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Genetic Analysis of Strawberry Root System Traits in Fumigated and Nonfumigated Soils I. Inheritance Patterns of Strawberry Root System Characteristics

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Abstract. **Seedling offspring of crosses among 10 selected strawberry genotypes (*Fragaria ×ananassa* Duch.) from the University of California strawberry improvement program were established in annual hill culture. Soil treatments consisted of 1) preplant fumigation using a mixture of methyl bromide and chloropicrin or 2) no fumigation. Root systems of individual plants were sampled with a soil probe in January, April, and July 1994 to determine root mass (RM), secondary root mass (SRM), and a subjective root appearance score (RAS). For each trait, genetic analyses of partial diallels were performed to quantify sources of genetic, environmental, and interaction variance. Root trait values differed significantly between soil treatments only for the April sampling date, with all trait values greater in fumigated soils than in nonfumigated soils. For RM and SRM, variance due to general combining ability (GCA) was significant in April and July. Narrow-sense heritabilities (h^2) for RM increased between January (0.14) and July (0.40); SRM showed a similar trend with a higher h^2 on each sampling date. GCA variances were nonsignificant for RAS, however, significant fumigation × GCA interaction variance was detected for RAS in January. Specific combining ability (SCA) variances were nonsignificant for all traits. To further quantify the extent of interactions, correlations (r_g) between genotypic expressions in fumigated soils and nonfumigated soils were calculated for each root trait. These r_g values were at or near unity (> 0.85) for RM and SRM on all sampling dates, implying that genetic variability for these traits is conditioned by genes with identical effects within each soil environment. Conversely, r_g between soil environments was 0.52, 0.62, and –0.18, for January, April, and July RAS, respectively. These findings suggest that genetic variability exists within this germplasm base for strawberry root mass characteristics. Genetic variation also exists for January root appearance score, but it is not conditioned identically across fumigation treatments.**

Deficient root growth or poor root health are known to have negative consequences for strawberry (*Fragaria ×ananassa*) productivity (Wilhelm and Paulus, 1980; Yuen et al., 1991). Currently, root development and health do not limit commercial production in California because soils are fumigated with a mixture of methyl bromide and chloropicrin before planting, and problems associated with weeds, nematodes, and soilborne fungi are minimized (Himelrick and Dozier, 1991; Wilhelm and Paulus, 1980). Due to the availability of cultural methods for insuring root health, the extent of genetic variation for strawberry root traits, their modes of inheritance, and their associations with production traits have not been investigated widely. However, the likely regulatory phaseout of methyl bromide use has renewed interest in surveying strawberry populations for genes conferring adaptation specific to soils with suboptimal preplant fumigation treatment (Watson et al., 1992). This adaptation may involve aspects of root system performance because of its direct interaction with the rhizosphere. Characterization of root system traits for genetic parameters in relevant soil fumigation environments is the initial step in evaluating these traits for use as selection criteria for cultivar development.

Most available information regarding strawberry root system performance concerns the primary effects of soil pathogens on root appearance and morphology (Wilhelm, 1965; Wilhelm et al., 1972; Yuen et al., 1991). Of particular relevance to California is a complex of sublethal soil pathogens, also known as the black root complex, which reduces productivity in nonfumigated soils (Wilhelm, 1961; Larson and Shaw, 1995). The identities and relative proportions of pathogens in this complex vary by location (Paulus, 1990), but all tend to attack feeder rootlets initially, resulting in their blackening and death, followed eventually by decay of the main, or primary, roots (Wilhelm, 1961). Fumigation trials conducted in soils with sublethal pathogen problems have confirmed that dead or diseased root fragments are recovered at higher frequency from plants in nonfumigated soils than in fumigated soils (Yuen et al., 1991). Further, significantly lower root masses and root densities have been detected for plants in nonfumigated soils than in fumigated soils, particularly at the time of peak fruit production (Larson and Shaw, 1996; Yuen et al., 1991). To characterize further these fumigation-related root system responses, Fort and Shaw (1998) developed a subjective measure of root health based on visual criteria and a feeder rootlet mass measurement. They found that plants in fumigated soils had healthier roots and greater root mass than plants in nonfumigated soils, but genetic analyses of these traits were not performed.

