Fruit Varieties Journal 44(2):54-62 1990

Germplasm Resources Available to Meet Future Needs for Blueberry Cultivar Improvement[1]

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The genus *Vaccinium* (blueberries, cranberries, bilberries, lingonberries) occurs on all continents except Australia and Antarctica (41). It also occurs on many islands and island groups. Wherever species occur, they readily colonize disturbed habitats during early stages of succession (44) and so are weeds in the ecological sense (i.e. pioneers of secondary succession). Distribution of species in nature is limited by the fact that they are acidophiles, largely intolerant of dense shade, and require light for seed germination (13, 20). Therefore continual opening up of appropriate disturbed habitats is essential for the long term perpetuation of species.

Worldwide, *Vaccinium* includes approximately 400 species and is most abundant in the montane tropics (41). The center of origin of the genus is believed to be northern South America, however the greatest concentration of species is currently in New Guinea. In North America, north of Mexico, the genus includes 10 sections (subgenera) (3). At the present time blueberries grown commercially for fruit production in temperate and subtropical regions are all derived from species or interspecific hybrids in *Vaccinium* section *Cyanococcus*, the true or cluster-fruited blueberries, which are largely restricted to acid soil regions throughout the eastern half of North America.

The true blueberries include from 10 to 26 species depending on taxonomic viewpoint (14, 42, 43, 44, 45). This results in a great deal of disagreement on species delimitation, mainly in regard to crown-forming species. There is a high incidence of polyploidy in *Vaccinium*, and species in section *Cyanococcus* occur at the diploid (2n = 2X = 24), tetraploid (2n = 4X = 48), and hexaploid (2n = 6X = 72) levels (13). The cultivated types are all polyploids. Rabbiteye blueberry is hexaploid, while standard highbush, southern (low-chilling) highbush, lowbush, and half-high cultivars are tetraploid.

Four species [sensu. Vander Kloet 1972 (42)], *V. angustifolium* Ait. (lowbush blueberry — 2n = 4X = 48), *V. ashei* Reade (rabbiteye blueberry — 2n = 6X = 72), *V. corymbosum* L [highbush blueberry — (2n = 4X = 48 forms)], and *V. darrowi* Camp (Darrow's evergreen blueberry — 2n = 2X = 24), have provided the majority of the germplasm utilized up to this time in cultivar development. The contributions of *V. darrowi* to cultivated blueberries have been possible because selected clones of this diploid species produce unreduced gametes.

The Gene Pool in Cultivated Blueberries

The germplasm base in highbush and rabbiteye blueberries is very narrow. Hancock and Siefker (24) determined that most of the nuclear genes in present highbush cultivars were contributed from the three native

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selections, 'Brooks,' 'Sooy,' and 'Rubel.' Likewise, seven of the 10 tetraploid cultivars which include *V. darrowi* germplasm in their background trace back to a single clone, 'Fla. 4-B.' A similar situation exists with rabbiteye cultivars where almost all of the nuclear genes were derived from four original wild selections, 'Myers,' 'Black Giant,' 'Ethel,' and 'Clara.'

A 1986 survey of diversity of cytoplasms in 50 tetraploid cultivars found that only four different cytoplasms were involved; two of those, 'Fla. 4-B' and 'North Sedgwick,' were represented by single cultivars (22). Since 1986 two additional cultivars, 'Cape Fear' and 'Sierra,' have been released that have 'Fla. 4-B' cytoplasm. In addition, 'Georgiagem,' released in 1986, has cytoplasm from 'Ashworth,' a clone of *V. corymbosum*. The cytoplasms of the most widely planted highbush cultivars in the U.S. were either 'Brooks' or 'Rubel' (22). A review of rabbiteye cultivars, where the female parent is known, shows that only three cytoplasms are involved. The cytoplasm of 'Centurion' comes from 'W-4,' while the cytoplasms of all other rabbiteye cultivars come from either 'Ethel' or 'Myers.'

The increased inbreeding accompanying consecutive generations of recombination within these narrow germplasm bases has been effective in concentrating desirable blocks of genes or gene combinations in single genotypes. However, inbreeding depression results in reduced plant vigor and fruit weight in highly inbred material in *Vaccinium* (25). Therefore, inbreeding within the present standard cultivated highbush and rabbiteye gene pools is probably severe enough to slow breeding progress.

