Genetic Interactions of Pillar (Columnar), Compact, and Dwarf Peach Tree Genotypes

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ABSTRACT. A study was conducted to determine genetic control of the columnar or pillar (PI) growth habit, and to evaluate the effects of interactions of various genes that influence peach [Prunus persica (L.) Batsch (Peach Group)] growth habit. The PI habit (brbr) examined in this study was inherited as a monogenic trait expressing incomplete dominance. The heterozygous Brbr derived from crosses between standard (ST) and PI genotypes was recognized as an upright (UP) tree with narrower branch angles than ST trees but wider than PI trees. The combination of brachytic dwarf (Dw, dw) and/or compact (CT, Ctc) produced dwarf-pillar (DWPI) trees. The effects of the heterozygous Brbr in combination with dw and/or compact (CT) (Ct) could not be recognized by visual observation. Compact pillar (CTPI) trees resulted from the expression of Ct_Brbr. These trees were distinguished from globe-shaped (GL) trees (Ct_Brbr) by the more upright growth habit of the CTPI trees. This genetic study highlights the genetic plasticity of tree growth habit in peach. The investigation of novel growth habits extends our concept of the peach tree. Some growth habits such as PI may have commercial potential for high-density peach production systems. Others, such as DWPI and CTPI may have potential as ornamentals.

Parental germplasm. The CT genotype (‘Com-Pact Redhaven’) was discovered in 1964 as a bud mutation of ‘Redhaven’ (Van Well, 1974). ‘Com-Pact Redhaven’ was crossed with ‘Empress Dwarf’ (Brooks and Olmo, 1971) and produced a number of seedlings, one of which, KV77119, a CT tree, was heterozygous for the compact gene (Ctc) and the brachytic dwarf gene (Dw, dw). KV77119 was crossed with a showy-flowered pillar (SFP) tree (see below). Progeny segregated in a ratio of 1:1 for globe-shaped (GL) : 1 upright (UP) (Scorza et al., 1989). A pedigree and proposed phenotypes and genotypes of parental, F1, F2, and F3 trees used in this study are presented in Fig. 1. Test for allelism in PI sources. Two sources of PI were used in this study. Both were obtained from L. F. Hough [Rutgers University, New Brunswick, N.J. (deceased)]. They were imported originally from Japan. The growth form of these two PI clones was similar. One genotype, SFP, produced double showy variegated flowers and small, bitter, melting, white-flesh fruit. SFP appears to be similar, if not identical, to the Japanese cultivar, Hoki (Yamazaki et al., 1987). The second genotype, a nonshowy-flowered pillar (NSP), produced nonshowy flowers and yellow, non-melting flesh fruit. Differences in fruit and flower phenotypes and the absence of information concerning their precise origins led to questions concerning the allelic identity of these two PI genotypes. In order to test for allelism between the PI genes in SFP and NSP, heterozygous red-leaf SFP, developed at the Appalachian Fruit Research Station, Kearneysville, W.Va., was used as a pollen parent to hybridize with NSF. While green-leaf pillar progeny from this cross could have resulted from self-pollination of the female green-leaf NSF parent, red-leaf trees could only result from hybridization between the red-leaf SFP and the green leaf NSF since there were no other red-leaf trees in the block or adjacent blocks. Hybrids were also produced between a tree heterozygous for both PI (from SFP) and red-leaf, and a green-leaf NSF. If the PI genes were allelic, a 1 PI : 1 UP ratio

Materials and Methods

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would be expected along with 1 red-leaf : 1 green-leaf. Red-leaf PI trees would be most diagnostic because these could only result from cross-hybridization as opposed to self-pollination of the green-leaf parent that could have occurred unintentionally.

