Lowbush Blueberry-Bunchberry Competition

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Abstract. The competitive effects of bunchberry *Cornus canadensis* L. on native stands of blueberries *Vaccinium angustifolium* Ait. was assessed in 1986 and 1987, and in the greenhouse in 1987 with replacement series experiments. In the field, blueberry and bunchberry fruit were harvested in August and all aboveground growth was cut, the species were separated, and dry weight was determined. The relative yield total (RYT), defined as the dry weight (DW) of the combined aboveground portions of the blueberry and bunchberry divided by their respective DW at 100% cover, was >1 and showed an increase with increasing proportion of bunchberry. Blueberry relative yield, defined as the DW of the aboveground portion divided by the DW at 100% cover, was >1, but bunchberry relative yield DW was ≤1. Regression of individual on associate DW yield indicates blueberry is as aggressive as bunchberry. Blueberry fruit count and yield decreased with increasing bunchberry density. In the greenhouse study, plant count and cover were assessed weekly, and leaf area index (LAI) and DW were obtained at the end of the study. RYT > 1, and combined DW increased with increasing proportion of bunchberry. The LAI of blueberry or bunchberry was higher in mixtures than in pure stands. Blueberries are competitive with bunchberry, but in native fields, open areas among clones allow faster growing bunchberry to spread without competition.

The principal lowbush blueberry species present in the commercial growing regions of Maine, the Maritime Provinces of Canada, and Quebec are the sweet lowbush blueberry *Vaccinium angustifolium* Ait. and the sourtop blueberry *V. myrtilloides* Michx. (Hall et al., 1979). Commercial fields in eastern Canada were developed from abandoned farms, whereas many fields in Maine are on land that was burned by Native Americans in the past or opened by logging. The lowbush blueberry industry exceeds 40,000 ha in Maine and Canada and produces an average of 32 million kilograms of fruit per year. Increased demand for the crop has produced needs for expanded productivity, mechanical harvesting, and increased acreage (Smagula and Yarborough, 1990).

Hall et al. (1979) separated species competing with the lowbush blueberry into four ecological site groups: natural or undisturbed, postlogging, old field, and blueberry crop. Vander Kloet and Hall (1981) and Hall et al. (1979) listed *Cornus canadensis* L. as a competitor with *V. myrtilloides* in the Acadian forest and with *V. angustifolium* in the Boreal forest. On postlogging sites, *C. canadensis* is listed as a major competitor by Hall (1959) and Hall and Sibley (1976). *Vaccinium angustifolium* is abundant in disturbed communities that result from clear cutting, forest fires, and the abandonment of agricultural land (Hall et al., 1979). Bouchard (1986) determined that lowbush blueberry yield in the Lac-Saint-Jean region of Quebec was negatively correlated with cover of other species and that *C. canadensis* had 19.5% frequency of occurrence and 80% cover in the plots on which it occurred. McCully (1988) indicated that *C. canadensis* was the most serious competitor in Nova Scotia blueberry fields after hexazinone treatment because it had the greatest relative abundance, a value which combines frequency,

uniformity, and density (McCully et al., 1991). Yarborough and Bhowmik (1989) found that *C. canadensis* increased in density and frequency after hexazinone application to blueberry fields in Maine. Although decreases in weed abundance and diversity and increases in blueberry yield have been associated with the use of hexazinone (Yarborough and Bhowmik, 1989; Yarborough et al., 1986), the competitive ability of individual species in lowbush blueberry fields has not been documented.

De Witt replacement series experiments have been the standard method for evaluating competition in two-species experiments over the past 25 years (Harper, 1977). Under this method, two monocultures and mixtures are compared at a single density, which is chosen to represent typical field densities. Expected and observed yields, measured as plant DW, seed count, fruit weight, etc., are compared where the expected yield is a linear function of the species proportions in a mixture. Harper (1977) described four possible outcomes or models for competition, which may be used in interpreting replacement series results from competition and allelopathy experiments (Fig. 1). Hill (1973) described an alternative approach to expressing the relationship of competing species in a substitutive experiment by regressing the individual mean, defined by plant biomass or commodity yield grown in combination with another species, on the associate mean, defined by plant biomass or commodity yield grown in monoculture. When a regression function is defined by these pairs, the relative competitiveness of the crop and weed may be determined (Hill, 1973) (Fig. 2).

The bunchberry is increasing in density and distribution in lowbush blueberry fields in Maine and in Canada, but since presence does not necessarily assure competition, there is a need to determine if bunchberry plants will adversely affect blueberries in native fields. Replacement series experiments were established in the field and greenhouse to determine the competitiveness of bunchberry in lowbush blueberry fields in Maine.

