Novel Peach Flower Types in a Segregating Population from ‘Helen Borchers’

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ABSTRACT. Several new peach (*Prunus persica*) flower types were discovered in an F₂ segregating population from an open-pollinated, non-showy-flowered F₁ seedling of ‘Helen Borchers’, a double-flowered ornamental cultivar. The novel flower types were white and red single-flowered, non-showy blooms, as well as double-flowered, non-showy red, pink, white, and yellow phenotypes. The double, non-showy flowers were very attractive, and resembled pom-pom chrysanthemums. Yellow flower color is unknown in peach. Flower type in the F₂ family segregated ≈3:1 for non-showy (*Sh*_) vs. showy (*shsh*), for anthocyanin-present vs. anthocyanin-absent, and for pink (*R*_) vs. red (*rr*), independently. Flower petal number segregated at about 9:3:4 for classes single:semi-double:double. Although both parents were late flowering, the F₁ was not. The F₂ seedlings showed a wide range in time of flowering. Higher petal number was correlated with later bloom, although it is unclear whether this is due to linkage or developmental differences in the flowers with extra petals. These novel flower types might be useful as ornamentals, and for use in genetics and breeding studies. Microsatellite analysis of possible pollen donors revealed that ‘Oldmixon Free’, a non-showy-flowered peach cultivar, was likely the pollen parent of the F₁.

Peach flowers normally have five separate, perigynous petals and sepals. Commercial peach fruit cultivars have pink flowers classified as one of two types, showy or non-showy, based on the corolla shape and size. Showy flowers have larger, overlapping petals that open nearly flat and hide the sepals. Non-showy flowers have smaller, narrower, slightly cupped petals with the sepals visible between them and the corolla also slightly cupped (campanulate). In non-showy flowers before anthesis, the anthers are often exposed and may dehisce, in contrast to showy flowers where the longer petals cover the anthers, inhibiting pollen shed before anthesis. Most of the oldest United States peach cultivars have non-showy flowers, which are the wild type. Many of the commercially important cultivars from the northern U.S. also have non-showy flowers. Although showy (*shsh*) is recessive to non-showy (*Sh*_) (Bailey and French, 1942), in recent decades more showy-flowered cultivars have been released, perhaps representing breeders’ bias toward showy flowers. The larger size of the unopened flowers makes them easier to emasculate and allows a longer window of availability for hand pollination. Also much of the recent breeding has been done in lower chilling regions, where much of the adapted germplasm was showy-flowered. The *Sh/sh* locus has been mapped, but the morphological and cellular bases of the different types is unknown, as is their relative value to the plant.

Pink is the characteristic peach flower color, but other colors have been reported (Bassi and Monet, 2008), including those designated white, dark pink, red, and variegated [with various combinations of white, pink and red, such as ‘Peppermint’ and ‘Candy Cane’ (Okie, 2013)]. Peaches with showy flowers having extra petals have been used as ornamentals for centuries, often in combination with novel growth forms like upright, weeping and/or dwarf (Hedrick, 1917; Hu et al., 2005; Lammerts, 1945). These “double-flowered” forms can have numbers of extra petals ranging from a few to 75 petals (Lammerts, 1945). For example, ‘Candy Cane’ has 35–40 petals (Okie, 2013). Other floral parts such as pistils and sepals may be multiplied as well. Most highly double-flowered peaches, particularly those with multiple pistils, set little to no fruit, making them desirable as ornamental trees but difficult subjects for genetic studies. We find no report of non-showy flowers in colors other than shades of pink, nor with extra petals.

Peach flower characteristics are useful in identifying cultivars, for verifying parents in crosses, and in genetic and linkage studies. Novel peach flower phenotypes can arise by mutation or from segregation in crosses between distant parents (Bailey and French, 1942; Blake, 1931). As a reproductive organ, the peach flower serves to attract insects. Peach flowers generally open before leaf growth, so changes in floral characteristics are readily visible. Under natural open-pollination, the likelihood of selfing is generally high in the perfect, self-compatible peach flower. The rate of cross-pollination (varying from 0% to 25%) by bees depends on bee populations and on the distances between trees (Bassi and Monet, 2008). Often, it is difficult to determine if a seedling is the result of self-pollination or outcrossing. Identification of the pollen parent of an outcross can be difficult if there are multiple possible pollen sources nearby with similar traits. Under this circumstance, codominant simple sequence repeat (SSR) markers, along with other types of DNA markers, are useful for distinguishing parentage (Chen et al., 2008a, 2008b; Dirlwanger et al., 2004). This approach is

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more effective and informative if the SSR markers contain polymorphic heterozygous alleles that will help distinguish among the possible pollen parents (Chen et al., 2008a).