Lack of diversity in the cultivated rabbiteye and highbush gene pools is also potentially disastrous from the standpoint of genetic vulnerability. Hancock and Krebs (22) suggested that the highbush blueberry industry could be seriously at risk from pathogen attack if cytoplasmic resistance ever becomes important. The same situation is also true for rabbiteye blueberries.

Genetic vulnerability in lowbush blueberries as currently established in native stands consisting of a mixture of many genotypes is not a serious concern. However, the advent of widespread establishment of lowbush fields utilizing a small number of elite clones could drastically change this situation.

In recent years blueberry breeders have made a conscious effort to broaden the germplasm base (or initiate programs with a fairly broad base) with the various cultivated types (2, 8, 17, 29, 31). This is evident in recent tetraploid cultivar releases. However, it is apparent that much greater efforts are needed, particularly in broadening cytoplasmic diversity.

Desired Characteristics in Future Cultivars

Previous reports have documented the recent changes in and current status of the various types of blueberries grown in North America, along with major and promising new cultivars in each production region. It is significant that 20 new cultivars have been released in recent years. These new cultivars represent improvements in fruit quality, fruit size, reliability of cropping, productivity, pest tolerance, broadened soil adaptation, and extension of the fruiting season. These cultivars are expected to complement or, in some cases, replace standard cultivars. The potential of the southern (low-chill) highbush and half-high types is particularly exciting because they have made possible the expansion of "highbush type" blueberry culture into more southern and northern regions, respectively.

The next question is what characteristics will be essential in cultivars of the future if the blueberry industry is to continue to thrive. Fruit and plant characteristics usually included in evaluation of potential cultivars were summarized by Galletta (20), and it is doubtful that any of these characteristics will be de-emphasized in the future. However, there are a number of characteristics that will be essential in future commercial cultivars, and thus should receive greatly increased emphasis. These are pest resistance, tolerance or resistance to environmental stresses, and adaptation to mechanized management.

Increasing restrictions on pesticide usage and dimmed prospects for new pesticide registrations for blueberries necessitate identifying genetic sources of resistance to major insects, mites, and diseases and incorporating these genes into commercial cultivars as rapidly as resources and personnel will permit. This will require major, sustained, efforts by teams of researchers, will involve interspecific and perhaps sectional hybridization in a number of cases, and in some instances, if genes for resistance do not appear to exist in *Vaccinium*, may involve the techniques of biotechnology. Disease problems of greatest concern (i.e. requiring the most immediate attention) include mummy berry and monilinia blight [*Monilinia vaccinii-corymbosum* Reade (Honey)], blueberry stunt (blueberry stunt mycoplasma), blueberry shoestring virus, stem blight [*Botryosphaeria dothidea* (Mouq. ex Fr.) Ces. & de Not.], stem canker [*Botryosphaeria corticis* (Demaree & Wilcox) Arx & Muller], and botrytis blight and fruit rot (*Botrytis cinerea* Ters. ex Fr.).[3] Insects of greatest concern include the blueberry maggot (*Rhagoletis pomonella* Walsh), sharp-nosed leafhopper (blueberry stunt vector) (*Staphytopius magdalensis* Prov.), blueberry aphid (shoestring virus vector) (*Illinoia pepperi* Mac. G.), cranberry fruit worm (*Mineola vaccinii* Riley), cherry fruit worm (*Grapholitha packardi* Zell), and plum curculio (*Conotrachelus nenuphar* Herbst.).[3]

