

Genetic correlations between vegetative growth traits and productivity at different within-season intervals for strawberries (*Fragaria X ananassa*)

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Summary. Genetic and environmental relationships between vegetative growth and production traits at different intervals within a single season were investigated using unselected strawberry genotypes from 20 biparental crosses and their parents. Vegetative growth and productivity patterns differed between test locations and larger yields were detected where fall growth was greatest. Positive genetic correlations were detected between fall growth increments and mid-season production traits, but fall growth was uncorrelated or negatively correlated with late-season production. Conversely, growth during the production season was genetically uncorrelated or negatively correlated to early production traits, but was positively correlated to mid and late-season production. Together, these results suggest that the growth pattern required for early vs sustained production may represent conflicting breeding objectives. Also, although vegetative and reproductive functions compete for assimilates in strawberry, sustained productivity appears dependent on adequate vegetative growth throughout the spring and early summer. Significant correlations were detected between fall plant growth and early yield, but these were attributed to environmental rather than genetic sources. Genetic correlations between spring growth and early production traits were significantly negative and large, suggesting that vegetative during this interval may indicate limited fall inflorescence development.

Key words: Heritability – Genetic correlations – Yield – Vegetative growth – Resource partitioning

Introduction

Productivity in strawberries depends on the quantity of photosynthate assimilated by individual plants and

on the distribution of assimilates to vegetative and reproductive functions throughout the season (Strick and Proctor 1988a, b; Galletta and Bringhurst 1990). An understanding of the genetic and environmental determinants of plant growth, and the consequences of seasonal variation in vegetative growth rate for resource partitioning, may lead to more efficient procedures for selecting highly productive cultivars.

Within individual strawberry cultivars, growth rate depends on photoperiod, growing temperatures, fertility, and vernalization treatment (Heide 1977; Dana 1980; Galletta and Bringhurst 1990). Within-cultivar variation for yield has been correlated with a number of vegetative growth characters, including initial plant size (Mason 1987; Olsen et al. 1985; Guttridge and Anderson 1981), leaf number (Lacey 1973; Albregts and Howard 1985), and crown number (Hancock et al. 1982). Environmental variables that control plant vigor, especially growing temperature and the degree of vernalization, have a large impact on resource partitioning in strawberry and ultimately affect both yield and production pattern (Darrow 1966; Durner et al. 1984, 1987). Several of the studies cited above demonstrate that vigorous vegetative growth is not always associated with high productivity. Excessive vigor in strawberries can reduce total yield by shifting plant resources from reproductive to vegetative functions (Voth and Bringhurst 1970; Shaw 1989; Galletta and Bringhurst 1990).

Differences in productivity among strawberry cultivars have been correlated with growth rate and with patterns of resource partitioning (Strick and Proctor 1988a). Genetic differences for growth rate during periods of inflorescence differentiation or fruit filling generate a substantial fraction of the variation for yield observed among commercial cultivars (Strick and Proctor 1988a, c). However, high innate vigor does not

always result in high yields, especially when vigorous genotypes are managed with cultural treatments that also condition high vigor (Shaw 1989). Large genetic \times environment and genetic \times cultural treatment interactions are commonly detected for strawberry yield (Shaw et al. 1989; Shaw 1989; Pritts and Luby 1990); these interactions may be partially a consequence of partitioning responses that differ among genotypes in different environments.

For strawberries grown using annual production systems (usually in mediterranean environments), vegetative growth and inflorescence differentiation occur concurrently and continuously throughout most of the production season (Darrow 1966). Obtaining high productivity in these systems requires a balance throughout the season between growing the vegetative structures that differentiate and support development of the fruit, and partitioning assimilate to the fruit itself. This study was conducted to investigate the inheritance of variables that describe vegetative plant growth during different portions of the annual cycle of field-grown strawberries and to quantify the genetic and environmental relationship between these vegetative growth variables and fruit production at different harvest intervals.

