Modeling climate change effects with provenance test data

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Summary

Provenance tests of forest trees, which were originally intended to identify suitable seed sources for planting at different locations, provide valuable data for assessing the response of populations to environmental change. Environmental differences between the location of origin and the planting (test) site have been calculated by principal component analysis and termed ecological distance. Based on ecological distance values, the growth response of tree populations can be modeled as a function of the test site macroclimate. These models can then be used to predict the effects of climatic change on growth and survival.

The growth response model predicts that increasing annual mean temperatures will result in accelerated growth if precipitation is sufficient, but only within the limits characteristic of the species. At the southern limits of distribution, growth and competitive ability of the species will decline, leading to successional changes.

Keywords: adaptation, distribution, ecological distance, growth, species survival, successional change.

Introduction

Climate changes have always accompanied evolution and to a large extent are responsible for it. There is even evidence that some paleoclimatic changes might have occurred at a rate similar to those forecast for the near future (Fairbanks 1993, Table 1). Forest trees, especially conifers, that have been evolving for hundreds of million years have survived these changes and some populations may be regarded as witnesses (relics) of such scenarios.

The predicted climate changes as a consequence of anthropogenic interference with atmospheric processes are of serious concern. Comparative studies of the

Table 1. Temperature differences of monthly means for July–August (in °C) between predicted climates (respective similar paleoclimates calculated by Budyko and Izrael (1987)) and the present zonal climates at different latitudes on the Northern Hemisphere (Farago et al. 1991).

Expected year and respective paleoclimate	Latitude (° N)					
	80–70	70–60	60–50	50–40	40–30	30–20
2000 AD (approx. 4000 B.C.)	4.4	3.0	1.9	1.0	0.3	−0.2
2025 AD (approx. 125000 years ago)	6.0	4.8	2.8	1.6	0.3	−0.2
2050 AD (approx.3.3–4.3 million years ago)	10.3	6.5	5.4	4.1	2.3	1.1

growth and productivity of populations in different environments provide a valuable tool for examining the nature of changes in biomass production and stability of forest ecosystems as a result of an altered climatic environment. For many years, foresters have been establishing such comparative plantations for the evaluation of provenances. The investigation of genetic variation among forest tree provenances has a tradition dating back to Vilmorin's experiments in Les Barres (1823) (Langlet 1971). The establishment and analysis of provenance tests are probably among the most important contributions that forestry has made to the natural sciences. Unfortunately, little of the knowledge available from provenance tests has been used in related scientific fields, unlike recent findings concerning the ecological genetics of herbaceous plants (e.g., Clausen et al. 1948).

Construction of growth response models

Provenance tests were originally intended to identify seed sources suitable for planting at particular locations. They have been used to describe intraspecific differences (taxonomy) and to study certain genetic phenomena (including phenotypic flexibility, genotype–environment interactions and ratio of inter- to intrapopulation variation). The performance of different seed sources also serves as a basis for delineating seed (planting) zones and breeding zones (Raymond and Namkoong 1990, D. Lindgren, unpublished observations).

As a result of adaptation to local conditions, the performance of populations transferred to a given environment (the test site) shows a certain correlation with ecological characteristics at the site of origin. Numerous authors have developed analytical approaches to predict expected performance based on ecological characteristics at the site of origin.

In general, the growth performance of populations originating from different parts of the species' range can be described by a simple polynomial as a function of an important environmental parameter, e.g., geographic latitude. Because variation patterns are strongly influenced by altitudinal gradients, geographical clines are difficult to trace in mountainous regions (Figure 1). The correlations are improved if elevational effects are excluded, thus species with a basically planar distribution are best suited to illustrate these effects, e.g., Scots pine (*Pinus sylvestris* L.) or jack pine (*Pinus banksiana* Lamb.).

