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Joint analysis of genotypic and environmental effects

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Summary. A definition of jointly contributing genotypic and environmental effects is introduced, from which a new concept of genotype × environment interactions is derived. Interaction is defined to be the failure of genotypic or environmental response functions to be separable. For separable response functions, the contributions of the genotypic and environmental effects must be related in terms of an operator which can describe their joint actions. A scale-free method of determining the simplest operator is developed in terms of comparative norms of reaction and a characteristic of the operator is given for several operators. With a defined operator, the genetic and environmental contributions can be derived, and biologically interpreted. These methods are applied to published data on *Pinus caribaea.*

Key words: Genotypic × environmental interaction – Joint action B

Introduction

The concept of genotypic × environment interaction as a departure from linear and independent genotypic and environmental "main effects" assumes that each factor contributes an effect to the phenotype (Falconer 1960). One of the foci of research has been the linearity of the genetic and non-genetic contributions and hence on how various scaling transformations may legitimize a linear model (Pooni and Jinks 1980). However, a problem exists in interpreting results when, for example, transformations which may linearize environmental effects, make genotypic effects non-linear, or the effects of genotypes on environments non-linear. If instead, it is desirable to use some natural scaling in which genotypes respond non-linearily to an environmental scale, then a problem exists with respect to the measure of the genotypic differences in non-linear response functions. In fact, the existence of a non-linear response function for a genotype, while commonly expected for most physiological processes, poses a problem in how we define environmental effects. The problem as described by Lewontin (1974) is that there is a tautology in most analyses of the model. Since we generally only measure the phenotypes resulting from specific genotype responses to specific environments, the environments are only defined by the sampled genotypes, and hence the factors cannot be separately defined or estimated. He proposed that we focus attention on the "Norm of Reaction", which is a concept originally introduced by Woltereck (1909). Similarly, Knight (1970, 1973) called attention to the potential value of analyzing "Response Functions" of genotypes over common ranges of environmental variables, and in both of these cases, the tautology was avoided by using independent measures of environmental variables. In these concepts, the paradigm for the development of the phenotypic expression is that it is a response function of the two variables, genetic and environmental. Their analyses and others (Roberds et al. 1976; Gupta and Lewontin 1982) indicate that physiologically reasonable norms of reaction are non-linear and that they vary among genotypes.

However, if we accept the general desirability of considering the phenotype as a response function of the

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two types of variables, we are then faced with the problem of defining and measuring these "genetic" and "environmental" effects. Since we now recognize that a genotypic effect does not exist independently of an environmental effect, the linear model concept of an interaction becomes meaningless, since every phenotypic expression would be an interaction effect. In terms of the Analysis of Variance, everything would be accounted for by interaction without "main effects". Instead, we consider the problem of defining genetic and environmental variables and their joint operation in such a way that genetic and environmental effects can be estimated and have clear meaning for general non-linear response functions. We generalize the approach of Gregorius (1977) which we believe will be found to be biologically reasonable, widely applicable, and mathematically tractable. This requires that we first define a minimal concept of interaction and, conversely, non-interaction. Conditional upon the absence of interaction, we then define a condition of separability of genetic and environmental functions which in this sense are "independent" and which includes the classical, linear cases of independence but is not limited to those effects or those linear functional relationships. We do not presuppose any particular kinds of functions or operators, nor continuity properties, in the derivations, but use some such properties in the development of specific examples.

Interaction

The phenotype of an individual is completely determined by its genotype and environment. Ideally, both genotype and environment of an individual are supposed to contribute mutually independent effects, the cooperation of which results in the phenotype. Independence of effects simply means that the contribution of a particular genotype to the formation of the phenotype does not depend on environment and, conversely, that a particular environment makes the same contribution when acting on different genotypes. If, in some system, these effects are not independently definable the term "interaction" is used. As was recently demonstrated by the present authors (Gregorius and Namkoong 1986), interaction is essentially a synonym for undefinability of effects of causal variables. Hence, in the present paper we shall concentrate on working out the conditions under which genotypic and/or environmental effects can be distinguished and represented. Given this, methods to characterize the mode of operation between genotypic and environmental effects in the formation of the phenotype shall be proposed.

It follows from the above that we are basically concerned with a set of phenotypic observations on a set G of genotypes in a set E of environments, and we can then hypothesize the existence of a phenotypic response function ϕ which specifies for each pair (g, e) of genotype g (from G) and environment e (from E), the phenotypic expression $\phi(g, e)$. Hence, we seek the mapping for ϕ which takes values in the set F such that

$$\phi\colon\ G \times E \to F,$$

describing the response of each genotype in each environment.

It can be noted for any given genotype g_1 that its response to an environmental set, or its reaction norm, is an expression of the environmental effects for that genotype. If these effects were consistent, i.e. if they would not change with the genotype, then, as a minimum requirement, two environments e_1 and e_2 having identical effects on g_1, i.e. $\phi(g_1, e_1) = \phi(g_1, e_2)$, should also have identical effects on the other genotypes, i.e. $\phi(g_i, e_1) = \phi(g_i, e_2)$. Analogously, e_1 and e_2 having different effects on g_1, i.e. $\phi(g_1, e_1) \neq \phi(g_1, e_2)$, should also be different in their effects on the other genotypes, i.e. $\phi(g_i, e_1) \neq \phi(g_i, e_2)$. In this case it can be consistently said that an environmental affect exists which is separable from genotypic effects. However, if the environmental effects are identical for one but different for another genotype, then the environmental effects are fundamentally inconsistent and are not separable from the genotypic effects. We term this kind of inconsistency an interaction, and define *separability of environmental effects from genotypic* as: the response functions for any two environments from E are either consistently identical or consistently different, i.e.

