

Sub-Montane Norway Spruce As Alternative Seed Source for a Changing Climate? A Genetic and Growth Analysis at the Fringe of Its Natural Range in Austria

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Insights into the intraspecific variation in climate response of forest trees and the utilization of suitable seed sources are required to maintain forest ecosystems under expected climate change. Individuals of Norway spruce with an anomalous spherical-shaped crown were characterized by genetic (using a mtDNA marker) and dendroclimatic analysis. Such trees occur frequently at the fringe of the spruce distribution in east/south-east Austria. We employed pair-wise comparisons between trees with spherical and “regular” conical crowns on 47 sites. No evidence was found for a different phylogeographic history of spherical and conical spruces, but the high allelic diversity at the *nad1* locus highlighted the importance of east/south-east Austria as refugium and migration corridor for Norway spruce. Analysis of mean annual increment revealed a larger amount of earlywood within the sapwood area and fewer negative pointer years for spherical spruces than for conical ones, pointing at a higher vitality and smaller interactions between climate and growth for spherical spruces. Although the results cannot explain the anomalous crown form, they suggest spherical trees to have a higher ability to cope the warm and dry climate of the region than “regular” conical spruces. We discuss the origin of spherical crowns in terms of population history and phenotypic plasticity and speculate on possible effects of crown architecture on canopy-atmosphere exchange.

Keywords climate-growth response, crown type, rear edge, mitochondrial DNA, *Picea abies*

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1 Introduction

The consequences of climate change to forest ecosystems and the mitigation of negative effects to ecosystem functions including wood production are major challenges of current forest science and management (Prentice et al. 1993, Lindner 1999, Maracchi et al. 2005). Among different silvicultural measures, planting of alternative tree species or different provenances better adapted or having a higher potential for adaptation to expected climate conditions has been discussed (species: e.g. Berry et al. 2002, Hamann and Wang 2006; provenances: e.g. Matyas 1996, Rehfeldt et al. 1999, Bradley St. Clair and Howe 2007). To identify those provenances, long-term common garden experiments in strongly differing climates are required (e.g. Rehfeldt et al. 2001). However, such trials are not available for most tree species. Alternatively, appropriate provenances might be found at fringe of the species' natural range. Populations growing in these areas are typically exposed to more extreme environmental conditions than those in the centre of the distribution.

With respect to the phylogeographic distribution of a species and its postglacial migration

routes, Hampe and Petit (2005) differentiate between populations at the northern-oriented leading edge (colonization front), and the rear edge, which is the eroding range margin at its southerly distribution limit. For future climate scenarios, mainly populations from the rear edge are considered as important. They are typically small, restricted to particular habitat patches, and expected to be more selected to local adaptation than for generalism, because of their long-term persistence to suboptimal growing conditions (Dynesius and Jansson 2000, Hampe and Petit 2005). These characteristics fit well to existing populations of Norway spruce (*Picea abies* [L.] Karst.) in the hilly countryside of east and south-east Austria (Fig. 1). The forest growth and provenance regions located here (Kilian et al. 1994) are characterised by low precipitation and long-standing drought periods (e.g. Auer et al. 2005, Efthymiadis et al. 2006, Nobilis and Godina 2006) affecting growth and survival of Norway spruce and limit its natural distribution. Recent paleobotanical studies of pollen and macrofossils demonstrate the existence of refugial populations of Norway spruce in the region of the East and South-east Alpine Foreland as well as in

