Genetic Interactions of Pillar and Weeping Peach Genotypes

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Abstract. Genetic interaction of the pillar (PI) and weeping (WE) growth habit genotypes was investigated in peach [Prunus persica (L.) Batsch] (Scorza et al., 2002). Inheritance of both the pillar (PI) and weeping (WE) growth habits has been reported. The PI growth habit, also designated as broom in the literature, is controlled by a single recessive gene designated br (Yamazaki et al., 1987). Incomplete dominance at the br locus allows heterozygotes to be distinguished from both homozygous classes in most genetic backgrounds, having an intermediate architecture referred to as upright (UP). Weeping growth habit is also controlled by a single recessive gene, designated pl (Monet et al., 1988, Yamazaki et al., 1987). Both of these reports proposed dominant gene action at the br locus. It was later reported that PI was epistatic to the expression of WE (plpl). A unique growth habit not previously described in peach, and referred to as archer (AR), was recovered in the F1 family. Arching trees showed an upright phenotype similar to Brbr heterozygotes, but had a distinct curvature in the developing shoots. Progeny testing of AR trees revealed their genotype is Brbrplpl.

Peach is a model organism for the genetic and physiological study of growth habit and architecture in woody plants. Several genes influencing tree architecture have been identified and described in peach [Prunus persica (L.) Batsch] (Scorza et al., 2002). Inheritance of both the pillar (PI) and weeping (WE) growth habits has been reported. The PI growth habit, also designated as broom in the literature, is controlled by a single recessive gene designated br (Yamazaki et al., 1987). Incomplete dominance at the br locus allows heterozygotes to be distinguished from both homozygous classes in most genetic backgrounds, having an intermediate architecture referred to as upright (UP). Weeping growth habit is also controlled by a single recessive gene, designated pl (Monet et al., 1988, Yamazaki et al., 1987). Both of these reports proposed dominant gene action at the PI locus, but Bassi and Rizzo (2000) noted that heterozygotes can be discerned from homozygotes, suggesting incomplete dominance. Limited studies have been conducted examining the interaction of the br and pl genes. Yamazaki et al. (1987) reported that F1 progeny derived from crosses between PI and WE parents produced normal progeny, while Scorza et al. (2002) reported that crosses between PI and WE PI produced normal progeny. F3 progeny derived from hybridization between ‘Pillar’ (brbr) × ‘White Glory’ (plpl). The source of ‘Pillar’ used in this study was initially obtained from L. F. Hough at Rutgers University, New Brunswick, NJ, representing material originally imported from Japan. According to Scorza et al. (2002), this material obtained by Hough appears to be similar or identical to the Japanese cultivar, ‘Hoki’. ‘White Glory’ is a weeping ornamental nectarine derived from ‘S37’ (Werner et al., 1985). ‘Pillar’ was used as the female parent in the original hybridization. The hybridization method was as described by Scorza and Sherman (1996).

Development of F1, F2, BC1P1, BC1P2, BC1P3, BC2P1, BC2P2, BC2P3, F3, and F4 families. The BC1P1 and BC1P2 families were generated using the same F1 hybrid plant as the female parent. The F2, F3, F4, and F5 families were obtained through self-pollination by covering trees with parachutes from prebloom until petal fall (Werner and Cain, 1985). Three F1 trees were self-pollinated for development of F2 families. A sample of plants were established in the field in the spring at a spacing of 0.6 m within rows and 6.7 m between rows. Growth habit was evaluated by two observers in the dormant season following two seasons of growth. Based on field observation, trees were placed into one of five phenotypic classes: standard (ST), upright (heterozygous PI, UP), pillar (PI), weeping (WE), and arching (AR). The AR phenotype has not been described previously in the literature, and is discussed below. Proposed phenotypes and genotypes of parental, F1, BC1P1, BC1P2, BC1P3, F2, and F3 trees used in this study are presented in Table 1.

