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The influence of composite traits on genotype by environment relations*

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Summary. In breeding for multiple trait value functions, the existence of genotype-by-environment interaction effects can vastly complicate the designation of optimum sets of genotype-environment pairings into Target Populations of Environments. In this paper it is shown that even in the absence of any changes in genotypic ranking over environments on a trait-by-trait basis, it is possible to generate changes in genotypic ranking in value in different environments. This is shown to be true even for linear value functions in a case example in pine breeding.

Key words: Genotype-by-environment – Interaction – Selection index

Introduction

In trials of plant varieties or genotypes over a range of environmental conditions, evaluation usually includes several traits that together express crop value. In forest trees, for example, tests often are conducted on sites that differ in climate and soil conditions and measured traits often include stem size, form, and disease resistance. A major objective is to identify a clustering of genotypes and environments within which there is little genotype-by-environment interaction (Horner and Frey 1957; Ramey and Rosielle 1983). The breeder may then subdivide breeding populations by Target Populations of Environments (TPE) as suggested by Comstock (1977). However, when crop value depends on several traits, defining TPE's becomes a multi-variate problem. In general, genotype-by-environment interactions are treated independently of multiple trait selection under the assumption that traits are independent, as for example in cotton (Abou-El-Fittouh et al. 1969). It is clear that genotype-by-environment interactions differ among traits in cotton (Miller et al. 1959), but it is not clear how the interactions should affect multiple trait selection (Lin 1978).

It is also not clear that rank changes of genotypes among environments in any component traits are either necessary or sufficient conditions for either different TPE's or genotype-by-value interactions to exist.

A linearizeable model

To analyze the simplest case, consider a set of i genotypes (g_i), in j environments (e_j), measured for k traits, without changes in rank of any genotype over the environments in any trait. To distinguish models in which the genotypic effect may vary with environment and hence g_{ij} denotes the i^{th} genotypic effect in the j^{th} environment, in our model we use $g_{i.}$ and $e_{.j}$ to denote constancy of effects over the dotted variable. For traits with constant linear and independent genetic and environmental contributions, we can denote yield as $Y_{ij} = \mu + g_{i.} + e_{.j}$. For the multivariate case, genotypic value is vector valued as $(Y_{ij1}, Y_{ij2}, \ldots, Y_{ijk})$, where

$$Y_{ijk} = \mu_k + g_{i.k} + e_{.jk}.$$

For a constant linear index value function of the k traits, we can denote the value of a genotype as

$$Y_{i..} = \sum_k \alpha_k (\mu_k + g_{i.k}),$$

where α_k is the constant index weighting given to trait k, and $\sum_j e_{.jk} = 0$. It can then be seen that the differ-

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ence between any i and i′ genotypes in any environment is the same for all environments, and for the index, the difference is

$$Y_{i..} - Y_{i'..} = \sum_k \alpha_k \, (g_{i.k} - g_{i'.k}) \,,$$

which is unaffected by environmental effects. Thus, any constant index will yield the same ordering of genotypes in any set of environments. However, if the assumption of linearity of genotypic and environmental effects is relaxed while still maintaining the rank order of genotypes in all traits in all environments, a quite different result is obtained. For example, if a trait, k′, is affected such that the environmental effect multiplies genotypic effects, such as

$$Y_{ijk'} = \mu_k + (g_{i.k'})\,(e_{.jk'}) \,,$$

then the rank order of genotypes is the same in any environment. That is,

$$Y_{ijk'} - Y_{i'jk'} = e_{.jk'}\,(g_{i.k'} - g_{i'.k'}) \,,$$

and obviously, for any set of j environments, the ordering of genotypes is maintained. However, even for linear, constant multiple trait value functions, it can be seen that the difference between two genotypes in environment j is: $\sum_k \alpha_k \, (Y_{ijk} - Y_{i'jk'})$, which for the two traits abvove is:

$$Y_{ij.} - Y_{i'j.} = \alpha_k \, (g_{i.k} - g_{i'.k}) + \alpha_{k'} \, e_{.jk'} \, (g_{i.k'} - g_{i'.k'})$$

while in environment j′, the difference is:

$$Y_{ij'.} - Y_{i'j'.} = \alpha_k \, (g_{i.k} - g_{i'.k}) + \alpha_{k'} \, e_{.j'k'} \, (g_{i.k'} - g_{i'.k'}) \,.$$

The genotypic differences are not the same in the two environments since $e_{.j.k'} \neq e_{.j'k'}$ and in fact, the order of genotype i vs i′, may be reversed depending on the sign and magnitude of

$$(g_{i.k} - g_{i'.k}) \text{ vs. } (g_{i.k'} - g_{i'.k'}) \quad \text{and} \quad e_{.jk'} \text{ vs. } e_{.j'k'} \,.$$

Thus, even if no genotype changes rank over environments in any component trait, genotypes can change value rank among environments. The mapping of the multi-variate space into a single composite value function creates a genotype-by-value interaction by the effect of adding the product of index weights by environmental effects. In effect, the mapping from a multi-dimensioned trait space to a single variable creates a joint effect which acts like an interaction effect even in the case of a linear value function.

