Use of long-term field trial datasets in forestry to model ecosystem responses to environmental change

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Summary

Common garden testing of populations of different origin started with forest trees more than two hundred years ago. Since then, so-called provenance tests have been established with most commercially important species. Beyond the strict silvicultural goals, the tests offer excellent opportunities to study genetic variation patterns and represent probably the most powerful available tool for testing hypotheses of responses to climatic change in wild plants. The use of existing provenance tests to predict such effects is based upon the concept that observed spatial (geographic) variation patterns are responses to transfer into new environments, and may be interpreted as a simulation of responses to environmental change over time. The performance of populations plotted against an ecological-climatic factor exhibits a characteristic pattern and can be described by response functions. Accordingly, calculated response regression of growth of transferred populations on thermal parameters may be interpreted as a model of response to temperature change scenarios.

In view of expected climate instability, genetic adaptability of forest trees causes serious concern due to their long lifespan, compared to the rapidity of expected changes in environmental conditions. The potential of provenance tests to interpret long-term adaptational processes should be utilized to analyze, model and predict response of trees to climate change. In this respect, provenance research, although seldom appreciated, might be among the most important contributions of forestry to biological sciences.

Keywords: climate change, adaptation, provenance research, natural selection, diversity

Introduction: response levels of forest ecosystems to environmental change

Domestication of forest trees is still in its beginnings. In the majority of cases forest tree populations still maintain their unimproved, "wild" condition; this provides a comparatively wide adaptability to the diverse site conditions encountered in forestry. With the widespread use of commercial tree species outside their natural range, however, forest stands became more susceptible to environmental extremes and changing ecological conditions. Mass mortality experienced e. g. in artificially established Norway spruce forests of Central Europe, following a prolonged drought period in the nineties, directed the interest of ecologists and foresters alike to the ability of forest tree populations to adjust to changing conditions, i.e. to their adaptation potential.

The issue of adaptedness appears as a crucial problem for forestry in view of the expected climate instability. The longevity of trees makes a fast adjustment to changed conditions more difficult than in agriculture. Long-term adaptedness and stability should be therefore of higher concern than possible gains in timber or fiber yield. Due to the lifespan of trees, climate fluctuations, secular changes and rare events must have shaped the natural

adaptive strategy both on individual and population level. Trees are therefore interesting objects for studying long-term adaptation to the environment.

Adaptation in a genetic sense means the change of the gene pool of a population in response to changes in external conditions. However, genetic consequences of climate or environmental changes in a population cannot be separated from processes in the ecosystem. There are at least three organizational levels of adjustment which have to be considered and are studied by different disciplines (ecology, coenology, plant geography, genetics and physiology):

1. On the ecosystem level, prolonged environmental stress or changing conditions will lead first to the loss of sensitive species of secondary importance, later to the substitution of dominant species. At the same time other, better adapted species will immigrate into the ecosystem. The tolerance limits of the species, and the stability of the species community will decide to which extent and how fast these changes occur. This phenomenon is described by ecologists as succession or degradation (depending on the direction and quality of species composition changes).

2. On the level of the population (or species) environmental stress triggers a selection process, which manifests itself through increased mortality. This process will change the gene frequency of the population: less adapted individuals will leave less progeny or disappear altogether. The rate of adjustment will be largely influenced by the availability of individuals with suitable traits, i. e. by the genetic variability contained in the population. This is the process of natural selection in the sense of Darwin, and termed genetic adaptation by geneticists. Genetic adaptation is understood as a change in gene frequency, directed toward a theoretical optimum in a given ecological situation. The genetic transformation is expected to increase the average fitness of the population.

3. Finally, on the individual level the question of survival or death is decided by the resistance or tolerance of the organism to cope with changing conditions. Plasticity (stability or homeostasis) is a physiological trait which is, of course, also determined by heredity. Phenotypic plasticity describes the ability of the organism to change its the expressed phenotype as a response to changing environmental conditions. It has to be stressed that phenotypic changes are transitory (mostly morphological) and do not involve genetic change of the organism itself.

