Fertility and Other Characteristics of F₁ and Backcross₁ Progeny from an Intersectional Blueberry Cross [(highbush cultivar × *Vaccinium arboreum*) × highbush cultivar]

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Abstract. Fertility and morphological traits were studied in the F₁ and BC₁ generations of intersectional crosses between tetraploid highbush blueberry cultivars (*Vaccinium* section *Cyanococcus*) and colchicine-induced tetraploid *V. arboreum* (*Vaccinium* section *Batodendron*). The goal of the introgression project was to combine desirable plant characteristics from *V. arboreum* with the large fruit and high fruit quality of highbush cultivars. Highbush × *V. arboreum* crosses were hard to make, but large numbers of BC₁ seedlings were easily obtained using the most fertile F₁ plants as parents in backcrosses to highbush. Anther awns, a character from *V. arboreum*, were present in all F₁ seedlings, but fruit sclerids, another *V. arboreum* trait, were absent in most seedlings. Berry size in the BC₁ generation was twice as large as in the F₁ generation and was twice as large in the F₁ as in *V. arboreum*. The BC₁ generation was extremely variable in vigor and berry quality. Although berries of most BC₁ plants were smaller, darker, and less desirable in texture and flavor than highbush berries, the high fertility of BC₁ plants and the high variability among plants indicate that useful clones could be selected or developed by further breeding.

Cultivated highbush blueberry, which is tetraploid (2n = 4x = 48), was developed by crosses and selection using plants in *Vaccinium* section *Cyanococcus*, including *V. corymbosum* and its close relatives. *Vaccinium arboreum* (section *Batodendron*) is a diploid wild blueberry, native and locally abundant in the southeastern United States. On favorable sites, where fire is infrequent, *V. arboreum* takes the form of a small tree, up to 10 m tall, with diameter at breast height up to 35 cm (Vander Kloet, 1988). In the southeastern United States, *V. arboreum* is used in native-plant landscaping and is valued for its ornamental, bushy, winter form, which is attractive to songbirds. Abundant white flowers are fragrant in springtime, and shiny black berries persist on the tree through fall and early winter.

Highbush blueberry cultivars have been crossed with *V. arboreum* with the long-range goal of obtaining cultivars with new characteristics (Lyrene, 2011). *Vaccinium arboreum* can develop a deep, wide-ranging root system when planted on deep, well-drained soil. A larger root system would

allow blueberry growers to irrigate less frequently and would reduce the amount of irrigation water used annually in areas where heavy rains alternate with dry periods. *Vaccinium arboreum* can tolerate higher soil pH than cultivated highbush blueberries. *Vaccinium arboreum* has long peduncles and pedicels, giving a very open flowering raceme. An open raceme has become more important as blueberry cultivars with larger berries have been developed. Large berries in a tight cluster make hand harvesting difficult and mechanical harvesting almost impossible. Crowded berries in a tight cluster can result in misshaped berries. Ripe berries of highbush blueberry and related species in section *Cyanococcus* have green or white flesh inside the blue or black skins. Native *Vaccinium arboreum* populations in the southeastern United States are polymorphic for internal flesh berry color. Berry flesh of some plants remains green or white when the berries are fully mature. On other plants, berries begin to develop internal anthocyanins at the start of the ripening season, and by the time all the berries on the plant are ripe, the flesh inside the skin is dark purple to black. The dark purple flesh of wild European bilberries (*Vaccinium myrtillus*) has market appeal, because consumers associate the purple color with health benefits. The ability of *V. arboreum* to produce a large plant on a single stem could be used to develop cultivars better suited to mechanical harvest. The late flowering of

V. arboreum (flowers typically open in mid-April and berries ripen in October in north Florida) avoids most spring freezes. Local wild races of tetraploid *V. corymbosum* flower in late February and early March in north Florida and ripen in May. Yields are often reduced by hard freezes in February and early March. Late-ripening blueberries are not of commercial interest in Florida but might be grown profitably for October harvest in states farther north. Home-garden blueberries that ripen in September and October in the southeastern United States, and are larger and more palatable than the berries of *V. arboreum*, would be valuable for gardeners and for wildlife. *Vaccinium arboreum* produces numerous berries, but these are small and scarcely edible. They contain large seeds and sclerids and have a dry and gritty texture. Berries from some plants are sweet, but sparkleberries are often astringent or have a “grassy” taste.

