

Genetic potential of plastic response to climate change

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Climate change: unfavourable prospects for SE Europe's continental lowlands

Scenarios of future climate of Europe forecast different conditions on the continent. While the Atlantic coast and boreal parts of Western Europe seem to profit from gradual warming, the continental lowlands of South-eastern Europe will probably experience a worsening of growing conditions. There the lower (semiarid) limit of closed forests is crossing the plains of SE Russia and the Ukraine, reaching its westernmost extension in the Carpathian Basin. The lower forest limit is an ecotone, a rather vaguely determined belt, influenced locally by edaphic and water regime conditions. It has been under strong human influence for millennia and little has remained from its original vegetation cover. Most forests are man-made and plantations. Apart from areas with surplus water supply, climate dependent zonal forests of the lowlands are extremely sensitive to seemingly minor changes of temperature and precipitation. The limits and presence of closed forests are determined by the tolerance capacity of the dominant species (oaks and towards the East, also Scots pine). It is visible in Table 1 that *even the mildest expected scenario of climate change is similar in magnitude to a whole vegetation zone difference*; the temperature and precipitation change might trigger a complete destabilisation or shift of zones (Mátyás 2000).

Table 1. Average temperature and precipitation data of zonal forest belts in the lowlands of the Carpathian Basin and the magnitude of expected changes (Mátyás, Czímber 2000)

	Annual precipitation (mm)	July temperature (°C)
<i>Beech zone</i>	734 ± 65.2	19.1 ± 0.95
<i>Hornbeam-oak zone</i>	702 ± 70.3	20.0 ± 0.79
<i>Turkey- sessile oak zone</i>	616 ± 49.0	20.2 ± 0.70
<i>Forest steppe zone</i>	563 ± 49.0	21.5 ± 0.56
<i>Average difference between zones</i>	57	0.80
<i>Expected mildest change scenario in the region</i>	-40	+1.1

Any prediction about the effects of future scenarios on stability and yield of low-elevation forests in this region requires information on the tolerance and adaptability of tree species involved. Although quasi easy questions, quantitative response and limits of tolerance have not been among the priority themes of current genetic research for a number of reasons, such as

- up to the present, growth and yield of populations on marginal sites had little practical relevance;
- research in quantitative trait variation is long-term, expensive and has limited scientific reputation;
- out of genetic forces structuring variability, primarily the random effects have been studied (effects of migration, mutation and drift); response to adaptive selection to a less extent;
- ecological interpretation of molecular marker variation patterns has remained dubious in most cases.

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Goal of study and approach

The analysis was aimed at answering the following questions:

- how do populations react to change of environmental conditions;
- are differences in response to climatic factors discernible; and
- do response differences at intraspecific level exist between populations from various climatic zones?

Potentially, response of an ecosystem (and of species dominating it) to changed external conditions has two alternatives:

- Response of populations (genotypes) to an altered environment during their lifetime; phenotypic adaptation through plasticity and/or differential mortality in the population;
- Change of distribution area of species, possible migration behavior and changes in interspecific interactions (competition, foraging, symbiosis etc.) in response to climatic shifts.

Ecologically oriented studies concentrate traditionally on the second case of apparently higher relevance. It has to be considered however, that most vegetation types of Europe are dominated (and determined) by a relatively small number of forest tree species, with a comparatively long life cycle – compared to the anticipated pace of changes.

In the present paper we concentrate therefore on the first question, i.e. how the genetic system of trees determines their response to changed environments *within the lifetime* of the present generation. In other words, how norm of reaction and plasticity describe phenotype adjustment.

Plasticity: favored in trees by evolution?

The analysis of response of populations and genotypes to different environments has been initiated by Woltereck (1909), a German zoologist, who coined the term *norm of reaction* (Reaktionsnorm) for observed changes of the phenotype with changing environmental conditions. The application of this concept to plants happened relatively late. Bradshaw (1965) defined *plasticity*, a genetically determined trait, as gene expression influenced by environmental conditions. He pointed out that plasticity is favored by evolution in two cases: 1. where the time scale of environmental changes is much less than the generation time of the species, i. e. if the changes cannot be followed effectively by genetic adjustment (adaptation) of the population. 2. Plasticity is similarly favored if spatial environmental differences appear on a much finer scale than the size of effectively mating neighbourhoods within the species' range – the latter being determined among others by the migrative potential and the genetic system.

