Genetic Influence on Flower Bud Density in Peach and Nectarine Exceeds That of Environment

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Abstract. Spring frosts often kill all or a portion of the flowers on peach [*Prunus persica* (L.) Batsch] trees in the southeastern United States. Increased flower bud density increases the likelihood of sufficient flowers surviving to produce a crop. The effect of environment on flower bud density (buds/node) was studied using two locations over 3 years. Bud density of 25 peach and nectarine varieties grown in completely randomized designs was measured in Georgia and North Carolina. Genotypic variability was greater than location or year effects. Varieties selected for high bud density at one location can be expected to have high densities at other locations with similar chilling.

Several times in the last decade the southeastern U.S. peach crop has been severely reduced by spring frosts. Survival of peach flower buds and flowers in the spring is a function of bud preconditioning, minimum temperature, bud hardiness, time of bloom, number of flowers, and uniformity of bud development. The number of flower buds depends on the length of shoot growth, number of nodes per unit length, and number of flower buds per node (density). Shoot growth and bud differentiation are a function of genotype and the growing conditions of the tree the previous summer. Nodes on moderately vigorous shoots typically have a single vegetative bud flanked by a pair of flower buds. Some nodes will have only a single flower bud or vegetative bud, or no visible bud at all, particularly on the younger part of the shoot, which reduces the mean flower bud count per node for the entire shoot. Blake (1933b) developed a rating scheme for flower bud density ranging from class 1 (≈ 1.3 to 2.0 buds/cm) to class 6 (< 0.3 buds/cm) and rated 135 genotypes over 3 years (Blake, 1933a). Werner et al. (1988) reported mean bud densities ranging from 1.59 flower buds per node for 'Harko' to 0.35 for 'Late Gold' during 1986–87 in North Carolina. Both authors reported consistent results from year to year for a given variety. Perez-Gonzalez (1993) lists bud densities of 50 varieties rated in Italy and categorized them on the basis of the number of buds per node.

Flower bud density is relatively easy to measure compared to other components contributing to bud survival. However, the relative contributions of genotype vs. environment on bud density are not known. A large genetic component would make selection for high bud density more effective. This study was designed to compare the effects of genotype and environment on the flower bud density of 25 peach and nectarine varieties.

Materials and Methods

We selected 25 peach and nectarine varieties from the United States and several foreign countries (Table 1) to obtain a wide range of flower bud densities. June-budded trees on Lovell rootstock were planted in Spring 1986 at sites in Byron, Ga. (Faceville fine sandy loam soil; lat. 32°40'N, long. 83°44'W), and Clayton, N.C. (Norfolk sandy loam; lat. 35°39'N, long. 78°30'W). Both sites annually average > 1100 h of chilling below 7 °C. Pertinent weather data were obtained from nearby National Weather Service sites (Table 2). Each site consisted of a completely randomized design using 25 varieties and four single-tree replications. Trees were maintained according to commercial recommendations for the area. Sample shoots were removed before trees were pruned in the spring. Beginning in 1988, as bud swell occurred (making it easier to distinguish flower from vegetative buds), typical 1-year-old shoots oriented at 45° angles from vertical were selected from around the canopy, and 10 were removed from each tree. Length, number of visible nodes, and number of flower buds were determined for each shoot. Bud density (flower buds/node) and internode length (nodes/length) were calculated. Data were analyzed by correlation and analysis of variance (ANOVA) (SAS Institute, 1987) using years as a split plot in time. Varieties and

locations were considered fixed effects. Variance components (Table 3) for genetic and environmental effects were calculated from the expected mean squares (EMS) (Schultz, 1955). Variance (V_v) of a variety mean was estimated as $V_v = \delta^2_{r(lv)}/r + \delta^2_{y}/y + \delta^2_{yr(lv)}/yrl + \delta^2_{srl}/srl + \delta^2_{srl}/srl$, where s , r , l , y , and v represent the number of shoots, replications, locations, years, and varieties, respectively (Jones et al., 1960). Corresponding estimated variance components for replication ($\delta^2_{r(lv)}$), year $\times$ variety (δ^2_{y}), year $\times$ replication ($\delta^2_{yr(lv)}$), shoot (δ^2_{srl}), and error (δ^2_e) are from Table 3. Broad sense heritability was estimated by the ratio of genetic variance : total phenotypic variance: $100 \times (\text{variety EMS})/(\text{sum EMS})$. Estimates of stability parameters were made following Fernandez (1991), as proposed by Shukla (1971) and Kang (1989).

