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Effect of Host Plant, *Rhizobium* Strain and Host x Strain Interaction on Symbiotic Variability in Peanut[1]

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ABSTRACT

Varability of the plant-*Rhizobium* symbiosis can be attributed to additive effects of the plant genotype and the *Rhizobium* strain and the nonadditive effects of specific plant and *Rhizobium* combinations. The relative contribution of these sources of variability is important in adopting the best procedure to maximize nitrogen fixation. Six peanut (*Arachis hypogaea* L.) genotypes were grown in all possible combinations with 10 *Rhizobium* strains in order to estimate the relative importance of the three genetic components of symbiotic variability. Additive genetic effects of host and *Rhizobium* genotype were significant for plant color, nodule number and weight, N_2 (C_2H_2) fixed, and shoot dry weight. Nonadditive variation attributable to specific host-strain combinations was significant for all traits measured except for shoot dry weight. The large additive effects of the host genotype for nodule weight and shoot weight suggest that the variability for these traits can best be exploited by selection of host plants. However, the large nonadditive effects for nodule number and $N_2(C_2H_2)$ fixed suggest that these traits can best be improved by simultaneous selection of both host and bacterium. Rhizobial strains NC123 and 3G4b21 were found to have significant stability variances indicating that these strains show host specificity, whereas strain RP182-13 exhibited a nonsignificant stability variance with a high mean for all traits in symbiosis with all host genotypes.

The poor response to inoculation of the spanish genotypes in comparison to the nitrogen control suggests that superior strains for these genotypes must be identified.

Key Words: *Arachis hypogaea*, nitrogen fixation, additive effects, nonadditive effects, plant breeding and genetics.

Enhancement of symbiotic nitrogen fixation is complex because the genetic systems of both the plant macrosymbiont and the *Rhizobium* microsymbiont are involved. Variability of the host plant-*Rhizobium* symbiosis can be attributed to general or additive effects of the plant genotype, the general or additive effects of the *Rhizobium* strain, and the specific or nonadditive effects of individual plant and *Rhizobium* combinations (9). The relative contribution of these sources to total variability is important in determining the best procedure to adopt in order to maximize nitrogen fixation.

The assumption that nitrogen fixation depends upon additive effects of plant and *Rhizobium* genotype is generally made. However, if large nonadditive effects are present, most rapid advance from selection is likely to be achieved by simultaneous selection of the most productive specific plant-*Rhizobium* associations.

The importance of the host, the strain and the host x strain interaction has been reported for several legumes although most investigators did not assign relative importance to additive effects of the host or strain and nonadditive effects of the host-strain interaction (1, 3, 5, 6, 7, 10, 14).

Mytton *et al.* (11) grew six *Vicia faba* populations in all possible combinations with six *R. leguminosarum* strains in order to estimate the relative importance of the three genetic components of symbiotic variability for shoot weight. Additive genetic effects of host and *Rhizobium* genotypes accounted for only 8.9 and 11.8% of the total phenotypic variation. Nonadditive variation attributable to specific host x *Rhizobium* interaction was the largest component accounting for 73.8% of the phenotypic differences. The greatest improvement in symbiotic nitrogen fixation, therefore, should occur from the simultaneous selection of both symbionts.

Mytton (8) grew four white clover cultivars without applied nitrogen in soil containing a natural population of rhizobia. Two large plants were selected from each cultivar and a single *Rhizobium* isolate was taken from a large nodule of each plant. When host plants and strains were tested in a factorial experiment, estimated proportions of the phenotypic variance for plant dry matter for general effects of plant genotypes, general effects of *Rhizobium* genotypes, and specific effects of individual plant and *Rhizobium* genotypes were 34, 5, and 23%, respectively. Despite selection of plants expected to have good general effectiveness with indigenous rhizobia, there was still a large specific component of variation.

Although few studies have investigated host and strain interactions for peanut (*Arachis hypogaea* L.), Burton (1) demonstrated a host x strain interaction although the

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peanut generally is considered to be promiscuous and effective with most cowpea miscellany rhizobia (4).

Nambiar and Dart (12) recently reported that the cultivar Robut 33-1 gave substantial increases in pod yield when inoculated with strain NC92 but gave no increase in pod yield when inoculated with other effective strains.

