Flower Age Affects Fruit Set and Stigmatic Receptivity in Rabbiteye Blueberry

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Abstract. Rabbiteye blueberry (*Vaccinium ashei* Reade) often exhibits problems with low fruit set. Little is known about the duration of flower receptivity in this species. The objective of this study was to investigate the effects of flower age at pollination on fruit set, seed number per fruit, and stigmatic receptivity. 'Brightwell' and 'Tifblue' rabbiteye blueberry plants were kept under controlled conditions in a growth chamber. Day/night temperatures during pollination were 23 °C/10 °C. Flowers were hand pollinated with self- or cross-pollen at 2-day intervals ranging from 0 to 8 days after anthesis (DAA). Flower age at pollination had a significant effect on both fruit set and seed number per fruit. Rabbiteye blueberry flowers were able to produce optimum fruit set during a period of at least five days. Fruit set was markedly reduced 6 to 8 DAA, depending on the cultivar. Flower age at pollination also had a significant effect on stigmatic receptivity, which was assessed as the number of germinated tetrads on the stigma 24 hours after pollination. Stigmas pollinated 0 DAA had a significantly lower number of germinated tetrads than those pollinated 8 DAA. Flower age at pollination and stigmatic receptivity were positively associated. To our knowledge, this is the first quantitative evidence of delayed stigma maturation in blueberry. Stigmatic receptivity and fruit set were not correlated. Overall, the data strongly suggest that stigmatic receptivity was not a limiting factor for fruit set of 'Brightwell' and 'Tifblue'. It is hypothesized that ovule longevity determines the duration of flower receptivity in these two rabbiteye blueberry cultivars.

Pollination involves the release, transport, and deposition of pollen from the anthers of a flower to a stigma. In blueberry (*Vaccinium* spp. L. section *Cyanococcus* A. Gray), the anthers and the stigma are spatially separated from each other to prevent autogamy (self-pollination with pollen from the same flower), so that pollination is mediated by biotic agents, primarily bees (Coville, 1910). After viable pollen has been deposited on the stigma, successful fertilization and fruit set of blueberry are determined by three maternal factors: the receptivity of the flower, the degree of self-fertility, and the availability of resources for fruit maturation. Rabbiteye blueberry often exhibits inadequate fruit set

(Scherer et al., 2001), and the problem is attributed in part to its low degree of self-fertility (El-Agamy et al., 1981).

Little is known about the duration of flower receptivity in rabbiteye blueberry. According to Young and Sherman (1978), adequate fruit set of 'Bluebelle' is expected to occur after pollination of flowers up to at least 5 d after anthesis (DAA). Cultivar effects on flower receptivity remain unknown for this species. Merrill (1936) and Moore (1964) assessed the length of flower receptivity in highbush blueberry (*V. corymbosum* L.) by recording fruit set after hand pollination at time intervals ranging from 0 to 5 DAA. 'Rubel' exhibited a gradual decrease in fruit set with increasing flower age, although adequate levels were obtained up to 5 DAA (Merrill, 1936). Fruit set of 'Bluecrop' declined sharply at 5 DAA (Moore, 1964). Wood (1962) investigated flower receptivity of lowbush blueberry (*V. angustifolium* Ait.) under field conditions. He found that flower receptivity declines with increasing flower age, although some fruit set can be expected after preventing bee visitation for a period of 7 d.

The effective pollination period, which is the number of days during which pollination of a flower is effective in producing a fruit, is determined by the longevity of the ovules minus the time lag between pollination and

fertilization, providing that this value does not exceed the length of stigmatic receptivity (Williams, 1965). As reviewed by Sanzol and Herrero (2001), the effective pollination period plays a clear role in controlling fruit set and yield of temperate fruit crops.