Results and Discussion

Bud density ranged widely across varieties (Table 4). Most of the genotypes with higher densities were developed in regions with colder winter temperatures and more frequent spring frosts, in contrast to those from California. 'Agua 6-4', from the highlands of Mexico, where spring frosts occur regularly, has the highest bud density and probably has been selected over many generations for ability to crop reliably. Density values in this study correlated well with those from North Carolina in an earlier study (Werner et al., 1988) for the few varieties in common. Our density range was somewhat smaller than that reported by Blake (1933a), but he measured shorter shoots that may have had fewer budless nodes at the shoot apex. The only variety in common with Blake was 'Amarillo Tardio',

Table 1. Origin of peach and nectarine varieties used in bud density study in Georgia and North Carolina.

Variety	Origin
Amarillo Tardio (PI55835?)	Spain
Agua 6-4	Mexico
Bicentennial	Louisiana
Blake	New Jersey
Clayton	North Carolina
Cresthaven	Michigan
Eagle Beak (PI43289)	China
Flavortop ²	California
Hardired ²	Ontario
Junegold	California
Majestic	Louisiana
Monroe	North Carolina
Norman	North Carolina
O'Henry	California
Parade	California
Pekin	North Carolina
Ta Tao #6 (PI101668)	China
Redhaven	Michigan
Redskin	Maryland
Reliance	New Hampshire
Sunhigh	New Jersey
Sunprince	Georgia
Surecrop	Louisiana
Topaz	Missouri
Winblo	North Carolina

²Nectarine.

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Table 2. Comparison of temperatures and rainfall pertinent to bud density, for Byron, Ga., and Clayton, N.C., for 1987–89. Data from the National Weather Service.

Year	Location	Monthly mean					Absolute minimum ^z	Annual total
		May	June	July	August	January ^z		
Temperature (°C)								
1987	Byron	23	26	27	28	5	−9	---
	Clayton	20	25	27	26	1	−12	---
1988	Byron	21	25	27	27	11	−7	---
	Clayton	20	25	28	29	7	−9	---
1989	Byron	21	26	26	26	11	−13	---
	Clayton	18	26	25	26	10	−12	---
Rainfall (mm)								
1987	Byron	110	90	60	120	---	---	1070
	Clayton	50	30	50	90	---	---	1400
1988	Byron	60	30	110	150	---	---	1000
	Clayton	60	90	110	100	---	---	940
1989	Byron	100	130	180	40	---	---	1270
	Clayton	140	180	120	120	---	---	1440

^zJanuary of the following year; absolute minimum for winter beginning the year listed and ending the following year.

Table 3. Analysis of variance for flower bud density for 25 peach and nectarine varieties evaluated in Georgia and North Carolina 1988–90. Values based on four single-tree replications (Rep) per location and 10 shoots per tree per year. Variance components calculated using fixed effects model for variety and location. ($R^2 = 0.78$; R^2 using tree means = 0.93.)

Source	df	Mean square	F value	P	Variance component
Location (Loc)	1	19.40	17.16	0.0437	0.0064
Variety (Var)	24	22.98	41.29	0.0001	0.0935
Loc × Var	24	0.64	1.24	0.2481	0.0011
Rep (Loc × Var)	150	0.24	1.38	0.0102	0.0023
Shoot (Rep × Loc × Var)	1800	0.07	1.04	0.1837	0.0009
Year	2	10.66	61.27	0.0001	0.0052
Loc × Year	2	1.03	5.95	0.0029	0.0009
Var × Year	48	0.48	2.77	0.0001	0.0038
Loc × Var × Year	48	0.44	2.52	0.0001	0.0066
Year × Rep (Loc × Var)	298	0.17	2.52	0.0001	0.0105
Error	3582	0.07			0.0689

Table 4. Mean, standard error, and coefficient of variation (cv) for bud density, shoot length, nodes per shoot, and internode length for 25 peach and nectarine varieties grown in Georgia and North Carolina in 1988–90 (four replications per location). Replication means are calculated using 10 shoots. Correlations calculated using tree means for each year, location, and replication.