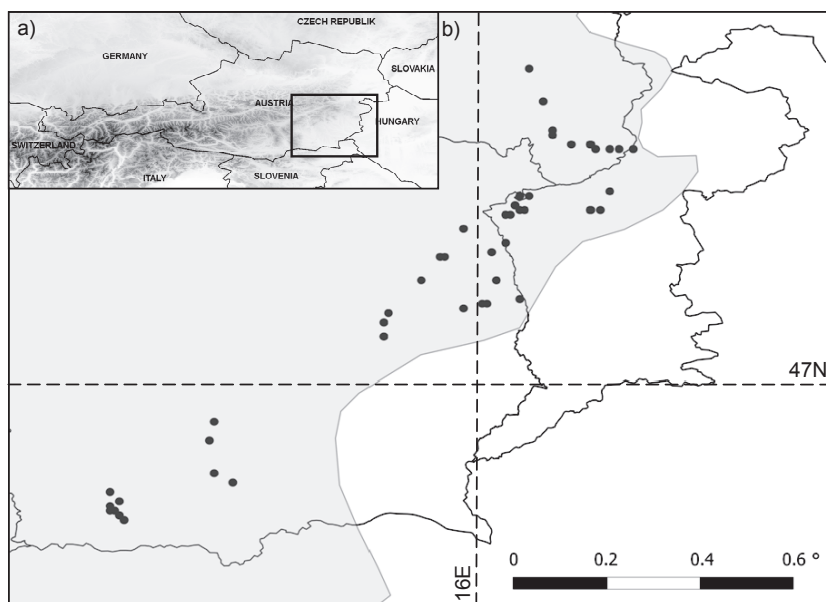


Fig. 1. Location of the study region in Austria (a) and position of the sample sites (b). The natural distribution of Norway spruce in Austria is indicated by the grey shading in b).



Fig. 2. Typical spherical (left) and conical (right) spruce trees for comparison.

the adjacent Hungarian/Danubian basin (Ravazzi 2001, Terhürne-Berson 2005). Extensive field observations on Norway spruce in east/south-east Austria also revealed a high diversity of tree morphotypes (Fig. 2). In particular, the frequent occurrence of crowns with a distinctive spherical shape, contrary to the typical conical shape, has attracted interest, because such trees seemed to be more vital during drought events than conical ones (Pollinger personal comm.). However, whether this crown diversity is due to genetically determined provenance or progeny variation or to phenotypic plasticity is unknown.

In general, spruce species exhibits a high plasticity in many characters, e.g. branching pattern (e.g. Sylvén 1909, Gruber 1988, Geburek et al. 2008), growth rhythm and frost hardiness (e.g. Johnsen 1989, Skroppa 1994), or needle morphology and photosynthesis (e.g. Ishii et al. 2007 in *Picea jezoensis*). On the other hand, provenance and progeny specific crown types were also observed (e.g. Holst and Teich 1969, Colin et al. 1993 in *Picea glauca*).

The aim of the present study is to test whether spruces with spherical crowns are individuals of

‘rear edge’ populations and really better adapted to the unfavourable conditions at low elevations. Our first hypothesis is that spherical trees are descendants of the former refugia while conical trees occurring in the same region are presumably allochthonous. This will be tested by comparing the descendance of spherical trees to conical trees by means of a maternally inherited mitochondrial marker. Secondly, we hypothesise that spherical trees are better adapted to the unfavourable mild climatic condition of the region than conical trees. Therefore, we study growth behaviour and the interaction between tree vigour and climate of both crown types.

2 Materials and Methods

2.1 Sites and Tree Samples

During regular visits of forest seed production stands in east and south-east Austria a number of spherical spruces as single trees or groups has been identified visually (see Fig. 2 for typical pictures of spherical and conical trees). In order to

confirm the spherical crown character, a variety of crown parameters have been measured and compared with “regular” conical trees growing on the same site, under the same silvicultural management and the same stand density. Throughout the study, these tree pairs were used for morphological, genetic, and dendroclimatic analysis.

For the present study, 47 sites with 58 spherical trees were selected. The sites are located from 15.2–16.3°E and from 46.7–47.6°N (Fig. 1). All sites are located within a rural landscape consisting of cultivated fields and forests. Forests are managed extensively by small-scale farmers, mainly for the production of fire wood. All sites are mixed stands of coniferous and broadleaved trees (*Fagus sylvatica*, *Quercus robur*, *Fraxinus excelsior*). For none of the stands a continuous forest management plan exists. The predominant silvicultural system is selective logging of single trees. Soils are cambisols with a clayic and silty character and an estimated pH-value between 6 and 7. The elevation of the sites varied between 300 and 650 m above sea level.