Therefore, the ability to withstand changes on all three levels, depend on the adaptive potential and adaptedness, the determination of which is however certainly a question of interpretation. In the followings mainly the genetic adaptation on the level of populations will be discussed.

Without disregarding conflicting opinions in this respect, to assess adaptedness, the suggestion of Ayala (1969) is used: *adaptedness of a population may be judged on the relative ability (as compared to responses under other conditions) to transform available nutrients and energy into its own living matter*. This corresponds to dry matter production, in forestry to growth and volume (timber) yield. Adaptational difficulties manifest themselves in deterioration of growth rate, hardiness and resistance, which affect volume production directly and are therefore of critical importance in forestry. Out of the components of yield of a forest stand height growth is under strong genetic control; only this growth trait will be discussed.

Throughout the paper "adaptive variation" is used for climate-related genetic variation between populations, although it is clear that other forms of variation support adaptation (and fitness) as well; however climate-related variation is the most prudent interpretation of adaptive genetic variation. The paper deals with phenomena observed on widespread, outbreeding tree

species, mostly conifers. Taxa with divergent reproduction systems or fragmented distribution areas may exhibit different patterns, also depending on their evolutionary past.

Discovering long-term effects of climatic factors on hereditary traits: a retrospective

The awareness that plant development is affected by climate can be traced back into antiquity. The understanding however, that species distributed across climatically different regions adapt to local ecological (climatic) conditions through adjusting their genetic variation, is relatively recent.

Interestingly it was forest trees that attracted attention first. 18th century naval shipyards were seriously concerned about the declining supply of good quality oak and pine timber, and became interested in the question whether seed provenance might influence growth and form of trees in man-made forest plantations. The inspector-general of the French navy, the prominent botanist, Duhamel du Monceau established the first comparative trials in France with Scots pine seed of Baltic origin between 1745 and 1755, however no records of his pioneering work survived. Seventy years later it was André de Vilmorin, who in the 1820's endeavored to repeat Duhamel's effort. His results were published after 36 years of observation in 1862, stating differences between provenances and proposing the existence of climate-related genetic variation within the species (Wright and Bull 1963). "Provenance" means simply the source of a population sample representing a defined area. The provenances (synonymously: sources) originate from seed collected from identified stands or regions.

Failures with plantations established from imported seed prompted numerous further experiments in the second half of the 19th century. Outstanding with respect to their extent and design were the provenance experiments in Russia. Similar experiments were established throughout Central and Northern Europe, in Germany, Austria and Sweden (for details see Langlet 1971). The interest in provenance trials with forest trees was so great, that when the International Union of Forest Research Institutions (IUFRO) was founded in 1892, it was among its first tasks to initiate international provenance experiments. The scope of some of these tests is impressive: e.g. the international provenance test with Norway spruce initiated in 1962 includes 1100 provenances from Siberia to Iberia; a total of 20 parallel experiments in 14 countries have been established (Weisgerber et al. 1976).

The importance of ecological factors, especially of climate, in shaping within-species (intraspecific) variability became widely recognized, however, only after experiments with herbaceous plants yielded similar results. The work carried out in California with various perennial species is presumably the best-known investigation of plant populations collected along altitudinal transects. The common-garden experiments proved the existence of climate-related genetic differences within the species. The results published in four volumes (Clausen *et al.* 1940, and following publications) became a citation classic in ecological literature.

Aims and significance of provenance research

Provenance research is the expression used in forestry for the analysis of common garden plantations of tree populations originating from geographically different locations.

Provenance tests of trees are time consuming, require large areas and are very costly; nevertheless provenance testing became a standard procedure because of the economic interest in maintaining vitality and growth vigor of forest stands until maturity. Provenance testing has been applied to practically all major forest tree species of the Northern hemisphere and also to numerous tropical species of economic interest. Many of them originate from international cooperation coordinated by IUFRO, FAO or other agencies.

