parents that escaped those early freezes. Crossing the 4 parents found in both selections should produce seedlings that are taller, have increased resistance to damage from spring frosts, and average 2% less compatibility than families from crosses among the 10 most compatible parents.

A slightly different ranking of parents for compatibility occurred when the rankings were based on field-test results versus rankings based on estimated breeding values derived from BLP analysis. Parents 23, 242, and 16131 were ranked 11 and 3, 21 and 10, 7 and 16 based on field tests and breeding values, respectively. Parents 23 and 242 seemed to have lower average compatibility based upon field tests because they had been crossed accidentally with a greater proportion of less compatible parents than normal. The reverse situation occurred with parent 16131; it was crossed only with highly compatible parents. The estimated breeding values are likely more accurate because the BLP procedure adjusts for crossing imbalance.

Phenological ranking of female buds will assist breeders in determining which parents can be easily crossed. The average 10-day difference in opening of buds separating the earliest and latest parents necessitates planning when deciding which parents to isolate for female strobili and which to use as males. Pollen can be collected, applied the same year, or preserved in cold storage (Copes, 1987; Webber, 1987) and used in future years. Phenology information was available only for 19 of the 27 parents, but that included 12 of the 14 most compatible parents. Unfortunately, phenology and growth data were not recorded for parent 312, the most compatible parent in this study.

Computer sampling indicated that the compatibility of a parent could be estimated with reasonable or high accuracy if as few as 5 to 7 or ≥ 10 crosses, respectively, were field tested. These results were likely influenced by the truncated nature of the parent population. The initial screening of potential parents by graft-testing before breeding resulted in selection of parents that were more compatible than the native, unselected population (91% versus 65% compatibility, respectively) (Copes, 1982). The ability to determine the compatibility of putative parents without more extensive field-testing should significantly reduce costs associated with developing new rootstocks.

Use of highly compatible families as rootstocks in seed orchards has saved considerable cost and time in orchard establishment as less mortality occurs and less regrafting of incompatibility losses is required. The economic benefit of more complete stocking of healthy trees is obvious. The unseen benefit of obtaining seed with greater genetic gain or diversity due to increased panmixia during pollination exists, but is more difficult to determine.

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The Environmental Dichotomy of Adaptation and the Role of Genetic Diversity

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Abstract

Consideration of the characteristics of the adaptational system are explicitly based on the principle that all manifestations of life emerge through realization of genetic information under the stimulus of environmental conditions; thus genotype and environment determine biological response. Because adaptation is the process of adjusting responses to environmental demands, it involves the effects of two types of environmental conditions, (*i*) the *modifying conditions* affecting manifestations of life (response), and (*ii*) the *adaptive conditions* to which these manifestations have to be adjusted such that survival and reproduction are guaranteed. Adaptational systems can therefore be viewed to serve the purpose of coordinating the effects of these two types of environmental conditions so as to maintain all biological functions relevant to survival and reproduction. This view is substantiated with the help of examples, and mechanisms of the genetic system are suggested that may enable adaptation in this sense. Among the main results of the analysis are (1) that disturbances in the adaptive environment of sessile organisms are likely to challenge the adaptational mechanisms of the genetic system much more than disturbances in the modifying environment, (2) that adaptational differentiation with moderate gene flow among the differentiated demes is probably the most efficient way of maintaining genetic variation for adaptation, (3) that the evolution of motility in animals may have taken place at the cost of their capacity to adapt to global adaptive changes as compared to plants, and (4) that in forest tree breeding, programs securing evolutionary flexibility have primacy because of poor controllability of both modifying and adaptive environments in forest practice.

Key words: adaptational system, modifying and adaptive environments, plasticity, flexibility, genetic system.

Introduction

This paper presents an elementary analysis of a central feature of adaptational systems that has attracted little explicit interest in the past. The feature concerns the dichotomous function of an organism's environment for adaptation consisting in *modifying* the manifestations of life within its genetic constraints and in selecting those manifestations which are fit for survival or reproduction (GREGORIUS, 1994). Such selection is commonly referred to as *adaptive.* Some immediate consequences for the genetic basis of adaptation will be drawn that result from various degrees of association (correlation) between these two functions of the environment.

