

Climatic adaptation of trees: rediscovering provenance tests

Csaba Mátyás

University of Sopron, Hungary, P.O. Box 132, 9401 Sopron, Hungary

Key words: adaptation, climate change, provenance research, phenotypic stability, natural selection, genetic, diversity

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 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.

Analysis of adaptive traits (mostly juvenile height growth) in provenance experiments indicate the existence of very effective constraints on adaptedness. The performance of populations plotted against an ecological-climatic factor exhibits a characteristic pattern and can be described by response functions. The population average of a fitness-related trait for a locally adapted population is often significantly lower than that of populations from other environments; usually the ones from milder climate perform better. The phenomenon is interpreted as adaptation lag. Suboptimal adaptation is compensated by a high level of genetic diversity. Molecular genetic studies confirm the high level of allelic and individual genetic diversity in forest trees. A consequence of individual homeostasis, phenotypic stability of populations is usually also high; the sensitivity to environmental changes is generally moderate. Phenotypically stable populations are valuable not only because of a wider range of potential cultivation but specifically because of a greater ability to adjust to unexpected changes. This trait should receive more attention in the future for obvious reasons.

The maintenance of a high within-population genetic variance is favored by the genetic system of the investigated species (effective gene flow, outbreeding, high genetic load, etc.). Random events and long-lasting biotic interactions are further effects impairing the efficiency of natural selection.

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. Although seldomly appreciated, provenance research might be among the most important contributions of forestry to biological sciences.

Introduction

Due to numerous reasons the domestication of forest trees is still in its beginnings. There are only few genera where monoclonal plantations of selected genotypes are in commercial use (e.g. *Populus*, *Salix*, *Cryptomeria*, some *Eucalypts*). In most cases forests are regenerated with generatively propagated seedling populations; this provides a comparatively wide adaptability to the diverse site conditions encountered in forestry.

Nevertheless the issue of climatic adaptation appears as a crucial problem for forestry in view of the expected climate instability. The longevity of trees make 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 fibre yield. The fact that breeding of forest trees has not progressed very far yet, offers some advantages. The use of practically wild populations in breeding experiments may offer infor-

mations which are valuable far beyond their immediate goal. Genetic variation of wild populations can be analysed to study mechanisms of climate adaptation. Due to the lifespan of trees, climate fluctuations, secular changes and rare events must have shaped the adaptational strategy both on individual and population level. Trees are therefore interesting objects for studying long-term climatic adaptation.

Climatic adaptation of plants involves both the genetic adaptation of populations and the ability of individuals to buffer environmental changes through modifying their phenotypical response. 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. 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.

Individual or 'physiological' homeostasis (acclimation or plasticity), appears on population level as phenotypic stability. Although clearly determined by hereditary factors, phenotypic stability does not involve genetic change in the population (therefore the often synonymously used term 'genotypic flexibility' is somewhat misleading). Phenotypic stability or plasticity denotes a change in the expressed phenotype as a function of changing environmental effects. (It is related to the term reaction norm, which, in a narrow sense, describes the reaction to a specific effect). The interpretation of adaptation in natural plant populations is difficult. The safest and simplest is the analysis of climatic adaptation, through observing differences in populations of different origins and relating their response to ecological conditions at their location of origin. To define or even quantify adaptedness is certainly a question of interpretation. Without disregarding conflicting opinions (Tigerstedt, 1992) in this respect, the suggestion of Ayala (1969) is adopted: to assess adaptedness, the ability of the population to transform available nutrients and energy into its own living matter is analyzed. This corresponds to dry matter production, in forestry to volume (timber) yield. (It cannot be denied that within a closed forest stand of high density, juvenile height growth plays a crucial role and is of high adaptive value – less so in open woodlands.) Adaptational differences between populations, manifesting themselves in growth, hardiness and resistance, 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 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 restricted or fragmented distribution areas may exhibit very different patterns, also depending on their evolutionary past.

Discovering effects of climatic factors on hereditary traits: a retrospective

The awareness that plant development is affected by climatic events can be traced back into antiquity. The understanding however, that widespread species adapt to different ecological conditions through adjusting genetic variation locally, is relatively recent.