**Hybridization of PI with ST, DW, and WE Phenotypes.** SFP and NSP were hybridized with standard (ST) growth habit peach cultivars, and DW and WE peach phenotypes. The PI parent was used as a male or female parent depending on the cross, but reciprocal crosses using the same parents were not performed. The general hybridization method was as described in Scorza and Sherman (1996). Self-pollination was achieved by covering trees with parachutes from pre-bloom until petal fall (Werner and Cain, 1985). Fruit were harvested, seeds were removed from the endocarps and stratified (moist pre-chilled) at 5°C for 2 months or until radicals appeared, planted in a medium of 3 peat: 1 perlite (by volume), and fertilized monthly with a water soluble fertilizer containing 10N–4P–8K. Seedlings were field planted, left unpruned, and evaluated for growth habit after 1 to 4 years in the field. Trees were fertilized with 325 kg·ha⁻¹ of 10N–4P–8K in the spring of each year. Herbicides, insecticides, and fungicides were applied as needed during the growing seasons.

**Development of F₂ and F₃ Populations.** Five F₁ GL and 10 UP trees from the cross KV77119 × SFP were self-pollinated by covering trees with parachutes. Following stratification and germination, seedlings grew for 9 months in a greenhouse and were planted in the field in September 1987 at a spacing of 2 m within rows and 6 m between rows. Growth habit was evaluated independently by two observers following two seasons of growth and again during the fourth season of growth in the field. Based on field observations, nondwarf trees were placed into one of six phenotypic classes: ST, UP, PI, CT, GL, or Compact Pillar (CTPI). DW trees were rated as DW or pillar dwarf (DWPI). The difference in growth between some of these tree types was subtle. Examples of some of these tree types were self-pollinated to produce F₃ populations to further clarify the combination of genes in particular trees expressing subtle differences in growth habit. The phenotypes selected included GL, CTPI, DW, and DWPI. Seeds were germinated and seedlings grown in a manner similar to that of the F₂ trees and evaluated after 1, 2, 3, and 5 years in the field.

**Results**

**Test for Allelism of Pi Gene.** Two populations of hybrid progeny (64 trees, and 11 trees) resulted from crosses of green-leaf NSP × red-leaf SFP. All progeny, whether green- or red-leaf, were PI (Table 1). Cross 1 produced an excess of green-leaf progeny indicating that some of the progeny were products of self-pollination of the green-leaf NSP. Both crosses of green-leaf NSP by red-leaf UP produced phenotypic ratios of 1 PI : 1 UP. These crosses also produced

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more green-leaf PI than expected again indicating some self-pollination. Over all crosses, these results indicated that the PI growth habit from SFP and NSP resulted from the expression of the same gene.

**Table 1. Tests of allelism of the pillar gene from SFP and NSP sources using green-leaf (grgr) parents and heterozygous red-leaf (Grgr) parents.**

| Cross | Pillar (no. trees) | Nonpillar (no. trees) | Red (no. trees) | Green (no. trees) | $\chi^2$ | P |
|-------|-------------------|-----------------------|-----------------|-------------------|---------|---|
| GR NSP x RL SFPy,x | 64 | 0 | 0 | 0.99 | 25 | 39 | 3.06 | 0.05–0.1 |
| GR NSP x RL SFPy,x | 11 | 0 | 0 | 0.99 | 6 | 5 | 0.09 | 0.70–0.80 |
| GR NSP x RL SFUPwx | 51 | 41 | 1.09 | 0.2–0.3 | 36 | 56 | 4.35 | 0.02–0.05 |
| GR NSP x RL SFUPwx | 57 | 59 | 0.03 | 0.8–0.9 | 50 | 66 | 2.21 | 0.10–0.20 |

$\chi^2$ ratio tested for growth habit = all PI.