'Helen Borchers' was introduced before 1939 by W.B. Clarke Nursery of San Jose, CA, for ornamental use, making it one of the oldest commercial ornamental peaches released in the United States. 'Helen Borchers' has very large flowers with 30–40 pink petals, 10 sepals, multiple pistils (Lammerts, 1945) and is late-flowering (late March in Byron, GA). The very rare fruit are small, ovate-shaped, unattractive with little-blush, white-fleshed, and clingstone (Okie, 1998).

This manuscript describes BY02P5129v, an open-pollinated F_1 seedling of 'Helen Borchers'. Segregation of floral traits in a selfed progeny of BY02P5129v is shown and several novel flower types are described. The likely pollen parent of BY02P5129v is identified through the use of SSR markers.

Materials and Methods

PLANT MATERIALS. All trees were grown at the USDA-ARS Southeastern Fruit and Tree Nut Research Laboratory in Byron, GA, using commercial management recommendations. Sixteen open-pollinated fruits (an unusually large crop) were harvested from two trees of 'Helen Borchers' in 2001. The resulting seedlings flowered in 2004. Most of the seedlings produced double-flowers with showy pink, red or white petals, as might be expected from self-pollination of 'Helen Borchers' if it were heterozygous for the genes controlling white and red flower color. However, seedling tree BY02P5129v had standard, light-pink, non-showy flowers mostly with five petals (a few flowers had one to five extra petals), suggesting it was the result of an outcross to a non-showy parent. An open-pollinated progeny of 24 seedling trees of BY02P5129v was grown to verify the parentage. These seedlings were segregated for flower type, flower color, and petal number, confirming that BY02P5129v parentage was 'Helen Borchers' $\times$ unknown non-showy parent. To produce a selfed F_2 population, the 7-year-old seedling tree of BY02P5129v was enclosed in a screen cage during bloom in Spring 2008. All seeds were collected and stratified, and 125 seedlings were planted in the field in Spring 2009 at a spacing of about 1×5 m.

EVALUATION OF FLOWER PHENOTYPES. Floral characteristics were evaluated in Spring 2011, 2012, and 2014. Flower traits were scored on each tree in the population: flower type (showy or non-showy), petal color (white, yellowish-white, yellow, pink, or red), petal number class (class 0 = only five petals per flower, class 1 = most 5 but a few 5–10, class 2 = most 8–12, and class 3 = most >20), and relative bloom stage (1 = no flower bud swelling to 9 = past bloom/petal fall). Fruit set (none, <20 fruit/tree, and >20 fruit/tree) was estimated in June 2011. Because petal color often gets darker as the flower ages, pink flower color was more difficult to categorize. Also, non-showy petals are often darker pink at the margins than at the base, while showy petals are more uniform in color, although they may darken in the center as they age. Because flowers opened over 2–3 weeks, not all trees were blooming at the same time, making comparisons more difficult. We used a consensus rating over 3 years.

STATISTICAL ANALYSIS. Trait frequency and a chi-square test for goodness of fit were performed using statistical functions in Excel (Microsoft, Redmond, WA) to determine whether each trait fit the expected segregation ratios. The critical values under 1 and 2 df are 3.84 and 5.99 ($P = 0.05$), respectively.

SSR GENOTYPING. To identify the possible pollen parent of BY02P5129v, all late-blooming non-showy cultivars located near the Helen Borchers seed source tree—Redhaven, Late Crawford, Champion, Oldmixon Free, and Early Crawford (Okie, 1998)—were included in the SSR analysis. The eight SSR primers (Table 1) were previously reported (Chen et al., 2014) and used in the study on peach to determine the probable pollen parent of 'Helen Borchers' seedling BY02P5129v. The PCR program and genotyping and allele scoring procedure were previously described in detail (Chen et al., 2014). The SSR allele table and chromatogram were generated by GeneMarker 2.4 (SoftGenetics, State College, PA). Each allele was presented in the table and chromatogram by bp, the size of the amplicon peak detected. Individual F_2 seedlings were also tested against a set of eight SSR markers that were heterozygous in BY02P5129v to confirm their selfing origin.

