From Villous Strawberry Shams to Hairy Huckleberries: The Wild Side of Berry Exploration

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***Abstract*. The U.S. Department of Agriculture (USDA), Agricultural Research Service, National Clonal Germplasm Repository in Corvallis was established as the U.S. National Plant Germplasm System's berry genebank in 1981. Since then, the USDA has sponsored numerous explorations throughout the United States and foreign countries to obtain berry plant genetic resources. Species of *Fragaria* L. (strawberries), *Ribes* L. (currants and gooseberries), *Rubus* L. (raspberries and blackberries), and *Vaccinium* L. (blueberries and cranberries) are native to both domestic and international localities. With limited gene pools for cultivated strawberries, raspberries, and blackberries, expeditions have provided a wealth of genetic resources to expand opportunities for breeders to develop new cultivars. Particularly given the diverse species inherent in the development of cultivated blueberries, these trips have discovered unusual new blueberry relatives and forms available for expanding the range of production, increasing plant yields, and improving fruit antioxidant content. Along the way, new fruit species and new uses for known species were observed. Gathering the bounty of the world's berries resulted in encounters with diverse fauna, from snakes, bears, and bison to butterflies, mosquitoes, ticks, and chiggers. Avenging *Toxicodendron* species have added their mark on intrepid explorers. Remote sites with nothing but clear night stars and the satellite markers on the global positioning system offer radiant beauty and an abiding hope for the conservation of plant genetic diversity for all people for all time.**

BEGINNINGS OF THE NATIONAL PLANT GERMPLASM SYSTEM

In 1898, the U.S. Department of Agriculture (USDA) Division of Botany, Bureau of Plant Industry established a "Seed and Plant Introduction Section" to acquire new germplasm for the United States (Hyland, 1977). Since then, plant exploration has been sponsored annually to acquire diverse genetic resources for U.S. agriculture (Williams, 2005). For more than 40 years after the establishment of the Seed and Plant Introduction Section, there were limited facilities for maintaining newly introduced plant materials. A high percentage of early PIs were lost (White and Briggs, 1989). Congressional legislation established the four Regional Plant Introduction Stations, the Interregional Potato Station, and the National Seed Storage Laboratory in the 1940s and 1950s. In the late 1970s, reorganization within the Agricultural Research Service and new national legislation gave rise to facilities specifically assigned to preserving horticultural plant resources in a clonal form. The U.S. National Plant Germplasm System (NPGS) currently includes ≈30 federal genebanks that store seeds and plants of economically important, food, fiber, and ornamental crops. The genebanks in the NPGS have a mandate to collect, maintain, distribute, evaluate, document, and capture diverse global genetic resources.

NATIONAL CLONAL GERMPLASM REPOSITORY–CORVALLIS

The USDA Agricultural Research Service (ARS) National Clonal Germplasm Repository (NCGR) at Corvallis, OR, was the first Clonal Repository to be established in the NPGS. It was dedicated in May 1981. Species of strawberries, raspberries and blackberries, currants and gooseberries, and blueberries and cranberries were assigned to the NCGR–Corvallis because of the commercial importance of berry crops to the economy of the Pacific Northwest United States and because of the excellent climate for their growth. Although each of these genera has centers of origin within North America, each also has much of their species diversity indigenous to other continents (Brennan, 1996; Daubeny, 1996; Hummer et al., 2010; Jennings, 1988).

As of the end of 2010, the NCGR conserved ≈6000 small fruit accessions (Table 1), including the previously mentioned berry genera in addition to hardy kiwifruit [*Actinidia arguta* (Siebold & Zucc.) Planch. ex Miq., *A. polygamma* (Siebold & Zucc.) Maxim. *A. kolomikta* (Maxim. & Rupr.) Maxim.], and blue honeysuckle (*Lonicera caerulea*). Approximately 40% of these accessions were collected from the wild during plant collection expeditions. The remaining NCGRP accessions are composed of named cultivars and selections with desirable well-characterized traits from breeding programs.

SMALL FRUIT COLLECTION EXPEDITIONS

The following section briefly summarizes some of the expeditions that have brought significant small fruit genetic resources to the NCGR–Corvallis during the past 30 years.

Strawberries. Approximately 20 species of strawberries exist throughout the northern hemisphere (Hummer and Hancock, 2009). The NCGR–Corvallis maintains accessions representing each of these species as well as many infraspecific taxa. The primary gene pool for the hybrid strawberry of commerce is octoploid ($2N = 8x = 56$, $x = 7$), although cultivars of diploid *Fragaria vesca* L. have been commercialized in Europe (Hummer and Janick, 2009; Hummer et al., 2010). Artificial decaploid strawberries have been developed through chemical-induced increases of ploidy in *F. vesca* crossed with *F. ×ananassa* in Sweden and Germany, which was named as a hybrid species, *F. ×vescana* Rud. Bauer and A. Bauer (Bauer, 1993).

