Table 1). Several collections (LH 9, LH 15, LH 17, LH 18, LH 45, LH 50) were made near the timberline where the growing season was typically very short (only 6 to 8 weeks, according to local reports) and frost or snow could occur at any time of the year (Table 1). Cold hardiness and blossom frost tolerance may be available from these and other high-altitude sites in the eastern Rocky Mountain ranges.

The sites were quite variable for the soil pH and content of K, P, and organic matter (Table 2). Collections from several sites with alkaline soils may be sources of tolerance to higher pH. Soils at sites LH 2 and LH 40

Table 1. *Fragaria* collections and site descriptors.

Site	Collections[z] of *Fragaria* *virginiana*	*vesca*	Locale and state[y]	Latitude (°N)	Longitude (°W)	Elevation (m)	Aspect/ slope (°)[x]	Vegetation zone[w]	Description
					1985 Collections				
Cascade Mountains (west slope)									
BL 2	S	S	Willamette NF, OR	44 00	122 20	1400	E/V	Douglas fir	Roadbanks
BL 50	S		Willamette NF, OR	44 30	122 00	1100	SSW/5	Douglas fir–Arborvitae-hemlock	Roadsides and open forest
BL 52		S	Willamette NF, OR	44 20	122 10	1370	NW/V	Spruce–fir	Young forest
BL 63	S		Gifford Pinchot NF, WA	45 50	121 40	1400	E/0-20	Arborvitae–hemlock	High meadow
BL 70	C H		Gifford Pinchot NF, WA	46 00	122 00	1100	E/45	Arborvitae-hemlock	Roadside, old clearcut
Cascade Mountains (east slope)									
BL 26	S		Winema NF, OR	43 00	123 30	1830	SW/20	Douglas fir	Roadside and roadbank
BL 27	S		Winema NF, OR	42 30	122 20	1810	NW/10	Douglas fir	Moist, open forest
BL 29		S	Winema NF, OR	42 30	122 10	1590	E/10	Douglas fir	Roadside and meadow
BL 30	S		Deschutes NF, OR	43 40	121 10	2100	E/10	Douglas fir	Sedge meadow
BL 39	S		Deschutes NF, OR	43 50	121 50	1530	E/V	Douglas fir	Roadbanks, open forest, and clearcut
BL 41		S	Deschutes NF, OR	43 30	121 30	1300	NE/V	Ponderosa pine–Douglas fir	Roadbanks
Siskiyou Mountains									
BL 18		S	Siskiyou NF, OR	42 10	123 30	1300	SW/45	Douglas fir	Roadbanks and meadow
BL 20	S		Rogue River NF, OR	42 10	123 00	1530	S/20	Ponderosa pine–Douglas fir	Old clearcut
BL 21	S	S	Rogue River NF, OR	42 30	123 10	1600	E/45	Douglas fir	Roadside and open forest
Coast Range									
BL 57	CSH		Siuslaw NF, OR	45 10	123 30	1000	V/0-20	Red fir	Mountaintop bald
Olympic Mountains									
BL 89	C H		Olympic NF, WA	47 00	124 00	970	S/5	Arborvitae-hemlock	Roadside
BL 93	C		Olympic NF, WA	47 40	123 00	1220	NW/45	Arborvitae-hemlock	Roadside, moist open forest
BL 96	C		Olympic NF, WA	48 00	123 10	500	S/10	Arborvitae-hemlock	Roadbank
					1989 Collections				
Black Hills									
LH 2	CS		Black Hills NF, SD	43 50	103 30	1600	NW/V	Ponderosa pine	Open forest
LH 3	C H		Black Hills NF, SD	43 40	103 30	1760	NE/30	Ponderosa pine	Open forest
LH 4	C H	C H	Black Hills NF, SD	43 30	103 20	1380	V/V	Oak–pine	Savannah
LH 5	C H		Black Hills NF, SD	44 10	103 40	1550	NW/V	Douglas fir	Grazed meadow, open forest
LH 6	CSH		Black Hills NF, SD	44 20	103 50	1840	V/V	Douglas fir	Moist streambanks
LH 7	C H		Black Hills NF, SD	44 30	103 50	1980	SW/10	Douglas fir	Open forest
Bighorn Mountains									
LH 8	C H	C H	Bighorn NF, WY	44 40	108 30	2210	NW/V	Spruce–fir	Grazed meadow, open forest
LH 9	C H		Bighorn NF, WY	44 30	108 30	2650	S/30	Spruce–fir	Montane grazed meadow
LH 10	C H	H	Bighorn NF, WY	44 30	108 40	1860	N/30-45	Ponderosa pine	Open forest
Absoroka Range and Yellowstone Plateau									
LH 11		C H	Shoshone NF, WY	44 20	109 40	2590	N/30-60	Spruce–fir	Scree slope
LH 12	C H	C H	Shoshone NF, WY	44 30	109 40	2070	V/V	Spruce–fir	Streambanks in open forest
LH 13	C H		Shoshone NF, WY	44 30	109 40	1980	V/V	Spruce–fir	Roadside in open forest
LH 14	C H		Shoshone NF, WY	44 40	109 40	2160	N/15	Spruce–fir	Roadside and open forest
LH 15	C H		Shoshone NF, WY	44 50	109 40	2470	N/15	Spruce–fir	Edge of alpine meadow
LH 17	C H		Shoshone NF, WY	45 00	109 30	2900	W/15	Spruce–fir	Montane meadow
LH 18	CSH		Shoshone NF, WY	45 00	109 30	2800	W/30	Spruce–fir	Gravelly roadbank
LH 19	H		Shoshone NF, WY	45 00	109 40	2070	Flat	Spruce–fir	Open forest
LH 20	SH		Gallatin NF, MT	45 00	109 50	2420	Flat	Spruce–fir	Recently burned forest
LH 52	C H		Gallatin NF, MT	45 20	110 10	1615	Flat	Douglas fir	Meadow, open forest
LH 21	S	S	Yellowstone NP, WY	44 40	110 30	2010	SE/V	Douglas fir	Gravelly roadbank
Madison, Tobacco Root, and Pioneer Mountains									
LH 22	C H	C H	Beaverhead NF, MT	45 20	111 30	1670	N/40	Douglas fir–juniper	Open forest and roadbank
LH 23		H	Beaverhead NF, MT	45 30	112 10	1990	N/V	Douglas fir	Roadsides
LH 24	C H		Beaverhead NF, NT	45 30	113 20	2160	W/10	Douglas fir	Recent clearcut
Bitteroot Range									
LH 26	CSH	H	Bitteroot NF, MT	45 30	114 20	1980	SW/20	Douglas fir	Open forest