Results and Discussion

SEGREGATION OF FLOWER CHARACTERS. The flowers of 'Helen Borchers', BY02P5129v, and putative paternal parent 'Oldmixon Free' (see below) are shown in Figure 1A. Segregation of different flower phenotypes in the F_2 progeny is shown in Table 2. Bloom type segregated 88 non-showy:37 showy, close to 3:1 as expected ($\chi^2 = 1.41$, $P = 0.24$). Flower color independently segregated 88 anthocyanin-present:37 anthocyanin-absent ($\chi^2 = 1.41$, $P = 0.24$) as well, also about 3:1 as expected. Lack of anthocyanin (W/w) is reported as recessive and results in trees with white flowers and green twigs (Creller and Werner, 1996; Lammerts, 1945). Color ratios were similar in the showy and non-showy types. In trees with anthocyanins present, flower color segregated 63 pink:25 red, about 3:1 ($\chi^2 = 0.55$, $P = 0.46$). There was an excess of red over pink for non-showy class 3 phenotypes, which may reflect scoring errors related to petal color of the small petals found in non-showy double types. Presumably some of the white-flowered (ww) phenotypes were also homozygous recessive for red-flower (rr), but could not be identified because red is epistatic to white due to the total disruption of anthocyanin biosynthesis. Whereas the dark pink petal trait (Dp/dp) is dominant (apparently not present in this population), the red petal trait (R/r) is recessive (Bassi and Monet, 2008; Lammerts, 1945).

Comparing petal number ratings across years (data not shown) showed that classes 0 (five petals only) and 1 (an occasional flower had an extra few petals) were not consistent from year to year. Perhaps these inconsistencies are only chance developmental events and not strictly genetic in origin. Therefore we merged classes 0 and 1 for analysis. Petal number then segregated 68 class 0/1: 29 class 2: 28 class 3, or about 9:3:4 ($\chi^2 = 1.73$, $P = 0.42$) or 9:7 if classes 2 and 3 are combined ($\chi^2 = 0.17$, $P = 0.68$). Although there is at least one dominant gene for double flowers (Beckman et al., 2011), Lammerts (1945) suggested two recessive genes, d_1 and dm_1 , were responsible for extra petals in crosses with 'Early Double Red', i.e., $D_1_Dm_1_$ and $D_1_dm_1dm_1$ for singles, $d_1d_1Dm_1_$ for 1–5 extra petals and $d_1d_1dm_1dm_1$ for 10–16 extra petals. He suggested 'Helen Borchers' might carry an additional allele (Dm_2) for petal number to account for its 30–40 petals. Although we did not count petals on all F_2 seedlings, several of the most highly double flowers had 65–70 petals each. We cannot confirm if 'Helen Borchers' carries the alleles that Lammerts described but the segregation suggests two genes

Table 1. Eight expressed sequence tag simple sequence repeat primers previously reported (Chen et al., 2014) and used in the study on peach to determine the probable pollen parent of ‘Helen Borchers’ seedling BY02P5129v.

Primer name	Forward primer (5'-3')	Reverse primer (5'-3')	Product size (bp)
CX1H01	CTTCCTCTGCATCTCTCTCTCTTT	CTGAGATAGAGAAAGAGTCGGGTC	291
CX1A03	GAGCTCTCAACTCCATAGCAAAA	CTGAAAACCTCCCAACATGATTGAT	111
CX1A05	GCGCTCAAAAGATACTGTGTGTAT	AGAAGATAGCAGATGGCTCAAAGT	180
CX1B07	CAAATAAAGAGAAGGCGAAGAGAG	GACAAAGAGAGAAACGAAAAGAGG	143
CX1E09	GGAAACATCTTTTGGTAATCTCG	AGACATCGTATGTCCATTTAGGGT	126
CX1E11	TGACACACCAAGTAGGAGAGAGAG	AGCTCTTGTCACTTCTTTCAACCT	156
CX1A12	AAACAAACAAAATGCATCTTCAAA	GGAGACAGACAGGGTAGATTAGGA	173
CX1E12	TCTGATATCAACGCTCTCAAACTC	TCTCTCTACCGAAGAGCCTAAAAA	294

