

Pollen Source Affects Yield Components and Reproductive Fertility of Four Half-high Blueberry Cultivars

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Abstract. Pollination of the half-high blueberry (*Vaccinium corymbosum* L./*V. angustifolium* Ait.) cultivars St. Cloud, Northsky, Northcountry, and Northblue with self, outcross, and outcross/self pollen mixtures suggests that outcross fertilization maximizes percent fruit set, berry weight, seeds per berry, and seeds per pollination while minimizing days to harvest. Based on these results, mixed plantings of at least two blueberry cultivars are recommended for these cultivars. Fruit and seed set were negatively associated with increased percentages of self pollen in outcross/self pollen mixtures. These responses were linear for 'Northblue' due to a tendency to parthenocarpy, and nonlinear for 'St. Cloud', 'Northsky', and 'Northcountry', due to low fruit set following self-pollination. These data indicate that post-fertilization abortion affected seed formation, which was, in turn, correlated positively with fruit set.

In 1921, Coville reported that, "When blueberry flowers are pollinated with pollen from their own bush the berries are fewer, smaller, and later in maturing than when the pollen comes from another bush. It is important, therefore, that a plantation should not be made up wholly from cuttings from one bush." Other researchers have observed similar results (Bailey, 1937; Beckwith, 1930), including correlations of seed count to berry size and days to maturity in highbush blueberry (Meader and Darrow, 1947; Morrow, 1943; White and Clark, 1938), rabbiteye blueberry, *V. ashei* Reade (Meader and Darrow, 1944), and lowbush blueberry, *V. angustifolium* Ait. (Aalders and Hall, 1961; Wood, 1968).

Merrill (1936) reported satisfactory commercial fruit set following self pollination in the highbush varieties Rubel, Cabot, Adams, and Pioneer, although fruit set was generally higher following cross pollination. Later, Merrill and Johnston (1939) added that fruit set and berry weight following self pollination were not significantly different than those results following open pollination in the highbush varieties Stanley, Jersey, Concord, and June. A controlled outcross treatment was not included in this study, and therefore, open pollination could have included significant amounts of self pollination within a large plantation of a single variety or among flowers on a single large bush.

Relationships between seed count per berry and other yield components have yet to be documented in "half-high" cultivars (*V. corymbosum* / *V. angustifolium* hybrid derivatives). The fruiting responses to self and cross pollinations have varied among half-high selections and cultivars in the Univ. of Minnesota's blueberry breeding program. Rabaey and Luby (1988) observed that apparent segregation for self-fruited fell in three classes: genotypes with no fruit following self pollination, genotypes showing no effect from pollen source, and an intermediate class. They sug-

gested 'Northblue' could be used in single cultivar plantations, because fruit set or berry weight were similar following self and cross pollination. 'Northcountry' and 'Northsky' were recommended for mixed plantings because of low levels of fruit set following self pollination.

The terms "incompatibility" and "self incompatibility" have been used in much of the recent literature to describe reduced reproductive fertility of blueberries following self pollination (Ballington and Galletta, 1978; El-Agamy et al., 1981; Garvey and Lyrene, 1987). By definition, self incompatibility is a prefertilization barrier (Mather, 1943). However, research in blueberry does not support the existence of a prefertilization barrier. Self pollen tubes reach the base of the style at about the same time as outcross pollen tubes in *V. ashei* (El-Agamy et al., 1981; Garvey and Lyrene, 1987) and *V. corymbosum* (Krebs and Hancock, 1988). Self pollen tubes also have been observed entering ovules in both of these species (El-Agamy et al., 1980; Krebs and Hancock, 1988) and fertilizing ovules in *V. corymbosum* (Vander Kloet, 1991). This evidence suggests that a post-zygotic mechanism, not self incompatibility, is causing the observed differences in reproductive fertility between self and outcross pollinations in *Vaccinium* spp. Research further suggests that the reductions in self fertility observed in blueberries are a function of inbreeding depression. Reduced fruit set and seeds per berry (Hellman and Moore, 1983) as well as increased seed abortion (Krebs and Hancock, 1988) have been correlated to increased inbreeding in *V. corymbosum*.