Compared to the main effects of soil fumigation, much less is known about the genetic responses of root traits to different fumigation treatments. Yuen et al. (1991) reported significant differences among cultivars with no evidence of cultivar × fumigation treatment interactions for root density in their fumigation study. However, the small number of genotypes sampled (three or fewer at all locations) prevents their results from being generalized to a broader germplasm sample. Some information about genetic × fumigation interactions for root characters might be inferred from evaluation of above-ground traits in fumigation experiments, which indirectly reflect rhizosphere conditions. While substantial genetic variance has been found for many above-ground growth and productivity traits in fumigation studies (Fort et al., 1996; Larson and Shaw, 1995; Shaw and Larson,

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1996), genetic × fumigation interaction variances generally have been nonsignificant and small relative to genetic variances. Although patterns of variation for root traits cannot be determined explicitly from these results, possible explanations include an absence of genetic or genetic × fumigation interaction variance for root traits or weak genetic correlations between root traits and above-ground traits.

This study was conducted to estimate components of genetic and genetic × fumigation treatment interaction variance for strawberry root traits in soils where sublethal pathogens were of primary concern. Root sampling was conducted on three dates within a season so that temporal trends for genetic parameter estimates could be assessed. Together, these parameter estimates were used to determine which seasonal root samples would provide an adequate description of the genetic variation observed for each root trait.

Materials and Methods

Ten strawberry genotypes were chosen as parents and crossed in two five-parent half-diallel mating designs (no reciprocal crosses or selfs) to generate 20 biparental crosses for testing and genetic analysis. The parental genotypes were a random sample of cultivars and advanced selections within the Univ. of California breeding program that had undergone several cycles of selection for commercial productivity, fruit quality, and disease tolerance. The effect of this prior selection on genetic variation for root traits is not known, but selection responses for production traits have been consistent for several breeding cycles indicating that substantial genetic variation remains in the population.

A total of 40 seedling offspring from each cross (20 in one instance) were planted at the Univ. of California Watsonville Strawberry Research Facility on 15 Sept. 1993 and managed according to established guidelines for experimental seedling trials (Shaw et al., 1989). Soils at the Watsonville facility had been planted in alternate years to strawberry and cover crops for several production cycles and had been consistently free of any identifiable lethal pathogen problems during that period (Larson and Shaw, 1995). Seedlings were tested using a randomized complete block design with blocks nested in fumigation treatments, which consisted of 1) standard soil fumigation with a 2 methyl bromide : 1 chloropicrin mixture (by weight, 392 kg·ha^{-1}) or 2) no fumigation. Blocks were nested within treatments because of the operational difficulty involved with randomizing fumigation treatments within blocks. The 40 seedlings per cross were distributed randomly between the two fumigation treatments and, subsequently, between the two blocks in each fumigation treatment. The 10 seedlings per cross within each fumigation–block combination were established as single experimental plots. These plots were further randomized within each of the four fumigation–block combinations before planting.

Soils at the Watsonville facility had been planted in alternate years to strawberry and cover crops for several production cycles and had been consistently free of any identifiable lethal pathogen problems during that period (Larson and Shaw, 1995). Nonfumigated soils had not been fumigated in over 5 years and had been cropped to strawberry twice since the last fumigation.

Sampling of root systems on an individual-plant basis was initiated on 3 Jan., 2 Apr., and 2 July 1994. Plants within a single block were sampled over a 2 d period, and the two replications were sampled 2 weeks apart. Root extractions were performed by inserting a 1.9 cm diameter × 24 cm length metal probe into the soil 10 cm from the center of each plant, at a 60 degree angle aimed underneath the plant, and along a line running through all plant centers in the row. Extractions were performed on alternate sides of each plant on successive sampling dates to minimize any adverse effects on plant development and yield. Root samples were refrigerated at 5 °C for up to 1 week, washed free of soil, and then assigned a subjective root appearance (health) score (RAS) on a scale of 1 to 5 (5 = best) based on the extent of their branching structure and the degree of blackening / decay (Fort and Shaw, 1998). Root samples were then dried for at least 3 d in a 60 °C oven and weighed to obtain total root mass (RM) and secondary root mass (SRM); SRM is a subset of RM from which root pieces >0.5 mm in diameter have been removed (Fort and Shaw, 1998). RM and SRM exhibited large differences in scale between fumigation treatments on all sampling dates, and appropriate power transformations were conducted before statistical analyses of these traits (Fernandez, 1992).