**Table 2. Segregation of peach tree growth type.**

| Cross | Progeny (no. trees) | Expected ratio | $\chi^2$ | P |
|-------|---------------------|----------------|---------|---|
| ST x PI | Pegaso x NSP | 4 | 105 | 0 | 1:0 | 1.43 | 0.20–0.30 |
| Suncrest x NSP | 17 | 103 | 0 | 1:0 | 0.089 | 0.30–0.50 |
| Supergem x NSP | 2 | 35 | 0 | 1:0 | 0.005 | 0.90–0.95 |
| Cesarini x NSP | 0 | 8 | 0 | 1:0 | 0.999 | 0.02–0.05 |
| IFF100 x NSP | 0 | 31 | 0 | 1:0 | 0.021 | 0.80–0.90 |
| IFF101 x NSP | 1 | 37 | 0 | 1:0 | 0.003 | 0.90–0.95 |
| City 32-82 x NSP | 0 | 9 | 0 | 1:0 | 0.001 | 0.90–0.95 |
| Fireseed x NSP | 0 | 28 | 0 | 1:0 | 0.999 | 0.02–0.05 |
| Maria Aurelia x NSP | 0 | 7 | 0 | 1:0 | 0.999 | 0.02–0.05 |
| Total | 24 | 363 | 0 | 1:0 | 1.43 | 0.20–0.30 |
| PI x ST | NSF x Springbelle | 0 | 67 | 3 | 1:0 | 0.089 | 0.30–0.50 |
| (Suncrest x NSP) x StarMay | 2 | 10 | 0 | 1:0 | 0.005 | 0.90–0.95 |
| (Pegaso x NSP) x StarMay | 30 | 29 | 5 | 1:0 | 0.999 | 0.02–0.05 |
| (NSP x Springbelle) x Royal Glory | 8 | 4 | 4 | 1:0 | 0.999 | 0.02–0.05 |
| Total | 40 | 43 | 9 | 1:0 | 0.979 | 0.50–0.70 |
| ST x UP | Springlady x (NSP x Springbelle) | 9 | 11 | 0 | 1:0 | 0.005 | 0.90–0.95 |
| (Suncrest x NSP) x (Pegaso x NSP) | 8 | 17 | 7 | 1:0 | 0.005 | 0.90–0.95 |
| (Suncrest x K2) x NSP | 11 | 18 | 9 | 1:0 | 0.005 | 0.90–0.95 |
| (Pegaso x NSP) x (SFP x Redskin) | 28 | 54 | 30 | 1:0 | 0.005 | 0.90–0.95 |
| (Pegaso x NSP) x (SFP x Redskin) | 8 | 13 | 9 | 1:0 | 0.005 | 0.90–0.95 |
| (Suncrest x NSP) x (SFP x Redskin) | 5 | 13 | 6 | 1:0 | 0.005 | 0.90–0.95 |
| Total | 60 | 115 | 61 | 1:2:1 | 0.999 | 0.02–0.05 |
| UP x PI | [(Bounty x NSP) x (Fire Red x NSP) (UP)]y | 0 | 29 | 38 | 1:0:1 | 2.1 | 0.10–0.20 |
| [Flavortop x NSP] x (Fire Red x NSP) (PI)] | 0 | 27 | 35 | 1:0:1 | 2.1 | 0.10–0.20 |
| PI self-pollinated | SFP | 0 | 0 | 13 | 0:1:0 | 0.999 | 0.02–0.05 |
| NSP | 0 | 0 | 19 | 0:1:0 | 0.999 | 0.02–0.05 |
| NSP | 0 | 0 | 22 | 0:1:0 | 0.999 | 0.02–0.05 |
| Total | 0 | 0 | 54 | 0:1:0 | 0.999 | 0.02–0.05 |
| WE x PI | 91459 x NSP | 0 | 47 | 0 | 0:1:0 | 0 | 0.999 |
| DW x PI | Empress (op op) x SFP | 0 | 18 | 0 | 0:1:0 | 0 | 0.999 |
| Empress (op op) x SFP | 0 | 19 | 0 | 0:1:0 | 0 | 0.999 |
| Empress (op op) x SFP | 0 | 21 | 0 | 0:1:0 | 0 | 0.999 |
| Valley Red x NSP | 0 | 31 | 0 | 0:1:0 | 0 | 0.999 |
| Total | 0 | 89 | 0 | 0:1:0 | 0 | 0.999 |
| PI x CT | NSF x Elbertita | 0 | 14 | 0 | 0:1:0 | 0 | 0.999 |

*ST = standard growth form, UP = upright; PI = pillar, NSP = nonshowy-flowered pillar, WE = weeping, DW = dwarf, op op = second generation derived from open pollinations, and SFP = showy-flowered pillar.

