A Proposed Model for Inheritance of Primocane Fruiting in Tetraploid Erect Blackberry

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ABSTRACT. Inheritance of the primocane-fruiting (PF) characteristic was studied in seedling populations of tetraploid (4x) blackberries (*Rubus* subgenus *Rubus*). Four selections (A-1836, A-593, A-830, and A-1680) and two cultivars ('Arapaho' and 'Shawnee') were used as parents in a full diallel crossing scheme. Selection A-593 was used as the main source for PF due to its origin ('Brazos' x 'Hillquist,' the latter an old PF cultivar). All parents except 'Shawnee' have A-593 in their parentage; among the parents, only A-1836 fully expresses PF. Selfing of A-1836 resulted in 100% PF offspring, indicating that A-1836 is homozygous for this trait. Selfing of A-593, A-830, and 'Arapaho' produced either a 35:1 or a 20.8:1 FF (floricane or summer-fruiting):PF segregation ratio, fitting a tetrasomic inheritance model under either random chromosome assortment (RCSA) or random chromatid assortment (RCTA), respectively, also suggesting that PF is controlled by a single recessive gene and that the parents are duplex (AAaa) for this trait. Selection A-1680 and 'Shawnee' selfed did not produce PF progeny, but when crossed with the nulliplex A-1836, gave a 27:1 FF:PF ratio, indicating RCTA and that they are triplex (AAAa) for PF. According to these research, both gametic outputs (RCSA and RCTA) seem to operate in 4x blackberry. The intensity in expression of PF had a negative relationship with time to harvest, with those seedlings showing the highest PF scores producing a crop in early to mid-August. This knowledge will be helpful in implementing breeding strategies to produce PF blackberry cultivars.

Evidence of the primocane-fruiting (PF) characteristic (also known as fall fruiting or tip fruiting) in *Rubus* was recorded as early as 1778 (Hedrick, 1925). It is found mainly in the subgenus *Idaeobatus* in wild and cultivated forms of *R. idaeus* L. (European red raspberry), *R. strigosus* (Michx.) Maxim (American brilliant red raspberry), *R. occidentalis* L. (black raspberry), and *R. illecebrosus* Focke (strawberry-raspberry) (Keep, 1961). Other sources of PF are *R. spectabilis* Pursh. (subgenus *Idaeobatus*), *R. odoratus* L. (subgenus *Anoplobatus*), and *R. arcticus* L. (subgenus *Cylactis*) (Daubeney, 1996). Plants possessing this trait flower and fruit on the tip (and a varying portion of the cane below the tip) of current year's growth (primocanes) in late summer or in the fall; after cropping, that portion of the cane dies leaving the remaining portion to bear a second crop the following summer (Keep, 1988). PF is also found in blackberry (subgenus *Rubus*, formerly *Eubatus*), but not as intensified as it is in raspberry (Moore, 1984). The trait occurs in 'Hillquist,' an old diploid cultivar (Jennings et al., 1992). 'Hillquist' was selected from the wild in Ashland, Va., by L.G. Hillquist, who sent it to Geneva, N.Y., in 1949 (K.E. Hummer, personal communication). This cultivar was crossed in 1967 at the University of Arkansas with the tetraploid cultivar Brazos, resulting in the selection A-593. The selection is tetraploid, suggesting it originated from an unreduced male gamete of 'Hillquist' fusing with a reduced female gamete of 'Brazos' (Moore, 1997). It has not expressed the PF characteristic, but progeny upon selfing segregated for the trait. Three of 46 seedlings showed the trait; the best of these was released as NC194 (Ballington and Moore, 1995). These preliminary observations indicate that PF is controlled by a simple recessive gene, but modifier genes probably affect its expression (Ballington and Moore, 1995).

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Somewhat contradictory results have been reported regarding inheritance of PF in raspberry. It has been attributed to a single recessive gene (Fejer, 1972; Haskell, 1960; Lewis, 1941). Based on an approximate 3:1 ratio in progeny derived from open-pollinated seed from wild *R. idaeus*, Haskell (1960) assigned the symbol *af* to this gene. On the other hand, the trait has been suggested to be under complex genetic control and its expression greatly influenced by environment (Fejer, 1977; Keep, 1961; Ourecky, 1976; Slate, 1939; Waldo and Darrow, 1941). Intercrossing or selfing PF clones very seldom produced 100% PF offspring (Keep, 1961; Oberle and Moore, 1952; Slate, 1939, 1948; Waldo and Darrow, 1941). In addition, no substantial gains in number of PF seedlings produced were observed in populations resulting from crosses between two PF parents as compared with crosses in which only one of the parents exhibited PF (Slate and Suit, 1944). Based on these observations, Fejer (1977), Keep (1961), and Ourecky (1976) concluded that the PF characteristic is controlled by minor genes with predominantly additive action.