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Abbreviations: C : W, crop : weed; DAT, days after transplanting; DW, dry weight; LAI, leaf area index; RYT, relative yield total.

Fig. 1. Theoretical models for interpreting results of replacement series experiments using relative yield.

Methods

Greenhouse. In Apr. 1987, five blueberry and bunchberry clones each were selected on a pruned blueberry field at the Blueberry Hill Experimental Farm at Jonesboro, Maine. Each of the clones was used for one replication of the greenhouse experiment. Sixteen dormant blueberry and bunchberry sods 5 cm in diameter and 8 cm deep were transplanted into $0.42 \times 0.42 \times 0.14$ m wooden boxes. Soil medium was a 1:1 (v/v) mixture of sand and peatmoss. The proportion of blueberry and bunchberry plants placed in the boxes corresponded to the following crop : weed (C : W) proportions: 1.0:0, 0.75:0.25, 0.50:0.50, 0.25:0.75, and 0:1.0. The placement of the plugs was four rows of four plugs for the 1.0:0 and 0:1.0; four blueberry placed diagonally among 12 bunchberry or four bunchberry placed diagonally among 12 blueberry for the 0.75:0.25 and 0.25:0.75, respectively, and every other plant for the 0.50:0.50.

The boxes were randomly placed on benches in the greenhouse at the Univ. of Maine in Orono. Plants remained in the greenhouse from 20 Apr. through 14 Aug. 1987; greenhouse

air averaged 20/18C (day/night). The number of stems were counted and boxes were photographed weekly from 30 Apr. through 14 Aug. Slides of the treatments were projected on a 0.42 m^2 grid with 2.5 cm squares. Area occupied by blueberry or bunchberry was marked to the nearest half square and totaled. Mean area and SE were calculated for each treatment and date.

On 14 Aug. 1987, all plant top growth was harvested. Leaf area of blueberry and bunchberry top growth was determined by measuring the total leaf area with a LI-COR portable leaf area meter, model LI-3000 (LI-COR, Lincoln, Neb.). The belowground portion of the plants, consisting of roots and rhizomes, was separated from the soil. The aboveground and belowground portions of the blueberry and bunchberry plants were placed in open paper bags, dried at 60C for 30 days, and weighed.

Field. Two blueberry fields with abundant blueberry and bunchberry cover at Blueberry Hill Farm were selected for the field replacement series experiment in June 1986. In 1985, field 7U was burned, 2.2 kg hexazinone/ha and 83.7 kg urea/ha (46% N) were applied preemergence. In 1986, field 5L was mowed,

Fig. 2. Theoretical association between individual and associate yield for interpreting results of replacement series experiments.

2.2 kg hexazinone/ha and 220 kg 15N-15P-15K/ha were applied preemergence. In 1987, field 7U was burned, 2.2 kg hexazinone/ha and 220 kg 15N-15P-15K/ha were applied preemergence. In 1986, field 5L was in the nonbearing or prune cycle and field 7U was in the crop cycle; in 1987 the sequence was reversed. In June 1986 and 1987, ten 0.42 m² quadrats were located for each of five cover proportions on both prune and crop cycle fields. The five C : W cover proportions were: 1.0:0, 0.75:0.25, 0.50:0.50, 0.25:0.75, and 0:1.0.

Blueberry and bunchberry fruit were harvested with a hand rake in August from all of the quadrats in the crop year cycle in 1986 and 1987. The number of berries and fresh weights were obtained from these samples. In Sept. 1986 and 1987, all aboveground blueberry and bunchberry growth was cut within quadrats at the ground level on both the prune and crop year fields. The number of stems were counted and fresh weights were obtained. The stems were placed in open paper bags and stored in the drying room at 60C, and the DW of the blueberry and bunchberry top growth were recorded.

Data conversion and analysis. Relative biomass of the blueberry and bunchberry was obtained by dividing the DW of the 0.25, 0.50, and 0.75 proportions by the DW at the 1.0 proportion. The RYT, as DW was obtained by adding the blueberry and bunchberry relative DW yields for each pair, i.e., the 0.75 blueberry DW, was added to the 0.25 bunchberry DW for in each plot. Means of relative yield in DW, RYT in DW, LAI, and their SE were calculated.

Regression of the individual mean (the monoculture DW mean times the proportion represented, i.e., the DW at 1.0 times 0.25, 0.50, or 0.75) on the associate mean (the DW mean of the yield at a certain crop component of the mixture, i.e., the DW obtained at the 0.25, 0.50, 0.75 mixture) was used to measure relative aggressiveness. The general linear models (GLM) program of SAS (SAS Institute, 1985) was used to regress the individual on the associate DW means of blueberry and bunchberry, respectively.

