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**Intraspecific variation in the response of Scots pine (*Pinus sylvestris*)
seedlings to multiple warmer drought periods**

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Abstract

Seedling performance and survival during extreme climatic events are crucial for the regeneration and persistence of forest ecosystems. Scots pine forests have suffered from frequent dieback events triggered by recent climate change. However, drought responses may depend on the interaction of water availability and temperature, on the seasonal timing of water shortage, and on acclimation stimulated by previous drought events. The genetic diversity and acclimation potential of Scots pine might prove some provenances resilient to future climatic conditions and consequently make them suitable for forest adaptation by assisted migration. Therefore, specific drought performance of seedlings is essential for the selection of appropriate provenances.

This thesis deals with the response of potted Scots pine seedlings from twelve provenances of the south-western distribution range to seasonal drought and elevated temperature. The provenance-specific drought response and recovery of the stomatal control were estimated using infrared thermography. Additionally, drought-induced mortality rates and its variation with acclimation after multiple drought events and temperature increase were investigated. Furthermore, the inter- and intra-annual growth and ecophysiological performance were examined during and after multiple seasonal drought events.

Above-ground dimensions of seedlings were the key determinants of drought-specific resistance and resilience as measured by plant water status, mortality rates and growth patterns, which in turn could be attributed to either water consumption or to specific drought adaptations as well as acclimation. Scots pine seedlings exhibited considerable inter- and intra-annual compensatory growth after drought stress release that mitigated drought impacts. Provenances from Mediterranean origins were less affected by drought than provenances from continental origins. This response was associated with summer dryness at their origin. Additionally, the acclimation potential against drought mortality of Scots pine seedlings differed between provenances. Provenance-specific drought resistance, resilience and acclimation potential may sustain seedlings establishment as well as support forest adaptation and therefore the persistence of Scots pine forest under future climatic extremes.

Zusammenfassung

Für die Regeneration und den Fortbestand von Waldökosystemen können die Reaktionen und das Überleben von Sämlingen während klimatischer Extremereignisse entscheidend sein. Insbesondere Kiefernwälder litten unter häufigen, durch den jüngsten Klimawandel ausgelösten, Dürreereignissen. Im Allgemeinen kann die Reaktion auf Trockenheit vom Zusammenspiel aus Wasserverfügbarkeit und Temperatur, vom saisonalen Zeitpunkt der Wasserknappheit und auch von der Akklimatisierung während vorangegangener Dürreperioden abhängen. Die Waldkiefer weist eine hohe genetische Vielfalt und ein hohes Akklimatisierungspotenzial auf. Manche Herkünfte könnten sich daher als widerstandsfähig gegenüber zukünftigen klimatischen Bedingungen erweisen und sich für eine Anpassung von Wäldern durch die sogenannte „assisted migration“ eignen. In diesem Kontext ist daher die herkunftsspezifische Reaktion von Sämlingen während einer Dürre ein grundlegendes Auswahlkriterium geeigneter Provenienzen.

Diese Dissertation befasst sich mit Kiefernensämlingen aus zwölf Herkünften des südwestlichen Verbreitungsgebietes und deren Reaktionen auf mehrmalig induzierten saisonalen Wassermangel und erhöhte Temperatur. Die provenienzspezifische Reaktion der Stomata auf Trockenheit und deren Erholung wurde anhand von Infrarot-Thermografie ermittelt. Die dürreinduzierten Sterblichkeitsraten wurden in Abhängigkeit einer Akklimatisierung an die vorangegangenen Dürreereignisse sowie die Temperaturerhöhung untersucht. Darüber hinaus wurden das inter- und intra-annuelle Wachstum und ökophysiologische Parameter während und nach den Dürreereignissen beobachtet.

Die oberirdischen Abmessungen der Sämlinge waren die Hauptfaktoren zur Bestimmung der Widerstandsfähigkeit und Belastbarkeit gegenüber Trockenheit, was anhand des Wasserstatus, der Mortalitätsrate und der Wachstumsmuster gezeigt werden konnte. Diese Reaktionen konnten wiederum entweder auf den Wasserverbrauch oder auf spezifische Trockenheitsanpassungen sowie auf Akklimatisierung zurückgeführt werden. Nach den Trockenphasen zeigten die Kiefernsetzlinge ein erhebliches Kompensationswachstum innerhalb und zwischen den Jahren. Dies schwächte die Auswirkungen der Dürre ab. Provenienzen mediterranen Ursprungs waren von der Dürre weniger betroffen als Provenienzen kontinentalen Ursprungs, was mit der klimatischen Wasserbilanz an ihrem Herkunftsort zusammenhing. Darüber hinaus unterschied sich das Akklimatisierungspotenzial der Herkünften gegenüber der Dürresterblichkeit. Die

provenienzspezifische Widerstandsfähigkeit, Belastbarkeit und das Akklimatisierungspotenzial können die Etablierung von Sämlingen und Setzlingen unterstützen sowie bei der Anpassung der Wälder und dem Fortbestand von Kiefernwäldern unter zukünftigen klimatischen Extremereignissen helfen.

1. Introduction

Forests are one of the most important ecosystems of the world. They supply a variety of provisioning, regulating, cultural and supporting ecosystem services such as food and fibre, erosion and natural hazard regulation, recreation and ecotourism, as well as soil formation and nutrient cycling (Shvidenko et al., 2005). Moreover, forests influence climate by altering energy fluxes, water and carbon cycles and vegetation dynamics (Bonan, 2008).

The formation and expansion of the world forests since the last glacial period back 10,000 years has always been affected by the interference of human mankind (Williams, 2006). Thus, we do not and will probably never know the amount of the potential natural world forest cover of the Holocene. Estimates suggest that the world forest cover during the last 5,000 years was reduced by one-third, covering around 30% of the land surface today (FAO, 2016b). Nevertheless, this area comprises only 36% primary forest and just 22% are considered as intact forest landscapes larger than 500 km², whereas 59% are production and multiuse forests (FAO, 2016a; Potapov et al., 2017).

Humans directly disturb forest development by removal of resources to be used as fuel, construction material and food. Forest use, logging and clearing, and converting forests to agricultural and urban areas result in major land cover changes (Williams, 2006). Over-exploitation of forests and depletion of its resources initiated the development of the concept of sustainability by Hans Carl von Carlowitz (1713) designated for forestry and forest management, but nowadays used in various fields of economic sectors and society.

Besides direct impact of human activity, indirect influence via anthropogenic climate change is affecting forest ecosystems. Climate change increased mean global temperature by around 0.9°C and changed precipitation patterns during the last century (Stocker et al., 2013). This development is likely to be continued since climate projections predict a further increase of global temperature and a regional decrease of summer precipitation including increasing severity and frequency of drought events (Kirtman et al., 2013). Forests will directly respond to changes of precipitation and temperature by altered tree species distribution and composition, productivity, growth and mortality and will be indirectly affected by climate change due to climate-driven disturbances such as pests and pathogen attacks and wildfire (Keenan, 2015).

Scots pine (*Pinus sylvestris* L.) is one of the most widely distributed conifer tree species stretching from Spain in the south-west to Scandinavia in the north and the far-east of Russia (Boratyński, 1991) favouring provenances adapted to local climatic conditions. This species accounts for a large proportion of trees in its distribution range and is economically important for building and construction timber, and for paper production (Houston Durrant et al., 2016).

Although Scots pine is considered a drought resistant species (Ellenberg, 1988), its stands have been more often affected by climate change mediated dieback events than stands of other forest tree species (Allen et al., 2010). Especially seedlings are vulnerable to drought events and suffer mortality (Lloret et al., 2004). Additionally, low water ability can decrease the ability of seedlings to compete with the herbaceous vegetation that leads to lower survival rates (Davis et al., 1998, 1999). The hampered seedling establishment can prevent forest regeneration and may result in species or even biome shifts (Anderson-Teixeira et al., 2013; Martínez-Vilalta and Lloret, 2016).

This thesis consequently will study intra-specific responses of Scots pine seedlings to multiple droughts and increased temperature in order to support the selection of suitable provenances with higher climate change resilience.

1.1. Future change of mean and extreme temperature and precipitation

Climatic conditions are likely to further change in the future (Kirtman et al., 2013). Nevertheless, it is not the mean conditions that have the strongest impacts on plant responses and species distribution, but the increased climatic variability resulting in more frequent and severe extreme events (Keenan, 2015; Reyer et al., 2013). Although many climatic variables and measures will exhibit extremes at both tails of their distribution, only changes in mean and extremes of precipitation, temperature and their interactions will be elaborated in this chapter.

