FRUIT BREEDING

Volume II.
Vine *and* Small Fruits

Edited by

Jules Janick • *James N. Moore*

FRUIT BREEDING

VOLUME II
VINE AND SMALL FRUITS

Edited by

Jules Janick
Purdue University

James N. Moore
University of Arkansas

John Wiley & Sons, Inc.

New York • Chichester • Brisbane • Toronto • Singapore

This text is printed on acid-free paper.

Library of Congress Cataloging in Publication Data:

Fruit breeding / edited by Jules Janick and James N. Moore.

p. cm.

Rev. ed. of: Advances in Fruit breeding. 1975.

Includes indexes.

Contents: v. 1. Tree and Tropical Fruits—v. 2. Vine and Small Fruits—v. 3. Nuts.

ISBN 0-471-31014-X (v. 1 cloth : alk. paper).—ISBN 0-471-12670-5 (v. 2 cloth : alk. paper).—ISBN 0-471-12669-1 (v. 3 cloth : alk. paper)

1. Fruit—Breeding. 2. Nuts—Breeding. I. Janick, Jules, 1931- . II. Moore, James N. III. Advances in fruit breeding.

SB359.35.F78 1995

634'.0423—dc20 95-16407

Printed in the United States of America

10 9 8 7 6 5 4 3 2 1

FRUIT BREEDING

CONTRIBUTORS

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

R.A. Beatson, DSIR Fruit and Trees, MT. Albert Research Centre, Auckland, New Zealand

Rex M. Brennan, Scottish Crop Research Institute, Invergowrie, Dundee DD 2 5DA, Scotland

Hugh A. Daubeny, Agriculture Canada, Research Station, 6660 NW Marine Drive, Vancouver, BC V6T 1X2, Canada

A.R. Ferguson, DSIR Fruit and Trees, MT. Albert Research Centre, Auckland, New Zealnd

L.G. Frazer, DSIR Fruit and Trees, MT. Albert Research Centre, Auckland, New Zealnd

Gene J. Galletta, USDA/ARS, Fruit Laboratory, Beltsville, MD 20705

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

C.F. Harvey, DSIR Fruit and Trees, MT. Albert Research Centre, Auckland, New Zealnd

F.J. Lawrence, Department of Horticulture, Michigan State University, East Lansing, MI 48824

M.A. McNeilage, DSIR Fruit and Trees, MT. Albert Research Centre, Auckland, New Zealnd

Charlotte Pratt,(Retired) Department of Horticultural Science, NY State Agricultural Experiment Station, Cornell University, Geneva, NY 14456

Bruce I. Reisch, Department of Horticultural Science, NY State Experiment Station, Cornell University, Geneva, NY 14456

A.G. Seal, DSIR Fruit and Trees, MT. Albert Research Centre, Auckland, New Zealnd

Donald H. Scott, (Retired) Fruit Laboratory, USDA/ARS, Beltsville, MD 20705

FRUIT BREEDING

CONTENTS

CHAPTER 1

BLUEBERRIES, CRANBERRIES, AND LINGONBERRIES

Gene J. Galletta and James R. Ballington

The genus *Vaccinium* L. includes approximately 400 species, which are concentrated in the montane tropics, but extend to all continents except Australia (Vander Kloet 1988; Luby et al. 1991). Species also occur on many islands and island groups. *Vaccinium* is in the tribe Vaccinieae of the subfamily Vaccinioideae of the Ericaceae (Stevens 1969). The Vaccinieae includes all Vaccinioideae with inferior ovaries and more or less fleshy fruits. Stevens (1969) lists 28 genera in Vaccinieae, however the only genus other than *Vaccinium* that extends into temperate latitudes is *Gaylussacia* H.B.K., which is found in eastern North America. A summary of early treatments of evolution and taxonomy in *Vaccinium* is included in Galletta (1975). *Vaccinium* is also commonly divided into sections (Stevens 1969), and fruits of species in a number of sections have been gathered from the wild by humans from time immemorial (Galletta 1975; Vander Kloet 1988; Luby et al. 1991). These sections, their general distributions, and representative species are listed in Table 1.

