Vaccinium

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Chapter 10
Vaccinium

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10.1 Basic Botany of *Vaccinium*

10.1.1 History, Origin, and Distribution

Vaccinium is a genus of terrestrial shrubs in the family Ericaceae (Syn. Heath) (Vander Kloet 1988). It consists of approximately 450 species with a wide geographic distribution in the Northern Hemisphere and also in the mountains of tropical Asia and Central and South America. A few species are also found in Africa and Madagascar, as well as 92 species (51 endemic) in China (Luby et al. 1991; Fang and Stevens 2005). High densities of *Vaccinium* species are distributed in the Himalayas, New Guinea, and the Andean region of South America (Luby et al. 1991; Hancock et al. 2008). The majority of species are found on open mountain slopes in the tropics (Camp 1942a, b, 1945). Southeast Asia (Malayan, Archipelago, New Guinea, India, China, and Japan) is the origin of almost 40% of the *Vaccinium* species. About 35% of the species are native to America including 25% in North America and 10% in South and Central America. The rest, about 25%, are widely scattered across the world (Luby et al. 1991). *V. uliginosum* L. is likely the most widely distributed *Vaccinium* species. Many of the *Vaccinium* species are invaluable ornamental plants due to their colorful leaves, flowers, and fruits (Galletta, and Ballington 1996).

Three major *Vaccinium* fruit crops (blueberry, cranberry, and lingonberry) have been domesticated in the twentieth century (Galletta and Ballington 1996; Hancock et al. 2003; Lyrene et al. 2003). Bilberry and the fruits of a number of other non-cultivated *Vaccinium* species also show great potential as new crops (Vorsa 1997). The most important *Vaccinium* crop species are found in the sections *Cyanococcus*, *Oxycoccus*, *Vitis-Idaea*, *Myrtillus*, and *Vaccinium* (Table 10.1). The taxonomy of these sections has been difficult to resolve due to complex polyploidy series ($x = 12$) and a general lack of chromosome differentiation and crossing barriers within sections. The primary mode of speciation has been through unreduced gametes (Camp 1945; Darrow and Camp 1945; Hancock et al. 2008).

Most production comes from species in section *Cyanococcus* including cultivars of *Vaccinium corymbosum* L. (highbush blueberry) and *Vaccinium ashei* Reade (rabbiteye blueberry; syn. *Vaccinium virgatum* Ait.) and native stands of *Vaccinium angustifolium* Ait. (lowbush blueberry). Highbush cultivars are further separated into northern or southern types depending on their chilling requirements and winter hardiness. *Vaccinium macrocarpon* Ait. (large cranberry), a member of section *Oxycoccus*, is also an important domesticated species. *Vaccinium myrtillus* L. (bilberry, whortleberry), *Vaccinium membranaceum* Douglas. Ex Torr. (tall bilberry, big huckleberry), *Vaccinium deliciosum* Piper (Cascade bilberry or huckleberry), and *Vaccinium ovalifolium* Sm. (oval-leaved huckleberry) in section *Myrtillus* and *Vaccinium vitis-idaea* (lingonberry) in section *Vitis-Idaea* are collected primarily from the wild.

10.1.1.1 Blueberries

The blueberries in the section *Cyanococcus* occur naturally only in eastern and northcentral North America

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Table 10.1 Important *Vaccinium* species ($2n = 2x = 24$)

Section	Species	Common name	Ploidy	Location	Potentially useful traits
Batodendron	*V. arboreum* Marsh	*Farkleberry*; Sparkleberry.	2*x*	S.E. North America	Drought tolerance, adaptation to basic mineral soils, open flower clusters, upright bush habit, stem blight resistance, resistance to sharp-nosed leafhopper
Cyanococcus	*V. angustifolium* Ait.	*Lowbush Blueberry*; Blueberry; Late Sweet Blueberry; Low Sweet Blueberry; Sweethurts; Upland Lowbush Blueberry	4*x*	N.E. North America	Winter hardiness, early ripening, blossom frost tolerance, adaptation to high pH, stem blight and Phytophthora root rot resistance, light blue fruit color, small scar, high soluble solids and low acidity
	V. ashei Reade. (syn. *V. virgatum* Aiton)	*Rabbiteye Blueberry*	6*x*	S.E. North America	Drought tolerance, low chilling requirement, upright plant habit, late ripening, long flowering to ripening period, fruit firmness, small scar, loose fruit cluster, cane canker, stem blight and Phytophthora root rot resistance, resistance to sharp-nosed leafhopper
	V. boreale Hall & Aald.	*Northern Blueberry*	2*x*	N.E. North America	Winter hardiness, blossom frost tolerance
	V. constablaei Gray	*Hillside Blueberry*	6*x*	Mountains of SE North America	Winter hardiness, high chilling requirement, light blue fruit color
	V. corymbosum L.	*Highbush Blueberry*; American Blueberry; Blueberry; Swamp blueberry; Aairelle d'Amérique; Amerikanische Blueberry; Arándano americano	2*x*	S.E. North America	Low chilling requirement, upright plant habit, early ripening, light blue fruit color, small fruit scar
	V. corymbosum L.	*Highbush Blueberry*	4*x*	E. North America	Low chilling requirement, upright plant habit, light blue and firm fruit color, small fruit scar, excellent flavor, stem canker resistance
	V. darrowii Camp	*Darrow's Blueberry*	2*x*	S.E. North America	Low chilling requirement, heat tolerance, resistance to mummy berry, adaptation to high pH, tolerance to mineral soils, late flowering, late ripening, long flowering to ripening period, fruit firmness, excellent complex flavor, small scar, light blue fruit color, fruit hold well in heat, high soluble solids and low acidity, loose fruit cluster
	V. fuscatum Ait.	*Black Highbush Blueberry*; Thick-leaf Blueberry; Downy Swamp-huckleberry	2*x*	Florida	Very low chilling requirement, upright plant habit, vigorous
	V. myrtilloides Michx.	*Velvetleaf Huckleberry*	2*x*	Central North America	Winter hardiness, early ripening, blossom frost tolerance, resistance to mummy berry, small scar, high soluble solids and low acidity

(*continued*)

Table 10.1 (continued)

Section	Species	Common name	Ploidy	Location	Potentially useful traits
	V. pallidum Ait.	*Blue Ridge Blueberry*; Lowbush Blueberry; Hillside Blueberry; Blueridge Blueberry; Hillside Lowbush Blueberry; Upland Low Blueberry	2*x*; 4*x*	Mid-Atlantic North America	Adaptation to mineral soils, early ripening, small scar, high soluble solids and low acidity
	V. tenellum Ait.	*Small Black Blueberry*	2*x*	S.E. North America	Adaptation to mineral soils, late ripening, firm fruit
	V. elliottii Chapm.	*Elliott's Blueberry*	2*x*	S.E. North America	Drought tolerance, adaptation to high pH, tolerance to mineral soils, low chilling requirement, upright plant habit, late flowering, early ripening, upright habit, small fruit scar, excellent flavor, cane canker, stem blight and Phytophthora root rot resistance, resistance to sharp-nosed leafhopper
	V. hirsutum Buckley	*Hairy Blueberry*	4*x*	S.E. North America	
	V. myrsinites L.	*Shiny Blueberry*; Evergreen Blueberry	4*x*	S.E. North America	Low chilling requirement, small scar, low acidity, firm fruit
	V. simulatum Small	*Upland Highbush Blueberry*	4*x*	S.E. North America	Large fruit, winter hardiness, adaptation to mineral soils, deep root system
Oxycoccus	*V. macrocarpon* Ait.	*Large Cranberry*; Cultivated Cranberry; American Cranberry	2*x*	North America	Large leaf, large fruit and seed, high antioxidant content
	V. oxycoccos L.	*Cranberry*; Small Cranberry; European Cranberry; Mossberry; Moosbeere; Tsuru-kokemomo; Bog Cranberry; Swamp Cranberry; Wild Cranberry	2*x*; 4*x*; 5*x*; 6*x*	Circumboreal	Cold hardiness
	V. erythrocarpum Michx.	*Southern Mountain Cranberry*	2*x*	S.E. North America and E. Asia	–
	V. microcarpum (Turcz. Ex Rupr.) Schmalh.	*Small Cranberry*	2*x*	Circumboreal	–
Vitis-Idaea	*V. vitis-idaea* L.	*Lingonberry*; Cowberry; Foxberry; Mountain Cranberry; Red Whortleberry; Lowbush Cranberry; Partridgeberry	2*x*	Circumboreal	High benzoic acid, resistance to bacterial fruit rots, highly ornamental value for colorful, evergreen leaves
Myrtillus	*V. cespitosum* Michx.	*Dwarf bilberry*; Dwarf Blueberry; Dwarf Huckleberry	2*x* 4*x*	North America	Cold hardiness, late bloom, early ripening

(*continued*)

Table 10.1 (continued)