The environmental dichotomy of modification and selection is probably long recognized. Levins, for example, uses this fact in his 1968 book to introduce the chapter on strategies of adaptation, and states explicitly (bottom of p. 12) that "the environmental factor to which the response is an adaptation" need not also be "the signal that evokes the response". Influenced by the earlier work of BRADSHAW (1965), CAVALLI-SFORZA (1974) recurred to this topic in connection with his study of the role of plasticity in biological evolution. Referring to a single environmental variable, CAVALLI-SFORZA (1974, p. 46) states that "the value of x (the environmental variable) that determines the fitness of an individual is not necessarily the same as that which determines the phenotype", and he mentions as obvious evidence that "there always is a lag in any kind of physiological adaptation" so that there is a "difference of x values (of the environmental variable) between the points at which the phenotype and fitness are determined". The same clear distinction between the two functions of the environment is made by MORAN (1992), whose analysis concentrates on conditions under which phenotypic plasticity ("polyphenism" in the author's terminology) gains a selective advantage.

The topic is also implicit in the more recent work on norms of reaction which is concerned with the problem of the evolution of phenotypic plasticity (for a brief survey see STEARNS, 1992, for more recent treatments see e.g. SCHLICHTING and PIGLIUCCLI, 1995; SCHLICHTING and VAN TIENDEREN, 1995; or VIA, 1994). In all of these considerations plasticity refers to "phenotypic plasticity" and thus to the capacity to change phenotype in response to environmental changes. Adaptation or selection are not objects of plasticity in this definition. Unlike the work of MORAN (1992), the evolution of plasticity is treated without explicit reference to the association between the modifying and adaptive environmental conditions.

This purely phenotypic concept of plasticity contrasts with that common in ecology, where "tolerance" is one of the central characteristics of plasticity. In this context, trait states are classified with respect to the extent to which they enable their carriers to tolerate particular environmental conditions and thus to represent adaptations. The ecological concept guides, for example, studies of the evolution of adaptations in response to diverging selection regimes (ecotypes), as well as of the genetic differentiation between the populations affected by the adaptational differentiation (for a typical example from forestry see e.g. KLEINSCHMIT et al., 1995, who studied the problem of alleged oak species). While the adjectives "adaptive" or "adaptational" are frequently applied to "plasticity" in order to address forms of phenotypic changes conforming with adaptational demands, THODAY (1953) suggested usage of the term "flexibility" to emphasize that adaptational plasticity implies a flexible response to adaptational demands. This does not assume that adaptational plasticity (flexibility) can be achieved only with phenotypic plasticity.

In all of these considerations, it has to be taken into account that the environmental variables determining the manifestations of life and those determining survival and reproduction can in fact be of a completely different nature. This becomes obvious in situations where parasites play the role of a biotic adaptive environment for plants displaying the desired host characteristics. The manifestation of these host characteristics is usually largely determined by the abiotic environment as modifying environment of the host plant. Modifying and adaptive environment of the plant's trait (the host characteristics) thus differ fundamentally and can even show no associations. An example in which both environments are of abiotic nature is given by the strong dependence of leaf shedding on photoperiod as the modifying condition in many pioneer tree species. It is a frequent observation in woody plants that "progressive decrease in day length induces the conclusion of the growth period and the transition to the dormant state" (see e.g. LARCHER, 1980, p. 53ff). Thus, the occurrence of early frost, which may vary largely independently of photoperiod, could have considerable negative selective effects on individuals displaying low sensitivity to photoperiod.

The fact that modifying and adaptive conditions are often likely to diverge poses the question as to the evolutionary mechanisms securing adaptability. This question is tackled in the present paper by developing an explicit concept of the adaptational system, inferring basic conditions for evolutionary mechanisms that may aid the coordination of the environmental dichotomy so as to allow adaptation, and discussing some general implications of the results for forest tree breeding and management.

Conceptual Characteristics of the Adaptational System

Any attempt to elaborate general characteristics of the biological adaptational system must be built upon the principle that all manifestations of life emerge through realization of genetic information under the stimulus of environmental conditions; thus genotype and environment determine biological response. Because adaptation is the process of adjusting responses to environmental demands, it involves the effects of two types of environmental conditions, as pointed out above:

▷ the *modifying conditions* affecting manifestations of life (response), and

▷ the *adaptive conditions* to which these manifestations have to be adjusted such that survival and reproduction are guaranteed.

