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Growth and Yield of F_1 Hybrid Peaches Developed from Doubled Haploids

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Abstract. **Doubled haploid peach [*Prunus persica* (L.) Batsch] lines were cross-pollinated to produce F_1 hybrids. F_1 hybrids were evaluated at 3, 7, 8, and 9 years after field planting for tree growth as measured by trunk cross-sectional area, and for fruit production as measured by total weight, total number, and production per unit trunk cross-sectional area. Fruit quality of most F_1 hybrids was within the range of quality observed in progeny of standard peach cultivars, and tree growth and productivity were similar to those of standard cultivars. F_1 hybrids present the possibility of developing scion varieties that can be produced from seed, thus eliminating the need for grafting scions onto rootstocks in situations where specific, adapted rootstocks are not necessary. They could also be used to develop genetically uniform seed-propagated rootstocks. The use of doubled haploid-derived F_1 peach hybrids, however, would require reliable, efficient production techniques.**

F_1 hybrids, produced by the mating of homozygous parents, allow the production of specific, uniform genotypes from seed (Fehr, 1987). Breeding programs for F_1 hybrids are based on the selection of inbred parental genotypes with superior combining abilities for traits of interest. While F_1 hybrids are utilized in large-scale production of maize (*Zea mays* L.) and for certain vegetable (Nienhuis and Sills, 1992) and flower crops, F_1 hybrids of tree fruits have not been tested because dependable, efficient technologies have not been developed to produce inbred lines. In certain tree fruit species such as apple (*Malus* ×*domestica* Borkh.), homozygosity leads to severe inbreeding depression, resulting in an inability to sustain highly inbred lines. Additionally, in many tree fruit species, seedlings exhibit long juvenile periods without fruit production, making the use of F_1 hybrid seed impractical for the propagation of scion cultivars. Clonal propagation of tree fruits is usually accomplished by grafting a scion variety onto a rootstock. The rootstock itself may be produced vegetatively or through seed.

There has been interest in the potential of F_1 hybrid apple (Höfer and Lespinasse, 1996; Lespinasse et al., 1983) and peach (Toyama, 1974). Peach is particularly suited for testing the potential of such hybrids because it has a relatively short juvenile period of 2 to 4 years, depending upon the length of the growing season and temperatures during the growing season (Sherman and Lyrene, 1983). Because peach is a predominantly self-pollinating species (Fogle, 1977), it does not suffer significantly from inbreeding depression. Lesley (1957) produced inbred lines that remained vigorous after four to seven cycles of self-pollination. In some cases, the F_1 hybrids produced by crossing these inbred lines exhibited heterosis as measured by trunk cross-sectional area. Monet et al. (1996) observed no decline in fruit weight after three cycles of self-pollination of peach. Fruit size of the hybrids produced from intercrossing these self-pollinated lines was closer in size to that of the larger parent but there was no clear heterosis for this trait.

Hesse (1971) described two monoploid (haploid) peach seedlings. Toyama (1974) isolated 24 naturally occurring haploid peach seedlings, which were identified by their distinctive morphology, from >20,000 seedlings resulting from open-pollination or controlled crosses. The frequency of haploids ranged from 0 to 0.7% of the seedling populations evaluated, and Toyama (1974) suggested that the frequency depended upon unidentified environmental factors. Ten haploids were doubled with colchicine to produce homozygous diploid lines. Toyama suggested using male-sterile lines for the development of F_1 hybrids to avoid hand emasculation of the female parents. Sanford (1983) stated "It is conceivable that the use of inbreds or F_1 hybrids could allow peach and black raspberry cultivars to be propagated by seed, eliminating a major expense in production. In both genera haploids do occur, and it is in these fruit crops that successful utilization of haploids might occur first." While the production of F_1 hybrid peaches is feasible, they apparently have not been produced or tested to date. The purpose of our work was to utilize the doubled haploid lines developed by Toyama (1974) to produce F_1 hybrids and to evaluate tree growth and fruit production of such hybrids.