Fig. 1. Flowers of peach parents and their F₁ (A), and non-showy flower types from their F₂ family (B). (A) Left: ‘Helen Borchers’ (seed parent, pink, class 3 double showy); middle: BY02P5129v (an open-pollinated F₁ progeny, pink, class 1 non-showy); and right: ‘Oldmixon Free’ (open pollen parent identified by expressed sequence tag simple sequence repeat markers, pink, single class 0 non-showy). The diameter of a hole in the top blue tray is 11 mm. (B) From left to right: white double non-showy (class 2), yellow double non-showy (class 3), pink (with yellowish cast) single non-showy (class 0), typical pink single non-showy (class 0), pink (with yellowish center) double non-showy (class 2), and red double non-showy (class 3).

are involved. If its parent was ‘Klara Meyer’, a flowering peach from Germany with 70–80 petals, as has been suggested (Jacobsen, 1996), ‘Helen Borchers’ might have been heterozygous for an additional factor producing the high number of

petals found in ‘Klara Meyer’. Segregation for this allele in the F₂ could produce the seedlings with petal numbers greater than ‘Helen Borchers’. Most trees with flowers rated class 3 for petal number set no fruit, although two such seedlings had a few fruit.

The chill hour requirements for ‘Helen Borchers’ and ‘Oldmixon Free’ are about 950 h or more below 7 °C (Okie, 1998). Most years at Byron, GA, ‘Helen Borchers’ blooms slightly later than ‘Oldmixon Free’, and both bloom with or later than ‘Contender’, one of the latest blooming U.S. commercial peach cultivars. ‘Contender’ is rated as having a chill hour requirement of about 1050 h below 7 °C (Okie, 1998). In contrast, the F₁ selection BY02P5129v blooms much earlier than either parent, comparable to peaches with a 750 chill hour requirement, suggesting its parents carry different recessive alleles for high chilling requirement. Time of bloom of the F₂ seedlings ranged from similar to the F₁ parent to later than either grandparent. The earliest blooming F₂ seedlings were past petal fall before the latest blooming seedlings had reached anthesis. Trees rated class 3 for petal number were later blooming than those with fewer petals (Fig. 2). In 2014, only two of the 28 class 3 trees were in bloom when the majority of the class 0 and 1 trees were in bloom. Only four of the 83 class 1 or 2 trees were as late blooming as most of the class 3 trees. The Pearson correlation coefficient between the classes of petal number and relative bloom time among all the F₂ progeny in

2011, 2012, and 2014 was –0.642, –0.448, and –0.711, respectively. Whether this effect on bloom time is related to gene linkages or alternately, to differences in floral development rate as a consequence of enhanced petal number, is unknown.

Table 2. Distribution of tree seedlings in a peach F₂ population from ‘Helen Borchers’ × ‘Oldmixon Free’.^z

PNC ^y	Flower color					Anthocyanin ^w		Subtotal	PNC total ^y
	White	Yellow	Y-W ^x	Pink	Red	Absent	Present		
Showy (no.)									
0	1	0	0	0	1	1	1	2	14
1	5	0	0	11	5	5	16	21	54
2	2	0	0	6	2	2	8	10	29
3	1	0	0	2	1	1	3	4	28
Subtotal	9	0	0	19	9	9	28	37	125
Non-showy (no.)									
0	1	0	1	10	0	2	10	12	
1	10	0	3	19	1	13	20	33	
2	4	0	2	9	4	6	13	19	
3	1	3	3	6	11	7	17	24	
Subtotal	16	3	9	44	16	28	60	88	
Color total	25	3	9	63	25	37	88	125	

^zDistribution is based on the counts of seedling trees with the following floral traits, including petal number class (PNC), flower color, presence/absence of anthocyanin, and flower type (showy or non-showy). The data are consensus of ratings over 3 years.

^y0 = only five petals per flower, 1 = most 5 but a few flowers with 5–10, 2 = most 8–12, and class 3 = most >20; PNC total = sum of the two subtotals in the same petal number class. For example, 14 in class 0 is the sum of 2 from showy flowers and 12 from non-showy flowers.

