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Doctoral Dissertation

Climate-Growth response of Norway spruce provenances in the Alpine Region – recommendations for alternative seed sources under climate change

submitted by

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in partial fulfilment of the requirements for the academic degree

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Affidavit

I hereby declare that I have authored this dissertation independently, and that I have not used any assistance other than that which is permitted. The work contained herein is my own except where explicitly stated otherwise. All ideas taken in wording or in basic content from unpublished sources or from published literature are duly identified and cited, and the precise references included. Any contribution from colleagues is explicitly stated in the authorship statement of the published papers.

I further declare that this dissertation has not been submitted, in whole or in part, in the same or a similar form, to any other educational institution as part of the requirements for an academic degree.

I hereby confirm that I am familiar with the standards of Scientific Integrity and with the guidelines of Good Scientific Practice, and that this work fully complies with these standards and guidelines.

Vienna, Sep. 1st, 2021 Stefan KAPELLER *(manu propria)*

Preface

This thesis is a synthesis of three scientific articles that have been published in peer-reviewed SCI journals. They can be found in the Appendix (section 7). Each article has a different structure and citation style due to particular journal requirements.

All analyses of these three papers are primarily based on data from the Austrian Norway spruce provenance trial established in 1978. Each paper focuses on a different aspect and presents different methods. This synthesis links the individual articles and provides an overall perspective of common research objectives. In detail, the specific methods, results, and their discussion can be found in the respective articles.

Please cite the thesis as Kapeller S (2021) Climate-Growth response of tree provenances in the Alpine Region – recommendations for alternative seed sources under climate change. Dissertation, University of Natural Resources and Life Sciences, Vienna (BOKU) or refer to the individual papers.

List of papers

I) Kapeller, S., Lexer, M. J., Geburek, T., Hiebl, J., & Schueler, S. (2012). Intraspecific variation in climate response of Norway spruce in the eastern Alpine range: Selecting appropriate provenances for future climate. *Forest Ecology and Management*, *271*, 46–57. https://doi.org/10.1016/j.foreco.2012.01.039

II) Schueler, S., Kapeller, S., Konrad, H., Geburek, T., Mengl, M., Bozzano, M., Koskela, J., Lefèvre, F., Hubert, J., Kraigher, H., Longauer, R., & Olrik, D. C. (2013). Adaptive genetic diversity of trees for forest conservation in a future climate: A case study on Norway spruce in Austria. *Biodiversity and Conservation*, *22*(5), 1151–1166. https://doi.org/10.1007/s10531-012-0313-3

III) Kapeller, S., Dieckmann, U., & Schueler, S. (2017). Varying selection differential throughout the climatic range of Norway spruce in Central Europe. *Evolutionary Applications*, *10*(1), 25–38. https://doi.org/10.1111/eva.12413

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Abstract

A major challenge in current forest management is safeguarding forest ecosystems' persistence under conditions of climate change. In addition to the conversion of the tree species composition of forest stands to species that are more suitable for future climates, utilizing the intraspecific genetic variation and employing well-adapted reproductive material for reforestation is considered a promising adaptation measure. Intraspecific variation in climate response among and within tree populations provides management options to mitigate adverse effects of drought or other climate related disturbance events. Beyond potential negative effects, there is also a potential for increasing productivity due to extended vegetation periods and higher photosynthetic rates. Evolutionary adaptation can probably not keep up with the pace of climate change. Therefore, the assumption that local seeds are best adapted to local conditions might not hold anymore in the mid to long run. Instead, other geographic origins of reproductive material (provenances) should be considered that might be adapted for future climatic regimes at a specific location. To provide provenance recommendations that fit to current and prospective climatic conditions, well-founded information about climatic tolerances of individual tree populations is necessary, as well as information about genetic variation within populations to examine the potential of tree populations to adapt to future conditions (adaptive potential).

In this thesis, Norway spruce (*Picea abies* (L.) Karst.) was used to demonstrate the intraspecific variation in climate response and its utilization. The Austrian Norway spruce provenance trial 1978, as one of the most comprehensive common garden tests (provenance test) in Central Europe, included seeds from 480 Austrian provenances and 60 provenances from other countries, planted at 44 trial sites. Tree heights were measured several times in the following years. These data were used in this study (1) to analyze the climate-growth response of individual populations, (2) to evaluate the existing network of gene conservation forests in Austria for its capability to safeguard genetic diversity, and (3) to assess the adaptive potential of tree populations at planting sites from the species' warm-dry to cold-moist distribution limits.

The study revealed that for most parts of Austria, height growth of Norway spruce is expected to increase under climate change conditions. The selection of appropriate reproductive material may increase productivity additionally. Variation of absolute tree heights at age 15 is higher at planting sites in warm and dry regions than at planting sites in cold and moist conditions. Promising provenances for future climate conditions originate from areas that today depict the warm and dry edge of the natural species distribution range. These hotspot areas of genetic diversity are insufficiently covered by the Austrian network of genetic conservation units. To preserve the existing genetic variation for future tree generations, the network should be extended, especially at the eastern fringe of the Alps.

Here, at the warm edge of the species distribution, climatic conditions are currently still not delimiting growth of Norway spruce, as no climatic constraints on phenotypic variation have been observed. The species distribution limits might instead be shaped by other selection drivers at the warm edge, such as bark beetles or competition by other tree species.

It can be concluded that genetic variation and climatic tolerance of tree populations affect the populations' suitability for future climatic conditions. Such information should complement the currently applied guidelines for provenance recommendations.

Keywords: *climate change, provenance trials, Norway spruce, climate-growth response, adaptation*

Kurzfassung

Eine große Herausforderung der aktuellen Waldbewirtschaftung ist die Bewahrung der Waldökosysteme und deren Funktionsfähigkeit im Klimawandel. Neben der Veränderung der Baumartenzusammensetzung hin zu an das zukünftige Klima besser angepassten Artenmischungen stellt die Nutzung der intraspezifischen genetischen Variation und die Verwendung von an zukünftige Bedingungen gut angepasstes Vermehrungsgut für die Waldverjüngung eine vielversprechende Anpassungsmaßnahme dar. Die intraspezifische Variation in Bezug auf Klimasensitivität zwischen und innerhalb von Baumpopulationen bietet Managementoptionen, um negative Auswirkungen von Dürreperioden und anderen klimabezogenen Störungsereignissen abzumildern. Neben der Milderung von negativen Auswirkungen einer Klimaänderung besteht auch das Potential, längere Vegetationsperioden, günstigere thermische Bedingungen und gesteigerte Photosyntheseraten für eine Produktivitätserhöhung zu nutzen.

Die natürliche evolutionäre Anpassung von Bäumen kann nicht mit dem Tempo des Klimawandels Schritt halten. Daher ist die Annahme, dass lokales Saatgut immer am besten an die lokalen Gegebenheiten angepasst ist, nicht mehr haltbar. Stattdessen sollten auch andere geografische Herkunftsgebiete (Provenienzen) in Betracht gezogen werden, die auch für zukünftige Klimaverhältnisse eines Ortes geeignet sind. Für Herkunftsempfehlungen, die aktuelle und zukünftige Klimaverhältnisse berücksichtigen, und um zukünftige Klimareaktionen modellieren zu können, sind fundierte Informationen zur Klimatoleranz einzelner Baumpopulationen notwendig sowie Informationen über die genetische Vielfalt innerhalb von Populationen, auf der das natürliche Anpassungspotenzial beruht.

In dieser Arbeit wurde die Fichte (*Picea abies* (L.) Karst.) untersucht, um die innerartliche Vielfalt der Klimareaktionen und deren Nutzung zu demonstrieren. Der österreichische Fichten-Herkunftsversuch 1978 ist einer der umfangreichsten Provenienzversuche in Mitteleuropa. Er umfasst Saatgut von 480 österreichischen Herkünften und 60 ausländischen Herkünften, die an 44 Versuchsstandorten gepflanzt wurden. In den folgenden Jahren wurden mehrmals die Baumhöhen gemessen. Diese Daten wurden in dieser Studie verwendet, (1) um die Klima-Wachstums-Funktionen einzelner Populationen zu kalibrieren, (2) um das bestehende Netzwerk der Generhaltungswäldern in Österreich hinsichtlich der Abdeckung der genetischen Vielfalt zu bewerten, und (3) um limitierende Faktoren des natürlichen Anpassungspotenzials der Baumpopulationen von der warm-trockenen bis kalt-feuchten Verbreitungsgrenze der Art zu untersuchen.

Die Studie ergab, dass im Großteil Österreichs im Klimawandel mit einer Zunahme des Höhenwachstums zu rechnen ist. Die Auswahl von geeignetem Vermehrungsmaterial kann die Produktivität zusätzlich steigern. Die Variation der absoluten Baumhöhen im Alter von 15 Jahren ist an warmen und trockenen Standorten höher als an Standorten mit kalten und feuchten Bedingungen. Die vielversprechendsten Herkünfte für zukünftige Klimabedingungen stammen aus Gebieten, die heute den warmen und trockenen Rand des natürlichen Verbreitungsgebiets der Fichte darstellen. Eine Analyse ergab, dass diese Hotspots der genetischen Vielfalt vom Netzwerk der Generhaltungswälder nur unzureichend abgedeckt werden.

Daraus lässt sich schließen, dass die derzeit angewandten Richtlinien für Herkunftsempfehlungen mit Information zur Genetik und zur Eignung einer Population für zukünftige Bedingungen ergänzen werden sollten. Um die genetische Variation für zukünftige Baumgenerationen zu erhalten, sollte das Netzwerk der Generhaltungswälder in Österreich erweitert werden, insbesondere am östlichen Rand der Alpen. Hier, an der warm-trockenen Grenze des natürlichen Artenareals, sind die Fichtenpopulationen nicht unbedingt schlecht an die Standortsbedingungen angepasst. Es konnten keine klimatischen Einschränkungen der phänotypischen Variation beobachtet werden. Stattdessen könnte das Verbreitungsgebiet hier von anderen Treibern der natürlichen Selektion, wie Borkenkäfer oder Konkurrenz durch andere Baumarten, geprägt sein.

Schlüsselwörter: *Klimawandel, Herkunftsversuche, Fichte, Klima-Wachstums-Reaktion, Anpassung*

Contents

1 Introduction

Climate change has manifold impacts on forests and associated ecosystem services (Lindner et al., 2010). Tree species and populations are adapted to the local environment, despite the enormous gene flow within and between populations (Savolainen et al., 2007). It is controversially discussed if and to what extent these adaptations will still be advantageous under anticipated climatic conditions and which tree species will be most suitable in future climates. Climate change can have positive effects on forestry in some regions, e.g., due to a prolonged vegetation period and higher water use efficiency through increased CO_2 in the atmosphere (Matala et al., 2006). More often, concerns are prevailing that disturbance events (storm, fire, drought), pathogens, or pest insects such as bark beetles threaten forest ecosystems (Jandl, 2020).

The economic damage to forest owners could be massive. Hanewinkel et al. (2013) assessed European forest land's current and future value based on prospective species range shifts and productivity differences between tree species groups. They estimate that by 2100, the value of European forest land will decrease between 14 and 50 % without adaptive forest management or the introduction of more productive species from outside Europe.

The vitality and stability of forests strongly depend on the local adaptation of tree populations to prevailing climatic conditions. Though trees are sedentary and long-living organisms, they have evolutionary means to cope with changing conditions. Tree species can migrate through seed dispersal. Also, tree populations harbor substantial genetic diversity that is maintained through extensive gene flow, i.e., seed and pollen dispersal (Savolainen et al., 2007). This standing genetic diversity, and strong selective pressures, define the ability of tree populations to adapt to rapidly changing environments (Alberto et al., 2013; Gauzere et al., 2020). Indeed, intensive gene flow among and within populations has been shown (Hamrick et al., 1992; Hamrick & Godt, 1996). However, means of evolutionary adaptation or range shifts through migration may be too slow to keep up with the pace of current climate change (Savolainen et al., 2007; Petit et al., 2008). Recently, the contribution of epigenetic variation to the adaptive capacity of tree species has been discussed (Bräutigam et al., 2013; Aitken & Bemmels, 2016). Environmentally induced epigenetic effects could significantly affect tree breeding and the interpretation of provenance trial data (Alberto et al., 2013). However, the role of epigenetics in adaptive processes remains largely unknown. Studies in conifers are especially challenging due to their large genomes (Estravis-Barcala et al., 2020; but see Heer et al., 2018, for epigenetic variation in Norway spruce).

Understanding constraints of species migration and genetic adaptation is a prerequisite for predicting the consequences of changing environments on forest ecosystems. Species distribution models (SDM) have been developed for many tree species to understand range limits (Kölling 2007, Iverson & McKenzie, 2013). Early modeling approaches were primarily based on correlations between occurrence data within the current species distribution range and environmental factors. In recent years, distribution models have been improved, e.g., by incorporating data from plantings beyond the natural distribution range (Booth, 2017) or including phenotypic variability and plastic response to environmental changes (Prober et al., 2016, Gauzere et al., 2020).

Generally, many different traits of trees exhibit considerable phenotypic plasticity, i.e., the capacity of a genotype to express various phenotypes in response to different environments (Nicotra et al., 2010). Phenotypic plasticity can facilitate population persistence even under rapid environmental change (Hultine et al., 2020). Examples of phenotypic plasticity have been examined in traits connected to growth and phenology (Franks et al., 2014). Still, there is limited knowledge of how genetic variation, phenotypic variation, and plasticity relate to each other and how these components together define the intrinsic capacity of a species to adapt to changing environments (Gauzere et al., 2020).

Beyond a better understanding of the natural means of adaptation, guidelines for active forest management are required to preserve forests and related ecosystem services. To mitigate adverse effects, forest managers have different options. Active conversion management is the transition to species or species compositions that are better adapted to anticipated climatic conditions. Generally, mixed-species forests are considered more resilient because the risk of damages spreads across a broader range of species-specific properties (Pretzsch et al., 2013; Pardos et al., 2021). Increasingly, there is an interest in considering non-native tree species, for example *Pseudotsuga menziesii* (Chakraborty et al., 2016) or *Robinia pseudoacacia* (Nicolescu et al., 2020). The introduction of non-native tree species is however controversial and evokes conflicts of interest between nature conservation and forestry (Vítková et al., 2017).

Apart from species conversion, the within-species variability among populations in adaptive traits may be utilized in forest management to ensure that native tree species survive and thrive under future conditions. Populations of the same tree species differ in their ability to cope with particular environments. Local populations reveal adaptations to current and past environmental conditions at their specific location. However, rapid climate change is now disrupting local adaptation. For example, Bradley St Clair & Howe (2007) analyzed the tradeoff between cold- and drought hardiness and the annual growth-cycle in Douglas-fir populations, and found that these genetically controlled traits may not be synchronized anymore in the future. Trees that set bud too early are prone to spring frost, and if the timing of bud burst is too late, trees may not finish their seasonal growth before the onset of summer drought (Bradley St Clair & Howe, 2007). Hence, the assumption that reproductive material (seeds, trees) from local populations is best adapted to local conditions does not hold anymore in many regions (Aitken & Bemmels, 2016). Climate change has already caused an adaptational lag in many tree populations (Browne et al., 2019), and will cause a further mismatch to prevailing climatic conditions in the future (Bradley St Clair & Howe, 2007; Frank et al., 2017). A careful selection of reproductive material for reforestations is necessary that considers current and predicted conditions. While current seed transfer guidelines are based on National provenance regions and altitudinal belts, recent studies suggest considering reproductive material from beyond traditional provenance recommendations – often referred to as assisted migration or assisted gene flow (Aitken & Bemmels, 2016). ‘Assisted migration’ refers to the intentional anthropogenic translocation of individuals within or outside the natural range of a species. The term ‘assisted gene flow’ in contrast is limited to the movement of individuals or gametes between populations within species ranges (Aitken & Whitlock, 2013).

Approaches used to identify promising provenances include association studies with genetic markers, analysis of wood cores samples, seedling tests in controlled environments (nurseries, chambers) or long-term field tests (e.g., provenance trials, also called common gardens). Provenance trials have been established for more than 200 years, involving different provenances of a species (i.e., populations of a species that come from particular locations) planted together in the same environment (Matyas, 1994). Many provenance trials were initially established to identify the most productive seed sources for wood production in a specific region. Today, these long-term trials provide valuable data for assessing climate-growth relationships (Breed et al., 2018).

Beyond phenotypic plasticity and climate tolerance, the natural capacity of tree species to adapt to changing environments is critically dependent on genetic diversity within and among populations. Therefore, identification and recommendation of reproductive sources should take existing genetic diversity into account. In Europe, the European Forest Genetic Resources Programme (EUFORGEN) is committed to fostering the conservation of genetic resources. A network of forest stands adapted to specific environmental conditions is cataloged in the EUFGIS Portal (European Information System on Forest Genetic Resources). These forest stands are referred to as genetic conservation units. The network facilitates the conservation of not only specific forest genetic resources, but also evolutionary processes within the conservation units are safeguarded. Hence, the aim is to maintain the full potential for continuous adaptation (Eriksson et al., 1993; Lefèvre et al., 2013).

This thesis focuses on Norway spruce (*Picea abies* (L.) Karst.). Norway spruce is a key species in Central European Forest ecosystems and for the wood economy. In Austria, the share of Norway spruce in total forest cover is decreasing since the 1980s, but it still covers 49,2 % of the productive forest area, according to the Austrian forest inventory (Austrian Research Center for Forests, 2019; Jandl, 2020). Silvicultural management measures and production processes in the wood-processing industry are tailored to this type of timber. Regarding climate change, a transition to other tree species is often demanded but forest owners may be hesitant due to expected economic losses.

In recent two decades, Norway spruce in regions outside its natural range has experienced severe pressure from drought and heat waves and related bark beetle disturbances. Productivity and tree health are expected to decline further from ongoing climate change accompanied by intensified disturbance regimes (Kölling, 2007; Honkaniemi et al., 2020). Particularly, biotic disturbance agents related to global warming, like spruce bark beetles, are causing extensive damages (Jandl, 2020). Forest managers have already reacted in many places with conversion to tree species that are better adapted to evolving conditions such as broadleaves, leading to a substantial reduction of the share of Norway spruce. An alternative under specific circumstances may be the choice of appropriate reproductive material of Norway spruce.

2 Objectives

The overall aim of this thesis is to assess the climate tolerance and adaptive potential of Norway spruce populations in Central Europe to current and future climatic conditions. In detail, three main objectives have been addressed:

1. To analyze the **growth potential** of Norway spruce provenances in Austria under current and potential future climates by calibrating climate-response functions from tree height data. Climate-response functions shall then be utilized to assess the current provenance recommendation scheme in Austria with regard to growth potential under future climate.
2. To review the existing **gene conservation network** of Norway spruce in Austria regarding its coverage of phenotypic and genetic diversity.
3. To explore the **evolutionary adaptive potential** of tree populations to cope with climate change by in-depth analysis of within-population variation of tree heights.

3 Material and Methods

3.1 Material

3.1.1 Austrian Norway spruce provenance trial 1978

The following analyses are primarily based on tree height measurements from a large provenance trial series with Norway spruce populations, established by Nather and Holzer in 1978 (Nather & Holzer, 1979). The trial series initially comprised 44 trial sites across Austria.

A selection of seed material of provenances was planted at each site, chosen from a pool of 480 Austrian Norway spruce populations and 60 populations from other countries. The seed material has been collected from presumably autochthonous stands during commercial seed harvests in 1971 (Nather & Holzer, 1979).

All sampled seeds were first sown at the experimental nursery Mariabrunn, belonging to the Austrian Research Centre for Forests (BFW) in Vienna, and at the central forest nursery of the Austrian Federal Forests (ÖBf AG) in Arndorf. Seedlings were then planted in nursery fields. In 1978 the 5-year-old trees were transferred to the trial sites (Nather & Holzer, 1979). At each site, only a sample of populations could be planted due to the large total number of involved populations: on average 29 populations (ranging from 20 to 53) have been planted per site.

The experimental setup was a randomized complete block design with three blocks at each trial site (except for sites No. 1, No. 20, and No. 24 with only one or two blocks). On average, 46.9 seedlings per single population per block were planted in rectangular plots (spacing of 1.5 m × 1.5 m).

Tree heights were measured in 1983 (at tree age of 10) and 1988 (at tree age of 15). In 1983, the shoot lengths for the preceding three years were surveyed, which also provided heights for the trees at the age of 7, 8, and 9 years.

In 1988, further tree height data were collected at 29 trial sites (out of initially 44) that were still part of the trial series. At these 29 sites, 83 304 trees were measured in 1988. For the duration of the trial (1978–1988), there had been no forest management activities at all sites. These 29 trial sites are located at altitudes from 250 to 1750 m above sea level, ranging from the warm and dry distribution limit at low altitudes to the cold distribution limit at the tree line. Thus, the trial series comprises a large part of the climatic niche of Norway spruce (except for both cold and dry conditions that do not occur in the Alpine area but only in Fennoscandia or in the Russian Plane; Fig. 1). Mean annual temperatures (MAT) at test sites range from 2.6 °C to 9.2 °C, and mean annual precipitation sums (APS) at test sites range from 535 mm to 2392 mm during the growing period at the trial sites (climate data from period 1978–1988).

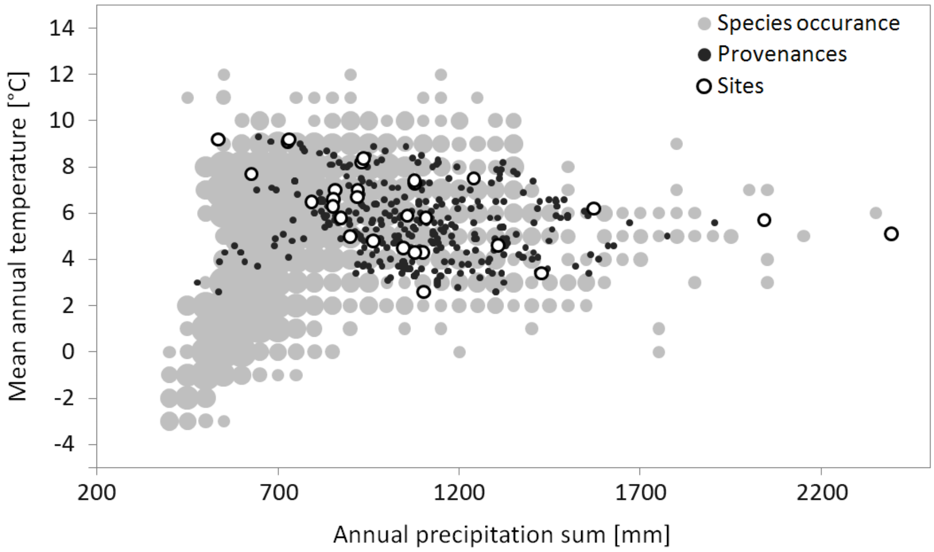

Fig 1 *Distribution of 29 trial sites (white circles) and provenance origins (black dots) within the climatic range of Norway spruce reflected by mean annual temperature and annual precipitation sums. Light gray circles indicate the complete Norway spruce distribution in Europe according to ICP Forests Level I monitoring plots (ICP Forests 2010). (Appendix 7.3 – Paper III)*

3.1.2 Neutral genetic diversity

For assessing neutral genetic diversity, DNA analyses were performed with Norway spruce twig samples from sample plots of the Austrian Forest Inventory period 2007/2009 and 2000/2002. The Austrian Forest Inventory samples Austrian forests from a 3.89 × 3.89 km grid. From each forestry grid point with Norway spruce, twig samples from four trees were collected.

Mitochondrial *nad1* markers (see Sperisen et al., 2001) were analyzed from 1493 individual tree samples and six nuclear microsatellite markers (see Rungis et al., 2004) from 2773 individual tree samples.

3.1.3 Climatic data

The Austrian meteorological service (Central Institute for Meteorology and Geodynamics) provided climatic data for each geographic location of both trial sites and population origins, including monthly time series of temperature means and precipitation sums from 1971 to 2008, mean monthly temperature and precipitation minima and maxima, length of vegetation period, growing degree days (i.e., a thermal index accumulating degree days above a threshold of 5 °C) and appearance of the first frost in autumn. Climate data for planting sites incorporate records during the growing period at the trial sites (1978–1988). Climate data of provenance origins are based on 38-years records (1971–2008).

For the scenario analyses in section 3.2.3 climate data were obtained from WorldClim data portal (Hijmans et al., 2005) in a resolution of 2.5 arc-minutes for the complete Norway spruce distribution range in Austria. Future climate conditions are represented by the MPI-Echam5 model for the emission scenario A1B (Nakičenovič & Swart, 2000). For these analyses, the term "current climate" refers to the period 1959-2000 and the term "future climate" refers to the period 2070–2099 (short: "2080s").

3.2 Methods

3.2.1 Climate response functions

The response of tree height to the climatic conditions of planting sites was determined with nonlinear regression analysis. The response variable "tree height at age 15" was fitted to a Gaussian normal distribution function using AHM as climatic predictor variable. Annual heat-moisture index (AHM; Wang et al. 2006) was used as the predictor variable in many of the here presented analyses. AHM combines mean annual temperature (MAT) and annual precipitation sum (APS) into a single parameter: AHM = (-MAT + 10)/(APS/1000). This measure reflects evapotranspiration and soil moisture content better than precipitation and temperature alone (Wang et al., 2006).

The three parameters of the Gaussian normal function reflect in ecological terms the maximum response, the location of this maximum (i.e., the 'climate optimum'), and climate sensitivity. Regression coefficients and standard deviation of residuals were calculated with curve fitting software CurveExpert (Hyams, 2005). Upper and lower confidence limits of estimated values were calculated with R-package nlstools (Baty et al., 2015).

Individual climate-response functions were calibrated all populations with available height data from at least six different sites.

3.2.2 Response of population clusters

In a second step, populations were grouped to population clusters applying three different approaches. Response functions were then calibrated to the pooled data from these population clusters.

(i) Populations grouped according to national provenance regions (Kilian et al., 1994) (referred to as “PR Cluster”),

(ii) populations grouped according to climatic similarity and geographical proximity (referred to as “CLI Cluster”), and

(iii) populations grouped according to altitudinal belts according to Kilian et al. (1994) (referred to as “ALT Cluster”).

For clustering according to climatic similarity (ii), the following climate parameters were considered: mean annual temperature (MAT), annual precipitation sum (APS), annual heat-moisture index (AHM), days of annual vegetation period (VP), growing degree days (GDD), mean coldest month temperature (MCMT), longitude, latitude, and altitude. In the first step, a principal component analysis was performed. The first four principal components (accounting for 97 percent of the variance in the data) were then used in the cluster routine ‘partitioning around medoids’ (in R-package cluster). The response functions of population clusters were calibrated on the 90th percentiles of all single tree heights for each population at each planting site. These percentiles reflect the potential for growth in height of a population on a specific site better than mean values.

3.2.3 Scenario analyses: best clusters under current and future climate conditions

Climate response functions were used to estimate the growth potential of the population clusters throughout the natural distribution range of Norway spruce in Austria. For each raster point of the species distribution maps of EUFORGEN (2009) the average estimated tree heights at age 15 were calculated, both according to current climate and according to future climate scenarios.

The population group with the best growth potential under current (period 1950–2000) and future (‘2080s’) climate was identified for each grid point of the natural distribution range of Norway spruce in Austria.

The percental change between current and future potential tree heights was calculated considering two scenarios: (i) selection of planting material according to the current provenance recommendations, i.e., from respective national provenance region, and (ii) selection of planting material of the locally best performing climate cluster according to previous analysis. The average difference in the tree heights at age 15 between both scenarios was calculated for all provenance regions.

3.2.4 Gene conservation network for Norway spruce in Austria

Results of climate-response-functions (see 4.2.1) were applied in a separate study to evaluate the current network of gene conservation units in Austria regarding its coverage of genetic diversity. In detail, the geographic distribution of gene conservation units was compared to the regional variation of (i) adaptive and (ii) neutral genetic diversity with a gap analysis (Maxted et al., 2008).

In particular, the Austrian territory was split into regular squares of 60 x 60 km. Numbers of existing genetic conservation units, measures of adaptive diversity, and measures of neutral genetic diversity were counted for each of these squares.

i) As a measure of adaptive genetic diversity, the phenotypic variability of the adaptive trait height-growth was used as determined in section 3.2.3. Therefore, climate population clusters with high growth potential (i.e., highest average tree heights at age 15) under future climate were identified. Then, a suitable index was calculated by rating populations from these clusters with the value 2 and populations with low growth potential under future climate with the value 1. The average value of all populations within a specific square rendered a regional index I_{clim} between 1 and 2.
ii) As a measure of neutral genetic diversity, allelic diversity was analyzed in individual twig samples. In detail, 1493 samples were genotyped for the mitochondrial nad1 marker, and 2773 samples were genotyped for 6 nuclear microsatellite loci.