Section	Species	Common name	Ploidy	Location	Potentially useful traits
	V. deliciosum Piper	*Cascade Bilberry*; Alpine Blueberry; Cascade Blueberry; Blueleaf Huckleberry; Rainier Blueberry		N.W. North America	Winter hardiness, blossom frost tolerance, light blue fruit color, excellent flavor
	V. membranaceum Dougl. Ex Hook.	*Mountain Bilberry*; Black Mountain Huckleberry; Black Huckleberry; Twin-leaved Huckleberry; Leaf Huckleberry; Tall Huckleberry	4*x*	W. North America	Cold hardiness, drought tolerance, high pH tolerance internal fruit pigmentation, large fruit size, excellent flavor
	V. myrtillus L.	*Bilberry*; Dwarf Bilberry; Myrtle Blueberry; Myrtle Whortleberry; Whortleberry	2*x*	Circumboreal	Winter hardiness, blossom frost tolerance, internal fruit pigmentation, excellent flavor
	V. ovalifolium Sm.	*Oval-leaved Bilberry*; Oval-leafed Blueberry; Mountain Blueberry; High-bush Blueberry	4*x*	Circumboreal	Large and firm fruit, small picking scar, light blue fruit color
	V. parvifolium Sm.	*Red bilberry*; Red Huckleberry	2*x*	N.W. North America	Drought tolerance
	V. scoparium Leiberg ex Coville	*Grouseberry*; Small-leaved Huckleberry; Dwarf Red; and Red Alpine Blueberry	2*x*	N.W. North America	Drought tolerance
Polycodium	*V. stamineum* L.	*Deerberry*; Highbush Huckleberry; Squaw Huckleberry: Southern Gooseberry	2*x*	Central and E. North America	Upland adaption, drought tolerance, adaptation to mineral soils, late ripening, very high soluble solids and low acidity, large and firm fruit size, small stem scar, excellent flavor, resistance to sharp-nosed leafhopper
Pyxothamnus	*V. consanguineum* Klotzch	*Costa Rican Blueberry*; Deerberry; Squaw Huckleberry; Gooseberry;	2*x*	S. Mexico and Central America	Blossom frost tolerance
	V. ovatum Pursh	*California Huckleberry*; Evergreen Huckleberry; Box Huckleberry; Evergreen Blueberry; Shot Huckleberry; California Huckleberry; Box Blueberry; Black Huckleberry	2*x*	N.W. North America	Adaptation to mineral soils, late ripening, ornamental value
Bracteata	*V. bracteatum* Thunb.	*Sea Bilberry*	2*x*	E. Asia; China and Japan	Tolerance to high pH
Vaccinium	*V. uliginosum* L.	*Bog Bilberry*; Bog Blueberry; Bog Whortleberry; Bog Huckleberry; Northern Bilberry	2*x*; 4*x*; 6*x*	Circumboreal	Cold hardiness, blossom frost tolerance, Fusicoccum canker resistance? tolerance to heavy metals

Source: from Ballington (1990), Luby et al. (1991), Galletta and Ballington (1996), Jacquemart (1997), Vander Kloet and Dickinson (1999), Suda (2003), Hancock et al. (2008)

(Hancock and Draper 1989). Prior to 1916, all blueberries were harvested from the wild. Today, blueberries are the most popular berry crop in *Vaccinium* and almost all of the commercial blueberries are harvested from three species (1) highbush (*V. corymbosum* L.), (2) rabbiteye [*V. ashei* Reade (syn. *V. virgatum* Ait.)], and (3) lowbush (*V. angustifolium* and *V. myrtilloides*). Highbush plants are crown-forming shrubs and generally 1.8–2.5 m tall. They are found in wetlands and drier upland wooded slopes from Nova Scotia west to Wisconsin, south to Georgia, and Alabama. The most winter hardy cultivars can be grown as Far North as plant hardness Zone 3 with −40 to −34.5°C average annual minimum temperature range (AAMTR). Most northern highbush blueberries do not grow well in the southern US because they require more than 700 chill hours to break dormancy in the spring. Lowbush blueberries, 0.30–0.60 m tall, include the low sweet blueberry (*V. angustifolium*) and the sour-tasting, velvet-leaf blueberry (*V. myrtilloides*). The low sweet blueberries are found from the Arctic to Minnesota and the mountains of New York and New Hampshire; the sour-tasting velvet-leaf blueberries are distributed wild throughout New England and west through plant hardness zone 2 with 45.6 to −40°C AAMTR. These cold-hardy bushes cannot tolerate too much summer heat, and their limit is about zone 7 with −17.8 to −12.3°C AAMTR. Rabbiteye blueberries (*V. ashei*) are crown-forming shrubs and generally 2.0–4.0 m tall. They are most adapted to regions with mild-winters including the southeastern US. Rabbiteye blueberries tolerate dry periods better than other blueberries. However, they are only cold hardy to the zone 6 or 7 with −23.3 to −12.3°C AAMTR (Encyclopedia of Plants 2008).

Many of the wild, edible *Vaccinium* species have been harvested for thousands of years by indigenous people (Moerman 1998). Native Americans in western and eastern North America intentionally burned native stands of blueberries and huckleberries to renew their vigor. Highbush and rabbiteye blueberries were domesticated at the end of the nineteenth century. Plants were initially dug from the wild and transplanted into New England and Florida fields. Most of the commercial production of blueberry now comes from highbush and lowbush types, although rabbiteyes are important in the North American southeast, and hybrids of highbush × lowbush (half-highs) have made a minor impact in the Upper Midwest of the USA. Rabbiteye cultivars are beginning to be grown in the Pacific Northwest and Chile for their very late ripening fruit. Highbush blueberries are grown in 37 states in the USA, in six Canadian provinces, and in Australia, Chile, Argentina, New Zealand, and a number of countries in Asia and Europe (Strik 2005; Strik and Yarborough 2005). The largest acreages of northern highbush are in Michigan, New Jersey, North Carolina, Oregon, and Washington in the USA, and British Columbia in Canada. The greatest amount of southern highbush acreage is in Florida, California, and Georgia. Commercial production of lowbush blueberries is mainly in Maine, Quebec, New Brunswick, and Nova Scotia (Strik 2005; Hancock et al. 2008). While the half-high blueberries are not a major contributor to the fruit market, they are very widely used as an ornamental plant for landscaping.

10.1.1.2 Cranberries

Cranberries are widespread throughout the cool temperate Northern Hemisphere and their native habitat is principally in wetland areas. There are four species of cranberry (Table 10.1). The domesticated large cranberry or the American cranberry, *Vaccinium macrocarpon* (Ait.) Pursh. is an endemic of eastern North America and is thought to be the most primitive species in section *Oxycoccus* (Camp 1945). Large cranberry plants, 10.2–15.2 cm tall, are woody perennials adapted to acid soils and a temperate climate, requiring approximately 1,200 h of chilling to break winter dormancy (Polashock and Vorsa 2002a). The first cultivation of large cranberries was reported in 1810 in Cape Cod, Massachusetts (Camp 1945; Polashock and Vorsa 2002a; McCown and Zeldin 2005). Common cranberry (*V. oxycoccos* L.) is widespread throughout northern Europe, northern Asia, and northern North America. Small cranberry (*V. microcarpum* (Turcz. Ex Rupr.) Schmalh.) occurs in northern Europe and northern Asia. Southern mountain cranberry, *V. erythrocarpum* (Michx.) Pers., is native to southeastern North America at high altitudes in the southern Appalachian Mountains and also in eastern Asia.

Currently, *V. macrocarpon* Ait. is grown as a commercial crop on approximately 40,000 acres across the northern United States and Canada, primarily in Wisconsin, Massachusetts, New Jersey, Washington, and Oregon, with limited plantings in British Columbia, Michigan, Nova Scotia, and Quebec. Chile and Germany also grow *V. macrocarpon* Ait.; Russia and eastern Europe are the two major regions for commercial production of *V. oxycoccos* L. (Roper and Vorsa 1997; McCown and Zeldin 2005). The small cranberry and southern mountain cranberry are seldom cultivated.

10.1.1.3 Lingonberries

V. vitis-idaea (common known as lingonberry) is a perennial, evergreen dwarf shrub in *Vaccinium* section *vitis-idaea* (Moench) Koch (Table 10.1) (Luby et al. 1991; Galletta and Ballington 1996; Gustavsson 2001). It is thought to be a cranberry–blueberry intermediate (Galletta and Ballington 1996). This species is distributed in circumboreal regions and prefers acid soils. It has been divided into a coarser, lowland subsp. *vitis-idaea* (L.) Briton and a circumpolar-Arctic Montane subsp. *minus* (Lodd.) Hult (Hultén 1949). The plant height of *V. vitis-idaea* (L.) Briton may exceed 30 cm, whereas the plant height for *V. vitis-idaea* spp. *minus* rarely exceeds 20 cm (Gustavsson 2001). The subsp. *vitis-idaea* (L.) grows in Europe and Asia. In Europe, it is restricted to the north, ranging from the British Isles, Fennoscandinavia and North Russia, south to the Pyrenees, northern Italy, the Balkans, and Caucasus. In Asia, it is distributed from the Urals to Okhotsk and Kamchatka, south to northern Mongolia, Korea, and Japan. The subsp. *minus* (Lodd.) is found mainly in North America, parts of Asia, and the alpine region of Scandinavia. In North America, the subsp. *minus* (Lodd.) ranges from eastern Kola Peninsula and Nova Zemlia to the Chukch Peninsula and Kamchatka and across North America to Greenland and Iceland (Luby et al. 1991).