A case example

Data on *Pinus caribaea* provenances reported by Gibson (1982) provide an example of change in genotypic value with environment, where no change in ranking exists for any component trait. In two locations, Puerto Rico and Chumporn, Thailand, six provenances were analyzed in detail. While rank changes were very common among provenances over all of the sites sampled, two planting sites produced consistent rankings for bark percent (BP) and for length of the longest internode (LI) (Table 1). These two traits affect the expected value of trees by their relationships with growth and susceptibility to mechanical damage. Their relative values may be approximated by a linear function with roughly equivalent economic weights. The differences among genotypes in LI are larger in Puerto Rico than in Chumporn and hence a multiplicative genotypic and environmental joint effect can exist, while the genotypic differences in BP are roughly similar in the two planting sites. However, the rankings of the provenances in the two sites are the same and if we gave equal weight to BP and LI, say 1 : 1, the rankings are no different for the two sites (Table 2). However, if the weighting for BP and LI were 1 : 1.3, the rankings are different in the two sites. Furthermore, with weightings of 1 : 1.6, there is a different change in ranking for the two sites. Thus, in general, selecting provenances to maximize or minimize both BP and LI depends on the relative weighting given the traits. For a linear value function,

Table 1. *Pinus caribaea* provenance performance in bark percent (BP) and longest internode length (LI) planted in Puerto Rico and Chumporn, Thailand. (From Gibson 1982)

Provenance name	Planting site			
	Puerto Rico		Chumporn, Thailand	
	BP	LI	BP	LI
Guanaja	38.0	1.40	33.5	0.80
Potosi	37.5	1.60	31.0	1.30
Brus Lagoon	35.5	2.55	30.6	1.60
Santa Clara	34.0	1.15	30.4	0.75
Poptun	32.5	2.60	28.5	1.75
Alamicamba	31.0	4.00	27.5	2.40

$$V(BP, LI) = a_1 BP + a_2 (LI),$$

values of a_2/a_1 exceeding 1.52 would give the provenance Santa Clara the highest ranking in both planting sites. For values of a_2/a_1 less than 1.05, the provenance Alamicamba, would consistently receive highest ranking. However, for $1.05 < a_2/a_1 < 1.52$, the highest provenance ranking would switch from Santa Clara in Puerto Rico to Alamicamba in Chumporn.

Implications

It is clear that genotype-by-value interactions large enough to alter genotypic ranking in different environments are possible, even if no shifts in genotypic ranking by trait occur. Since the ultimate purpose of selection and breeding is to increase genotypic value, the appropriate response to the situation seems obvious. We must compute genotypic values as a function of the relevant traits in various environments. When we hope to identify TPE's or clustering, this step is necessary even though no significant genotype-by-environment interactions exists in the individual traits.

When genetic and environmental effects contribute non-linearly to the phenotype, or when genotypes

Table 2. Provenance values for relative weightings of BP:LI

Provenance name	Planting site					
	Weighting of BP:LI					
	1:1		1:1.3		1:1.6	
	Puerto Rico	Chumporn	Puerto Rico	Chumporn	Puerto Rico	Chumporn
Guanaja	39.4 (1)	34.3 (1)	39.82 (1)	34.54 (1)	40.24 (1)	34.78 (1)
Potusi	39.1 (2)	32.3 (2)	39.58 (2)	32.69 (2)	40.16 (2)	33.08 (3)
Brus Lagoon	38.05 (3)	32.2 (3)	38.82 (3)	32.68 (3)	39.58 (3)	33.16 (2)
Santa Clara	35.15 (4)	31.15 (4)	35.50 (6)	31.38 (4)	35.84 (6)	31.60 (4)
Poptun	35.10 (5)	30.25 (5)	35.88 (5)	30.78 (5)	36.66 (5)	31.30 (6)
Alamicamba	35.00 (6)	29.90 (6)	36.20 (4)	30.62 (6)	37.40 (4)	31.34 (5)

change rank in any component trait on any set of environments, any change in genotypic value rank will depend on the composite trait value function and the environmental effects. Clearly, if the value function changes, different rankings can occur. In soybeans, which exhibit little genotype-by-environment interaction, changes in linear index weights sometimes lead to different selection results (Brim et al. 1959). In forest trees, such changes can lead to selecting different populations for different value functions (Namkoong 1978).

A change in the value function with a shift in environment can easily create rank changes. In trials of *Eucalyptus grandis* provenances along an elevational gradient in Brazil, Namkoong et al. (in press) observed no provenance rank changes in either volume growth or disease resistance. However, because disease incidence is high at low elevations, disease resistance has greater value for forestation at low than at high elevations. The result is a difference in choice of provenances for high and low elevation plantings.

The recommended value functions need not be linear (Goddard 1983; Bulmer 1980). Even if these functions are nonlinear, however, genotypes and environments can be clustered using existing techniques. The dimensionality of the clustering method would only have to be increased if separate traits or distinct trait functions were used to cluster genotypes according to environment-trait likenesses.

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