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Beech adaptation to climate change according to provenance trials in Europe

Doctoral (PhD) Dissertation

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Beech adaptation to climate change according to provenance trials in Europe

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Abstract

Beech adaptation to climate change according to provenance trials in Europe

Based on common garden experiment data, using a mixed-effect modeling approach, the 9-year-old height growth response of beech populations to changes in climate has been modelled. According to climate zones of origin, populations were divided into three groups (Alpine, Atlantic and continental) and separate height growth response models were created. Winter minimum temperature has been identified as main climate factor to determine the mean performance of the Atlantic provenances. Provenances adapted to colder winters performed generally better across the sites, their performance was more stable than of others. In terms of ecological distance of transfer of Atlantic provenances, the change in Ellenberg drought index was one of the most significant parameter. In case of the continental group the climatic moisture deficit showed the strongest relationship with the mean performance of provenances. The ecologically marginal populations (with too low or too high climatic moisture deficit) performed poorer than populations from optimal climate conditions. The effect of climatic transfer was best described with the difference in maximum temperature in April.

By projection the early survival and height growth data, the group of the best performing provenances was determined at the Hungarian trial site, Bucsuta. The transfer function showed that the magnitude of changes slightly exceeded the adaptability of the local provenance.

The result of phenological observations in Bucsuta confirms the strong geographical trends in beech flushing previously reported. The high variability in this trait refers to an adaptation to the climate of provenance origin. Comparing the mean bud burst of provenances in five different years, it is concluded that warmer winters may delay the bud burst of trees due to the insufficient chilling.

Kivonat

A bükk klimatikus alkalmazkodóképességének vizsgálata származási kísérletek adatai alapján

9 éves bükk populációk klímaváltozásra adott növekedési válaszreakciójának modellezését végeztem el mixed - effect modell segítségével, származási kísérletek adatai alapján. A modellezést a populációk származási helye alapján létrehozott csoportokban (alpin, atlanti és kontinentális) külön - külön valósítottam meg. A modell alapján az atlanti régióba

tartozó származások átlagos teljesítménye leginkább a téli minimum hőmérséklet alapján volt elkülöníthető. Az alacsonyabb téli minimum hőmérsékletű helyről származó populációk jobb és stabilabb teljesítményt mutattak. Az áttelepítés hatása ugyanezen származások esetében az Ellenberg aszályossági index különbségével volt legjobban mérhető. A kontinentális származások átlagos teljesítményét jól meghatározta a származási helyük nedvességi hiány mértéke. A marginális helyzetben levő populációk gyengébb teljesítményt mutattak, mint az optimális klimatikus helyről származók. A kontinentális származások áttelepítése szempontjából az áprilisi maximum hőmérséklet volt a legmeghatározóbb klimatikus paraméter.

A korai megmaradás és magassági adatok segítségével meghatározható volt a legjobban teljesítő származások köre a magyarországi kísérleti helyszínen, Bucsután. Az áttelepítési függvény alapján elmondható, hogy az éghajlatváltozás mértéke már kissé meghaladta a helyi populáció alkalmazkodóképességét.

A Bucsután végzett fenológiai vizsgálatok megerősítik korábbi vizsgálatok eredményeit, miszerint a bükk fakadása határozott földrajzi mintázatot mutat. A fakadásban mutatkozó genetikai változatosság a helyi klimatikus viszonyokhoz való erős alkalmazkodottságra utal. A származások különböző években mért átlagos fakadása alapján kimondható, hogy az enyhébb telek késleltethetik a rügyfakadást az elégtelen hideghatás teljesülése miatt.

1. Introduction

Climate is a major determinant for the phenology, physiology, distribution and development of trees. Current climate change shows a substantial increase in average temperature and change in precipitation patterns, which is significantly changing these processes (IPCC 2014). Successful adaptation of trees in the future depends on how they can cope with these environmental changes.

Long-lived organisms such as trees have to tolerate relatively broad fluctuations of environmental conditions without the chance of escaping to more favorable habitat, therefore there is increased interest to predict the potential growth responses of forest trees to climate change. Common garden experiments provide a powerful tool for studying climate tolerance and population-specific response of trees (MÁTYÁS 1994, 1996). The importance of these experiments lies in their potential to mimic projected climate change effects (REHFELDT ET AL. 1999, 2001, 2002). Reaction norms provide an opportunity to predict the impact of climate change on one population based on data collected on multiple sites of provenance tests.

Dissertation deals with the modeling of adaptive response of one of the dominant tree species in Europe, beech (*Fagus sylvatica* L.). The aim was to construct a prediction of juvenile growth performance across the potential sites within the distribution range, based on the IUFRO provenance trial network. The concept of the analysis was that the growth and vitality of a population at a test site is determined by the inherited adaptation to the site of origin and by the experienced different conditions at the planting site (MÁTYÁS AND YEATMAN 1992).

106 provenances and 31 trial sites were included in the analysis in order to model population height as a function of climate at seed source, climatic transfer distance (i.e. ecodistance) as well as their interaction.

Aim of research and working hypothesis

Climate conditions are major selective forces that result in physiological and morphological adaptation of tree population to local climate. Climate will be warming by average 2°C by the end of the century according to climate models (IPCC 2014). Seed transfer guidelines for reforestation has to be developed in order to avoid sub-optimal productivity and mal-adapted forests in the future. For planning large-scale transfers of forest reproductive material (FRM), the understanding of anticipated changes and delineating suitable seed source regions is needed.

The aims of this study were as follows:

- to assess the adaptive variability of beech at the intraspecific level,
- to define ecological variables which are best associated with vitality parameters of beech,
- to create a model which can describe the growth response of trees to environmental changes,
- to provide concrete data for guidelines for use and transfer of FRM in the future.

The following hypotheses were applied in this study:

- The growth potential of populations from various parts of the distribution area is different, which is the result of long-term adaptation to the past climate at the site of origin.
- Quantitative, adaptive responses measured in common garden experiments can be used to predict the reactions of populations to climate change.
- Survival and growth success of trees in the future depends on how they can cope with the difference between their past, long-term climate and the future environmental conditions.

2. Analysis of adaptation and adaptability – a literature review with special reference to European beech

2.1. Ecological demands of beech and characteristics of its distribution

Beech survived the last glacial period in multiple refuges, the glacial-interglacial cycles left a signature on the genetic diversity of species (COMPS ET AL. 2001, MAGRI ET AL. 2006). The different refuges contributed to different extent to the colonization of Europe. The main refuge areas from where beech likely spread to central and northern Europe are Slovenia, the eastern Alps, the French Alps and south Moravia (MAGRI ET AL. 2006). The surface occupied by beech increased exponentially from the late glacial until about 3500 cal. yr. BP, then slowed down towards an equilibrium (MAGRI 2008).

At present, European beech is a wide-spread forest tree species that spreads from the Atlantic influenced climate in West-Europe to the continentally influenced areas in Central and South-Central Europe. In the northern part of its natural range it is mainly planar phytogeographic element, but in southern part beech is a mountain species.

Minimum temperatures in winter, high temperatures in summer and precipitation are the most important factors limiting the occurrence of the tree, but often the soil may have a similar importance (JEDLIŃSKI 1953 in SULKOWSKA ET AL. 2011). In North Europe, where the climate is colder and more humid, beech populations prefer light, dryer and warmer limestone soils while in the west part of the range they occupy very acid sites (SULKOWSKA ET AL. 2011). In Central Europe, beech is the most competitive tree species on sites with moderate soil moisture and acidity (BOHN 2004). It has been demonstrated that beech seedlings developed much better where soil was rich in calcium, magnesium and potassium (HARLEY 1949, LEPOUTRE AND TEISSIER DU CROS 1979, STICKAN 1988, OOSTERBAAN AND JAGER 1988). Extremely dry sites with flooding and high groundwater levels are less favourable (ELLENBERG 1988).

The distribution limit of many tree species is closely related to growing season temperature and precipitation. The upper/northern distributional limit of species is primarily associated with thermal factors. Minimum temperatures are particularly important in limiting the poleward expansion of plant species (JUMP ET AL. 2009). In contrast to the expanding edge, the rear edge or low-latitude/xeric limit (MÁTYÁS ET AL. 2009b) is understudied. The ecological features, dynamics and conservation requirements of these populations differ from populations in other parts of the range (HAMPE AND PETIT 2005). Available moisture will affect responses to climatic changes: while climatic warming in the northern part of the range, with sufficient moisture, may lead to production increase, at the xeric limit under stressful and uncertain conditions growth depression and vitality loss are expected (MÁTYÁS ET AL. 2009c).

Xylem cavitation resistance is known as a key physiological trait correlated with species tolerance to extreme drought stress. Vulnerability to xylem cavitation of beech is greater compared to oak species or spruce, making it more sensitive to drought (MAHERALI ET AL. 2004). WORTEMANN ET AL. (2011) assumed that beech trees have the capacity to acclimate their hydraulic traits to local climatic conditions by high phenotypic plasticity.

Limited water availability can restrict nitrogen supply enhancing the negative effect of drought (GESSLER ET AL. 2004).

Numerous attempts were made to identify the most influential climatic factors defining the probability of presence of beech (FANG AND LECHOWICZ 2006, CZÚCZ ET AL. 2011, FÜHRER 2010, RASZTOVITS ET AL. 2012), considering the whole range or the lower/xeric part of the distribution.

2.2. Effects of climate change on forest trees

Forest trees exposed to climate conditions outside their climatic niches face risk of productivity loss and increased vulnerability to insects and pathogens.

In the Montseny Mountains in Catalonia the basal area increment (BAI) of beech showed a strong negative relationship with mean annual temperature (JUMP ET AL. 2006). In Central Europe, in Bavaria beech decline have been observed caused by *Phytophthora* disease associated with excessive rainfalls and drought (JUNG 2009). At high altitudes, high temperatures promoted the growth and establishment of beech seedlings, whereas at low altitudes the opposite pattern was seen in Northeast Spain (JUMP ET AL. 2007). Here, the beech forest shifts upwards and is replaced by the more drought resistant Mediterranean holm oak (PEÑUELAS ET AL. 2007). Plant range shifts are most frequently reported from mountain regions compared to the poorly defined latitudinal distributions in the lowlands. Climate dependent zonal forests of lowlands are extremely sensitive to minor changes of climatic factors (MÁTYÁS AND NAGY 2005). Vegetation zone shift may happen due to even small changes in temperature and precipitation (Table 1). For instance, an altitudinal range shift of 10m is predicted to correspond to 10km latitudinal shift based on temperature gradient (JUMP ET AL. 2009).

Table 1: Average temperature and precipitation data of zonal forest belts in the lowlands of the Carpathian Basin, compared to the magnitude of expected changes (MÁTYÁS AND CZIMBER 2000)

	Annual precipitation (mm)	**July temperature (°C)**
Beech zone	734±65.2	19.1±0.95
Hornbeam-oak zone	702±70.3	20.0±0.79
Turkey-sessile oak zone	616±49.0	20.2±0.70
Forest steppe zone	563±49.0	21.5±0.56
Average difference between zones	57	0.8
Expected mildest change scenario in the region	-40	1.1

The xeric limit of closed forest belt, where the predicted frequency of drought events endangers the stability of forest ecosystem, extends across the woodland ecotones of the Mediterranean, Southeast Europe, South Siberia and North America (MÁTYÁS ET AL. 2009b).

Observed mortality events close to the lower (xeric) distribution limit of the species indicate that populations are most threatened close to the xeric limits, especially at low elevations (BERKI ET AL. 2009). Extreme weather events may weaken physiological condition of trees relatively fast and may lead to insect and disease outbreaks also in regions generally suitable for the species. For instance, the prolonged drought period from 2000 to 2004 has weakened trees and resulted on a typical damage chain causing mass mortality of beech in Hungary (LAKATOS AND MOLNÁR 2009). According to regional climate models, beech will lose a large part of its habitat by the end of the century in Hungary and in Serbia (RASZTOVITS 2011, STOJANOVIĆ ET AL. 2013). MÓRICZ ET AL. (2013) showed that only 35% of beech and 75% of present sessile oak area will remain at their current sites by the middle of the century, while Turkey oak (*Quercus cerris*) may occupy large areas of current sessile oak habitat. The same situation is already occurring in Central Germany where the area of beech forest at lower elevation has decreased in favour of oak forests (FRANKE AND KÖSTNER 2007). According to a statistical species distribution model, most of the current beech habitats which are located in the South of France, Italy, ex-Yugoslavia and Greece may become unsuitable by 2050 (KRAMER ET AL. 2010).

2.3. Natural options for adaptation in changing environments

Trees have to withstand large environmental fluctuations during their lifetime and are not able to escape if environmental conditions get worse. Some studies suggest trees will be unable to adapt to projected changes because the rate of climate change is too rapid compared to the longevity of trees (DAVIS AND SHAW 2001) and it is unlikely that they have enough genetic diversity to adapt to the changing environmental conditions (DAVIS AND KABINSKI 1992). According to other opinions, trees have high phenotypic plasticity that allows them to cope with greater environmental changes (REHFELDT ET AL. 2002) and some paleo-ecological studies suggest that large fluctuations in species range have been achieved without loss of genetic diversity (HAMRICK 2004, MAGRI ET AL. 2006).

Annual plants can adapt faster to changing environment due to their short generation time. Species with long generation time and long lifespan need much more time to adaptation because the delayed reproductive maturity will reduce the number of generations and the long lifespan will reduce the opportunity to establish new genotypes which could be able to adapt to changed climate conditions (SAVOLAINEN ET AL. 2004).

Forest tree species have adapted to the long-term (millennial) conditions of their sites where they were growing. This adaptation has occurred at the species and also at the population level. Populations may differ genetically which means that they are partially different in several quantitative characters. Allelic frequency of populations may be altered by natural processes which are not always necessarily promoting adaptation. The only directed process increasing or maintaining adaptation to actual conditions is natural selection.

2.3.1. Natural selection

The selective response to environmental stress is the result of complex processes which is ultimately determined by the fitness of the genotype or population in the given conditions (Figure 1). Several selective forces may operate on forest trees, some simultaneously and some at different life stages or during different seasons of the year.

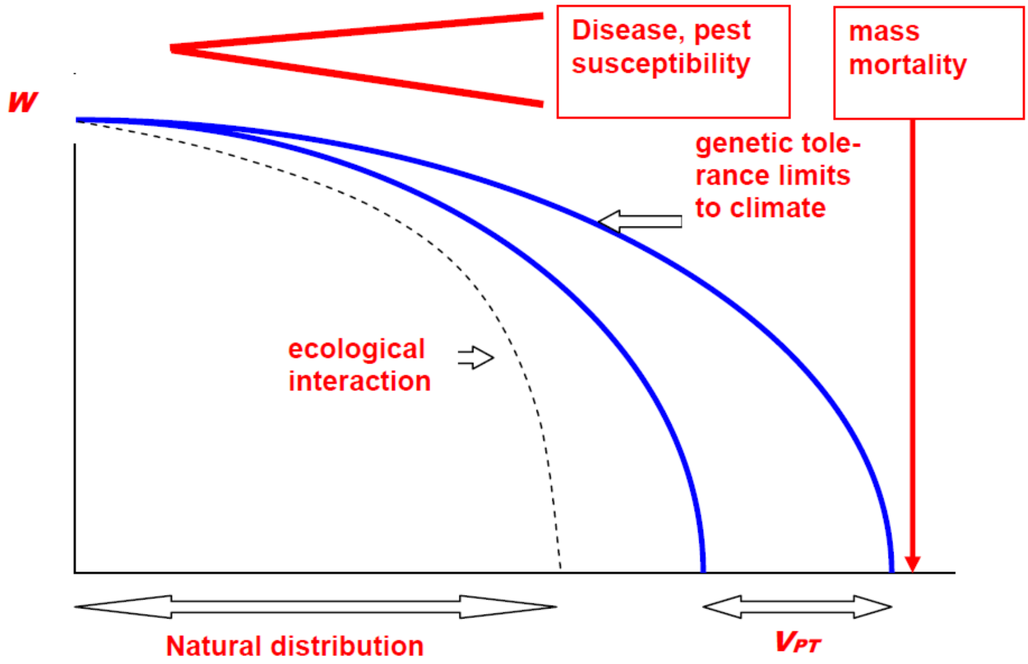


Figure 1: Ecological-genetic hypothesis of fitness change along a climatic cline: tolerance decline and mortality triggered by worsening of climatic conditions. The genotypic variance of limits of tolerance (VG) represents the basis of natural selection. The dashed line marks the ecological limitations of the species (MÁTYÁS 2006)

Natural selection has occurred when individuals in a population can deliver their alleles to the progeny generation more successfully than others. This ability is attributable to a better fitness under the environmental conditions where the population grows (ERIKSSON ET

AL. 2013). In other words, natural selection is a key mechanism of evolution which eliminates the genotypes with low fitness, thus improving the average fitness of a population to changing conditions. Temporal and spatial environmental variability across the natural distribution of forest trees results in within-species differentiation of populations and simultaneously in a continuous shift in gene frequencies or phenotypic values of traits (KREMER 2007). The efficiency of natural selection is detected by provenance tests in which significant variation between populations has been observed for fitness-related traits.

The higher the genetic diversity, the more successful the future adaptation, i.e. the response to natural selection is proportional to the level of genetic diversity (FISHER 1958). Marginal populations could be under stress, the effectiveness of adjustment through selection may decrease and mass mortality may occur (MÁTYÁS 2007). Decline of genetic diversity due to extreme stress was detected e.g. in sessile oak populations in Hungary. Allelic diversity of allozyme loci strongly correlated with severity of climatic stress (BOROVICS AND MÁTYÁS 2013).

Based on phenological variation of conifers in boreal conditions, genetic adjustment to expected climatic changes was estimated as 10 or more generations (SAVOLAINEN 2004). If we calculate 100 years per generation, it would take 1000 years to catch up climatic changes. This balancing effect is far below the rate of expected changes. It has to be noted, however, that selection may be much faster. For instance, extreme occurrence of natural selection has happened at one beech provenance trial in Slovenia (Figure 2). A sudden early snow event at the end of October in 2012 heavily damaged the provenances. The late flushing provenances with prolonged growing season still had leaves on the trees and suffered heavily, in particular the Atlantic provenance, Plateaux du Jura (France, Fig. 2.).

Figure 2: The Atlantic beech provenance ‘Plateaux du Jura’ (France) damaged by snowbreak in Slovenia (photo: Gregor Božič)

2.3.2. Gene flow and migration

Gene flow is achieved by seed or pollen dispersal. In beech, gene flow through seed dispersal is limited (more than 90% of the seeds are situated within 30m of the adult tree) therefore gene flow by pollen is a particularly important mechanism for bringing new genetic variants into a population (KRAMER ET AL. 2008). Seed dispersal may directly contribute to the shift of the distribution area, i.e. to migration.

While populations at higher latitudes expand northwards under climate change, the populations at the southern edge of the distribution range will lose habitat and may go extinct. If gene flow is restricted among population, it can result ecotypic or racial differentiation, however, if gene flow is large, an ecoclinal variation can develop (ERIKSSON ET AL. 2013). Tree species are usually wind pollinators and exhibit in general an abundant pollen flow, nevertheless tree populations typically show strong local adaptation despite of high levels of gene flow (HOWE ET AL. 2003).

Migration is effective when it is able to follow the environmental changes. According to a pessimistic scenario, the average temperature will increase in Central Europe by 2 degrees Celsius during the next 35 years, thereby isotherms would shift horizontally with 3km/year to north and 12m/year in altitude (MÁTYÁS 2006). If this rate is compared with the natural migration rate of species which is 0.1-0.4 km/year (DAVIS AND SHAW 2001), it can be seen that horizontal migration will not be able to keep up with the expected changes. Even if migration would catch up with the speed of isotherm shift, the very fragmented landscapes in most of Europe prevent the spontaneous seedling recruitment in new areas. Habitat fragmentation may increase the risk of genetic drift and inbreeding, together with a potential reduction of gene flow from adjacent populations (YOUNG ET AL. 1996). If these impacts are coupled simultaneously with changes in demographic processes, such as altered mating systems and changes in pollinator behavior (in case of insect pollinated species, like linden or wild cherry), can result in reduction of individual fitness and increased risk of population extinction (LANDE 1988, ELLSTRAND AND ELAM 1993). An additional problem in mountain regions is that it may happen that there is no more possibility for species to migrate to higher elevation (ERIKSSON ET AL. 2006) and other populations or species need to replace them (CASTELLANOS-ACUÑA ET AL. 2015).