Materials and Methods

Parental germplasm and hybridization for development of F1 families. Interaction of the br and pl genes was tested in numerous families derived from hybridization between ‘Pillar’ (brbr) × ‘White Glory’ (plpl). The source of ‘Pillar’ used in this study was initially obtained from L. F. Hough at Rutgers University, New Brunswick, NJ, representing material originally imported from Japan. According to Scorza et al. (2002), this material obtained by Hough appears to be similar or identical to the Japanese cultivar, ‘Hoki’. ‘White Glory’ is a weeping ornamental nectarine derived from ‘S37’ (Werner et al., 1985). ‘Pillar’ was used as the female parent in the original hybridization. The hybridization method was as described by Scorza and Sherman (1996).

Development of F1, F2, BC1P1, BC1P2, BC1P3, F3, and F4 families. The BC1P1 and BC1P2 families were generated using the same F1 hybrid plant as the female parent. The F2, F3, F4, and F5 families were obtained through self-pollination by covering trees with parachutes from prebloom until petal fall (Werner and Cain, 1985). Three F1 trees were self-pollinated for development of F2 families. A sample of plants were established in the field in the spring at a spacing of 0.6 m within rows and 6.7 m between rows. Growth habit was evaluated by two observers in the dormant season following two seasons of growth. Based on field observation, trees were placed into one of five phenotypic classes: standard (ST), upright (heterozygous PI, UP), pillar (PI), weeping (WE), and arching (AR). The AR phenotype has not been described previously in the literature, and is discussed below. Proposed phenotypes and genotypes of parental, F1, BC1P1, BC1P2, BC1P3, F2, and F3 trees used in this study are presented in Table 1.

Table 1. Parental phenotypes and genotypes, and genotypes and predicted phenotypes of F1, BC1P1, BC1P2, F2, F3 progeny.

| Parental Genotype | F1 Progeny | BC1P1 Progeny | BC1P2 Progeny | BC1P3 Progeny | F2 Progeny | F3 Progeny |
|------------------|------------|--------------|--------------|--------------|------------|------------|
| (P.) × (P.) | BrbrPlPl (UP) | BrbrPIPI (UP) | BrbrPIPI (UP) | BrbrPIPI (UP) | BrbrPIPI (UP) | BrbrPIPI (UP) |
| P1 × P1 | BrBrPlPl (UP) | BrBrPIPI (UP) | BrBrPIPI (UP) | BrBrPIPI (UP) | BrBrPIPI (UP) | BrBrPIPI (UP) |
| F1 × F1 | BrBrPlPl (ST) | BrBrPlPl (ST) | BrBrPlPl (ST) | BrBrPlPl (ST) | BrBrPlPl (ST) | BrBrPlPl (ST) |
| F2 × F2 | BrBrPlPl (UP) | BrBrPlPl (UP) | BrBrPlPl (UP) | BrBrPlPl (UP) | BrBrPlPl (UP) | BrBrPlPl (UP) |
| F3 × F3 | BrBrPlPl (AR) | BrBrPlPl (AR) | BrBrPlPl (AR) | BrBrPlPl (AR) | BrBrPlPl (AR) | BrBrPlPl (AR) |

Figure 1 photographs taken by Herman Lankford, Agricultural Research Service (NCARS) and North Carolina State University. Support for assistance with field plot management. Research supported by funds provided by the North Carolina Agricultural Research Service (NCARS) and North Carolina Foundation Seed Producers, Inc. (NCFSPI). Figure 1 photographs taken by Herman Lankford, Dept. of Communication Services, North Carolina State University.

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Fig. 1. Minimally pruned (lower branches removed) F₂ peach seedlings, 4 years in the field (pillar in A only 2 years old). (A) Pillar (PI) phenotype, (B) weeping (WE) phenotype, (C) upright (UP) phenotype, and (D) archer (AR) phenotype.
individuals from ST homozygous (Br Br) individuals in F₂ and BC families was sometimes difficult. In contrast, pillar (PI) and weeping (WE) trees could be unambiguously classified in segregating families.

A distinctly different and novel phenotype was identified in the F₂ family. Trees demonstrating this phenotype showed upright to semi-upright branch angles between the main trunk and primary branches, suggestive of heterozygosity at the Br locus (UP). However, unlike normal upright individuals, these trees showed a semi-weeping appearance manifested as a distinct curvature in the developing shoots. We classified these trees as arching (AR). Figure 1 shows a typical AR tree compared to UP, WE, and PI trees.