This research was undertaken to study inheritance of primocane-fruiting in tetraploid blackberry germplasm developed at the University of Arkansas in order to facilitate future development of PF cultivars. Based on previous observations (Ballington and Moore, 1995), we hypothesized that PF is controlled by a single recessive gene.

Materials and Methods

Four selections (A-1836, A-593, A-830, and A-1680) and two blackberry cultivars ('Arapaho' and 'Shawnee') were chosen as parents to cross in a diallel scheme to produce 36 progenies. The main source of PF used was A-593 due to evidence that it produces PF offspring (Ballington and Moore, 1995). Among the parents, A-1836 (Fig. 1) is the only clone that expresses PF, and among the remaining parents, only 'Shawnee' (Moore et al., 1985) does not have A-593 in its parentage. Therefore, the progeny of 'Shawnee' were not expected to segregate for PF and was used as a control. 'Arapaho' (Moore and Clark, 1993) was used as a potential source for both PF and thornlessness. Parent plants were dug from the field

Fig. 1. Pedigree of A-1836, a primocane-fruited blackberry.

at the University of Arkansas Fruit Substation, Clarksville on 21 Dec. 1993 and transported to the Arkansas Agricultural Research and Extension Center, Fayetteville, where they were potted and kept in a greenhouse. Crossing was initiated on 1 Mar. 1994. Due to low fruit set in the greenhouse, additional pollinations were made in the field at Clarksville in late April 1994 [inflorescences were covered with No. 535 Lawson bags (Lawson Bags, Northfield, Ill.) after emasculation and pollination]. Seeds were germinated following standard procedures (Moore et al., 1974) in our program.

Seedlings were field-planted on 15 to 17 May 1995 at the Arkansas Agricultural Research and Extension Center, Fayetteville.

Populations were set in a randomized complete block design with four replicates. The number of seedlings per population per block varied from 40 in most cases, to only seven in two (A-593 x 'Shawnee' and A-830 x 'Arapaho'). Additionally, five parent plants propagated asexually from root cuttings were included in each block. Plants were spaced 0.60 m apart within rows spaced 1.22 m apart and 24 m long. The plots were maintained following standard cultural practices.

Scoring for primocane fruiting was done in Summer through Fall 1995–97. The dates of first flower buds to reach anthesis and first fruit to ripen (picking maturity) in 1997 were recorded for each seedling showing the PF characteristic. Additionally, each PF seedling was assigned a score, based on a 1 to 10 scale (1 = the weakest, 10 = the strongest), on the intensity of expression of the PF trait (PF score) in the 1997 season.

The Pearson chi-square test was used to compare segregation ratios for reciprocal crosses. In the case that only one phenotype was produced by both crosses, and it was the same phenotype for both, the test statistic could not be computed; the *P* value was set to 1.0 because of the perfect agreement between the phenotypic distributions of the two crosses. The observed data for the segregation ratios in the selfed progenies of the six parents were used to propose a single gene model for inheritance of PF. To test the model, the Pearson chi-square goodness-of-fit test was applied to the observed segregation ratios of the crosses. Since some seedlings did not show the PF trait until 1997, only 1997 data were used in the analyses. Linear regression was used to show the relation of time to harvest and PF score among PF progeny. Statistical computing was done using SAS software (SAS Inst. Inc., Cary, N.C.).

Results

Some seedlings expressed the PF characteristic in the greenhouse about 2 months after transplanting. By late Sept. 1995, over 50% of the progeny from selfing A-1836, and smaller percentages (ranging from 1.3 to 10.1) of progeny from five crosses in which A-1836 was the female parent, had flowered (data not presented). By late Sept. 1996, PF was observed in 27 of 36 populations. At this time, all progeny resulting from selfing A-1836 had flowered on primocanes while in remaining progeny the highest percentage of PF seedling populations was only 19.8% (i.e., A-1836 x A-593), suggesting that PF is recessive and that A-1836 is homozygous for this trait. Anthesis of terminal flowers of inflorescences occurred as

Table 1. Total number of seedlings^z in population and percentage progeny^y expressing the primocane-fruited trait in diallel crosses of tetraploid blackberries during the 1997 growing season.