Materials and Methods

Pollination. Crosses between doubled haploid peaches were made in Spring 1988. The choice of parents was based on pollen fertility rather than on fruit quality or yield. Two doubled haploid lines, ELB (from open-pollinated 'Elberta' peach) and FLA (from open-pollinated 'Flavortop' nectarine) are pollen sterile and were used as female parents. Male parents included doubled haploids from open pollination of 'Alamar' (ALA), 'Lovell' (LOV), 'Redglobe' (RED), and selection P21-5 (selected by T. Toyama from a cross of 'Redhaven' x 'Veefreeze'). Female parent trees were covered with parachutes when the flower petals were tightly closed to exclude foreign pollen. Pollen was applied directly to the stigmas at anthesis, and the parachute covering was removed after petal fall. Nonpollinated flowers served as controls to evaluate the possibility of self-pollination due to a rare occurrence of fertile pollen on sterile trees or cross-contamination from foreign pollen resulting from tears in the parachute covering.

Seed germination and tree care. The resulting seeds were stratified for 90 d at ≈4 °C and planted in individual 10-cm pots in the greenhouse in Jan. 1989. Seedlings ≈0.7 m tall were field-planted on 1 June 1989. Trees were fertilized from 1989 to 1996 with applications of 10N–4.3P–8.3K at 300 $kg \cdot ha^{-1}$ or urea at 250 $kg \cdot ha^{-1}$ in alternating years. Trees were trained to an open center by yearly pruning in late March to early April. Fruit were thinned to produce a commercial crop with ≈20 cm between fruit. Insecticides and fungicides were applied as necessary. Rows were at least 6 m apart, with 1.75 m between trees. In the fourth year of growth (1993), an in-row spacing of 3.5 m was achieved by removing every other tree.

Data collection. At the end of each growing season in 1992 to 1998, trunk diameter of all test trees was measured at 25 cm above the soil surface. In 1992, sibling F_1 hybrid progeny from each of four hybridizations were evaluated, and data were collected from five to 25 trees of each hybridization. In 1996, 1997, and 1998, five sibling F_1 hybrid progeny trees of each of six to seven hybridizations were selected for good tree health and uniformity in size and fruit load. Trees from the cross FLA x P21-5 were evaluated in 1992 and 1996 only. The experimental design in all years was completely randomized with each sibling F_1 hybrid tree considered as a single plot. All fruit were removed from all trees of a hybrid when the majority of the fruit reached the firm-ripe stage as determined by the change in ground color from green to yellow-green (Delwiche and Baumgardner, 1983). In 1992, total weight

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of fruit from each tree and the diameters of five fruit per tree were measured. In 1996 to 1998, all fruit from each of the five trees of each F_1 hybrid were passed through a commercial grader and electronic weight-sizer (Omnisort, Durand-Wayland, La Grange, Ga.) and the total number and total weight of fruit were recorded. Data were converted to fruit weight per unit trunk cross-sectional area (TCSA) for fruit productivity calculations based on tree size.

Fruit quality of doubled haploid parents, F_1 hybrids, and standard cultivars was subjectively evaluated. Ripening date was recorded based on color change as described above. A numerical score of 7 indicated a level for that characteristic typical for commercial cultivars. Ratings lower or higher than 7 were below or superior to commercial standards, respectively (Layne, 1985).

Statistical analyses. Data for tree growth and fruit production were analyzed by SAS PROC GLM and PROC MEANS with mean separation using Duncan's multiple range test (SAS Institute, 1990).

