Genetic Analysis of Strawberry Root System Traits in Fumigated and Nonfumigated Soils II. Relationships among Root System and Above-ground Traits of Strawberry Seedlings

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ABSTRACT. Genotypic and phenotypic relationships among root system and above-ground traits of strawberry (*Fragaria × ananassa* Duch.) were evaluated for seedlings grown in annual hill culture, with soil treatments consisting of 1) preplant fumigation with methyl bromide and chloropicrin or 2) nonfumigation. Seedlings were from crosses among 10 genotypes within the University of California strawberry improvement program that had been selected previously for yield and other production traits. Root mass had positive genotypic correlations with plant diameter 5 months after planting in both fumigated ($r = 0.58$) and nonfumigated ($r = 0.69$) soils. Genotypic correlations between root mass and two production traits, yield and fruit size, were nonsignificant. However, plant diameter had positive genotypic correlations with yield ($r = 0.36$ to 0.51) and negative genotypic correlations with fruit size ($r = -0.47$ to -0.60). In general, root appearance scores were uncorrelated with production traits, but their genotypic correlations with vegetative traits were occasionally strong. Genotypic path coefficient analyses conducted separately for fumigated soils and nonfumigated soils both indicated that plant diameter had positive direct effects on yield that were twice the magnitude of that for any other trait. Root mass had a small negative direct effect on yield in each fumigation environment, while root appearance scores had small to moderate direct effects on yield that were more positive for samples obtained after fruiting (in April) versus before fruiting. Pleiotropic relationships appear to exist between root traits and plant diameter, but plant diameter is the best single predictor of genotypic variation for yield in both soil fumigation environments.

Nearly 20,000 strawberry seedlings (*Fragaria × ananassa*) are generated every year from crosses performed in the University of California (UC) breeding program. These seedlings are screened for cultivar potential both as seedlings and in multiple clonal evaluations. Genotypes identified as potential cultivars during preliminary trials display exceptional productivity and fruit quality in commercial environments. Direct selection for these production traits is likely to be accompanied by indirect selection for other characteristics that contribute to their expression. Selection for these associated traits along with production traits could be used to increase overall selection efficiency (Falconer, 1981). Consequently, vegetative growth traits have been evaluated for their relationships to productivity and fruit size and their potential as indirect selection criteria (Shaw, 1993; Shaw and Hansen, 1993). However, root system characteristics have not been assessed for use in cultivar development despite the possible role of roots in adaptation to different soil environments.

Assessments of root system performance could improve the strawberry cultivar development procedure under certain circumstances. First, methods must be available for sampling small root fractions without negatively impacting subsequent plant growth and productivity, and these root fractions must reflect the entire root system accurately. Yuen et al. (1991) developed root sampling methods for strawberry with these attributes by using soil cores, and these methods were standardized further by Fort and Shaw (1998) to measure root masses (RM) and root appearance

scores (RAS). Second, traits measured on fractional root samples must express sufficient genetic variability to be used in selection programs. Within the UC breeding program, significant genetic variation was detected for RM and RAS obtained with soil cores among segregating seedling populations (Fort and Shaw, 1999a). Third, root traits must have strong genetic correlations with production traits or serve as reliable environmental covariates. Genetic and phenotypic relationships between root traits and production traits have received little experimental attention to date. Shaw and Hansen (1993) found that total root weight for growth chamber plants was correlated with some yield measures for field-grown plants, but genetic variation for total root weight was relatively small. Root measures based on field samples have not been correlated to production traits in strawberry, nor have these trait interrelationships been examined using multivariate analysis methods.

Soil differences may affect associations between root traits and production traits, thereby altering their impact on selection efficiency. Of importance to strawberry production in California are the effects of preplant fumigation treatments. Soil fumigation controls a highly variable complex of soilborne fungal pathogens with sublethal effects on plant vigor (Larson and Shaw, 1995; Wilhelm and Paulus, 1980), as well as lethal soil pathogens (Wilhelm, 1961). However, the use of methyl bromide, a compound in standard fumigation mixtures, may be phased out (Watson et al., 1992). The potential need for widespread strawberry production in soils prepared with suboptimal fumigation treatments dictates that breeding strategies be formulated for these new target environments.