Apart from other issues, the question of plasticity gained actuality with the raising issue of climate change and adaptation to it. The study of adaptation to different environments embraces both ecology *and* genetics (this is reflected also in the denomination of this interdisciplinary field: *ecological genetics* or *evolutionary ecology* respectively).

Plasticity represents a fast growing field in biological research, however with some constraints: the overwhelming majority of studies are conducted with genetically screened, sometimes cloned material in controlled, laboratory conditions, mostly with animals of small body size (such as *Daphnia*, *Caenorhabditis*, *Drosophila* sp.) or with microorganisms.

Plasticity is especially promoted by the sessile nature of plants. In contrast to animals that will move in space to avoid unfavourable environmental conditions, plants may buffer the changes by adequate phenotypic response. The well known and often cited studies of Clausen

et al., Bradshaw and Antonovics analysed natural populations of plants, but the investigated perennials and especially annuals „perceive” their environment on a completely different temporal and spatial scale than long-lived trees. Local adaptation and low plasticity has been demonstrated in response to a number of strong selection agents against plants such as toxicity of soil, maritime exposure, clipping and grazing, use of herbicides etc., however exclusively on herbs (Linhart and Grant 1966). (In addition, the suspicion may arise that clonally reproduced groups instead of true populations have been observed.)

Most traits showing plasticity in changing environments contribute to fitness. In plants, and especially in trees, size (height) is one of the most important fitness components. It could be shown (Mátyás and Varga 2000) that size-generated plasticity responds clearly to changing competitive situations also in trees, by favouring reproductive capacity over growth in low-competition situations (allometric change). Therefore the use of height growth response to analyse plasticity is certainly justified.

Given the fact that economically important forest trees are managed in generation cycles of hundred and more years, and that adaptively homologous areas (AHA's, Mátyás 2004) are presumed to be on a scale of tens, even hundreds of kilometers, both temporal and spatial heterogeneity in climate and site conditions must have generated a high level of plasticity in forest trees.

For this reason common garden tests with natural-state populations of forest trees offer highly valuable, even unique opportunities to investigate responses of a life form with extremely long generation times, incomparably high within-population genetic variability and heterozygosity, and by area and numbers, immense population sizes (AHA's).

There are relatively few studies of provenance tests of forest trees endeavouring on ecological genetic analysis of adaptive response (e.g. Mátyás and Yeatman 1992, Mátyás 1994, Rehfeldt 2003 and earlier studies, for review see Morgenstern 1996). Common garden datasets are well suited for analysis of adaptation and response to changing conditions. The growth and survival of natural populations in changed environments of common garden tests can be interpreted as a simulation of anticipated changes on a selected location. The idea of transfer analysis, i.e. modeling of responses and forecasting responses to scenarios based on provenance data has been proposed originally by Mátyás (1994). *The calculation of regressions height response versus ecological distance (i.e. ecologically / climatically interpreted distance of transfer) provides estimates of the norm of reaction and is an indication of plasticity.*¹

In the followings a case study of Scots pine is presented; a species with extreme parameters: the largest distribution area among forest trees, with a very effective gene flow and negligible discontinuities within the area limits. Propagation by seed is simple, economic importance is high and therefore it is no wonder that Scots pine became one of the flagships of provenance studies in forestry from the early days on.

Case study: transfer analysis of Scots pine

Scots pine (*Pinus silvestris* L.) has served for large scale provenance studies numerous times. An experimental series on the largest scale has been initiated by the late Y.P. Prokazin of the All-Soviet Research Institute of Forest Melioration (VNIILM). Between 1973 and 1975 a total of 110 provenances have been outplanted at 44 locations in the one-time Soviet Union and at 3 locations in Hungary (not all provenances are represented at every location). Results

¹ It has to be pointed out that the environment-dependent height response of genetically different populations is the broadest possible interpretation of plasticity.

of height growth measurements and survival data have been published after two decades for a large number of „Soviet” test locations by Shutyaev and Giertych (1997).