Variety	Bud density ^z		Shoot length (cm)	Nodes (no.)	Internode length (cm)
	Buds/node	cv			
Agua 6-4	1.66 ± 0.05	16.2	50.4 ± 1.4	34.5 ± 1.1	1.48 ± 0.04
Eagle Beak	1.46 ± 0.05	17.9	53.6 ± 2.2	27.6 ± 1.2	1.97 ± 0.06
Hardired	1.13 ± 0.03	12.2	51.9 ± 1.7	26.0 ± 0.8	2.00 ± 0.04
Reliance	1.10 ± 0.05	23.3	52.5 ± 2.3	27.2 ± 1.0	1.93 ± 0.05
Cresthaven	1.03 ± 0.04	20.6	48.8 ± 1.9	27.7 ± 1.0	1.77 ± 0.04
Blake	0.99 ± 0.03	15.1	45.2 ± 2.0	27.3 ± 0.9	1.65 ± 0.03
Amarillo Tardio	0.88 ± 0.03	15.1	49.9 ± 2.0	27.0 ± 0.8	1.84 ± 0.04
Norman	0.86 ± 0.04	22.5	49.8 ± 1.7	24.6 ± 0.6	2.03 ± 0.05
Surecrop	0.85 ± 0.03	19.6	47.9 ± 2.3	27.2 ± 0.8	1.76 ± 0.07
Clayton	0.85 ± 0.04	20.4	52.5 ± 2.5	27.7 ± 0.9	1.88 ± 0.05
Pekin	0.83 ± 0.04	24.4	49.3 ± 2.0	26.8 ± 0.7	1.84 ± 0.05
Redhaven	0.77 ± 0.04	24.6	51.4 ± 2.3	26.4 ± 0.8	1.94 ± 0.05
Junegold	0.73 ± 0.04	25.6	47.3 ± 2.2	27.9 ± 1.0	1.70 ± 0.06
Redskin	0.72 ± 0.04	24.0	53.2 ± 2.4	28.4 ± 0.9	1.87 ± 0.05
Bicentennial	0.70 ± 0.04	30.5	51.5 ± 2.1	30.6 ± 1.1	1.69 ± 0.05
Sunprince	0.70 ± 0.04	26.6	46.1 ± 1.8	27.7 ± 0.9	1.67 ± 0.05
Parade	0.69 ± 0.03	22.9	51.3 ± 2.0	26.8 ± 0.9	1.91 ± 0.04
Flavortop	0.65 ± 0.02	18.3	47.2 ± 1.9	23.2 ± 0.8	2.04 ± 0.04
Majestic	0.65 ± 0.03	23.6	56.1 ± 3.2	28.8 ± 1.1	1.96 ± 0.10
Sunhigh	0.57 ± 0.03	24.7	50.8 ± 2.0	26.9 ± 0.7	1.96 ± 0.05
Winblo	0.56 ± 0.03	28.4	51.4 ± 2.1	27.5 ± 0.6	1.87 ± 0.05
Monroe	0.54 ± 0.04	33.9	46.9 ± 1.7	26.9 ± 0.7	1.75 ± 0.05
O'Henry	0.42 ± 0.03	35.2	45.3 ± 1.8	26.6 ± 0.7	1.71 ± 0.05
Topaz	0.39 ± 0.02	29.5	46.4 ± 1.9	27.3 ± 0.7	1.69 ± 0.05
Ta Tao #6	0.31 ± 0.03	51.8	53.4 ± 2.8	33.2 ± 1.3	1.59 ± 0.03
Overall mean	0.80		50.0	24.5	1.83
Correlation ^y	1.00		0.14	0.16	0.02

^zWaller–Duncan minimum significant difference for density = 0.08.

^yPearson correlation (r) with density.

which he rated at 0.6 buds/cm compared to 0.5 buds/cm in our test. Most of the varieties Blake tested are extinct. We only tested two varieties in common with Perez-Gonzalez (1993), 'O'Henry' and 'Redhaven', which he rated at 0.64 and 0.93 buds/node, respectively, both higher than our values of 0.42 and 0.77. Extremes of bud density are readily observed without counting buds. 'Agua 6-4' often has three flower buds per node, in contrast to 'Ta Tao', which has mostly single buds per node, and many nodes with no flower buds.

Results from ANOVA show location, variety, and year main effects to be more important than any interactions in determining bud density (Table 3). The higher mean densities at Clayton than at Byron (Table 5) probably relate to growing conditions and crop load the previous year; trees at Byron were less heavily thinned, which commonly reduces return fruit bud set. Since the variety effect is much larger than any interaction, a given variety would tend to perform similarly across locations similar to ours. Although we used a fixed effects model, which limits the ability to extrapolate beyond our situation, the varieties tested represent most of the commercial peach germplasm in use in the medium-high chilling zones of the southeastern United States. In climates where peaches suffer significant mid-winter bud death, spring bud counts may be misleading if the dead buds dehisce. In contrast, varieties that crop poorly in a location may have bud densities biased upwards the next spring. Mean bud density was not well correlated with shoot length, number of nodes per shoot, or internode length (Table 4). Results from ANOVA for shoot length and number of nodes (data not shown) showed year and location factors and their interaction to be highly significant and of primary importance.