Fruit set and berry weight are major components influencing yield; however, days from bloom to harvest also can be important, as growers often are interested in earlier harvests to market their crop at a time when the commodity faces less competition and receives a premium price. The objective of this study was to determine the effects of self, outcross, and mixed pollinations on various yield components, and the correlations among those components, in four half-high blueberry cultivars.

If zygotic abortion occurs as a result of selfing, fertility should be proportional to the ratio of outcross : self pollen used in pollination. For example, pollination with a mixture of self and outcross pollen should result in fruit set or seed production intermediate to the results from self and outcross pollinations. Therefore, the hypothesis is that as the outcross : self pollen ratio increases, the fertility of the pollination will increase proportionally.

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Materials and Methods

Four Univ. of Minnesota half-high blueberry cultivars, St. Cloud, Northsky, Northcountry, and Northblue, were studied. In Mar. 1989, the plants were forced into flower in a greenhouse following a 4-month cold treatment. Pollination treatments contained pollen from outcross and self flowers in ratios of 0:1 (self pollination), 1:3, 1:1, 3:1, and 1:0 (outcross pollination) to approximate 0%, 25%, 50%, 75%, or 100% outcross pollen. Pollen was extracted by rolling the flowers between the thumb and index finger. The extracted pollen was deposited onto the thumb nail of the other hand and touched to the stigmas of emasculated flowers.

To minimize the effects of inbreeding, the outcross pollen sources varied depending on the cultivar used as the female. 'St. Cloud' and 'Northblue' have one of their parents in common, US 3, while the other parents, B19A for 'St. Cloud' and B10 for 'Northblue', are full siblings from G65 x 'Ashworth'. 'Northcountry' and 'Northsky' are full siblings and one parent, B6, represents a third sibling from G65 x 'Ashworth'. Consequently, to minimize inbreeding, 'Northblue' was the outcross pollen source for 'Northcountry' and 'Northsky', and outcross pollen for 'St. Cloud' and 'Northblue' was randomly taken from either 'Northsky' or 'Northcountry'. Outcross pollen sources were not mixed within an experimental unit.

Ripe berries were harvested every other day, and data for each inflorescence were collected for percent fruit set, days to harvest, berry weight, seeds per berry, and seeds per pollination. Shrunken or light-colored ovules were considered aborted, while plump and dark-colored seeds were included in seed counts. The number of seeds per pollination was calculated as seeds per berry weighted by percent fruit set.

Data were analyzed as an incomplete block design. Five inflorescences at a similar stage of development constituted a block. There were between three and 20 blocks per plant depending on plant size and available inflorescences. Each inflorescence within a block was then randomly assigned one of the five treatments.

Eight blocks were assigned to each of the four cultivars for a total of 32 blocks. Because a plant was labeled incorrectly, three blocks had to be dropped, leaving 29 blocks for analysis.

In the analysis of variance, cultivar and cultivar x treatment effects were tested by partitioning degrees of freedom from the block and block x treatment effects, respectively. Orthogonal contrasts partitioned from the treatment sums of squares and linear regression were used to test for linear and quadratic effects of the treatments and to estimate Y intercept values. Correlations among certain yield components were calculated using the Pearson product-moment method.

Initially, the experiment was designed as a randomized complete block design, but several factors determined the switch to incomplete blocking. First, environmental factors were assumed to affect self fertility; therefore, blocks needed to be as small as possible to better control environmental variability. Using incomplete blocking reduced the number of treatments per block from 20 to five. Also, having only one cultivar included per incomplete block minimized the effects of any inconsistencies of the treatments between cultivars.