Adaptational systems can therefore be viewed to serve the purpose of coordinating the effects of these two types of environmental conditions so as to maintain all biological functions relevant to survival and reproduction. In the following, when applied to the two environmental conditions, the term *association* will refer to their quantitative and qualitative correspondence, and the term *coordination* will be used to indicate an individual's or population's struggle for adaptation in relation to the two conditions. It might be useful to realize that, on the population level, adaptation usually requires selection, while, however, selection may take place without necessarily implying adaptational progress.

While the examples of distinct modifying and adaptive conditions given in the Introduction are more or less obvious, one of the probably most important phenomena of adaptational relevance, stress, might be less clearly classifiable with respect to the environmental dichotomy. Accepting stress as a state of metabolic and energetic imbalance, stress symptoms are phenotypic indications of this state, which itself is caused by environmental conditions referred to as stressors. Hence, stress symptoms are responses to stressors as modifying environmental conditions. Yet, at the same time, these responses signal the demand for adaptation to the stressing conditions. This demand is satisfied, and physiological adaptation to the stressor is said to have taken place, if under persisting stressing conditions the initial stress symptoms fade away. Consequently, the stressing conditions act as both modifying conditions for the stress response and adaptive conditions to which adjustment is required. The effects of the adaptational mechanism, in turn, result in a change in stress response signalling adaptedness to the stressor. Apparently, the latter must have implied a change in physiological state that, under the action of the same stressing conditions, yields a modified response.

This typical example of physiological adaptation demonstrates the major components involved in an adaptational process. These components provide the basis for a generalized system theoretical characterization of an *adaptational system.* In fact, there are three subsystems involved (see *Figure 1*). One produces a response to an environmental stimulus (the modifying environment) acting upon a specific state of the system. Depending on the level considered, this state may be the physiological state of an individual (as level) as in the above stress model. On other levels such as populations, states are characterized by a number of components comprising aspects of demographic or genetic structure, for example. This subsystem will be referred to as the *modifying system.*

In a second subsystem termed *comparator system,* the response of the first acts as system state, the comparison of which with another environmental stimulus (the adaptive environment) produces an output that serves as a corrective (action) referring to the adaptational demand. The degree of adaptedness of the response in relation to the adaptive environment is measured in terms of some valuation function. The criterion for valuation may vary with the definition of the system's integrity. Recall that modifying and adaptive environments may or may not be identical. While in the stress model of physiological adaptation the demand is specified by metabolic or energy gradients, for example, regimes of phenotypic selection could appropriately specify the corrective reflecting adaptational demand on the population level. Here, the application of phenotypic selection requires phenotypic structures as response of the modifying system.

The function of the third subsystem is to organize the regulation of the state of the modifying system according to the corrective provided by the comparator system. Therefore, the state of this *regulation system* is specified by the corrective which has to be applied to a state of the modifying system as input in order to yield the altered state as output. On the population level, the regulation system for the genetic structure as state component includes, for example, modes of inheritance and mating systems.

In summary, this introduces adaptational processes as *feedback systems* in which three subsystems – the modifying, com-