It is very likely that mean global and regional temperatures will further increase till the end of the 21st century also with distinct seasonal patterns of warming (Collins et al., 2013; Kirtman et al., 2013). Based on the RCP scenarios that assume respective peaks in radiative forcing from approximately 3 W/m² to 8.5 W/m² and subsequent decrease to 2.6 W/m² for RCP2.6 till the end of the century, the number of warm days and nights will increase while the number of cold days and nights will decrease (Sillmann et al., 2013). Additionally, respective absolute temperatures will increase (Sillmann et al., 2013). These global projections can also be found on the regional scale in Europe while being stronger than in other regions across the globe (Sillmann et al., 2013). Additionally, Europe is likely to experience stronger and longer heat waves and warm spells more often (Seneviratne et al., 2012; Sillmann et al., 2013). Moreover, based on the older SRES scenario A2 (~RCP8.5), the percentage of hot days with temperatures above 30°C will rise as well as the 20-year extreme daily maximum temperature will increase up to 5°C. The return period of annual extreme hot days will shorten from 20 years to five to two years, depending on the region (Seneviratne et al., 2012).

Regional precipitation changes are likely to have diverging patterns across the globe, with precipitation increases in the high and mid latitudes and a precipitation decrease in the subtropics also varying among seasons. For example, precipitation may decrease in the Mediterranean Basin during all seasons, whereas Central Europe may become wetter during winter, spring and autumn, and drier during summer (Kirtman et al., 2013).

The length of dry periods (CDD; precipitation of consecutive days < 1 mm CDD) will similarly to mean precipitation patterns vary among seasons and regions, whereas the duration of dry periods may get longer in Central Europe during summer (Seneviratne et al., 2012). However, southern Europe may experience longer dry periods independent of the season and the length of dry periods may not change in Northern Europe (Sillmann et

al., 2013). Regarding soil moisture conditions, it is not only precipitation that is determining the level of dryness, but also temperature, which is increasing evapotranspiration driven by the vapour pressure deficit (Seneviratne et al., 2012). Additionally, seasonal reduction of soil moisture can accumulate to an annual shortage of soil water storage (Wang et al., 2009).

1.2. Scots pine climatic requirements

Scots pine can colonize and inhabit fundamentally different habitats varying in climate (alpine to Mediterranean) and soil (acid to alkaline, water logged to dry) conditions (Ellenberg, 1988). Some of these are not suitable for other tree species (Ellenberg, 1988) and thus natural as well as planted Scots pine stands can have a high value in means of nature and biodiversity conservation (Heinrichs et al., 2019; Lust et al., 2001).

Scots pine occur when mean annual precipitation and summer temperatures exceed 300 mm and 13°C, respectively (Boratyński, 1991), while growth patterns are influenced by multiple factors. Optimum height growth of Scots pine depends on the interplay of various climatic variables, e.g. mean annual temperature, degree-days and annual moisture index, and its populations are balancing growth potential with cold hardiness (Rehfeldt et al., 2002). Northern populations from cold climates may grow under suboptimal temperature conditions whereas southern provenances from warm climates are already at their height growth vertex (Rehfeldt et al., 2002; Reich and Oleksyn, 2008). Moreover, height growth might be linked to the moisture deficit during spring (Taeger et al., 2013). Radial growth of Scots pine increases with temperature if this relationship is not reversed by dry conditions and thus correlates with water ability during summer (Martínez-Vilalta et al., 2008, 2012; Weber et al., 2007).

Scots pine can be considered as a drought tolerant species (Ellenberg, 1988), because of its relatively strong isohydric stomatal response reducing evaporative water loss, avoiding low needle and stem water potentials, and thus minimizing hydraulic failure (Irvine et al., 1998; Martínez-Sancho et al., 2017). Drought acclimation comprises a reduction of the needle area and the needle to sapwood area ratio, the adjustment of xylem conduits, a lower investment in above-ground structures and a higher investment into roots compared to shoots (Dobbertin et al., 2010; Eilmann et al., 2009; Martínez-Vilalta et al., 2009; Taeger et al., 2015). Nevertheless, a recent study on the Swiss forest inventory data revealed that Scots pine mortality increases with the site dryness deviating from the long-

term mean and that mortality increased especially for large individuals since the 1960s (Etzold et al., 2019).

The colonization of fundamentally different habitats favoured the establishment of Scots pine provenances with specific adaptations and responses to prevailing climatic conditions. Provenances show temperature-specific height growth optima, drought resistance, seedling establishment and height growth (Reich and Oleksyn, 2008; Richter et al., 2012; Taeger et al., 2013, 2015). With ongoing climate change, provenance-specific adaptations to current conditions may be suboptimal at the place of origin (Keenan, 2015). Research on provenance responses to climatic extremes may lead to recommendations for appropriate assisted migration to adapt forests and forest management to future environmental conditions (Bussotti et al., 2015).

1.3. Responses of trees and forests to climate, drought and warmer temperatures

Onset of phenological spring development of temperate and boreal tree species is triggered by seasonal temperatures, especially in winter and spring, as well as partially by day length (Laube et al., 2014). Sensing day length ensures that a critical time in spring is passed to reduce the risk of exposure to unfavourable cold temperatures (Hanes et al., 2013). After surpassing this threshold of daylight, it is the interaction with increasing temperature that is driving the onset of phenophases (Rossi et al., 2014a). A certain temperature sum of forcing is needed to initiate phenological development, what may be modulated by the exposure to cold temperatures (chilling) during winter to break quiescence. Phenology of trees comprises the seasonal formation of leaves or needles, flowers, wood and roots (Radville et al., 2016; Rossi et al., 2014a; Tooke and Battey, 2010) and thus effects growth and physiological processes.

Tree growth is generally influenced by current year climatic conditions (Fritts, 1976). However, depending on the species, previous year conditions matter too. Theoretically, tree growth follows an optimum curve in dependence of temperature and water availability (Pretzsch, 2009). This simple tree climate-growth response is modulated by many other factors such as the actual dose of temperature or precipitation, age, competition, fertilization, light and disturbance (Pretzsch, 2009; Thomas et al., 2010).

Moreover, on the cellular level, sufficient supply of water is required for cell division and expansion, and accurate temperature drives the speed of molecular reactions.

Ecophysiological processes of trees are influenced by climatic conditions as well, e.g. photosynthesis relies on sufficient water supply and a certain temperature range. Cellular respiration provides the basis for energy demanding metabolic processes which increase with temperature until a certain threshold and decline with water stress. Both processes are effected by temperature dependent enzymatic reactions (Lambers et al., 2008). Stomatal control is regulating plant water relations and has thus an impact on gas exchange and photosynthesis, transpiration, hydraulic conductance and sap flow (Tyree and Zimmermann, 2002).

A future increase in climatic variability causing extreme events such as drought and heat may have additional major impacts on tree responses and mortality (Bauweraerts et al., 2014; Neumann et al., 2017; Reyer et al., 2013). How a meteorological drought affects tree responses or is even leading to mortality depends on several factors such as the severity, the length and the seasonal timing of the drought itself, the depth and water capacity of soils, the access to ground water and finally on the tree species-specific mechanisms to cope with drought (Anderegg et al., 2013). Drought and temperature extremes exceeding optimum species-specific conditions have negative impacts on growth, ecophysiological processes, and survival (Allen et al., 2010; Peñuelas et al., 2013; Teskey et al., 2015). Nevertheless, trees are able to tolerate or acclimate to drought and heat (Niinemets, 2010; Peñuelas et al., 2013) by, among others, stomata closure to reduce water loss, evaporative cooling to reduce tissue temperature, reduction of the canopy leaf area by growth reduction or leaf shedding, growth allocation to roots, osmotic and elastic adjustment, or altered gene expression to synthesize specific water stress or heat shock proteins (Chaves et al., 2003; Kozłowski and Pallardy, 2002; Peñuelas et al., 2013). These responses require a certain degree of phenotypic plasticity to a changing environment that is species- or even provenance-specific and occurs within their climatic niche breadth (Duputié et al., 2015; Gratani, 2014). Acclimation to drought or heat is triggered by stress severity or duration that do not surpass a certain species-specific threshold giving individuals the ability to, at least, partially recover after stress release (Niinemets, 2010). As a consequence, acclimation can partially compensate drought-induced secondary growth reduction and stabilize the relationship between relative growth and leaf area during long-term drought (Barbeta et al., 2013; Cinnirella et al., 2002; Schönbeck et al.,

2018). Moreover, it can decrease mortality during reoccurring drought events (Cregg, 1994; Seidel and Menzel, 2016).

1.4. Mechanisms and consequences of drought-induced mortality

More than 150 drought-induced tree mortality events have been documented during the last 50 years (Hartmann et al., 2018). These phenomena have been observed throughout the globe and cover all kinds of woody ecosystems (from boreal to tropical), various tree functional types (deciduous to evergreen, broadleaf to conifer, isohydric to anisohydric) and tree ages from seedlings to mature trees (Adams et al., 2017; Mitchell et al., 2013; Zhang et al., 2017). There is strong evidence that climate warming will increase the risk of tree mortality during drought even more (Allen et al., 2015). The vapour pressure deficit increases with temperature and thus may intensify drought impacts by increased evaporation and transpiration.

