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Genetic Correlations Derived from Full-sib Relationships in Soybean (*Glycine max* Merr.)

R. Ecochard and Y. Ravelomanantsoa
E.N.S.A.T. University of Toulouse, Toulouse (France)

Summary. Spaced plants of a segregating soybean hybrid population in the F_6 generation were scored for fourteen quantitative traits related to yield, foliage development and growth duration. Full-sib relationships were used to estimate the genetic additive components of variation and covariation. All genetic correlations between traits, as well as phenotypic and environmental correlations, were estimated separately. A principal component analysis was further performed in all three cases. Genetic correlations identified four different groups of traits comprised of: (I) seed number per pod; (II) mean seed weight; (III) dry weight and chlorophyll content per unit leaf area; (IV) all the other characters, including seed yield and total plant weight at maturity. Among these traits, stem diameter at ground level appeared to be a good indicator of yield. This distribution remained about the same for the environmental correlations, except that growth duration traits and foliage development traits became independent of yield. The implications of these results are discussed in relation to soybean breeding for climatic adaptation.

Key words: Genetic correlations – Full-sib covariance – Physiological traits

Introduction

Correlations between characters to be improved in a segregating plant population is a matter of concern to breeders in several respects. The progress achieved for a given trait frequently entails an undesirable response in another trait. For example, Hartwig and Hinson (1972) demonstrated a negative association between seed yield and protein content in soybeans (*Glycine max* Merr.), though Brim and Burton (1977) reported a few cases where these two parameters could be increased simultaneously. Because yield is usually characterized by low heritability, it is more advantageous to base selection on physiological criteria correlated with yield (Cooper 1976).

In both cases the correlations involved are genetic correlations. It is important to differentiate the genetic correlations from the environmental correlations (Falconer 1964; Cahaner and Hillel 1980), although what is commonly observed is a combination of both. Such a distinction is still too often neglected, especially in studies dealing with plants. Recently, Gardner (1977) urged quantitative geneticists to conduct investigations on simultaneous selection for several traits.

The basic nature of the genetic correlations is complex: pleiotropy, linkage disequilibrium and change in gene frequencies upon selection may contribute (Rutledge et al. 1973). Measurable traits are likely to be correlated if they share at least a proportion of the genes that are involved in their expression. Falconer, as early as 1952, suggested that a trait measured in two different environments should be considered not as one but as two traits associated by a genetic correlation.

In soybeans, the heritability of a number of quantitative and physiological parameters controlling yielding capacity were recently investigated (Ecochard et al. 1979). Interesting phenotypic correlations between two traits in the same segregating populations were also assessed and discussed (Paul et al. 1979).

The aim of the present study was to estimate separately the genetic, environmental and phenotypic correlations between fourteen traits. The corresponding correlation matrices were analysed separately, using the principal components method (Seal 1964) in order to elucidate the mode of association of the fourteen traits.

Full-sib rather than parent-offspring relationships were used as resemblance between relatives (Definitions) for the development of the genetic model. All determinations were thus carried out using the same generation under the same environmental conditions during the same year. This procedure provided a good control of the non-genetic causes of variation.

Materials and Methods

1) Plant material: The soybean population used in this study was kindly provided by H. Voldeng (Ottawa, Canada) under the code number X 514. It came from a complex hybridization program involving six strains belonging to maturity groups 00

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to III; these strains were characterized by different growth types and protein contents. The broadly segregating population derived from this hybrid population was initiated from a single F_1 individual, and was bred as single seed descent (Definitions) throughout five generations before the onset of the experiments.

2) Experimental procedure: The trial was performed in 1979 in the INRA experimental farm at Toulouse-Auzeville in a deep loamy soil with unlimited water supply due to irrigation. Two replicate series of plants were established side by side. Each series comprised 64 individuals of the population X 514 so that full-sib comparisons could be made between replicates. A 50 cm distance between plants eliminated competition effects. Each replicate contained eight plants of each of the following control varieties: 'Altona', 'Swift', 'Hodgson' and 'Amsoy 71'.

