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The inheritance of vegetative growth traits in strawberries (*Fragaria* × *ananassa*) grown at low temperatures and their relationship to field productivity

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Abstract. The genetic relationship between vegetative growth at low temperatures and productivity was investigated for strawberries grown in controlled and field environments. Genotypes from 20 biparental crosses were grown in controlled environments with 11 °, 14 °, and 17 °C days, 11 °C nights, and 11-h daylength to simulate a range of winter growing conditions expected in mediterranean environments. Individual plants were scored for two initial runner traits and eight vegetative growth traits. Significant main effects of temperature and cross were detected for all growth chamber traits, and conservative estimates of the broad sense heritability (h^2) for these traits were 0.10–0.28. None of the temperature X cross interaction effects were significant, suggesting that genetic potential for vegetative growth and vigor is expressed similarly at low and optimal growing temperatures. Highly significant genetic correlations were detected between many growth chamber trait pairs, indicating pleiotropic effects for the genes that condition these traits. Complementary field trials were established, and individual plants were scored for traits that describe yield, production pattern, and plant size. Significant negative genetic correlations were detected between traits that describe growth in the chambers and early production in the field trials, but genetic correlations between chamber growth traits and mid-season or total production were significantly positive and occasionally large. Several of the yield and field growth variables were genetically correlated to initial runner plant traits, suggesting that indirect selection using traits scored in the nursery can be used to improve yield and modify production pattern in the field.

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Introduction

Strawberry plantations grown in mediterranean or arid subtropical environments are characterized by exceptional productivity and an extended fruiting season. In these environments, inflorescence initiation and/or differentiation in individual plants occur throughout the winter, provided that temperature and other environmental factors permit plant growth (Darrow 1966; Dana 1980). Although many factors may contribute to superior performance in these environments, the ability to sustain growth at low temperature is perhaps the most important (Bringhurst and Voth 1984).

The importance of cultural treatments that enhance strawberry growth during periods of inflorescence differentiation is well established (Strick and Proctor 1988a); several reports have suggested that genetic factors contribute to variable flowering responses as well. For example, variation for vegetative growth rate during critical periods within the production cycle has been correlated with differences in productivity among strawberry cultivars (Strick and Proctor 1988b). Also, Guttridge (1969) reported variation among strawberry cultivars adapted to specific regions for the temperature and photoperiod regimes they required for floral initiation. Shaw (1993) demonstrated that, in a segregating population of strawberries, vegetative growth traits of field-grown plants were genetically correlated to several components of yield and production pattern. Fall and winter growth increments were positively correlated with mid-season and total production traits, but were uncorrelated or

negatively correlated with late-season production. None of the vegetative traits scored in the field were genetically correlated with early productivity.

The primary objective of this study was to supplement the results obtained for field-grown strawberries (Shaw 1993) with information about strawberry plants grown in controlled environments. A large number of factors impact flower initiation and differentiation (Guttridge 1985); the intent here was to quantify the genetic variation for vegetative growth in strawberry in controlled environments that simulate a range of winter temperatures in mediterranean environments. An eventual goal of this research is to use vegetative growth traits to facilitate early-cycle indirect selection for production traits. Thus, a second objective of this study was to determine the genetic relationship between traits scored in growth chambers and traits that describe growth and productivity in the field.

Materials and methods

Seedlings from each of 20 bi-parental crosses among nine parent genotypes were planted in a nursery at the Wolfskill Experimental Orchard near Winters, Calif. in June, 1989. Both growth chamber studies and field evaluations were conducted using runner plants obtained from this population.

Growth chamber experiments

Runners from 8–12 seedling genotypes per cross were harvested on December 27–30 and stored at −2 °C for at least 8 weeks before planting. Response to vernalization varies among strawberry genotypes (Guttridge 1969), but all plants tested in growth chamber studies had received cold treatments sufficient to ensure maximum growth response.

After cold storage, runner plants were planted in 10 cm square pots (10 × 10 × 9) and grown in a common greenhouse for 10 days. A single runner from each genotype was then transferred to controlled environments with 11 °, 14 °, and 17 °C daytime temperatures and a common night temperature of 11 °C. Treatments were chosen to simulate realistic winter conditions for mediterranean environments, but also to avoid temperatures below 7.2 °–10 °C, which could induce vernalization (Galletta and Bringhurst 1990). Further, short daylengths (11 h) were chosen to mimic winter conditions and to normalize the flowering response of short-day and day-neutral genotypes (Guttridge 1985), both of which were present in the sample population. Light intensity was a minimum of 700 μmol/m^2 per second, which is close to saturation levels reported for strawberries (Hancock 1991).