2.3.3. Phenotypic plasticity/stability

Phenotypic plasticity is the environmentally sensitive production of alternative phenotypes by existing genotypes (DEWITT AND SCHEINER 2004) which allows individuals for rapid acclimation to adverse environmental conditions.

The role of phenotypic plasticity in evolution is ambiguous: Firstly, the phenotypic plasticity can hide the genotype which means that natural selection will not be effective. Secondly, phenotypic plasticity may contribute to the fitness of a genotype, it is especially important for long-lived organisms, which must tolerate relatively broad fluctuations of environmental conditions (ERIKSSON ET AL. 2006).

Phenotypic plasticity is an often underestimated issue both in forest genetics and ecology, in spite of the fact that considering the speed and magnitude of predicted changes, phenotypic plasticity is the primary natural buffering mechanism (MÁTYÁS AND NAGY 2005). MCLEAN ET AL. (2014) suggest that species with greater phenotypic plasticity are able to respond more rapidly to adverse environments and selective pressures.

The term plasticity has been often used to describe differentiation of productivity (growth) of identic genotypes/populations on different sites, for instance in common garden tests, which is not exactly the content of the original term: change in growth rate is not necessarily an alternative phenotype. Therefore, the new term phenotypic stability has been introduced. It means the ability to maintain the fitness of the individual or population under changing environmental conditions without genetic changes. Nevertheless, stability fulfills largely the criteria described by ERIKSSON et al. (2006), first of all the ability to *withstand selection pressure under changed conditions.*

2.3.4. Mutation

Mutation is an alteration in a gene or a chromosome which can be caused by several factors. It may happen due to a cell division error, exposure to radiation or harmful chemicals, etc. Most spontaneous mutations that persist in the population are neutral, which means that they are insignificant for natural selection. Other mutations are often deleterious and will therefore be selected if natural selection is allowed to act (ERIKSSON ET AL. 2013). Mutation may promote the differentiation among populations, although mutation rate at individual loci is generally low and the probability that the mutation will improve the fitness of the population is even lower. Mutation considered as the source of diversity but its effect on short-term population adaptation is negligible.

2.3.5. Other options for adaptation

Environmental impacts may affect the gene expression without altering the DNS nucleotide sequence. They are commonly known as epigenetic effects. These changes may even be transferred to the progeny generation, which is in contradiction with the classical dogma of genetics.

The extent of epigenetics in adaptation of trees is still not sufficiently clarified. Up to now, the only example thoroughly investigated is the case of “after-effects” in Norway spruce, discovered by BJÖRNSTAD in Norway (SKROPPA AND JOHNSEN 1994, in MÁTYÁS 2002), where spruce seed orchards were established in warm climates in order to enhance seed production. Graftings of plus trees from the northern and central part of the country (lat.63-67°N) have been planted in southern Norway for a seed orchard (lat.58°N). Surprisingly, offspring from the orchard showed a different behavior from their parents under northern condition. Their behavior was similar to southern populations with later flushing and less autumn frost hardiness. It was found that the temperature conditions during flowering and fertilization caused the different phenological behavior, likely caused by genomic imprinting, probably methylation (SKROPPA-JOHNSEN 1994, in MÁTYÁS 2002).

In order to understand adaptation of an individual or a population to a certain environment we must examine ecological, demographic and genetic processes together. None of the above mentioned type of adaptation seems be able to fully counterbalance the impacts of climate change due to the speed of recent changes or artificial obstacles such as fragmentation. For these reasons, it is important to be able to predict the effects that are expected in the future and thereby we can give an appropriate support to natural processes. In this respect, the investigation of results of common garden tests is indispendable.

2.4. Common garden experiments

In order to understand how trees are adapted to different environmental conditions the provenance trials are the most appropriate means. The term “provenance” is used in forestry for populations of the same species of identified origin, i.e. collected in different parts of the geographic distribution of that species.

These experiments have a long tradition in forest research. The main objective of most provenance tests was to identify populations with highest growth potential which can be used as best seed sources for reforestation. Data collected from these trials enable to compare such important traits like frost resistance, drought tolerance or growth characteristic between populations. Results of common garden experiments can provide guidance how the use and transfer of forest reproductive material has to be adjusted in the face of climate change. If the reforestation material is not well adapted to the plantation site, the risk of growth decline and damages by antagonist organisms may increase, causing huge economic losses.

In early works, geographic variables of given seed-source were used to compare the performance of populations (e.g. CAMPBELL 1974). The relationship between growth traits and climate gradients has been studied only in recent decades. It was MÁTYÁS (1994, 1996) who first interpreted the differentiation between provenances, not on geographical distance basis, but as effect of different ecological adaptations, first of all related to local climate. Therefore growth differentiation was investigated as the result of the difference between the climate at the seed source and at the test site where provenances were planted (MÁTYÁS AND YEATMAN 1992). This difference termed “ecodistance” (also known as climatic transfer distance), is based on the idea that populations adapted to certain ecological (climatic) conditions, and if they are transferred to a new environment, their phenotypic response to climate depends not only on the climatic conditions where the population is tested, but also on the magnitude and direction of environmental change experienced due to the transplanting, related to the macroclimate they had been adapted to originally (MÁTYÁS ET AL. 2009c).

Through the comparison of ecodistance and growth in provenance trials, it is possible to determine the environment where a particular provenance performs best. The mathematical description of the performance of a single, individual population across test site environments is the norm of reaction. On the other hand, when analyzing single provenance tests with multiple provenances, the regression of (climatic) ecodistance on growth resoponse of various provenances produces nonlinear functions termed transfer functions. The optimal (climatic) ecodistance of populations designate the adaptively homogeneous areas where they perform well, in other words, indicate the optimum provenance for a particular site (MÁTYÁS 1994, 1996, REHFELDT ET AL. 1999, WANG ET AL. 2006, AITKEN ET AL. 2008). In consequence, provenance tests received a new role: they can be considered as climate-change experiments. These trials provide a powerful tool for studying climate tolerance and population-specific response of trees (MÁTYÁS 1994). The response of provenances to climatic changes experienced through transplantation can be interpreted as simulations of response to future predicted changes in climate. Data collected from these experiments offer information about adaptive genetic variation within and between populations for fitness related traits. A limitation, however, is that in the past, provenance tests were nearly never established outside the suitable climatic habitat of the species, and even more, generally were planted at the best climatic sites; contrasting sites with large ecodistance values are now needed, given the speed and dramatic amount of the climate change.

Common garden trials of many trees indicate that forest trees are adapted to their past environment; therefore the growth and survival of existing forests will depend on their ability to adjust phenotypical response to rate of environmental changes. In spite of the fact that populations are adapted to the local climate, it is often observed that local population is not necessarily the best; the strong ‘genetic x environment’ interaction may promote but may be have negative influence on the performance of a given population at one particular site. Some authors question even the existence of local adaptation; e.g. GÖMÖRY ET AL. (2010) found that in the beech provenance trial series, the optimum environments were almost the same for all provenances, due to the strong phenotypic plasticity of beech. Populations may respond differently to improving conditions. In a Norway spruce experiment, it has been observed that provenances originating from southern limit were growing better when transferred to cooler climate compared to their local climate, while the northern provenances showed the opposite behavior. This effect was explained also by phenotypic plasticity or stability (MÁTYÁS ET AL. 2009a).

The basic concept to interpret the results of common garden experiments is summarized by MÁTYÁS and coauthors (2007) as follows:

- distributional limits of zonal tree species have been determined primarily by climatic factors,
- much of the intraspecific genetic differentiation among populations of dominant tree species with large distributional ranges is linked to climatic adaptation,
- fitness related traits (growth, phenology, vitality) measured in comparative tests may be utilized to predict the impacts of climatic change, as the response of populations at the test site can be interpreted as a simulation of environmental changes,
- given climatic conditions (at test sites) trigger different responses, depending on the adaptedness of populations to the site of origin, i.e. on ecodistance
- limits of tolerance are genetically determined; if the environmental conditions get worse, the fitness of populations may decline depending on their genetic variability, and when the genetic and ecological possibilities of adaptation are no longer sufficient, mass mortality can occur.

On the other hand, provenance trials also have limitations (KONNERT ET AL. 2015):

- they may represent only a mixture of few open-pollinated families (if too few trees were sampled),
- seeds from selected mother trees do not necessarily represent the genetic structure of the whole stand,
- optimal nursery conditions may prevent natural selection during germination, establishment and early growth,
- planting monospecific plots and protection against competitive vegetation in trials may distort ability to compete with other species and tolerate pests and herbivores,
- number of populations and sites involved in tests are often insufficient to represent the whole climatic range,
- with increasing age the measurements become less reliable and biased by competition between genotypes,
- a part of trees needs to be removed by thinning which may falsify mortality data,
- most studies are based on measurements at juvenile age which results may not be simply extrapolated to adult age.

Despite of these limitations, provenance experiments provide the most reliable information for practical recommendations.

In principle, determination of the adaptability of populations should be supported also by molecular genetic studies. A high level of adaptive genetic diversity in a population increases the probability of higher fitness. To identify genes related to adaptive traits that respond to environmental changes is, however, still a main challenge to molecular genetics. Quantitative traits are generally controlled by a large number of genes and most of current molecular markers are neutral, they cannot be linked to the distribution of adaptive variation. During the last decades many molecular techniques have been developed such as isozymes, RFLPs, RAPDs, AFLPs, microsatellites and SNP markers. These markers provide information about the level of genetic diversity, colonization routes and lineages but do not offer specific, reliable information about phenotypic or adaptive variation. Therefore, common garden experiments remain – for the time being – the main source of information about adaptive processes and adaptability of populations.

2.4.1. Approaches of modeling growth response in common garden experiments

MÁTYÁS AND YEATMAN (1992) investigated growth response of 15 year-old jack pine (*Pinus banksiana* Lamb.) provenances in order to model the effect of climate change. Eight test sites across Ontario with 56 sources originating mainly from Ontario, western Quebec and adjacent areas have been analyzed. Ecodistance between test site and the site of origin has been calculated from the heat sum and latitude values. It was found that southward transfer, up to a certain limit, resulted positive growth response but transfer outside the distribution area caused significant height decline. They demonstrated that an increase in temperature affects growth positively but only within a certain physiological and ecological tolerance limit, and if temperature changes exceed this limit, it may cause decrease in production and ultimately lead to mortality.

Reactions of three forest tree species were compared by MÁTYÁS ET AL. (2007) in order to investigate tolerance limit of species. It has been demonstrated that close to the lower distribution limit populations are under stress and even little unfavorable change in climate conditions resulted in growth decline for both investigated species. MÁTYÁS ET AL. (2007) compared three beech provenance trials relatively close to the south-eastern continental limit of the species. The concept of transfer analysis and ecodistance has been used and Ellenberg drought index was selected to determine ecodistance between the test site and the site of origin. A linear surface model has been applied to model height growth response of 10 provenances (Figure 3). At the warmest site in Bucsuta, Hungary, all provenances were moved into warmer and drier conditions. Figure 3 shows a clear decline of height growth with increasing ΔEQ value. However, growth decline was not detectable when provenances transferred into cooler and moister environment. Different behavior of provenances indicates that response to climatic change is regionally divergent, depending on testing conditions and inherent facilities.

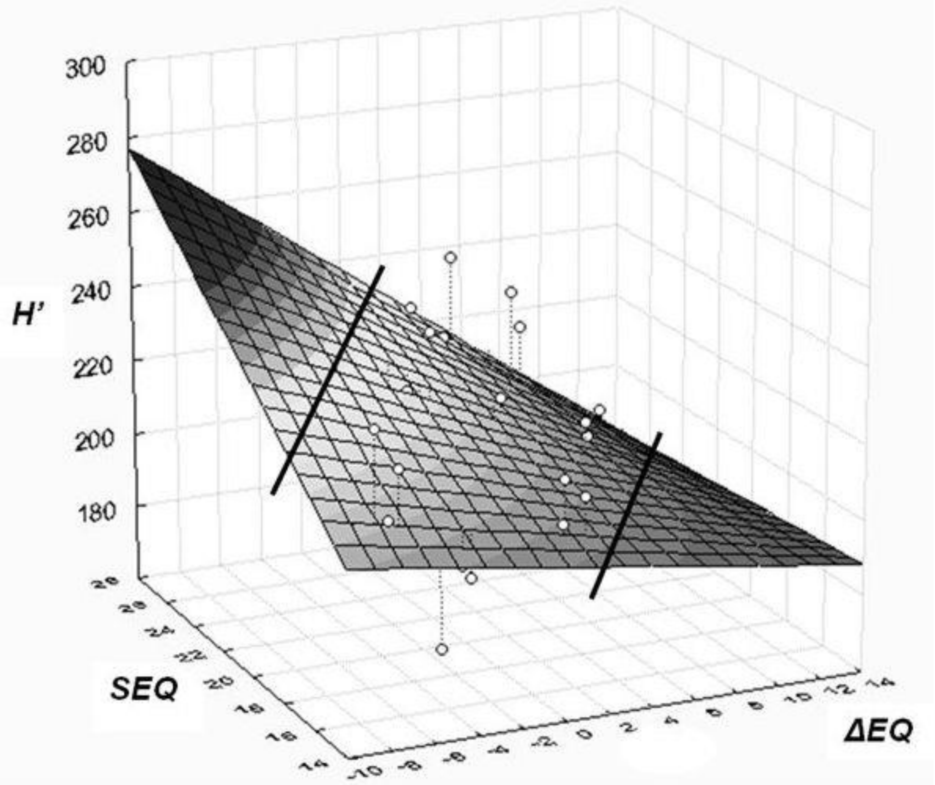


Figure 3: Linear surface model of height growth response of provenances. The model shows corrected height (*H'*) as dependent, and ecodistance of provenances (*ΔEQ*), respectively *EQ* value of sites (*SEQ*) as independent variables. Positive *EQ* values of ecodistance (to the right on the *X* axis) stand for simulated warming effect. Lines indicate the part of the fitted surface not supported by observed data (MÁTYÁS ET AL. 2009c)

Similarly, NAGY (2009) predicted 15% growth decline for Scots pine (*Pinus sylvestris* L.) with increasing annual mean temperature by 2°C, according to provenance trial data using regression analysis.

WANG ET AL. (2006, 2010) developed a universal response function (URF) to predict the influence of climate on phenotypes based on data of an extensive lodgepole pine (*Pinus* *contorta* Dougl. ex Loud.) provenance trial. A multiple regression analysis has been applied to build URF, in which climate of seed source, test sites climate and geographic variable of provenances were used as independent variables. The mean annual temperature of test site and provenance origin explained the main source of variation, its environmental and genetic effects have been quantified and compared (Figure 4).

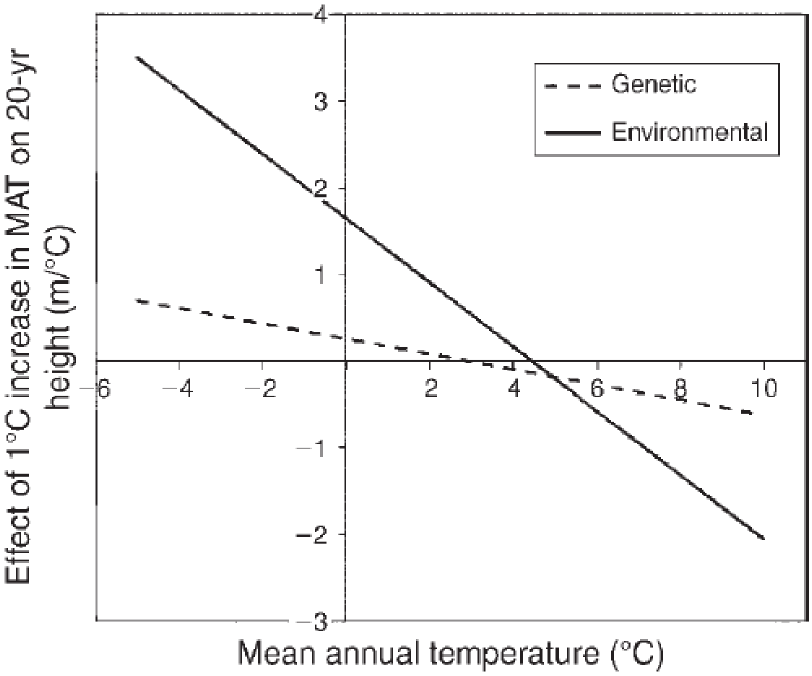


Figure 4: Environmental vs. genetic effects of mean annual temperature (MAT) on lodgepole pine 20-yr height. Effects are expressed by the rate of change in 20-yr height with an increase of MAT by 1°C at a given MAT (WANG ET AL. 2010)

A novel analysis of historical data was applied in the study of LEITES ET AL. (2012a) to model differences in height of three-year-old Douglas-fir (*Pseudotsuga menziesii*) populations in response to climate transfer. They used a mixed-effect model which is able to accommodate the data structure by selection of fixed and random effects. The modeling approach is based on the idea that genetics of populations shaped by long-term environment (climate at seed source) and the recent/short-term environment (climate at test site) determine the particular phenotype, the realized growth of populations (Figure 5).

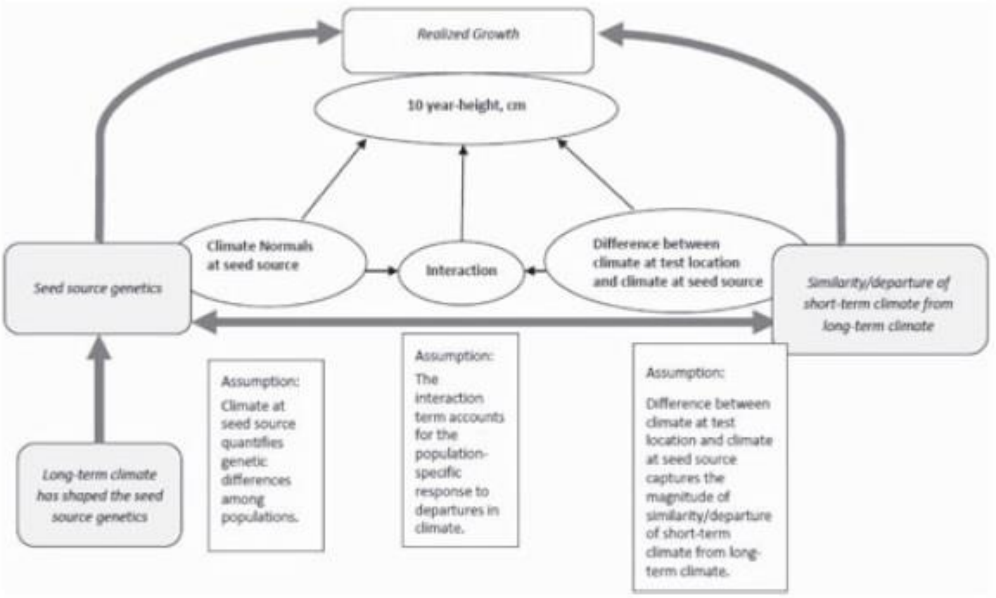


Figure 5: The conceptual diagram used for model by LEITES ET AL. (2012b)

The most sensitive indicator was the mean temperature of the coldest month. All populations showed optimum height growth when transferred to climates with warmer winters but populations originating from warmest winters were taller across sites and the optimal transfer distance was close to zero; in contrast, populations from colder climates performed poorly and had optimum height growth when transferred the farthest (it has to be pointed out that the sites were positioned mostly in cold boreal climate).

Practical application of common garden test has been realized also in Mexico in order to select the most appropriate Mexican conifer populations, which will able to cope with altitudinal shift due to climate change. It was found that an assisted migration upwards of 300m in altitude was viable strategy to mitigate the effects of climate change (CASTELLANOS-ACUÑA ET AL. 2015).

2.5. Phenology observations

Phenology is considered as one of the most important factors determining growth and survival of trees. Changes in the phenological patterns caused by climatic warming may change the productivity of trees and disturb the plant-animal interactions (VISSER ET AL. 2001). Understanding the genetic and environmental factors driving the annual development cycle of trees is of great importance in practical forestry under climate change (HÄNNINEN 1990).