Currently, breeding materials are screened and selected in soils receiving standard fumigation treatments. Incentives to modify this practice depend on whether rankings of genotypic performance shift as fumigation treatments are modified. Studies

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using seedlings and runner plants have indicated that production traits show little or no variance for genotype $\times$ fumigation treatment interactions in response to sublethal soil pathogens (Larson and Shaw, 1995; Fort et al., 1996), suggesting no need to alter current breeding practices. Conversely, significant genotype $\times$ fumigation interaction variances have been detected for RAS (Fort and Shaw, 1999a). These interactions imply that correlations involving RAS may differ across fumigation treatments. Therefore, the best prediction of genotypic value for production traits based on RAS in combination with other correlated characters may also differ across soil fumigation environments.

The present study was conducted to examine the genotypic and phenotypic relationships between root traits and measures of above-ground vegetative growth and productivity in strawberry. Further objectives were to evaluate the consistency of these relationships in soils with and without standard preplant fumigation and to address their potential significance for development of selection strategies.

Materials and Methods

Generation of experimental strawberry seedling populations, characteristics of parental genotypes, and field testing procedures at the UC Strawberry Research Facility (Watsonville, Calif.) were described in a companion study (Fort and Shaw, 1999a). In brief, 40 seedlings from each of 20 biparental crosses were planted in Watsonville on 15 Sept. 1993 in annual hill culture. Field testing was conducted using a randomized complete block design with blocks nested in treatments consisting of 1) preplant soil fumigation with a mixture of 2 methyl bromide : 1 chloropicrin (by weight, 392 kg·ha⁻¹) or 2) nonfumigation.

Fruit harvests were conducted from 13 Apr. until 29 June, a period of 12 consecutive weeks, and captured an estimated 85% to 90% of the yield expected for the season in total. Fruit number and yield in grams were recorded for individual plants once each week. Fruit size was calculated by dividing the total yield by the total number of fruit. Cross-sectional plant diameters (Shaw, 1993) were obtained on 15 Feb. and 1 July as a measure of above-ground vegetative growth; the former date corresponds to a transition from initial plantation establishment to the initiation of fruiting, whereas a majority of seasonal yield had been harvested by the latter date. Root systems were sampled on 3 Jan., 2 Apr., and 2 July 1994 using a 1.9 cm diameter $\times$ 24 cm length soil corer. The soil corer was inserted into the soil 10 cm from the center of each plant at a 60° angle aimed underneath the plant (Fort and Shaw, 1998). Roots extracted on each sampling date were washed free of soil and assigned a subjective root appearance score (RAS) on a scale of 1 to 5 (5 best) based on their degree of darkening and decay as a primary criterion (dark brown and black = 1, light beige = 5) and their degree of branching and secondary rootlet growth as secondary criterion; RAS is intended to be a rough measure of root health (Fort and Shaw, 1998). Root samples were then measured for root mass (RM) after drying for at least 3 d in a 60 °C oven. Fruit size, yield, and RM exhibited large differences in scale between fumigation treatments on all sampling dates, and power transformations were conducted before statistical analyses of these traits (Fernandez, 1992).

Data for yield, fruit size, February plant diameter, and the February to July diameter increment were analyzed initially on a univariate basis. Methods of univariate analysis for these traits were identical to the methods presented for root traits in a companion study (Fort and Shaw, 1999a). Briefly, analyses of

variance (ANOVAs) were conducted on each of two half-diallel mating designs using the least-squares procedure DIALL (Shaffer and Usanis, 1969) to conduct significance tests for general combining ability (GCA), specific combining ability (SCA), and their interactions with fumigation treatments and blocks within treatments.