Results

Fruit quality evaluations of F_1 hybrids. Observations of F_1 hybrid fruit demonstrated that, within an F_1 hybrid, fruit characteristics (Table 1) were uniform within the range that we generally observe on budded trees (data not presented). Most of the hybrids did not meet commercial standards for all characteristics evaluated (Table 1); in general, fruit did not have the size, attractiveness, red overcolor, or firmness necessary for a commercial cultivar. Ripe fruit flavor was rated acceptable to good in all hybrids. The doubled haploid parental lines varied in fruit quality, and ELB and LOV were rated as particularly unattractive. Fruit of FLA, LOV, and RED was less than the minimum size necessary for a commercial cultivar (≈6.4-cm diameter), whereas that of P21-5 was of particularly high quality.

Fruit production and tree growth, 1991–92. Production of fruit began in 1992, 3 years after the seedlings were field-planted (Table 2). Greater TCSA of F_1 hybrids was generally associated with lower total fruit weight and lower yield/cm^2 TCSA (Table 2). Yield in 1992 ranged from 10.8 to 17.3 kg/tree. Trees from the hybridization ELB x P21-5 produced the greatest weight of fruit, and close to the greatest number. Fruit diameter in this first year of cropping ranged from 5.20 to 5.78 cm on thinned trees (data not shown).

Tree growth and fruit production, 1996–98. Parental influence on TCSA and fruit production was evaluated by analyzing the data after grouping F_1 hybrids based on common parents. In 1992, only two parents, FLA and P21-5, could be compared. The differences between these two parents were nonsignificant (data not presented). Parental clone affected weight or number of fruit per tree in 1996, 1997, and 1998 (Table 3). The parents FLA and LOV generally appeared to influence production positively, but this effect was not evident when measured as fruit production per TCSA.

Discussion

Comparisons of growth and productivity within the group of F_1 hybrids revealed few differences that were consistent over years, although one hybrid, FLA x LOV, appeared to be superior to the others in both 1996 and 1997. Analysis of parental effects indicated that the parents of this hybrid, FLA and LOV, generally exerted a favorable influence on their hybrid offspring (Table 3). The effect appeared to be related to vigor rather than to production efficiency. Fruit yields and TCSA were highest in hybrids from these parents, but fruit production/unit TCSA was not.

Direct comparisons between F_1 hybrids and conventionally budded trees would be misleading because the trees are propagated on different schedules and these schedules could affect tree growth and fruit production. In the conventional tree production system, rootstock seeds germinate in the nursery in the spring and are bud-grafted either in the summer or the fall of that year. The summer "June-budded" trees are then planted as small caliper trees in the next season. The fall-budded trees are grown for another season and are planted as larger caliper trees in the fall of the next year. These propagation systems affect tree performance, which would differ from that of seed-planted trees, especially in the early years of growth. Thus, instead of making direct comparisons with "June-budded" or fall-budded trees, we chose to compare data obtained from the F_1 hybrids in this study with the historical performance of budded peach trees using the published data from previous studies carried out at the Appalachian Fruit Research Station research plots (Glenn and Miller, 1995; Glenn and Welker, 1996; Glenn et al., 1995; Hammerschlag and Scorza, 1991) (Table 4). Such a comparison may provide a broader-based evaluation of F_1 hybrid performance. Only data for trees that were grown under the same general conditions as the F_1 hybrids (nonirrigated, herbicide weed control within the row, no root pruning) were selected. Over all previous studies, 3-year budded trees yielded an average of 17.6 kg/tree (Table 4), whereas the mean for all F_1 hybrids in the present study was 12.9 kg/tree in 1992. In prior studies, 6- to 8-year-old trees yielded an average of 27.5 kg/tree, vs. an average of 32.8 kg/tree for 7- to 9-

Table 1. Fruit characteristics of F_1 hybrid peaches and doubled haploid parents.[z, y]