Frost and freezing temperatures during and following bloom often seriously reduce yields of all types of blueberries and in all production areas (21, 23). Incorporation of genes for either delayed bloom (to avoid frost and freeze injury) and/or for tolerance to low temperatures during and following bloom are needed to assure regular annual cropping. In all northern production regions tolerance of flower buds to low temperatures during the dormant season is especially needed (19). Adaptation of "highbush type" cultivars to upland mineral soils could be potentially important if blueberry culture continues to expand at the present rate. Korcak et al. (28) demonstrated that hybrid seedlings from a number of different genetic backgrounds including *V. angustifolium*, *V. ashei*, *V. darrowi*, and also *V. corymbosum*, could be selected for adaptation to mineral soils. Adaptation to mechanized management, particularly pruning and harvesting, is rapidly being necessitated by shortages of hand labor and the rising labor costs. Mechanical harvesting for processing outlets has been a standard commercial practice in most highbush and rabbiteye production areas for many years (20). When grown under cool climatic conditions, selected highbush cultivars can be harvested mechanically for the fresh market outlets. Rabbiteye cultivars are also reasonably well adapted to mechanical harvesting for the fresh market (3). However, major efforts are now required to develop highbush (and perhaps lowbush) cultivars which possess all the necessary plant and fruit characteristics for successful mechanical harvesting for the fresh market. Plant architecture and resistance to cane diseases must be considered along with fruit characteristics in

[3]Genetic Vulnerability Statement on Cultivated *Vaccinium* in North America, Small Fruits Crop Advisory Committee.

breeding for adaptation to mechanical harvesting (20). Plant architecture, vigor, and precocious flower bud formation are also very important selection criteria in breeding for adaptation to mechanical pruning.

Based on Galletta (20), the ideal highbush or rabbiteye cultivar for mechanical harvesting and pruning would possesss the following characteristics: moderate vigor; at least a moderate number of narrowly-upright canes (suitable for training in a narrow hedgerow); a large number of flower buds/cane; a high level of resistance to wound pathogens (to withstand cane injury during harvesting operations); small to moderate fruit size (1.0 to 1.5 g); very light blue fruit color; a very small picking scar; loose fruit clusters; moderate ease of fruit removal; crisp flesh texture and superior firmness; a moderately tough but elastic skin on the fruit; and a desirable sugar/acids ratio to assure extended shelf-life of fruit. For lowbush cultivars, maximization of the number of fully erect fruiting shoots per unit surface area and synchronous ripening would appear to be essential, along with the fruit characteristics listed for highbush and rabbiteye.

Germplasm Resources Available to Meet Future Needs

In recent years there has been a much increased awareness of potential genetic vulnerabilities and other problems associated with a narrow germplasm base in cultivated crops. Serious economic losses in major crops such as maize brought this sharply into focus (1). A number of organized plant explorations have been carried out during the last 20 years (particularly in the last 10 years) to increase the amount and diversity of *Vaccinium* germplasm available, and these materials (mainly seeds) have often been deposited with the National Clonal Germplasm Repository, Corvallis, Oregon, for long-term maintenance. However, the materials maintained at the Repository, as well as those in the working collections of breeding programs, by no means represent a significant percentage of the germplasm available. Therefore, what germplasm resources are available to meet future needs for blueberry cultivar improvement?

Lyrene and Ballington (30) pointed out the *Vaccinium* germplasm resources fall into three categories referred to as primary, secondary, and tertiary gene pools.

There is a primary gene pool within each of the main cultivated types. Thus the primary gene pool for lowbush and rabbiteye blueberries consists of *V. angustifolium* and *V. ashei*. respectively. For standard and southern highbush blueberry the primary gene pool consists of tetraploid genotypes of wild and cultivated *V. corymbosum*. Half-high blueberry cultivars present a different situation in that both *V. angustifolium* and *V. corymbosum* are major components (29). In this case the primary gene pool involves two completely interfertile species (16).

The range of tetraploid *V. corymbosum* extends from southern Canada across to Michigan, and southward into east Texas and Florida (42), and within this range literally millions of genotypes occur in the wild (37). Approximately the same situation exists for *V. angustifolium* within its range in eastern Canada and the northeastern and Great Lakes areas in the United States (42). The range of *V. ashei* in the wild is more restricted. Originally this species occurred only in southern Georgia, northern Florida, and southeastern Alabama (14). However, *V. ashei* is very adaptable and escaped plants from commercial plantings, which were made in the early part of the 20th Century, and later abandoned, have become established in the wild as far west as Mississippi, and at least as far north as Geogetown County, South Carolina (10). Thus *V. ashei* germplasm resources, while perhaps not on the same scale as *V. angustifolium* and *V. corymbosum*, are still quite extensive and appear to be increasing.