The GAREML program (Huber, 1993), which applies the restricted maximum likelihood method of Geisbrecht (1983) to diallel analysis, was used to estimate general combining ability (σ^2_{GCA}), specific combining ability (σ^2_{SCA}), and interaction variance components. Variance component estimates were used to calculate narrow-sense (h^2) and broad-sense (H^2) heritabilities for each trait according to the expectations for a diallel mating design (Griffing, 1956; Hallauer and Miranda 1981).

GAREML also was used to obtain predictions of GCA and SCA effects for each parent within fumigated and nonfumigated soils independently. GCA and SCA effects were used to construct genotypic effects for each trait by adding the sum of the two parental GCA effects for each cross to twice their SCA effect. Genotypic correlations (r_g) were then calculated among all pairs of above-ground and root traits within each treatment as the product-moment correlation of their estimated genotypic effects. As r_g is calculated using the full complement of additive and dominance genetic effects, it corresponds directly to H^2 . Phenotypic correlations between traits were also calculated for each fumigation treatment as the product-moment correlation of individual plant measurements.

Separate path coefficient analyses (Li, 1975) were applied to genotypic correlations obtained in fumigated and nonfumigated soils with yield as the response variable in each instance. General interrelationships among traits within each fumigation treatment were evaluated by use of path coefficients and genotypic correlations. Path coefficients were also examined for their relative consistency across fumigated and nonfumigated soils to compare patterns of plant growth in these environments. In fumigated soils, inclusion of both January RAS and April RAS in the path coefficients model resulted in high multicollinearity, i.e., the multiple correlation coefficients (R) of January RAS and April RAS with all other traits in the model, including each other, were above $R = 0.95$ (variance inflation factors >10). April RAS was excluded from the path analysis model in favor of retaining January RAS for three reasons: 1) to reduce multicollinearity, 2) to preserve as much of the entire seasonal trend for RAS in fumigated soils as possible, and 3) April RAS had a smaller direct effect on yield than January RAS.

Results and Discussion

Means for the four vegetative growth and fruit quality and productivity measures were greater for seedlings grown in fumigated soils than nonfumigated soils (Table 1). The largest difference was observed for yield, with seedlings in nonfumigated soils yielding only 48% as much as those in fumigated soils. In February, plant diameters in nonfumigated soils were 88% of those in fumigated soils, and plant diameter increases between February and July were 78% as great. Fruit harvests were conducted from April to June, so plants in fumigated soils had greater vegetative growth during the production season than plants in nonfumigated soils despite bearing twice as much fruit. Fruit sizes in nonfumigated soils were 84% as great as those in fumigated soils. This result differs from a prior seedling trial (Fort et al., 1996), where fruit sizes did not differ between fumigation

Table 1. Means and standard deviations (in parentheses) for four vegetative growth and production traits of strawberry seedlings with and without preplant fumigation treatments.

Fumigation treatment ²	February plant diam (cm)	February to July diam increment (cm)	Fruit size (g)	Yield (g)
Nonfumigated	22.6 (3.9)	22.6 (8.2)	19.9 (5.8)	930.9 (445.5)
Fumigated	25.7 (3.9)	28.9 (8.3)	23.7 (5.7)	1920.0 (626.1)

²Nonfumigated and fumigated indicate no preplant soil fumigation and soil fumigation with 2 methyl bromide : 1 chloropicrin (by weight) at 392 kg-ha⁻¹, respectively; N = 341 for nonfumigated treatment means and N = 352 for fumigated treatment means.

treatments, but it is consistent with the results of a genotypic trial (Larson and Shaw, 1995).