3) Data: Eleven traits previously described elsewhere (Paul et al. 1979; Ecochard et al. 1979) as well as three additional traits were characterized in this study. These traits were:

VPD: vegetative phase duration, from emergence to beginning of seed setting, expressed as "Heat Units" (see Definitions below); TCD: total cycle duration to maturity, also in Heat Units; MLA: mean leaf area; TNL: total number of leaves; LAP: leaf area per plant (= MLA × TNL); HTP: plant height; NPP: number of pods per plant; SPP: number of seeds per pod; MWS: mean weight of seeds; TPW: total plant weight at maturity, before threshing; TWS: total weight of seeds (= yield); CAC: chlorophyll "A" content per unit leaf area (determined in fully developed leaflets at the top of the foliage); SLW: specific leaf weight (oven-dry weight per unit leaf area in the same leaves as CAC); SDG: stem diameter at ground level.

The foliar parameters were determined at the beginning of seed set, at the end of the vegetative phase; the foliage build-up was then considered to be complete. The other traits were measured after harvest.

4) Data analysis: The $\frac{14\times(14-1)}{2}$ correlation coefficients between traits were calculated using the model detailed below. A principal component analysis was then carried out for each correlation matrix with a C.I.I. – IRIS 80 computer. Principal component matrices were generated and the variances corresponding to the various components were computed. The projection of the fourteen trait vectors into the plane defined by the plot of the principal components provided the diagrams of the various kinds of correlations.

Definitions

Heritability: ratio of additive genetic variance to phenotype variance (Falconer 1964).

Genetic correlation: correlation calculated from the genetic component of covariances and variances (Falconer 1964).

Resemblance between relatives: covariance between pairs of related individuals (offspring and one parent, full-sibs, etc.). Both genetic and environmental causes contribute to the covariance of relatives. The degree of resemblance may also be expressed by regression or correlation coefficients, dividing the covariance by the appropriate variances (Falconer 1964).

Single seed descent: procedure used in self-fertilizing crops, such as soybeans, for advancing generations to the desired level of inbreeding, without selection. In the F_2 and succeeding generations, only one seed from each plant in the population is used (Brim 1966). For genetic experiments, it is of interest to trace individually each progeny throughout the procedure.

Heat Unit: unit of growth based on the actual growth of corn and of soybean, as a function of temperature. For a given photoperiodism, the summation of the daily heat units is a more reproducible expression of the duration of a developmental phase than the mere number of days. Among the various heat units reported in the literature, those of Brown and Chapman (1972) were selected:

$$HU = 0.9[T_{C^\circ\min}-4.5] + 1.67[T_{C^\circ\max}-10]-0.042\,(T_{C^\circ\max}-10]^2\,.$$

Model

1 Full-sib Relationships

As in the present experiment there is a biallelism with an equal distribution of the alleles, if epistasis is assumed to be negligible, the covariance between two relatives in an inbred progeny (Chevalet and Gillois 1977; 1978) approximates to its additive component throughout successive generations of inbreeding:

$$\mathrm{Cov}_{A_iA_j/A_i'A_j'} \rightarrow 2\varphi_{i/i}\,V_A \qquad (1)$$

where $\varphi_{i/i}$ is the probability that $i \equiv i'$.

In the present case, these two individuals are full-sibs, then $\varphi_{i/i}=\frac{1+f_{n-1}}{2}$ where f is the coefficient of inbreeding.

After six generations of selfing the covariance becomes:

$$\mathrm{Cov}_{FS} = 2V_A\,. \qquad (2)$$

Equation (1) also represents the genotypic variance of the individuals in the population, if $A_iA_j \equiv A_{i'}A_{j'}$. Then $\varphi_{i/i}=\frac{1+f_n}{2}$ and, in the present case:

$$V_G = 2V_A\,. \qquad (3)$$

2 Estimated Correlations Between Traits

The observed phenotypic variance of a character X at the generation considered can be derived from Eq. (3):

$$V_{P(X)} = 2V_{A(X)} + V_{E(X)}\,. \qquad (4)$$

Similarly the observed covariance between two traits X and Y is:

$$\mathrm{Cov}_{P(XY)} = 2\,\mathrm{Cov}_{A(XY)} + \mathrm{Cov}_{E(XY)}\,. \qquad (5)$$

2.1 Phenotypic Correlations

In the experiments reported here, the phenotypic variances and covariances of the segregating population were estimated as the residual variances and covari-

ances of the data in replicates 1 and 2, namely total variation or covariation minus the replicate effect with degrees of freedom = 126. Thus, the phenotypic correlation between X and Y, after simplification, can be estimated as:

$$r_{P_{(XY)}} = \frac{Cov_{(X_1,Y_1)} + Cov_{(X_2,Y_2)}}{\sqrt{V_{(X_1)} + V_{(X_2)}} \cdot \sqrt{V_{(Y_1)} + V_{(Y_2)}}}.$$

