

Effectivity of genetic regulation in buffering environmental changes with special reference to forest trees

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Changing environment and the resilience of living systems

All individuals and populations of living organisms are affected by inhomogeneity of the environmental conditions causing phenotypical change and eventual mortality. It is generally accepted that both plant and animal species are adapted to their environment but there is no general agreement on the closeness of the relation between the environment and the structure of populations and communities. Similarly, it is often overlooked in ecological studies that individuals of the species do not respond uniformly, as depending on their inherited traits substantially different responses may be observed.

In contrast to closed systems of classical physics, living systems (ecosystems) are open, dynamically reacting systems of co-existing populations. The openness is determined by the constant energy and matter flux through the system such as solar light/heat, water, nutrients - commonly referred as *environmental factors*. On the various timescales (daily, annual, secular, geological) this energy flux exhibits considerable fluctuation and irregularity, yet ecosystems show a remarkable resilience to changes and maintain compositional, structural and functional characteristics within a broad spectrum of conditions. This resilience (and especially its limits) gains special importance in view of growing environmental loads and expected climate instability.

The resilience and stability of ecosystems has its ecological explanation in the tolerance of organisms and in the complexity of trophic relations of living systems, expressed in various dimensions of *biodiversity*. Specific importance is attributed in this respect to diversity on the species level, while the genetic dimension is often not appreciated according to its real weight in regulating system processes.

Regulation of adaptation

The maintenance of the structure and function of the living system requires a *constantly adjusted ability to convert available matter and energy into its own living matter*; which is maintained by the process of physiologic and genetic adaptation. On the ecosystem level species composition of the community (biocoenosis) is a visible indication of the adjustment to the external conditions. The "fine-tuning" of the adjustment is provided on the infraspecific level through genetic processes. To keep the identity of the system, a stable information background is required which remains relatively unchanged across generations and in changing environmental situations. It is apparently the hereditary matter in the living cells providing for the necessary continuity of identity (Gregorius 1997).

Physiologic or regulatory adaptation on the individual level is apparently determined by hereditary factors but does not involve genetic changes. The ability of the organism to maintain its functions within a given spectrum of environmental conditions is described by the term *physiological homeostasis*. The width of the spectrum is determined primarily by physiologic and ontogenetic constraints.

The regulation of the expression of genetic information stored in the DNA in the cell nucleus allows for a certain flexibility in the manifestation of traits. *Phenotypic plasticity* describes the change of expressed phenotype across environments. It is known for instance, that certain *Ranunculus* species may change their leaf form according to changing annual weather conditions so significantly that they may be mistaken for a different species. *Drosophila* flies may change their body coloration and organ sizes (wing size) according to temperature conditions they were raised in etc.

Through the testing of the response of organisms against environmental variables, *reaction norms* may be calculated. Reaction norms of growth response have special importance in forestry as they determine the site spectrum where a population (or clone) may be cultivated with best results. Contrary to the bell-shaped curves shown in textbooks, reaction norms for tree growth are usually fairly linear across tested environments.

Some investigations demonstrate that the change in *allocation ratio* between plant parts also contribute to the adaptive potential. E.g. it could be shown with Scots pine, that the increase of spacing from closed stand to solitary tree status changed profoundly organic matter allocation streams. The ratio of annual stem increment and cone crop (both calculated in dry matter weight) has switched from 95 : 5 to approximately 25 : 75 in genetically identical trees (Mátyás 1991).

Phenotypic changes caused by environmental factors are not thought to have hereditary consequences. Temperature as well as nutrient status conditions were found however to cause inherited changes in flax and tomato plants. In tomato, e.g. crossing at lower temperature resulted in faster root growth of the progeny. In forest trees such observations are very recent. Investigations on Norway spruce (Johnsen, Skroppa 1992) have shown for example that temperature conditions during the fertilization stage may determine the future phenologic behaviour of the plant (heat sum needed for flushing, length of vegetation cycle). The effects last for at least two decades (age of oldest experiments of this kind). Observations of similar character have been made on Scots pine (Beuker 1996).

Genetic adaptation is understood as a change in gene frequency, directed toward a theoretical optimum in a given ecological situation. It acts on the level of populations. The genetic transformation is expected to increase the average fitness of the population through the elimination of less fit individuals. Genetic adaptation should be understood not only as an adjustment to the current conditions, it also includes the ability to adapt to future (unspecified) changes. Covering relatively short periods in time, adaptational changes in the population may be regarded as reversible. This is the tool of natural selection, leading to evolutionary changes on the long run.