Results

Analysis of variance was performed on pooled data of all four cultivars to test for cultivar x treatment interactions (data not presented). The interactions were significant at $P \leq 0.05$ for percent fruit set, days to harvest, and seeds per berry and at $P \leq 0.11$ and 0.12, respectively, for berry weight and seeds per pollination.

When 'Northblue' was excluded from the pooled analysis, no significant interactions were found among the remaining three cultivars ($P > 0.05$; Table 1A). Therefore, data from 'St. Cloud' are used to represent these three cultivars (Fig. 1), however, treatment means for all four cultivars are presented in Table 2. Berry weight, seeds per berry, and seeds per pollination increased and days to harvest decreased with increasing proportions of outcross pollen for all four cultivars. In each case, slope estimates were signifi-

Table 1. Analysis of variance for fruit set, days to harvest, berry weight (g), seeds per berry, and seeds per pollination on (A) pooled data of the cultivars St. Cloud, Northsky, and Northcountry, and (B) 'Northblue'.

Source	Percent fruit set		Days to harvest		Berry weight (g)		Seeds per berry		Seeds per pollination	
	df ^a	Mean squares	df	Mean squares	df	Mean squares	df	Mean squares	df	Mean squares
A										
Blocks (B)	23	0.13	23	117.79	23	0.38	23	61.23	23	65.66
Cultivar (C)	2	0.18*	2	180.50**	2	3.21**	2	19.81	2	35.07
Residual	21	0.13	21	111.82	21	0.11	21	65.18	21	68.58
Treatment (T)	4	1.54**	4	421.63**	4	0.34**	4	535.68**	4	847.78**
Linear	1	4.78**	1	1564.64**	1	1.29**	1	2110.48**	1	3233.93**
Quadratic	1	1.14**	1	442.61**	1	0.21**	1	153.29**	1	90.91*
B x T	90	0.04	78	25.82	78	0.02	78	16.31	90	20.01
C x T	8	0.02	8	42.30	8	0.02	8	24.00	8	34.10
Error	82	0.04	70	23.93	70	0.02	70	15.43	82	20.94
B										
Blocks	4	0.01	4	11.39	4	0.08	4	162.89	4	170.51
Treatment	4	0.01	4	46.07**	4	0.37**	4	483.28**	4	466.65**
Linear	1	0.03	1	117.05**	1	0.91**	1	1462.97**	1	1548.46**
Quadratic	1	0.01	1	63.18**	1	0.20**	1	451.61**	1	306.23**
Error	16	0.02	16	6.87	16	0.04	16	27.55	16	26.80

^aDegrees of freedom.

*,** F tests significant at $P \leq 0.05$ and 0.01, respectively.