An important foreign small fruit collection trip to Chile was led by George Darrow (Perdue and Christenson, 1989) to collect wild and landrace strawberries in 1956–1957 (Table 2). Several genotypes for wild small red-fruited *F. chiloensis* subsp. *chiloensis* f. *patagonica* Staudt and the larger white-fruited landrace *F. chiloensis* subsp. *chiloensis* f. *chiloensis* Staudt were obtained from that expedition. This white-fruited landrace was the maternal progenitor for the large-fruited cultivated hybrid red-fruited strawberry that consumers recognize. Four genotypes, representatives of both types of Chilean strawberries collected in 1956, are conserved and remain available at NCGR–Corvallis. The limited availability of available Chilean strawberry plant material in the United States inspired return expeditions led by J. Scott Cameron with colleagues in 1990 and 1992 (Table 2). A broad range of Chilean strawberries representing ≈60% of the country's area was obtained as a result of those two plant expeditions. Subsequently, several hundred Chilean strawberry representatives were donated and are maintained by the NCGR–Corvallis.

Several subspecies of *Fragaria chiloensis* have been collected from native habitats in California, Oregon, Washington, British Columbia, Alaska, and Hawaii (Table 2). Around the Pacific Rim, *Fragaria orientalis*

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Losinsk. was collected from the Russian Far East; *F. iturupensis* Staudt from Iturup Island in the Greater Kurile Island chain (Hummer et al., 2009); *F. iinumae* and *F. nipponica* were collected from Sakhalin Island, Russia, and Hokkaido and Honshu, Japan (Hummer and Sabitov, 2008; Hummer et al., 2010; Iketani et al., 2010) . Diverse diploid and tetraploid strawberry species have also been collected from India, China, and Kyrgyzstan and donated to the NCGR–Corvallis.

The paternal progenitor species of the hybrid strawberry of commerce is *Fragaria virginiana* Mill. subsp. *virginiana*. This species is endemic to northeastern North America. James Ballington, James Luby, and Otto Jahn collected strawberry species and many other small fruit taxa through the northwestern North America in 1985 and 1986. Finn, Luby, and Hancock also collected strawberry species from the Rocky Mountains. Ballington and Hummer also collected eastern populations of *F. virginiana* as well as additional small fruit species in subsequent trips. The maternal progenitor species is *F. chiloensis* subsp. *chiloensis* f. *chiloensis*, a cultivated landrace from Chile.

Table 1. Berry accessions at the USDA ARS National Clonal Germplasm Repository at Corvallis as of 31 Dec. 2010.[z]

Genus	Unique	Seed
Actinidia[y]	185	36
Fragaria	1665	455
Lonicera	79	48
Ribes[x]	1148	551
Rubus	1750	1300
Vaccinium	1327	847
Total	6154	3237

[z]"Unique" accessions include unusual plant genotypes preserved as living collections. "Seed" denotes germplasm accessions that are stored as seed lots at –18 °C.

[y]Will be transferred to National Clonal Germplasm Repository, Davis, CA, in 2011.

[x]Will be transferred to Arctic and Subarctic Plant Gene Bank, Palmer, AK, in 2011.

Another Rosaceae genus, *Potentilla* L., is found almost everywhere *Fragaria* is distributed. In some environments, *Potentilla* species may be trifoliate and can be morphologically similar to strawberries. The yellow petal color of *Potentilla* is a distinguishing character compared with the white petals of *Fragaria*. *Potentilla villosa* Pall. ex Pursh is native to the Aleutian Islands, Kodiak Island, and continental Alaska. This plant appears to be a "most pubescent strawberry" until the yellow flower petals are viewed. Another Rosaceae species, *Duchesnea indica* L., has been introduced from Asia to many regions of the world, including Europe and eastern North America. *Duchesnea* can also be distinguished by yellow petals, although it is a trifoliate and produces runners with red stolons, somewhat similar to those of *Fragaria*. Several representatives of these non-*Fragaria* strawberry relatives are housed in the collections at NCGR–Corvallis. The main collection for Potentilla in the NPGS is at the Regional Plant Introduction Station at Ames, IA.