Individual plants were scored for crown caliper and initial fresh weight prior to planting. Final plant measurements were taken after 6 weeks of growth in the different controlled environments for cross-sectional plant diameter, leaf number, and the length of the longest petiole. After final measurements, the plants were removed from their pots and dissected. Total leaf area of each plant was then measured using a Panasonic WV-CD20 Video Camera, a personal computer, and Digital Image Analysis System v. 1. 02. (DIAS II by Decagon Devices). The plants were then dried in a desiccating air dryer for 5–10 days, and dry root weights and dry shoot weights were recorded. A relative growth rate based on 6th-week diameter and an intermediate diameter obtained 2 weeks after transfer to the growth chambers was calculated according to Roberts et al. (1985) as:

$$\frac{\ln(\text{6-week diameter}) - \ln(\text{2-week diameter})}{\ln(\text{2-week diameter})} \quad [1]$$

Treatments means for the dry-weight variables were proportional to their standard deviations and were transformed using natural logarithms prior to further analyses (Bulmer 1985); all other variables were analyzed untransformed.

Because growth chamber space was limited, plants were removed from cold storage and planted on three dates, and planting dates were treated as replicates in time. Crosses were represented by 2–4 genotypes in each replicate. ANOVAs for growth chamber trials were conducted with replications and temperatures as fixed effects and crosses as random effects (Steele and Torrie 1980) using Type III model expectations obtained from SAS procedure GLM (SAS Institute 1988). Also, because the number of genotypes per cross in each replication was small, cross X replication and cross X temperature X replication interaction effects were confounded with variation due to within-cross genetic sampling; sums of squares and degrees of freedom from these sources were pooled to form the residual within-cross variance. Model variance components were calculated using linear functions of the expected mean squares in Table 1 (Searle 1971).

Genotypic heritabilities were calculated for growth chamber traits as (Hallauer and Miranda 1981)

$$h^2 = \frac{2(\sigma_c^2)}{\sigma_c^2 + \sigma_{ct}^2 + \sigma^2} \quad [2]$$

and cross-mean heritabilities were calculated as (Namkoong 1979)

$$h_c^2 = \frac{2(\sigma_c^2)}{\sigma_c^2 + \sigma_{ct}^2/n_t + \sigma^2/n_t n_g} \quad [3]$$

In [3], n_t and n_g are coefficients representing the number of temperature treatments and number of genotypes per cross, respectively, and were estimated using Type III model expectations (SAS Institute 1988). The genetic expectation of σ_c^2 for biparental crosses is: $\sigma_c^2 = \frac{1}{2}\sigma_a^2 + \frac{1}{4}\sigma_d^2$, plus small fractions of epistatic components (Comstock and Robinson 1948); thus, h^2 is a conservative estimate of the broad-sense heritability.

Genotypic correlations among growth chamber traits were calculated as (Searle 1971):

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

Table 1. Form and expected mean squares for analyses of variance for strawberry vegetative growth trait variables, using seedling genotypes from 20 biparental crosses grown a three temperatures

Source	*df*	Expected mean squares[a]
Replication (R)	2	$\sigma^2 + k_5\sigma_r^2$
Temperature (T)	2	$\sigma^2 + k_1\sigma_{tc}^2 + k_4\sigma_t^2$
R × T	4	$\sigma^2 + k_3\sigma_{rt}^2$
Cross (C)	19	$\sigma^2 + k_1\sigma_{tc}^2 + k_2\sigma_c^2$
T × C	38	$\sigma^2 + k_1\sigma_{tc}^2$
Within cross	487	σ^2

[a] $k_1 = 9.2$, $k_2 = 27.4$, $k_3 = 58.0$, $k_4 = 183.0$, $k_5 = 176.6$

In [4] $\sigma_{c(xy)}$ is the component of covariance for traits x and y due to crosses; this value was calculated from linear functions of expected and experimental cross products obtained using the MANOVA option of SAS Procedure GLM (SAS Institute 1988). $\sigma^2_{c(x)}$ and $\sigma^2_{c(y)}$ are cross variance components for traits x and y, calculated as described above.