Little is known about the parameters determining the effective pollination period of blueberry. Young and Sherman (1978) concluded that adequate pollen tube growth can be expected to occur up to at least 5 DAA in tetraploid and hexaploid cultivars. To our knowledge, stigmatic receptivity and ovule longevity have not yet been quantified for blueberry. Indirect evidence suggests that stigmatic receptivity might limit effective pollination period of the species. Dichogamy is the temporal separation of male and female functions within a flower (Bertin and Newman, 1993). The most widespread type of dichogamy among the members of the Ericaceae family is protandry, in which the male function precedes the female. According to Drummond and Groden (2000, p. 6), pollen of lowbush blueberry "is ready for dispersal a few days before the stigma becomes receptive"; however, quantitative data to support this statement was not provided. Vander Kloet (1988, p. 15) indicated that *Vaccinium* flowers are generally protandrous, and that the onset of stigmatic receptivity is "heralded by the presence of a creamy exudate." Based on these observations, we formulated the hypothesis that stigmas of rabbiteye blueberry flowers are not fully receptive on the day of anthesis. The objective of the current study was to investigate the effects of flower age at pollination on fruit set, seed number per fruit, and stigmatic receptivity of two rabbiteye blueberry cultivars after self- and cross-pollination.

Materials and Methods

Plant material and experimental conditions. The rabbiteye blueberry cultivars Brightwell and Tifblue were chosen for this study because of their commercial importance and their differences in fruit set. 'Brightwell' is usually very productive, whereas 'Tifblue' often exhibits low fruit set (Lyrene, 2002; NeSmith and Krewer, 1999). Six plants of each cultivar were used in this 2-year study. Three 4-year-old plants and three 5-year-old plants were evaluated in 2003 and 2004, respectively, under the same controlled conditions. All plants were grown in 19-L containers using pine bark as a growing medium. After chilling under natural conditions outdoors, dormant plants were stored at day/night temperatures of 10 °C/5 °C to slow bud development and to help synchronize bloom. To initiate the experiment, plants with floral buds at stages 1 to 2 (Spiers, 1978) were transferred into a growth chamber located at the University of Georgia Griffin Campus. Flowers were hand pollinated under the following growth chamber conditions: 23 °C/10 °C day/night temperature, 40%/85% day/night relative humidity, and a 13-h photoperiod. These environmental conditions are near

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average for the rabbiteye blueberry growing area in southeastern Georgia. To simulate natural seasonal changes, the temperature was increased to 28 °C/15 °C 4 weeks after pollination and to 30 °C/18 °C 2 weeks later. Plants were fertilized with a 15N–3.9P–10K controlled-release fertilizer and watered daily.

Flower age and pollen source treatments. Flowers with their tubular corolla fully elongated but not yet open were selected for emasculation. Typically, these flowers were just a few hours from anthesis, so that the day of emasculation was considered to be the same day when anthesis would have occurred. Flower age at pollination had five treatment levels: 0, 2, 4, 6, and 8 DAA. Flowers were emasculated every 2 d so that all treatment levels could be pollinated on the same day. ‘Brightwell’ and ‘Tifblue’ flowers were either self-pollinated or reciprocally crossed using fresh pollen collected from newly opened flowers. Pollen was applied onto the stigma using the surface of a steel rod. Pollen viability in the two studied cultivars is high (>80% tetrad germination) according to *in vitro* assays (Brevis et al., 2006). One hundred flowers were pollinated per plant—that is, 10 flowers per flower age × pollen source combination. In 2004, fruit set and stigmatic receptivity were evaluated on the same plants, so the number of pollinated flowers was doubled to 200 per plant. Flowers for both fruit set and stigmatic receptivity evaluations were pollinated with similar pollen on the same day. Flowers of a given treatment combination were randomly located throughout the plant.

Evaluation of fruit set and seed number per fruit. In 2003 and 2004, fruit were harvested when ripe (>90% blue in color). Fruit set was estimated as the proportion of pollinated flowers that produced ripe berries. Harvested fruit were stored in a freezer so that seed counts could be made at a later date. In 2003, all seeds were counted under a dissecting microscope regardless of their degree of development. In 2004, fully developed seeds were counted as a separate class within total seeds, as described by Krebs and Hancock (1991).

Evaluation of stigmatic receptivity. In 2004, stigmatic receptivity was assessed on detached flowers as the number of germinated tetrads on the stigmatic surface 24 h after pollination. Flowers were detached from the plant one day after pollination and fixed in formaldehyde acetic acid alcohol as described by Ngugi et al. (2002). Styles were then softened in 1 N NaOH overnight on a hot plate (60 °C). After softening, styles were mounted in squash preparations with 0.1% water-soluble aniline blue in 0.1 N K₃PO₄ (Martin, 1959). Tetrad germination was examined by fluorescence microscopy. Germinated tetrads on the stigma can be easily identified because those that do not germinate are washed off during the softening and mounting procedure.