The timing and regulation of flushing is mainly controlled by temperature (ROMBERGER 1963). The developmental cycle from budset to budburst is affected by several processes with different temperature regime. Chilling temperature in winter and forcing temperature in early spring are considered as the most important factors releasing dormancy and triggering the onset of growth of trees (KRAMER 1994b). SARVAS (1974) defined different phases during dormancy, rest and quiescence. During rest period buds remain dormant because inhibitor compounds inside the plant prevent it to begin unfolding. This condition is released when buds are exposed to the sufficient chilling temperature sum which can vary from species to species and may differ also within species. In the quiescence phase the plant is ready to grow but if the ambient environmental conditions are unfavorable for growth, buds will still remain dormant. Trees enter active phase when buds receive the sufficient forcing temperature sum. Some studies also emphasize the importance of photoperiod in bud dormancy (HEIDE 1993, FALUSI AND CALAMASSI 1990, VITASSE AND BASLER 2013). KÖRNER AND BASLER (2010) assumed that photoperiod is more important for species with oceanic distributions than for continental species, because temperature increase is a less reliable signal of spring in oceanic climates. LAUBE ET AL. (2013) found that beech was sensitive to photoperiod when chilling requirements was not satisfied. LI ET AL. (2003) observed that bud flush of silver birch is a consequence of local temperature or photoperiod or their interaction.

Species with large geographical distribution range show differences in bud burst among populations which refers to site specific selection. The existence of clear geographic (better: climatic) clines and strong correlation with the temperature regime of the site of origin points out that bud burst is a highly heritable trait in beech (VON WÜHLISCH ET AL. 1995).

With global warming, an advance in spring leaf phenology has been reported worldwide (CHMIELEWSKI AND ROTZER 2001, PEÑUELAS ET AL. 2002, KARLSSON ET AL. 2003, VITASSE ET AL. 2011). Shift in the timing of leaf unfolding may increase the risk of late frost damage (CANNELL AND SMITH 1986, HÄNNINEN 2006), however, KRAMER (1994a) concluded that the probability of spring frost damage will decrease for tree species in the Netherlands and Germany. Significant correlation was detected between frost damage and bud burst date referring to the trade-off between the length of the growing season and the risk of frost damage (GÖMÖRY AND PAULE 2011, LEINONEN AND HÄNNINEN, 2002). As a consequence, changes in spring phenology may change the distribution range of foraging insects too. For instance, increasing winter temperature in southern Spain resulted on the occurrence of the pine processionary caterpillar in high elevations (HÓDAR ET AL. 2003).

3. Materials and Methods

3.1. The International Beech Provenance Trials of 1993/95 and 1996/98 in Europe

In 1995 and 1998 international beech provenance trials were established across Europe, organized by the Institute for Forest Genetics, Grosshandorf, Germany, initiated by H.J. MUHS and G. VON WÜHLISCH (VON WÜHLISCH 2007). With support of a large number of participants, 42 tests were successively planted across Europe (Figure 6). One site of the 1998 provenance test series has been planted out in Bucsuta, SW Hungary. Seeds were collected from the whole distribution area and raised in Hamburg, in a nursery until age two. After two years they were planted out to the European trial sites. The layout of the planting was the same at each site. Provenances were planted in randomized plots with 10 m x 10 m plot size, 50 plants per plot (5 rows each with 10 plants) and replicated in three blocks across the site (Figure 7). The main objective of these experiments was to identify intraspecific variation in adaptive traits in order to be able to determine the most suitable population at a given site, and to make predictions for future distribution range of beech under changing environmental conditions. An important support for international cooperation and creation of a central dataset was initiated by the European COST E52 cooperative action which provided a platform for the participants of the experimental series. The conclusions of the COST action have been published in Spain by ALIA ET AL. (2011).

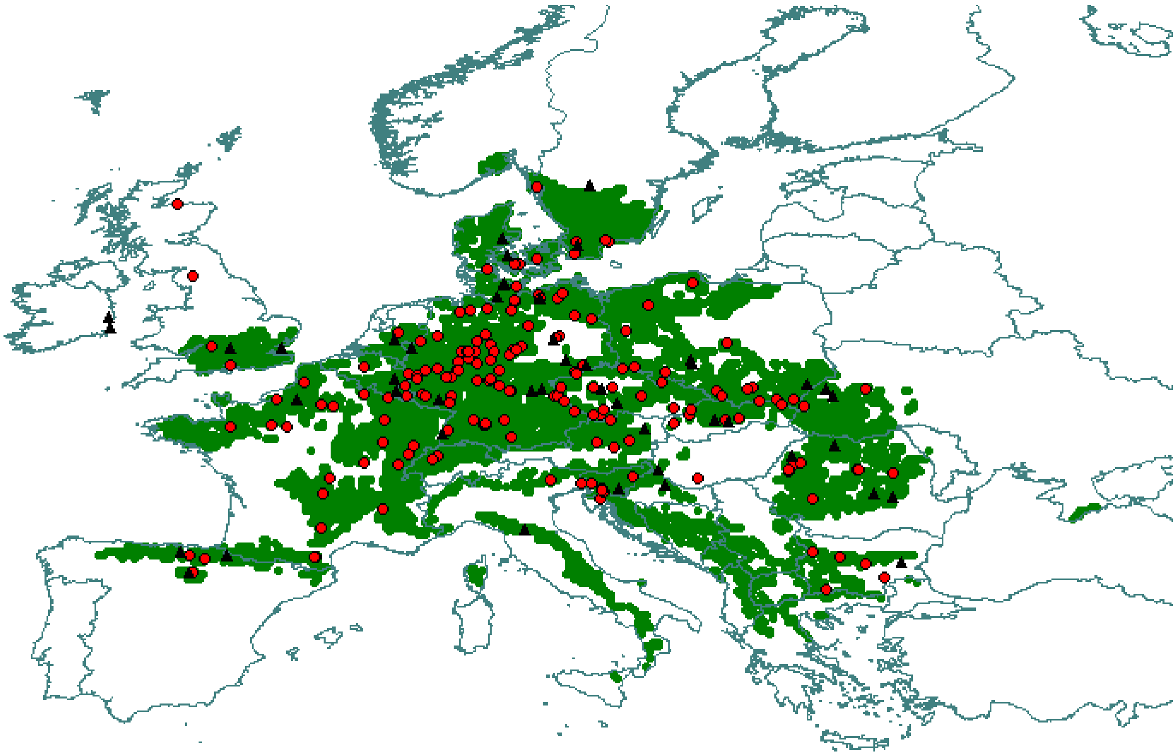


Figure 6: Test sites (▲) and origins of beech provenances (●) of the 1995 and 1998 International Beech Provenance Trial, projected on the distribution map of European beech (map source: EUFORGEN)

The measured traits made in the experiments were proposed as follows:

- Height,
- DBH,
- Survival, Flowering phenology,
- Flowering quantity,
- Stem quality,
- Branching,
- Wood anatomy,
- Wood physical quality,
- Wood chemical quality,
- Biological resistance insects,
- Biological resistance pathogens,
- Biomass,
- Bud flush,
- Bud set,
- Abiotic resistance wind,
- Abiotic resistance cold,
- Abiotic resistance drought.

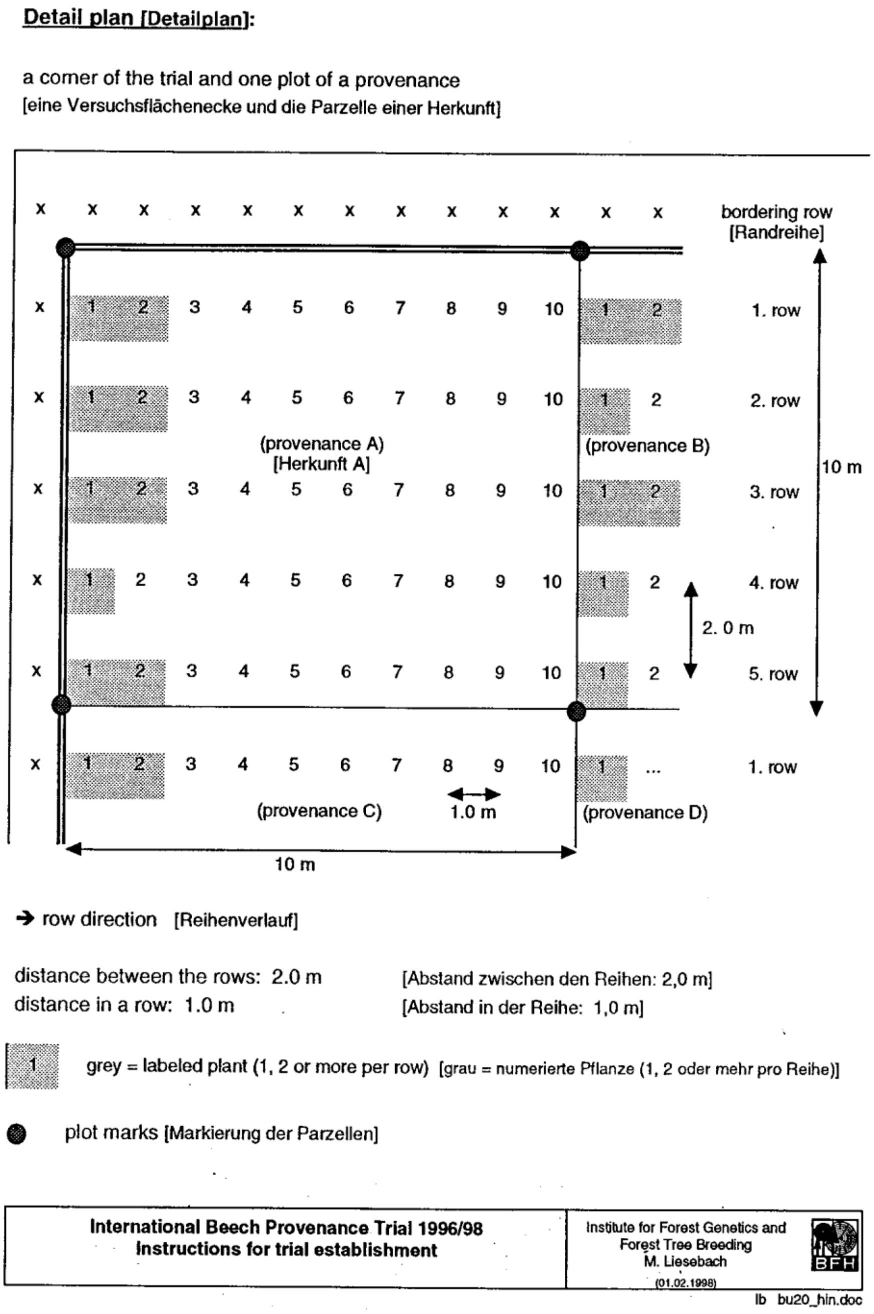


Figure 7: The general layout of planting

The provenances represented in the parallel trials were not always the same and the dates of measurements were also different. The first, detailed analysis of the survival and performance data of the international beech provenance trials was published by ALÍA ET AL. (2011). They found significant differences in phenotypic plasticity among the different provenances. Populations from Germany and Sweden showed higher stability while from France, Denmark and the Netherlands performed poorer across sites. A comprehensive analysis of leaf flushing was done by ROBSON ET AL. (2011). They observed that heat accumulation during the winter and spring was the most important determinant of the timing of budburst. They confirmed the existence of clinal variation along geographical gradients as determined by VON WÜHLISCH ET AL. (1995). Provenances from the south-east of Europe in Mediterranean and warm-continental regions flushed earlier than provenances from the north and west of Europe, where the oceanic influences on the climate are strong. There were other summarizing analyses concentrating on certain traits such as budburst, growth decline or analyzing regional tests, partly mentioned in the previous chapter (e.g. MÁTYÁS ET AL. 2009a, HORVÁTH AND MÁTYÁS 2014, GÖMÖRY ET AL. 2010).

3.2 Mixed model analysis of height growth of provenances in 31 trial sites

3.2.1. Analyzed data

Out of the measured traits, height was selected for analysis because it is highly heritable, easy to measure (at least in the juvenile phase) and it was available for most of the sites at relatively the same ages. For individual provenances replication mean data were pooled and site mean per provenance has been used for analysis. As trial sites did not include always the same provenances, those provenances that were present at least at five locations have been selected for further analysis. Because of the different years of measurement, the 9 years old height (counted from outplanting) was considered as reference age for all experiments. Where it was not available, height data have been predicted for 9 years of age using mean annual increment data. Finally, 11 trial sites of the year 1995 series with 57 provenances, 20 sites of the year 1998 series with 49 provenances were selected. Thus, for the analysis 106 provenances and 31 trial sites were included, with a total of 990 mean height data compared. The data originated from the database compiled by G. VON WÜHLISCH in cooperation with the COST E52 project partners.

3.2.2. Construction of the model

The main goal of the analysis was to create a model which best describes the response of provenances to environmental changes triggered by transplantation. The importance of the modeling lies in its potential to mimic projected climate change effects. The concept was that the growth and vitality of a population at a test site is determined by the inherited adaptation to the site of origin and by the experienced different conditions at the new site (MÁTYÁS AND YEATMAN 1992). Two reference climates, i.e. climate of origin and climate of the test site, had to be calculated for different periods: for climate of provenance (origin) the past climate characterizing the conditions during the lifetime of the parent population has to be calculated.

For climate at the test site, the data of the years starting from the outplanting until the actual measurement have to be considered, even if this period is much shorter than the standard climate reference period (30 years). The difference between the two variables is considered as "climatic distance" (or *ecodistance*, MÁTYÁS AND YEATMAN 1992, as opposing the *geographic distance* used earlier) which expresses the assumed magnitude of maladaptation of the population at the test site. Maladaptation is defined as the difference between the adaptedness as spontaneously developed at the origin and the current adaptive requirements of a population, expressed in fitness trait units such as in height growth.

For the data analysis a mixed-effect model was applied (REHFELDT ET AL 2002, LEITES ET AL. 2012a, b). Mixed-effect regression model takes into consideration the source of variation that is not attributable to independent variables. The great advantage of the mixed-effects method is that random effects can be incorporated in the model. In this study provenance and site were considered as random effects. For the model construction, the most efficient variables had to be selected. The main steps were the followings:

1. Selecting the best climate variables at seed source.
2. Selecting the best climate transfer distance variables.
3. To combine the previous two functions, compare results of full models (on what is called "competing models" , LEITES ET AL. 2012b) and select the best one.

Measured mean height of provenances served as dependent variable. To identify the climate variables at the site of origin that best describe the performance of the populations across sites, Spearman's rank correlation was applied. Climate variables with the highest ρ value have been selected.

Climate transfer distance was calculated as the difference between test site climate and seed source climate. For modeling growth response to climate transfer, a quadratic function has been used based on results of previous studies (MÁTYÁS AND YEATMAN 1992, MÁTYÁS 1994, REHFELDT ET AL.1999).

After selecting the most relevant and significant climate variables in the first two steps, they have been combined in all possible way. Finally, the full models were compared according to their AIC values (AKAIKE 1992).

The model predicts the height growth at 9 years of age of a provenance at a given site as determined by the following variables: the climate at the origin of the provenance, the climatic change (climatic distance) caused by transferring the adapted provenance to the test site and the interaction of the two. The general model form was as follows:

$$y_{ij}=b_0 + b_1x_{1j} + b_2x_{2ij} + b_3x_{2ij}^2 + b_4x_{1j}x_{2ij} + \mathit{site} + \mathit{provenance} + e_{ij}$$

where y_{ij} is the height growth response of j^{th} provenance at the i^{th} site, x_{1j} is climate variable for seed source *j*, x_{2ij} is climate transfer distance for provenance *j* at the test site *i*, x_{2ij}^2 is the quadratic term of transfer distance and $x_{1j}x_{2ij}$ is the interaction; *b'*s are the intercept and regression coefficients and e_{ij} is the residual. Provenance and site were incorporated in the model as random effects.

All statistical analyses were conducted using the R package lme4 (R-3.2.2.) and STATISTICA 12 software.

3.2.3. Climate data for mixed model analysis

As neither trial site descriptions nor provenance data did include reliable, comparable climatic information, climate data for the test sites and the seed sources were obtained from the ClimateEU database. Climate variables have been generated with the ClimateEU v4.63 software package, available at http://tinyurl.com/ClimateEU, based on methodology described by HAMANN ET AL. (2013). This software can calculate monthly, seasonal and annual climate variables for specific locations based on latitude, longitude and elevation. In total 85 climate variables (Table 2) have been calculated for each trial site and each provenance origin.

In the case of trial sites weather data has been computed from the date of planting to the date of measurement (e.g. 1998-2006), while a climate normal (1961-1990) has been determined for seed sources which represents the past climate.

3.3. Assessing the provenance trial in Hungary

3.3.1. Location of the trial

Out of the 1998 series of the international beech provenance trials, one experiment was established in Bucsuta, SW Hungary. The experiment was initiated by CSABA MÁTYÁS. The site selection and establishment was carried out by VALÉRIA HORVÁTH and SZILÁRD SZABÓ. The trial is located in the Forest District of Bánokszentgyörgy (Zala County) which belongs to the Zalaerdő State Forest Company. The trial is located in the forest subcompartment Bucsuta 10B (46°35'N, 16°51'E). It is situated at the altitude of 220 m above sea level on a southeast-facing slope with an inclination of about 5-10° (Figure 8).

Table 2: List of climate variables used for analysis (based on ClimateEU database)

Annual variables	
MAT	mean annual temperature
MWMT	mean warmest month temperature
MCMT	mean coldest month temperature
TD	continentality (temperature difference between MWMT and MCMT)
MAP	mean annual precipitation
MSP	mean summer precipitation (May to Sept)
AHM	annual heat moisture index ((MAT+10)/(MAP/1000))
SHM	summer heat moisture index ((MWMT)/(MSP/1000))
DD<0	degree-days below 0°C
DD>5	degree-days above 5°C
DD<18	degree-days below 18°C
DD>18	degree-days above 18°C
NFFD	the number of frost-free days
FFP	frost-free period
bFFP	the Julian date on which FFP begins
eFFP	the Julian date on which FFP ends
PAS	precipitation as show (mm) between August in previous year and July in current year
EMT	extreme minimum temperature over 30 years
Eref	Hargreaves reference evaporation
CMD	Hargreaves climatic moisture deficit
EQ	Ellenberg's climate quotient ((Tave07/MAP)*1000))
Seasonal variables	
TAV_wt	winter mean temperature (Dec.(prev. year) - Feb.)
TAV_sp	spring mean temperature (Mar. - May)
TAV_sm	summer mean temperature (Jun. - Aug.)
TAV_at	autumn mean temperature (Sep. - Nov.)
TMAX_wt	winter mean maximum temperature
TMAX_sp	spring mean maximum temperature
TMAX_sm	summer mean maximum temperature
TMAX_at	autumn mean maximum temperature
TMIN_wt	winter mean minimum temperature
TMIN_sp	spring mean minimum temperature
TMIN_sm	summer mean minimum temperature
TMIN_at	autumn mean minimum temperature
PPT_wt	winter precipitation
PPT_sp	spring precipitation
PPT_sm	summer precipitation
PPT_at	autumn precipitation
Monthly variables	
Tave01 - Tave12	mean temperatures from January to December
Tmax01 - Tmax12	maximum mean temperatures from January to December
Tmin01 - Tmin12	minimum mean temperatures from January to December
PPT01 - PPT12	precipitation from January to December

The site belongs to the Göcsej forest region with temperate-continental climate with some Alpine sub-mediterranean influence. Bucsuta is a particularly interesting location to study adaptive responses, because it is situated at the edge of the distribution area (xeric limit), most provenances experience warmer and drier climate here than at the site of origin.

The dominant tree species in the region is beech but frequently associated with sessile oak (*Quercus petraea*), non autochthonous Scots pine (*Pinus sylvestris* L.) and hornbeam (*Carpinus betulus* L.). On the selected site there was a 31-year-old Norway spruce forest stand damaged by spruce bark beetle (*Ips typographus*). The stand was clear cutted the previous winter, tree stumps were removed and the trial area was fenced.