To each single or group of spherical spruces one conical spruce from the same location was used for comparison (in total, 47 conical spruces). Criteria for the selection of tree pairs were: i) height ($\pm 20\%$ difference), ii) diameter at breast height (d.b.h. $\pm 30\%$ difference), iii) geographical distance (max. 100 m), and iv) both trees should belong to the same dominance class. Since the sampling focused on spherical trees in few cases we could not find a comparable conical tree in close proximity to the chosen spherical spruce. In such cases, smaller and very likely younger trees were chosen for comparison. Trees affected by biotic harming excitors (e.g. *Sirococcus conigenius* [DC.], *Pucciniastrum epilobii* [Pers.], *Pristiphora abietina* [Christ]) were excluded. Overall, the selection of tree pairs aimed at finding comparable trees for which the soil and site characteristics and the forest management was the same.

2.2 Tree and Crown Morphology

For each tree (spherical and conical spruces), a range of parameters has been determined: diameter at breast height (*dbh* – measured in a height of 130 cm), height (*ht* – measured with a Fores-

tor Vertex, Haglöf Sweden), the height of start of crown (*hc* – measured with a with a Fores-tor Vertex at the lowest green branches), crown length (*cl* = *ht* – *hc*), crown width (*cw* – measured as a projection of the maximum width), and the canopy dominance class according to Kraft (1884). These measures were used to calculate several indicators of tree crown structure: first, the crown ratio *cr* = *cl* / *ht*, second, the height to diameter at breast height ratio *hdr* = $100 * ht / dbh$, third, the crown thickness index *cti* = *cw* / *cl*, and fourth, the crown spread index *csi* = *cw* / *ht*. T-tests were used to test for differences between spherical and conical trees.

2.3 Genetic Analysis

To infer the ancestral history of spherical spruces, variation in the fragment length of the mitochondrial gene locus *nad1* (Sperisen et al. 2001) was analysed. Due to the maternal inheritance (Grivet et al. 1999) and the low sequence evolution of the mitochondrial genome (Palmer 1992) this locus is known to provide information on postglacial migration of Norway spruce (see also Gugerli et al. 2001, Tollefsrud et al. 2008).

The genomic DNA was extracted from needle tissue using DNeasy plant minikit (QUIAGEN). PCR and enzyme restriction was done according to Sperisen et al. (2001). Fragments were analysed using the capillary electrophoresis system CEQ 8000 - Genetic Analyzing System (Beckmann-Coulter).

2.4 Dendrochronological Analysis

The analysis of dendrochronological and dendroclimatic parameters unfolds a subset of 30 pairs of trees, where forest owners agreed on the drilling of the stem. From each tree, two cores were taken at right angle to each other in a height of 130 cm.

2.4.1 Radial Growth and Sapwood Area

The sapwood area was determined on basis of differences in translucence immediately after getting

the core (Münster-Swendsen 1987). Early- and latewood, as separated according to qualitative aspects by one single person, was measured microscopically with the measurement device Lintab (Rinntech). Data were processed with the software TSAP (Rinn 1996). Absolute dating was synchronised by software Cofecha (Holmes 1994).

In addition to the annual ring width, as indicator of tree vigour we calculated the total area of the earlywood within the sapwood area (hereafter referred to as early sapwood) by summing up the earlywood area of each tree ring within the sapwood region (Waring et al. 1980, Eckmüller and Sterba 2000). According to Eckmüller and Sterba (2000), early sapwood is strongly correlated to needle biomass and foliage and can therefore be used as good indicator for tree vigour and vitality.

For each crown type, arithmetic means of annual increment and the early sapwood were calculated. Since tree pairs from a single location could show age differences (see above), we compared the mean ring width according to the cambial age of the trees. The analysis of radial growth within a defined age class, i.e. according to the cambial tree age, has the advantage that the age trend towards declining radial growth is eliminated and trees or groups of trees with different real ages can be compared (Barnett and Jeronimidis 2003, Grabner 2005). If the defined cambial age period is large enough (> 10 years) also the effect of different weather conditions during the various growth period can be neglected. We defined three different cambial age classes: 1) the entire growing period available for each sample, 2) the cambial age period of 20 to 35 years representing the growth at the pole wood stage, and 3) the age period of 60 to 75 years representing adult growth.