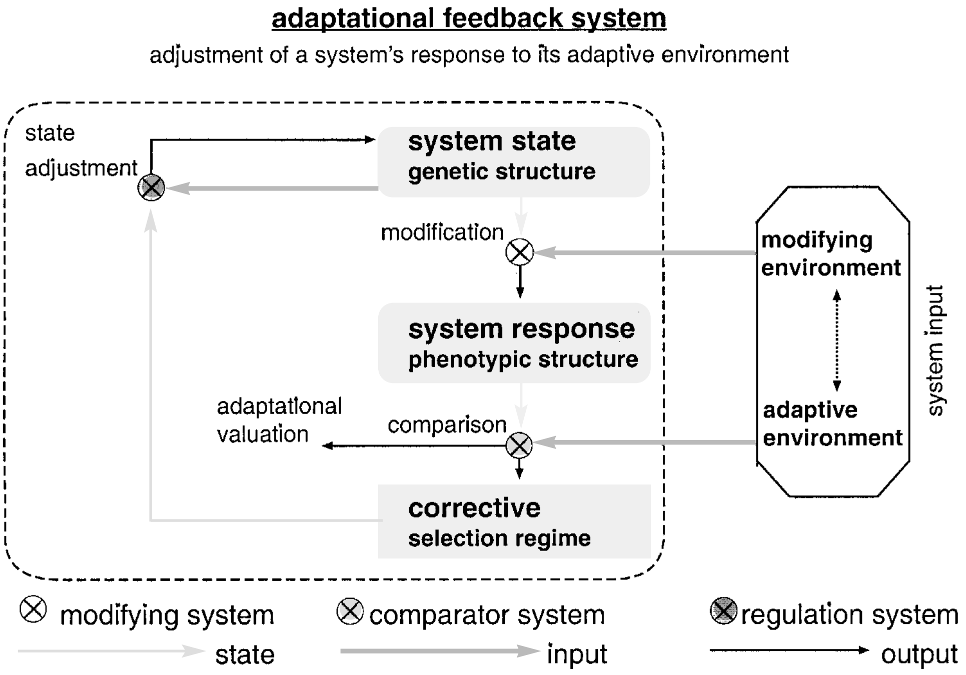

Figure 1. – The adaptational feedback system with its three constituent subsystems: modifying, comparator, and regulation system. Small script in boxes refers to populations as example of an adaptational system. The outcome of the adaptational valuation need not directly affect state regulation.

parator, and regulation system – are sequentially coupled such that the output of the preceding subsystem specifies the state of the succeeding subsystem. In the following chapter, this concept will be applied to the population level to address some basic problems of evolutionary adaptation associated with the environmental dichotomy. Particular attention will be paid to the role of genetic diversity in a population's capacities to coordinate its modifying and adaptive environmental conditions. As has become clear now from the definition of the adaptational system, coordination of the two conditions can be realized only through adjustment of the system responses (phenotypes or phenotypic structures) to the adaptational demands of the adaptive environment. This can be achieved only by changes in the state of the modifying system.

Adaptive Evolution and the Environmental Dichotomy

There are two basic relations among modifying and adaptive environments (see *Figure 2*): (*i*) the same environment acts as modifying and as adapting agent on a trait, (*ii*) modifying and adapting effects on a trait are realized through separate environments. A third relation, which will be shown later to be of elementary significance, is characterized by situations where (*iii*) the adaptive environment in relation (*ii*) also functions as modifying environment for a second trait. The above consideration of stress constitutes an example of relation (*i*). Examples of relation (*ii*) have also been given earlier in the Introduction. The central question to be addressed here concerns the basic evolutionary mechanisms that allow for adaptation under the constraints of these relations.

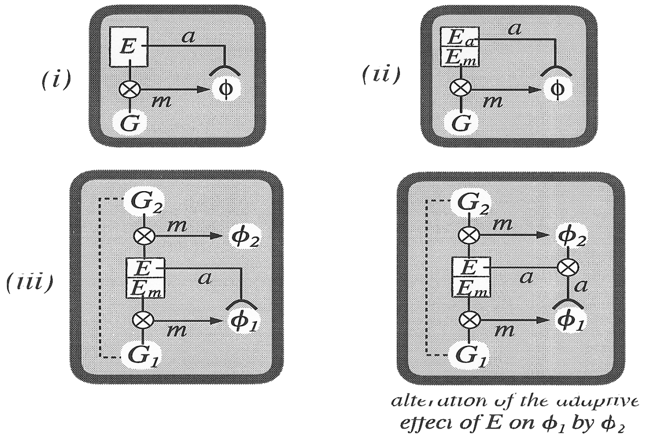

Figure 2. – Three elementary ways in which modifying and adaptive environments may interact in adaptation. E = environment, G = genotype, Φ = trait, m = modifying, a = adaptive. *(i)* the same environments acts as modifying and adaptive agent on the trait Φ; *(ii)* modifying and adaptive components of the environment act separately; *(iii)* the adaptive environment in *(ii)* also acts as modifying environment for a second trait Φ_2.

In order to simplify the presentations of the respective results, it is useful to agree upon the terminology of adaptational (selectional) and modifying phenomena at the three levels of the individual, the genotype, and the population as specified in *table 1.* At the outset, modificatory variability will be referred to as *plasticity,* as is common usage in connection with phenotypic plasticity, while *flexibility* will be reserved for adaptational versatility, following THODAY (1953).