2.2 Genetic Correlations

Equation (2) gives the covariance of full-sibs for a character X, when the contribution of dominance can be neglected:

$$Cov_{(X_1,X_2)} = 2V_{A_{(X)}}.$$

Similarly, the covariance between the value of X in a plant and the value of Y in its full-sib ("cross-covariance", Falconer 1964), using Eq. (2), is:

$$Cov_{(X_1,Y_2)} = 2\,Cov_{A_{(XY)}}$$

and:

$$Cov_{(X_2,Y_1)} = 2\,Cov_{A_{(XY)}}.$$

The best estimate of the additive covariance between X and Y is thus:

$$Cov_{A_{(XY)}} = \frac{1}{4}[Cov_{(X_1,Y_2)} + Cov_{(X_2,Y_1)}]$$

In the case of covariances, the arithmetic mean would be preferred to the geometric mean used by Cahaner and Hillel (1980). From the above equations, the genetic additive correlation between X and Y can be estimated as:

$$r_{A_{(XY)}} = \frac{\frac{1}{2}[Cov_{(X_1,Y_2)} + Cov_{(X_2,Y_1)}]}{\sqrt{Cov_{(X_1X_2)}} \cdot \sqrt{Cov_{(Y_1Y_2)}}}.$$

2.3 Environmental Correlations

Environmental correlations are derived from the phenotypic and genetic correlations:

$$V_{E_{(X)}} = V_{P_{(X)}} - V_{A_{(X)}}$$

$$V_{E_{(Y)}} = V_{P_{(Y)}} - V_{A_{(Y)}}$$

$$Cov_{E_{(XY)}} = Cov_{P_{(XY)}} - Cov_{A_{(XY)}}.$$

Therefore:

$$r_{E_{(XY)}} = \frac{Cov_{P_{(XY)}} - Cov_{A_{(XY)}}}{\sqrt{V_{P_{(X)}} - V_{A_{(X)}}} \cdot \sqrt{V_{P_{(Y)}} - V_{A_{(Y)}}}}.$$

The environmental variances and covariances can also be estimated directly from the control varieties. They are residual variances and covariances, namely total variance or covariance minus replicate effects, minus variety effects, minus replicate × variety interactions, with degrees of freedom = 56. Subtracting this environmental component from the observed variances or covariances of the population X 514, provides the genetic component. Equations (2) and (3) in their more general form ($f \neq 1$) would then allow two unknowns, the additive and dominance components, to be calculated. Such calculations led to a number of nonsensical results, such as negative variances, suggesting that the control varieties considered are poorly representative of the range of segregating genotypes for most traits.

Nevertheless, the data derived from these control varieties provide an alternative estimate of the environmental correlation between two traits, independently from the population X 514.

The principal component analysis carried out using the environmental correlation matrices corresponding to both plant populations leads to comparable conclusions, as substantiated below.

Table 1. Correlations between different traits in segregating soybean plants. Traits coded as in the text. Top: phenotypic correlations; bottom: genetic correlations

	VPD	TDC	MLA	TNL	LAP	HTP	NPP	SPP	MWS	TPW	TWS	CAC	SLW	SOG
VPD		0.545	0.361	0.679	0.660	0.615	0.640	0.156	−0.156	0.565	0.541	−0.115	−0.443	0.450
TCD	0.867		0.314	0.345	0.416	0.522	0.354	0.037	−0.026	0.389	0.307	−0.214	−0.263	0.426
MLA	0.524	0.560		0.286	0.737	0.356	0.354	0.258	0.085	0.501	0.418	0.016	−0.274	0.500
TNL	0.863	0.624	0.444		0.809	0.456	0.671	0.170	−0.125	0.565	0.582	−0.086	−0.414	0.432
LAP	0.877	0.684	0.770	0.894		0.519	0.651	0.215	−0.019	0.675	0.628	−0.078	−0.419	0.569
HTP	0.796	0.961	0.647	0.645	0.776		0.627	0.197	−0.136	0.622	0.546	−0.085	−0.246	0.620
NPP	0.833	0.846	0.478	0.830	0.861	0.754		0.225	−0.003	0.908	0.946	−0.049	−0.399	0.696
SPP	0.133	0.069	0.274	0.116	0.082	0.351	0.230		−0.258	0.258	0.295	−0.042	−0.139	0.288
MWS	−0.126	0.167	0.127	−0.093	0.021	−0.138	−0.004	−0.328		0.206	0.240	−0.061	−0.078	0.165
TPW	0.783	0.899	0.667	0.712	0.879	0.769	0.939	0.257	0.242		0.939	−0.024	−0.388	0.801
TWS	0.730	0.841	0.520	0.735	0.825	0.688	0.952	0.243	0.255	0.939		−0.055	−0.385	0.744
CAC	−0.221	−0.184	−0.036	−0.233	−0.155	−0.205	−0.258	−0.256	−0.100	−0.223	−0.304		0.263	−0.066
SLW	−0.710	−0.544	−0.540	−0.630	−0.689	−0.423	−0.698	−0.063	−0.139	−0.708	−0.691	0.400		−0.337
SDG	0.711	0.943	0.862	0.608	0.856	0.725	0.772	0.513	0.183	0.891	0.847	−0.044	−0.544	