Lingonberry plants are extremely hardy, tolerating −40°C or lower, but grow poorly where summers are hot. They are found in diverse habitats, ranging from lowland to upland and mountain areas, in largely acidic soils to pure peat bog (Gustavsson 1997). Lingonberry has a long history of being commercially harvested from native stands in Europe and parts of northern North America (Gustavsson 2001; Finn and Mackey 2006). The fruits are traditionally used in jams, jellies, juices, sauces, pies, and wines.

10.1.1.4 Berry Fruits in Genus *Vaccinium*, Section Myrtillus

The *Vaccinium* section *Myrtillus* Dumortier includes seven species (Table 10.1) (Vander Kloet 1988). This section is restricted to the Northern Hemisphere within a radius of 100 km of 50° N latitude, 110° W longitude. It has its center of diversity along the Pacific Rim from Japan to Guatemala (Vander Kloet and Dickinson 1999). A secondary center of diversity occurs in the mountains of Honshu, Japan (Vander Kloet 1983). The origin and habitats of the seven species were summarized in Table 10.2. The common name bilberry is derived from the Danish word *bollebar,* which means dark berry (Grieve 1979). It is most often referred to as *V. myrtillus* L. There is an increasing demand for the berries of *V. myrtillus* due to their high nutritional value (Barney 2003; Martinussen et al. 2009).

10.1.1.5 Other Sections in *Vaccinium*

The section *Vaccinium* includes *V. uliginosum* L., which is an Arctic and boreal circumpolar species occurring in cool temperate regions of the Northern Hemisphere, at low altitudes in the Arctic and at high altitudes south to the Pyrenees, the Alps, and the Caucasus in Europe, the mountains of Mongolia, northern China and central Japan in Asia, and the Sierra Nevada mountains in California and the Rocky Mountains in Utah in North America (Tables 10.1 and 10.3) (Luby et al. 1991). This species grows on wet acidic soils on heathland, moorland, open tundra, and in the understory of coniferous forests, from sea level in the Arctic up to 3,400 m altitude in the south of the range (Hanson 1953; Young 1970; Vander Kloet 1988; Kelso 1989). The edible berries were the most popular fruit of the Native Americans in the Fort Yukon region (Holloway and Alexander 1990). They are usually used for jam, juice, pie, jelly, and wine making (Iwagaki et al. 1977; Rui 1982). Leaves can be used for tea (Robuck 1989). In addition, both the leaves and fruits are consumed by many species of wildlife (LeResche and Davis 1973; Wolff 1978; West 1982; MacHutchon 1989).

In Section *Pyxothamnus*, at least three species produce edible berry fruits (Table 10.3) (Luby et al. 1991; Finn 1999). These evergreen species have similar berries

Table 10.2 *Vaccinium* species in section *Myrtillus* Dumortier

Species	Origin	Habitat	Fruit diameter (mm)	Fruit color	Fruit flavor	Other traits of interest for breeding	References
V. cespitosum Michx.	In the early Tertiary and migrated east across North America in the early Pleistocene	Wet meadows, mountain slopes, moist rocky ledges, subalpine forests, and alpine tundra at 2,000–3,000 m	3–7	Blue	Good	Cold hardiness, late bloom, early ripening	Camp (1942a), Schultz (1944), Szczawinski (1962)
V. deliciosum Piper	A hybrid between *V. cespitosum* Michx. and *V. ovalifoliu* Smith	Open areas in subalpine forest and meadows and alpine tundra at 1,400–3,000 m	5–6	Light blue	Excellent	Cold tolerance, blossom forest resistance	Camp (1942a), Schultz (1944), Szczawinski (1962)
V. membranaceum Dougl. Ex Hook.	Derivative of several diploid species in section *Myrtillus*	Clear cut tracks, mountain slopes at 900–2,000 m, and dry, open sites in coniferous forests	6–20	Purple or red blue	Fair to good	Cold hardiness, drought tolerance, high pH tolerance	Camp (1942a), Schultz (1944), Szczawinski (1962)
V. myrtillus L.	An ancient circumboreal group	(1) In lowland to alpine open pine or spruce forests in northern Europe and Asia; (2) At 1,800–3,000 m in moist, open sites, mountains of subalpine communities in the Pacific Northwest and rock mountains of the USA	5–10	Dark blue	Good, tart	Cold hardiness, high fruit quality	Vander Kloet (1983), Ritchie (1956), Schultz (1944), Szczawinski (1962), Flower-Ellis (1971)
V. ovalifolium Sm.	In the Pacific Northwest of North America	On raw humus in moist, coastal, coniferous, forests from seal level to 1,000 m	8–12	Light blue	Fair	Large, firm fruit, small picking scar	Schultz (1944); Vander Kloet (1988), Ballington et al. (1988b)
V. parvifolium Sm.	Northern West America	(1) At low to intermediate elevations on the west slopes of coastal ranges from Alaska to northern California; (2) Inland to southern–eastern British Columbia	7–9	Pink to dark red	Fair	Drought tolerance	Schultz (1944), Vander Kloet (1988)
V. scoparium Leiberg ex Coville	An ancient circumboreal group	At 1,500–3,000 m in open to partially open sites or in alpine meadows above the timberline in the Cascades	2–5	Pink to dark red	Fair, acidic	Drought tolerance	Camp (1942a), Schultz (1944), Szczawinski (1962), Ballington et al. (1988b)

Source: adapted from Luby et al. (1991)

Table 10.3 Species in other *Vaccinium* sections

Section	Species	Origin	Habitat	Fruit diameter (mm)	Fruit color	Fruit flavor	Other traits of interest for breeding	References
Polycodium	*V. stamineum* L.	Central and E. North America	Dry uplands	10	Green to yellow	Good, tart	Upland adaption, drought tolerance	Vander Kloet (1988)
Pyxothamnus	*V. consanguineum* Klotzch.	Southern Mexico, Central America	In cooler, subtropical climates or in part-shade in warmer climates.	5–6	Reddish to blackish purple	Fair	Frost and freeze resistance during bloom	Camp (1945), Wilbur and Luteyn (1978)
	V. ovatum Pursh.	The North Pacific coast	Coastal coniferous forests	4–7	Purplish-black	Considerable variation in flavor, tart	Drought tolerance	Schultz (1944), Camp (1945), Szczawinski (1962)
	V. floribundum Kunth.	Southern Mexico, Central America	Mainly in high alpine regions.	5–8	Blue–black	Pleasantly flavored	Frost and freeze resistance during bloom	Wilbur and Luteyn (1978), Popenoe (1924), Macbride (1959)
Bracteata	*V. bracteatum* Thunb.	Eastern Asian	Light woodland, moist soil with low pH	6	Purplish black with bloom	Good	Resistant to honey fungus	Iwagaki et al. (1977), Huxley (1992a,b)
Vaccinium	*V. uliginosum* L.	The smaller diploid is common at latitudes over 60°N or at high elevations compared to the coarser tetraploid. Hexaploid forms are known from Japan	On wet or moist, organic or inorganic soils	6–15	Dark blue to glaucous	Good	Cold hardiness, Fusicoccum canker resistance?, Tolerance to heavy metals	Camp (1945), Schultz (1944), Szczawinski (1962), Vander Kloet (1988), Young (1970), Iwagaki et al. (1977), DiLabio and Rencz (1980), Finn (1999)

(Finn 1999). *Vaccinium floribundum* Kunth is distributed in Costa Rica, Venezuela, Colombia, Ecuador, and Peru. *Vaccinium consanguineum* Klotzch is native to Costa Rica and W. Panama. The range of *V. ovatum* spans the Pacific northwest of North America, from British Columbia, Washington, Oregon, and Nevada, south to California (Camp 1945). *V. consanguineum* Klotzch is found in Costa Rica, Honduras, and Panama.

10.1.2 Botanical Features, Cytology, and Germplasm Resources

As a large genus, *Vaccinium* is taxonomically complex. Although Sleumer (1941) divided the genus into 33 sections based on morphological phylogenetics, sectional species composition and evolutionary relationships have been the subject of much debate (Powell and Kron 2002). Many of the characters traditionally used to delimit genera based on flower, fruit, seeds, and vegetative parts fail to adequately distinguish among taxa (Stevens 1972; Kron et al. 2002).

Hundreds of the *Vaccinium* species that are native to tropical highlands are little-known, although many have potential as ornamentals or in fruit production. More on-site botanical studies are critically needed to provide information and broad-based seed. More collections should be made to safeguard genetic resources in these species until they are better understood.