For any two elements e_1, e_2 from E,
either $\phi(g, e_1) = \phi(g, e_2)$ for all g from G (1 a)
or $\phi(g, e_1) \neq \phi(g, e_2)$ for all g from G.

Conversely, we can analogously define *separability of genotypic effects from environmental* if and only if the response functions (reaction norms) for any two genotypes from G are either consistently identical or consistently different, i.e.

For any two genotypes g_1, g_2 in G,
either $\phi(g_1, e) = \phi(g_2, e)$ for all e in E (1 b)
or $\phi(g_1, e) \neq \phi(g_2, e)$ for all e in E.

If separability is realized in both directions, we may speak of *mutual separability,* or simply separability of genotypic and environmental effects. *Interaction* is then defined as the failure of separability which occurs if either (1 a) or (1 b) fails. Thus we may encounter two types of interaction:

a) if the environmental effects are not separable from the genotypic, then at least one of the environmental effects interacts with the genotypic effects, and

b) if the genotypic effects are not separable from the environmental, then at least one of the genotypic effects interacts with the environmental effects.

Obviously, there is a broader class of genotypic response functions which can be included in a set and still be called non-interacting, including non-quantitative and discontinuous functions.

For continuous, one-dimensional environmental variables, this formalization of interaction implies some intuitively pleasing results. Consider, for example, the class of all strictly monotonic functions for genotypic responses over an environmental range. Strict monotonicity of the reaction norms implies that condition (1 a) is fulfilled and, hence, the environmental effects are separable from the genotypic. Mapping each norm on the (ϕ, e)-plane, we can directly determine that interaction exists if any of two different norms intersect, since if they do, condition (1 b) for separability of genotypic from environmental effects is invalidated. Thus, in this case, interaction is equivalent to a change in ranking. Therefore, mutual separability is realized if the reaction norms of all genotypes are strictly monotonic and non-intersecting (Fig. 1).

For reaction norms with local maxima and/or local minima, mutual separability requires, besides non-intersection, that, by condition (1 a), wherever a genotype produces the same phenotype, that in those environments, all genotypes act similarly (Fig. 2).

By these conditions, we can include a mixture of response functions in sets which are intuitively reasonable to define as being joint products of the two factors, but which are separable and hence, "non-interactive". Clearly, the additive mode of action is a special case of a set of straight-line, parallel functions. Many other joint effect functions such as multiplicative or exponential joint functions are definable as particular modes of action between separable environmental and genetic effects. In the additive case, the effects can be transformed into functions which can be combined in a linear form. We now seek to define these transformations of separable functions in order to discriminate among forms of joint actions.

Separability of genotypic and environmental contributions

When a separable ϕ exists in the sense of (1 a) and (1 b), it is desirable to then derive functions of genotypes which in some sense are "independent" of environments and vice versa. Thus for any ϕ which satisfies (1 a) and (1 b), we would like to define genetic (γ) and environmental (ε) contributions which are not functions of the other variable, and which can be combined in some form of mathematical operation (Ω) to form the ϕ. That is, we wish to decompose ϕ into an operation (Ω) on mutually separable genotypic and environmental contributions (specified effects) and to be able to clearly define $\gamma(g)$, $\varepsilon(e)$, and $\Omega(\gamma, \varepsilon)$. For these purposes consider two functions

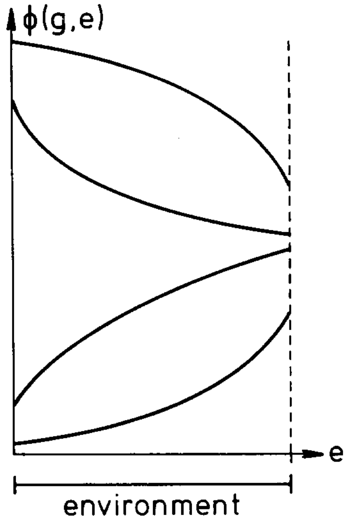

Fig. 1. Separability of genotypic and environmental effects for monotonic norms of reaction (e = environment, g = genotype, ϕ = response function)

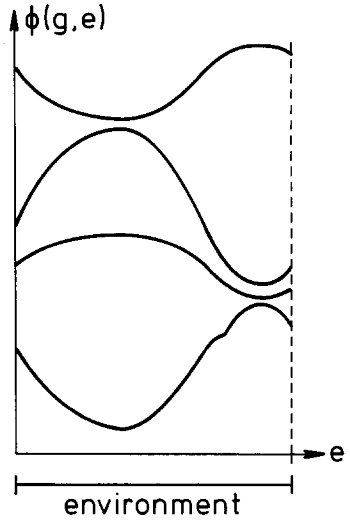

Fig. 2. Separability of genotypic and environmental effects for non-monotonic norms of reaction

$$\gamma\colon G \to C_\gamma \quad \text{and} \quad \varepsilon\colon E \to C_\varepsilon,$$

where the contribution of each genotype as an element from C_γ takes the form $\gamma(g)$ and is combined by the operation Ω with a contribution from C_ε for each environment to completely map the joint response function. Thus