Blueberry breeders have the potential of almost seemingly unlimited genetic resources in the primary gene pool of the cultivated species. Both the diversity, and in some cases lack of diversity, in these gene pools is very interesting, as illustrated by the following examples. Most of the characteristics desired in cultivars adapted to mechanical management appear to occur in both *V. corymbosum* and *V. ashei* (20). Genes for large fruit size apparently occur throughout the range of tetraploid *V. corymbosum*. From 1978 through 1984 elite germplasm for large fruit size was collected in southern Georgia, southeastern and south central North Carolina, and southern Michigan (9, 10, 11). Genes for large fruit size appear to be more widespread in populations of *V. ashei* from west Florida than in populations from southern Georgia (6, 11). Genes for upland adaptation occur in *V. angustifolium*, *V. ashei*, and also in *V. corymbosum* (9, 10, 11, 20). Genes for early ripening occur in *V. angustifolium*; however, in one study involving native tetraploid *V. corymbosum* populations from New Jersey, North Carolina, and northern Florida, there was no variation for early ripening (4). Likewise, no variation for nonpreference feeding resistance to the sharp-nosed leafhopper (blueberry stunt vector) has been observed in either wild or cultivated *V. corymbosum*, while a wide range in resistance occurs in *V. ashei* (18, Meyer & Ballington—Annals Ent.—In press). Genes for resistance to mummy berry are known to occur in cultivated and wild *V. corymbosum*, and resistance to stem canker in wild and cultivated *V. corymbosum* and *V. ashei* (20). Keeping abreast of the appearance of new races of the stem canker fungus complicates breeding for resistance (15, 35). No variation for resistance to stem blight has been found in wild *V. corymbosum*, but it does occur in cultivated *V. corymbosum*, and *V. ashei* and *V. angustifolium* (12, 34, Buckley & Ballington—In preparation).

For each of the cultivated blueberry types there is a secondary gene pool made up of the other species in *Vaccinium* section *Cyanococcus*. For example, *V. angustifolium* would be in the secondary gene pool for standard highbush and *V. darrowi* [or *V. elliottii* Chap. (2n = 2X = 24), *V. myrsinites* Lam. (2n = 4X = 48), or *V. ashei*] for southern highbush. Species diversity and abundance in the secondary gene pool are also extremely great. Examples of species in this gene pool which have contributed to, or are promising for incorporation of genes into, cultivated blueberries are as follows:

Vaccinium darrowi is a main secondary gene pool species involved in all present southern highbush cultivars. It has contributed genes for drought and heat tolerance (36), superior fruit quality and fruit firmness under warm humid conditions (2, 6, 20). This species is abundant on dry sandy uplands throughout much of Florida, and also occurs in southern Georgia, southeastern Alabama, and along the Gulf Coast in Louisiana (42).

Vaccinium elliottii is a fairly wide ranging crown-forming species of southern latitudes with an extremely broad ecological amplitude (11, 14, 42). It is adapted to a wide range of soils from droughty sands to heavy clays (11), and is notable for high acid flavor, a favorable soluble solids/acids ratio, a very small picking scar, and for ease of fruit removal (6). These last three traits are very important for adaptation to mechanical harvesting. This species also exhibits a wide range of resistance to the sharp-nosed leafhopper and the stem blight fungus (12, Meyer & Ballington, Annals Ent.—In press).

Vaccinium simulatum Small (2n = 4X = 48) is a crown-forming species of intermediate to high elevations in the Appalachians, ranging from northern Alabama and Georgia to Kentucky and West Virginia (14). It is well adapted to upland soils and produces a deep root system even on clay soils (11). Plant height averages from 4 to 6 m, and dormant buds must be extremely hardy, considering that plants crop regularly on exposed sites at 2000 m elevation. The fruit has a pleasant subacid to acid flavor, and is quite variable for traits such as color and size. The range in fruit size is equal to wild tetraploid *V. corymbosum* (9). Vander Kloet (42, 44) includes this taxon in *V. corymbosum*, and admittedly, it is difficult, if not impossible, to separate the two based on plant, leaf and fruit morphology in summer (9). However, the two are distinct in phenological development, and based on systematic crosses among three clones of each species, and attempts at intercrossing *V. simulatum* with cultivated *V. corymbosum*, they do not appear to be fully interfertile (Ballington—unpublished). In addition, they are distinct for percentage of individual anthocyanins in fruits (5). Therefore, it appears that *V. simulatum* and *V. corymbosum* are distinct gene pools. *Vaccinium simulatum* could easily become the primary gene pool for an additional type of cultivated blueberry for the Appalachian region. It also has potential as a source of bud hardiness and upland adaptation in northern growing regions.