Finally, the various adaptive and neutral genetic diversity measures were compared with the numbers of gene conservation units in each square of the Austrian territory.

3.2.5 Evolutionary adaptive potential

To analyze the evolutionary adaptive potential of tree populations, various measures of tree height variance were employed. First, to analyze among-population variance at test sites, among-population variance (σ^2_{ap}) was partitioned from the total phenotypic variance at each site (σ^2_s) with a linear model. To compare individual test sites, these variance components were standardized as coefficients of variation (CV_{ap}, CV_s) to remove the effects of different growth rates among sites.

After calculating these variation measures for each of the 29 sites separately, their relation to climate indicators was analyzed by linear regression analysis. Therefore, two subsuming predictor variables were calculated by a principal component analysis. The first principal component aggregates primarily temperature-related climate variables (hereafter referred to as “TempPC”). The second principal component aggregates primarily precipitation-related variables (hereafter referred to as “PrecPC”).

Additionally, the ratio of among-population variation to the total site variation CV_{ap}/CV_s was calculated to test whether the portion of explained variance by population relative to the total site variance relates to site climate.

Second, to analyze climatic effects on within-population variance, the standardized within-population variation CV_{wp} was calculated for each population and test site as $CV_{wp} = \sigma_{wp}/\mu_{wp}$, where σ_{wp} and μ_{wp} refer to all individual tree heights measured for a specific population at a particular site. CV_{wp} was then related to the climate of the trial site and the climate of the population origin. CV_{wp} was also calculated for the same trees in different years at the ages of 7, 8, 9, 10, and 15 years to assess the temporal changes in within-population variation throughout the juvenile stage.

Third, to better understand the environmental and genetic effects on phenotypic variation, the density distributions of tree heights were analyzed with mixture-model analysis. Mixture-models are clustering methods designed to describe and discern mixtures of distributions (Benaglia et al., 2009). They allow to differentiate phenotypic subgroups and can also be used to describe the shape of a particular density distribution (Ni et al., 2014). Finally, the robustness of the results was validated regarding potential bias effects by an unequal climatic distribution of tested populations across sites or varying survival rates between trial sites.

4 Results

4.1 Growth potential of Norway spruce provenances

Significant differences were found in mean tree height at age 15 among populations at each planting site, and significant differences among different planting sites. Therefore, both the climate at population origin and climate at planting sites affect growth performance of trees. The effect of site climate is however stronger than the effect of climate at populations origins. Response functions for maximum attainable tree height (i.e., the 90th percentile) at age 15 to Annual-Heat-Moisture-Index (AHM) are shown in Fig. 2. These functions were calibrated for clusters of populations grouped according to (i) national provenance regions, (ii) climate similarity, and (iii) altitudinal belts.

Generally, tree heights were larger at sites with higher AHM-indices (i.e., warmer and dryer sites) throughout all tested populations and population clusters. The graphs of the calibrated functions revealed peaks (climate optima) at AHM-indices between 31.5 to 35.7. These values are close to maximum current levels of the Norway spruce distribution range in Austria, indicating that a further increase in tree height cannot be expected under even warmer conditions in future.

With each of the three clustering approaches, considerable differentiation was found in the parameters of the Gaussian functions among population clusters. At current mean AHM level, differentiation between climate-response-functions is lower than at current maximum or prospective 2080 maximum levels (Fig. 2). The most pronounced differentiation was found with the climate-clustering approach at AHM levels above 30.

Map of best clusters reveal hardly any declines in tree height of Norway spruce across its current distribution range in Austria. For most parts, even an increase in productivity can be expected. For each raster point on the Norway spruce distribution map of EUFORGEN (2009), best performing population clusters were determined. Clusters 4, 7, and 9 revealed greatest potential tree heights within different parts of the distribution range: Cluster 9, with populations from warm and dry sites in northern Upper and Lower Austria,

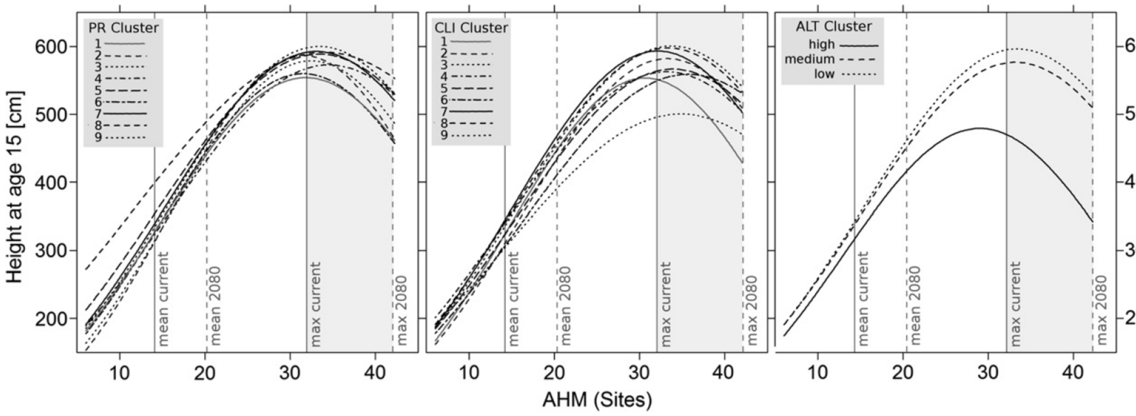

Fig. 2 *Response of tree height at age 15 to annual heat-moisture index (AHM) at trial sites. Tree height is calculated as the maximum attainable tree height in cm. Results with different clustering approaches are shown: Left: Clustering according to national provenance regions (PR Cluster); Middle: Clustering according to climatic similarity (CLI Cluster); Right: Clustering according to altitudinal belts (ALT Cluster). Response was fitted as Gaussian functions to the 90th percentiles of all populations belonging to a specific cluster. Also, mean and maximum values of AHM in Austrian territory are indicated with vertical lines, both for current (1950–2000) and future climate in 2080s (i.e. average of period 2070–2099). (Appendix 7.1 - Paper I)*

i.e., with highest AHM indices, performed best at the north-eastern margin of Norway spruce distribution range (parts of Weinviertel in lower Austria, eastern Styria, and Burgenland). Cluster 4, with populations from relatively warm and dry but more mountainous sites in central Styria and northern Carinthia, performed best at mountainous regions in western Austria. Cluster 7, with populations from easter Carinthia and eastern Styria, performed best in many parts of Upper and Lower Austria and on the fringe of the Alps.

Under future climate scenarios (“2080s”), the spatial distribution of these three clusters with maximum potential tree heights changes. The share of area, where cluster 9 and 7 reveal best performance, increases, while the area where cluster 4 is most suitable decreases.

Throughout the entire Norway spruce distribution area in Austria, the percental change of potential tree heights was estimated under future climate conditions. Rising temperatures and AHM values will induce an overall increase in productivity in most regions in Austria. Only at the very eastern edge of the distribution range, a further increase cannot be expected. There it seems that Norway spruce has already reached maximum potential tree heights. On average, potential tree heights may increase by 45% until the 2080s in the study area (Fig.3, top).

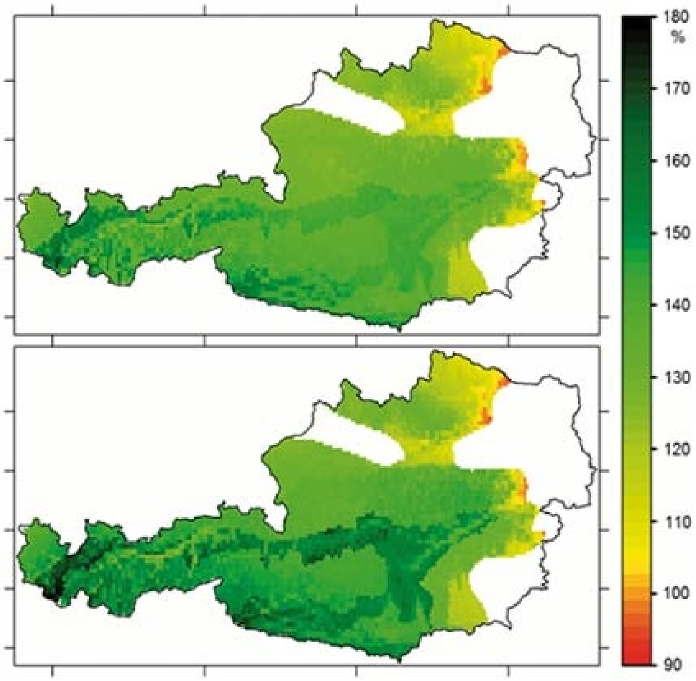

Fig. 3 *Map of natural Norway spruce distribution range in Austria. Colors at each grid point indicate the percental change of estimated tree heights from current conditions until the 2080s, assuming two different provenance selection scenarios.* ***Top:*** *"Local provenancing" - seed material from respective national provenance regions is used.* ***Bottom:*** *"Climate-adjusted provenancing" - seed material from locally best climate clusters is used. Colors indicate the respective percental change of potential tree heights at age 15. (Appendix 7.1 - Paper I)*

In addition, in most areas, potential tree heights could be significantly further increased by selecting reproductive material from population clusters that performed best in this analysis, instead of selecting seeds of the same provenance regions. Especially in the mountainous areas of western Austria an additional increase of up to 11 % of potential tree heights at the age of 15 could be estimated (Fig.3, bottom).

4.2 Gene conservation network

The distribution of existing gene conservation units across Austrian territory was compared with the regional variation of adaptive and neutral genetic diversity. The genetic diversity in climate response was indexed as the regional suitability of provenances for future climates (I_{clim}). Under current conditions the climate response of tree height at age 15 varies within a relatively small range among population clusters in Austria. Under anticipated future climates, however, the range of variation will increase (see section 4.1). Norway spruce populations with highest growth potential under future climatic conditions ("2080s") originate from the Bohemian Massif, the northern alpine foreland, and the eastern and southern fringe of the Alps.

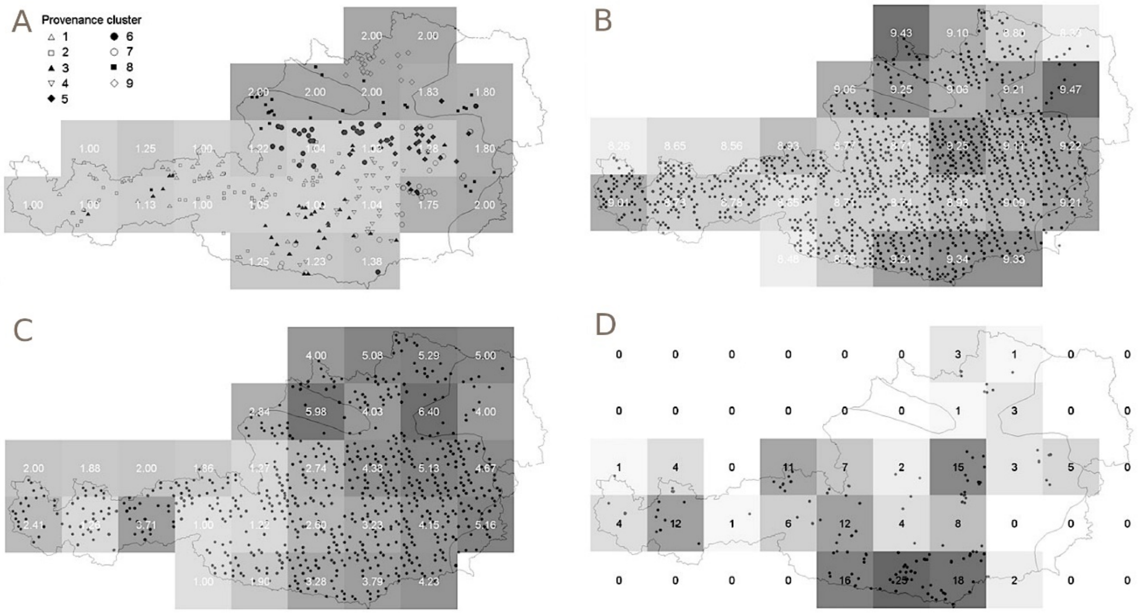

***Fig. 4** Comparison of provenance suitability, nuclear diversity, mitochondrial diversity and distribution of gene conservation units in Austria.*

***A:** Distribution of provenances tested within the Austrian Norway spruce provenance test 1978, the allocation of provenances (marked by different symbols) to nine provenance clusters and the regional Index I_clim summarizing the occurrence of provenance clusters within regions. The greyscale indicates the suitability of provenances for future climate conditions (the darker, the better)*

***B:** Number of alleles of 6 nuclear microsatellites analyzed on 2,773 samples of Norway spruce from all over Austria (dots mark the sampling locations). The greyscale indicates the corrected number of alleles within a region*

***C:** Numbers of mitochondrial DNA haplotypes analyzed on 1,493 samples of Norway spruce from all over Austria (dots mark the sampling locations). The greyscale indicates the corrected number of haplotypes within a region*

***D:** Spatial distribution of genetic conservation units (dots) of Norway spruce in Austria. The greyscale indicates the sum of gene conservation units within each region. (Appendix 7.2 – Paper II)*

As a measure of neutral genetic diversity, the allelic diversity in twig samples was analyzed. The results were similar to the analyses of the allelic diversity of nuclear microsatellites and mitochondrial DNA haplotypes. Largest diversity was found within the northern, eastern and south-eastern regions of Austria. Western and central regions revealed lower diversity, i.e., fewer alleles in nuclear and mitochondrial DNA.

The 164 currently existing gene conservation units for Norway spruce in Austria are very unevenly distributed, with the highest numbers of units south of the Alpine main ridge (Fig. 4D) and in the western parts of Austria. Only a few units are located in the Bohemian massif and the eastern fringe of the Alps. However, populations from these regions have high growth potential under future climate regimes and harbor high genetic diversity. The gap analysis corroborates this mismatch shown in Fig. 4.

4.3 Adaptive potential of Norway spruce populations

Frequency density distributions of juvenile tree heights at age 15 indicate how climatic constraints shape the genetic variation in tree populations.

In a first step, the total phenotypic tree height variance was partitioned at each site. The among-population variance was 47 % of the total variance. This portion of variance can be attributed to tree populations irrespective of the local climate.

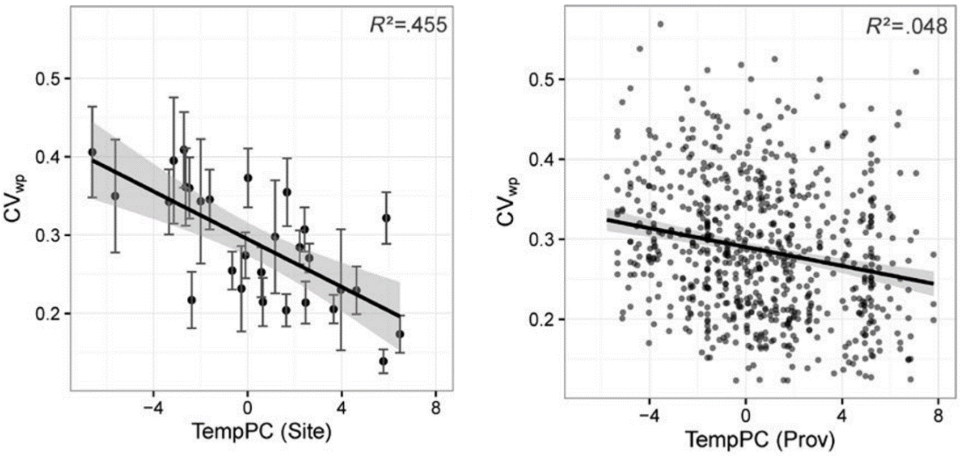

Fig. 5 *Within-population variation (CVwp) for each population–site combination. Coefficients of variation for within-population variation are shown along the climate gradient TempPC, where large values of TempPC represent warm and dry locations.* ***Left:*** *response along climate at the test sites. Error bars represent* CV_{wp} *values from all populations tested at a respective site;* ***Right:*** *response along population climate. Points represent* CV_{wp} *values of one population tested at one specific site. (Appendix 7.3 – Paper III)*

The tree height variation within populations (CV_{wp}) is higher at cold and moist sites than at warm and dry sites (Fig. 5, left). Moreover, tree height variation is higher within populations originating from regions with cold and moist climatic conditions, irrespective of climate at trial site (Fig. 5, right).

Analysis of temporal changes in within-population variation throughout the juvenile stage revealed differences between cold-moist sites and warm-dry sites. At cold-moist sites, variation within population increases or accumulates over the years between tree ages of 7 to 15. In contrast, at warm-dry sites, tree height variation remains at about the same level during early tree development.

Finally, the frequency density distributions of tree heights differ between cold-moist and warm-dry trial sites. At cold-moist sites tree height distributions are left-skewed, whereas at warm-dry sites tree height distributions are not skewed (Fig. 6).

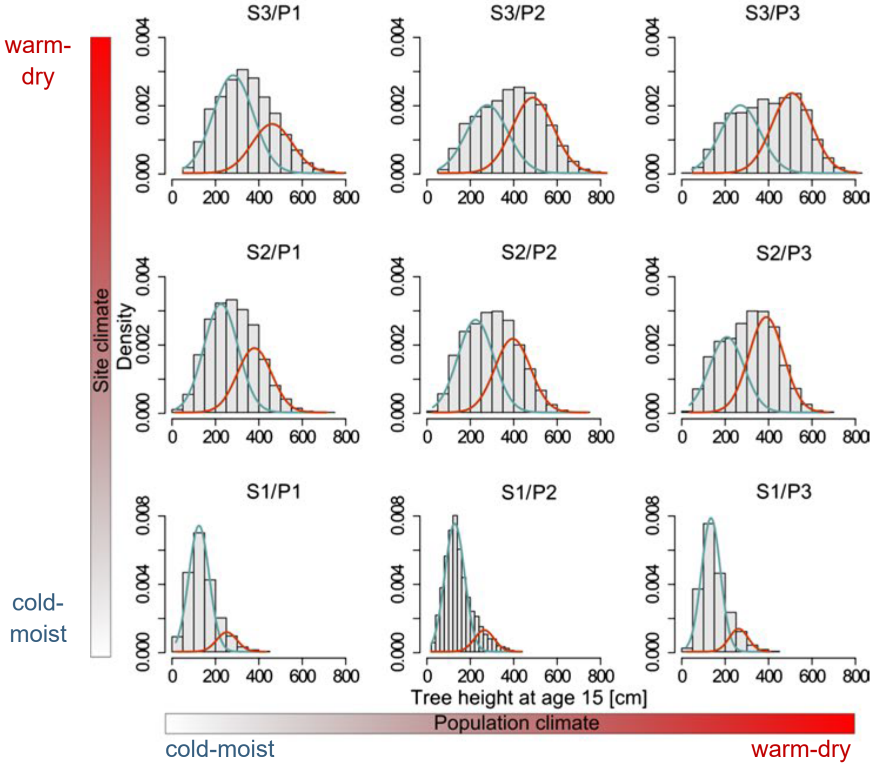

Fig. 6 *Frequency density distributions of absolute tree heights at the age of 15. All records were divided into nine climate subsets by TempPC. Each subset aggregates records from one of three test site groups (S1, S3, or S3) and from one of three population groups (P1, P2, or P3). Red and blue curves are the results from a mixture-model analysis and represent density probabilities of two hypothetical subcomponents for "small" and "high" trees within each subset. (Appendix 7.3 – Paper III)*

5 Discussion and conclusion

5.1 Methodological issues

5.1.1 Data from provenance trials

Provenance trials provide valuable data to calibrate models of growth response to current and future climatic conditions. In the Alpine space, provenance trials have been established for many tree species since the last 200 years, primarily to detect most productive provenances for specific regions. Today, such data are employed to analyze the intraspecific variation of climate response of tree species in the light of climate change. Theoretical, statistical, and computational methods for such analyses have been significantly improved within the last decades. Climate data is easily accessible at high spatial and temporal resolution. Therefore, data from tree measurements conducted 50 years ago or more, can render valuable new insights if analyzed with novel statistical approaches. They are vital for our understanding of climate growth relationships and the underlying evolutionary processes of adaptation.

Unfortunately, the necessary raw data from old provenance trials are often difficult to get and process. In many old experiments, tree measurements have not been recorded electronically. If evaluations and analyses already exist, data are often scattered across journal articles, conference proceedings, government reports, and other sources (Risk et al., 2021). In addition, in many cases, the data have been collected by state authorities and are not readily made freely available for scientific research. Therefore, before any statistical analyses can be started, a lot of effort must first be put into the collection and preparation of measurement data.

Furthermore, at the time when many provenance trials have been established, their aim was usually first and foremost to find most productive seed sources for specific test sites and not to investigate general climate - growth relations. Consequently, most trial sites were set up in locations within the natural distribution range of the tree species. Only a few trial sites exist at the edges of the natural climatic range of tree species. However, to detect niche limits of tree species and tree populations and to calibrate well-founded response functions, sites at climatically extreme locations are most valuable. Ideally, future provenance trial series should also include planting sites beyond the natural distribution range.

The experimental design of newly established provenance trials should therefore ensure, that (1) both the trial sites and the origins of the tested provenances cover a broad climatic spectrum, (2) all trial sites are laid out according to a uniform trial design, and (3) silvicultural measures are carried out as uniformly as possible across sites, so that the measurement results are comparable.

The Austrian Norway spruce provenance trial of 1979 is one of the most comprehensive trials with consistent study design. After 10 years of growth at respective trial sites (at the tree age of 15 years), most trial sites were left standing and measured again after another 15 years. Unfortunately, at this time, the trial sites were no longer managed uniformly, so that a joint evaluation is not very robust.

The analyses in this study focus measurements of tree heights at age 15. Tree height is an important phenotypic trait and can be interpreted as a proxy for juvenile fitness and productivity (Aitken & Bemmels, 2016). Trees experience strong intra- and interspecific density-dependent competition for light. Hence, fast-growing trees are more likely to dominate their neighbors close by (Vieilledent et al., 2010). Later on, large trees are more likely to survive and to produce more offspring than smaller competitors. Also, tree height is easily measured than direct measures of a trees’ fitness as survival and reproduction.

5.1.2 Selection of climatic predictor variables

To grow and reproduce, trees are adapted to a variety of local climatic and environmental conditions. For the model calibration, a set of quantitative variables is necessary that describe local climatic conditions. The selection of suitable variables that serve as predictor variables is crucial for the informative value and significance of the model. Which climate variables to use is a difficult decision because the parameters that limit tree growth and drive evolutionary selection forces may varausy from site to site. For example, in mountainous areas, the limiting factor for tree productivity might rather be cold hardiness. Instead, in warm regions tree productivity might rather be limited by the extent of drought periods (Aitken & Hannerz, 2001; Honkaniemi et al., 2020).

Especially in heterogeneous climates of Alpine regions, where manifold microclimates can occur within small geographic ranges, a large number of selection forces may play a role: for example, growth performance of Norway spruce was found to be positively related to temperature in May and June at higher altitudes and negatively related to temperatures of the same months at lower elevation (Mäkinen et al., 2002). In higher altitudes, frost tolerance and stability are of paramount importance. In lower altitudes, best exploitation of the vegetation period has higher priority (Howe et al., 2003).

For the calibration of climate-response functions, a selection of climatic predictor variables is critical. Strong correlations were found between the various monthly climate parameters. Therefore, subsuming variables proofed suitable. The annual heat-moisture index (AHM), according to Wang et al. (2006), integrates temperature and precipitation into one single parameter and better reflects evapotranspiration (related to temperature) and soil moisture than precipitation and temperature alone (Wang et al., 2006). For the analyses of within-population variation, the large number of available climate variables was reduced through a principal component analysis, resulting in two predictor variables, which combine temperature-related on one hand (“TempPC”), and precipitation-related variables on the other (“PrecPC”).

However, for provenance trial sites with heterogeneous soil characteristics such as water holding capacity, the use of variables like AHM or principal components may not be sufficient to characterize ecological gradients. Chakraborty et al. (2019) analyzed tree height, climate, and soil characteristics from the Austrian Norway spruce provenance trial 1978. He found that climate and soil characteristics at the planting sites are dominant drivers of growth compared to climate and soil at provenance origins. However, the relative effects of climate and soil vary among different provenance groups: For planting material originating from cold-moist areas (at high altitudes), climatic drivers are dominant. For materials originating from warm-dry locations (at low altitudes), soil and climate conditions are equally important (Chakraborty et al., 2019).

Especially in the Alpine region, other environmental factors are considered essential for Norway spruce, e.g., bud burst (Søgaard et al., 2008) or frost hardiness (Johnsen & Skrøppa, 2000). For seed recommendations, such traits should be considered as well.

5.2 Limiting factors of potential tree heights along the climatic gradient

The presented analysis covers different aspects of climate-growth relations: projected juvenile tree heights in future climatic conditions, utilization and conservation of intraspecific genetic variance, and the role of tree height variation within populations in evolutionary processes. Despite these different aspects, some overall findings become apparent throughout. Significant effects of climate at planting sites on tree growth are evident. However, the effects vary along the climatic gradient from cold temperature sites at high altitudes to low-temperature sites at low altitudes. Many montane regions of Austria (above approximately 700 m a.s.l.) are currently still providing favorable climatic conditions for *Picea abies* regarding mean temperature and precipitation. For these regions, the presented results indicate that Norway spruce has not reached an upper heat-moisture limit yet. Instead, the trees seem to even tolerate a further increase in temperature. Rising mean temperatures and extended vegetation periods will increase tree heights. By an optimized choice of seed material accounting for prospective future climates, the height growth can additionally be increased.

These findings are in line with Frank et al. (2017), who analyzed seedling heights, day of the year of bud break and growth cessation in Norway spruce, silver fir and European beech in Swiss common garden tests. They estimated the risk of genetic maladaptation to future climates, here defined as difference between the predicted phenotype of an adaptive trait in the past and current climate, where it evolved, and the value of that trait that is expected to be adapted to the future climate at a specific location (Frank et al., 2017). They found that populations of spruce, fir and beech are sufficiently adapted to the projected climate of 2021 to 2050, however, the risk of maladaptation will significantly increase for spruce and beech by 2061-2090.

From the presented climate-response functions in this study, a further increase in juvenile tree height cannot be expected in colline to submontane lowland regions of Austria, though hardly any decrease can be derived neither. Similarly, analyses of tree height variation revealed no climatic constraints on tree height variation even at the warmest trial sites in Eastern Austria. Hence, climatic conditions are currently still suitable for Norway spruce provenances regarding tree physiology even at the warm edge of its distribution range. It is, however, clear, that many Norway spruce forests are especially threatened in the submontane region (Trujillo-Moya et al., 2018). Here, extrinsic biotic factors, like spruce bark beetles, rather than climatic factors are expected to be the main drivers that hinder tree health and growth.

5.3 Climate-adjusted provenancing

Norway spruce populations in Austria harbor varying climatic optima even within small geographic distances. Differences between tested provenances were especially pronounced at test sites with cold climates, i.e., primarily test sites in the montane and submontane vegetation belt. At test sites with warmer climates in lower regions, the differences among provenances were less distinct.

Currently, seed transfer guidelines in Austria follow a static concept based on National provenance regions and altitudinal belts. This concept should be complemented with information about provenance-specific climate-response and genetic variation. Both the local climatic conditions and genetic preconditions, i. e., the origin of planted seed material, should be taken into account. Also, seed material from beyond respective provenance regions should be considered, i.e., planting material originating from locations that are currently already similar to future climate of the respective planting sites. Seed transfer guidelines with such a more dynamic concept could contribute to mitigate negative consequences of deploying seed sources unsuitable for future conditions on the one hand, and use the full capacity of potential positive effects such as increased productivity on the other hand.

5.4 Gene conservation network does not cover genetic and phenotypic variation

Forest tree species harbor large genetic diversity, which is considered crucial for the conservation of forest ecosystems under ongoing climate change. Therefore, exploring and utilizing available genetic variation and planting provenances suitable for future climatic conditions is considered an important adaptation measure. The existing network of genetic conservation units safeguard the hotspots of adaptive and neutral genetic diversity and may provide appropriate genetic resources to forest management.

In Austria, Norway spruce represent a particularly high intrinsic natural value due to refugial areas during the last ice age within or adjacent to Austria (Tollefsrud et al., 2008).