$$\Omega\colon C_\gamma \times C_\varepsilon \to F$$

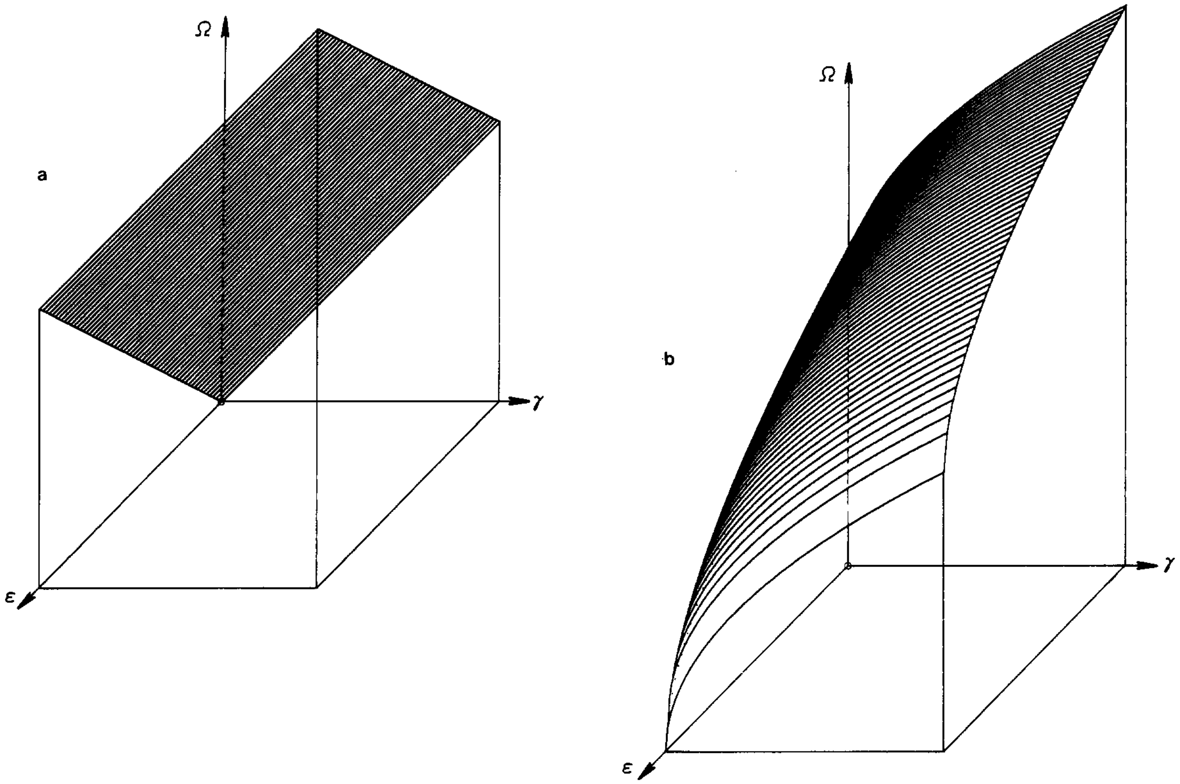

Fig. 3a, b. Additive operation (Ω) of genotypic (γ) and environmental (ε) effects. **a** Untransformed effects; **b** The operation Ω after a transformation $\sqrt{\gamma}$ and $\sqrt{1-\varepsilon}$ of the genotypic and environmental effects

and it obeys the relation $\Omega(\gamma(g), \varepsilon(e)) = \phi(g, e)$. This then corresponds to the characterization of the response by ϕ for mutually separable effects. Neither effect should obscure the effect of the other and, therefore, for mutually independent contributions, we require that

$$\Omega(x, y_1) = \Omega(x, y_2) \quad \text{only if} \quad y_1 = y_2 \tag{2a}$$

$$\Omega(x_1, y) = \Omega(x_2, y) \quad \text{only if} \quad x_1 = x_2 . \tag{2b}$$

For each x from C_γ and y from C_ε, $\Omega(x, \cdot)$ and $\Omega(\cdot, y)$ can be considered as functions

$$\Omega(x, \cdot) : C_\varepsilon \to F \quad \text{and} \quad \Omega(\cdot, y) : C_\gamma \to F .$$

Then the conditions (2a) and (2b) are equivalent to: $\Omega(x, \cdot)$ and $\Omega(\cdot, y)$ being one-to-one functions and thus are invertible. Therefore, we only need to know what the operation is and either a $\gamma(g)$ or an $\varepsilon(e)$ to derive the other.

Moreover, it is shown in Appendix A that each separable trait allows for an $\Omega(\gamma, \varepsilon)$-representation. This representation is *canonical* in the sense that it applies to all situations of separability. However, if an $\Omega(\gamma, \varepsilon)$ exists, it remains to be proven that it is unique, i.e. do there exist different Ω's, γ's and ε's all representing the same separable trait ϕ, and what the relationships are, if any, between these. In Appendix B we show that it is possible to have different Ω's with different γ's and ε's even for the same operator. Yet, they are all in one-to-one correspondence, so that the differences are just due to scaling and, consequently, uniqueness of the representation is guaranteed to mere scaling effects.

Thus, if ϕ is separable, and therefore no interaction exists, there is always some operator on a genetic contribution function and an environmental contribution function which can be derived. Furthermore, each genotype and each environment in the set can be uniquely characterized by its contribution function taken with respect to an appropriate average or other reference genotypic or environmental sample. We can therefore decompose the ϕ representation into genetic and environmental component contributions ($\gamma(g)$ and $\varepsilon(e)$) and can describe how the separate functions jointly operate (Ω) in what we are now calling "non-interactive" conditions. These are not only intuitively pleasing concepts of independent effects within a system of joint operations, but the definitions are operable.

Thus, the Ω-representation of response functions lays bare the essential way that a genetic contribution and an environmental contribution jointly operate to

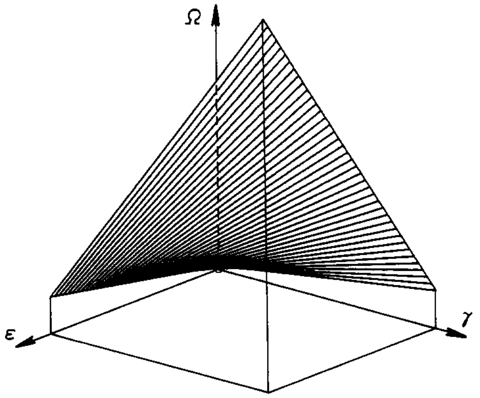

Fig. 4. Multiplicative operation (Ω) of genotype (γ) and environmental (ε) effects

produce the phenotypic responses. The separable contributions themselves may be some complicated functions of the genetic, g, or environmental, e, effects, but as long as $\gamma(g)$ and $\varepsilon(e)$ are additive, they will form the Ω as in Fig. 3a. Each set of response functions will have an associated γ and an ε function, and each genotype and environment will determine a point on the Ω-surface. If the Ω is a product of $\gamma(g)$ and $\varepsilon(e)$, then, the form of the operator will be as in Fig. 4.