Female parents	Male parents					
	A-1836	A-593	A-830	Arapaho	A-1680	Shawnee
A-1836	108^z	81	108	120	51	147
	100.0^y	19.8	14.8	15.0	3.9	1.4
A-593	75	126	71	147	148	30
	13.3	4.8	1.4	4.1	1.4	0
A-830	150	153	144	25	153	114
	3.3	3.9	4.1	4.0	0.6	0
Arapaho	138	148	153	144	148	157
	14.5	4.7	1.9	1.4	0.7	0
A-1680	141	142	148	149	140	155
	0.7	0.7	1.4	0.7	0	0
Shawnee	139	143	141	152	148	139
	1.4	0	0	0.7	0	0

early as 15 June in some seedlings and, in some cases, plants continued to flower until the end of the growing season (late October). Similar results were obtained in 1997, but the number of PF seedlings in eight populations was slightly higher (0.7% to 4.0%) than in 1996 (data not presented), and one more population (A-1680 x A-593), showed a PF seedling for the first time (Table 1). Severe winters during 1995–96 and 1996–97 killed several seedlings, causing differences in the total number of plants per population among years (data not presented).

Selfing of A-1836 produced only PF offspring, suggesting this parent is homozygous recessive (nulliplex) for the PF trait (Table 2). Selfing of A-593 gave <5% PF progeny, an indication that PF might be controlled by a single recessive gene in tetrasomic inheritance. Chi-square test revealed a better fit for this type of inheritance under

the assumption of random chromosome assortment (RCSA) (Allard, 1960) for this particular progeny, also suggesting that A-593 is heterozygous duplex (*AAaa*). An approximate 35:1 florican (FF):PF segregation ratio was observed when A-830 and ‘Arapaho’ were selfed, also indicating tetrasomic inheritance, this time with a better fit for random chromatid assortment (RCTA). Therefore, these two clones are also duplex for PF (Table 2). A-1680 and ‘Shawnee’ selfed did not give PF progeny but both clones segregated for PF when in combination with other parents. Crosses between the nulliplex A-1836 and any duplex parent (A-593, A-830, and ‘Arapaho’), or between two duplexes produced the expected FF:PF segregation ratios for either RCSA or RCTA model. The exception to this model was the cross A-830 x A-1836 which did not give enough PF seedlings to conform to the expected ratio; the reciprocal

Table 2. Chi-square test and goodness-of-fit for a single recessive gene controlling primocane (fall)-fruiting in offspring resulting from crosses of tetraploid blackberries.