A detailed analysis of the VNIILM data with respect to climatic response was carried out by Rehfeldt et al. (2003). They used all available data of 36 tests in Russia and also North American results.

In the present paper the goal was set to investigate the response of populations in a relatively restricted climatic-geographic range in Russia, where locations close to the lower distribution limit were duly represented (Table 2), which puts the emphasis on responses closer to the southern limits of distribution.

Table 2. Experimental locations of the VNIILM test series analysed in the present paper

Expt. No.	Government district	Location	Decimal geographic		Temp. sum of veget. period (STVEG)
			latitude N.	longitude E.	
17	Voronezh	Davidovka	51.00	39.00	57.5
18	Penza	Lunino	53.00	45.00	47.5
26	Kurgan	Zeverinogolovsk	54.78	64.97	45.0
22	Tatarstan	Zelenodolsk	55.00	52.00	42.5
24	Perm	Kungur	57.43	56.75	35.0
25	Ekaterinburg	Revda	56.83	59.97	32.5

Climatic data for the sites of origin of the tested provenances, as well as for the test sites have been determined (in absence of other reliable data) from monthly average precipitation and temperature maps for Eurasia, compiled by the World Meteorological Organisation². The following data have been selected or calculated from the monthly averages:

- Annual mean temperature
- Range of monthly temperature means (indicator for continentality)
- Sum of monthly average temperatures above 5°C in the vegetation period (STVEG)
- Sum of temperature means of summer months
- Sum of temperature means of winter months
- Negative sum of months with temperatures below 0°C
- Annual mean rainfall
- Sum of precipitation of the vegetation period
- Precipitation sum of months above 15°C mean temperature
- Sum of precipitation in winter (accumulation) months
- Monthly moisture index: $\Sigma(P/3-T)$ calculated from monthly precipitation and temperature averages

The 95 provenances analysed in the six tests cover the whole distribution of Scots pine in the one-time Soviet Union, from the Baltic to the Russian Far East. The range of the vegetation period length (STVEG) extend from 10.0 (Bratsk) to 65.0 (Volgograd) degreemonths (the values for tests sites are presented in Table 2).

In the analysis, height of provenances measured at age 17 has been processed as *relative heights, expressed in percents of height of the local, adapted population* at the experimental site. These data have been used to compare responses of the same provenances at the 6 selected locations and to compensate for the effect of different site potentials of the test sites.

² Monthly averages were used because these are the only available standard data which are comparable to areas outside the Soviet Union. Our dataset contains a number of other (European) sources as well (not shown here)

Results

Provenances have been grouped by the STVEG data at their location of origin. The medium group B ($30 < \text{STVEG} < 45$) had most observations (Table 4), its data are therefore the most reliable.

Correlation coefficients relative height vs. changes of climate components (Table 3) indicate that sensitivity of Scots pine to changes is significantly higher for temperature than to precipitation. Highest correlations were calculated for temperature changes during the growth period, such as heat sum in the vegetation period or summer temperature mean.

*Table 3. Correlation of relative heights at age 17 versus climate component ecodistances³ i.e. actual change; provenances grouped by STVEG temperature sum at location of origin (**bold values are significant at $P = 5\%$**)*

Climate component ecodistance (actual change)	northern (A)	central (B)	southern (C)
	correlation coeff. (r) of group		
Annual mean temperature	0,58	0,68	0,36
Range of monthly temperature (continentality)	-0,26	-0,33	-0,39
Temperature sum in the veget. period (STVEG)	0,69	0,84	0,43
Sum of temperature means of summer months	0,64	0,81	0,42
Sum of temperature means of winter months	0,42	0,54	0,50
Negative sum of temperatures below 0 °C	0,47	0,60	0,53
Annual mean rainfall	-0,24	-0,38	-0,11
Precipitation mean of months above 15°C	0,59	0,60	0,27
Sum of precipitation of the vegetation period	-0,33	-0,41	-0,16
Sum of precipitation in winter months	-0,02	0,10	-0,24
Moisture index	-0,42	-0,66	-0,26

Changes in precipitation show also significant effects, but to a less extent; e.g. the effect of winter rainfall changes on growth seems to be minor. Highest correlation was found with precipitation changes in the warm months ($T > 15^{\circ}\text{C}$).