1.4.1. Physiological mechanisms of drought-induced mortality

The currently intensively debated hypotheses of physiological mechanisms leading to drought-induced tree mortality are carbon starvation, hydraulic failure and their interrelation causing phloem transport failure (Hartmann et al., 2018; McDowell et al., 2008, 2013; Mencuccini et al., 2015; Sala et al., 2010). Carbon starvation is caused by reduced carbon assimilation and a depletion of carbon reserves leading to negative carbon balance till the point when respiration cannot be maintained anymore or by failure of phloem carbon translocation to sink tissues (Adams et al., 2013; Galiano et al., 2011; McDowell et al., 2008, 2013; Mencuccini et al., 2015; Sevanto, 2014). Hydraulic failure represents the inhibition of water transport in roots, stems or leaves by partial or complete collapse of water columns in the xylem causing dehydration and ultimately desiccation of supporting and assimilating tissue (Brodribb and Cochard, 2009; McDowell et al., 2008; Nardini et al., 2013; Urli et al., 2013). These mechanisms may be interdependent when phloem turgor loss is restricting access to carbon assimilates or when xylem hydraulic conductivity is constrained by a limitation of carbon reserves (Sevanto et al., 2014).

The ultimate reason of mortality may depend on the severity and duration of drought which refers to the drought response strategies in the continuum between isohydric and

anisohydric species (Mitchell et al., 2013) and the ability to recover functional xylem while maintaining sufficient carbon gain (Trugman et al., 2018). The mechanism behind mortality may also depend on the time lag between drought and mortality that can be considered as concurrent-drought mortality and post-drought mortality (Adams et al., 2017; Trugman et al., 2018). While hydraulic failure may be more likely the reason for concurrent-drought mortality during severe drought events in more anisohydric species or tall individuals, carbon starvation may act during longer drought periods in more isohydric species, seedlings or during post-drought mortality (Bennett et al., 2015; Galiano et al., 2017; Hartmann et al., 2013; McDowell and Allen, 2015; Mitchell et al., 2013; Niinemets, 2010; Trugman et al., 2018). Drought can have a more negative impact on the hydraulic system in tall trees than in small trees (McDowell and Allen, 2015). Anisohydric species have a loose stomatal control in relation to water supply in order to sustain photosynthesis at the risk of hydraulic failure, whereas isohydric species that close stomata even under mild drought conditions may suffer prolonged periods of negative net assimilation (Martínez-Sancho et al., 2017; Meinzer et al., 2009; Mitchell et al., 2013). However, isohydric species may switch to a more anisohydric drought response strategy under prolonged drought to sustain carbon gain and to prevent overexploitation of carbon reserves (Salmon et al., 2015; Timofeeva et al., 2017). Mature trees and thus generally larger trees may rely on more extensive carbon pools than seedlings to bridge periods of reduced carbon gain (Niinemets, 2010). Additionally, Salazar-Tortosa et al. (2018) assume that a tight stomatal control of isohydric species impairs drought survival by nutrient deficits and stoichiometry imbalance.

1.4.2. Impact of drought-induced mortality on ecosystems

Tree mortality can have profound impacts on the biosphere as well as on the atmosphere (Anderegg et al., 2012, 2016; Martínez-Vilalta and Lloret, 2016; Ruiz-Benito et al., 2017). In general, mortality occurs on diverse spatial and temporal scales from cells to regions and from days to years (Breshears et al., 2018; Guadagno et al., 2017; Hartmann et al., 2018). Since present forest ecosystems exhibit diverse characteristics in terms of structure, diversity, demography and functional composition, also the outcome of climatic change induced mortality may be manifold additionally depending on prevailing climatic conditions, forest stand characteristics and the magnitude of disturbance (Allen et al., 2015; Jump et al., 2017; Martínez-Vilalta and Lloret, 2016; Ruiz-Benito et al., 2017). These outcomes may range from complete regeneration to pre-disturbance conditions,

succession to alternative forest ecosystems or even biome shifts (Martínez-Vilalta and Lloret, 2016). A recent analysis of National Forest Inventories showed that climate change driven mortality favoured angiosperm-like traits, such as high wood density as well as higher vulnerability to xylem embolism, promoted the reduction of gymnosperms and led to the shift in dominant functional groups (Ruiz-Benito et al., 2017). Although Martínez-Vilalta and Lloret (2016) could only attribute eight out of 35 global large scale mortality events to a vegetation shift after disturbance, they classified the outcome of 24 cases as uncertain what highlights the fact that we have limited evidence how forested vegetation will develop after drought-induced mortality.

In most cases, forest die-off may alter ecosystem fluxes of water and carbon leading to decreased evapotranspiration and net productivity (Anderegg et al., 2012, 2016). Despite a strong initial impact, effects on ecosystem fluxes might be buffered or recover on relatively short time scales by compensatory mechanisms (e.g. light use and water use efficiency, nutrient availability, soil evaporation) after moderate disturbances (Anderegg et al., 2016). Contrary, feedbacks between the biosphere and the atmosphere may further exacerbate impacts on vegetation and climate (Allen et al., 2015; Anderegg et al., 2016; Martínez-Vilalta and Lloret, 2016; Peñuelas et al., 2013).

1.5. Objectives

Seedling establishment is critical for Scots pine forest regeneration and persistence. When climatic conditions change faster than the pace of natural adaptation, the selection of adapted provenances and its use in assisted migration programs might be useful (Bussotti et al., 2015). We thus screened seedlings from a set of provenances originating from diverse climatic origins and hypothesize that provenances from drier and warmer locations are better adapted to water stress and higher temperatures. We employed different techniques on various characteristics to assess the drought resistance of those provenances.

Conventional methods to evaluate drought stress responses are frequently time consuming or invasive (Fiorani and Schurr, 2013). To evaluate the drought responses of different provenances in a relatively rapid and non-destructive way, we employed thermal imaging of the canopy that reflects needle surface temperatures and thus stomatal response to water availability (chapter 3.1).

Seedling survival during drought is the outcome of all physiological mechanisms counteracting water stress (Giuggiola et al., 2010) and therefore may offer a good indication of provenance suitability during extreme and long lasting drought conditions. Additionally, acclimation due to previous droughts may play a role for seedling survival (chapter 3.2).

Greater growth of seedlings and high performance of ecophysiological processes are critical for competition success, thus seedling establishment, and can be altered by site conditions like water availability (Grossnickle, 2012). Some provenances of Scots pine may better meet these characteristics what is qualifying them as candidates for assisted migration in a warmer and drier future (chapter 3.3).

2. Overview of methods

This thesis presents results of four experiments on subsequent drought events conducted on Scots pine seedlings from twelve provenances. The seedlings were grown in a vegetation hall (glass roofed building with open sidewalls) and/or a greenhouse to simulate ambient and elevated temperatures. Not all experiments dealt with similar numbers of provenances (Figure 1 B) or were conducted in both buildings. The experiments were partially subsequently built upon each other.

An overarching experiment with ten provenances was conducted in 2013 and 2014 in both buildings to investigate responses of growth, phenology and physiology to seasonal drought and temperature increase (Seasonal Drought 2013 - 2014). Individuals of six provenances, being part of the seasonal drought experiment in the greenhouse, were used to evaluate drought stress responses of provenances via thermal imaging in 2013 (Thermography 2013). Two mortality experiments were conducted in the greenhouse. In the first mortality experiment in 2014, native drought mortality responses of individuals from all twelve provenances were examined (Mortality 2014). In the second mortality experiment in 2015, drought and temperature acclimation effects on mortality were studied on three provenances (Mortality 2015). These individuals were equally taken from the seasonal drought experiment.

While the methods used as well as the scientific state of the art are fully presented in the publications associated with this thesis, a brief overview of the experimental setup and of the evaluation of drought impacts is given here.

2.1. Provenances

In total, twelve Scots pine provenances that originate from the south-western distribution range between 53°N to 40°N and 03°W to 24°E (Table 1, Figure 1 B) were available for the experiments reported in this thesis. All seeds were derived from autochthonous populations except Alpenkiefer and Plantage Pornopati that had been collected from seed orchards. The mean climatic conditions at the origin of provenances are between 3.2°C and 10.8°C mean annual temperature, between 570 mm and 1170 mm annual precipitation sum and a ratio of precipitation to potential evapotranspiration of the driest month from 0.3 to 1.45 (Table 1).

Northern provenances (lat. $\geq 45^\circ\text{N}$) originated from temperate regions with a precipitation maximum in summer (Figure 1 A) and southern provenances (lat. $< 45^\circ\text{N}$) from Mediterranean regions with a precipitation minimum in summer (Figure 1 C). These provenances were used in differing numbers in the four experiments from 2013 to 2015 (Figure 1 B).

Table 1. Origin of seed sources and respective climatic conditions. Provenances are arranged in decreasing order of latitude.