Materials and methods

Several runner plants from each of nine strawberry genotypes, and seedlings from each of 20 biparental crosses among these nine parent genotypes, were planted in a nursery at the Wolfskill Experimental Orchard near Winters, California, in June, 1989. Forty runners from each of the parent genotypes and four runners from each of 20 randomly-sampled seedling genotypes per cross were harvested on 27 October and stored at 2°C until planting. Field trials were established at Winters and at Watsonville, California, on 8 and 9 November, respectively. The Watsonville environment is representative of those used for commercial production in the central coast of California, with a mean January temperature of 10.0°C and a mean summer temperature of 17.2°C. The climate at Winters is more extreme, with mean January and June temperatures of 7.5°C and 23.9°C, respectively. As a consequence, fruit yield at Watsonville is typically larger and the fruiting season is usually longer than for Winters. Large main effects of these locations have been detected (Shaw 1989), and much of the variation for yield among seedlings grown at both locations has been attributed to genetic \times location interaction (Shaw 1989; Shaw et al. 1989).

Each parent genotype was represented by 20 runners and each seedling genotype by two runners at each location. Parent genotypes were evaluated using a randomized complete block design with two blocks per location, and a single plot of ten runners for each genotype in each block. Seedling genotypes were tested using a randomized complete block design with two blocks per location; each block included a single runner from each genotype, thus all blocks initially contained an identical complement of 400 seedling genotypes. To facilitate randomization, the 20 genotypes from each bi-parental cross were further distributed between two plots within each block, with each plot containing ten genotypes.

Plants at Winters were established in single-row beds, with 1.4 m between rows and 45 cm between plants within rows. Plants at Watsonville, were established using two-row diagonal beds on 1.5 m centres, with 60 cm between plants along rows and 30 cm between rows (Welch 1989). Rows with a SE exposure were warmer for the Watsonville trials, and preliminary analyses detected large and significant bedside effects for most of the variables evaluated, with mostly small and non-significant genetic \times bedside interactions. To simplify the comparison of results between test locations, all variables for Watsonville observations were corrected for bedside main effects prior to further analyses.

Data for individual-plant growth and productivity traits were collected throughout the season. Plant diameters were obtained on 23 or 27 February, 23 or 27 March, and 7 or 9 July, for the Watsonville and Winters trials respectively. Variables to describe vegetative plant growth during three intervals were generated as the change in plant diameter between plantation establishment and these three sets of dates. The variables generated were intended to describe plant growth from planting to winter rest (fall/winter growth), during early spring prior to the development of fruiting structures, and during the flowering and production season of late spring and early summer. Individual plant yield and fruit number were scored for 16 consecutive weeks beginning 7 April at Watsonville and for 12 consecutive weeks beginning 15 April at Winters. Production traits were generated and evaluated as yield or fruit number sums for 4-week intervals, and seasonal (total) yield and fruit number. ANOVAs were conducted for parent genotypes at each location separately, with blocks treated as fixed effects and genotypes as random effects; the model variance components given in Table 1 were calculated using linear functions of their expected mean squares (Searle 1971). Because preliminary analyses indicated that observations on runners obtained from a single seedling were correlated, multiple observations on each seedling genotype could not be considered statistically independent, and analyses of seedling data were somewhat more complicated. Runners obtained from a single mother plant share a common developmental and nutritional status, nursery micro-environment, and timing of runner development. Correlations induced by these common environmental effects, or 'C' effects, can confound genetic analyses by downward bias of putative error variance (Burdon and Shelbourne 1974). To minimize the consequences of correlated observations, ANOVAs for seedling genotypes were conducted separately for each block/location combination. Mean squares and degrees of freedom were then averaged across blocks to provide a single test for each location. This treatment sacrifices some of the information available from the repeated measurements on each seedling genotype, but prevents the inflated significance levels and genetic parameter estimates

Table 1. Expected mean squares for analysis of variance of ten production variable and four plant growth variables for parental genotypes