Genotype	Ripe Date[x]	Flesh[w]	Set[y]	Diam[y] (cm)	Shape[v]	Pubesc.[y, u]	Red overcolor[y]	Firmness[y]	Pit free[y, t]	Attr[y, s]	Notes[r]
F_1 hybrids											
ALA x P21-5	227	M	8	6.2	R	7	6	5	6	7	---
ELB x LOV	234	M	7	6.2	R	7	4	7	7	6	GGC
ELB x P21-5	233	M	6	6.0	R	7	6	7	8	7	---
ELB x RED	219	M	7	6.6	R	7	6	7	7	7	GGC
FLA x LOV	227	M	8	5.7	R	6	4	4	6	6	---
FLA x P21-5	224	M	8	5.8	R	8	7	6	6	6	RIF
FLA x RED	206	M	6	6.5	R	6	7	5	6	6	RIF, SPLT
Doubled haploids											
ALA	239	M	6	7.0	R	8	7	6	7	7	TP, LFLAV
ELB	237	M	5	6.5	R	7	3	3	7	4	TP, RIF
FLA	219	N	7	5.1	O	N	7	6	7	6	RIF
LOV	239	M	7	5.1	R	5	2	---	7	4	GGC
P21-5	232	M	7	6.7	R	8	7	8	7	8	---
RED	219	M	7	5.7	---	---	9	7	7	5	---

[z]Doubled haploid peach trees derived from open pollinations of 'Alamar' (ALA), 'Elberta' (ELB), 'Flavortop' nectarine (FLA), 'Lovell' (LOV), 'Redglobe' (RED), and a seedling peach selection from a cross of 'Redhaven' x 'Veefreeze' (P21-5).

[y]Subjective ratings on a scale of 1–9 with 7 and above commercially acceptable, averaged over 2 to 3 years, using five to 10 fruit samples per year (one sample year for ALA x P21-5 and FLA x LOV).

[x]Day of the year.

[w]M = melting; N = non-melting.

[v]R = round; O = oval.

[u]Amount of pubescence, lower numbers = more pubescence; N = nectarine.

[t]Freeness of the stone from the flesh, lower numbers are less free.

[s]Overall attractiveness of the fruit.

[r]GGC = green ground color; RIF = red coloration of the flesh; TP = fruit is tipped; LFLAV = low flavor level; SPLT = split pits.

Table 2. Tree growth and yield of F_1 hybrid peaches, 1992, 3 years after field planting.

			Fruit		
F_1 hybrid[z]	n	TCSA[y] (cm^2)	No.	Total wt (kg)	$g \cdot cm^{-2}$ TCSA
ELB x P21-5	10	37.1 b[x]	193 ab	17.3 a	497 a
FLA x LOV	15	44.2 a	168 ab	10.8 b	274 b
FLA x P21-5	5	28.2 b	132 b	11.0 b	397 ab
FLA x RED	25	38.9 a	227 a	13.3 b	349 ab
Pooled SE		3.4	28.1	1.7	067

[z]Doubled haploid peach trees derived from open pollinations of ‘Alamar’ (ALA), ‘Elberta’ (ELB), ‘Flavortop’ nectarine (FLA), ‘Lovell’ (LOV), ‘Redglobe’ (RED), and a seedling peach selection from a cross of ‘Redhaven’ x ‘Veefreeze’ (P21-5).
[y]Trunk cross-sectional area.
[x]Mean separation by Duncan’s multiple range test ($P \leq 0.001$).

Table 4. Performance of F_1 hybrid compared with historical peach performance of budded peach trees in Appalachian Fruit Research Station research plots.

Tree age (yrs)	Yield/tree (kg/tree)	Yield/TCSA[z] ($g \cdot cm^{-1}$)
	Historical[y]	
3	17.6	34
6–8	27.5	36
	F_1 hybrids	
3	12.9	36
7	26.0	30
8	37.2	31
9	35.3	28

[z]Trunk cross-sectional area.
[y]Historical data from: Glenn and Miller, 1995; Glenn and Welker, 1996; Glenn et al., 1995; Hammerschlag and Scorza, 1991.

Table 3. Tree growth and fruiting of F_1 hybrid peaches, 1996–98, 7, 8, and 9 years after field planting.