Label	Provenance	Country	Lat.	Long.	Alt. (m a.s.l)	T ($^\circ\text{C}$)	PPT (mm)	Min AI_{month}
PL9	Suprasl	Poland	53°15'N	23°23'E	181	6.6	584	0.61 _{Aug}
D8	Mittel-/Ostdt. Tiefland	Germany	53°04'N	13°29'E	75	8.5	574	0.51 _{Jul}
D6	Hauptsmoorwald	Germany	49°51'N	10°58'E	250	8.8	646	0.59 _{Jul}
D7	Alpenkiefer	Germany	47°30'N	11°20'E	1150	3.2	1106	1.45 _{Sep}
HU14	Plantage Pernoapati	Hungary	47°20'N	16°28'E	300	10	598	0.51 _{Jul}
CH5	Wallis	Switzerland	46°18'N	07°39'E	900	8.7	861	0.69 _{Jul}
I4	Emilia Romagna	Italy	44°30'N	10°27'E	460	10.8	888	0.36 _{Jul}
F12	Mont Ventoux	France	44°10'N	05°16'E	1600	3.9	1166	0.68 _{Jul}
F3	Prealpes du Sud	France	43°45'N	06°40'E	1185	7.6	955	0.39 _{Jul}
ES1	Alto Ebro	Spain	42°59'N	03°17'W	860	10.1	940	0.43 _{Jul}
BG10	Garmen	Bulgaria	41°43'N	23°54'E	1300	6.6	649	0.41 _{Aug}
ES2	Montes Universales	Spain	40°28'N	01°53'W	1670	7.8	644	0.30 _{Jul}

Geographic location, altitude, annual mean temperature (T), mean annual sum of precipitation (PPT) and the aridity index of the driest month (AI_{month}) defined as the ratio of precipitation to potential evapotranspiration. T and PPT are shown as means for the period 1950–2000 (WorldClim data base; Hijmans et al., 2005). The potential evapotranspiration to calculate AI was computed according to Thornthwaite (1948).

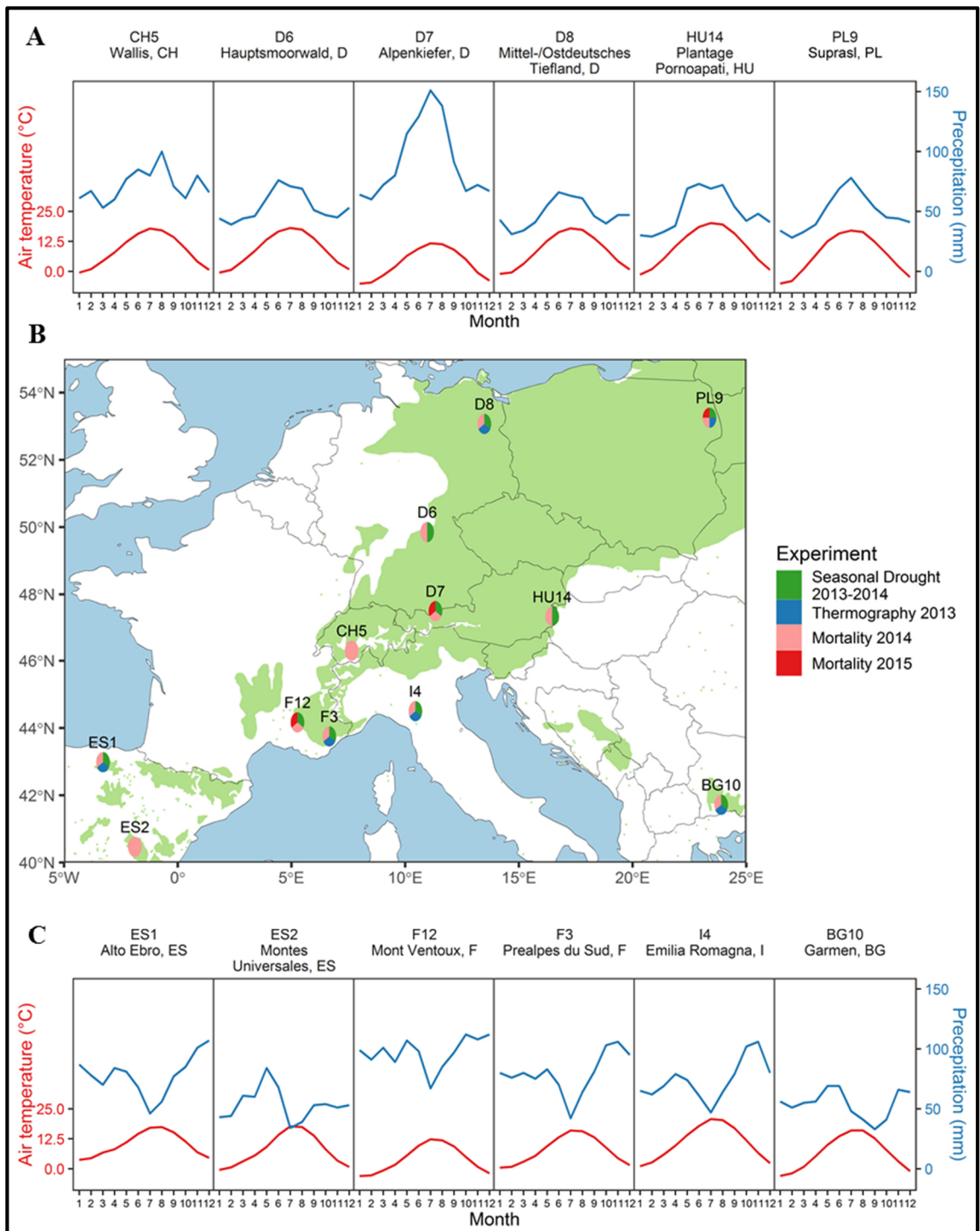


Figure 1. Climate diagrams of the (A) temperate and (C) Mediterranean origins of provenances used for the experiments as well as (B) the geographic origin within the natural distribution in Europe (modified after Caudullo et al., 2017) and the use of provenances in the different experiments. Temperature and precipitation are shown as monthly means for the period 1950–2000 (WorldClim data base; Hijmans et al., 2005).

2.2. Growing conditions

One-year-old seedlings were obtained from the Bavarian Office of Forest Genetics (Bayerisches Amt für Waldgenetik, Teisendorf, Germany). They were potted into 3l containers with peat substrate ('Basismischung Bayer. Staatsforsten AöR', Klasmann-Deilmann GmbH, Geeste, Germany) in April 2012 at the Gewächshauslaborzentrum (GHL) near Freising, Germany, and placed in a greenhouse (Figure 2 A) and in a vegetation hall (Figure 2 B). Potted seedlings were able to acclimate to respective conditions till the start of the observations and measurements in January 2013.

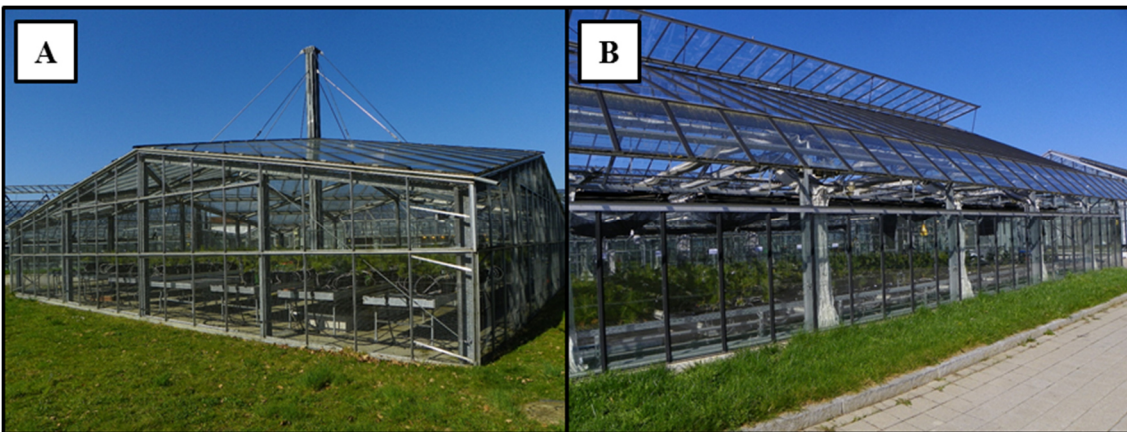


Figure 2. Scots pine seedlings were either grown (A) in a glass roofed building with open sidewalls (vegetation hall) or (B) in a greenhouse. Passive warming of the greenhouse resulted in a mean temperature increase of 3°C in comparison to almost ambient conditions in the vegetation hall.

For the seasonal drought experiment, twice 1200 seedlings of ten provenances (Figure 1 B) were placed in the vegetation hall and in the greenhouse and were equally distributed across three tables within each building. Out of those, 40 individuals of seven provenances (PL9, D6, D7, HU14, F12, F3, BG10) per building were replanted into 20 l containers in March 2014 and placed on six tables (Figure 3) for the second year of the seasonal drought experiment. Besides, 760 individuals in total of all 12 provenances were grown in the greenhouse for the first mortality experiment in 2014 with 31 to 187 seedlings per provenance on separate tables. From the seasonal drought experiment, 48 seedlings were used for the thermography experiment in 2013. After the seasonal drought experiment in 2014, 139 individuals of three provenances (PL9, D7, F12) that had experienced the previous experimental conditions were used in the second mortality experiment in 2015.