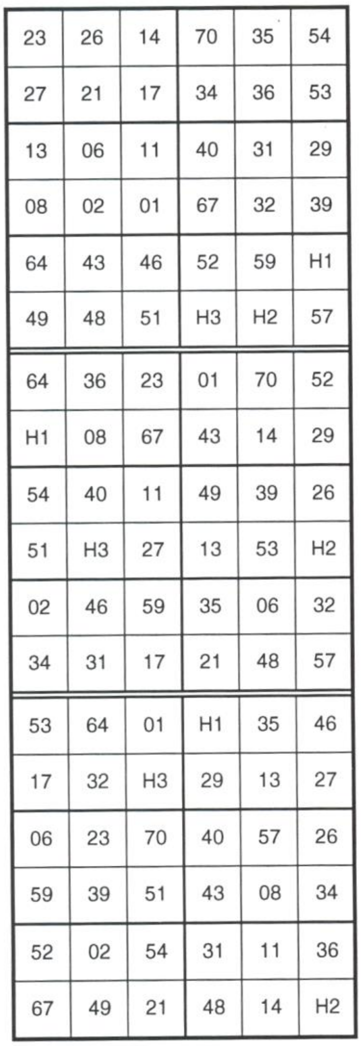
3.3.2. Soil and site characteristics

In the Göcsej forest region soils are developed on loess in the east and on loam in the west of the region. Due to erosion also the Pannonian clay, sedimented in the Holocene/Pleistocene, may appear on the soil surface. The soil characteristics of the trial site have been investigated by BIDLÓ ET AL. (2013). Based on four soil profiles they found that the soil conditions are uniform in the compartment. Humification and clay lessivation were observed in the soil profiles, and in some parts of the investigated profiles stagnosol development was detectable which refers to water accumulation. The depth of the soil exceeded 100 cm for all soil profiles. Despite of the fact that the exploration was during a dry summer period, each horizon of the soil contained sufficient moisture for vegetation. The soil pH test showed acid and slightly acid values, which is favorable for forest trees. The soil type has been identified as lessivated brown forest soil. The trial site has good water storage capacity, sufficient nitrogen content and there is no soil defect which could prevent the growth of trees. In the middle of the area there is an erosion gully, the third replication is located on the bottom of the hill, it is cooler and moister than the rest of the trial site. Due to relatively uniform soil properties within the site, the observed differences in growth of provenances are not attributable to soil variability.

Figure 8: The trial site Bucsuta on the Google map

3.3.3. The experimental layout and material

The Hungarian trial consists of 36 provenances. Four provenances out of the 36 are Hungarian (Table 3), one, Nr 52 Magyaregregy belongs to the international set, i.e. it is represented in some other trials, while three other provenances were added to complete the trial set of 36. One of these, H1 Bánokszentgyörgy, originates from the nearby forests and may be considered as local. The provenances were planted in randomized plots according to the uniform plan and replicated in three blocks across the site (Figure 9). Each rectangular (10 x 10 m) plot consists of five rows, each with 10 trees at a spacing of 2 m between rows and 1 m between plants within the rows. By 4th of April 1998 all seedlings have been planted out. During the planting the weather was very favourable, it was mild sunny time with regular rainfall.



23	26	14	70	35	54	
27	21	17	34	36	53	
13	06	11	40	31	29	
08	02	01	67	32	39	I.
64	43	46	52	59	H1	
49	48	51	H3	H2	57	
64	36	23	01	70	52	
H1	08	67	43	14	29	
54	40	11	49	39	26	
51	H3	27	13	53	H2	II.
02	46	59	35	06	32	
34	31	17	21	48	57	
53	64	01	H1	35	46	
17	32	H3	29	13	27	
06	23	70	40	57	26	
59	39	51	43	08	34	III.
52	02	54	31	11	36	
67	49	21	48	14	H2	

Figure 9: The experimental layout in Bucsuta. Provenance ID codes as in Table 4

Table 3: Name and main geographical and climate data of provenances of the Bucsuta trial

Id	Name of provenances	**Country**	**Latitude**	**Longitude**	**Altitude**	**Mean annual precipitation (mm)**	**Mean annual temperature (°C)**
1	Perche	FR	48.42	0.55	205	697	9.8
2	Bordure Manche	FR	49.53	0.77	80	696	10.2
6	Plateaux Du Jura	FR	46.80	5.83	600	1550	8.6
8	Pyrenées	FR	42.92	2.32	670	810	11.2
11	Heinerscheid	LU	50.08	6.12	423	886	7.9
13	Soignes	BE	50.83	4.42	110	810	9.9
14	Aarnink	NL	51.93	6.73	45	787	9.4
17	Westfield	GB	57.40	-2.75	10	839	8.2
21	Grasten	DK	54.92	9.58	45	777	7.8
23	Torup	SE	55.57	13.20	40	641	7.7
26	Farchau	DE	53.65	10.67	55	676	8.2
27	Graf Von Westphalen	DE	51.52	8.78	375	952	7.6
29	Dillenburg	DE	50.70	8.30	520	789	7.1
31	Urach	DE	48.47	9.45	760	943	7
32	Ebrach	DE	49.85	10.50	406	680	7.9
34	Oberwil	CH	47.17	7.45	570	1109	8.3
35	Hinterstoder	AT	47.72	14.10	1250	1334	3.6
36	Eisenerz	AT	47.53	14.85	1100	1245	4.2
39	Jaworze	PL	49.83	19.17	450	884	7.5
40	Tarwana	PL	49.47	22.33	540	705	5.3
43	Jawornik	PL	49.25	22.82	900	759	4.2
46	Domazlice-Vyhledy	CZ	49.40	12.75	760	845	5.7
48	Jablonec	CZ	50.80	15.23	760	739	5.1
49	Brumov Sidonie	CZ	49.05	18.05	390	762	7.8
51	Horni Plana	CZ	48.85	14.00	990	1114	4.8
52	Magyaregregy	HU	46.22	18.35	400	691	9.5
53	Postojna	SI	45.63	14.38	1000	1742	7.2
54	Idrija	SI	46.00	13.90	930	2266	7.7
59	Pidkamin	UA	49.95	25.38		618	7
64	Nizbor	CZ	50.00	14.00	480	531	6.9
65	Koino	PL	49.92	20.42	400	716	7.4
67	Bilowo	PL	54.33	18.17	250	633	5.7
70	Buchlovice	CZ	49.15	17.32	410	683	7.7
H1	Bánokszentgyörgy (local)	HU	46.60	16.85	200	751	9.9
H2	Farkasgyepü	HU	47.20	17.65		627	8.9
H3	Ördöglyuk	HU	48.49	21.36	450	660	7.4

3.3.4. Early survival assessment

One year after planting in 1999, a supplementary planting was necessary due to vole damage. Provenances experienced one of the driest and warmest year in 2000, before survival assessment. Assessment has been performed in 2001 in each replication.

3.3.5. Scoring bud phenology

Scoring method

In most cases for recording a five point scale was used (Figure 10). The following scoring scale (VON WÜHLISCH ET AL. 1995) was applied for phenological stages:

1. Dormant winterbud
2. Buds expanding
3. Bud burst
4. Leaves are flushing
5. Leaves are fully expanded

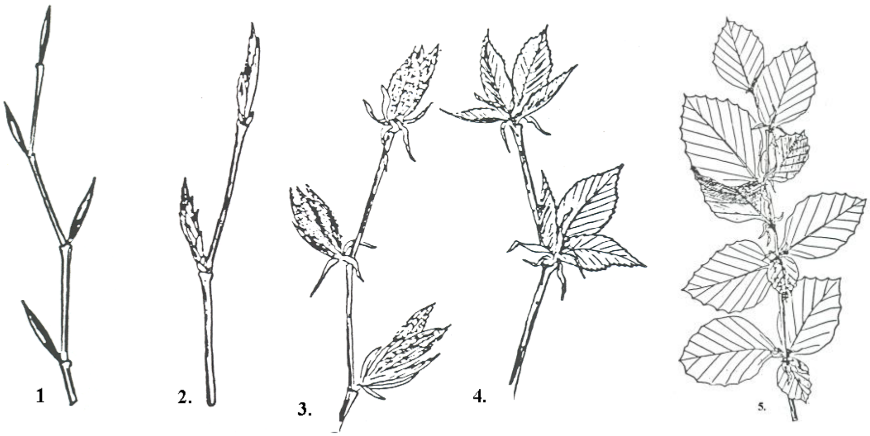


Figure 10: Picture of bud development classes

Phenophases were scored at 3-7 day intervals between early April and mid-May. Data were collected from each tree per plot in each replication. The trial site is located on a slope and because the temperature gradient was not measured, only the data of one block on the top have been used. Data from lower blocks showed later bud burst date for each provenance. Mean data per provenance was used in the analysis. Table 4 shows an example of recording protocol.

	PHENOPHASES				
DATE OF CENSUS	**1**	**2**	**3**	**4**	**5**
IV.13.	26				
IV.16.	18	3	2	2	1
IV.20.	5	12	1	2	6
IV.23.	3	6	6	3	8
IV.27.		3	1	5	17
IV.30.				4	22
V.04.					26

Table 4: The number of trees in different phenophases for provenance 14 (Aarnink, NL)

Because of the difficult accessibility of the trial, phenological observations were carried out irregularly. In the years of 1999 and 2000, only the 5th phenophase was recorded. In 2001, 2002 and 2003 every phenophase was assessed but in many cases flushing completed too quickly. Next assessment was in 2006 but only 11 provenances were recorded. The best survey was performed in the year of 2007. Unfavorable weather conditions prevented to perform enough censuses in 2014. In 2015 the assessment was successful.

Weather data

The phenological comparison of provenances in different years needed daily observation data. Because there is no meteorological station on the spot, the data of the nearest station (Nagykanizsa, latitude: 46.45; longitude: 16.967; elevation: 141m) have been used for the analysis. Comparisons of local weather measurements with those of Nagykanizsa station have shown close agreement.

Determination of bud burst date

To compare the flushing duration of each provenance a logistic sigmoid function was fitted on the data. The mathematical form of this function is $y=k/(1+e^{(-c*(x-m))})$, where *k*, *c* and *m* are constants: *k* is the horizontal asymptote for maximum value, *c* the shape parameter which determines the slope rate and *m* the inflection point of the ‘S’ shape function. As the limit values of the function are *0* and *k*, every phenophase stage has been reduced with 1 in order to represent the curve. This transformation does not affect the outcome.

The fitting was performed by STATISTICA software with Nonlinear estimation module.

<u>Calculation of chilling and heat requirements</u>

In order to compare temperature characteristics of different years and find the most appropriate model to predict budding, two methods, alternating and sequential have been applied.

Several methods have been developed to assess chilling and heat requirement necessary for dormancy release and budburst. Some models work with accumulated chilling units and others use number of chilling days to evaluate the chilling requirement of species and applied different function (linear or logistic) to describe the rate of forcing (Sarvas 1974, Cannell and Smith 1983, Murray et al. 1989, Kramer 1994 a,b). Threshold temperatures, start and end dates for chilling and forcing accumulation also varied in different studies.

Murray et al. (1989) used alternating model where the rate of forcing (F) and the rate of chilling (C) are respectively:

$$F=\begin{cases} 0 & T \le Tbf \\ T - Tbf & T > Tbf \end{cases}, \quad C=\begin{cases} 1 & T \le Tbc \\ 0 & T > Tbc \end{cases}$$

where *T* is the ambient temperature, *Tbf* and *Tbc* the base temperature which in most cases 0°C or 5°C. Forcing temperatures were not summed for days when the average daily temperature equal or lower than the base temperature. If the average daily temperature exceeded the threshold value, the temperature unit was summed based on the formula. Forcing accumulation started on the first of January to the date of bud burst. Chilling days were counted as the number of days when the average daily temperature was equal or below the base temperature (*Tbc*). In this study two temperature criteria were used. The number of chilling days below 5°C was calculated from the first of November to the end of February and for the same time period between 0 and 10°C.

Kramer (1994b) applied a model developed by Sarvas (1974) and refined by Hänninen (1990) and estimated parameters for *Fagus sylvatica* data collected in the Netherlands:

$$F=\begin{cases} 0 & T \le 0°C \\ \frac{1}{1+e^{-0.1(T-33.1)}} & T > 0°C \end{cases}, \quad C=\left\{\begin{matrix} 0 & T \le -19.4 \\ \frac{T-(-19.4)}{-0.2-(-19.4)} & -19.4 < T \le -0,2 \\ \frac{T-77}{-0.2-77} & -0.2 < T < 77 \\ 0 & T \ge 77 \end{matrix}\right\}$$

where T is the average daily temperature. The rest and quiescence phases are strictly separated, there is no transition from rest to quiescence unless the critical state of chilling is attained. To get this critical value, chilling unit (C) has to be summed from the first of November based on the formula. From the date when critical value (C=117.6) is fulfilled, the rate of forcing (F) can be calculated by an exponential function and summed. According to the results of Kramer (1994a), the bud burst date occurred when the exponential function reached the value 3.6.

Both methods have been applied for the climate data of Nagykanizsa in five different years (2001, 2002, 2003, 2007, 2015) and the results have been compared with the observed bud burst date of provenances at the trial site Bucsuta. Models with better estimates can be used to predict changes in phenology in the future according to climate change scenarios. Fortunately, the five years had different weather characteristics, thus it was possible to compare flushing variability with various weather conditions.

4. Results

4.1. Mixed model analysis: population's height-growth response to environmental changes

4.1.1. Separating the distribution range into main climate zones

The role of different climatic factors in climatic adaptation should be different according to the character of the selective environment. Investigations on reaction norms of Norway spruce provenances indicated, that the adaptive response of provenances from different parts of the range is not parallel (ÚJVÁRI-JÁRMAI ET AL. 2016). Similar results were achieved earlier with East European Scots pine populations (MÁTYÁS 1981). It seems logical that response models should be separately built for different climatic environments, to increase precision of predicting and to identify the regionally decisive climate variables. Therefore provenances were divided into three climatic regions (Alpine, Atlantic and continental) according to the map of Environmental Stratification of Europe (METZGER ET AL. 2005). Figure 11 shows location of provenances. The map contains originally 13 regions, in this study only three regions were used, merging different regions. Alpine regions (ALN, ALS) and Mediterranean Mountains (MDM) were considered as Alpine; Atlantic (ATC, ATN) and Lusitanean (LUS) regions were pooled as Atlantic, and finally Continental (CON), Nemoral (NEM) and Pannonian-Pontic (PAN) regions formed the continental group. Other high altitude provenances were included in the Alpine group. The groups of provenances by regions are listed in the Annex 1.

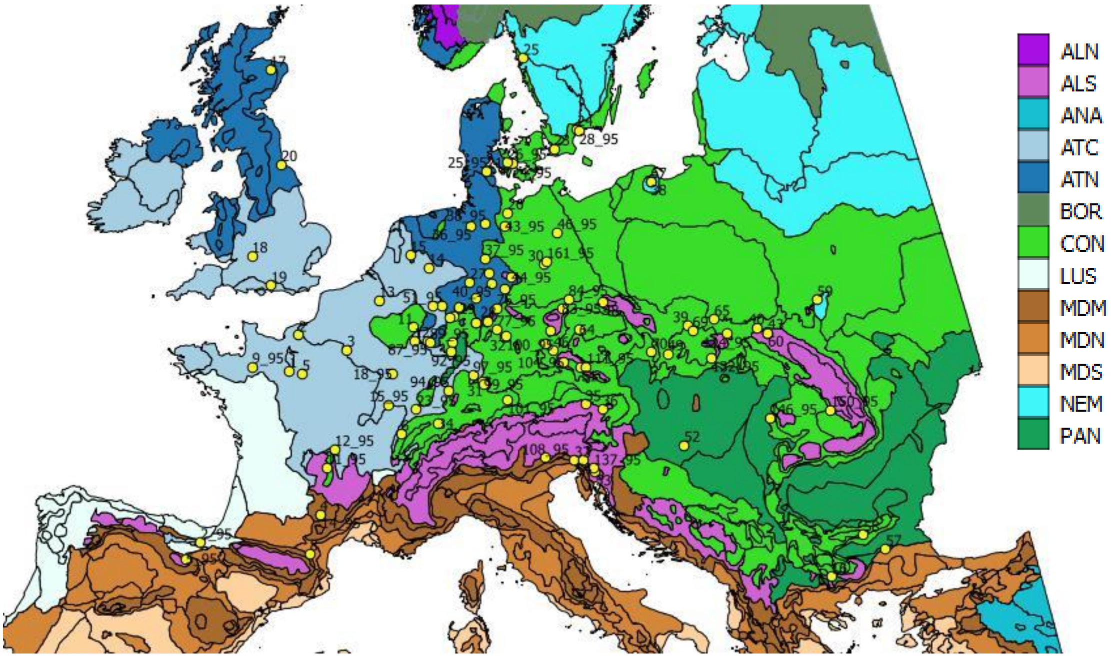


Figure 11: Provenances included in the analysis projected on the map of European Environmental Stratification (http://www.wageningenur.nl/en)

4.1.2. Alpine group

The Alpine group included the least number of provenances, namely 20 at 30 test sites. Spearman correlation showed no significant relationship between 9-year old height and any climatic parameters, so a mixed model analysis was not feasible for this group. Presumably, in the case of Alpine group the number of provenances was insufficient to create a reliable height growth response model.

4.1.3. Atlantic group

The Atlantic group contained 37 provenances and 31 test sites, in total 341 data points. According to Spearman correlation eighteen climatic parameters of seed source have been selected which were significant at level p<0.01 (Table 5). For abbreviations, see in Table 2.

Table 5: Climate parameters significantly correlating with the mean height of Atlantic provenances across sites

Climate variable	Spearman 'ρ'	Climate variable	Spearman 'ρ'
Tmin_wt	*-0.526*	**bFFP**	*0.457*
Tmin01	*-0.518*	**Tave12**	*-0.455*
Tmin10	*-0.511*	**Tave_wt**	*-0.454*
EMNT	*-0.511*	**Tmin_at**	*-0.449*
Tmin12	*-0.502*	**DD<0**	*0.447*
NFFD	*-0.499*	**Tmin11**	*-0.443*
eFFP	*-0.499*	**Tmin03**	*-0.443*
FFP	*-0.487*	**Tave01**	*-0.434*
Tmin02	*-0.473*	**MCMT**	*-0.432*

Parameters in Table 5 are of thermal character and mostly related to winter temperature which means that the mean performance of provenances regarding their origin has been mostly determined by winter temperature. The negative correlations show that provenances adapted to colder winters performed better than provenances from milder winter climate. Because there is a strong interrelation among variables only the best one, the winter minimum temperature (*Tmin_wt*) has been selected.

In order to recognize how Atlantic provenances respond to translocation, quadratic functions have been fitted and compared according to AIC values. Autumn precipitation (*PPT_at*), precipitation in January (*PPT_01*), in October (*PPT_10*) and November (*PPT_11*), maximum temperature in April (*Tmax04*) and Ellenberg drought index (*EQ*) transfer distances showed the lowest AIC values with negative trend. Due to the small difference in AIC value of the six transfer distance variables, only one, the Ellenberg drought index has been selected. *EQ* includes temperature and also precipitation data and several previous studies emphasized the role of this drought index in the distribution of beech (Ellenberg 1986, Mátyás et al. 2010, Czúcz et al. 2011, Rasztovits et al. 2012, Stojanović et al. 2013, Móricz et al. 2013).

The results of the two selection methods can be combined into one model. The full model include winter minimum temperature (*Tmin_wt*) as seed source climate variable and Ellenberg drought index (*EQ*) as transfer distance variable and their interaction. Table 6 shows the statistical parameters of the model.

$$\text{Height growth}_{\text{atlantic provenance}} = \text{Tmin\_wt} + \Delta\text{EQ} + (\Delta\text{EQ})^{\wedge 2} + \text{Tmin\_wt}^{\text{x}}\, \Delta\text{EQ}$$

Table 6: Statistical parameters of full growth response model for Atlantic group

Parameter	Parameter estimate	Confidence intervals (α=0.95)		Contribution to total variance (%)
		lower	upper	
Fixed effects				
Intercept	223.2648	195.0446	251.2730864	
Tmin_wt	3.0017	-1.63439	7.67461371	8.9
ΔEQ	-2.1729	-3.86961	-0.43622111	34.8
(ΔEQ)^2	-0.0481	-0.16185	0.0704704	0.6
Tmin_wt x **ΔEQ**	-0.4893	-1.04886	0.08040413	17.1
Total contribution of fixed effects:				61.4
Random effects	**Std.Dev.**			
provenance	7.681			0.3
site	75.217			32.4
residual	32.003			5.9
Total contribution of random effects:				38.6

The Pearson correlation coefficient between the observed and predicted values using fixed and random effects was 0.883. 61.4% of the total phenotypic variation between provenance height growths could be explained by climate. Genetic differentiation due to other factors (e.g. genetic drift) accounted for only 0.3 of the total variance. The planting site had a large contribution to total variance (32.4%). This random site effect includes all factors (e.g. local soil conditions, different management practices) which were not possible to measure. Box-whisker plots represent the variability of height by sites (Figure 12).