**Table 2. Segregation of peach tree growth type.**

**Inheritance of Pi.** Self-pollinated PI trees produced only PI (Table 2). PI crossed with ST produced primarily one tree type (UP) characterized by a more upright growth than ST trees (Fig. 2). This upright growth was more clearly evident in some crosses than in

more green-leaf PI than expected again indicating some self-pollination. Over all crosses, these results indicated that the PI growth habit from SFP and NSP resulted from the expression of the same gene.
INTERACTION OF PI, DW, CT—F2 GENERATION. Pillar. Segregation data from progeny of self-pollinated F1 parents, supported previous data indicating that the PI phenotype is controlled by a single gene (Yamazaki et al., 1987). Over all crosses, progeny segregated into 3 nonpillar (BrBr, Brbr) : 1 pillar (brbr), with acceptable chi-square values (Table 3). Independent evaluations by two observers resulted in consistent classification of trees as pillar or nonpillar. The difference between the BrBr genotype (ST tree phenotype) and the Brbr genotype (UP tree phenotype) in these F2 populations was more dependent on the subjective interpretation of the observer, as evidenced by a large number of discrepancies in classification between standard (BrBr) vs. upright (Brbr) (data not presented). Chi-square values on total trees observed using a 1 \( \chi^2 \) 2 : 1 model of no dominance were unacceptably large (pooled \( \chi^2 = 90.59, P < 0.001 \); sum of \( \chi^2 = 99.16, P < 0.001 \)). This difficulty in discrimination between BrBr and Brbr in these populations may have been due to confounding effects of environmental and interlocus interactions related to the genetic backgrounds of the original parental germplasm including 'Com pact Redhaven' and 'Empress'.

Compact. Previous work has shown that the compact allele is inherited as a simple Mendelian dominant (\( C_t \)), producing a 3:1 segregation of compact to noncompact progeny (Mehlenbacher and Scorza, 1986). In the current study, expression of the \( C_t \) gene was evaluated by grouping all trees that expressed characteristics typical of compact growth, specifically dense branching habit, increased tree canopy, and decreased tree height.

Table 3. Summary of segregation of the pillar (PI) phenotype in progeny of self-pollinated UP (Brbr) trees.

| Parent no. | Progeny (no. trees) | Nonpillar | pillar | \( \chi^2 \) | P |
|-----------|---------------------|-----------|-------|-----------|---|
| 64        | 174                 | 35        | 7.11  | <0.01     |
| 66        | 266                 | 104       | 1.91  | 0.10–0.20 |
| 72        | 93                  | 37        | 0.83  | 0.30–0.50 |
| 76        | 154                 | 76        | 7.93  | <0.01     |
| 79        | 42                  | 16        | 0.21  | 0.10–0.20 |
| 81        | 173                 | 60        | 0.07  | 0.70–0.80 |
| 83        | 81                  | 24        | 0.26  | 0.10–0.20 |
| 84        | 132                 | 37        | 0.87  | 0.30–0.50 |
| 91        | 56                  | 20        | 0.07  | 0.70–0.80 |
| 94        | 16                  | 3         | 0.86  | 0.30–0.50 |

Expected ratio 3 nonpillar : 1 pillar

\( \chi^2 \)

Pooled 0.46 0.30–0.50

Sum 20.12 0.02–0.05

Heterogeneity 19.66 0.02

*Parent trees were upright tree form (UP) F1 progeny of the cross KV77119, a compact (CT) growth habit tree, and a showy-flowered pillar (SFP) tree.