Three *Vaccinium* fruit crops (blueberries, cranberries and lingonberries) have been domesticated recently, almost entirely in the twentieth century. Modern cultivars of these crops offer a most dramatic example of the results of fruit crop breeding and selection. In most instances, these cultivars have greatly extended cultural ranges and ripening seasons, and improved plant health, productivity, and fruit quality, compared to wild clones. Moreover, cultivation of improved blueberries and cranberries is usually on acidic, often imperfectly drained sandy soils formerly classed as agriculturally worthless. Galletta (1975) gave an account of previous blueberry and cranberry breeding history, biology, methods and aims. Recent progress in domestication, exploration, broadening of the germplasm base,

Fruit Breeding, Volume II: Vine and Small Fruits Crops, edited by Jules Janick and James N. Moore
ISBN 0-471-12670-5

TABLE 1. Sections of the Genus Vaccinium. Don. Which Includes Species From Which Fruits Have Been Harvested in the Wild

Section of the genus	Common name	Distribution	Representative species
Batodendron (Nutt.) A. Gray	Sparkleberry	Disjunct distribution: S. eastern & S. central N. America; Mexico; Cuba	*V. arboreum* Marsh *V. leucanthum* Schlecht.
Bracteata Nakai	—	Japan and southeast Asia, to Papau New Guinea	*V. bracteatum* Thumb. *V. myrtoides* (Blume) Miq.
Ciliata Nakai	—	East Asia	*V. oldhamii* Miq.
Cinctosandra (Klotzsch) Hooker fil.	—	Disjunct distribution; S. and E. Africa, Madagascar	*V. andringitrense* Perr.
Cyanococcus A. Gray	Blueberry	Eastern North America (to British Columbia with *V. myrtilloides* Michx.)	*V. corymbosum* L. *V. angustifolium* Ait.
Hemimyrtillus Sleumer	—	Disjunct distribution: Caucaus Mts, Azores, Madeira: east Asia	*V. arctostaphylos* L.
Macropelma (Klotzsch) Hooker fil.	Ohelo	Hawaiian Islands	*V. reticulatum* Sm.
Myrtillus Dumort.	Bilberry	Circumpolar, (to central America in the Rocky Mts.)	*V. myrtillus* L.
Oxycoccoides Hooker fil.	S. Mtn. cranberry	Disjunct distribution: S. Appalachians in N. America and east Asia	*V. erythrocarpum* Michx.
Oxycoccus (Hill) Koch	Cranberry	Circumpolar (south to mid-Atlantic region and S. Appalachian with *V. macrocarpon* Ait.	*V. oxycoccus* L. *V. macrocarpon* Ait.
Polycodium (Ref.) Rehder	Deerberry	Eastern N. America (with disjunct popls. in Mexico)	*V. stamineum* L.
Praestantia Nakai	—	East Asia	*V. praestans* Lamb.
Pyxothamnus (Nutt.) Sleumer	Mortina	Disjunct distribution: Calif. to Brit. Columbia; Mexico; C. Amer. Andes	*V. floribundum* H.B.K.
Vaccinium L.	Bog blueberry	Circumpolar	*V. uliginosum* L.

TABLE 1. (*continued*)

Section of the genus	Common name	Distribution	Representative species
Vitis-idaea (Moench) Koch	Lingonberry	Circumpolar	*V. vitis-idaea* L.

Source: From Galletta (1975), Stevens (1969), Vander Kloet (1988), Luby et al. (1991).

systematics, biotechnology, and basic understanding of the *Vaccinium* genome has been considerable.