Two hexaploid species *V. amoenum* Ait. (2n = 6X = 72) and *V. constablaei* Gray (2n = 6X = 72) continue to show great promise in the secondary gene pool of *V. ashei* (2, 8). *Vaccinium amoenum* has contributed genes for improved fruit quality and mineral soil adaptation, and *V. constablaei*, genes for delayed bloom, short bloom to ripe period, and improved winter hardiness. Intercrosses of F_1's among *V. constablaei* and *V. ashei* produced seedlings blooming later than and ripening with the standard mid-early North Carolina highbush cultivar 'Croatan' (8). Hybrids among *V. amoenum* and *V. constablaei* also combine many of the desirable traits of both species.

Finally, diploid populations of *V. corymbosum* (sensu, Vander Kloet 1972) represent a distinct gene pool that has only been used in genetic and taxonomic studies (7, 32, 33, 42, 44). yet the populations making up this gene pool are even more numerous and widely-occurring on a broader range of habitats than tetraploid *V. corymbosum* (10, 44). Therefore, diploid *V. corymbosum* represents a potentially valuable and virtually untapped resource for blueberry improvement.

With the secondary gene pool the concepts of homoploid (within ploidy level) and heteroploid (between ploidy levels) interfertility become significant. Camp (13) indicated that there appear to be no fundamental sterility barriers between members of the same phyletic section in *Vaccinium* so long as they have the same chromosome number. While the idea of complete homoploid interfertility has been disputed by several workers (7, 44), it does appear that if a fairly large number of parents are utilized in any homoploid interspecific combination, it is likely that one or more combinations will be successful. Complete homoploid interfertility between *V. angustifolium* and 4X *V. corymbosum* has already been noted (16); therefore, transfer of resistance to stem blight from *V. angustifolium* to *V. corymbosum* may be facilitated almost as readily as between cultivated *V. corymbosum* parents.

Heteroploid crosses in *Vaccinium* are generally much less successful than homoploid crosses (30). However, certain clones in most diploid section *Cyanococcus* species produce some unreduced gametes making 2X-4X combinations feasible (7, 31, 33, 44). Crosses between sharp-nosed leafhopper resistant clones of *V. elliottii* (2X) and susceptible cultivated *V. corymbosum* (4X) usually result in only a small number of usually tetraploid hybrids (31, 33); however, it may be possible to transfer resistance via this route. A number of studies (27, 46, 48, 49, 50) indicate that gene transfer is feasible from 4X-6X crosses, in particular those involving *V. corymbosum* and *V. ashei* through backcrossing the most fertile pentaploids from the F_1 to *V. corymbosum*. Recently Vorsa (47) has also demonstrated the feasibility of backcrossing pentaploids to hexaploids. Transfer of sharp-nosed leafhopper resistance from *V. ashei* to *V. corymbosum* using resistant pentaploids as a bridge appears quite feasible because larger progenies are more readily generated. Using this methodology, transfer of resistance to BC_1 genotypes has been successful recently (Ballington & Meyer—unpublished). Other examples of success with 4X-6X backcross derivatives include the tetraploid cultivars 'Flordablue,' 'Avonblue,' 'O'Neal,' and 'Sierra' (38, 40, Draper—unpublished).

The tertiary gene pool for cultivated blueberries is comprised of species from sections of *Vaccinium* other than *Cyanococcus*. F_1 sterility and hybrid weakness, which separates even closely related species in many genera, appear to operate largely at the sectional level, viable F_1 hybrids with at least partial fertility may be produced if enough parental combinations are attempted. Backcrossing one hybrid between 'Rancocas' and *V. uliginosum* L. (2n = 4X = 48) (section *Vaccinium*) to 'Rancocas' produced the cultivar 'Aron' in Finland (26). Several *V. darrowi* x *V. stamineum* L. (2n = 2X = 24) (section *Polycodium*) hybrids have produced tetraploid seedlings in crosses with tetraploid highbush (30), and Draper (unpublished) produced one tetraploid seedling (US 65) between the highbush cultivar 'Coville' and *V. ovatum* Pursh (2n = 2X = 24) (section *Pyxothamnus*). These latter two examples involve both heteroploid and sectional gene transfer. Therefore, gene transfer among fairly widely separated taxa in *Vaccinium*, where necessary to achieve specific goals, appears to be a realistic possibility.