No studies have been reported on the relative importance of the host, the rhizobial strain, or the host x strain interaction for the peanut-*Rhizobium* symbiosis. The objectives of this greenhouse study were to compare the relative importance of the host, strain, and host x strain interaction for several peanut host-rhizobial strain combinations for shoot weight, nodule number and weight, plant color, and $N_2(C_2H_2)$ fixed as measured by acetylene reduction. These traits have been demonstrated to adequately describe the host-strain symbiosis in peanut (15).

Materials and Methods

Six peanut genotypes, representing a range in genetic diversity, were inoculated with 10 strains of *Rhizobium* also chosen to represent a range in diversity. The six peanut genotypes included two virginia (ssp. *hypogaea* var. *hypogaea*) cultivars, Florigiant and NC 4, two valencia (ssp. *fastigiata* var. *fastigiata*) cultivars, A-1 and A-2, and two spanish (ssp. *fastigiata* var. *vulgaris*) cultivars, Spantex and Argentine. The 10 rhizobial strains included four isolated at North Carolina from nodules collected from South America (NC6, NC123, NC56.1, and NC70.1), a commercial strain (RP182-13), and two strains recommended by the USDA (176A22 and 3G4b21). The rhizobial strains had been shown to be effective with either NC 4 or Argentine peanuts in earlier greenhouse studies. An uninoculated and an uninoculated-plus-mineral nitrogen treatment was also included.

Individual plants of the six cultivars were grown with each of the 12 rhizobial or control treatments in a factorial experiment arranged in a randomized block design with four replicates in a greenhouse.

Plants were grown in modified Leonard jars containing an autoclaved 1:1 sand:vermiculite medium. Seeds of each genotype were surface sterilized in calcium hypochlorite solution (61 g/liter) for 10 min followed by rinsing in sterile water five times. Seeds were then pregerminated in sterilized vermiculite and placed at a depth of 25 mm in the medium in the Leonard jars. The rhizobial strains were grown to stationary growth phase in yeast extract mannitol broth (YEM) (13). Before covering the seed, a 10-mL suspension of the proper rhizobial strain (about 10^9 cells/mL) was added to the seeds of all treatments except for the uninoculated controls where sterile YEM alone was added. The nitrogen control received 10 ml of a 1 mg N/mL solution of NH_4NO_3 applied three times during the test. Nutrient solution consisting of Bond's stock mixture (2) supplemented with zinc, molybdenum, and cobalt was added twice during the 54-day growing period. At harvest plant color was rated on a scale of 1 to 3 with 1 = yellow and 3 = green. N_2 fixed was measured for the root system of each plant using acetylene reduction methodology. Specific nitrogen-fixing activity was computed as the ratio of N_2 fixed and nodule dry weight. Nodules were removed, counted, and weighed after drying. The roots and shoots were also dried and weighed.

The relative importance of the three genetic components of symbiotic variability was estimated using the methods of Mytton *et al.* (11).

The statistical model used in the analysis of variance was:

$$Y_{ijk} = \mu + B_i + H_j + S_k + (HS)_{jk} + \varepsilon_{ijk}$$

where Y_{ijk} was the value of the j^{th} host and k^{th} strain in the i^{th} block, μ the population mean, B_i the i^{th} block effect, H_j the j^{th} host effect, S_k the k^{th} strain effect, $(HS)_{jk}$ the effect of interaction between the j^{th} host and k^{th} strain, and ε_{ijk} the experimental error associated with the ijkth observation.

An interaction deviation was computed for each host-strain combination,

$$d_{jk} = \bar{Y}_{.jk} - \bar{Y}_{.j.} - \bar{Y}_{..k} + \bar{Y}_{...}$$

where dot subscripts indicate summation over the index. These deviations were used to compute a stability variance for each host, V_{h_j} with s-1 degrees of freedom, and for each strain, V_{s_k} with h-1 df, having the following expectations:

$$E\{V_{h_j}\} = E\{\frac{bh}{(h-1)(s-1)} \sum_{k}^{s} d_{jk}^2\} = b(\frac{1}{h-1})\{\frac{1}{s-1} \sum_{k}^{s} (HS)_{jk}^2\} + \sigma^2$$

$$E\{V_{s_k}\} = E\{\frac{bs}{(h-1)(s-1)} \sum_{j}^{h} d_{jk}^2\} = b(\frac{s}{s-1})\{\frac{1}{h-1} \sum_{j}^{h} (HS)_{jk}^2\} + \sigma^2$$

These stability variances were tested with F-tests using the residual error term from the analysis of variance. It should be noted that there were only h-1 independent V_{h_j}'s and s-1 independent V_{s_k}'s and that the V_{h_j}'s were not independent of the V_{s_k}'s. A low stability variance indicated that the particular host was consistent across strains. A strain with high V_{s_k} would be one exhibiting host specificity. Individual d_{jk}'s were inspected to detect the source of such interaction.