10.1.2.1 Blueberry

Species delineation has been difficult to resolve in *Cyanococcus* due to polyploidy, overlapping morphologies, continuous introgression through hybridization, and a general lack of chromosome differentiation. In the first detailed taxonomy of the group, Camp (1945) described nine diploid, 12 tetraploid, and three hexaploid species, but Vander Kloet (1980, 1988) reduced this list to six diploid, five tetraploid, and one hexaploid taxa. He included all the crown-forming species into *V. corymbosum* with three chromosome levels. Most horticulturists and blueberry breeders feel that the variation patterns in *V. corymbosum* are distinct enough to retain Camp's diploid *Vaccinium elliottii* Chapm. and *Vaccinium fuscatum* Ait., tetraploid *Vaccinium simulatum* Small and hexaploid *V. constablaei* A. Gray and *V. ashei* Reade, which is more properly denoted *V. virgatum* Ait (Ballington 1990, 2001; Galletta and Ballington 1996; Lyrene 2006).

All the polyploid *Cyanococcus* are likely of multiple origins, and active introgression between species is ongoing. The tetraploid highbush blueberry *V. corymbosum* has been shown to be genetically an autopolyploid (Draper and Scott 1971; Krebs and Hancock 1989), as well as an interspecific tetraploid hybrid of *V. darrowii* Camp and *V. corymbosum* (Qu and Hancock 1995; Qu et al. 1998). Wenslaff and Lyrene (2003) found considerable chromosome homology in tetraploid southern highbush × *V. elliottii* hybrids. The lowbush blueberry, *V. angustifolium*, appears to be a direct descendant of *V. pallidum* Ait. × *V. boreale* Hall & Aalders, but introgression with *V. corymbosum* may have also influenced its subsequent development (Vander Kloet 1977). The primary mode of speciation in *Vaccinium* has been through unreduced gametes, as there is a strong but not complete triploid block (Lyrene and Sherman 1983; Vorsa and Ballington 1991). The unreduced gametes are produced primarily through first division restitution (Qu and Hancock 1995; Qu and Vorsa 1999), although some second division restitution occurs (Vorsa and Rowland 1997). Embryo culture was not successful in recovering triploids of *V. elliottii* × tetraploid highbush (Munoz and Lyrene 1985).

Interspecific hybridization within *Vaccinium* section *Cyanococcus* has played a major role in the development of highbush blueberries (Ballington 1990, 2001). Most homoploids freely hybridize, and interploid crosses are frequently successful (Lyrene et al. 2003). Genotypes have been found in many blueberry species that produce unreduced gametes (Ballington et al. 1976; Cockerman and Galletta 1976; Ortiz et al. 1992), and colchicine can be used to produce fertile genotypes with doubled chromosome numbers (Perry and Lyrene 1984). Even pentaploid hybrids of diploid × hexaploid crosses have been shown to cross relatively easy to tetraploids (Jelenkovic 1973; Chandler et al. 1985a, b; Vorsa et al. 1987).

Numerous interspecies crosses have been made by breeders within section *Cyanococcus* including (1) tetraploid *V. corymbosum* × tetraploid *V. angustifolium* (Luby et al. 1991), (2) tetraploid *V. myrsinites* L. × tetraploid *V. angustifolium* and *V. corymbosum* (Darrow 1960; Draper 1977), (3) colchicine-doubled diploid hybrids of *V. myrtilloides* Michx. × tetraploid *V. corymbosum* (Draper 1977), (4) diploid *V. darrowii* × hexaploid *V. ashei* (Darrow et al. 1954; Sharp and Darrow 1959), and (5) diploid *V. elliottii* × tetraploid highbush cultivars (Lyrene and Sherman 1983). Probably the most widely employed interspecific hybrid has been US 75, a tetraploid derived from the cross of diploid *V. darrowii* selection Fla 4B × the tetraploid highbush cultivar Bluecrop. In spite of being a hybrid of an evergreen, diploid species crossed with a deciduous, tetraploid highbush, US 75 is completely fertile and is the source of the low chilling requirement of many southern highbush cultivars (Draper and Hancock 2003).

Many of the highbush types now being released are complex hybrids. Some of the most dramatic examples are "O'Neal", which contains genes from four species (*V. corymbosum*, *V. darrowii*, *V. ashei*, and *V. angustifolium*), and "Sierra", which possesses the genes of five species (*V. corymbosum*, *V. darrowii*, *V. ashei*, *V. constablaei*, and *V. angustifolium*). "Biloxi" contains the genes from five taxa [*V. corymbosum* (diploid and tetraploid), *V. darrowii*, *V. ashei*, and *V. angustifolium*] and has fewer *V. corymbosum* than non-*V. corymbosum* genes in its genome.

Intersectional crosses have generally proved difficult, although partially fertile hybrids have been derived from *V. tenellum* Ait. and *V. darrowii* (section *Cyanococcus*) × *V. stamineum* L. (section *Polycodium*) (Lyrene and Ballington 1986), *V. darrowii* and *V. tenellum* × *V. vitis-idaea* (section *Vitis-Idaea*) (Vorsa 1997), *V. darrowii* × *V. ovatum* Pursh (section *Pyxothamnus*), *V. arboreum* Marshall (section *Batodendron*) and *V. stamineum* (section *Polycodium*) (Ballington 2001), and tetraploid *V. uliginosum* (section *Vaccinium*) × highbush cultivars (Rousi 1963; Hiirsalmi 1977; Czesnik 1985). Genes of *V. arboreum* have also been moved into tetraploid southern highbush using *V. darrowii* as a bridge (Lyrene 1981; Brooks and Lyrene 1998a, b). Genes from *V. ovatum* have been incorporated into ornamental highbush selections in the US Department of Agriculture (USDA), Agricultural Research Service (ARS), Oregon, program via NC 3048.

There are several important collections of native blueberry germplasm and hybrids (Ballington 2001). The most extensive is held at the USDA-ARS's National Clonal Germplasm Repository at Corvallis Oregon, where representatives of most species can be found along with almost all named non-patented cultivars. James Ballington at North Carolina State University has a particularly large collection of southern species material. Paul Lyrene at the University of Florida and James Hancock at Michigan State University also have large collections of southern and northern adapted material, respectively.

10.1.2.2 Cranberry

Cranberries have the basic chromosome number of 12 and a polyploid series of 2*x*, 4*x*, or 6*x* (Table 10.1). Large cranberries, *V. macrocarpon* (Ait) Pursh. ($2n = 24$), are the most closely related to diploid *V. oxycoccus* (Camp 1944). They are low, creeping perennial shrubs or vines up to 2 m long and 5–20 cm in height. Natural polyploid populations of *V. macrocarpon* have not been reported (Zeldin and McCown 2002). Gene exchange between *V. macrocarpon* and diploid *V. oxycoccus* is now severely limited due to a disjunctive distribution and a flowering date difference of 3 weeks (Vander Kloet 1988). Compared to *V. macrocarpon*, *V. oxycoccus* plants have small (5–10 mm) leaves. The fruit is a small pale pink berry, with a refreshing sharp acidic flavor.

The largest collections of cranberry germplasm are held by Nicholi Vorsa at Rutgers University and Eric Zeldin and Brent McCown at the University of Wisconsin. In addition, the USDA National Clonal Germplasm Repository in Corvallis, OR, has 123 accessions of *V. macrocarpon* (large-fruited cranberry), three accessions of *V. microcarpon* (small-fruited cranberry), and 41 accessions of *V. oxycoccus* (2x/4x wild cranberry) (National Plant Germplasm 2005).

10.1.2.3 Bilberry and Lingonberry

Compared to sections *Cyanococcus* and *Oxycoccus*, the section *Myrtillus* has drawn little attention from plant breeders. Bilberries (*V. myrtillus* L.) are closely related to blueberries and are diploid ($2n = 24$) (Table 10.1; Vander Kloet 1988). The plants grow 10–60 cm tall. Their fruit is dark blue and is smaller, softer, and juicier than that of the blueberry (Table 10.2). The easiest way to distinguish the bilberry from the blueberry is that it bears one to three individual berries instead of clusters of berries.

The lingonberry (*V. vitis-idaea* L.) is a diploid ($2n = 24$), low-growing (15–30 cm tall), evergreen groundcover (Sorsa 1962; Rousi 1967). Lingonberries thrive in acidic soils (pH 3.5–5) and reproduce vegetatively through rhizomes and sexually by seeds. The ripe fruit is bright red, 6–10 mm in diameter, tart and smaller than cranberries but with a finer flavor. Wild lingonberry populations are variable in nearly all important horticultural traits (Gustavsson 2001; Persson and Gustavsson 2001; Paal 2006).

10.1.3 Economic Importance

Vaccinium fruits are perceived by the public to be a health-promoting food. According to the latest ARS report from the USDA, cranberries and blueberries rank number one and two, respectively, in antioxidant values of 19 common fruits (USDA-ARS 2007). Demand for berries from the various *Vaccinium* species (blueberries, cranberries, bilberry, and lingonberry) will likely continue to grow due to their nutritional and therapeutic properties (Prior et al. 1998; Sun et al. 2002; Ferguson et al. 2006; Neto 2007a, b; Neto et al. 2008).