In the field replacement series experiment, the fresh weight of the blueberry top portion, the fruit count, and fruit yield were

regressed against the number of bunchberry stems using the GLM program of SAS.

Results

Greenhouse. The number of blueberry stems increased rapidly at all cover proportions up to 41 days after transplanting (DAT) and then increased slowly, reaching a maximum at 109 DAT (Fig. 3). Blueberry cover showed a similar trend with cover increasing at a faster rate starting at 46 DAT (Fig. 3). Bunchberry buds were formed the year before and were aboveground, so there were more buds at the beginning. Stems initially increased slowly, but increased more rapidly after 46 DAT (Fig. 3). Bunchberry cover exceeded blueberry cover up to 46 DAT, but blueberry cover increased to exceed or equal the bunchberry cover by the end of the study (Fig. 3).

The relative DW yield of the aboveground portions of both blueberry and bunchberry grown in combination exceeded DW when grown separately (Fig. 4). The RYT was >1, with the 0.50:0.50 and 0.75:0.25 bunchberry : blueberry proportion providing the highest DW yields. The relative DW yields of the belowground rhizome portions were more erratic (Fig. 4). The RYT DW was >1.25 at the 0.50:0.50 bunchberry : blueberry proportion, but slightly <1 at the 0.25:0.75 and 0.75:0.25 proportions.

LAI was >1 for both blueberry and bunchberry (Fig. 5). Bunchberry LAI was higher when the proportion of the bunchberry was less than the blueberry in the mixture. Blueberry LAI increased with the higher proportions of bunchberry.

Regressing the individual vs. the associate yield for the blueberry DW and bunchberry DW of the aboveground portions of the plants produced similar trends (Fig. 6).

Field. Stem counts of blueberry and bunchberry obtained at the termination of the study indicated a higher density of blueberry than bunchberry stems at the same cover proportions (Table 1). For most of the cover proportions, there were more stems in the prune than in the crop cycle and in 1987 than in 1986.

In the prune cycle of 1986, the relative DW yields of the aboveground portions of blueberry grown in combination with bunchberry exceeded the DW yield if grown in monoculture. But the DW yield of bunchberry grown in combination with blueberry exceeded the yield grown in monoculture only at the 0.75:0.25 bunchberry : blueberry proportion (Fig. 7). In the yield cycle of 1986; the relative yield in DW of blueberry exceeded that of bunchberry, and the RYT in DW was >1, with the 0.50:0.50 and 0.75:0.25 blueberry : bunchberry proportions providing the highest yields.

In the prune cycle of 1987, the relative DW yields of the aboveground portions of blueberry grown in combination exceeded the DW yield grown in monoculture, but, for the bunchberry, the DW yield grown in combination was less than the DW yield grown in monoculture at the 0.50:0.50 blueberry : bunchberry proportion (Fig. 7). The RYT DW was >1, with the 0.75:0.25 blueberry : bunchberry proportion providing the highest DW yield.

The results for the crop cycle of 1987 were similar, with the relative DW yields of blueberry grown in combination with bunchberry exceeding the DW monoculture yield, and with the bunchberry DW yield grown in combination was less than in monoculture (Fig. 7). The RYT in DW was >1 with the 0.25:0.75 and 0.75:0.25 blueberry : bunchberry proportions providing the highest yields.

Regressing the individual on the associate yield for the blueberry and regressing the bunchberry DW on the aboveground

Fig. 3. Number of blueberry or bunchberry stems or percent cover over time by cover ratio from greenhouse in 1987.

portions of the plants produced similar relationships in prune and crop years for 1986 and 1987 (Fig. 8). Significant regressions were obtained for bunchberry in both cycles and in both years. The regression for blueberry was significant in 1987 but not in 1986 (Fig. 8).

Regressing the blueberry fresh weight of aboveground portions of the plant, blueberry fruit count, and fruit weight in grams per plot vs. the number of bunchberry stems per plot gave significant quadratic regressions in 1986. Regressions for fruit count and weight were not significant for 1987 (Fig. 9).

Discussion

Greenhouse. Bunchberry had more stems and more cover than blueberry at 10 DAT. The bunchberry buds were on or near the soil surface, whereas the blueberry plant initiated buds from a woody rhizome. Bunchberry cover exceeded blueberry cover up to 46 DAT, but thereafter blueberry cover equaled or exceeded that of bunchberry. The number of blueberry stems increased rapidly up to 46 DAT and then increased at a slower rate. Bunchberry stem count, conversely, showed little increase up to 46 DAT, but then began to increase at a higher rate.