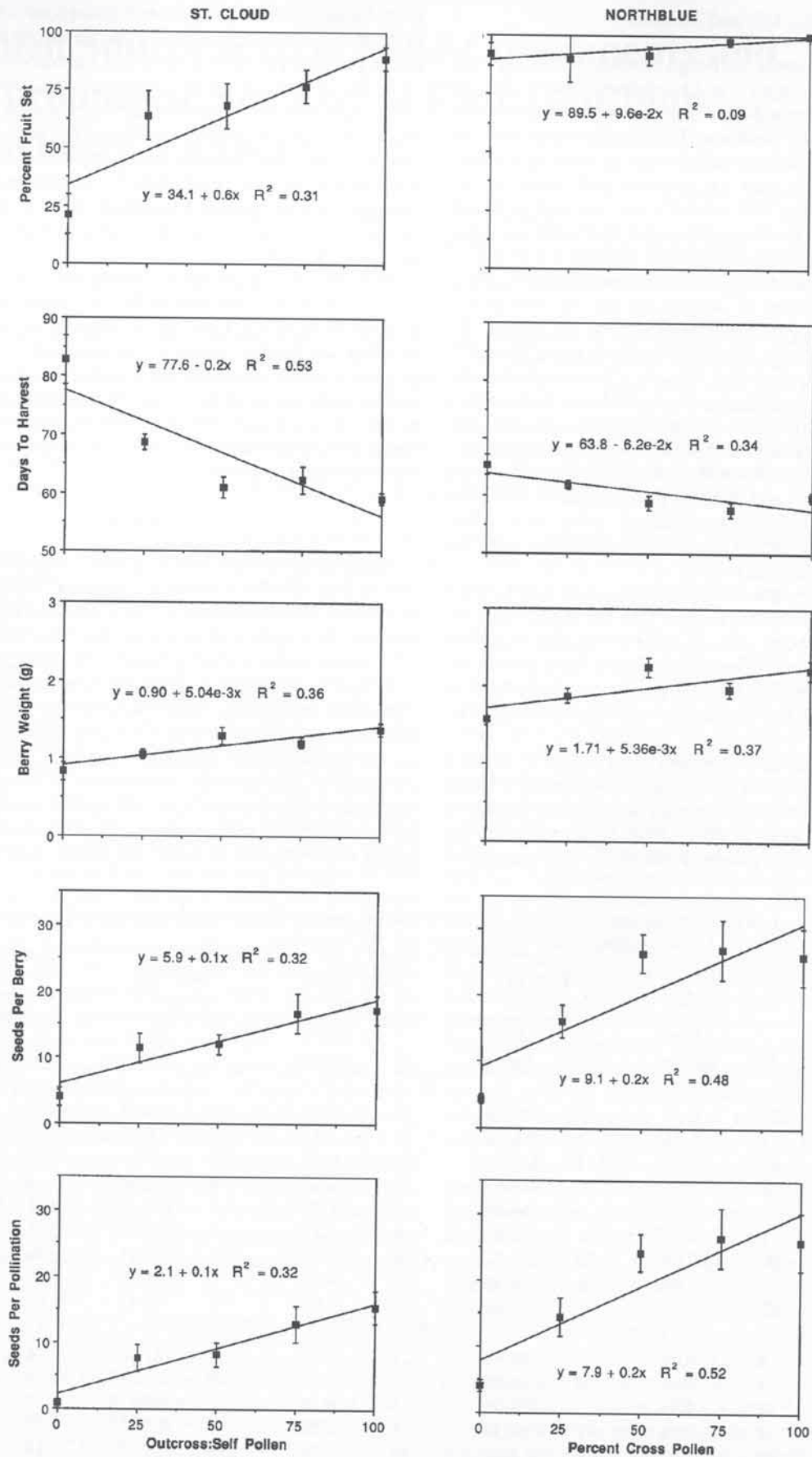


Fig. 1. From the top, regressions of percent fruit set, days to harvest, berry weight (g), seeds per berry, and seeds per pollination responses on outcross : self pollen ratios for 'St. Cloud' and 'Northblue' on a per observation basis. Points and vertical bars represent treatment means and standard errors, respectively.

Table 2. Means for percent fruit set, days to harvest, berry weight (g), seeds per berry, and seeds per pollination following five outcross : self pollen treatments of the cultivars St. Cloud, Northsky, Northcountry, and Northblue.

Cultivars	SE	Outcross : self pollen				
		0:1	1:3	1:1	3:1	1:0
Percent fruit set						
St. Cloud	4.1	21.3	63.8	68.0	76.5	88.9
Northsky	3.5	21.3	74.5	83.9	89.9	84.6
Northcountry	4.1	19.8	51.3	67.4	73.5	75.3
Northblue	3.1	92.0	90.0	91.6	98.0	100.0
Days to harvest						
St. Cloud	1.1	82.9	68.7	60.9	62.3	59.1
Northsky	0.9	70.3	60.6	59.9	57.7	58.7
Northcountry	1.1	61.5	64.1	61.8	63.3	60.9
Northblue	0.7	65.4	61.9	58.8	57.7	59.8
Berry weight (g)						
St. Cloud	0.05	0.82	1.05	1.28	1.20	1.38
Northsky	0.03	0.49	0.68	0.74	0.80	0.77
Northcountry	0.02	0.55	0.49	0.55	0.58	0.64
Northblue	0.05	1.58	1.88	2.25	1.96	2.21
Seeds per berry						
St. Cloud	0.6	4.0	11.4	11.9	16.7	17.2
Northsky	0.9	4.0	12.5	12.9	18.5	18.3
Northcountry	0.6	5.7	14.2	13.8	14.9	22.9
Northblue	1.3	4.3	16.2	26.4	27.0	25.9
Seeds per pollination						
St. Cloud	0.9	0.9	7.6	8.2	12.9	15.5
Northsky	0.9	0.9	9.3	11.6	16.5	16.9
Northcountry	0.9	1.2	7.3	9.7	11.5	17.3
Northblue	1.3	4.1	14.5	24.2	26.4	25.9