Table 4. Segregation of compact (CT) and non-CT growth types [grouping CT and CT pillar (CTPI) as CT, and standard and pillar as non-CT] in progenies of four self-pollinated CtctBrbr trees. Chi-square values are based on the expected frequency of 3 CT : 1 non-CT (Mehlenbacher and Scorza, 1986).

| Self-pollinated parent | Progeny (no.) | Compact (no. trees) | Noncompact (no. trees) | \( \chi^2 \) | P |
|------------------------|--------------|---------------------|------------------------|-----------|---|
| Tree 63                | 27           | 8                   | 0.081                  | 0.70–0.80 |
| Tree 65                | 60           | 25                  | 0.662                  | 0.30–0.50 |
| Tree 87                | 43           | 15                  | 0                      | 0.99      |
| Tree 89                | 104          | 49                  | 4.19                   | 0.02–0.05 |

\( \chi^2 \)

Pooled 1.73 0.10–0.20

Sum 4.93 0.20–0.30

Heterogeneity 3.20 0.30–0.50

*Parent trees were globe-shaped (GL) tree form, F1 progeny of the cross KV77119, a compact (CT) growth habit tree and a showy-flowered pillar (SFP) tree. For genotypes of progeny see Fig. 1.

Table 5. Phenotypes, expected genotypes, expected frequencies, and mean observed frequencies of six observed classes of progeny from self-pollinated CtctBrbr peach trees.

| Phenotype | Expected genotype | Expected frequency | Mean observed frequency |
|-----------|-------------------|--------------------|------------------------|
| Compact   | CtCtBrBr          | 1/16               |                        |
|           | CtctBrBr          | 2/16               |                        |
| Globe     | CtCtBrBr          | 2/16               | 3/16 (19%) 25%         |
|           | CtctBrBr          | 4/16               |                        |
|           | CtctbrBr          | 6/16 (38%)         | 27%                   |
| Compact pillar | CtCtbrBr       | 1/16               |                        |
|           | CtctbrBr          | 2/16               |                        |
| Standard  | ctcBrBr           | 3/16 (19%)         | 19%                   |
| Upright   | ctcBrBr           | 1/16 (6%)          | 8%                    |
| Pillar    | ctcbrBr           | 2/16 (12%)         | 12%                   |
|           | ctcbrBr           | 1/16 (6%)          | 9%                    |

*Mean phenotypic frequency in four F2 populations (63, 65, 87, 89).
branch angle, and reduced height (Mehlenbacher and Scorza, 1986; Scorza et al., 1989), as CT genotypes. These evaluations confirmed the expected 3:1 ratio (Table 4). In the F1 populations that we studied, the CT phenotype (Ct_BrBr) was not well distinguished from GL (Ct_Brbr), a tree type characterized by a uniformly round, dense canopy, the former being over-represented and the latter under-represented.

Interaction of pillar and compact. Segregation of the PI (br) and CT (Ct) genes appeared to be independent, based on an insignificant contingency chi-square (2.104, P = 0.1–0.25). Expected dihybrid ratios of Ct and br are indicated in Table 5, and segregation data of the Ct and br genes from four self-pollinated CtctBrbr individuals are presented in Table 6.

Dwarf. The brachytic dwarf used in this study is controlled by a single recessive gene (dw) (Lammerts, 1945). Tree KV77119 which is heterozygous for the dwarfing gene (Dwdw) was crossed with SFP, which contains no known dwarfing alleles. The progeny would have segregated in a 1 Dwdw : 1 Dwdw ratio. As expected, approximately half of the offspring trees evaluated were heterozygous for the dwarfing gene (nine out of 15 trees, chi square = 0.6, P = 0.25–0.50), as indicated by the presence of dwarf trees in their progeny derived from self-pollination (F2 generation). In the F2 generation there were fewer DW trees from each DW-producing parental combination than expected (pooled $\chi^2 = 35.75$ P = <0.001; sum of $\chi^2 = 56.95$ P = 0.001–0.01), probably due to relatively high seedling mortality of the dwarf phenotype in the greenhouse due to shading from non-DW seedlings grown at close spacing.