2.4.2 Climate Response and Pointer Year Analysis

Climate response of both crown types was analysed by response and correlation functions considering monthly precipitation and mean temperature data for August of the preceding year to September of the current year as independent climate variables.

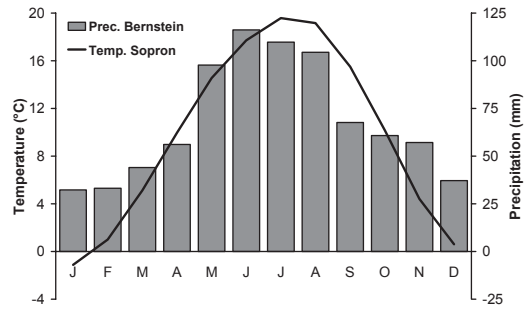


Fig. 3. Climate diagram of the closest meteorological stations where homogenized data of temperature (Sopron: 16.6°E, 47.68°N) and precipitation (Bernstein: 16.26°E, 47.35°N) were available (Auer et al. 2005).

Response functions are a multiple regression technique where the principal components (PC) of the monthly climate data are being used to estimate indexed values of ring width (Fritts 1976, Fritts and Wu 1976). The obtained regression coefficients are multiplied with the PC of climate to obtain an improved set of regression coefficients in relation to the original climate. Correlation functions are the temporal sequence of univariate correlation coefficients using Pearson's correlation between the monthly climate data and the tree ring chronologies (Biondi 1997). To derive response and correlation functions, the long-term growth trend of the tree ring data was eliminated with a spline-function of 30 years base length in the software Arstan (Cook 1985). Response and correlation functions were exclusively calculated for the Northern sub-sample (located from 15.8–16.3°E and from 47.1–47.6°N), because here climate strongly limits the spruce distribution. This sub-sample contained 30 spherical and 20 conical spruces. Using the variability between individual trees, the significance of the response and correlation functions (95% confidence limits based on a 1000 bootstraps) were calculated with DendroClim2002 (Biondi and Waikul 2004). Meteorological stations chosen due to their geographic proximity and availability of homogenized data (ZAMG: Auer et al. 2005) provided the precipitation and temperature data (Fig. 3). Temperature data were taken from the station Sopron (Location 16.6°E, 47.68°N), where the mean annual

temperature is 9.7 °C and the mean temperature in the vegetation period (May–August) 17.8 °C. The meteorological station Bernstein (Location 16.26°E, 47.35°N) provided precipitation data with average precipitation of 817 mm per annum and 502 mm in the vegetation period.

Another method to investigate intraspecific differences in annual growth reactions is pointer year analysis. Pointer years are defined as years, where rapid changes in environmental conditions cause remarkable annual growth reactions (Neuwirth et al. 2004, Schweingruber et al. 1990). Therefore, for each individual tree ring widths were transformed into z -values using the equation: $RW_z = (RW_t - RW_n) / SD_n$ (Cropper 1979). Here, RW_z is the z -value of the year t , RW_t represents the total ring width of the year t , RW_n is the mean ring width averaged for a window of 5 years and SD_n stands for the standard deviation of the same 5 years. This transformation deleted the age trend and harmonized means and standard deviations. Due to the distribution of tree pairs over a wider region instead of single stands, positive pointer years were defined for z -values >0.75 and negative pointers for z -values <0.75 . In order to compare spherical and conical trees, only those years within each group were considered as pointer years, where all individual trees had z -values >0.75 , respectively <0.75 . In general, trees showing lesser negative pointer years and/or more positive pointer years can be interpreted as having a higher vitality under the prevailing climate conditions.

