Journal American Pomological Society 57(1):26-31 2003

Investigations of Metaxenia in Northern Highbush Blueberry (*Vaccinium corymbosum* L.) Cultivars

MARK K. EHLENFELDT[1]

Abstract.

Metaxenia is a change in the tissue of a mother plant as effected by pollen source. A group of 10 cultivars with early to late ripening times were used as females and were cross-pollinated, in a greenhouse, with 10 cultivars (9 matching the female group) to examine the potential for ripening time and fruit-size metaxenia in northern highbush blueberries. Significant differences due to pollen sources were found both across and within cultivars as females; however, no single pollen source had a completely consistent effect on ripening (either accelerating or delaying). Within females, however, the use of 'Duke', 'Bluejay', 'Rube', and 'Elliott' as males, accelerated ripening in 8 of 9 possible combinations. The largest relative effects were delays of ripening, suggesting that poor pollination, poor fertilization, or inbreeding effects may have been factors contributing to the observed variation in ripening times. No correlation was observed between ripening interval of pollen source parents and the effect on the ripening interval of the cultivars as females (i.e. early-ripening males did not induce the fruit on females to ripen earlier). Similarly, for fruit weight, no correlation was found between the ripening interval of cultivars used as pollen sources and fruit weight on females pollinated by those sources. The ability of a pollen source to accelerate ripening was very highly correlated with ability to enhance fruit weight. In general, pollen that enhanced ripening and fruit weight on other cultivars came from cultivars that are regarded as self-fruitful.

In many blueberry growing areas, growers are interested in producing fruit as early as possible to take advantage of the premium market price paid for early-ripening fruit. Thus, any practice that might significantly accelerate ripening date without reducing yield or berry weight, would be beneficial. Conversely, growers in a few states (such as Michigan because of its northern location), might wish to delay ripening and take advantage of late-season prices, if there was no penalty to pay in yield or berry weight.

Xenia is a phenomenon in which a characteristic of the pollen source is expressed in the tissue of the embryo or endosperm (8). Xenia has been documented primarily for endosperm characteristics such as endosperm pigmentation and starch/sugar composition. Similarly, metaxenia is defined as effects of pollen on the characteristics of the maternal tissue, such as a change in the weight or size of the pericarp (8). Metaxenia is of greatest practical interest where it influences characteristics which might have an impact on yield or marketability. Cases of metaxenia for fruit weight and ripening date have been reported in fruits such as cherry (*Prunus avium* L.) (16), pear (*Pyrus communis* L.) (14), raspberry (*Rubus idaeus* L.) (1), date palm (*Phoenix dactylifera* L.) (17), and blueberry (*Vaccinium corymbosum* L. and *V. ashei* Reade) (4).

Growers have long recognized the need for cross-pollination in blueberry to improve fruit set and fruit weight, and cultural recommendations normally suggest planting two or more cultivars in proximity to obtain cross-pollination (5). Various researchers have documented the effect of specific pollen sources on fruit production or fruit quality (6, 7, 10), but did not show any consistent effect of pollen source. A few papers have documented differences in pollen viability (9), and viability effects on fruit development (18).

Gupton (4) observed 'xenia" (his useage) in southern highbush blueberry (*V. corymbosum* introgressed with significant

[1]Research Geneticist. U.S. Department of Agriculture, Agricultural Research Service, Fruit Laboratory, Henry A. Wallace Agricultural Research Center, 10300 Baltimore Ave., Beltsville, MD 20705. Mailing address: Marucci Center for Blueberry and Cranberry Research and Extension, 125A Lake Oswego Road, Chatsworth, NJ 08019

percentages *of V. darrowi)* and in rabbiteye blueberry (*V. ashei* Reade) across more than 14 cultivars. He reported a tendency for early-ripening pollen sources to produce earlier-ripening, larger fruit (i.e. directed metaxenia).