Source	<i>df</i>	<i>EMS</i> ^a
Block (B)	1	$\sigma^2 + k_1\sigma_{bg}^2 + k_3\sigma_b^2$
Genotype (G)	8	$\sigma^2 + k_2\sigma_g^2$
B \times G	8	$\sigma^2 + k_1\sigma_{bg}^2$
Within plot	148 (156) ^b	σ^2

^a $k_1 = 9.2$ or 9.6 , $k_2 = 18.4$ or 19.2 , $k_3 = 82.1$ or 86.1 for Winters and Watsonville trials, respectively

^b Within plot degrees of freedom for Winters and Watsonville trials, respectively

Table 2. Expected mean squares for analysis of variance of ten production variable and four plant growth variables for offspring genotypes

Source	df	EMS ^a
Cross	19	$\sigma^2 + k_1\sigma_c^2$
Within cross	WCDF ^b	σ^2

^a $k_1 = 15.5, 14.6, 18.6$, and 17.8 for blocks 1 and 2 at Winters, blocks 1 and 2 at Watsonville, respectively

^b Within cross degrees of freedom = 290, 272, 352, and 336 for blocks 1 and 2 at Winters, blocks 1 and 2 at Watsonville, respectively

that would result from an underestimation of error variance. Similarly, model variance components for seedling genotypes were calculated for each block/location combination separately, using linear functions of the expected mean squares in Table 2, and a single value for each parameter was calculated by averaging the estimates for the two blocks at each location.

Individual-plant repeatabilities (R) were calculated for parent genotypes as:

$$R = \frac{\sigma_g^2}{\sigma_g^2 + \sigma_{bg}^2 + \sigma^2} \quad (1)$$

In (1), σ_g^2 , σ_{bg}^2 , and σ^2 are components of variance for genotypes, block \times genotype interaction, and pooled within-plot error. The term repeatability is used rather than broad-sense heritability because parent genotypes represent a population that has been selected but not recombined.

Individual-plant heritabilities were calculated for seedling genotypes as:

$$h^2 = \frac{2(\sigma_c^2)}{\sigma_c^2 + \sigma^2} \quad (2)$$

In (2), σ_c^2 and σ^2 are the components of variance among and within biparental crosses respectively. The genetic expectation of σ_c^2 for biparental crosses is: $\sigma_c^2 = (1/2)\sigma_a^2 + (1/4)\sigma_d^2$, in which σ_a^2 and σ_d^2 are the additive and dominance genetic variances, with small fractions of epistatic variance components ignored (Comstock and Robinson 1948). Thus, h^2 is a conservative estimate of the broad-sense heritability and will allow realistic predictions of short-term selection response when individual genotypes are retained and vegetatively propagated.

Correlations among traits due to genetic effects were calculated as:

$$r_{gy} = \frac{\sigma_{g(xy)}}{\sqrt{\sigma_{g(x)}^2 * \sigma_{g(y)}^2}} \quad (3)$$

for parent genotypes, and as:

$$r_c = \frac{\sigma_{c(xy)}}{\sqrt{\sigma_{c(x)}^2 * \sigma_{c(y)}^2}} \quad (4)$$

for the genetic effects that are expressed between biparental crosses (Searle 1971). In (3) and (4), $\sigma_{g(xy)}$ and $\sigma_{c(xy)}$ are the components of covariance for traits x and y due to genotypes or crosses, respectively. Components of covariance were calculated from linear functions of expected and experimental cross products obtained using the MANOVA option of SAS Procedure GLM (SAS Institute, Cary, N.C.); $\sigma_{g(x)}^2$, $\sigma_{g(y)}^2$, $\sigma_{c(x)}^2$, and $\sigma_{c(y)}^2$ are genotypic and biparental cross variance components for traits x and y, calculated as described above.