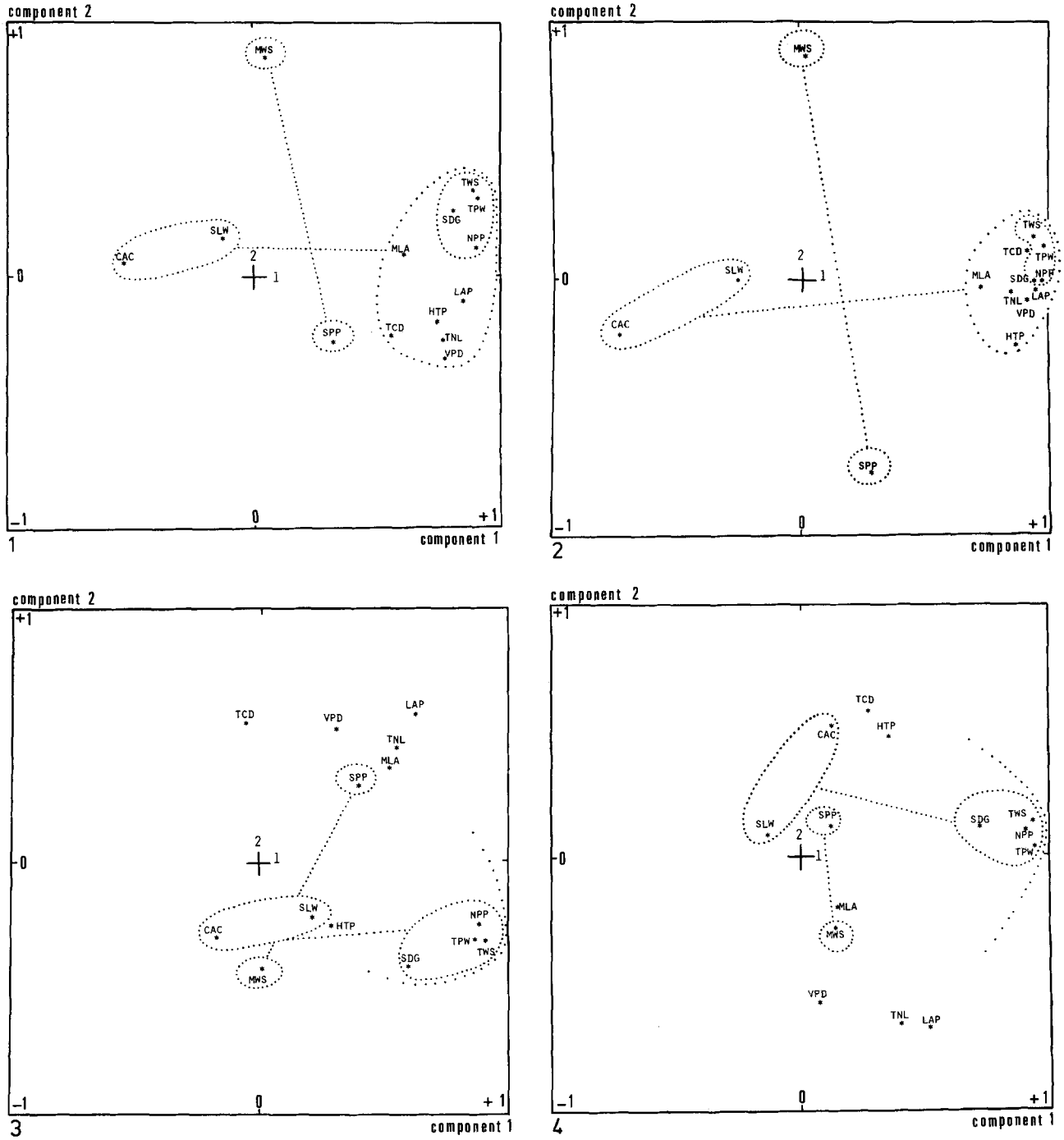

Fig. 1–4. **1** Principal component analysis of the Phenotypic correlations, graphically represented as described in the text. **2** Principal component analysis of the Genetic correlations. **3** Principal component analysis of the Environmental correlations (a). **4** Principal component analysis of the Environmental correlations (b)

Results

Correlation matrices between the fourteen characters in all possible combinations were tabulated in four sets as follows:

(1) phenotypic correlations, as directly observed in the segregating population (Table 1, top); (2) genetic additive correlations calculated from that population as explained in 2.2 (Table 1, bottom); (3) environmental correlations (a) deduced as shown in 2.3 (Table 2, top); (4) environmental correlations (b) derived from intra-class variations and covariations of the control varieties (Table 2, bottom).

The principal components analysis of the four different correlation sets provided the contribution (%) of

Table 2. Correlations between different traits in space soybean plants. Traits coded as in the text. Top: environmental correlations (a) derived from the segregating population; bottom: environmental correlations (b) derived from the control varieties

	VPD	TCD	MLA	TNL	LAP	HTP	NPP	SPP	MWS	TPW	TWS	CAC	SLW	SDG
VPD		0.238	0.205	0.329	0.312	0.123	0.242	0.196	−0.228	0.098	0.110	0.010	−0.141	−0.065
TCD	−0.030		0.161	0.086	0.195	0.003	−0.148	0.014	−0.126	−0.150	−0.207	−0.223	−0.076	−0.080
MLA	0.158	0.039		0.137	0.729	−0.010	0.244	0.249	0.043	0.354	0.336	0.052	−0.089	0.143
