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Development of Highbush Blueberry Cultivars Adapted to Florida

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Abstract

The low-chill southern highbush blueberries now being grown in Florida were developed by crossing northern highbush cultivars, which had large fruit, high fruit quality, and early ripening but were poorly adapted in Florida, with Florida native blueberry species, which were well-adapted but were late-ripening and had small fruit. In formulating the foundation populations for recurrent selection during the 1950s, most of the parentage was northern highbush, and less was Florida native. This paper presents the hypothesis that faster progress could have been made if a higher percentage of the original gene pool had been derived from the adapted natives. The hypothesis is based on the observation that good environmental adaptation depends on many independent components, most of which are hard to evaluate accurately in small plots in one year, whereas large fruit, high fruit quality, and early ripening are easier to evaluate in single-plant plots in a single year. The ability to evaluate young plants in small plots allows rapid cycles of recurrent selection during which the selected characters can quickly be improved. Florida native blueberry species that could have been used more in breeding include diploid *Vaccinium darrowi* Camp, diploid highbush blueberry (*V. corymbosum* L.) from the Florida peninsula between Ocala and Lake Okeechobee, and tetraploid highbush blueberry (*V. corymbosum* L.) from northeast Florida and southeast Georgia.

The highbush blueberry, *V. corymbosum*, is the principal cultivated blueberry of the world. It is native from coastal Maine and Nova Scotia west to central lower Michigan and south to south-central Florida (1,8,9). Like many perennial woody species that have a long north-south native distribution on the coastal plain of eastern North America, individual plants are adapted to the climate at their latitude of origin, and cannot be successfully transplanted long distances in a north-south direction within the range of the species.

Improved northern highbush blueberry cultivars bred by the USDA were being planted in southern New Jersey by 1930 (2), and within a few years, the New Jersey selections were being tested in other parts of the range of *V. corymbosum*, both to the north and to the south. The New Jersey cultivars grew well and were productive along the southwest shore of Lake Michigan, and Michigan became an important state for highbush blueberry production. The New Jersey highbush cultivars succeeded as far south as the coastal plain of southeastern North Carolina, where nearly 4 million quarts (about 3 million kg) of blueberries were being harvested annually by 1960 (2). Harvest of highbush blueberries in eastern North Carolina began each spring about May 20. Farther south, on the coastal plains of Georgia and Florida, the New Jersey highbush were tested but were not well enough adapted to be commercially successful.

In 1948, Ralph Sharpe began breeding highbush blueberries at the University of Florida in Gainesville (6,7). His goal was to develop cultivars which, when cultivated in north and central Florida, would produce blueberries a month earlier than the northern highbush cultivars being planted in southeastern North Carolina. Sharpe recognized that at least the following characteristics would be needed to make highbush blueberries commercially successful in Florida: low chilling requirement, tolerance to summer heat, tolerance to the major diseases of Florida, the ability to continue growing through late summer and early fall (most northern highbush cultivars set flower buds and stop growing by mid-summer in Florida), and the ability to produce large, high-quality fruit, most of

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which could be picked before harvest began in North Carolina.

Sharpe and his cooperator, George Darrow, then the USDA blueberry breeder in Washington, D.C., embarked on a program to develop highbush blueberry cultivars for Florida by combining the best features of the northern highbush cultivars from New Jersey and Michigan, which had large fruit and short bloom-to-ripe intervals, with the best features of one or more of the blueberry species that were native and well-adapted in Florida. At least conceptually, two alternative procedures were available to them. One was to use the Florida native blueberries as the principal founding population to start a recurrent selection breeding program, using the New Jersey highbush cultivars only enough to provide genes for large, high-quality fruit. The second alternative, which Sharpe and Darrow adopted, was to base the program largely on the improved northern highbush cultivars, using the Florida native species only enough to provide genes for lower chilling requirement and improved adaptation. Because Sharpe and Darrow chose the second strategy, most of the genes in the southern highbush cultivars now being grown in Florida derive from northern highbush cultivars, not from Florida native blueberry populations. It will probably never be known with certainty which of these two breeding strategies would have been more efficient in producing commercially profitable cultivars. In this paper I propose the hypothesis that, because large fruit, high fruit quality and early ripening-traits largely from northern highbush cultivars — are easy to evaluate in young seedlings, whereas good adaptation to the Florida environment — which came largely from the Florida native species — can only be evaluated in older plants over a period of years, the more efficient strategy might have been the one not followed — to base the recurrent selection program mainly on low-chill blueberry selections from Florida and southeast Georgia.