Statistical analysis. The experimental design was a randomized complete block split plot with cultivar as the main plot and

a factorial arrangement of flower age × pollen source as subplots, with 10 hand-pollinated flowers per subplot. All response variables were transformed before analysis to reduce heterogeneity of variance. Fruit set was arcsine square root transformed. Averages per plant were calculated for the variables germinated tetrads on the stigma and total number of seeds per fruit, and then the means were square root transformed. Data were analyzed using the SAS statistical package (SAS Institute, Cary, N.C.).

Results

A 2-year study was conducted to evaluate the effects of pollen source and flower age on fruit set and seed number per fruit of ‘Brightwell’ and ‘Tifblue’ rabbiteye blueberry. Preliminary statistical tests indicated that year main effects and interactions were not significant ($P > 0.05$); therefore, data from both years were combined before analysis.

The effect of pollen source on fruit set and seed number per fruit. Pollen source main effect and cultivar × pollen source interactions were significant for fruit set (Table 1). Self-pollination reduced fruit set relative to cross-pollination, although the extent of this decrease depended upon the cultivar (Table 2). ‘Brightwell’ was more self-fertile than ‘Tifblue’. Overall, fruit set of ‘Brightwell’ and ‘Tifblue’ after self-pollination represented 66% and 29% of that after cross-pollination respectively.

Pollen source also had a significant effect on the total number of seeds per fruit (Table 1). Self-pollination reduced total seeds relative to cross-pollination (Table 2). The number of fully developed seeds was correlated with the total number of seeds per berry. Correlation coefficients for ‘Brightwell’ and ‘Tifblue’ were 0.84 and 0.79 respectively ($P < 0.0001$ in both cases). In ‘Brightwell’, fully developed seeds represented 8% and 10% of the total seed content after self- and cross-pollination respectively, whereas in ‘Tifblue’, these percentages were 5% and 8%. Self-pollination caused a slight reduction in the proportion of seeds reaching full development relative to cross-pollination.

The effect of flower age on fruit set and seed number per fruit. Flower age main effect and cultivar × flower age interactions were significant for both fruit set and total number of seeds per fruit (Table 1). Overall, the effect of flower age at pollination was more pronounced on fruit set than on seed number per fruit (Table 2). This is because the variable “seed number per fruit” only takes into account the subset of flowers retained by the plant and developed into a ripe fruit. Flower age did not interact with pollen source, which means that the trends of fruit set and seed number per fruit across flower age were similar following either self- or cross-pollination.

Maximum fruit set for ‘Brightwell’ occurred 2 DAA (Table 2). Flowers of this cultivar produced optimum fruit set (i.e., not statistically different from the maximum

value) during a period of at least 5 d (from 0 to 4 DAA, inclusive). By 6 DAA, fruit set declined to a significantly lower level, although 42% was still a considerable value for a rabbiteye cultivar. Fruit set at 8 DAA was nearly zero for ‘Brightwell’. With ‘Tifblue’, fruit set reached its maximum at 4 DAA (as observed in cross-pollination); fruit set was similarly high from 2 to 6 DAA. The period for optimum fruit set for ‘Tifblue’ (as described earlier) was 5 d, similar to ‘Brightwell’, although its timing appeared to be delayed about 2 d.

Stigmatic receptivity. Cultivar had a significant effect on stigmatic receptivity, which was defined as the number of germinated tetrads on the stigma (Table 3). Overall, the number of germinated tetrads in ‘Tifblue’ was slightly higher than in ‘Brightwell’ (Table 4).

Flower age at pollination had a significant effect on stigmatic receptivity (Table 3). The number of germinated tetrads increased linearly as flower age increased (with contrast confidence at $P < 0.0001$). Stigmas pollinated 8 DAA had significantly more germinated tetrads than those pollinated 0 DAA, regardless of cultivar or pollen source (Table 4). The high receptivity of stigmas from 6 to 8 DAA, as evidenced by the number of germinated tetrads, contrasted with the rapidly decreasing fruit set observed among flowers of similar age. Stigmatic receptivity and fruit set were not positively correlated. Coefficients of correlation for each cultivar after self- and cross-pollination were as follows: ‘Brightwell’, -0.49 and -0.43 ; ‘Tifblue’, -0.14 and 0.08 ($n = 15$ in each case). None of these estimates was statistically significant ($P > 0.05$).