Southern highbush and rabbiteye blueberry represent germplasms which differ in many respects from northern highbush blueberry. If directed metaxenia occurs in northern highbush blueberry, it would be of considerable interest to northern blueberry growers. To investigate this possibility, pollinations were made among a group of 10 northern highbush (*V. corymbosum*) cultivars, to evaluate whether the ripening-time of pollen-source cultivars influenced the berry weight or ripening time of fruit on the female parents.

Materials and Methods

Plant material and pollination procedures - This study employed 10 cultivars as females and 10 cultivars as males with 9 of the cultivars common to both groups (Table 1). Cultivars represented a range of ripening times ranging from the third week of June to the second week of August in the field in New Jersey. The cultivars used are commercially available, and information about them is readily accessible except for 'Bonus'. 'Bonus' is a selection being marketed by a nursery in Michigan, and is reported to be a sibling of 'Elliott'. It is late-ripening and large-fruited. Maternal parents were 4-year old plants grown in 3-L pots in a 50:50 mixture of peat and sand. Pollinations were performed the third week of March in 1997, using freshly collected pollen applied with a pencil tip. A minimum of 100 pollinations were made on unemasculated flowers of each fruiting cultivar with each pollen parent (excluding selfs) in an insect-free greenhouse. Number of pollinations and date of pollination were recorded for each cluster. Pollinations were distributed across five plants of each cultivar to minimize plant-to-plant variation, and all crosses were performed over a period of one week. Ripe fruit were harvested every Monday, Wednesday, and Friday, and date of harvest was recorded to allow calculation of ripening interval. Individual fruit were weighed to 0.01g. To make the results more conservative and more likely to show actual differences, only the earliest ripening 75% of fruit were used for analysis. This eliminated fruit presumed to be poorly pollinated, have few seed, and have substantially extended ripening times.

Statistical analysis of ripening interval and fruit weight — For each fruiting cultivar the data were analyzed as a one-factor general linear model using PROC MIXED (15) with pollen source as the treatment, and the assumptions of the general linear model were tested. To correct for variance heterogeneity, the treatments were grouped into similar variance groups for the analysis when necessary. To evaluate effects of pollen source across fruiting cultivars, the data were also modeled as a two-factor general linear mixed model with pollen source as the fixed effect and fruiting cultivar as the random effect. The assumptions of the general linear model were met. When the treatment effects were statistically significant, mean comparisons were done with Sidák adjusted p-values so that the experiment-wise error rate was 0.05.

Results and Discussion

Highly significant variance was observed both within fruiting cultivars (across all pollen sources) (Table 2a) and across fruiting cultivars for ripening interval (Table 2b). Only 'Legacy' exhibited non-significant variance for ripening interval ($F=1.80$, $p=0.08$). Similarly, for fruit weight, highly significant variance was observed both within fruiting cultivars (across all pollen sources) (Table 2a) and across fruiting cultivars (Table 2b). Only 'Duke' exhibited non-significant variance for fruit weight ($F=1.37$, $p=0.21$).

Ripening times of the fruiting parents under greenhouse conditions ranged from 43.3 days for 'Bluetta' to 76.3 days for 'Elliott'. These results are consistent with the behavior of these cultivars in the field (personal observations) (Table 3). For ripening time, significant differences due to pollen sources were found (across females); however, no single pollen source had a fully consistent general effect on ripening (either accelerating or delaying). However, 'Duke', 'Bluejay', 'Rubel', and 'Elliott' accelerated ripening in 8 of 9 cross combinations. Deviations from the female ripening time mean ranged from relative accelerations of 9% ('Bluecrop' x 'Bluejay') to relative delays of 22% ('Bonus' x 'Legacy'). The only fruiting cultivar with no significant variability (as a female) was 'Legacy', which had a ripening range of only 5 days, relatively brief for a mid-late ripening cultivar. Among the crosses that took longer to ripen, several combinations can be recognized that are relatively inbred: 'Duke' x 'Bluetta', 'Weymouth' x 'Bluetta', 'Blueray' / 'Bluecrop' x 'Bluetta', 'Blueray' x 'Bluecrop' (and reciprocal), and 'Jersey' x 'Bluecrop' / 'Blueray'. Many of the other delayed-ripening combinations had no easily discernable causation. Delays outnumbered enhancements among the observed deviations.