3 Results

3.1 Tree and Crown Morphology

Measuring 57 spherical and 47 conical spruces revealed strong differences in tree and crown morphology (Table 1). Significant differences have been found for the tree morphology and size parameters dbh and cw . On average, spherical trees had a dbh of 60 cm and a crown width cw of 8.1 m, whereas conical trees had a dbh of 46 cm and a cw of 6.1 m. This is also shown in Fig. 4a, where spherical spruces belong to higher dbh size classes than conical trees. However, comparing the average height and the crown length shows only negligible differences

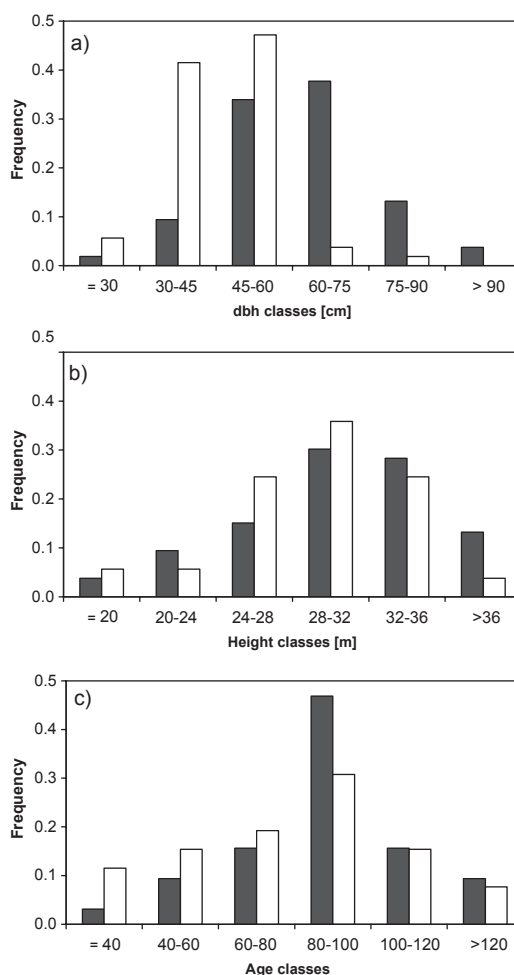


Fig. 4. Frequency distribution of dbh (a), height (b), and age (c) of spherical (black bars) and conical (white bars) spruces.

and the height class distribution of both types is very similar (Fig. 4b). This is mainly, because conical trees have a significantly higher ratio of height to dbh (hdr) and can be considered to be more slender than spherical trees.

In addition to the tree size parameters, also the crown shape parameters cti and csi showed significant differences and support the a priori discrimination between the two crown types. All trees of both crown types belonged to the dominant type.

Table 1. Tree and crown measures of spherical and conical spruces given as average and standard deviation of the respective crown types. Averages between the tree types were compared with t-statistics.

| | Spherical spruce | Conical spruce | p-value |
|--|------------------|----------------|--------------|
| Tree height <i>ht</i> (m) | 29.8 ± 5.4 | 28.3 ± 4.7 | 0.154 |
| Diameter at breast height <i>dbh</i> (cm) | 60.3 ± 14.3 | 46.0 ± 10.4 | <0.001 |
| Crown length <i>cl</i> (m) | 18.3 ± 4.9 | 18.0 ± 5.2 | 0.812 |
| Crown width <i>cw</i> (m) | 8.1 ± 2.2 | 6.1 ± 1.3 | <0.001 |
| Crown ratio <i>cr</i> (%) | 61.6 ± 13 | 63.7 ± 15.8 | 0.440 |
| Height to diameter at breast height ratio <i>hdr</i> | 50.7 ± 9.5 | 63.3 ± 12.1 | <0.001 |
| Crown thickness index <i>cti</i> | 0.46 ± 0.15 | 0.36 ± 0.12 | <0.001 |
| Crown spread index <i>csi</i> | 0.27 ± 0.07 | 0.22 ± 0.06 | <0.001 |
| Tree age ^{a)} | 90 ± 25 | 81 ± 31 | 0.216 |

^{a)} Tree age according to the dendrochronological analysis of 30 tree pairs.

3.2 Genetic Analysis

Eight size variants (haplotypes) were identified at the mitochondrial gene locus *nad1*. The most frequent haplotype was ht815 with a frequency of 42% in spherical and 52% in conical trees, respectively. The second most frequent type was ht842 with 26% and 22%, respectively. Haplotype ht983 was found only in spherical spruces, but in low frequency. No significant differences (χ^2 -test) in the frequency distribution of haplotypes between spherical and conical trees were detected (Fig. 5).

