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Impact of heat and drought on provenances of Scots pine (*Pinus sylvestris* L.)

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ABSTRACT

Background and Aims

Impacts of climate change on ecosystems are already visible. Rising temperatures and more frequent climatic extremes will particularly affect forest trees as they are long-living, immobile organisms. The future suitability of tree species adapted to current, local conditions is therefore questioned in many regions of the world. This is corroborated by an increasing number of reports on climate effects including mortality events. One of the species controversially discussed in this context is Scots pine (*Pinus sylvestris* L.). Known as a “survivor-species” with a wide physiological tolerance, this species covers a vast geographic range. On the other hand, species distribution models predict a considerable loss of habitats for Scots pine under climate change, not only at the warm and dry margin of its distribution. So far, these models neglect possible intraspecific differences in the response to drought and warming that could have the potential to buffer those impacts. Therefore this thesis aims to elucidate the role of provenances in the context of climate change by exploring provenance differences in response to increased temperature and drought events. Combining manipulative experimental approaches on seedlings with a retrospective observation study on a provenance trial initiated in 1982, the following leading research questions are addressed:

1. Do the chosen provenances differ in genetic composition, phenology and growth?
2. How does Scots pine respond to elevated temperatures and drought events?
3. Do provenances of Scots pine differ in their response to climatic effects?
4. Which role do provenances play in the face of climate change?

Material and Methods

Two experiments on seedlings and a dendroclimatic study of a 30 year old provenance trial are subject of this thesis. For the experimental approach, ten provenances from the southwestern margin to the central part of the distribution range of Scots pine were gathered and genetically characterized. The first experiment conducted in the greenhouse focused on the germination and the development of the provenances during the first vegetation period under two contrasting water regimes. In the second experiment provenances were sown into the field and were exposed to experimental warming and drought conditions for two years following a factorial design. A complex infrastructure consisting of a heating system and a rain-out shelter was established. This set-up allowed heating the air surrounding plants directly while preventing excessive soil heating and manipulating drought while permitting almost natural radiation including high-light stress. Plant responses were assessed as changes in phenology, growth and biomass allocation. The dendroclimatic study focused on eleven provenances of the IUFRO 1982 provenance trial at two macroclimatic different sites in Germany. Provenance origins range from Bosnia-Herzegovina to Russia. Chronologies of tree-ring width and annual height increment were measured and climate/growth relationships were explored. The response of tree growth to the most severe drought event per site was examined using tolerance indices of resistance, recovery and resilience. Overall provenance performance was summarized with a multivariate archetype analysis based on drought tolerance as well as on growth metrics.

Results and Discussion

As a first major result, significant genetic differences among the ten provenances selected for the experimental approaches were exhibited. Genetic variability and genetic diversity increased from southwestern provenances to those originating from central parts of the distribution. According to the genetic distance, the provenances could be classified into four groups consisting of a Spanish, a French, an Italian group and a group with the remaining provenances (Germany, Poland, Bulgaria and Switzerland). Significant geographic clines were revealed in the greenhouse experiment in terms of a faster seedling development and an earlier bud set of northern provenances. Reduced water availability slowed bud set and decreased above ground growth for all provenances. The lowest sensitivity of growth increment to drought was found for Spanish provenances, although this could not be proved within the field experiment. Drought at the field led to significant effects regarding almost all measured growth traits, whereas warming had only a minor effect by advancing spring phenology and influencing bud biomass and diameter increment depending on water availability. A high potential of phenotypic plasticity of Scots pine seedlings in response to drought was detected in terms of considerable adjustment of root morphology, measured as an increase of tap-root length and root-shoot ratio. Southwestern provenances revealed conservative aboveground growth but responded to drought with the strongest root adjustment. In all treatments of both experiments the German alpine provenance, derived from plus trees of a seed orchard, showed best growth performance. The dendroclimatic study confirmed the relationship between growth parameters and moisture deficit of Scots pine provenances. Height growth was sensitive to moisture deficit during May whereas basal area increment was sensitive to moisture deficit during May to July of the current year. Drought response depends on timing and duration of the event. Differences of drought responses among provenances were pronounced for recovery and resilience. Mirroring the experimental results, specific drought adaptations at the cost of low aboveground growth were found for the southernmost provenance of the dendroclimatic study. Both approaches showed that provenances from the southwestern margin of the distribution do not take advantage of favorable conditions and show aboveground growth on a low, but rather constant level.

Conclusions

The results of this thesis demonstrate the importance of considering the provenance level in the discussion of future suitability of tree species using the example of Scots pine. With both approaches, the experiments and the dendroclimatic study, differences among provenances were found for various traits and in particular regarding the response to climatic effects. The phenotypic plasticity of root morphology in response to drought emphasizes root growth as a key response to moisture deficit. Drought response among provenances was not uniform. Due to specific drought adaptations, southwestern provenances could be able to better cope with future conditions which are associated with an increase of extreme drought events. However, due to their low aboveground growth level, they do not seem to be an alternative to replace local provenances under a forest management perspective so far, since local provenances combine still superior growth performance with resilient drought responses. Nevertheless, seed transfer guidelines should be continuously updated to allow the supplementation of stands with pre-adapted ecotypes following the concept of assisted migration.

KURZFASSUNG

Hintergrund und Ziele

Der Klimawandel hat bereits heute sichtbare Auswirkungen auf Ökosysteme. Weiter ansteigende Temperaturen sowie eine Zunahme von klimatischen Extremereignissen werden Bäume als langlebige und unbewegliche Organismen besonders stark treffen. In vielen Regionen der Erde wird die künftige Eignung von Baumarten in Frage gestellt, da diese an derzeitige lokale Verhältnisse angepasst sind. Diese Unsicherheit wird durch eine zunehmende Anzahl von Berichten über klimatisch bedingte Absterbeerscheinungen von Bäumen verstärkt. In diesem Kontext wird insbesondere auch die Zukunft der Kiefer (*Pinus sylvestris* L.) kontrovers diskutiert. Einerseits als Überlebenskünstler bekannt, hat die Kiefer einen weiten physiologischen Toleranzbereich und nimmt nicht zuletzt deshalb auch ein riesiges Verbreitungsgebiet ein. Andererseits prognostizieren Artverbreitungsmodelle vor dem Hintergrund des Klimawandels nicht nur an der warm-trockenen Verbreitungsgrenze einen erheblichen Rückgang an geeigneten Lebensräumen. Allerdings lassen diese Modelle bislang innerartliche Unterschiede in der Reaktion auf Dürre und höhere Temperaturen unberücksichtigt, welche möglicherweise solche Rückgänge puffern könnten. Diese Dissertation versucht deshalb zu klären, welche Rolle die Herkunftsfrage vor dem Hintergrund des Klimawandels spielt. Dazu werden Herkunftsunterschiede bezüglich der Reaktion auf Temperaturerhöhungen und Trockenheitsereignisse beleuchtet. Mit zwei komplementären Ansätzen aus Manipulationsexperimenten an Jungpflanzen und einer retrospektiven Untersuchung am Herkunftsversuch IUFRO 1982 stehen innerhalb dieser Dissertation folgende Fragestellungen im Vordergrund:

1. Unterscheiden sich die ausgewählten Herkünfte bezüglich ihrer Genetik, der Phänologie und des Wachstums?
2. Wie reagiert die Kiefer auf Temperaturerhöhung und Trockenheit?
3. Unterscheiden sich die Herkünfte der Kiefer in ihrer Reaktion auf klimatische Effekte?
4. Welche Rolle spielen Herkünfte vor dem Hintergrund des Klimawandels?

Material und Methoden

Zwei Experimente an Jungpflanzen und eine dendroklimatische Studie an einem knapp 30-jährigen Herkunftsversuch wurden für diese Doktorarbeit durchgeführt. Für die Experimente wurden zehn Herkünfte vom südwestlichen Rand des Verbreitungsgebietes der Kiefer bis nach Polen und Bulgarien ausgewählt und genetisch charakterisiert. Innerhalb des ersten Experimentes im Gewächshaus standen die Keimung und die Entwicklung der Herkünfte während der ersten Vegetationsperiode unter zwei unterschiedlichen Bewässerungsregimes im Fokus. Im zweiten Experiment wurden die Herkünfte auf der Freifläche ausgesät und zwei Jahre lang in einer faktoriellen Versuchsanordnung beheizt und ausgetrocknet. Dazu wurde eine komplexe Infrastruktur aus einem Heizungssystem und einem Rain-Out-Shelter aufgebaut. Diese ermöglichte ein direktes Erwärmen der Umgebungsluft der Pflanzen, wodurch eine übermäßige Bodenerwärmung verhindert wurde. Es erlaubte zudem die Simulation von Trockenheitsphasen unter annähernd natürlichen Strahlungsbedingungen und damit gegebenenfalls auch unter Starklichtstress. Als Pflanzenreaktionen wurden Veränderungen der Phänologie, des Wachstums und der Biomasseallokation erfasst. Gegenstand der dendroklimatischen Studie waren elf Herkünfte des Herkunftsversuches IUFRO 1982 an zwei makroklimatisch unterschiedlichen Standorten in Deutschland. Die geographische Spanne der Herkünfte reichte von Bosnien-Herzegowina bis nach Russland. Auf Basis der Messung von Jahrringbreiten und des jährlichen Höhenwachstums wurden Klimawachstumsbeziehungen untersucht. Die Zuwachsreaktion auf das extremste Trockenheitsereignis je Standort wurde mit Toleranzindizes hinsichtlich der Resistenz, der Erholungsreaktion und der Resilienz untersucht. Eine Gesamtbeurteilung der Herkünfte erfolgte durch eine multivariate Archetypenanalyse, die sowohl die Trockenheitstoleranz als auch das Wachstumsverhalten mit einbezieht.

Ergebnisse und Diskussion

Als erstes wichtiges Ergebnis konnten für die zehn Herkünfte, die für die Experimente ausgewählt wurden, signifikante Unterschiede hinsichtlich ihrer Genetik nachgewiesen werden. Die genetische Variabilität und die genetische Vielfalt nehmen von den Herkünften aus dem Südwesten des Verbreitungsgebietes hin zu zentral gelegeneren Herkünften zu. Auf Basis der genetischen Distanz lassen sich die Herkünfte in vier Gruppen einteilen, die aus einer spanischen, einer französischen, einer italienischen und einer Gruppe mit den übrigen Herkünften (Deutschland, Polen, Bulgarien und Schweiz) bestehen. Signifikante, geographische Gradienten der Merkmalsausprägung konnten im Gewächshaus in Form einer schnelleren Keimlingsentwicklung und einer früheren Knospenbildung bei nördlichen Herkünften nachgewiesen werden. Eine geringere Wasserverfügbarkeit führte zu einer späteren Knospenbildung und verminderte zudem das oberirdische Wachstum aller Herkünfte. Die geringste Trockenheitssensitivität des Zuwachses zeigten die spanischen Herkünfte, was sich jedoch im Freilandexperiment nicht nachweisen ließ. Trockenheit führte im Freilandexperiment bei fast allen gemessenen Wachstumsparametern zu signifikanten Effekten. Eine Erwärmung hatte geringere messbare Auswirkungen, neben einem früheren Austreiben ließ sich jedoch in Abhängigkeit von der Wasserverfügbarkeit ein Einfluss auf die Knospenbiomasse und den Durchmesserzuwachs feststellen. Das große Potential von Kiefernsämlingen hinsichtlich ihrer phänotypischen Plastizität in der Trockenheitsreaktion wurde durch die enorme Anpassung der Wurzelmorphologie deutlich, die als eine Zunahme der Hauptwurzellänge und der Wurzel-Spross Verhältnisse messbar war. Südwestliche Herkünfte, die durch ein konservatives Zuwachsverhalten oberirdischer Kompartimente charakterisiert sind, reagierten auf Trockenheit mit der stärksten Anpassung der Wurzelmorphologie. In beiden Experimenten und allen Behandlungsvarianten erwies sich die deutsche Herkunft Alpenkiefer, deren Samen von Plusbäumen aus einer Samenplantage stammen, als die wüchsigste. Bei der dendroklimatischen Analyse konnte die Sensitivität von Wachstumsparametern auf Wassermangel nachgewiesen werden. Für den Höhenzuwachs sind hierbei die Bedingungen im Mai, für den Grundflächenzuwachs die Bedingungen von Mai bis Juli des laufenden Jahres entscheidend. Die Trockenheitsreaktion ist abhängig von Zeitpunkt und Dauer solcher Dürreereignisse und unterscheidet sich bei den Herkünften vor allem im

Hinblick auf Erholungsreaktion und Resilienz. Wie schon in den experimentellen Ergebnissen sind spezifische Trockenheitsanpassungen mit einem geringen oberirdischen Wachstum verbunden, was in der dendroklimatischen Analyse für die südlichste der Herkünfte nachgewiesen werden konnte. Beide Ansätze verdeutlichen somit, dass Herkünfte vom südwestlichen Rand des Verbreitungsgebietes günstige Bedingungen weniger gut ausnutzen können, da sie oberirdisch eher ein konstantes Wachstum auf niedrigem Niveau zeigen.

Schlussfolgerungen

Die Ergebnisse dieser Dissertation demonstrieren am Beispiel der Kiefer eindrücklich die Bedeutung der Herkunftsfrage in der Diskussion um zukünftige Baumarteneignungen. Zwei komplementäre Ansätze, bestehend aus Experimenten an Jungpflanzen und aus einer dendroklimatischen Studie am Herkunftsversuch IUFRO 1982, ergaben sowohl für zahlreiche Wachstumsparameter als auch hinsichtlich der Reaktion auf klimatische Faktoren wesentliche Herkunftsunterschiede. Die große phänotypische Plastizität der Wurzelmorphologie verdeutlicht die Bedeutung der Wurzelentwicklung als eine der Schlüsselreaktionen auf Trockenheit. Die Herkünfte zeigen keine deckungsgleiche Trockenheitsreaktion. Südwestliche Herkünfte könnten aufgrund ihrer spezifischen Trockenheitsanpassungen mit zukünftigen Bedingungen besser zurechtkommen, sofern diese durch eine Zunahme von extremen Trockenheitsereignissen geprägt sind. Aus forstwirtschaftlicher Sicht sind sie jedoch wegen ihres geringen oberirdischen Wachstums bislang keine Alternative zu lokalen Herkünften, da diese derzeit ein überdurchschnittliches Wachstumsverhalten mit einer resilienten Trockenheitsreaktion vereinen. Um eine Anreicherung von Kiefernbeständen mit vor-angepassten Ökotypen nach dem Konzept der *„assisted migration“* zu ermöglichen, sollten Herkunftsempfehlungen fortlaufend angepasst werden.

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1 GENERAL INTRODUCTION

1.1 CLIMATE CHANGE

1.1.1 Observations and projections

The earth is exposed to an anthropogenic climate change. Since the late 19th century (period 1880 – 2012), the mean global air temperatures increased by 0.85°C (±0.2°C) (IPCC 2013). Warming was especially high during the last four decades (Luterbacher 2004; Hansen et al. 2006; Hansen et al. 2010) and the period 1983 – 2012 was likely the warmest 30-year period of the last 1400 years in the northern hemisphere (IPCC 2013). Furthermore, the years 2001 to 2012 were all among the warmest years since the beginning of temperature records (WMO 2013).

Global warming is very likely caused by an increase of anthropogenic greenhouse gas emissions such as CO_2, CH_4 and N_2O since 1750 (IPCC 2013). Due to human activities pre-industrial levels of these greenhouse gases are exceeded by far. Major drivers of the increase are the combustion of fossil fuels (CO_2) land use change (CO_2) and agriculture (CH_4 and N_2O).

Emission scenarios and climate projections predict a further increase of global temperature of 1.0 °C (±0.7°C) to 3.7 °C (±1.1°C) for the period 2081-2100 relative to the period 1986-2005 (IPCC 2013). Even when assuming the absence of future greenhouse gas emissions a rise of temperature would have to be expected due to climate feedback processes (Solomon et al. 2009). The rise of temperatures will most probably be accompanied by changes in precipitation. For Germany an increase of winter precipitation and a reduction of summer precipitation are projected for the end of the 21st century (Jacob 2008; Tölle et al. 2013).

In addition, changes regarding extreme climatic events could already be detected in the past decades since 1950 (Frich et al. 2002; IPCC 2012). In southern Germany for example the probability of hot and dry summers doubled compared to the period before 1970 (KLIWA 2012). Due to the fact that they occur rarely by definition, the prediction of future extreme event occurrences is associated with higher uncertainties compared to the prediction of changes in means. Nevertheless, rising temperatures of observed climatic trends as well as of future projections are linked with increasing climatic variability (Easterling et al. 2000). Globally it is projected that the frequency, the duration and/or the intensity of extreme climatic events such as warm spells, heatwaves, heavy precipitation events or droughts will further increase (Salinger 2005; Beniston et al. 2007; Rahmstorf and Coumou 2011; IPCC 2012). Heatwaves experienced in Europe during the summer of 2003 are therefore expected to occur more often in the future (Schär and Jendritzky 2004; Ciais et al. 2005). At a regional scale, a higher probability of heatwaves and drought events is projected for southern Germany (KLIWA 2012).