Although four species have contributed the vast majority of the genes in present blueberry cultivars, useful genes occur in many other species. An exhaustive compilation of potential sources of genes for economic traits including pest tolerance or resistance, environmental factors, and fruit and plant traits has recently been published in a Genetic Vulnerability Statement on Cultivated *Vaccinium* in North America by the Small Fruits Crop Advisory Committee. This summary includes known sources within cultivars, breeding selections, elite wild clones and species. It does not suggest genetic solutions to all problems associated with blueberry improvement and production; however, it does indicate that there are real possibilities for improvement in a significant percentage.

Summary and Conclusions

1. *Vaccinium* is a genus of widespread occurrence and diversity and includes hundreds of species, most of which appear to be only of limited genetic vulnerability due to their generally "weedy" nature. This is not to say that some genetic erosion is not occurring through habitat destruction or alteration.
2. The primary and secondary gene pools in *Vaccinium* section *Cyanococcus* (the true blueberries) are extremely large and diverse, and appear to include many of the desirable genes needed in blueberry improvement. These genes are basically available for exploitation.

3. Transfer of genes from the essentially worldwide tertiary gene pool in *Vaccinium* (in relation to section *Cyanococcus*) appears to be possible, though much more difficult than within and among the primary and secondary gene pools.
4. If we are to realize the full potential of the *Vaccinium* germplasm available, organized efforts to systematically collect, evaluate, utilize, and preserve these resources are essential. At the present time we have barely begun the necessary work in any of these endeavors.