Field experiments

Runners from 20 randomly sampled seedling genotypes per cross (occasionally fewer) were harvested on October 27, stored at 2 °C, and planted at the Watsonville Research Facility on November 9. Plants were established using two-row diagonal beds on 1.5 m centers, with 60 cm between plants along rows and 30 cm between rows (Welch 1989). Seedling genotypes were planted in a randomized complete block design, with a single runner from each genotype in each of two blocks. Genotypes from each cross were distributed between two plots within each block, and all blocks initially contained an identical complement of seedling genotypes. The experimental results described here for field performance are a subset of those reported previously (Shaw 1993). They are included, with some re-analysis described below, to facilitate the comparison of growth chamber experiments with field performance in a realistic production environment.

Data for individual plant growth and productivity traits were collected throughout the annual plantation establishment and production season, and variables to describe plant growth and productivity were generated as reported previously (Shaw 1993). Briefly, plant size was evaluated as the change in cross-sectional plant diameter during the fall/winter, in early spring, and during the flowering and fruiting season. Productivity was scored as yield sums for 4-week intervals over the 16-week harvest season and as seasonal (total) yield. Rows with a SE exposure were warmer for the Watsonville trials, and all variables for field observations were corrected for main bedside effects prior to further analyses (Shaw 1993).

ANOVAs were conducted with crosses treated as random effects and Type III model expectations obtained from SAS procedure GLM (SAS Institute 1988). Model variance components were calculated using linear functions of the expected mean squares in Table 2 (Searle 1971).

Genotypic heritabilities were calculated for field productivity and growth traits as (Hallauer and Miranda 1981)

$$h^2 = \frac{2(\sigma^2_c)}{\sigma^2_c + \sigma^2} \qquad [5]$$

and cross-mean heritabilities were calculated as (Namkoong 1979)

$$h^2_c = \frac{2(\sigma^2_c)}{\sigma^2_c + \sigma^2/n_g}$$

In [6], n_g is the number of genotypes per cross. The analyses reported here for field trials were conducted using the means of two runners per seedling genotype (genotypic means) as observations, and the heritabilities generated from this analysis differ slightly from those reported earlier (Shaw 1993). This procedure was adopted to simplify the comparison of field and growth chamber results.

Table 2. Form and expected mean squares for analyses of variance for nine productivity and vegetative growth variables, using seedling genotypes from 20 biparental crosses grown in field trials

Source	*df*	Expected mean squares[a]
Cross	19	$\sigma^2 + k_1\sigma^2_c$
Within cross	356	σ^2

[a] $k_1 = 18.8$

Field/growth chamber comparisons

Genotypic correlations between field and growth chamber traits were calculated as (Burdon 1977)

$$r_{g(xy)} = \frac{r_{c(xy)}}{\sqrt{h^2_{c(x)} \cdot h^2_{c(y)}}} \qquad [7]$$

In [7], $r_{c(xy)}$ is the phenotypic correlation of cross means after correction for the main effects of temperature, $h^2_{c(x)}$ and $h^2_{c(y)}$ are cross-mean heritabilities for field and growth chamber traits, respectively.

Results and discussion

Growth chamber experiments

Plants grown at higher temperatures had greater growth response for all vegetative traits except root dry weight (Table 3). Above-ground vegetative growth rate is expected to change substantially between 11 °C and 17 °C (Heide 1977), whereas Proebsting (1957) determined that root growth was unaffected between 7.2 °C and 17 °C. Means for initial caliper and fresh weight did not differ among temperature treatments; these traits were evaluated prior to the application of differential temperature environments, and their uniformity suggests that randomization among temperature treatments was effective.

ANOVA result confirm that temperature effects were highly significant ($P < 0.01$) for all growth chamber traits except root dry weight (Table 4). Replication effects were significant for initial runner traits and for a number of growth variables; temperature × replication interactions usually were significant where replication effects were not. When replication effects were significant, plants established after longer periods of storage had lower trait values. Similarly, when temperature × replication interactions were significant, high temperatures were detrimental in combination with later planting dates. Together, these results suggest that replication effects reflect the detrimental consequences of long-term storage rather than any enhancement of plant vigor by continued accumulation of cold (Voth and Bringhurst 1970).