		Fruit		
Genotype	TCSA[z] (cm^2)	No./tree	Total wt (kg)	$g \cdot cm^{-2}$ TCSA
		F_1 hybrids[x] *1996*		
ELB x LOV	109 b[y]	357 ab	40.1 a	369 a
ELB x P21-5	77 c	205 c	20.1 c	266 ab
ELB x RED	84 bc	74 d	11.3 d	134 b
FLA x LOV	146 a	415 a	34.3 ab	251 ab
FLA x RED	92 bc	238 c	29.3 b	321 a
ALA x P21-5	81 c	281 bc	29.9 b	378 a
FLA x P21-5	50 d	281 bc	16.8 cd	350 a
Pooled SE	8.9	42.6	3.3	39
		Parents[w] *1996*		
ELB	90 a	212 b	23.8 a	256 a
FLA	96 a	311 a	26.8 a	307 a
LOV	127 a	386 a	37.2 a	310 a
P21-5	63 c	256 b	22.2 b	331 a
RED	88 b	156 c	20.3 b	228 a
Pooled SE	17.7	69.9	6.0	72
		F_1 hybrids[x] *1997*		
ELB x LOV	115 b	634 a	40.0 ab	345 a
ELB x P21-5	113 b	346 b	30.9 b	274 a
ELB x RED	94 bc	212 c	29.8 b	326 a
FLA x LOV	180 a	672 a	49.2 a	284 a
FLA x RED	150 a	373 b	44.9 a	336 a
ALA x P21-5	90 bc	312 bc	28.6 b	310 a
Pooled SE	12.8	40.8	3.9	35
		Parents[w] *1997*		
ELB	110 b	397 a	33.6 b	314 a
FLA	164 a	523 a	47.1 a	310 a
LOV	159 a	653 a	44.6 a	315 a
P21-5	103 b	329 b	29.7 b	290 a
RED	126 b	292 b	37.4 ab	331 a
Pooled SE	10.2	38.1	3.0	25
		F_1 hybrids[x] *1998*		
ELB x LOV	122 b	552 ab	36.1 ab	300 bc
ELB x P21-5	136 ab	350 c	30.6 b	227 d
ELB x RED	122 b	333 c	29.6 b	247 cd
FLA x LOV	183 a	573 ab	34.9 ab	205 d
FLA x RED	150 ab	673 a	45.4 a	318 ab
ALA x P21-5	99 b	456 bc	35.4 ab	375 a
Pooled SE	15.8	46.9	7.8	22
		Parents[w] *1998*		
ELB	127 ab	412 b	32.1 a	258 a
FLA	168 a	618 a	39.7 a	256 a
LOV	155 ab	564 a	35.4 a	248 a
P21-5	115 b	403 b	33.0 a	301 a
RED	136 ab	503 ab	37.5 a	282 a
Pooled SE	16.1	46.9	7.9	22

[z]Trunk cross-sectional area.
[y]Mean separation by Duncan’s multiple range test ($P \leq 0.001$).
[x]Doubled haploid trees derived from open pollinations of ‘Alamar’ (ALA), ‘Elberta’ (ELB), ‘Flavortop’ nectarine (FLA), ‘Lovell’ (LOV), ‘Redglobe’ (RED), and a seedling peach selection from a cross of ‘Redhaven’ x ‘Veefreeze’ (P21-5). Hybrid data based upon five single tree replications per year.
[w]Data based upon 15 trees per year for ELB, FLA, and P21-5; 10 trees per year for LOV and RED.

year-old F_1 hybrids. Similar values for productivity were 34 $g \cdot cm^{-2}$ and 36 $g \cdot cm^{-2}$ for 3- and 6- to 8-year-old budded trees, respectively (Glenn and Welker, 1996; Hammerschlag and Scorza, 1991), vs. 36 $g \cdot cm^{-2}$ and 30 $g \cdot cm^{-2}$, respectively, for F_1 hybrids after 3 or 7–9 years in the field. While data presented here are means for all F_1 hybrids, values for individual hybrids in 1998 ranged from 29.6 to 45.4 kg/tree and 205 to 375 $g \cdot cm^{-2}$ TCSA. These comparisons show that the yields of F_1 hybrid trees were well within the ranges expected for bud-grafted peach trees grown in research plots at the Appalachian Fruit Research Station.