Differences between fumigation treatments were significant ($P \leq 0.05$) for February plant diameter and yield (Table 2). Variance due to GCA (σ^2_{gca}) was significant for February plant diameter, yield, and fruit size. SCA variance (σ^2_{sca}) was nonsignificant in all instances. Significant GCA $\times$ fumigation or SCA $\times$ fumigation interaction variances ($\sigma^2_{\text{gca} \times \text{f}}$, $\sigma^2_{\text{sca} \times \text{f}}$) were not detected for any of the four above-ground traits. Moreover, the variance estimates attributed to these interactions were essentially zero for February plant diameter, fruit size, and yield, indicating that similar genes with identical effects conditioned expression of these traits in fumigated and nonfumigated soils. Narrow-sense heritabilities were low to moderate for yield ($h^2 = 0.23 \pm 0.14$), February plant diameter ($h^2 = 0.40 \pm 0.21$), and fruit size ($h^2 = 0.40 \pm 0.22$) (Table 2), reflecting the presence of additive genetic variance for these traits and the absence of confounding interactions. The heritability for the February to July diameter increment was very low ($h^2 = 0.06 \pm 0.09$).

Analysis of genotypic and phenotypic correlations indicated that associations between vegetative growth traits were similar within fumigated and nonfumigated soils (Tables 3 and 4). Correlations between RM and February plant diameter were positive and moderately strong (r_g and $r_p = 0.58$ to 0.69 , $P \leq 0.01$) in both fumigation environments. The narrow ranges for r_g and r_p indicate that genetic and environmental effects were correlated to a similar extent for these traits. Conversely, correlations between RM and above-ground growth during the production season (February to July diameter increment) were weak in both fumigation environments (r_g and $r_p = 0.09$ to 0.27).

Relationships between traits describing vegetative growth and fruit quality or productivity were also consistent across fumigation treatments (Tables 3 and 4). Genetic correlations between February plant diameter and fruit size were negative in both fumigated ($r_g = -0.60$, $P \leq 0.01$) and nonfumigated ($r_g = -0.47$, $P \leq 0.05$) soils. Analogous correlations between RM and fruit size were also negative ($r_g = -0.35$ to -0.36), though nonsignificant, suggesting that genes conditioning excessive vegetative growth above and, possibly, below ground may have negative consequences for fruit size. Phenotypic correlations between these vegetative traits and fruit size were weak in both fumigation environments ($r_p = -0.22$ to 0.03), so the environmental effects of these traits appear to be uncorrelated. In fact, environmental effects appeared to be either positively correlated or uncorrelated

for nearly all trait pairs. Genotypic correlations between February plant diameter and yield were consistently positive in fumigated ($r_g = 0.36$) and nonfumigated ($r_g = 0.50$, $P \leq 0.05$) soils, while all correlations between RM and yield were weak ($r_g = -0.19$ to 0.17).

Genotypic correlations involving the three RAS sampling dates differed noticeably between fumigation treatments (Tables 3 and 4), consistent with the genotype $\times$ fumigation interaction variance estimated for these traits (Fort and Shaw, 1999a). January RAS had genotypic correlations with February plant diameter ($r_g = 0.58$, $P \leq 0.01$) and RM ($r_g = 0.85$, $P \leq 0.01$) that were positive and strong in fumigated soils (Table 3); analogous correlations involving April RAS and July RAS were also positive, but smaller in magnitude. In nonfumigated soils, the genotypic correlation between January RAS and February plant diameter was positive ($r_g = 0.45$, $P \leq 0.05$), whereas July RAS had negative genotypic correlations with RM and February plant diameter (both $r_g = -0.49$, $P \leq 0.05$) (Table 4). The correlation between January RAS and RM differed significantly ($P \leq 0.01$) across fumigation treatments. The stronger association between these traits in fumigated soils may result from a relative absence of root decay with this soil treatment for an unspecified period following plantation establishment (Wilhelm, 1961). Apparently, the amount of secondary rootlets and their branching structure contribute more to early variation for RAS in fumigated soils than root decay, while root decay and secondary rootlet structure affect January RAS jointly in nonfumigated soils. The only significant genotypic correlation between RAS and produc-

Table 2. Results of analysis of variance for four vegetative growth and production traits of strawberry seedlings in soils with two preplant fumigation treatments.