Blueberry Species Native in Florida

Blueberries, including section Cyanococcus of the genus *Vaccinium*, to which the cultivated highbush (*V. corymbosum* L., lowbush (*V. angustifolium* Ait.), and rabbiteye (*V. ashei* Reade) blueberries of the eastern U.S. belong, are undergoing rapid evolution, and taxonomists do not fully agree on the most useful way of delineating the species. For reasons which I need not enumerate here, in discussing the blueberries of the southeastern U.S., I largely follow the taxonomic treatment of Camp (1945), although I have made some modifications in light of chromosome number information that was not available to Camp.

The blueberry species of Florida occur in three sections or subdivisions of the genus *Vaccinium* (1). Section Polycodium is represented in Florida by only one species, *Vaccinium stamineum* L., the deerberry. Section Batodendron is represented in Florida by one species, *V. arboreum* Marsh, the sparkleberry. *Vaccinium arboreum* makes vigorous hybrids with some of the cultivated blueberries. Despite its long-range promise in breeding upland-adapted blueberry cultivars, *V. arboreum* ripens too late and has too many undesirable berry quality characteristics to make it an attractive choice for developing early-ripening blueberry cultivars in the short term.

All the other native Florida blueberry species are in section Cyanococcus. All produce edible fruit, with flavors and textures similar to cultivated highbush blueberry, but the fruit is small, except for some plants of V. *ashei* and tetraploid V. *corymbosum*. Two species are rhizomatous, evergreen, and low-growing, and are adapted to occasionally-burned pineland. One of these (V. *darrowi*) is diploid and the other (V. *myrsinites* Lamarck) tetraploid. Although they have many features in common and sometimes grow in close proximity, they probably hybridize infrequently due to the triploid block in *Vaccinium*.

On land that is not frequently burned over in Florida, there occur both diploid and tetraploid forms of a tall (3 to 4 m), upright blueberry that has leaves much larger than those of V. *darrowi* and V. *myrsintes* and is adapted to moist but well-drained, acid, sandy soils that are high in organic matter. Camp (1), who did not know the chromosome numbers in this taxon, did not distinguish between the diploid and tetraploid forms, and called them both *V. fuscatum* Ait. I will refer to them here as diploid and tetraploid *V. corymbosum*, because the tetraploid forms are similar morphologically and ecologically to the tetraploid *V. corymbosum* that extends from south Georgia to southern New England. The tetraploid form is rare or nonexistent in the Florida peninsula south of Gainesville, but the diploid form is locally abundant along streambanks and in swampy areas as far south as Lake Placid in southern Highlands County.

Vaccinium elliottii Chapmn., a distinct and abundant small-leafed, tall-growing, highly-deciduous, diploid species, extends from Gainesville north and west through the Florida panhandle. Specimens collected farther south in the Florida peninsula as *V. elliottii* are, instead, hybrids between diploid *V. corymbosum* and *V. darrowi*. At certain times of the year, these hybrids resemble *V. elliottii* in leaf and bush morphology but are much more evergreen and do not have the flower structure of *V. elliottii*, which is typified by a style that is much shorter than the corolla tube. *Vaccinium elliottii* also has a wide range outside of Florida in the southeastern U.S. Despite being diploid, *V. elliottii* produces a few unreduced gametes, and breeders can obtain a few tetraploid hybrids by crossing it with tetraploid highbush cultivars. These hybrids are usually highly vigorous and have been used somewhat in breeding, but experience in Florida indicates that they are a less useful gene source for quick progress than the diploid *V. corymbosum* from the central and southern parts of the Florida peninsula.