The determination of the operator would be highly informative not only of how genetically and environmentally defined elements jointly operate, but as shown in Appendix B, we can invert the operation, and then can determine $\gamma(g)$ from $\varepsilon(e)$ and vice versa. Obviously, each operator would have some unique characteristics, and the estimation of the appropriate operator might be aided by further determination of the characteristic operators. However, it is possible that alternative scalings of $\varepsilon(e)$ and $\gamma(g)$ functions could yield other Ω's, and hence, some choice might exist among models. For example, consider a rescaling of the genotypic and environmental contributions in the additive model such that the new γ and ε result from the old ones by the transformations $\sqrt{\gamma}$ and $\sqrt{1-\varepsilon}$ ($0 \leqq \gamma, \varepsilon \leqq 1$), respectively. Hence, the operator is still additive, but the Ω-representation now looks as in Fig. 3b. Comparing this with Fig. 3a, it is evident that the characteristic of Ω, i.e. additivity, may be obscured by rescaling procedures. It is desirable to remove any such ambiguities and to be able to describe the simplest Ω operator possible.

A phenotypic mapping

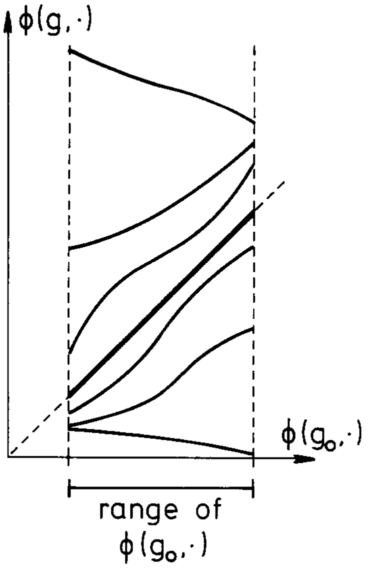

Fig. 5. Separability of genotypic and environmental effects: representation by way of plotting reaction norms $\phi(g,\cdot)$ of genotypes g against the reaction norm of a reference genotype g_0

To reduce the Ω to its simplest representation, consider an alternative form of the $\phi(g,\varepsilon)$ graphical representation of the norms of reaction which is similar to that used by Gregorius (1977). Consider that we designate a certain genotype as a reference genotype, g_0, any other genotype as g_i, and their norms of reaction as $\phi(g_0,\cdot)$ and $\phi(g_i,\cdot)$ for a separable trait ϕ.

In Appendix B it is shown that to each value of $\phi(g_0,\cdot)$ there can be assigned exactly one value of $\phi(g_i,\cdot)$ such that $\phi(g_0,e) \rightarrow \phi(g_i,e)$, and that this assignment constitutes a one-to-one mapping of the range of $\phi(g_0,\cdot)$ onto the range of $\phi(g_i,\cdot)$. If the trait is real-valued and continuous (i.e. the ranges of the norms $\phi(g,\cdot)$ are intervals), then the above assignment $\phi(g_0,e) \rightarrow \phi(g_i,e)$ can be represented as a function in a two-dimensional coordinate system. Thus, on the horizontal coordinate, we can plot the $\phi(g_0,\cdot)$ values and on the vertical coordinate, the $\phi(g_i,\cdot)$ values. In particular, if $g_i = g_0$ or the norm of reaction of g_i is identical to that of g_0, then the resulting function is the 45°-line passing through the origin.

Now consider all such functions resulting from different g_i's for the fixed g_0. Then, according to the condition (1b) for separability, the functions do not cross in the two dimensional coordinate representation. If these functions are continuous, then the plot of the $\phi(g_i,\cdot)$ relative to $\phi(g_0,\cdot)$ are strictly monotone since they are one-to-one by condition (1a) (Fig. 5). Hence, separability of genotypic from environmental effects means that the curves in Fig. 5 don't cross and separability of environmental from genotypic effects implies strict monotonicity for these curves.

As previously shown by Gregorius (1977), there are certain characteristic behaviours of the $(\phi g_i, \phi g_0)$

plotting for certain operators. If there is an additive relationship between separable genotypic norms of reaction, the $(\phi g_i, \phi g_0)$ graph will consist of parallel straight lines of 45° slope, each of which maps the ϕ for each i genotype vis-a-vis the g_0 (see Fig. 6). If the relationship is multiplicative, the graph will consist of straight lines, emanating from the origin at angles determined by each genotype (see Fig. 7). If the functional relationship among the $\phi(g_i, \cdot)$ is of the form such that the Ω function of γ, ε is exponential, the graph will be as shown in Fig. 8. In Appendix B we derive that $\phi(g_i, \cdot)$ can be described as a function of $\phi(g_0, \cdot)$ which is unique for an $\varepsilon(e)$ and Ω operation. We designate this as $\Phi_i(\phi g_0)$. From this it can also be seen that the environments need not be continuous variables, but it is necessary only that ϕ be real-valued in order to conduct an analysis of $\Phi_i(\phi g_0)$. Thus, a powerful analysis of separable functions and their operator is available simply by analyzing the $\Phi_i(\phi g_0)$ function. Furthermore, since the $\phi(g_i, \cdot)$ are the canonical forms of $\gamma(g_i)$, the $\Phi_i(\phi g_0)$ is free of any scale effects. Thus, even if we do not know what the $\gamma(g)$ or $\varepsilon(e)$ functions are, if the $\Phi_i(\phi g_0)$ fall into one form or another, that form is unique for an operation no matter what scalar or other 1 : 1 transformations are used in $\gamma(g)$ or $\varepsilon(e)$. The estimation of the operator then becomes merely a matter of estimating the $\Phi_i(\phi g_0)$. If $\Phi_i(\phi_0) = b_i + (\phi g_0)$, the operator is additive. If $\Phi_i(\phi g_0) = b_i \cdot (\phi g_0)$, the operator is multiplicative, etc.