4.1.3. Continental group

Because of the weak ρ values, it has been assumed that the relationship between climate variables and 9 year-old height is not monoton. Therefore, instead of Spearman correlations, quadratic functions have been fitted and climate variables with the highest significance were selected (Table 7, Figure 13). Highest significance was calculated for Hargreaves climatic moisture deficit (*CMD*). If *CMD* is equal to 0, it means that precipitation is larger than the evaporation in every month. High *CMD* value refers to high temperature and low amount of precipitation. The decline of the function towards high *CMD* values (towards the “xeric limit”) indicates the selective importance of moisture conditions.

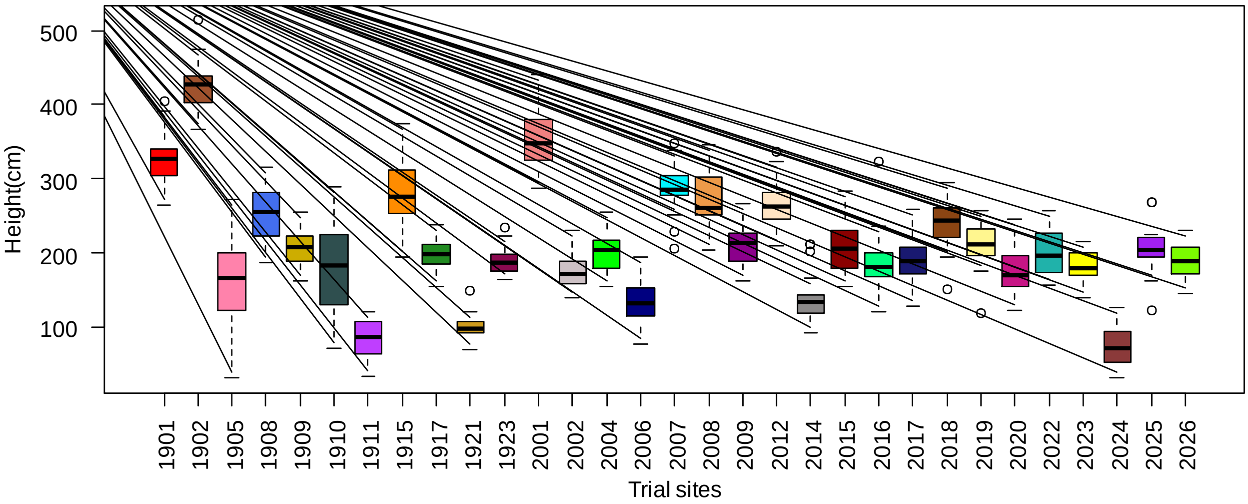


Figure 12: Box-whisker plot of site variability of height for Atlantic provenances. The code list for the test sites is in the Appendix

Table 7: Significant ($p < 0.05$) climate parameters, correlating with the mean height of continental provenances across sites, based on quadratic functions

Climate variable	p	Climate variable	p
CMD	*0.0002*	**Tmax05**	*0.0236*
Eref	*0.0019*	**Tmax12**	*0.0237*
Tmax09	*0.0019*	**Tmax_sp**	*0.0240*
SHM	*0.0020*	**Tave_sp**	*0.0241*
Tmax08	*0.0022*	**Tave08**	*0.0328*
Tmax_sm	*0.0024*	**Tmax04**	*0.0341*
Tmax06	*0.0035*	**Tave09**	*0.0357*
Tmax_at	*0.0039*	**Tave07**	*0.0364*
Tmax07	*0.0042*	**MWMT**	*0.0365*
DD18	*0.0057*	**MAT**	*0.0397*
Tmax11	*0.0064*	**Tmax_wt**	*0.0404*
Tmax10	*0.0162*	**Tave_sm**	*0.0435*
Tave11	*0.0173*	**Tmax01**	*0.0473*
DD5	*0.0178*	**Tave_at**	*0.0486*
Tave04	*0.0200*		

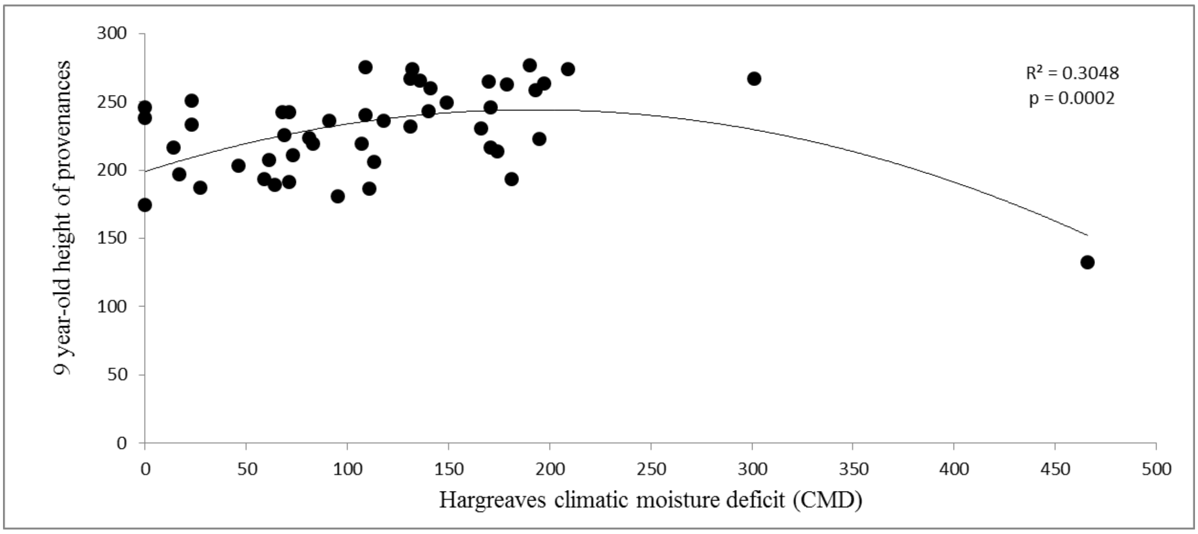


Figure 13: Significant relationship between continental provenance mean for height (averaged across sites) and Hargreaves climatic moisture deficit

Transfer distance variables have been chosen in the same way as in the Atlantic group. Climate variables with the lowest AIC value were maximum temperature in April (*Tmax04*), May (*Tmax05*), July (*Tmax07*), September (*Tmax09*) and summer maximum temperature (*Tmax_sm*). In total, 145 candidate models were run and compared. The best full model with the lowest AIC value included Hargreaves climatic moisture deficit (*CMD*) as seed source variable and maximum temperature in April (*Tmax04*) transfer distance variable (Table 8).

$$\text{Height growth}_{\text{continental provenance}} = \text{CMD} + (\text{CMD})^{\wedge 2} + \Delta\text{Tmax04} + (\Delta\text{Tmax04})^{\wedge}2 + \text{CMD}^{\text{x}}\ \Delta\text{Tmax04}$$

Table 8: Statistical parameters of the selected full growth response model for continental provenances

Parameter	Parameter estimate	Confidence intervals (α=0.95) lower	 upper	Contribution to total variance (%)
Fixed effects				
Intercept	217.80	188.60	247.34	
CMD	0.14	-0.03	0.3	0.01
(CMD)^2	-0.0005	-0.001	-0.00003	19.10
ΔTmax04	-4.40	-9.16	0.35	41.51
(ΔTmax04)^2	-0.52	-1.03	-0.007	15.94
CMD x **ΔTmax04**	0.0007	-0.025	0.026	0.01

			Total contribution of fixed effects:	76.58
Random effects	**Std.Dev.**			
provenance	14.08			0.72
site	73.7			19.72
residual	28.66			2.98
			Total contribution of random effects:	23.42

In this model the Pearson correlation coefficient between the observed and predicted values using fixed and random effects was 0.903. 76.58% of the total phenotypic variation between provenance height growths could be explained by climate. Genetic differentiation due to other factors (e.g. genetic drift) accounted for only 0.72 of the total variance. The planting site had a large contribution to total variance (19.72%). This random site effect includes all factors (e.g. local soil conditions, different management practices) which were not possible to measure.

4.1.4. Prediction of height growth response using the selected models

The fixed-effects response of three Atlantic provenances to changes in the Ellenberg drought index shows a quite different picture (Figure 14). Populations from milder winters (Tmin_wt = 1.5; -1.1, red and green lines) respond to increasing *EQ* value negatively. These populations originated from the edge of the continent, close to the coast. However, population from location with cold winters (Tmin_wt = -5) which originated from inside the continent shows a very plastic reaction to the changing *EQ* value. Most trial sites were established in the continental region; provenances close to the continental border (Tmin_wt = -5) experienced less extreme ‘climate change’ by transplanting, which may explain the flat response of the function.

The fixed-effects response of the continental provenances (Figure 15) was similar, however, the mean performance of populations (intercepts of the functions) was well separated, particularly, the performance of provenance with high *CMD* value (which refers to dry and warm climate) showed much lower height growth across sites. Presumably, this marginal provenance (from Southeast Europe) is under stress due to strong climatic selection, which is reflected in its performance.

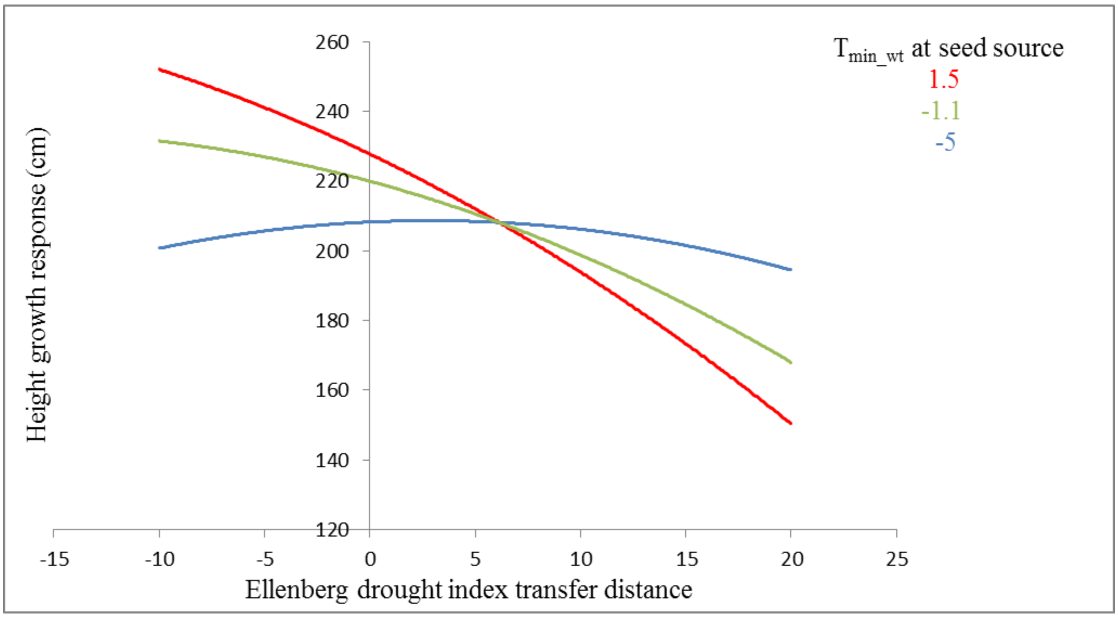


Figure 14: Illustration of the model's fixed-effects predictions for three provenances with different winter minimum temperature values (Tmin_wt)

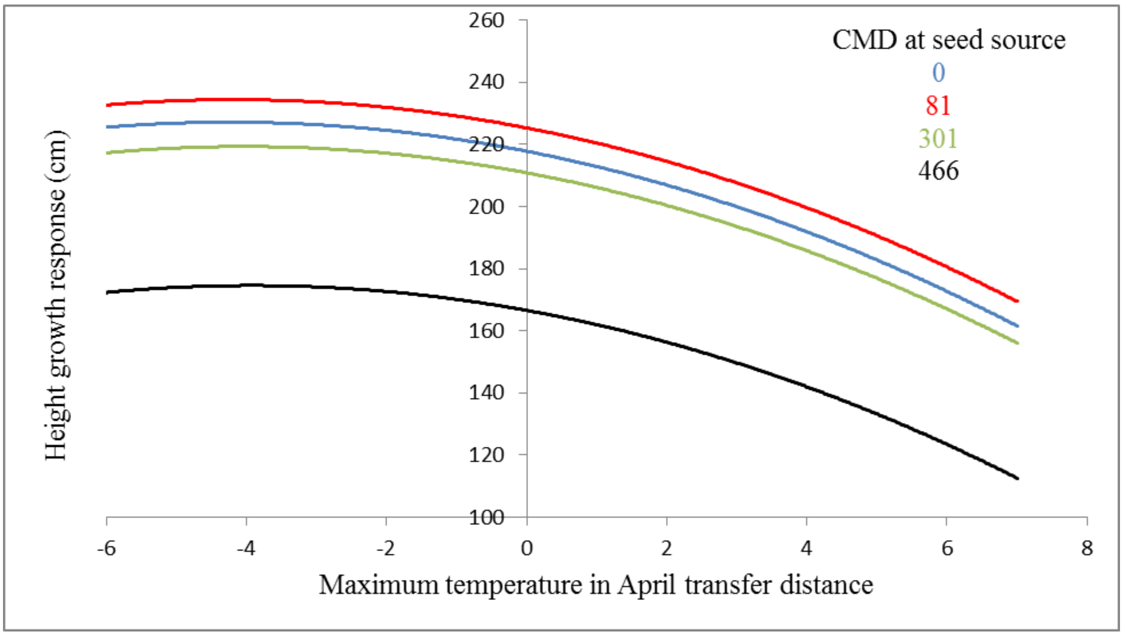


Figure 15: Illustration of the model's fixed-effects predictions for four provenances with different climatic moisture deficit values (CMD)

4.1.5. Illustration of the mean height of provenances in the Atlantic and the continental zones

In order to illustrate the distribution of the mean performance of populations, the result of Spearman correlation (in Atlantic group) and the result of quadratic function (in continental group) have been used.

In each group, the first map shows the distribution of the climate parameter (Figure 16, 18) which was the most significant according to Spearman analysis and quadratic function and the second map shows the mean performance of provenances by region (Figure 17, 19) based on the climate parameter. In the case of second maps (Figure 17, 19) height growth was interpolated according to the linear equation for winter minimum temperature at seed source, and to the quadratic equation for Hargreaves climatic moisture deficit at seed source.

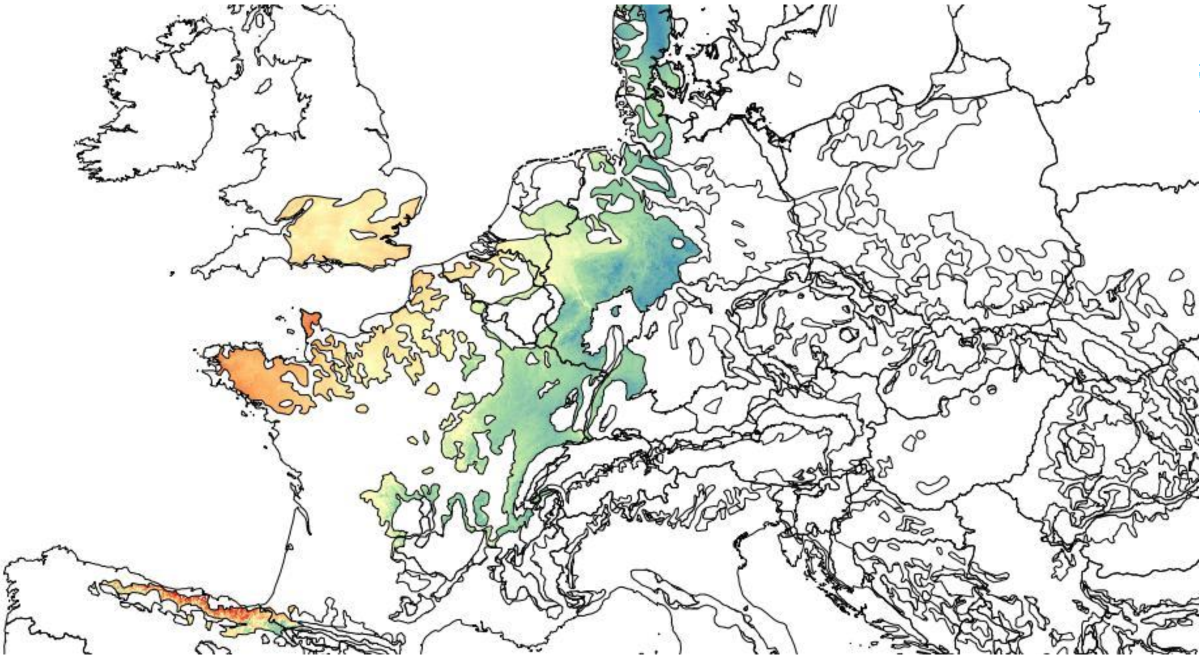


Figure 16: Winter minimum temperature (*Tmin_wt*, 1961-1990) projected on the map of beech distribution in the Atlantic climate zone

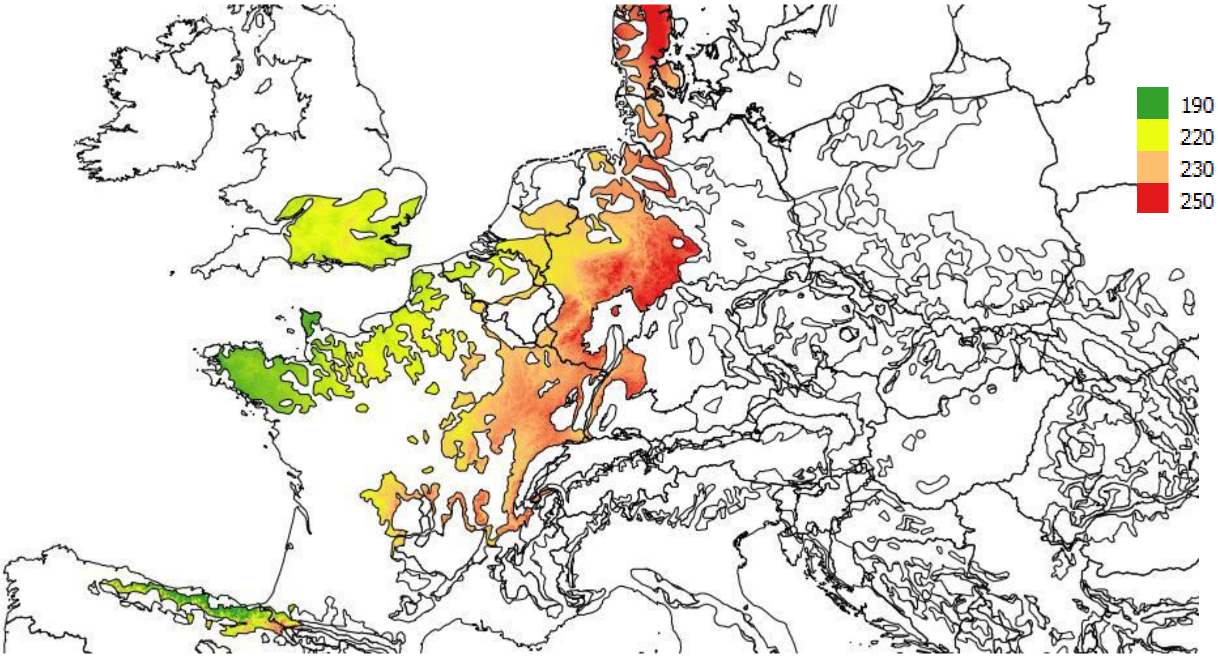


Figure 17: Pattern of mean height response of Atlantic provenances across all test sites according to winter minimum temperature (*Tmin_wt*) at origin