Significant genetic diversity of mitochondrial and nuclear markers was observed in eastern and south-eastern populations (Mengl et al., 2009). This diversity results from refugial areas in close proximity to the eastern Alpine foreland, the south-east Alpine foreland, as well as in the Hungarian plain (Ravazzi 2002; Tollefsrud et al., 2008). This area was presumably a migration corridor of Norway spruce through which the entire Alpine region was re-colonized after the last glaciation (Petit et al., 2003). A recent study from Trujillo-Moya et al. (2018) confirms the significant adaptive genetic variation Norway spruce populations in the Eastern Alpine range and the Bohemian Massif as a consequence of the postglacial migration history. However, neutral genetic variation was found to be relatively low, potentially as a result of extensive gene flow via pollen.

Analyses of climate response in tree height also revealed high variation among provenance clusters from these areas. The most productive and promising provenance clusters for future climate conditions in Austria originate from the Bohemian massif, the south-eastern fringe of the Alps, and the northern Alpine foreland. These clusters depict the warmest and driest regions of the natural spruce distribution range in Austria. Here, tree populations are probably adapted to warm and dry climate regimes. The observed above-average tree heights at age 15 likely result from an adaptation towards the extended growing season in these warmer regions. In the future, also Norway spruce populations in other parts of Austria will be confronted with such conditions.

The southern-most regions with high genetic diversity and long population history are well covered in the current gene conservation network. Unfortunately, areas in east and north-east Austria with high genetic diversity and high adaptive variation are less well covered. Here, at the eastern and the northern fringe of the Alps and on the Bohemian massif, further conservation measures on a regional scale are necessary to conserve important adaptive genetic variation.

5.5 Varying adaptive potential of tree populations to anticipated climate

Tree height variation among individual trees within populations is higher at cold trial sites. While climate conditions at the colder trial sites increase the differentiation among trees within populations, climate conditions at warm sites do not affect within-population variation.

One possible explanation for high within-population tree height variation at cold mountainous sites could be related to the characteristics of the trial sites. While lowland trial sites are rather flat and homogeneous, cold trial sites are more likely to harbor a larger heterogeneity regarding topography, soil characteristics, or snow cover, thus advantageous microhabitats for individual trees that are able to outperform their competitors.

Another potential cause for the differing tree height variation along the climatic gradient from the cold to the warm edge could be the strong relation between height growth and phenology, especially flushing and bud set (e.g., Kleinschmidt et al., 1981). These traits reveal significant additive genetic variation (Hannerz et al., 1999; Søgaard et al., 2008). At cold sites, small differences in temperature sum requirements for flushing and the onset of growth among individual trees can accumulate into large differences in tree heights. In warm environments, temperature sums are accumulating faster. Here, the effect of genetic variation in temperature sum requirements is more negligible. Such behavior was also observed for other species (Davi et al. 2011).

Large tree height variation suggests that at cold sites, a few well-performing trees will likely dominate and outcompete the slower-growing trees close by. The enormous intraspecific competition among juvenile trees (Vieilledent et al., 2010) results in a strong climatic selective pressure at the cold edge of the spruce distribution. From analyses of within-population variation of tree height density distributions, it can be concluded that Norway spruce is not under strong selection pressure by climate constraints at the warm-dry temperature limit of the species range.

These results on climate constraints at the cold distribution edge are in good agreement with other traits in conifers related to cold adaptation (Aitken & Hannerz, 2001; Howe et al., 2003; Morgenstern, 2011). Besides bud burst and bud set, a significant variation among Norway spruce provenances in frost hardiness has been found (Skrøppa, 1991). Howe et al. (2003) concluded that such adaptive traits are under strong natural selection in cold environments. In contrast, there is fewer evidence for genetic adaptation of Norway spruce to warm temperatures, e.g., drought resistance. This may be because fewer studies have addressed the intraspecific variation in adaptive traits at the warm temperature edge (but see (Mátyás et al., 2009). It may also corroborate the conclusion that climatic drivers at its warm edge do not immediately limit the species distribution of Norway spruce. Thus, the realized niche is defined by non-climatic factors (e.g., bark beetles, inter-species competition) and does not reflect the fundamental niche.

Under prospective climate change, the altitudinal or latitudinal range, where Norway spruce trees can grow, is supposed to shift upwards. In this process, the cold distribution limit is the leading edge, and the warm distribution limit is considered to be the trailing edge (Sykes et al., 1996).

At the trailing edge, Norway spruce will suffer area reductions with consequences for forest ecosystems and wood production (Hanewinkel et al., 2013). Moreover, losses of genetic diversity are expected (Schueler et al., 2014).

Natural selection at this trailing edge is limited, hence means of natural evolutionary adaptation are too slow considering the velocity of climate change. Forest management can mitigate adverse effects by assisted migration and anticipatory choice of genetic planting material. Also, the existing genetic diversity at the warm (trailing) edge should be utilized and preserved by establishing gene conservation forests in such areas.

5.6 Implications and conclusions

Norway spruce populations are increasingly challenged by climate change in Central Europe, particularly at dry, low-elevation sites (e.g., Honkaniemi et al., 2020; Jandl, 2020). Despite threats like bark beetle outbreaks and increasing drought and storm events, Norway spruce continues to find climatically suitable habitats, mainly at higher altitudes. Hence, Austrian forestry might not only aim at mitigating negative effects but instead seek to utilize potential positive effects on tree growth, e.g., exploitation of an extended vegetation period.

For this purpose, static seed transfer guidelines should be complemented by provenance-specific information such as phenotypic plasticity or adaptive capacity. Provenance trials can provide such information (Prober et al., 2016). Climate-response functions can help to identify suitable provenances from beyond the National provenance regions or respective altitudinal belts. Data sets and analyses similar to those presented for Norway spruce in the current study are available for many tree species and have been used to select appropriate populations for future reforestations (e.g., Leites et al., 2012; Lu et al., 2014; Rehfeldt et al., 2002). Therefore, unpublished data from provenance trials should be made available. More resources are needed for the preparation and digitization of this data.

Also, the Austrian gene conservation network should be expanded with focus on the eastern and northern fringe of the Alps. Ideally, the establishment and sustainment of the gene conservation network is coordinated internationally by the European Forest Genetic Resources Programme (EUFORGEN) with neighboring countries to cover the entire area of the species distributions range and beyond. Gene conservation forests are especially essential in warm climates. Here, tree populations are particularly vulnerable. At the same time, a high genetic diversity has been found within tree populations, that could provide urgently needed information on drought-resistance and heat-tolerance.

Finally, the in-depth analysis of the phenotypic variation within such datasets can provide additional knowledge on the population's adaptive capacity. Along the climatic gradient, different selection factors seem to drive tree productivity and health. At low altitudes, biotic factors limit the growth and survival of the Norway spruce trees. In these regions, pest insects such as bark beetles or pathogens are the strongest selection factors. At higher altitudes, the small-scale climatic conditions are of greater relevance for the tree heights, mainly due to limiting effects of the temperature regime.

This work deals mainly with juvenile tree heights as a proxy for productivity. However, productivity is not the only goal of forest management in the Alpine region. Especially at higher altitudes, forests provide a range of protective services regarding gravitational hazards, such as avalanche, rockfall and landslides. Therefore, along with tree height, many other adaptive traits could be in focus. Seventeen percent of the forests in Austria are protective or other forests without commercial yield. Here, rapid growth during the juvenile stage of a tree is of less importance than, for example, stability and resilience to disturbances. At lower altitudes near cities, the recreational value of forests is becoming increasingly important. The demands on forest management are becoming increasingly diverse and even more challenging to meet in the future regarding climate change.

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7 Appendix

7.1 Appendix – Paper I

Kapeller, S., Lexer, M. J., Geburek, T., Hiebl, J., & Schueler, S. (2012). Intraspecific variation in climate response of Norway spruce in the eastern Alpine range: Selecting appropriate provenances for future climate. *Forest Ecology and Management*, *271*, 46–57.

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Intraspecific variation in climate response of Norway spruce in the eastern Alpine range: Selecting appropriate provenances for future climate

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ABSTRACT

Enhancing adaptation of forest ecosystems to prospective climate change is a major challenge in current forest management. Beyond potential negative effects of climate change such as decreasing productivity due to an increasing number of drought periods and damages from intensified disturbance regimes, there is also a potential for increasing productivity due to prolonged vegetation periods and higher photosynthetic rates. Quantitative genetic variation is crucial for adaptability of species towards environmental changes. The use of suitable reproductive material for forest regeneration will be a key factor essential for both, mitigating negative effects and making the most of potential positive effects. Therefore, insights into intraspecific variation within and among tree populations in climate response are of paramount importance.

In our study we investigated intraspecific variation in climate response among Norway spruce (*Picea abies*) populations in the eastern Alpine range. Results from a comprehensive Austrian provenance test, comprising tree heights at age 15 from 379 populations planted at 29 test sites across Austria, were used to calibrate climate response functions for groups of Norway spruce populations. Potential future changes in productivity for climate change conditions as represented by a regionalized A1B scenario were estimated using height at age 15 as a productivity proxy. Climate response functions were calculated for single populations and aggregated clusters of populations from climatically similar origins.

Our results hardly revealed any declines in employed proxies for productivity of Norway spruce throughout its current distribution range in Austria. For most parts of Austria an increase of tree heights up to 45 percent can be expected until 2080. However, the impact of a warming climate is different for individual population groups. Generally, variation in climate response increases with higher temperatures and less precipitation. Thus, an optimized choice of seed material according to prospective future climate conditions has the potential for an additional increase of productivity up to 11 percent.

In general, populations from currently warm and drought prone areas seem to be well adapted to respective climate conditions and may be appropriate candidates for extended utilization in future. Furthermore, populations showing the best productivity indices originate from regions, which are phylogenetically distinct from the core distribution area of Norway spruce, suggesting that population history might explain part of the variation in climate response among populations.

1. Introduction

Potential consequences of climate change for forest ecosystems and the mitigation of negative impacts on ecosystem services and functions are major challenges of current forest science and management (Prentice et al., 1993; Maracchi et al., 2005; Lindner et al., 2010). Impacts of climate change on forest ecosystems in Europe have been discussed controversially. It is generally agreed, that increasing temperatures will lead to higher photosynthetic activity, faster growth and therefore higher potential forest net productivity, at least in large parts of northern and western Europe (Peltola et al., 2002; Matala et al., 2006; Lindner et al., 2010). However, more intense and increasing numbers of drought periods are assumed to be major limiting factors for tree growth in the future (Modrzynski, 2002; Bréda et al., 2006), and some tree species very likely will not be able to survive under such future conditions in all parts of their current natural range or cultivation area respectively (Davis and Shaw, 2001; Pearman et al., 2010). Also, biotic and abiotic disturbance regimes may be affected by a changing climate with generally increasing intensity of disturbance events (e.g. Lindner et al., 2010).

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Forest growth, as well as stand vitality and stability strongly depend on the natural adaptedness of tree populations to prevailing climate conditions. Sedentary and long-living organisms like trees have evolutionary developed means to adapt to changing conditions, e.g. by intensive gene flow among and large intraspecific genetic variation within populations (Hamrick et al., 1992; Hamrick and Godt, 1996). However, a number of recent publications corroborate the assumption that means of natural adaptation or range shifts through migration may be too slow to keep up with the current speed of climate change (Savolainen et al., 2007; Petit et al., 2008). Therefore, the exclusive utilization of local seed sources for reforestation, which has been until now regarded as the most efficient way to avoid maladaptation under stable environmental conditions, must be challenged in the future (Wang et al., 2006; O'Neill et al., 2008). Instead, the selection of appropriate seed sources for forest regeneration needs to consider future rather than current climates, thus providing tree genotypes well adapted for the future conditions (Bower and Aitken, 2008).

Adaptive genetic variation of forest trees and its correlation with the climate conditions of individual populations have long been investigated in provenance experiments (e.g. Langlet, 1971; Morgenstern, 1996) and it has been suggested to consider genetic variation between populations for the development of seed transfer and utilization schemes as adaptation measure (e.g. Matyas, 1994; Rehfeldt et al., 1999; Wang et al., 2006; McLachlan et al., 2007; St. Clair and Howe, 2007; Ukrainetz et al., 2011). In Austria, seed zones are bio-geo-climatic regions, delineated on the basis of natural forest types, geology and soil, and altitudinal belts rather than genetically different groups of populations (Kilian et al., 1994).

Climate-response functions and climate transfer functions have been developed to describe the correlations between tree growth characteristics and climate parameters (e.g. Carter, 1996; Rehfeldt et al., 2002; Wang et al., 2006; Matyas, 1994; O'Neill and Nigh, 2011). The former characterize the performance of a specific population across many planting sites, the latter describe the performance of different populations at one planting site in dependence on climatic differences between local planting site and population origin site. The mathematical approach usually employs univariate or multivariate curve fitting techniques to link tree growth traits such as height with environmental or geographic predictor variables (Hamann et al., 2011).

In this study we investigate the climate response of Austrian Norway spruce (*Picea abies* (L.) Karst.) populations, employing tree heights at age 15 from a comprehensive provenance test. Norway spruce is the economically most important forest tree species in Austria. It has been promoted heavily as a productive timber species at sites naturally supporting broadleaved and mixed species forests (Seidl et al., 2007). However, in respect to ongoing climate change a transition from pure Norway spruce stands to broadleaved or mixed broadleaved-conifer stands has been suggested especially at low-elevation sites in Austria (Lexer et al., 2002). Besides its economic importance, spruce populations in Austria also harbor high genetic diversity and differentiation among populations, mainly due to the long population history. For example, refugial populations have survived at the transition between the Bohemian Massif and the northern Alpine foreland, but also at the south-eastern fringe of the Alps (Tollefsrud et al., 2008; Schiessl et al., 2010). Although this neutral diversity as assessed with mitochondrial and nuclear genetic markers is not granting for high quantitative and adaptive genetic variation, the long population history suggests that local adaptation to the highly heterogeneous environment of the alpine landscape facilitated also high quantitative variation among tree populations (Yeaman and Jarvis, 2006), which might today be advantageous for mitigating negative climate change impacts on spruce forests.

Main objectives of this study are (1) to fit climate response functions to data from a Norway spruce provenance test in Austria (2) to aggregate Norway spruce populations in Austria and analyze climate response of these population clusters, (3) to map the best performing population clusters for current and future climate scenarios and (4) to compare future growth performance of seed material which has been selected due to different recommendation schemes.

2. Material/methods

2.1. Austrian provenance test with Norway spruce 1978

Norway spruce seeds from 480 Austrian populations (i.e. provenances) and 60 populations from other countries were included in the Austrian provenance test in 1978. Seed material had been collected during commercial seed harvests in 1971. These harvest comprised presumably autochthonous stands with tree ages between 80 and 200 years involving several trees as representative sample of the stand. After pre-cultivation in climatic chambers in 1973, the young seedlings were transplanted to nursery beds. In 1978, 5-year old trees were planted at 44 sites across Austria (Nather and Holzer, 1979) in a uniform experimental random block design. The number of tested populations on each planting site ranged from 20 to 53 (29 on average). Trees of each population where split in three randomized blocks (repetitions), though, on few sites only one or two blocks could be established. Each single population within a block consisted of 50 plants initially, usually planted with 1.5 m × 1.5 m spacing. Tree height has been recorded at age 15 at 29 of these 44 trial sites. Further information about tree numbers per population and planting site and on coordinates of provenances and test sites are provided as online supplement (Table S1).

At age 15, data from many test sites and trees were still available and no forest management interventions had been implemented so far. In young tree plantations, tree height can be considered as a measure for productivity and ecophysiological fitness because it approximates the correspondence of the trees phenotype with the environmental conditions of the site and the trees competitiveness towards neighboring plants (Savolainen et al., 2007). For statistical analysis, we used the 90% percentile of all tree heights of a given provenance respectively a given provenance cluster, because in managed spruce stands, the best growing and most promising individuals (i.e. social dominating trees) are typically favored by stand tending interventions. Thus, the 90% percentile better approximates potential productivity than the average tree growth performance of a population.

For single sites, additional measurements of diameter (dbh) at age 25 and age 31 are available. These data were used for juvenile-age correlations to test for the representativeness of our data.

2.2. Climate data

Climate data for each test site and the geographical source of the populations were provided by the Austrian meteorological service, the Central Institute for Meteorology and Geodynamics. These include monthly time series of temperature means and precipitation sums from 1971 to 2008, as well as mean monthly temperature and precipitation minima and maxima, length of vegetation period, growing degree days (i.e. a thermal index accumulating degree days above a threshold of 5 °C) and appearance of the first frost in autumn. For each location of the trial sites and the population origin, climate data from the nearest 15 stations have been selected, weighted according to horizontal distance and processed in a linear regression against altitude. By selecting (the fixed number of) 15 stations (instead of a fixed search radius) a solid climate parameter-altitude dependency is guaranteed (in all cases). The emphasis of regional climate specifics is achieved by geographical weighting. By means of the regression equation, the climate value was assigned to the location according to its altitude. Averaged climate data for planting sites take into account records during the growing period (1978–1988), whereas averaged data of populations are based on 38-years records (1971–2008). The selection of sites and populations of the Austrian provenance test covers almost the whole climatic range of current Norway spruce habitats (Fig. 1). Climate conditions at test sites are ranging from 2.6 °C to 9.2 °C and annual precipitation values from 535 mm to 2392 mm.

The relationship between tree growth and climatic conditions at the trial sites has been analyzed by means of uni- and multivariate regression analysis (Schueler and Kapeller, 2010). For the analysis of climate-response functions, the annual heat-moisture index (AHM) according to Wang et al. (2006) has been applied, because it integrates mean annual temperature (MAT) and annual precipitation sum (APS) into one single parameter: AHM = (-MAT + 10)/(APS/1000).

The advantage of using AHM instead of precipitation and temperature is, that this combined measure better reflects evapotranspiration and soil moisture content than precipitation and temperature alone (Wang et al., 2006).

2.3. Response functions

To understand the response of single populations to the climatic conditions of its planting sites, we tested several model candidates (quadratic, Gaussian, Richards, saturation-growth, linear, Gompertz, logistic) among which the Gaussian normal distribution (Eq. (1)) in general showed best values for Pearson's correlation coefficient r and residual pattern.

$$y = ae^{\frac{-(x-b)^2}{2c^2}}, \tag{1}$$

where y is the response variable (height at age 15), x is the climatic predictor (AHM) and a, b, c are model parameters. The parameters of the Gaussian normal function can be interpreted in an ecological meaningful way. Parameter a reveals the maximum response (i.e. tree height at age 15), parameter b indicates the location of this maximum, i.e. the 'climate optimum' and parameter c can be interpreted as an indicator of climate sensitivity. The lower the c-value, the more pronounced is the climate optimum.

We applied the Gaussian function in a non-linear regression technique to link tree heights to AHM indices at the planting sites. Regression coefficients and standard deviation of residuals were calculated with the curve fitting software *CurveExpert* (Hyams, 2005). Upper and lower confidence limits of estimated values were calculated with R-package *nlstools* (Baty and Delignette-Muller, 2011) as defined by Beale (1960). In addition, normality of residuals was tested with Shapiro–Wilks test and independence of residuals with runs test (see Appendix).

Climate response functions were calculated for individual populations, which had been tested at least on six sites. In addition, we grouped populations and calibrated response functions to pooled data from all populations within each group. The grouping was based on three approaches: (i) populations were grouped according to national provenance regions (Kilian et al., 1994), (ii) population clusters were built with provenances from climatically similar and geographically proximate origin, and (iii) clusters were built with populations from similar altitudinal belts. Since the climatic conditions of the same altitude are strongly different between the southern and northern Alps, physiological elevation levels based on geobotanical community characteristics and climate according to Kilian et al. (1994) were used instead of simple altitude above sea level.

For the climate clustering of populations the following parameters were taken into account: mean annual temperature (MAT), annual precipitation sum (APS), annual heat-moisture index (AHM), days of annual vegetation period (VP), growing degree days (GDD), mean coldest month temperature (MCMT), longitude, latitude and altitude. For clustering, a principal component analysis implemented in the R programming environment (R Development Core Team, 2010) was performed in a first step. The first four principal components (accounting for 97 percent of variance in the data) were then used in the cluster routine 'partitioning around medoids' (in R-package *cluster*). This method allowed us specifying the number of clusters and ensuring that enough populations of each cluster were available at all test sites.

For the cluster response functions we first calculated the 90% percentiles of single tree heights for each population at each planting site. Then, Gaussian functions were fitted by regression of these

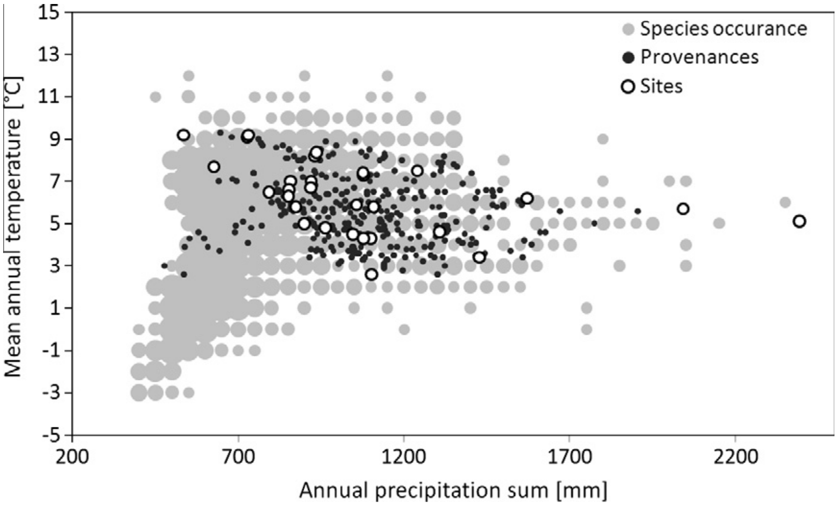

Fig. 1. Distribution of 29 test sites (white circles) and provenances (black dots) in bioclimatic parameter space (some sites are climatically very similar and can hardly be distinguished on the map). Grey circles indicate the climate envelope of Norway spruce according to mean annual temperature and annual precipitation following Kölling (2007).

90% percentiles from all populations belonging to a population cluster against AHM values of test sites.

2.4. Scenario analysis

The climate response functions were used to calculate the performance of the different population groups for the complete natural distribution range of Norway spruce in Austria according to the species distribution maps of EUFORGEN (2009) for current climate and climate change scenarios. Climate data for this analysis were obtained from WorldClim data portal (Hijmans et al., 2005), where 'current' (1950–2000) climatic conditions and downscaled climate change scenarios for the 2050s (i.e. average of period 2040–2069) and 2080s (i.e. average of period 2070–2099) are available in a resolution of 2.5 arc-minutes (Ramirez and Jarvis, 2008). To represent climate change conditions we used the MPI-Echam5 model for the emission scenario A1B (Nakicenovic et al., 2000) downscaled to 2.5 arc-minutes using the delta approach for downscaling (Ramirez and Jarvis, 2010). The results of the MPI-Echam5 model provide a good average of the various global circulation models available and it has been rated as one of the most reliable global climate models (Connolley and Bracegirdle, 2007). For each point of this raster we calculated the annual heat-moisture index with current values of temperature and precipitation, as well as with data for the 2050s and 2080s under climate change conditions. Using the cluster-specific parameter estimates from regression, potential tree heights at age 15 were calculated for each grid point of the natural distribution range of Norway spruce in Austria. Thus, we were able to identify the population groups with the best growth performance under current climate and climate change conditions.

In addition, the percental change in tree heights between current and future growth performance was calculated for two management scenarios with (1) planting material from respective national provenance region according to the current provenance recommendations and (2) planting material of the locally best performing climate cluster according to our previous analysis. For all national provenance regions, the mean difference in the performance between the regional provenance recommendation and the most productive population group was calculated.

3. Results

3.1. General

Analysis of tree heights at age of 15 years confirmed that growth performance of tree populations is strongly affected by climate conditions at both the trial sites and the provenance origins. Due to its mountainous landscape character, strong variation of climatic conditions can be found in the eastern Alps even within small geographic ranges. Climate conditions of the provenance origins span mean annual temperatures between 2.6 and 9.3 °C and precipitation sums between 539 mm and 1905 mm. AHM indices for the whole natural distribution range of Norway spruce in Austria average 14.2 (max. 32). Under prospective climate change conditions in the 2080s (Ramirez and Jarvis, 2008), AHM indices for the same area will average 20.4 (max. 42.3). One test site (Porrau) is already located beyond current AHM ranges of the natural distribution area of Norway spruce in Austria.

Significant differences in growth performance (i.e. mean tree height at age 15) were found at trial sites among populations as well as for provenances at different trial sites (Schueler and Kapeller, 2010). The average survival of populations per site was 77%. Significant differences in survival were found among sites (Anova, $p < 0.01$), but not among populations.

Response functions of the two standard populations Schneegattern (ST1) and Murau (ST2), which have been tested at every site, are shown in Fig. 2. Tree heights for both populations increase with rising AHM-values. However, it seems that at very drought prone sites with high AHM-indices an upper level of maximum tree height has been reached. Therefore, a further increase beyond the maximum values under current climate cannot be expected under warming scenarios (Fig. 2, grey area). Most other populations have been planted at fewer sites and thus statistically valid parameter estimates were not possible (results for other populations are given in the online supplement in Table S2).

Populations were grouped in climate similarity clusters according the first four principal components, which account for a cumulative proportion of 97% of the variation in the climate parameters of provenance sites. A scatterplot of the first two principal components is shown in Fig. 3. This clustering generated a well-balanced distribution of populations according their climatic characteristics (Table 1, CLI 1 to CLI 9). AHM values are ranging from 11.3 (CLI 2) to 20.5 (CLI 9). When mapping the geographic regions which are enveloped by each of the nine climate based population clusters, it is shown that these regions partly overlap (in particular the groups 3, 4, 5 and 7), indicating that the alpine landscape provides strong climatic differences at geographically close distances, mainly due to different altitudinal levels (Fig. 4).

Grouping populations according to the national provenance region (Table 1, PR1 to PR 9), AHM values group vary between 12.7 (PR 2) and 24.3 (PR 8). The latter group however is excluded from detailed comparisons as it comprises only two populations (Table 1).

Additionally a simple altitudinal grouping based on three elevation belts based on Kilian et al. (1994) was used to cluster populations, resulting in clusters with AHM values ranging from 13.2 to 18.3 (Table 1, ALT 1 to ALT 3).

3.2. Climate response of population clusters

Regression parameters describe maximum attainable tree heights at age 15 and related climate optima. Maximum heights (parameter *a*), representative for populations from provenance regions, range from 554 cm to 600 cm, with AHM optima (parameter *b*) ranging from 31.5 to 34.5. Maximum heights of climate based population groups range from 500 cm to 601 cm, with AHM optima ranging from 30.7 to 35.7. Maximum heights of altitudinal clusters range from 479 cm to 596 cm, with AHM optima ranging from 29 to 33.4 (compare Table 2).

Mean values of all involved climate parameters show that there is a considerable differentiation among clusters, even after aggregation of data from many provenances (Table 1, see Appendix for details). The cluster group based on climate similarity showed a better differentiation than other groupings, especially at high AHM values (Fig. 5). At current mean AHM level, differentiation between clusters is rather small for all group structures, but increases with higher AHM indices.

3.3. Map of best clusters under future conditions

Cluster-specific estimates of potential tree heights at age 15 over the whole natural distribution range of Norway spruce in Austria show that Cluster 4, 7 and 9 reveal the best performance within different parts of the distribution range (Fig. 6, top). Other clusters did not show maximum heights at any point. Cluster 9 shows the best performance at the north-eastern margin of the distribution range under current climate conditions (Fig. 6, light grey dots). This cluster includes populations that origin from sites

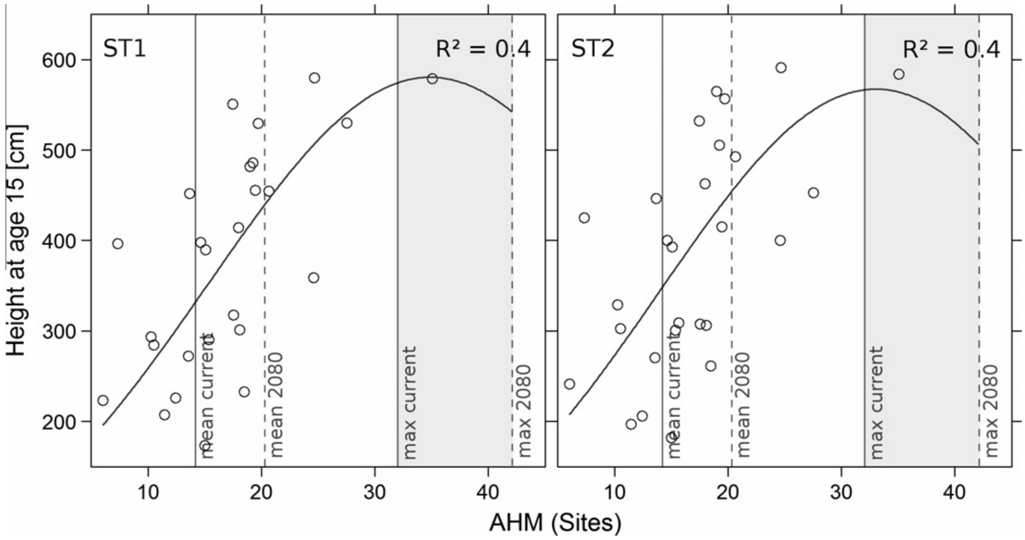

Fig. 2. Climate response functions for two standard provenances ST1 (Schneegattern) and ST2 (Murau). Each circle shows the 90% percentile of tree heights at annual heat-moisture (AHM) indices of respective planting sites. Vertical lines indicate mean and maximal AHM-values within Norway spruce species range in Austria for current (continuous line) and future (dashed lines) climates. Grey area denotes AHM-regions beyond current maximal limits.