The response regression polynomials usually display a gradual clinal variation, where a number of provenances show similar or better performance than the local population. Provenances may outperform local populations for a number of reasons (Namkoong 1969), including genetic constraints on the adaptability of local populations (Rose et al. 1987). Except for test sites close to the northern distributional limit of the species, highest yield values at the test site are achieved by populations originating from milder environments. Applying the lag–load concept for relative deficiency in fitness (Maynard Smith 1978), the inferiority of local populations in terms of growth and yield is defined as an adaptation lag (Matyas 1990, 1991). Because of this lag effect, the response polynomial is usually not symmetric as

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N = 252
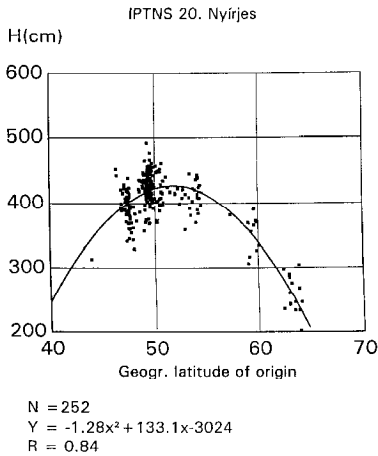Y = -1.28x² + 133.1x-3024
R = 0.84

Figure 1. Average height of Norway spruce (*Picea abies* Karst.) provenances in the IUFRO 64/68 test at age 10 in Nyirjes, Hungary (Experiment No. 20, Ujvari and Ujvari 1994). The graph shows data for sources between 15° and 20° E longitude as a function of latitude of origin (horizontal axis). The broad scatter of points between latitudes 47° and 51° N illustrates the effect of elevation (sources from the Alps and the Carpathians).

proposed, e.g., by Ujvari and Ujvari (1994) and Lindgren (unpublished observations), but is steeper toward milder environments. By introducing more than one environmental parameter, regression surfaces can be constructed (Namkoong 1979). Such response regressions have been applied to seed source studies (Kung and Clausen 1984).

Flexibility of response models can be improved by combining data from different planting sites. For this purpose, the calculation of ecological distance or ecodistance has been proposed (Matyas 1987). The effect of environmental change on a provenance planted at a given location can be expressed as the difference between the ecological characteristics of the test site and the site of origin. The main environmental (climatic) parameters determining growth response differences among provenances are heat sum, humidity and latitude. Because these parameters are usually confounded, principal component analysis can be applied to integrate the effects of more than one parameter. The principal component values calculated from parameter differences between the site of origin and the test site are termed ecological distance or ecodistance. Accordingly, at any test site, the local source takes the value of zero ecological distance, sources transferred northward take negative values, and sources transferred southward take positive values, depending on the direction and distance of transfer. Thus, ecological distance is a measure of environmental change for transferred populations, expressed as the difference in ecological characteristics between the site of origin and the test (planting) site (Matyas and Yeatman 1992).

In addition to ecological distance, the climatically determined site potential of the location (characterized by the growth of the local source) also significantly influences the average growth performance and between-provenance variation (i.e., on good sites, growth differences among provenances are enhanced, whereas on harsher

sites, growth differences among provenances are minimized). The two variables, ecological distance and site potential, provide the basis for determining a three-dimensional model of growth response, where the data of test sites are pooled. Because genotype × environment interactions are negligible in such wide-range studies, the response of individual provenances over test sites is more or less linear resulting in a regression surface of relatively low complexity (Figures 2 and 3).