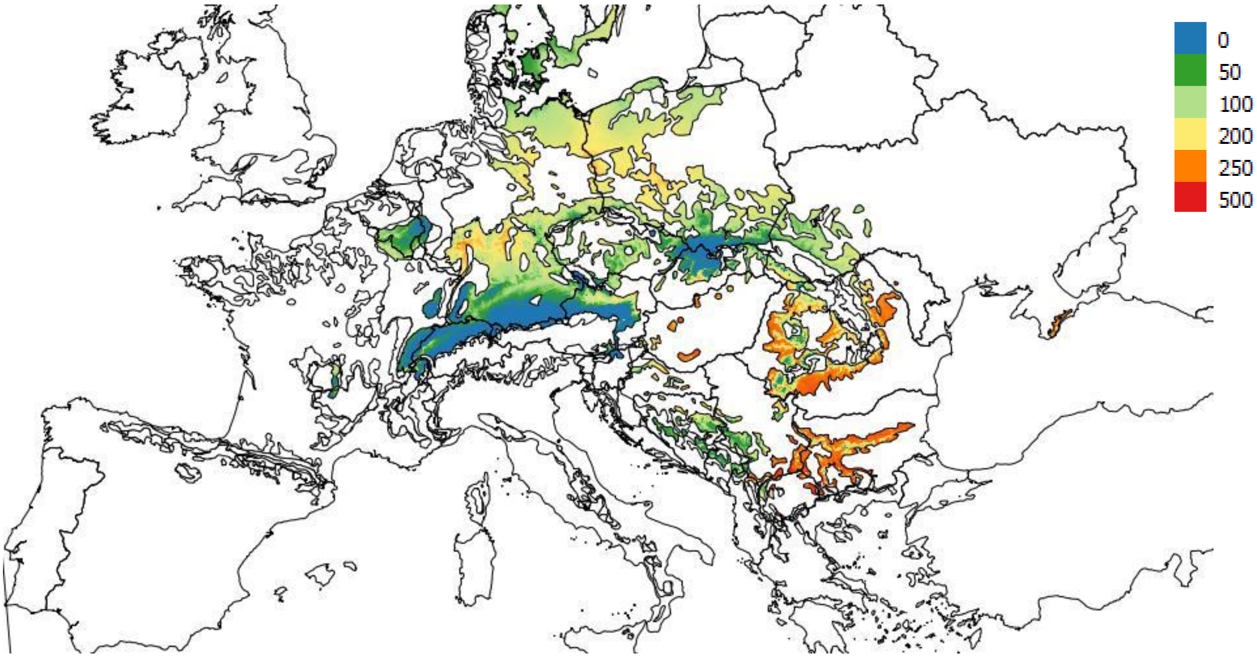


Figure 18: Hargreaves climatic moisture deficit (*CMD*, 1961-1990) projected on the map of beech distribution in the continental climate zone

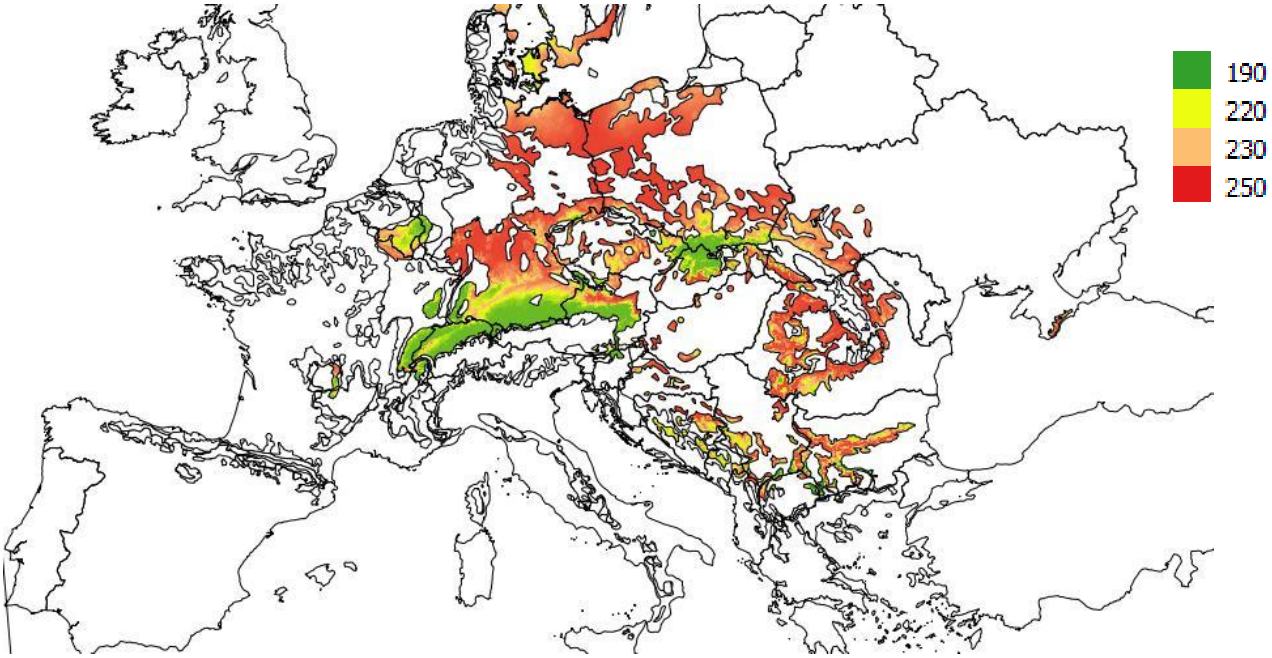


Figure 19: Pattern of mean height response of continental provenances across all test sites, according to Hargreaves climatic moisture deficit (*CMD*, 1961-1990) at origin

In the Atlantic climatic zone (Figure 16) the minimum winter temperature is continuously decreasing towards the inside of the continent. Provenances from seed source with lower winter temperature showed generally better performance across sites than provenances originated from sites with mild winter. Because most trial sites were situated in continental region, it is assumed that provenances originating from milder Atlantic climate (close to the coast) tolerated less the environmental changes (higher *ΔEQ*s).

In the continental zone the base climatic parameter was the Hargreaves climatic moisture deficit at seed source. If this value is 0, it means that precipitation is larger than the evaporation in every month. High *CMD* value refers to high temperature and low amount of precipitation. Provenances with lower *CMD* value have performed worse in the average of all sites, however, provenances with extreme high *CMD* value (in the South Balkans) also performed poorly (Figure 18, 19).

4.2. A detailed analysis of the Hungarian trial, Bucsuta

4.2.1. Response of provenances to transfer

Bucsuta is the most extreme site among the trial sites. Almost all provenances which are planted here experience drier and warmer conditions compared to their original site (Figure 20).

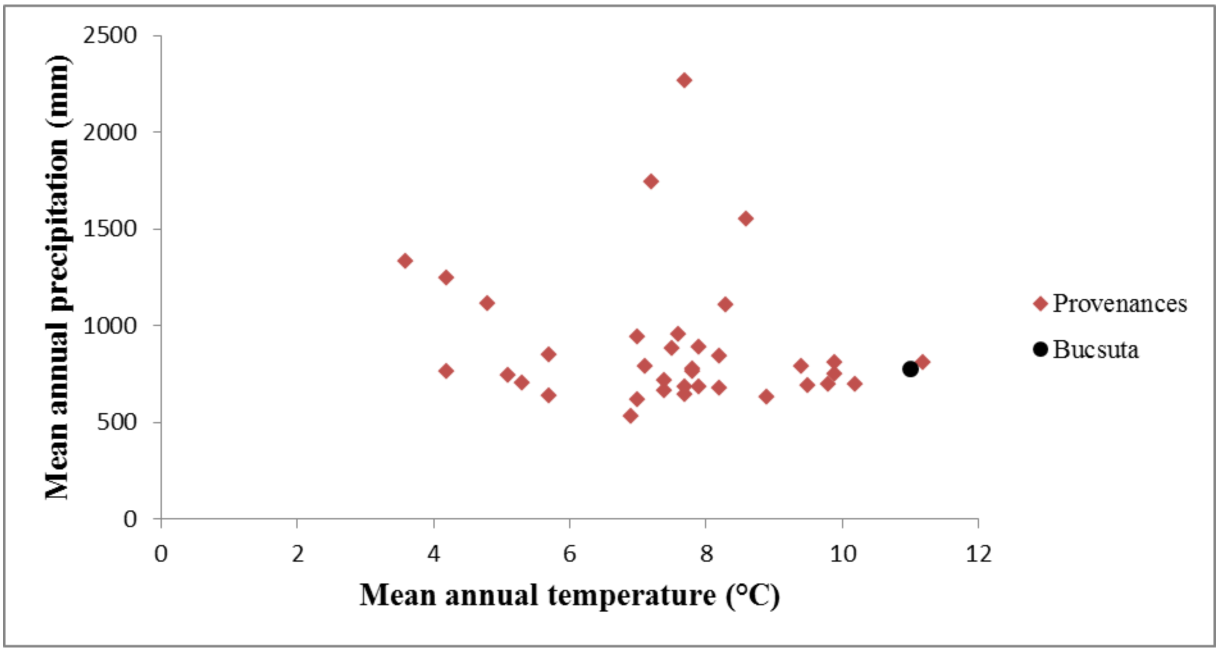


Figure 20: Climate location of Bucsuta and of tested provenances

A transfer function for provenances at Bucsuta has been calculated based on height data measured in 2006. On the basis of the results of the mixed model analysis, maximum temperature in April as transfer distance variable (ΔTmax04 = maximum temperature of April in Bucsuta (1998-2006) minus maximum temperature of April of the provenance origin (1961-1990) has been used. Figure 21 shows a decline towards warming which confirms the previous result of the author (Figure 22, HORVÁTH AND MÁTYÁS 2014). A linear response regression of diameter growth vs. *ΔEQ* has been presented in Figure 22. It explains 25% of the total variation between provenances ($R^2 = 0.247$, $p = 0.0006$). The function predicts the increment loss caused by sub-optimal adaptedness, i.e. if a population is planted in an environment to which it is not fully adapted. The function may be interpreted also as indicating the growth decline of native populations caused by projected rapid climate change.

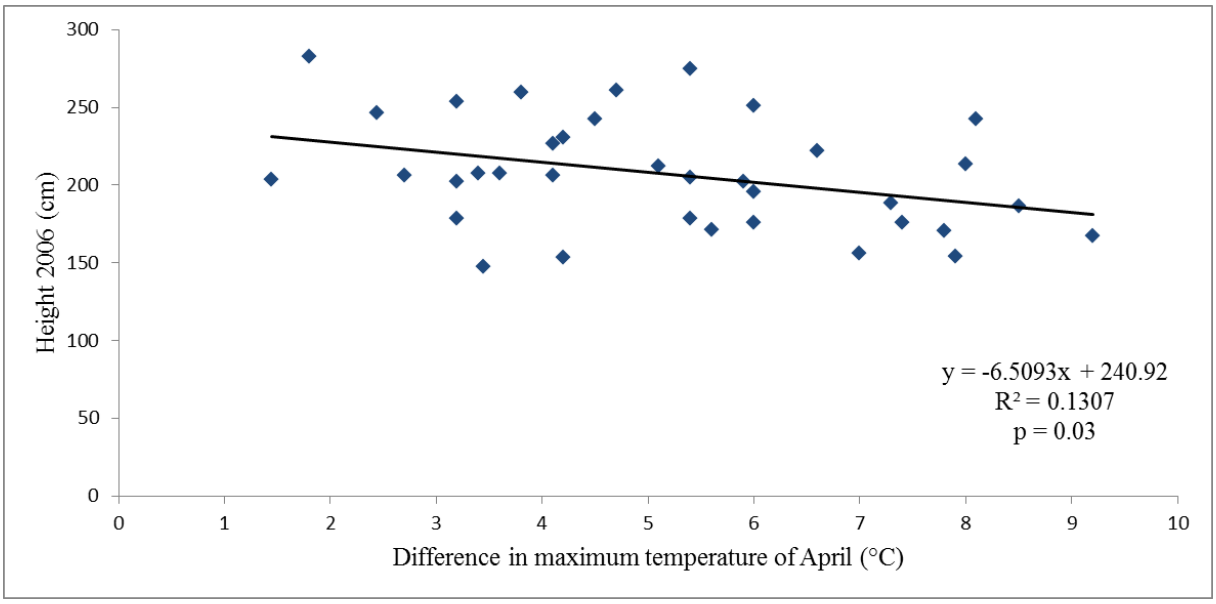


Figure 21: Observed growth decline of provenances with increasing transfer distance of maximum April temperature at the trial site Bucsuta

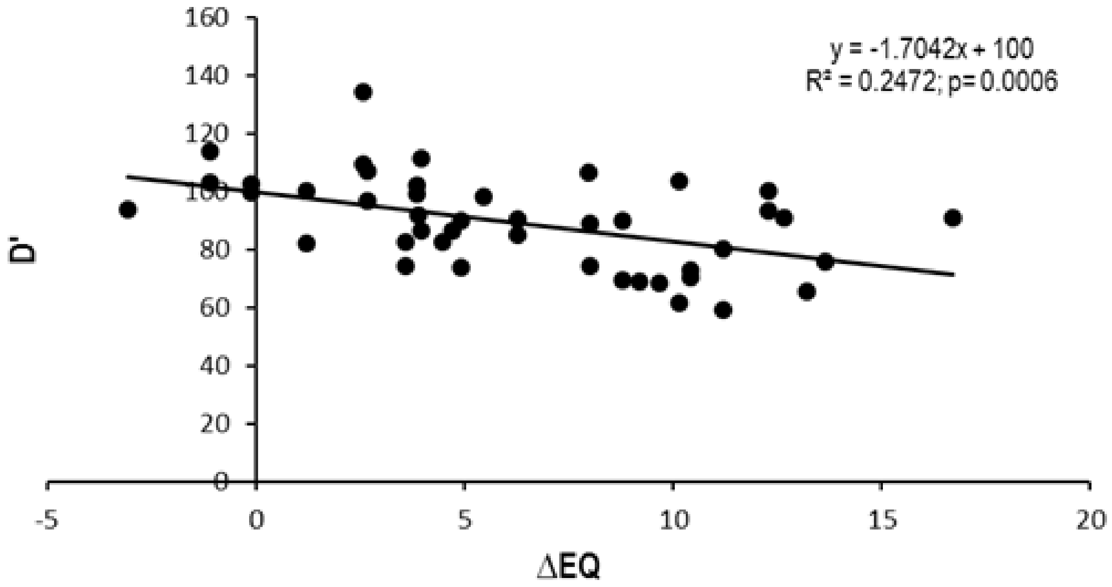


Figure 22: Increment decline caused by sub-optimal adaptedness, in function of the change of the Ellenberg drought index (HORVÁTH AND MÁTYÁS 2014)

In order to get the group of the best provenances in Bucsuta, the early survival (2001) was combined with height growth (2008) (Figure 23).

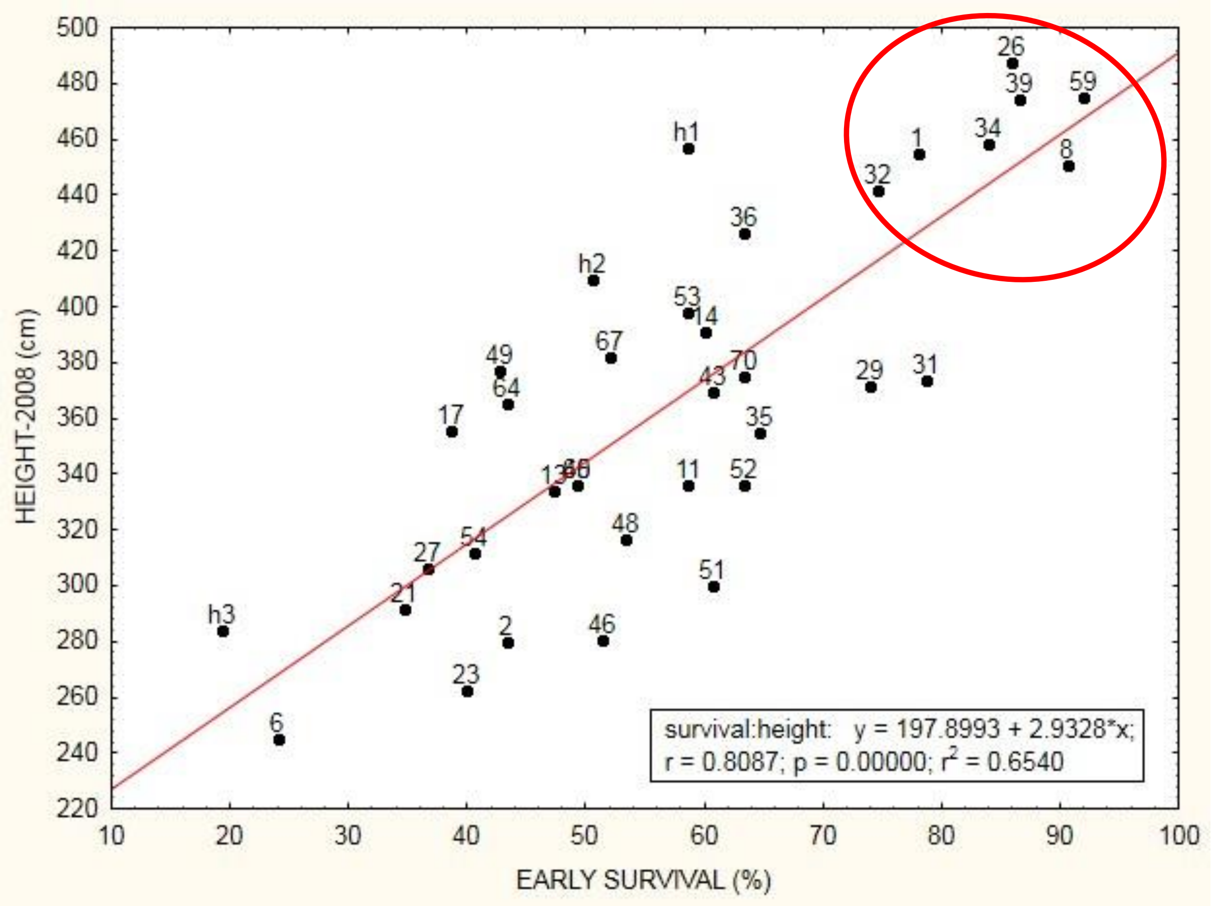


Figure 23: Early survival (2001) and height measured in 2008 shows a strong relationship. The best performers are situated the top right of the figure

Five continental (26, 32, 34, 39, 59), one Atlantic (1) and one Alpine (8) provenances had the highest survival rate with good growth characteristics in Bucsuta. Figure 24 introduces the map of survival of provenances, indicating the best performers with red circles.