Two barriers make it hard to cross cultivated highbush blueberries with *V. arboreum*. First, the cultivars are tetraploid and *V. arboreum* diploid. The triploid block is strong in *Vaccinium*, and if the diploid parent makes few or no unreduced gametes, as seems to be the case with *V. arboreum*, few hybrids are obtained from crosses between diploids and tetraploids. The second barrier is the evolutionary divergence that separates section *Cyanococcus* from section *Batodendron*. This barrier is not highly restrictive; crosses between diploid *V. darrowii* of section *Cyanococcus* and *V. arboreum* give hybrids rather easily (Brooks and Lyrene, 1998; Chavez and Lyrene, 2010). Some of these diploid hybrids are vigorous and flower heavily but are sterile, except that they make a few unreduced gametes, which allow them to be crossed with tetraploid cultivars. Some BC₂ and BC₃ (backcrosses were to highbush cultivars) selections that were grown for 10 years in 15-plant field plots were vigorous, early-ripening, and produced berries of commercial quality. The success of the crosses that used *V. darrowii* as a bridge to bring *V. arboreum* genes into highbush cultivars made it seem desirable to attempt direct crosses between the cultivars and *V. arboreum*. We attempted such crosses with several thousand highbush flowers pollinated in several different years and obtained no seedlings. Subsequently, over a period of eight years, we treated thousands of *V. arboreum* seeds with colchicine as a pre-germination seed soak and selected plants that looked like they might be tetraploid. Initial selection was by seedling morphology, and the retained seedlings were re-selected when they flowered based on the size of pollen tetrads. Information on these crosses has been published (Lyrene, 2011). I report the results of intercrossing 34 BC₁ seedlings and present information on the phenotypes of F₁ and BC₁ plants.

Materials and Methods

Vaccinium arboreum parents FL 06-730 and FL 06-753 were selected from plants

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grown from colchicine-treated seed because they produced unusually large pollen tetrads. In 2007, crosses were made by pollinating flowers of 16 southern highbush cultivars with pollen from either FL 06-730 or FL 06-753 (Lyrene, 2011). Additional F₁ hybrids were made in 2008 using different highbush parents and the same two *V. arboreum* plants. Seedlings were grown in a field nursery, and 450 seedlings from the first year's crosses were verified as F₁ hybrids in late winter, 2009, based on morphology after one growing season in the field. Hybrids were easily distinguished from non-hybrids based on leaf shape and color, on the appearance of bark on one-year-old wood, and on the presence or absence of obvious flower buds in mid-winter. Highbush seedlings that flowered in the spring had large, conspicuous flower buds by midwinter, whereas F₁ hybrids that flowered in the spring showed no indication of flower buds until 1 or 2 weeks before the corollas became visible. When they flowered, hybrids were confirmed by raceme morphology and by the presence of anther awns (Camp, 1945). Anther awns are absent in section *Cyanococcus*, present in section *Batodendron*, and were present (although reduced in size) on the anthers of all F₁ hybrids that were examined.

In Feb. and Mar. of 2009 and 2010, 57 F₁ plants were selected for use in backcrosses to highbush cultivars. The plants were selected because they were vigorous, had the most flower buds after one growing season in the field, shed the most pollen, and had pollen that appeared, under the microscope, to include at least some potentially viable microspores. The selected F₁ plants included one or more seedlings from each of the crosses 'Lenoir' × *V. arboreum* 'FL06-753' and 'Carteret' × *V. arboreum* 'FL06-753' plus one or more seedlings from each of 11 crosses of highbush × *V. arboreum* 'FL06-730', where the highbush parents were 'Abundance', 'Bluecrisp', 'Brigitta', 'Jewel', 'Scintilla', 'Springhigh', 'FL95-50', 'FL95-138', 'FL01-151', 'FL01-297', and 'FL06-526'. The selected F₁ plants were dug, potted, and moved to a bee-proof greenhouse. Each F₁ plant was crossed with one highbush clone that was not one of its parents. Seeds from these backcrosses were sown in a greenhouse in Nov. 2009, and the seedlings were transplanted to a field nursery in Apr. 2010. The number of seedlings transplanted to the field nursery varied from cross to cross depending on the number of seeds that germinated and the vigor of the seedlings in the greenhouse grow-on trays. For each of nine crosses, 200 to 300 BC₁ seedlings were transplanted to the field. For each of 10 additional crosses, 50 to 100 seedlings were transplanted. For the nine crosses having the fewest seedlings, five to 15 seedlings per cross were placed in the field.