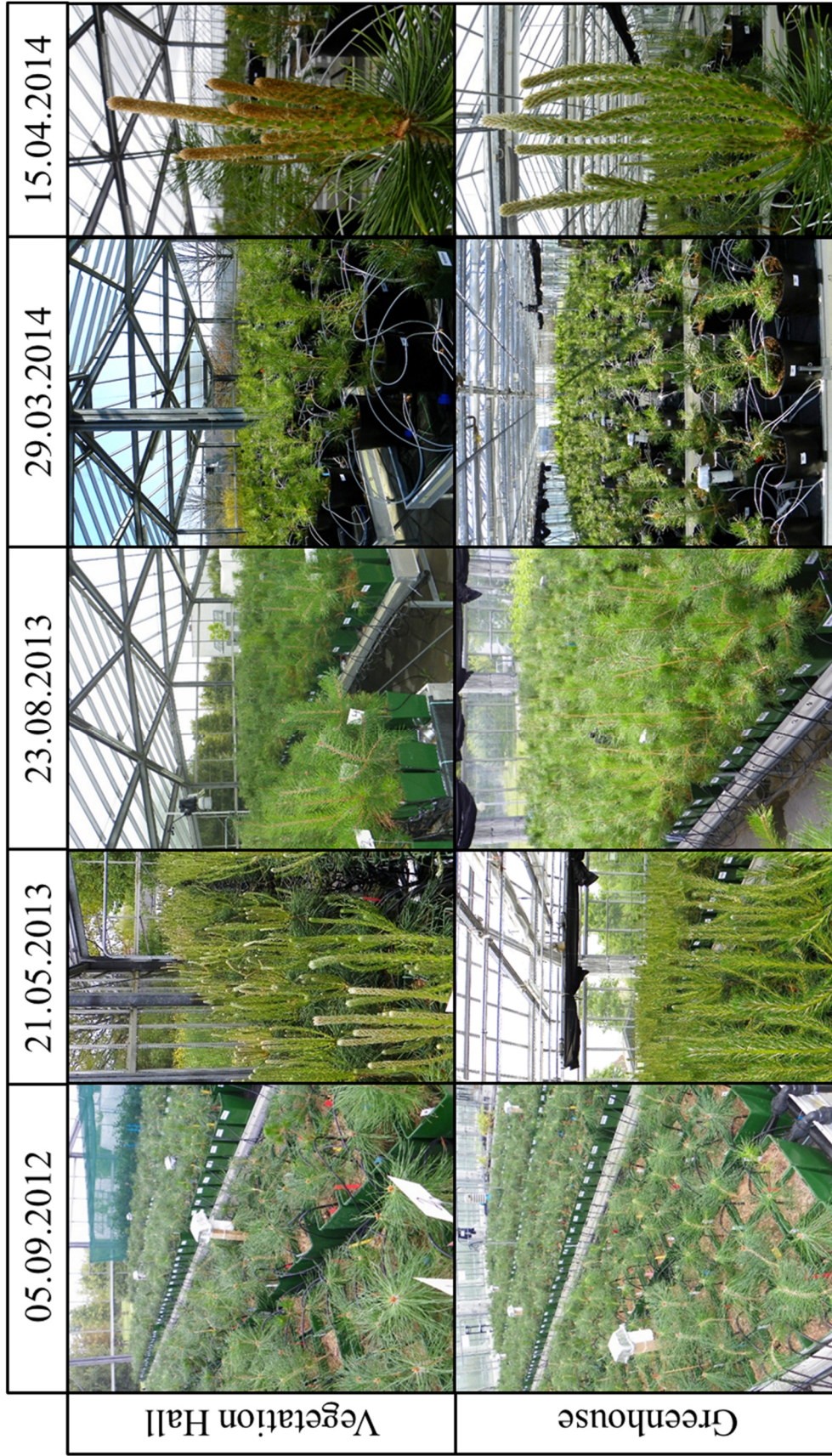


Figure 3. Potted seedlings in the vegetation hall and the greenhouse. Seedlings were re-potted from 3 l containers into 20 l containers in March 2014. Phenological development was advanced in the greenhouse as seen in the pictures of May 2013 and April 2014. The main water distribution lines and micro tubes connected to each pot for irrigation can be seen at the frames and in the centre of each table.

Air temperature and relative humidity (RH) within each building were recorded in 10-min intervals with a temperature/RH data logger (HOBO U23 Pro v2, Hobo, Onset Computer Corporation, Bourne, MA, USA). Passive warming of the greenhouse resulted in an annual mean temperature increase of $\sim 3^{\circ}\text{C}$ in comparison to the almost ambient conditions in the vegetation hall. This temperature increase was likely to induce an advanced phenological development (Figure 3). Mean daily temperature differences between greenhouse and vegetation hall were more pronounced during the winter (Figure 4) when the greenhouse had to be kept frost free because of water filled installations for irrigation and heating. On frost days, mean daily temperatures in the vegetation hall were 0.5°C to 15.3°C lower than in the greenhouse, whereas differences on frost free days ranged between -0.3°C and 6.1°C . In 2013 and 2014 respectively, this resulted in 4.0°C and 5.8°C higher mean temperatures in the greenhouse during frost periods (periods from the first to the last day having frost within each winter season) but only 1.3°C and 2.3°C higher temperatures during frost free periods. Overall, the 10-min temperature records ranged between -18°C and 42°C in the vegetation hall and 1°C to 42°C in the greenhouse.

The vapour pressure deficit (VPD) had a daily maximum of up to 6.5 kPa in the vegetation hall and the greenhouse. The daily mean VPD vapour pressure deficits during the vegetation period from March to November ranged between almost 0 kPa and 2.2 kPa , whereas the overall mean was around 0.15 kPa higher in the greenhouse than in the vegetation hall and 0.1 kPa lower in 2013 compared to 2014 (Figure 4).