Negative correlation values for precipitation, moisture index and continentality need an explanation: in the investigated part of distribution, moisture supply and continentality is increasing north- and eastward. Transfers to milder environments have therefore an inverse effect on increment and growth.

The comparison of responses of populations from the central zone with the northern boreal ones shows that response are essentially similar, with somewhat lower statistical reliability due to lower number of observations. The same comparison with the southern group indicates differences in response, which is a result of opposite transfer: these populations have been moved mostly northward to the trial locations (see STVEG data in Table 4). For these populations changes in winter temperatures and winter precipitation seem to be more important than for the others (Table 3).

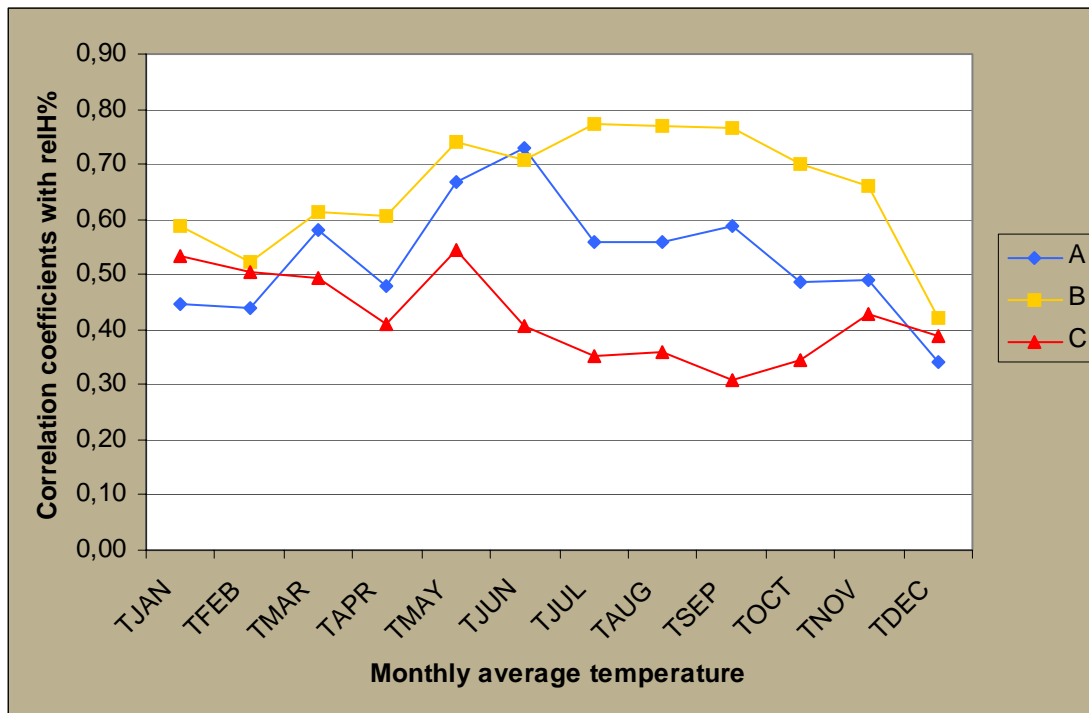
A more detailed view on the „perception” of temperature and moisture conditions in the annual cycle is provided by correlation values of monthly means. Figure 1 shows that temperature data of May to October correlate the strongest with height growth of transferred populations, at least for the central group. Provenances from the mildest part of the investigated area (group C) however, seem to be somewhat less sensitive to temperature changes.

³ difference of value at site of origin minus value at test location

Table 4. Effect of change of temperature sum in the vegetation period (STVEG) on relative height performance of populations in 6 tests (see also Figure 3)

Provenance group	Number of observations (N)	Mean of STVEG change	R ²	<i>Equation</i>
			of regression STVEG change vs. relative height	
Northern (A)	29	- 27.5	0.471	0.88 + 96.6
Central (B)	176	- 5.54	0.700	1.00 + 99.1
Southern (C)	72	+ 5.14	0.188	0.68 + 89.6

Figure 1. Correlation between relative height growth of the transferred populations (in percents of locally adapted) and changes in monthly average temperatures, by zone groups



In Figure 2 correlations with monthly precipitation changes are presented. It is obvious that these data support again the generally lower sensitivity to precipitation changes (of course this might be somewhat enhanced by the lower reliability of rainfall data interpolations). For the central group summer precipitation (June-August) appears as most significant. Southern populations transferred into harsher environments react to increases of January precipitation the strongest.