In Feb. and Mar. 2011, 37 BC₁ plants were selected from the field based on high vigor and the presence of visible flower buds. These were potted and moved to a greenhouse. When the BC₁ plants flowered, 100 to

200 flowers on each plant were emasculated and pollinated with pollen from a different BC₁ plant. BC₁ plants were assigned to crosses in such a way that each seedling from the crosses would have two different *V. arboreum* plants (FL 06-730 and FL 06-753) in its ancestry. All BC₁ plants were verified as the intended hybrids based on raceme morphology, the presence of anther awns, and on many other morphological features, particularly features related to flower morphology and bark structure. The parent species are so distinct that the validity of the F₁ hybrids and BC₁ plants was beyond doubt. Fertility data for F₁ plants were obtained in 2007 and 2008 and for BC₁ plants in 2011. In all three years, the crosses were made in the same greenhouse by the same worker using the same techniques. The plants used as female parents were of similar age and size each year and were dug from the same field nurseries. Conditions for fruit set in the greenhouse were good in all three years, as indicated by the fact that numerous highbush cultivar × highbush cultivar crosses made each year in the same greenhouse gave high fruit set and berries with many seeds. Flower thrips (*Frankliniella* spp.) and other pests that can interfere with fruit set were eliminated with insecticides. Fertility of F₁ and BC₁ plants was estimated in three ways: 1) percent good microspores: 100 microspores were examined at 250× using pollen tetrads shed from flowers gathered from the greenhouse. The percentage of the microspores that appeared well formed and potentially viable was recorded; 2) percent fruit set in crosses. One hundred to 200 flowers were emasculated and pollinated on each plant. F₁ plants were pollinated with pollen from highbush cultivars that were not closely related to their highbush parent. The F₁ plants used in crosses were not a random sample of all F₁ plants; they had been selected for high vigor in the field and for having above-normal male fertility as judged by the amount of pollen shed and by microscopic examination of the pollen. The BC₁ plants used in crosses were selected only for high vigor in the field and for having enough flower buds for use in crosses. They were not selected for high pollen fertility; and 3) number of well-developed seeds in the first 10 berries that ripened on each plant. The first ripe berries are usually the largest and have the most seed. Each berry was individually opened and the well-developed seeds were counted. Based on previous experience with blueberry seeds from many crosses, it is thought that most of the counted seeds were capable of germinating. The seeds of most crosses were sown and gave excellent germination.

Several phenotypic characteristics were examined for each F₁ and BC₁ plant used as a female parent. The average weight of the first 10 berries harvested from each plant was recorded. Flowers were examined for anther awns (Camp, 1945), because anther awns are a key character separating section *Cyanococcus* (no anther awns) from section *Batodendron* (anther awns present). The berries were

examined for presence or absence of sclerids, which are conspicuous in *V. arboreum* and not noticeable in highbush blueberry. Fruit color, flavor, picking scar, and firmness were noted for each plant used as a female parent.

Results and Discussion

The two *V. arboreum* plants used in crosses shed an abundance of pollen, and the pollen appeared to be well formed under the microscope, but the success rate for obtaining hybrid seedlings when this pollen was placed on stigmas of highbush cultivars was low (Lyrene, 2011). To produce several hundred verified F₁ hybrid seedlings, tens of thousands of highbush flowers were pollinated in this study and in highbush × *V. arboreum* crosses made later using other tetraploid *V. arboreum* plants. These crosses gave far fewer hybrids per pollinated flower than analogous intersectional hybrids made at the diploid level (*V. darrowii* section *Cyanococcus* × *V. arboreum*; Lyrene, 1991). Colchicine-derived autotetraploids produce numerous aneuploid gametes (Crane and Lawrence, 1952; Hagberg and Ellerstrom, 1959; Sanford, 1983). Nonfunctional aneuploid gametes may have reduced the fertility of the tetraploid *V. arboreum* parents.