Interestingly it were forest trees that attracted attention first. Eighteenth 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 (Langlet, 1971).

Seventy years later it was André de Vilmorin, who in the 1820's endeavored to repeat Duhamel's effort and established plantations of Scots pine populations of various origin and other introduced exotic species on his estate Les Barres (Durand, 1984). Vilmorin's results were published after 36 years of observation in 1862, stating differences between geographic provenances and proposing the existence of continuous (clinal) variation (Wright & Bull, 1963). The experiments attracted so much attention in forestry circles, that the posthumous report was soon translated into other languages.

Simultaneously botanists and agronomists began investigating possible links between the origin of pop-

ulations or cultivated varieties and their phenologic behavior (Schübeler, 1862; Linsser, 1867; De Candolle, 1872; Kerner, 1875 – cit. in Langlet, 1971). In forestry, failures with plantations established from imported seed prompted numerous experiments in the second half of the 19th century, following Vilmorin. Outstanding with respect to their extent and design were the provenance experiments in Russia. Turskiy established between 1877 and 1892 numerous experiments with Scots pine populations near Moscow, which were maintained and reviewed for a century to come (Timofeev, 1973). Later, Ogievskiy established tests with a large number of provenances at 20 different locations – already a network-type experiment (Giertych & Oleksyn, 1981). Similar experiments were outplanted throughout Central and Northern Europe, in Germany, Austria and Sweden (discussed in the excellent paper of Langlet, 1971).

The interest in provenance trials with forest trees was so great, that when the Union of Forest Research Institutions (IUFRO) was founded in 1892, it was among its first tasks to initiate international provenance experiments. The first in a long sequence of IUFRO-coordinated provenance tests with various species was established in 1907 in 9 countries (Giertych, 1979). 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).

It became evident already around the turn of the century that forest trees harbor a great wealth of intraspecific variability which at least in part reflects the climatic differences within the area of distribution of the species. It was obvious that the morphological and growth differences between the populations may be utilized to improve the quality of cultivated forests (such a proposal may be traced in the archives of the Swedish navy as early as 1759; cit. in Langlet, 1971).

The importance of ecologic factors, especially of climate, in shaping intraspecific variability became widely recognized, however, only after experiments with herbaceous plants yielded similar results. The work initiated by the Carnegie Institution of Washington is presumably the best-known investigation of herbaceous plants collected along altitudinal transects. The common-garden experiments proved the existence of genetic differences within the species. The results published in four volumes (Clausen et al., 1940, 1945, 1948, 1958) became a citation classic in ecological literature, especially the work on *Achillea* (Hiesey et al.,

1942, respectively Clausen et al., 1948) and was often used as an illustration of continuous, clinal variation along an altitudinal (climatic) transect, which was not the conclusion of the authors.

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' 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 which need not be indigenous. (Therefore in tree improvement literature and forest legislation a distinction is made between provenance and origin, the latter meaning the ancestral, original population.)

Due to their size and lifespan, forest trees seem to be very difficult objects for common garden or controlled environment tests. Although growth chamber tests can be carried out barely beyond the early juvenile stage, early growth, developmental and physiology traits correspond satisfactorily to initial field results on the level of provenances, and correlate well with climatic data at the locations of origin (Giertych & Farrar, 1962; Yeatman, 1966; Ledig, 1992). Nursery tests are also frequently used to establish adaptive differences in a geographic area (Rehfeldt, 1988; Sorensen & Weber, 1994).

Provenance tests of trees are time consuming, require large areas and are very costly – nevertheless, as documented in the earlier chapter, provenance testing was conceived more than two hundred years ago and became a standard procedure for a century because of the economic interest in maintaining vitality and growth vigor of forest stands over decades 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 original intention and 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. In course of time the tests have been used to study quantitative genetic phenomena (e.g. juvenile-mature correlation, ratio of inter- and intrapopulation variation, genotype-

environment interactions, etc.). Provenance data also serve as a basis to delineate seed (planting) zones as well as breeding zones (Kung, 1981; Raymond & Lindgren, 1986, 1990). Beyond strongly practice-oriented intentions serving silviculture, the tests offer an excellent opportunity to analyse intraspecific diversity in other than growth traits (allozymic, chemical, physiological, morphological variation) which was exploited also for taxonomic purposes.