Population	Proposed parental genotype	Segregating phenotype		Random chromosome assortment ^x			Random chromatid assortment ^x		
		A	a	Expected ratio	χ^2	P	Expected ratio	χ^2	P
A-1836 selfed	<i>aaaa</i>	0	108	0:1	0	1.00	0:1	0	1.00
A-593 selfed	<i>AAaa</i>	120	6	35:1	1.84	0.17	20.8:1	0.01	0.92
A-830 selfed	<i>AAaa</i>	141	3	35:1	0.26	0.61	20.8:1	2.06	0.15
Arapaho selfed	<i>AAaa</i>	142	2	35:1	1.03	0.31	20.8:1	3.37	0.07
A-1680 selfed	<i>AAAA</i>	139	0	1:0	0	1.00	783:1	0.18	0.67
Shawnee selfed	<i>AAAA</i>	134	0	1:0	0	1.00	783:1	0.17	0.68
A-1836 x A-593	<i>aaaa</i> x <i>AAaa</i>	65	16	5:1	0.56	0.45	3.7:1	0.11	0.74
A-1836 x A-830	<i>aaaa</i> x <i>AAaa</i>	92	16	5:1	0.27	0.60	3.7:1	2.69	0.10
A-1836 x Arapaho	<i>aaaa</i> x <i>AAaa</i>	102	18	5:1	0.24	0.62	3.7:1	2.82	0.09
A-1836 x A-1680	<i>aaaa</i> x <i>AAAA</i>	49	2	1:0	---w	0	27:1	0.02	0.89
A-1836 x Shawnee	<i>aaaa</i> x <i>AAAA</i>	145	2	1:0	---w	0	27:1	2.09	0.15
A-593 x A-1836	<i>AAaa</i> x <i>aaaa</i>	65	10	5:1	0.60	0.44	3.7:1	2.82	0.09
A-593 x A-830	<i>AAaa</i> x <i>AAaa</i>	70	1	35:1	0.49	0.48	20.8:1	1.64	0.20
A-593 x Arapaho	<i>AAaa</i> x <i>AAaa</i>	141	6	35:1	0.93	0.33	20.8:1	0.09	0.76
A-593 x A-1680	<i>AAaa</i> x <i>AAAA</i>	146	2	1:0	---w	0	130:1	0.68	0.41
A-593 x Shawnee	<i>AAaa</i> x <i>AAAA</i>	143	0	1:0	0	1.00	130:1	1.10	0.29
A-830 x A-1836	<i>AAaa</i> x <i>aaaa</i>	145	5	5:1	19.2	<0.0001	3.7:1	28.83	<0.0001
A-830 x A-593	<i>AAaa</i> x <i>AAaa</i>	147	6	35:1	0.74	0.39	20.8:1	0.16	0.69
A-830 x Arapaho	<i>AAaa</i> x <i>AAaa</i>	24	1	35:1	0.14	0.71	20.8:1	0.02	0.89
A-830 x A-1680	<i>AAaa</i> x <i>AAAA</i>	152	1	1:0	---w	0	130:1	0.02	0.89
A-830 x Shawnee	<i>AAaa</i> x <i>AAAA</i>	114	0	1:0	0	1.00	130:1	0.88	0.35
Arapaho x A-1836	<i>AAaa</i> x <i>aaaa</i>	118	20	5:1	0.47	0.49	3.7:1	3.79	0.06
Arapaho x A-593	<i>AAaa</i> x <i>AAaa</i>	141	7	35:1	2.06	0.15	20.8:1	0.01	0.93
Arapaho x A-830	<i>AAaa</i> x <i>AAaa</i>	150	3	35:1	0.38	0.54	20.8:1	2.41	0.12
Arapaho x A-1680	<i>AAaa</i> x <i>AAAA</i>	147	1	1:0	---w	0	130:1	0.02	0.89
Arapaho x Shawnee	<i>AAaa</i> x <i>AAAA</i>	157	0	1:0	0	1.00	130:1	1.21	0.27
A-1680 x A-1836	<i>AAAA</i> x <i>aaaa</i>	140	1	1:0	---w	0	27:1	3.39	0.07
A-1680 x A-593	<i>AAAA</i> x <i>AAaa</i>	141	1	1:0	---w	0	130:1	0.01	0.92
A-1680 x A-830	<i>AAAA</i> x <i>AAaa</i>	146	2	1:0	---w	0	130:1	0.68	0.41
A-1680 x Arapaho	<i>AAAA</i> x <i>AAaa</i>	148	1	1:0	---w	0	130:1	0.02	0.89
A-1680 x Shawnee	<i>AAAA</i> x <i>AAAA</i>	155	0	1:0	0	1.00	783:1	0.20	0.65
Shawnee x A-1836	<i>AAAA</i> x <i>aaaa</i>	137	2	1:0	---w	0	27:1	1.84	0.17
Shawnee x A-593	<i>AAAA</i> x <i>AAaa</i>	143	0	1:0	0	1.00	130:1	1.10	0.29
Shawnee x A-830	<i>AAAA</i> x <i>AAaa</i>	141	0	1:0	0	1.00	130:1	1.08	0.30
Shawnee x Arapaho	<i>AAAA</i> x <i>AAaa</i>	151	1	1:0	---w	0	130:1	0.02	0.89
Shawnee x A-1680	<i>AAAA</i> x <i>AAAA</i>	148	0	1:0	0	1.00	783:1	0.19	0.66

^zA and a stand for florican (summer)-fruiting and primocane (fall)-fruiting, respectively.

^yAssuming complete dominance.

^xFrequency of double reduction (a) = 0 and 1/7 for segregation under random chromosome assortment and random chromatid assortment, respectively (Allard, 1960).

^wChi square value is noncalculable.