cantly different than zero ($P \leq 0.01$). However, the slopes of the percent-fruit-set responses for the cultivars St. Cloud, Northsky, and Northcountry differed from that of 'Northblue' (Fig. 1 and Table 1B). Although the sum of squares for linear effects accounted for much of the variability in the traits with significant treatment effects, there was still a relatively small but significant quadratic response ($P \leq 0.05$; Table 1).

The means of the self-pollination treatments seemed to deviate slightly from the expected, based on a linear response of the other four treatment levels, and were apparently the basis for the quadratic effects noted in the previous analysis. Therefore, the analysis was repeated without the self-pollination treatment. The four remaining treatments produced a linear response for all three traits ($P \leq 0.01$; Table 3), and the quadratic effect was nonsignificant ($P > 0.05$).

Linear regressions based on the treatments, excluding self pollination, were used to predict Y-intercept values. If the hypothesis of linear fertility responses in relation to proportion of outcross pollen was correct, then the Y intercept from this regression analysis should predict the value of the self-pollination treatment. Using Bonferroni's simultaneous confidence intervals, the Y intercepts from these analyses were found to be significantly higher than the observed responses of the self-pollination treatments for percent fruit set, seeds per berry, and seeds per pollination ($P \leq 0.05$). No significant differences ($P > 0.05$) were found between the predicted Y intercepts and the observed values of the self-pollination treatments for days to harvest and berry weight.

'Northblue' set $\approx 94\%$ fruit with no significant differences ($P > 0.05$) among the pollination treatments (Figure 1 and Table 1B). Sixteen percent of the fruit set following the self pollination treatment was parthenocarpic for 'Northblue'. When all five

pollination treatments were included in the analysis, treatment effects were significant for all other traits ($P \leq 0.01$). The responses were largely linear with a significant quadratic effect ($P \leq 0.01$; Table 1B). In plots of the means for seeds per berry and seeds per pollination, 'Northblue' responded linearly from self pollination treatment to treatment 1:1, and level responses were reached for subsequent outcross proportions (Fig. 1).

The number of seeds per berry correlated negatively with days to harvest and correlated positively with berry weight for all four cultivars (Table 4). Seeds per berry also correlated positively with percent fruit set for 'St. Cloud', 'Northsky', and 'Northcountry', but not for 'Northblue' (Table 4).

Discussion

Yield components

For 'St. Cloud', 'Northsky', 'Northcountry', and 'Northblue', the yield component responses of percent fruit set, days to harvest, berry weight, and seeds per berry suggest that earlier and larger yields can be expected with increasing amounts of outcross pollination. The significant correlations of seeds per berry with percent fruit set, days to harvest, and berry weight further suggest that this is largely a function of seeds per berry. Percent fruit set in 'Northblue' was the only case in which no such response or correlation was observed. 'Northblue' can form parthenocarpic fruit and, therefore, the responses to self pollination that were absent in other yield components of 'Northblue' were absent for percent fruit set.