Mean fruit weights for cultivars ranged from 0.73 g for 'Bluetta' to 2.29 g for 'Bonus' (Table 1). Significant differences due to pollen sources were found (across females); however, no single pollen source had a fully consistent general effect on fruit weight; however, 'Rubel' increased fruit weight in 8 of 9 cross combinations. Deviations from the female fruit weight mean ranged from relative increases of 34% ('Weymouth' x 'Duke') to relative decreases of 50% ('Weymouth' x 'Bluejay'). In this group, the only cultivar with no significant variability was 'Duke' which had a fruit weight range of 1.19 to 1.39g, with a mean fruit weight of 1.30g. Among the crosses that had lower fruit weights, several combinations can be recognized that are relatively inbred: 'Bluetta' x 'Duke', 'Weymouth' x 'Bluetta', and 'Blueray' x 'Bluecrop' (and reciprocal). Many other low weight combinations have no obvious cause. Similar to ripening time, low weight deviations outnumbered weight heterosis deviations.

Significant effects were produced by pollen sources for ripening time (Tables 2b, 4) and fruit weight (Tables 2b, 4). Across females, 'Rubel' produced the greatest average acceleration in ripening time, and 'Blueray' produced the greatest average delay. Table 4 shows that both early- and late-ripening cultivars were found to have "beneficial" effects on ripening interval and fruit weight. 'Duke', 'Bluejay', 'Bluecrop',

Table 1. Fruit weight means (in grams) and comparisons for specific crosses. Cultivars on both margins are arranged in ripening order from earliest to latest.

	Cultivar as female									
Pollen source	Bluetta	Duke	Weymouth	Bluejay	Blueray	Bluecrop	Legacy	Jersey	Bonus	Elliott
Bluetta	—	1.25	1.06 b	0.88 ab	0.82 ab	1.20 cd	1.63 ab	0.61 bcd	2.51 ab	1.19 abc
Duke	0.64 bc[1]	—	1.62 a	0.88 ab	0.90 ab	1.28 bcd	1.65 ab	0.87 ab	2.44 ab	1.28 ab
Weymouth	0.67 abc	1.19	—	0.68 ab	1.12 ab	1.54 abc	1.50 b	0.66 d	2.51 ab	0.89 cd
Bluejay	0.81 abc	1.22	0.60 c	—	1.27 ab	1.56 abc	2.00 ab	0.93 a	2.46 ab	0.77 d
Blueray	0.69 abc	1.32	1.28 ab	0.83 ab	—	1.02 d	1.63 ab	0.68 bd	2.12 abc	1.06 bcd
Bluecrop	0.68 abc	1.35	1.28 b	0.94 a	0.81 b	—	1.73 ab	0.79 abd	2.17 bc	1.23 ab
Legacy	0.75 abc	1.37	1.20 b	0.67 b	0.86 ab	1.62 ab	—	0.89 a	1.68 c	1.44 a
Jersey	0.87 a	1.21	0.96 bc	0.76 ab	0.95 ab	1.34 a-d	2.01 a	—	1.67 bc	1.03 bcd
Rubel	0.87 ab	1.35	1.43 ab	0.95 a	1.13 ab	1.67 a	1.68 ab	0.74 abd	2.24 abc	1.37 ab
Elliott	0.63 c	1.39	1.07 b	0.83 ab	1.32 a	1.60 ab	1.70 ab	0.86 ac	2.68 a	—
Mean	0.73	1.30	1.21	0.83	1.10	1.44	1.72	0.78	2.29	1.17
Range	0.63-0.87	1.19-1.39	0.60-1.62	0.67-0.95	0.81-1.32	1.02-1.67	1.50-2.01	0.66-0.93	1.67-2.68	0.77-1.44

[1]Means within columns with different letters are different at the 0.05 significance level.

Table 2a. Analysis of variance for pollen source effects within cultivars (as females) for ripening interval and fruit weight.