10.1.3.1 Blueberry

Blueberry has become the second most important berry crop in the USA. The highbush blueberry is by far the most important commercial crop in *Vaccinium*. Over 110,000 t of highbush fruit are produced annually in the US on over 20,000 ha (USDA Agricultural Statistics). The estimated area of rabbiteye production is currently about 3,000 ha, with half the surface planted in Georgia. The total annual production is over 5,500 t. Half-high production is restricted to a few hundred hectares in Minnesota and Michigan. Annual production of lowbush blueberries ranges from 40,000 to 55,000 t on about 40,000 ha in primarily Maine and the Maritime provinces of eastern Canada.

From 1995 to 2007, worldwide blueberry acreage grew by 254%, from 23,116 ha to 58,601, and most of that growth was in the western Hemisphere, including 20,315 additional hectares in South America and 312,950 more hectares in North America, primarily the US and British Columbia (Lehnert 2008). The estimated area of blueberry production in China increased from 24 ha in 2001 to 1,363 ha in 2007 (Li and Yu 2009).

About 50% of the highbush crop is marketed fresh and the remainder is processed. Blueberries are used primarily in pie fillings, yogurts, ice cream, and prepared muffin and pancake mixes. Syrups, jams, and preserves are also produced but in limited quantities. The juice of blueberries is rarely consumed directly due to its strong flavor and dark color.

Blueberries are one of the richest sources of antioxidant phytonutrients among the fresh fruits, with a total antioxidant capacity ranging from 13.9 to 45.9 μmol Trolox equivalents/g fresh berry (Prior et al. 1998; Conner et al. 2002a, b; Zheng and Wang 2003). Many factors including genetics, growing condition, fruit maturity at harvest, and other variables affect nutritious levels in blueberry fruits. General information on nutritional value indicates that blueberries are a source of vitamin A, vitamin C, potassium, and foliate. An average blueberry fruit is composed of approximately 83% water, 0.7% protein, 0.5% fat, 0.5% ash, and 15.3% carbohydrate (Hancock et al. 2003).

The overall acidic content of *Vaccinium* fruit is relatively high. Ripe blueberries range from 1 to 2%, and the primary organic acid is citric acid (1.2%). They also contain significant amounts of ellagic acid, a compound thought to reduce the risk of cancer (Maas et al. 1991). Total anthocyanins in blueberry fruit range from 85 to 270 mg per 100 g, and species in the subgenus *Cyanococcus* carry the same predominant anthocyanins, aglycones, and aglycone-sugars, although the relative proportions vary (Ballington et al. 1988). The predominant anthocyanins were delphinidin-monogalactoside, cyanidin-monogalactoside, petunidin-monogalactoside, malvidin-monogalactoside, and malvidin-monoarabinoside. Anthocyanin is responsible for the blue color of blueberries and has been shown to be among the most powerful antioxidants that are known to reduce urinary tract infections and protect against cancer, diabetes, heart and vascular diseases, and neurodegenerative diseases in humans (Ehlenfeldt and Prior 2001; Seeram et al. 2006). The major volatiles contributing to the characteristic aroma of blueberry fruit are *trans*-2-hexanol, *trans*-2-hexanal, and linalool (Hancock et al. 2003). The predominant volatiles in the bilberry are *trans*-2-hexanal, ethyl-3-methyl butyrate, and ethyl-2-methyl butyrate.

10.1.3.2 Cranberry

Humans have consumed cranberry fruits for several centuries (McCown and Zeldin 2005). Since the seventeenth century, cranberries have been used for an assortment of medicinal purposes: stomach ailments, liver problems, and blood disorders. In North America, cranberry consumption has been associated with the holidays of Thanksgiving and Christmas when cranberry sauce is served with roast turkey meat. However, cranberry consumption has become a year round activity, largely through juice products. Cranberry production in North America is about 380,000 t annually on 21,700 ha. About 95% of cranberries are processed into products such as juice drinks, sauce, and sweetened dried cranberries. The remaining 5% is sold fresh to consumers and used in baking (muffins, scones, and cakes). Unlike many other berries, cranberries are normally too tart to be eaten unaccompanied.

Cranberries have medium levels of vitamin C, dietary fiber and the essential dietary mineral, manganese, and other essential micronutrients (Table 10.3). The overall acidic content in ripe cranberries ranges from 2 to 3%. The cranberry contains high levels of several organic acids, including quinic (1.3%), citric (1.1%), malic (0.9%), and benzoic (0.6%). Additionally, Cranberries have long been prized for their brilliant red fruit. The deep-colored pigments are made up of anthocyanins, which are a subclass of flavonoids. Therefore, raw cranberries are excellent food sources of the anthocyanidin flavonoids, cyanidin, peonidin, and quercetin (Duthie et al. 2006). When 19 common fruit crops were compared, cranberries had the highest antioxidant capacity with the Oxygen Radical Absorbance Capacity (ORAC) of 9,584 units per 100 g of fresh fruit (USDA-ARS 2007). Antioxidants reduce the effect of free radical oxidants, which weakens the immune system and is linked to several diseases, by binding with them and decreasing their destructive power and repairing damage. A high antioxidant activity could potentially make this berry crop a candidate for cancer chemoprevention and treatment (Sun et al. 2002; Wang et al. 2005; Sun and Liu 2006; Ferguson et al. 2006; Neto 2007a, b; Neto et al. 2008). Ingestion of cranberries leads to increased acidity of the urine through conversion of its high quinic and benzoic acid contents to hippuric acid by the body. The high acidity and possible antibacterial effects of hippuric acid or proanthocyanidins may relieve urinary tract infections and reduce some types of kidney stones (Kessler et al. 2002; Linsenmeyer et al. 2004; Jepson and Craig 2007).

10.1.3.3 Bilberry

V. myrtillus fruits are an ancient food in northern Europe (Kardell 1980; Raatikainen and Raatikainen 1983; Kostov and Stojanov 1985). The berries contain antioxidants and other compounds beneficial to human health. They are harvested commercially from the wild in Finland and other European countries. In Europe, the berries are used for fruits, pies, tarts, syrups, jellies, and wine making (Tyler 1994). In North America, native people historically ate the fruit fresh or dried and continue to use it today (Turner 1997). Herbalists and physicians have used bilberry fruit in traditional European medicine for nearly 1,000 years (Morazzoni and Bombardelli 1996). Traditionally, bilberry preparations have been used as an astringent for treatment of diarrhea and dysentery (Bone and Morgan 1997). In addition, they are used to help stop the flow of breast milk and to relieve scurvy, dysentery, and vascular disorders (Grieve 1979; Bruneton 1995). As herbal medicines, bilberry has shown vasoprotective, antiedematous, antioxidant, anti-inflammatory, and astringent actions (Bone and Morgan 1997).

10.1.3.4 Lingonberry

In Europe, lingonberries have long history of medicinal uses for treatments of inflammatory diseases, wounds, gastric distress, and rheumatism. In addition, the antioxidant compounds in lingonberries may play an important role in cancer chemoprevention and treatment (Wang et al. 2005). Lingonberry leaves have been used as medicine for curing kidney and bladder diseases (Paal 2006). Lingonberries are rich in active antioxidants such as anthocyanin and phenolic compounds (Zheng and Wang 2003; Wang et al. 2005) and are rich in benzonic acid. In comparison with blueberries (cv. Serra) and cranberries (cv. Ben Lear), lingonberries (cv. Amberland) had a significantly higher antioxidant activity that was associated with a higher content of anthocyanin and phenolic compounds (Zheng and Wang 2003). When Wang et al. (2005) evaluated fruits of 11 selected lingonberry cultivars, he found fruit soluble solids, titratable acids, anthocyanins, phenolics, and antioxidant activities to vary greatly among the cultivars.

To date, commercial production of lingonberry from cultivated fields is far less common than from wild plants (Hendrickson 1997; Gustavsson 2001; Paal 2006). However, there is clearly an increasing demand for lingonberry products due to its rich antioxidant content, medicinal properties, and expanding fresh market (Galletta and Ballington 1996; Penhallegon 2003; Wang et al. 2005; Finn and Mackey 2006). In Sweden, lingonberry is called "red gold" due to its economic importance (Persson and Gustavsson 2001). Major lingonberry exporting countries are Sweden, Finland, and counties of the former Soviet Union (Paal 2006).

10.2 Breeding and Genetics

10.2.1 History of Breeding

10.2.1.1 Blueberry

Highbush breeding began in the early 1900s in New Jersey, with the first hybrid being released in 1908 by Frederick Coville of the USDA. He conducted the fundamental life history studies of the blueberry that served as the basis of cultivation such as soil pH requirements, cold and day-length control of development, pruning strategies, and modes of propagation. Working with Elizabeth White and others, he collected several outstanding wild clones of *V. corymbosum* and *V. angustifolium*, which he subsequently used in breeding improved types. Over 75% of the current blueberry acreage is still composed of his hybrids, most notably "Bluecrop", "Jersey", "Weymouth", "Croatan", "Blueray", "Rubel", and "Berkeley" (Mainland 1998).