The results of this study are similar to those of Rabaey and Luby (1988), who compared the self and outcross fertility of 10 half-high blueberry genotypes, including the cultivars under investigation

Table 3. Analysis of variance for percent fruit set, days to harvest, berry weight (g), seeds per berry, and seeds per pollination on 'St. Cloud', 'Northsky', and 'Northcountry', including only the 1:3, 1:1, 3:1 and 1:0 (outcross) treatments.

Source	Percent fruit set		Days to harvest		Berry weight (g)		Seeds per berry		Seeds per pollination	
	df ^a	Mean squares	df	Mean squares	df	Mean squares	df	Mean squares	df	Mean squares
Blocks (B)	23	0.11	23	111.67	23	0.40	23	64.79	23	78.37
Cultivar (C)	2	0.21**	2	119.02**	2	3.51**	2	18.30	2	42.40
Residual	21	0.10	21	110.97	21	0.11	21	69.22	21	81.80
Treatment (T)	3	0.18**	3	89.36**	3	0.13**	3	220.45**	3	322.41**
Linear	1	0.51**	1	228.73**	1	0.35**	1	641.02**	1	967.06**
Quadratic	1	0.04	1	15.58	1	0.01	1	15.88	1	0.85
B × T	67	0.04	66	17.78	66	0.02	66	17.28	67	21.71
C × T	6	0.02	6	23.70	6	0.03	6	32.35	6	10.74
Error	61	0.04	60	17.19	60	0.02	60	15.78	61	22.79

^aDegrees of freedom.

**F tests significant at $P \leq 0.01$.

here. Most yield component responses tested in both studies were similar. However, the lack of self sterile cultivars and the increase in berry weight of 'Northblue', as the percentage of outcross pollination increased, were unexpected results based on their study. There are at least two explanations for the discrepancies between the two studies. First, experimental precision was increased in the current study by using more replications and a wider range of pollination treatments, which included self/outcross pollen mixtures. Environmental differences provide another source of variation between the experiments. Although both experiments were done under similar greenhouse conditions, environmental differences are likely to occur due to differences between years. This is seen as year-to-year differences in the results of Rabaey and Luby (1988), and similar environmental effects could be expected between the two experiments.

Reproductive fertility

'St. Cloud', 'Northsky', and 'Northcountry'. In an extreme manifestation, inbreeding depression could presumably result in

no seed production with self pollination; all ovules fertilized by self pollen would abort. In this situation, pollination with mixtures of self and outcross pollen would result in intermediate amounts of seed, and outcross pollination would give maximum seed formation. Positive, linear responses of the reproductive traits would be expected as the outcross : self pollen ratio increased, and the Y intercept would pass through the origin.

Self pollination did not result in total lethality for zygotes in this study; a certain percentage of the self pollen did contribute to seed formation. A proportional response from the minimum value in the self-pollination treatment to the maximum value in the outcross pollination treatment represents the hypothesis, with reproductive fertility solely a function of the relative amounts of self and outcross pollen. Such a response, without nonlinear effects, occurred only if the self-pollination treatment was not included in the regression analyses. High levels of berry abscission associated with the self-pollination treatment may have led to the nonlinear responses. Berries that lack the minimum number of seeds necessary for fruit development are aborted before harvest, reducing percent-fruit-set and seeds-per-pollination responses. Similar responses have been observed in apple (*Malus domestica* Borkh.) (Heinicke, 1917; Roberts, 1946) and tomato (*Lycopersicon esculentum* Mill.) (Varga and Bruinsma, 1976).

In this study, as the proportion of outcross pollen increased, more seeds developed, thereby allowing more berries to ripen fully. This increase in fruit set, in turn, may have saved zygotes that were lost in aborted berries in the self-pollination treatment. Similar response reductions in the self-pollination treatment were not evident for days to harvest and berry weight. These traits probably reached some physiological level at which point further reductions in seed count per berry, observed in the self-pollination treatment, had little effect.