		Ripening interval		Fruit weight	
Culivar as female	DF	F-value	p-value	F-value	p-value
Bluetta	8	8.43	<.0001	3.53	0.0007
Duke	8	4.97	<.0001	1.37	0.2105
Weymouth	8	6.79	<.0001	14.13	<.0001
Bluejay	8	12.16	<.0001	2.56	0.0108
Blueray	8	7.26	<.0001	3.50	0.0013
Bluecrop	8	20.29	<.0001	7.33	<.0001
Legacy	8	1.80	0.0807	2.37	0.0236
Jersey	8	7.31	<.0001	5.71	<.0001
Bonus	9	18.43	<.0001	5.84	<.0001
Elliott	8	13.67	<.0001	8.46	<.0001

'Legacy', 'Rubel', and 'Elliott' produced statistically similar effects even though they represent a range of ripening times. No significant correlation was observed between mean ripening interval of pollen source cultivars (Table 3) and the mean ripening interval across all fruiting cultivars when that cultivar was used as a pollen source (Table 4) ($r = -0.48$, $p = 0.19$). This suggests that no generalized metaxenia effect for ripening interval occurs, or if it does, its magnitude is overwhelmed and/or masked by other factors. Analogous results were seen for fruit weight. Across fruiting cultivars, 'Rubel' and 'Elliott' produced the greatest average weight enhancement, and 'Blueray' produced the greatest weight reductions. No significant correlation was observed between cultivar fruit weight mean (Table 1) and the mean fruit weight across all fruiting cultivars when that cultivar was used as a pollen source (Table 4) ($r = -0.53$, $p = 0.14$). It is perhaps not surprising that the cultivars with the greatest "beneficial" effect on ripening interval also showed the most beneficial effect on fruit weight, and the effect was strongly correlated across pollen sources ($r = -0.95$, $p \leq 0.0001$). Many previous studies have demonstrated similar correlations among pollination effectiveness (as measured by seed number and fruit set), ripening interval, and fruit weight (2, 3, 7, 11, 13).

Directed metaxenia for fruit ripening interval did not occur in this group of northern highbush cultivars. Metaxenia was observed, but it occurred as specific cultivar interactions. The primary positive evidence for directed metaxenia in blueberries was the study of Gupton (4) which found significant differences in fruit development period and fruit weight between different cultivars used as pollen sources. Gupton reported that there was a trend for pollen from late-ripening cultivars to produce fruit with a longer interval from pollination to the ripe-berry stage, and for pollen from early-ripening cultivars to produce fruit with a shorter ripening interval. In light of the current results, Gupton's published values were reexamined. A conservative reanalysis of the data suggested correlations between female effect and paternal effect (pollen source) for fruit development period for both rabbiteye and southern highbush were non-sig-

Table 2b. Analysis of variance for pollen source effect across cultivars for ripening interval and fruit weight.

		Ripening interval		Fruit weight	
Treatment	DF	F-value	p-value	F-value	p-value
Pollen source	9	19.22	<.0001	6.17	<.0001

Table 3. Ripening interval means (in days) and comparisons for specific crosses. Cultivars on both margins are arranged in ripening order from earliest to latest.