More than half of the F₁ hybrids obtained in this study were weak and died in the field nurseries before they flowered. Other seedlings flowered but were not vigorous; still others were highly vigorous. Some crosses produced only weak hybrids; others that involved different highbush cultivar parents but the same *V. arboreum* parents produced mostly vigorous hybrids.

It was easy to obtain large numbers of BC₁ seedlings by crossing the most fertile F₁ hybrids, either as pollen or seed parent, with highbush cultivars. As would be expected, seedlings of the BC₁ generation were extremely variable in vigor and morphology. Some plants were more vigorous than typical highbush seedlings after three years in the field; others were relatively weak. Many of the F₁ and some BC₁ seedlings were more susceptible to powdery mildew [*Microspheera penicillata* var. *vaccinii* (Schw.) Cooke] and other leaf diseases than typical highbush seedlings. Leaves of both F₁ and BC₁ plants tended to be shiny green or green with an orange or golden cast, and most lacked the blue and gray hues common in the summer leaves of highbush seedlings. Flowering racemes of most F₁ seedlings and of many BC₁ seedlings were long and flower and berry clusters were unusually open with long pedicels and peduncles, a characteristic from *V. arboreum*. Anther awns were present, although much reduced in size, in most but not all BC₁ plants.

Berry weight in the F₁ generation averaged approximately twice that of typical *V. arboreum* (data not shown) but was much closer to *V. arboreum* than to the highbush cultivar parents. Berry weight in the BC₁ generation averaged almost exactly twice that in the F₁ generation (Table 1). Still,

Table 1. Three measures of fertility in plants of the F₁ and BC₁^z generations from highbush cultivar × *V. arboreum* crosses and mean weight of the first 10 berries that ripened on each plant.^y

	Good pollen (%) ^x		Fruit set (%) ^w		Seeds per berry (no.) ^v		Berry wt (g) ^y	
	F ₁	BC ₁	F ₁	BC ₁	F ₁	BC ₁	F ₁	BC ₁
N ^u	86	37	38	34	29	34	28	34
Mean	39.7	70.3****	38.4	61.8***	7.79	22.2***	0.83	1.74***
Median ^a	40	70	34	59	7.0	20.8	0.79	1.67
Highest plant	98	98	100 ^r	85.0	17.2	51.2	1.67	2.80
Second highest	98	98	100 ^r	83.6	15.2	40.1	1.50	2.43
Third highest	98	95	74.3	81.8	14.6	38.2	1.22	2.41
Lowest plant	0	20	0	35.3	1.3	8.6	0.38	0.98
Second lowest	0	20	0	36.9	1.4	9.3	0.39	1.02
Third lowest	0	40	0	42.1	1.5	10.0	0.52	1.06
SD	28.15	23.30	27.07	13.77	4.56	9.523	0.305	0.468

^xBackcrosses were made by crossing F₁ hybrids back to highbush cultivars. The cultivar used in the backcross was always different from the one used to make the F₁ hybrid.

^yTo get the fruit set and berry data, each F₁ plant was pollinated with pollen from one unrelated highbush cultivar and each BC₁ plant was pollinated with pollen from one unrelated BC₁ plant.

^vBased on 100 microspores viewed at 250×.

^wBased on 100 to 200 flowers per plant emasculated and hand-pollinated in a greenhouse.

^zBased on the first 10 berries to ripen on each plant, a total of 290 berries from F₁ plants and 340 from BC₁ plants. The first berries tend to be largest and have the most seeds. Only seeds that appeared to be plump and viable were counted.

^uNumber of plants on which the data in each column are based.

^aIndicates that the means of the F₁ and BC₁ populations differ at *P* = 0.001 according to the *t* test. Percentage data were transformed by the arcsin square root transformation to calculate *t*.