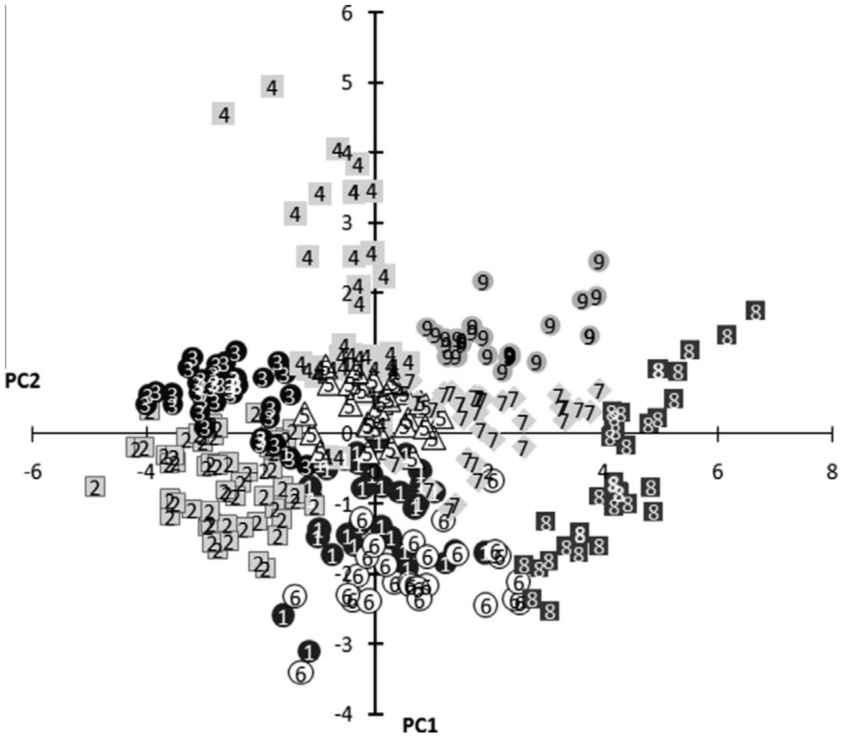

Fig. 3. The scatter plot of the first two principal components for all populations, accounting for 81% of the variation within provenance climates. Numbers in the plot refer to the climate similarity cluster (CLI 1 to CLI 9), which each population was attributed (according to a clustering method involving the first four principal components).

with the highest AHM indices (Table 1, CLI 9), i.e. where a relatively warm and dry climate is currently prevailing. A displacement of locally best performing populations under scenarios with increasing temperature is clearly observable. The share of forests where cluster 9 shows the best performance under climate change conditions increases with prospective climate warming until the 2050s and even more until the 2080s. Similarly, the area where cluster 7 performs best (Fig. 6, dark grey dots) increases, while the area where cluster 4 is most suitable (Fig. 6, black dots) decreases.

Our calculation of the percental change of height growth performance under current and future climate conditions indicates that rising temperatures and AHM values will cause an overall increase in productivity in Austria (Fig. 7). Only for some areas at the eastern edge of the distribution range, a further increase is unlikely. Here, Norway spruce already reached the maximum growth performance and a loss of productivity can be expected. Even an employment of locally best performing climate clusters at the eastern range limits does not translate into enhanced productivity. However, in most other areas, the choice of best climate cluster improves productivity significantly more than it could be expected from using populations from respective provenance region (Fig. 7).

Table 1
Mean climatic parameters of each group of populations of the various national provenance regions (PR*), climatic similarity clusters (CLI*) and altitudinal clusters (ALT*). MAT – Mean annual temperature, APS – Annual precipitation sum (mm), AHM – annual heat moisture index, Alt – Altitude (m), VP – vegetation period (days), GDD – growing degree days (>5.5 °C), WT – winter temperature (coldest month), nPop – number of populations aggregated in this cluster.

Clust	MAT	APS	AHM	Alt	VP	GDD	WT	nPop
PR1	3.9	1089	12.9	1423	182	774	−4.5	104
PR 2	5.2	1222	12.7	1135	198	1031	−3.8	42
PR 3	5.2	923	17.0	1170	202	1015	−3.6	46
PR 4	5.6	1203	13.8	1014	205	1116	−3.4	101
PR 5	6.9	916	18.7	833	224	1387	−2.3	23
PR 6	5.9	1178	13.9	1035	207	1204	−3.7	13
PR 7	8.1	1019	18.3	499	238	1658	−1.5	21
PR 8	8.8	771	24.3	450	247	1848	−1.4	2
PR 9	6.6	802	20.8	708	215	1332	−2.9	34
CLI1	6.0	1172	13.8	984	211	1195	−3.4	38
CLI 2	4.1	1269	11.3	1379	181	801	−4.4	64
CLI 3	3.8	1077	12.9	1441	180	757	−4.6	82
CLI 4	4.8	817	18.9	1216	198	958	−4.0	40
CLI 5	5.3	1068	14.4	1073	203	1035	−3.3	34
CLI 6	6.5	1451	11.5	850	217	1276	−2.7	29
CLI 7	7.0	967	17.7	782	225	1410	−2.6	33
CLI 8	8.4	970	19.7	448	242	1740	−1.4	36
CLI 9	6.3	802	20.5	748	212	1276	−3.1	31
ALT1	3.7	1100	13.2	1474	177	724	−4.6	77
ALT2	5.6	1082	15.2	1025	205	1108	−3.4	194
ALT3	7.9	1017	18.3	558	236	1630	−1.9	61

Table 2
Parameter estimates for each cluster. Clust – population cluster; *a* – parameter defining the maximum response (potential height at age 15 in cm); *b* – parameter defining the AHM value of the maximum response (climate optimum); *c* – parameter defining the variance of the distribution; p(*a*,*b*,*c*) – *p*-values of respective parameter estimation; r – correlation coefficient between observed and fitted data; Res. SE – Standard error of residuals.

Clust	*a*	p(*a*)	*b*	p(*b*)	*c*	p(*c*)	r	Res. SE
PR 1	553.9	<0.001	31.8	<0.001	17.3	0.001	0.69	104.0
PR 2	586.5	<0.001	31.6	<0.001	15.6	0.001	0.71	113.1
PR 3	578.7	<0.001	32.5	<0.001	16.6	0.002	0.7	105.2
PR 4	572.8	<0.001	34.5	<0.001	19.1	0.009	0.65	112.0
PR 5	588.6	<0.001	33.4	0.004	19.2	0.045	0.59	118.4
PR 6	559.8	<0.001	31.5	<0.001	16.8	0.005	0.64	122.0
PR 7	592.6	<0.001	33.1	<0.001	18	0.004	0.66	118.2
PR 8	591.5	0.028	34	0.298	22.4	0.547	0.5	169.3
PR 9	599.9	<0.001	33.4	<0.001	17.8	0.005	0.67	121.4
CLI 1	553.3	<0.001	30.7	<0.001	15.9	0.002	0.66	121.5
CLI 2	582	0.021	33.3	0.0515	17	0.078	0.69	104.7
CLI 3	500.3	<0.001	34.8	0.0106	20.6	0.05	0.61	100.5
CLI 4	562.6	<0.001	33.2	<0.001	18.9	0.004	0.66	106.6
CLI 5	566.5	<0.001	33.9	<0.001	18.6	0.005	0.68	107.5
CLI 6	558.9	<0.001	35.7	0.008	19.6	0.031	0.61	125.0
CLI 7	593.2	<0.001	32.1	<0.001	17.2	0.001	0.69	112.0
CLI 8	597.7	<0.001	33.4	<0.001	18.1	0.005	0.65	121.8
CLI 9	600.5	<0.001	33.7	<0.001	18.1	0.006	0.67	120.4
ALT1	479.2	<0.001	29	0.012	16.1	0.048	0.65	100.9
ALT2	576.6	<0.001	33.2	<0.001	18.2	0.003	0.67	109.1
ALT3	596.3	<0.001	33.4	<0.001	18.1	0.006	0.65	121.9

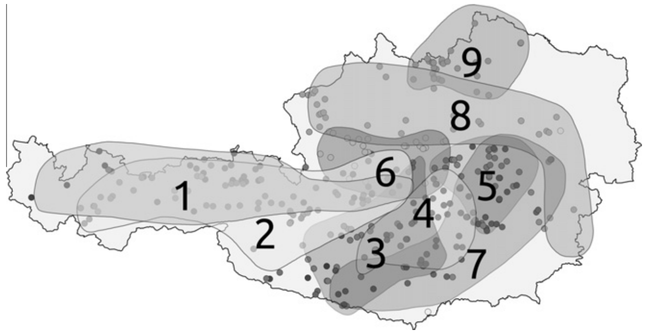

Fig. 4. Geographic location of climatic population clusters. Clusters are overlapping since they are based on geographic and climatic similarity. See climatic details of each climatic cluster in Table 1 (CLI1 – CLI9).

The mean change of tree heights from today until 2080 averaged for the provenance regions is given in Table 3. Using seeds according to best climate clusters is especially favorable in provenance regions which are located at more mountainous areas in western Austria (1, 2, 3, 4, 6), whereas provenance regions in the east (5, 7, 8, 9) will not benefit from this strategy (Table 3).

4. Discussion

4.1. Relevance of the study

Norway spruce as one of the most productive conifers in Central Europe is expected to suffer significantly from ongoing climate change (Kölling, 2007), leading to a strong reduction of spruce forests either by active conversion management or by intensifying disturbance regimes accompanied by decreasing profitability of forest management (Hanewinkel et al., 2010). Although quantitative genetic diversity and productivity of spruce have been analyzed in several national and range-wide provenance trials (e.g. Giertych, 1976; Krutzsch, 1992; Collignon et al., 2002; Liesebach et al., 2010), only few and regionally restricted analysis of the intraspecific variation in climate response have been made (e.g. Matyas, 1994; Schmidtling, 1994; Liesebach et al., 2001; Gömöry et al., 2011). Although the present study sets focus on populations of the eastern Alps and the Bohemian Massif in Austria, some results can be generalized beyond the Austrian border. Firstly, the Norway spruce test series of 1978 comprised a huge number of provenances from locations that cover nearly the complete climatic distribution of spruce in Central Europe (Fig. 1). Secondly, although the provenances origin from a relatively small part of the natural range of Norway spruce, they cover the three main refugial lineages which build the basis of all natural Norway spruce populations in Central and Western Europe. With various molecular markers the long population history of these lineages can still be observed (e.g. Maghuly et al., 2006; Mengl et al., 2009; Konrad et al., 2011). These two facts suggest that if quantitative genetic variation in climate response exists in Norway spruce it should be visible within our dataset. Thirdly, the provenance trial series has been established along a wide gradient of climate conditions ranging from 2.6 °C to 9.2 °C and annual precipitation values from 535 mm to 2392 mm, thus covering not only a large part of current Norway spruce habitats (Fig. 1), but also extends into sites at the warm and dry edge of its distribution, making it highly suitable to analyze the potential response to a changing climate.

In the present study, tree height at age 15 was considered as a proxy for productivity, because at this age no management interventions have shaped growth performance. Correlation of this juvenile height with measurements of d.b.h. at age 31 at five sites that are still under observation revealed significant juvenile-age correlations with coefficients between 0.19 and 0.83 for the different sites (Table 4). The differences are mainly due to the diverse forest management interventions after age 15.

4.2. Implications for climate change adaptation

The two main intentions of climate change adaptation in forest management are (i) to mitigate negative effects of maladaptation

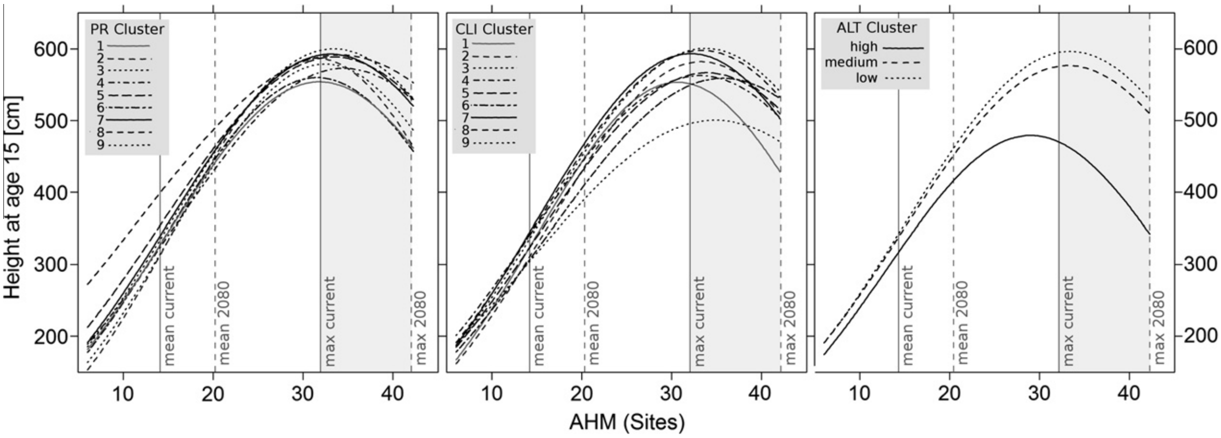

Fig. 5. Fitted Gaussian functions to the 90% percentiles of all populations belonging to certain clusters to site AHM. These percentiles were calculated from single tree heights for each population and test site. Left: Clusters of national provenance regions (PR1 – PR9). Center: Climate similarity clusters (CLI1 – CLI9). Right: Altitudinal clusters (ALT1 – ALT3). See climatic details for each cluster in Table 1 and respective parameter estimations in Table 2. Vertical lines indicate mean and maximal AHM-values within Norway spruce species range in Austria for current (continuous line) and future (dashed lines) climates. Grey area denotes AHM-regions beyond current maximal limits.

to changing climate and (ii) to maximize potential positive effects of increasing productivity. Which of the two has priority depends on the local climatic conditions of respective planting sites.

Most regions of Austria are still providing favorable heat-moisture conditions for growing *Picea abies* and seem to be able to tolerate further increase in temperature. Response curves of all population groups used in this study indicate that for most parts of Austria Norway spruce has not reached an upper heat-moisture limit yet. It can be assumed that rising temperatures will lead to increasing tree growth and forest management may benefit from global warming. Ninety percent of the Norway spruce occurrences in Austria have AHM-indices below 21.8. Hence, most of Austrian forestry might not primarily aim at mitigating negative effects, but instead seek to utilize potential positive effects on tree growth. The choice of appropriate seed material is one crucial decision for that purpose.

However, we detected locations at the eastern range limit of the natural Norway spruce distribution, where increased AHM does not translate into higher productivity. Here, under very dry conditions (compared to Austrian average) we cannot assume any Norway spruce populations to benefit from climate warming. The advantages of a long vegetation period, late frost events in autumn and higher photosynthetic activity are outweighed by insufficient water supply and related drought events. Ultimately, these unfavorable conditions will make Norway spruce vulnerable to damaging forest pests and insects. Our study shows that at such warm and dry areas, seeds of local provenances might generally be a good choice, since there were no other populations available, which had the chance to adapt to even drier climates. Populations from dry regions perform best at dry sites due to former adaption processes. Nevertheless, even populations adapted to dry climates will suffer from ongoing temperature increase, if we assume that further adaptation processes are too slow to keep up with climate change. In regions at the edge of the climatic distribution range it will be especially important to use appropriate genetic material to mitigate negative effects of climate change.

Studies estimating potential tree height and volume of conifers under climate change conditions in North America reveal considerable productivity losses under very warm and dry climate conditions. Wang et al. (2006) for example predict productivity of *Pinus contorta* in British Columbia to decline by −9% until 2087 (instead, +23% increase could be achieved if optimal seed sources were deployed). O'Neill et al. (2008) estimated the production decline for *Pinus contorta* in some southern areas of British Columbia as high as up to -70% by 2085. Andalo et al. (2005) found significantly lower productivity in seedlings of *Picea glauca* in Quebec, when planted at sites with an annual mean temperature by 4 °C higher and precipitation by 10% higher than at the site of origin. Other examples of productivity loss at warmer or dryer planting sites can be found for *Abies balsamea*, *Larix laricinia* and *Pinus banksiana* (Carter, 1996) or *Pseudotsuga menziesii* (Griesbauer et al., 2010). In contrast, although several test sites of the Austrian provenance test with Norway spruce are located at the edge of its natural distribution range or even beyond, we mainly found an increase of tree height under conditions of climate change. The rate of increase, however, decreases at sites with initially high AHM values and stagnates at high levels.

Results of the present study concern only climatic effects. For successful cultivation of *Picea abies* in future, we suspect other limiting factors including insect pest (e.g. European spruce bark beetle, small spruce fly) to be essential in combination with climate parameters. Such factors might very well inhibit an increase of productivity, even at sites which were climatically advantaged regarding rising temperatures and prolonged vegetation periods.

The most productive and promising population groups for future climatic conditions as represented by the scenario data in our study origin from the Bohemian Massive (climate cluster 9), the south-eastern fringe of the Alps (climate cluster 7) and the Northern Alpine foreland (climate cluster 8). The origin of these three clusters depicts today the warmest and driest regions of the natural spruce distribution in Austria, suggesting that local adaptation to past and current climate can be used as good approximation for a qualification to the conditions of climate warming. A main part of this local adaptation is very likely due to an extended growing season in these warmer regions.

In addition to the environmental differences among regions, provenances of the climate clusters 7 and 9 origin from regions with a different phylogenetic history. Within the present study, we have not used molecular markers to analyze the genetic structure. However, a very recent analysis of mitochondrial and nuclear DNA using 2800 spruce samples from the national forest inventory showed that populations from the Bohemian Massive (climate cluster 9), but also from the south-eastern fringe of the Alps (more or less climate cluster 7) differ significantly from Alpine populations (Mengl et al., 2009; Konrad et al., 2011), suggesting that population history also might have played a role in quantitative genetic variation and climate response. Already, Collignon et al. (2002) showed that populations of the Hercynian-Carpathian

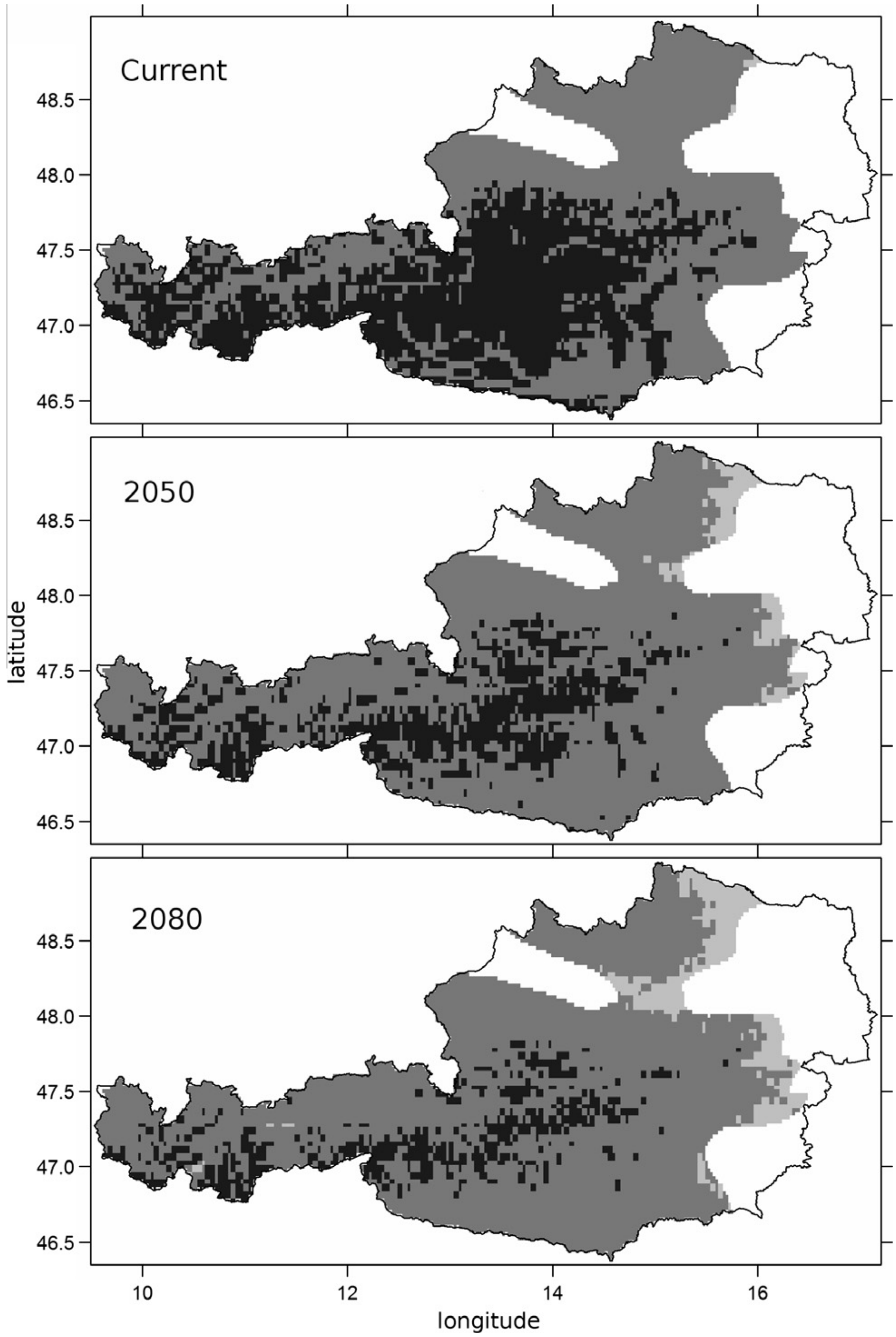

Fig. 6. Map of Norway spruce distribution range in Austria. Greyscale at each grid point indicates the population cluster with maximum potential tree heights at age 15 according to local AHM indices under (i) present climate conditions (top), (ii) for prospective AHM indices for the 2050s (center) and (iii) prospective AHM indices for the 2080s (bottom). Square colors refer to provenance clusters: Black = cluster 4, dark grey = cluster 7, light grey = cluster 9.

domain show on average a better growth performance than provenances from the Alpine domain, although both domains partly overlap and the Hercynian-Carpathian domain must be divided into two phylogenetic clusters according to more recent studies (Tollefsrud et al., 2008).

4.3. Statistical analysis and climate parameter

Several mathematical functions have been used so far for modeling climate response of tree populations among which quadratic functions have gained most attention recently (Matyas, 1994; Rehfeldt et al., 2002) for their simple application without complicate assumptions. Rehfeldt et al. (1999) state that other functions than quadratic that are asymptotic at zero and can be either asymmetrical or symmetrical were the most appealing conceptually. Weibull functions have also successfully been applied to describe climate response (Rehfeldt et al., 2003, 2008). However, the Weibull function requires four different parameters and therefore, assumptions about symmetry and inflection points. Especially if the empirical data basis is scarce, parameterization will either fail

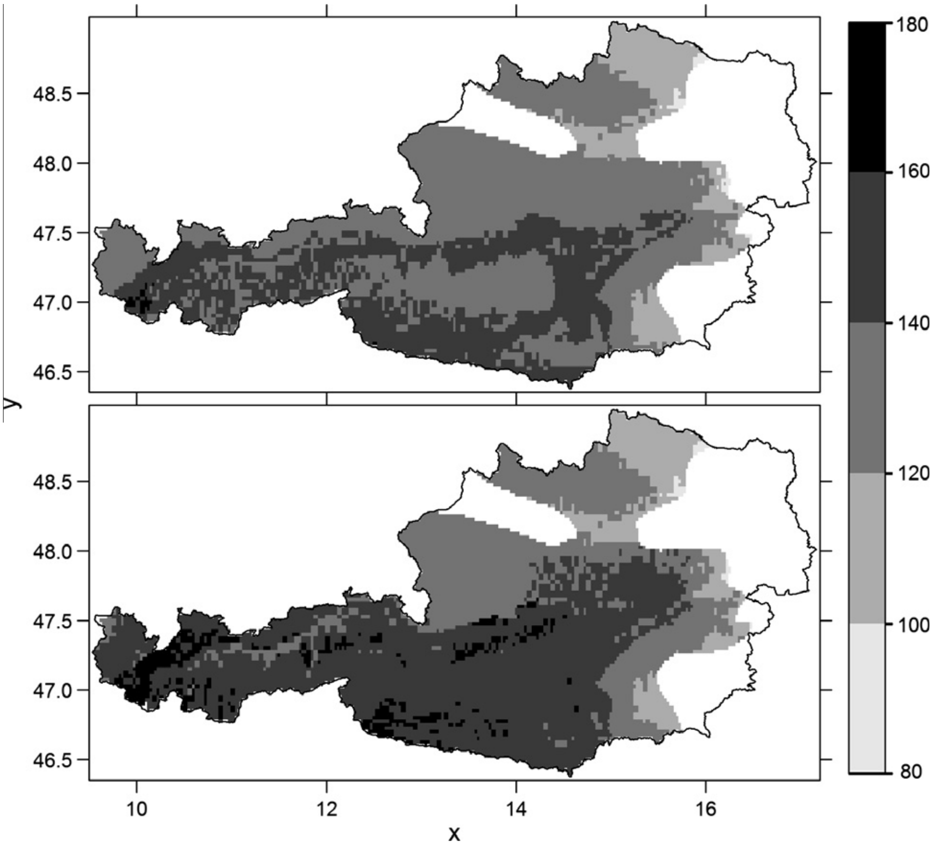

Fig. 7. Map of Norway spruce distribution range in Austria. Greyscale at each grid point indicates the percental change of estimated tree heights from current conditions until the 2080s given that (i) seed material of respective national provenance regions are used (top) or (ii) seed material of locally best climate clusters (as in fig. 6) are used (bottom). Level bar at the right side gives respective percental change indicated by greyscale levels. A colorized version of this figure is available as online supplement (Fig. S1).

Table 3
Percental change of average tree heights for national provenance region. PR – national provenance region; PR_2080 – change until 2080 using seeds of same provenance region; CLI_2080 – change until 2080 using seed material of locally best climate cluster; Diff – Difference between these two strategies.

PR	PR_2080	CLI_2080	Diff
1	139.6	147.7	+8.1
2	145.1	155.9	+10.8
3	143.3	153.3	+10
4	130.1	139.1	+9
5	123.0	124.6	+1.6
6	141.5	148.1	+6.6
7	122.3	124.2	+1.9
8	101.7	100.9	−0.8
9	120.2	121.5	+1.3

Table 4
Pearson's correlation coefficients between tree heights at age 15 and d.b.h. at age 31 of population means for five sites, which are still under observation. r – Pearsons correlation coefficient; p – p-value of correlation; df – degrees of freedom.

Site	r	p	df
9	0.4	0.06	20
10	0.61	0.001	23
23	0.38	0.064	22
39	0.83	<0.001	17
40	0.19	0.42	17

or provide weak parameter estimations. If data cannot fully sample a broad climatic range (at best the whole fundamental niche) of each population, too many assumptions about the shape of response curves have to be made and eventually may not be supportable (Rehfeldt et al., 1999). For data with skewed distributions within upper and lower limits, the Beta-distribution function has been proposed as alternative by Austin et al. (1994). Gaussian normal distribution functions have received less attention in recent climate-response modeling, though species distributions along environmental gradients are generally considered to be Gaussian curves (Gauch and Whittaker, 1972). Methods of fitting data to Gaussian distributions are straightforward and parameter estimates can easily interpreted (Gauch and Chase, 1974; Oksanen et al., 2001).