Several assumptions are required for valid interpretation of the genetic parameters estimated here, most of which have been discussed previously (Shaw et al. 1988; Comstock et al. 1958). Two features of this study require additional discussion. First, although blocks at all locations initially contained identical sets of seedling genotypes, plant mortality and the failure of certain genotypes to flower generated imbalance. Differences between blocks within locations were very slight. However, approximately 14% of the seedling genotypes planted failed to produce fruit at Winters and were excluded from analyses at this location. As a result, between-location comparisons for segregating populations were made between complements of genotypes that differ slightly. A second caution for interpretation concerns the comparison of results for parent and seedling genotypes. Seedling genotypes were included in the study without conscious selection, whereas parental genotypes had been selected for commercial potential. The parents were a representative sample of the advanced selections used to perform crosses in the University of California varietal improvement program; thus, genetic parameters estimated using their segregating offspring are appropriate for predicting response to selection within this population. Also, comparison of a select group with their unselected offspring may reveal differences in their respective patterns of resource partitioning. However, because parental genotypes represent a truncated population, differences between R and h^2 may result either from the consequences of selection or from differences in the genetic expectations of genotypes and crosses. Similarly, r_{gy} reflects the correlation of total genetic effects for a truncated population, whereas r_c better reflects the correlation in an unselected population, but contains fractional additive, dominance, and epistatic genetic covariance components.

Results and discussion

Consistent with previous results (Shaw et al. 1989), yields and fruit numbers were larger at Watsonville than at Winters (Table 3). Plant diameters at the end of the production season were similar for the two test locations (42.7 and 41.4 cm for Winters and Watsonville, respectively), but within-season patterns of vegetative growth differed substantially. Both parent and seedling diameters increased more during fall/winter at Watsonville than at Winters (14.7 vs 7.5 cm, Table 3). Conversely, early spring diameter increments were smaller for Watsonville than for Winters (7.4 vs 13.5 cm, Table 3). Also, diameter change during flowering and production was slightly larger at Winters than at Watsonville (21.7 vs 19.5 cm, Table 3). Short photoperiods during late fall and winter promote inflorescence differentiation in strawberry, provided that temperatures are sufficient to sustain active plant growth (Dana 1980). The difference in fall/winter diameter increments detected between the two locations suggest that the Watsonville environment allowed more growth during short photoperiods than for Winters, and associated increases in flower induction at Watsonville may explain the differences detected for yield and fruit number as well. However, between-location differences were detected for production traits at all harvest intervals (Table 3), and superior produc-

Table 3. Means and standard errors (in parentheses) for ten production variables and four plant growth variables for parent and offspring populations at two test locations

Location	Yield for weeks (grams/plant)				Total yield	Fruit number for weeks				Total fruit number	Diameter growth (cm)			
	1-4	5-8	9-12	13-16		1-4	5-8	9-12	13-16		Fall	Early Spring	Prod. season	Total season
Winters														
Parents	185 (6.5)	127 (7.6)	126 (10.8)	—	438 (14.4)	11.5 (0.4)	6.9 (0.4)	7.2 (0.6)	—	27.5 (0.9)	7.5 (0.2)	13.4 (0.2)	20.8 (0.4)	41.7 (0.3)
Offspring	145 (3.0)	130 (4.6)	110 (6.1)	—	385 (9.3)	8.8 (0.2)	7.3 (0.3)	6.7 (0.4)	—	24.9 (0.7)	7.6 (0.1)	13.6 (0.1)	22.5 (0.2)	43.7 (0.2)
Watsonville														
Parents	200 (8.0)	443 (15.6)	492 (16.1)	510 (19.9)	1644 (38.9)	8.5 (0.3)	19.6 (0.8)	27.6 (0.8)	52.0 (1.7)	107.7 (2.7)	14.7 (0.2)	7.5 (0.2)	18.7 (0.4)	40.9 (0.3)
Offspring	170 (4.4)	429 (7.5)	431 (7.0)	429 (8.8)	1460 (16.7)	8.2 (0.2)	21.7 (0.1)	27.3 (0.1)	49.7 (0.1)	106.9 (1.3)	14.7 (0.1)	7.3 (0.1)	19.8 (0.2)	41.8 (0.2)

tion at Watsonville late in the production season may depend more on sustained flowering during the cooler spring than on active fall/winter growth (Galletta and Bringhurst 1990).