The hexaploid rabbiteye blueberry is widespread, abundant, and well-adapted in the Florida panhandle and in northeast Florida. This species was used to a small extent by Sharpe and Darrow in the early years of the Florida highbush blueberry breeding program. By crossing hexaploid *V. ashei* with diploid *V. darrowi*, they produced a few seedlings which they believed to be tetraploid (they were later found to be pentaploid). These hybrids were crossed with tetraploid northern highbush selections and contributed somewhat to the foundation gene pool from which southern highbush cultivars were developed. Although *V. ashei* is extremely vigorous and well-adapted in north Florida and produces large berries, its usefulness as a parent for breeding early-ripening tetraploid blueberry cultivars is reduced by the fact that it is hexaploid and late-ripening, and its hybrids with highbush cultivars have reduced pollen fertility due to pentaploidy and almost always produce dark berries that lack the desired blue color.

Low-chill Blueberry Species that Could Have Been More Widely Used in Breeding Southern Highbush Blueberries

The strategy of breeding southern highbush blueberry cultivars starting principally with native selections from Florida and southeast Georgia could have been implemented by much heavier use of three taxa that seem particularly useful for this purpose — tetraploid *V. corymbosum* from northeast Florida and southeast Georgia, roughly in the area from Gainesville, Florida to Valdosta, Waycross, and Brunswick, Georgia; diploid *V. corymbosum* from the Florida peninsula between Ocala and the southern end of the species range around Lake Placid; and the tallest, most upright forms of *V. darrowi* from the Florida peninsula. These three taxa are discussed further below and in (3).

Lowchill tetraploid *V. corymbosum*. This taxon is widespread and abundant in northeast Florida and southeast Georgia on moist, acid, sandy soils. In Florida, all or almost all plants produce shiny-black fruit. In southeast Georgia, some populations are polymorphic for black and glaucous-blue fruit. Camp (1945) separated the glaucous-fruited form as *V. australe*, but this no longer seems warranted in that black and blue-fruited plants are clearly members of one cross-pollinating population at several locations in southeast Georgia. Furthermore, the glaucous vs black-fruited polymorphism also occurs in *V. elliottii* from west Florida, in the northeast Florida-southeast Georgia race of hexaploid *V. ashei*, and in *V. darrowi* in the Florida peninsula. Tetraploid *V. corymbosum* from northeast Florida and southeast Georgia has a low chilling requirement, berries that are large for a wild section-Cyanococcus blueberry, vigorous, upright growth habit with a desirable level of basal sprouting, medium-early fruit ripening, and good berry quality. The best selections from southeast Georgia are probably similar in berry size and quality to the wild New Jersey highbush selections that were used to start breeding northern highbush blueberries in 1910.

Lowchill diploid *V. corymbosum*. This taxon occurs from Gainesville, Florida (and probably farther north) south to near the north end of Lake Okeechobee. The plants resemble the tetraploid highbush blueberries described above, but have somewhat smaller leaves and berries, are more evergreen, are diploid, and have a lower chilling requirement. Until recently, these plants were abundant along streams, in swampy "bayheads", and on the margins of the numerous lakes that dot the central Florida peninsula. In recent decades, urbanization and agriculture have decimated or destroyed populations of this species in many localities. The highbush populations around Lake Placid in southern Highlands County thrive where mean January temperatures are about 63°F (17 °C), which is 6°F warmer than at the southern end of the range of tetraploid *V. corymbosum* in north-central Florida. In places where fire has been excluded and habitats have been disturbed, much hybridization and introgression of characters has occurred between diploid *V. corymbosum* and *V. darrowi*. Plants that are intermediate between the two species and plants that resemble one species in some morphological characteristics and the other species in other characteristics are common.

In the Florida, crosses between diploid wild *V. corymbosum* from Lake Placid and tetraploid advanced selections from the breeding program have produced a few triploid and a few tetraploid hybrids. The tetraploids have been fertile, highly vigorous, very low in chilling requirement, and surprisingly large-fruited. Fruit size in the interspecific hybrids is probably increased as a result of 2n gamete formation in the diploid parent. Increased cell size is typical when chromosome numbers are doubled in a plant.