Coefficient of determination for height growth with temperature sum change due to transfer is relatively strong for pooled data ($R^2 = 0.54$) and even stronger if calculated for the central group B ($R^2 = 0.70$; Table 4). Figure 3 shows the linear regressions calculated separately for provenance groups A, B and C. Height growth expressed in percents of height of the local provenance shows a clear downward trend with growing ecodistances towards warmer and drier environments. *In other words, transferred provenances experiencing rising temperatures are increasingly inferior to locally adapted populations.* Growth performance compared to the locally adapted populations improves at the same time if provenances are transferred into cooler conditions – an effect of obviously improved moisture supply, even if moisture plays a secondary role in responses.

Figure 2. Correlations between relative height growth of the transferred populations (in percents of locally adapted) and changes in monthly average precipitation, by zone groups

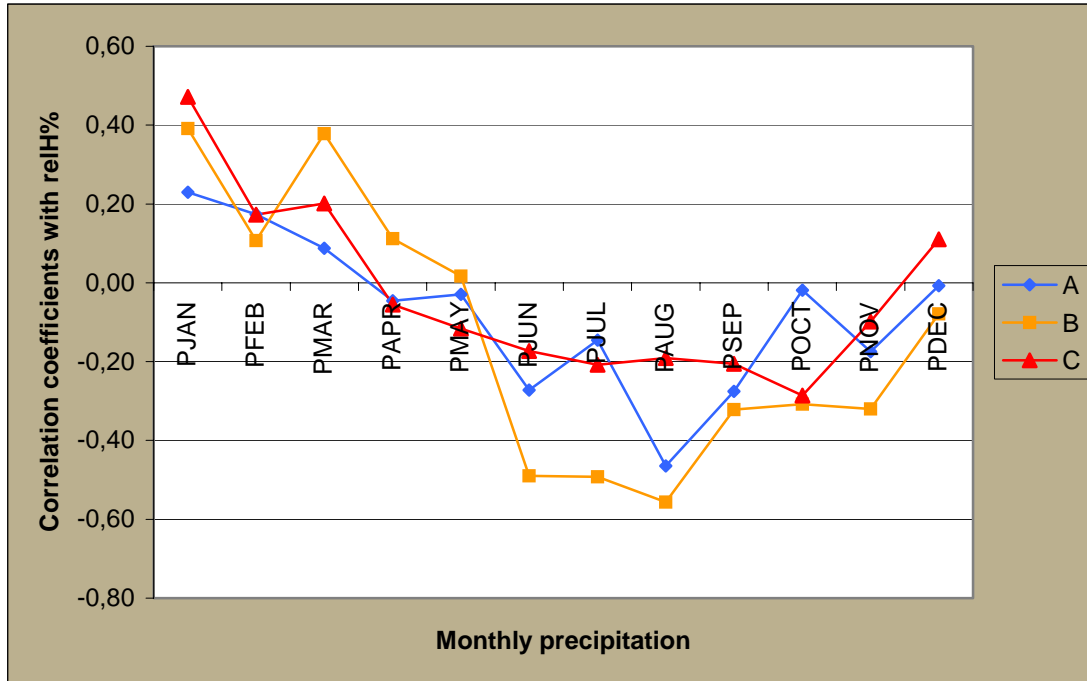
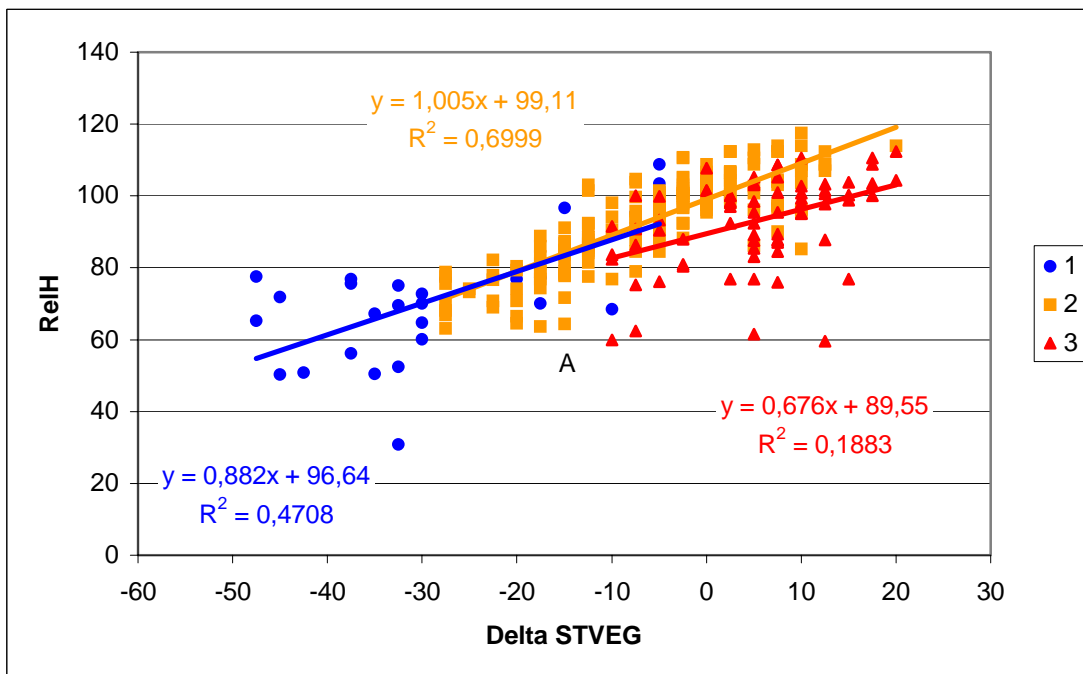