continued

Table 1. *continued.*

Site	Collections[z] of *Fragaria virginiana*	*vesca*	Locale and state[y]	Latitude (°N)	Longitude (°W)	Elevation (m)	Aspect/ slope (°)[x]	Vegetation zone[w]	Description
LH 28	C H		Bitteroot NF, MT	45 50	114 20	1460	S/5	Ponderosa pine	Open forest
LH 29	C H		Clearwater NF, ID	46 40	114 30	1610	Flat	Spruce–fir	Sedge meadow
LH 30	C H		Lolo NF, MT	46 50	114 20	1060	Flat	Douglas fir	Meadow, open forest
LH 32	C H	H	Lolo NF, MT	47 20	115 10	820	S/V	Douglas fir	Old clearcut
LH 37	C H		Coeur d'Alene NF, ID	47 30	115 40	1580	W/10	Spruce–fir	Gravel roadside
LH 38	C H		Kootenai NF, MT	47 50	115 40	730	Flat	Ponderosa pine	Open forest
Cabinet and Selkirk Ranges									
LH 34	C H		Coeur d'Alene NF, ID	47 30	116 20	790	Flat	Douglas fir	Wet, grazed meadow
LH 35	C H	H	Coeur d'Alene NF, ID	47 50	116 40	730	N/10-20	Douglas fir	Powerline clearcut
LH 36	C H	C H	Kaniksu NF, ID	48 40	116 50	700	Flat	Arborvitae-hemlock	Powerline clearcut
Flathead and Whitefish Ranges									
LH 39	C H		Kootenai NF, MT	48 00	115 20	1065	Flat	Douglas fir	Old clearcut
LH 40	C H		Flathead NF, MT	48 30	114 10	1340	ENE/V	Douglas fir	Roadbanks and open forest
LH 42	C H		Flathead NF, MT	48 40	114 30	1800	NE/V	Spruce–fir	Gravel roadside
LH 43	C H		Flathead NF, MT	48 50	114 40	1465	Flat	Douglas fir	Open forest
LH 44	C H	H	Kootenai NF, MT	48 40	114 50	975	Flat	Douglas fir	Mature open forest
Lewis Range									
LH 45	S		Glacier NP, MT	48 40	113 40	2075	NW/15	Spruce–fir	Gravel roadside, timberline
LH 46	C H	H	Flathead NF, MT	48 00	113 50	915	Flat	Ponderosa pine	Meadow
LH 47	C H		Lolo NF, MT	47 10	113 30	1220	Flat	Douglas fir	Mature open forest
LH 48	C H		Helena NF, MT	47 00	112 20	1870	Flat	Douglas fir	Roadside clearcut
Big Belt, Little Belt, and Crazy Mountains									
LH 49	C H		Helena NF, MT	46 20	111 10	1430	NNE/45	Douglas fir	Gravelly roadcut
LH 50	CSH		Lewis & Clark NF, MT	46 40	110 40	2255	Flat	Spruce–fir	Roadside clearcut
LH 51	CSH	H	Gallatin NF, MT	46 00	110 20	1965	V/V	Douglas fir	Open forest