^rHalf of the seedlings were above this value and half were below.

^sSome of the berries in this cross and probably some of the berries in other crosses were seedless.

berries from BC₁ seedlings that were open-pollinated in field plots were usually smaller than those typical of seedlings from highbush × highbush crosses (data not shown). Berries of the F₁ plants were mostly shiny black, although a few showed traces of the epicuticular wax that gives many highbush blueberries their powdery blue color. Most BC₁ seedlings also had dark fruit, but traces of wax were more common than in the F₁. The berries of most F₁ plants derived from FL 06-730 and FL 06-753 (more than 100 seedlings examined) were free of obvious sclerids, but some F₁ hybrids produced subsequently, using other *V. arboreum* clones as parents, have had sclerids. Sclerids were not apparent in the berries of any BC₁ seedlings in this study. Picking scar and berry firmness in most F₁ and BC₁ plants were as good as in seedlings from highbush blueberry cultivars. Berry post-harvest characteristics were not studied. When tasted, berries of most F₁ and BC₁ plants had both sugars and acids. Berries from some, but not all, plants had an unpleasant “grassy” flavor with traces of astringency in some. Berries of some plants in both generations had a pasty, dry texture, but others seemed quite juicy. Berry flavor and texture in most BC₁ seedlings were inferior to that of the highbush cultivar parents but much better than that of *V. arboreum*. *V. arboreum* in Florida is polymorphic with respect to the amount of visible anthocyanin in the flesh (as opposed to the skin) of the mature berries. The two *V. arboreum* plants used in these crosses lacked visible flesh anthocyanin as did the highbush parents and all the hybrid progeny.

The 86 F₁ seedlings for which pollen was examined under the microscope ranged from 0% to 98% in percentage of the individual microspores that appeared well developed

and potentially viable (Table 1). The median value for these plants was 40% and the mean 39.7%. Two of the F₁ plants that were completely male-sterile were placed outside among flowering highbush plants the next year, and both set a full crop of seedy berries. Of the 38 F₁ seedlings that were hand-pollinated with highbush pollen in the greenhouse, fruit set averaged 38.4% and ranged from 0% to 100% for individual plants (Table 1). The number of well-developed seeds per pollinated flower averaged 7.8. This compares with an average of more than 26 large seeds per berry obtained in 74 highbush cultivar × highbush cultivar crosses made in the Florida blueberry breeding program (Chavez and Lyrene, 2009). Some fertility reduction in the F₁ seedlings could be explained by aneuploidy resulting from aneuploid gametes from the colchicoid *V. arboreum* parents. Burnham (1962) reviewed four studies of chromosome numbers in progeny of colchicine-induced tetraploid maize. On average, only 60% of the progeny were exactly tetraploid. Most of the other progeny lacked one or two chromosomes.

Percent well-developed microspores averaged much higher for the BC₁ seedlings than for the F₁ seedlings (Table 1). Comparisons of the fertility of the F₁ and BC₁ generations as deduced from the crosses are complicated by the fact that the crosses were made in different years and the pollen placed on the stigmas of the F₁ plants was from highbush cultivars and that used in the BC₁ × BC₁ crosses was from BC₁ seedlings.

In the crosses, percent fruit set and number of well-developed seeds per berry were much higher in the BC₁ × BC₁ crosses than in the F₁ × highbush crosses. The highbush cultivars used to pollinate the F₁ seedlings typically produce 95% to 99% well-developed

microspores, whereas the BC₁ plants used in the BC₁ × F₁ crosses averaged only 70.3% well-developed pollen. Despite this, fruit set and seed number were higher in the BC₁ than in the F₁. Taken as a whole, the data indicate that the BC₁ plants are more fertile than their F₁ parents.