Figure 3. Linear regressions relative height vs change of temperature sum due to transfer (delta STVEG) by groups of provenances (1: northern, 2: central, 3: southern group)

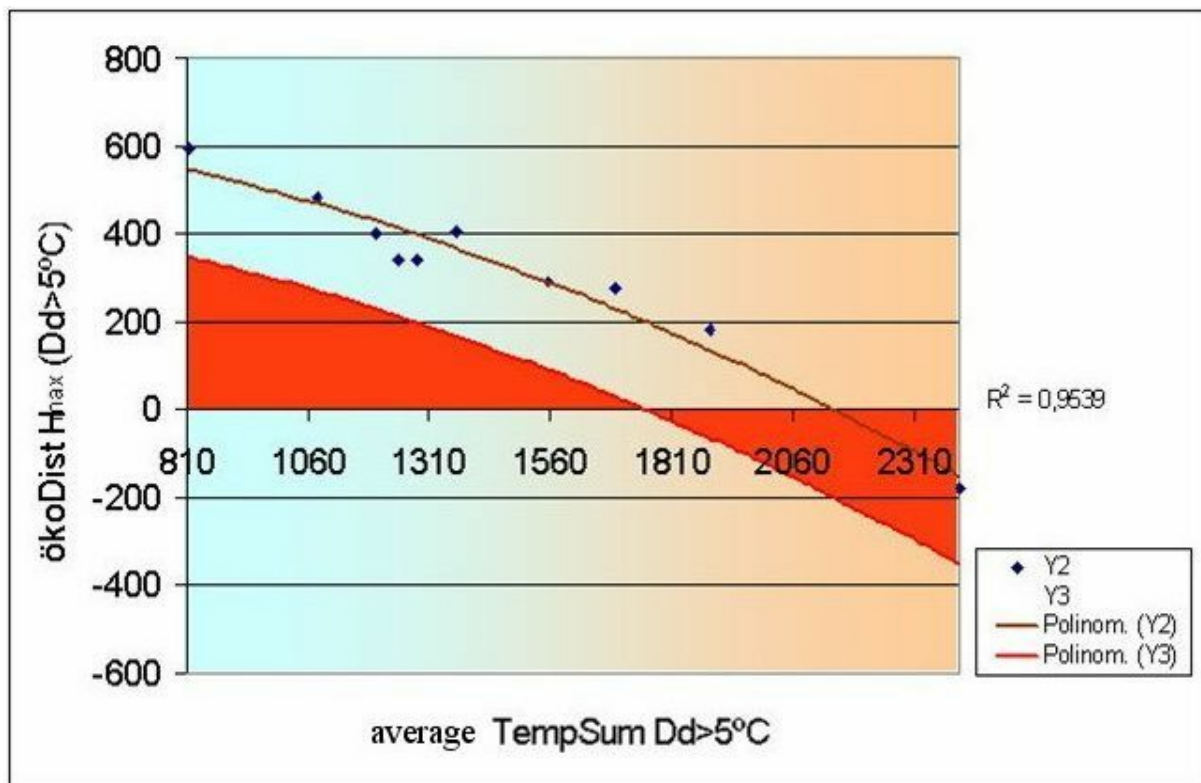


An estimate for the transfer distance, where local populations are theoretically equally performing than transferred ones may be calculated from the regression equations. E.g. for

group B it is a site 6.89 degree-months cooler than the origin, which is a transfer distance of approximately 2 degrees of latitude (see STVEG values in Table 2).

What does this mean *in concreto* with respect to growth and performance of populations in environments experiencing gradual changes in climate? To answer this question, results of Rehfeldt *et al* (2003) have been processed further. Analysing the same set of populations, Rehfeldt and his co-workers calculated transfer functions developed from Weibull regressions of height response to changed climatic conditions for 36 test sites in Russia. The transfer functions of measured (absolute) heights are curvilinear. The optimum value is measured at locations other than the original site, which has been attributed by Mátyás (1990) to adaptation lag, a general feature of transferred populations. Rehfeldt also found that „most populations inhabit climates either cooler ... or warmer than their optima and benefit from a transfer”.

Figure 4. Response to an “annual temperature rise of +200 degree-days” change scenario along an ecological transect of differently adapted populations (see explanation in text)



Using Rehfeldt’s calculated maximum heights for the optimum transfer and the temperature sum differences belonging to these values, we constructed a response curve for maximum height performance (Figure 4). The curve (Y2) was calculated from average responses of groups (dots in figure) which represented provenances from sites with different temperature sums from 810 to 2310 average degree-days above 5°C. The response is expressed in temperature difference between site of origin and site of maximum height performance (ökodist H_{max}). Figure 4 shows that these sites of maximum growth performance are found in milder than original environments toward the upper (cooler) end of the distribution. On the other hand, close to the lower end of distribution the maxima are found at cooler sites.