Table 1. Mean squares for fruit set and total number of seeds per berry for ‘Brightwell’ and ‘Tifblue’ rabbiteye blueberry pollinated from 0 to 8 d after anthesis with self- and cross-pollen under growth chamber conditions, 2003–2004.^z

Source	df	Mean squares	
		Fruit set ^y	Total seed no./berry ^x
Block	5	0.185	20.62**
Cultivar (C)	1	1.676*	50.16***
Main plot error	5	0.233	0.90
Pollen source (P)	1	3.142***	136.69***
C × P	1	0.206*	5.05
Flower age (A)	4	1.422***	19.78***
C × A	4	0.848***	10.27***
A × P	4	0.078	1.43
C × A × P	4	0.040	1.22
Subplot error	90 ^w	0.047	1.77

^zData from both years were combined because year main effects were not significant ($P > 0.05$). Sample size was thus six plants.

^yAnalysis performed on arcsine square-transformed data.

^xAverages per plant were calculated before analysis. Analyses were performed on square root-transformed data.

^wThe df value of the error term for seed number per berry was 68 because of missing values (seed count data were not available when fruit set was equal to zero).

*, **, ***Significance at $P \leq 0.05$, 0.01, and 0.001 respectively.

Table 2. Fruit set and total number of seeds per berry for 'Brightwell' and 'Tifblue' rabbiteye blueberry pollinated from 0 to 8 d after anthesis with self- and cross-pollen under growth chamber conditions, 2003–2004.^z

Flower age at pollination (days after anthesis)	Brightwell				Tifblue			
	Fruit set (%)		Seeds per berry (n)		Fruit set (%)		Seeds per berry (n)	
	Crossed	Selfed	Crossed	Selfed	Crossed	Selfed	Crossed	Selfed
0	75 a ^y	57 a	70 a	41 a	23 b	5 b	29 b	—
2	87 a	62 a	72 a	54 a	43 ab	23 a	45 ab	13 ab
4	78 a	48 a	69 a	45 a	63 a	13 ab	50 a	19 a
6	42 b	17 b	64 a	36 a	53 a	15 ab	53 a	9 ab
8	3 c	3 b	— ^x	—	25 b	5 b	37 ab	8 b

^zData from 2 years were combined (n = 6 plant replicates).

^yMeans followed by different letters (within columns) are significantly different according to LSD test at $P \leq 0.05$.

^xMeans are not shown if less than three observations were available (seed counts were unavailable when fruit set was equal to zero).

Table 3. Mean squares for number of germinated tetrads on the stigma for 'Brightwell' and 'Tifblue' rabbiteye blueberry pollinated from 0 to 8 d after anthesis with self- and cross-pollen under growth chamber conditions, 2004.

Source	df	Mean squares ^z
Block	2	0.977
Cultivar (C)	1	1.606*
Main plot error	2	0.081
Pollen source (P)	1	0.074
C × P	1	0.685
Flower age (A)	4	6.526***
C × A	4	0.083
A × P	4	0.700
C × A × P	4	0.452
Subplot error	36	0.405

^zAverages per plant (n = 3) were calculated before analysis. Analyses were performed on square root-transformed data.

*, **, ***Significance at $P \leq 0.05$, 0.01, and 0.001 respectively.

Discussion

Self-pollination reduced fruit set and seed number per fruit relative to cross-pollination. The effect of pollen source on fruit set and seed number is well documented for blueberry, and the results from the current study agree with previous research (Garvey and Lyrene, 1987; Meader and Darrow, 1944, 1947; Morrow, 1943). Rabbiteye blueberries are reported to have a low degree of self-fertility relative to highbush blueberries (El-Agamy et al., 1981). Our results emphasize the fact that there can be important differences in self-fertility among rabbiteye cultivars. 'Brightwell' had a comparatively high degree of self-fertility relative to 'Tifblue', which likely contributes to its better field performance with regard to fruit set (Lyrene, 2002; NeSmith and Krewer, 1999).