The ϕ to Ω transformation

Consider that $\Phi_i(\phi g_0)$ is a function of $\phi(g_0, \cdot)$, which is the reaction norm of g_0, and that $\phi(g_0, \cdot)$ is a function of e for a given g_0. If we let this $\phi(g_0, \cdot)$ be our $\varepsilon(\cdot)$, then it can be seen that our $(\phi g_i, \phi g_0)$ is a plotting of the Ω operator corresponding to that choice of $\varepsilon(e)$. That is, in terms of real-valued ϕ, we choose a particular rescaling of the environment which forces the Ω to pass through the origin, be linear, and be of unit slope for the chosen g_0. Thus, more generally, the rescaling of $\varepsilon(e)$ is specified by the inverse $\Omega_{\gamma_0}^{-1}$, of $\Omega(\gamma(g_0), \cdot)$ which implies that $\varepsilon(e) = \Omega_{\gamma_0}^{-1}(\phi(g_0, e))$. Therefore, if we let $\mathrm{f} = \phi(g_0, e)$, and $\gamma = \gamma(g)$, we can always rewrite $\phi(g, e)$ as another function of f and γ, namely: $\phi(g, e) = \varrho(g, \mathrm{f})$. Clearly, ϱ is a function ϱ: $C_\gamma \times F_0 \to F$, where $F_0 =$ range of $\phi(g_0, \cdot)$ is a subset of F. ϱ is 1 : 1 in both of its components $\varrho(\gamma, \cdot)$ and $\varrho(\cdot, \mathrm{f})$, and it is equal to f for a $\gamma = \gamma_0$. Any such function with these properties is appropriately called a characteristic function, and therefore we call $\varrho(\gamma, \mathrm{f})$ *the characteristic of* $\Omega(\gamma, \varepsilon)$. Essentially, this characteristic consists in specifying the procedure according to which the norms of reaction of the various genotypes can be obtained from the norm of a reference genotype g_0. Thus, ϱ enables the direct comparison of the reaction norms of the genotypes and facilitates the biological interpretation.

In Table 1 and the accompanying Figs. 6, 7, 8 a few operators and their associated ϱ-characteristics are presented in their most general forms.

Table 1. Operators and their characteristics. a and b are real-valued one-to-one functions

Type	$\Omega(\gamma, \varepsilon)$	$\varrho(\gamma, \mathrm{f}) =$
Additive	$a(\gamma) + b(\varepsilon)$	$\mathrm{f} + (a(\gamma) - a(\gamma_0))$
Multiplicative	$a(\gamma) \cdot b(\varepsilon) + c$	$\frac{a(\gamma)}{a(\gamma_0)} \cdot \mathrm{f} + c \cdot \left(1 - \frac{a(\gamma)}{a(\gamma_0)}\right)$
	$a, b \neq 0$	$\mathrm{f} \neq c$
Exponential	$c_1 + c_2 \cdot e^{a(\gamma) \cdot b(\varepsilon)}$	$c_1 + c_2 \cdot \left(\frac{\mathrm{f} - c_1}{c_2}\right)^{\frac{a(\gamma)}{a(\gamma_0)}}$
	$a, b \neq 0;\ c_2 \neq 0$	if $c_2 > 0$ then $\mathrm{f} > c_1$, if $c_2 < 0$ then $\mathrm{f} < c_1$, $\mathrm{f} \neq c_1 + c_2$

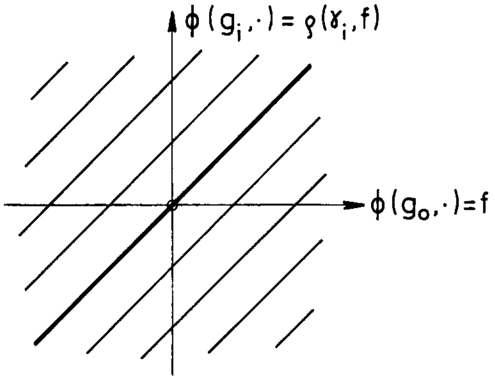

Fig. 6. Additive separability of genotypic and environmental effects (cf. Table 1)

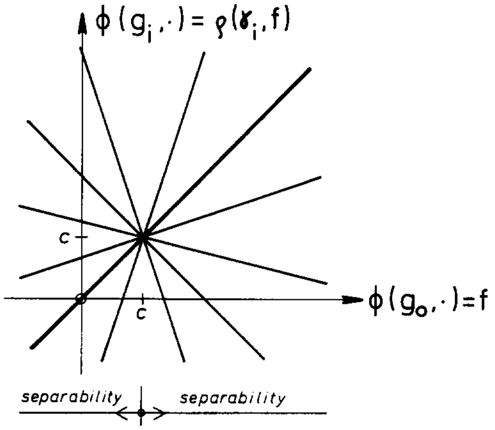

Fig. 7. Multiplicative separability of genotypic and environmental effects (cf. Table 1)