Tree breeding research, advancing toward clonal selection, advanced-generation breeding and genetic engineering, regarded until recently provenance tests as a useful but already somewhat redundant starting point. With the increasing understanding of the significance of genetic diversity, provenance tests became interesting as valuable archives of genetic diversity both for breeding and conservation.

The tracing of between-provenance variation probably represents the most powerful available tool for testing hypotheses of climatic adaptation in trees. Instead of analysing genetic changes in subsequent generations, an unthinkable task in forestry, the observed geographic variation is interpreted as an adaptive response to changes in climate conditions. The outplanting of the tests may be regarded as a simulation of environmental change over time and may be modeled (Mátyás & Yeatman, 1987, 1992; Mátyás, 1994; Schmidting, 1995). This approach offers direct applications in forecasting climate change effects on trees and forests.

Provenance tests covering different habitats may be utilized also for biological site indication. The growth and vigor of populations used as standards characterize the environment, the growth potential and possible risks (Lindgren & Persson, 1995). Compared to common garden experiments with short-lived plants, an advantage might be the long duration of the tests. Effects of annual weather fluctuations and rare anomalies are integrated in the end result. The longevity of the objects themselves binds the organisms stronger to the given environment, than in the case of ephemeral plants. This is not to imply a much closer adaptation to local conditions; a 'perfect' adaptation would result in the long run in the extinction of the species. On the contrary: adaptive strategies seem to include 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 applica-

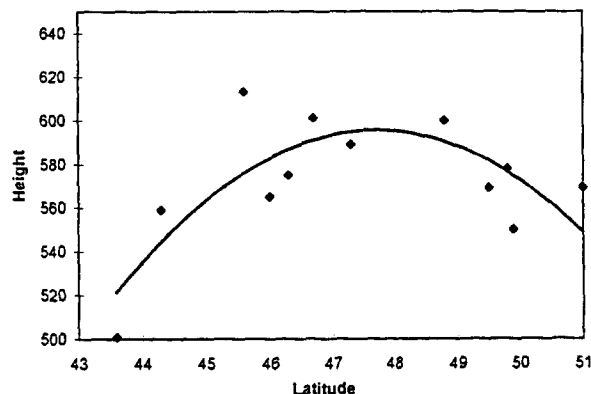


Figure 1. Mean height of 12 jack pine (*Pinus banksiana*) provenances from West Ontario in Swastika, Ont., plotted against the latitude of their origin. The scatter of values indicates a fairly weak adaptation to latitudinal effects in spite of simple topography ($R^2 = 0.52$, sign. at $P = 5\%$ level). The latitude of the test site is 48° O'N (Mátyás 1987).

tions. 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 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 location of origin (Figure 1). Depending on the nature of the observed trait, adaptive genetic variation may exhibit certain geographic patterns; although linked to climate, the various traits may show independent patterns depending on the effect the climate has on that specific trait. Correlations between trait variation and climate parameters may suggest the adaptive pressure exerted on the trait – in a sense demonstrating its adaptive significance (Table 1). Comparing different types of traits, the variation of growth- and phenology-related traits seems to be in closest agreement with cli-

Table 1. Correlation of growth and morphology traits of 35 East European Scots pine populations with climate factors at the location of origin (measured in Kámon, Hungary; from Mátyás 1987)

	Number of frost-free days	Geograph. latitude (photoperiod)	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

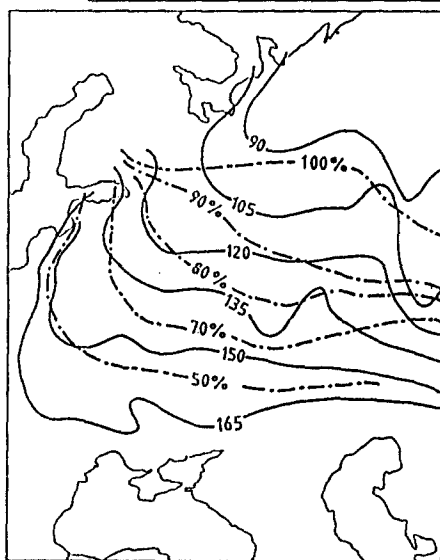


Figure 2. Variation of budset of one year old East European Scots pine (*Pinus sylvestris*) seedlings in early September in Hungary (broken line: percentage of seedlings with buds). The geographic pattern of phenology closely follows thermal conditions (full line: number of frost-free days) (Mátyás, 1981).

matic factors. Morphological and allozyme variation generally do not correlate well with climate.