1.1.2 Impact of climate change on forest ecosystems

Climate change impacts on ecosystems are already visible: various studies from all over the world show that anthropogenic climate change has affected physical and biological systems by now (Walther et al. 2002; Parmesan and Yohe 2003; IPCC 2007; Rosenzweig et al. 2008). Generally, possible responses of plants to climate change are phenotypic plasticity (responses within the plants' reaction norm), evolutionary adaptation or migration (Nicotra et al. 2010). If these strategies fail, plant species will extinct. The rise in temperature led to an earlier timing of spring events such as leaf unfolding or flowering and to an extension of the growing season (Menzel and Fabian 1999; Sparks and Menzel 2002; Menzel et al. 2006; Parmesan 2006). Climate change is a major driver of changes in biodiversity (Sala et al. 2000; Hansen et al. 2001) and widespread extinctions already led to a significant reduction of the number of species (Thomas et al. 2006). Further high extinction risks predicted for the future put global biodiversity at risk (Davis 2001; Maclean and Wilson 2011). Climate change induces species to migrate following altitudinal or latitudinal gradients (Grace et al. 2002; Parmesan and Yohe 2003; Lenoir et al. 2008; Jump et al. 2009; Pauli et al. 2012; Iverson and McKenzie 2013). These range shifts of species are in particular driven by extreme climatic events and consequently lead to altered compositions of species communities (Jentsch and Beierkuhnlein 2008).

Forests are especially sensitive to changes in site conditions, since forest trees are long-living, immobile organisms. Forest experts and practitioners are very concerned about the possible impacts of climate change, as revealed in a recent inquiry (Spathelf et al. 2013). Since the middle of the last century changes of forest productivity due to climate change are already noticeable. On a global scale, a positive effect on growth was found as long as water was not the limiting factor (Boisvenue and Running 2006). Due to their ability to sequester carbon forests can serve as a sink of CO_2 and therefore provide a negative feedback mechanism in the climate/carbon cycle system (Friedlingstein et al. 2006). In combination with a fertilizing effect of CO_2 and nitrogen depositions, climate change could lead to an increase of vegetation productivity and to enhanced carbon sequestration in some regions as simulated for Oregon, USA (Hudiburg et al. 2013). Tree growth and wood production are generally expected to increase in the northern and western part of Europe, at least for a certain period of time, whereas southern and eastern parts of Europe could be negatively affected by an increase of disturbance risks (Lindner et al. 2010). A projection of the economic consequences shows that European forests in general could considerably lose economic value due to a shift of forest types to low productive Mediterranean oak forests by the end of the century (Hanewinkel et al. 2012).

Extreme events

Extreme climatic events, becoming more frequent under climate change, will have detrimental impacts on agriculture as well as on forests and forest productivity (Fuhrer et al. 2006). They are likely to trigger ecosystem-level disturbances and are more important to biological systems than changes in mean conditions (Parmesan et al. 2000; Gutschick and BassiriRad 2003; Jentsch and Beierkuhnlein 2008; Vasseur et al. 2014). In terms of evolution, Gutschick and

BassiriRad (2003) were able to show that selection is mainly occurring during extreme events rather than during ordinary, normal conditions. Furthermore, extreme events actually shape distribution ranges of species. This is particularly true for immobile, long-living organism such as trees, because in this case events with a low frequency of occurrence and long return periods also are of importance. Their consideration and explicit integration substantially improves tree distribution range models (Zimmermann et al. 2009). On the other hand, phenotypic plasticity and genetic variability are suggested to counteract extreme events (Lloret et al. 2012). In addition, consequences of extreme events such as lowered competition or enhanced recruitment could attenuate their severe impacts (Lloret et al. 2012).

The extremely hot and dry summer of 2003 in Europe serves as an example of possible impacts of future events. Its heatwave and exceptional drought reduced about 30 percent of gross primary production in Europe and converted European forests overall to a net source of carbon by offsetting the net ecosystem carbon sequestration of four years (Ciais et al. 2005). The impact of extreme events depends on the type of the climatic event, its timing and intensity (Breda and Badeau 2008; Lebourgeois et al. 2010; Lloret et al. 2011). The response of forest trees is also species specific and differs between sites (i.a. Bugmann and Pfister 2000; Pichler and Oberhuber 2007). In addition to immediate responses such as growth reductions, extreme climatic events can trigger time-lagged effects such as delayed mortality, fires or pest outbreaks. If those events become more frequent in the future, they will very likely negate the expected increase of forest carbon sequestration as described before (Reichstein et al. 2013).

Dieback events

In fact, in recent years an increasing number of studies from all around the world reports mortality events of forest trees that were linked to climate change. Widespread tree mortality events could be due to climate induced range shifts and could affect ecosystems and ecological functioning on a broad scale (Adams et al. 2010; Wang W et al. 2012; Anderegg et al. 2013). Despite the great number of such reports, there is still a lack of understanding of the underlying physiological causes and mechanisms of mortality which hampers its prediction (Wang W et al. 2012). Mortality is found to be a nonlinear threshold process, triggered by multiple factors, causing immediate as well as delayed multi-year effects (Franklin et al. 1987; Allen et al. 2010; Wang W. et al. 2012). Nevertheless, mortality events could be attributed to extreme climatic events, especially to severe droughts. In this context, various authors describe drought events under warmer temperatures as global-change-type droughts, which are expected to occur more frequently in the future (Breshears et al. 2005; Wang W et al. 2012). Allen et al. (2010) provided a global overview of drought and heat induced mortality events and were able to show that the increasing number of such reports is consistent with projections of increased forest mortality due to climate change. But not only the number of dieback events seems to increase, there is also evidence for increasing background mortality rates due to regional warming in unmanaged forests (van Mantgem et al. 2009).

Huge dieback events due to climate extremes have been reported for North America. Regional die-off of *Pinus edulis* (ENGELM.) in southwestern North America was attributed to drought as the dominant factor - although this event was accompanied by bark beetle infestations (Breshears et al. 2005). Recent declines of *Populus tremuloides (MICHX.)*, the most widely distributed tree species in North America, were also related to drought events (Worrall et al. 2013). Numerous reports also come from Europe, regarding various tree species (Peñuelas et al. 2001; Bréda et al. 2006; Allen et al. 2010). In particular, there is a striking number of reports on dieback events of Scots pine (*Pinus sylvestris L.)* (Allen et al. 2010; Giuggiola et al. 2010). Diebacks, mainly observed at the rear edge of the distributions, could cause far-reaching consequences since this possibly leads to losses of genetic diversity (Hampe and Petit 2005; Borovics and Mátyás 2013).

Adaptedness and adaptive capacity

Considering the reports about species extinctions and these numerous reports on dieback events, the question arises whether plants and in particular forest trees can adapt to future climates. In situ, plants can respond to changing conditions by phenotypic plasticity or evolutionary development (Nicotra et al. 2010). Immediate plant responses are enabled through phenotypic plasticity, whereas evolutionary responses become more important on the long run (Franks et al. 2014). Phenotypic variability, which will be the focus of this thesis (see also Chapter 1.4), facilitates the persistence of plants and therefore allows for subsequent evolutionary development to take place (Jump and Peñuelas 2005; Nicotra et al. 2010). On the contrary, the enhanced persistence may delay the evolutionary response by reducing selection processes (Savolainen et al. 2007; Savolainen et al. 2011). However, trees are characterized by individual longevity, the potential of high rates of pollen flow and high within-population genetic variability, which could prevent tree species from extinction (Hamrick 2004).

The potential of genetic adaptations to different environmental conditions is evident by the extent of local adaptations of forest tree populations (Alberto et al. 2013). The basis of a high adaptive capacity is provided by a high genetic variability within tree species (Müller-Starck et al. 1992) and in particular within populations of tree species (Salmela et al. 2013). In addition, epigenetic effects could contribute to the adaptive capacity (Nicotra et al. 2010; Bräutigam et al. 2013). Nevertheless, so far it remains unclear if the evolutionary response can keep pace with rates of climate change (Nicotra et al. 2010). The velocity of climate change could exceed the adaptive capacity of trees in fragmented habitats at the rear edge (Rehfeldt et al. 2002; Jump and Peñuelas 2005) or in general (Franks et al. 2014). On the contrary, some authors describe rapid evolutionary responses of shrubs and trees to climate change on basis of high genetic variability (Jump et al. 2008; Kramer et al. 2010).

1.2 SCOTS PINE

Scots pine is known as a weak competitor but is at the same time characterized as a “survivor” species (Roloff 2008). It has one of the largest distribution ranges of European tree species, extending from northern Spain to Scandinavia, covering most of Europe and reaching deep into Russia (Giertych and Mátyás 1991; Lang et al. 2007; EUFORGEN 2009). The wide distribution of this sub-boreal species reflects its tolerance to contrasting environmental conditions. Low temperatures limit the distribution in the northernmost parts, whereas the southern margin of the species is terminated by a combination of high temperatures and drought (Castro et al. 2004; Matías and Jump 2012).

Therefore, climate change impacts are not expected to be uniform across its distribution range. Congruent with general trends of forests in Europe, growth of Scots pine is likely to increase in the north and as long as water availability is sufficient, whereas growth might decrease in southern parts (Martínez-Vilalta et al. 2008; Reich and Oleksyn 2008). Along with impacts on seed production, seed establishment and mortality, this could finally lead to a shift of its distribution range (Parmesan 2006; Matías and Jump 2012).

At northern tree lines severe climatic conditions limit further expansions (Morin et al. 2007), thus an increase in temperature will positively affect pollen production (Savolainen et al. 2011), seed viability and recruitment (Kullman 2007; Matías and Jump 2012). At the same time higher temperatures and an increasing number of droughts will have negative consequences for southernmost populations of Scots pine, as concluded from observations of responses to recent heatwaves and drought events. Crown development, cone production and growth of Scots pine in the French Mediterranean region were affected by an exceptional drought period from 2003 to 2005 (Thabeet et al. 2009). In spite of relatively stable emergence rates, an increase of temperature and summer droughts will diminish natural rejuvenation of Scots pine at southernmost sites, since drought is found to be the main mortality agent of seedlings (Castro et al. 2004; Castro et al. 2005). Furthermore, boosted summer droughts are also associated with the increasing number of dieback events of Scots pine and with range shifts of species at the southern limit of its distribution. Such reports concern the Pyrenees in Spain (Galiano et al. 2010; Hereş et al. 2012), the Aosta Valley in Italy (Vacchiano et al. 2012) and the Valais in Switzerland (Dobbertin et al. 2005a; Bigler et al. 2006). Reductions of radial growth and an increase of mortality were also associated with drought at a dry inner-alpine valley in Austria (Oberhuber et al. 1998; Pichler and Oberhuber 2007). In addition to drought, there may be other factors contributing to these responses. Described range shifts of species towards oak dominated forests at the Valais or at the Pyrenees are to some extent due to former forest management or the abandonment of practices such as litter removal, forest pasture or forest management (Rigling et al. 2013; Vilà-Cabrera et al. 2013). Increasing tree mortality of Scots pine can be triggered by biotic factors such as mistletoe (Dobbertin et al. 2005b) or insects (Dobbertin et al. 2007). Nevertheless, drought is identified to be the major driving factor of Scots pine`s decline (Sánchez-Salguero et al. 2012).

The observed growth reductions, diebacks and vulnerability to extreme drought events at its southern margin led to a discussion about the suitability of this species in the face of expected climate change in Germany and other European countries (Vennetier et al. 2007; Spellmann 2008; Jandl et al. 2012). Forecasts derived from bioclimatic envelope models query the future role of Scots pine. Based on the ecological niche theory, bioclimatic models describe the climatic component of the fundamental ecological niche; thus, the climatic conditions in which a species can survive and grow (Pearson and Dawson 2003). Following this concept, Scots pine is characterized as a boreal tree species not being adapted to warm and dry conditions (Walentowski et al. 2007). Even a moderate warming scenario of 1.8 °C would put warm areas of Germany (e.g., current annual mean temperature 9.5°C) way beyond the suitability range of this species (Kölling 2007). In contrast to this assessment, other authors expect Scots pine to gain under climate change scenarios and to experience increasing appreciation as suitable tree species for future European forests, due to its wide range of physiological tolerance and adaptability (Roloff 2008; Spellmann 2008). This is supported by studies that found Scots pine to be more resistant to warm and dry conditions than other economical important tree species, for example *Picea abies ([L.] KARST.)* or *Fagus sylvatica (L.)* (Beck 2010).

Obviously, these contrasting assessments of the suitability of Scots pine in the face of climate change reveal a lack of understanding of physiological thresholds and the potential of possible adaptations. Bioclimatic envelope models can provide a useful first approximation for possible impacts of climate change, but they often ignore the complexity of factors other than climate that shape species' distributions (Pearson and Dawson 2003; Ibáñez et al. 2008). In particular, these models do not account for provenance effects or possible genetic adaptations (Bolte et al. 2008). Considering intraspecific variation in species distribution models explicitly will help shedding light on this complex issue (Benito-Garzón et al. 2011).

Scots pine reveals high genetic diversity, a large genetic reaction norm and high potential of genetic adaptability: as an r-strategist, the species is characterized by short generation times, high fecundity, early and frequent fructification and the ability to disperse offspring widely (Kätzel 2008; Kätzel et al. 2008). Nevertheless, some authors fear that genetic adaptation could be slow in contrast to the pace of climate change (Rehfeldt et al. 2002). However, covering a large geographic range with contrasting environmental conditions, Scots pine evolved a wide phenotypic plasticity and genotypic variation (Lang et al. 2007). Considerable differences in phenology, morphology and growth traits are found among different Scots pine populations or provenances (e.g., Giertych 1979). Due to these differences, the provenances vary in growth potential and, even more crucial, in response to climate variables (Rehfeldt et al. 2002). Hence, climate change impacts on the species Scots pine are expected not to be uniform regarding intraspecific variation.

1.3 THE ROLE OF PROVENANCES

"Provenance" in forestry refers to a population of a tree species growing at a defined area (Callaham 1963). The research of provenances has a long tradition in forestry comprising various tree species (Rohmeder and Schönbach 1959; Ruetz et al. 1997; Konnert and Ruetz 2001), with first provenance trials of Scots pine already being established in 1820 (Giertych 1991). Originally, the focus was on the definition of genetic and environmental components of phenotypic variability between trees from different geographic regions (Callaham 1963).

Even in the absence of climate change, the consideration of the provenance level of tree species is of great importance. The use of suitable, locally best adapted provenances can be way more crucial than silvicultural measures or even the choice of tree species (Rossmässler 1967; Kramer et al. 1988; Ebert 1997). But at the same time, these provenance trials include observations of tree reactions of populations transferred to other environmental conditions. Allowing valuable insights regarding climatic adaptations these trials can be used to assess responses to expected future conditions (Mátyás 1996; Schneck 2007; Leites et al. 2012). Acknowledging provenance trial data by explicitly considering intraspecific variation and phenotypic plasticity was found to significantly alter the outcomes of species distribution models: severe impacts of climate change could be buffered and the extinction risk of southern populations could be alleviated (Benito-Garzón et al. 2011; Oney et al. 2013).

1.3.1 Conventional findings of provenance trials

The need of adequate stems for the use as ship masts was the motivation of early provenance trials of Scots pine during the 18th century (Schneck 2007). From then on provenance trials were mainly established to identify seed sources of populations with favorable traits in terms of commercial use, e.g., superior height and diameter growth, straight stem forms, low number of branches, thin branches (Rohmeder and Schönbach 1959; Rohmeder and Eicke 1969; Liesebach and Stephan 1998; Bachmann 2001). The International Union of Forest Research Organizations (IUFRO) organized provenance trials distributing international provenances of Scots pine to various participating countries in the years 1907, 1938, 1939 and 1982 (Giertych and Oleksyn 1992). In addition, provenance trials focusing on regional populations were established in Germany during the last century (Bachmann 2001; Nickel et al. 2007; Steinacker et al. 2007).

These trials reveal huge intraspecific variation within Scots pine. Morphological differences among provenances range from needle color (Rohmeder and Eicke 1969), needle length and needle weight (Stimm and Utschig 1994; Androsiuk et al. 2011) to branching and stem forms (Rohmeder and Schönbach 1959; Stimm and Utschig 1994; Bachmann 2001). At German sites, provenances from lowlands of central Europe, the Baltic region and Poland revealed superior growth yields (Giertych 1979; Stimm and Utschig 1994). With increasing longitude growth performance declines whereas quality augments at the same time (Schneck 2007). The cultivation of provenances derived from origins south of 45° N and north of 55° N seems not to be promising because of observed poor growth yields and low survival (Giertych 1979; Stimm and Utschig 1994; Stephan and Liesebach 1996a; Kohlstock and Schneck 1998). Furthermore local provenances or provenances from proximate origins were generally found to be among the better ones (Rohmeder and Eicke 1969; Giertych 1991; Giertych and Oleksyn 1992), although this was not always the case (Chmura et al. 2012). Despite the fact that differences among provenances can be found from the very beginning, the ranking of provenances regarding growth traits does not necessarily have to be constant (Giertych and Oleksyn 1992). In addition to growth rates, there are observations of divergent vulnerability to late frost, needle cast disease and insect attacks, with local provenances exhibiting best adaptations in many cases (Rohmeder and Eicke 1969; Stephan and Liesebach 1996b). Unsurprisingly, the provenances thus show unequal survival rates as well (Liesebach and Stephan 1998; Schneck 2007).