TNL	0.253	−0.200	−0.028		0.686	0.005	0.378	0.243	−0.195	0.321	0.321	0.073	−0.187	0.120
LAP	0.355	−0.157	0.308	0.733		0.006	0.323	0.272	−0.091	0.347	0.340	−0.005	−0.161	0.134
HTP	−0.175	0.368	0.062	−0.099	−0.047		0.308	−0.058	−0.130	0.220	0.225	0.137	−0.001	0.376
NPP	0.119	0.231	0.057	0.242	0.317	0.221		0.228	0.000	0.844	0.938	0.198	−0.058	0.520
SPP	−0.087	0.058	0.048	−0.050	0.027	−0.095	0.071		−0.170	0.256	0.367	0.132	−0.203	0.005
MWS	0.047	−0.159	0.006	0.170	0.121	0.094	−0.065	−0.114		0.120	0.213	−0.015	−0.001	0.126
TPW	0.000	0.198	0.101	0.298	0.443	0.231	0.952	0.060	0.029		0.859	0.223	0.006	0.624
TWS	−0.115	0.189	0.058	0.239	0.329	0.327	0.925	0.185	0.160	0.928		0.217	−0.059	0.564
CAC	−0.048	−0.072	−0.031	−0.048	−0.148	−0.075	0.014	−0.071	−0.185	−0.086	−0.114		0.162	−0.091
SLW	−0.262	0.283	−0.081	−0.099	−0.093	0.206	0.186	−0.112	−0.197	0.146	0.100	−0.045		−0.112
SDG	0.033	0.288	0.056	0.161	0.184	0.279	0.570	0.050	0.259	0.596	0.627	−0.041	0.028	

Table 3. Principal component analysis of the correlation matrices: contribution (%) of the first four components to the total variance

	Comp. 1	Comp. 2	Comp. 3	Comp. 4
(1) Phenotypic correlations	46.50%	10.11%	8.96%	7.23%
(2) Genetic correlations	61.56%	10.43%	8.55%	8.01%
(3) Environmental correlations (a)	29.40%	15.44%	9.45%	9.22%
(4) Environmental correlations (b)	27.66%	15.96%	9.08%	8.56%

the first four components to the total variance, as listed in Table 3.

Figures 1 to 4 illustrate the principal component analysis of the various types of correlations: the plot of principal component 1 versus principal component 2 corresponds to the projection of the trait vectors into the plane thus defined, plane (1 : 2).