Raspberries and blackberries. The brambles (*Rubus* L.) include ≈750 species classified within 12 to 15 subgenera (Daubeny, 1996; Hall et al., 2009; Hummer and Janick, 2009; Jennings, 1988). The majority of *Rubus* species are native to Asia and Oceania, although Europe and the Americas also have many endemics. In 2011, the NCGR–Corvallis maintained germplasm representing 167 *Rubus* species and 15 infraspecific taxa. The primary gene pool for commercial raspberries is diploid ($2N = 2x = 14$, $x = 7$), and the primary gene pool for blackberry is hexaploid ($2N = 6x = 42$, $x = 7$). Hybrid berries with both red raspberries and blackberries in their pedigrees have been developed by genetic manipulation to reach compatible ploidy levels. Various fruit color mutants from yellow to dark purple or black occur in many *Rubus* species. Leaf and seed morphology in *Rubus* species are as diverse as any genus on the planet; *Rubus* leaf form includes entire, lobed, dissected, palmately compound, pinnately compound, and more. Wada and Reed (2010) recently examined seed morphology for identity determination.

Significant USDA plant expeditions for *Rubus* have occurred in Guizhou and northeastern provinces of China; Primorye, Khabarovsk, and Sakhalin Territories of Russia; Hokkaido and Honshu, Japan; Scandinavia, the United Kingdom, and other parts of Europe; Ecuador, Bolivia, and Chile; New Zealand; and throughout North America (Table 2).

The available black raspberry (*Ribes occidentalis* L.) gene pool has been limited over the past century to wild material from the northeastern United States (Dossett and Finn,

Table 2. Some of the small fruit expeditions for the National Plant Germplasm System (NCGR) 1956–2011.

Collectors	Years	Countries	Crop	Amount extant in NCGR–Corvallis in 2011
G. Darrow	1956–57	Chile	*Fragaria*	4
J. Galletta	1965	US (FL, GA, NJ, WI)	*Vaccinium*	12
D.D. Dolan	1976	US (NE)	*Fragaria*	Unknown
M. Faust	1976	US (NE)	*Fragaria*	Unknown
M. Faust	1977	US	*Fragaria*	Unknown
W. Sherman and P. Lyrene	1981	US (SE)	*Vaccinium*	10
M.N. Westwood	1981	Japan, Taiwan, Korea	*Fragaria, Ribes, Rubus, Vaccinium*	40
O. Jahn	1982/1985	England/Scandinavia	*Rubus*	13
T. Sjulin and C. Shanks, Jr.	1983	US (CA, OR)	*Fragaria*	250
J. Ballington, J. Luby, and O. Jahn	1985	US (CA, OR, WA)	*Fragaria, Ribes, Rubus, Vaccinium*	210
N. Fredricks	1987	Oregon	*Ribes*	15
M. Thompson, D. Brenner	1988	Pakistan	*Fragaria, Ribes, Rubus, Vaccinium*	300
K. Hummer	1990	US (NE)	*Fragaria, Ribes, Rubus, Vaccinium*	20
M. Thompson, J. Ballington, J. Leutyne	1990	Ecuador	*Vaccinium* and relatives	16
J.S. Cameron	1990	Chile	*Fragaria, Rubus*	171
J. Allen	1991	US (NE)	*Vaccinium*	21
M. Thompson and J. Young	1992	China (Guizhou)	*Rubus*	200
J.S. Cameron, T. Sjulin	1992	Chile	*Fragaria*	200
N. Vorsa	1992	US (SE)	*Vaccinium*	11
C. Finn, J. Luby, R. Harrison	1993	US	*Fragaria, Ribes, Rubus, Vaccinium*	55
W. Messinger, J. Ballington	1995	Bolivia, also US collecting	*Ribes, Rubus, Vaccinium*	103
K. Hummer and K. Wright	1996	Alaska	*Fragaria, Ribes, Rubus, Vaccinium*	52
M.M. Thompson, C. Finn, J. Postman	1996	China (NE)	*Fragaria, Ribes, Rubus, Vaccinium*	70
K. Hummer	1998	Alaska, Pacific NW US	*Fragaria, Ribes, Rubus, Vaccinium*	15
K. Hummer and N. Vorsa	2001	Russia (Far East)	*Fragaria, Ribes, Rubus, Vaccinium*	87
J. Postman and P. Meyer, A. Whitmore	2002	Armenia	*Rubus*	9
A. Sabitov and K. Hummer	2003	Russia (Far East) Iturup, Sakhalin	*Fragaria, Ribes, Rubus, Vaccinium*	128
K. Hummer and T. Davis	2004	Japan (Hokkaido)	*Fragaria, Ribes, Rubus, Vaccinium*	171
K. Hummer and P. Lyrene	2006	US (Florida)	*Vaccinium*	44
K. Hummer, C. Finn and M. Dossett	2007	US (SE and MW)	*Rubus* (black raspberries)	78
K. Hummer and J. Postman	2009	Japan (Hokkaido and Honshu)	*Fragaria, Ribes, Rubus, Vaccinium*	139
Total				2444