1.3.2 Geographic clines

In addition to the described classical form of provenance research, the exploration of genetic variation among provenances is complemented with many studies at the original provenance trials or conducted in growth chambers and separate field experiments. Clines along geographic origin and environmental gradients are described for various traits of Scots pine. This is typical for forest tree species since they are usually adapted to local climate conditions (Howe et al. 2003). Relating to 112 provenance trial studies including 309 analyses of temperate and boreal tree species from the Northern hemisphere a recent review found 78% of provenance trial analyses provide evidence of clinal variation regarding different quantitative traits (Alberto et al. 2013).

With increasing latitude bud set of Scots pine populations is observed to occur earlier (Mikola 1980; Hurme et al. 1997; Oleksyn et al. 1998; Repo et al. 2000; Savolainen 2004; Chmura et al. 2012; Notivol et al. 2007). Longitudinal effects are found for frost hardiness (Andersson and Fedorkov 2004) and for above ground biomass production (Oleksyn et al. 1999). Bud flush is also found to be earlier of northern provenances (Chmura et al. 2012) and seems to be earlier of provenances from higher altitudes (Salmela et al. 2011; Salmela et al. 2013) although this cline is weaker compared to bud set (Alberto et al. 2013). This could be due to the fact that bud flush strongly depends on chilling, forcing and only to some degree on photoperiod (Laube et al. 2014). Among populations of the same species, high phenotypic plasticity rather than genetically determined thresholds could be critical for the weak clines (Hänninen and Tanino 2011; Alberto et al. 2013). Furthermore, provenances from northern origins display higher nutrient concentrations compared to southern provenances, which is a possible adaption to limited nutrient availability (Oleksyn et al. 2002). Differences are also found for photochemical capacity among Scots pine populations of Scotland (Salmela et al. 2011). Less information exists about adaptations to drought or heat, but a study of Cregg and Zhang (2001) points out better adaptations to drought of Scots pine seedlings from Asian seed sources. Compared to European provenances they had a higher water-use efficiency and overall a lower mortality rate when exposed to drought. Alia et al (2001) found evidence for drought adaptation of Spanish provenances.

1.3.3 Differences in genetic structure

Differences in genetic structure among Scots pine provenances were revealed although studies showed that genetic variability within populations was high compared to among-population differences (Müller-Starck et al. 1992). High within-population variability accompanied by low genetic differentiation among populations (Prus-Glowacki and Stephan 1994; Robledo-

Arnuncio et al. 2005; Pyhäjärvi et al. 2008) is typical for wind pollinated species such as Scots pine due to effective gene flow (Harju and Muona 1989). Today's genetic structure is the result of post glacial migration, climate and environmental conditions and anthropogenic influences (Prus-Glowacki et al. 2003; Bilgen and Kaya 2007; Matías and Jump 2012 and citations therein). Floran et al. (2011) suggest that Spain, Northern/Central Europe and Fennoscandia can be distinguished as evolutionary units of Scots pine. Spanish, Italian and Turkish populations most probably did not take part in the last post glacial colonization of Europe (Puglisi and Attolico 2000; Naydenov et al. 2007; Prus-Głowacki et al. 2012). These populations represent unique material as they possibly represent ancient tertiary gene pools (Prus-Glowacki et al. 2003). Therefore it is suggested that populations in Central Europe originate mainly from Eastern or Northeastern Europe rather than from southern refugia (Pyhäjärvi et al. 2008; Prus-Głowacki et al. 2012).

1.3.4 Shortcomings and challenges

The motivation of provenance trials often was commercially driven, as described above. Consequently, existing provenance trials usually are established on sites with average site conditions or conditions close to the optimum avoiding harsh environments. Furthermore, provenances have been used, which are promising regarding quality and productivity provenance trails. These usually contain provenances derived from narrow ranges of climatic transfer distances (Leites et al. 2012). Thus, the existing trials often neglect populations of the southern margin. In the context of climate change, exactly these populations at the rear edge are of particular interest, because they could store special genetic diversity or adaptations to heat or drought (Nielsen and Jørgensen 2003; Hampe and Petit 2005; Prus-Głowacki et al. 2012). Furthermore, testing of provenances beyond the distribution range of the species and under climate conditions of expected climate change scenarios is urgently needed (Alberto et al. 2013). Classical provenance trials are set up with seedlings usually older than two years; therefore, they miss out on capturing the phase of germination and first establishment. Since every tree of a future stand has to undergo this crucial development and has to survive during this early phase of selection, detailed knowledge has to be established (Alberto et al. 2013). This would provide the required basis to implement the concept of assisted migration of suitable provenances as a valuable tool of "active adaptation" of forestry to climate change (Savolainen 2004; Bolte and Degen 2010; Chmura et al. 2012).

1.4 EFFECTS OF RISING TEMPERATURES AND DROUGHT ON TREES

1.4.1 Effect of high temperature

Rising temperatures, as predicted under climate change scenarios, will affect boreal and temperate plant ecosystems and forest trees since temperature influences all biochemical processes, phenological development, plant growth and survival. In temperature limited ecosystems warming will clearly have a positive effect on growth and survival, inducing range expansions of forests and forest trees (Grace et al. 2002; Parmesan and Yohe 2003; Morin et al. 2007). A positive effect could also be expected in other European regions as long as water availability is not limited (Boisvenue and Running 2006) and critical temperature thresholds are not exceeded. Heat stress directly affects plant metabolism (Rennenberg et al. 2006). In conifers, temperatures above 44 to 50°C cause severe damages, due to beginning denaturation processes of proteins (Larcher 2001).

Changes in leaf chemistry and photosynthesis due to moderate warming are described for several species, e.g., recently for *Abies faxoniana (FRANCH.)* (Wang J et al. 2012) and *Quercus pubescens (WILLD.)* (Contran et al. 2013). The net photosynthesis of saplings for three European oak species increased in an open top chamber experiment (Arend et al. 2013), whereas the photosynthetic response of 25 year old Scots pine trees was found to be negative (Wang et al. 1995). Respiration is also promoted by temperature, offsetting at least parts of gross photosynthesis, although in general a positive effect is expected for many species (Saxe et al. 2001; Way and Oren 2010). The effect of increased temperatures on photosynthesis is species-specific and depends on the ontogenetic stage of the tree, the position of the tree within the forest and even on soil properties (Chung et al. 2013; Contran et al. 2013). The effect on photosynthesis cannot simply be translated into changes in growth, since other factors such as nitrogen, water or light availability may be of importance (Chung et al. 2013). Generally an increase of temperature is observed to promote plant growth as summarized by recent reviews and a meta-analysis (Way 2011; Wu et al. 2011; Chung et al. 2013). However, this relationship is not always evident in experiments (Olszyk et al. 1998; Thiel et al. 2012; Kuster et al. 2013a).

Plant development and phenological phases are strongly driven by temperature. Due to the temperature rise during the last decades an extension of the growing season was already detected (Menzel and Fabian 1999). It is well established that leaf unfolding advanced by 2-5 days per decade and leaf senescence delayed by 1-2 days per decade (Menzel and Fabian 1999; Parmesan and Yohe 2003; Root et al. 2003; Menzel et al. 2006). The effect of temperature on phenology has also been found in a set of warming experiments of shrubland (Prieto et al. 2009) or tree species (Junttila 1986; Repo et al. 1996; Bronson and Gower 2010; Morin et al. 2010; Richter et al. 2012). Experimental results of phenology have to be interpreted with care as they can be influenced by the chosen heating system (Bronson et al. 2009) and tend to underestimate observed plant responses (Wolkovich et al. 2012). Temperature induced advances in phenology are also described for some plants located in temperate and tropical cities due to the urban heat island effect (Jochner et al. 2013). In general, higher temperatures do not necessarily lead to an increased rate of advancement of spring phenology (Morin et al. 2010). Furthermore, the response to temperature is found to be species- (Prieto et al. 2009) and provenance-specific (Richter et al. 2012).

In addition to direct effects of temperature, plants also are indirectly affected by temperature dependent processes, such as soil nitrogen mineralization or leaf litter decomposition (Melillo et al. 2011; Chung et al. 2013). Furthermore, interactions with herbivore insects could be altered under future climate conditions and impact forest ecosystems (Bale et al. 2002; Zvereva and Kozlov 2006; Bauerfeind and Fischer 2013). Changes of characteristics and frequency of cold events are also of importance regarding species distributions of trees (Kreyling et al. 2012; Gloning et al. 2013), but are not subject of this thesis.

1.4.2 Drought effect

There is no physiological process of plant life that is unaffected by moisture stress (Larcher 2001; Rennenberg et al. 2006). Water stress impacts growth more than any other environmental factor (Kozlowski et al. 1991), accounting for up to 80% of year-to-year growth variability in temperate forest stands (Bréda et al. 2006). Drought is triggering mortality, especially if multi-year events occur (Bigler et al. 2006) and is related to the increasing number of mortality events (Allen et al. 2010; Anderegg et al. 2013).

The response of radial increment to drought differs among tree species, as many comparative studies show (Weber et al. 2007; Vila et al. 2008; Bouriaud and Popa 2009; Linares et al. 2011; Michelot et al. 2012; Martin-Benito et al. 2013; Schuster and Oberhuber 2013). Numerous dendroclimatic studies analyze drought impacts on Scots pine (i.a. Oberhuber et al. 1998; Wilczynski and Skrzyszewski 2002; Seo et al. 2011; Vilà-Cabrera et al. 2011; Xenakis et al. 2012), but there is just a very limited number of studies considering differences among provenances, e.g., of Scots pine (Savva 2000), *Picea abies* (Nicke and Wolf 2009) or *Pinus contorta (DOUGL.)* (McLane et al. 2011). Furthermore, drought response depends on tree size (Zang et al. 2012) and tree age (Bogino et al. 2009; Lloret et al. 2011; Martínez-Vilalta et al. 2012). Stand structure has also to be considered as an effective factor (Candel-Pérez et al. 2012). It also has been shown that thinning alters drought response (Sohn et al. 2012) and inter-specific facilitation in mixed forest stands can offset drought stress at least to some degree (Pretzsch et al. 2013).

Growth response varies among leaf, shoot and root (Kozlowski et al. 1991) because allocation processes within trees are modified under drought conditions (Delucia et al. 2000; Bréda et al. 2006). This may also be attributed to seasonality effects. The formation of leaves, height growth and radial increment during the vegetation period rather take place subsequently than concurrently, although they overlap to some extent (Chmura et al. 2011). The maximum rate of root growth occurs late in the growing season and could therefore be less affected by droughts earlier in the year (Iivonen et al. 2001). Resulting higher root-shoot ratios seem to be more common in seedlings than in mature trees (Joslin et al. 2000).

Regeneration of forests is severely hampered by drought since seedlings are in particular prone to water stress (Chmura et al. 2011). It is therefore unsurprising that summer drought is the main mortality factor of Scots pine seedlings in the southernmost distributions (Castro et al. 2005; Benavides et al. 2013). But it is by far not clear how future recruitment rates will develop (Chmura et al. 2011). Provenance differences could be crucial, as it is indicated by studies on *Fagus sylvatica* (Nielsen and Jørgensen 2003; Czajkowski and Bolte 2006) or *Pseudotsuga menziesii* ([MIRB.] FRANCO) (St Clair and Glenn 2007). On the other hand, no considerable differences could be found in some experiments on *Pinus nigra (ARN.)* (Mataruga et al. 2012; Thiel et al. 2012).

Similar to the effect of temperature, indirect effects of drought may also be of importance for tree growth and survival. For example, drought alters the mobility and availability of soil nutrients (Ozolincius et al. 2009). Reduced nutrient uptake due to limited transpiration could be deteriorated at the same time by reduced decomposition and consequently lower nutrient availability (Kreuzwieser and Gessler 2010). Predisposition to insects or diseases caused by drought is also attributed to mortality events (Breshears et al. 2005; Griess and Knoke 2011).

1.4.3 Combination of temperature and drought effect

High temperatures could enhance negative drought effects by increasing vapor pressure deficit and further decreasing soil water potential (Pichler and Oberhuber 2007). The combination of warming and drought does not lead simply to additive effects and due to the existing lack of knowledge, further experiments exploring this interaction are strongly needed (Wu et al. 2011; Reyer et al. 2013). In addition, hot and dry weather situations are usually joined by high-light, constraining the plant to get rid of excess radiation (Chaves et al. 2003).

The combination of an increase in temperature with drought events is likely to be responsible for the rising number of tree mortality reports (Breshears et al. 2005; Adams et al. 2009; Allen et al. 2010, see also Chapter 1.1.2). Two alternative hypotheses triggering mortality in trees are discussed (Hartmann 2011). Following the carbon starvation hypothesis, reduced stomatal conductance as a response to drought finally leads to the depletion of carbon reserves and would be temperature dependent (McDowell et al. 2008). On the other hand, hydraulic failure, due to pronounced embolism under drought conditions, is suggested as the primary mechanism of mortality (Martínez-Vilalta et al. 2002). Due to low hydraulic safety margins across forest species worldwide, forest biomes are suggested to be equally vulnerable to this potential mortality effect (Choat et al. 2012).

The carbon starvation hypothesis has been questioned due to the lack of evidence (Sala et al. 2010) which is emphasized in some recent case studies (Anderegg et al. 2012; Gruber et al. 2012; Voltas et al. 2013). However, Adams et al. 2009 explained temperature dependent mortality rates in an experiment focusing on *Pinus edulis* with the depletion of carbon. Similarly, some authors suggest the importance of carbon reserves regarding mortality events of Scots pine observed in Spain (Galiano et al. 2011). There is evidence that the two hypotheses are mutually independent, but that they are non-exclusive (McDowell 2011; McDowell et al. 2011; Wang W et al. 2012). Therefore, mortality would occur when one or more of the processes associated with either of the hypotheses exceed a threshold, which probably is promoted by feedbacks across such processes (McDowell et al. 2011).

1.5 ASSESSING TREE RESPONSES TO CLIMATIC EFFECTS

The response of trees to climatic effects can be assessed generally by three different approaches, all of them including specific advantages and drawbacks. In experiments, climatic conditions can be set up imitating possible climate change scenarios, including climatic variability and extreme events (Jentsch et al. 2007; Reyer et al. 2013). Due to the fact that extreme events per definition occur rarely, their effects are more difficult to capture within observational studies, although this can be solved via retrospective analysis focusing on past events or by long-term observations (Menzel et al. 2006; Reyer et al. 2013). On the other hand observations provide the possibility to analyze effective variables and their interactions concurrently. Lastly, modeling approaches are a valuable tool for testing hypothesis derived from experimental or observational methods.

1.5.1 Experiments

There is already a large number of existing experiments on the response of plants to various factors such as ozone (Matyssek et al. 2010; Paoletti and Grulke 2010; Stampfli and Fuhrer 2010), CO_2 (Wang et al. 1995; Jach and Ceulemans 1999; Asshof et al. 2006), warming (see Chung et al. 2013 for overview) or drought (see Wu et al. 2011 for overview). Unquestionably, these experiments have increased our knowledge of possible consequences of global change, although they often focus on effects of a single factor due to experimental limitations. Therefore, important information gaps have still to be filled, interactions among factors being one of them (Boisvenue and Running 2006; Luo et al. 2008). Experiments including combined effects of precipitation and temperature are especially needed (Wu et al. 2011), which in addition would explicitly account for intraspecific variation and differences among populations (Alberto et al. 2013).

Experimental warming

The relevance of results and conclusions depends on the experimental design. The set up of an experiment will inevitably inhibit unwanted side effects to some degree. Therefore it is of importance to consider and to minimize possible artifacts in order to meet a relevant and realistic treatment (Beier et al. 2012). Different methods can be used to attain experimental warming of plants. Open top chambers provide a passive method of warming during the day, but are limited in heating capacity (Godfree et al. 2011). Infrared lamps overcome these constraints, but they do not imitate climate change warming realistically (Amthor et al. 2010). In addition, soil heating cables may disproportionately affect below ground parts of plants. Therefore, in the warming experiment of this thesis the air surrounding Scots pine seedlings is heated directly, which is a reasonable method to simulate global warming impacts (Amthor et al. 2010).