Table 1. – Terminology.

Levels of plasticity and flexibility:

Physiological plasticity – phenotypic variability of an *individual* in response to temporally varying environmental conditions.
Phenogenetic plasticity – phenotypic variability of the carriers of a *genotype* in response to different environmental conditions. This includes temporally and spatially variable conditions.
Phenotypic plasticity – refers to physiological as well as to phenogenetic plasticity.
Physiological flexibility – adaptability of an *individual* to temporally varying (heterogeneous) environmental conditions.
Phenogenetic flexibility – adaptability of the carriers of a *genotype* to a wide range of environmental conditions. This includes temporally and spatially variable conditions.
Evolutionary flexibility – adaptability of a *population* to a wide range of environmental conditions.

The distinction between physiological and phenogenetic flexibility emphasizes the difference between environmental variability as experienced by an individual of given genotype and between individuals of that genotype. Even for a motile organism experiencing environmental variation through confrontation with variable localities, it is the temporal sequence of the environmental conditions that defines its individual environment. An implication of this distinction is that high physiological flexibility need not imply high phenogenetic flexibility. For example, a genotype the carriers of which have high adaptational valuation under temporally heterogeneous conditions may have low valuation in temporally homogeneous conditions.

Implicit in this example is a basic difference between the genotypic and the other two levels of flexibility. While individuals and populations are subject to adaptational processes following the above characterization of an adaptational system, a genotype is intrinsically incapable of undergoing adaptation. A genotype may or may not contain the information that enables its individual carrier to adjust to certain adaptive environmental conditions and thus specifies its carrier's adaptedness to this possibly temporally variable condition. The pertaining processes involve changes in physiological state. Yet, by definition, a genotype is not allowed to undergo state changes to reach adaptedness. Hence, although the genotype itself cannot adapt, it codes for the capacity of its carriers to adapt and tirus codes for the individual adaptational system.

Returning to the relations (*i*) and (*ii*) among modifying (E_m) and adaptive (E_a) environments, some elementary evolutionary consequences of these result from the fact that to each state of the trait considered there corresponds a pattern of correctives solely determined by E_a, while each genotype is characterized by its reaction norm for that trait in response to E_m. Trait states and genotypes constitute system states in two separate subsystems, the comparator and the modifying system, with input variables E_a and E_m and output variables given by the correctives and trait modifications, respectively. In the overall adaptational system, the two environmental classes E_m and E_a may be associated to various degrees. The demands on the adaptational system resulting from these associations will now be analyzed for the extreme cases of identity and independence between the two environments.

Identity of modifying and adaptive environment

For relation (*i*) with $E_m = E_a = E$ (see *Figure 2*) and thus complete association between the two environmental classes, it is possible that for each genotype there exists an environmental condition in which its trait modification has highest adaptational valuation. In terms of the adaptational system, this is a consequence of the complete coupling between the modifying and comparator system via identity of the two environments (consult *Figure 1*). Hence, an increase in the adaptational valuation at the population level (average fitness, for example) can be achieved, if the population's regulation system is directed towards concentrating within each environmental condition those genotypes which there produce phenotypes with high adaptational valuation (consult *Figure 1*). This leads to genetic differentiation between the environmental conditions. In combination with moderate amounts of gene flow among them (as part of the regulation system), this constitutes one of the most frequently cited mechanisms for the maintenance of genetic diversity and evolutionary flexibility.

Another possibility could consist in the existence of a genotype such that in each environmental condition its response receives highest adaptational valuation among the responses of all genotypes. In most population regulation systems (mating systems and modes of inheritance), such a genotype would replace the others and would by this increase the adaptational valuation. The genotype would also establish high flexibility in the sense that all carriers of the genotype have the capacity to respond to each adaptational demand by expressing an adapted phenotype.

According to the terminology in *table 1,* the latter case represents a situation of phenogenetic flexibility, irrespective of the degrees of physiological flexibility involved. Since high phenogenetic plasticity is required here to achieve high flexibility for variable adaptive effects of *E,* phenogenetic plasticity can be said to have evolved (selective advantage of polyphenism, see MORAN, 1992). However, since high phenogenetic plasticity is likely to be maintained only at considerable metabolic and energy costs, the situation of global adaptational superiority of a single genotype may be of limited biological significance. Both evolutionary consequences are extendable in weaker form to the case of strong association between E_m and E_a.