Blueberries were harvested from wild plants of many North American species prior to the first shipment of fruit of F. V. Coville's hybrid highbush blueberry seedlings from Elizabeth White's farm at Whitesbog, New Jersey, in 1916 (Coville 1921). The introduction of the 'Pioneer', 'Cabot', and 'Katherine' cultivars from Coville's breeding program in 1920 (Coville 1937) served as the basis for an entirely new agricultural industry. This industry has continued to thrive and expand with the continuing development of newer and better cultivars of all five domesticated classes of blueberries (see below). There are over 62,000 ha (153,202 acres) of cultivated blueberries in North America at present, of which two-thirds of the producing area is in lowbush blueberries (Hancock 1989). However, two-thirds of the total production comes from highbush blueberries, and 5 to 10% of the highbush blueberry area is planted to rabbiteye blueberries.

There are now commercial industries in Europe and Oceania (Australia and New Zealand), and there is considerable interest in expanding blueberry culture in Chile and Japan (Eck 1988; Hanson and Hancock 1990; Spiers 1990). The outlook is good for a greatly increased world production of blueberries, but the realization of this expansion is dependent on further developments in blueberry breeding, genetics, and culture.

The large or American cranberry (*Vaccinium macrocarpon* Aiton) has long been prized for its acid red fruit, which is high in vitamin C, cellulose, and pectin content, and possesses organic acids beneficial to the digestive and urinogenital tracts (Eck 1990). Henry Hall of Dennis, Massachusetts, on Cape Cod, started the culture of this native American crop in about 1816, and the fruit began to be marketed about 1845 (Peterson et al. 1968). Cranberries are now grown on approximately 9000 ha in the United States and 700 ha in Canada; they are important in Massachusetts, Wisconsin, New Jersey, Washington, and Oregon in the United States, and British Columbia and the Maritime Provinces in Canada (Dana 1990). Cranberry culture has shown promise in recent years in experimental trials in Poland, Austria, Germany, Russia, Latvia, and Finland (Soczek and Scholz 1969; Klein 1971, 1977; Liebster 1971; Kolupaeva 1971; Haeckel 1977; Schmid 1977; Eschenbecher and Jost 1977; Holfelder and Ross 1977; Gronskis and Snickovskis 1989; Hiirsalmi 1989; Ripa 1989). Cultural promise is greatest for the bog or European cranberry (*V. oxycoccus* L. = *Oxycoccus quadripetalus* Gilib.) in Latvia, Finland, and Russia (Gronskis and Snickovskis 1989; Hiirsalmi 1989), although interest in the American cranberry is intense in these countries also.

Consumption of cranberries in North America was once limited to Thanksgiving and Christmas fare in the form of jellies and sauces. Starting in the early 1960s, new products, such as cranberry juice, cran-grape and cran-apple juices, and cranberry-orange relish began to be vigorously promoted. In 1968 the industry voted to accept a marketing order that permits withholding part of the crop each year to stabilize prices. Although the U.S. crop area has remained essentially the same since 1905 (9000 ha), production had risen almost seven-fold by 1985 (171.4 t) due to improved cultural practices such as weed control, fertilizer management, and water harvesting in eastern areas (Dana 1990). The value of the crop tripled in the period from 1963 to 1971, due largely to the impact of new products, especially juice, and is now worth several hundred million dollars annually in North America (Dana 1989). Cranberries are now consumed the year round and they are being exported in quantity. The industry today appears sound and healthy.

The circumboreale cranberry–blueberry intermediate, *V. vitis-idaea* L. (known as lingonberry or cowberry, foxberry, rock cranberry, redberry, and, in Newfoundland, partridgeberry), has long been prized for jelly and juice, and as a condiment with meat by northern Europeans, residents of Newfoundland, and native Americans of northern North America (Vander Kloet 1988). Starting in the 1960s commercial plantings of lingonberries were established in northern Europe, based on cultivation of selections from the wild and recently introduced open-pollinated seedlings (Fernqvist 1977; Lehmushovi 1977; Blasing 1989; Hiirsalmi 1989; Stojanov 1989; Luby et al. 1991). In the United States, Elden Stang of the University of Wisconsin (at Madison) is conducting selection and domestication trials of lingonberries, based largely on Finnish seed stocks.