Interaction of dwarf with compact and pillar. In the field, young DW trees, due to their small size, can be easily damaged by herbicides and cultivation equipment, and, in fact, 45% of DW trees died within a few years of planting in the field. Many of the surviving DW trees could be classified as DW or DWPI (Fig. 3). However, an interaction of DW with Brbr (UP) could not be distinguished and it is not known if dwdwBrbr trees would be more likely classified as DWPI or DW. Further, the growth habit of trees combining dwdw with Ct and Brbr is unclear and could have influenced the classification of growth habits. If it is assumed that any tree expressing dwdw would, in fact, be a DW tree there is the possibility that some of these combinations, particularly DW + CT could produce very small, compact-dwarf trees, more prone to seedling mortality. Specific studies of dwarf trees expressing combinations of growth habit genes may be necessary to assess the interactions of these genes with dwdw.

$\chi^2$ GENERATION. Selfed trees classified as GL. Prior work with GL trees (Scorza et al., 1989) suggested that this phenotype was a result of expression of both the PI and CT genes. In the F1 hybrids described in that report, the GL trees would have been the result of combining PI in a heterozygous state with the CT heterozygote, the
Table 7. Segregation of peach tree growth habit in the F3 generation progeny of self-pollinated F2 trees with or without overall grouping (pooling) of Compact (CT) and non-CT trees.

| F2 parent’ growth habit | Progeny growth habit | χ² | P |
|-------------------------|----------------------|----|---|
|                         | Pooled CT | Pooled Non-CT |    |   |
| KV872526 GL             | 60        | 32        | 4.19 | 0.02–0.05 |
| KV87962 GL              | 77        | 19        | 1.17 | 0.20–0.30 |

Expected ratio 3CT : 1 non-CT

|          | Pooled |         |     |      |
|----------|--------|---------|-----|------|
|          | χ²     |         |     |      |
|          | P      | Sum     | Heterogeneity |     |
|          | 4.35   | 5.36    | 5.01 | 0.02–0.05 |

Expected ratio 12 CT : 1UP : 2 ST : 1 PI

|          | Pooled |         |     |      |
|----------|--------|---------|-----|------|
|          | χ²     |         |     |      |
|          | P      | Sum     | Heterogeneity |     |
|          | 4.81   | 10.37   | 5.56 | 0.10–0.20 |

Expected ratio 3 CT : 6 CTUP : 3 CTPI : 2 UP : 1ST : 1PI

|          | Pooled |         |     |      |
|----------|--------|---------|-----|------|
|          | χ²     |         |     |      |
|          | P      | Sum     | Heterogeneity |     |
|          | 46.8   | 58.3    | 11.5 | 0.20–0.30 |

KV87962 is an F2 progeny of self-pollinated globe-shaped (GL) F1 seedling tree 63 from the cross KV77119, a compact (CT) growth habit tree, and a showy-flowered pillar (SFP) tree. KV872526 is an F2 progeny of self-pollinated globe-shaped (GL) F1 seedling tree 87 from the cross KV77119, a compact (CT) growth habit tree, and a showy-flowered pillar (SFP) tree.