From a forestry point of view, growth and survival traits are the most important. In temperate and boreal forests, the adaptive variation of growth-related traits (height increment, bud break and formation, hardiness, etc.) are primarily shaped by the thermoperiod (Sarvas, 1972, 1974; Prokazin & Bogachev, 1975; Morgenstern, 1978). 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 (Giertych & Farrar, 1962; Yeatman, 1966).

The effect of photoperiod on trees has been also widely investigated, especially because latitude data are usually more precise and easier to establish than thermal parameters. Vaartaja's (1959) classic work led even to the definition of 'photoperiodic ecotypes'. Dormling (1979) was able to prove the importance of photoperiod in case of Norway spruce for budbreak and bud formation, as well as in initiating and terminating dormancy. This seems to be in strong contradiction with the beforesaid. In fact, there is certainly a synergism in photo- and thermoperiodic regulation of growth (Koski & Sievänen, 1985), where the importance of photoperiod seems to increase toward the arctic timberline and high elevation sites (Mátyás, 1981). On the other hand, in most cases there is a strong confounding effect between photoperiod (latitude) and thermal conditions for obvious reasons. The two effects can be successfully separated only in mountainous areas or in anomaly regions, such as Eastern Europe, where – as a consequence of the Gulf stream – isotherms run partially perpendicular to latitude. For this area, the clear dominance of the thermal factor is obvious (Figure 2). The increased importance of photoperiod appears in climatically severe areas receiving less heat. Sarvas proposed the limit for dominant thermal regulation of growth of conifers around 62 ° N. latitude (which corresponds in Scandinavia to roughly 1000 degree-days). More recent investigations in provenance tests support this (Eriksson, 1980; Mátyás, 1981).

The effect of precipitation seems to be minor in affecting climatic adaptation of trees, even if the species is at its limits regarding moisture conditions; moisture-related intraspecific differentiation has not been demonstrated.

Table 2. Ten-year height and survival of some transferred Scots pine provenances in an experiment near Moscow (from Mátyás, 1989)

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

Phenotypic stability in tree populations

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. Provenances transferred over large distances into very different environments are able to grow and even compete with the native, local populations (Table 2). This indicates a very high level of individual homeostasis. As a consequence, the phenotypic stability of populations is usually high. Reaction norms of individual populations are usually not well expressed within considerably large geographic areas, and growth differences between adjacent areas are difficult to detect in absence of steep gradients (e.g. mountain slopes). On geographically not fragmented plains the distance between populations with measurable growth differences may exceed 50 to 100 km along ecological gradients.

Stability differences have also been observed among provenances in some coniferous species. Furthermore, stable provenances seem to concentrate in certain 'stable' areas. While the value of stable populations is very great, the evolutionary causes for their appearance are not clear. Phenotypic stability *per se* need not be adaptive. However various theoretical models agree upon the fact that environmental heterogeneity in time favors the evolution of stability by increasing individual homeostasis (Mitton & Grant, 1984; Parsons, 1987; Powers et al., 1991; Scheiner, 1993). Indications that high climatic instability may be responsible for the evolution of phenotypically stable populations, has been found for some coniferous species (Mátyás, 1986).

Phenotypically stable populations are valuable not only because their potential cultivation area is considerably larger than that of unstable populations, but specifically because they have a greater potential to adjust

to unexpected environmental fluctuations. Therefore, stability as a trait should receive even more attention in the future.

Adaptive growth patterns and climate: an example of lodgepole pine

The shape and distinctness of between-population adaptive genetic variation depends on the climate gradients. Low lapse rates correspond to less expressed patterns and *vice versa*. An example of pattern changes is presented with data of lodgepole pine (*Pinus contorta*) in western North America.