[z]Type of collection from each site: C = clonal (vegetative); S = seed; H = herbarium specimen.
[y]Abbreviations for states are Oregon (OR), Washington (WA), South Dakota (SD), Wyoming (WY), Montana (MT), Idaho (ID).
[x]V = aspect varied or slope varied by more than 30° over the collection site.
[w]Vegetation zones defined by Daubenmire (1943), Munz and Keck (1959), and Peet (1988).

were low in P and/or K and these collections may be sources of nutrient-efficient genotypes. The high organic matter content (nearly 10%) at some sites was indicative of generally cool, moist conditions that would be conducive to plant growth but might hinder rapid decomposition. Other sites with low organic matter content usually had young soils (e.g., gravel or talus) and tended to be more xeric.

Fragaria virginiana exhibited extensive variability for fruit traits including internal and external color (various shades of pink, orange, and red), flavor, size (< 5 to 15 mm diameter), shape, firmness, and degree of seed sunkeness. Several collections, notably BL 2, BL 39, BL 52, LH 18, and LH 51, were especially outstanding for large fruits. We could not accurately determine the gender ratios in most populations because plants did not have flowers or fruits. However, some staminate plants bearing fruit were observed. Day-neutral flowering was observed at sites LH 34, LH 44, LH 45, LH 46, LH 50, and LH 51 and has been observed in the greenhouse on plants from several other sites.

Fragaria vesca was common throughout the collection area. It was often in the same habitats as *F. virginiana* but frequently occupied sites with drier, coarser soils where *F. virginiana* was absent, suggesting that it may be a source of extreme drought tolerance. *Fragaria vesca* occurred at elevations from 700 to 1600 m in Oregon and 120 to 1000 m in Washington. In the Rocky Mountains it was commonly found with *F. virginiana* at the lower elevation sites but usually was absent at the high elevation subalpine sites.

SYSTEMATICS OF OCTOPLOID *FRAGARIA* IN WESTERN NORTH AMERICA

The mountains of western North America may be a key sampling area for clarification of certain systematic and evolutionary aspects of octoploid *Fragaria*. Variation patterns in *F. virginiana* have perplexed taxonomists for decades. Rydberg (1922, 1932) assigned species rank to 10 octoploid taxa that would fit within Staudt's (1962) concept of *F. virginiana* in the most recent taxonomic revision of the genus. Staudt himself recognized four subspecies of *F. virg niana* that are regarded as varieties in several recent flora (Hitchcock and Cronquist, 1973; McGregor, 1986; Scoggan, 1978; Weber, 1987; Welsh et al., 1987). *Fragaria virginiana* ssp. *virginiana* and ssp. *grayana* (E. Vilm.) Staudt represent the species in its eastern range with the former being more common in the north (Nova Scotia to Manitoba to Oklahoma to Georgia) and the latter in the south (New York to Alabama, Louisiana and Texas) (Rydberg, 1932; Staudt, 1989).