3.3 Dendrochronological Analysis

3.3.1 Radial Growth and Sapwood Area

The age of the trees varied between 33 and 170 years. Spherical trees were on average 90 years old, whereas conical trees were approximately 81 years old (Table 1). The age class distribution for both types is dominated by trees in the age of 80–100 years (Fig. 4c). However, younger age classes contain more conical than spherical trees.

For all age classes, a trend was found with larger tree rings for spherical spruces than for conical ones. For the entire period, rings of spherical trees were on average 3.28 mm (standard deviation SD=1.09 mm) wide, while rings of conical trees

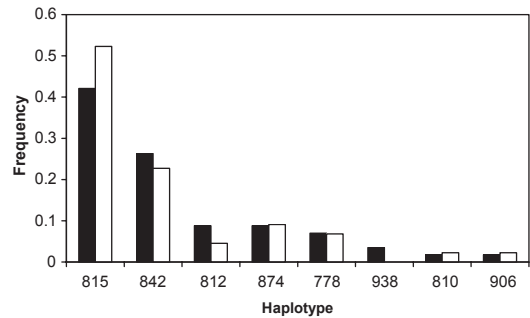


Fig. 5. Haplotype frequency distribution of spherical (black bars) and conical (white bars) spruces.

were 2.96 mm (SD=1.12 mm; *t*-test: *p*=0.13). The age class of 60 to 75 years revealed significant differences in ring width between the crown types (*t*-test: *p*=0.05): 3.22 mm (SD=1.45 mm) for spherical and 2.37 mm (SD=1.52 mm) for conical spruces. The smallest difference (*t*-test: *p*=0.3) was found for trees at the pole wood stage (cambial age of 20–35 years). Here, rings of spherical tree had an average width of 2.58 mm (SD=1.51 mm), and rings of conical trees 2.48 mm (SD=1.44 mm).

The early sapwood, as indicator of tree vigour, was significantly larger (*p*<0.01) for spherical spruces having an early sapwood of 1013 mm² (SD=391 mm²) than for conical ones having 683 mm² (SD=331 mm²).

Table 2. Climate response of spherical and conical spruces for significant response (RF) and correlation functions (CF). RF – regression coefficient of the multivariate response function; CF – Pearson’s product moment correlation coefficient. The significance was determined by 1000 bootstraps using the software DendroClim2002 (Biondi and Waikul 2004).

| | | | Preceding year | | | | | Current year | | | | | | | | |
|---------------|-----------|----|----------------|------|-----|-----|-----|--------------|------|-----|-------|-------|------|-------|-----|-----|
| | | | Aug | Sep | Oct | Nov | Dec | Jan | Feb | Mar | Apr | May | Jun | Jul | Aug | Sep |
| Precipitation | Spherical | RF | 0.23 | 0.19 | - | - | - | - | - | - | - | 0.26 | 0.19 | - | - | - |
| | | CF | 0.33 | 0.24 | - | - | - | - | - | - | - | 0.42 | 0.27 | 0.26 | - | - |
| | Conical | RF | 0.23 | 0.24 | - | - | - | - | 0.17 | - | - | 0.28 | 0.22 | - | - | - |
| | | CF | 0.28 | 0.28 | - | - | - | - | 0.19 | - | - | 0.41 | 0.29 | 0.29 | - | - |
| Temperature | Spherical | RF | - | - | - | - | - | - | - | - | -0.18 | - | - | - | - | |
| | | CF | - | - | - | - | - | - | - | - | -0.35 | -0.34 | - | -0.25 | - | |
| | Conical | RF | - | - | - | - | - | - | - | - | -0.15 | - | - | - | - | |
| | | CF | - | - | - | - | - | - | - | - | -0.31 | -0.31 | - | -0.19 | - | |

Table 3. Positive (+) and negative (-) pointer years of spherical- and conical spruces for the northern part of the study region for the time period 1920–2006.

| Year | 1922 | 1926 | 1933 | 1935 | 1958 | 1968 | 1973 | 1975 | 1976 | 1988 | 1989 | 1997 | 2003 | 2006 |
|-----------------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|
| Spherical trees | | + | | | - | | | | | - | | + | - | + |
| Conical trees | - | + | + | - | - | - | - | + | - | - | + | | - | |

3.3.2 Climate Response and Pointer Years

Climate-growth analysis revealed similar climate dependencies for spherical and conical spruces (Table 2). By means both of bootstrapped response and correlation functions, negative associations were obtained for May temperature and positive ones for precipitation in May and June of the current year. Positive effects were also found for precipitation in August and September of the previous year.