Cross variances were significant or highly significant for all growth variables, demonstrating the presence of genetic variation (Table 4). Conversely, none of the cross × temperature interactions were significant, indicating that vegetative growth traits were expressed consistently regardless of temperature treatment. Heritabilities were moderate for initial runner conditions ($h^2 = 0.22-0.28$, Table 4), but low for all growth chamber traits ($h^2 = 0.05-0.17$, Table 4). Cross × temperature in-

Table 3. Means and standard deviations (in parentheses) for ten vegetative growth variables, using seedling genotypes from 20 biparental crosses grown at three temperatures

Chamber Temperature (°C)	*n*	Initial caliper (mm)	Initial weigth[a] (g)	Leaf number	Petiole length (cm)	Plant diameter (cm)	Leaf area (cm^2)	Crown weight[a] (g)	Root weight[a] (g)	Total weight[a] (g)	Growth rate[b]
11	184	9.4 (1.7)	6.8 (2.2)	3.4 (1.3)	8.3 (2.1)	17.9 (3.0)	336.8 (115.4)	3.9 (1.2)	2.4 (1.0)	6.3 (2.0)	0.15 (0.07)
14	180	9.5 (1.7)	6.6 (1.9)	4.5 (1.6)	11.4 (2.2)	21.1 (2.9)	448.4 (128.5)	4.8 (1.3)	2.4 (0.9)	7.2 (1.8)	0.20 (0.09)
17	189	9.4 (1.8)	6.6 (2.2)	5.7 (1.9)	15.8 (3.1)	26.1 (3.8)	546.6 (153.3)	5.4 (1.5)	2.1 (0.7)	7.6 (2.0)	0.26 (0.10)

[a] Initial weight on a fresh basis, all others on a dry weight basis
[b] See Eq. 1

Table 4. Results for analysis of variance and heritabilities for ten vegetative growth variables, using seedlings genotypes from 20 biparental crosses grown at three temperatures

Source	Mean squares for									
	Initial caliper	Initial weight	Leaf number	Petiole length	Plant diameter	Leaf area	Crown weight	Root weight	Total weight	Growth rate
Replication (R)	20.83**	30.43*	32.43	330.3	335.8*	1.39	1.54*	3.24*	2.08*	0.209*
Temperature (T)	1.32	2.17	215.47**	2136.2**	678.6**	10.52**	5.25**	0.44	1.88**	0.444**
R × T	1.06	2.91	5.89*	59.0**	21.0*	0.27	0.12	0.33	0.14	0.021*
Cross (C)	10.11**	18.60**	6.64**	14.4**	30.4**	0.27*	0.26**	0.20*	0.18*	0.014**
T × C	1.91	2.11	1.75	5.9	9.1	0.10	0.05	0.07	0.04	0.004
Within cross	2.74	3.99	2.35	4.25	8.7	0.17	0.11	0.12	0.09	0.006
h^2	0.22	0.28	0.17	0.14	0.16	0.10	0.15	0.05	0.13	0.09
SE (h^2)	(0.07)	(0.09)	(0.05)	(0.06)	(0.06)	(0.03)	(0.05)	(0.03)	(0.04)	(0.04)
h_c^2	0.79	0.84	0.75	0.67	0.73	0.69	0.79	0.38	0.77	0.56
SE (h_c^2)	(0.36)	(0.40)	(0.33)	(0.29)	(0.31)	(0.31)	(0.40)	(0.28)	(0.48)	(0.32)

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

teractions were uniformly non-significant; thus the low heritabilities reflect large sampling variances for these traits rather than confounding interactions. The resolution of genetic differences could be improved by evaluationg clonal propagules within each treatment (Shaw and Hood 1985).

Genotypic and phenotypic correlations between pairs of growth chamber traits were usually similar in sign but occasionally differed in significance and magnitude (Table 5). Large differences were detected only for correlations that involve root dry weight. Differences between phenotypic/genotypic pairs may reflect complementary genetic and environmental relationships, but are most likely the result of high sampling error associated with genetic correlations. Because the genetic variation detected for root weight was small, genetic correlations that use this trait must be regarded with caution.