West of the Great Plains, ssp. *glauca* (Wats.) Staudt ranges from the southern Rocky Mountains to the parklands of northwest Canada and central Alaska (Staudt, 1989). *Fragaria virginiana* ssp. *platypetala* (Rydb.) Staudt is distributed not only through the Rocky Mountains but also in the ranges farther west, from the Sierra Nevada and Cascades to British Columbia (Staudt, 1989) or central Alaska (Hitchcock and Cronquist, 1973). It is distinguished from ssp. *glauca* by its spreading rather than appressed pubescence on the petiole and scape and by its broader petals and leaflets (Hitchcock and Cronquist, 1973). Welsh et al. (1987) noted, however, that these two forms completely intergrade and suggested that all material be referred to a single taxon, the oldest epithet being var. *glauca* Wats. Other authors of recent flora of the region apparently adhered to this thinking and recognize only var. *glauca* (Scoggan, 1978; Weber, 1987) or do not distinguish infraspecific taxa (Dorn, 1977, 1984).

The basis for taxonomic confusion was evident in our collections. Populations in the Black Hills and the eastern front ranges of the Rocky Mountains (e.g., LH 3, LH 7, LH 15, LH 47, LH 50, LH 51, LH 52) appeared to be introgressive swarms between ssp. *glauca* and ssp. *virginiana,* supporting the designation of these taxa as varieties rather than subspecies. McGregor (1986) previously noted the phenomenon in this region: "A number of taxa have been isolated from this variable species but intergrade rather completely. They are not at all clearly delimitable in our area."

In the late Pleistocene, the Great Plains region of North America was mainly boreal forest (Kaul, 1986). This plant community would have provided a continuous habitat across the continent for *Fragaria* and, there-

Table 2. Soil characteristics (0 to 0.15-m depth) from *Fragaria virginiana* collection sites in the northern Rocky Mountains.

Site	P (mg·kg⁻¹)	K (mg·kg⁻¹)	pH	Organic matter (%)	Description[z]
LH2	5[y]	67	7.9	3.0	Sandy and gravelly
LH3	32	133	6.7	4.8	Gravelly (granite, quartzite)
LH4	31	164	6.6	6.3	Clay and silt
LH5	21	191	6.8	6.7	Thin clay layer over shale
LH6	18	206	7.6	9.9	10–15 cm of clay with high organic matter, some gravel
LH7	23	167	6.3	8.2	No comments
LH8	54	197	5.8	7.5	Loose humus
LH9	75	279	5.6	7.2	Deep loam
LH10	13	248	7.2	7.2	Gravelly humus
LH11	50	256	6.3	4.7	Silty, thick humus
LH12	51	133	6.6	5.3	No comments
LH13	54	420	6.5	6.1	Deep, moist, heavy texture
LH14	15	91	7.8	6.0	No comments
LH15	8	111	7.9	6.1	High organic matter with weathered gypsum
LH17	17	194	6.5	4.6	Deep, high organic matter
LH22	12	187	7.6	4.6	Deep, gravelly
LH24	71	157	5.4	4.3	Silty
LH26	28	145	5.9	4.1	10–15 cm light soil over rock
LH28	58	142	5.2	6.1	Thin organic layer over rock
LH29	17	164	5.4	7.5	Highly organic
LH30	28	115	6.3	7.7	No comments
LH32	53	167	6.5	5.2	No comments
LH34	24	140	5.9	7.1	High clay and organic matter
LH35	64	203	6.6	6.0	Deep, moist, red clay
LH36	46	93	6.7	3.2	Deep, red loamy sand
LH38	136	404	6.4	3.5	Gravelly
LH39	180	149	6.1	2.2	Deep, very dry
LH40	3[y]	64	7.7	2.5	No comments
LH43	81	110	6.1	5.3	No comments
LH44	60	136	6.0	2.9	No comments
LH46	97	112	6.1	6.1	Gravelly, alluvial
LH47	100	98	5.5	4.3	Deep sandy loam
LH48	69	139	6.4	5.0	Clay with gravel
LH49	4[y]	162	8.0	3.2	Shale chips and clay
LH50	25	125	6.4	3.8	No comments
LH51	56	228	6.0	8.4	No comments
LH52	13	157	6.9	4.2	No comments

[z]Comments recorded at the collection site.
[y]Olsen P value presented where the Olsen value exceeded the Bray value at sites with pH >7.2.

fore, extensive opportunity for gene flow between eastern and western populations as they spread north with the retreating ice sheet and coalesced (Staudt, 1989). Hybridization and introgression may have occurred between *F. virginiana* ssp. *glauca* and eastern *F. virginiana* ssp. *virginiana* in the Black Hills and eastern Rocky Mountains. When the plains later became hotter and drier, these populations were left as Ice Age relics in which the characters that distinguish the two contemporary taxa have not become uniformly intermediate or lost due to selective pressure. We were unable to find populations in central South Dakota or central or western North Dakota that might provide a link between the two subspecies. However, sampling was quite limited and further exploration in the area is critical.