	Cultivar as female									
Pollen source	Bluetta	Duke	Weymouth	Bluejay	Blueray	Bluecrop	Legacy	Jersey	Bonus	Elliott
Bluetta	—	46.7 a	51.6 a	52.2 ab	58.3 a	62.8 b	65.2	68.9 abc	61.5 b	75.9 cd
Duke	43.1 bc[1]	—	47.3 ab	56.2 a	51.8 ab	58.8 bcd	63.7	58.8 e	62.6 b	73.0 d
Weymouth	44.3 ab	45.5 a	—	55.2 ab	50.0 ab	59.7 bc	66.6	69.8 a	60.5 b	82.1 a
Bluejay	42.0 bc	45.1 ab	47.9 ab	—	52.0 ab	54.6 d	61.5	59.4 de	65.1 b	82.6 abc
Blueray	45.2 a	46.2 a	46.9 ab	51.4 b	—	70.8 a	66.6	65.3 ab	63.5 b	81.6 ab
Bluecrop	43.1 bc	41.9 b	46.8 ab	46.7 d	57.2 a	—	62.3	64.1 a-d	64.6 b	76.2 bcd
Legacy	42.9 bc	44.8 ab	46.0 ab	48.9 bcd	55.4 a	55.2 cd	—	58.3 e	79.4 a	72.2 d
Jersey	42.0 c	45.5 ab	50.0 a	49.6 bc	53.9 a	61.4 bcd	64.1	—	77.5 a	75.6 a-d
Rubel	41.8 c	44.2 ab	45.1 b	49.2 bcd	55.1 a	55.2 cd	63.1	60.1 cde	64.4 b	71.5 d
Elliott	44.5 ab	44.4 ab	45.4 b	48.0 cd	49.7 b	58.9 bcd	64.7	61.0 b-e	62.2 b	—
Mean	43.3	44.6	47.4	50.5	53.4	59.5	64.2	62.7	65.2	76.3
Range	41.8-45.2	41.9-46.7	45.1-51.6	46.7-56.2	49.7-58.3	54.6-70.8	61.5-66.6	58.3-69.8	60.5-79.4	71.5-82.6

[1]Means within columns with different letters are different at the 0.05 significance level.

nificant, as were correlations between female effect and paternal effect for fruit weight. Using data from Gupton (4), correlations between fruit development period in rabbiteye versus pollen parent are r = 0.57, p = 0.17 (7 cvs., Table 1). Similarly, for fruit development period in southern highbush versus pollen parent, r = 0.29, p = 0.53 (7 cvs.,Table 2), and for berry weight in southern highbush versus pollen parent, r = 0.38, p = 0.40 (7 cvs., Table 3). Other results in that publication were not directly analyzable, but the results were suggestive of non-significant correlations.

If the reinterpretation of Gupton's data is correct, it seems unlikely that any directed metaxenia occurs in blueberry. For both ripening time and fruit weight, significant differences due to pollen sources were found for specific combinations, suggesting that these combinations can be particularly desirable (or undesirable). Negative effects (of smaller magnitudes) were observed more frequently than positive effects for both ripening interval and fruit weight suggesting that poor pollination, poor fertilization, or inbreeding effects may have been factors contributing to the observed variation. Coupled with the observation that pollen source ability to enhance ripening interval was very highly correlated with ability to enhance fruit weight strongly suggests that these effects are largely fertility issues. No single pollen source had fully consistent effects on either ripening or fruit weight; however, 'Duke', 'Bluejay', 'Bluecrop', 'Legacy', 'Rubel', and 'Elliott' were among the better pollen sources. 'Duke', 'Bluejay', 'Rubel', and 'Elliott', enhanced ripening in 8 of 9 cross combinations. These culti-

Table 4. Ripening interval and fruit weight effects of cultivars used as pollen sources (averaged across all females.)

Pollen source	Ripening interval mean (days)	Fruit weight mean (g)
Bluetta	59.1 ab[1]	1.18 bc
Duke	56.2 cd	1.29 ab
Weymouth	58.8 ab	1.18 bc
Bluejay	55.5 d	1.27 abc
Blueray	59.9 a	1.15 c
Bluecrop	55.7 cd	1.27 abc
Legacy	55.3 d	1.31 ab
Jersey	57.7 bc	1.19 bc
Rubel	54.6 d	1.35 a
Elliott	55.5 d	1.34 a

[1]Treatment means with different letters are different at the 0.05 significance level.

vars are generally regarded as self-fruitful. 'Duke' and 'Legacy' were shown in an earlier study to be self-fruitful (3) and 'Rubel' has long been regarded as self-fruitful (12). 'Bluecrop' has proven productive in large blocks, and has parthenocarpic tendencies (personal observation) which suggests it too is self-fruitful. This suggests that cultivars generally regarded as self-fruitful, will serve as pollen sources which can help maximize yields in other cultivars, and that fertility is a critical issue in promoting ripening and fruit size.