The F_1 hybrids evaluated in this study were inferior to commercial cultivars in some fruit quality characteristics. This was not unexpected. Doubled haploid parents were selected based on fertility, not on fruit quality, and they had not been subjected to the selection pressure for fruit quality that is applied to commercial cultivars. Yet the fruit quality of most of the F_1 hybrids was within the range of fruit quality seen in the progeny produced by intercrossing standard peach cultivars (data not presented).

F_1 hybrid peaches present new possibilities for both breeders and peach growers. Peach breeding programs utilizing F_1 hybrids could be directed toward the development of prepotent parental lines with desirable traits fixed in the homozygous state. The development of these lines could be aided by using molecular markers to screen potential parents for the presence of particular single genes (such as male sterility, flesh color, or nectarine) or quantitative trait loci (QTL). Currently, breeding programs concentrate on developing large populations of segregating seedlings with the goal of selecting those with the optimum number of desired traits. Testing the combining ability of parental lines would require evaluating only a few progeny of each combination since the F_1 hybrids from each cross would be uniform. On the other hand, considerable numbers of parents would be necessary for breeding programs aimed at developing cultivars over a wide range of cropping dates (Hesse, 1975).

A major difficulty in further testing F_1 hybrid systems for peaches is the inability to produce haploids reliably. Without haploids, at least six generations of selfing are necessary to produce a high level of homozygosity (Sanford, 1983). This requires at least 18 to 24 years of breeding. Even at this level of inbreeding, Lesley (1957) showed that enough heterozygosity can exist in the selfed lines to preclude the development of F_1 hybrids with enough uniformity for scion cultivars. Pollination of peaches with viable but infertile heat-treated pollen has been proposed as one method of producing peach haploids (Pooler and Scorza, 1997). Pollinating peach with pollen from incompatible *Prunus* species may also produce haploids. If haploids, doubled haploids, and F_1 hybrids produced from mating doubled haploids could be produced consistently, F_1 hybrids could have a number of practical applications in the peach industry. They would have immediate potential for the development of seed-propagated peach rootstocks. Since almost all such rootstocks currently grown in the United States and much of the rest of the world are of seedling origin, F_1 hybrid seed would immediately fit into current rootstock production technology. The benefits of F_1 hybrid rootstocks could accrue through the ability to fix in a homozygous state desirable genes such as those for disease and nematode resistance in seed-produced rootstocks. The male sterility trait in peach, controlled by a single recessive gene, *ps* (Scott and Weinberger, 1944), could be used to produce female parents that could be easily pollinated. Additional alleles for pollen sterility have been reported (Chaparro et al., 1994).

F_1 hybrids are potentially useful with high-density production (HDP) systems. The elimination of grafting and the direct sale of seed or nongrafted seedlings could significantly reduce the cost of trees, making HDP more economically attractive, assuming no need for a specifically adapted rootstock.

The ability to produce uniform seedlings with high fruit quality may be of particular interest in developing countries where seed propagation is the dominant peach production system (Perez, 1989; Perez et al., 1993; Sherman and Lyrene, 1984).

Our study demonstrates that the growth and productivity of F_1 hybrid peaches is similar to those of standard cultivars. F_1 hybrids offer advantages in the production of uniform seedling scion and rootstock cultivars. Future utilization of F_1 hybrid peaches from doubled haploid lines will depend, in part, on the development of efficient systems for producing peach haploids.

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