The percentage of seeds reaching full development was only 8% to 10% in cross-pollinated fruit, which compares with 37% in 'Tifblue' as reported by Moore et al., (1972). This low percentage of fully developed seeds was likely the result of "cross-incompatibility" (Darnell and Lyrene, 1989), given that 'Tifblue' was reciprocally crossed with its progeny 'Brightwell' (Lyrene, 2002). Nevertheless, fruit set after cross-pollination was high in both cultivars, providing that flower

Table 4. Stigmatic receptivity^z of 'Brightwell' and 'Tifblue' rabbiteye blueberry pollinated from 0 to 8 d after anthesis with self- and cross-pollen under growth chamber conditions, 2004.

Flower age at pollination (days after anthesis)	Germinated tetrads (n)			
	Brightwell		Tifblue	
	Crossed	Selfed	Crossed	Selfed
0	6.6 c ^y	5.0 c	4.2 b	11.6 b
2	10.7 bc	8.3 bc	11.6 a	10.3 b
4	15.2 ab	12.5 ab	15.0 a	14.8 ab
6	18.7 a	12.7 ab	21.2 a	15.5 ab
8	15.3 ab	18.4 a	21.8 a	23.7 a

^zDefined as the number of germinated tetrads on the stigma 24 h after pollination.

^yMeans followed by different letters (within columns) are significantly different according to LSD test at $P \leq 0.05$.

receptivity at pollination was adequate. It may be possible that seeds that are unable to reach full size could still contribute to fruit retention and enlargement by providing hormonal stimuli before abortion. These issues have not yet been adequately investigated in blueberry.

Flower age at pollination had a significant effect on fruit set and seed number per fruit. At day/night temperatures of 23 °C/10 °C, rabbiteye blueberry flowers were able to produce optimum fruit set during a period of at least 5 d. Fruit set was markedly reduced 6 to 8 DAA, depending on the cultivar. The information available for blueberry (Merrill, 1936; Moore, 1964; Young and Sherman, 1978) suggests that there are no major differences in flower longevity between highbush and rabbiteye cultivars, although the number of studies conducted so far is limited. The trends of fruit set and seed number per fruit across flower age were different between cultivars, as indicated by significant cultivar × flower age interactions. Flower performance was markedly different on the day of anthesis, with 'Brightwell' at its optimum level and 'Tifblue' at its lowest. These findings have practical implications in the selection of flowers for controlled crosses in blueberry breeding programs. If the aim is to maximize production of viable seeds, it is recommended to select unopened flowers that are as close to the stage of anthesis as possible for emasculation and pollination. If consistently poor results are obtained with a given

genotype as a mother plant, it may be desirable to repeat pollination around 2 to 3 DAA.

Flower age at pollination and stigmatic receptivity were positively associated. Low stigmatic receptivity limited pollen germination in flowers pollinated on the day of anthesis. To our knowledge, the results from the current study are the first quantitative evidence for delayed stigma maturation in blueberry, although some researchers have suggested that blueberries are generally protandrous (i.e., pollen is released a few days before the stigma becomes receptive) (Drummond and Groden, 2000; Vander Kloet, 1988). Delayed stigma maturation would be consistent with protandry, although the effects of flower age on anther dehiscence and pollen release remain unknown.

Flower age × pollen source interactions were not present for fruit set, which indicated that the trends observed across flower age were unaffected by paternal effects. Therefore, the variability in fruit set associated with flower age was likely the result of maternal parameters. Under the conceptual framework of the effective pollination period, the maternal parameters determining fruit set are two: stigmatic receptivity and ovule longevity (Sanzol and Herrero, 2001; Williams, 1965). In this study, stigmatic receptivity was not correlated with fruit set of either cultivar, which strongly suggest that this parameter was not limiting for fruit set. It is proposed that ovule longevity limits fruit set of 'Brightwell' and 'Tifblue' rabbiteye blueberry. Under this hypothesis, the low performance of 'Tifblue' flowers at 0 DAA could be the result of a lack of embryo sac maturation. Presence of immature ovules at anthesis is characteristic of some almond [*Prunus dulcis* (Mill.) D.A. Webb] (Pimienta and Polito, 1983), apricot (*P. armeniaca* L) (Burgos and Egea, 1993), and pear (*Pyrus communis* L.) (Herrero, 1983) cultivars. Moreover, the low fruit set of 'Brightwell' and 'Tifblue' at 8 DAA could be explained by a loss in ovule viability. Additional research would be needed to test these hypotheses.

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