George Darrow assumed the USDA program after Coville died in 1937 and made important contributions on the interfertility and phylogeny of the native *Vaccinium* species in cooperation with the taxonomist W.H. Camp (Hancock 2006a). He formed a large collaborative testing network that encompassed private growers and Agricultural Experiment Station scientists in Connecticut, Florida, Georgia, Maine, Massachusetts, Michigan, New Jersey, and North Carolina. From 1945 to 1961, he sent out almost 200,000 seedlings to his cooperators for evaluation.

Arlen Draper followed Darrow and focused on incorporating the genes of most wild *Vaccinium* species into the cultivated highbush background (Draper 1995; Hancock 2006b). He maintained and strengthened Darrow's collaborative network and released a prodigious number of southern and northern highbush cultivars, with improved fruit color and firmness, smaller pedicle scars, and higher productivity (Hancock and Galletta 1995). His "Duke" and "Elliott" have been major successes, along with the newer release "Legacy". Mark Ehlenfeldt assumed the USDA-ARS program in 1998.

Ralph Sharp began working in the 1950s in Florida on the development of southern highbush types in collaboration with Darrow (Sharp and Darrow 1959; Lyrene 1998). He was the first collector of *V. darrowii* for breeding, and until very recently, all southern highbush cultivars contained genes from his wild clones. Sharp and his colleague Wayne Sherman developed several successful cultivars, including "Sharpblue", which was grown commercially until very recently. Paul Lyrene took over the breeding work in Florida in 1977 and has released a number of important cultivars including "Star" and "Jewel".

Stanley Johnson at Michigan State University spent a considerable amount of time in the 1950s and 1960s improving the cold tolerance of highbush by crossing it with *V. angustifolium*. Out of this work came the "half-high" cultivar Northland and the mostly pure highbush type "Bluejay", which was released by his successor James Moulton. The program was abandoned in 1978 but was renewed in 1990 by James Hancock. He has released three important cultivars, "Aurora", "Draper", and "Liberty".

In the Pacific Northwest, Joseph Eberhart, in Olympia, Wash., released three cultivars, Pacific, Olympia, and Washington, in the 1920s and 1930s. "Olympia" is still widely grown today.

Outside of the USA, blueberry breeding work was conducted in Australia, Germany, and New Zealand. Johnston sent open-pollinated seed to D. Jones and Ridley Bell in Australia in the 1960s that generated the important cultivar "Brigitta Blue" along with several others. Narandra Patel at HortResearch in New Zealand released the cultivars Nui, Puru, and Reka from breeding material initially provided by the University of Arkansas and the USDA at Beltsville in the 1960s and 1970s. Walter Heermann in Germany, working with seed provided by Frederick Coville, released several varieties in the 1940s and 1950s including “Blauweiss-Goldtraube”, “Blauweiss-Zukertraube”, “Heerma”, “Rekord”, “Ama”, and “Gretha”.

Rabbiteye breeding was initiated in 1939 by George Darrow in collaboration with Otis J. Woodard at the Georgia Coastal Plain Experiment Station (Tifton, Ga.) and Emmett B. Morrow at the North Carolina Experiment Station, although a collection of wild selections from Florida and Georgia had been planted at Tifton in the 1920s (Austin 1994). This work was continued by Max Austin and then Scott NeSmith in Georgia, Gene Galletta followed by James Ballington in North Carolina, and Ralph Sharp, Wayne Sherman, and then Paul Lyrene in Florida (Lyrene 1987). These breeding programs have resulted in significant improvements in fruit color, size, texture, and appearance over the original wild selections. The most important cultivars have been “Tifblue” (1955) and “Brightwell” (1971) from Georgia, “Bluegem” (1970) and “Bonita” (1985) from Florida, and “Powderblue” and “Premier” (1978) from North Carolina. Rabbiteye cultivars were also bred in the New Zealand HortResearch, Inc. program of Narandra Patel. Several releases came from this program in the 1990s including “Maru” and “Rahi”.

Lowbush blueberry breeding has generally received little attention. The primary effort has been centered with Agriculture and Agri-Foods Canada (Kentville, NS), currently overseen by Andrew Jamieson. At this station, wild selections from Maine and the Maritime Provinces were tested and crossed, resulting in a number of releases including “Augusta”, “Blomidon”, “Brunswick”, “Chignecto”, and “Fundy”. Recently, a seed-propagated lowbush cultivar, “Novablue”, was released by Andrew Jamieson from the cross of “Fundy” × “Brunswick”. The hybrids have unusually large berries and spread more rapidly by rhizomes than the parent clones.

Lowbush blueberries have been hybridized with *V. corymbosum* to produce “halfhigh” cultivars (Finn et al. 1990). The major releases of this type were “Northland” developed by Stanley Johnston in Michigan and “Northblue”, “Northsky”, “Northcountry”, “St. Cloud”, “Polaris”, and “Chippewa” released by James Luby in Minnesota. The “half-highs” have much higher yields and larger fruit than lowbush but have low enough stature to be protected by snow in areas with extreme winter cold.

10.2.1.2 Cranberry

Breeding of cranberries has been sporadic since the mid-1900s. However, during the last decade of the twentieth century, much of the acreage previously planted to native selections “Early Black”, “Howes”, “McFarlin”, and “Searles” has been renovated with first generation hybrids (Galletta and Ballington 1996), the cultivar Stevens being the most widely planted. In 1929, the USDA began a major cooperative cranberry-breeding project with the New Jersey, Massachusetts, and Wisconsin Agriculture Experiment Stations to develop varieties resistant to false blossom disease, a phyoplasma (Chandler et al. 1947). Resistance to false bottom was based on developing varieties that would be less attractive to the blunt-nosed leaf hopper, the vector of the false blossom agent. The majority of the seedlings were planted in New Jersey because of the severity and prevalence of false bottom in the state. Out of this program came “Pilgrim”, “Wilcox”, and “Stevens”. “Pilgrim” was released for improved productivity, size, color (purplish red), keeping quality, productivity, and resistance to the blunt-nosed leafhopper. “Stevens” was selected and released for its improved productivity, color (deep red), firmness, and resistance to softening (Dana 1983). “Crowley” was introduced from the Washington Agriculture Station in the 1960s as a better pigmented replacement for “McFarlin” but has lost favor due to variable and generally low productivity.

10.2.1.3 Bilberry

Although commercial prospects for medicinal and nutritional supplement products may be promising, bilberry (*V. myrtillus* L.) has not been commercially cultivated. In 1994, evaluations of bilberry selections obtained from a wide area of western North America and northern Europe was begun at the University of Idaho. To date, 13 bilberry selections have been selected for advanced testing, although no bilberry cultivars have been released.

10.2.1.4 Lingonberry

Beginning in the 1960s, domestication of lingonberry was initiated in Sweden, Finland, Lithuania, Germany, and Latvia (Teär 1972; Luby et al. 1991; Gustavsson 2001; Paal 2006). In the USA, cultivation of lingonebrry started in 1987 (Stang et al. 1993). From the 1960s–1990s, lingonberry breeding focused on selection and evaluation of wild clones and seedlings. To date, 24 cultivars have been released (Table 10.4), with some selections still under field trails (Finn and Mackey 2006).

10.2.2 Breeding Objectives

In general, the major breeding objectives for *Vaccinium* species are either for improved fruit production (high productivity, fruit quality, and resistance to pests, diseases, and abiotic stresses) or for modified ornamental characteristics (colorful flowers and leaves, wide adaptability of habitat, and distinguished plant architectures).

10.2.2.1 Blueberries

The current goals of southern highbush breeders are to obtain early ripening cultivars with high plant vigor, improved disease resistance, and later flowering dates (particularly in the southeastern USA, where late freezes are a problem). Higher yields, better flavor, and characteristics favorable for mechanical harvest are also being sought. Cultivars and advanced breeding lines are being used to breed southern highbush, along with hybrids derived from native, low-chill highbush selections from Florida and Georgia (*V. ashei*, *V. elliottii*, and *V. darrowii*). Because of their low chill requirement and the influence of genes from *V. darrowii*, many southern highbush cultivars can be grown as evergreens that avoid dormancy in areas with mild winters, with a harvest season that extends for several months through the winter and early spring (Darnell and Williamson 1997). Rabbiteye breeders hope to expand harvest dates, improve berry size and fruit quality, reduce susceptibility to rain cracking, and extend storage life.