The principal goal of provenance tests is to identify stands, populations or areas which provide the most desired traits and commercially best results at the test location. Beyond strongly practice-oriented intentions serving silviculture, the tests offer an excellent opportunity to analyze intraspecific diversity in other than growth traits (molecular genetic, biochemical, physiological, morphological variation) which was exploited also for taxonomic purposes.

The tracing of between-provenance variation probably represents the most powerful available tool for testing hypotheses of climatic adaptation in trees. *Instead of analyzing genetic changes in subsequent generations, an unthinkable task in forestry, the observed geographic variation can be interpreted as an adaptive response to changes in climate conditions. The transfer of populations to provenance test sites may be regarded as a simulation of environmental change over time and the response may be modeled* (Mátyás and Yeatman l987, 1992; Mátyás 1994). This approach offers direct applications in forecasting climate change effects on trees and forests.

Compared to common garden experiments with short-lived plants, the long duration of the tests is of great advantage. Effects of annual weather fluctuations and rare anomalies are integrated in the end result. Longevity provides for a more reliable response to the given environment than in the case of ephemeral plants. This does not imply a much closer adaptation of trees to local conditions; a "perfect" adaptation would result in narrowing genetic variation, reduced adaptability and on the long run in the extinction of the species. On the contrary: adaptive strategies must provide for the maintenance of a sufficient level of variability to adjust to continuous and unpredictable fluctuation of conditions during the tree's lifespan and into an obscure future.

These distinct evolutionary and ecological implications make provenance tests important and interesting objects to study beyond direct silvicultural applications. *Although provenance research might be among the most important contributions of forestry to biological sciences, up to now its results have failed to capture much attention outside the forestry community.* Even the fact that much of the climatic adaptation research has been initiated and studied on forest trees first, is not generally known.

Genetic variation and climate factors

To demonstrate the effects of climate on intraspecific genetic variation, it is sufficient to plot provenance data against an important climate (or geographic) factor of the locations of origin (Table 1.). The various traits show independent patterns depending on the effect the climate has on that specific trait. Correlation between trait variation and climate parameters suggest the selective pressure exerted on the trait - in a sense demonstrating its adaptive significance. Comparing different types of traits, the variation of growth- and phenology-related traits seems to be in closest agreement with climatic factors. Essentially neutral traits, such as morphological and molecular genetic variation, generally do not correlate well with climate factors.

Table 1. Correlation of growth and morphology traits of 35 East European Scots pine populations with climate factors at the location of origin. Correlation coefficients indicate the varying selection pressure on the respective trait (measured in Kámon, Hungary; from Mátyás 1996)

	Number of frost-free days	Geograph. latitude (photoper.)	Average July temperature	Annual precipitation
11-year height	0.81	-0.69	0.62	-0.14
Height incr., 11th year	0.86	-0.74	0.69	-0.17
Branch number, top whorl	0.44	-0.56	0.41	-0.18
Branch angle	0.70	-0.54	0.35	-0.08
Needle-cast resistance	0.46	-0.15	0.06	0.29
Bud break	-0.84	0.72	-0.62	0.11
Bud set	-0.82	0.75	-0.58	0.17
Winter color of needles	0.80	-0.72	0.75	-0.29

From a forestry point of view, growth and survival traits are the most important. In temperate and boreal forests, the adaptive *variation pattern of growth-related traits* (height increment, bud break and formation, hardiness etc.) *are primarily shaped by the thermoperiod.* Growth and phenology data of provenances correlate best with thermal parameters whereas heat sum, temperature average, maxima and minima yield roughly the same results. This is also in agreement with experiments in controlled environments (Mátyás 1997).

The effect of *photoperiod* on trees has been demonstrated already by early studies, especially because latitude data of the origins are by far easier to obtain than thermal parameters (a classical study is that by Vaartaja 1959). In most cases, however, there is a strong confounding effect between photoperiod (latitude) and thermal conditions for obvious reasons. Surprisingly, moisture-related intraspecific differentiation is difficult to demonstrate (see Table 1), its effect is probably included in the thermal component.