In our dataset, a linear relationship could as well be assumed from plotting tree heights at age 15 of single populations against climatic parameters as in Fig. 2. Statistically, a simple linear model could have been supported as well, though with a slightly lower correlation coefficient *r* (0.64) and higher standard error of residuals (111.7). Moreover, it is biologically more meaningful to assume a nonlinear Gaussian niche model, since the current distribution of Norway spruce shows, that an upper climatic growth limit exists, even it is not completely reached in the study area (yet).

Annual heat-moisture index (AHM) (Wang et al., 2006) was selected as predictor variable as it integrates temperature and precipitation into one single parameter and better reflects evapotranspiration (related to temperature) and soil moisture than precipitation and temperature alone (Wang et al., 2006). Within a previous study (Schueler and Kapeller, 2010) we analyzed the correlation of various climate parameters to the average growth data and found annual measures of temperature, precipitation or AHM as the most important factors for height growth. This is mainly because all test sites of the present study are located within a geographically small region along a strong environmental gradient which is mainly shaped by altitude. Thus, strong correlations exist between the various climate parameters. In addition, the sensitivity of Norway spruce to monthly measures of temperature and/or precipitation strongly depends on the respective environment: for example, in lower altitudes summer precipitation is positively and temperature negatively correlated to annual increment, whereas in higher altitudes summer precipitation is negatively and summer temperature positively correlated to annual growth (Mäkinen et al., 2002). Therefore, we focused on simple annual measures of AHM as an appropriate predictor for modeling tree heights, growth rates or drought tolerance. However, in case of strongly varying soil characteristics such as water holding capacity, AHM may not be sufficient to characterize ecological gradients. Our study did not include other environmental factors, which are considered as essential in cold and mountainous environments, e.g. bud burst (Søgaard et al., 2008) or frost hardiness (Johnsen and Skroppa, 2000). Obviously, such traits should be considered as well, if profound seed recommendations for any given planting site are desired.

5. Conclusions

National provenance regions in Austria have been delineated according to natural forest types, climate and geomorphological characteristics. In combination with altitudinal belts these regions are used for seed transfer guidelines. This rather static concept should be complemented with information about genetic variation. Regarding climate change, seed transfer guidelines should contribute to both mitigate negative effects of maladaptation and make most of potential positive effects such as increasing productivity. Which of the two approaches has priority depends on the current and future climatic conditions of the respective planting sites. In this study it has been shown that there is a large genetic variation among Norway spruce populations in Austria. Natural adaptation processes have led to varying climatic optima even within small geographic distances. This variation in climate response can be used to improve the selection of appropriate seed sources in a changing climate.

Further analysis of intraspecific genetic variation will be necessary and essential in adapting forests to climate change. Differentiation in climate response among populations is increasing under warmer and dryer conditions. Therefore, the choice of appropriate seeds improves productivity already under current climates and will even be more important in future.

Acknowledgements

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Appendix A

See Table A1.

Appendix B. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.foreco.2012.01.039.

Table A1

Details of parameter estimation including confidence regions of estimates and results of Shapiro–Wilk normality test and Runs-test of independence of residuals. Clust – population cluster; *a*, *b*, *c* – parameter estimates; _low and _up – lower and upper limits of confidence intervals; _SE – standard error of parameter estimation; _p – p-value of parameter estimation; r – correlation coefficient between observed and fitted data; Res. SE – Standard error of residuals; S-W(p) – p-value of Shapiro–Wilks; Run(p) – p-value of runs test.

Clust	*a*	a_low	a_up	a_SE	a_p	*b*	b_low	b_up	b_SE	b_p	*c*	c_low	c_up	c_SE	c_p	r	Res. SE	S-W (p)	Run (p)
PR1	553.9	347.8	760.0	66.8	<0.001	31.8	13.8	49.8	5.8	<0.001	17.3	2.8	31.7	4.7	0.001	0.69	104.0	0.702	0.090
PR2	586.5	364.6	808.5	71.5	<0.001	31.6	15.4	47.7	5.2	<0.001	15.6	2.6	28.5	4.2	0.001	0.71	113.1	0.654	0.230
PR3	578.7	352.4	805.0	32.5	<0.001	32.5	13.7	51.2	6.0	<0.001	16.6	1.7	31.6	4.8	0.002	0.7	105.2	0.822	0.310
PR4	572.8	270.1	875.5	98.2	<0.001	34.5	6.1	63.0	9.2	0.001	19.1	−1.6	39.8	6.7	0.009	0.65	112.0	0.334	0.090
PR5	588.6	300.0	877.2	91.6	<0.001	33.4	1.8	65.1	10.1	0.004	19.2	−8.9	47.3	8.9	0.045	0.59	118.4	0.810	0.508
PR6	559.8	307.5	812.2	80.9	<0.001	31.5	11.3	51.8	6.5	<0.001	16.8	−0.1	33.7	5.4	0.005	0.64	122.0	0.760	0.676
PR7	592.6	323.3	861.9	87.3	<0.001	33.1	10.1	56.1	7.5	<0.001	18.0	0.4	35.5	5.7	0.004	0.66	118.2	0.989	0.014
PR8	591.5	−109.4	1292.3	146.8	0.028	34.0	−95.3	163.3	27.1	0.298	22.4	−135.6	180.5	33.1	0.547	0.5	169.3	0.166	0.361
PR9	599.9	311.1	888.6	93.3	<0.001	33.4	9.2	57.6	7.8	<0.001	17.8	−0.2	35.9	5.8	0.005	0.67	121.4	0.153	0.171
CLI1	553.3	336.8	769.8	69.9	<0.001	30.7	13.8	47.5	5.4	<0.001	15.9	2.0	29.8	4.5	0.002	0.66	121.5	0.695	0.031
CLI2	582.0	−146.7	1310.6	233.6	0.021	33.3	−17.0	83.5	16.1	0.052	17.0	−11.6	45.6	9.2	0.078	0.69	104.7	0.634	0.211
CLI3	500.3	210.8	789.8	92.2	<0.001	34.8	−3.8	73.4	12.3	0.011	20.6	−10.3	51.6	9.9	0.050	0.61	100.5	0.353	0.662
CLI4	562.6	317.7	807.4	79.4	<0.001	33.2	9.3	57.0	7.7	<0.001	18.9	0.3	37.5	6.0	0.004	0.66	106.6	0.885	0.090
CLI5	566.5	295.7	837.4	87.7	<0.001	33.9	8.6	59.3	8.2	<0.001	18.6	−0.2	37.4	6.1	0.005	0.68	107.5	0.765	0.123
CLI6	558.9	166.6	951.3	126.7	<0.001	35.7	−2.5	73.9	12.3	0.008	19.6	−6.9	46.1	8.6	0.031	0.61	125.0	0.319	0.171
CLI7	593.2	363.4	822.9	74.5	<0.001	32.1	13.6	50.7	6.0	<0.001	17.2	2.6	31.8	4.7	0.001	0.69	112.0	0.881	0.090
CLI8	597.7	310.4	884.9	93.2	<0.001	33.4	8.9	57.8	7.9	<0.001	18.1	−0.3	36.5	6.0	0.005	0.65	121.8	0.947	0.090
CLI9	600.5	302.2	898.9	96.4	<0.001	33.7	8.4	59.1	8.2	<0.001	18.1	−0.5	36.7	6.0	0.006	0.67	120.4	0.168	0.171
ALT1	479.2	160.2	798.3	102.3	<0.001	29.0	−4.1	62.1	10.6	0.012	16.1	−7.9	40.1	7.7	0.048	0.65	100.9	0.566	0.404
ALT2	576.6	325.3	827.9	81.5	<0.001	33.2	10.6	55.7	7.3	<0.001	18.2	1.0	35.5	5.6	0.003	0.67	109.1	0.779	0.090
ALT3	596.3	308.6	884.0	93.3	<0.001	33.4	8.8	57.9	8.0	<0.001	18.1	−0.4	36.6	6.0	0.006	0.65	121.9	0.904	0.090

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7.2 Appendix – Paper II

Schueler, S., Kapeller, S., Konrad, H., Geburek, T., Mengl, M., Bozzano, M., Koskela, J., Lefèvre, F., Hubert, J., Kraigher, H., Longauer, R., & Olrik, D. C. (2013). Adaptive genetic diversity of trees for forest conservation in a future climate: A case study on Norway spruce in Austria. *Biodiversity and Conservation*, *22*(5), 1151–1166.

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ORIGINAL PAPER

Adaptive genetic diversity of trees for forest conservation in a future climate: a case study on Norway spruce in Austria

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Abstract Genetic resources of forest trees are considered as a key factor for the persistence of forest ecosystems because the ability of tree species to survive under changing climate depends strongly on their intraspecific variation in climate response. Therefore, utilizing available genetic variation in climate response and planting alternative provenances suitable for future climatic conditions is considered as an important adaptation measure for forestry. On the other hand, the distribution of adaptive genetic diversity of many tree species is still unknown and the predicted shift of ecological zones and species' distribution may threaten forest genetic resources that are important for adaptation. Here, we use Norway spruce in Austria as a case study to demonstrate the genetic variation in climate response and to analyse the existing network of genetic conservation units for its effectiveness to safeguard the hotspots of adaptive and neutral genetic diversity of this species. An analysis of the climate response of 480 provenances, clustered into 9 groups of climatically similar provenances, revealed high variation among provenance groups.

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The most productive and promising provenance clusters for future climates originate from three regions that today depict the warmest and driest areas of the natural spruce distribution in Austria. Gap analysis of the Austrian genetic conservation units in the EUFGIS Portal suggests adequate coverage of the genetic hotspots in southern parts of Austria, but not in eastern and northern Austria. Therefore conservation measures and sustainable utilization of the valuable genetic resources in these regions need to be expanded to cover their high adaptive genetic variation and local adaptation to a warmer climate. The study shows that current conservation efforts need to be evaluated for their effectiveness to protect genetic resources that are important for the survival of trees in a future climate.

Keywords Forest genetic resources · Climate response · Intraspecific variation · Adaptation · *Picea abies* · Genetic variation

Introduction

The Convention on Biological Diversity recognizes genetic diversity as a key component of biodiversity together with the diversity of species and ecosystems (CBD 2002). Genetic diversity is being appreciated for its intrinsic value and its various benefits for ecological, economic, and social systems but the genetic diversity of wild species is often less regarded by policy makers and the human society as compared to the diversity of domesticated animals and plants. Communication of the value of genetic diversity requires understanding the processes that shape genetic diversity and demonstrating the importance of genetic diversity for the societal challenges of the future.

Forest ecosystems are strongly shaped by predominant forest tree species, which can be considered mainly as 'wild' plant species. Indeed, the selectively neutral genetic diversity of forest trees has been found to be affected primarily by population history and postglacial migration pattern (Petit et al. 2005), whereas adaptive genetic variation is rather driven by selection and local adaption (Savolainen et al. 2007). Adaptive genetic variation can be defined as a phenotypic trait that evolved through local adaptation in order to confer a tree the ability to survive in a given environment or to increase its fitness (Kremer et al. 2012). Because many tree species occur over a wide range of environments within their distribution range with different directions and intensities of selection, the variability of adaptive genetic traits is tremendous. In comparison with neutral genetic diversity, adaptive genetic variation generally shows higher levels of diversity and stronger differentiation on adaptive traits (Karhu et al. 1996; Kremer et al. 2010).

The value of adaptive genetic variation has been recognized in forest management, conservation biology and conservation genetics. For example, in forest management adaptive genetic variation has been used as a basis for the delineation of breeding zones and provenance regions in many countries (e.g. Crowe and Parker 2005; Hamann et al. 2011), and in conservation biology adaptive genetic variation is increasingly considered as an important factor in restoration projects to match phenotypes with given habitats (Bischoff et al. 2006; O'Brien et al. 2007). The high differentiation of adaptive genetic variation and its strong correlation to environmental variables gives it a paramount importance for developing adaptation strategies for forests to cope with climate change, which has been regarded one of the greatest challenges of the 21st century. Making good use of the variation in survival and growth response shown by different populations grown in various environments (Mátyás 1996; Rehfeldt et al. 1999; Wang et al. 2006) or phenotypic and phenological characters of seedlings (e.g. St. Clair et al. 2005; St. Clair and

Howe 2007) adaptation strategies have been developed for several tree species. However, long-term common garden experiments in strongly differing climates (e.g. Rehfeldt et al. 2001) are needed to understand the correlations between climate and adaptive traits, i.e. reaction norms and to develop adaptation schemes for single species. Such data are not available for many species and results of new experiments cannot be expected shortly and might be too late for management decisions in the present day. In particular, populations at the warmer distribution limit of many European species will be affected by climate change, because the climate habitats of these ecological zones are expected to shift north-eastwards (Thuiller 2003) with varying velocity for the various ecological zones (Loarie et al. 2009).

Beyond existing phenotypic variation and plasticity, future adaptation will also include genetic evolution from an initial reservoir of genetic diversity. Although adaptive genetic variation indicates per se the functional importance of genetic diversity in the current environment, it does not necessarily reflect all components of the genetic diversity that will be important in other or future environments (e.g. in the case of an emerging parasite, the genes that confer resistance to the host, if any, could have no other effect before the parasite appears and lie within the neutral diversity at that time). Population history, demographic events (e.g. bottlenecks) or isolation processes are other important factors which affect genetic diversity and leave imprints in both neutral and adaptive genetic variation. Thus, patterns of neutral genetic diversity as revealed by nuclear or plastid DNA analysis should be considered as additional basis for the conservation of forest genetic resources (e.g. Crandall et al. 2000).

In Europe, efforts for the conservation of genetic resources of forest trees are promoted by the European Forest Genetic Resources Programme (EUFORGEN). As part of EUFORGEN, the EUFGIS Portal (European Information System on Forest Genetic Resources) was developed for cataloguing dynamic conservation units of forest trees. Dynamic conservation of genetic diversity means that not only specific forest genetic resources are conserved, but that the evolutionary processes within the conservation units are safeguarded to maintain their potential for continuous adaptation (e.g. Eriksson et al. 1993).

The objective of the present study is to use Norway spruce (*Picea abies* [L.] Karst.) in Austria as a case study (1) to demonstrate the importance of genetic variation for adapting forests to climate change and (2) to evaluate whether the gene conservation network in Austria covers the hotspots of adaptive and neutral genetic diversity within the country.

Materials and methods

Genetic variation in climate response

To analyse intraspecific phenotypic variation regarding climate conditions, we used data from an Austrian Norway spruce provenance test (Nather and Holzer 1979). This provenance test includes 480 Austrian provenances and 60 provenances from other countries. The trial was established in 1978 with 5-year old seedlings planted on 44 sites across Austria in random block designs (Fig. 1). In 1988, survival and stem height of the young trees were measured after 10 years in the field.

Climate data for each test site and for the locations of the provenance origins were provided by the Central Institute for Meteorology and Geodynamics Austria (ZAMG). The relationship between tree growth and the climatic conditions at the trial sites was analyzed by means of uni- and multivariate regression analyses (Schüler and Kapeller 2010). For the analysis of climate-response functions, the annual heat-moisture index (AHM) according

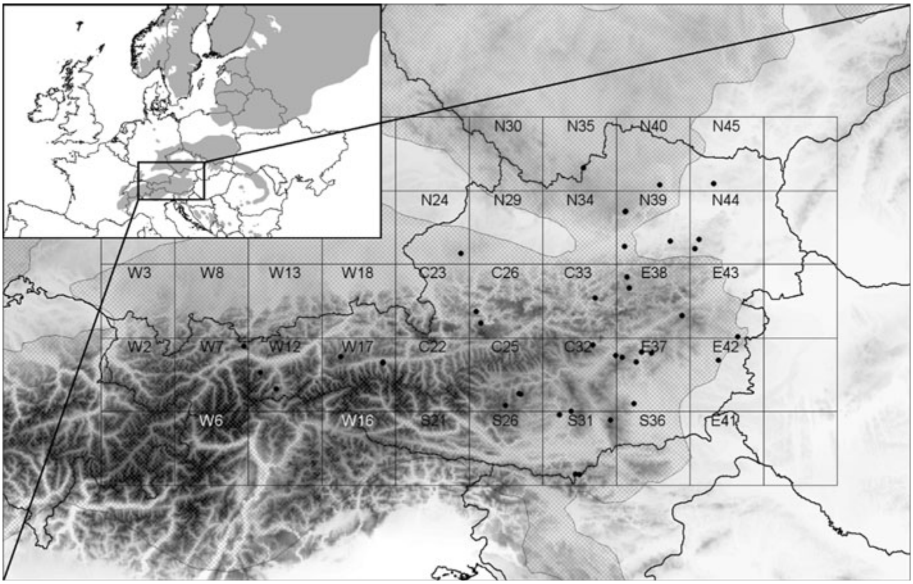

Fig. 1 Natural distribution range (*grey area* and *cross-diagonal shape*) of Norway spruce in Austria (EUFORGEN distribution map) and the setup of the present study. *Dots mark* the location of provenance trial sites and the *grid* indicates the regions for gap-analysis. *Each square* has a size of 60 × 60 km

to Wang et al. (2006) was selected as the most significant climate parameter, because it integrates mean annual temperature (MAT) and annual precipitation sums (APS) into one single parameter [AHM = (MAT + 10)/(APS/1,000)]. Further details of the current and future climate data used are described in Kapeller et al. (2012). Climate response functions were calculated for nine provenance clusters that were constructed according to the similarity of climate and geographical proximity (Kapeller et al. 2012). The climate response of the provenance clusters were modelled as a Gaussian response model using non-linear regression. Parameters of Gaussian function can be directly interpreted in an ecological meaningful way, where parameter *a* reveals the maximum response (potential tree height), *b* indicates the location of this maximum, i.e. the ‘climate optimum’ and *c* the variation of the distribution.

Neutral genetic variation

Twig samples of Norway spruce were collected during the 2007 Austrian Forest Inventory, for which the national territory of Austria is divided into 3.89 × 3.89 km grids and only forested grid points were sampled. Each sampled grid point consisted of four sampling plots, arranged in a quadratic way with a distance of 200 m between them. From each sampling plot with Norway spruce, twig samples were collected. Additional samples had been collected during the inventory period 2000–2002. A comprehensive sample of the Austrian Norway spruce populations was obtained using this approach. DNA was extracted using the DNeasy 96 Plant Kit (Qiagen). Subsequently, the mitochondrial *nad*1 marker described by Sperisen et al. (2001), and six nuclear microsatellite loci: WS0023.B03, WS00716.F13, WS0092.A19, WS0022.B15, WS0073.H08, and WS00111.K13 (Rungis et al. 2004) were facilitated for genotyping. PCR conditions were as described in the respective papers. Forward primers were labelled with WellRed dyes (Sigma-Aldrich) and fragment analysis was done on a CEQ 8000 capillary sequencer (Beckman Coulter). For the analysis of the *nad*1 intron region, both forward and reverse primers were dye-labelled and digested with *EcoR*V prior to capillary gel electrophoresis. In this way a total of 1,493 and 2,773 individual tree samples were genotyped for *nad*1 and nuclear microsatellite markers, respectively.

Gap analysis of the Austrian network of genetic conservation units

To assess how much of the adaptive and neutral genetic diversity is included in the current network of genetic conservation units in Austria, we performed a gap analysis (e.g. Maxted et al. 2008), in which the regional variation in neutral and adaptive genetic diversity was compared to the conservation measures undertaken. Due to different sampling strategies and intensities in our assessments of adaptive and neutral genetic diversity, we subdivided the Austrian territory in regular 60 × 60 km squares (see Fig. 1 for schematic presentation of the grid system). For each of these squares, we calculated measures of genetic diversity and the number of genetic conservation units. For adaptive genetic diversity in climate response, we considered the growth potential for populations in future climates. Thus, populations from provenance clusters with high productivity under futures climates were rated with 2, whereas populations from clusters with low growth potential in the future were rated with 1. For the regional index, we calculated the average of all provenances from the respective square obtaining an index I_{clim} between 1 and 2. For the measures of neutral genetic diversity we calculated the number of alleles (nuclear SSRs), respectively (haplotypes) as well as the unbiased heterozygosity (nuclear SSRs) and the unbiased haplotype diversity using GenAlEx 6.0 (Peakall and Smouse 2006). In order to correct for the unequal samples sizes within regions a rarefaction analysis was performed with HP-Rare 1.0 (Kalinowski 2005) using 18 genes per region fur nuclear SSRs and 15 genes for haplotypes.

Results

Genetic variation in climate response

The analysis of tree height at age of 15 years demonstrated that growth performance is strongly affected by climate conditions at both the trial sites and the provenance origins. Due to its mountainous landscape character, strong variation of climatic conditions can be found within small geographic ranges in the Eastern Alps. Climate conditions of the provenance origins span between 2.6 and 9.3 °C in mean annual temperatures and between 539 and 1,905 mm in precipitation sums.

Non-linear regression of the provenance performance (tree height) to the annual-heat-moisture index (AHM) resulted in significant models with correlation coefficients r of 0.61 to 0.69 between observed and fitted values for the different provenance clusters. The parameter estimates of the nine clusters varied considerably: maximum tree heights of provenance clusters are ranging from 500 to 601 cm, with AHM optima (parameter b) from 30.7 to 35.7 (Fig. 2). Climate responses varied within a relatively small range among the clusters from Austria under the current climate. However, the range of the variation will become substantial under climates predicted for the future. Further details of the analysis can be found in Kapeller et al. (2012). In our study, the most productive and

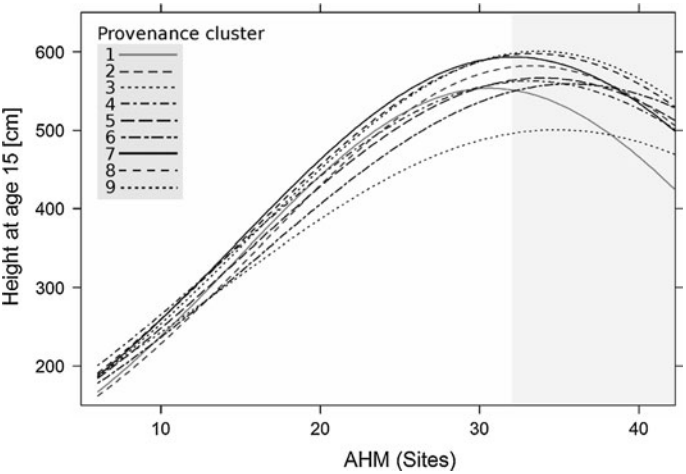

Fig. 2 Climate response functions of Norway spruce provenance clusters. The Gaussian functions resulting from fitting provenance cluster heights (90 % percentile) to site annual heat moisture index AHM. The *grey area* denotes AHM-regions beyond current maximal limits. For further details see Kapeller et al. (2012)

promising provenance clusters for future climate conditions (Fig. 3) origin from the Bohemian massif (provenance cluster 9), the eastern fringe of the Alps (provenance cluster 7) and the northern alpine foreland (provenance cluster 8).

Neutral genetic variation

Considerable differences were found in the average number of nuclear microsatellites alleles among regions ranging from 9.5 up 20.5 (Table 1). When corrected for unequal sample size by rarefaction analysis with 18 sampled genes (Kalinowski 2005), the differences among regions were much smaller, ranging now from 8.26 to 9.47. However, in both cases—corrected and uncorrected—we found the highest number of alleles within northern, eastern and south-eastern regions of Austria (Fig. 4; Table 1). Western and central Austrian regions show much lower allelic diversity. The analysis of mitochondrial DNA revealed a very similar picture revealing the highest numbers of haplotypes and haplotype diversity in the northern and eastern regions (Fig. 5) for corrected and uncorrected measures.

Gap analysis of genetic conservation units

In Austria, 164 forest areas have been declared as genetic conservation units for Norway spruce. These units cover between 5 and 470 ha (average size: 40 ha; 6,470 ha in total) at elevations from 360 up to 2,100 m a.s.l. The highest number of units can be found south of the alpine main ridge: there about one-third of the units can be found within a relatively small area (Fig. 6). Other hotspots of genetic conservation are located in the western part of Austria (approximately within the Lechtaler Alps, Rofan, and Grossglockner massif), whereas only one hotspot can be found in the Eastern Alps (approximately within the Ennstaler Alps). The Bohemian massif (i.e. north of the Danube valley) and the eastern fringe of the Alps have only very few units, although many populations here can be

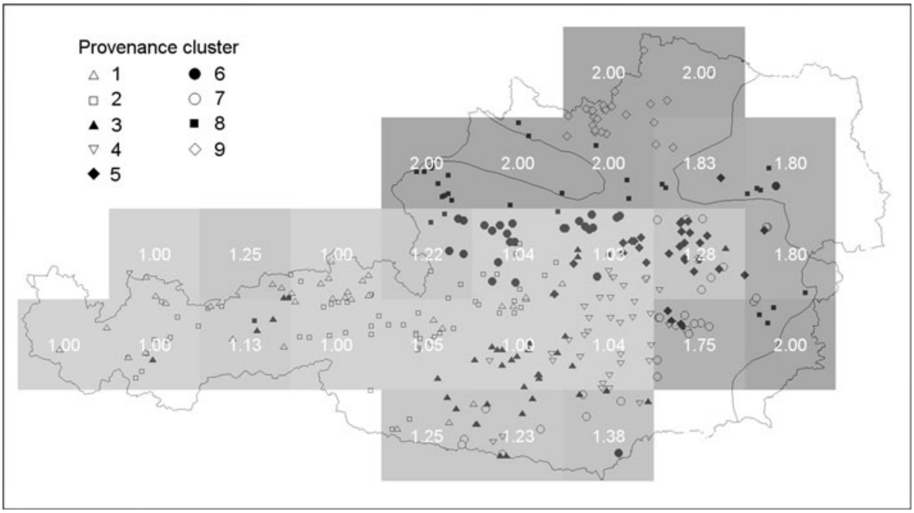

Fig. 3 Distribution of provenances tested within the Austrian Norway spruce provenance test 1978 (Kapeller et al. 2012), the allocation of provenances (marked by *different symbols*) to nine provenance clusters (see Fig. 2) and the regional Index I_clim summarizing the occurrence of provenance clusters within regions. The *greyscale* indicates the suitability of provenances for future climate conditions (the *darker* the better)

considered autochthonous given that Norway spruce started the colonisation of the Alps from these regions.

Based on the variation in climate response, populations from the northern Alpine foreland (provenance cluster 8), the Bohemian massif (provenance cluster 9), and the eastern fringe of the Alps (provenance cluster 7) have a higher growth potential in the future. These are actually those regions (Fig. 4), where so far only very few units were established. A very similar picture can be obtained when comparing the distribution of neutral genetic diversity with the location of genetic conservation units: although the high nuclear diversity in the southern regions S26 and S31 is well-covered by the high number of units, only few conservation units exist within the most variable eastern and northern regions but also in the southern region S36 indicating a distinct gap in the current conservation network. The mismatch between the putative high value of populations for adaptation measures, neutral genetic diversity and the low number of genetic conservation units in the eastern and northern regions is shown in Fig. 7. In order to weight up the different conservation goals in case of limited conservation resources, i.e. whether an improved conservation strategy should focus rather on adaptive genetic variation or on preserving neutral nuclear or mitochondrial DNA variation, correlations between the different measures of genetic variation were made across regions. Highly significant and strong correlations were found between the index of suitability for future climates and the various measures of mitochondrial DNA variation (Table 2). However, from the measures of nuclear DNA variation, the total number of alleles and number of rare alleles were not correlated to any other variation measure, while the unbiased heterozygosity of the nuclear microsatellites was correlated to the number of haplotypes and haplotype diversity.