Adaptedness of the individuals is not necessarily equivalent to adaptedness on the population level. While the status of individual adaptation is set by the actual environmental conditions, the long-term survival of populations depend on the ability to cope with fluctuating, often dramatically changing conditions and a wide range of potential environments. E.g. late flushing (i.e. a high heat sum demand for budbreak) is of high advantage in a frost pocket but a competitive drawback on other sites. On a site of low competition pressure, e.g. in the initial stage of colonization, a higher allocation rate to reproductive organs will provide better fitness for the individual; while if competition is high, such as in a densely closed forest stand, a higher allocation to growth will determine survival. Accordingly, there is always a certain antagonism in adaptational demands which will cause constraints on the precision of adjustment.

Forest trees as objects of study

Most species are ephemeral features of the Earth system - an average species exists for about 10 million years. Forest trees, especially evolutionarily ancient conifers certainly belong to the more persisting class of species. Trees have not only successfully survived changing geological periods as species, but also endure during an individual's lifetime considerable fluctuations of environment without the chance of migration or short-term genetic adaptation on the population level as in case of annual plants and many animals.

The present interglacial period, the Holocene, has lasted for approximately 10,000 years; radiocarbon dating confirmed a relatively recent migrational past of forest trees in the temperate-boreal forest zone of a few thousand years only (Davis 1980). This timespan is very short with regard to possibilities of close adaptation when compared to the lifespan of trees. In extreme, for the oldest bristlecone pines (*Pinus aristata*) of the Californian White Mts., reaching ages over four thousand years, the whole Holocene might appear as a period of only three generations.

On the timescale of the generation cycle of trees, long-term climate changes appear much faster as for shorter-lived organisms. The adaptive strategy of trees is therefore an interesting subject to study, especially in the perspective of the expected uncertainty of future climate conditions. Another reason to give trees special consideration is that trees are keystone species in every ecosystem where present; their stability and vitality determines the presence and vitality of the majority of other species at all trophic levels of the ecosystem. Finally, although human interference in their genetic constitution cannot be neglected any more, forest trees may still be regarded as being closer to the wild state compared to any agricultural crop plant.

It is obvious that the key element in maintaining adaptability of populations to environmental changes is the genetic diversity both on genic and individual level. This is determined by the evolutionary past and the genetic system of the species (e.g. way of gene exchange between individuals and populations; see Hamrick and Godt 1990). The recent years have yielded an increasing wealth of information on the genetic diversity of forest trees; the majority of these studies, however, deal with diversity on the molecular level. Although molecular polymorphism may be a conditionally useful marker for loci of adaptive significance (Ledig *et al.* 1983, Devey *et al.* 1995), the importance of quantitative (growth) traits as measured in long-term field tests cannot be stressed enough as these traits are the most reliable, quantitative expressions of long-term plant-environment interactions.,

Common garden testing of populations of different origin started with forest trees more than two hundred years ago (Langlet 1971). Since then, so-called provenance tests have been established with most commercially important species. Beyond the strictly silvicultural goals, the tests offer excellent opportunities to study intraspecific genetic variation patterns and represent probably the most powerful available tool for testing hypotheses of climatic adaptation in trees. (Mátyás 1996,1997).

Constraints on adaptation

Analysis of adaptive traits (mostly juvenile height growth) in provenance experiments indicate the existence of very effective constraints on adaptedness. The population average of a fitness-related trait for a locally adapted population is often lower than the average of other populations introduced from other environments; a phenomenon termed as *adaptation lag* (Mátyás 1991). Suboptimal adaptation has to be compensated for by a sufficiently high level of individual homeostasis. In case of weakly expressed, constrained adaptation to the environment,

a high level of diversity has to be expected in trees both on individual and population level.