Manipulation of precipitation

Studies conducted in greenhouses have the advantage that many factors can be controlled and that some unwanted effects can be excluded, for example browsing and damages caused by mice. In such studies precipitation regimes can be easily controlled via irrigation. On the other hand, when conducted as pot experiments, they neglect natural root development, the most effective trait of drought tolerance (Bréda et al. 2006). Furthermore the advantages come at the cost of various artifacts such as possible differences of water chemistry, shading or passive warming (Beier et al. 2012). The latter two are also the case in field studies using permanent shelters. Since radiation and especially high-light stress are impacting plants especially during heatwaves, shading can actually alleviate possible plant stress (Boeck and Nijs 2011). Therefore, the use of retractable shelters in field studies is recommended (Beier et al. 2012).

1.5.2 Observations

Long-term phenological observations contribute significantly to the detection of climate change impacts in terms of changes in average trends (Parmesan and Yohe 2003; Menzel et al. 2006). Observational studies can also explore plant responses to extreme events if they happen to capture these. This is more likely in long-term data analyzes and could be accidentally the case in short-term observations (Reyer et al. 2013). Well established are dendroclimatic approaches using radial growth of trees as proxy for tree vitality (Dobbertin 2005) and they are widely used to study the drought response of trees (Ferrio et al. 2003, Breda and Badeau 2008; Vila et al. 2008; Bouriaud and Popa 2009; Linares et al. 2011; Pasho et al. 2011; Eilmann and Rigling 2012; Toromani et al. 2011; Fischer and Neuwirth 2013, Martin-Benito et al. 2013). The use of height growth in this context is less common, since height growth of trees shows a higher variability and is more difficult to assess without cutting the whole tree (Mäkinen 1998).

As disadvantage, observations are limited to actually observed conditions and do not elucidate possible conditions beyond that. Furthermore, long-term analyzes integrate overall effective factors that led to the observed response. In order to be able to draw conclusions regarding a specific factor, they have to account for these contributing factors. Regarding long-term growth changes, additional effects such as tree aging or possible fertilization processes due to nitrogen depositions or increasing atmospheric CO_2 concentrations have to be taken into account (Kahle 2008).

1.5.3 Models

Models are an important tool for testing hypotheses that are derived from observations, experiments or theories (Luo et al. 2011; Reyer et al. 2013). They are also widely used to transfer established knowledge to forest management (Pretzsch et al. 2007). Developed growth simulation models can be used to study possible impacts of climate change, as long as the conditions do not exceed those from the parameterization data too much (Pretzsch et al. 2002). In addition to such approaches, species distribution models are commonly used to assess climate change impacts (Morin et al. 2007; Mellert et al. 2011; Gloning et al. 2013). Possible drawbacks of this method including the disregard of provenance effects or climatic extremes are already described in Chapter 1.2. Nevertheless the use of models, especially if combined with observational methods and/or experiments, is essential to evaluate future climate change and their impacts on plants and forests (Luo et al. 2011; Wang W et al. 2012). However in the absence of a physiological understanding their predictive ability remains limited (Wang W et al. 2012).

2 BACKGROUND AND OBJECTIVES

The study was funded by financial resources of the “Klimaprogramm Bayern 2020”, a program of the Free State of Bavaria initiated to support climate change research. The project KLIP 10 “Trees in an extreme future” was one of 25 research projects supported by the Bavarian Ministry of Food, Agriculture and Forestry from 2009 to 2012.

The project KLIP 10 focused on the impact of extreme events on trees and consisted of two subprojects. The first part, as subject of this thesis, explores impacts of temperature and drought on provenance of Scots pine and was conducted by myself. The integration of extreme events into distribution models by implementing tools of extreme value theory was the task of Philipp Gloning and complemented the project.

The Bavarian Office for Forest Seeding and Planting as our project partner was responsible for the genetic analysis within this study. The forest tree nursery at Laufen of the Bavarian State Forestry Enterprise (Bayerische Staatsforsten) supported the experimental designs with practical suggestions.

2.1 STUDY DESIGN

In this thesis the so far contrasting assessment of the future suitability of Scots pine is addressed by exploring provenance differences in response to temperature and drought. In order to get a more comprehensive picture, experimental approaches are complemented with a retrospective observation study. Furthermore, within the project KLIP 10 the presented dissertation was accompanied by a modeling approach focusing on distribution models and the integration of extreme events with help of extreme value statistics, which is not part of this thesis. For the presented dissertation, two experiments of relative short duration focusing on the development of seedlings and a dendroecological analysis on mature Scots pine provenances were realized.

Ten provenances of Scots pine from the southwestern rim to the central part of the distribution range (Figure 2.1, Table 3.1) were chosen for the experimental investigation. Seeds were derived from different institutions who had harvested them for commercial reasons or research purposes. Prior to the experiments, the provenances were genetically characterized. Both experiments, set up as a greenhouse and a field study, were established at Freising within the campus of the Technische Universität München.

The first experiment is subject of the article summarized in Chapter 4.1 (Taeger et al. 2013a) and is hereinafter referred to as “greenhouse experiment”. It focused on the germination and the development of the provenances during the first vegetation period in 2010. The experiment was conducted in the greenhouse. Seedlings were exposed to two water regimes and an extreme heat event. Phenology and growth development were thoroughly observed to detect differences among provenances and to reveal geographic clines. Harvesting of all seedlings and biomass measurements completed the experiment after the first vegetation period.

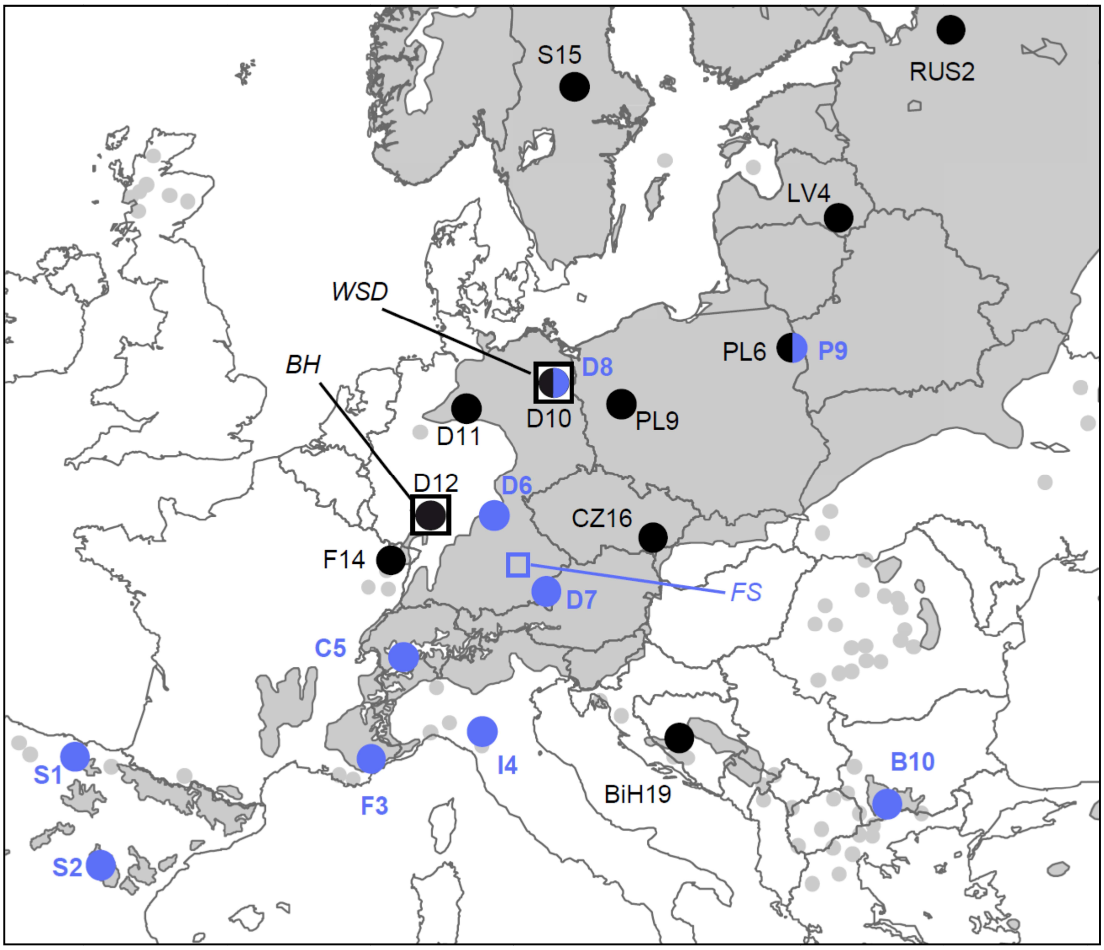

Figure 2.1 Map of investigated provenances of the experiments (blue circles) and the IUFRO 1982 trial (black circles); additionally the location of the experiments (blue square) and the two sites Waldsieversdorf (WSD) and Bensheim (BH) of the IUFRO 1982 trial (black squares) are shown; gray area representing the distribution of Scots pine (EUFORGEN 2009); for details about provenances see Table 3.1

In the second experiment the response of the ten provenances to experimental warming and drought was investigated under field conditions. The experiment, hereinafter referred to as "field experiment", is outlined in Chapter 4.2 and described in the article of Taeger et al. (2014). With the help of a complex infrastructure, consisting of a rain-out shelter and a self-developed heating system, these experimental manipulations were set up and facilitated at the same time natural radiation regime and natural root development. After sowing in 2010, huge losses of seedlings were caused by needle cast disease irrespective of provenance. Therefore a restart of the experiment in spring 2011 was inevitable. Consequently, the duration of the experiment was reduced by one year. Phenology and growth responses were recorded during two years of observation. All plants were thoroughly excavated and separate biomass measurements of buds, needles, shoot and roots were the final step of the experiment in fall 2012.

A dendroclimatic study of the IUFRO 1982 international provenance trial complemented the investigations on germination and seedling development (see Chapter 4.3, Taeger et al. 2013b). The growth responses to temperature, precipitation and drought events of eleven provenances of this trial were investigated at two sites (Bensheim, Waldsieversdorf) located in Germany (Figure 2.1). Climate/growth relationships were explored by measurements of tree-ring width chronologies and annual height increment.

2.2 RESEARCH QUESTIONS

Based on the state of knowledge and the outlined research needs briefly described in the introduction a series of research questions were addressed within this thesis.

The leading research questions were:

1. Do the chosen provenances differ in genetic composition, phenology and growth?
2. How does Scots pine respond to elevated temperatures and drought events?
3. Do provenances of Scots pine differ in their response to climatic effects?
4. Which role do provenances play in the face of climate change?

To pursue these research goals, experimental manipulations were combined with an observational, dendroclimatic study. The prediction of future performance of Scots pine to increased climate variability should be based on the exploration of responses of genetically characterized provenances to extreme events (Martínez-Vilalta et al. 2012). For this reason, two experiments were established in order to answer the following questions:

- Do the chosen provenances differ in their genetic composition?
- Do these provenances exhibit geographic clines in their development or growth?

To assess the response of Scots pine to climatic factors experimental manipulations were conducted in the greenhouse and under field conditions. A complex infrastructure was set up in order to minimize artifacts while simulating elevated temperatures and drought events. On basis of these experimental preconditions the second and third lead question were addressed focusing on following effects:

- How are the provenances impacted by drought treatments?
- How are the provenances impacted by warming or heat?
- Are there interactions regarding the response to drought and warming?

The experimental approaches were complemented by a dendroclimatic study in order to explicitly elucidate responses of mature trees of Scots pine provenances. The focus within the dendroclimatic study was on the second and third lead question, which were addressed in detail with following questions

- Can we identify general climate-growth relationships?
- How do the provenances respond to drought regarding height increment and radial growth?
- Do provenances differ in resistance, recovery and resilience to drought events?

Overall the thesis elucidates the last leading question in particular with respect to recommendations to future forest management.

3 MATERIAL AND METHODS

3.1 PROVENANCES

Provenances from southwestern to central parts of the species' distribution range were chosen for the two experiments (Figure 2.1, Table 3.1). This approach was taken, because populations from the rear edge are usually neglected in provenance trials, but could bear special genetic diversity (Hampe and Petit 2005) or provide adaptation to heat and drought (Alia et al. 2001; Nielsen and Jørgensen 2003). Using two similar provenances (P9-PL6; D8-D10) this selection ties the experiments up to the IUFRO 1982 trial and expands the original setting of this trial further southwest. All seeds came from natural, autochthonous populations of Scots pine, except for the German progeny "Alpenkiefer" (D7), which was derived from a seed orchard in Laufen, Germany (origin of parent trees: Bavarian alps, above 900m a.s.l.). Throughout the study all material will be referred to as "provenances" or "populations".

Table 3.1 Origin of the provenances investigated in the experiments (blue) and the IUFRO 1982 trial (black) characterized by latitude, longitude, altitude as well as mean annual temperature (T) and annual sum of precipitation (PPT); climatic data is derived from WorldClim database (1950-2000; Hijmans et al. 2005). Labels of the IUFRO 1982 according to original description (Giertych and Oleksyn 1992).

No.	Country	Origin	Lat.	Long.	Alt. (m a.s.l.)	T (°C)	PPT (mm)
S1	**Spain**	**Alto Ebro**	**42°59' N**	**03°17' W**	**860**	**10.1**	**937**
S2	**Spain**	**Montes Universales**	**40°28' N**	**01°53' W**	**1670**	**7.4**	**667**
F3	**France**	**Prealpes du Sud**	**43°45' N**	**06°40' E**	**1185**	**7.8**	**947**
I4	**Italy**	**Emilia Romagna**	**44°30' N**	**10°27' E**	**460**	**10.8**	**886**
C5	**Switzerland**	**Wallis**	**46°18' N**	**07°39' E**	**900**	**6.7**	**1089**
D6	**Germany**	**Hauptsmoorwald**	**49°51′ N**	**10°58' E**	**250**	**8.5**	**625**
D7	**Germany**	**Alpenkiefer**	**47°57′ N**	**12°54' E**	**420**	**8.7**	**1114**
D8	**Germany**	**Ostdeutsches Tiefland**	**53°04' N**	**13°29' E**	**75**	**8.4**	**571**
P9	**Poland**	**Supraśl**	**53°15' N**	**23°23' E**	**181**	**6.6**	**580**
B10	**Bulgaria**	**Garmen**	**41°43' N**	**23°54' E**	**1300**	**6.2**	**657**
RUS2	Russia	Kondežskoe	59° 58' N	33° 30' E	70	3.3	703
LV4	Latvia	Silene	55° 45' N	26° 40' E	165	5.5	650
PL6	Poland	Supraśl	53° 12' N	23° 22' E	160	6.9	571
PL9	Poland	Bolewice	52° 24' N	16° 03' E	90	8.5	554
D10	Germany	Neuhaus	53° 02' N	13° 54' E	40	8.5	567
D11	Germany	Betzhorn	52° 30' N	10° 30' E	65	8.8	626
D12	Germany	Lampertheim	49° 30' N	8°30' E	97	10.1	643
F14	France	Haguenau	48° 49' N	7° 46' E	157	10.0	657
S15	Sweden	Sumpberget	60° 11' N	15° 52' E	185	4.6	660
CZ16	Czech Republic	Zahorie	48° 46' N	17° 03' E	160	9.5	623
BiH19	Bosnia-Herzegovina	Prusačka Rijeka	44° 06' N	17° 21' E	885	8.1	1009

The dendroclimatic study focused on eleven of the 20 provenances of the international IUFRO 1982 provenance trial. The original setting of the trial consists of two gradients: north-south and west-east, which could be maintained with the chosen selection. However, progenies from seed orchards were not included. Details about the original concept and a complete list of all provenances can be found in Oleksyn (1988) and Giertych and Oleksyn (1992). The original labels introduced in these articles are kept throughout this thesis.

3.2 FIRST EXPERIMENT – EARLY TESTING AT THE GREENHOUSE

This experiment focused on the first vegetation period. The set up enabled a close and detailed assessment of the development during the first growing season of the chosen Scots pine provenances. Plant evolution was followed on a high resolution, with observation rhythms of several times per week up to daily observations.

All seeds were sown into plastic boxes (40 x 60 x 13 cm) with sealed bottom and side walls (Figure 3.1) on 10 May 2010. A prefertilized peat culture substrate (TKS 1, Floragard) was used as substrate. Per provenance 300 seeds were sown into a regular grid following a split plot design. Two treatments were established, each treatment consisted of ten boxes. Each of the boxes was divided into three plots containing 50 seeds of one provenance, resulting in a seed spacing of 3.5 x 3.5 cm. Provenances were randomly allocated, with the precondition that each box contained three different provenances.

Seedlings were grown under natural light conditions in the greenhouse. Watering was done every day on a gravimetrical basis, from August on the interval was changed to every second day. The resulting soil moisture regime was 30.7 % and 23.6 %, after the 1 August 28.3 % and 11.8 %, respectively for the control and the dry regime. Seedlings of the dry regime were exposed to a drought event, when watering was stopped from 13 July to 1 August. All seedlings were harvested after the first vegetation period in the second week of November 2010.