^xY-W = yellowish-white.

^wAnthocyanin-absent = the sum of the values under White, Yellow, and Y-W; Anthocyanin-present = the sum of the values under Pink and Red; Subtotal = sum of Anthocyanin-absent and Anthocyanin-present.

Fig. 2. Distribution of bloom time of F₂ peach seedlings of ‘Helen Borchers’ × ‘Oldmixon Free’ relative to flower petal number class. Bloom time based on 3 years of observations normalized for each year. Bloom time categories range from A (earliest bloom, about 750 chill units required) to G (latest bloom, over 1000 chill units required). Petal number classes are: class 0 = only five petals per flower; class 1 = most five but a few 5–10; class 2 = most 8–12; and class 3 = most >20.

NOVEL PEACH FLOWER TYPES. The red and white single, non-showy flower phenotypes listed in Table 2 have apparently never been reported. The red, pink and white double, non-showy flowers, also novel, are quite attractive, resembling pom-pom chrysanthemums (Fig. 1B). Three of the seven anthocyanin-absent, double non-showy flower types were not pure white as expected, but showed a distinct yellow tint, unlike any previously reported in peach (Fig. 1B), and most showed a slight yellowish cast. About half the class 1 or 2 non-showy anthocyanin-absent trees showed flowers with some slight yellowish color. The yellowish-white color class was somewhat variable from year to year for unknown reasons. None of the trees with white showy flowers had this cast but the population size was smaller (nine trees), especially of the class 3 double types (only one tree). Two of the six class 3 pink non-showy phenotypes also showed a distinct yellowish tint in the center of flower (Fig. 1B).

The sample size is too small to discern the inheritance of this yellow color.

The yellow-colored flowers are unique in peach, and perhaps in *Prunus* as a genus. It is unclear whether the yellow color is the result of a novel pigment, enhanced production of an existing pigment, or concentration of an existing pigment due to the structure or developmental rate of the double non-showy flower. Water-soluble anthocyanins are generally believed the primary source for the pink and red in peach flower and fruit, but peach fruit reportedly also contain a variety of lipid-soluble carotenoids (Gil et al., 2002; Mackinney, 1937; Vizzotto et al., 2006). Unfortunately it appears no one has reported on the pigments in peach flowers or petals. There are anthocyanin and carotenoid pigments that can produce yellow colors (Cazzonelli, 2011; Winkel-Shirley, 2001), making it difficult to speculate whether the yellow color in these flowers is derived from an anthocyanin, a carotenoid, or a mixture of either class. However, some year-to-year variation in the intensity of yellow in the yellow-white phenotypes may imply the pigment(s) belong to the anthocyanin class, such as luteolin or quercetin. It has been reported that the biosynthesis of certain anthocyanins in many genotypes are induced/enhanced by favorable temperature and/or influenced by other environmental factors, whereas that of most carotenoids is development-related and less influenced (Cazzonelli, 2011; Winkel-Shirley, 2001). Although the yellow color was primarily visible in white-flowered phenotypes in which anthocyanin pathways are disrupted, some non-red intermediates may still be produced. A further analysis and determination of the yellow pigment(s) are needed to answer the question.

THE POLLEN PARENT OF BY02P5129v. Among the non-showy-flowered peach cultivars surrounding the showy-flowered Helen Borchers tree, only Oldmixon Free could have been the pollen parent, according to the alleles of eight EST-SSR markers (Fig. 3). ‘Oldmixon Free’ is a very old white-fleshed peach cultivar, dating back to the early 1800s (Okie, 1998). ‘Champion’, ‘Early Crawford’, ‘Late Crawford’, and

Fig. 3. The genotyping chromatograph of an expressed sequence tag simple sequence repeat marker from peach, CX1A03. The size of each detected allele was marked below each peak. From top to bottom, the samples were 'Helen Borchers', BY02P5129v, 'Champion', 'Early Crawford', 'Late Crawford', 'Oldmixon Free', and 'Redhaven'. 'Helen Borchers', showy-flowered, was the seed parent of BY02P5129v, a non-showy-flowered open-pollinated seedling. The other five non-showy-flowered cultivars, near the Helen Borchers tree, were the pollen parent candidates.