Fig. 2. Relationship between harvest date and degree of expression of the primocane-fruiting characteristic (PF score) in offspring resulting from diallel crossing tetraploid blackberries. Numbers in the biplot indicate the number of observations (seedlings). Scale for PF score: 1 = the weakest (only a few floral buds at the tip of canes), 10 = the strongest (numerous inflorescences cover at least one third of the cane's length).

cross, however, fit the model. When A-1680 was crossed with A-1836 or with any of the duplex parents, segregation for PF occurred at low frequencies. Similar results were observed in the cross 'Shawnee' x A-1836 (and its reciprocal) and 'Shawnee' x 'Arapaho.' Since A-1680 and 'Shawnee' did not segregate for PF when selfed so as to be considered duplex, it was postulated these two clones are triplex (AAAA) and that segregation could occur only under the assumption of RCTA (Allard, 1960). Under this hypothesis, a 27:1 FF:PF segregation ratio can be expected from the cross between a triplex and a nulliplex. Low fit to this expected ratio was observed when either A-1680 or 'Shawnee' was crossed with A-1836. Crossing of A-1680 with a duplex, and of 'Shawnee' with 'Arapaho,' gave a better fit to a 130:1 FF:PF ratio, which is the expected segregation ratio from the combination of a triplex with a duplex under RCTA. These results show some evidence that A-1680 and 'Shawnee' are triplex.

Bloom date, harvest date, and PF score (intensity of expression of the PF characteristic) were recorded for each seedling showing PF (data not presented). The PF parent, A-1836, started to bloom on 30 June, the first fruits matured on 10 Aug. and, on a 1 to 10 scale, was assigned a score of 10 (all canes showing abundance of inflorescences over at least one third of their length) for expression of PF. Earliest recorded dates for bloom and harvest in seedling populations were 15 June and 25 July, respectively, while the latest bloom date and harvest date were 14 Sept. and 15 Oct., respectively. Mean bloom date of PF seedlings in the experiment was 12 July. Bloom date and harvest date were highly correlated ($r = 0.94$, $P \leq 0.001$) (data not presented), and a negative relationship ($P \leq 0.001$) was observed when harvest date was regressed against PF score (Fig. 2) in the offspring populations.

Discussion

Total expression of the PF characteristic in A-1836 can be attributed to the genetic contribution of both parents of this blackberry selection. In the female parent, the source for PF can be traced

back to A-593, a parent that has been used as a key component in the present research (Ballington and Moore, 1995). On the other hand, we hypothesize that a source for PF also exists in 'Brazos,' a cultivar that is found repeatedly in the pedigree of the male parent of A-1836 (Fig. 1). 'Brazos' is an F_2 that resulted from the cross 'Lawton' (*R. allegheniensis* Porter x *R. frondosus* Bigel) x 'Nessberry,' the latter an F_3 from the cross *R. rubrisetus* Rydb. (*R. trivialis* Smith) x *R. strigosus* (Hall, 1990). *Rubus strigosus* is a major source for PF that has also contributed to increased branching habit of PF red raspberries (Daubeny, 1996). 'Brazos,' therefore, must be a heterozygous clone carrying a recessive allele (i.e., triplex) for PF originating from *R. strigosus*. This could explain the occurrence of PF offspring in some combinations with 'Shawnee' in the present study (Table 2). 'Shawnee' was used as a homozygous A parent because it does not have A-593 in its parentage. Thus, no PF progeny were expected in crosses involving 'Shawnee' if the PF trait was controlled by a single recessive locus. Unexpectedly, PF seedlings resulted from the crosses 'Shawnee' x A-1836 (and its reciprocal) and 'Shawnee' x 'Arapaho.' Since 'Shawnee' selfed did not segregate for PF (Table 2), it was postulated that this cultivar is triplex having inherited a recessive allele for PF from 'Brazos,' a cultivar that is present in the pedigree of both parents of 'Shawnee' (Moore et al., 1985).

Results of this research present some evidence that PF is controlled by a single recessive gene, being consistent with a tetrasomic inheritance model. The chromosome behavior, however, varies among genotypes; some crosses segregate according to a RCTA pattern while others do so following a RCTA pattern (Allard, 1960). Under the hypotheses of RCTA, the model for tetrasomic inheritance had a better fit ($P > 0.20$) in 17 out of 36 populations (Table 2). Even though true random chromatid segregation has been reported to occur very rarely (Sanford, 1983), postulation of this type of inheritance could explain segregation for PF in the crosses triplex x duplex and triplex x nulliplex (and vice versa) which, under the assumption of RCTA, should not produce PF offspring (Allard, 1960). Goodness-of-fit for PF being controlled by a major recessive gene was greater under the hypothesis of RCTA in one self (A-593) and in 14 more populations, with low fit in two progenies (A-1839 x 'Shawnee' and A-1680 x A-1836) (Table 2), indicating that both types of gametic outputs can occur in tetraploid blackberry. These results agree with postulation of a single recessive gene controlling PF in raspberry (Fejer, 1972; Haskell, 1960; Lewis, 1941). There is a possibility that small seedling population sizes prevented the observation of PF segregates in some populations (i.e., A-1680 and 'Shawnee' selfed; A-593, A-830, A-1680, and 'Arapaho' x 'Shawnee'; and 'Shawnee' x A-593, A-830, and A-1680).