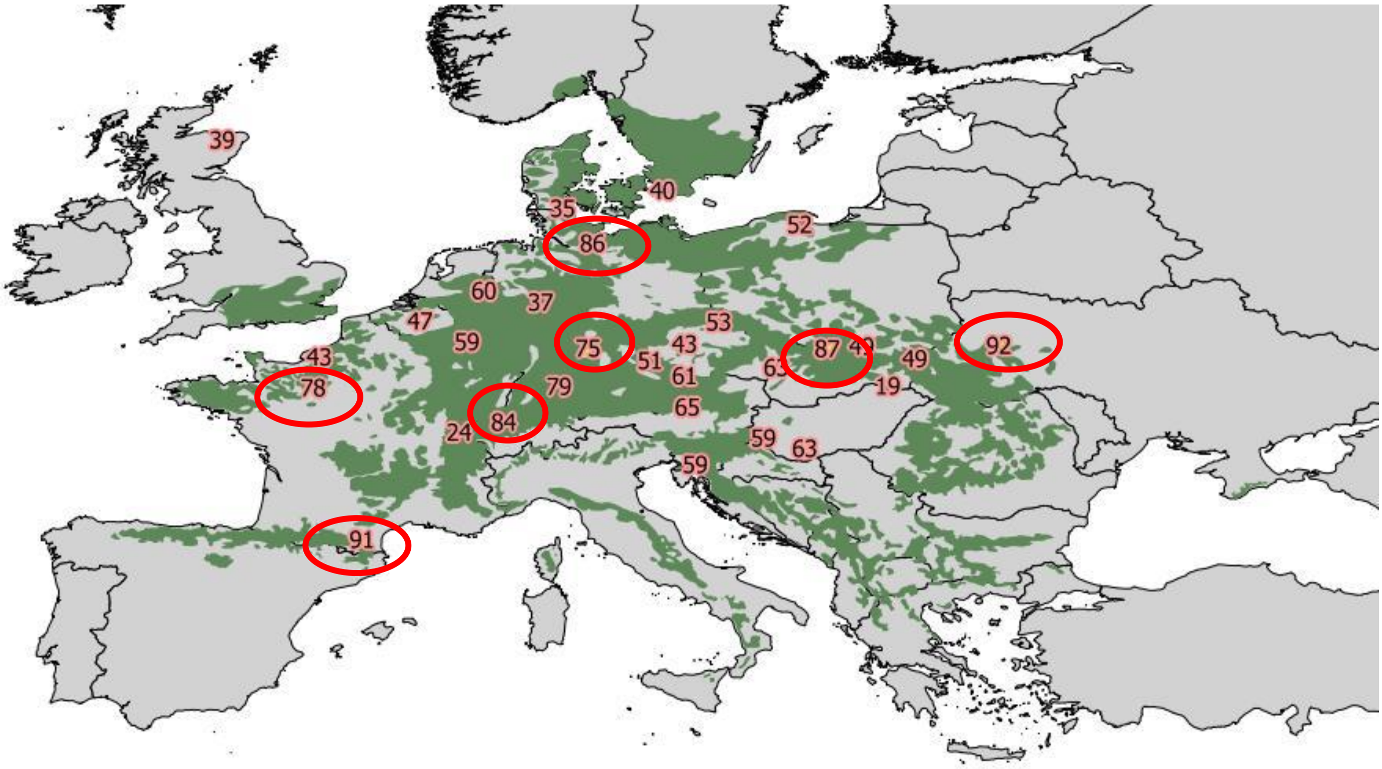


Figure 24: The mean survival rate (%) of provenances at the trial site Bucsuta projected to the site of origin. Red circles indicate provenances which have high survival rate and robust height growth

4.2.2. Phenological characteristics of provenances in Bucsuta

Fortunately, the investigated years are characterized by contrasting climate conditions. The winter in 2001, 2007 and 2015 was much warmer than in the other two years. Difference in spring temperature among years was less. The year of 2007 was the warmest both in winter and in spring (Table 9).

Table 9: Winter and spring temperatures in phenology assessment years

Year	Average temperature from 1 November to the end of February	Average temperature from 1 March to the end of April
2001	3.98	9.06
2002	0.81	8.50
2003	0.65	7.25
2007	*4.62*	*9.57*
2015	3.93	8.56

Logistic sigmoid function has been fitted for phenological data of each provenance in each year (Figure 25). In total, 180 functions were evaluated. The inflection point of each function has been determined as bud burst date (see Annex 2). Degree days for bud burst date have been computed according to two different methods.

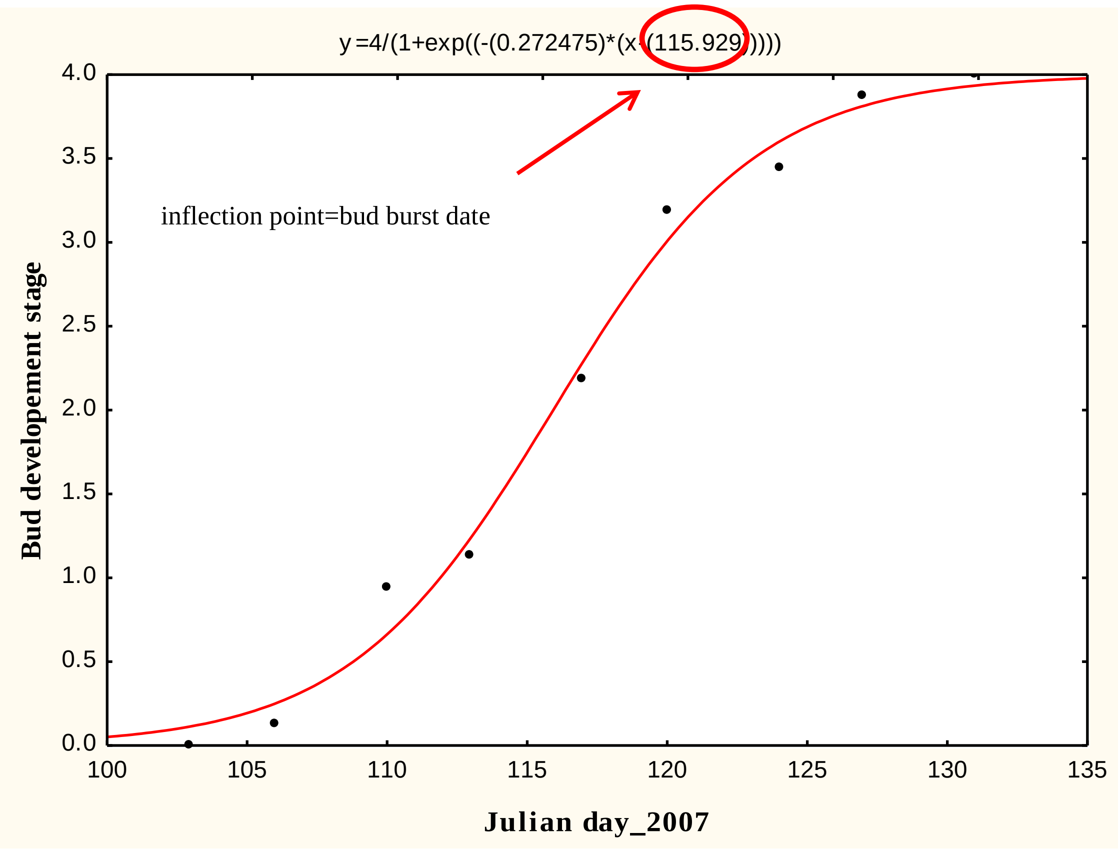


Figure 25: Sigmoid function of “Idrija” which is the one of the latest flushing provenance.

Improved sequential model

The model of KRAMER (1994b, Table 10) was tested using phenology observation data which were assessed in different years: 2001, 2002, 2003, 2007 and 2015. Pooled bud burst dates of all provenances per year are considered as mean bud burst date.

Table 10: Parameter values of the KRAMER (1994b) model

MODEL PARAMETERS	MODEL VALUES
minimum temperature for chilling	-19.4
optimal temperature for chilling	-0.2
maximum temperature for chilling	77
critical value of state of chilling	117.6
critical value of state of forcing	3.6
constant ‘b’	0.1
constant ‘c’	33.1

Applying the model in each year, expected results significantly differed from the observed data. According to the model the bud burst date occurs when the exponential function takes the value *3.6* which equivalent to around 23.5°C. In all cases this value was reached much later than the observed bud burst date. The least deviation was found in 2003, it is likely because there was a rapid warming in that year and therefore the mean temperature have been reached earlier the critical value, *3.6*. Table 11 shows the observed and predicted values.

Table 11: Observed and predicted values for bud burst (BB) date

Year	Observed mean BB date	Model prediction
2001	116	149
2002	110	165
2003	115	129
2007	109	146
2015	110	163

Why did the prediction not work?

The parameters of the model (Table 10) have been developed for Atlantic conditions where due to warm winters the chilling requirement fulfilled only later, therefore the bud burst delayed. Observing the average temperature values of two warm years 2001 and 2007, it can be seen they are almost the same (Table 9) and the model prediction is also similar (Table 11). If we compare the temperature profile of April month in each year (Figure 26, Table 12), the fluctuation in 2001 is more significant and thereby the bud burst delayed, which is well reflected in the observed data. Figure 26 shows that in April in 2001 there was a suddenly decrease in temperature just before the first bud burst would have been occurred.

Table 12: Basic statistics of temperature for April month in each year

Years	N	Mean	Minimum	Maximum	Range	Variance
2001	30	9.29815	2.611111	16.61111	14.00000	8.68720
2007	30	11.96407	7.000000	15.61111	8.61111	5.24110
2003	30	9.39259	-0.388889	17.72222	18.11111	20.69752
2002	30	9.89630	2.055556	14.61111	12.55556	11.71152
2015	30	10.88519	4.333333	17.83333	13.50000	16.93719

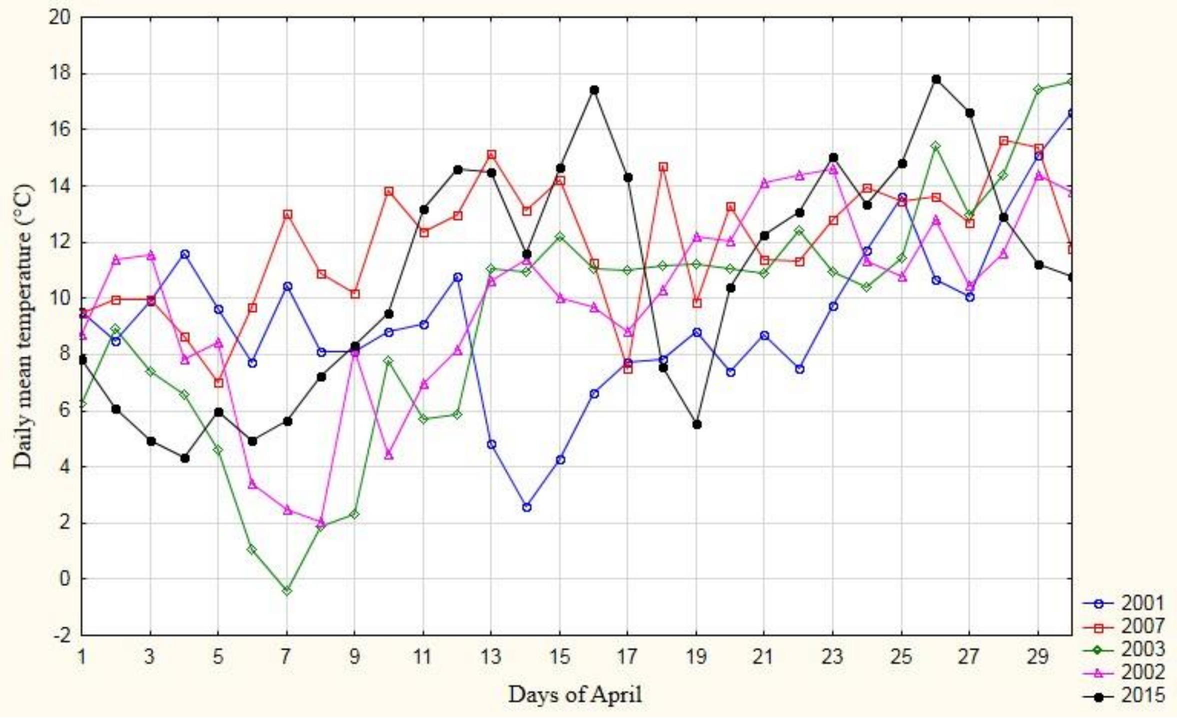


Figure 26: Temperature profile of April in five different years according to climate data of Nagykanizsa

Alternating model

The alternating model (MURRAY ET AL. 1989) applies linear relationships to predict bud burst. The start date for forcing accumulation was January 1 with 5°C base temperature. The number of chilling days was calculated below 5°C from the first of November to the end of February and between 0 and 10°C from the first of November to the end of February.

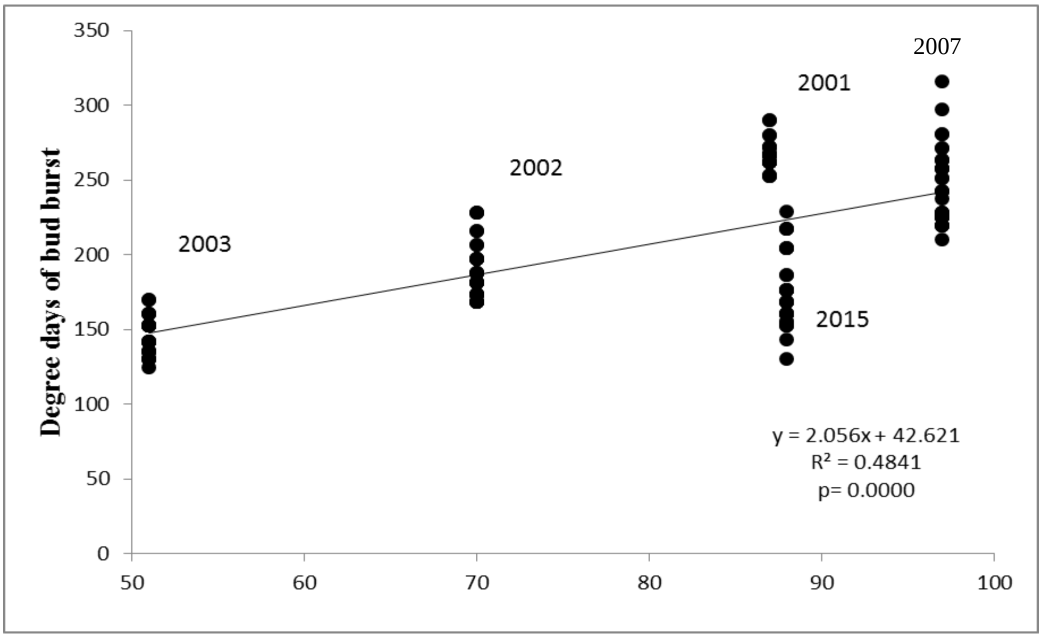


Figure 27: Number of days between 0 and 10°C from November 1 to March 1

The warm winters in 2001 and 2007 resulted more days with temperature between 0 and 10°C and higher heat requirement (Figure 27). This outcome confirms the results of previous study (MURRY ET AL. 1989) that the insufficient chilling due to warm winters increases the heat requirement. This result also verifies why the sequential model does not work at a continental site, like in Hungary at Bucsuta. Sequential model has been developed for Atlantic conditions where winters are milder and thereby bud burst occurs later (VON WÜHLISCH ET AL.1995, ROBSON ET AL. 2011). An opposite outcome was obtained with calculating the number of days below 5°C (Figure 28). The more number of days below 5°C daily average temperature (including negative values) decreases the heat requirement. Results show that the warmer the winters, the longer the flushing.

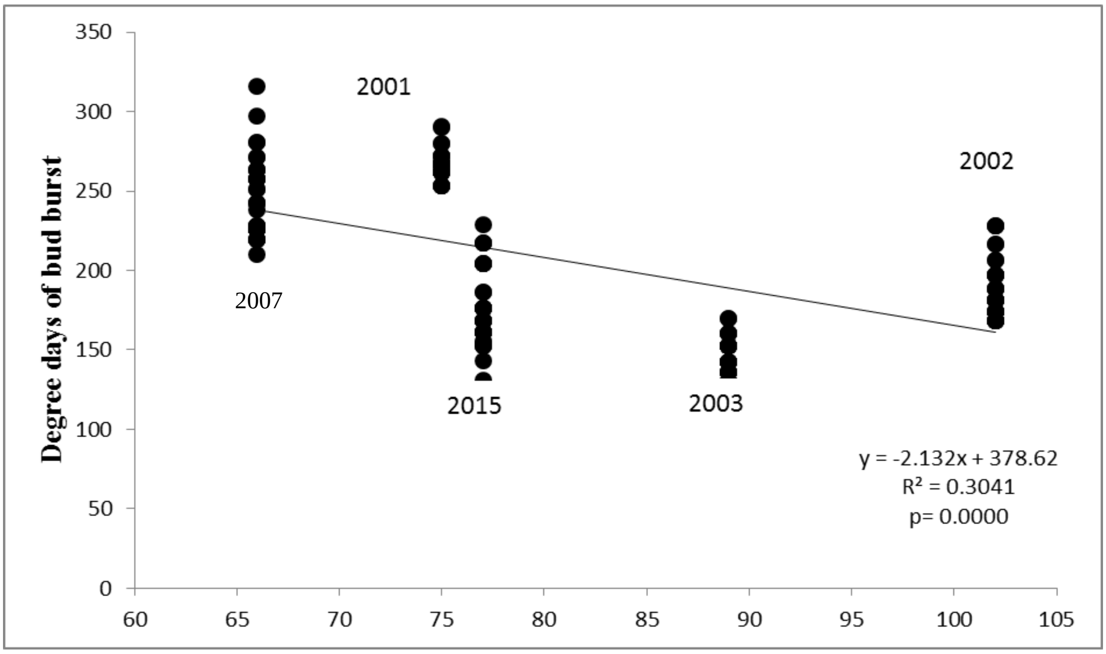


Figure 28: Number of days below 5°C between November 1 and March 1

Bud burst is known as a highly heritable, adaptive trait. To identify what climatic factors affect the bud burst, a simple Pearson correlation was performed between the required degree days to bud burst of provenances and 85 climatic parameters of the site of origin (Table 2). Positive significant correlation were detectable with minimum and average temperature in January and February, winter mean and mean minimum temperature, mean coldest month temperature, extreme minimum temperature over 30 years. Continentality (temperature difference between mean warmest month temperature and mean coldest month temperature) showed the strongest negative relationship with average heat requirement of provenances for bud burst (Figure 29). It means that the more continental provenances, which receive sufficient chilling earlier due to colder winters, are flushing earlier.

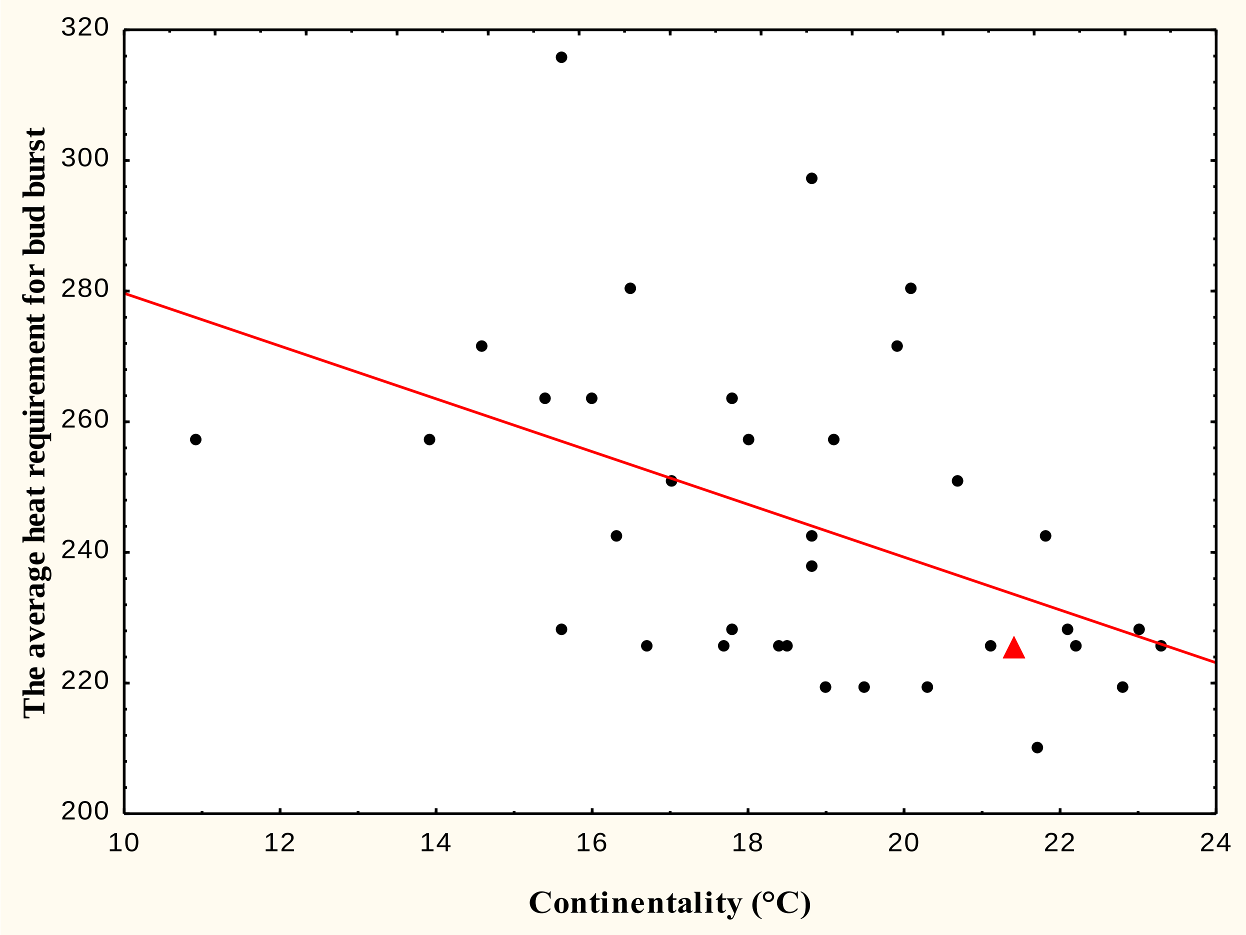


Figure 29: Mean heat requirement of provenances for bud burst as a function of continentality of the site of origin, at Bucsuta in 2007. Red triangle indicate the local provenance, Bánokszentgyörgy

Results show that both variability in bud burst among years and among provenances are mostly affected by winter temperature. In order to compare the effect of differences among years and the differences among provenances on bud phenology, an analysis of variance (ANOVA) has been performed (Table 13). Both effects were significant, but according to F statistics the effect of year is much stronger than the effect of provenances.