Yields were larger for parent genotypes than for seedling genotypes at both locations, but fruit number was larger for parents only at Winters. Differences in productivity between the selected parents and their unselected offspring may result either from differing rates of flower bud initiation or from different patterns of assimilate partitioning during fruit development. The yield component most limiting to productivity apparently differed depending on the location. Also, parent diameters were smaller than their offspring at both locations (Table 3), perhaps as a consequence of unconscious selection for resource partitioning.

Significant ($P < 0.05$) and occasionally large genetic effects were detected for vegetative growth traits ($R = 0.19-0.54$; $h^2 = 0.05-0.39$) and production traits ($R = 0.02-0.56$; $h^2 = 0.06-0.43$) at nearly all seasonal intervals (Tables 4 and 5). Genetic effects for yield and fruit number during the second production interval were not significant for plants tested at Winters ($R = 0.02$; $h^2 = 0.06$), but where the only exception. Final plant diameters depended mostly on growth during the production season, and genetic parameters estimated for seasonal and production season diameter increments were nearly identical (Tables 4 and 5). Repeatabilities were slightly larger than heritabilities for all traits ($\bar{X}_R = 0.37$, $\bar{X}_{h^2} = 0.24$), consistent with the presence of some non-additive genetic effects (Shaw et al. 1989).

The relationship between vegetative growth and production traits was further resolved by examination of genetic and phenotypic correlations within each location. Fall/winter diameter increments were phenotypically correlated ($r = 0.24-0.59$, $P < 0.01$) with early

and mid-season production traits for parent and seedling genotypes at both locations (Tables 6 and 7). Corresponding genetic correlations between fall/winter diameter and mid-season production traits were uniformly positive (r_{gy} and $r_c = 0.29-0.57$) and occasionally significant (Tables 6 and 7). However, significant genetic correlations between fall/winter diameters and early production traits were detected only for parent genotypes tested at Winters. Although significant genetic effects were detected for fall/winter diameters and early production traits, the positive phenotypic correlations between fall vegetative growth and early productivity resulted primarily from correlated environmental effects rather than pleiotropy. Phenotypic and genetic correlations between fall/winter diameters and late-season production traits were generally either non-significant or significantly negative (Tables 6 and 7). Negative genetic correlations between fall/winter vegetative growth and late-season production traits suggest that rapid early establishment may be somewhat competitive with sustained production, and that selection for one trait may inhibit response to selection for the other.

The relationship between seasonal productivity and fall vegetative growth differed depending on the test location. Seasonal yield and fruit number at Watsonville were positively correlated with fall/winter diameter increments, both phenotypically and genetically (Tables 6 and 7). Conversely, negative genetic correlations (r_c and $r_{gy} = -0.15$ to -0.86) were detected between seasonal production traits (especially fruit number) and fall/winter diameter increase at Winters. Genetic differences for fall/winter growth may reflect differences in innate vigor. High innate vigor combined with excessive vernalization inhibits inflorescence differentiation in strawberry and promotes allocation of

Table 4. Results of ANOVAs and repeatabilities for ten production variables and four plant growth variables for parental genotypes tested at two locations

