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Influence of the Value Function on Genotype-by-Environment Relations[1]

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Summary

In provenance trials of tree species over several sites where tree value is a composite function of several traits, it is generally supposed that the lack of a change in provenance rank in any trait is sufficient reason to select a single best provenance for all sampled sites. In this paper, we show that provenance values may change rank in the absence of rank changes in any component trait. When the value function is affected by the environment, ranking of provenance values may change in the absence of changes in ranking of composite traits.

Key words: Selection index, Genotype-by-environment, Provenance trials, Selection.

Zusammenfassung

Hierbei wird allgemein angenommen, daß das Ausbleiben von Rangverschiebungen bei irgendeinem Merkmal Grund genug ist, um für alle Standorte eine einzige, am besten geeignete Provenienz zu selektieren. In dieser Arbeit zeigen wir, daß die Rangfolge der Provenienzwerte insgesamt sich ändern kann, obwohl bei den einzelnen Merkmalen keine Rangverschiebungen vorkommen. Dies ist der Fall, wenn die Funktion, die den Provenienzwert bestimmt, durch Umweltfaktoren beeinflußt wird.

Introduction

In provenance trials of tree species over several test sites, where tree value is a composite function of several traits, it is generally supposed that the lack of a change in provenance rank in any trait is sufficient reason to select a single best provenance for all sampled sites. For example, a set of provenances may exhibit no shifts in ranking for either growth or fire resistance, and it may then be assumed that a single best provenance exists for all sites. Alternatively, if rank changes occur over sites in only one trait, it is generally assumed that subdividing planting environments into appropriate genotypic sets according to that one trait, will maximize value (Abou-El-Fittouh *et al.*, 1969). Such conclusions, however, are valid only if two underlying assumptions are satisfied:

1) All genetic and evironmental effects are linear and independent in their contribution to the phenotype in all traits, and
2) The composite value function is constant.

It has been shown that departures from the first assumption can result in changes in provenance ranks in their composite value function over environments (Namkoong, 1985). That is, a provenance by environment interaction can exist for composite value even if no rank changing interaction exists in any component trait.

In this paper, we indicate that failures of the second assumption may also occur and results in changes in rank of provenance values in the absence of rank changes in any component trait. Using data from a provenance trial of *Pinus caribaea* (Gibson, 1982), we demonstrate that the possibility is neither remote nor trivial. In this trial, and in other situations that can easily be imagined, the value function is dependent on the environment. As a result, the choice of best provenance varies with environment even without failure of the first assumption.

The Model

Consider a simple case of linear and independent genetic ($g_{i.}$) and environmental ($e_{.j}$) effects for a trait, k. Since genotype-by-environment interactions and departure from linearity are absent, the model can be written as:

$$Y_{ik} = \mu_k + g_{i.k} + e_{.jk} \tag{1}$$

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when the dot indicates constancy over that subscript. Under the usual assumptions,

$$\sum_{i} g_{i.k} = \sum_{j} e_{.jk} = 0, \text{ for all } k. \tag{2}$$

The value function $V(Y_{ij1}, Y_{ij2}, \ldots Y_{ijk})$, may take any one of many forms, a simple one being the linear selection index with weights $a_1, a_2, \ldots a_L$:

$$V(Y_{ij.}) = \sum_{k} a_k \, (Y_{ijk}). \tag{3}$$

Obviously, the difference between any genotypes, i. vs i', is the same for any environment:

$$Y_{ijk} - Y_{i'jk} = g_{i.k} - g_{i'.k} = Y_{i.k} - Y_{i'.k}. \tag{4}$$

Then, for any set of weights, the difference between genotypes is:

$$V(Y_{i..} - Y_{i'..} = \sum_{k} a_k (g_{i.k} - g_{i'.k}). \tag{5}$$

It is clear that any constant value function will yield a consistent ranking of genotypes over all environments.

If assumption 1 fails, the $g_{i.}$ and $e_{.j}$ may independently affect the phenotype in a nonlinear fashion (Namkoong, 1985). For example certain planting sites may magnify provenance differences without changing their rank. Such phenomena lead to the breeders' quest for optimum test sites but, more importantly, can cause provenance rank changes in the composite value function (Namkoong, 1984). Thus, an interaction of genotype value with environment is introduced when the component traits are reduced to a single value function, even though no interaction exists on a trait by trait basis.

However, even if the g_i and e_j linearly affect the phenotype for all traits, differences in the composite value function in different environments can change the value ranking of genotypes for different planting sites. In equation 5 it is obvious that changes in the relative sizes of the a_k can change the size and sign of the difference between genotypes in these linear value functions. It can be further seen that, if the relative sizes of the a_k are functions of the environment, the differences between genotypes becomes a function ($f_k(e)$) of the environment,

$$V(Y_{i..} - Y_{i'..}) = \sum_{k} f_k(e) \; (g_{i.k} - g_{i'.k}).$$

That is, there is a genotypic value-by-environment interaction created by the a_k actually becoming functions of e_j.

A Case Example

We illustrate this effect by an analysis of a provenance trial of *Pinus caribaea* reported by Gibson 1982), which included planting on many sites around the world. Two sites (Puerto Rico and Chumporn, Thailand) in particular produce consistent provenance rankings and no genotype-by-environment interaction in either height growth (Ht) or bark percent (BP). Bark thickness is thought to be important in the survival of trees exposed to ground fires, and hence high BP is a measure of fire resistance (Gibson, 1982).

In this case, the composite value of Ht and BP can be a linear function in which BP is positive in fire-prone areas, but is of little or perhaps even slight negative value where fire incidence is low. The provenance mean performances in the two traits on the two sites shown in *Table 1* display no rank changes and no consistent pattern of nonlinear genotype-by-environment interaction.