BLUEBERRIES

ORIGIN AND EARLY DEVELOPMENT

All present cultivated blueberries are included in the section *Cyanococcus* of *Vaccinium*. This group has often been referred to as the "true" or cluster-fruited blueberries (Camp 1945). Based largely on his cooperative investigations (with G. M. Darrow, E. B. Morrow, and F. B. Chandler) with species in this section, Camp (1942) made the following observations in regard to speciation in *Vaccinium*: (1) a lack of fundamental sterility barriers between species of the same ploidy level; (2) a high incidence of polyploidy ($x = 12$), with many natural tetraploid ($2n = 4x = 48$) and hexaploid ($2n = 6x = 72$) species; (3) individuals of many species are functionally self-unfruitful, which promotes the incidence of interspecific hybrid swarms in combination with homoploid interfertility; (4) intolerance of dense shade and alkaline soil, which restricts habitats and encourages speciation through ecological separation; and (5) results from migrations caused by geologic events or changes in distribution patterns as a consequence of the antiquity of the genus. These events permitted formerly disjunct species to come together, hybridize, and recede. Blueberries are excellent primary colonizers of disturbed areas, either natu-

ral or man-made, and since blueberry seeds are widely disseminated in nature by birds, opening-up of new disturbed areas permits colonization opportunities for hybrid segregants as well as species.

Camp (1945) presented the first comprehensive treatment of *Vaccinium* section *Cyanococcus* in his 1945 monograph. He concluded that the section included 9 diploid species, 12 tetraploid species and 3 hexaploid species. The section has since received major revisions by Vander Kloet (1972 1983b 1988). He considered the diploid lowbush species the basic elements of the section, and also considered the diploid highbush blueberry *V. corymbosum* to be of hybrid origin, from combinations among the lowbush species (Vander Kloet 1983b 1988). He included a total of 6 diploid taxa, 5 tetraploid taxa, and 1 hexaploid, and also listed *V. corymbosum* as occurring at all three chromosome levels. Additional evidence, from both traditional and nontraditional sources, now indicates that further revisions, largely with highbush blueberry, appear to be in order (Ballington et al. 1987a 1993; Bruderle and Vorsa 1990 1994; Bruderle et al. 1991; Buckley 1990; Meyer and Ballington 1990; Vorsa et al. 1988). The most recent circumscription by Vander Kloet (1988) of species in *Vaccinium* section *Cyanococcus*, along with proposed changes in circumscription based on recent evidence, is presented in Table 2. The table also lists the plant habit, habitat, general distribution of the species, and presumed origin of the polyploids. For a discussion of "blueberries" in other sections of the genus, see Vander Kloet (1988) and Luby et al. (1991).

HISTORY OF IMPROVEMENT

There are five major classes of blueberries grown commercially for fruit today. These include the lowbush, half-high, highbush, southern highbush, and rabbiteye blueberries.

Lowbush Blueberries

Stems are less than 0.5 m tall, and plants are typically rhizomatous. The lowbush group includes predominantly the tetraploid "sweet lowbush blueberry," *V. angustifolium* Aiton (including var. *nigrum*), but also includes Canada blueberry, *V. myrtilloides* Michaux, particularly in newly cleared fields, and occasionally *V. boreale* Hall and Aalders. Production entails managing native stands by burning (or mowing) on a biennial basis, usually in combination with chemical weed control. Commercial production is confined mostly to Maine, Quebec and the Canadian Maritime Provinces (Luby et al. 1991).