Source	Mean squares													
	Yield for weeks				Total yield	Fruit number for weeks				Total fruit number	Diameter growth (cm)			
	1-4	5-8	9-12	13-16		1-4	5-8	9-12	13-16		Fall	Early Spring	Produc. season	Total season
Winters														
Block	31	66440**	2819	-	111310	13.4	235.1*	0.0	-	240	3.4	1.7	184.3*	170.3*
Genotype	51818**	12094	232694**	-	173878**	106.8**	40.1	664.4**	-	1108**	27.5**	27.0**	253.7**	205.3**
BxG	7482	11558	23511	-	59762	17.9	31.9	69.1	-	120	4.2	5.7	30.4	31.3
Within plot	4562	8916	7995	-	25828	19.8	24.2	39.6	-	89	3.5	4.2	14.6	14.2
R	0.35	0.02	0.56		0.22	0.19	0.03	0.49		0.37	0.27	0.27	0.39	0.39
SE(R)	(0.18)	(0.04)	(0.27)		(0.12)	(0.11)	(0.04)	(0.24)		(0.19)	(0.15)	(0.12)	(0.22)	(0.22)
Source	Yield for weeks				Total yield	Fruit number for weeks				Total fruit number	Diameter growth (cm)			
	1-4	5-8	9-12	13-16		1-4	5-8	9-12	13-16		Fall	Early Spring	Produc. season	Total season
Watsonville														
Block	59686	273024**	2	233799**	1567241*	55.3*	995.9*	35.1	1127*	6161*	165.4*	161.1*	0.1	0.1
Genotype	40100**	349193**	414903**	746647	2877001**	130.1**	959.9**	993.0**	5621**	13349**	44.4**	21.0**	171.3**	319.5**
BxG	9600	37036	40331	2997	150855	9.4	88.9*	110.3	178	648	8.2	19.2	21.1	35.0*
Within plot	6230	19974	28492	35340	113049	11.3	40.7	74.6	253	571	2.5	2.4	14.6	15.5
R	0.22	0.45	0.41	0.52	0.56	0.36	0.51	0.38	0.53	0.54	0.42	0.19	0.54	0.45
SE(R)	(0.12)	(0.22)	(0.20)	(0.25)	(0.27)	(0.18)	(0.25)	(0.19)	(0.25)	(0.28)	(0.20)	(0.10)	(0.18)	(0.22)

* and ** indicate statistical significance at the 0.05 and 0.01 probability levels, respectively

Table 5. Results of ANOVAs and heritabilities for ten production variables and four plant growth variables for seedling genotypes tested at two locations

Source	Mean squares									
	Yield for weeks				Fruit number for weeks				Diameter growth (cm)	
	1-4	5-8	9-12	13-16	Total yield	1-4	5-8	9-12	13-16	Total fruit number
Winters										
Cross	12838**	19480	69777**	-	94889*	45.3**	65.3	231.2**	-	652.7**
Within cross	4921	12673	18860	-	48427	17.5	45.8	70.4	-	227.1
h^2	0.17	0.06	0.28	-	0.11	0.17	0.06	0.22	-	0.20
SE(h^2)	(0.09)	(0.06)	(0.13)	-	(0.07)	(0.10)	(0.06)	(0.12)	-	(0.10)
Watsonville										
Cross	36355**	102518**	113724**	139820**	532491**	76.1**	373.0	559.0**	1951.5**	5703.1**
Within cross	9970	33169	31089	52275	170299	24.7	91.7	112.1	377.6	962.0
h^2	0.25	0.21	0.27	0.17	0.21	0.21	0.29	0.36	0.37	0.43
SE(h^2)	(0.12)	(0.10)	(0.12)	(0.08)	(0.10)	(0.10)	(0.12)	(0.14)	(0.14)	(0.16)
Mean squares										
Fruit number for weeks										
Diameter growth (cm)										
Product season										
Total season										

* and ** indicate statistical significance at the 0.05 and 0.01 probability levels, respectively

Table 6. Genotypic (r_{gy}) and phenotypic (r) correlations between production traits and plant diameter growth during the fall (D_f), early spring (D_s), during fruit production (D_p), and for the entire season (D_t), for parental genotypes tested at two locations