Modifing environment different from adaptive environment

In relation (*ii*), where E_m and E_a differ and show little or no association (see *Figure 2*), two extreme cases can be distinguished, one in which E_a is largely invariant and E_m is variable, and the other in which the role of the two environmental classes is reversed. The case of invariant E_a can actually be considered as a special case of relation (*i*) if the adaptive effect of the environment is there considered to remain the same over the possibly variable modifying effects of this environment. Adaptational valuation is then solely determined by phenotype, so that one or more phenotypes with consistently highest adaptational valuation exist. The situation of the evolution of phenogenetic flexibility considered above for relation (*i*) now requires low sensitivity of the genotype to the effects of E_m at a high level of adaptedness. Adaptive evolution may therefore favour low phenogenetic plasticity in this situation. Again genetic differentiation among the modifying environmental conditions could be another opportunity, since different genotypes may express the same phenotype (with constant adaptational valuation) under different modifying environmental conditions.

At the other extreme with largely invariant E_m, the trait shows no modification and can thus be considered as a "genetic trait" under environmentally heterogeneous selection. Hence, sufficient levels of adaptedness (adaptational valuation) in a population cannot be maintained by only one or a few genotypes, since different adaptive conditions may require different genotypes for generating adapted phenotypes. Consequently, to persist in this situation, a population must be able to maintain large amounts of genetic diversity in such a way that it can recruit and multiply the genotypes required for varying adaptational demands in sufficient number at sufficient speed. Regulation systems supporting genetic differentiation among the adaptive environmental conditions may again provide the most cost effective and stable solution.

As the variability of both modifying and adaptive conditions increases in an uncorrelated manner, it becomes increasingly difficult for a population to evolve adapted genetic structures. This can be taken directly from the representation of the adaptational system in *figure 1* by considering the fact that the regulation system cannot explicitly react to modifying and adaptive conditions. This problem could be avoided by developing mechanisms that allow a population to reinforce relation (*i*) or one of the above-mentioned extremes of relation (*ii*) for the trait under consideration. Such mechanisms could either act through alteration of the adaptive environment or through alteration of the current trait modifications. Both cases require the emergence of new genetic information which replaces extant genetic information in an evolutionary process.

Reinforcement of the extreme case of relation (*ii*) with invariant E_m can be achieved through the emergence of mutants which code for low phenogenetic plasticity (low sensitivity to, low penetrance of the variation in the modifying environment). This could be realized by homologous mutation (at the loci involved in the control of the trait variation) or by non-homologous mutation. In the case of homologous mutation, the resulting genotype would show little or no phenogenetic plasticity, but the pertinent trait state may receive different adaptational valuation in the different adaptive environments. The mutant could thus replace the extant genetic variants at least in those adaptive environments where it has (consistently) higher adaptational valuation. For a non-homologous mutant it is furthermore conceivable that, by realizing all associations through recombination, it could lower the phenogenetic plasticity of all of the extant genetic variants. Such a mutant could be evolutionarily successful by providing for each adaptive environmental condition a genotype with consistently highest adaptational valuation. Genetic differentiation among adaptive environmental conditions would be a consequence of this mode of gene action, and this would again be in support of the above-mentioned mechanisms for the maintenance of genetic diversity and evolutionary flexibility.

The reverse case, where the variability of the effects of the adaptive environment on the reference trait is to be reduced, is more involved. In effect, some new genetic information would be required such that each modification that it affects would receive largely the same adaptational valuation across all of E_a. However, this contradicts the understanding that E_a determines the corrective and adaptational valuation of each trait modification irrespective of the genotypes and environments that bring about this modification. Hence, as a rule, identical adaptational valuation is associated with identical trait state, and, to realize this situation, a genotype must accomplish low degrees of phenogenetic plasticity. This, in turn, guides us back to the previous case. It thus appears that a reduction in variability of the effects of the adaptive environment on a given trait is probably impossible to achieve by evolutionary changes at this trait.