Through the lowering of the regression line by 200 degree-days (Y3 in Figure 4) we have simulated a virtual climate change scenario where the temperature conditions increased

uniformly by this value, which might equal to approx. 0.5 °C annual temperature rise. As populations stay in place, the ecological distance to the maximum performance points diminish accordingly by 200 degree-days. The shaded areas represent the still existing performance difference between locally adapted and transferred populations. These indicate that on the northern limits of distribution (left side of the graph) further temperature sum may be added through transfer to achieve maximum performance, while on the southern limits (right side) populations perform much below their potential at the site of origin.

If one bears in mind that Rehfeldt's data set contains more northern-continental test site observations than ours, the comparison of the response curve with Figure 3 shows strong similarities.

Discussion and summary

From a genetic viewpoint, response to climatic changes is an adaptation and – in a wider perspective – an evolutionary problem. Fundamental basis of genetic adaptation is the genetic variability in natural populations. Adaptedness may be characterised by growth traits, first of all by height at a given age. If adaptation to changed conditions happen without significant selection within a generation, than *adaptation through plasticity* is involved.

Results of the transfer analysis show the remarkable width of adaptability (and, in consequence, the extended width of „local” adaptation) to even dramatic changes in thermal conditions, photoperiod and, to a less extent, in moisture supply. This phenomenon indicates the substantial conservatism in climatic adaptation of Scots pine, shared also by other conifers (e.g. *P. banksiana*: Mátyás and Yeatman 1992), which has inherent genetic reasons and may have been enhanced by evolution. This conservatism is supported by the presumably polygenic character of quantitative traits (Kremer 1999), hindering a more precise phenotypic adjustment.

An important outcome of the transfer analysis results is the asymmetry of the response: the regression line does not cross 100% relative height at 0 ecodistance value for relative height data (Figure 3).