Southern highbush cultivars are being developed at several locations, including Arkansas, California, Florida, Georgia, Mississippi, Australia, Chile, and Spain. Paul Lyrene at the University of Florida has the most active program dealing with very low chill genotypes and has released many high impact cultivars including

Table 10.4 Lingonberry cultivars

Source	Cultivar (year of release)	References
Dutch cultivars	“Koralle” [1969]; “Red Pear” [1981]	Liebster (1977), Gustavsson (1999), Pliszka and Kawecki (2000)
German cultivars	“Erntedank” [1975]; “Erntekrone” [1978]; “Erntesegen” [1981]; “Ammerland” and “Erzgebirgeperile” [1993]	Zillmer (1985), Pliszka and Kawecki (2000)
Swedish cultivars	“Sussi” [1986]; “Sanna” [1988]; “Ida” and “Linnea” [1999]	Gustavsson (1993, 1999), Gustavsson and Trajkovski (1999), Trajkovski and Sjöstedt (1986), Eckerbom (1988)
Norwegian cultivar	“Scarlet” [unknown]	Gustavsson (1997)
Polish cultivars	“Masovia” [1985]; “RunoBielawskie” [1996]	Pliszka and Kawecki (1985, 2000)
Canadian cultivars	“Utopia” [1998]	Estabrooks (1998)
Russian cultivars	“Kostromskaya rozovaya” and “Kostromichka” [1996]; “Rubin” [1998]	Tyak et al. 2000
Latvian cultivars	“Salaspils 1”, “Salaspils 2”, “Salaspils 4”, and “Salaspils 5”	Audrinja (1992)
American cultivars selected from Finnish seeds	“Splendor” and “Regal” [1987]	Stang et al. (1994)

"Emerald", "Jewel", "Misty", and "Star". James Ballington in North Carolina has the most significant program operating at the interface between northern and southern highbush types and has generated a number of important cultivars including "Lenore", "New Hanover", "O'Neal", "Reveille", and "Sampson". James Moore and now John Clark at the University of Arkansas have focused on mixing southern wild species with northern types and recently released "Ozarkblue", a very high quality late type. Scott NeSmith at the University of Georgia has generated several new early varieties including "Rebel", "Camellia", and "Palmetto". He also has an active rabbiteye breeding program and his late season cultivar Ochlockonee has generated considerable interest. Steven Stringer, Arlen Draper, and James Spiers at the USDA-ARS in Mississippi have developed a number of southern highbush types including "Biloxi", "Gupton", and "Magnolia". Several private breeding programs have also emerged that are developing southern highbush types including Atlantic Blue in Spain (Ridley Bell), Berry Blue in Michigan and Chile (Edmond Wheeler), Driscoll Associates in California (Brian Caster), Mountain Blue Orchard in Australia (Ridley Bell), and Vital Berry in Chile (James Ballington). Berry Blue is also devoting some effort to rabbiteye types.

Northern highbush breeders are concentrating on flavor, longer storing fruit, expanded harvest dates, disease and pest resistance, and machine harvestability. Established breeding lines are being used in these efforts along with complex hybrids made up of *V. darrowii*, *V. angustifolium*, *V. constablaei*, and most of the other wild species. Even though it has limited winter hardiness, *V. darrowii* has proven to be an interesting parent in colder climates because it passes on a powder blue color, firmness, high flavor, heat tolerance, and upland adaptation (Hancock 1998).

Northern highbush blueberries are currently being bred in New Jersey, Michigan, Oregon, and Chile. James Hancock at Michigan State University is focusing on late maturing, long storing genotypes and has released three new northern highbush cultivars that show high promise, "Aurora", "Draper", and "Liberty". Mark Ehlenfeldt of the USDA program in New Jersey is focusing on identifying genotypes with high disease resistance and tolerance to winter cold and has released several cultivars including "Chanticleer" and "Hannah's Choice". Nicholi Vorsa at the Cranberry and Blueberry Research Station of Rutgers University has begun a program in New Jersey to develop locally adapted highbush cultivars with machine harvestability and high fruit quality. Chad Finn of the USDA in Oregon is active in identifying genotypes that are well suited to the Pacific Northwest. Other worldwide northern highbush breeding projects include "Berry Blue" in Michigan and Chile, Fall Creek Farm and Nursery in Oregon, Driscoll Associates in California and Washington, and the University of Talca and Vital Berry in Chile.

Danny Barney at the University of Idaho, and to a lesser extent the USDA-ARS (Ore.), is selecting superior genotypes of *V. membranaceum*, *V. ovalifolium*, and *V. deliciosum* that may have potential as commercial "huckleberry" cultivars, and some of these are in commercial trial. They have also attempted to cross these species with highbush blueberry with very limited success.

Rabbiteye breeders hope to expand harvest dates and improve flavor and storage life. The northern highbush breeders are concentrating on flavor, longer storing fruit, expanded harvest dates, disease and pest resistance, and machine harvestability. Established breeding lines are being used by northern highbush breeders along with complex hybrids made up of *V. darrowi*, *V. angustifolium*, *V. constablei*, and most of the other wild species. Even though it has limited winter hardiness, *V. darrowii* has proven to be an interesting parent in colder climates, because it passes on a powderblue color, firmness, high flavor, heat tolerance, and potential upland adaptations.

10.2.2.2 Cranberry

Cranberry breeding efforts are being focused on early maturing fruit, uniform large size, intense color (total anthocyanin content – TACy), keeping quality, high productivity, disease resistance, and plant vigor. The greatest emphasis is being placed on productivity and resistance to fruit rot organisms. Cranberries are currently being bred by Nicholi Vorsa at Rutgers University in New Jersey and Eric Zeldin and Brent McCown at the University of Wisconsin. The Wisconsin team recently released the first new cranberry cultivar in over 30 years – "HyRed", which is distinguished by its earliness and deep red color (McCown and Zeldin 2003). The Rutgers program released three cultivars in

2006, "Crimson Queen", "Mullica Queen", and "Demoranville". "Crimson Queen" and "Demoranville" have tested for high TACy, large fruit size, and productivity. "Mullica Queen" is being released for high production potential and improved TACy relative to "Stevens".

10.2.2.3 Bilberry

Bilberry domestication efforts started with evaluation of elite selections. Danny Barney at the University of Idaho has made a number of advanced selections of bilberry (*V. myrtillus*), Cascade huckleberry (*V. deliciosum*), mountain huckleberry (*V. membranaceum*), and oval-leaved bilberry (*V. ovalifolium*, a.k.a. Alaska blueberry, *V. alaskaense*) since 1994. The selection criteria include canes (numerous, vigorous, upright, many fruiting laterals), physiology (late-blooming, self-fruitful, suitable ripening period), leaves (thick, tough, leathery), fruit (flavor, color, high anthocyanin and antioxidant capacity, and size), and disease resistance (mummy berry, blight, twig blight, and bacterial canker) (Danny Barney personal communication).

10.2.2.4 Lingonberry

Lingonberry breeding efforts are being focused on broadly adapted cultivars with high productivity, increased fruit size, insect- and disease-resistance, tolerance to abiotic stresses, suitability for mechanical harvesting, high flavor and aroma retention, and enhanced polyphenolic (flavonoid) profiles beneficial for human health (Galletta and Ballington 1996).

The first and best known cultivar, "Koralle", was initially selected as an ornamental plant by H. Van der Smith in Holland in 1969 (Liebster 1977). It was first cultivated in Germany as a fruit crop because of its suitability for machine harvesting and fall cropping habit (Gustavsson 1999). In terms of overall agronomic worth, "Koralle" is still one of the best cultivars for commercial cultivation (Finn and Mackey 2006).

A number of additional cultivars have been released in Europe. "Red Pearl" selected by Blanke in Boskoop and "Ammerland" selected by Krüger in Westerstede are similar to "Koralle" in plant growth and berry yield but have larger fruits (Dierking and Beerenobst 1993). The now closed Balsgård Research Station released a number of cultivars and selections (Trajkovski and Sjöstedt 1986; Eckerbom 1988; Gustavsson and Trajkovski 1999). Of these, "Ida" and 8723-10 showed the best characteristics for commercialization (Finn and Mackey 2006). In Germany, "Erntekrone", "Erntedank", and "Erntesegen" were released by Albert Zillmer in 1970s. "Erntesegen" has particularly large and aromatic berries (Zillmer 1985). "Ammerland" and "Erzgebirgeperle" were selected by Krüger in 1993 (Pliszka and Kawecki 2000). In Latvia, four cultivars "Salaspils 1", "Salaspils 2", "Salaspils 4", and "Salaspils 5" were selected from natural habitats by Ripa and Audrinja in the 1980s (Audrinja 1992). "Salaspils 2" has particularly high yield (about 900 g m^{-2}) and large fruits (4.0 g) (Paal 2006). In Poland, Kawecki selected two cultivars "Masovia" and "Runo Bielawskie" (Pliszka and Kawecki 1985, 2000). In Russia, three one-time blooming cultivars "Kostromskaya rozovaya", "Kostromichka", and "Rubin" were selected by Tyak and Cherkasov in 1990s (Tyak et al. 2000). In Estonia, a number of lingonberry selections are currently in field trials (Paal 2006).

In North America, "Regal" and "Splendor" were selected from Finnish seeds in Wisconsin by Stang et al. (1994). They showed high productivity and adaptability to North American climatic conditions (Stang et al. 1994; Galletta and Ballington 1996). In Canada, selections of *V. minus*, including F91-3, F91-5, and F91-1 ("Utopia"), have shown promise (Estabrooks 1998).