Location	Interval		Yield for weeks				Total yield	Fruit number for weeks				Total fruit number
			1-4	5-8	9-12	13-16		1-4	5-8	9-12	13-16	
Winters	D_f	r_{gy}	0.76**	0.37	-0.88**	-	-0.60	0.35	0.02	-0.88**	-	-0.86**
		r	0.59**	0.30**	-0.21**	-	0.26**	0.34**	0.30**	-0.16*	-	0.09
	D_s	r_{gy}	0.19	0.19	-0.22	-	-0.13	-0.20	-0.56	-0.21	-	-0.37
		r	0.16*	0.21**	-0.92	-	-0.16*	-0.03	0.14	0.01	-	-0.03
	D_p	r_{gy}	-0.43	-0.13	0.98**	-	0.95**	-0.36	-0.27	0.99**	-	-0.94**
		r	-0.37**	-0.14	0.55**	-	0.18*	-0.33**	-0.20**	0.50*	-	-0.26**
	D_t	r_{gy}	-0.11	0.04	0.56	-	0.64*	-0.28	-0.39	0.57	-	0.49
		r	-0.06	0.07*	0.48**	-	0.37**	-0.22**	-0.02	0.47**	-	0.33**
Watsonville	D_f	r_{gy}	-0.10	0.42	0.29	0.04	0.26	-0.32	-0.32	0.26	0.03	0.14
		r	0.46**	0.49**	0.09	0.14	0.40	0.36**	0.52**	0.23**	0.13	0.35**
	D_s	r_{gy}	-0.47	-0.12	0.24	0.50	0.34	-0.79**	-0.69**	-0.03	0.32	-0.03
		r	-0.40**	-0.15	0.22**	0.12	0.01	-0.47**	-0.39**	0.00	0.12	-0.10
	D_p	r_{gy}	0.02	0.67*	0.71*	0.28	0.65*	-0.29	0.42	0.48	0.25	0.37
		r	-0.21**	0.11	0.48**	0.28**	0.34	-0.26**	-0.05	0.25**	0.28**	0.20**
	D_t	r_{gy}	-0.18	0.68**	0.78**	-0.09	0.54*	-0.60**	-0.06	0.24	-0.12	-0.09
		r	-0.12**	0.17**	0.43**	0.09*	0.27**	-0.22**	-0.08*	0.24**	0.15**	0.10**

* and ** indicate statistical significance at the 0.05 and 0.01 probability levels, respectively

Table 7. Genotypic (r_c) and phenotypic (r) correlations between production traits and plant diameter growth during the fall (D_f), early spring (D_s), during fruit production (D_p), and for the entire season (D_t), for seedling genotypes tested at two locations

Location	Interval		Yield for weeks				Total yield	Fruit number for weeks				Total fruit number
			1-4	5-8	9-12	13-16		1-4	5-8	9-12	13-16	
Winters	D_f	r_c	0.14	0.31	-0.36	-	-0.15	-0.18	0.46**	-0.26	-	-0.21
		r	0.36**	0.24**	0.02	-	0.24**	0.10*	0.27**	0.05	-	0.17**
	D_s	r_c	-0.55**	-0.15	-0.02	-	-0.29	-0.61**	-0.22	-0.14	-	-0.33
		r	0.09*	-0.02	-0.13**	-	-0.07	-0.04	-0.02	-0.12**	-	-0.11**
	D_p	r_c	-0.29	0.32	0.69**	-	0.65**	-0.48*	0.16	0.74**	-	0.56**
		r	-0.26**	0.05	0.11**	-	0.01	-0.32**	0.01	0.08*	-	-0.00
	D_t	r_c	-0.51*	0.38	0.57**	-	0.54*	-0.70**	0.23	0.62**	-	0.42*
		r	-0.10**	0.11**	0.04	-	0.05	-0.27**	0.08	0.03	-	0.00
Watsonville	D_f	r_c	-0.02*	0.55**	0.57**	0.23	0.65**	0.08	0.45*	0.59**	0.40	0.52*
		r	-0.50**	0.49**	0.08*	0.17**	0.48**	-0.49**	0.58**	0.24**	0.24**	0.47**
	D_s	r_c	-0.28	-0.12	-0.20	-0.28	-0.28	-0.45*	-0.39	-0.26	-0.09	-0.36
		r	-0.25**	0.00	0.25**	-0.10**	-0.02	-0.33**	-0.24**	0.09*	-0.03	-0.12**
	D_p	r_c	-0.06	0.68**	0.71**	-0.15	0.57**	-0.54*	-0.07	0.12	-0.24	-0.14
		r	-0.25**	-0.03	0.33**	0.07	0.10**	-0.31**	-0.24**	0.12**	0.09*	-0.04
	D_t	r_c	-0.18	0.68**	0.78**	-0.09	0.54*	-0.60**	-0.06	0.24	-0.12	-0.09
		r	-0.12**	0.17**	0.43**	0.09*	0.27**	-0.22**	-0.08*	0.24**	0.15**	0.10**