Because the distributions of datum points in planes (1 : 3), (1 : 4), and (2 : 3) are nearly the same as in plane (1 : 2), the discussion below concerns only the (1 : 2) projection.

Discussion

The diagrams of the phenotypic, genetic and environmental correlations (Figs. 1–4) show a distribution of traits into 4 groups: yield and related traits (I); chlorophyll content and specific leaf weight (II); number of seeds per pod (III); and the mean weight per seed (IV).

These results show that the seed yield is closely related to a number of characters, including those of NPP, TPW, SDG, etc. The contribution of the seeds to the total dry matter synthesized was close to fifty percent in the experiments reported here, the same as in those mentioned previously (Ecochard et al. 1979). These results also corroborate the finding that seed yield markedly depends on the number of pods per plant (Kaw and Menon 1972). Interestingly, whereas the mean weight of the seeds is negatively associated with their number per pod, the product of these two traits, SPP × MWS, is independent from the number of pods per plant, genetically as well as environmentally. Therefore, the search for a higher number of heavier pods might thus lead to an increase in yield. Also, the diameter of the stem at ground level in spaced plants is a good predictor of yield. This trait can be measured very easily prior to harvesting. Unexpectedly, the chlorophyll "A" content per unit leaf area is negatively correlated with yield, genetically as well as environmentally. Although it is only a component of the total leaf chlorophyll, the CAC × LAP product can provide some information on the assimilation capacity at the plant level.

Yield has been shown to be positively correlated with the total leaf area in spaced plants (Paul et al. 1979). But in the presence of interplant competition for light, as in a normal crop density planting, physiological limitations will prevent a simultaneous increase in foliage development and assimilation rate per unit leaf area. An association between chlorophyll content and specific leaf weight can also be observed: CO_2-exchange rate is known to be related to the former (Buttery and Buzzell 1977), as well to the latter trait (Dorn-

hoff and Shibles 1976). Finally, the stem diameter and the number of pods per plant are closely correlated with the seed weight and the total plant weight. This could be a consequence of the anatomical features of the plant: more pods can be formed, and more dry matter can be synthesized when larger or more numerous vascular bundles are present.

In the environmental correlations traits which were highly correlated with yield in the phenotypic and genetic analysis appear to be markedly less associated with yield. These characters include plant height, total cycle duration, vegetative phase duration, as well as foliar parameters (Tables 1, 2).

In spaced plants, these structural characteristics, although they are partly determined by the same genes as yield capacity, undergo different influences from the environment. These influences are not the same in the segregating population X 514 as among the varieties chosen as a standard. For example, leaf development is acting on seed weight in one case, and on the number of seeds in the other case. This may explain why the control varieties could not be used directly for developing the genetic model (i.e. they were not representative). Leaf development might have a beneficial effect on the weight of seeds per pod (i.e. SPP × MWS). This point deserves further physiological investigation.

Environmentally as well as genetically the total leaf area is positively correlated with each of its components, namely the number of leaves and their average area. As already mentioned elsewhere (Paul et al. 1979), the former component prevails.

Furthermore, in spaced plants as well as in normal density planting (Paul et al. 1979; Ecochard et al. 1979), the foliage area markedly depends on the duration of the vegetative phase. This dependency is the result of genetical rather than environmental factors (Tables 1 and 2).

The genetic and phenotypic correlations investigated above are not basically different. Because the influence of the environment was purposely minimized by the experimental procedure selected, the genetic correlations are adequately accounted for by the phenotypic correlations observed in the segregating population. Perhaps the situation would have been different had some agronomic parameter such as population density or water supply been included. The nature of correlations found between traits is not always clear, especially when different growth conditions and varieties are involved. A partitioning of covariances as well as of variances before calculating correlations is the most reliable approach. Using this method, interesting genotype × environment interactions can be brought out.

With respect to the genetic model, the fact that the selfed progeny analysed were derived from a single F_1 plant substantiates the assumption of a biallelism with an equal distribution of the alleles. Furthermore, epistasis and dominance were assumed to be negligible. More general models have been developed to account for the former (Gallais 1970), as well as for the latter (Chevalet and Gillois 1977, 1978). After six generation of selfing, the dominance component has decreased dramatically. However, for sampling reasons, an unselected segregating population derived from hybridization is then an attractive alternative to a varietal assortment.