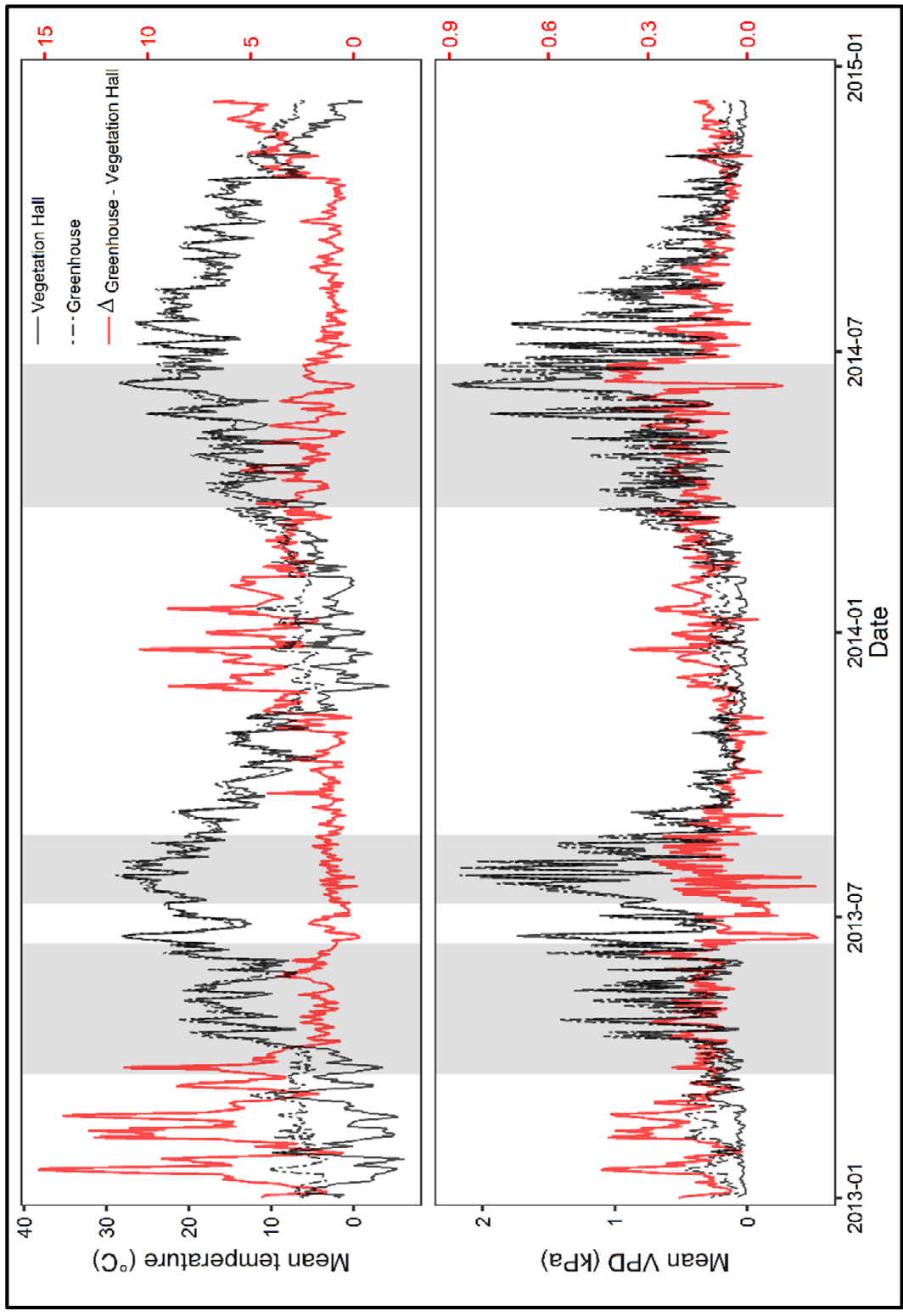


Figure 4. Mean daily temperature and vapour pressure deficit (VPD) in the vegetation hall and in the greenhouse as well as differences between those buildings. Gray shaded areas indicate the three periods when drought was applied during the seasonal drought experiment 2013- 2014.

2.3. Irrigation and drought treatments

General irrigation of seedlings in the seasonal drought experiment and derived further experiments (thermal imaging 2013, mortality 2015) was performed with a time-controlled irrigation system (AMI 1000, DGT-Volmatic, Senmatic, Søndersø, Denmark) in each building. The irrigation system was constructed out of four main distribution lines which therefore enabled a maximum of four watering regimes. Each pot was separately connected to the distribution lines by pressure compensating on-line drippers (PC drippers, Netafim Ltd., Tel Aviv, Israel) and micro tubes (Figure 3). Pots assigned to the first mortality experiment 2014 were well-watered manually on separate tables.

In the seasonal drought experiment, the drought treatments were applied in spring and summer 2013 from March 22 to June 14 and July 10 to August 21, respectively, as well as in spring 2014 from March 23 to June 23. The combination of all possible drought treatments and well-watered control groups in a full factorial design resulted in eight treatment groups in total (Figure 5 A). Individuals used in the thermography experiment 2013 were part of the respective summer treatments. The soil moisture in pots of the drought treated groups in 2013 was adjusted to oscillate around the permanent wilting point by withholding water intermitted by minor irrigation events (Figure 5 B). In contrast, irrigation was totally stopped in the drought treatment of 2014. All treatments were applied simultaneously in the vegetation hall and the greenhouse. During the spring drought in both years (2013 and 2014) soil moisture persisted at or fell below the permanent wilting point for five and six weeks in the vegetation hall and the greenhouse, respectively. The permanent wilting point was reached for about four weeks during the summer drought treatment of 2013. Between the drought treatments, all seedlings got well-watered to allow drought-treated seedlings to recover. In total, 240 pots equally distributed across provenances and treatments were used to monitor soil moisture with a hand-held sensor (UMP1, Umwelt-Geräte-Technik GmbH, Müncheberg, Germany) twice a week. In the vegetation hall, a malfunction of the irrigation system in 2014 caused a drop of soil moisture during spring in the well-watered control group (~13 vol%) and during summer in the previously assigned well-watered and drought treatment groups with a mean soil moisture minimum of around 11 vol% and around 20 vol%, respectively (Figure 5 B).

In both mortality experiments in 2013 and 2014, the lethal drought treatments were applied by totally intermitting irrigation. These drought events lasted from March 26 to July 1, 2014, and from May 22 to August 31, 2015, respectively (Figure 6).

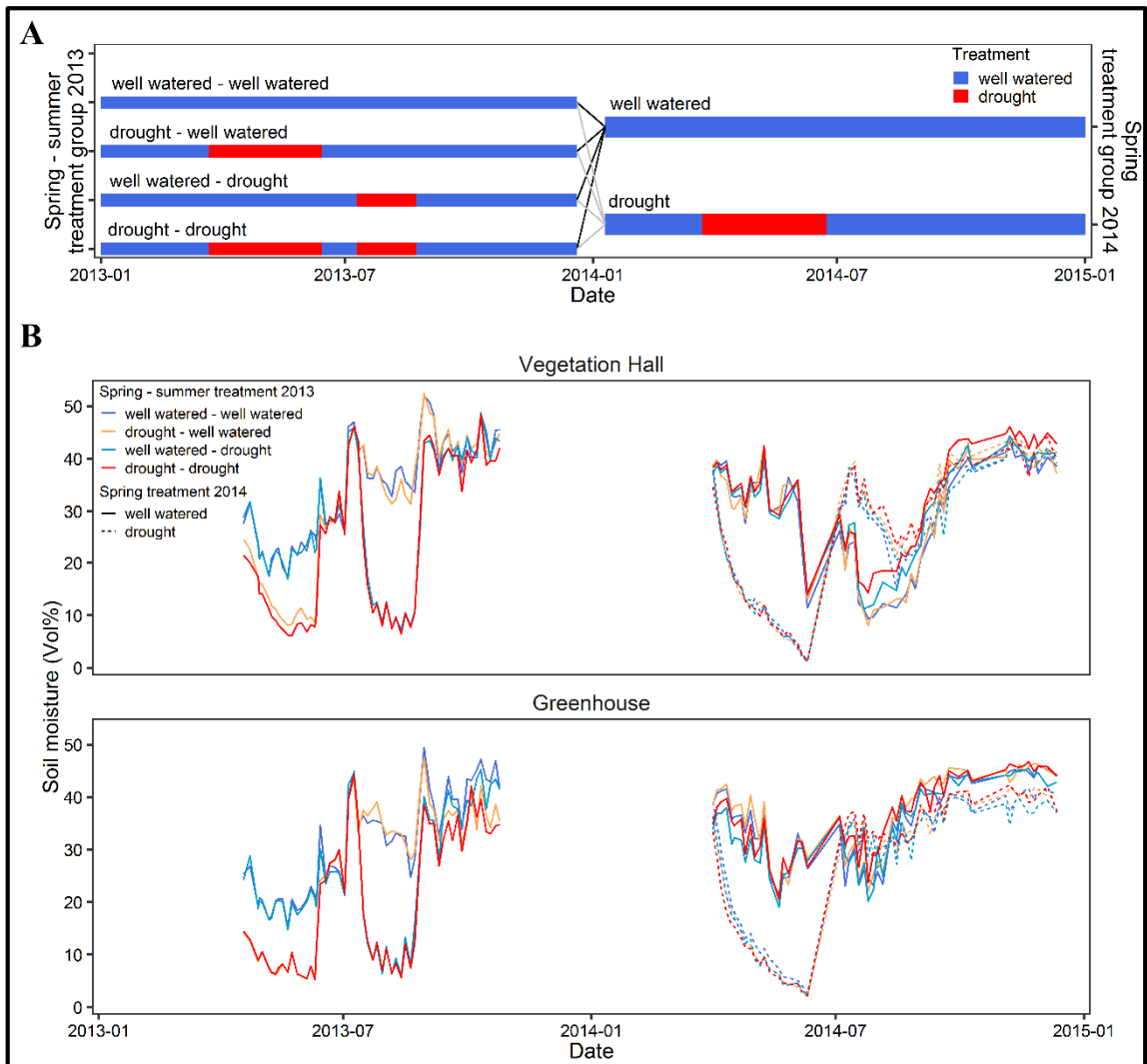


Figure 5. Drought treatments in the seasonal drought experiments. (A) Multiple droughts were applied in spring and summer 2013 as well as in spring 2014 and created eight different treatment groups in total. (B) The soil moisture in pots ($n = 240$) during the drought treatments was adjusted to oscillate around the permanent wilting (12 vol%) point in 2013 and was able to dry out by totally withholding irrigation in 2014.

2.4. Methods to evaluate drought responses and timetable

Drought responses in the experiments were evaluated by morphological and physiological traits using non-destructive to invasive techniques (Figure 6). Non-destructive methods represent the observation of spring phenology, the measurements of morphological parameters and of chlorophyll fluorescence as well as thermal imaging in the thermography experiment. Sampling of needles for carbon isotope analyses and the mortality assessment should have been of minor influence on seedling vitality whereas a destructive harvest of above-ground biomass was conducted on a subset of seedlings in the seasonal drought experiment at the end of 2013 and on all seedlings in the mortality experiments.

During the seasonal drought experiment, spring phenology was examined once a week 17 times in 2013 and 12 times in 2014. Height, diameter and needle length were measured at the beginning of 2013, after each seasonal drought treatment period (June and August 2013, June 2014) and additionally after drought recovery periods in 2013 (July and November 2013). Chlorophyll fluorescence was determined six times during the summer drought treatment 2013, after a recovery period of two weeks in September 2013, and at the end of the spring drought treatment 2014. Needles for stable carbon isotope analysis and above-ground biomass were harvested at the end of the summer drought and in November 2013, respectively.