Results and Discussion

The six host genotypes were significantly different for nodule number, nodule weight, shoot weight, $N_2(C_2H_2)$ fixed, and plant color in spite of a significant host x strain interaction for all traits except for shoot weight (Table 1). The two virginia cultivars of subspecies *hypogaea*, Florigiant and NC 4, generally produced larger plants and had greater nodulation than the cultivars from subspecies *fastigiata*–A-1, A-2, Argentine, and Spantex (Table 2). Although host differences were also significant for $N_2(C_2H_2)$ fixed and plant color, the virginia cultivars were not superior to the fastigiate cultivars. A valencia cultivar, A-1, had the highest mean for $N_2(C_2H_2)$ fixed and the other valencia cultivar, A-2, had the highest score for plant color. Although the differences observed among the host genotypes could be confounded with maturity differences, similar host differences have been observed in field tests (16).

Table 1. Relevant mean squares from analysis of variance of host-strain factorial experiment with uninoculated controls excluded.

Source	df	Mean squares				
		Nodule number	Nodule weight	Shoot weight	$N_2(C_2H_2)$ fixed	Plant color
Host	5	5898*	68308**	137.34**	60.96**	209.63**
Strain	9	21378**	10331**	32.44**	39.23**	242.26**
Host x Strain	45	4549**	2100**	2.23	9.39*	26.02**

*,**Indicates significance at p = 0.05 and 0.01, respectively.

There were similar differences among strains of *Rhizobium* for all traits measured (Table 1). High means for shoot weight were produced by strains NC70.1, NC123, RP182-13, 32H1, and CB756 while low shoot weights were produced by strains NC6, NC56.2, and 3G4b21 (Table 2). Nodule weight and $N_2(C_2H_2)$ fixed was highest for strains RP182-13 and NC56.2. Strain RP182-13 also had the highest mean for plant color.

The relative contribution of the three genetic components of symbiotic variability, *i.e.*, the additive effects of host and of *Rhizobium* strain and the nonadditive effects of host x strain interactions, was quantified by computing appropriate components of variance and comparing the relative size of each component. The host plant accounted for 43.7 and 49.4% of the total phenotypic variability for nodule weight and shoot weight, respectively; however, the host plant only accounted for 14.4, 14.0,

Table 2. Shoot and nodule weight, $N_2(C_2H_2)$ fixed and plant color of six host cultivar of peanuts with 10 strains of *Rhizobium* and uninoculated and nitrogen controls.