In the field, blueberry plants emerge after pruning in early

May when air temperatures have exceeded 6 to 10°C for 3 to 5 days (Hall et al., 1979; Vander Kloet and Hall, 1981). Bunchberry emerges and grows earlier, with weather affecting emergence by as much as 2 weeks (McCully, 1988). The time of emergence suggests that bunchberry has the initial advantage in the number of stems emerging and cover, but that the blueberry is able to equal or exceed the bunchberry later in the season, so that most of the growth of each species is occurring at different times.

The replacement series diagram (Fig. 7) for the relative DW yield of the top growth of the blueberry and bunchberry grown in combination reveal that both produced more DW than if grown in monoculture, so the RYT in DW exceeds 1. This relationship indicates that nutrients were not limiting, or that blueberry and bunchberry compete for nutrients at different times. This rhizome portion had a RYT in DW >1 at the 0.5:0.5 bunchberry : blueberry proportion and <1 at the other proportions. In the understory of the Acadian forest, Flinn (1980) found that blueberry rhizomes occur at 6 ± 1 cm and bunchberry rhizomes at 8 ± 2 cm so that their proximity would indicate no physical separation in depth. In this study, an equal mixture of blueberry and bunchberry resulted in better growth than either alone.

Fig. 4. Relative yield of blueberry, bunchberry, and combined top or rhizome portion dry weights by relative proportion of blueberry : bunchberry from greenhouse in 1987.

The LAI may be adversely affected by competition (Radosovich and Holt, 1984). The LAI of blueberry increased as the proportion of blueberry decreased or the proportion of bunchberry increased. The bunchberry showed a similar response to the blueberry, but with much smaller differences. This result suggests that blueberry leaf growth, when grown in association with bunchberry, exceeds that grown in monoculture.

The associate DW yield exceeded individual DW yield for blueberry and bunchberry and was stronger than a mutually exclusive relationship, indicating that both species were able to produce more DW in mixtures than alone. The slopes of blueberry and bunchberry are both significant, indicating their competitive ability is not frequency dependent (Hill, 1973).

Fig. 5. Effect of relative proportion of blueberry : bunchberry on LAI from greenhouse in 1987.

Fig. 6. Individual vs. associate yield of blueberry and bunchberry dry weight of top portions from greenhouse in 1987.

Field Study. Replacement series experiments were established on native stands and represent well-managed fields using recommended herbicide and fertility practices. Since lowbush blueberries have been developed from a wild population, a wide range in variation among clones is expected (Hepler and Yarborough, 1991). Density of blueberry stems in the monoculture varied between years and crop cycles. When the data are converted to a stems per 0.1 m^2 for comparison to past experiments, blueberry stand varied from a high of 170 in the 1972 prune cycle to 84 in the 1986 crop cycle. A blueberry plant stand at 97 stems/ 0.1 m^2 produced optimal yield and profit from 13 locations in 1981 (Yarborough et al., 1986), and the highest

Table 1. Stem density of blueberry and bunchberry from field replacement series, Jonesboro Maine, 1986-87.

Relative proportions blueberry : bunchberry (%)	Number of stems (SE)			
	Blueberry		Bunchberry	
	1986	1987	1986	1987
<i>Prune cycle</i>				
100:0	262 (20)	300 (25)	2 (1)	4 (2)
75:25	240 (13)	281 (21)	55 (7)	44 (6)
50:50	162 (15)	243 (13)	105 (11)	85 (5)
25:75	59 (9)	99 (13)	152 (10)	145 (11)
0:100	0 (0)	1 (1)	201 (12)	224 (6)
<i>Crop cycle</i>				
100:0	149 (9)	202 (16)	3 (1)	4 (1)
75:25	119 (12)	181 (18)	51 (9)	37 (5)
50:50	132 (17)	166 (11)	87 (8)	80 (11)
25:75	58 (9)	42 (7)	129 (13)	175 (13)
0:100	0 (0)	0 (0)	199 (16)	224 (14)

yield was obtained from a field with a stem density of 116 stems/0.1 m² from Township 18, Maine in 1987 (Yarborough and Bhowmik, 1989). Bunchberry stem density varied from 113 to

127 stems/0.1 m², much less variation than the blueberry McCully (1988) found a maximum of 54 bunchberry stems/0.1 m² in mixed stands. Compared to blueberry and bunchberry stands from earlier experiments, the stand density in this study was high, indicating that interspecific and intraspecific competition should occur.