* and ** indicate statistical significance at the 0.05 and 0.01 probability levels, respectively

available resources to vegetative functions (Voth and Bringham 1970; Shaw 1989). Vigorous genotypes may be highly productive at Watsonville, but too vegetative, and therefore less productive, at the colder Winters location.

Correlations between diameter increase in early spring and production traits were generally negative (Tables 6 and 7) at both locations. Genetic correlations between spring diameter increments and first-interval fruit number were consistently negative and large (r_{gy} and $r_c = -0.20$ – -0.79 , Tables 6 and 7) and were statistically significant in three of four cases. Corresponding positive correlations were not detected between spring diameter increments and late-season production traits, which suggests that vigorous spring growth is associated with reduced inflorescence number rather than a shift in the timing of fruit development. Plants that grow most rapidly during the early spring may do so because they lack reproductive sinks, and vegetative activity during this interval may indicate limited fall/winter inflorescence differentiation. Spring growth might serve as a predictor of low productivity, and could be included as an indirect trait in a selection index.

Diameter increase during the production season was either uncorrelated or negatively correlated to early production traits, but was positively correlated to mid- and late-season production (Tables 6 and 7). Genetic correlations between yield during the third harvest interval and production-season diameter increments were uniformly large and highly significant (r_{gy} and $r_c = 0.69$ – 0.98 , Tables 6 and 7). Although vegetative and reproductive functions compete for assimilates in strawberry, sustained productivity appears dependent on adequate vegetative growth throughout the spring and early summer. The relationship between production-season growth and fruit number differed somewhat from that observed for yield. Genetic correlations between late-season fruit number and production season diameter increments were positive and large for plants tested at Winters (r_{gy} and $r_c = 0.74$ – 0.99 , $P < 0.01$), but were small and non-significant for plants tested at Watsonville (r_{gy} and $r_c = 0.24$ – 0.48 , $P > 0.05$). Low winter temperatures probably limited the opportunity for fall/winter inflorescence differentiation at Winters, and fruit number may have been the limiting yield component at this location. At Watsonville, fall/winter inflorescence differentiation was not as constrained by temperature and competition for available photosynthate during fruit development, rather than absolute fruit number, may have been the limiting yield component.

Correlations for final diameter were similar in sign but differed in magnitude from those that use production-season diameter (Tables 6 and 7). Because

plant diameter at the end of the season depends largely on production-season growth, correlations between production traits and final diameter add little information. Further, correlations between final diameter and production traits summarize a relationship that involves several partially-correlated traits, and express little of the information demonstrated for seasonal growth components.

Genetic correlations between diameter change and production traits suggest that patterns of vegetative growth and production patterns are conditioned in part by similar sets of genes. As a consequence, selection for yield will modify the growth patterns of vegetative structures, and vice versa. Plant diameters are a crude indicator of plant growth, but are easily scored and could be used in an index for selection of cultivars with desired levels of vigor and specific patterns of resource partitioning. Further, a more detailed knowledge of the genetic factors that determine plant growth, and their interactions with specific environmental variables, could narrow the targets of future cultivar development programs.

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