Rhizobial strain/ treatment	Virginia		Valencia		Spanish		Mean
	Florigiant	NC 4	A-1	A-2	Spantex	Argentine	
	Shoot weight (g/plant)						
CB756	6.2	5.6	3.4	4.7	4.1	3.2	4.5
RP182-13	6.7	4.9	5.1	4.4	3.1	4.0	4.7
NC70.1	7.9	4.5	4.8	3.9	5.3	4.1	5.1
NC6	4.3	3.3	4.8	3.5	0.8	2.1	2.8
NC123	8.4	6.5	3.9	3.9	3.3	3.1	4.9
SMS-2	6.3	4.1	3.6	2.6	3.1	3.1	3.8
176A22	6.6	4.1	4.6	3.6	4.0	3.3	4.3
3G4b21	3.5	2.0	0.8	1.4	1.0	1.1	1.6
NC56.2	3.8	4.1	2.6	1.3	2.0	1.8	2.6
32H1	6.2	6.7	3.5	3.3	4.4	4.2	4.7
Mean	5.8	4.5	3.5	3.2	3.1	3.1	
N_2 control	6.6	6.1	4.5	4.3	5.4	6.0	5.5
Uninoculated	3.4	2.2	2.0	1.2	0.6	0.8	1.7
	$S_{\bar{x}} = 0.63$						
	Nodule weight (mg/plant)						
CB756	129.8	97.1	79.1	81.3	95.5	78.5	93.5
RP182-13	160.7	168.4	142.4	97.0	100.4	94.4	127.2
NC70.1	125.7	64.5	100.1	60.9	72.0	72.1	83.3
NC6	124.6	86.2	105.2	107.5	43.6	77.5	89.3
NC123	177.4	130.3	62.5	46.4	48.8	31.5	82.8
SMS-2	129.7	123.9	102.3	91.6	74.6	100.5	103.8
176A22	137.3	90.1	116.1	101.8	96.4	89.9	105.3
3G4b21	185.1	107.7	41.1	101.8	29.0	40.7	81.8
NC56.2	210.1	168.5	140.2	104.2	116.1	131.7	145.1
32H1	133.0	119.0	94.0	61.4	103.6	82.0	98.8
Mean	131.6	104.4	85.2	72.8	68.8	69.1	
	$S_{\bar{x}} = 17.7$						
	$N_2(C_2H_2)$ Fixed (μM/hr/plant)						
CB756	5.22	3.31	7.62	5.45	7.20	5.84	5.77
RP182-13	7.02	5.94	11.09	11.08	8.27	7.66	8.51
NC70.1	4.82	2.20	8.36	6.16	5.83	5.19	5.54
NC6	6.00	4.29	8.36	6.51	4.20	5.94	5.75
NC123	7.07	5.35	3.82	5.17	4.62	3.57	4.93
SMS-2	7.40	4.16	8.27	6.84	6.52	6.82	6.67
176A22	5.14	3.58	9.38	4.95	7.97	5.93	6.15
3G4b21	8.74	5.44	2.28	6.87	2.41	3.50	4.87
NC56.2	8.78	6.55	9.55	7.06	0.28	8.64	8.31
32H1	4.75	5.39	5.66	5.36	6.75	5.49	5.57
Mean	5.74	4.11	6.40	5.57	5.58	5.13	
	$S_{\bar{x}} = 1.20$						
	Plant color						
CB756	2.8	3.0	2.9	2.8	2.4	2.9	2.8
RP182-13	2.9	2.9	3.0	3.0	2.9	2.9	2.9
NC70.1	2.6	2.5	2.5	3.0	2.8	2.9	2.7
NC6	2.7	2.8	2.9	3.0	1.6	2.3	2.5
NC123	2.9	3.0	2.4	3.0	2.6	2.8	2.8
SMS-2	2.8	2.9	2.6	3.0	2.6	2.6	2.8
176A22	2.6	2.9	2.6	3.0	3.0	2.9	2.8
3G4b21	2.4	2.0	1.0	3.0	1.3	1.9	1.8
NC56.2	2.6	2.8	2.4	2.6	2.3	2.1	2.5
32H1	2.9	2.9	2.4	3.0	2.8	2.6	2.8
Mean	2.6	2.7	2.4	2.8	2.4	2.5	
N_2 control	2.5	2.6	2.6	3.0	3.0	3.0	2.8
Uninoculated	1.6	1.3	1.3	1.3	1.3	1.3	1.3
	$S_{\bar{x}} = 1.9$						

and 3.5% of the phenotypic variability for $N_2(C_2H_2)$ fixed, plant color, and nodule number, respectively (Table 3). Rhizobial strains accounted for 27.1% of the phenotypic variability for plant color, 21.4% for nodule number, 19.5% for shoot weight, and only 11.0% and 9.3% for nodule weight and $N_2(C_2H_2)$ fixed, respectively.

These results suggest that increases in nodule weight and shoot weight can best be improved by selection of superior host plants since the additive effects for hosts predominate for these traits. Nodule number, shoot weight, and plant color can all be improved by selection of rhizobial strains; however, since nonadditive effects are important for nodule number, $N_2(C_2H_2)$ fixed, and plant color, these traits can best be improved by simultaneous selection of both host and bacterium. These data demonstrate that improvement in traits indicative of symbiotic nitrogen fixation can be achieved by selection of superior hosts or strains, but both should be considered simultaneously in programs for improvement of nitrogen fixation of the peanut.