Literature Cited

1. Colbert, S. and D. de Olivera. 1990. Influence of pollen variety on raspberry (*Rubus idaeus* L) development. J. Hered. 81:434-437.
2. Eaton, G. W. 1967. The relationship between seed number and berry weight in open pollinated highbush blueberries. HortScience 2:14-15.
3. Ehlenfeldt, M.K. 2001. Self- and cross-fertility in recently released highbush blueberry cultivars. HortScience 36:133-135.
4. Gupton, C.L. 1997. Evidence of xenia in blueberry. Acta Hort. 446:119-123.
5. Highbush Blueberry Production Guide (NRAES-55). 1992. Pritts, M.P. and Hancock, J.F. (Eds.) Northeast Regional Agricultural Engineering Service, Ithaca, New York.
6. Harrison, R.E., J.J. Luby, and P.D. Ascher. 1993. Pollen source affects yield components and reproductive fertility of four half-high blueberry cultivars. J. Amer. Soc. Hort. Sci. 119:84-89.
7. Hellman, E.W. and J.N. Moore. 1983. Effect of genetic relationship to pollenizer on fruit, seed, and seedling parameters in highbush and rabbiteye blueberries. J. Amer. Soc. Hort. Sci. 108: 401-405.
8. Kiesselback, T.A. 1980. The Structure and Reproduction of Corn. University of Nebraska Free Press. Lincoln, Nebraska.
9. Lang, G.A. and E.J. Parrie. 1992. Pollen viability and vigor in hybrid southern highbush blueberries (*Vaccinium corymbosum* L. x spp.). HortScience 27:425-427.
10. Lyrene, P.M. 1989. Pollen source influences fruiting of 'Sharpblue' blueberry. J. Amer. Soc. Hort. Sci. 114: 995-999.
11. Meader, E. M. and G. M. Darrow. 1944. Pollination of the rabbiteye blueberry and related species. Proc. Amer. Soc. Hort. Sci. 45:267-274.
12. Merrill, T.A. 1936. Pollination of the highbush blueberry. Michigan Agr. Expt. Sta. Tech. Bul. No. 181.
13. Moore, J. N., B. D. Reynolds, and G. R. Brown. 1972. Effects of seed number, size, and development on fruit size of cultivated blueberries. HortScience 7:268-269.
14. Nyeki, J. 1972. Metaxenia studies of pear varieties. Acta Agron. Acad. Sci. Hungaricae 21:75-80.
15. SAS Institute Inc., SAS/STAT® User's Guide, Version 8, Cary, NC: SAS Institute Inc., 1999. 3884 pp.
16. Stancevic, A.S. 1971. Metaxenia in the sweet cherry: The effect of pollen of the parental variety on the time of ripening of some varieties of sweet cherry (in Croatian: English abstract). Jugoslovensko Vocarstvo 15:11-17.
17. Swingle, W.T. 1928. Metaxenia in the date palm, possibly a hormone action by the embryo or endosperm. J. Hered. 19:257-268.
18. Vander Kloet, S.P. 1983. The relationship between seed number and pollen viability in *Vaccinium corymbosum* L. HortScience 18:225-226.

Five Apple Training Systems Compared

'Royal Gala' on M.9 was grown under four training systems at a planting density of 2976 trees/ha. The systems were slender spindle (SS), Geneva Y-Trellis (GY), Solen Y-Trellis (SY), and V-trellis (LDV). An additional system was the high-density V (HDV) with a planting density of 7143 trees/ha. After 8 years, the differences among the four systems at the lower density were minimal. The two Y-shaped systems had 11-14% more yield than SS but did not intercept more light at maturity. There were no consistent differences in fruit size or color among the four systems at 2976 trees/ha. Especially in the early years, the HDV system yielded much more fruit than did the LDV, but fruit size was reduced, and pruning requirements were much greater. With the similar performance of the four lower density systems, the authors concluded that cost and ease of management should be the major considerations when choosing a tree training system. From: Hampson, C.R., H.A. Quamme, and R.T. Brownlee. 2002. HortScience 37:627-631.