In the nonparthenocarpic cultivars, the expectation of a linear response to increasing percentages of outcross pollen in mixtures of self and outcross pollen was shown to be inappropriate. A more realistic expectation is a response that is linear over the mixture and outcross treatments that then drops in a nonlinear manner to a lower response for the self-pollination treatment.

Other factors may be affecting seed formation in this study. Krebs and Hancock (1990) found that outcross pollen, applied up to 48 h after self pollination, resulted in seed set similar to an outcross pollination. This suggests that outcross pollen may be able to 'outcompete' self pollen for ovule fertilization. Similar phenomena have been described recently in half-high cultivars

Table 4. Correlations, by cultivar, of percent fruit set, harvest date, berry weight, and seeds per berry using pooled pollination treatments. *P* values are given in parentheses.

Cultivar and variables	n ^a	Seeds per berry
St. Cloud	33	
Fruit set (%)		0.48 (0.0043)
Days to harvest		-0.43 (0.0134)
Berry weight		0.45 (0.0090)
Northsky	38	
Fruit set (%)		0.68 (0.0001)
Days to harvest		-0.73 (0.0001)
Berry weight		0.80 (0.0001)
Northcountry	35	
Fruit set (%)		0.35 (0.0380)
Days to harvest		-0.51 (0.0016)
Berry weight		0.55 (0.0006)
Northblue	25	
Fruit set (%)		0.15 (0.4700)
Days to harvest		-0.49 (0.0122)
Berry weight		0.58 (0.0025)

^aNumber of observations used for each cultivar.

(Harrison, 1991) and accessions of wild, diploid *V. corymbosum* (Vander Kloet, 1991). Therefore, the presence of the more effective outcross pollen in treatments 1:3, 1:1, 3:1, 1:0 (outcross pollination), in conjunction with increased fruit abortion after self pollination may be responsible for the lack of agreement between the observed and expected responses in this study. Alternatively, these results could suggest a 'mentor pollen effect', in which fertilization by less compatible pollen is stimulated by the presence of compatible pollen (Settler, 1968). In our study, paternity of the progeny was not established, and these hypotheses could not be tested.

'Northblue'. The expectation of a linear increase in seeds per pollination as the outcross : self pollen ratio increases likely was not confounded by berry abscission in 'Northblue', because of the insignificant effect of seeds on fruit set. The observation of a linear response for seeds per berry, which reaches a maximum level, can be explained by the presence of a physiological limit to seeds per berry in this cultivar (Fig. 1). If the maximum number of seeds per berry was reached with the 1:1 treatment, then a linear response for treatments 0:1 (self pollination), 1:3, and 1:1 followed by a level response for the remaining treatments would be consistent with the original hypothesis of this experiment.

The results of this experiment suggest that outcross pollination should be maximized to increase half-high blueberry yields. Percent fruit set and berry weight were positively correlated with seeds per berry, while days to harvest was inversely related. The highest number of seeds per berry was associated with increased levels of outcross pollination. Consequently, mixed plantings of at least two blueberry cultivars should be recommended to obtain a larger crop that ripens earlier when choosing from 'St. Cloud', 'Northsky', 'Northcountry', or 'Northblue'. Even in 'Northblue', which sets fruit regardless of pollen source, increased outcross pollination likely will have a positive effect on yield.

When the confounding effects of fruit abscission are removed, as in the parthenocarpic 'Northblue', a response is seen that appears to be consistent with the original hypothesis of this study: as the outcross : self pollen ratio increases, the fertility of the pollination will increase proportionally. In nonparthenocarpic cultivars, the expectation of a linear response should be modified to account for low fruit and seed set following self pollination.

Linear responses to increasing percentages of outcross pollen suggest that post-fertilization abortion is affecting seed formation. As the percentage of self pollen was reduced, more seeds were formed. The low self fertility observed in this study is consistent with other research on half-high (Harrison et al., 1993) and highbush blueberries (Hellman and Moore, 1983; Krebs and Hancock, 1988, 1990), in which negative effects on reproductive traits were interpreted as manifestations of inbreeding depression.

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