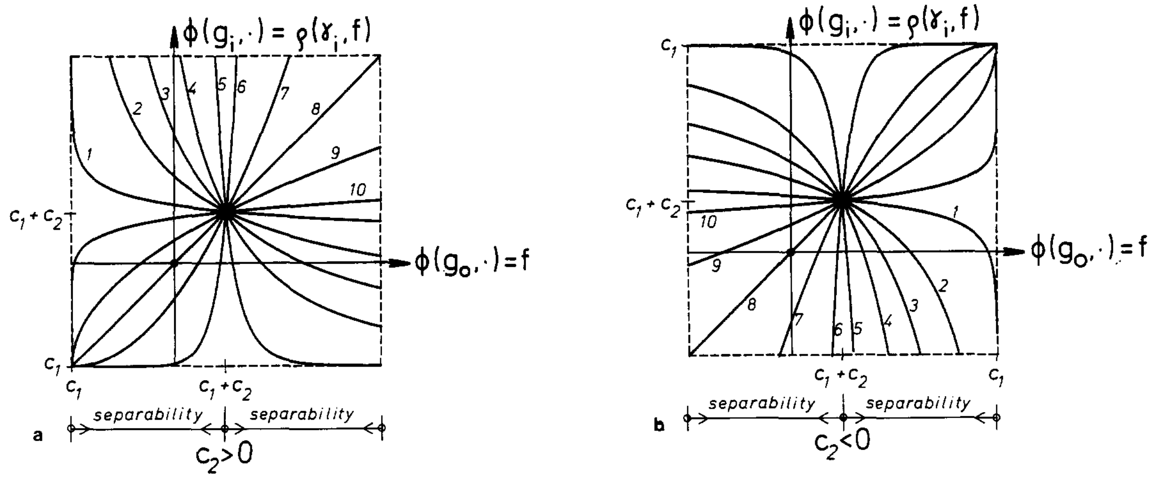

Fig. 8 a, b. Exponential separability of genotypic and environmental effects (cf. Table 1)

In the case of a real-valued, separable trait, the general basis for the interpretation of ϱ is provided by the linear ordering of environmental conditions as specified by the reaction norm $\phi(g_0, \cdot)$ of the reference genotype g_0. Hence, $\phi(g_0, \cdot)$ defines an environmental gradient along which the trait expression of the genotype g_0 strictly increases. All of the remaining genotypes are evaluated with respect to their responses along this gradient. Some of the more basic features of such an evaluation concern convergent or divergent behaviour of the reaction norms for the extremes of the environmental gradient. Divergent behaviour towards the upper extreme is typical in the multiplicative case for $\mathrm{f} > c$ (consult Fig. 7) and in the exponential case for $\mathrm{f} > c_1 + c_2$ and $c_2 > 0$ (consult Fig. 8a). Convergent behaviour towards the upper extreme occurs for $\mathrm{f} < c$ in the multiplicative case and for $\mathrm{f} < c_1 + c_2$ and $c_2 < 0$ in the exponential case (consult Fig. 8b). Initial divergence may be followed by convergence for exponential separability provided $c_2 > 0$ and $c_1 < \mathrm{f} < c_1 + c_2$ (consult Fig. 8a), or $c_2 < 0$ and $c_1 + c_2 < \mathrm{f} < c_1$ (consult Fig. 8b). These considerations also accentuate the special position occupied by additive separability, since there neither divergence nor convergence of the reaction norms takes place. In this sense, additivity appears to be the most ideal form of absence of interaction between genotype and environment.

However, as the other examples of Figs. 6, 7, and 8 demonstrate, even drastic deviations from additivity do not always indicate interaction, so that the analysis of variance is not a satisfactory tool for detecting interaction. An appropriate statistical analysis has to be based on data obtained for response functions, or at least approximations of these, and should provide means for estimating the probabilities of failure of conditions (1 a) and/or (1 b).

A note on statistical problems

So far, genotypes and environments have been considered to be deterministic units which can be uniquely described. While this is possible for genotypes if the species can be cloned and genetically identical individuals can be obtained, identical repetitions of environmental conditions are rarely, if ever, possible. However, in most cases, even the genotype of individuals can be specified only within certain limits of precision, in that they are offspring from selfing, full sibs, half sibs, provenances, etc. Hence, identical repetitions of genotypes and environmental conditions, as they are ideally required for the determination of response functions, are generally impossible.

Therefore, our genotypes g and environments e have to be replaced by random variables. The two types of random variables, genetic and environmental, are then to be considered as the factors of the experiment or model, and their levels are defined by the families, provenances, etc. (for the genetic factor) or the temperature, sites, areas, etc. (for the environmental factor). Thus the genotypes correspond to the levels of the genetic factor, and the environments correspond to the levels of the environmental factor.

Based on this framework, it was reasoned by the present authors (Gregorius and Namkoong 1986) that the appropriate stochastic representation of the response function is obtained by considering its probability distribution for each combination of a genetic and an environmental level. Distributional parameters, such as the expectation, higher moments, or quantiles, are then defined to be the *stochastic responses*. Hence, all of the previously derived concepts and results are applicable without any restrictions when genotypes are replaced by genetic levels, environments by environmental levels, and response functions by the distributional parameters considered.

Problems of estimating and testing distributional parameters from samples can be approached with the help of the available statistical methods. For example, for continuously distributed traits, separability or interaction can be detected in some cases by performing statistical sign tests (Dixon and Mood 1946) with respect to pairs of genetic and/or environmental (stochastic) response functions. The failure of a test to produce significant differences may then be provisionally accepted as 'statistical identity' or 'inseparability'. However, the development of more satisfactory concepts and methods of treating the idea of 'statistical identity' seem still to be wanting.