In a range-wide test of lodgepole pine on Vancouver Island, Ying & Liang (1994) found an unexpectedly narrow band of populations adapted to the local climate. At this test location the area represented by sufficiently adapted populations has a maximum width of only 60 km, however it extends over 3° latitude. The elevational band is even more restricted: only 250 m.

In the rugged mountains of Idaho and Wyoming the species is distributed over more than 2000 m of elevational difference and grows across comparably steep gradients: the frost-free period varies from 120 days to less than 30 (!) days. Instead of expected 'local' strains, a clearcut elevational (thermal) cline can be detected across a topographically complex area, in spite of numerous disjunctions in distribution. Most of the geographic variation found is elevational (Rehfeldt, 1988).

There is no reason to interpret any of the described patterns as local (ecotypic) or non-clinal adaptation. Usually the lack of proper ecological data may create such impressions. E.g. in Idaho, 300 m in elevational change resulted in measurable genetic differences. Although seemingly small, this change equals to 24 days in length of growing season: a very essential difference which clearly has its genetic consequences.

Similarly, the suggested 'very close' adaptation in coastal British Columbia populations is the result of a very steep east-west gradient from very long and mild growing season at sea level to the harsh climate in the nearby Coast Range. Altitudinal differentiation is by no means more explicit than latitudinal; it is the thermal lapse rate which differs.

For the central Sierra Nevada in California, altitudinal and latitudinal lapse rates have been calculated for temperature. The latitudinal gradient is $0.46^{\circ}\text{C}/\text{lat. degree}$, the elevational gradient $0.55^{\circ}\text{C}/100\text{ m}$. Converted for the conditions on the generalized west slope of the Sierra Nevada 1°C of average temperature change occurs over 222 km distance in N-S (latitudinal) direction, while over only 5 km along the slope (elevation) – a difference of two orders of magnitudes, in terms of directional selection pressure, which explains the development of narrow bands of similarly adapted populations (Mátyás, 1995).

Genotype-environment interactions measured in tests are relatively weak, but increase generally toward the climatic limits of the species, indicating a growing climatic selection pressure. This phenomenon is observable in numerous conifers near the boreal forest limits (Ericsson, 1980). Lodgepole pine exhibits this effect as well on the northwestern limits of distribution. In the very harsh climate of Northern British Columbia and the Yukon lodgepole pine occurs in a narrow elevational band between 600 and 1200 m, however over a latitudinal range of 10° . Ying & Illingworth (1986) tested sampled populations at two Yukon locations:

	Elev. (m)	Aver. temp ($^{\circ}\text{C}$)	January	Precip. (mm)*
Whitehorse	663	- 1.0	- 19.0	172
Watson Lake	710	- 3.0	- 23.7	288

At Whitehorse the response differences were remarkably moderate. At Watson Lake in the Rocky Mts., however, the conditions are closer to the climatic tolerance limit of the species: the same populations show strongly accentuated differences (Figure 3).

Constraints on climatic adaptation

The presented features of adaptive genetic variation in trees illustrate very effective constraints on 'perfect' adaptation. Provenance tests prove the inefficiency