Evolutionary alteration of adaptive environments

As indicated above, changing the adaptive effects of environmental conditions on a reference trait requires a process in which new traits evolve in response to these conditions. Consequently, the considered environmental conditions act in two ways: adaptive on the reference trait and modifying on a new trait. The states of the new trait are then considered to alter the adaptive effects on the reference trait (particularly by reducing their variation), by this means coordinating adaptive and modifying conditions for the reference trait. The above relation (*iii*) covers this case (also see *Figure 2*).

In essence, alteration of the adaptive effects amounts to a situation, in which the states of the new trait at least partially adopt the role of the adaptive environment for the reference trait. It may not cause a problem to specify genetic mechanisms that could realize such a trait. For example, if the adaptive environment is of a biotic nature and acts through differential parasitising of certain phenotypes, any mutant coding for defence or resistance mechanisms would alter the effect of this environment. In order to make this alteration an adaptive environment for the reference trait, the defence mechanism ought to act independently of the state of the reference trait. This can be achieved by letting the mutant go to fixation. Furthermore, the defence mechanism can be assumed to act such that its response to the parasite attack compensates the attacks on a constant level. This reinforces relation (*ii*) with constant effect of the adaptive environment.

It may, however, be a more challenging task to design biologically relevant mechanisms that evolve by drawing a selective advantage from altering the adaptive effects on the reference trait. As the above example demonstrated, such mechanisms would be required for the evolution of altered adaptive effects of environmental conditions. This topic will, however, not be expanded on in the present paper.

Discussion

In the above analysis, physiological flexibility played no particular role. The reason for this is that the differences between environmental conditions were not further classified. Basically, environmental conditions are classified with respect to their degrees of temporal and spatial heterogeneity. Temporal heterogeneity, in turn, can be divided into a component affecting individuals within a single generation and a larger scale component becoming effective between generations. It is the within-generation component of temporal environmental heterogeneity that relates to physiological flexibility. According to one of the most frequently defended theories, large temporal heterogeneity in an individual's adaptive environment requires large genetic diversity within the individual (large degrees of heterozygosity) in order to produce the adapted responses. Obviously, this theory assumes that a strong coordination between modifying and adaptive environmental conditions has been established in the evolutionary past.

Between-generation scales of temporal environmental heterogeneity may make adaptational demands that are, in some sense, similar in effect to those of spatial environmental heterogeneity. The similarity lies in the fact that in both cases the environmental heterogeneity can be experienced only by *different* individuals rather than by the same individual as in the situation of physiological flexibility. Hence, with respect to the adaptational systems of individuals, a difference in environment has the same effect irrespective of the time or location at which it occurs. Adaptation to this type of environmental heterogeneity takes place at the population level and follows the principles discussed above for the different relations between modifying and adaptive environments. This discussion implies that evolutionary flexibility can be realized either with a small number of genotypes, each with high phenogenetic flexibility, or with a large number of genotypes, each with low phenogenetic flexibility. The latter requires adaptational differentiation among environmental conditions and moderate degrees of gene flow among them.

For reasons of metabolic and energy balances, the above considerations also suggest that evolutionary flexibility can be maintained more effectively and stably through sufficient genetic diversity in combination with adaptational differentiation. This should not be misinterpreted as an argument against heterozygosity, since heterozygosity may be required for physiological adaptation of an individual to temporally heterogeneous environments, which may be characteristic of some but not of other locations in a population's habitat. In such a situation the adaptational differentiation would be expected to be mirrored by a genetic differentiation for the degree of heterozygosity.

Another important implication of the present approach to adaptational systems concerns the understanding of human impacts on ecosystems. Detrimental effects of human activities on the stability of forest ecosystems could be due to the disruption of existing coordinations of modifying and adaptive environmental conditions. As an example consider the transfer of northern provenances of birch from Finland and Sweden to 5 southern locations in Lower Saxony, Germany, reported by KLEINSCHMIT and OTTO (1980) and KLEINSCHMIT and SVOLBA (1982). The traits which have been studied are phenology and height growth. The Finnish provenances exhibited the earliest conclusion of growth period (CGP in the following) and reached only 65% to 82% of the height growth compared with the mean height at the experimental site. In order to demonstrate the relations to our present approach, we concentrate on CGP as modified trait. Since photoperiod is likely to have a major effect on the CGP (see LARCHER, 1980, p. 53ff), it is considered as a modifying environmental factor of this trait. When the selective effects of early frost are taken into account, the earlier leaf shedding of northern as compared to southern provenances after the transfer could *per se* be considered as an adaptive advantage, since this would reduce the danger of damage by early frost as adaptive environmental factor.