Table 3. Relative importance of components of symbiotic variability.

Source	% of total phenotypic variance				
	Nodule number	Nodule weight	Shoot weight	$N_2(C_2H_2)$ fixed	Plant color
Host	3.5	43.7	49.4	14.4	14.0
Strain	21.4	11.0	19.5	9.3	27.1
Host x Strain	27.3	13.4	7.9	22.2	17.6
Error	47.8	31.9	23.2	54.1	40.3

Responses of plant genotype and rhizobial strain are specific enough that it is not possible to reliably predict the general symbiotic performance. It would be hazardous to specify a strain of *Rhizobium* as being fully effective or having reduced effectiveness on peanuts without specifying the particular host. In order to determine if rhizobial strains could be specified for a group of hosts, the host x strain interaction was partitioned into two components, one arising from differences among botanical varieties and the second arising from differences within botanical varieties (Table 4). Most of the specificity of host and strains can be accounted for by differences in response of the strains to different botanical varieties, specifically in response of the strains to subspecies *hypogaea* (virginia) and subspecies *fastigiata* (spanish and valencia). This was unlike the additive effects of the host where both among botanical varieties (primarily *hypogaea* vs. *fastigiata*) and within botanical varieties (primarily within *hypogaea*) was significant for nodule weight, shoot weight, plant color, and $N_2(C_2H_2)$ fixed.

The specificity of a strain for a specific botanical type was determined by examining the significant estimates of interaction effects and the means over botanical types (Table 2). Significant ($p = 0.05$) interaction effects were found for strain NC123 which showed specificity for the virginia type for all traits; for strain 3G4b21 which also showed specificity for the virginia type for nodule number, nodule weight, and $N_2(C_2H_2)$ fixed; for strain NC56.2 which was specific for the spanish and valencia types for nodule number and for strain NC6 which showed specificity for the valencia and spanish types for shoot weight. The specificity of strains for particular host genotypes for nodule number is illustrated in Figure 1. Strain NC123 nodulates the virginia cultivars well but is poor in symbiosis with the spanish and valencia cultivars. NC56.2 nodulates the valencia cultivars extremely well and also does well with the remaining cultivars. Strain 3G4b21 is similar to NC123 in response while RP182-13 is consistent over all botanical types.

Stability variances for strains computed over all hosts were significant for strain NC123 for all traits, for 3G4b21 for all traits except shoot weight, for NC6 for shoot weight, and for NC56.2 for nodule number. Thus these strains show host specificity, whereas strain RP182-13 with a low stability variance and a high mean for all traits is a superior genotype that shows little host specificity.

These data suggest that strains may be selected that are specific for a group of host cultivars or strains can be selected that have general adaptation for peanut. Since only two cultivars of each botanical type were utilized in this study, further experimentation with a larger number

Table 4. Relevant mean squares for partitioning of host x strain interaction.

Source	df	Nodule number	Nodule weight	Shoot weight	$N_2(C_2H_2)$ fixed	Plant color
Host x Strain	55					
Host x (Negative control vs others)	5	658	2207	0.54	2.06	14.10
Among botanical varieties	2	1514	5248*	1.00	4.51	9.16
Ssp. hypogaea vs ssp. fastigiata	1	1767	10387**	0.38	8.88	10.92
Var. fastigiata vs var. vulgaris	1	1261	109	1.62	0.13	7.40
Within botanical varieties	3	87	180	0.24	0.43	17.40
Within var. hypogaea	1	223	97	0.13	0.07	17.52
Within var. fastigiata	1	1	442	0.48	0.40	30.68
Within var. vulgaris	1	37	0	0.12	0.82	4.00
Host x (Applied N vs Rhizobium)	5	1831	2422	2.90	6.86	33.92
Among botanical varieties	2	1490	2745	6.26*	15.29	81.80**
Ssp. hypogaea vs ssp. fastigiata	1	481	2575	2.81	1.56	115.82**
Var. fastigiata vs var. vulgaris	1	2499	2915	9.71*	29.02*	47.78
Within botanical varieties	3	2059	2206	0.66	1.25	2.00
Within var. hypogaea	1	4559	5950*	0.97	2.73	0.96
Within var. fastigiata	1	214	91	0.01	0.36	0.26
Within var. vulgaris	1	1403	579	1.01	0.65	4.80
Host x (Among strains)	45	4549**	2100**	2.23	9.39*	26.02**
Among botanical varieties	18	8987**	3485**	2.85*	14.75**	34.49**
Ssp. hypogaea vs ssp. fastigiata	9	15826**	5697**	3.02	23.40**	28.43
Var. fastigiata vs var. vulgaris	9	2148	1273	2.68	6.09	40.56**
Within botanical varieties	27	1590	1177	1.81	5.82	20.38
Within var. hypogaea	9	1889	1333	2.88	2.59	6.90
Within var. fastigiata	9	1540	1465	1.35	12.15*	35.45*
Within var. vulgaris	9	1340	732	1.19	2.71	18.78