Literature Cited

1. Anonymous. 1972. Genetic vulnerability of major crops. National Academy of Sciences, Washington, D.C.
2. Ballington, J. R. 1979. Blueberry improvement through interspecific hybridization: Recent progress and potential in North Carolina, pp. 35-39. In: J. N. Moore (ed.) Proc. 4th N. Am. Blueberry Research Workers Conf., Univ. Arkansas, Fayetteville, Ark.
3. Ballington, J. R. 1981. A brief overview of blueberry culture in North America, pp. 434-448. In: Proc. Florales, 1980, No. 15, Montreal, Quebec, CAn.
4. Ballington, J. R., W. E. Ballinger, C. M. Mainland, W. H. Swallow, E. P. Maness, G. J. Galletta, and L. J. Kushman. 1984a. Ripening season of *Vaccinium* species in southeastern North Carolina. J. Amer. Soc. Hort. Sci. 109:392-396.
5. Ballington, J. R., W. E. Ballinger, and E. P. Maness. 1987. Interspecific differences in the percentages of anthocyanins, aglycones, and aglycone-sugars in the fruit of seven species of blueberries. J. Amer. Soc. Hort. Sci. 12:859-864.
6. Ballington, J. R., W. E. Ballinger, W. H. Swallow, G. J. Galletta, and L. J. Kushman. 1984b. Fruit quality characterization of 11 *Vaccinium* species. J. Amer. Soc. Hort. Sci. 109:684-689.
7. Ballington, J. R. and G. J. Galletta. 1978. Comparative crossability of diploid *Vaccinium* species. J. Amer. Soc. Hort. Sci. 103:544-560.
8. Ballington, J. R., Y. M. Isenberg, and A. D. Draper. 1986. Flowering and fruiting characteristics of *Vaccinium ashei* and *Vaccinium ashei*-*Vaccinium constablaei* derivative blueberry progenies. J. Amer. Soc. Hort. Sci. 111:950-955.
9. Ballington, J. R., W. B. Kirkman, D. V. Barkley, and A. F. Huyler. 1979. *Vaccinium* germplasm collections, North Carolina and South Carolina, 1978 and 1979. Hort. Crops Res. Series No. 51, North Carolina State University, Raleigh, N.C.
10. Ballington, J. R., W. B. Kirkman, W. H. Gensel, Y. M. Isenberg, and C. A. Walker. 1982. *Vaccinium* germplasm collections, 1980-1982. Hort. Crops Res. Series No. 60, North Carolina State University, Raleigh, N.C.
11. Ballington, J. R., W. B. Kirkman, C. A. Walker, B. L. Shoemaker, and D. Finch. 1985. Small fruit crops germplasm collections, 1983-1985. Hort. Crops Res. Series No. 71, North Carolina State University, Raleigh, N.C.
12. Buckley, Blair and J. R. Ballington. 1987. Screening native *Vaccinium* species for resistance to stem blight. HortScience 22:101.
13. Camp, W. H. 1942. On the structure of populations in the genus *Vaccinium*. Brittonia. 4:189-204.
14. Camp, W. H. 1945. The North American blueberries with notes on other groups of Vacciniaceae. Brittonia 5:203-275.
15. Cline, W. O. and R. D. Milholland. 1988. Identification of a new race of *Botryosphaeria corticis* on highbush and rabbiteye blueberry in North Carolina, Plant Disease 72:268.
16. Darrow, G. M. and W. H. Camp. 1945. *Vaccinium* hybrids and the development of horticultural material. Bull. Torrey Bot. Club 72:1-21.
17. Draper, A. D., G. J. Galletta, and J. R. Ballington. 1982. Breeding methods for improving southern tetraploid blueberries. J. Amer. Soc. Hort. Sci. 107:106-109.
18. Etzel, R. W. and J. R. Meyer. 1986. Resistance in blueberries to feeding and oviposition by the sharp-nosed leafhopper, *Scaphytopius megdalensis* (Provancher) (Homoptera: Cidadelidae). J. Econ. Entomol. 79:1513-1515.
19. Fear, C. D., F. I. Lauer, J. J. Luby, R. L. Stucker, and C. Stushnoff. 1985. Genetic components of variance for winter injury, fall growth cessation, and off-season flowering in blueberry progenies. J. Amer. Soc. Hort. Sci. 110:262-266.
20. Galletta, G. J. 1975. Blueberries and cranberries, pp. 154-196. In: J. N. Moore and J. Janick (eds.) Advances in fruit breeding. Purdue Univ. Press, Lafayette, Ind.
21. Gupton, C. L. 1983. Variability among rabbiteye blueberry cultivars for tolerance of flowers to frost. HortScience 18:713-714.
22. Hancock, J. F. and S. J. Krebs. 1986. Cytoplasms of highbush blueberry cultivars. Fruit Var. J. 40:49-50.

23. Hancock, J. F. and J. W. Nelson. 1985. Factors influencing yields of *Vaccinium corymbosum* L. in Michigan. Acta Hortic. 165:107-113.

24. Hancock, J. F. and J. H. Siefker. 1982. Levels of inbreeding in highbush blueberry cultivars. HortScience 17:363-366.

25. Hellman, E. W. and J. N. Moore. 1983. Effect of genetic relationship and pollinizer on fruit, seed, and seedling parameters in highbush and rabbiteye blueberries. J. Amer. Soc. Hort. Sci. 108:401-405.

26. Hiirsalmi H. and A. Lehrnushovi. 1982. A Finnish highbush blueberry variety 'Aron.' Ann. Agr. Fenniae. 21:151-154.

27. Jelenkovic, G. and A. D. Draper. 1973. Breeding value of pentaploid interspecific hybrids if *Vaccinium,* pp. 237-244. In: Proc. Int'l. Symposium on Breeding *Ribes, Rubus,* and *Vaccinium.* Yugoslavia Society for Pomological Science.

28. Korcak, R. F., G. J. Galletta, and A. D. Draper. 1982. Response of blueberry seedlings to a range of soil types. J. Amer. Soc. Hort. Sci. 107:1153-1160.

29. Luby, J. J. and C. E. Finn. 1984. Inheritance and relationships of bloom date, ripe date, fruit filling period, and fruit weight in blueberry, pp. 15-22. In: T. E. Crocker and P. M. Lyrene (eds.) Proc. 5th N. Am. Blueberry Research Workers Conf., Univ. Florida, Gainesville, Fla.