The most striking feature of provenance tests is the generally *low sensitivity of populations to changing environments*, even with regard to highly adaptive traits such as height growth. Tree populations transferred over large distances into very different environments are able to grow and compete with the native, local populations, even if survival data indicate that only a certain fraction of the population exhibits the necessary plasticity (Table 2). Numerous studies verified a high level of individual and population homeostasis (for Norway spruce and Scots pine: Eriksson 1982, Southern pines: Wells 1969, white ash: Kung and Clausen 1984 etc.). As a consequence, between-population genetic differences are not well differentiated within considerably large geographic areas in absence of steep gradients (e.g. mountain slopes). On contiguous plains the distance between populations with measurable growth differences may exceed 50 to 100 km along ecological gradients.

Table 2. 10-year height and survival of some transferred Scots pine provenances in an experiment near Moscow. Note the comparable growth of populations from substantially warmer environments. Maladaptation is indicated by the decline of survival (from Mátyás 1996)

Provenance	Average height(cm)	Survival (%)	Annual mean temperature	Geographic latitude
	in the Moscow test		at the location of origin	
Moscow (local)	400	87	3.4	56
Minsk	409	88	5.0	54
Brest	435	92	7.0	52
Volynsk	397	65	7.0	50
Donetsk	418	68	8.0	48

Predicting effects of climate change

There are a number of approaches to estimate the transfer effect along an ecological gradient (Westfall 1992), which might be used for modeling the effects of environmental change. The assessment of effects of climate change with the help of multiple regression analysis has been proposed by the author (Mátyás 1994,1996). The use of existing provenance tests to predict such effects is based upon the above mentioned concept that spatial (geographic) variation may be interpreted as a simulation of responses to environmental change over time. Accordingly, response regressions of growth of transferred populations on thermal parameters may be interpreted as a model of response to temperature change scenarios.

The investigation of some conifers indicate that a relative growth increase until a certain limit of transfer into cooler environments is a phenomenon regularly encountered in provenance tests; at least into environments not too close to the upper distribution limits (= physiological tolerance limits) of the species. (Relative growth means that data are related to the performance of the local populations. In absolute terms, growth decreases naturally under conditions where the temperature sum is lower.) It is the result of complex hereditary and other biotic effects which demonstrate the repressive character of biological regulation (Mátyás 1996). On the other hand, the increase of temperature negatively affects growth. As an example, table 3 shows the interpretation of the general response of populations calculated from the dataset of 45 families of ponderosa pine (*Pinus ponderosa*) from the Sierra Nevadas in California at 4 sites. The data were obtained from three-dimensional response regression functions, where the transfer effect, i.e. the "ecological distance" was one of the variables, and the ecological conditions at the test site the other (Mátyás 1997, see also Morgenstern 1996, Westfall 1992 etc.).

Table 3. Estimated change of height growth of Californian ponderosa pine families at age 12 as a result of different annual average temperature change scenarios. Responses are calculated for three elevational positions (No reliable estimates are available for the empty cells)

test site		annual mean temperature change (°C)					
		4.5	4	3	2	1	0
high elev.	cm	406.9	422.4	449.1	474.8	506.9	537.8
	%	75.6	78.5	83.5	88.3	94.3	100
mid-elev.	cm			475.1	496.7	520.0	544.0
	%			87.3	91.3	95.6	100
low elev.	cm					504.6	524.1
	%					96.3	100

It is visible that the growth rate decreases with increasing pace as average annual temperature climbs higher. An increase of 1°C (or 1.8 F°) means already a growth loss of roughly 5%; and 3°C (or 5.4 F°) a loss of 13% of the original height at mid-elevation. The sensitivity difference between high-elevation and mid-elevation conditions, exhibiting a stronger response at higher altitudes, has to be treated with caution and needs further confirmation.