Theoretically, this technique allows an approximate prediction of the performance of any source transferred to any location (Matyas and Yeatman 1992). Nonclinal genetic variation and differences in phenotypic stability appear as deviations from
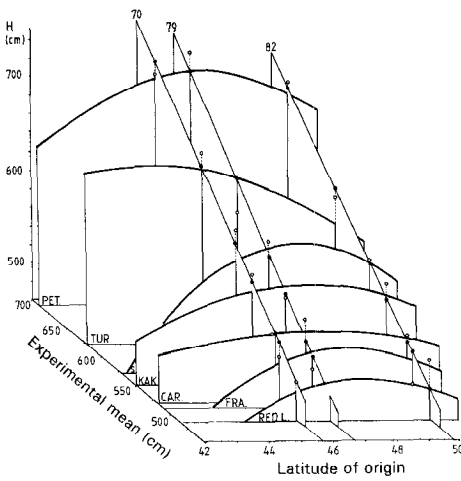

Figure 2. Height response curves of 15-year-old jack pine (*Pinus banksiana* Lamb.) provenances in seven Ontario experiments (Petawawa (PET), Turkey Point (TUR), Swastika (S), Kakabeka (KAK), Caramat (CAR), Fraserdale (FRA) and Red Lake (RED L.)) as a function of latitude of origin (horizontal axis). The test sites are arranged on the basis of the experimental means, scaled on the diagonal axis. Expected (●) and measured heights (O) of three sources (No. 70, 79 and 82) illustrate the approximately linear response to changing environmental conditions.
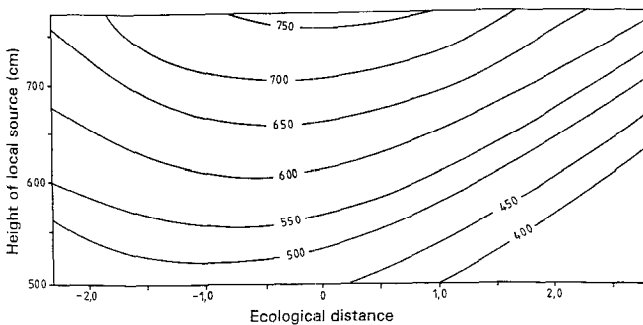

Figure 3. Contour plot of expected source heights of 15-year-old jack pine (*Pinus banksiana* Lamb.) from experiments in Ontario as a function of site potential (height of local source) and transfer distance (ecological distance).

the predicted performance.

Application of the model to predict effects of climate change

Because the growth response to geographic transfer can also be used to simulate climate change effects, the model can be used to predict performance directly. In the following application of the model, I have used the jack pine (*Pinus banksiana* Lamb.) data described in detail by Matyas and Yeatman (1987, 1992). The experimental series analyzed had eight test sites across Ontario, with 56 sources originating mainly from Ontario, western Quebec and adjacent areas in the United States. The model was constructed for average heights of sources, measured at 15 years of age. Figure 3 shows the calculated response regression surface. The interpretation of ecological distance values in terms of heat sum and latitude differences is given in Figure 4.

The practical application of the model is illustrated by the growth responses of provenances identified as local sources at three Ontario test locations: Turkey Point, Petawawa and Swastika. (Some important data about the locations are listed in Table 2.)
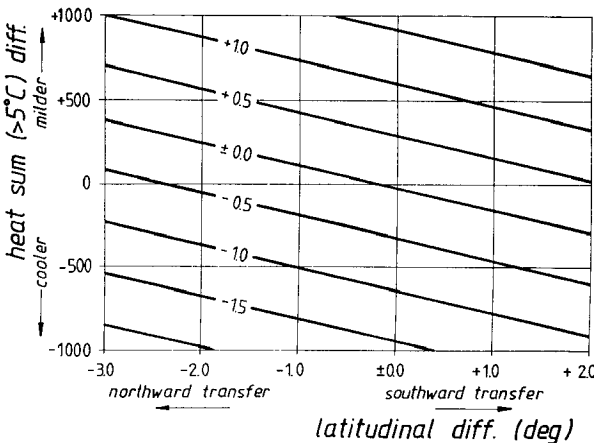

Figure 4. Graph of ecological distance values calculated for the jack pine (*Pinus banksiana* Lamb.) experiments in Ontario. The heat sum and latitude values refer to differences between the origin of the population and the test site (from Matyas and Yeatman 1992).

Table 2. Data for three jack pine provenance test sites in Ontario.