Of the hundreds of different crosses that were made in this hybridization project, only part of which are described here, the least productive (measured as number of seedlings per 100 pollinated flowers) have been highbush cultivar × tetraploid *V. arboreum*. Pollinations of F₁ hybrids with highbush pollen were far more productive, and pollinations of BC₁ plants with either highbush pollen or with pollen from other BC₁ plants produced the most seedlings. In 2012 we made five crosses to generate BC₂ seedlings. These crosses gave high fruit set and high seed numbers per berry, but along with the good seeds were many small, underdeveloped seeds. Similar underdeveloped seeds are found with the good seeds from most highbush × highbush crosses, so those found in the BC₂ were not necessarily the result of *V. arboreum* introgression. Pollination of flowers on F₁ hybrids with pollen from tetraploid *V. arboreum* was attempted in 12 crosses. Most of these crosses gave few fruit and seed, but from each of three crosses, each with several hundred flowers pollinated, several hundred seedlings were obtained. Backcrossing F₁ hybrids to tetraploid *V. arboreum* was harder than backcrossing them to highbush. The results of the *V. arboreum* backcrosses were highly dependent on both the highbush and the *V. arboreum* plants used as parents.

Crosses among species within *Vaccinium* section *Cyanococcus*, and autotetraploid segregation ratios of genes in the tetraploid species of *Cyanococcus*, indicate that chromosomes of the species within the section are homologous and do not show preferential pairing (Qu et al., 1998). The high sterility of diploid intersectional hybrids between sections *Cyanococcus* and *Batodendron* (examples are *V. darrowii* × *V. arboreum* and *V. elliottii* × *V. arboreum*) suggested that chromosomes from these sections might pair poorly in diploid F₁ hybrids and produce irregular anaphase separations during meiosis. Tetraploid intersectional hybrids would be expected to have two sets of homologous chromosomes from each section. This should enable reliable chromosome pairing and anaphase separation and could account for the increased fertility of the tetraploid hybrids (Lyrene and Olmstead, 2012). Accurate chromosome segregation during meiosis depends on crossing over between paired homologous chromosomes (Crismani et al., 2012). Rousi (1966) thought the surprisingly high fertility of intersectional F₁ hybrids between highbush blueberry and tetraploid *V. uliginosum* (section *Vaccinium*) was possible because each parent had contributed two sets of chromosomes to the hybrids and these like sets paired with each other. If this mechanism were operating in the crosses reported here,

the BC₁ hybrids should be less fertile than F₁ hybrids because they would have three sets of chromosomes from one section and only one from the other (Hiirsalmi, 1977). Instead, the BC₁ hybrids appear to be more fertile, implying that genic rather than chromosomal factors account for the increase in fertility in the BC₁ generation.

It is too soon to judge the extent to which desirable *V. arboreum* characteristics are present in the F₁ and BC₁ hybrid seedlings. Neither of the *V. arboreum* plants used in the initial crosses had much internal berry pigmentation, and fruit of the hybrids was green to white inside. Nearly all the F₁ seedlings and many BC₁ seedlings had longer peduncles and pedicels than is typical for highbush cultivars. Many of the F₁ seedlings and some BC₁ seedlings were exceptionally upright in growth habit. In Jan. 2011, more than 1300 BC₁ seedlings and 1900 highbush seedlings of the same age were transplanted from a high-density field nursery, where they had been planted as small seedlings the previous April to a test field at 1 m × 3 m spacing. Despite tremendous variation in vigor among the BC₁ seedlings, it was obvious when the plants were being dug that the roots of the BC₁ plants had spread more widely than the roots of highbush seedlings that were similar in size aboveground.

Our data support Ballington's (2001) observation on *Vaccinium* hybrids: "Cytogenetic and morphological irregularities are often evident to varying degrees with tetraploid intersectional hybrids; however, fertility and normal morphological development can

sometimes be restored with backcrossing, as in the case of *V. corymbosum* × *V. uliginosum* (section *Vaccinium*) crosses." Ballington cited the example of the Finnish blueberry cultivar Aron, which was derived by backcrossing the F₁ intersectional hybrid *V. uliginosum* × *V. corymbosum* to *V. corymbosum*. Whatever the reasons for the fertility, the fact that many BC₁ seedlings are quite fertile indicates that genes from *V. arboreum* and highbush blueberry cultivars can be brought together to produce potentially useful clones. Producing clones with desirable combinations of characteristics will probably require several generations of recurrent selection, starting with BC₁ or F₂ plants depending on the objectives, selecting parents in each generation that are nearest the desired type.

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