In fact, *genic diversity* of trees seems to be relatively high compared to other organisms, this is supported by biochemical marker studies (Hamrick and Godt 1990). Highest level of allozymic variation is observed in widely distributed, strictly outbreeding, wind-pollinated and wind-dispersed species, such as most conifers and many of the broadleaved tree species. Even though there are observations which support certain correlations between climate factors and frequency patterns of molecular markers (Bergmann and Gregorius 1993), adaptation seems to have rather limited effect on the genic diversity indicated by isozymes (Prus-Glowacki 1991, Savolainen 1994), resulting in low inter- and high intrapopulation variation. A similar variation pattern is exhibited by several other traits of less adaptive significance, such as certain morphological traits and wood characteristics (fibre length and other anatomic traits, chemical composition etc.).

In case of highly adaptive traits, displaying a clear climate-related variation on the between-population (provenance) level, diversity can be still substantial among individuals. A conspicuous manifestation is the diversity in the length of the growing season; phenophases within one population may differ considerably and may appear in form of polymorphisms (late- and early flushing types). In a Scots pine test, the variation range in termination of growth in autumn was more than 70 days within one population; this is considerably larger than the difference between the averages of extreme northern and extreme southern populations (Mátyás 1987).

The importance of genic diversity itself for the survival and reproductive success of a species or population, although generally recognized, should not be overestimated (Ledig 1986). Many studies propose a link between protein heterozygosity and consistency of performance (Mitton and Grant 1984). Considering the limited predictive value of enzymatic diversity on heterozygosity of loci determining adaptive traits, these results cannot be generalized. Homeostasis is not a function of average observed heterozygosity, it is likely regulated both through changing allelic expression and changing interactions among loci in relation with environmental conditions (Scheiner 1993), which means that it is the genic diversity of certain loci only, which matters - and those may not be evaluated by molecular analytic methods.

The role of the environment in adaptation is generally understood in two ways: first, by setting the fitness function and selecting the fittest individuals, and second, affecting the developmental process of the individual by determining the phenotype. In maintaining the adaptation lag, both the genetic system of the species and random effects play a role, which is seldom recognized. The *genetic system* of many commercially important temperate-boreal tree species is characterized by very effective gene flow through wind-pollination, an outbreeding mating system with strong mechanisms to prevent inbreeding and a high genetic load (Ledig 1986, Koski 1991). These genetic factors act against genetically related neighborhoods and local adaptation. Peculiarities of reproductive ecology (e.g. differential fertility, polyembryony, non-random mating; see Müller-Starck 1991) prevent further a straightforward action of abiotic selective forces.

Randomness, the occurrence of stochastic events may have a very important role in shaping diversity. Rare and irregularly occurring circumstances are usually disturbances contributing to a high level of temporal heterogeneity on time scales which are difficult to follow. On an evolutionary scale, the random effect of migration, fragmentation, isolation and can be demonstrated on the genetic structure of populations and species, which contributes to the presently observed patterns of diversity (Hamrick and Godt 1990, Ledig 1986). On the scale of the lifespan of trees, regeneration success and biotic interactions have strongly random components. The possibility for regeneration through appearance of suitable niches is unpredictable, depending on some catastrophic event or mortality of neighbors. *Biotic*

interactions include long-lasting competition with the same and other species, and incidental interactions with consumers, parasites, pathogens etc. In the entirety of ecosystems, it seems that evolution promotes rather the complexity of biotic interactions at the expense of the proper fitting of the organism-environment relation. The effectiveness of natural selection is further impaired by the random character of accessibility to abiotic limiting factors. It is interesting that heat, the main factor clearly distinguished for shaping climatic adaptation, is the only abiotic factor beside the atmosphere, which can be regarded as conditional, i.e. less affected by competition and other biotic interactions in the ecosystem (on the other hand moisture and light conditions are strongly determined by canopy dynamics).

In summary, it may be stated that the functioning of ecosystems and their successful adjustment to changing environmental conditions require the regulatory effect of genetics. However, due to permanent environmental instability and both phylo- and ontogenetic constraints on adjustment, populations cannot be regarded to ever reach an ideal or optimum state; this can neither be expected therefore for the whole living system. This lends the ecosystem a certain robustness in response to unexpected and strong changes. It has to be remembered however, that adjustment and adaptation follows presumably the "Red Queen" principle, which means that directed changes happen only to the minimum necessary extent. The corollary is that the buffering is far more effective in the direction of the optimum than towards the existential minimum requirements. This may be proven easily from modelling response data to environmental change (Mátyás 1997). It is therefore not unexpected that in spite of well developed homeostasis and genetic buffering, environmental deterioration is instantly signaled by declining biomass production and eventual mortality.

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