In a breeding program one would want to be able to select for bud density based on single tree performance, as seedlings are rarely replicated. Variances of individual tree means (based on 10 shoots/tree) were mostly below 0.06 (detailed data not shown), which translates to an LSD ($P = 0.05$) of 0.23 buds/node. The variance of a mean using one replication; one location; 1 year; and 3, 5, or 10 shoots per tree would be 0.040, 0.031, or 0.024, respectively. Resulting LSD values would be 0.70, 0.31, or 0.16 buds/node, respectively. These values would be applicable to single-budded trees of a variety, such as might be interplanted as controls, assuming seedling spacing was not so close as to interfere with bud development. Assuming cultural practices (tree density, fruit thinning) were suitable, single-tree selection among seedlings, using at least five shoots per tree, could be effective for increasing bud density. However, we did not sample seedling trees, and their flower bud development may differ from that of budded trees. Because the largest variance component was that of the error term, increasing the number of years, shoots, locations, or replications would (increasingly, in that order) reduce the variance and allow better discrimination among bud density. Clearly, it is easiest to increase the number of shoots evaluated.

Table 5. Means $\pm$ standard errors over years and locations for mean flower bud density (buds per node) for 25 peach and nectarine varieties.

Year	Flower bud density (no./node)		
	Location		Mean over locations
	Byron, Ga.	Clayton, N.C.	
1988	0.68 ± 0.04	0.75 ± 0.03	0.72
1989	0.75 ± 0.03	0.92 ± 0.03	0.84
1990	0.80 ± 0.04	0.91 ± 0.04	0.85
Mean over years	0.75	0.86	0.80

Table 6. Stability parameter estimates² for mean bud density of 25 peach and nectarine varieties grown in Georgia and North Carolina in 1988–90.

Variety	Ecovalence	δ^2_i	s^2_i
Amarillo Tardio	0.10527***	0.08937***	0.06826**
Agua 6-4	0.09102***	0.07699***	0.09623***
Bicentennial	0.04324	0.03544	0.04370*
Blake	0.10360***	0.08792***	0.07600**
Clayton	0.03111	0.02489	0.03110
Crethaven	0.07854**	0.06614**	0.05917**
Eagle Beak	0.15581***	0.13333***	0.15001***
Flavortop ^y	0.02209	0.01705	0.01516
Hardired ^y	0.04605	0.03788	0.02953
Junegold	0.06390**	0.05340**	0.06157**
Majestic	0.01219	0.00844	0.00813
Monroe	0.14466***	0.12362***	0.15388***
Norman	0.03954	0.03222	0.03617
O'Henry	0.07313**	0.06143**	0.07011**
Parade	0.03870	0.03149	0.03121
Pekin	0.03844	0.03126	0.03643
Ta Tao #6	0.12091***	0.10298***	0.08110***
Redhaven	0.04066	0.03320	0.00432
Redskin	0.02421	0.01889	0.01579
Reliance	0.07188**	0.06034**	0.06486**
Sunhigh	0.01322	0.00934	0.01154
Sunprince	0.04303	0.03525	0.04323*
Surecrop	0.02507	0.01964	0.01618
Topaz	0.01856	0.01398	0.01707
Winblo	0.04715*	0.03884*	0.04495*

²Ecovalence stability index (wi) (Kang, 1989); stability variance (δ^2_i) and adjusted stability variance (s^2_i) (Shukla, 1972).

^yNectarine.

*, **, *** Significant at $P = 0.05$, 0.01 , or 0.001 , respectively.

When shoot variation is removed by using means for trees, the ANOVA R^2 value for bud density based on location, year, and variety effects is very high (0.93). Calculations of variance components show that variety effects

(genetic variation) were from 9 to 100 times as large as environmental effects or interactions. Estimates of stability parameters indicate which varieties would tend to react similarly across environments. Varieties with nonsig-

nificant estimates would be more stable (Table 6), those with the most highly significant values are less stable. The same varieties are shown as unstable by all three parameters. Although this instability reflects nontypical performance across environments, the relative ranking was similar in most cases. Broad sense heritability was calculated as $100 \times 0.0935/0.2009 = 47\%$. This value indicates selection for high bud density would be effective. Selection would also be effective for low bud density, which would allow development of varieties for areas without spring frost, to reduce thinning costs.

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