Vaccinium darrowi. *Vaccinium darrowi*, nearly a Florida endemic (a few populations occur in coastal Alabama and Mississippi and in southeast Georgia), is a diploid, evergreen, rhizomatous species that grows on acid soils in pinelands that are subject to fires. In the Florida panhandle, *V. darrowi* conforms to the description given by Camp (1), occurring in extensive colonies 0.15 to 0.40 m high. In the Florida peninsula, however, *V. darrowi* often reaches a height of 1.0 to 1.5 m (Lyrene, 1986). This increased height is probably a result of long-term introgression between *V. darrowi* and diploid *V. corymbosum*.

Vaccinium darrowi, specifically clone FL 4B, a glaucous plant collected in the Florida peninsula, has been widely used in breeding southern highbush cultivars. This selection contributed genes for light-blue berry color to the southern highbush gene pool. The strong contrast in characteristics between lowbush, evergreen *V. darrowi* and tall-growing, deciduous northern highbush cultivars from New Jersey and Michigan has given rise to highly variable hybrid populations that permit breeders to select a wide range of plant types.

Adaptive Traits Needed in Highbush Blueberry Cultivars for Florida

Good growth and yield of blueberries requires that the cultivars be well-adapted to the local environment. To be well adapted, a plant must respond favorably to the many facets of the climate as they manifest throughout the year. It must also grow well on the available soil and be resistant or tolerant to the major insect and disease pests that cannot be readily controlled by cultural practices. The plant must also respond favorably to the management practices needed to produce high-quality berries during the preferred market window. Bad response to one insect, one disease, one soil characteristic, or one aspect of the local climate can make a cultivar unprofitable in a particular area. Good adaptation involves many diverse interactions between cultivar and environment and thus requires many years to recognize in a test selection. Southern highbush selections in North Florida are often discarded after years of testing because the most recent growing season has revealed some previously unnoticed problem. By noting, over a series of years, the principal reasons why clones must be discarded in advanced stages of testing, the most important elements of good adaptation in southern highbush blueberries in Florida can be determined. Some of these elements are listed below.

1. Inherently high vigor and biomass production. The highest annual blueberry yields in North America come from northern highbush cultivars in the western parts of Oregon, Washington, and British Columbia and from rabbiteye cultivars such as 'Brightwell' and 'Powderblue' on excellent blueberry soil with irrigation in the southeastern U.S. In both situations, the plants show extremely high vigor, and are capable of supporting very high crop loads while simultaneously making an abundance of strong new vegetative growth for fruiting the following year. Southern highbush selections in the Florida breeding program vary enormously in vigor. Many are too weak or too slow-growing to produce heavy annual crops.

2. Low chilling requirement. It is hard to represent the chilling requirement of a southern highbush blueberry clone by assigning it a number, because the adverse effects of lack of chilling are manifested in such a variety of ways in different clones. Some clones respond to insufficient winter chilling by aborting their flower buds in late March or early April in Gainesville, after which they leaf prolifically and grow vigorously throughout the summer, producing a copious load of flower buds in the fall, only to abort these again the following spring, unless the winter has been unusually cold. Other clones, when underchilled, begin flowering in early February and continue flowering through early April, opening only a few flowers each day. Still other clones open their flowers with good synchrony, but flower very late in the spring, thus missing the preferred harvest window. Some clones flower early and synchronously, but are very slow to make new leaves, and the harvest may be small, delayed, or low in quality due to insufficient leaves to support berry development. The most practical way to designate the chilling requirement of a southern highbush clone may be to state the mean temperature of the three coldest months in the warmest area where the clone has been commercially successful.

A common manifestation of lack of chill with blueberries in Florida is failure to leaf well in the spring. In Michigan, New Jersey, and in the Pacific Northwest, where northern highbush cultivars receive much chilling, plants normally begin to produce new leaves before they reach full bloom. In Florida, most southern highbush cultivars are in full bloom before they produce new leaves, a much less desirable chronology. Recent observations with potted plants suggest that chilling the plants at lower temperatures promotes earlier leafing relative to the time of flowering. For several years, 100 dormant southern highbush plants from the breeding program, each a different genotype, were dug and potted from the field in late December. These plants were placed in refrigerators with no light for 60 days, after which they were moved to a warm greenhouse for flowering. Two refrigerators were used each year, one kept at 5 to 7°C, the other at 0 to 2°C. Although all the plants were placed in the refrigerators and moved to the greenhouse at the same time, those from the colder refrigerator showed a marked tendency to leaf abundantly before they flowered, whereas those from the warmer refrigerator tended to flower before they leafed. The fact that most of the chilling hours received in Florida tend to be at the higher range of where chilling is effective may explain why so many clones that flower well in the spring have trouble leafing.