Table 13: Analysis of variance of heat requirement by effects of provenance and year

	SS	Degr. of	MS	F	p
Intercept	7507468	1	7507468	66319.09	0.00
year	359868	4	89967	794.75	0.00
prov	43362	35	1239	10.94	0.00
Error	15848	140	113		

Based on the accumulated degree days, three groups, “early”, “medium” and “late” flushing provenances have been determined based on phenology data in Bucsuta (Figure 30). For the analysis, the data of 2007 has been used because this year has shown the best differentiation between provenances due to the favorable environmental conditions.

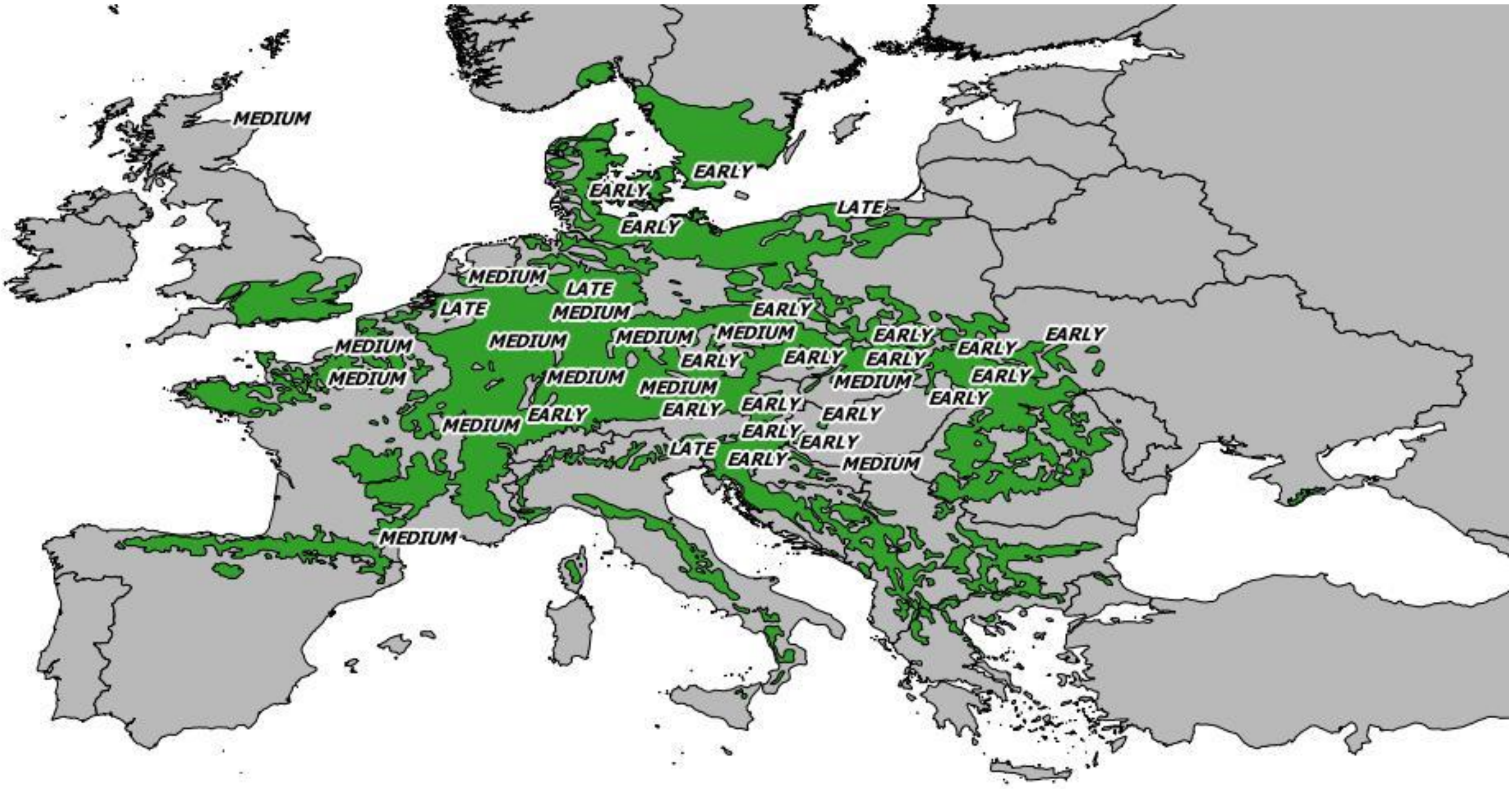


Figure 30: Map of early, medium and late flushing provenances at the trial site, Bucsuta

5. Discussion

The aim of mixed model analysis was to select the main climate variables which have the most influential effect on height growth of 9 years old beech seedlings and to build up a model which allows predict how different populations will respond to environmental changes based on common garden experiment data.

Because the role of the climate variables at the different part of the area is different, using one model for the whole area may increase error variance. In order to improve model prediction, provenances were divided into three groups (Alpine, Atlantic, continental) according to the map of Environmental Stratification of Europe based on climate, ocean influence and geographical data (METZGER ET AL 2005).

The Alpine group, including provenances from high elevation, showed no significant relationship between height growth and any climate parameter. This confirms the results of previous studies which also detected the divergent behavior of beech populations from higher elevations (GÖMÖRY 2010, MÁTYÁS ET AL. 2011). However, the small number of populations in this group has likely contributed to the weak statistical results.

Winter minimum temperature has been identified as main climate factor to determine the mean performance of the Atlantic provenances. The negative trend of Spearman correlation suggests that provenances adapted to colder winters performed generally better across the sites, their performance was more stable than of others. This phenomenon is clearly discernible in the map (Figure 17). Almost all significant climate variables related to winter temperature (Table 5) which is the main factor in regulating phenology (LANDSBERG 1974, HÄNNINEN 1990, KRAMER 1994a, b, MURRAY ET AL. 1989, KOBAYASHI ET AL. 1982, VEGIS 1964, CHUINE ET AL. 1999). Bud burst is a highly heritable trait (VON WÜHLISCH ET AL. 1995), it is assumed that within the Atlantic region, provenances close to the continental border are flushing earlier than the coastal provenances thereby prolonging their growing season which is reflected in their performance. In terms of ecological distance of transfer, the difference (change) in Ellenberg drought index was one of the most significant parameter. The important role of Ellenberg drought index is supported by other studies (MÁTYÁS ET AL. 2010, CZÚCZ ET AL. 2011, RASZTOVITS ET AL. 2012, STOJANOVIC ET AL. 2013, MÓRICZ ET AL. 2013, HORVÁTH AND MÁTYÁS 2014). According to model prediction (Figure 14) Atlantic provenances from milder winters respond to increasing *EQ* value quite negatively. These populations are located close to the coast with typical maritime climate. In contrast, populations from inside the continent adapted to cold winters show a very plastic reaction to the changing *EQ* value. The distribution of the trial sites was, however, unbalanced; most of the sites were established in the continental region (with higher *EQ* values). Consequently, Atlantic provenances close to the continental border experienced less extreme ‘climate change’ by transplanting than the coastal provenances. This may partly explain the flat response of the function.

In case of the continental group the climatic moisture deficit showed the strongest relationship with the mean performance of provenances (Figure 13). This quadratic relationship indicates that the ecologically marginal populations (with too low or too high climatic moisture deficit) performed poorer than populations from optimal climate conditions (Figure 19). The effect of climatic transfer was best described with the difference in maximum temperature in April. CZÚCZ ET AL. (2011) also confirmed the role of spring temperature for beech. Based on model prediction, the response of the continental provenances (Figure 15) was similar, however, the mean performance of populations was well separated (see intercepts of the functions), particularly the performance of one provenance from Southeast Europe with remarkably high *CMD* value (which refers to dry and warm climate) showed much lower height growth across sites. Presumably, this marginal provenance is under strong stress selection at its original site and its gene pool depleted, therefore, it can not adapt to rapidly changing environmental conditions. This provenance went extinct in most trial sites.

For both models, the contribution of fixed effects to total variance was larger than the contribution of random effects (Table 6, 8). It is indicating that the total phenotypic variation of provenance height growth could be well explained by climate. Among random effects, the effect of planting site was much larger than the provenance random effect. It is general for all common garden experiment networks with large extension, due to the strongly varying local ecological conditions of the test sites.

The Hungarian trial site Bucsuta has a great importance. Because of its high temperature and low precipitation conditions it is the most extreme of all trial sites. The transfer function (Figure 21) shows a decline towards warming which confirms the previous result of the author (Figure 22, HORVÁTH AND MÁTYÁS 2014). Here, the local provenance is not the best; another Hungarian provenance, Magyaregregy from South Hungary, adapted to less precipitation amount and less temperature value performed best (Figure 21). Due to the recent climate change in Bucsuta, which is represented here as climate difference between the past climate (1961-1990) and the weather conditions from outplanting to the date of measurement (1998-2006), the magnitude of changes slightly exceeded the adaptability of the local provenance. However, the flat response of the function underlines the high plasticity of beech.

By projection the early survival (measured in 2001) and height data (measured in 2008), the group of the best performing provenances was determined. High survival rate (above 70 %) and significantly better than average growth (above 440 cm) were observed for five continental (26, 32, 34, 39, 59), one Atlantic (1) and one Alpine (8) provenances (Figure 23, 24).

A detailed phenology assessment was conducted in five different years in Bucsuta. Variance between provenances and between years were significant, however the effect of year was much stronger. Depending on winter and spring temperature characteristic for the particular year, all provenances were flushing earlier or later relative to another year. Winter temperature had a dominant role on bud burst date. The role of winter temperature of different years was compared based on the number of days below 5°C between November 1 and March 1 and on the number of days between 0 and 10°C between November 1 and March 1. In the future, the mean bud burst date could be predicted with the functions Figure 27 and 28; however this requires a very accurate weather forecast. In generally, warmer winters delay the bud burst of trees due to the insufficient chilling which confirms the results of MURRAY ET AL. (1989). The correlation between the continentality of provenances and the accumulation of degree days verify the finding by VON WÜHLISCH ET AL.(1995) and ROBSON ET AL. (2011) that bud burst of beech shows a west-east cline, from late to early flushing. Based on heat requirement for bud burst, three groups of provenances (early, middle and late flushing) were distinguishable at the trial site Bucsuta (Figure 30).

6. Conclusions

The success of tree planting efforts depends on the use of appropriate forest reproductive material that will survive and grow at the planting site. Selecting suitable planting stock for reforestation is a key question of adaptive forest management strategy to mitigate negative impacts of climate change (MÁTYÁS 2016).

Results show the existence of macroclimatic adaptation patterns in juvenile growth of beech. Climate effects that shaped population differentiation in the past and the climate change simulated by transfer of populations explain a significant part of the differentiation among provenances of beech. According to the mixed-effects model analysis, 61.4% of the phenotypic variation for Atlantic provenances and 76.58% for continental provenances could be explained by climate factors. In order to define recommended directions and limits of transfer of reproductive material, it would be advisable to use ecologically-based criteria instead of geographical criteria. Transfer effects are not the same between regions and it was different also within region in the case of Atlantic provenances. Especially at exposed sites, growth decline is expected with worsening climate conditions. Using growth response models (Table 6, Table 8), the height growth of one particular provenance can be projected for a given planting site.

The stability of performance of provenances across a range of environmental conditions is of primary importance in the selection and use of forest reproductive material. Stability of provenances was well separated within regions.

The transfer function in Bucsuta confirms that the speed of changes may overtake the adaptive potential of a population. There is relatively limited space left for adjusting natural processes. The 'local is the best' is a valid argument, as long as changes in temperature and precipitation remain within the tolerance limits ensuring acceptable growth and vitality (MÁTYÁS 2016). Still, it would be advisable to use climatically matcing (preadapted) provenance which is assumed to be adjusted to future climate conditions.

The result of phenological observations in Bucsuta confirms the strong geographical trends in beech flushing previously reported. The high variability in this trait refers to an adaptation to the climate of provenance origin. Warmer winters delayed the bud burst of trees due to the insufficient chilling. Applying a vigorously growing continental provenance on an Atlantic site with milder winters, it is expected that the provenance will not show the same performance due to the shortened vegetation period.

In summary, the results draw attention to the importance of using appropriate planting stock, matching with the future climate conditions at the planting site.

7. Recommendations for the future

Based on the comprehensive analysis, transferring Atlantic provenances to continental sites is not recommended because it may lead to growth decline due to the worsening temperature and precipitation conditions to which Atlantic provenances are not adapted. Moreover, Atlantic provenances show later bud burst and the duration of flushing is also relatively long (ROBSON ET AL. 2011), they are less prepared to unpredictable events such as early snow damage (e.g. in Slovenia, Figure 2).

Warmer winters due to projected global warming may delay the bud burst of trees resulting shorter growing season with decreasing production. Applying early flushing provenances in order to maintain production and vitality is a primary task, at least under continental conditions. Selection for earlier budburst could be a mechanism to ensure sufficient early growth before summer drought becomes a limiting factor. Further, the selection of appropriate provenances based on late frost resistance would be also a desirable task in the future.

Climate is a main selective force that has shaped adaptive traits of trees over the last few thousands of years; therefore, in order to use appropriate reproductive material, the revision of reproductive material policies is advisable, on the basis of discussed ecological principles.

Provenance trials provide a unique tool to investigate climate change effects on forest trees. Establishing new provenance trials based on accumulating new knowledges should be considered.

Finally, it has to be noted that the success of evaluation depends on the characteristic of the dataset: number and quality of provenances and test sites, the quality and reliability of recording. Furthermore it has to be pointed out that the author is fully aware that the results obtained at juvenile age may change in later age. Further observations are indispensable to increase reliability. Still, due to the irreplaceability and importance of the observations, the presented analysis is considered as relevant for research and forest management.

8. Theses

1. Beech populations from the different part of the distribution area showed different phenotypic response to the environmental changes. This response can be characterised with a growth response model based on long-term climate, i.e. climate at seed source and current climate i.e. weather at the test site from the outplanting to the date of measurement and their interaction.

2. The selective role of climatic factors in the different parts of the distribution area are different, therefore separating provenances based on climatic zone may improve future predictions. It is recommended to separate, at least, the Atlantic, continental and Alpine regions.

3. Genetic variability in bud burst has been detected between provenances at the trial site Bucsuta. The high variability in this trait refers to an adaptation to the climate of

provenance origin. Genetic variability in bud burst date showed a west-east cline, from late to early flushing.

4. Winter temperature had a dominant role on bud burst date of provenances.Warmer winters delayed the bud burst of trees due to insufficient chilling.

5. Winter temperature, which is important for phenology, can be characterized both by the number of days below 5°C between November 1 and March 1 and the number of days between 0 and 10°C between November 1 and March 1.

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11. Annex

1. List of provenances by regions.

ALPINE				
5_95	108_95	137_95	35	48
14_95	110_95	4	36	51
83_95	111_95	8	37	53
104_95	114_95	16	43	54
ATLANTIC				
2_95	37_95	80_95	2	18
9_95	38_95	87_95	3	19
12_95	39_95	88_95	5	20
15_95	40_95	89_95	12	21
18_95	44_95	92_95	13	27
23_95	51_95	94_95	14	
25_95	66_95	97_95	15	
36_95	68_95	1	17	
CONTINENTAL				
11_95	73_95	102_95	26	49
24_95	74_95	132_95	28	52
26_95	76_95	146_95	30	57
28_95	77_95	150_95	31	59
43_95	84_95	161_95	32	64
46_95	90_95	6	34	65
67_95	93_95	11	38	67
69_95	99_95	23	39	69
70_95	100_95	24	40	70
72_95	101_95	25	46	

2. Julian days and accumulated degree days for bud burst of provenances in different years in Bucsuta.

Provenances	**Julian day of bud burst in 2007**	**Accumulated degree days for bud burst in 2007**	**Julian day of bud burst in 2003**	**Accumulated degree days for bud burst in 2003**	**Julian day of bud burst in 2001**	**Accumulated degree days for bud burst in 2001**
1	113	271.48	116	152.61	116	267.33
2	111	257.37	116	152.61	116	267.33
6	112	263.70	116	152.61	116	267.33
8	109	242.70	115	142.17	115	261.67
11	112	263.70	117	160.56	116	267.33
13	118	315.76	118	169.94	119	290.39
14	112	263.70	118	169.94	116	267.33
17	111	257.37	116	152.61	115	261.67
21	107	228.17	114	135.72	115	261.67
23	106	225.67	113	130.33	115	261.67
26	107	228.17	114	135.72	115	261.67
27	114	280.42	116	152.61	117	272.39
29	110	250.98	116	152.61	116	267.33
31	111	257.37	116	152.61	115	261.67
32	109	242.70	115	142.17	115	261.67
34	106	225.67	115	142.17	115	261.67
35	106	225.67	113	130.33	115	261.67
36	105	219.39	112	124.39	114	253.06
39	107	228.17	114	135.72	116	267.33
40	106	225.67	113	130.33	116	267.33
43	106	225.67	115	142.17	116	267.33
46	105	219.39	114	135.72	115	261.67
48	108	237.87	115	142.17	116	267.33
49	110	250.98	116	152.61	117	272.39
51	111	257.37	116	152.61	117	272.39
52	109	242.70	116	152.61	117	272.39
53	106	225.67	113	130.33	116	267.33
54	116	297.48	117	160.56	119	290.39
65	105	219.39	114	135.72	115	261.67
59	107	228.17	115	142.17	116	267.33
64	113	271.48	117	160.56	118	280.28
67	114	280.42	117	160.56	118	280.28
70	105	219.39	115	142.17	116	267.33
H1	106	225.67	116	152.61	114	253.06
H2	104	210.17	113	130.33	114	253.06
H3	106	225.67	115	142.17	114	253.06

Provenances	**Julian day of bud burst in 2002**	**Accumulated degree days for bud burst in 2002**	**Julian day of bud burst in 2015**	**Accumulated degree days for bud burst in 2015**
1	111	197.28	114	204.44
2	111	197.28	112	186.28
6	111	197.28	115	217.28
8	109	181.11	111	176.22
11	111	197.28	114	204.44
13	115	228.39	115	217.28
14	112	206.67	112	186.28
17	110	188.17	114	204.44
21	110	188.17	110	168.17
23	108	173.89	111	176.22
26	108	173.89	111	176.22
27	113	216.28	115	217.28
29	110	188.17	111	176.22
31	111	197.28	111	176.22
32	111	197.28	111	176.22
34	107	168.61	110	168.17
35	107	168.61	109	160.89
36	107	168.61	109	160.89
39	109	181.11	109	160.89
40	107	168.61	109	160.89
43	108	173.89	110	168.17
46	108	173.89	106	152.39
48	109	181.11	109	160.89
49	109	181.11	111	176.22
51	112	206.67	110	168.17
52	110	188.17	104	130.61
53	109	181.11	108	155.50
54	115	228.39	116	228.89
65	109	181.11	107	154.94
59	109	181.11	109	160.89
64	113	216.28	110	168.17
67	115	228.39	114	204.44
70	108	173.89	109	160.89
H1	107	168.61	106	152.39
H2	107	168.61	105	143.06
H3	108	173.89	106	152.39