30. Lyrene, P. M. and J. R. Ballington. 1986. Wide hybridization in *Vaccinium.* HortScience 21:52-57.

31. Lyrene, P. M. and W. B. Sherman. 1983. Mitotic instability and 2n gamete production in *Vaccinium corymbosum* x *V. elliottii* hybrids. J. Amer. Soc. Hort. Sci. 108:339-342.

32. Megalos, B. S. and J. R. Ballington. 1987. Pollen viability in five southeastern United States diploid species of *Vaccinium.* J. Amer. Soc. Hort. Sci. 112-1009-1012.

33. Megalos, B. S. and J. R. Ballington. 1988. Unreduced pollen frequencies vs. hybrid production in diploid-tetraploid *Vaccinium* crosses. Euphytica 39:271-278.

34. Milholland, R. D. 1972. Histopathology and pathogenicity of *Batryosphaeria dothidea* on blueberry stems. Phytopathology 62: 658-660.

35. Milholland, R. D. 1984. Occurrence of new race of a *Botryosphaeria corticis* on highbush and rabbiteye blueberry. Plant Disease 68:522-523.

36. Moon, J. W., J. F. Hancock, A. D. Draper, and J. A. Flore. 1987. Genotypic differences in the effect on temperature of CO_2 assimilation and water use efficiency in blueberry. J. Amer. Soc. Hort. Sci. 112:170-173.

37. Pritts, M. P., J. H. Siefker, and J. F. Hancock. 1984. Yield component variation in wild and cultivated blueberries, pp. 30-37. In: T. E. Crocker and P. M. Lyrenne (eds.) Proc. 5th N. Am. Blueberry Workers Conf., Univ. Florida, Gainesville, Fla.

38. Sharpe, R. H. and W. B. Sherman. 1976a. 'Flordablue' blueberry. HortScience 11:65.

39. Sharpe, R. H. and W. B. Sherman. 1976b. 'Sharpblue' blueberry. HortScience 11:65.

40. Sharpe, R. H. and W. B. Sherman. 1977. 'Avonblue' blueberry. HortScience 12:510.

41. Stevens, P. F. 1971. A classification of the Ericaceas: subfamilies and tribes. Bot. J. Linn. Soc. 64:1-53.

42. Vander Kloet, S. P. 1972. The North American blueberries revisited: A taxonomic study of *Vaccinium* section *Cyanococcus* Gray. Ph.D. Dissertation, Queen's Univ., Kingston, Ontario, Can.

43. Vander Kloet, S. P. 1978. The taxonomic status of *Vaccinium pallidum,* the hillside blueberries including *Vaccinium vacillans.* Can. J. Bot. 56:1559-1574.

44. Vander Kloet, S. P. 1980. The taxonomy of the highbush blueberry *Vaccinium corymbosum.* Can. J. Bot. 58:1187-1201.

45. Vander Kloet, S. P. 1983. The taxonomy of *Vaccinium Cyanococcus:* A summation. Can. J. Bot. 61:256-266.

46. Vorsa, N. 1987. Meiotic chromosome pairing and irregularities in blueberry interspecific backcross-1 hybrids. J. Hered. 78:395-399.

47. Vorsa, N. 1988. Differential transmission of extra genomic chromosomes in pentaploid blueberry. Theor. Appl. Genet. 75:585-591.

48. Vorsa, N., G. Jelenkovic, A. D. Draper, and M. V. Welker. 1986. Aneuploid seedlings derived from pentaploid *Vaccinium australe* x *V. ashei* hybrids. J. Hered. 77:114-118.

49. Vorsa, N., G. Jelenkovic, A. D. Draper, and G. J. Galletta. 1987a. Crossability of BC^1 aneuploid and tetraploid progeny derived from *Vaccinium ashei/corymbosum* pentaploid hybrids. J. Amer. Soc. Hort. Sci. 112:998-1004.

50. Vorsa, N., G. Jelenkovic, A. D. Draper, and M. V. Welker. 1987b. Fertility of 4X-5X and 5X-4X progenies derived from *Vaccinium ashei/corymbosum* pentaploid hybrids. J. Amer. Soc. Hort. Sci. 112:993-997.