In 1986 and 1987, the RYT in DW was >1 in both prune and crop fields, with blueberry producing more DW in mixture than in monoculture and bunchberry producing an equivalent or slightly lower DW in mixture compared to monoculture. Over the two cycles and years, the trend is for blueberry top DW to be higher in mixture than in monoculture and for bunchberry DW to be the same or slightly less. A RYT >1 indicates that the blueberry and bunchberry are not competing and suggests that they may be acquiring resources at different times.

In 1986, blueberry at the lower associate DW yield levels was weaker and bunchberry was stronger, but at higher associate DW yields, blueberry was stronger and both were higher than mutually exclusive. The slope for blueberry on the individual vs. associate yield was not significant, indicating blueberry had a frequency-dependent competitive ability. In 1987, both blue-

Fig. 7. Relative yield of blueberry, bunchberry, and combined top portion dry weights by relative proportion of blueberry : bunchberry from field 1986 and 1987.

Fig. 8. Individual vs. associate yield of blueberry and bunchberry dry weight of top portions from prune and crop year fields in 1986 and 1987.

berry and bunchberry slopes were similar and closer to the mutually exclusive slope, indicating equivalent growth. However, both had slopes that were significant, implying that they are able to compete aggressively over a wide range of mixed proportions.

Regressing the fresh weights of the leaf and stems, fruit weight, and fruit count of the blueberry against the density of bunchberry stems will give an indication of the effect of bunchberry density on blueberry productivity (Cudney et al., 1989). In 1986, increasing bunchberry stems resulted in a significant reduction of blueberry fresh weight of the leaf and stems, fruit count, and weight. In 1987, increasing bunchberry stems resulted in less blueberry leaf and stem fresh weight, but the low R^2 values and nonsignificant slope indicate other factors were more important in affecting the fruit count and yield. Levels of pollination and moisture may have had more effect on fruit set and development than the presence of the bunchberry stems.

Evidence from replacement series experiments in the greenhouse and field at blueberry and bunchberry densities that could be expected on well-managed stands indicates that there is little competition between blueberry and bunchberry and that their

growth is equivalent. Blueberry and bunchberry occur naturally in association in many communities throughout North America (Bouchard, 1986; Flinn, 1980; Hall et al., 1979), and the species may have evolved niches to allow both species to survive in association.

Use of the herbicide hexazinone creates open areas among the blueberry clones, varying in size from 15% to 40% of the fields (Yarborough and Bhowmik, 1989), depending on how long the field has been in production. In these open areas, there is no competition until the plants fill in, so the most rapidly growing species have the initial advantage. The bunchberry plant is more herbaceous than the blueberry, and the rate of radial spread is reported to be up to 30 cm per year by Hall and Sibley (1976). Blueberry spread on mineral soil is reported as 10 cm per year, but up to 50 cm spread per year may be obtained on organic soils (Hall et al., 1979). In the field, bunchberry is spreading more rapidly in the open mineral areas produced by the reduction in weed cover. Since blueberry and bunchberry grow equivalently in mixed stands, bunchberry could prevent blueberry plants from spreading in the field. The ability of bunchberry to spread more rapidly

Fig. 9. Effect of density of bunchberry stems (BS) on blueberry count, top weight, and fruit weight in 1987 and 1988. Bold line is blueberry top weight (TW) in 1987 $TW = 112.7 - 0.58BS + 0.0005BS^2 R^2 = 0.68 L^{**}$ in 1988 $TW = 130 - 0.70BS + 0.0008BS^2 R^2 = 0.66 L^{**}$; dashed line is blueberry fruit count (FC) in 1987 $FC = 257.9 - 1.96BS + 0.0034BS^2 R^2 = 0.60 L^{**} Q^{**}$ in 1988 $FC = 319.9 - 0.21BS - 0.004BS^2 R^2 = 0.30 NS$; solid line is fruit weight (FW) in 1987 $FW = 92.1 - 0.74BS + 0.0014BS^2 R^2 = 0.60 L^{**} Q^{**}$ in 1988 $FW = 116.2 - 0.14BS + 0.0012BS^2 R^2 = 0.33 NS$.

and establish itself before the blueberry makes it a better competitor than the blueberry.

In the agricultural ecosystem, productivity of the crop species is the objective. Pruning and the use of herbicides has increased the productivity of native lowbush blueberry fields. Herbicide-resistant species need to be controlled to maintain and increase the productivity of native blueberry stands. Although bunchberry does not limit blueberry growth when grown in association with lowbush blueberry, its presence limits the spread of the blueberries and prevents an increase in the potential yield of the field. Therefore it will be necessary to reduce bunchberry to encourage blueberry growth.

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