Application to an experimental data set

A data set on seed source trials of *Pinus caribaea* is provided by Gibson (1982) which are derived from replicated trials in several locations. We extract the data on stem straightness scores for seed source means in five of the test planting sites (Table 2). By analyzing the sources Alamicamba, Santa Clara, Guanaja, and Potosi, the ϱ characteristic seems to reflect an exponential type of operation (Fig. 9). This suggests that the straightness scores for these source populations are jointly exponential effects of the source genotypic contributions and the planting environmental contributions. However, as can be seen in Fig. 10, the two other source populations tested, Brus Lagoon and Poptun, do not have the same kind of joint operation and with respect to each other, a linearity of genotypic and environmental effects is apparent. The interaction between these two sets of source populations lies not only in their different forms of reaction norm, but also in the manner in which the environmental contributions affect their genetic effects.

Table 2. Stem straightness scores for six seed sources in five environments[a]

Planting environment	Seed source					
	ALA	STA	GUA	POT	BRU	POP
Chati	3.8	3.7	3.0	1.9	4.2	3.3
Mariti	4.2	3.8	3.4	2.0	3.3	2.9
San Pedro	10.3	8.9	7.7	5.0	7.1	6.8
Cardwell	9.3	8.7	7.0	4.9	9.0	8.5
Bukit Tapah	10.5	9.4	8.8	7.7	9.1	8.0

[a] From Gibson (1982)

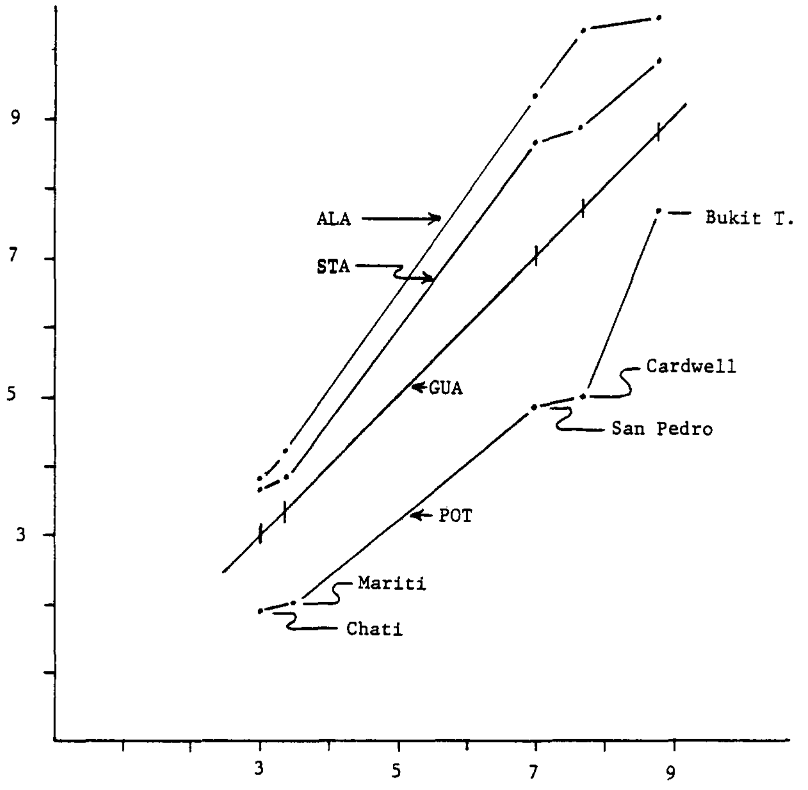

Fig. 9. Characteristic function for four sources in five environments of exponential form

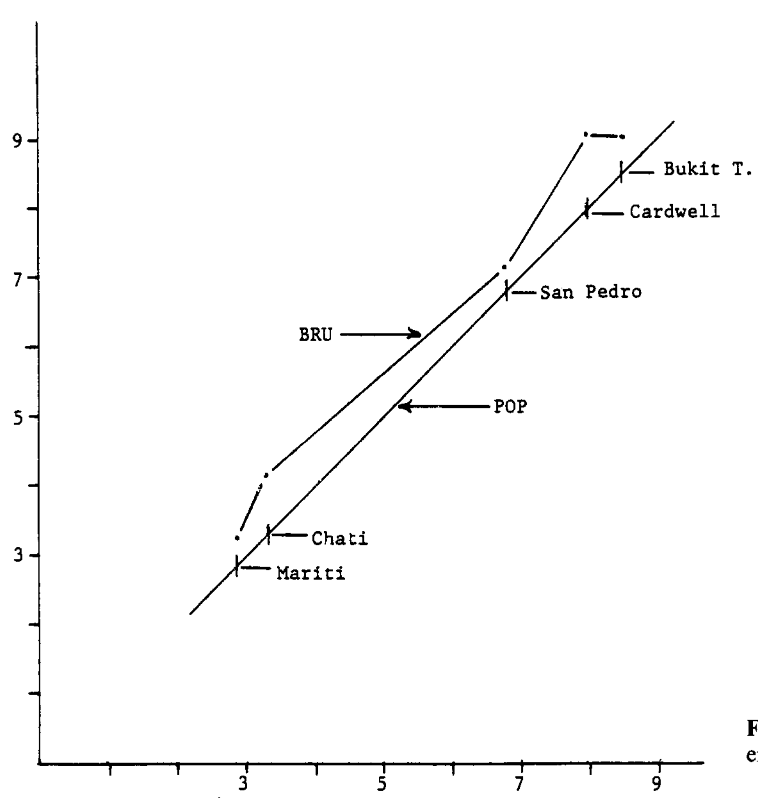

Fig. 10. Characteristic function for two sources in five environments of linear form

The concept of interaction: conclusion

If the concept and utility of the analysis of separable response functions is accepted and is clearly distinguishable from what we term interaction, we can apply the above analyses only within "non-interactive" sets of genotypes and environments (as was done in the last section). When our basic concept of consistent effects, as defined by (1 a) and (1 b), breaks down, then we cannot define generally valid gene or environmental effects. However, if there are subsets of genotypes and environments within which consistency exists, then we can describe the amount of such sub-setting which may be required and discuss other features of those subsets. It is also possible to explore the nature of relationships between subsets in order to jointly interpret some possibly piece-wise separable functions. It is not our intention here to further explicate the measures and interpretations of these interactions, but rather to extract as much interpretability as possible out of some basic concepts of non-interaction.