Genotypic correlations among leaf number, petiole length, plant diameter, leaf area, crown weight, and total dry weight were all significant (all but one were highly significant) and large (Table 5). Heritable variation for these traits apparently is conditioned by genes that have widespread consequences for plant growth and vigor. Because these traits give largely the same genetic information, a subset would probably suffice for future studies. Also, significant and highly significant genotypic correlations were detected between initial caliper or initial fresh weight, and several vegetative growth variables (Table 5), suggesting that genes that affect runner growth and development in the nursery are pleiotropic with those that condition later vegetative growth.

Field experiments

Descriptive statistics for growth and productivity variables in field trials have been reported previously (Shaw 1993). ANOVAs conducted using genotypic means detected highly significant cross variances for all yield variables and all diameter increments (Table 6). Heritabilities for yield components were generally larger than those estimated for growth traits ($h^2 = 0.18-0.32$ versus $h^2 = 0.14-0.18$). Heritabilities estimated for field diame-

Table 5. Genetic (above the diagonal) and phenotypic correlations (below the diagonal) among ten strawberry vegetative growth traits, using seedling genotypes from 20 biparental crosses grown at three temperatures

	Initial caliper	Initial weight	Leaf number	Petiole length	Plant diameter	Leaf area	Crown weight	Root weight	Total weight	Growth rate
Initial caliper		0.60**	0.44*	0.41	0.05	0.38	0.23	1.15**	0.55**	−0.17
Initial weight	0.47**		0.31	0.44*	−0.27	0.12	−0.18	0.98**	0.12**	−0.19
Leaf number	0.12*	0.14**		0.75**	0.50*	0.66**	0.62**	0.89**	0.82**	−0.06
Petiole length	0.50**	0.00	0.44**		0.57**	1.10**	0.76**	0.84**	0.89**	−0.04
Plant diameter	0.01	−0.02	0.51**	0.78**		0.94**	0.95**	0.17	0.74**	0.29
Leaf area	0.00	0.06	0.51**	0.49**	0.67**		1.05**	0.34	1.01**	0.17
Crown weight	0.11*	0.11*	0.43**	0.43**	0.69**	0.74**		0.23	0.95**	0.01
Root weight	0.23**	0.39**	0.07	−0.04	0.14**	0.30**	0.51**		0.95**	−0.24
Total weight	0.17**	0.24**	0.35**	0.31**	0.57**	0.67**	0.94**	0.77**		−0.11
Growth rate	−0.12**	−0.15**	0.17**	0.41**	0.35**	0.03	−0.18**	0.41**	−0.29**	

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

Table 6. Results for analyses of variance and heritabilities for nine productivity and vegetative growth variables, using seedling genotypes from 20 biparental crosses grown in field trials

Source	Mean squares for:								
	Yield for weeks: (g/plant)				Seasonal yield	Diameter increments for: (cm)			Seasonal diameter
	1–4	5–8	9–12	13–16		Fall	Spring	Produce season	
Cross	30 018**	64 825**	98 436**	130 113**	417 852**	5.46**	5.44**	59.2**	83.4**
Within cross	6 448	22 212	19 840	35 641	118 641	2.22	2.24	21.0	28.4
h^2	0.32	0.18	0.36	0.25	0.25	0.15	0.14	0.17	0.18
SE(h^2)	(0.13)	(0.07)	(0.10)	(0.09)	(0.09)	(0.07)	(0.06)	(0.08)	(0.08)
h_c^2	0.78	0.65	0.80	0.73	0.73	0.60	0.60	0.63	0.65
SE(h_c^2)	(0.39)	(0.28)	(0.30)	(0.31)	(0.31)	(0.31)	(0.31)	(0.33)	(0.32)

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

ter increments were similar in magnitude to those for growth chamber traits. The relatively low heritabilities for growth traits may reflect errors of measurement or the response to variable microenvironments.

Field/growth chamber comparisons

Several of the traits scored in the growth chamber experiments had strong genetic relationships with traits scored in the field. Plant diameter, leaf area, crown dry weight, and total dry weight obtained for plants in growth chambers had significant positive genotypic correlations with field diameter growth during the spring and during the production season (Table 7). Almost all other vegetative traits scored in the growth chambers were positively correlated with spring and production season diameter increments, but not significantly. Conversely, none of the vegetative traits scored in the chambers were correlated with fall diameter increment in the field. This result is consistent with previous observations: genes that condition heritable variation for fall growth in the field are independent of those that affect growth later in the season (Shaw 1993).