The first seedlings expressing the PF trait began to flower in the greenhouse 4 months after the seeds were sown. By the end of the 1995 growing season, flowering was observed in 2% of the seedlings field-planted in May. With the exception of Keep (1961), none of the workers dealing with breeding of PF raspberries (Fejer, 1977; Slate, 1939, 1948; Slate and Suit, 1944; Waldo and Darrow, 1941) have reported fruiting of seedlings in their first year. Keep (1961) noted that PF raspberry seedlings very rarely flowered the year of planting, the vast majority flowered the second year, a considerable proportion fruited the third year, and a few did not fruit until the fourth year. In the present research, percentages of seedlings showing the PF characteristic were 5.29% and 5.33% for the 1996 and 1997 season, respectively, as opposed to only 2% for 1995 (data not presented). Obviously, some seedlings did not flower on primocanes until 2 years after planting. In addition to juvenility, Keep (1961, 1988) attributes the annual difference in number of PF seedlings in red raspberry to environmental effects. In a study conducted in

Ontario, Canada, with PF red raspberries, above ground (heat units) and soil temperatures as well as solar radiation, mainly those prevailing in the middle of the growing season, were the factors that had the greatest influence at the time of floral initiation (Privé et al., 1993). It may be that plants growing in a short season and low heat unit environment do not express the PF trait, while non-PF plants might become PF given enough heat units before the onset of winter. Differences in heat unit accumulation among years and other environmental and physiological factors (i.e., juvenility, biomass, etc.) along with the possibility of modifying genes might explain why the observed phenotypic segregation in the cross A-830 x A-1836 deviated greatly from the expected ratio (Table 2). The number of PF seedlings in this population went from zero in 1995, to two in 1996, to five in 1997. The number of PF seedlings might have increased in 1998, increasing the chances for this population to fit the expected segregation ratio.

In red raspberry, expression of PF within a population of seedlings can vary from weak to very strong (Fejer, 1977). Some plants flower at the tip of one cane only, others at the tip of several canes, and still others in all canes (Keep, 1961). It therefore seems probable that, although under genetic control, there is a physiological threshold for expression of the PF trait. In the present research, expression of PF varied from very weak to very strong, even within populations, intensity in expression correlating negatively with harvest date. Seedlings with the strongest expression of PF fruited from late July to mid-August, whereas those seedlings with the lowest scores tended to fruit later in the season (Fig. 2). Since each of the parents used in this study has a diverse genetic background, the action of modifying genes might also have contributed to different outcomes. Therefore, the discrepancies from the model of tetrasomic inheritance (RCSA vs. RCTA) might be the result of either the operation of modifying genes, of physiological and environmental factors, or of a combination of both.

Blackberry seedlings scoring highest for PF also showed some degree of cane branching (data not presented), which agrees with findings in PF red raspberry that branching is correlated with early summer flowering (Lawrence, 1976). Keep (1961) indicated that season of fruiting of the PF parent and the capacity of the latter to transmit the PF characteristic to its progeny are correlated in raspberry. If this also holds true in blackberry, the best PF individuals could be selected early in the season to use as potential parents to maximize production of PF seedlings.

Some seedlings possessing the PF trait began to flower the same year of planting. This fact and the knowledge that PF seems to be simply inherited could be useful in obtaining PF blackberry cultivars in a shorter period of time as compared to breeding for the traditional summer-fruited types, since the breeding cycles for PF could be shortened. Selection of the best PF genotypes to use as parents in crosses with superior summer-fruited cultivars, followed by crossing between outstanding F_1 half sibs would allow production of PF individuals with superior horticultural characteristics in a fairly short period of time (i.e., two breeding cycles). Of paramount importance would be the identification of F_1 individuals with outstanding horticultural characteristics that are simplex, since crosses among these would allow optimization of PF progeny (i.e., a 3:1 FF:PF ratio, instead of the 35:1 FF:PF ratio that can be expected from the cross duplex x duplex, assuming random chromosome segregation).

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