Pointer year analysis (1920–2006) revealed more negative hits for conical spruces in comparison to spherical trees (Table 3). The number of positive pointer years is almost equal for both crown types.

4 Discussion

Insights into the intraspecific variation in climate response of a species and the utilization of suitable

seed sources for forest management are required to maintain the current tree species composition under expected climate change. To counteract the negative impacts of climate warming, we believe that it is necessary to combine actual knowledge about the phylogeographic history of trees with an analysis of the climate response either retrospectively, as done in our study, or prospectively by exposing offspring, for instance selected from the rear edge (Hampe and Petit 2005), to differing climate regimes. The present analysis of sub-montane Norway spruce at the boundary of its natural range indicates intra-specific variation in climate sensibility among individuals growing at the same location and within the same dominance class. Based on our a priori discrimination between trees with spherical and conical crowns, trees with spherical crowns seem to be more suitable to the environmental conditions of that region than “regular” conical spruces. Spherical trees are characterized by larger early sapwood and show smaller interactions between growth and climate than conical spruces.

However, it is not clear if and how crown shape is responsible or correlated to climate-growth relationships. The present sampling design, based on a selection of visually recognizable crown types, which were confirmed by measurements, does not allow evaluating the full variation of climate-growth response or all potential crown geometries at lower elevations. More extensive field studies with an unbiased random selection of trees are necessary in south-east Austria to test whether spherical and conical trees represent two distinct types or if intermediate forms exist. Nevertheless, we have good reasons to believe that correlations between crown form and climate suitability exist. In many coniferous species, crown shape is at least partly provenance and/or genotype specific (e.g. Holst and Teich 1969, Colin et al. 1983, Kärki and Tigerstedt 1985, Emhart et al. 2007). Also, it is known that crown shape depends on the environment: higher altitudes and latitudes favour conical shapes, because the conical form together with the layered branch architecture allows a more efficient sunlight interception over the entire crown (Smith and Brewer 1994). Also, it is assumed that wide crowns have severe drawbacks in regions with high snow loads, similar as it was found for provenances from lower elevations in Poland (König 2002). Therefore, the historical occurrence of spherical trees in lower elevations of east/south-east Austria and a correlation of the crown form with adaptations to the mild climate of the region seem reasonable. In higher altitudes or in lower elevations of the northern alpine foreland, harsher conditions and higher snow loads likely limit the distribution of such spherical trees. Another explanation for the advantage of spherical crowns in comparison to conical ones could be an effect of crown architecture on the canopy-atmosphere exchange. Possibly, the crown shape affects rainfall interception and transpiration functions (see Breda et al. 2006 for review) and therefore decreases the water loss in dry periods. Also the sunlight penetration to lower branches is reduced and might help to reduce transpiration.

Another explanation for differences in tree crown morphology could be the silvicultural treatment and the resulting tree density (e.g. Kuuluvainen 1988, Kantola and Mäkelä 2004, Hein et al. 2007). However, in our comparison,

spherical trees and conical trees were growing side by side under the same management regime and the same soil conditions. Although on average spherical trees are slightly older (not significant) than conical ones, also the age class distribution is very similar and does not support systematic effects of varying stand treatment of different age cohorts.

Our genetic analysis did not aim to detect differences in genes controlling the phenotype nor the adaptation to the environmental conditions. Instead, the idea was to infer the origin of spherical and conical spruces by means of the mitochondrial DNA locus *nad1*, which is proven to be an excellent marker for studies of population subdivision and postglacial immigration (Tollefsrud et al. 2008). However, our hypothesis that spherical spruces originate from other refugia than conical trees was not confirmed, because no differences in the haplotype frequency distribution were observed. Very likely this intensive admixture of haplotypes is due to a long standing contact among refugial lineages. In our very limited study region, we found an unusual high diversity of haplotypes (see also Maghuly et al. 2007) including the predominant types of the three major refugial lineages occurring in South and Central Europe. The most frequent haplotype ht815 originates in the eastern Alps and western Carpathian mountains from where it expanded west- and northwards. Second most frequent ht842 is the dominant type in the Bohemian Massif and in the northern Alpine Foreland. Moreover, also ht778, which originates from the disconnected refugial populations of the southern Carpathians, Rhodope and Pirin Mountains and the northern Dinaric Alps, has been found in our analysis in lesser frequency. This mixture of three major types demonstrates that east and southeast Austria not only harboured refugial populations, but that this region was also an important migration corridor for different lineages.