2010). In 2007, Dossett, Finn, and Hummer explored the southern and western edges of the distribution of the eastern North American black raspberry, *Rubus occidentalis* L. Particular genotypes with insect resistance, soilborne pathogen resistance, unusual leaf morphology, and desirable anthocyanin content (Dossett and Finn, 2010; Dossett et al., 2010) have been found from recent plant collections. New breeding efforts to develop cultivars with improved traits have begun.

Currants and gooseberries. The currants and gooseberries (*Ribes* L.) include ≈150 species (Barney and Hummer, 2005; Brennan, 1996) distributed primarily throughout the Northern Hemisphere, but also at higher latitudes in Central and South America and northwestern Africa. Worldwide, black currants are the primary cultivated *Ribes* crop for juice production; however, red and white currants and gooseberries are produced for fresh eating and preserves. *Ribes* serves as a cohost for the white pine blister rust disease caused by the fungus *Cronartium ribicola* J. C. Fisher, thus limiting *Ribes* production and consumption in North America. Twelve states still have restrictions on *Ribes* production because of this disease, but in 2010 and 2011, U.S. black and red currant production increased. In the United States, powdery mildew, caused by *Podosphaera mors-uvae* (Schwein) U. Braun & S. Takam., is a major fruit production problem. Mildew-resistant genotypes have been identified in gooseberries and currants (Picton and Hummer, 2003). Evaluation of the NCGR–Corvallis *Ribes* collection for white pine blister rust and powdery mildew resistance is ongoing.

Currants and gooseberries have been collected for the NCGR–Corvallis, from Europe, the Russian Far East, China, Japan, Bolivia, Chile, and across the United States. The Pacific Northwestern United States is a center of diversity for gooseberries. Of Nancy Fredrick's 1987 collection throughout Oregon, 15 genotypes of *Ribes* remain available (Table 2). Sets of Native American species of *Ribes aureum* Pursh, *R. americanum* Mill., *R. pinetorum* Greene, and *R. mescalerium* Coville are represented. In addition, ornamental flowering currants such as *R. sanguineum* Pursh, *R. speciosum* Pursh, *R. viburnifolium* A. Gray, *R. watsonianum* Koehne, and *R. menziesii* Pursh are being evaluated.

With recent budget limitations, the NPGS genebanks located at Corvallis, OR, and Palmer, AK, have been merged under one management unit. The primary responsibility for the genus *Ribes* assigned has recently changed from NCGR–Corvallis to the Arctic and Subarctic Plant Gene Bank, at Palmer, AK. Corvallis will continue to maintain a backup field collection and representation of *Ribes* species native to lower latitudes in support of the Palmer Gene Bank.

Blueberries. The genus *Vaccinium* contains ≈400 species (Galletta and Ballington, 1996), which are predominantly endemic in Oceania, although many economically important species are native to North America and circumpolar boreal forests.

The original highbush blueberries (*Vaccinium corymbosum* L.) were selected by E. White and bred by F. Coville from endemic northeastern North American germplasm beginning in 1906. This species ranges from Nova Scotia south to Florida along the eastern coast of North America and is found inland as far west as Wisconsin. Since the early 1900s, A. Draper, G. Galletta, P. Eck, P. Hepler, R. Sharp, J. Ballington, J. Luby, N. Vorsa, J. Hancock, P. Lyrene, and other breeders have been making blueberry crosses with native *Vaccinium* species to extend the range of production (Perdue and Christenson, 1989). Galletta, Lyrene, and Ballington collected additional blueberry germplasm of southern distributions. For example, Galletta's collection of *V. constablaei* A. Gray from Grandfather Mountain in near North Carolina provided genes for later bloom, earlier ripening, cold-hardiness, and improved fruit quality (Galletta and Ballington, 1996).

Crosses between highbush blueberry and the northern lowbush species, *V. angustifolium* Aiton, produced a group of blueberries called "half high" blueberries (Finn et al., 1990). The stature and other morphological characteristics of this group are intermediate between the low and highbush blueberries. In northern latitudes, these plants typically remain under snow cover and are insulated from the cold and desiccation of winter. The half high blueberries successfully expanded the blueberry production range through the northern midwestern United States and Canada. Recently, half high blueberries were being trialed on the Kenai Peninsula for Alaskan production (Barney and Hummer, 2011).