DW gene being either homozygous dominant or heterozygous (CtctDwDwBrbr). Selfing such a tree would be expected to produce ST, UP, CT, PI, and DW progeny and progeny expressing interactions between these alleles (Fig.1). Field observations placed F1 progeny of F2, GL trees into six phenotypes: CT, CTPI, GL, PI, UP, and ST (Fig. 4). Pooled chi-square values for F1 progeny of GL parents, KV878962 and KV872526, supported classification of CT vs non-CT trees as was the case for the evaluations of the F2 generation (Table 7). Distinguishing non-CT trees as UP, ST, or PI also resulted in acceptable chi-square values for the segregation of these F1 progeny (Table 7). Classification into the six predicted groups (CT, CTUP, CTPI, UP, ST, and PI) was not supported by chi-square analyses (Table 7) apparently due to the difficulty of distinguishing between the various CT classes resulting from interactions with PI growth form. Although not supported by significant chi-square values, observations of F1 progeny suggested that the F2 parents KV87962 and KV872526 were CtctDwDwBrbr, the same genotype as had been determined for GL trees evaluated in the F1 generation.
The peach displays a diverse range of genetically-controlled tree forms controlled by expression of multiple loci. Simply inherited tree forms include DW, PI, CT, and WE. The PI habit examined in this study was inherited as a monogenic trait expressing incomplete dominance. Homozygous \( BrBr \) produced ST trees, homozygous \( brbr \) produced PI, and the heterozygote \( Brbr \) was UP. This finding furthers the work of Yamazaki et al. (1987) and Chaparro et al., (1994) who proposed a simple recessive model of the \( Br \) allele. The segregation of trees into 1 ST \( (BrBr) \) : 2 UP \( (Brbr) \) : 1 PI \( (brbr) \) was clearly evident in ST x PI crosses. The production of F1 UP trees from crosses of DW x PI and WE x PI also support the incomplete dominance model. F2 populations developed from parents containing \( br, dw \), and \( Ct \) alleles produced trees that could not be classified accurately as ST and UP. Because tree form involves cumulative families (Fig. 1). These observations included CT and PI F1 trees, trees with apparent interactions of these two growth types, the presence of non-CT trees, and the absence of DW trees.

F2 trees rated as CTPI were difficult to distinguish from those rated as GL, the differences being generally perceptible, but often subtle (Fig. 5). Two CTPI trees were self-pollinated to test if the differences between GL and CTPI trees in the F2 generation, perceived through visual observation, were due to genotypic differences. Progeny of the two F1 CTPI trees displayed segregation markedly different from the GL trees and different from each other. Progeny of the CTPI F2 tree KV872522 were evaluated as PI, CTPI, and DWPI (Fig. 6). Significant chi-square values indicated that KV872522 was CTctDwDwbrbr (Table 8). Another CTPI F2 tree (KV87961), upon self-pollination, produced 96 F3 progeny nearly identical in CTPI growth habit (Fig. 7). The genotype of KV87961 appeared to have been CticDwDwbrbr. Apparently, the CTPI phenotype is a result of an interaction of the \( brbr \) and \( Ct \), whereas the GL phenotype results from an interaction of \( Brbr \) and \( Ct \). The difference between these two trees in phenotype is that CTPI trees present a form that is more dense and upright than the GL tree which also has a high density of branching, but in a canopy that is subtly less upright. This difference is apparently due to the difference in expression between \( Brbr \) and \( brbr \).

F2 DW trees were self-pollinated; KV87938, evaluated as an upright dwarf (DWUP) and KV87613, a DWPI (Fig. 8). KV87613 produced all DWPI progeny indicating a dvwdwbrbr genotype. KV87938 produced 76 DW : 14 DWPI (5.4:1). This parent was expected to be heterozygous for \( Br \) and homozygous for \( dw \) in which case an F2 ratio of 1 dvwdwBrBr : 2 dvwdwBrbr : 1 dvvdwbrbr (phenotypically 1 DW : 2 DWUP : 1 DWPI) would have been expected. The deviation from the expected is likely due to difficulties in distinguishing \( dvwdwBrBr \) (DWUP) from \( dvvdwBrBr \) (DW). The difficulty in distinguishing \( Brbr \) heterozygotes was also encountered in some segregating progenies of standard sized trees as discussed previously.