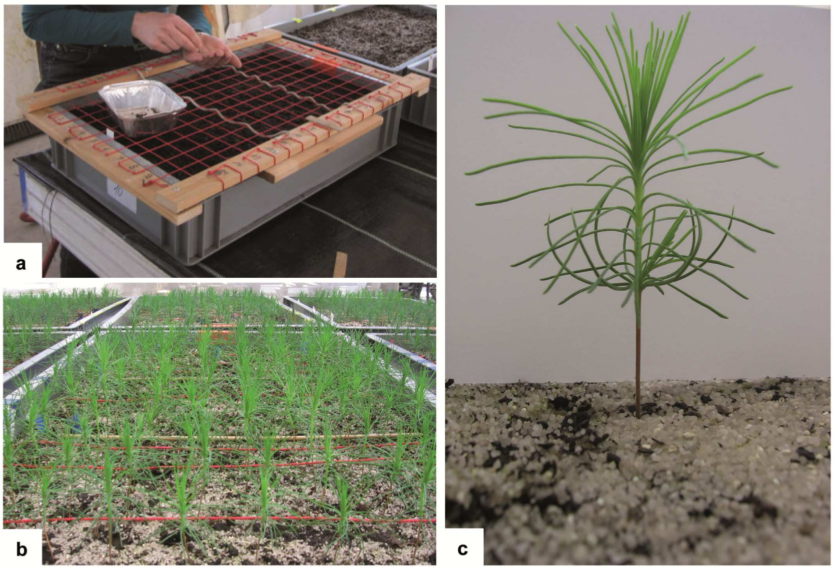

Figure 3.1 Scots pine seedlings in the greenhouse experiment: a) sowing on May 10 2010 following the regular grid, b) 9 week old seedling c) 10 week old seedlings across the boxes

3.3 SECOND EXPERIMENT - MANIPULATION EXPERIMENT AT THE FIELD

At the field, seeds were sown into a sandy loam with increasing clay proportion by depth. A split-plot design was applied. Seedlings were exposed to two temperature levels (ambient, heated) and two levels of precipitation (ambient, dry), resulting in four treatments (control, warm, dry, warm+dry) as displayed in Figure 3.2.

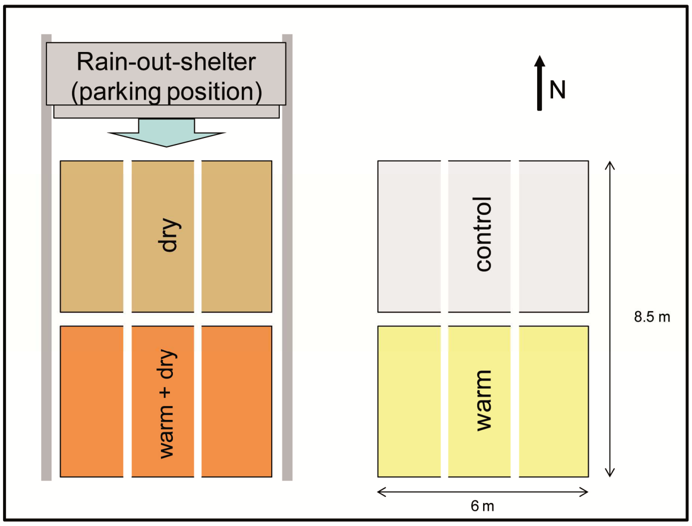

Figure 3.2 Experimental design of the field experiment with the four treatments: control, warm, dry, warm+dry; the treatments are subdivided in three subplots; the plots of the dry and warm+dry treatment are equipped with a rain-out shelter.

Each treatment contained three replicates of all ten provenances (each with twelve individuals) in randomized order. Overall, 1440 seedling locations were designated for measurements. Additional buffer rows were used to install measurement devices within the plots and surrounded the seedlings under investigation.

Air temperature and relative humidity were measured 10 cm above the surface (representing plant height) in each of the twelve subplots with shaded HOBO sensors (HOBO Pro v2 U23-002, Onset, USA). At 10 cm depth, soil temperature was monitored with HOBO sensors (HOBO TMC20-HD, Onset, USA) and volumetric soil water content with ECH_2O EC-5 sensors (Decagon Devices, Inc., USA). All devices recorded data at 10 minute intervals.

For the climatic manipulations an extensive infrastructure was established at the experimental field. An automated, transparent rain-out shelter was installed to simulate drought events (Figure 3.3). It was controlled by a rain sensor and covered the dry plots only during rain events of simulated drought periods. A heating system was developed, which aimed to heat the air surrounding the seedlings directly and to prevent excessive soil heating (Figure 3.4). A hot-water system heated a grid of corrugated, black plastic tubes, which were placed in a distance of 9 cm from the seedlings. The tubes were mounted 2 cm above ground on top of wooden strips to avoid disproportionate soil heating (Figure 3.5). The computer based regulation allowed a maximum warming of the seedlings of 4 K (measured 10 cm above ground) compared to control plots (Figure 3.7). For additional heating in 2012, 50% of the ground was with stripes of a black, water-permeable geomembrane.

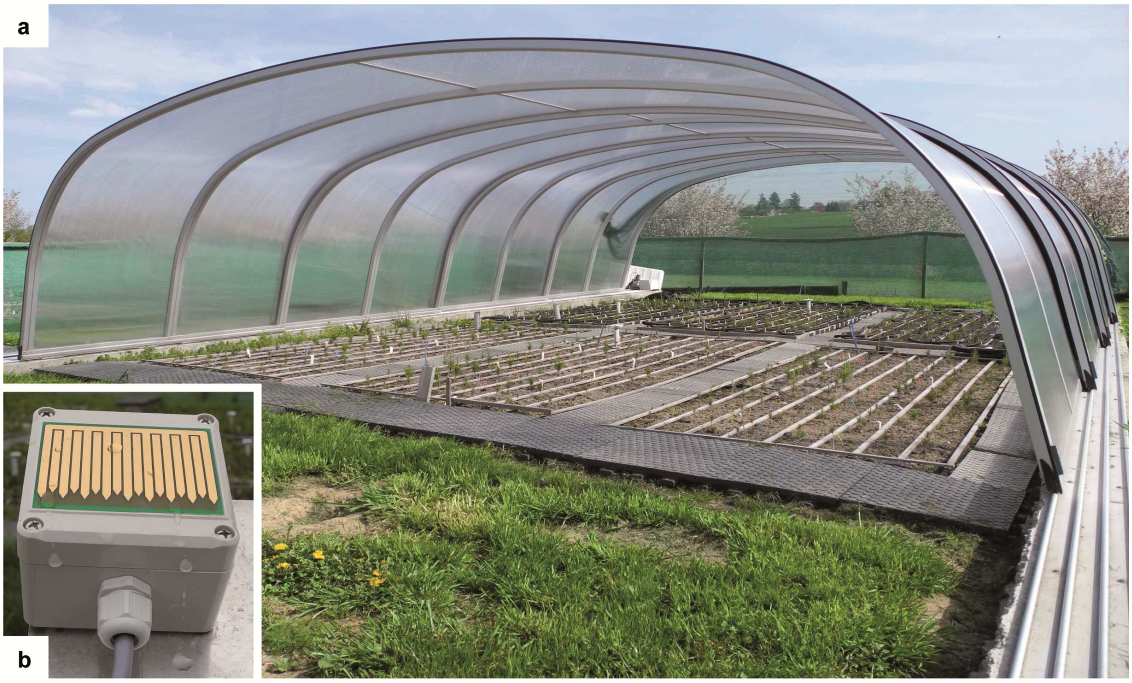

Figure 3.3 Installation for manipulation of precipitation with a) the rain-out shelter covering the dry and warm+dry treatment plots and b) the rain sensor that closes the rain-out shelter in case of rain

Figure 3.4 Heating system at the field experiment consisting of a) the boiler, b) the water distributor, c) the computer-control, d) the tubes and stripes of black, water-permeable geomembrane at the heated plots

Figure 3.5 Seedling during heating period 2012 surrounded by black plastic tubes (mounted on top of wooden strips to prevent disproportionate soil heating) and the stripes of black water-permeable geomembrane

Figure 3.6 Seeds and seedlings during the experiment with a) sowing into a regular grid, b) reduction of seedlings to one seedling per seeding location in March 2012, c) measurement of water potential in August 2012, and d) seedlings at end of the second vegetation period 2012

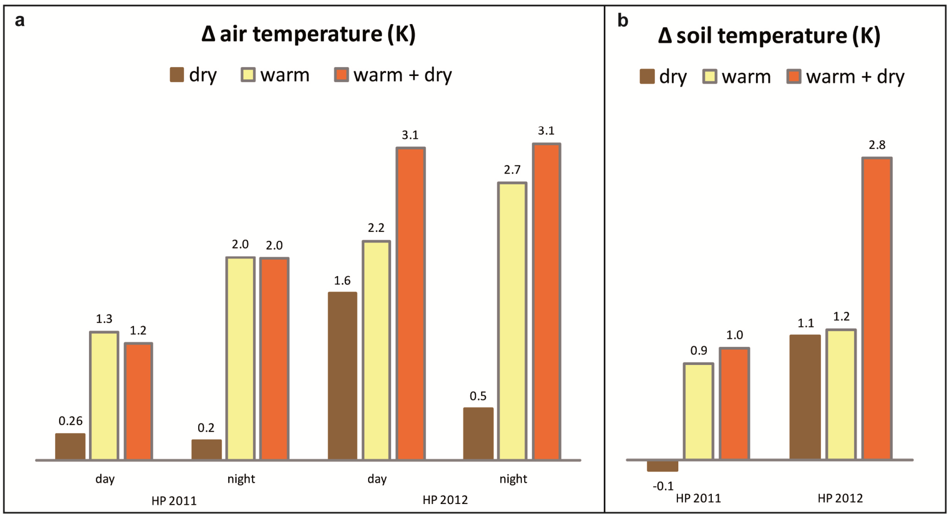

Figure 3.7 Temperature differences of the treatment plots (dry, warm, warm+dry) compared to the control plots during the heating period 2011 (HP 2011) and 2012 (HP 2012) of a) air temperature measured at 10 cm height and b) soil temperature measured at 10 cm depth. Shown are average values per treatment.

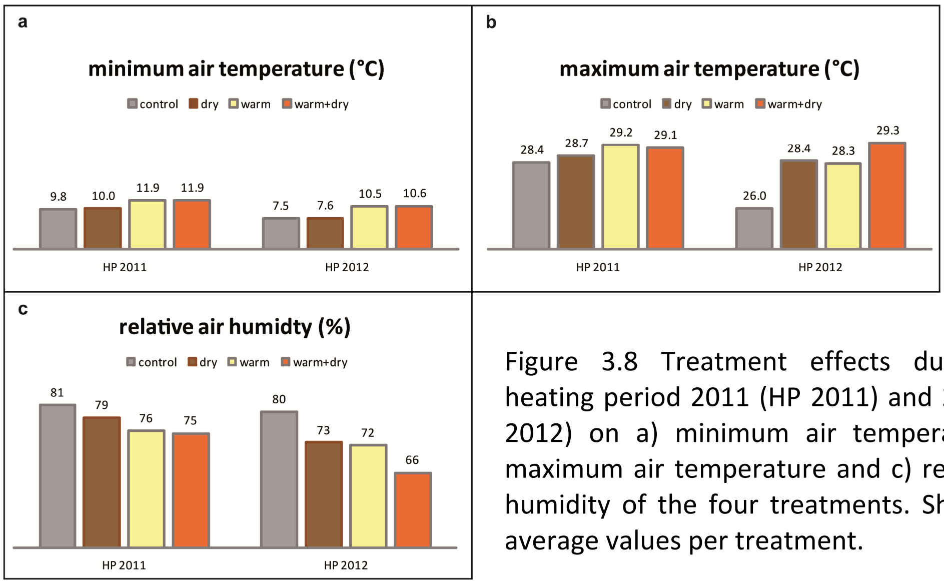

Figure 3.8 Treatment effects during the heating period 2011 (HP 2011) and 2012 (HP 2012) on a) minimum air temperature, b) maximum air temperature and c) relative air humidity of the four treatments. Shown are average values per treatment.

Besides to the detailed description of the climate manipulations in the article summarized in Chapter 4.2 (Taeger et al. 2014), some information about the temperature manipulation is provided here. The heating system allowed direct heating of the air surrounding the plants and prevented disproportionate soil heating, as can be seen in Figure 3.7. The temperature increase of the dry treatment in 2012 is due to reduced precipitation and consequently reduced soil moisture. In addition to average temperature, also minimum and maximum temperatures could be manipulated successfully (Figure 3.8). Furthermore, the reduction of relative air humidity is important in order to simulation drought periods (Beier et al. 2012). With the chosen heating system and infrastructure the relative air humidity could be reduced by 6% in 2011 and by 14% in 2012 (Figure 3.8c).

3.4 DENDROCLIMATIC STUDY OF THE IUFRO 1982 PROVENANCE TRIAL

At two sites in Germany (Figure 2.1) various growth traits of eleven provenances (Table 3.1) of the IUFRO 1982 provenance trial were sampled in January and February 2011. Both stands were unthinned so far. It was a unique opportunity, since destructive sampling could be integrated into the first thinning measure. Therefore, it was possible to gather stem discs as well as accurate measurements of annual height growth on harvested trees.

Per site and provenance 12 trees were selected, with the exception of provenance F14 (11) at Bensheim, RUS2 (11) and BiH19 (10) at Waldsieversdorf. Overall, 142 trees at Waldsieversdorf and 132 trees at Bensheim were sampled, all of them co-dominant trees (social tree class 2 according to Kraft (1884)). Tree height, crown length, the length of annual shoots (measured as distance between branch whorls) and diameter at breast height (1.3 m) were recorded. Stem discs were taken at breast height to determine annual tree-ring width. Tree-ring width was standardized as basal area increment following Biondi and Qeadan (2008).

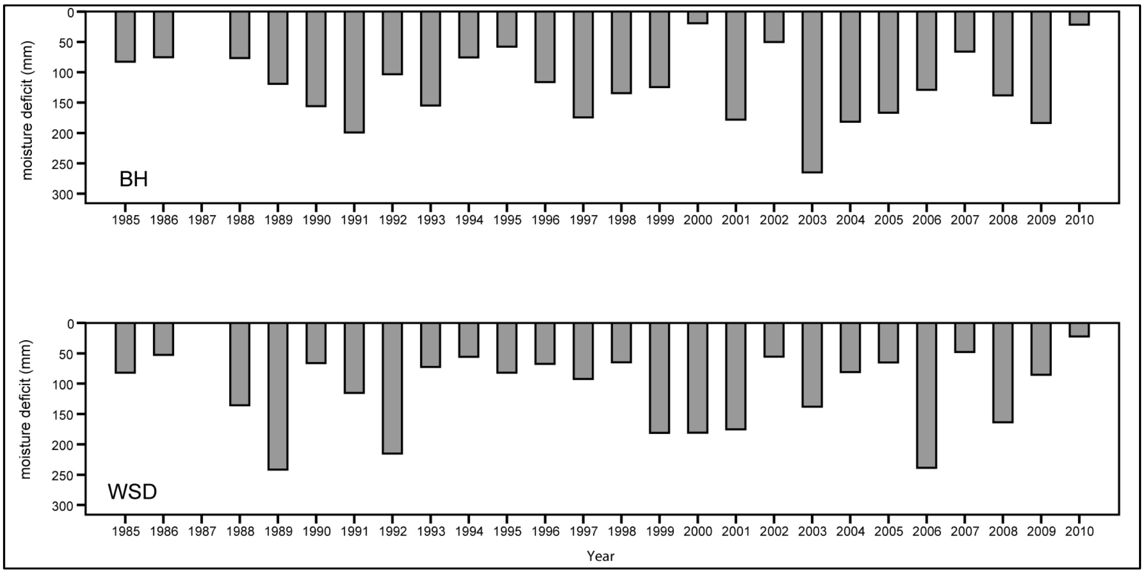

Figure 3.9 Moisture deficit during the vegetation period at Bensheim (BH) and Waldsieversdorf (WSD) for the years 1985 to 2010

Local climate of the two sites was characterized by daily values of climatic parameters obtained from nearby stations (distance less than 10 kilometers) of the German Meteorological Service (Deutscher Wetterdienst). The Thornthwaite monthly water-balance model (McCabe and Markstrom 2007) was run for each site and the moisture deficit was derived as the difference of potential and actual evapotranspiration. This moisture deficit is a good proxy for water supply of trees (Stephenson 1998). Then the most extreme drought year was identified as the year with the highest moisture deficit during the vegetation period. At Bensheim 2003 was the most extreme drought year, whereas at Waldsieversdorf 1989, 1992 and 2006 were considered as extreme years. Since no information on tree-ring width before 1990 was available the analysis of drought impacts on growth parameters was conducted for 2003 at Bensheim and 2006 at Waldsieversdorf.