Improvement of the lowbush blueberry has been initiated with the selection of horticulturally superior wild clones at various times by the United States Department of Agriculture (USDA), Canada Department of Agriculture, and the Maine, Michigan, Wisconsin, Minnesota, and West Virginia Agricultural Experiment Stations. Kender (1966) listed the objectives of improved lowbush phenotypic selection: large fruit size, good blue color, fine flavor, heavy productivity,

TABLE 2. Habitats and General Distribution of Species in *Vaccinium* Section Cyanococcus and the Proposed Origins of the Polyploid Species

Species			
Vander Kloet (1988)	Proposed Circumscription	Habit, Habitat and Distribution	Presumed Origin
DIPLOID ($2n = 2x = 24$)			
V. boreale Hall & Aald.	*V. boreale* Hall & Aald.	Lowbush[a]: Forest–tundra, alpine meadows, exposed coastal headlands, occas. on rocky uplands: Northern Quebec, Laborador, Newfoundland, Cape Breton, and Gaspe, south to outlying stations on mountain summits in Maine, New Hampshire, New York, and Vermont	
V. myrtilloides Michx.	*V. myrtilloides* Michx.	Lowbush: Muskeg or upland barrens, subalpine and boreal forests: British Columbia and Mont. to Laborador, S. to N.Y., Ind. and the mountains to W. Va.	
V. pallidum Ait.	*V. pallidum* Ait.	Lowbush to half-high: Dry upland woods, rocky ledges and abandoned farm land: Minn. and Ont. to Me., south to Ark., Tenn., Ala., and Ga.	
V. tenellum Ait.	*V. tenellum* Ait.	Lowbush: Pine savannahs, upland open forest and meadows: SE Va. to N. Fla. and Ala.	
V. darrowii Camp	*V. darrowii* Camp	Lowbush to highbush: Dry sandy uplands: La. to Fla.	Appears close to the progenitor species of the other diploids[b]
V. corymbosum L.	*V. corymbosum* L.[c,d]	Highbush: Coastal plain and inland bogs, pine flatwoods, and open wooded slopes: C. Fla. to E. Tex. and Ark, N. to N.Y. and Me.	

	V. elliottii Chapm.[d]	Highbush: River basins, upland woods and abandoned fields: SE Va. to N. Fla., then west along the Gulf to La. and Tex., and north to Ark.	
TETRAPLOIDS ($2n = 4x = 48$)			
V. angustifolium Ait.	*V. angustifolium* Ait.	Lowbush: Headlands, high moors, dry upland woods, rocky outcrops, abandoned pastures and bogs: Laborador and Newfoundland, W. to S. Manitoba and Minn., S. to N. Ill., Penn. and Del., and to Va. and W.Va. in the mountains	Proposed allotetraploid of either *V. boreale* × *V. pallidum* or *V. boreale* × *V. myrtilloides*[e]
V. pallidum Ait.	*V. pallidum* Ait.	Same as diploid *V. pallidum*	Autotetraploid of diploid *V. pallidum*
V. hirsutum Buckley	*V. hirsutum* Buckley	Lowbush: Dry ridges and meadows in the mountains: N.C., Tenn., Ga.	Unknown
V. myrsinites Lam.	*V. myrsinites* Lam.	Lowbush: Pine flatwoods and dry sandy areas: Gulf Coast to La.; Fla. Ga., and southeast S.C.	Proposed allotetraploid of *V. darrowii* × *V. tenellum*[f]
V. corymbosum L.	*V. corymbosum* L.[g,i]	Highbush: Coastal plain and inland bogs, pine flatwoods, occas. on upland slopes: N. Fla. to Me., Ont. N.S., W. to E. Tex., N. to Mich.	Basically an autotetraploid of diploid *V. corymbosum*, but introgression with other species is often evident[h]
	V. simulatum Small[g]	Highbush: Open mtn. slopes and meadows: from N. Ala. and Ga. to Ky. and Va.	Proposed autotetraploid derived taller forms of diploid *V. pallidum*[f]
HEXAPLOIDS ($2n = 6x = 72$)			
V. corymbosum L.	*V. ashei* Reade[i,j]	Half-high to principally highbush: Stream and lake margins, pine flatwoods, upland slopes slopes, abandoned fields: north Fla. to east	Complex origin[f]

TABLE 2. (*continued*)

Species			
Vander Kloet (1988)	Proposed Circumscription	Habit, Habitat and Distribution	Presumed Origin
		Tex. and central Ark., north along the Atlantic coast to central S.C.	
	V. constablaei Gray[i]	Half-high to highbush: Shrub "balds" and rocky outcrops above 1000 m elev.: northern Ga. western N.C. and eastern Tenn.	Proposed to be *V. alto-montanum* (4*x*, *V. pallidum*, sensu. Vander Kloet) × *V. simulatum* through production of unreduced gametes by one parent[f]

Note: Species circumscriptions modified from Vander Kloet (1988), based on recent evidence.