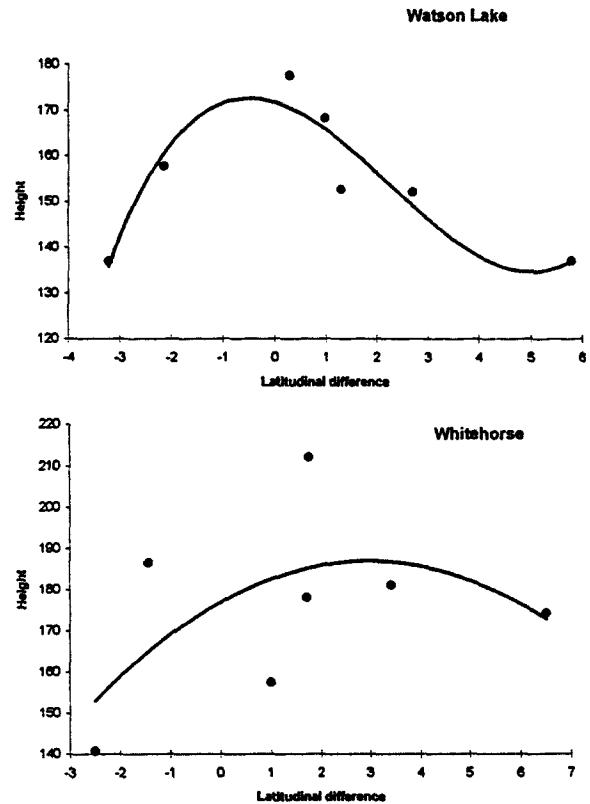


Figure 3. Mean height of 7 lodgepole pine (*Pinus contorta*) provenances from northwestern Canada in two experiments, plotted against the latitudinal difference between the original location and the test site. Negative values indicate southern provenances transferred northward; populations from the North got positive values. While both test sites are close to the northern limit of distributional range of the species, Watson Lake is the harsher location. Note the more accentuated response ($R^2 = 0.65$) at Watson Lake, as compared to Whitehorse (data from Ying & Illingworth, 1986).

of natural selection to shape a genetic makeup which provides for phenotypes attaining the optimum for a given trait at a given site. 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 & 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 & Gregorius, 1993), climatic adaptation seems to have however 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.). Interestingly, fertility (cone or seed yield) seem to follow this pattern as well: individual variation in this trait is overwhelming compared to certainly existing, but by far weaker geographic effects.

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 in termination of growth in autumn was more than 70 days within one population (Mátyás 1987). Likewise, a single elevational cline at one location may encompass nearly all the adaptive genetic variation observed within a range of distribution (Rehfeldt, 1988).

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 & 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 effect of migration, fragmentation, isolation and drift induced by climatic shifts across geologic times, can be demonstrated on the genetic structure of populations and species, which contributes to the presently observed patterns of diversity (Hamrick & 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).

Aspects of breeding

The concepts of fitness and adaptedness seem to gain more importance in cultivated ecosystems, partially because of concerns that high inputs are affecting the environment and because of projected climate instability. In re-considering sustainability and low-input management, it may be of value to analyze successful adaptive strategies of wild plants, including trees. In forestry, it is proposed to breed in favor of generalists, i.e. phenotypically stable populations. Individual and population diversity should be enhanced by introducing a maximum of different lines which produce the reproductive material for artificial regeneration (Ledig & Kitzmiller, 1992). It seems also worthwhile to increase efforts to understand the genetic mechanisms of high-level homeostasis and to trace naturally stable populations and strains – a valuable natural phenomenon which should be utilized.