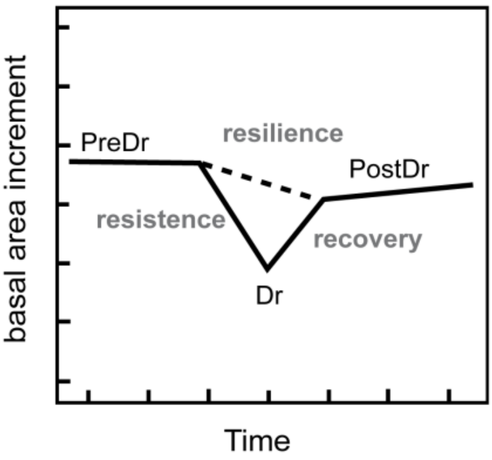

Figure 3.10 Individual tree response of basal area increment to a drought event over time, characterized by the period before the drought event (PreDr), growth during the drought event (Dr), and after the drought event (PostDr)(modified after Lloret et al. (2011)).

Individual tree tolerance to drought events was analyzed using indices for resistance, recovery, resilience and relative resilience introduced by Lloret et al. (2011) (Figure 3.10, Table 3.2). Drought events were identified as years with highest moisture deficit during the vegetation period and growth during such a drought year was assessed (Dr). The periods before (PreDr) and after the drought event (PostDr) were calculated as mean growth of three respective years, similar to the study of Pretzsch et al. (2013).

Table 3.2 Tolerance indices resistance, recovery, resilience and relative resilience calculated following Lloret et al. (2011).

Resistance = Dr / PreDr
Recovery = PostDr / Dr
Resilience = PostDr / PreDr
Relative Resilience = ((PostDr – Dr) / (PreDr – Dr)) (1 – (Dr / PreDr))

Provenance performance was summarized with an archetypal analysis (Cutler and Breiman 1994). This type of analysis aims at synthesizing a set of multivariate observations through a few points (the archetypes), that do not necessarily have to be observed. These archetypes lie on the boundary of the data scatter, and all observations can be represented as their convex combinations. The set of performance metrics for this analysis included measures for growth (height growth, diameter at breast height, stem volume), general climate sensitivity (regarding basal area increment and annual height growth) and drought tolerance (resilience of basal area increment and height growth). The ideal performer was defined as being high on growth metrics, low on general climate sensitivity and high on drought tolerance. More details about this analysis are given in the article (Taeger et al. 2013b).

4 SUMMARIES OF THE PUBLISHED ARTICLES

4.1 LARGE-SCALE GENETIC STRUCTURE AND DROUGHT-INDUCED EFFECTS ON EUROPEAN SCOTS PINE (PINUS SYLVESTRIS L.) SEEDLINGS

Steffen Taeger[1], Barbara Fussi[2], Monika Konnert[2], Annette Menzel[1]

2013. European Journal of Forest Research, Volume 132, Issue 3, pp. 481–496.

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Seedlings of ten provenances of Scots pine (*Pinus sylvestris* L.) from the south-western to the central part of the species` distribution range were investigated in a greenhouse experiment under dry conditions compared to a well-watered control. We conducted an isozyme study and recorded phenology as well as growth traits during the first year of growth. Genetic variability and genetic diversity increased from the westernmost provenances to those central to the distribution.

Provenances from the Apennines and Spain revealed the strongest genetic differentiation compared to all others, whereas populations from Germany, Poland and Bulgaria were found to belong to the same gene pool. Seedling development and bud set were faster in northern populations. Shoot length was highest for Polish and German provenances within both regimes, populations from France and Spain had the longest roots. Reduced soil moisture slowed later development stages and delayed bud set for all provenances by about 5 days. Shoot growth decreased considerably under the dry regime for all provenances. German provenances were the most sensitive to drought whereas Spanish provenances showed adaptation to drought conditions indicated by the lowest reduction in shoot growth relative to optimum conditions.

The results of this pilot study show that under more pronounced drought conditions with repeated drought events the so far established superiority of north-eastern provenances compared to south-western ones could diminish in the future.

Individual contribution

Barbara Fussi and Monika Konnert conducted the genetic analyses and contributed to the manuscript. Annette Menzel provided suggestions for statistical analysis, corrections and proof reading. I did about 75% of the work including design of the experimental set up, experimental work, data processing, statistical analysis and writing the manuscript.

4.2 EFFECTS OF TEMPERATURE AND DROUGHT MANIPULATIONS ON SEEDLINGS OF SCOTS PINE PROVENANCES

Steffen Taeger[1], Tim H. Sparks[1,2,3,4,5], Annette Menzel[1,2]

2014. Submitted to Plant Biology.

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Rising temperatures and more frequent climatic extremes as a consequence of climate change are expected to affect growth and distribution of tree species that are adapted to current, local conditions. Species distribution models predict a considerable loss of habitats for *Pinus sylvestris* not only at the warm and dry edge of its distribution. These models do not consider possible intraspecific differences in response to drought and warming that could buffer those impacts.

We tested 10 European provenances of *P. sylvestris*, from the southwestern to the central part of the species distribution, in their response to warming and drought in a factorial design. In this common-garden experiment the air surrounding plants was heated directly to prevent excessive soil heating, and drought manipulation, using a rain-out shelter, permitted almost natural radiation including high-light stress. Plant responses were assessed as changes in phenology, growth increment and biomass allocation.

Warming had a minor effect on growth but advanced phenological development and had a contrasting effect on bud biomass depending on water availability. Seedlings of *P. sylvestris* reveal a plastic response to drought by increased tap-root length and root-shoot ratios. Strongest root growth response was found for southwestern provenances indicating a specific drought adaptation at the cost of overall low growth of aboveground structures even under non-drought conditions.

The intraspecific variation of *P. sylvestris* provenances could buffer climate change impacts although additional factors such as the adaptation to other climatic extremes have to be considered before assisted migration could become a management option.

Individual contribution

Tim Sparks gave statistical advice and edited the manuscript; Annette Menzel provided suggestions for experimental set up, statistical analysis, corrections and did proof reading. I did about 90% of the work including the experimental design, all observations and measurements, data processing, statistical analysis and writing the manuscript.

4.3 IMPACT OF CLIMATE AND DROUGHT EVENTS ON THE GROWTH OF SCOTS PINE (*PINUS SYLVESTRIS* L.) PROVENANCES

Steffen Taeger[1], Christian Zang[1], Mirko Liesebach[2], Volker Schneck[3], Annette Menzel[1]

2013. Forest Ecology and Management, Volume 307, pp. 30- 42

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We explored the growth response of Scots pine to temperature, precipitation, and drought focusing on eleven provenances from the IUFRO 1982 international provenance trial. At two macroclimatically different sites in Germany we measured chronologies of tree-ring widths and annual height increment. We estimated general climate/growth relationships and examined growth response, based on tolerance indices of resistance, recovery, resilience and relative resilience, to the most severe drought event per site. Using multivariate benchmarking of provenance archetypes, we established a ranking of the individual provenances in terms of general performance.

In addition to considerable differences in overall growth between provenances, growth metrics differed between sites which were mostly attributable to climate. Basal area increment depended mainly on water availability from May to July, whereas annual height growth was influenced by moisture deficit during May of the current year. The reaction to drought events was shown to depend on the timing and duration of the drought event. Differences between provenances in resistance were modest, but more pronounced for recovery and especially for resilience and relative resilience. The results indicate a better adaptation to drought of the provenance from Bosnia Herzegovina and of local German provenances compared to other provenances. We summarized the findings by aligning the eleven provenances between two multivariately defined archetypes, one of which represented best general performance defined by good overall growth, low climate sensitivity and high resilience to drought. This approach confirmed the superior performance of the local German populations. Provenances from France and Poland were ranked above average whereas northern provenances and that from Bosnia Herzegovina were found to be least suitable at the sites under investigation. Our results clearly demonstrate the importance of considering provenance in the discussion about future adaptedness and adaptability of tree species under climate change scenarios.

Individual contribution

Christian Zang provided suggestions for statistical analysis and the archtype analysis. Mirko Liesebach and Volker Schneck supported sampling and provided additional information about the sites. Annette Menzel provided suggestions for statistical analysis, corrections and did proof reading. I did about 85% of the work including the experimental work, data processing, statistical analysis and writing the manuscript.

5 DISCUSSION

5.1 PROVENANCE DIFFERENCES IN GENETIC COMPOSITION, PHENOLOGY AND GENERAL GROWTH TRAITS

5.1.1 Genetic composition

The prediction of future performance of Scots pine in the face of increased climate variability can adequately be explored by the investigation of genetically characterized provenances and their responses of to extreme events (Martínez-Vilalta et al. 2012). It is reasonable to expect differences in response patterns from genetically differing provenances (Thiel et al. 2012). Therefore, the exploration of the genetic composition of provenances, conducted as an isoenzyme analysis (Taeger et al. 2013a), forms the basis of the seedling experiments at the greenhouse and at the open field presented in this thesis.

Genetic variability, measured as mean number of alleles and genotypes per locus, increased from southwestern European populations to Central European populations. The low variability of provenances from Spain (S1, S2) and Italy (I4) is probably due to fragmented habitats at the trailing edge of the species distribution, which could have led to genetic erosion and bottleneck effects (Jump and Penuelas 2006). However, the high genetic variability and genetic diversity of the Bulgarian provenance (B10) contradicts this hypothesis and remains unexplained. The variability values found in the genetic analysis of this thesis differ slightly from those found in an European wide study of Prus-Głowacki et al. (2012), probably due to different isozyme loci used.

The highest separation based on Nei's genetic distance (Nei 1972) of the Italian provenance (I4) to all other provenances is conform with studies from Scalfi et al. (2009) and Belletti et al. (2012), who could demonstrate the distinctiveness of populations from the Apennine as relict populations. The subpopulation differentiation clearly separated the ten provenances into west and east. Furthermore, using Nei's genetic distance it was possible to divide the provenances into a mid-European to eastern group (C5, D6, D7, D8, P9, B10), and three southwestern groups (S1, S2 / F3 / I4), which is in accordance to findings for other conifer species (such as *Abies alba (MILL.)*, Konnert and Bergmann 1995).

The distinctiveness of the western populations could be due to adaptations to special environmental conditions such as high temperatures and frequent drought events. Climatic stress might drive selection at such sites close to the xeric limit and could be responsible for declines of genetic diversity resulting in a higher level of fixation (Borovics and Mátyás 2013). However, since genetic variation determines the adaptability of trees to future environmental conditions (Müller-Starck et al. 1992; Kramer et al. 2010), the lower variability of these provenances could be a drawback in case of changing conditions under climate change scenarios.

Prus-Głowacki et al. (2012) also found differences in genetic composition among ten of the eleven provenances investigated in the IUFRO 1982 dendroclimatic study (BiH19 not included in their study). The German and Polish provenances (D11, D12, PL6) displayed the highest values of genetic variability compared with other provenances of this trial. The key finding of the study of Prus-Głowacki et al. (2012) is a clear separation of Spanish provenances from all other provenances investigated. This confirms the findings presented in this thesis and the hypothesis that Spanish provenances did not take part in the recolonization of northeastern habitats.

5.1.2 Seedling development

Due to the genetic differences, emergence and phenology of seedlings differed among provenances in both experiments even in the absence of climatic manipulations (Taeger et al. 2013a, Taeger et al. 2014). Unsurprisingly, emergence percentages were higher in the greenhouse (75-90%) than in the field experiment (58-84%), both being slightly above or within the range of other studies (Reich et al. 1994; Castro 1999; Lang et al. 2007). Emergence was positively correlated to latitude and negatively to altitude of seed origin. However, since seeds from low latitude concurrently were derived from higher altitudes, this effect cannot be disentangled. Number of cotyledons and needle color showed also geographic clines. Needles of Spanish and French provenances, subjective with a more gray-bluish appearance, were proved to be significantly less green compared to the remaining provenances. The less pronounced greenness of needles of southwestern provenances is probably an adaptation to prevent radiation-induced stress (Larcher 2001).

Geographical clines were also found in terms of the seedlings' phenological development. Northernmost provenances showed on average 11 days earlier bud swelling and 2 days earlier bud burst compared to provenances from southern origins, which confirms other findings for Scots pine (Beuker 1994; Chmura et al. 2012) and for several other pine species (Steiner 1979). In addition, provenances from northern origins ceased growth on average 10 days earlier than southern populations, which is in accordance with literature and is explained with a photoperiodic effect (Hurme et al. 1997; Repo et al. 2000; Savolainen 2004). Analog geographic clines regarding bud set or growth cessation also exist for provenances of the IUFRO 1982 trial, as shown by Oleksyn et al. (1992) and Oleksyn et al. (1998).

5.1.3 Growth traits

Differences among provenances were found for most measured growth traits, both in the two experiments and in the dendroclimatic analysis. Early development and growth of seedlings can depend on seed mass; therefore, the experimental results on seedlings were checked for such a seed mass effect. In contrast to other studies that considered single seed masses (Wrzesniewski 1982; Reich et al. 1994; Castro 1999), just a small effect on early seedling performance was found. This concerned the number of cotyledons and the rate of accomplishing first development stages (Taeger et al. 2013a).

Throughout both experiments the growth performance of the German alpine provenance D7 was remarkable: D7 dominated the provenance rankings of almost all biomass and growth parameters at the greenhouse as well as at the field, regardless of the climatic manipulations. Within a principal component analysis, conducted for the field experiment and comprising 20 variables, D7 is therefore clearly separated from all other provenances (Taeger et al. 2014). Its unique behavior is at least partially due to a genetic gain of its seeds, since they have been derived from plus trees of a seed orchard (Wennström et al. 2007). This could consequently result in considerable yield improvements of mature trees as suggested by Ahtikoski and Pulkkinen (2003) and Ahtikoski et al. (2012), which would also be of financial interest regarding forest management. However, long-term measurements are required to prove the persistence of this predominance effect.

Spanish and French provenances tend to develop longer roots than central or northern provenances, as indicated by significant longer roots within the greenhouse experiment. Accordingly, these provenances had the longest tap-roots within the drought treatments of the field experiment, but this finding was not significant. Nevertheless, a long tap-root length of southern provenances and in particular of Spanish provenances was described by Brown (1969) in an experiment including 45 different European provenances, which supports that this finding could be a general characteristic of those provenances.

In both experiments, the German provenances D7 and D6 revealed superior height growth, followed by provenances D8 and P9 within the greenhouse experiment and by I4 within the manipulation experiment. On the contrary, southwestern provenances and in particular Spanish provenances had the lowest height growth. Similar patterns were found for height growth of mature trees at the IUFRO 1982 trial (Taeger et al. 2013b). Provenances from Germany (D10, D12), Poland (PL6, PL9) and northeastern France (F14) had superior higher height growth compared to northern or southern provenances such as those from Russia (RUS2), Sweden (S15) or Bosnia-Herzegovina (BiH19). The superior height growth of German and Polish provenances compared to those from northern or southern origins, as revealed by the experiments and the dendroclimatic study, are in accordance with results of an IUFRO 1982 trial site in Poland (Oleksyn et al. 1999) or other provenance trials (Giertych 1979; Stimm and Utschig 1994). Furthermore, Alia et al. (2001) observed low height growth of Spanish seedlings compared to German ones at various experimental sites in Spain.

In a recent study encompassing 59 tree species Alberto et al. (2013) could show that genetic differentiation among provenances and clinal variation along environmental gradients are very common. These authors associated these findings with climatic selection. The development of such local adaptations, also found in herbaceous plants and grasses, consequently shows the potential of adaptation to environmental conditions (Franks et al. 2014), which of course is of relevance under predicted climate change. The basis of future adaptability in terms of evolutionary responses to novel conditions is provided by genetic variability within a species and within populations (Salmela et al. 2013). In addition, other strategies of plant species adjustment to environmental changes consist of plant responses within their genetic reaction norm, defined as phenotypic plasticity, or migration to suitable habitats in order to prevent extinction (Gimeno et al. 2008; Nicotra et al. 2010). Phenotypic plasticity of Scots pine is addressed in particular in the field experiment and will be discussed in the following chapters.

5.2 RESPONSE OF SCOTS PINE PROVENANCES TO DROUGHT OR / AND WARMING

5.2.1 Response to drought

Responses of Scots pine provenances to reduced water availability and to drought events were demonstrated to be significant in both experimental approaches as well as in the retrospective, dendroclimatic study. Due to the magnitude of drought effects it was also possible to detect differences among provenances. Drought responses of provenances evidently were not uniform, neither in the experiments nor in the dendroclimatic study, contradicting the findings of Thiel et al. (2012) on provenances of *Pinus nigra* in a manipulation experiment.

Species-specific response

The importance of drought impacts on plant growth is well established (Kozlowski et al. 1991; Larcher 2001; Bréda et al. 2006), including changes in growth cessation (Nielsen and Jørgensen 2003; Eilmann et al. 2011). In contrast, drought induced changes of phenology such as bud burst or bud set are less commonly reported or are not observed (Lotan and Zahner 1963; Morin et al. 2010). However, moisture deficit delayed bud set in the greenhouse experiment by about 5 days on average of all provenances, which is in accordance with findings of a seedling experiment on *Pseudotsuga menziesii* (Khan et al. 1996).