Source	Mean squares			
	February plant diam	February to July diam increment	Fruit size (g)	Yield (g)
Fumigation (F)	766.0*	1833.9	911.6	2480.3*
Replication (R)	32.8	523.1**	93.9*	65.7**
GCA	211.9*	329.4	365.3**	77.6*
SCA	7.0	127.9	44.8	13.5 ^z
GCA $\times$ F	27.2	78.3	23.1 ^z	10.9 ^z
SCA $\times$ F	13.2 ^z	116.4	38.5	26.9
GCA $\times$ R	19.9	153.9	38.6	19.2
SCA $\times$ R	29.8**	110.8*	32.8	16.7**
Error	12.1	60.8	23.4	7.5
σ^2_{gca}	1.65	1.06	1.97	0.11
σ^2_{sca}	0	0.62	0.15	0
$\sigma^2_{\text{gca} \times \text{f}}$	0	0.57	0	0
$\sigma^2_{\text{sca} \times \text{f}}$	0	0	0	0
$\sigma^2_{\text{rf} \times \text{cross}}$	1.25	7.05	1.19	0.26
h^2	0.40	0.06	0.40	0.23
SE (h^2)	(0.21)	(0.09)	(0.22)	(0.14)
H^2	0.40	0.10	0.44	0.23
SE (H^2)	(0.21)	(0.20)	(0.30)	(0.14)

^zMean 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 $P < 0.05$ and 0.01 , respectively; mean squares and variance components for yield and fruit size have been divided and multiplied by 100, respectively, for ease of presentation.

tion traits occurred between January RAS and fruit size ($r_g = -0.61$, $P \leq 0.01$) in fumigated soils.

Path analysis of genotypic correlation coefficients indicated that the direct effects of February plant diameter on yield were positive in fumigated (1.131) and nonfumigated (1.146) soils and roughly twice as large as those of any other trait (Tables 5 and 6). Fruit size also had consistently positive direct effects on yield in the two soil fumigation environments (0.495 to 0.613). Conversely, root mass (−0.255 to −0.307) and the February–July plant diameter growth increment (−0.159 to −0.171) had small, but negative direct effects on yield in both fumigation environments. The direct effects of RAS on yield were inconsistent across soil treatments and sampling dates. In both soil fumigation environments, the direct effects of RAS on yield became more positive between January and July. January RAS had a negative direct effect on yield in fumigated soils (−0.451) and almost no direct effect in nonfumigated soils (0.048), while July RAS had a small direct effect on yield in fumigated soils (0.158) and a much greater direct effect in nonfumigated soils (0.516).

The positive direct effects of February plant diameter on yield were consistent with the positive genotypic correlations between these traits; in fact, they were even larger than anticipated on the basis of these correlations. Examination of the indirect effects of February plant diameter on yield show that many were negative and moderately large, thereby reducing the genotypic correlation between February plant diameter and yield. For example, nega-

tive indirect effects on yield were generated by greater February plant diameters via increased RM (−0.148, −0.211) and decreased fruit size (−0.370, −0.234) in fumigated and nonfumigated soils, respectively (Tables 5 and 6).

The small direct effect of the February to July plant diameter growth increment on yield, combined with its low heritability, indicate that environmental influences on above-ground vegetative growth increase in importance as the plantation matures. February plant diameter exerted virtually no indirect effect on yield through subsequent diameter increases in either fumigation environment (−0.004 to −0.008), so the genes influencing vegetative growth before and after initiation of fruiting response appear to be unrelated.

The small, negative direct effects on yield caused by greater RM were more than canceled by correlated increases in February plant diameter in fumigated (0.657) and nonfumigated (0.789) soils (Tables 5 and 6). Therefore, total yields depended upon root growth only to the extent necessary to support rapid initial diameter increase. Partitioning of plant resources specifically to root system development at the expense of above-ground growth likely would have negative consequences for yield. A possible explanation for this result may derive from the standard cultural practice in California of supplying water and fertilizer to strawberry through drip tape following initial plantation establishment: if water and essential nutrients are readily available in the rooting zone at all times, then the most productive plants might be

Table 3. Genotypic and phenotypic correlations (above and below the diagonal, respectively) among root traits and above-ground vegetative growth and production traits for strawberry seedlings grown in fumigated soils.