In the primary phase of analysis, univariate analyses were used to resolve root trait data from each of the three sampling dates. Analyses of variance (ANOVAs) were conducted independently for the two half-diallels with fumigation treatments and replicates treated as fixed effects and general combining ability (GCA) and specific combining ability (SCA) as random effects, using the least-squares procedure DIALL (Shaffer and Usanis, 1969). Sums of squares for interactions of SCA with treatments or blocks were found by subtracting sums of squares for GCA interactions from Type I sums of squares for cross interactions obtained using SAS procedure GLM (Shaw et al., 1989). Sums of squares and degrees of freedom for the two diallels were pooled into a joint analysis, then significance tests were conducted for the joint diallel analysis using hierarchial expected mean squares (Table 1). To insure conservative tests of significance, ANOVA sources that yielded negative variance component estimates, i.e., those with mean squares less than their respective error terms, were adjusted before pooling by resetting the variance component to zero and modifying the experimental sums of squares. Variances

Table 1. Expected mean squares for analysis of variance of three strawberry root system traits in the Watsonville fumigation trial.

Source	df	Expected mean squares
Fumigation (F)	1	$\sigma^2 + 172.7\,\sigma^2_{r/f} + 346.4\,\sigma^2_f$
Replication (R/F)	2	$\sigma^2 + 172.7\,\sigma^2_{r/f}$
GCA	8	$\sigma^2 + 8.6\,\sigma^2_{sca\times r/f} + 25.8\,\sigma^2_{gca\times r/f} + 17.1\,\sigma^2_{sca\times f} + 51.5\,\sigma^2_{gca\times f} + 34.2\,\sigma^2_{sca} + 103.6\,\sigma^2_{gca}$
SCA	10	$\sigma^2 + 8.6\,\sigma^2_{sca\times r/f} + 17.1\,\sigma^2_{sca\times f} + 34.2\,\sigma^2_{sca}$
GCA × F	8	$\sigma^2 + 8.6\,\sigma^2_{sca\times r/f} + 25.8\,\sigma^2_{gca\times r/f} + 17.1\,\sigma^2_{sca\times f} + 51.5\,\sigma^2_{gca\times f}$
SCA × F	10	$\sigma^2 + 8.6\,\sigma^2_{sca\times r/f} + 17.1\,\sigma^2_{sca\times f}$
GCA × R/F	16	$\sigma^2 + 8.6\,\sigma^2_{sca\times r/f} + 25.8\,\sigma^2_{gca\times r/f}$
SCA × R/F	20	$\sigma^2 + 8.6\,\sigma^2_{sca\times r/f}$
Error	617	σ^2

due to general combining ability (σ^2_{GCA}), specific combining ability (σ^2_{SCA}), and interactions were estimated using the GAREML program, which applies the restricted maximum likelihood method of Geisbrect (1983) in computer software by Huber (1993). Narrow-sense (h^2) and broad-sense (H^2) heritability estimates were calculated using σ^2_{GCA} and σ^2_{SCA} according to the expectations for a diallel mating design (Hallauer and Miranda, 1981). The suitability of applying diploid genetic expectations to strawberry (a fully diploidized octoploid) has been established (Comstock et al., 1958; Shaw et al., 1989).

Genotypic correlations were calculated for RM, SRM, and RAS on each sampling date by treating individual trait expressions within fumigated and nonfumigated soils as separate but genetically correlated (Burdon, 1977):

$$r_g = r_{p(c)}/\sqrt{[h^2_{c(fum)}] \times [h^2_{c(non)}]} \quad [1]$$

where $r_{p(c)}$ is the product-moment correlation of cross means between the fumigated and nonfumigated environments, and $h^2_{c(non)}$ and $h^2_{c(fum)}$ are the cross-mean heritability estimates in fumigated and nonfumigated soils, respectively (Namkoong, 1979). Values obtained using Eq. [1] quantify the extent to which genotypic variances within each soil fumigation environment are conditioned by the same genes and facilitate calculation of the indirect gain from selection (Falconer, 1981) expected when selection and response soil fumigation environments differ. The variance components used to calculate cross-mean heritabilities were obtained using GAREML, accounting for only those sources of variation expressed among seedlings within individual fumigation treatments. Individual-plant heritabilities for traits expressed within each fumigation treatment were also obtained using these components (Shaw, 1993).