Significant negative genotypic correlations were detected between plant diameter, leaf area, crown weight, and growth rate in the chambers and early production in the field trials, but genotypic correlations between these traits and mid-season or total production were significantly positive and occasionally large (Table 7). Excess vigor in strawberries, whether genetically or environmentally induced, promotes competition between vegetative and reproductive functions and can delay or inhibit inflorescence differentiation (Dana 1980). The observation that vigor in the growth chamber predicts delayed fruiting in the production field suggests that early yield and total yield may be partially conflicting breeding objectives.

Several of the yield and field growth variables were genotypically correlated to initial runner caliper and weight scored for growth chamber trials (Table 7). Run-

Table 7. Genetic correlations between ten strawberry vegetative growth traits obtained using seedling genotypes grown at three temperatures and nine vegetative and production traits obtained in field trials

	Initial caliper	Initial weight	Leaf number	Petiole length	Plant diameter	Leaf area	Crown weight	Root weight	Total weight	Growth rate
Yield: wks 1–4	0.20	−0.31*	−0.05	−0.48**	−0.57**	−0.56**	−0.37*	0.11	−0.21	−0.37**
wks 5–8	0.36*	0.24	0.41	0.44*	0.58**	0.54**	0.68**	0.65*	0.77**	0.10
wks 9–12	0.25	0.20	0.25	0.22	0.44*	0.46**	0.54**	0.28	0.54**	0.06
wks 13–16	0.61**	0.44**	0.35*	0.32	0.31	0.29	0.20	0.06	0.15	0.55**
Total yield	0.69**	0.37*	0.47**	0.32	0.42*	0.45*	0.54**	0.46	0.50**	0.20
D_f[a]	0.22	0.47*	0.07	0.16	0.28	0.22	0.11	0.08	0.07	0.31
D_s	0.20	−0.06	−0.06	0.02	0.11	0.44*	0.41*	0.41	0.45*	−0.15
D_p	−0.21	−0.10	0.15	0.11	0.33	0.50**	0.67**	0.41	0.71**	−0.32
D_t	−0.08	0.01	0.13	0.13	0.37*	0.60**	0.64**	0.46	0.75**	−0.24

* and ** indicate significance at the 0.05 and 0.01 probability levels, respectively; tests based on the significance of cross-mean correlations

[a] D_f, D_s, D_p, and D_t are plant diameter increments for fall and winter, spring, production season, and total season intervals, respectively

ners for field and growth chamber studies were sampled independently and harvested separately at differing times of the year. Heritable variation for runner traits in the nursery is apparently pleiotropic with variation for production traits.

Conclusions

The variation for vegetative growth traits in our segregating strawberry population was attributable in part to genetic differences among individuals, and differences in genetic potential for vegetative growth were expressed similarly at low and optimal growing temperatures. We found no evidence of genetic effects that favor growth specifically at low temperatures; genotypes that grow well at low temperatures also do well at higher temperatures.

Commercial production systems generally use partially vernalized runners (Bringhurst and Voth 1989), whereas our growth chamber evaluations were conducted using fully vernalized plants. Interactions between vernalization sensitivity and growing temperature may impact vegetative growth responses substantially. However, large genetic correlations were detected between crown diameters in the field and several of the traits scored in the growth chamber experiments, suggesting that genetic effects for at least some indicators of vegetative growth are relatively stable to variable vernalization treatments.

Plant vigor has important consequences for both yield and production pattern in field performance trials. Several of the genotypic correlations between chamber growth traits and total yield were greater than $r_c = 0.5$; when r_c^2 is used as an indicator of shared genetic variance, our results suggest that greater than 25% of the genetic variance for total yield can be explained by variation in vegetative growth in controlled environments. An even greater fraction of the genetic variance for total yield is shared with initial caliper, suggesting that the evaluation of runner traits in the nursery could be valuable in obtaining indirect selection response for yield. Conversely, high genetically conditioned plant vigor was clearly detrimental to early production. Because vigor has conflicting consequences for early and total yield some tradeoffs are inevitable, and indirect selection using vegetative growth traits might be substantially improved by the inclusion of indexes of resource partitioning.

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