Thermal imaging was performed almost twice a week during the six weeks long summer drought 2013 and a subsequent recovery period of two weeks.

The mortality assessment was conducted on six occasions in 2014 and on 13 dates in 2015. Biomass was harvested at the end of both mortality experiments. Height was measured at the beginning of the drought in 2014 (Figure 6).

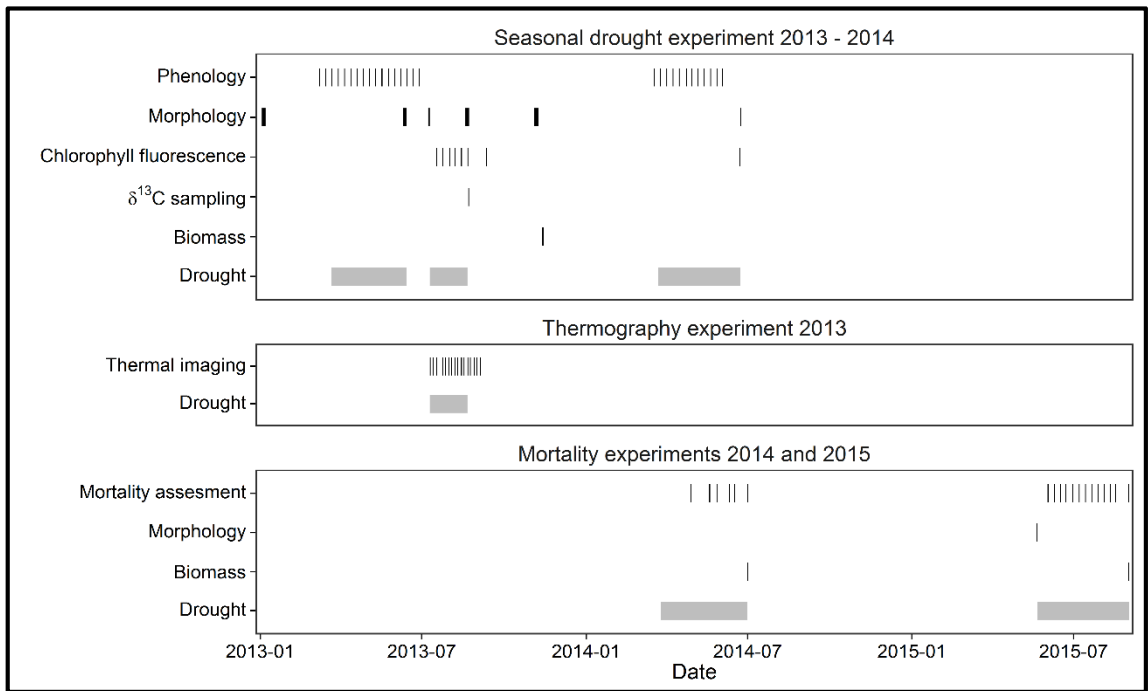


Figure 6. Dates of observations, measurements and samplings as well as respective seasonal and lethal drought periods in the four drought experiments (see Figure 1 B for provenances investigated in each experiment).

3. Publications: Abstracts and contributions

3.1. Diverging Drought Resistance of Scots Pine Provenances Revealed by Infrared Thermography

Seidel, H., Schunk, C., Matiu, M., and Menzel, A. (2016). *Front. Plant Sci.* 7, 1247. doi:10.3389/fpls.2016.01247.

With recent climate changes, Scots pine (*Pinus sylvestris* L.) forests have been affected by die-off events. Assisted migration of adapted provenances mitigates drought impacts and promotes forest regeneration. Although suitable provenances are difficult to identify by traditional ecophysiological techniques, which are time consuming and invasive, plant water status can be easily assessed by infrared thermography. Thus, we examined the stress responses of 2-year-old potted Scots pine seedlings from six provenances (Bulgaria, France, Germany, Italy, Poland, and Spain) based on two thermal indices (crop water stress index and stomatal conductance index). Both indices were derived from infrared images during a 6-week drought/control treatment in a greenhouse in the summer of 2013. The pines were monitored during the stress and subsequent recovery period. After controlling for fluctuating environmental conditions, soil moisture or treatment-specific water supply was the most important driver of drought stress. The stress magnitude and response to soil water deficit depended on provenance. Under moderate drought conditions, pines from western and eastern Mediterranean provenances (Bulgaria, France, and Spain) expressed lower stress levels than those from both continental provenances (Germany and Poland). Moreover, pines from continental provenances were less resilient (showed less recovery after the stress period) than Mediterranean pines. Under extreme drought, all provenances were equally stressed with almost no significant differences in their thermal indices. Provenance-specific differences in drought resistance, which are associated with factors such as summer precipitation at the origin of Scots pine seedlings, may offer promising tracks of adaptation to future drought risks.

Contributions

HS developed the experimental design, collected data, analysed, and interpreted the data and wrote the paper. CS assisted in collecting the data, contributed to the experimental design, and contributed to writing the paper. MM contributed to the experimental design, advised concerning the data analyses, contributed to writing the paper. AM contributed to the conception of the work, interpreted the data and revised the paper writing.

3.2. Above-Ground Dimensions and Acclimation Explain Variation in Drought Mortality of Scots Pine Seedlings from Various Provenances

Seidel, H., and Menzel, A. (2016). *Front. Plant Sci.* 7, 1014.

doi:10.3389/fpls.2016.01014

Seedling establishment is a critical part of the life cycle, thus seedling survival might be even more important for forest persistence under recent and future climate change. Scots pine forests have been disproportionately more affected by climate change triggered forest-dieback. Nevertheless, some Scots pine provenances might prove resilient to future drought events because of the species' large distributional range, genetic diversity, and adaptation potential. However, there is a lack of knowledge on provenance-specific survival under severe drought events and on how acclimation alters survival rates in Scots pine seedlings. We therefore conducted two drought-induced mortality experiments with potted Scots pine seedlings in a greenhouse. In the first experiment, 760 three-year-old seedlings from 12 different provenances of the south-western distribution range were subjected to the same treatment followed by the mortality experiment in 2014. In the second experiment, we addressed the question of whether acclimation to re-occurring drought stress events and to elevated temperature might decrease mortality rates. Thus, 139 four-year-old seedlings from France, Germany, and Poland were subjected to different temperature regimes (2012-2014) and drought treatments (2013-2014) before the mortality experiment in 2015. Provenances clearly differed in their hazard of drought-induced mortality, which was only partly related to the climate of their origin. Drought acclimation decreased the hazard of drought-induced mortality. Above-ground dry weight and height were the main determinants for the hazard of mortality, i.e., heavier and taller seedlings were more prone to mortality. Consequently, Scots pine seedlings exhibit a considerable provenance-specific acclimation potential against drought mortality and the selection of suitable provenances might thus facilitate seedling establishment and the persistence of Scots pine forest.

Contributions

HS collected data, contributed to the experimental design, analysed and interpreted the data, and wrote the paper. AM suggested the study, contributed to the framing of the work and experimental design, interpreted the data, and assisted in writing the paper.

3.3. Compensatory Growth of Scots Pine Seedlings Mitigates Impacts of Multiple Droughts Within and Across Years

Seidel, H., Matiu, M., and Menzel, A. (2019). *Front. Plant Sci.* 10, 519.
doi:10.3389/fpls.2019.00519.

Tree seedling resistance to and recovery from abiotic stressors such as drought and warming are crucial for forest regeneration and persistence. Selection of more resilient provenances and their use in forest management programs might alleviate pressures of climate change on forest ecosystems. Scots pine forests in particular have suffered frequent drought-induced mortality, suggesting high vulnerability to extreme events. Here, we conducted an experiment using potted Scots pine seedlings from ten provenances of its south-western distribution range to investigate provenance-specific impacts of multiple drought events. Seedlings were grown under ambient and elevated temperatures for 1.5 years and were subjected to consecutive droughts during spring and summer. Growth (height, diameter, and needle) and spring phenology were monitored during the whole study period and complemented by biomass assessments (bud, needle, wood, and needle/wood ratio) as well as measurements of chlorophyll fluorescence and of needle stable carbon isotope ratio. Phenology, growth and biomass parameters as well as carbon isotope ratio and their (direct) responses to reoccurring droughts differed between provenances, indicating genotypic adaptation. Seedling growth was plastic during drought with intra- and inter-annual compensatory growth after drought stress release (carryover effects), however, not fully compensating the initial impact. For (smaller) seedlings from southern/drier origins, sometimes greater drought resistance was observed which diminished under warmer conditions in the greenhouse. Warming increased diameter growth and advanced phenological development, which was (partly) delayed by drought in 2013, but advanced in 2014. Earlier phenology was linked to higher growth in 2013, but interestingly later phenology had positive effects on wood and needle biomass when subjected to drought. Lastly, stable carbon isotope ratios indicated a clear drought response of carbon assimilation. Drought-induced reduction of the photosystem II efficiency was only observed under warmer conditions but showed compensation under ambient temperatures. Besides these direct drought impacts, also interactive effects of previous drought events were shown, either reinforcing or sometimes attenuating the actual impact. Thus, depending on amount and timing of events, Scots pine seedlings, particularly from southern origins, might be well adapted and resilient to drought stress and should be considered when discussing assisted migration under changing climatic conditions.