To assess the similarity of genetic effects expressed at different within-season intervals for each root trait, genotypic correlations (r_g) were calculated between sampling dates as the product-moment correlation of their estimated genotypic effects. These effects were constructed on a per-cross basis using predictions of GCA and SCA effects provided by GAREML; the two parental GCA effects for each cross were added to twice their SCA effect to reflect the total genotypic effect and to provide correspondence with H^2.

Preliminary univariate assessments of RM and SRM by sampling date revealed 1) nonsignificant GCA × fumigation treatment and SCA × fumigation treatment interactions for each sampling date and 2) genotypic correlation coefficients approaching unity ($r_g > 0.85$) between all pairs of sampling dates. Thus, data from independent sampling dates were combined to produce single estimates describing RM and SRM, thereby eliminating redundancy of genetic information and simplifying further analyses. Composite scores for RM and SRM were obtained by converting individual-plant transformed data from each sampling date to standardized Z scores (Steel and Torrie, 1980), followed by finding the arithmetic mean of scores across the three sampling dates. Significance tests, estimation of genetic and interaction components of variance, and calculation of heritabilities were then performed for composite RM and SRM following methods described previously for individual sampling date data. RAS had a complex seasonal expression pattern which precluded the construction of a single composite score.

To further assess the complex genetic expression pattern for RAS, genotypic correlations between sampling dates were obtained for the fumigated and nonfumigated soil treatments independently. This was done by obtaining predictions of genotypic effects for sources of variation expressed within fumigation treatments using GAREML, followed by calculation of genotypic correlations between pairs of sampling dates as described above.

Results and Discussion

RAS was greater in fumigated soils than in nonfumigated soils on all three sampling dates, with the largest treatment differences in April (Table 2). Over the course of the season, RAS declined

Table 2. Means and standard deviations (in parentheses) for three root performance traits of strawberry seedlings sampled on three dates in soils with two preplant fumigation treatments.

Fumigation treatment[z]	Sampling date	Root appearance score (RAS)[y]	Total root mass (RM) (mg/plant)	Secondary root mass (SRM) (mg/plant)
Nonfumigated	January	2.52 a[x]	37.3 b	21.7 b
		(0.88)	(23.4)	(12.5)
	April	2.03 b	44.3 a	27.8 a
		(0.65)	(25.2)	(15.3)
	July	1.85 c	43.0 a	29.5 a
		(0.63)	(25.1)	(17.3)
Fumigated	January	3.28 b	39.4 b	24.9 c
		(0.91)	(23.1)	(14.5)
	April	3.73 a	56.0 a	35.1 a
		(0.68)	(27.2)	(16.4)
	July	2.77 c	40.5 b	27.6 b
		(0.86)	(24.1)	(14.5)

[z]Nonfumigated and fumigated indicate no soil fumigation and preplant soil fumigation with 2 methyl bromide : 1 chloropicrin (by weight) at 392 kg·ha^{-1}, respectively.
[y]RAS is scored visually on a scale of 1 to 5, 5 = best.
[x]Within each treatment/trait combination, means followed by identical letters do not differ at $P < 0.05$ for a paired t test; N = 352 for fumigated treatment means, and N = 341 for nonfumigated treatment means.

Table 3. Results of analysis of variance for three root performance traits of strawberry seedlings at three sampling dates in soils with two preplant fumigation treatments.

	Mean squares								
Source	Jan. RAS[z]	Apr. RAS	July RAS	Jan. RM	Apr. RM	July RM	Jan. SRM	Apr. SRM	July SRM
Fumigation (F)	48.16	227.87**	57.64	2.40[y]	54.90*	0.00[y]	9.55	40.03*	1.16[y]
Replication (R/F)	2.96*	0.44[y]	5.96**	12.79**	1.84[y]	6.41	5.86	1.70[y]	6.15
GCA	9.56	3.09	1.67	16.04	35.02*	56.63**	38.07	47.26*	63.73**
SCA	0.86	0.87	1.16[y]	5.35	4.69	5.28	9.59	8.17	5.59
GCA × F	3.52*	0.50	2.08	1.64[y]	6.53	6.12	3.24	5.91	5.28
SCA × F	0.67[y]	1.02	1.29	2.86	2.55	3.74	3.30	3.02	3.88
GCA × R/F	1.19	0.26[y]	0.93	2.89[y]	2.47	2.94	4.38[y]	3.09	2.57
SCA × R/F	0.90	0.71*	0.56	3.05	3.97*	2.91[y]	5.61*	4.25**	3.24
Error	0.64	0.45	0.46	2.02	2.23	3.22	2.57	2.20	2.67
σ^2_{gca}	0.050	0.018	0	0.139	0.245	0.416	0.214	0.302	0.479
σ^2_{sca}	0	0	0	0.127	0.049	0.036	0.161	0.154	0.043
$\sigma^2_{gca\times f}$	0.048	0	0.008	0	0.042	0.022	0	0.036	0
$\sigma^2_{sca\times f}$	0	0.012	0.031	0	0	0.044	0	0	0.084
$\sigma^2_{r/f\times cross}$	0.038	0.027	0.047	0.162	0.111	0	0.192	0.152	0.061
h^2	0.23	0.16	0.00	0.14	0.32	0.40	0.26	0.39	0.54
SE (h^2)	(0.20)	(0.11)	(0.00)	(0.11)	(0.22)	(0.22)	(0.18)	(0.29)	(0.32)
H^2	0.23	0.16	0.00	0.27	0.38	0.44	0.45	0.59	0.58
SE (H^2)	(0.20)	(0.11)	(0.00)	(0.23)	(0.31)	(0.30)	(0.33)	(0.44)	(0.42)