In conclusion, an evaluation of the genetic correlations, restricted to their additive component when necessary, is a prerequisite allowing the matters raised in the introduction to be met. Genetic correlations, together with heritabilities, allow the prediction of the favourable or unfavourable response of a trait to the selection of another trait. Productivity can thus be improved by applying selection to some morphological or physiological criteria.

Also, when the selection conditions, e.g. spaced plants, or plants grown in a growth chamber, are remote from the field conditions where its effects will be finally assessed, the expression of a given trait in two different environmental situations is to be considered as two different traits related by a genetic correlation (Falconer 1964).

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Literature

Brim, C.A. (1966): A modified pedigree method of selection in soybeans. Crop Sci. **6,** 220

Brim, C.A.; Burton, J.W. (1977): Recurrent selection for increased seed protein content in two soybean populations [Abst.]. In: Agronomy Abstracts. p. 50. Madison, Wisc.: Am. Soc. Agron.

Brown, D.M.; Chapman, L.J. (1972): Heat unit for corn in Southern Ontario. Min. of Agric. and Food. AGDEX 111–131

Buttery, B.R.; Buzzell, R.I. (1977): The relationship between chlorophyll content and rate of photosynthesis in soybeans. Can. J. Plant Sci. **57,** 1–5

Cahaner, A.; Hillel, J. (1980): Estimating heritability and genetic correlation between traits from generations F_2 and F_3 of self-fertilizing species: a comparison of three methods. Theor. Appl. Genet. **58,** 33–38

Chevalet, C.; Gillois, M. (1977): Estimation of genotypic variance components with dominance in small consanguineous populations. (E. Pollak, O. Kempthorne, T.B. Bailey jr., eds.) In: "Proc. Intern. Conf. Quant. Gen." Ames (USA) Aug. 1976, pp. 271–296. Amer. (Io.): Iowa State Univ. Press

Chevalet, C.; Gillois, M. (1978): Inbreeding depression and heterosis: expected means and variances among inbred lines and their crosses. Ann. Génét. Sél. Ani. **10** (1), 73–98

Cooper, R.L. (1976): Modifying morphological and physiological characteristics of soybeans to maximize yields. Proc. p. 231–236. World Soybean Research Conference, Rayleigh (USA) Sept. 1976

Dornhoff, G.M.; Shibles, R.M. (1976): Leaf morphology and anatomy in relation to CO_2-exchange rate of soybean leaves. Crop Sci. **8,** 670–674

Ecochard, R.; Gallais, A.; Paul, M.H.; Planchon, C. (1979): Héritabilité et réponse à la sélection de caractères physiologiques liés au rendement chez le soja. Ann. Amélior. Plantes **29,** (5), 493–514

Falconer, D.S. (1952): The problem of environment and selection. Am. Nat. **86,** 293–298

Falconer, D.S. (1964): Introduction to quantitative genetics. Edinburgh: Oliver & Boyd

Gallais, A. (1970): Covariances entre apparentés quelconques avec linkage et épistasie. II. Evolution en régime d'autofécondation. Ann. Génét. Sel. Ani. **2,** 417–427

Gardner, C.O. (1977): Quantitative research in plants; past accomplishments and research needs. (E. Pollak, O. Kempthorn, T.B. Bailey jr., eds.) In: Proc. Intern. Conf. Quant. Gen. Ames (USA) Aug. 1976, pp. 29–37. Amer. (Io.): Iowa State Univ. Press

Hartwig, E.E.; Hinson, K. (1972): Association between chemical composition of seed and seed yield of soybean. Crop. Sci. **12,** 829–830

Kaw, R.N.; Menon, P.M. (1972): Association between yield and components in soybean. Indian J. Genet. Plant Breed. **32** (2), 276–280

Paul, M.H.; Planchon, C.; Ecochard, R. (1979): Etude des relations entre le développement foliaire, le cycle de développement et la productivité chez le soja. Ann. Amélior. Plantes **29** (5), 479–492

Rutledge, J.J.; Eisen, E.J.; Legates, J.E. (1973): An experimental evaluation of genetic correlation. Genetics **75,** 709–726

Seal, H.L. (1964): Multivariate statistical analysis for biologists. London: Methuen

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Prof. R. Ecochard
Dr. Y. Ravelomanantsoa
Laboratoire d'Amélioration des Plantes
Ecole Nationale Supérieure Agronomique
Institut National Polytechnique
145 avenue de Muret
31076 Toulouse Cédex (France)