The results indicate, that *the response of populations in different parts of the distributional range are divergent*, as different climatic factors exert their selection pressure. The boreal limit of distribution is temperature-dependent. Populations close to the upper limit show their maximum performance in much warmer conditions. The transfer distance to the (warmer) maximum diminishes with increasing temperature sum.

At the lower limit of distribution, drought stress is the main controlling factor. Transfer toward cooler climate (= better moisture supply) results in accelerated growth. Transfer distance to optimum diminishes with decreasing thermal values.

Accordingly, *the reaction of indigenous populations to changing conditions will be different* by climatic zones. In the northern-boreal zone, expected rise of temperature will lead to a strong growth acceleration for Scots pine without any significant genetic change. In the temperate-maritime zone, growth will accelerate too, along with higher temperatures and increasing or at least unchanged rainfall.

In the temperate-continental zone however, even relatively minor temperature increases, coupled with growing drought stress, will trigger loss of compatibility, higher susceptibility to diseases and increase of mortality – a selection of tolerant individuals. In semiarid climates at the lower forest limit mass mortality may lead to local extinctions and shift of distribution area northward, or upward in altitude.

Expectable genetic changes will be minor not only due to the speed of forecast changes. At least in the northern part of the range *improved growing conditions can be utilised through the plasticity potential of populations*. As inherited plasticity will determine the response to

changes, there is little room left for genetic adaptation. The stability of temperate-Atlantic populations will also be well buffered by their adaptability. *In drought stress climates increment loss and higher frequency of diseases and pests* will challenge the economy of forest operations and will put emphasis on maintenance of ecological functions and conservation of stability and of genetic resources.

Post-script: are silvicultural mitigation measures necessary?

The above conclusions have far reaching consequences with respect to timber yield and also carbon sequestration, however genetic aspects have not penetrated yet most climate change studies. Here only the question of necessity to prepare mitigating measures in forestry is briefly highlighted. Some scientists (e.g. Hamrick 2004) argue that no silvicultural measures will be needed to mitigate the effects of changing conditions because

- there is enough genetic variability in the populations, which might be further replenished by migration;
- regeneration is secured through the persistence, phenotypic plasticity and long life cycle of forest tree populations;
- paleoecologic data indicate that enough variation accumulates and is saved in refugia, and the selection pressure of recent climatic fluctuations was without effect;
- genetic adaptation may happen in relatively short periods, 2-3 generations.

These arguments may be valid first of all in boreal regions with predominantly nature-close conditions, where human land use had no serious impact yet. In nature conservation areas, national parks cyclical changes of vegetation do not pose serious threats as long as ecological space for retreat is available. In landscapes and regions transformed by humans there is however no room left for such fluctuations, especially not close to the lower distribution limits of a vegetation type or a species (this is a frequent misconception of many models counting with spontaneous buffering processes). And last not least, consequences of response to changes on forestry are left completely unconsidered.

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Summary

Transfer analysis of Scots pine shows the remarkable width of adaptability to even dramatic changes in thermal conditions, photoperiod and, to a less extent, in moisture supply. This phenomenon indicates the conservatism in climatic adaptation of conifers, which has inherent genetic and evolutionary reasons.

The results show that the response of populations in different parts of the distributional range is divergent, as different climatic factors exert their selection pressure. Accordingly, the reaction of indigenous populations to changing conditions will be different by climatic zones. In the northern-boreal zone, expected rise of temperature will lead to a strong growth acceleration for Scots pine without any significant genetic change. In the temperate-maritime zone, growth will accelerate too, along with higher temperatures and increasing or at least unchanged rainfall.

In the temperate-continental zone however, even relatively minor temperature increases, coupled with growing drought stress, will trigger loss of compatibility, higher susceptibility to diseases and increase of mortality. In semiarid climates at the lower forest limit, mass mortality may lead to local extinctions and shift of distribution area northward, or upward in altitude.

As inherited plasticity will determine the response to changes, there is little room left for genetic adaptation. In drought stress climates however, resistance selection, increment loss and higher frequency of diseases and pests will challenge the economy of forest operations and will put emphasis on maintenance of ecological functions and conservation of stability and of genetic resources.

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