For lower latitudes, where winter chilling hours are insufficient to accommodate the chilling requirement of standard *V. corymbosum* cultivars to initiate spring budbreak and growth, southern lowbush species such as *V. darrowii* have been incorporated into parental breeding stock. *Vaccinium darrowii* Camp, native to Florida, has no chilling requirements. Crosses resulted in group of "southern highbush" blueberries, which have shorter chilling requirements. This breeding innovation has allowed for the production of blueberries in the warm climates of North Carolina, Georgia, Florida, southern California, and Mexico and has expanded blueberry production to other countries such as New Zealand, Mexico, Chile, Argentina, Uruguay, Portugal, and Spain. Recent trials have demonstrated that southern highbush blueberries can be produced in Hawaii as well (Hummer and Zee, 2007; Zee et al., 2006). The NCGR–Corvallis expanded its collection of *V. darrowii* when Hummer and Lyrene traveled in 2006 to collect *V. darrowii* and the southern distribution of *V. corymbosum* (also known as *V. fuscatum* Aiton) from three separate metapopulations in the Panhandle, the central region, and the southern peninsula of Florida. These species, found on pine sand barrens, are seriously endangered as a result of human encroachment and the booming development in that region. During that expedition, many cuttings were taken and representative seed samples are being generated to represent the diversity of those southern taxa.

Rabbit eye cultivars (*V. virgatum* Aiton, formerly known as *V. ashei* J. M. Reade) are a second type of economically important low-chilling blueberry species native to the southeastern United States. Rabbit eye cultivars require growing degree-days. When grown in the Pacific Northwestern United States, these species extend the production season and ripen in late summer to early fall after the head has been sufficient to ripen the fruit.

Recently interest has been increasing in fruit anthocyanin pigment content. Blueberries have been touted as high in anthocyanin in comparison with red-ripening fruits (Moyer et al., 2002). In standard blueberry cultivars, high anthocyanin concentrations occur in the fruit skin, not in the fruit flesh. Other species in *Vaccinium* section *Myrtillus* include species with dark flesh. Recent interest has increased plant-collecting efforts to obtain blueberry relatives such as *V. myrtillus* L., *V. membranaceum* Douglas ex Torr., *V. deliciosum* Piper, and *V. ovalifolium* Sm. in this section. Crosses have been made to increase the internal pigment content of blueberries. In Hawaii, two native species in section *Myrtillus*, *V. reticulatum* Sm. and *V. calycinium* Sm., were the subject of recent study to advance the development of cultivars for fruit and ornamental plant production (Zee et al., 2010). These species could provide a good model for local production of other indigenous wild berries.

Cranberries. A second economically important *Vaccinium* species is the red-fruited American cranberry, *Vaccinium macrocarpon* Ait., native to northeastern North America. Many cultivars were initially selected from wild populations in New Jersey, New York, Massachusetts, New England, and Wisconsin. Breeding programs in the USDA, New Jersey, Massachusetts, and Wisconsin have developed new disease-resistant, high-yielding cultivars (Galletta and Ballington, 1996; Eck, 1990). Plant material has been collected throughout the northern range. In 1991, Jeannie Allen worked with the Forest Service and state heritage botanists to collect cranberries from their southern and western range in the Appalachians, in states such as Tennessee, Kentucky, Maryland, and West Virginia where this species is on watch lists.

Hummer, Vorsa, Postman, and others collected *V. oxycoccos* L., a cranberry relative from Asia and the Russian Far East. These fruits, unlike those of the small-fruited species in North America, were similar in size to *V. macrocarpon*. Ploidy differences may explain this observation and are under evaluation.

CONCLUSIONS

The USDA plant exploration grants (Williams, 2005) and the NCGR–Corvallis unit funds have significantly supported collection of small fruit species during the past 60 years. Diverse species have been obtained that have contributed significantly to breeding improvements for small fruit cultivars to increase the production range, modify the blooming and ripening seasons, and improve fruit qualities, yield, disease resistance, insect resistance, plant habit, and many other traits. The global small fruit industry has increased over this time. Many countries in both the northern and southern hemispheres are producing these healthful fruits for local use and also for export to population centers. The use of diverse species in breeding programs has broadened gene pools and has been the foundation for global berry production. Many small fruit species have not yet been collected or evaluated for breeding potential or crop development. Exploration for small fruit must be supported for the next century for continued growth of the small fruit industry.

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