10.2.3 Traditional Breeding Techniques

Vaccinium are crops propagated through cuttings and micropropagation, so elite genotypes can be directly utilized without the need to develop pure lines. The breeding of *Vaccinium* species has evolved, as with other woody crops, from casual selection of elite wild clones to the use of controlled crosses and rigorous field selection. Techniques involving marker-assisted selection are just beginning to emerge to maximize the efficiency of plant breeding. Currently, *Vaccinium* cultivars are obtained exclusively through traditional breeding approaches.

10.2.3.1 Crosses Within Species

Self-pollinations are rarely used in *Vaccinium* breeding due to reduced seed set, germination, and because seedlings from selfing tend to be weak. Most breeding programs have relied primarily on pedigree breeding where elite parents are selected each generation for intercrossing. However, the Florida southern highbush and rabbiteye breeding programs have utilized recurrent selection (Lyrene 1981, 2005). About 150 different genotypes are used in the Florida program each year, in random pairwise combinations.

Blueberries are all primarily outcrossing with varying levels of self-fertility, depending on species and genotype. In general, northern highbush blueberries have the highest levels of self-fertility, followed by southern highbush and then rabbiteye. Cultivars that are not highly self-fertile display reduced fruit set and berry size when self-pollinated (Morrow 1943; El-Agamy et al. 1981; Rabaey and Luby 1988; Gupton and Spiers 1994; Ehlenfeldt and Prior 2001). Highbush are generally planted in solid blocks, although having a pollinizer would be beneficial for most cultivars. All rabbiteye cultivars need pollinizers and alternate row plantings are recommended. Lowbush fruit is harvested from highly variable native stands, with abundant opportunity for cross-pollination. Self-infertility in blueberries has been shown to be the result of late-acting inbreeding depression (Krebs and Hancock 1988, 1990; Hokanson and Hancock 1998). Harrison et al. (1993) found that parental self-fertility was not predictive of the self fertility of progeny in segregating families of half-high and highbush genotypes.

Cranberries are generally self-fertile, but cross-pollination can enhance seed production (Sarracino and Vorsa 1991; Galletta and Ballington 1996). For lingonberries, cross-pollination gives twice the fruit and seed set of self-pollination (Fernqvist 1977; Lehmushovi 1977).

Interspecific Hybridization

To enhance levels of genetic variability within a species (primary genepool), interspecific hybridization followed by backcrossing is commonly used to introgress desirable genes from related species within the genus (secondary genepools) to commercial cultivars (Ballington 2009; Vorsa et al. 2009). Interspecific hybridization has played a significant role in development of blueberry cultivars for fruit production (Brevis et al. 2008; Ballington 2009).

Ballington (2009) has recently summarized the successful role of interspecific hybridization in blueberry improvement as following (1) For highbush blueberry improvement, the species used in interspecific hybridization include *V. angustifolium* (lowbush blueberry), *V. darrowii* (Darrow's evergreen blueberry), *V. ashei* or *V. virgatum* (rabbiteye blueberry), *V. tenellum* (southern lowbush blueberry), *V. elliottii* (Mayberry), and *V. constablaei* (Constable's blueberry). (2) For improvement of hexaploid rabbiteye blueberries (*V. virgatum*), interspecific hybridization has only played a minor role to date. (3) Cultivar improvement in tetraploid lowbush blueberries has been confined exclusively to the primary gene pool of *V. angustifolium* to date. (4) *V. pallidum* holds promise for contributing to future highbush and half-high blueberry improvement. (5) *V. constablaei* and hexaploid southern highbush will probably contribute significantly to rabbiteye blueberry improvement in the future. (6) Intersectional crosses among tetraploid species also may be promising for future blueberry cultivar improvement.

Genetics and Marker-Assisted Selection (MAS)

A wide array of markers have been utilized in blueberry for fingerprinting and linkage mapping including proteins (Bruederle et al. 1991; Hokanson and Hancock 1998), restriction fragment length polymorphisms (RFLPs) (Haghighi and Hancock 1992), random amplified polymorphic DNA (RAPD) (Aruna et al. 1993; Levi et al. 1993; Qu and Hancock 1997), simple sequence repeat (SSR), and express sequence tag-polymerase chain reaction (EST-PCR) (Rowland et al. 2003a, b; Boches et al. 2005, 2006).

More limited numbers of marker studies have been conducted in cranberry, although isozymes were used to measure diversity patterns in native *V. macrocarpon* (Bruederle et al. 1996), and RAPDs were utilized to determine cultivar identity and heterogeneity in commercial beds (Novy et al. 1994). Polashock and Vorsa (2002a, b) used the sequence-characterized amplified region (SCAR) technique to fingerprint over 500 accessions and to estimate the degree of genetic similarity.

Most recently, blueberry markers, 39 EST-SSRs and 10 genomic SSRs, have been tested for the ability to amplify a polymorphic marker in American cranberry accessions. Sixteen SSRs resulted in informative and polymorphic primer pairs and were used to fingerprint 16 economically important cranberry cultivars (Bassil et al. 2009).

Rowland and Levi (1994) developed the first blueberry map using a diploid population segregating for chilling requirement. Their population was a cross between an F_1 interspecific hybrid (*V. darrowii* × *V. elliottii*) and another clone of *V. darrowii*.

They have continued to periodically add markers and at the last report, the map had 72 RAPD markers on 12 linkage groups, which is in agreement with the basic chromosome number of blueberry (Rowland and Hammerschlag 2005). Later, Rowland et al. (1999, 2003b) constructed RAPD-based maps of diploid *V. corymbosum* (*V. caesariense* Mack.)× *V. darrowii* hybrids crossed with other *V. darrowii* and *V. corymbosum* selections. The goal was to develop populations that were segregating for chilling requirement and cold tolerance. First RAPD and more recently EST-PCR markers were added to this map and a quantitative trait loci (QTL) was identified that explained about 20% of the genotypic variance associated with cold hardiness (Rowland et al. 2003a, b, c; Rowland and Hammerschlag 2005).

Qu and Hancock (1997) constructed an RAPD-based genetic map of a tetraploid population resulting from the cross of US 75 × tetraploid *V. corymbosum*, "Bluecrop". One hundred and forty markers were mapped to 29 linkage groups. The map was essentially that of *V. darrowii*, as US 75 was produced from an unreduced gamete of *V. darrowii* and only unique markers for Fla 4B were used. Fla 4Bwas one of the *V. darrowii* clones used by Rowland and Levi (1994) and Rowland et al. (1999). As was previously noted, Fla 4B hybrids (in particular US 75) have been used extensively in breeding to produce low-chilling types.

SSR markers are powerful tools for fingerprinting blueberry cultivars. Thirty SSRs were derived from either EST or genomic DNA libraries of highbush blueberry cv. Bluecrop (Boches et al. 2005, 2006). One or just two (NA-1040 + CA421) selected SSRs allowed identification of each of the 75 tested cultivars (Hinrichsen et al. 2009). In addition, the EST-SSRs were also very effective at estimating genetic relationship as well as at distinguishing closely spaced lowbush blueberry cultivars (Bell et al. 2008; Brevis et al. 2008). Most recently, Brevis and Hancock at Michigan State University used these SSRs to develop a linkage map of the tetraploid cross "Jewel" (southern highbush) × "Draper" (northern highbush). The ultimate goal is to identify QTL for the chilling requirement. Polashock and Vorsa (2006) are using bulked segregant analysis to tag genes for mummy berry resistance in segregating blueberry populations with *V. darrowii* as the source of resistance.

Kreher et al. (2000) found that 15 RAPD markers distinguished 67 genets of 99 total samples of deerberry (*V. stamineum* L.) from 22 patches in a 1-ha site. There was genetic diversity within individual patches (Kreher et al. 2000). For *V. vitis-idaea* L., genetic and genotypic diversity of four Swedish populations was investigated using automated image analysis of leaf shape and RAPD analysis (Persson and Gustavsson 2001). Forty-three RAPD allowed for the identification of 29 different genotypes among 129 plants from two populations. Most of the variation could be attributed to within-population variation. RAPDs were also used to determine genetic diversity in 15 lingonberry (*V. vitis-idaea* L.) populations in Sweden, Finland, Norway, Estonia, Russia, Japan, and Canada (Gustavsson et al. 2005).

10.2.4 Genomic Resources

The rapid advance in DNA sequencing technology has accelerated the accumulation of plant genome sequence data, including whole genome sequencing, genome survey sequencing, and ESTs of genomic resources. For *Vaccinium* species, collection of genomic resources began with the generation about 1,300 ESTs (Dhanaraj et al. 2004). These ESTs were subsequently demonstrated to be a reliable genomic resource for effective analysis of gene expression associated with cold acclimation.

cDNA microarrays were also used for gene expression studies under field and cold room conditions (Dhanaraj et al. 2007). Based on these ESTs and microarray data, the blueberry genomics database (BBDG) was developed (Alkharouf et al. 2007). This database is presently focusing on identification of genes associated with cold acclimation and freeze tolerance in blueberry (Alkharouf et al. 2007).

More recently, a fruit ripening-related EST library has been generated for bilberry (*V. myrtillus* L.), and the ESTs will be used to characterize genes involved in fruit development and ripening (Jaakola et al. 2009).

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