Appendix A

It is fairly obvious that a trait ϕ which allows for the representation $\phi(g,e) = \Omega(\gamma(g), \varepsilon(e))$ is separable, provided the operator Ω satisfies the conditions (2 a) and (2 b).

On the other hand, each separable trait ϕ allows for at least one $\Omega(\gamma,\varepsilon)$-type of representation. To see this, consider an arbitrary but fixed $e_0 \in E$ and $g_0 \in G$, and let $\varepsilon(e) := \phi(g_0, e)$, $\gamma(g) := \phi(g, e_0)$, $C_\varepsilon :=$ range of $\phi(g_0, \cdot)$, $C_\gamma :=$ range of $\phi(\cdot, e_0)$, and $\Omega(x,y) := \phi(g,e)$, where $x = \gamma(g)$, $y = \varepsilon(e)$. Ω is in fact well defined, since $\gamma(g) = x = \gamma(g')$ implies $\phi(g,e) = \phi(g',e)$ for all e, and, analogously, $\varepsilon(e) = \varepsilon(e')$ implies $\phi(g,e) = \phi(g,e')$ for all g. Clearly, in this case both C_γ and C_ε are subsets of F.

All we have to prove is that Ω satisfies the conditions (2 a) and (2 b). For this purpose, let $x = \gamma(g)$, $y_1 = \varepsilon(e_1)$, $y_2 = \varepsilon(e_2)$ and $\Omega(x,y_1) = \Omega(x,y_2) \Rightarrow \phi(g,e_1) = \phi(g,e_2) \Rightarrow$ by (1 b), $\phi(g_0,e_1) = \phi(g_0,e_2) \Rightarrow \varepsilon(e_1) = \varepsilon(e_2) \Rightarrow y_1 = y_2$, which proves (2 a). The proof of (2 b) proceeds analogously.

Consequently, both formalizations of the concept are equivalent, and the above-derived $\Omega(\gamma,\varepsilon)$-representation of ϕ may be referred to as canonical.

Appendix B: Uniqueness of the representation of a separable trait

Let ϕ be separable and consider a particular $\Omega(\gamma,\varepsilon)$ representation of ϕ, i.e.

$$\phi(g,e) = \Omega(\gamma(g), \varepsilon(e)) .$$

As the first step, we will show that the genotypic (γ) and environmental (ε) contributions are in fact uniquely specified by the operator Ω and the trait function ϕ. For this purpose let $\Omega_x: C_\varepsilon \to F$ be defined by $\Omega_x(y) = \Omega(x,y)$ for a particular $x \in C_\gamma$ and arbitrary $y \in C_\varepsilon$. Recall that for each $x \in C_\gamma$, the function Ω_x is one-to-one, so that the inverse Ω_x^{-1} of Ω_x exists. $\Omega_y: C_\gamma \to F$ is defined analogously for each $y \in C_\varepsilon$.

Now, consider a particular genotype g_0 and a particular environmental situation e_0, and let $x = \gamma(g_0)$, $y = \varepsilon(e_0)$. Then it follows that for any $g \in G$ and $\varepsilon \in E$,

$$\gamma(g) = \Omega_y^{-1}(\phi(g, e_0)) \quad \text{and} \quad \varepsilon(e) = \Omega_x^{-1}(\phi(g_0, e)) .$$

Consequently, the contributions γ and ε are completely determined by the operation Ω and an arbitrary but fixed pair (g_0, e_0), and for this pair the trait functions $\phi(\cdot, e_0)$ and $\phi(g_0, \cdot)$ are to be taken into account. Moreover, this representation of γ and ε corresponds directly to the canonical representation. There, the two contributions were given by $\phi(\cdot, e_0)$ and $\phi(g_0, \cdot)$, so that the present γ and ε result from these by the one-to-one transformations Ω_y^{-1} and Ω_x^{-1}, respectively. However, g_0 and e_0 need not be the same in the canonical and in the $\Omega(\gamma, \varepsilon)$-representation in order to guarantee a one-to-one correspondence of genotypic and environmental contributions between these two representations. It is easy to show for separable ϕ that the range of $\phi(g, \cdot)$ has the same power for all g, and that the range of $\phi(\cdot, e)$ also has the same power for all e. Consequently, all admissible representations of genotypic and environmental contributions within the canonical representation result from each other by one-to-one transformations, i.e. $\phi(g_0, \cdot) = h_1(\phi(g_1, \cdot))$, $\phi(\cdot, e_0) = h_2(\phi(\cdot, e_1))$, where $h_1, h_2\colon F \rightarrow F$ are one-to-one mappings. According to the preceding finding, this property is carried over to all representations, including other operators, so that we can state:

All $\Omega(\gamma, \varepsilon)$-representations of a separable trait ϕ can be obtained as follows:

Let $F_{g_0} :=$ range of $\phi(g_0, \cdot)$, $F_{e_0} :=$ range of $\phi(\cdot, e_0)$ and consider any pair of one-to-one mappings $h_\gamma\colon F_{e_0} \rightarrow C_\gamma$, $h_\varepsilon\colon F_{g_0} \rightarrow C_\varepsilon$. Then for $\gamma(g) := h_\gamma(\phi(g, e_0))$ and $\varepsilon(e) := h_\varepsilon(\phi(g_0, e))$, the Ω-operator belonging to these contribution functions is given by $\Omega(\gamma(g), \varepsilon(e)) := \phi(g, e)$.

The last equality establishes the identity of operators via rescaling of the genotypic and environmental contribution functions.

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