Test location	Latitude (° N)	Average annual temp (°C)	Precipitation (mm)	Annual heat sum (> 5 °C)	Ecological distance from Petawawa
Swastika	48.0	1.3	856	1450	−1.17
Petawawa	45.8	5.3	812	1900	0
Turkey Point	42.8	9.2	888	2200	+1.1

Information about the sources selected as local at the three test sites is presented in Table 3. The southward transfer of local sources to the respective test sites provides an indication of the expected growth changes at least for the juvenile growth period (10–20 years). There are indications that adaptation to changed climatic environment may improve with maturation, which may result in diminishing increment differences between local and transferred populations as has been observed in older provenance tests (Beuker 1994).

Taking the scenario of 2050 AD (Table 1) for latitudes 40° to 50°, Farago et al. (1991) predict an increase in summer temperatures of about 4 °C. The annual mean temperature differences between the Petawawa and Swastika locations, and between the Turkey Point and Petawawa locations are similar (Table 2).

The southward transfer of source Gowganda Lake from its local environment in Swastika to Petawawa, where the annual mean temperature is 4 °C higher and the heat sum increases by 450 degree days (above 5 °C), corresponds approximately to the temperature scenario predicted. The ecological distance calculated for the transfer is +1.17. The average height of the Gowganda Lake source measured in Petawawa was 729 cm at age 15 (expected value was 690 cm), which equals a height growth increase of approximately 20% compared with the original location in Swastika (Table 3). Compared with Swastika, Petawawa offers conditions close to optimum for jack pine and these conditions were obviously utilized by the Gowganda population which originated from a more limiting environment. The mean height of provenance Gowganda Lake at Petawawa (729 cm) was not significantly different from that of the local source (726 cm).

The transfer of the local source from Petawawa to Turkey Point at the southern distribution limits of the species is not such a favorable change in environment. The 300 degree day increase in temperature sum resulted in a height loss of 20%; the mean height was only 604 cm (expected value was 585 cm), which was significantly below the height of the selected local source (646 cm).

Based on a comparison of the height growth response of the population moved southward within the area of distribution (Gowganda Lake) with the growth response of the population that was transferred outside the area of distribution (Petawawa population planted at Turkey Point), it is evident that an increase in temperature affects growth positively only within the physiological and ecological tolerance limits of the species. Temperature changes exceeding this limit will obviously lead to losses in production and, in more extreme cases, to increased mortality. Such effects may be expected at the southern limits of the species' distribution area.

Table 3. Data for the sources selected as "local" at three test sites in Ontario (na = not available).

Test location	Source	Latitude (° N)	Precipitation (mm)	Annual heat sum (> 5 °C)	"Local" height (cm)
Swastika	Gowganda Lake	47.7	800	1460	606
Petawawa	Petawawa	45.8	812	1900	726
Turkey Point	Marl Lake	44.5	na	2090	646

Increased temperature sum and unfavorable humidity conditions will decrease the competitive ability of the species leading to successional changes. This is a particular problem at the woodland–steppe (prairie) ecotone, where the existence of forests is endangered (Matyas 1992).

The model has limitations. One serious drawback is that, at the time of planning and establishing the earlier provenance experiments, the importance of selecting and including truly local seed sources in the tests was not foreseen. Therefore, local sources are missing in some tests and the nearest stand has to be considered the local source (see also Schmidtling 1994). Furthermore, the predictions do not take account of the fact that transfers are accompanied by changes in photoperiod, the exact effect of which is not to known (Beuker 1994). The reliability of available climatic data and their relevance to the growth of forest trees is also limited for many locations, because of the lack of nearby meteorological stations, and inadequate information about altitude and microclimate effects.

Despite these shortcomings, the value of provenance tests should not be underestimated. They provide growth and yield data for long time series that cannot be generated otherwise. The responses of these tree populations to sudden environmental changes indicate the extent of genetic and physiological buffering that has evolved through millennia of evolution and adaptation.

Acknowledgments

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