Characteristic	RM ²	January RAS	April RAS	July RAS	February plant diam	February to July diam increment	Fruit size	Yield
RM		0.85**	0.58**	0.38	0.58**	0.27	−0.36	−0.19
January RAS	0.31**		0.81**	0.43	0.61**	0.10	−0.61**	−0.30
April RAS	0.07	0.31**		0.31	0.32	−0.02	−0.25	−0.27
July RAS	−0.05	0.11*	0.07		0.18	0.23	−0.19	−0.08
February plant diameter	0.62**	0.24**	0.05	−0.07		0.05	−0.60**	0.36
February to July diameter increment	0.11*	0.00	0.11*	0.10	−0.03		−0.09	−0.13
Fruit size	0.03	−0.15**	−0.01	−0.01	0.01	0.41**		0.26
Yield	0.10	−0.02	−0.02	−0.08	0.44**	−0.01	0.19**	

²RM = root mass, RAS = root appearance score

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

Table 4. Genotypic and phenotypic correlations (above and below the diagonal, respectively) among root traits and above-ground vegetative growth and production traits for strawberry seedlings grown in nonfumigated soils.

Characteristic	RM ²	January RAS	April RAS	July RAS	February plant diam	February to July diam increment	Fruit size	Yield
RM		0.41	0.32	−0.49*	0.69**	0.09	−0.35	0.17
January RAS	0.15**		0.47*	−0.20	0.45	0.16	−0.12	0.39
April RAS	0.01	0.26**		−0.03	0.10	0.41	−0.04	0.26
July RAS	−0.14**	−0.03	−0.03		−0.49*	0.17	0.00	0.06
February plant diameter	0.66**	0.14**	−0.07	−0.17**		0.02	−0.47*	0.50*
February to July diameter increment	0.03	0.04	0.18**	0.18**	−0.23**		0.08	0.09
Fruit size	−0.10	−0.05	0.16**	0.02	−0.22**	0.35**		0.03
Yield	0.25**	0.04	0.01	0.10	0.46**	0.02	0.24**	

²RM = root mass, RAS = root appearance score

*,** Significant at $P \leq 0.05$ and 0.01 , respectively.

Table 5. Direct (underlined) and indirect relationships of root and above-ground vegetative growth and production characteristics on strawberry yield in fumigated soils using path coefficient analysis.

Characteristic	Root mass (RM)	January RAS ^z	July RAS	February plant diam	February to July diam increment	Fruit size
Root mass (RM)	<u>-0.255</u>	-0.216	-0.096	-0.148	-0.070	0.093
January RAS	-0.382	<u>-0.451</u>	-0.193	-0.275	-0.047	0.273
July RAS	0.059	0.067	<u>0.158</u>	0.029	0.036	-0.029
February plant diameter	0.657	0.689	0.205	<u>1.131</u>	0.057	-0.681
February to July diameter increment	-0.043	-0.016	-0.036	-0.008	<u>-0.159</u>	-0.014
Fruit size	-0.224	-0.371	-0.114	-0.370	0.052	<u>0.613</u>
Correlation with yield ($R^2 = 0.754$)	-0.188	-0.299	-0.076	0.358	-0.130	0.255

^zRAS = root appearance score.

Table 6. Direct (underlined) and indirect relationships of root and above-ground vegetative growth and production characteristics on strawberry yield in nonfumigated soils using path coefficient analysis.