Table 1 Measures of genetic diversity, suitability of local Norway spruce provenances for future climates according to the provenance experiment and climate response, and the number of genetic conservation units of Norway spruce in different regions of Austria

Region	Grid	I_clim	N_ht	n_ht	nc_ht	nr_ht	uh_ht	N_ssr	n_ssr	nc_ssr	nr_ssr	UHe_ssr	N_unit
West	2	1.00	32	4	2.4	0.002	0.181	72	17.17	9.01	0.080	0.866	4
	3		10	2	2.0	0.000	0.200	13	9.50	8.26	0.040	0.867	1
	6**							1	1.67	1.67	0.060	0.667	0
	7	1.00	57	2	1.3	0.000	0.035	124	17.67	8.73	0.050	0.854	12
	8	1.00	17	2	1.9	0.000	0.118	34	14.33	8.65	0.030	0.857	4
	12	1.13	40	6	3.7	0.010	0.487	70	16.00	8.78	0.030	0.862	1
	13	1.25	15	2	2.0	0.000	0.133	26	13.50	8.56	0.030	0.854	0
	16		15	1	1.0	0.000	0.000	33	13.33	8.48	0.040	0.853	0
	17	1.00	51	1	1.0	0.000	0.000	102	17.67	8.65	0.050	0.853	6
	18	1.00	35	3	1.9	0.000	0.113	70	16.17	8.93	0.070	0.882	11
South	21	1.25	50	4	1.9	0.001	0.118	109	17.83	8.79	0.050	0.856	16
	26	1.23	66	6	3.3	0.012	0.350	146	19.50	9.21	0.1	0.871	25
	31	1.38	48	6	3.8	0.004	0.582	97	19.00	9.34	0.08	0.873	18
	36		41	6	4.2	0.211	0.596	55	17.17	9.33	0.05	0.876	2
Central	22	1.05	67	2	1.2	0.000	0.030	116	16.50	8.71	0.02	0.852	12
	23	1.22	55	2	1.3	0.000	0.036	106	18.83	8.77	0.07	0.851	7
	27	1.00	87	6	2.6	0.001	0.235	153	18.00	8.74	0.04	0.854	4
	28	1.04	66	4	2.7	0.199	0.397	157	18.83	8.71	0.06	0.851	2
	32	1.04	85	6	3.2	0.078	0.476	179	20.00	8.93	0.1	0.859	8
	33	1.03	121	9	4.4	0.097	0.660	220	20.50	9.25	0.08	0.872	15

Table 1 continued

Region	Grid	I_clim	N_ht	n_ht	nc_ht	nr_ht	uh_ht	N_ssr	n_ssr	nc_ssr	nr_ssr	UHe_ssr	N_unit
North	24	2.00	31	4	2.8	0.000	0.295	43	15.67	9.06	0.11	0.856	0
	29	2.00	21	7	6.0	0.664	0.714	39	16.17	9.25	0.17	0.871	0
	30	0.00	10	4	4.0	0.000	0.644	15	12.17	9.43	0.15	0.880	0
	34	2.00	39	5	4.0	0.004	0.668	68	16.83	9.06	0.05	0.862	1
	35	2.00	24	6	5.1	0.034	0.732	41	15.00	9.1	0.01	0.867	3
	39	1.83	26	9	6.4	0.794	0.794	61	17.67	9.21	0.1	0.869	3
	40	2.00	26	7	5.3	0.484	0.748	57	16.50	8.8	0.06	0.851	1
	44*	1.80	8	4	4.0	0.000	0.857	10	10.00	9.47	0.14	0.883	0
	45*		7	5	5.0	0.000	0.905	9	8.33	8.33	0.1	0.864	0
East	37	1.75	87	7	4.1	0.029	0.546	142	18.67	9.09	0.06	0.865	0
	38	1.28	131	9	5.1	0.037	0.756	235	20.67	9.11	0.07	0.866	3
	41**							2	3.33	3.33	0.15	0.861	0
	42	2.00	37	7	5.2	0.031	0.692	53	16.83	9.21	0.07	0.869	0
	43	1.80	88	9	4.7	0.006	0.676	112	18.50	9.22	0.07	0.867	5

I_clim regional index of suitability of provenances for future climate, *N_ht* number of samples for mitochondrial analysis, *n_ht* number of haplotypes, *nc_ht* number of haplotypes corrected for sample size by rarefaction analysis, *nr_ht* number of private haplotypes, *uh_ht* unbiased haplotype diversity, *N_ssr* number of samples for the nuclear analysis, *n_ssr* number of nuclear SSR alleles, *nc_ssr* number of SSR alleles corrected for sample size by rarefaction analysis, *nr* number of private SSR alleles, *UHe_SSR* unbiased expected heterozygosity of the SSRs, *N_unit* number of dynamic gene conservation units

* These mitochondrial diversity measures should be treated carefully, because they were not corrected with rarefaction analysis due to the low sample size (n_ht = nc_ht), ** similar for nuclear SSRs

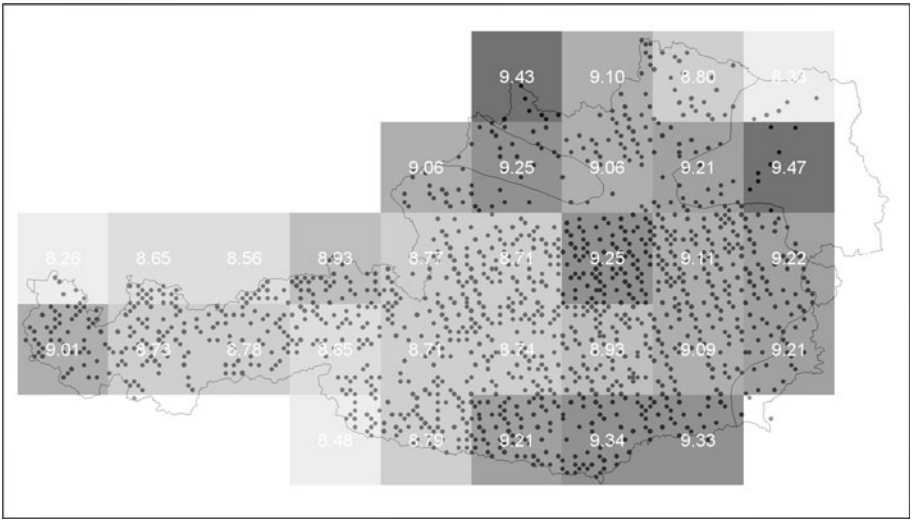

Fig. 4 Number of alleles of 6 nuclear microsatellites (nc_ssr) analysed on 2,773 samples of Norway spruce from all over Austria (*dots mark* the sampling locations) corrected for unequal sample size by rarefaction analysis with 18 genes. The *greyscale* indicates the corrected number of alleles within a region

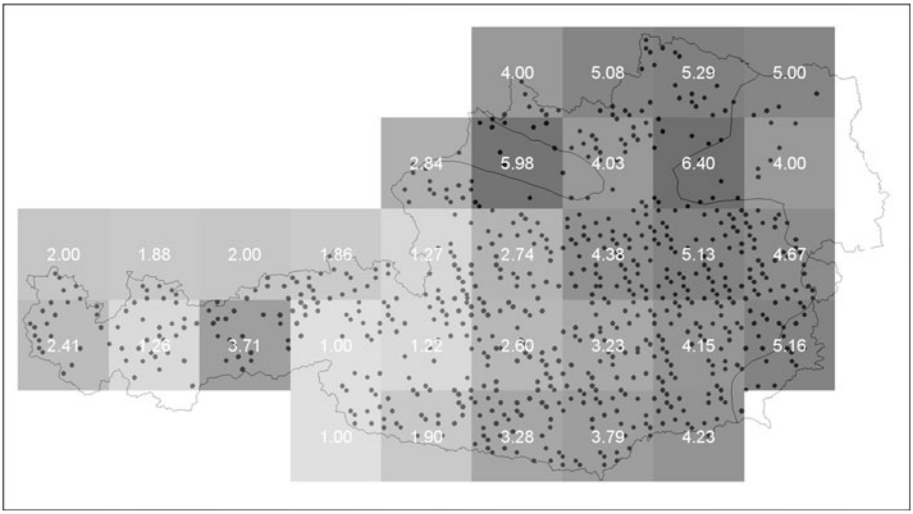

Fig. 5 Numbers of mitochondrial DNA haplotypes (nc_ht) analysed on 1,493 samples of Norway spruce from all over Austria (*dots mark* the sampling locations) corrected for unequal sample size by rarefaction analysis with 15 genes. The *greyscale* indicates the corrected number of haplotypes within a region

Discussion

Genetic conservation of Norway spruce and its population history in Austria

Conserving biodiversity within forest stands of Norway spruce seems contradictory to many people (Häusler and Scherer-Lorenzen 2002), because in Central Europe Norway

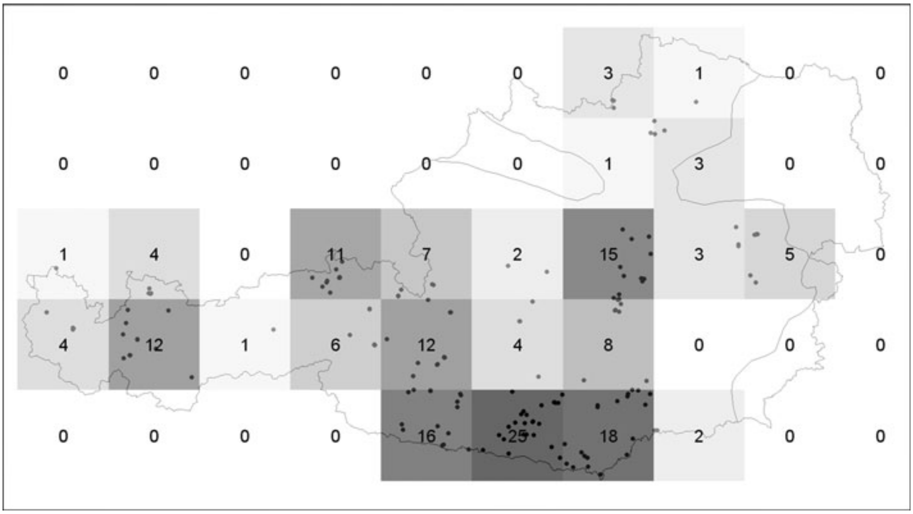

Fig. 6 Spatial distribution of genetic conservation units (*dots*) of Norway spruce in Austria. The *greyscale* indicates the sum of genetic conservation units within each region

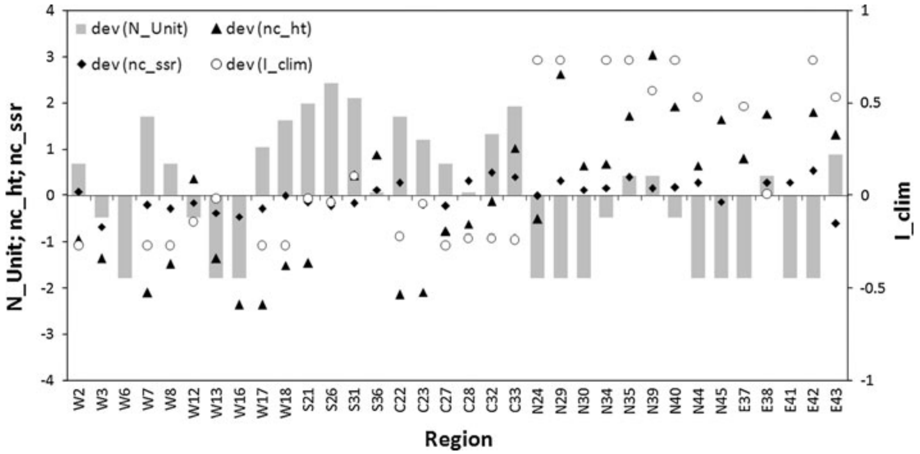

Fig. 7 Comparison between the regional genetic diversity and the number of genetic conservation units (N_unit) within the respective region (see Fig. 1 for region codes). All diversity indices are given as deviation from the average of all regions [e.g. dev (nc_ssr) = $\text{nc\_ssr}_{W2} - \text{nc\_ssr}_{\text{mean}}$]. Thus, *indices* below *zero* indicate genetic diversity and/or number of genetic conservation units below the average. *nc_ssr* number of SSR alleles corrected for sample size, *nc_ht* number of mitochondrial haplotypes corrected for sample size, *I_clim* adaptive genetic variation and potential use under climate change scenarios. The number of genetic conservation units is given as deviation from the average on a logarithmic scale: dev (N_Unit) = $\ln(\text{N\_unit}_{W2} + 3/8) - \ln(\text{N\_unit}_{\text{mean}} + 3/8)$

spruce is often regarded as a tree species of secondary forests harbouring low structural and species diversity, and being sensitive to storm damage and bark beetle attacks (Spieker 2003; Pawson et al. in press). Although this may be partly true at lower altitudes, Norway spruce is a key species in many montane and subalpine forest ecosystems and occurs natively in 85 % of all spruce forests in Austria (Prskawetz and Gschwantner 2005).

Table 2 Correlation between the regional measures of genetic diversity and the suitability of local Norway spruce provenances for future climates for the identification of putative cross-purposes between different conservation objectives

	I_clim	nc_ht	nr_ht	uh_ht	nc_ssr	nr_ssr	UHe_ssr
I_clim	–	**0.559**	**0.385**	**0.497**	−0.099	0.157	0.017
nc_ht	**0.002**	–	**0.605**	**0.944**	0.029	0.172	**0.473**
nr_ht	**0.043**	**0.001**	–	**0.432**	0.135	0.086	0.040
uh_ht	**0.007**	**0.000**	**0.022**	–	0.056	0.219	**0.543**
nc_ssr	0.615	0.883	0.495	0.778	–	−0.225	0.036
nr_ssr	0.426	0.381	0.662	0.262	0.250	–	0.024
UHe_ssr	0.930	**0.011**	0.841	**0.003**	0.856	0.902	–

Significant correlations are bold

Above diagonal correlation coefficient *r*, *below diagonal P* values

I_clim regional index of suitability of provenances for future climate, *nc_ht* number of haplotypes corrected for sample size by rarefaction analysis, *nr_ht* number of private haplotypes, *uh_ht* unbiased haplotype diversity, *nc_ssr* number of SSR alleles corrected for sample size by rarefaction analysis, *nr* number of private SSR alleles, *UHe_SSR* unbiased expected heterozygosity of the SSRs

In addition, Norway spruce is also the most important tree species in Central Europe from an economic point of view. In Austria, Norway spruce covers about 51 % of forests area and amounts to 69 % of the annual timber harvest (Österreichische Waldinventur 2007/2009). Thus it forms the basis for the forest and wood sector, one of the most important branches of the Austrian economy with a foreign trade surplus of about 3.42 billion Euro and a total of 292,000 employees, many living in structurally weak rural areas (FHP 2010). The on-going transformation of spruce forests to more stable mixed and deciduous forests is predicted to create significant financial losses for the forest owners and managers (Hanewinkel et al. 2010). This economic significance alone makes the genetic resources of Norway spruce a valuable 'biological resource' in terms of Article 2 of the CBD. However, in addition to its 'potential use and value for humanity' (CBD 2002), genetic resources of Norway spruce also represent a high intrinsic natural value particularly in Austria. Within and in close proximity to Austria, paleobotanical and genetic data provide evidence of the existence of refugial areas during the last ice age (Terhürne-Berson 2005). This natural heritage is still shaping the genetic diversity of current tree populations, because the high diversity of mitochondrial and nuclear diversity observed mainly in eastern and south-eastern populations result from the adjacent refugia in the eastern Alpine foreland, the south-east Alpine foreland as well as from the Hungarian/Danubian plain (Ravazzi 2002; Terhürne-Berson 2005). The mixed occurrence of the major Central European lineages in east and south–east Austria also demonstrate its role as a migration corridor and melting pot of diversity (Petit et al. 2003) through which the entire Alpine region was colonized by Norway spruce.

Adaptive potential of Norway spruce for future forestry

Although the present analysis of provenance-specific climate response is limited to provenances from Austria, high variation among provenance clusters has been found. As regards the phenotypic response to climatic conditions in the test sites, we showed that the most productive and promising provenance clusters for future climate conditions in Austria originate from the Bohemian massif (provenance cluster 9), the south-eastern fringe of the

Alps (provenance cluster 7) and the north alpine foreland (provenance cluster 8). The origin of these three clusters depicts today the warmest and driest regions of the natural spruce distribution in Austria, suggesting that local adaptations to past and current climate can be used as a proxy for matching provenance with predicted climate. The main part of this local adaptation is very likely the result of an extended growing season in these warmer regions. In addition to the environmental differences in the climate of the other regions, provenances of the cluster 7 and 9 origin from regions with a different phylogenetic history. In the present study, we provided only a general view into the diversity pattern in the Austrian Alps, but no detailed analysis of the postglacial migration pattern and population structure. The analysis of Tollefsrud et al. (2008), Mengl et al. (2009) and Konrad et al. (2011) showed that populations from the Bohemian massive (provenance cluster 9), but also from the eastern fringe of the Alps (provenance cluster 7) differ significantly from the alpine population, suggesting that not only genetic diversity, but also the population history of this diversity might have played a role in quantitative genetic variation and climate response. The significant correlations obtained in the present study between the measures of mitochondrial DNA variation and the adaptive performance in the future also support this view. Collignon et al. (2002) showed that populations from the Hercynian–Carpathian domain show on average a better growth performance than provenances from the Alpine domain, although both domains partly overlap and the Hercynian–Carpathian domain consists of two phylogenetic clusters (Tollefsrud et al. 2008). Besides growth performance also other adaptive characteristics exhibit high phenotypic and genetic variation in the Eastern Alps: For example high variation in climate-growth response and crown phenotypes has been found in the eastern Alpine foreland, suggesting adaptations to warmer and dryer conditions (Schiessl et al. 2010). Another dendroclimatic study provided evidence for high genetic variation in the response of populations to extreme drought events (Grabner et al. 2010), while on the other side strong phenotypic plasticity of the crown shape to the conditions of higher altitudes has also been demonstrated (Geburek et al. 2008). Overall, our study demonstrates the potential impact of genetic variation of forest trees for the adaptation of forests to climate change.

Implications for genetic conservation

The results of our gap analysis show that current conservation measures for Norway spruce do not include the high genetic diversity found in east Austria and the high adaptive variation found in north–east Austria. This is mainly because the Austrian network of genetic conservation units was established by a bottom-up approach from 1990 to 2002. Locally important genetic resources of preferentially autochthonous stands were designated as genetic conservation units in close cooperation with forest owners and experienced forest practitioners. Recent findings of integrated paleobotanical and genetic studies were not available at that time (e.g. Tollefsrud et al. 2008). However, the southern-most regions with high genetic diversity and long population history are well covered. At the eastern and the northern fringe of the Alps as well as on the Bohemian massif further conservation measures on regional scale would be required for both the conservation of important adaptive genetic variation for future climates and for the conservation of high neutral genetic diversity. As revealed by correlation analysis between the various diversity measures, adaptive variation and mitochondrial DNA variation are connected in eastern and northern Austria, while the allelic diversity of the nuclear microsatellites shows lesser correlation with mitochondrial and adaptive variation. This is likely because the allelic diversity of the nuclear markers varies only to a limited extent among the regions, whereas the mitochondrial variation shows a decisive spatial variation. Differences between nuclear and mitochondrial diversity might also be due to the fact that mitochondrial DNA is maternally inherited in conifers and can thus only migrate through seed dispersal, whereas nuclear DNA can be migrated through both pollen and seeds, while gene flow through pollen is about 10-fold higher than through seeds (Petit et al. 2005). Therefore, we suggest using the mitochondrial DNA variation and the adaptive performance under future climates as main criteria for an improved conservation strategy. However, the present case study only includes few measures of neutral genetic diversity and the growth potential of populations under future climate conditions. Adaptations to other environmental conditions or the variation of other phenotypic traits (wood density, resistance to pests, etc.) are not included. Theoretically, the consideration of such additional traits will lead to cross-purposes that require weighting up the different objectives. In addition to different conservation objectives for the conservation of genetic diversity of a single species, the conservation of other forest species or ecosystems might create additional cross-purposes (Milad et al. in press). For example, at lower altitudes in northern and eastern Austria forest transformations to more mixed and deciduous forests are already taking place aiming at higher forest stability towards pests and storms. Nevertheless, our study shows that conservation and utilization of valuable resources are strongly required here. These conflicting forest management and conservation objectives need to be thoroughly discussed with forest owners and policy makers. The existing genetic conservation units are maintained according to dynamic principles, which emphasize a complete genetic system and the maintenance of evolutionary processes, rather than focusing on specific individual genes (e.g. Eriksson et al. 1993). This conservation strategy should at least partly allow the local tree populations to adapt to environmental changes as long as the adaptive potential is sufficient and active measures for natural regeneration are taken (Schaich and Milad in press).

In addition to dynamic genetic conservation of Norway spruce within its natural environment, the use of the respective seed sources in regular forestry should also be evaluated. In particular, improved provenance recommendation schemes may help not only to conserve but also to deploy the most favourable genetic resources for future climatic conditions. The present analysis of adaptive variation in growth performance can be considered only as a first step. For practical guidelines and provenance transfer schemes other adaptive traits and phenotypic plasticity also need to be considered. For example, the transfer of tree populations from lower altitudes to higher ones might be limited to certain environmental distances above which maladaptation is likely to have negative fitness effects (e.g. St. Clair and Howe 2007).

In addition to focused regional conservation efforts, national measures also need to be coordinated on international level. Recently, the EUFGIS Portal (http://portal.eufgis.org) was established to support the national efforts to conserve forest genetic resources. For example, coordinated efforts within the region of Slovenia and Carinthia might help to better manage the regional hotspots of Norway spruce diversity.

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7.3 Appendix – Paper III

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ORIGINAL ARTICLE

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Varying selection differential throughout the climatic range of Norway spruce in Central Europe

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Abstract

Predicting species distribution changes in global warming requires an understanding of how climatic constraints shape the genetic variation of adaptive traits and force local adaptations. To understand the genetic capacity of Norway spruce populations in Central Europe, we analyzed the variation in tree heights at the juvenile stage in common garden experiments established from the species' warm-dry to cold-moist distribution limits. We report the following findings: First, 47% of the total tree height variation at trial sites is attributable to the tree populations irrespective of site climate. Second, tree height variation within populations is higher at cold-moist trial sites than at warm-dry sites and higher within populations originating from cold-moist habitats than from warm-dry habitats. Third, for tree ages of 7–15 years, the variation within populations increases at cold-moist trial sites, whereas it remains constant at warm-dry sites. Fourth, tree height distributions are right-skewed at cold-moist trial sites, whereas they are nonskewed, but platykurtic at warm-dry sites. Our results suggest that in cold environments, climatic conditions impose stronger selection and probably restrict the distribution of spruce, whereas at the warm distribution limit, the species' realized niche might rather be controlled by external drivers, for example, forest insects.

KEYWORDS
adaptive capacity, among-population variation, climate change, conifers, gene flow, intraspecific variation, phenotypic variation, *Picea abies*, provenance trials, within-population variation

1 | INTRODUCTION

Understanding the constraints and drivers of species' distribution ranges is a prerequisite for predicting the consequences of climate change on natural ecosystems and for managing endangered species and populations. Within the last decade, ecologists have developed a wide variety of species distribution models to understand species' climatic and migrational limitations and to analyze the impact of climate change on biodiversity, ecosystem functions, and conservation activities (Araújo, Alagador, Cabeza, Nogués-Bravo, & Thuiller, 2011; Hanewinkel, Cullmann, Schelhaas, Nabuurs, & Zimmermann, 2012; Randin et al., 2013; Summers, Bryan, Crossman, & Meyer, 2012; Svenning & Skov, 2004; Sykes, Prentice, & Cramer, 1996; Thomas et al., 2004; Thuiller et al., 2011). Beyond the scope of immediate abiotic and biotic interactions, evolutionary biologists aim to understand which traits determine the species' genetic capacity to adapt and expand their present ranges across certain limits (Bridle & Vines, 2007; Polechova & Barton, 2015). Strong gene flow toward marginal habitats and across heterogeneous environments was found to be the major cause of restricted ranges because it results in higher genetic load and prevents local adaptation (Haldane, 1956; Kirkpatrick & Barton, 1997; Ronce & Kirkpatrick, 2001). A key determinant of the adaptive capacity of a population in a peripheral habitat and under changing environmental conditions is the genetic variation of traits related to survival, growth, and reproduction within such populations. Populations at range limits are expected to harbor lower genetic variance within populations, because they experience stronger selection than populations under optimal conditions (Kopp & Matuszewski, 2014). On the other hand, models that allow for evolving genetic variance show that a gradually changing environment with moving optima tends to increase the genetic variance as a result of an increase in rare alleles, particularly if the population size is large (Burger & Lynch, 1995; Burger, 1999; Kopp & Matuszewski, 2014). Thus, understanding whether genetic variance varies among populations throughout a species' range and how environmental constraints affect genetic variance is required for evaluating the long-term prospects of species in times of global change.

For trees, climate conditions are among the most important determinants of species' distributions (e.g., Araújo & Pearson, 2005; Prentice et al., 1992), meaning that the patterns of population phenotypic traits and patterns of climate conditions are related (e.g., Hannerz, Sonesson, & Ekberg, 1999; Hurme, Repo, Savolainen, & Pääkkönen, 1997; Rehfeldt et al., 2002). Provenance trials, where tree populations from a wide range of the natural distribution are planted in one or more climates, have revealed that these phenotypic responses are often based on both phenotypic plasticity and local adaptation (Morgenstern, 1996). The plastic response of populations can be used to model mean trait values both with uni- and multivariate climate response and genecological functions (Rehfeldt, Wykoff, & Ying, 2001; Wang, Hamann, Yanchuk, O'Neill, & Aitken, 2006) and with combined universal response functions (Wang, O'Neill, & Aitken, 2010). Such models have been found to be valuable tools for estimating the effect of climate change on growth traits and tree productivity, and for improved provenance selections (Kapeller, Lexer, Geburek, & Schueler, 2012; Mátyás, 1994; Rehfeldt et al., 2002). However, the variance of the trait means and the contribution of phenotypic plasticity to trait variance have rarely been analyzed in relation to the environmental conditions.

For Norway spruce (*Picea abies* [L.] Karst.), the most widespread conifer in Central Europe, we recently analyzed the intraspecific variation in climate response on the basis of an extensive provenance test (Nather & Holzer, 1979) where populations from almost the complete climatic distribution in Central Europe were tested across an equally wide range of test environments (Kapeller et al., 2012). This provenance test provides a unique opportunity to analyze the trait plasticity and variation throughout the species' climatic range, as Norway spruce occurs naturally from approximately 300 m up to 2,000 m above the sea level. Although a significant part of populations at low elevations are considered as secondary spruce forests, there is a long history of spruce populations in Austria, dating back to a refugial population in the alpine forelands (Ravazzi, 2002; Terhürne-Berson, 2005). Our previous analysis (Kapeller et al., 2012) focused on the relationship between trait means and climate parameters and thus on the immediate phenotypic response to climate. Based on the observed phenotypic plasticity and the genetic variation among provenance groups, we found that populations from warm and drought-prone areas may be appropriate candidates for extended silvicultural utilization under future climate conditions. In the present study, we aim to complement the previous analysis by investigating the phenotypic variance within and among populations across the main climate factors. The objective of this study was to quantify the phenotypic variation of height growth within and among populations of Norway spruce. To account for environmental and genetic sources of phenotypic variation, we test for the relationships between height variation and the climate of both trial sites and population origin. Moreover, we study the temporal development of phenotypic variation at the juvenile stage. Finally, we explore the distribution of the potential selection differential in populations across the species climatic niche. For this purpose, we analyze the density distributions for climatically similar groups of populations and trial sites.

2 | MATERIALS AND METHODS

2.1 | Phenotypic data: Norway spruce provenance test 1978

We used tree height measurements from 29 trial sites of a Norway spruce provenance test series established in 1978 in the eastern Alpine region by Nather and Holzer (1979). The original trial series comprised 44 test sites, but measurement data are available for only 29 sites. These span a wide range of altitudes from 250 to 1,750 m above the sea level; they thus comprise a large part of the climatic niche of the Norway spruce, where sites at low altitudes mark the warm and dry distribution limit and sites at high altitudes close to the tree line indicate the cold distribution limit (Fig. 1).

The seed material for the trial series was collected from 480 Austrian Norway spruce populations during commercial seed harvests in 1971. Sixty populations from other countries were also included. The Austrian harvest comprised presumably autochthonous stands and included several trees as a representative sample of the stand (Kapeller et al., 2012; Nather & Holzer, 1979). Seeds were sown over six repetitions at the central forest nursery of the Austrian Federal Forest in Arndorf (Austria) and one repetition at the experimental nursery Mariabrunn of the Austrian

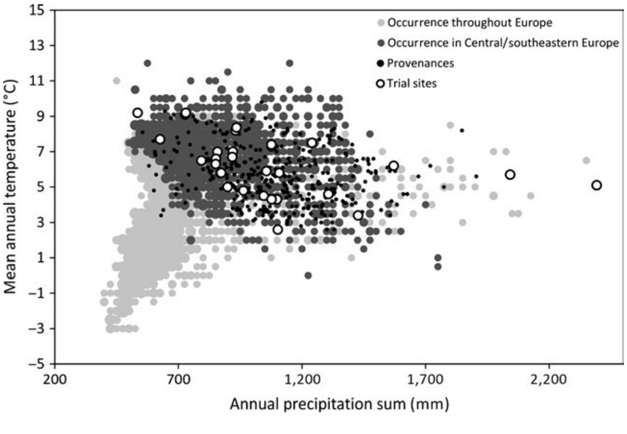

FIGURE 1 Distribution of 29 test sites (white circles) and tested populations (black dots) within the climatic range of Norway spruce. Light gray circles indicate mean annual temperature and annual precipitation of the complete Norway spruce distribution in Europe according to ICP Forests Level I monitoring plots (ICP Forests 2010). As the natural distribution in Europe can be divided into two nonoverlapping, genetically distinct ranges with different population history (Tollefsrud et al., 2008), dark gray circles indicate the central and southeastern distribution, which represent the majority of provenances

Federal Research and Training Centre for Forests, Natural Hazards and Landscape (BFW) in Vienna (Schulze, 1985). After 2 years, the seedlings were transferred into rows of tree nursery fields with 15 cm distance between seedlings (Schulze, 1985). In 1978, 5-year-old trees were transferred to the trial sites (Nather & Holzer, 1979). Each trial site was set up in a randomized complete block design with three blocks, except for sites 1 and 20, where there was only one block, and site 24, where only two blocks could be established. Because of the large number of populations sampled, not all populations could be planted at all sites. Instead, the number of tested populations per site ranged from 19 to 53 populations with an average of 28 (Table S1). The initial number of seedlings per single population per block averaged to 46.9. The seedlings of each population were planted in rectangular tree plots at a spacing of 1.5 m × 1.5 m.