[z]RAS = root appearance score; RM = root mass; SRM = secondary root mass.
[y]Mean squares corresponding to these sources were adjusted before conducting F tests to compensate for small, negative variance component estimates. Unadjusted mean squares are presented above.
*,**Significant at $P < 0.05$ or 0.01, respectively; mean squares and variance components for RM and SRM have been multiplied by 1000 for ease of presentation.

Table 4. Separate analysis of variance results for three root performance traits of strawberry seedlings at three sampling dates in soils with and without preplant fumigation treatments.

		Mean squares								
Fumigation treatment	Source	Jan. RAS[z]	Apr. RAS	July RAS	Jan. RM	Apr. RM	July RM	Jan. SRM	Apr. SRM	July SRM
Nonfumigation (NF)	Replication (R)	3.63*	0.05[y]	3.30**	1.13[y]	0.92[y]	2.93	7.25	2.92	1.84[y]
	GCA	5.12*	1.14	1.49	17.46	39.22**	29.65**	17.62	22.42	33.57**
	SCA	0.30[y]	1.21	0.68	10.96	6.18[y]	4.75	8.97	10.08	6.99
	GCA × R	1.41*	0.28[y]	0.79	5.05	2.52[y]	3.08	2.35[y]	2.41[y]	3.79
	SCA × R	0.60[y]	0.40	0.57	6.77	6.96**	3.95	6.70**	5.63**	4.37
	Error	0.64	0.39	0.33	4.3	2.86	2.77	2.48	2.16	2.80
	h^2	0.40	0.00	0.16	0.05	0.52	0.44	0.15	0.56	0.43
	SE (h^2)	(0.22)	(0.00)	(0.14)	(0.14)	(0.34)	(0.29)	(0.21)	(0.39)	(0.31)
	H^2	0.40	0.27	0.20	0.30	0.57	0.51	0.50	0.75	0.61
	SE (H^2)	(0.22)	(0.13)	(0.37)	(0.40)	(0.51)	(0.44)	(0.52)	(0.62)	(0.51)
Fumigation (F)	Replication (R)	2.21	0.39	8.62**	11.47**	2.91	10.48	4.25	0.08[y]	0.72[y]
	GCA	8.12**	2.48*	2.20	4.29	12.57	31.68*	22.04*	27.52*	33.49**
	SCA	1.09	0.65[y]	1.62	1.12[y]	2.95	3.97	3.76	6.77	2.93
	GCA × R	1.27	0.24[y]	1.06	1.65	4.16	2.57	6.00	5.32	1.26
	SCA × R	1.20*	1.01**	0.55	1.49	2.95	1.50[y]	4.08	4.28	1.97
	Error	0.61	0.39	0.62	0.92	2.74	3.63	2.49	3.61	2.02
	h^2	0.52	0.22	0.00	0.16	0.19	0.41	0.34	0.29	0.67
	SE (h^2)	(0.29)	(0.16)	(0.09)	(0.12)	(0.13)	(0.22)	(0.21)	(0.19)	(0.35)
	H^2	0.52	0.22	0.35	0.16	0.19	0.44	0.34	0.41	0.74
	SE (H^2)	(0.29)	(0.16)	(0.35)	(0.12)	(0.13)	(0.32)	(0.21)	(0.37)	(0.45)
NF vs. F	r_g	0.52	0.62	–0.18	1.27	0.90	0.87	1.06	0.99	0.86