Characteristic	Root mass (RM)	January RAS ^z	April RAS	July RAS	February plant diam	February to July diam increment	Fruit size
Root mass (RM)	<u>-0.307</u>	-0.126	-0.098	0.149	-0.211	-0.027	0.106
January RAS	0.020	<u>0.048</u>	0.023	-0.010	0.022	0.008	-0.006
April RAS	0.103	0.152	<u>0.323</u>	-0.010	0.034	0.131	-0.011
July RAS	-0.250	-0.103	-0.016	<u>0.516</u>	-0.251	0.087	0.002
February plant diameter	0.789	0.511	0.119	-0.557	<u>1.146</u>	0.024	-0.542
February to July diameter increment	-0.015	-0.027	-0.070	-0.029	-0.004	<u>-0.171</u>	-0.013
Fruit size	-0.171	-0.061	-0.017	0.002	-0.234	0.038	<u>0.495</u>
Correlation with yield ($R^2 = 0.660$)	0.168	0.393	0.264	0.062	0.502	0.090	0.031

^zRoot appearance score.

those that partition a greater share of plant resources to increasing initial photosynthetic area versus establishing extensive root systems.

Increased fruit size had positive direct effects on yield that were nullified by associated decreases in February plant diameter in fumigated (-0.681) and nonfumigated (-0.542) soils (Table 5 and 6). These negative indirect effects correspond to the negative genotypic correlations between February plant diameter and fruit size reported above. Together, these path coefficients indicate that fruit size and early above-ground vegetative growth contribute positively to yield, but their contributions are competitive.

The absence of strongly positive direct effects for January RAS on yield in either fumigation environment suggests that light root color and extensive root branching are not positive indicators of root health at this point in the growing season. Particularly in fumigated soils, there may be little genotypic variation for root health this soon after plantation establishment due to low soil pathogen levels. Together, the direct (-0.451) and indirect effects of January RAS in fumigated soils indicate that increases in this trait were associated with excessive vigor via increased RM (-0.216), increased February plant diameter (0.689), and decreased fruit size (-0.371) (Table 5). The direct effects of RAS on yield were more positive in July than in January in both fumigation environments, so the visual criteria that contribute to RAS seem to have a stronger relationship to root health as the plantation ages.

The positive direct effects of January RAS (0.048) and April RAS (0.323) in nonfumigated soils matched the sign of their indirect effects on yield through February plant diameter (0.511

and 0.119, respectively) (Table 6). The only other trait to show a positive correspondence between these effects was July RAS in fumigated soils (Table 5). In fact, the pattern of direct and indirect effects for July RAS in fumigated soils resembled those of January RAS and April RAS in nonfumigated soils, suggesting that soil pathogen levels, or other factors, influencing RAS in nonfumigated soils may be found 4 to 6 months later in fumigated soils. Consistent with this interpretation, means for RAS declined between April (3.73 ± 0.68) and July (2.77 ± 0.86) in fumigated soils, approaching the mean of January RAS (2.52 ± 0.88) in nonfumigated soils (Fort and Shaw, 1999a).

Genotypic correlations and path coefficients indicate that the most useful indirect trait for predicting genotypic value for yield is February plant diameter in both fumigation environments. RM, also a component of vegetative growth, had genotypic and phenotypic correlations with yield and fruit size that shared sign with February plant diameter. Despite these similarities, direct-effect path coefficients for February plant diameter were positive and large, unlike those for RM. Apparently, the seedlings in this study were homeostatic in their expression of above- and below-ground vigor, with root growth responding proportionally to increases in plant diameter, and not the reverse. RAS correlation and path coefficients were inconsistent across sampling dates and soil fumigation treatments, perhaps reflecting the interrelated effects of soil pathogen concentration, root aging, and secondary rootlet development. The RAS sampling dates with the largest direct effects on yield also conditioned indirect effects through February plant diameter that were equal in magnitude and opposite in sign. Together, these results suggest that the majority of

genetic information available from root traits regarding yield is available from plant diameters. However, these results do not preclude the possibility that root traits may be useful as environmental covariates for production traits.

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