The F₂ data (Table 2) showed an excellent fit to a recessive epistasis model, with br br being epistatic to expression of pl pl. Hence, the weeping phenotype is not expressed in a homozygous br br background. Backcross data was in general agreement with the F₂ data. Both BC families supported the recessive epistasis model in that no WE or PI individuals were recovered in the BC₂ₚₚ families, while the BC₂ₚl families showed a good fit to the expected 1:1 (PI:ST) ratio. The presence of two AR trees in this family was unexpected and cannot be explained by the model, but could be due to accidental self-pollination. The BC₂ₚₚ segmentation fit the expected 1:1 (ST: WE) ratio, but showed a deficiency in the WE class. However, population size in this family was small.

Based on the epistatic interaction observed between the br and pl genes and the observed frequency of AR trees recovered in the F₂ family, we hypothesized that trees showing the AR phenotype had a genotype of Br br pl pl. If so, F₂ families derived from self-pollination of AR trees would produce PI, AR, and WE offspring in an expected ratio of 1:2:1, respectively. Accordingly, seven AR trees were selected at random from the F₂ family, selfed, and progeny were evaluated. Six of the seven families fit the expected 1:2:1 (PI:AR: WE) test ratio. Archer family #3 showed the poorest fit, having a deficiency in the number of AR individuals, probably resulting from the small population size of this F₂ family. These results provide strong support that trees classified as AR are of genotype Br br pl pl, and that the epistatic effect of the br allele on the expression of weeping is operative even in Br br heterozygotes, although not to the extent found in br br homozygotes.

Scorza et al. (2002) reported the production of distinct new tree forms through recombining genes controlling the dwarf (DW), compact (CT), and PI growth forms. In this study, we demonstrate the production of a novel growth form called archer previously unreported in peach, through the combination of the br and pl genes. This form, demonstrating upright branch angles near the juncture between the lateral branch and main trunk, but showing a distinct curvature in the developing shoots, may have potential for commercial production. In agreement with Scorza et al. (2002), this study confirms the plasticity in peach tree growth, and the potential for developing novel growth forms through combination of different genes controlling growth habit.

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| Cross                  | Family       | Progeny (no. trees) | Expected ratio | Chi-square | P     |
|------------------------|--------------|---------------------|----------------|------------|-------|
| PI selfed              | F₁           | ST 0 0 0 0 23 0     | 0:0:1:0:0     | 1.0        | 0     |
| WGL selfed             | F₁           | 0 12 0 0 0 0       | 0:1:0:0:0     | 0          | 1.0   |
| PI × WG                | F₁           | 0 3 0 0 0 0       | 0:1:0:0:0:0   | 0          | 1.0   |
| PI × WG F₁ self        | F₂           | 60 115 21 82 43    | 3:6:1:4:2     | 0.56       | 0.97  |
| (PI × WG) × PI BCₚₚₚ  | Fₐ           | 1 19 0 22 2       | 0:1:0:0:0:0   | 0.22       | 0.64  |
| (PI × WG) × WG BCₚₚₚ  | Fₐ           | 3 5 2 0 0        | 1:1:0:0:1     | 5.20       | 0.16  |
| AR-1 self              | F₁           | 0 9 8 11 11       | 0:1:1:2:1:2   | 6.70       | 0.04  |
| AR-2 self              | F₁           | 0 16 18 33        | 0:0:1:1:2:2   | 1.33       | 0.94  |
| AR-3 self              | F₁           | 0 3 10 7         | 0:0:1:1:2:2   | 2.56       | 0.28  |
| AR-4 self              | F₁           | 0 23 33 67        | 0:0:1:1:2:2   | 0.15       | 0.93  |
| AR-5 self              | F₁           | 0 15 17 31        | 0:0:1:1:2:2   | 1.44       | 0.49  |
| AR-6 self              | F₁           | 0 21 22 55        | 0:0:1:1:2:2   | 1.49       | 0.47  |
| AR-7 self              | F₁           | 0 31 23 60        | 0:0:1:1:2:2   | 1.44       | 0.49  |
| PI-1 self              | F₁           | 0 1 0 17 0        | 0:0:1:1:2:2   | 0          | 1.0   |
| PI-2 self              | F₁           | 0 0 0 8 0         | 0:0:1:1:2:2   | 0          | 1.0   |