[a]Lowbush = less than 50 cm, half-high = 50 cm[1] m, highbush = over 1.5 m tall.

[b]Vander Kloet (1983b); Vorsa et al. (1988), Bruederle and Vorsa (1994).

[c]Diploid *V. corymbosum* sensu. Vander Kloet (1972).

[d]These two species separated based on anthocyanins in fruits (Ballington et al. 1987a); isozymes (Vorsa et al. 1988; Bruederle & Vorsa 1990, 1994), differential reaction to *Botryosphaeria dothidea* (Buckley, 1987), and *Scaphytoptus magdalensis* (Meyer and Ballington, 1990).

[e]Vander Kloet (1977a, 1978)

[f]Camp (1945).

[g]Species separated based on differences in anthocyanin in fruits (Ballington et al. 1987a) and incomplete crossability (Ballington 1989).

[h]Luby et al. (1991).

[i]Includes *Vaccinium amoenum* Ait. (sensu. Camp 1945) as recommended by Lyrene (1988b).

[j]Species separation based on Differences in anthocyanins in fruits (Ballington et al. 1987a) (*V. ashei* and *V. constablaei* vs. tetraploid *V. corymbosum*), isozyme differences between *V. ashei* and *V. corymbosum* (Vorsa et al. 1988), differential reaction to *Scaphytoptus magdalensis* (Meyer and Ballington 1990) and *Botryosphaeria dothidea* (Milholland and Ballington, unpublished) (*V. ashei* vs. *V. constablaeil* and *V. corymbosum*), and experience with generally very poor crossability between *V. constablaei* and tetraploid *V. corymbosum* (Ballington, unpublished).

self-fruitfulness, late blooming, uniform ripening, disease resistance, vigorous rhizome growth, easy propagation, and upright, vigorous, tall stems. All improvement work has been with *V. angustifolium*.

The lowbush breeding program in Nova Scotia introduced six improved cultivars ('Augusta', 'Blomidon', 'Brunswick', 'Chignecto', 'Cumberland', and 'Fundy') from 1975 through 1988 (Aalders et al. 1975, 1977; Hall and Aalders 1982; Hall et al. 1977, 1988). These cultivars represent significant improvements over typical wild genotypes, but their acceptance by the lowbush industry has been hindered by difficulties and expense of propagation (Hall 1979). While stem or rhizome cuttings are relatively easy to root, their extreme precocity of flowering results in very slow establishment of plantings. This problem can be largely avoided by using plants produced through micropropagation (Smagula and Lyrene 1984). However, micropropagated lowbush plants may still be too expensive to be utilized for widespread planting. Seedlings are also much more successful than rooted cuttings for establishment of new lowbush fields, and there has been a good deal of interest in establishing lowbush fields derived from seedling progenies from elite clones (Hall 1979, 1983). In addition to the above cultivars, 'Tophat', an extreme low-growing and relatively large-fruited later generation segregate from interspecific hybridization between *V. angustifolium* and *V. corymbosum*, was released in Michigan in 1977 (Moulton, et al. 1977).

Vaccinium angustifolium has contributed genes through 'Russell', 'North Sedgewick', and Michigan Lowbush #1 to over half the highbush blueberry cultivars introduced through state and USDA cooperative breeding programs in the United States (Galletta 1975; Ballington 1984a). It is also an integral component in the "Halfhigh" breeding program at the University of Minnesota. Recently *V. angustifolium* has been identified as a source of genes for resistance to stem blight caused by *Botryosphaeria dothidea* (Mouq. ex Fr.) Ces & de Not (Buckley 1990). Stem blight is now the most serious fungal disease of highbush blueberries in warmer regions of the United States, and no stem blight-resistant highbush genotypes have been identified that do not include germplasm from *V. angustifolium*.