*,**Indicates significance at p = 0.05 and 0.01, respectively.

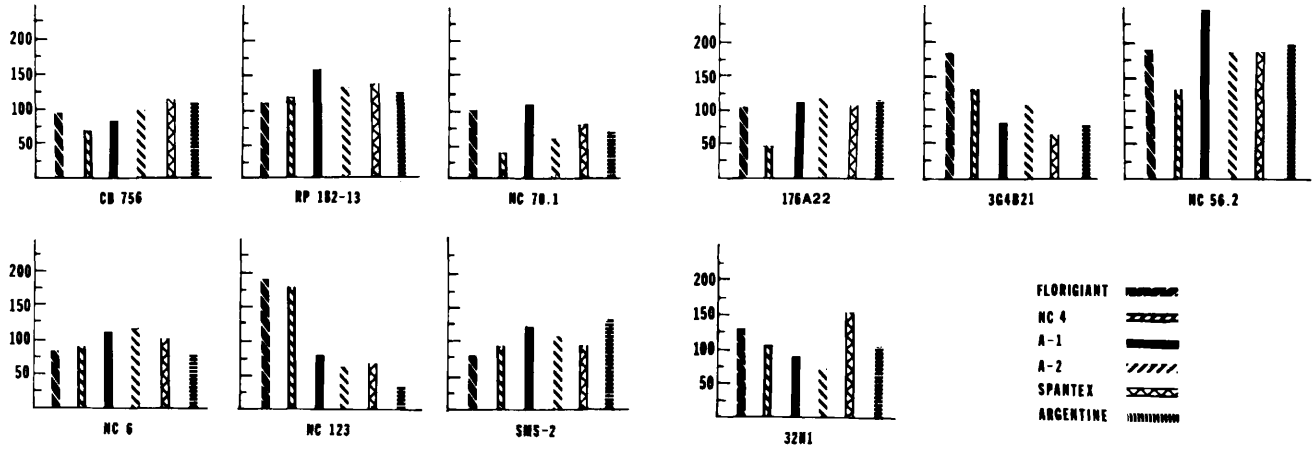

Fig. 1. Effect of specific peanut host and rhizobial strains on nodule number.

of hosts within a botanical variety are needed.

A comparison of the strain means for shoot weight for each host (Table 2) with the nitrogen control indicates that strains equal to the nitrogen control were found for all hosts except the two spanish cultivars. This and related studies (16) suggest that special emphasis is needed to identify superior strains for spanish cultivars.

The results from this and other studies conducted here (16) and at ICRISAT (12) suggest that two general approaches to breeding for improved symbiosis is possible in peanut. One approach is to select both host and rhizobial genotypes with general effectiveness against a range of genetically different partners. A second approach is to select for maximum nonadditive expression. Mytton (9)

suggests three ways of breeding for this specific association: (a) screen plant populations for individuals giving maximum expression with a *Rhizobium* genotype of good general effectiveness, (b) select plants with good general effectiveness and then identify rhizobial strains which maximize effectiveness, or (c) select both symbionts simultaneously choosing those combinations showing maximum effectiveness. Since peanut show significant additive effects for traits indicative of nitrogen fixation for both host and strains, it may be advantageous to improve the host first and then identify supeior strains for the improved host.

Regardless of the strategy adopted, the selection procedure must produce symbionts which have the capacity to reform the proper association under competition in the field. The evidence to data suggests that the capacity to infect and the capacity to be effective are under separate genetic control and a selection index involving both traits may be necessary.

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