Yet, the disruption of coordination between modifying and adaptive environmental conditions is evident from the considerable reduction of height growth signaling reduced physiological efficiency and thus lowered adaptational value. This could be explained by the earlier CGP of the northern provenances, which prevents them from utilizing the increased energy supply provided by the delayed timing of first frost in the southern latitudes. Hence, timing of first frost turns out to be an adaptive environmental factor that assigns higher adaptational value to later CGP. It then becomes apparent that the transfer of northern provenances to the south resulted in a change in both modifying (photoperiod) and adaptive conditions for the trait CGP of these provenances. Hence, the required new process of coordination involves optimizing the utilization of photoperiod and timing of first frost. If the association between modifying and adaptive conditions should be low, the adaptational demand showing up in the reduced height growth might be difficult to adjust for.

In breeding programs, the adaptive environment is invariant in that the breeder invariably gives highest adaptational value to the same trait state. In some programs the modifying environment is also controlled and thus largely invariant. The state regulation system is controlled by artificial selection (access to reproduction) and mating design. The degree of control of the adaptational system decreases in most breeding programs from the comparator to the regulation and to the modification system. Contrasting with most of the breeding products in agriculture, the utilization of breeding products in forestry implies more or less complete abandonment of control over all of the three subsystems of the adaptational system in the production populations. Consequently, forest tree breeding programs are forced to establish states in each of the three adaptational subsystems, which still may develop evolutionary flexibility when control ceases; genetic diversity and its maintenance or conservation is an indispensable prerequisite to this.

To conclude this paper, a more general adaptational characteristic of plants shall be addressed that refers to low associations among variable modifying and adaptive conditions. This characteristic concerns the individual sessility of plants as opposed to the individual motility of most animals. Motility can be considered to have evolved as a capacity to respond to unfavourable conditions by evasion. In essence, this ability puts animals into the position to reduce both the temporal and spatial variability of their adaptive environments and thus to generally avoid the implied considerable adaptational challenges. In contrast, the sessility of plants forces them to face these challenges by repeatedly evolving mechanisms of altering the effects of their adaptive environments in ways such as demonstrated in the above relation (*iii*). This requires maintenance of genetic diversity that is not needed in animals. As a consequence of this situation, it is conceivable that environmental changes that are global in the sense that they cannot be escaped may create adaptational problems solvable by plants but not by animals.

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Isozyme Variation of Natural Populations of Sal *(Shorea robusta)* in the Terai Region, Nepal

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Abstract

Genetic variation of sal *(Shorea robusta)* was investigated in three natural populations in the Terai region, Nepal, using 12 loci from 8 isozyme systems. The mean number of alleles per locus was 2.16 and 58.3% of loci were polymorphic (95% criterion for polymorphism). The mean observed and expected heterozygosities ranged from 0.105 to 0.129 with an average of 0.117, and from 0.130 to 0.158 with an average of 0.143, respectively. Only 4.7% of the total genetic diversity was due to differentiation among the populations and the mean value of genetic distance was 0.018. The results indicated that the majority of species' genetic variation was found within the studied populations and there was high genetic similarity among three natural populations of *S. robusta.* The sharing of one gene pool among the studied populations suggests a lack of barriers to gene flow.

Key words: gene flow, genetic differentiation, isozymes, populations, *Shorea robusta.*

Introduction

Knowledge of the distribution of genetic variation within and between the populations is of substantial benefit in the conservation of plant genetic resources (HEDRICK, 1985; BROWN et al., 1990; ADAMS et al., 1992). Isozyme variation in species, and within and among the populations has been extensively studied in many woody plants (HAMRICK and GODT, 1990; HAMRICK et al., 1992; MUONA, 1990; YANG et al., 1997). There are different conclusive evidences which show significant or no correlations between isozyme variation distribution and quantitative traits (KNOWLES and MITTON, 1980; KNOWLES and

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