The 29 trial sites were measured in 1983 and 1988, at 5 and 10 years after their establishment. This provided height data for the trees at the age of 10 and 15 years. During the 1983 measurement, the shoot length for the preceding 3 years was also measured, which provided heights for the trees at the age of 7, 8, and 9 years. Of the 109,101 trees initially planted in 1978, 83,304 could be measured in the year 1988 (on average 38.8 trees per plot). This reduction was caused by mortality, because there had been no forest management activities for the duration of the trial (1978–1988).

2.2 | Climate data

Climate data from all the trial sites and population origins were compiled by the Austrian Central Institute for Meteorology and Geodynamics for a previous analysis (Kapeller et al., 2012). The mean climate data of trial sites strictly refer to the growing period from 1978 to 1988, whereas the climate data of population origin are based on long-term means (1971–2008). These data include mean temperatures, mean monthly minima and maxima, and precipitation sums for both the complete year and the approximate growing season from April to September. In addition, the length of vegetation period (given as the number of days with an average temperature above 5°C), growing degree days (i.e., a thermal index accumulating degree days above a threshold of 5°C), the average day of the first frost in fall, and an annual heat moisture index according to Wang et al. (2006) were used as climate parameters.

To reduce the number of climate predictors and to obtain uncorrelated variables for the subsequent analysis, we performed a principal component analysis (PCA) using the statistical environment R (R Core Team 2014), with PCA functions from the R package "FactoMineR" (Husson, Josse, Le, & Mazet, 2015). The contribution of climate variables to each dimension of the PCA is given in Table S2. The first principal component explains 59.7% of observed variance and aggregates mainly temperature-related climate parameters. The second principal component adds another 17.3% variance and aggregates mainly precipitation- and drought-related parameters (Fig. 2). Therefore, we refer to the first dimension as "temperature-related principal component" (TempPC; large values indicate warm conditions) and to the second dimension as "precipitation-related principal component" (PrecPC; large values indicate moist conditions).

2.3 | Statistical analyses

Our analyses were performed in four steps. First, we applied a linear model at each test site to partition among-population variance from the total phenotypic variance. Second, we calculated the standardized within-population variation for each population and test site and related it to the climate of the trial site and the climate of the population origin. The standardized within-population variation of tree height was calculated for the same trees in different years at the ages of 7, 8, 9, 10, and 15 years; this was performed to assess the temporal changes in within-population variation throughout the juvenile stage. Third, we analyzed the density distributions of tree heights with mixture-model analysis to understand the environmental and genetic effects on phenotypic variation. In a fourth step, we validated the robustness of our results with respect to the potential biases introduced by unequal climatic distribution of tested populations across sites and varying survival rates between trial sites.

2.3.1 | Among-population variation

To estimate the variance among populations from the total variance at the individual trial sites, we used a linear model in the R package "lme4" (Bates, Maechler, Bolker, & Walker, 2014). Populations and repetitions (blocks) were treated as random effects, which allowed us to extract the estimates of the among-population variance σ^2_{ap}, the among-block

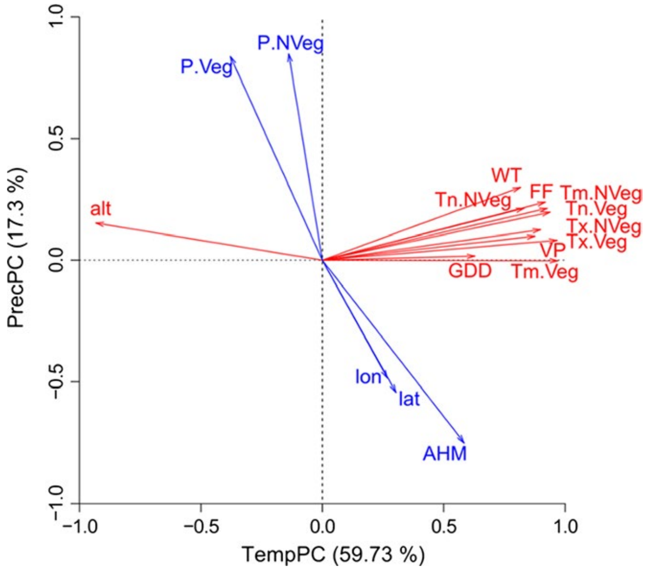

FIGURE 2 Principal component analysis of climatic parameters. The biplot shows that temperature-related factors and altitude (red) are oriented along dimension TempPC (first principal component). Precipitation and drought index (blue) are oriented along PrecPC (second principal component). Parameters included in this analysis were temperature mean (Tm), temperature maximum (Tx), temperature minimum (Tn) and mean precipitation sums (P) during the vegetation season (.Veg) and outside the vegetation season (.NVeg), growing degree days (GDD), length of vegetation period (VP), annual heat moisture index (AHM; see Wang et al., 2006), mean winter temperature (WT), average day of first frost in fall (FF), as well as longitude (lon), latitude (lat), and altitude (alt)

variance σ^2_b, and the total site variance σ^2_s of tree heights from the fitted models. To remove the effects of different growth rates among sites and to allow for comparisons between the individual test sites, these variance components (σ^2_s, σ^2_{ap}, σ^2_b) were standardized as coefficients of variation using the formulas $CV_s = \sigma_s/\mu_s$, $CV_{ap} = \sigma_{ap}/\mu_s$, and $CV_b = \sigma_b/\mu_s$, where μ_s is the mean tree height at the site. After calculating these variation measures for each of the 29 sites separately, the relationship of the standardized total variation CV_s and the standardized among-population variation CV_{ap} to the first two principal components of site climate TempPC and PrecPC was analyzed by linear regression analysis. Additionally, the ratio of among-population variation to the total site variation was calculated as CV_{ap}/CV_s (which equals σ_{ap}/σ_s) to test whether the portion of explained variance by population relative to the total site variance relates to site climate. Therefore, we applied linear regression analyses using the first two PCA components of the climate parameters (TempPC and PrecPC) from the test sites as explanatory variables.

2.3.2 | Within-population variation

To analyze the within-population variation along a climatic gradient of test sites and populations, we calculated the coefficient of variation of tree heights at age 15 for each population on each site separately as $CV_{wp} = \sigma_{wp}/\mu_{wp}$, where σ_{wp} and μ_{wp} refer to all individual tree heights measured for a specific population at a specific site. The coefficient of variation was calculated to remove the effect of different growth rates among sites. In total, we obtained 819 values of CV_{wp} for all population–site combinations. We used multiple linear regression analysis to investigate the potential relations between within-population variation CV_{wp} and the first two PCA components of the climate parameters (TempPC and PrecPC) from the test sites as well as from the population origins. This analysis of the within-population variation CV_{wp} was repeated with tree heights measured in earlier years, when trees aged 7, 8, 9, and 10 years, in order to identify the temporal changes in tree height variation within the juvenile stage. In addition, interactions between site and population climate were assessed in bivariate plots.

2.3.3 | Mixture-model analysis

To understand the effect of site and population climate on phenotypic variation, test sites and populations were both categorized into three climatic groups. The climatic ranges of the first two PCA components (TempPC and PrecPC) were subdivided into equal intervals and populations and sites were then assigned to the corresponding climatic subgroup. The groups were labeled S1, S2, and S3 for sites and P1, P2, and P3 for populations, referring to low, medium, and high levels of TempPC or PrecPC, respectively. For low TempPC, group S1 and P1 pooled "cold" sites and populations originating from a "cold" environment, respectively, while for low PrecPC, S1 and P1 represented "dry" sites and populations originating from dry locations. The density distributions of all nine subset combinations (three population subsets X three site subsets) were plotted separately and analyzed with mixture model analysis (R package "mixtools"; Benaglia & Chauveau, 2009). Mixture model analysis provide the density probabilities of hypothetical normal-distributed subgroups within each subset. Such probabilistic models have been used to identify subpopulations within an overall population (Benaglia & Chauveau, 2009; Ni, Baiketuerhan, Zhang, Zhao, & Von Gadow, 2014) and to test for admixture within populations using quantitative trait data. Here, we used mixture model analysis not to identify truly distinct subpopulations in a strict sense of population genetics, but to visualize the subtle patterns in the density distributions of tree heights. With our data, the mixture-model analysis allowed us to differentiate two phenotypic subgroups of "tall" and "small" trees within each of the climatic subsets. The ratios of these subgroups provided by the mixture model analysis can be used as additional statistics to describe the shape of a density distribution.

2.3.4 | Robustness to stratification

The distribution of provenances to the trial sites did not follow a fully randomized procedure, but was specified in some cases according to the altitude of the test sites and populations. Thus, some populations from higher altitudes (with colder and wetter climate) were preferentially tested on (colder and wetter) sites at higher altitudes, and vice versa (see Fig. 3). As this provenance distribution had the potential to affect our analysis, we aimed to reduce the data imbalance and tested for the effects of a slightly unequal population distribution by applying two different data stratification approaches. Stratification was performed by weighting each test unit (=population × site combination) according to its relative frequency in the bivariate climate spectrum of populations and sites (Fig. 3). We divided the bivariate climate spectrum into 25 climate strata according to regular subdivisions of TempPC at sites and population origins. We then calculated weights for each unit using the relative frequency of each unit in relation to

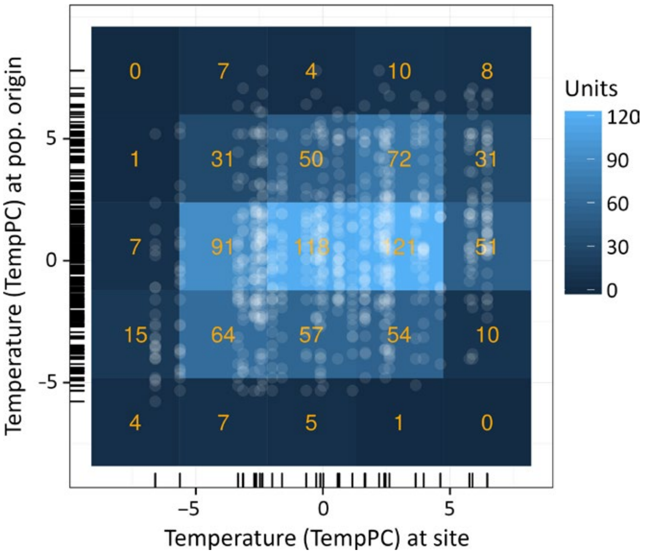

FIGURE 3 Climatic distribution of sites and populations. The bivariate climate spectrum of sites and population origins was subdivided into 25 climate strata, each representing a class of climatic site–population combinations. Relative frequency of test units, that is, site–population combinations (transparent white dots), was utilized to weight each unit and to test whether the stratification of the trial design has an effect on the outcomes of the study

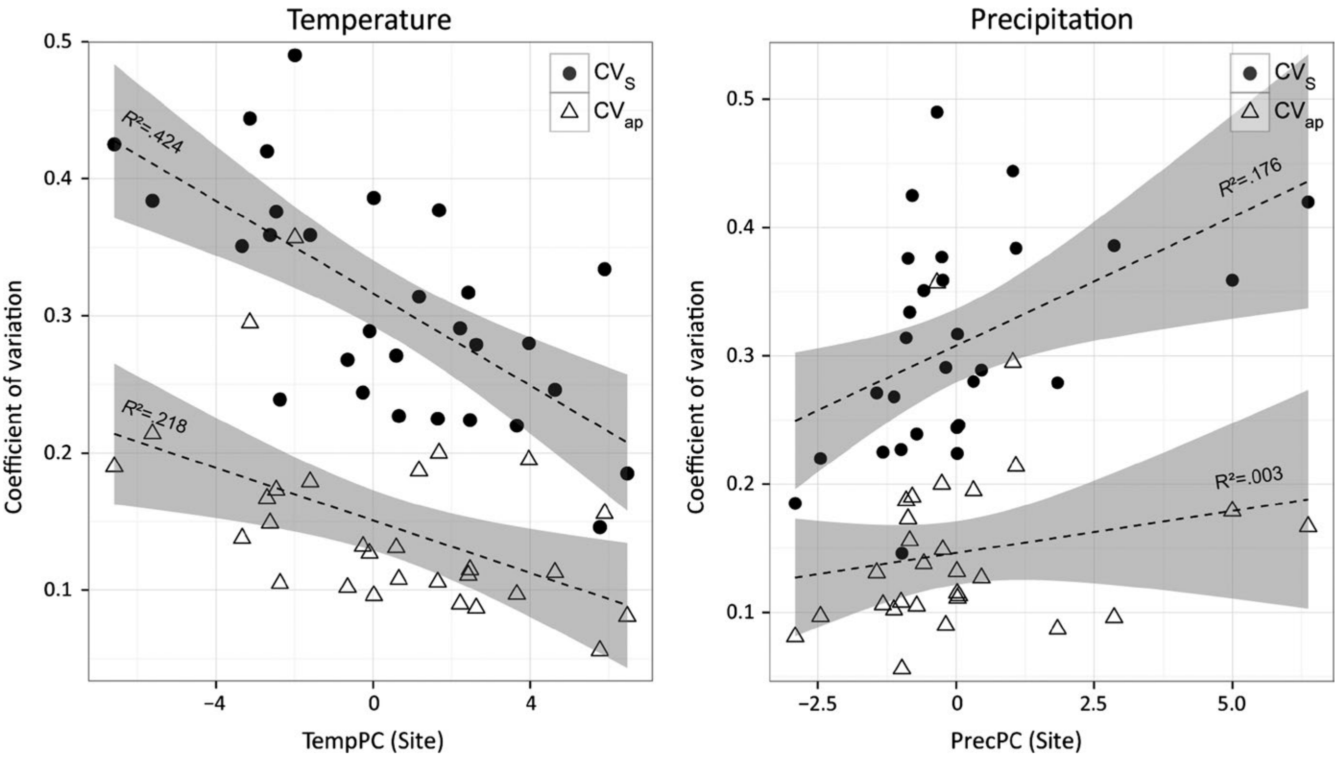

FIGURE 4 Total and among-population variation at trial sites. Coefficients of variation at each site (CV_S, full circles) and among-population variation (CV_{ap}, open triangles) are shown for each site along the climatic gradients of TempPC (left) and PrecPC (right). CV_S are high at cold-moist sites (low TempPC, high PrecPC) and low at warm-dry sites (high TempPC, low PrecPC)

the total number of units (weight#1) or its deviation from the joint frequency probability of the populations and sites of each respective stratum (weight#2). Taking into account these weights for all population x site combinations, we reanalyzed our multiple linear regression analyses of CV_{wp}.

2.3.5 | Effects of mortality

Of the 109,101 trees planted in 1978, 76% survived and could be measured in the year 1988 (i.e. 83,304 trees). The remaining 24% of trees died off for unknown reasons. As this mortality might also bias our estimates of height variation, we tested for the differences in the survival rate of individual populations across both the climate gradients of the trial sites and the gradient of the population origin using multiple regression analysis.

3 | RESULTS

3.1 | Total tree height variation and among-population variation are negatively related to temperature at trial sites

The mixed-effect model yielded variance components for each site, with one variance component explained by the differences among tested populations (on average 21.8% of the total variance σ^2_s), one component explained by the differences among repetition blocks (on average 4.2% of σ^2_s), and a residual variance (on average 74% of σ^2_s). Results for each site are given in supplementary Table S1.

Standardized coefficients of variation allow for comparisons among trial sites. The standardized total variation in tree heights CV_s ranged from 0.15 to 0.49 between the trial sites (Fig. 4, Table S1). When we partitioned the among-population variation from the total tree height variation at each site, the standardized among-population variation CV_{ap} ranged from 0.06 to 0.36 (Fig. 4, Table S1). The CV_{ap}/CV_S ratio ranged across all sites from 0.25 to 0.73 and averaged 0.47.

The overall variation in tree heights CV_S was found to be significantly related to the climate of test sites for both TempPC (adjusted $R^2 = 0.44$, $p < 0.001$) and PrecPC (adjusted $R^2 = 0.19$, $p = 0.011$). Here, CV_s was found to be high at cold-moist sites (low TempPC, high PrecPC) and low at warm-dry sites (high TempPC, low PrecPC). The ratio of among-population variation (CV_{ap}) to the overall variation (CV_{ap} / CV_s) was not significantly related to the climate at test sites for either TempPC ($p = 0.48$) or PrecPC ($p = 0.58$).

3.2 | Within-population variation is negatively related to temperatures at trial site and population origin

The variation within populations CV_{wp} ranged from 0.12 to 0.58 for individual population–site combinations with an average of 0.28. Across single trial sites, the average CV_{wp} ranged from 0.14 to 0.41 (Table S1).

Multiple regression analysis revealed a significant relationship between the within-population variation (CV_{wp}) and the climate at the test sites and the population origin (see summary of the multiple linear model fit shown in Table 1). Regression analyses were performed separately for

TABLE 1 Parameter estimates of multiple regression analyses, predicting CV_{wp} by climate parameters TempPC and PrecPC at test sites (*_S) and population origins (*_P) (adjusted R^2 = 0.424, *F*-statistic = 151.3 on 4 and 814 degrees of freedom)

	Estimate	*SE*	*t* value	Pr (>|*t*|)	
(Intercept)	0.2896	0.0024	123.1	<0.001	***
TempPC_S	−0.0116	0.0007	−15.5	<0.001	***
TempPC_P	−0.0017	0.0008	−2.1	0.0333	*
PrecPC_S	0.0134	0.0013	10.6	<0.001	***
PrecPC_P	0.0024	0.0014	1.8	0.0746	.

TempPC and PrecPC and for site and population-origin climate (Fig. 5). Regressions of CV_{wp} to the site climate revealed negative relationships with TempPC and positive relationships with PrecPC. Therefore, at warm and dry sites, within-population variation is low. In contrast, at cold and moist sites, within-population variation is high (Fig. 5, left). Moreover, within-population variation (CV_{wp}) is negatively related to the climate of the population origin for TempPC (Table 1; Fig. 5, center).

The multiple regression analysis for the 15-year-old trees demonstrated clear effects of trial site climate on CV_{wp} after the trees had been growing for 10 years in the field. When the trees were planted at the age of 5 years, they had a similar variation within populations CV_{wp} at all test sites. To reveal the temporal course of CV_{wp} development throughout the growing period in the field, we also analyzed CV_{wp} for trees aged 7, 8, 9, and 10 years and compared CV_{wp} for populations at the coldest trial site (i.e., the lowest TempPC at site 11) and the warmest site (i.e., the highest TempPC at site 42) (Fig. 6). In 7-year-old trees, the variation within populations CV_{wp} after two growing periods was already higher at the coldest trial site than at the warmest site. At the coldest site, the within-population variation increased from age of 10 to 15. A contrasting pattern was found at the warmest trial site on the upper temperature limit. Here, within-population variation increased only slightly from tree ages of 7–10, but then remained constant at a relatively low level until the tree age of 15 years (Fig. 6).

These differences in CV_{wp} temporal development between trials at cold and warm sites can be observed at all trial sites (Fig. 7; the results of multiple regression analyses in Table S3): During the period from tree age of 7 to 15 years, CV_{wp} stayed at a more or less constant level at sites with warm (high TempPC) and dry (low PrecPC) climates, while CV_{wp} increased with tree age at sites with cold (low TempPC) and moist (high PrecPC) climates (Fig. 7, row 1, row 3). Thus, the significant relationships found between trial climate and CV_{wp} when a tree is 15 years old are due to increasing CV_{wp} at cold sites, but not to decreasing CV_{wp} at warm sites. We found the most pronounced response of CV_{wp} to site climate in 15-year-old trees. However, these

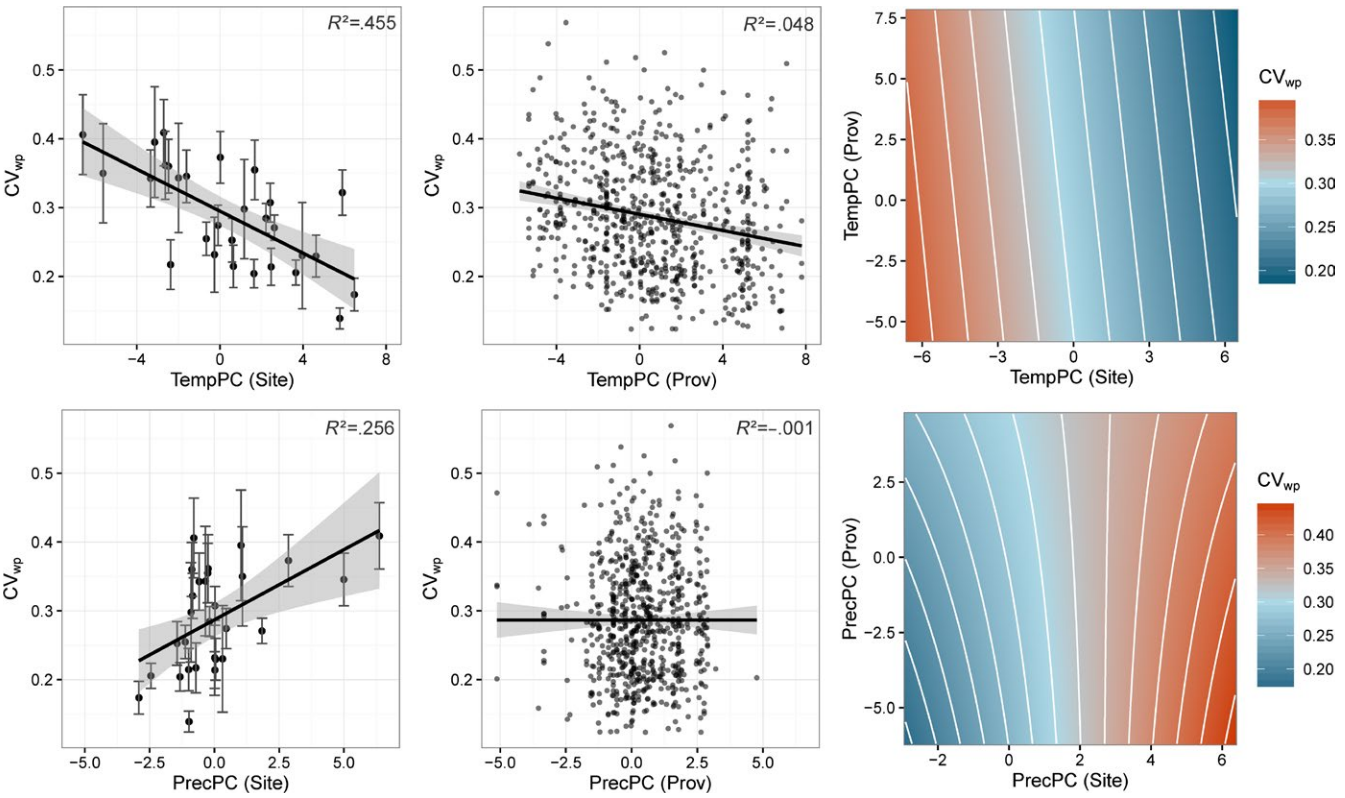

FIGURE 5 Within-population variation for each population–site combination. Coefficients of variation for within-population variation (CV_{wp}) are shown along the climate gradients TempPC (top) and PrecPC (bottom), where large values of TempPC and PrecPC represent warm and wet locations, respectively. Left: response along climate at the test sites. Error bars represent CV_{wp} values from all populations tested at a respective site; Center: response along population climate. Points represent CV_{wp} values of one population tested at one specific site; Right: bivariate plot along both site and population climates. Color indicates the level of within-population variation (CV_{wp}) (see legend)

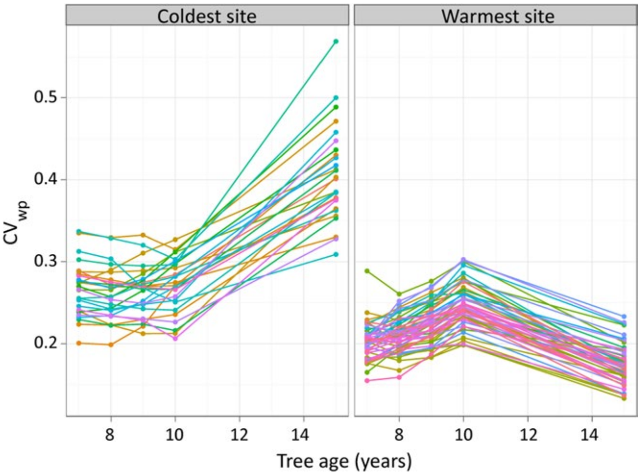

FIGURE 6 Within-population variation and tree age. CV_{wp} of populations at climatically most extreme sites 11 (coldest) and 42 (warmest) at tree ages of 7, 8, 9, 10, and 15 years

relationships (including a significant linear regression) between sites climate and CV_{wp} were already found for trees at the age of 7, 8, 9, and 10 (Table S3), but the slope of the relationship increased with tree age.

Beyond a significant relation of CV_{wp} to site climate, we found a significant relation of CV_{wp} to the temperature-related climate predictor (TempPC) of population origins for trees at the age of 7, 8, 9, 10, and 15 (Fig. 7, row 2; Table S3).