Drought effects regarding growth traits of all provenances vary to some extent between the two experiments. This is due to differences in intensity, duration and timing of drought conditions, caused by the experimental design (pot vs. field experiment) and the different observation periods. Nevertheless, similar general trends were found. Drought reduced aboveground growth significantly, including shoot length, diameter increment and aboveground biomass. Reductions of diameter and height increment due to limited water availability were also found for mature Scots pine provenances in the dendroclimatic study (Taeger et al. 2013b). These findings are in accordance with drought induced reductions of aboveground growth of various tree species described for seedlings (Sonesson and Eriksson 2000; Cregg and Zhang 2001; Nielsen and Jørgensen 2003; Rose et al. 2009; Aranda et al. 2010) and for dendroclimatic studies (Oberhuber et al. 1998; Thabeet et al. 2009; Dobbertin et al. 2010; Sangüesa-Barreda et al. 2013). Wu et al. (2011) showed that reduced water availability reduces aboveground biomass and productivity of plants and can even cause a decrease in net carbon uptake of ecosystems. Surprisingly, within the field experiment final stem length was not, total above ground biomass was less reduced by drought compared to the greenhouse experiment. Provenances at the field showed significant reductions of bud biomass (-40%) and stem biomass (-37%), whereas no significant differences regarding needle biomass could be detected. The less pronounced or the absence of drought induced reductions of these traits are explained by the fact that drought conditions at the field came into effect after the bulk of the stem length growth and needle biomass were already completed (Chmura et al. 2011), similar to the results of the experiment by Thiel et al. (2012).

At the end of both experiments root length and root biomass were measured, since the development of a deep and dense root system is the most important trait of drought tolerance (Reader et al. 1993; Bréda et al. 2006). The determination of root length and reliable estimates of root biomass are generally hampered, because the recovery of all root compartments is rather challenging, especially in field experiments (Robinson 2004; Poorter et al. 2012). In particular, the separation of roots among individuals is often difficult and fine roots can easily be lost during harvest (Poorter et al. 2012). These constraints cause sampling errors and most likely mask clear provenance differences, e.g., regarding root biomass at the greenhouse or tap-root length at the field. Furthermore, results of pot experiments, such as the greenhouse experiment of this thesis, have to be interpreted with care. They entail specific artifacts, particularly due to the prevention of unhindered root development (Ray and Sinclair 1998; Passioura 2006). This artifact is strongly depending on pot size and the available space for rooting (Climent et al. 2011). Therefore those effects should have limited impact on the results of the greenhouse experiment, since observations were restricted to the first vegetation period only and relatively big boxes (30 liters) were used. Furthermore, such artifacts were completely avoided in the field experiment, where seeds were sown directly into the soil.

On average of all provenances a significant increase of root length was observed as response to drought in the greenhouse (+15%) and even more clearly for tap-root length in the field experiment (+60%). In contrast, root biomass did not respond to drought treatment in the field, but was reduced in the greenhouse (-14%). A strong increase of root length in response to drought but little change of total root biomass matches the findings of Joslin et al. (2000) and Poorter et al. (2012). Besides, an increase of rooting depth or a shift of root biomass to deeper soil layers were interpreted as drought responses in recent seedling experiments of *Fagus sylvatica* (Goisser et al. 2013) and of *Quercus* species (Kuster et al. 2013b).

Goisser et al. (2013) also observed an increase of root-shoot ratios due to low water availability. This mirrors the results of the greenhouse experiment, where lower root-shoot ratios of seedlings facing lower water availability were mainly caused by a disproportionate reduction of total shoot biomass. Such changes of the root-shoot ratios were not apparent at the field, partially because needle biomass, accounting for 40% of the total plant biomass, did not differ among treatments. The bulk of foliage was completed at the field before drought treatment severely came into effect. When needle and bud biomass are excluded, a drought induced allocation change becomes apparent in terms of a significant increase in root-stem biomass ratios. These observed drought effects are in accordance with a suggested general drought response mechanism in terms of allocation changes from needle to stem to root, which consequently result in higher root-shoot ratios (Oleksyn et al. 1992; Delucia et al. 2000; Bréda et al. 2006; Poorter et al. 2012). This allocation shift is an important measure to avoid drought induced cavitations, by increasing the leaf specific conductance (Bréda et al. 2006).

Allocation changes as response to environmental effects are usually explained with the optimal partitioning theory: plants allocate resources in an optimal pattern by enhancing compartments to overcome limiting factors (Gedroc et al. 1996). However, it has been questioned that this theory is a general mechanism regarding all major environmental factors and suggested that other plant responses regarding changes of metabolism, chemistry or morphology are of greater importance (Reich 2002). Poorter et al. (2012) argue accordingly and demonstrate in a recent meta-analysis that plants generally have a greater ability to change organ morphology than to adjust allocation. Their findings correspond exactly to our results of the field experiment. Compared to a relatively small change of root-stem biomass ratios, root morphology showed a much stronger drought response, indicated by the root-stem length ratio and the length of tap-roots. Furthermore, we did not find any impact on needle biomass but on needle morphology: the specific leaf area was significantly higher under drought conditions. Morphology changes seem to be realized faster than changes in allocation, thus, allocation changes might have been observed more clearly after a longer observation period or in a long-term experiment.

Within the dendroclimatic study the assessment of drought responses focused on annual radial growth (standardized as basal area increment) and annual height increment of chosen provenances of the IUFRO 1982 trial. First of all, climate-growth relationships were explored by modeling annual growth parameters as a function of several time windows of climatic parameters in a linear model. No correlations of annual growth were detected for temperature or precipitation solely, but for moisture deficit. Moisture deficit was derived from the Thornthwaite monthly water-balance model (McCabe and Markstrom 2007) as calculated difference of the potential and actual evapotranspiration. Basal area increment was significantly reduced by moisture deficit during the period from May to July of the current year, which is in accordance to studies of Scots pine in temperate regions (Lebourgeois et al. 2010; Lebourgeois et al. 2012; Zang 2012). Conditions of the current year are shown to be the main driver of basal area increment (Oberhuber et al. 1998, Martínez-Vilalta et al. 2008; Michelot et al. 2012; Martin-Benito et al. 2013), whereas for height growth the relation is more complex: while annual height growth is significantly correlated to moisture deficit during May of the current year, an influence of the previous year could be demonstrated by a strong correlation of annual height growth with basal area increment of the previous year (Mäkinen 1998). Shoot formation depends on conditions of the previous year during the phase of bud formation (Kozlowski et al. 1991; Salminen and Jalkanen 2005), as well as on conditions of the actual year during the phase of shoot elongation (Kozlowski 1964; Larcher 2001; Bréda et al. 2006). For the climate-growth relationships, no significant effects of provenances or sites were found. On the contrary, the exploration of responses to severe drought events using tolerance indices introduced by Lloret et al. (2011) revealed significant differences among provenances and will be discussed in the following.

Provenance-specific response

Responses of Scots pine provenances differed significantly within both experiments as well as at both sites of the dendroclimatic study. In both experiments, provenances from Spain and France had higher root-shoot ratios (within the article Taeger et al. 2014 denominated as "below-aboveground biomass ratio") and showed lower investment in aboveground structures compared to German and Polish provenances. During the drought event at the greenhouse, growth was less reduced for these southwestern provenances and they showed complacent shoot growth continuously at low level throughout the first vegetation period. This finding could not be confirmed within the second experiment. At the field, the only provenance with significant lower reduction of aboveground growth under drought was found to be the German provenance D8, but this was clearly due to a very poor performance of the seedlings at the control plots rather than due to a specific drought response.

Biomass partitioning to roots and shoots is partially under genetic control, as shown for provenances of *Pinus contorta* (Martinsson 1986), *Pinus ponderosa (LAWS.)* (McMillin and Wagner 1995), *Pinus pinaster (AIT.)* (Aranda et al. 2010) and Scots pine (Chmura et al. 2013). Low investment in aboveground structure in combination with high root-shoot ratios are generally interpreted as specific drought adaptations (Reich 2002; Valladares et al. 2007). This adaptation was observed for xeric provenances of *Pinus pinaster* (Corcuera et al. 2012b) and was also suggested for southern provenances of Scots pine (Oleksyn et al. 1998; Oleksyn et al. 1999). Accordingly, Alia et al. (2001) showed lower height growth of 16 Spanish provenances in comparison to six German provenances at five sites in Spain and, mostly important, demonstrated that this lower height growth was linked to lower mortality during dry years. In an experiment by Cregg and Zhang (2001), Asian provenances of Scots pine exhibited lower growth, allocated more biomass to roots and had higher integrative water-use efficiency than European provenances, which also resulted in higher drought tolerances of these provenances.

The most striking result of the field experiment is the phenotypic plasticity of root development. The magnitude of the observed increase of tap-root length of all provenances exposed to drought conditions was not expected, although Richter et al. (2012) proved plastic drought response as increased biomass allocation to roots for both continental and Mediterranean Scots pine provenances. This plastic response obviously prevented drought induced mortality at the field, since no treatment effect on mortality could be detected. Nevertheless, significant provenance differences regarding root development were found. In particular, southwestern provenances from Spain and France exhibited the greatest increase of tap-root length and of root-stem ratios (length and biomass). They also had the longest tap-roots of the drought treatments, but this finding was not significant. Significant longer roots of these provenances were observed in the greenhouse experiment and are believed to be an adaptation to climatic conditions at the provenance origin (Brown 1969).

Provenance differences regarding phenotypic plasticity of drought responses are described for other tree species, such as *Fagus sylvatica* (Meier and Leuschner 2008) and *Pinus pinaster* (Aranda et al. 2010), although in both studies no difference in biomass partitioning expressed as root-shoot ratio was significant. The plasticity of rooting depth is found to be species-dependent (Reader et al. 1993) and such short term adaptations are of major importance in regard to extreme events and climate change (Valladares et al. 2007; Vitasse et al. 2010). The experimental results described in this thesis demonstrate clearly a greater phenotypic plasticity for southwestern provenances compared to those of central origins. This contradicts the findings of Richter et al. (2012). These authors suggested a lower phenotypic plasticity of southern Scots pine provenances compared to more central ones, which was observed during the first vegetation period focusing on root-shoot ratios. In contrast, the findings presented here include a greater number of provenances and show in particular a plastic response of root morphology, changeable more easily than biomass allocation (Poorter et al. 2012). However, in accordance with Richter et al. (2012) it was shown that drought adaptations of southwestern provenances come at the cost of low aboveground growth.

This is also in agreement with the findings of the dendroclimatic study, in which the southern provenance from Bosnia-Herzegovina (BiH19) revealed a specific adaptation to drought accompanied by poor overall aboveground growth. Drought tolerance was elucidated by the analysis of tree responses to the most extreme drought events. The tree responses were calculated as tolerance indices (for definitions see Chapter 3.4) for each site of the IUFRO 1982 trial under investigation. At both sites provenances showed almost uniform resistance (Dr/PreDr) to the analyzed drought events. Only at Waldsieversdorf, the northern provenances from Sweden (S15) and Latvia (LV4) showed a significantly stronger drought induced reduction of basal area increment. Overall northern provenances revealed low resilience (PostDr/PreDr), which is explained by low drought intensities at their sites of origin. In contrast, the drought response of the southern provenance from Bosnia-Herzegovina (BiH19) at both sites was very resilient in terms of annual height growth as well as in terms of basal area increment, indicating a special adaptation to such events. In addition, the performance of the local provenances, D10 at Waldsieversdorf and D12 at Bensheim (here followed by the provenance F14, originating from a nearby location with similar climatic conditions), was found to be remarkable. But in contrast to the southern provenance, their high tolerance to drought events was accompanied by superior aboveground growth yields. This confirmed the well-established conclusion that local effects are responsible for specific adaptations of provenances (Alia et al. 2001; Jump et al. 2009), although this does not generally imply that local provenances are always the best ones (Chmura et al. 2012).

5.2.2 Response to warming

The effect of warming on Scots pine provenances was explicitly assessed within the field experiment. Overall magnitudes of tree responses to warming were considerably lower than those induced by drought.

Nevertheless, warming significantly advanced spring phenology of Scots pine seedlings as expected, due to the well known strong correlation of temperature and spring phenology (Menzel et al. 2006). The advance of bud swelling, bud burst and the promotion of an earlier shoot length growth corresponds to other experimental findings for Scots pine (Repo et al. 1996), *Pinus nigra* (Thiel et al. 2012) or *Quercus* species (Morin et al. 2010). A warming of 3° K led to an advance of 11 days for bud swelling and 3.5 days for bud burst on average of all provenances. A simple extrapolation of these results to future climate conditions is hampered, since phenological responses can vary among warming methods to some degree (Bronson et al. 2009). However, Chung et al. (2013) pointed out that the effect of phenology depends rather on species and degree of warming than on the warming method. Furthermore, experiments tend to underestimate phenological responses of trees as shown by Wolkovich et al. (2012). Thus the observed advance can be even more pronounced under natural conditions. On the other hand, experimental warming did not start before early spring, therefore chilling effects, which could influence and even confine an immoderate advance, were not considered in this study. Higher temperatures during winter finally could affect chilling requirements and consequently even delay bud development, although pioneer species such as Scots pine seem to be less impacted by this effect than climax species (Laube et al. 2014).

Elevated temperatures affect plant physiology of various tree species including Scots pine by changing leaf chemistry and net photosynthesis (Wang et al. 1995; Wang J et al. 2012; Arend et al. 2013; Contran et al. 2013), as described in Chapter 1.4.1. Furthermore, increased temperatures generally tend to enhance shoot height, stem diameter and biomass of trees (Way 2011; Wu et al. 2011). A significant temperature effect on growth traits within the field experiment was therefore expected, not least because of the extended growing season caused by the heating at the warm treatments. However, the only significant effect caused solely by warming was found in terms of an increase in the number of developed buds averaged for all provenances. Other short term experiments also observed only minor temperature effects on growth of seedlings and saplings of trees (Arend et al. 2011; Thiel et al. 2012; Richter et al. 2012). The meta-analysis of Wu et al. (2011) suggests that biomass increases due to warming are rather reported in long-term experiments. Moreover, the significant effect on bud development most likely would have caused a considerable carry-over effect, which would have come into appearance in the following year (Sanz-Pérez and Castro-Díez 2010). One such carry-over effect was observed for example regarding shoot length of Scots pine (Junttila 1986; Salminen and Jalkanen 2005). Height growth is known to be a two year process, depending on conditions of the phase of bud development and of the phase of shoot elongation during the following year (Kozlowski et al. 1991; Larcher 2001). Due to the limited effects of temperature found in the experiment, no temperature-induced provenance differences could be detected.

5.2.3 Interactions of warming and drought

So far, plant responses were described exclusively based on either the factor drought or the factor warming. Since responses to the combination of both effects are not simply additive

(Wu et al. 2011), interactions of both effects regarding tree growth are of particular interest. A major question is also whether elevated temperatures enhance drought stress for Scots pine provenances, as suggested by recent dendroclimatic studies (Büntgen et al. 2013). This could finally lead to an increase in tree mortality under climate change, either due to a rise of water pressure deficit (Park Williams et al. 2012) inducing hydraulic failure (Martínez-Vilalta et al. 2002; Martínez-Vilalta et al. 2009) or the depletion of carbon reserves pronounced by elevated temperatures (McDowell et al. 2008; Adams et al. 2009).

Consequences of the combined effect of drought and high temperature were observed within both experiments and the dendroclimatic study. However, only the field experiment (Taeger et al. 2014) using a factorial design allowed explicitly testing for interactions between both climatic effects. In accordance with results of a modeling approach by Luo et al. (2008) and a review of experiments by Wu et al. (2011), the interactive effects of temperature and drought were found to be smaller than expected from single-factor responses within the field experiment. In fact, significant interactive effects were only found for diameter increment during the drought period as well as for the development of buds (number and biomass). In these cases, warming only had a positive effect on growth, whereas it reinforced growth reduction under drought conditions. The impact on bud development could have caused a carry-over effect (see Chapter 5.2.2).