Table 1. — Height and bark percent for *Pinus caribaea* provenances in two environments.

Provenance name	Planting site: Puerto Rico	Planting site: Chumporn
	Height in meters	
Alamicamba	11.3	11.4
Poptun	10.4	11.1
Potosi	10.0	10.8
Santa Clara	9.6	10.5
Guanaja	9.3	10.5
Brus Lagoon	8.9	9.8
	Bark percent	
Guanaja	38.0	33.5
Potosi	37.5	31.3
Brus Lagoon	35.5	30.6
Santa Clara	34.0	30.4
Poptun	32.5	28.8
Alamicamba	31.0	27.5

If the relative economic values for Ht (a_1) and BP (a_2) are 6.67 to 1 or greater, which might occur in areas of low fire hazard, the highest value provenance is Alamicamba in both Puerto Rico (A) and Chumporn. However, for a_1/a_2 ratios less than 1 to 1, which might occur where fire hazard is high, the highest value provenance would then be Guanaja in both areas. If a_1/a_2 ratios varied because fire hazard differed among sites, then provenance ranking would obviously vary also, and this switch in provenance value ranking with planting site would be independent of any ranking changes in any constituent trait.

Another type of ranking change may occur if there are nonlinear response differences among provenances. Even though there is no regular nonlinearity of provenance differences over sites, differences between specific pairs of provenances may be irregular. Hence, even when a_1/a_2 ratios are constant over planting sites but lie between 6.67 and 1, the highest valued provenance would be Potosi in Puerto Rico but could switch to Guanaja or Alamicamba in Chumporn.

A similar situation may exist for growth and insect resistance among provenances of *Eucalyptus viminalis* in southern Africa. It has been observed by Johnson (pers. comm.) that the provenances maintain fairly consistent rankings in height growth and resistance to the snout beetle *Gonipterus scutellatus*. If an average weighting were given to growth and resistance, it might be expected that one of the provenances would be ranked highest and might then be expected to yield the best average value. However, the snout beetle is a problem for *E. viminalis* primarily in high elevation plantings. Hence, a division of planting zones by elevation is feasible. At high elevations provenance preference would be for beetle resistance as well as growth. At lower elevations, rapid growth would be favored regardless of beetle resistance.

In effect, we may often have to consider the relative economic weights to be variables instead of known, fixed parameters. Value then becomes a function in which these economic variables may multiple the trait performance variables. Where the economic value is related to an environmental variable, nonlinear genotype-by-environment interactions are created. The environmental effect on value may be due to biotic variations or to a purely geographic effect such as closeness to a mill. Such a situation is described by Ohba (1984) for *Cryptomeria japonica.*

Implications

Since most genotype or provenance values are multiple trait composites for forestry, and since any departures from the simple assumptions of linearity and constancy can induce unexpected effects,, the existence of rank-changing interactions may be very common in most tree breeding programs. Thus, in forest genetics research where multiple regression techniques are used with familiarity, there is obviously a need for multivariate analyses (Namkoong, 1967). As basis for provenance selection, multivariate analysis can be a substantial aid for any explicit value function (Namkoong, 1982).

Multiple-trait evaluations are needed to breed within populations and to choose individuals for single or multiple population breeding (Namkoong, 1976). Even in the absence of departures from linearity, the multiplicity of selection objectives may require such a diversity of performance types and value functions that multiple populations are required for economically efficient breeding. From an initial single provenance or population, several populations may be developed. In such cases, the set of individual genotypes in the separate breeding groups may abruptly switch among groups such that no individual is a member of more than one foundation population. Switching occurs if the objective functions are widely different, but it can also occur with small changes in the function, if the genotypic set is not convex in the trait space. That is, if all of the genotypes available for selection are good for some traits or sites, and poor for others, and none are good for all, then even small changes in the value function can completely change the selected set of genotypes. Hence, selection must jointly consider the multiple nature of trait-by-environment responses, and the mutiplicity of value functions.

In this paper, we have presented only linear models and value functions. The results are not qualitatively different for nonlinear functions, though they are more diffecult to program.

It is significant that environmental effects on selection can commonly occur in the absence of traditionally defined genotype-by-environment interactions. These effects are uncovered only when multiple traits are evaluated. When nonlinear effects exist and value functions are not constant, there is no generally valid way to predict whether selection will be more or less complicated or will involve multiple or single populations. The effects of traits and values must be analyzed in detail for each environment.

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Are the EEC Directives on Forest Reproductive Material Genetically Adequate?1)

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Summary

Directives issued by the Council of the European Communities regulate the marketing of forest reproductive material in the member countries. In view of the long-term process of biological production in forestry, the genetic properties of forest seed are more important than those of short-lived crops. It is therefore desirable to have legislation which increases the purchaser's confidence in the phenotypic potential of forest reproductive material and the validity of the accompanying documents.

Because the Directives reflect the level of forest genetic knowledge of more than 20 years ago, their general conception as well as certain individual regulations conflict with insights since gained in the field of population genetics. A discussion of these shortcomings illustrates the need for a revision of these Directives.

Key words: Forest reproductive material, certification, seed legislation, population genetics.

Zusammenfassung

Vom Rat der Europäischen Gemeinschaften erlassene Richtlinien regeln das Inverkehrbringen forstlichen Saat- und Pflanzguts in den Mitgliedsländern. Angesichts der langen Lebensdauer der Waldbäume sind in der Forstwirtschaft die genetischen Eigenschaften des Saat- und Pflanzgutes von größerer Bedeutung als bei der Begründung kürzerlebiger Pflanzenbestände. Es erscheint daher wünschenswert, eine Gesetzgebung zu haben, welche das Ver-

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1) Dedicated to Prof. Wolfgang Langner on occasion of his 80th birthday.