References

- Ayala, R.J., 1969. An evolutionary dilemma: fitness of genotypes versus fitness of population. *Canad. J. Genet. Cytol.* 11: 439–456.
- Bergmann, F. & H.R. Gregorius, 1993. Ecogeographical distribution and thermostability of isocitrate dehydrogenase (IDH) allozymes in European silver fir (*Abies alba*). *Biochem. Syst. Ecol.* 21: 597–605.
- Clausen, J., D.D. Keck & W.M. Hiesey, 1940, 1945, 1948, 1958. Experimental studies on the nature of species. Vol. 1 to IV. Carnegie Inst. Publ. Nr. 520, 564, 581 and 615, Washington, D.C.
- Dormling, I., 1979. Influence of light intensity and temperature on photoperiodic response of Norway spruce provenances. *Proc. IUFRO Norway Spruce Breeding Conf.*, Bucharest, 398–408.
- Durand, R., 1984. *L'arboiretum National des Barres*. Paris.
- Ericsson, G., 1980. Severity index and transfer effects on survival and volume production of *Pinus sylvestris* in Northern Sweden. *Stu. For. Suec.* Nr. 156.
- Giertych, M., 1979. Summary of results of Scots pine height growth in IUFRO provenance experiments. *Silvae Gen.* 28 (4): 136–152.
- Giertych, M. & J.L. Farrar, 1962. A provenance study of jack pine seedlings. *Silvae Gen.* 11: 111–114.
- Giertych, M. & J. Oleksyn, 1981. Summary of results on Scots pine volume production in Ogievskij's pre-revolutionary Russian provenance experiments. *Silvae Gen.* 30 (2–3): 57–74.
- Hamrick, J.L. & M.J. Godt, 1990. Allozyme diversity in plant species. In: A.H.D. Brown, M.T. Clegg, A.L. Kahler & B.S. Weir (Eds). *Plant population genetics, breeding and genetic resources*. pp. 43–63. Sinauer Ass.
- Hiesey, W.M., J. Clausen & D.D. Keck, 1942. Relations between climate and intraspecific variation in plants. *Am. Natur.* 72.
- Koski, V., 1991. Generative reproduction and genetic processes in nature. In: M. Giertych & Cs. Mátyás (Eds). *Genetics of Scots pine*. pp. 59–72. Elsevier Publ. & Akadémiai Kiadó Budapest.
- Koski, V. & M. Sievänen, 1985. Timing of growth cessation in relation to the variations in the growing season. In: P.M.A. Tigerstedt, P. Puttonen & V. Koski (Eds). *Crop Physiology of Forest Trees*. pp. 167–193. Helsinki Univ. Press.
- Kung, F.H., 1981. Delineating seed collection zones based on multi-plantation provenance tests. *Proc. 16th South. For. Tree Impr. Conf.* May 22–28, 1981. pp. 83–96. Virginia, USA.
- Langlet, O., 1971. Two hundred years of genecology. *Taxon* 20 (5/6): 653–722.
- Ledig, F.T., 1986. Heterozygosity, heterosis and fitness in outbreeding plants. In: M. Soule (Ed). *Conservation biology: the science of scarcity and diversity*. pp. 77–106. Sinauer Assoc., Sunderland, Mass.
- Ledig, F.T., 1992. Genecology: the fitness of the organism and the fitness of the environment. *Proc. 12th North Am. For. Biol. Workshop*, Aug. 17–20, 1992. pp. 27–49. Sault Ste Marie, Ont., Canada.
- Ledig, F.T. & J. Kitzmiller, 1992. Genetic strategies for reforestation in the face of global climate change. *For. Ecol. Manage.* 50: 153–169.
- Lindgren, D. & A. Persson, 1995. Vitalization of results from provenance tests. *Proc. XXth IUFRO World Congr.*, Tampere (in press).
- Mátyás, Cs., 1981. Phenological variability of East European Scots pine provenances. *Erdészeti Kutat.*, Budapest, 74: 71–80 (in Hungarian).
- Mátyás, Cs., 1986. Improved planting stock in forestry. *Akademiai Publ.*, Budapest (in Hungarian).
- Mátyás, Cs., 1987. Adaptation processes in forest tree populations. *Dr. Sci. Thesis*, Sopron, 195 pp. (in Hungarian).
- Mátyás, Cs., 1989. Genetic and ecological constraints of adaptation. *Proc. IUFRO Int. Symp. on Forest Genetics, Breeding and Physiology*. pp. 79–90. Voronezh, USSR.
- Mátyás, Cs., 1991. Adaptation lag: a general feature of natural populations. *Proc. Joint Meeting of WFGA and IUFRO Working Parties*, Olympia, Wa. (USA) Aug. 20–25, 1990. Pap. Nr. 2.226.
- Mátyás, Cs., 1994. Modeling climate change effects with provenance test data. *Tree Physiol.* 14: 797–804.
- Mátyás, Cs., 1995. Climate of the Sierras. Unpubl. report, USDA PSW Expt. Sta., IFG Placerville, 30 pp.
- Mátyás, Cs. & C.W. Yeatman, 1987. Adaptive variation of height growth of *Pinus banksiana* populations. *Erd. Faip. Egy. Közl.* 1–2: 191–197 (in Hungarian).
- Mátyás, Cs. & C.W. Yeatman, 1992. Effects of geographical transfer on growth and survival of jack pine populations. *Silvae Gen.* 43 (6): 370–376.
- Mitton, J.B. & M.C. Grant, 1984. Associations among protein heterozygosity, growth rate, and developmental homeostasis. *Ann. Rev. Ecol. Syst.* 15: 479–499.
- Morgenstern, E.K., 1978. Range-wide variation of black spruce. *Can. J. For. Res.* 8: 463–473.
- Müller-Starck, G., 1991. Genetic processes in seed orchards. In: M. Giertych & Cs. Mátyás (Eds). *Genetics of Scots pine*. pp. 147–162. Elsevier Publ. & Akadémiai Kiadó Budapest.
- Parsons, P.A., 1987. Evolutionary rates under environmental stress. *Evol. Biol.* 21: 311–347.
- Powers, D.A., T. Lauerma, D. Crawford & L. DiMichele, 1991. Genetic mechanisms for adapting to a changing environment. *Ann. Rev. Genet.* 25: 629–659.
- Prokazin, E.P. & A.V. Bogachev, 1975. Hereditary adaptation of Scots pine to climate factors and possibilities of its assessment and prognosis. In: *Genetics, selection and seed production*. VNIILM, Pushkino (USSR) (in Russian).
- Prus-Glowacki, W., 1991. Biochemical polymorphism. In: M. Giertych & Cs. Mátyás (Eds). *Genetics of Scots pine*. pp. 73–81. Elsevier Publ. & Akadémiai Kiadó Budapest.