Vaccinium angustifolium can contribute the following desirable features to a hybrid gene pool: low stature, early fruit maturation season, concentrated ripening, precocity, drought resistance, bud hardiness, fine picking scar, productivity, and sweetness (Galletta 1975; Ballington et al. 1984a, b). Undesirable lowbush traits include self-infertility, small fruit size, small stature (in some instances), spreading habit, softness of fruit, and low fruit acidity (Galletta 1975).

Half-high Blueberries

Stems of this group are 0.5 to 1.0 m tall, and plants are suckering to crown forming. These are species hybrids or backcross derivatives of lowbush–highbush hybrids, at present usually involving *V. angustifolium* and *V. corymbosum* parentage. Small commercial plantings of half-high cultivars have been established in the upper Midwest and New England in the United States, and in eastern Canada

(Luby et al. 1991). Present cultivars are basically crown forming, so their culture is similar to that of the highbush blueberry (Hoover et al. 1984).

Breeding programs based on lowbush–highbush hybridization have been carried on in Michigan, West Virginia and Minnesota (Galletta 1975). Only the Minnesota program is continuing at present. Moore (1966) summarized the early generation results of lowbush–highbush crosses up to the F_2 and BC_1 generations from work at Michigan and several eastern United States locations. Noteworthy was the F_1 generation uniformity for intermediate plant height, extreme productivity, early maturity, small to moderate fruit size, dark color, soft fruit, and fair flavor.

F_2 and subsequent hybrid generations from lowbush–highbush crosses usually segregate for growth habit and fruit size and color. The lowbush–highbush improvement program in Michigan was carried through five generations (Johnson and Moulton 1968), and emphasized developing large-fruited, half-high segregates for commercial cultivation in northern Michigan, where they would overwinter under a snow cover for cold protection. The goals of the on-going Minnesota half-high improvement program are similar (Luby 1991). The Michigan program also looked for extreme lowbush segregates with large berries, and lower growing "highbush" segregates that would be easier to harvest.

The Minnesota breeding program released the 'Northblue', 'Northsky', 'Northcounty', and 'St. Cloud' half-high blueberry cultivars (Luby et al. 1986; Finn et al. 1990). None of the cultivar releases from the Michigan program of Johnston and Moulton fit into the half-high category. The half-high cultivar 'Friendship' was released from Wisconsin in 1990 (Stang et al. 1990). It is an open-pollinated seedling from native Wisconsin *V. corymbosum*, and based on plant habit, appears to be of *V. corymbosum* × *angustifolium* derivation. The West Virginia program released a half-high hybrid originating from a cross between a tetraploid genotype of the upland-adapted, drought-resistant lowbush to half-high species *V. pallidum* Aiton and 'Concord' (*V. corymbosum*) parentage, which they named 'Ornablue' (Childs 1969). Development of half-high cultivars involving the combination of tetraploid *V. pallidum* × *V. corymbosum* is also currently underway on a small scale in North Carolina.

Highbush Blueberries

These are crown forming plants, trained to 2.0 m tall or higher. Cultivars of this species are derived basically from tetraploid genotypes of *V. corymbosum*. However, many cultivars also have *V. angustifolium* in their background (Galletta 1975). This is the most important cultivated type worldwide, with commercial production taking place in 17 states in the United States, in three Canadian provinces, and in Europe, Australia, New Zealand and Chile (Hanson and Hancock 1990).

Credit for the domestication of the highbush blueberry must go to Frederick Vernon Coville (USDA botanist during the period 1888–1937) and his associates, who recognized the potential of this fruit species early. Reviews dealing with the domestication and subsequent improvement of the highbush blueberry have been