3.3 | Shapes of density distributions of tree height

The frequency density distributions of tree heights at the age of 15 reveal contrasting patterns for the categorized climatic subsets of the site and population climate. Figure 8 displays histograms of different site and population subsets (S1, S2, S3, P1, P2, P3) where the effects of the site climate are shown on the vertical axis and the effects of the climate at population's origins on the horizontal axis. With respect to site climate, we found increasing mean tree heights with increasing

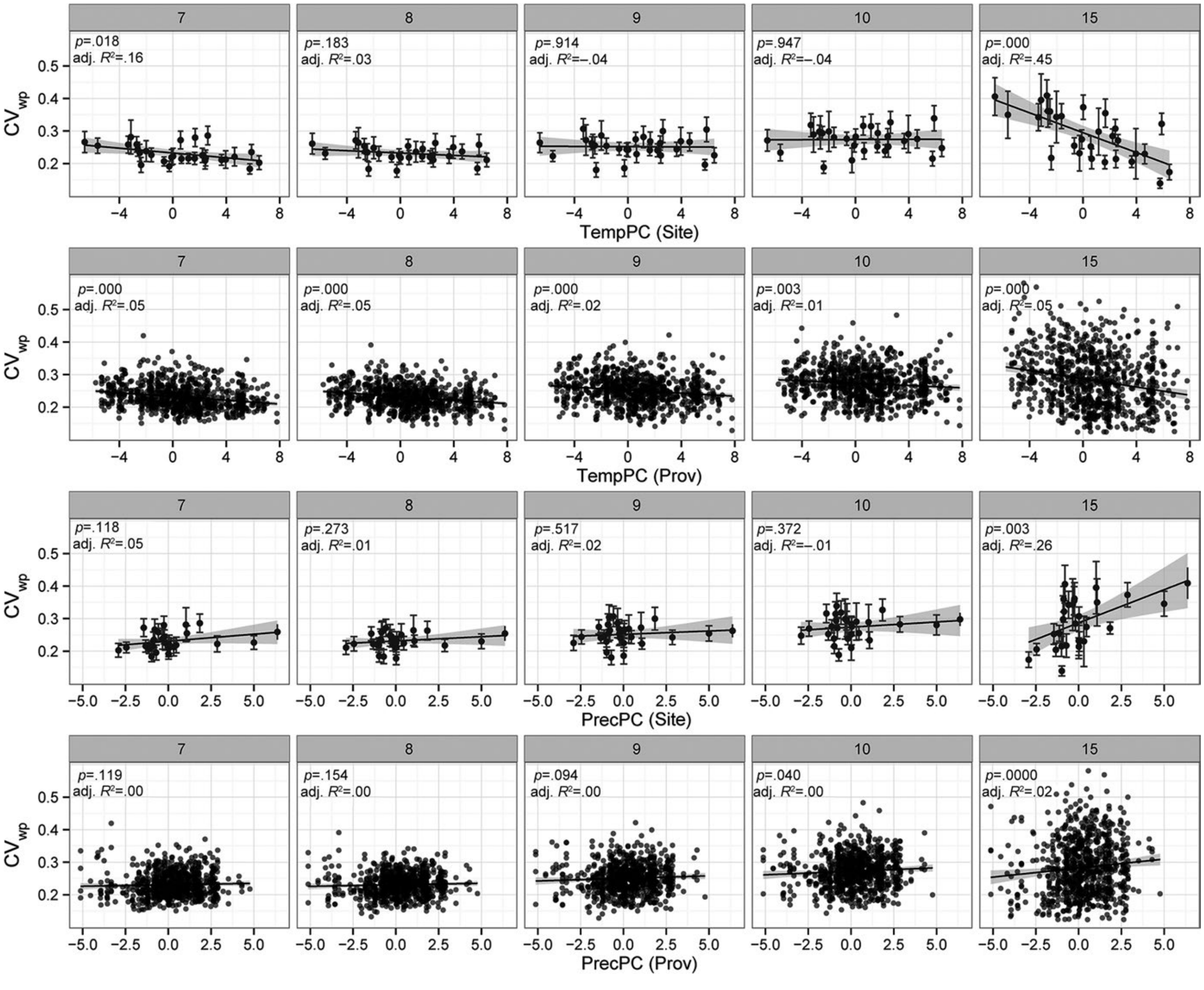

FIGURE 7 Within-population variation, tree age, and climatic gradients. Values of CV_{wp} are shown along climatic gradients of TempPC (1st and 2nd row) and PrecPC (rows 3 and 4) for tree ages of 7, 8, 9, 10, and 15 years. Error bars in site climate responses (rows 1 and 3) represent within-population variations of all populations on a site (mean ± *SD* of CV_{wp}). Dots in population climate responses (rows 2 and 4) represent within-population variation of a specific population at a specific site

TempPC and decreasing PrecPC. The shape of the density distributions suggests that at warm and dry sites, the variation in tree heights is also larger than at cold and moist sites (in contrast to our previous analyses, where we used the coefficient of variation). We found tree height distributions at cold and moist sites to be left-skewed, whereas at warm and dry sites they were not skewed or slightly right-skewed (see Table 2 for mean, variance, skewness, and kurtosis of the distributions). Kurtosis refers to the presence or absence of pronounced peaks in a density distribution. At cold sites, we found "peaked" (leptokurtic) distribution shapes (positive kurtosis) and "flat" (platykurtic) distribution shapes (negative kurtosis) at warm and dry sites.

Population subsets (P1, P2, P3) reveal only small differences in histogram patterns (Fig. 8). Overall, the mean tree height and the variation increased from (cold) P1 populations to (warm) P3 populations. Moreover, skewness increases from cold/moist populations to warm/dry populations, whereas kurtosis decreases. Thus, the populations from cold/moist sites are rather left-skewed and peaked, whereas the populations from warm/dry sites are nonskewed or slightly right-skewed and flat.

Density probability functions from mixture analyses provide additional insights into these patterns. In mixture analysis, each tree in a subset combination is attributed to one of two hypothetical components of the distribution (curves in Fig. 8), representing "relatively small" and "relatively tall" trees. Means and standard deviations of each component, as well as probabilities of data being classified as one of these components, are shown in Table S4. At warm S3 sites (high TempPC), 67% of trees from cold populations are classified as small (blue curve), while 33% of trees are classified as tall (red curve). Trees from warm populations at the same S3 sites are classified as 46% small and 54% tall. At intermediate S2 sites, we again have a larger number of "small trees" in P1 populations, but conversely a larger number of "tall trees" in P3 populations. At cold S1 sites, most trees are classified as small, regardless of population climate.

3.4 | Robustness to stratification

To avoid the biases in our analyses due to the unbalanced distribution of populations to trial sites, we corrected our dataset by stratifying population x site combinations according to their relative frequency in the bivariate spectrum of the population and site climate (see Fig. 3). The reanalysis of the multiple linear regression analyses of the response variable CV_{wp} and the predictors TempPC and PrecPC of site and population origins (Table 1) with the two stratification weights (weight#1 and weight#2) did not alter the significance of the regression analysis compared to the unweighted model (Table S5). Using weight#1 resulted in a higher significance level for TempPC of population origin, and using weight#2 resulted in a higher significance level even for PrecPC of population origin. Therefore, stratification

TABLE 2 Statistics describing forms of distribution of each of the nine combinations of climate subset (see Fig. 8)

S	P	Trees	Sites	Pop	Mean	Var	Skew	Kurt
TempPC								
1	1	8,019	8	60	141.4	4,084.1	0.87	0.92
1	2	9191	8	82	147.7	4,356.0	0.96	0.93
1	3	2346	8	20	153.1	3,929.0	0.95	0.94
2	1	7457	11	45	282.8	11,796.4	0.25	−0.39
2	2	15436	11	109	300.4	13,894.7	0.17	−0.57
2	3	4811	11	29	309.1	14,496.8	0.00	−0.69
3	1	6109	10	35	341.8	15,792.7	0.30	−0.35
3	2	21266	10	122	388.8	20,029.1	0.03	−0.70
3	3	9413	10	38	398.4	22,514.9	−0.04	−0.87
PrecPC								
1	1	3,635	18	17	353.5	24,419.5	−0.10	−1.04
1	2	39,289	21	184	310.5	22,335.8	0.28	−0.89
1	3	15,619	21	74	294.8	21,815.6	0.31	−0.91
2	1	1,225	4	9	361.3	34,765.4	0.35	−0.81
2	2	11,230	6	90	293.9	24,381.4	0.60	−0.02
2	3	7,081	6	74	291.8	23,994.6	0.62	−0.07
3	1	129	1	1	295.4	13,147.1	0.15	−0.91
3	2	3,436	2	29	214.4	11,627.4	0.60	−0.28
3	3	2,404	2	19	214.3	11,596.1	0.75	−0.01

S, P = IDs of the climate subsets of sites and populations indicating the levels of the respective climate variable TempPC or PrecPC (1 = low, 2 = medium, 3 = high); trees = the number of individual trees pooled in the combination of climate subsets; sites = the number of pooled sites; pop = the number of pooled populations; mean = mean tree height at the age of 15; var = variance of tree heights; skew = skewness of tree height distribution; kurt = kurtosis of tree height distribution

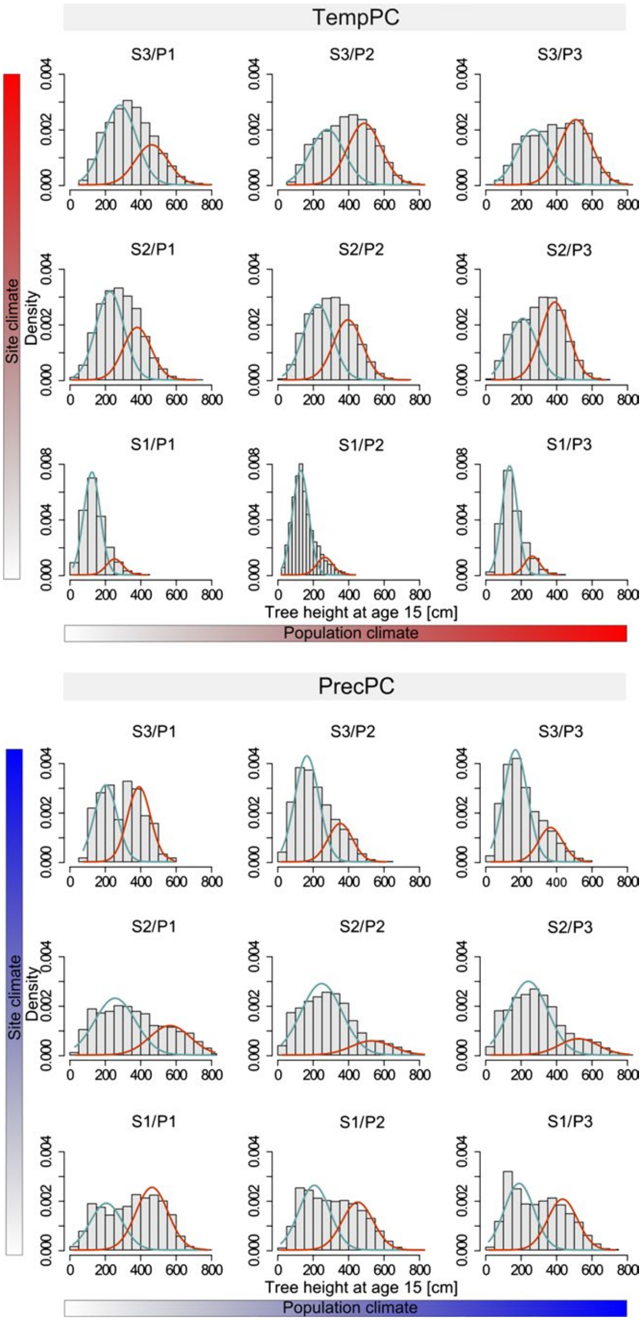

FIGURE 8 Density distributions of absolute tree heights at the age of 15. All records were divided into nine climate subsets by TempPC (top) and PrecPC (bottom). Each subset aggregates records of one of three test site groups (S1, S3, or S3) and one of three population groups (P1, P2, or P3). Red and blue curves are the results from a mixture-model analysis and represent density probabilities of two hypothetical subcomponents for "small" and "high" trees within each subset. Parameter estimates from the mixture-model analysis (portions of attributed data to each component, means of components and standard deviations) are presented in supplementary Table S4

by using two different weighting methods did not reveal any false significant model parameters in the linear regression analysis of the unweighted data. Instead, both weighted models resulted in a slightly stronger relevance of TempPC of population origins (compare Table 1 and Table S5).

3.5 | Effect of mortality

The analysis of survival rates across our trial sites did not indicate a bias of tree height variation measures. A significant relationship was found between the survival rate (calculated as the proportion of surviving trees after 10 years in the field) and TempPC of the trial sites, but not to TempPC of provenance origin. However, the total effect of site climate on mortality seems to be negligible, as the coefficient of determination of this relationship is very low (adjusted $R^2 = 0.023$) and the regression slopes close to zero (Table 3). Also, the relation of survival to PrecPC was not found to be significant for trial sites and provenance origin.

4 | DISCUSSION

The persistence of tree populations in future climates depends crucially on their adaptive capacity to adjust to new environmental conditions. Phenotypic variation in fitness-related traits is both a result of environmental selection pressures and a prerequisite for the adaptation to changing environments. Here, we used one of the largest common garden trial series of Norway spruce established more or less throughout its complete climate distribution in Central Europe and tested for the effects of climate conditions on the phenotypic variation within and among populations. Both the climate at trial sites and the climate at the geographic origin of populations had a significant impact on the phenotypic variation within populations (Fig. 5). The effect of site climate on phenotypic variation was much larger than the effect of climate of population origins, as previously shown also for other conifers (Chakraborty et al., 2015; Wang et al., 2010). The observed effect of site climate suggests stronger climatic selection pressures at the colder end of the species distribution resulting in increasing tree height variation in colder and moister environments. Survival rates were neither affected by site climate nor by provenance origin climate (see the numbers of planted and measured trees in Table S1).

4.1 | Environmental sensitivity of selection

Absolute mean heights were found to be strongly associated with site climate as a result of phenotypic plasticity. At the age of 15, trees

TABLE 3 Parameter estimates of multiple regression analyses predicting the survival rate by climate parameters TempPC and PrecPC at test sites (*_S) and population origins (*_P)

	Estimate	*SE*	*t* value	Pr (>|*t*|)	
(Intercept)	0.9713	0.0093	104.03	<0.001	***
TempPC_S	0.0131	0.0029	4.41	<0.001	***
TempPC_P	−0.0058	0.0032	−1.78	0.0757	.
PrecPC_S	0.0125	0.0050	2.48	0.0135	*
PrecPC_P	0.0090	0.0054	1.69	0.0923	.

Survival rate was calculated for each population–site combination as the percentage of living trees after 10 years in the field. We used arcsine transformation to meet normality assumptions. Adjusted $R^2 = 0.023$, *F*-statistic = 5.73 on 4 and 814 *df*.

reached on average 5 m at the warmest site and 1.2 m at the coldest site. Trees at warm sites also showed a higher absolute variance of tree heights. However, the overall coefficient of variation per trial site decreased significantly with increasing temperatures and ranged from 0.49 at the coldest site to 0.15 at the warmest (Fig. 4). This higher variation at colder sites was found to result mainly from the variation within populations (CV_{wp}), because the ratio of variation among populations to the total variation was not related to the site climate.

The strongest relationship between CV_{wp} and climate was found at tree age of 15 years (i.e., growing for 10 years in the field). The analysis of the temporal course of CV_{wp} by including data from earlier height measurements showed that CV_{wp} increased from age 7 to age 15 at the coldest trial sites, whereas CV_{wp} remained approximately constant at trial sites at the warm end of the species distribution (Figs. 6 and 7). This suggests that the climate conditions at the colder trial sites increase the differentiation among trees within populations, but climate conditions at warm sites do not affect CV_{wp}. Thus, at cold sites, relatively few well-performing trees have an advantage in height growth and will likely dominate and outcompete the slower-growing trees in the future stand. Given the huge intraspecific competition among juvenile trees (Vieilledent, Courbaud, Kunstler, & Dhôte, 2010), this will ultimately result in a higher potential selection differential at the cold edge of the spruce distribution. This is also supported by the mixture-model analysis across different environments (Fig. 8 and Table S4). At cold sites (labeled S1 in Fig. 8), we found right-skewed, leptokurtic distributions with a pronounced peak (negative kurtosis) resulting in a prevailing component of relatively small trees and a second much smaller component of taller trees. If climate was of similar importance at the upper temperature limit of the species' niche, we would expect a left-skewed distribution at the warmer trial sites (labeled S3 in Fig. 8), where physiological limits set a threshold for height growth. Instead, we did not find left-skewed distributions at the warmest trial sites, but nonskewed, platykurtic (positive kurtosis) distributions without pronounced peaks (Fig. 8, top). From such shapes of tree height density distributions, we conclude that Norway spruce is not under strong selection by climate constraints at any of our warm-dry test sites—some of which are located at the upper temperature limit of the species range (Fig. 1).

Potential reasons for the increasing height variation within populations at cold sites are manifold. One possible explanation for the increasing height variation at colder sites could be the strong relation between height growth and phenology (e.g., Kleinschmit, Sauer-Stegmann, Lunderstadt, & Svolba, 1981). In particular, tree height is strongly correlated with flushing and bud set within and across populations. Both traits, flushing and bud set, possess high additive genetic variation (Hannerz et al., 1999) and are driven by the annual temperature course in spring and late summer (Søgaard, Oystein, Jarle, & Olavi, 2008). Thus, at cold sites, small differences in temperature sum requirements for flushing among individual trees may accumulate into large differences in the onset of growth and resulting height growth pattern. As temperature accumulates much faster at warm sites, the same genetic differences in temperature sum requirements result in smaller differences of bud burst and height growth in warmer environments. Such behavior was also observed for other species: Davi et al. (2011), for example, analyzed flushing of various tree species from 960 to 1530 m a.s.l. and found a significant altitude effect for *Pinus sylvestris*, which decreased with faster spring development. Generally, our results on climate constraints at the cold end of the species distribution are in good agreement with the manifold traits that were found to be related to cold adaptation in conifers (Aitken & Hannerz, 2001; Howe et al., 2003; Morgenstern, 1996). Besides bud burst and bud set, a significant variation within and among families of Norway spruce has been found for frost hardiness (Skrøppa, 1991) and populations from southern Finland were found to be more sensitive to frost events than northern populations (Pulkkinen, 1993). Narrow-sense heritability of frost resistance ranged from 0.04 to 0.28 in a Swedish progeny trials (Hannerz et al., 1999). Howe et al. (2003) concluded that cold adaptation traits appear to be under strong natural selection. In contrast, evidence for genetic adaptations of Norway spruce to warm temperatures, namely drought resistance or stomatal conductance, is limited. In part, this may be due to the fact that fewer studies have addressed the intraspecific variation in adaptation to the warm temperature edge of a species' range (but see Mátyás, Nagy, & Jármay, 2009 or Lamy et al., 2011); but it may also be that Norway spruce rarely reaches its physiological limits and has thus developed fewer local adaptations. Another potential cause for the unequal climate selection could be the structure of the trial sites itself: Warm trials are rather located at low elevations with relatively flat and homogeneous site conditions. In contrast, cold trial sites are located on mountain slopes and likely provide higher on-site heterogeneity that may result into increasing differentiation among individual trees. A larger heterogeneity of both land surface and soil structure might provide advantageous microclimatic or edaphic conditions under which a few young trees are able to outperform their competitors. Also, snow cover in early spring is likely to increase the variation among trees, as it may delay the onset of growth for small trees completely covered with snow in particular. Larger trees that extend already beyond the snow cover are able to receive environmental signals for the start of the growing period much earlier than their smaller counterparts.

4.2 | Phenotypic evolution and environmental heterogeneity

Besides the climate at the trial sites, the climate of population origin was also related to CV_{wp} with higher variations within populations from colder regions (Fig. 7, row 2; Table S3). This finding seems counterintuitive, considering that with stronger selection at colder sites one might expect lower phenotypic variation. One explanation could be the ongoing phenotypic evolution at a marginal habitat and within changing environments where, for large and recombining populations, the genetic variance was found to increase under directional selection as a result of an increasing frequency of rare alleles (e.g., Burger, 1999; Burger & Lynch, 1995). This type of situation has been observed in several theoretical studies and may fit for Norway spruce at its cold edge, namely at higher elevations in its alpine distribution. Here, permanent selection pressures might cause maladaptations and thus a permanent lag of the population mean behind the environmental optimum (see

Kopp & Matuszewski, 2014). Another explanation for the increased variation could be the immediate effect of phenotypic plasticity, which was found to increase the genetic variation within one generation because of variations in the slope of reaction norms (Chevin & Lande, 2011). To differentiate between the effects of phenotypic plasticity or directional selection as described by Burger (1999), the immediate effects of mortality during changes in the genetic variance need to be considered. Our analyses of survival rates at trial sites indicated only a negligible effect of climate on mortality, as the coefficient of determination of this analysis is very low (adjusted $R^2 = 0.023$) and regression slopes are close to zero (Table 3). This indicates that between the age of 5–15 years, tree height variation is rather shaped by phenotypic plasticity than natural selection. Theoretical analysis of plasticity and phenotypic variation in populations within marginal habitats along environmental gradients support this conclusion. Chevin and Lande (2011), for example, found an increase in genetic variance within one generation. However, the effects of changing environments on variance and the contributions of plasticity are still not fully understood, because genetic variances are often assumed to be constant in quantitative models (Kopp & Matuszewski, 2014). Another explanation for higher variation within populations from colder origins could be intensive gene flow and environmental heterogeneity in such environments. In our experiment, cold populations originate mainly from alpine locations at higher elevations. Within its distribution in the Alpine region, Norway spruce occurs from the valley floors up to subalpine habitats near the tree line. This high environmental heterogeneity likely results in manifold local adaptations. The intense gene flow caused by pollen flow across spatially close but climatically distant populations could increase the genetic variation by introducing maladapted genotypes, as shown, for example, by Yeaman and Jarvis (2006). The gene flow and environmental heterogeneity explanation is supported by a recent meta-analysis of progeny tests of Norway spruce in Sweden (Kroon, Ericsson, Jansson, & Andersson, 2011). This study compared the genetic variation across a latitudinal gradient from 56°N to 65°N covering a similar climatic range. In contrast to our study, Kroon et al. (2011) found a significant decrease in genetic variation with increasing latitude and thus decreasing temperatures. Across the large spatial distance in Sweden, gene flow is much less likely to connect the same environmental gradients as in the Alpine landscape.

4.3 | Among-population variation

The ratio of among-population variation to the total phenotypic variation ranged from 25% to 73% (with a mean of 47%, Table S1) and did not change along the climatic gradient of TempPC or PrecPC. This is in agreement with our initial hypothesis that the distribution of populations across trial locations (although not completely balanced) results in similar differences between populations at each site. However, the higher selection differential acting on within-population variation at colder trial sites would imply that selection also increases the differences among populations. Instead, the ratio of among-population variation was found to be independent from site climate, indicating that besides local adaptations to climate, other factors might contribute to differentiation among populations. Such a factor is most likely the phylogeographic pattern of *P. abies*. The majority of tested populations originated from the eastern Alpine range and from surrounding countries. Indeed, the geographic origins of the populations cover the three main refugial lineages of Norway spruce in Central and Western Europe. The long population history of these lineages can still be observed with various molecular markers (e.g., Maghuly, Pinsker, Praznik, & Fluch, 2006; Mengl, Geburek, & Schueler, 2009), and provenance trials throughout Europe have recognized a strong variation among regional groups (Giertych, 1992; Krutzsch, 1992). In comparison with other provenance experiments with Norway spruce, the provenance effects on tree height variation in our study (25%–73%) seems higher than observed elsewhere (e.g., Weisgerber, Dimpflmeier, Ruetz, Kleinschmitt, & Widmaier, 1984; : 44%; Liesebach, Rau, & König, 2010: 0%–26%; Ujvári-Jármay, Nagy, & Mátyás, 2016: 12.6%). This is, however, because we calculated the coefficient of variation in order to correct for the strong variation in height growth among trial sites. The untransformed ratio of the among-population variation to total phenotypic variation ranged from 6% to 53% and is comparable to the values reported by Weisgerber et al. (1984), Liesebach et al. (2010), and Ujvári-Jármay et al. (2016).

4.4 | Understanding Norway spruce range limits

The focus of our empirical study is on tree height data, but not on direct measures of a tree's fitness in terms of survival and reproduction. Such direct measures of fitness for tree species are difficult to obtain, because many forest trees do not flower below the age of 20 years and unbiased estimates of reproductive performance would require reproductive success to be measured throughout an individual tree's life cycle. Nevertheless, measures of growth performance at the juvenile age are considered to be closely connected to fitness, as the intraspecific competition among trees is strongest among seedlings and juvenile trees (Vieilledent et al., 2010); only the very few trees that are able to dominate others will win the race for light and survive. During periods of extreme environmental conditions (e.g., drought or frost) as well as at later life stages, other physiological or phenological traits may have a higher impact and obscure height growth performance, but then the selection for tree height is expected to have already shaped the genetic structure of populations.

Under the assumption that tree height is strongly correlated with fitness, the varying selection differential at opposite ends of the spruce distribution can be discussed in terms of the species' fundamental and realized niche. At the cold end of the species distribution, we see high selection differential that very likely translates into a sharp range margin. Polechova and Barton (2015) recently demonstrated such an intrinsic limit to adaptation by modeling the joint evolution of trait mean and population size along environmental gradients within a genetic model. The existence of such range margins depends on the relation between fitness costs and the efficacy of selection relative to genetic drift (Polechova & Barton, 2015). Even small environmental gradients are able to generate intrinsic genetically determined range limits in the case of interspecific competition (Case & Taper, 2000), which tends to be the reality in a subalpine forest ecosystem. Our data neither allow us to estimate the model parameters of Polechova and Barton (2015) nor to prove the effects of interactions with other conifers, but they clearly demonstrate that climate selection in Norway spruce acts at the cold, but not the warm species distribution limit. Thus, the colder species distribution limit can be considered close to the limits of its fundamental niche, whereas the warm limit rather mirrors the species realized niche. Here, the species distribution might instead be defined by drivers other than climate, such as bark beetle attacks or competition with other tree species, which were found to be important drivers of species niches on ecological timescales (Hellmann, Prior, & Pelini, 2012; Meier, Edwards, Kienast, Dobbertin, & Zimmermann, 2011). However, given the short observation time in relation to a trees life span, it is also possible that we are not able to identify direct causes of mortality, or reduced reproduction at the warm temperature limit, which might also be related to intrinsic limits of the species range. To test whether the observed differences in selection differential are being carried into adult tree populations, we could design a simple genetic experiment: as our analysis predicts that no selection on tree height occurs on populations growing on the warm temperature limit, we would expect low heritability for height growth performance in the offspring of such trees. In contrast, offspring from populations growing at cold sites should have a higher degree of genetic determination.

Under climate change, the cold distribution limit is the leading edge that might spread to higher altitudes and latitudes (Sykes et al., 1996). The warm distribution limit is considered to be the trailing edge, where Norway spruce is expected to experience strong reductions in its present range with significant consequences for forest ecosystems, wood production (Hanewinkel et al., 2012), but also with losses of genetic diversity (Schueler et al., 2014). As our analysis indicates that natural selection at this trailing edge is limited, local adaptation at such sites seems to be impossible, in particular if we consider the high velocity of change. Thus, management actions to conserve the existing genetic diversity, for example, the establishment of gene conservation forests, are urgently needed at the warm limit of the species distribution range.

4.5 | Implications for forest tree breeding and distribution modeling

Our analysis aims to improve tree genetic conservation and to guide assisted migration measures. Assisted migration, that is, the translocation of forest reproductive material to areas with expectably favorable climates in the future, is widely discussed as a key forest management strategy to reduce climate maladaptation (e.g., Lu et al., 2014; McLachlan, Hellmann, & Schwartz, 2007; Wang et al., 2010). Based on the same Norway spruce dataset, we have already shown that populations from currently warm and drought-prone areas are appropriate candidates for continued silvicultural use in the future (Kapeller et al., 2012). In the mountainous area of the eastern Alps, this mainly means a shift of seed material upward in order to keep pace with global warming. In the present analysis, we found significantly stronger selection differential at the species colder distribution limit, although this has not resulted in reduced genetic variation in populations originating from such sites, likely because of intensive gene flow and environmental heterogeneity in alpine environments. This suggests that reasonable seed transfers upward bears only a small risk of maladaptations, as the variation within the populations is only weakly correlated with the temperature gradient, and thus, also populations from warmer seed origin display a broad adaptive capacity to grow and survive on colder sites. In general, however, genetic conservation and seed transfer activities should not be based on the variation in single traits alone. A valid risk-benefit analysis might also consider further physiological or phenological traits related to the adaptive potential of populations (e.g., frost hardiness, drought resistance, and pest insect tolerance).

Similarly, attempts to model future tree species distributions need to take into account the variable selection differential along climatic gradients and the relative importance of adaptive traits at specific areas within the species range. For Norway spruce, it is widely believed and shown with various species distribution models that the species will undergo strong reductions in its present range mainly on the species' warm and dry distribution limit (e.g., Hanewinkel et al., 2012; Sykes et al., 1996; Zimmermann et al., 2013). This is in contrast to our data as they do not show signs of climate selection on tree height on warm trial sites, whereas cold conditions impose a stronger selection with highly skewed density functions. Thus, our analysis helps to decipher individual mechanisms that may trigger range contractions or expansions that should be included in future mechanistic distribution models. This will help to improve models of the species' fundamental niche because under climate change it is more important to understand where a species *could* occur than where it *currently* occurs (Wiens, Stralberg, Jongsomjit, Howell, & Snyder, 2009).

5 | CONCLUSIONS

Under climate change, populations throughout the entire climatic range will experience shifts of mean temperatures, related climate parameters, or both. In Norway spruce, populations at the currently cold sites harbor higher phenotypic variation and will likely be able to adapt to the prospective conditions. At the warm edge of its distribution, populations are not necessarily maladapted, as we have not observed climatic constraints on phenotypic variation even in our warmest trial sites at the border of the climatic range. In our analysis, temperature shapes the phenotypic variation much more strongly than precipitation-related parameters. As climatic predictions for temperature are more reliable than for precipitation, our results could be integrated into mechanistic models of population persistence and species distributions. Datasets similar to those used in the present study are available for many tree species and have been used to select appropriate populations for future reforestations based on the population's mean climate response (e.g., Leites, Robinson, Rehfeldt, Marshall, & Crookston, 2012; Lu et al., 2014; Rehfeldt, Tchebakova, & Barnhardt, 1999; Rehfeldt et al., 2001, 2002). Our analysis suggests that an in-depth analysis of the phenotypic variation within such datasets can provide additional knowledge on the population's adaptive capacities.

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DATA ARCHING STATEMENT

Data files used for the analyses in this study are available at the Dryad Digital Repository: doi: http://dx.doi.org/10.5061/dryad.877ts.

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