3. Ability of the plants to continue growth through the summer. By the end of harvest on northern highbush blueberries in Michigan and the Pacific Northwest, most of the vegetative growth that will produce next year's crop has been made, flower buds are beginning to form, and the end of the growing season is at hand. In Florida, with blueberry harvest occurring in April and early May and with the growing season continuing through October, the end of harvest means that 5 warm, rainy months lie ahead before the plants enter dormancy. Many of the flower buds that were differentiated in March and April on the new vegetative flushes of early spring will die before November. Many clones are hard to keep growing during the summer, except on the best soils. The selections vary greatly in how they respond to post-harvest hedging, a common procedure in Florida blueberry production fields. Some sprout vigorously from the cut branches and make a canopy of new shoots that produce flower buds during September and October; others sprout back only weakly. Because of the long growing season, it is important that blueberry selections in Florida sprout vigorously after June pruning and continue vegetative growth through late August.

4. Resistance to the disease and insect pests of north Florida. In well-tended plantations on good blueberry soil in north Florida, the main causes of plant loss and poor growth are three diseases—phytophthora root rot (pathogen *Phytophthora cinnamomi*), stem blight (*Botryosphaeria dothidea*), and cane canker (*Botryosphaeria corticis*). There are also numerous fungi that cause leaf spots, some of which can defoliate susceptible plants during the summer and fall. Seedlings from the Florida highbush blueberry breeding program show great variability in resistance to all the major diseases. Occasionally, 20-plant clonal plots have been established in which almost every plant was dead of phytophthora root rot or stem blight within two years, in the same field in which most clones lost few or no plants. Except for phytophthora root rot, which is believed to have come to the U.S. after 1492, the serious blueberry pathogens in Florida are probably native, and the native blueberries probably have high levels of horizontal resistance.

The two insect pests that have had the most adverse effect on highbush blueberry production in Florida during the past ten years have been blueberry gall midge (*Dasineura oxycoccana*), which can damage flower buds and inhibit leafing in the spring (4), and flower thrips (*Frankliniella* spp.), which damage flowers and can greatly reduce fruit set. The level of resistance to these pests in the Florida blueberry species has not been studied, but casual observations indicate considerable clonal variation in levels of damage.

5. Ability to maintain high fruit quality in hot weather. Although temperatures are usually favorable for blueberry harvest in north and central Florida during April and early May, high temperatures during harvest occasionally reduce berry firmness, sugar content, and skin pigmentation. Many of the southern highbush blueberry selections seem to surpass the northern highbush cultivars in their ability to maintain high berry quality when temperatures are high during harvest. *Vaccinium darrowi* genes are present in all southern highbush cultivars. *V. darrowi* ripens in June, a hot month in Florida, and is believed to have contributed to the hot-weather tolerance of southern highbush berries.

Summary and Conclusions

Southern highbush cultivars from the Florida Agricultural Experiment Station were developed by many generations of recurrent selection during which genes from northern highbush cultivars were combined with genes from wild Florida blueberry species. Pedigrees indicate that most of the genes in the Florida cultivars came from northern highbush cultivars selected in New Jersey and Michigan. The best of the southern highbush cultivars produce berries that ripen in April and early May in Florida and southeast Georgia and are equivalent in quality to the berries that are harvested during June and July from northern highbush cultivars in New Jersey, Michigan, and the Pacific northwest. However, the cost of production per pound of berries is higher in Florida, in part because the cultivars have lacked vigor, longevity and high productivity. It is hoped that production costs in Florida can be lowered by breeding southern highbush cultivars better adapted to the Florida environment. Further use in breeding of wild *V. corymbosum* and *V. darrowi* selections from Florida and southeastern Georgia should be helpful in reaching this goal.

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