[z]RAS = root appearance score; RM = root mass; SRM = secondary root mass.
[y]Mean squares corresponding to these sources were adjusted before conducting F tests to compensate for small, negative variance component estimates. Unadjusted mean squares are presented above.
*,**Significant at $P < 0.05$ or 0.01, respectively; mean squares and variance components for RM and SRM have been multiplied by 1000 for ease of presentation.

steadily in nonfumigated soils, whereas RAS peaked in fumigated soils in April before declining in July. The decline in RAS in fumigated soils between April and July is consistent with root aging processes, which include the browning of primary roots (Wilhelm, 1961). Alternatively, protection from soil pathogens afforded by preplant fumigation may have dissipated during the production season (Wilhelm, 1961).

Secondary root mass (SRM) as a proportion of total root mass (RM) ranged from 63% in April to 75% in January (Table 2). Plants grown in fumigated soils had greater RM and SRM than their nonfumigated counterparts in January and April, but not in July. RM and SRM increased between January and April in both fumigation environments, but between April and July, root masses were static in nonfumigated soils and declined in fumigated soils. Seedling fruit production peaked in May and June in both soil environments, and surges of reproductive growth have been associated with the temporary growth inhibition of roots and other vegetative plant structures (Larson and Shaw, 1996). This may explain the lack of root growth between April and July.

Fumigation treatment effects were highly significant ($P \leq 0.01$) for April RAS and nonsignificant, though borderline ($0.05 \leq P \leq 0.10$), for January RAS and July RAS (Table 3). Significant fumigation treatment effects were attributed to the effects of sublethal pathogens, as plant mortality was low (<1%) and did not differ across fumigation treatments. Variances due to GCA (σ^2_{gca}) and SCA (σ^2_{sca}) were nonsignificant for RAS on all three sampling dates. Narrow-sense heritability estimates ranged from $h^2 = 0.23$ (±0.20) for January RAS to $h^2 = 0.00$ (±0.00) for July RAS (Table 3). GCA × fumigation treatment interaction variance ($\sigma^2_{gca\times f}$) was significant for January RAS and was similar to the σ^2_{gca} estimate in magnitude; however, $\sigma^2_{gca\times f}$ was not significant for April RAS or July RAS. SCA × fumigation treatment interaction variance ($\sigma^2_{sca\times f}$) was not significant for RAS on any sampling date.

Fumigation treatment effects for RM and SRM were significant only in April (Table 3), which is consistent with Yuen et al. (1991) and Larson and Shaw (1996). In these studies, root masses were always greater in fumigated soils at the time of initial fruit harvest (April), but not necessarily before or after. Significant σ^2_{gca} was detected for RM and SRM in April and July, but not in January, while σ^2_{sca}, $\sigma^2_{gca\times f}$, and $\sigma^2_{sca\times f}$ were not significant on any sampling date. Narrow-sense heritabilities for RM increased between the January ($h^2 = 0.14 \pm 0.11$) and July (0.40 ± 0.22) sampling dates (Table 3). Heritability estimates for SRM also had an increasing seasonal trend ($h^2 = 0.26 - 0.54$), with h^2 greater for SRM than RM on all three sampling dates.

Because SRM is a subset of RM, the two traits are necessarily correlated, and similar seasonal inheritance patterns were expected. For this reason, the subset of RM due to primary root mass was assessed for each sampling date in a manner analogous to SRM. Narrow-sense heritabilities for the primary root subset of RM ranged from $h^2 = 0.06$ (July) to $h^2 = 0.15$ (April), compared to the range of $h^2 = 0.26$ to 0.54 for SRM. Therefore, most additive genetic variation for RM appears to be due to secondary root mass (SRM) and not primary root mass.

These results demonstrate the existence of significant genetic variation for RM and SRM, particularly in April and July. Further, the absence of significant $\sigma^2_{gca\times f}$ and $\sigma^2_{sca\times f}$ for RM and SRM on all sampling dates indicates that genotypic expression for root mass traits is consistent across fumigation treatments. Conversely, estimates of genetic × fumigation interaction variance for January RAS and July RAS were significant and substantial in relation to σ^2_{gca} and σ^2_{sca}, suggesting that only a subset of the genes that condition variability for RAS within fumigated or nonfumigated soils are identical and confer similar phenotypic responses.