### Table 8. Proposed genotype of compact pillar (CTPI) tree KV87522 and genotypic and phenotypic segregation of progeny from self-pollination and phenotype evaluation of progeny of KV87522 and Chi square analysis based on predicted phenotypic ratios.

| Genotype       | Phenotype |
|----------------|-----------|
| CticDwDwbrbr (x) | 1         |
| CticDwDwbrbr      | CTPI      |
| CticDwDwbrbr      | CTPI      |
| CticDwDwbrbr      | CTDWPI    |
| CticDwDwbrbr      | CTDWPI    |
| CticDwDwbrbr      | PI        |
| CticDwDwbrbr      | PI        |
| CticDwDwbrbr      | DWPI      |

Predicted phenotypic ratios = 3 PI: 9 CTPI: 4 DWPI1

Chi square analysis based on the above phenotypic ratios

| KV87522 (x) | PI | CTPI | DWPI | \( \chi^2 \) | P |
|-------------|----|------|------|-------------|---|
| 13          | 49 | 25   |      | 1.21        | 0.50–0.70 |

1KV87522 is an F2 progeny of self-pollinated compact pillar (CTPI) F1 seedling tree 87 from the cross KV77119, a compact (CT) growth habit tree, and a showy-flowered pillar (SFP) tree.

2CTDWPI and DWPI could not be visually distinguished, thus all were classified as DWPI

### Discussion

The peach displays a diverse range of genetically-controlled tree forms controlled by expression of multiple loci. Simply inherited tree forms include DW, PI, CT, and WE. The PI habit examined in this study was inherited as a monogenic trait expressing incomplete dominance. Homozygous \( BrBr \) produced ST trees, homozygous \( brbr \) produced PI, and the heterozygote \( Brbr \) was UP. This finding furthers the work of Yamazaki et al. (1987) and Chaparro et al., (1994) who proposed a simple recessive model of the \( Br \) allele. The segregation of trees into 1 ST \( (BrBr) \) : 2 UP \( (Brbr) \) : 1 PI \( (brbr) \) was clearly evident in ST x PI crosses. The production of F1 UP trees from crosses of DW x PI and WE x PI also support the incomplete dominance model. F2 populations developed from parents containing \( br, dw \), and \( Ct \) alleles produced trees that could not be classified accurately as ST and UP. Because tree form involves cumulative

Fig. 7. F3 progeny of compact pillar (CTPI) peach KV87961. Proposed genotype of parent and progeny, CticDwDwbrbr. Tree heights are ≈2.7 m.
growth and development of the entire tree over several years, it is likely that environmental effects and epistatic (interlocus) interactions contributed to difficulties in tree classification in these particular populations. In the F1 generation segregating for br, Ct, and dw alleles, we also noted difficulty in classifying trees with a mixture of traits, especially trees that were thought to be heterozygous for the br trait combined with DW and/or CT growth habit. Trees expressing combinations of DW and CT, and DW, CT, and PI growth habits could not be distinguished. Future emphasis on DW populations may lead to clarification of these allelic interactions.

In this report we show that distinctly new forms can be produced through a combination of genes. These forms include DWPI (also reported by Yamazaki et al., 1987), CTPI, and GL. Yet there remain other predicted gene combinations (Fig. 1) that we were unable to recognize, perhaps because the differences were too subtle to be readily detected by standard field observa-

Some of the tree forms that have been discussed in this report may have potential for commercial production. The PI and UP forms appear to be particularly suitable to high-density tree wall, fusseto, and central leader-based systems (Bassi et al., 1994; Scorza et al. 2000). Others, such as the DWPI and CTPI, not only present a novel growth form, but these trees maintain a rather small size and compact form. Some bloom profusely and consistently on spurs (Scorza, 1987) requiring little if any pruning in our tests (unpublished). Continued hybridization and development and testing of peach tree growth habits may increase productivity of commercial peach orchards and expand use of the peach as a garden fruit crop and as an ornamental species.

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