Another reason for the observed phenotypic variation in crown type could be phenotypic plasticity, which is defined as an environmentally based variation of the phenotype (e.g. Via et al. 1995). For Norway spruce, a high phenotypic plasticity has been described for various traits, one of which is the morphological plasticity of the second order branching system (Sylvén 1909,

Gruber 1988, Geburek et al. 2008). An explanation for the higher plasticity of sub-montane Norway spruce could be the population history in this region. This view is supported by the dendrochronological analysis, because the two crown types did not differ in their pole wood growth (cambial age of 20–35 years), but the annual increment of adult trees (cambial age of 60–75 years) was significantly larger for spherical spruces. Thus, a spherical crown, which has larger crown volume and very likely a higher needle biomass for photosynthesis, seems to develop after an age of 35 years. Afterwards, this crown type contributes to a better growth performance explaining the observed higher annual increment. In addition to larger ring widths, we found significantly larger early sapwood for spherical spruces indicating better water conduction. According to Eckmüller and Sterba (2000) the size of the early sapwood is a reliable estimator of needle biomass in Norway spruce and can be considered as a good predictor of vitality.

Significant negative correlations for May temperature and positive correlations for precipitation during May and June point at the general limitations of spruce growth at lower altitudes and dryer sites. Both correlations are directly related to the water regime, because high spring temperatures increase evaporation and decrease soil water availability while precipitation in May and June increase soil water. In Germany, the same climate response pattern was observed for Norway spruce at lower altitudes but not in stands at high-elevated sites (Mäkinen et al. 2002). This is also supported by a Belgian study in *Picea abies*, when Laurent et al. (2003) found radial growth at a dry stand to be directly dependent on water supply during the first months of the vegetation period compared to the growth at humid sites. More general, Lebourgeois (2007) found early- and latewood growth of spruce strongly depending on the soil water deficit conditions of the current summer.

Comparing the climate-growth response of spherical and conical spruces indicates only slight intraspecific variation when response and correlation functions were applied. However, while these techniques provide average relationships between climate and tree rings, they neither validate the temporal stability of the climate response

nor the effect of extreme climate events. Both aspects are important for the understanding of tree growth under changing climate conditions. These limitations can be overcome by the analysis of pointer years, as they indicate those years where abrupt changes in environmental conditions cause changes in the annual growth rhythm of trees (Schweingruber et al. 1990). Our comparison of spherical and conical spruces from the same locations revealed a greater number of negative pointer years for conical spruce, suggesting spherical spruces to be less susceptible to abrupt weather changes. Compared with previous studies in spruce our results did not show any coincidence in pointer years and suggest that growth conditions and climate in sub-montane east and south-east Austria differs strongly from the conditions in Western and Central Europe (Neuwirth et al. 2004, Neuwirth et al. 2007, Lebourgeois 2007).

5 Conclusion

In the present study, we describe the morphological characteristics, the phylogeographic history, and the climate-growth relationships of a regional Norway spruce variety with a distinct spherical crown in comparison to “regular” conical spruces. Besides the characteristic crown phenotype, spherical spruces were found to have a better water conduction and lesser sensitivity to unfavourable climate conditions. These traits are important in the warm and dry climate of south-east Austria. Although the genetic analysis could not explain the history of spherical trees, it confirmed the importance of eastern Austria as a migration corridor and refugium during the last ice age. Altogether, the results do not only encourage further studies about the physiological and genetic status of spherical trees, but suggest also raising awareness to provenances which were not recognised so far, but which could help to implement mitigation measures for forestry under climate change.

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