- Raymond, C.A. & D. Lindgren, 1986. A model of genetic flexibility. In: D. Lindgren (Ed). Provenances and forest tree breeding for high latitudes. pp. 159–177. Kempe Symp. Rapp. 6, Umea.
- Rehfeldt, G.E., 1988. Ecological genetics of *Pinus contorta* from the Rocky Mountains (USA): a synthesis. *Silvae Gen.* 37 (3–4): 131–135.
- Sarvas, R., 1972, 1974. Investigations on the annual cycle of development of forest trees. Part I and II. Comm. Inst. For. Fenniae 76.3 and 84.1.
- Savolainen, O., 1994. Genetic variation and fitness: conservation lessons from pines. In: V. Loeschke, I. Tomink & S.K. Jain (Eds). Conservation genetics. pp. 27–36. Birkhauser Verl., Basel.
- Scheiner, S.M., 1993. Genetics and evolution of phenotypic plasticity. *Ann. Rev. Ecol. Syst.* 23: 1–14.
- Schmidtling, R.C., 1995. Developing a seed transfer model for short-leaf pine. Proc. 8th Bienn. South. Silv. Conf. Auburn AL, Nov. 1994 (in press).
- Sorensen, F.C. & J.C. Weber, 1994. Genetic variation and seed transfer guidelines for ponderosa pine in the Ochoco and Malheur National Forests of Central Oregon. USDA Dor. Serv. Res. Pap. PNW-RP 468.
- Tigerstedt, P.M.A., 1992. Why do exotic trees often exceed the yield of endemic trees? In: D. Lindgren (Ed). *Pinus contorta* – from untamed forests to domesticated crop. pp. 60–68. Umea.
- Timofeev, V.P., 1973. Growth traits of Scots pine of various origin at the forest experimental fields of the Timiryazev Agric. Academy. *Izd.-vo Kolos, Moscow*, 2: 130–146 (in Russian).
- Vaartaja, O., 1959. Evidence of photoperiodic ecotypes in trees. *Ecol. Monogr.* 29: 91–111.
- Weisgerber, H., W. Dietze, J. Kleinschmidt, J. Racz, H. Dietrich & R. Dimpfleier, 1976. Ergebnisse des internationalen Fichten-Provenienzversuches '1962. Teil 1: Phenologische Beobachtungen und Höhenwachstum bis zur ersten Freilandaufnahme. *Allg. Forst- und Jagdztg.* 147: 227–235.
- Wright, J.W. & W.I. Bull, 1963. Geographic variation in Scots pine. *Silvae Gen.* 12: 1–40.
- Yeatman, C.W., 1966. Geographic variation in jack pine seedlings. Ph.D. Thesis. 128 pp.
- Ying, Ch.C. & K. Illingworth, 1986. Lodgepole pine provenance research in northwestern Canada with particular reference to the Yukon territory. In: D. Lindgren (Ed). Provenances and forest tree breeding for high latitudes. pp. 189–200. Kempe Symp. Rapp. 6, Umea.
- Ying, Ch.C. & Q. Liang, 1994. Geographic pattern of adaptive variation of lodgepole pine within the species' coastal range: field performance at age 20 years. *Forest Ecol. Manage.* 67: 281–298.