An extreme event occurring during the greenhouse experiment (Taeger et al. 2013a) illustrated the impact of the combination of drought, heat and high-light on Scots pine seedlings. On 31 July 2010 (a hot summer day with clear sky), a dysfunction of the ventilation system caused temperatures in the greenhouse of above 45° C between 11 a.m. and 4 p.m., with maximum temperatures reaching 48.5° C. Therefore, seedlings of the drought treatment (not watered for 18 days) and the non-drought treatment were suddenly exposed to high-light stress and simultaneously to extreme temperatures, which were close to the maximum temperatures that can be endured by conifers (Larcher 2001). Within the non-drought treatment no visible damage such as needle discoloration or yellowing could be detected at any of the seedlings, whereas there was massive damage and considerable mortality within the drought treatment. Seedlings of the latter treatment were not any more able to cool their needles via transpiration. Therefore, tissue temperatures of those seedlings that were concurrently exposed to high-light exceeded the critical values of beginning protein denaturation and photodamage (Bréda et al. 2006; Rennenberg et al. 2006). The needle texture of such seedlings was visibly destroyed and differed clearly from “regular” shriveled seedlings generated in preliminary studies. Provenance effects could not be detected, which is at least partially due to the fact that this event was unplanned and the high-light stress during the relevant time period was not exactly similar for all seedlings due to shading of construction bars. However, this extreme event demonstrates the possible impacts of heatwave events, which are characterized by the exact combination of the three factors drought, heat and high-light (Chaves et al. 2003; Boeck and Nijs 2011). Drought was evidently the predisposing factor regarding damages and mortality, since within the non-drought treatment - regardless of high temperatures and high-light exposure - no damage was detected. Seedlings exposed to drought and very high temperatures were affected by high-light stress, finally triggering mortality.

In addition to the experimental findings, general growth differences of provenances between the two sites of the dendroclimatic study were proved to be mainly due to climatic effects of temperature and water availability (Taeger et al. 2013b). Despite a longer growing season of 33 days, provenances at Bensheim exhibited lower overall growth on average. In contrast to similar soil and site conditions, temperature during the vegetation period is 2° K higher at this site and exhibits climate conditions beyond the climatic envelope of Scots pine (Kölling 2007). The higher temperatures lead to a higher water vapour pressure deficit and, during drought events to further reduced soil water potential (Pichler and Oberhuber 2007). Since Scots pine is an isohydric species (Gruber et al. 2012), it closes its stomata already at an early stage of drought events to prevent drying-out (Zweifel et al. 2009; Hartmann 2011), resulting in a reduction of photosynthetic activity and finally in a reduction of growth (Ciais et al. 2005; Zang 2012). A shift in allocation as response to dry conditions can further reduce aboveground growth in favour of belowground parts (Nikolova et al. 2011; Poorter et al. 2012). This hypothesis is supported by the development of height growth, which was synchronous during the first years but considerably diverging after the year 2003. After 2003, which was a severe drought year at Bensheim, height growth during the following years was significantly reduced compared to the site Waldsieversdorf.

5.3 FACTORS INFLUENCING TREE RESPONSE TO DROUGHT OR / AND WARMING

The response of Scots pine provenances can be affected by various additional factors. First of all, the response depends on the seasonal timing of the occurrence of drought or / and high temperatures itself, as it was found for other forest trees and plants (McMillin and Wagner 1995; Robertson et al. 2009; Ruffault et al. 2013). The extreme event, which occurred accidentally at the greenhouse, was obviously an example of timing and the coincidence of several factors. Seasonal timing also explained the absence of a drought response regarding needle biomass or total shoot length in the field experiment. In the dendroclimatic study site differences of drought tolerance were due to differences of timing of the drought event. Therefore it is important to consider the seasonal timing of such events, particularly if results are to be generalized.

In addition, there is still lack of knowledge of how tree age affects drought tolerance of trees, since previous studies either describe an increase (Candel-Pérez et al. 2012) or a decrease of resilience (Bogino et al. 2009). However, responses of trees and also of whole-forest ecosystems to environmental factors are age dependent as pointed out by a recent review of Anderson-Teixeira et al. (2013). For this reason, in this thesis seedling responses as well as responses of mature trees were explored, which allows to get a more comprehensive picture of response pattern of Scots pine provenances to predicted climate change.

Allocation changes, addressed in the presented seedling experiments, are not expected to be constant during plant development due to ontogenetic effects (Reich 2002; Poorter et al. 2012). The response of mature trees to climatic effects can also be altered by tree size (Zang et al. 2012; Martínez-Vilalta et al. 2012) or social class (Martín-Benito et al. 2008). However, within the presented dendroclimatic study such effects were excluded by the experimental set up and the choice of the sampled trees.

Provenance differences regarding growth and the sensitivity to climatic factors are also found to be dependent on planting density to some degree (Egbäck et al. 2012) and on site effects (Alia et al. 2001; McLane et al. 2011). This might be associated with differences of colonization of mycorrhiza (Rudawska et al. 2011), which can affect provenance differences (Leski et al. 2010). Mataruga et al. (2012) suggested that even the site conditions within the origin of a certain provenance can have an influence on provenance performance.

Moreover, plant response can be modified by various additional factors such as light availability (Goisser et al. 2013), soil type (Lindsey and Kilgore 2013) or changes in the atmospheric condition (Huttunen and Manninen 2013). In addition, interactions with pests and pathogens were not considered in the experiments and did not play a major role regarding the results of the dendroclimatic study. However, such interactions could have substantial impacts (Weed et al. 2013; Haynes et al. 2014). For example, mistletoe infections can considerably exacerbate drought stress affecting resilience patterns of Scots pine and will gain in importance under climate change conditions (Dobbertin et al. 2005b; Sangüesa-Barreda et al. 2013). Clearly, these additional factors influencing tree responses also entail complex interactions which could be of interest (Gimeno et al. 2008; Luo et al. 2008; Luo et al. 2011; Wolkovich et al. 2012) and should be addressed in further experiments and studies.

The focus of this thesis was on the assessment of the impact of drought and high temperature as well as the interaction of warming and drought on provenances of Scots pine. Reckoning each experiment and the dendroclimatic study separately, these analyzes would have only pilot character. But since in this thesis two seedling experiments based on genetic analyzes are combined with a dendroclimatic study on mature trees, a more comprehensive picture of climate effects on Scots pine provenances is provided. Nevertheless, in order to further interpret and generalize the presented findings, additional factors touched above have to be taken into consideration.

5.4 SUMMARY AND CONCLUSIONS

5.4.1 Major findings

The results of this thesis emphasize the importance of drought effects on seedlings and mature trees of Scots pine (Kozlowski et al. 1991; Larcher 2001; Rennenberg et al. 2006). Warming solely revealed to be of minor importance, but was found to enhance drought stress for some traits especially if accompanied by high-light stress. Thus, measures to adapt to predicted climate change including increasing temperatures and drought events are recommended (Lindner et al. 2010; Chmura et al. 2011). In this context, the choice of tree species is of major importance (Kölling 2007; Chmura et al. 2011). This thesis demonstrates the fundamental role of provenances in the discussion of future suitability of tree species based on the analysis of Scots pine. Considerable differences of growth traits and of responses to climatic effects were found among provenances – for seedlings as well as for 27 year old trees. Therefore, the importance of considering the provenance level in the face of predicted climate change is corroborated (Mátyás 1996; Alberto et al. 2013). The incorporation of intraspecific variation and provenance effects refines simple species distribution models (Joyce and Rehfeldt 2013). This advancement might lead to a more positive assessment of the future suitability of Scots pine under climate change conditions, as simulation examples on Scots pine and *Pinus pinaster* for the Iberian Peninsula (Benito Garzón et al. 2011) and on *Pinus contorta* (Oney et al. 2013) for North America demonstrate.

Specific drought adaptations of southern provenances were observed for seedlings of the experiments (Taeger et al. 2013a, Taeger et al. 2014) and trees of the IUFRO 1982 trial (Taeger et al. 2013b). The magnitude of phenotypic plasticity of root development within the seedling experiments was remarkable, with provenances from Spain and France revealing the strongest responses. These provenances develop longer and deeper roots, have higher root-shoot ratios and their root morphology exhibits to be more plastic compared to provenances from central or northeastern origins under investigation. They would accordingly be better adapted to projected increases of drought events, since root development is one of the key traits of drought tolerance (Bréda et al. 2006). Specific drought adaptations (i.e., resilience of basal area increment and height growth to drought events) were observed for the southernmost provenance (Bosnia-Herzegovina) of the dendroclimatic study as well.

The detected drought adaptations of seedlings and trees come at the cost of low aboveground growth, which seems to be a general finding (Alia et al. 2001; Richter et al. 2012). An evaluation from a forest management perspective includes - besides the response to climatic factors - total growth yields that are likely achieved. Consequently, within the dendroclimatic study an archetype analyzes was conducted, based on measures for growth (height growth, diameter at breast height, stem volume), general climate sensitivity (regarding basal area and height growth) and drought response (resilience of basal area increment and annual height growth). The ideal performer was expected to be high on growth metrics, low on general climate sensitivity metrics and high on drought tolerance metrics. Local provenances, D10 at Waldsieversdorf and D12 at Bensheim (followed by the nearby provenance F14), were closest to the desired archetype, combining drought tolerance with superior growth yields. Polish provenances were also ranked close to the ideal performer, whereas the provenance from Bosnia-Herzegovina was least, despite its specific drought adaptation. Similarly, the results of growth traits within the field experiment were summarized with a principal component analysis confirming an overall superiority of the German alpine provenance (D7) regardless of the treatment. In addition, the provenance derived from Italy (I4) also revealed above average performance, whereas Spanish provenances followed most conservative growth strategies with low aboveground growth under all treatments. These results mirror the findings of the dendroclimatic study, although long-term studies on provenances from Italy and Spain are still missing.

5.4.2 Implications for forest management

Southern provenances entailing specific drought adaptations could become an alternative for forestry in central Europe, but not before frequency and severity of extreme drought and heat events increase considerably beyond levels experienced up to the present. Then they could diminish or even outreach the so far established superiority of German and Polish provenances (Alia et al. 2001). These provenances might also exhibit lower mortality rates under drought conditions (Cregg and Zhang 2001), but this still has to be proved. For this reason, long-term trials and manipulation experiments including additional provenances from the southwestern margins would be of particular interest. However, such provenances do not seem to be able to take advantage of favorable conditions in non extreme years concerning aboveground growth so far, as shown in the dendroclimatic study of this thesis and mirroring the findings of Richter et al. (2012). In addition, southwestern provenances contain less genetic variability and diversity, which could reduce their adaptability to future conditions. Therefore, local provenances that proved to be fairly drought resilient and exhibited strong growth performance seem to be an adequate option for forests management at least for the near future.

Nevertheless, in the long run the concept of assisted migration could become an interesting forest management option regarding the adaptation to climate change. This concept has gained rising attention during the last years in restoration ecology and forestry (McLachlan et al. 2007; St Clair and Glenn 2007; Bolte and Degen 2010; Kreyling et al. 2011; Breed et al. 2013). As a forest management measure, the colonization of non-local, climatically adapted species could help to maintain ecosystem services in the future (Buma and Wessman 2013). On the other hand, the introduction of new species always implicates the risk of negative effects on the respective ecosystem. This general problem of invasion biology can be avoided by focusing on the intraspecific level within a species distribution range (Kreyling et al. 2011). The assisted migration of pre-adapted ecotypes or provenances seems to be promising, since it can enhance forest productivity (Schreiber et al. 2013) and buffer against climate change impacts (Aitken and Whitlock 2013; Oney et al. 2013). Hence, general seed transfer guidelines should be periodically revised and updated to allow assisted migration measures of provenances containing specific adaptations as presented within this study (Chmura et al. 2011; Breed et al. 2013). Rather than a replacement of local provenances, the replenishment with such pre-adapted genotypes is recommended, which could enable the adaptation to novel climate conditions (Thiel et al. 2012). Due to the fact that this bears the risk of maladaptation in particular to non-climatic factors, more experiences from experiments of long-term trials are needed (Aitken and Whitlock 2013).

Gene conservation and assisted migration are integral parts of genetic strategies enabling adaptation to climate change (Chmura et al. 2011). The findings presented in this study suggest that these measures should promptly focus on genotypes derived from the southern margin of the species distribution range, since they contain specific adaptations but are at high risk of climate change induced extinction (Sánchez-Salguero et al. 2012). Yet, in addition to genetic importance further prioritizing might be necessary considering also cultural, historical and biogeographic factors (Matías and Jump 2012). The seed sources of such populations could then be preserved in identified climatic refugia, areas which are to some extent decoupled from regional climate trends (Hampe and Jump 2011). The natural stability of such climatic refugia of forest stands in general can be improved by silvicultural approaches in order to conserve them as long as possible. The most important measure in this context is the reduction of density to alleviate the competition for water and nutrients (Chmura et al. 2011; Matías and Jump 2012; Giuggiola et al. 2013). Besides, natural regeneration should be promoted whenever possible for genetic reasons and, as demonstrated within this thesis, because of the importance of natural root development.

6 FUTURE RESEARCH PERSPECTIVE

The results of this thesis confirm the importance of considering the provenance level regarding the future suitability of tree species in the face of predicted climate change. The combination of experimental approaches on seedlings with an observational study on older trees of Scots pine provenances has proved to be effective, since this provides a comprehensive of the assessment of provenance responses. Nevertheless, the experiences made during the analysis led to continuative questions and exposed some shortcomings, which could be addressed in future research projects.

Within the field experiment the shortened observation period did not allow an analysis of carry-over effects and long-term consequences of climatic impacts. In addition to demonstrated significant changes in morphology, longer observation periods could reveal significant changes in allocation, as morphology is easier changeable than allocation (Poorter et al. 2012). Moreover, impacts of warmer temperatures are more likely observed in experiments of longer duration (Wu et al. 2011). On the other hand a longer time period will allow the seedlings to establish a more extensive root system, which will be even more complicated to excavate completely. More severe drought treatments are recommended, in order to be able to study mortality rates. However, treatments close to the tolerance level of provenances of the same species always bear the risk of total die-off.

The incorporation of additional factors influencing tree responses, such as increasing atmospheric CO_2 or ozone concentration, would enable the integration of interaction effects adequately (Luo et al. 2008). This kind of multifactor experiments implies an increasing effort on experimental infrastructure. Yet, considering factors such as timing or the recurrence of extreme climatic events or the influence of soil properties seem accomplishable more easily from an experimental point of view and would thus be of specific interest.

There is still a lack of a mechanistic understanding of recent and future climate change impacts on the population level in particular (Alberto et al. 2013). A more detailed look at physiological and biochemical processes could help to further reduce the gap between presented genetic composition and growth responses. Analyzing water-use efficiency on the provenance level seems to be promising, since differences on the individual level in this trait trigger selective mortality events of Scots pine (Hereş et al. 2014). This should be complemented by the assessment of biochemical stress indicators among provenances (Corcuera et al. 2012a).

Since southwestern provenances have not been included in provenance trials, long-term observations are missing so far. Therefore I recommend the establishment of such trials, as initiated by the Bavarian Office for Forest Seeding and Planting with provenances gathered for this study. Overall I support the proposal of Chung et al. (2013) to combine manipulation experiments with long-term studies and to complement these with modeling approaches as this seems to be the most effective strategy to assess ecosystem responses to climate change (Luo et al. 2011).

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8 PUBLICATION LIST

Reviewed publications

Taeger S, Fussi B, Konnert M, Menzel A (2013) Large-scale genetic structure and drought-induced effects on European Scots pine (Pinus sylvestris L.) seedlings. European Journal of Forest Research 132, pp. 481–496. doi: 10.1007/s10342-013-0689-y

Taeger S, Zang C, Liesebach M, Schneck V, Menzel A (2013) Impact of climate and drought events on the growth of Scots pine (Pinus sylvestris L.) provenances. Forest Ecology and Management 307, pp. 30–42. doi: 10.1016/j.foreco.2013.06.053

Submitted publications

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Further publications

van der Maaten ECD, Spathelf P, Köthke M, Schall P, Taeger A, Menzel A, Bolte A, Ammer C, Spiecker H. (2009) Country Report Germany. In the frame of COST Action FP0703 ECHOES: Expected Climate cHange and Options for European Silviculture. http://docs.gip-ecofor.org/public/echoes/Echoes_Germany_Report_oct09.pdf

Taeger S, Zang C, Liesebach M, Schneck V, Menze, A (2013) Wie reagieren Herkünfte der Kiefer auf Trockenheit? LWF aktuell 98, pp 44-48.

Conference proceedings and abstracts

Oral presentations

Taeger S, Menzel A (2013) Effects of heat and drought on seedlings of Scots pine (Pinus sylvestris L.) provenances. Climtree - International Conference on Climate Change and Tree Responses in Central European Forests. Zurich, Switzerland. 1.-5. September 2013.

Taeger S, Zang, C, Liesebach, M, Schneck V, Menzel A (2012) Wachstumsreaktionen der Herkünfte der Waldkiefer auf Witterungsextreme – Herkunftswechsel statt Baumartenwechsel? Forstwissenschaftliche Tagung. Freising, Germany. 19.-22. September 2012.

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Gloning P, Taeger S, Seifert H, Schäffler U, Kölling C, Schilcher M, Menzel A (2011) Potential and actual distribution of tree species - influences of varying data sets on climate envelopes derived. EGU General Assembly. Vienna, Austria. 3.-8. April 2011.

Poster presentations

Seidel H, Taeger S, Menzel A (2013) Influence of seasonal drought and increased temperature on Scots pine provenances. Climtree - International Conference on Climate Change and Tree Responses in Central European Forests. Zurich, Switzerland. 1.-5. September 2013.

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