The calculated decline in height growth is only an indication for actual productivity loss, as a similar decline in diameter and basal area has a quadratic effect on stem volume. In addition to growth loss, other consequences of maladaptation increase as a function of growing temperature (or ecological) distances, such as susceptibility to snow break; or the loss of resistance to diseases and pests, which are otherwise often harmless or of minor importance; e.g. saprophytic fungi may turn into real parasites. A direct link between ecological distance and mortality could be proven for *Pinus banksiana* (Mátyás and Yeatman 1992).

Temperature increase will trigger an upward shift of species distribution bands and, in consequence, of elevational vegetation zones. It has to be stressed that within the elevational band of distribution, plant species are clearly structured into altitudinal "races" or clines, as already proven by the classical study of annuals by Clausen. The same is true for tree populations. Because of the altitudinal genetic differences, 300 m of elevation is generally proposed as the critical limit of safe transfer by ecological genetic studies on some western conifers. The temperature lapse rate for the Sierras was established as 0.54°C/100 m or 2.98°F/1000ft. 300 m of elevation equals then a temperature increase of 1.62 °C of yet relatively "safe" adaptation (Mátyás 1997). A further increase of temperature will inevitably lead to significant losses in productivity as shown in table 3.

Considering the long regeneration cycle of trees, the pace of the forecasted climate changes will be too fast to provide enough time for proper genetic adaptation of populations. A temperature shift will in any case negatively affect most of the populations. At low elevations, close to the lower limit of the species, temperature increase certainly will lead to the thinning out and disappearance of the species, losing its competitive ability against other species. At the upper limits, temperature increase will bring an improvement of site conditions. This offers the possibility of a migration advance for the species on the long run, as often modeled in climate scenarios. It has to be considered, however, that apart from the fact that natural migration speed of forest trees is relatively low, even on the long run the utilization of climatically improved zones off the present distribution range will be limited by soil conditions. The development of soil profiles takes millennia and the usually shallow, less developed soils of high altitudes and high latitudes will not change for a long time. Thus, contrary to general belief, the site potential will not follow the improvement in climate.

Concluding remarks

Common garden tests are carried out in forestry with easy-to-propagate, widely distributed species. The majority of species in large-scale test networks are up to now conifers, which occupy predominantly the initial phases of succession in temperate forest communities. It is therefore not certain that the observed phenomena apply to all widely distributed tree species. The described modeling method has its limitations as well, as the effect of climate variables at a given test location cannot be evaluated in its full complexity. In the described approach the effects of latitudinal (north-south) transfer have been neglected, although changes in the photoperiod might have some effect on light-sensitive species.

With the above limitations, the described effects of temperature change on growth and productivity of tree populations seem to have a rather general validity, even though the magnitude and type of response is determined by the actual genetic structure and tolerance of the species. It may be assumed that contrary to the general perception of physiological reaction to environmental change, the response of adapted, local populations is asymmetric due to the manifold constraints of biologic regulation. As a result, temperature increase leads to relatively fast growth and productivity loss and selective mortality. Apart from economic consequences, growth decline affects also the functioning of the forest ecosystem as carbon sink in a twofold manner. With increasing temperature, the quantity of sequestered carbon decreases and simultaneously the decomposition rate of dead organic matter accelerates, causing additional carbon release into the atmosphere.

An important feature of the modeling of climate change effects as presented in the example, is the fact that it is based on directly measured data and therefore the conclusions are fairly realistic. Such information is available in provenance tests for many commercially important tree species in many parts of the world. Their evaluation may contribute to a better understanding of natural processes triggered by environmental changes and help in formulating protective strategies.

The results indicate that because of the conservative nature of the genetic adaptation process, and of the relative speed of expected changes, even agricultural crops will demand a strategy to facilitate adaptation. Long-lived, immobile organisms, such as trees will especially need human interference in order to enhance gene flow and adaptation to altered conditions, in spite of an impressing hereditary capacity. National forest policies have to incorporate this task into the agenda of the next decades (Ericson *et al*. 1993). To counteract genetic erosion and extinction, populations along the southern (or low-elevation) limits of species distribution areas will need special attention.

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