The extent to which genes conditioning variation for root traits shared identity and/or effects across fumigation treatments was quantified more precisely by calculating the genotypic correlation (r_g) between expressions of individual traits within fumigated and nonfumigated soils (Table 4). Estimates of r_g ranged from 0.86 to 1.27 for RM and SRM for the three sampling dates, as expected for traits with little or no genotype × fumigation interaction variance. Analogous genotypic correlations for RAS were much weaker; r_g was 0.53 in January, 0.63 in April, and –0.18 in July. The proportion of genotypic variance conditioned identically across fumigation treatments is described by r_g^2. Therefore, only about 30% of genotypic variance for is conditioned identically across soil fumigation environments for January RAS, while the other 70% is conditioned as soil-specific adaptation.

For RM and SRM, genotypic correlations (r_g) between all pairs of sampling dates were 0.86 or above ($P \leq 0.01$), suggesting that differences among crosses were consistent across sampling dates for these traits. These correlations, along with an absence of genetic × fumigation interactions, indicate that seasonal samples for RM and SRM convey nearly identical genetic information and represent repeated measures of the same genetic phenomenon. On this basis, data for RM and SRM were combined across dates on an individual-plant basis to form composite traits. Heritabilities for composite RM and SRM were greater than those of any of their constituent sampling dates (Table 5), suggesting that environmental effects for the separate seasonal measures were largely uncorrelated.

Table 5. Results of analysis of variance for two composite root performance traits of strawberry seedlings in soils with two preplant fumigation treatments.

	Mean squares	
	Composite	
Source	RM[z]	SRM
Fumigation (F)	2.25	2.53
Replication (R/F)	1.19	1.47*
GCA	10.33**	14.80**
SCA	1.52	2.06
GCA × F	0.77	0.76
SCA × F	0.61	0.71
GCA × R/F	0.46[y]	0.61[y]
SCA × R/F	0.78*	1.00**
Error	0.42	0.42
σ^2_{GCA}	0.070	0.101
σ^2_{SCA}	0.027	0.042
$\sigma^2_{GCA\times f}$	0	0
$\sigma^2_{SCA\times f}$	0.003	0
$\sigma^2_{r/f\times c}$	0.021	0.039
h^2	0.46	0.58
SE (h^2)	(0.27)	(0.33)
H^2	0.64	0.82
SE (H^2)	(0.41)	(0.49)

[z]RM = root mass; SRM = secondary root mass.

[y]Mean squares corresponding to these sources were adjusted before conducting F tests to compensate for small, negative variance component estimates. Unadjusted mean squares are presented above.

*,**Significant at $P < 0.05$ or 0.01, respectively.

Genotypic correlations between January RAS and April RAS were strong and positive ($r_g = 0.91, P \leq 0.01$), while July RAS was not correlated with January RAS and April RAS ($r_g = 0.00$). However, because these correlations were constructed using GCA and SCA estimates, they reflect only that fraction of the genotypic variance that is conditioned identically across fumigation treatments. Because the genetic expression of RAS was inconsistent across fumigation treatments, r_g between RAS sampling dates were conducted separately for fumigated and nonfumigated soils. January RAS and April RAS remained strongly correlated ($r_g = 0.81$; $P \leq 0.01$) in fumigated soils, but their correlation was much lower ($r_g = 0.47$, $P \leq 0.05$) in nonfumigated soils. Apparently, soil-specific genetic effects originating primarily within nonfumigated soils distinguish January RAS from April RAS. Genotypic correlations between July RAS and the other RAS sampling dates were weak in both fumigation environments ($r_g = -0.20 - 0.43$). As most genetic correlations between RAS sampling dates were weak, particularly in nonfumigated soils, they were not combined to form a composite RAS trait.

Genotype × fumigation interactions have been detected for few strawberry traits in prior studies and the ratio of genetic to interaction variance has been large in all instances (Fort et al., 1996; Larson and Shaw, 1995; Shaw and Larson, 1996). Therefore, the existence of variance conferring specific adaptation to individual soil fumigation environments for RAS is atypical. Alternatively, genotypic variation for root mass traits was expressed identically across fumigation environments, which is a pattern more consistent with prior studies. The practical consequences of genes that confer differing root quality in fumigated and nonfumigated soils depends ultimately on the relationship between root appearance and traits that condition productivity in these respective environments.

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