'Redhaven', also non-showy-flowered, were clearly excluded as the pollen parent by the four markers in bold because two conflicts in allele inheritance were observed. First, specific alleles (bold italic) at CX1H01, CX1E11, and CX1E12 in the four peach cultivars were not found in BY02P5129v (Table 3). These alleles should be inherited by the progeny if any of these four were the pollinator for 'Helen Borchers'. For example, at CX1E11, 'Early Crawford' had the homozygous alleles of 167 whereas 'Helen Borchers' possessed the heterozygous alleles of 169/171, so the cross-pollination should produce hybrids with either 167/169 or 167/171 alleles, but was unlikely to produce a progeny like BY02P5129v that had the homozygous alleles of 171. Secondly, a new allele, 129 (bold underlined), at CX1A03 was found in BY02P5129v but was not possessed by any of the four peach cultivars (Fig. 3). After the exclusion, only 'Oldmixon Free' had no allelic inheritance conflict for all eight markers, and notably possessed that unique allele, 129, that was also found in BY02P5129v. The marker CX1A03 was most informative among the eight markers used here, because it unambiguously excluded 'Champion', 'Early Crawford', 'Late Crawford', and 'Redhaven' as the pollen parent, and supported 'Oldmixon Free' as the only possible parent among those tested. In addition, analysis of all the F₂ progeny with a set of eight EST-SSR

Table 3. Eight EST SSR markers and their detected alleles used to determine the pollen parent of peach BY02P5129v, an open-pollinated seedling of 'Helen Borchers'.

Cultivar	Marker (allele) ^z													
	CX1H01		CX1A03		CX1A05		CX1B07		CX1E09		CX1E11		CX1E12	
Helen Borchers	307	309	156		302	327	151		145		169	171	182	310 312
BY02P5129v	309		<u>129</u>	156	302	327	151		145		171		182	310 312
Champion	309		156		325	327	151		145		171		182	310 312
Early Crawford	307		156		ND ^y		151	153	145	149	167		182	284 310
Late Crawford	307	309	156	168	302	306	151		145		167	171	182	282 284
Oldmixon Free	307	309	<u>129</u>		302		151		145		169	171	182	310 312
Redhaven	307	309	156		302	327	151		145		167	171	182	282 312

^zEach marker is either heterozygous or homozygous in peach. Only one allele is listed at homozygous loci. Each value is the size (bp - base pair) of the detected allele. The four markers (CX1H01, CX1A03, CX1E11, and CX1E12) in bold were informative with trackable alleles for parental determination. The alleles in bold italic (307 at CX1H01, 167 at CX1E11, and 282 and 284 at CX1E12) excluded these cultivars as a parent. The bold underlined allele (129 at CX1A03) provided unique support that 'Oldmixon Free' was the pollen parent.

^yNot detected.

markers heterozygous in BY02P5129v (with a and b alleles) showed only aa, bb, and ab alleles were inherited in the progeny, suggesting all were F₂ seedlings and none were from outcrossing (data not shown). SSR marker analysis of allelic inheritance scenarios can in some cases confirm a relation (or non-relation) between parent(s) and progeny. In other cases it may yield only a maximal likelihood if the relation is not contradicted by additional markers (Chen et al., 2008b). In other words, it is straightforward to confirm a cultivar is not a parent as long as any allele specific to the cultivar does not segregate into the progeny, or to confirm a progeny is derived from outcross if any allele in the progeny is not from its parent(s). But it is theoretically possible to incorrectly claim a cultivar as a parent because the genome coverage of these markers is limited (Chen et al., 2008b). Due to its high reliability and reproducibility, identification of parents based on limited informative markers has been widely used in various kinship determinations.

Based on the F₂ segregation, parental genotypes appear to be: ‘Helen Borchers’ (*Ww Rr shsh D_xd_x D_yd_y*), ‘Oldmixon Free’ (*WW RR ShSh D_xD_x D_yD_y*), and BY02P5129v (*Ww Rr Shsh D_xd_x D_yd_y*), where *D_x* and *D_y* represent genes for extra petals that may or may not be identical to those of Lammerts. The heterozygous genotype of BY02P5129v was fortuitous in that it allowed segregation of additional genes in the F₂ population.

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