The western exploration areas were equally interesting from an evolutionary standpoint. The distributions and habitats of *F. virginiana* and *F. chiloensis* are geographically close in the Pacific Northwest (Hitchcock and Cronquist, 1973). Putative hybrids between *F. virginiana* and *F. chiloensis* were noted at four sites (BL 57, BL 70, BL 89, BL 93) in the Coast Range, the western Cascades, and the Olympic Mountains. Populations in western Montana and Idaho (LH 29, LH 34, LH 35, LH 37, LH 47) also had a combination of characters reminiscent of *F. chiloensis* — thick runners, thick, rounded leaves, and red petioles. These plants were similar to the woods-meadow populations of *F. chiloensis* described by Hancock and Bringhurst (1979) as having characters of *F. virginiana.* They are also similar to plants described by Staudt (1962) from Vancouver Island and Washington, and by Scoggan (1978) from southwest Alberta assigned to *F. ananassa* nm. *cuneifolia* (Nutt. ex. Howell) Staudt as putative hybrid derivatives of *F. chiloensis* and *F. virginiana.* Staudt (1989) noted that "hybrid populations of *F. chiloensis x F. virginiana* still exist from Vancouver Island along the coast south to Ft. Bragg, California" and that "the further one goes from the coastal area the more the *F. chiloensis* characteristics decrease, Plants with somewhat thinner leaves but some other characteristics of *F. chiloensis* are combined in ssp. *platypetala* of *F. virginiana...* considered to be the final link of an introgression of *F. chiloensis* into *F. virginiana* ssp. *glauca.*"

The timing and extent of possible gene flow between the species are intriguing questions as the Montana and Idaho sites are nearly 1000 km from the coastal habitat of *F. chiloensis.* Introgression from the cultivated strawberry could have occurred, although many of our collection sites were isolated from human settlements. Staudt (1989) speculated that hybidization probably occurred after glaciation in the Fraser River valley of British Columbia. Another possibility is that *F. chiloensis* and *F. virginiana* ssp. *glauca* are alternative forms of a single biological species, separated during the Pleistocene, and altered by selection for adaptation to coastal or montane, continental habitats. This change would be consistent with an origin for octoploid strawberries in east Asia and dispersal along the northern Pacific islands, through Alaska, and south throughout North America. Indeed, *F. iturupensis* of the western Pacific has glaucous leaves like *F. virginiana* ssp. *glauca* (Staudt, 1973). In South America, *Fragaria chiloensis* ranges through the habitats that contain *F. chiloensis* and *F. virginiana* ssp. *glauca* in North America-from Pacific Ocean beaches and headlands to montane forests at 1900 m elevation (Bringhurst et al., 1989; Cameron et al., 1991; Darrow, 1966). At high elevations in Chile, plants also have the glaucous, thin leaves characteristic of *F. virginiana* ssp. *glauca* (Bringhurst et al., 1989). Bringhurst et al. (1989) note that the glossy-leaved *F. chiloensis* characteristic of the coastal fog belt in California is rare in Chile and that most of the Chilean material more nearly resembles the North American types that derived from putative hybridization of *F. chiloensis* with *F. virginiana* (Hancock and Bringhurst, 1979).

In addition to collections that suggested gene exchange among octoploid taxa, *F. virginiana* plants at one location (BL 63) had characteristics of the diploid *F. vesca* including very erect, long peduncles and nonsunken achenes. These plants (of unknown ploidy) may be derivatives of interploid hy bridization similar to the natural pentaploid hybrids between *F. chiloensis* and *F. vesca* described from several Pacific coast sites in California (Bringhurst, 1990; Bringhurst and Senanayake, 1966).

These various introgressed populations could yield horticulturally interesting combinations of genes from divergent types. Numerical and biochemical taxonomic characterization and further intense collection from these geographic areas may clarify the evolutionary and taxonomic relationships. Evaluation of recent Chilean collections (Cameron et al., 1991) and future collections in Alaska, the northern and western Pacific islands, and the east Asian mainland will be critical in furthering the understanding of *Fragaria* speciation at the octoploid level, (Staudt, 1989).

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