Contributions

HS collected data, contributed to the experimental design, analysed and interpreted the data, and wrote the manuscript. MM contributed to data analyses and interpreted the data. AM contributed to the conception of the work, interpreted the data, and assisted in writing the paper.

4. Discussion

4.1. Immediate drought effects

Bud phenology during the two years of observations was not consistently affected by drought. While bud phenology showed a drought-induced delay in the first year, it was advanced by drought in the following year (chapter 3.3). Other studies have also presented a drought-induced delay (Adams et al., 2015; Swidrak et al., 2013) that can be explained by drought constrained tissue formation (Körner, 2015; Peñuelas et al., 2013). Contrary, Bernal et al. (2011) attributed an advance of phenology to an increase of tissue temperature caused by drought-induced stomatal closure and thus reduced transpirational cooling. In our experiment, the overall phenological timing and speed of development were fundamentally different between both years. Bud phenology started earlier and developed slower in the first year but began later and was faster in the second year. Thus, there was a longer temporal overlap of drought with the decisive phenological development, partly under more severe conditions, in the first year of the experiment. A straight-forward explanation of phenological drought response is therefore difficult since the ultimate outcome might be a matter of the relation between phenological timing and drought occurrence as well as drought severity that all can be altered by temperature (Deng et al., 2019; Peñuelas et al., 2004). The complex interplay of the various drivers that alter phenology highlights their importance for and the challenges to predict drought impacts on forest ecosystems as well as on forest productivity.

Scots pine seedlings survived between 7 and 14 weeks in our mortality experiments (chapter 3.2) that mimicked a fast and strong drought event comparable to similar studies with conifers (Cregg and Zhang, 2001; Hartmann et al., 2013) but might be longer than for many angiosperm seedlings (Barigah et al., 2013; Blackman et al., 2019; Urli et al., 2013). The longer survival time during these conditions is probably primarily related to a more isohydric behavior of Scots pine and the resulting conservation of water. This may suggest that the depletion of carbohydrates causes mortality instead of hydraulic failure. Anyway, the ultimate reason of Scots pine mortality triggered by drought is not yet clear. Salmon et al. (2015) showed increased rates of transpiration, stomatal conductance and therefore net assimilation of Scots pine trees under drought conditions after having suffered from previous drought events. Additionally, Bachofen et al. (2017) and Rehschuh et al. (2020) found no evidence of lethal carbon depletion in Scots pine seedlings during drought. But fast as well as strong soil and atmospheric drought

conditions can cause considerable loss of hydraulic conductivity (Rehseh et al., 2020). Although there is no direct indication in literature that a shortage of water causes carbon starvation and ultimately tree death, a lack of water may additionally impede the utilization of carbon (Hartmann et al., 2013; Paljakka et al., 2017).

Annual growth was reduced by drought (chapter 3.3). Tissue temperature derived drought stress indices (chapter 3.1), stable carbon isotope ratios and quantum efficiencies of the PSII indicated a limitation of photosynthesis under drought conditions (chapter 3.3). The decline of growth during drought is well documented for plants. The lack of water impedes the formation of new tissue and consequently reduces growth (Hsiao and Acevedo, 1974; Muller et al., 2011; Peñuelas et al., 2013). Moreover, *P. sylvestris* has a tight stomatal control and a reduced photosynthesis under drought conditions (Eilmann et al., 2010; Irvine et al., 1998; Semerci et al., 2017). In general, growth constraints may be primarily controlled by carbon sinks since thresholds for growth termination are lower than for photosynthesis that is influenced by stomatal closure (Körner, 2015; Muller et al., 2011).

Survival and drought resistance was lower when growth was higher during well-watered conditions (chapter 3.2 and 3.3). A long-term Europe-scale study on ring width indices found similar results (Bose et al., 2020a). Our results of seedling dimensions increasing the hazard for drought-induced mortality are in line with a recent multi-year and regional-scale study that determined size as the strongest predictor of individual tree mortality during severe drought conditions (Stovall et al., 2019). This finding might be due to a higher ratio of above- to belowground biomass and thus to relatively increased demand for water resulting in a faster dehydration during drought conditions.

Contrary to shoot elongation, which was completed in early summer when growth rates can be already small (Swidrak et al., 2013), annual needle and diameter growth were modulated by inter-annual negative carryover effects, compensation growth or acclimation (chapter 3.3), which are discussed in the following.

4.2. Interaction between growth phenology and drought timing

Growth cessation occurred earliest for shoot growth in early summer, followed by needle growth in late summer and finally for radial growth in autumn (chapter 3.3). The observed pattern of growth terminations is only partly confirmed by Swidrak et al. (2013) who

found that radial growth stops before needle growth. However, the location of their study site and rainfall patterns suggest general water limitations that could have affected wood formation (Eilmann et al., 2011; Pichler and Oberhuber, 2007). Consequently, Swidrak et al. (2013) argues that growth phenology of different organs can be influenced by site-specific environmental factors.

The influences of drought treatments on growth and possible recovery varied between different compartments and seasons. Additionally, drought impacts were low when growth rates were small at the end of respective growth periods (chapter 3.3). In general, drought can only have direct or immediate impacts on growth if respective compartments are actually developing or growing during the period of low water availability. The same applies to recovery during favorable conditions. Consequently, unlike needle and radial growth which lasted at least till end of August and therefore was influenced by spring and summer water availability, shoot growth was not affected by summer drought conditions anymore. Mature Scots pine trees growing in Germany in the field only showed a very weak relationship of shoot elongation with late spring water deficit (Taeger et al., 2013), indicating that also under natural temperate conditions shoot elongation terminates before water shortage occurs. Although Dougherty et al. (1994) stated that height growth of single flushing species is closely linked to weather conditions during bud formation in the previous year, this can only be true if tissue formation during bud outgrowth and the resulting shoot elongation is not impeded by actual water shortage (Hsiao and Acevedo, 1974; Muller et al., 2011; Peñuelas et al., 2013). Radial growth is divided into two phases by the formation of early- and latewood divides while diameter growth can be high during the whole growing season (Dougherty et al., 1994). The impact of spring as well as of summer drought on diameter increment and wood formation was shown by Pichler and Oberhuber (2007). They also found that the impact of summer drought on latewood did not affect total ring width, which is supporting our observation of smaller drought impacts at the end of growth periods. Although dry conditions can stop wood formation and annual diameter increment in *Pinus sylvestris* (Gruber et al., 2010), we observed a resumption of radial growth after drought stress release. This is in line with the frequent observation of intra-annual density fluctuations in tree rings that can indicate the return to unimpeded growth after environmental conditions become favorable again (Battipaglia et al., 2016).

Our experiments showed that higher temperatures advanced bud outgrowth. Therefore, it was quite evident that (later occurring) drought did not affect advanced phenophases

under warmer growing conditions. Additionally, warming resulted in higher spring growth despite water shortage when onset of bud break occurred well before the development of severe drought constrains. Moreover, warming partially buffered drought impacts by extending the growing season (chapter 3.3). The promotion of leaf phenology and the prolongation of growth periods by rising temperatures is a global phenomenon linked to climate change (Reyer et al., 2013). Similarly, wood phenology can start earlier and can last longer under higher temperatures in Scots pine (Gruber et al., 2010) and other pines (Deslauriers et al., 2008; Gruber et al., 2009). Gruber et al. (2010) also reported that the difference in radial growth between a xeric and a dry-mesic site is smaller in a year with higher spring temperatures. Nevertheless, an escape from drought stress triggered by temperature induced advanced growth might not be translated into superior annual growth due to negative carryover effects of warmer droughts or growth constrains by higher summer temperatures. Since the occurrence of drought in relation to growth timing is important, it is crucial to consider temperature mediated changes of phenology when predicting outcomes of drought events under future climate change.

4.3. Negative carryover effects

After stress release, drought can still have impacts within and across years or can amplify the impact of a consecutive drought. We found intra-annual (short-term) negative drought effects for needle and diameter growth as well as for photosynthesis as indicated by chlorophyll fluorescence and transpiration derived from needle tissue temperatures. Inter-annual (long-term) negative effects were observed for height growth only under ambient temperatures (chapter 3.3).

Short-term recovery might be due to a restoration of the plant water status and resumption of physiological processes to pre-drought conditions whereas the long-term recovery might be a consequence of persistent constrains like leaf shedding, the reduction of sapwood area or the loss of functional xylem (Guadagno et al., 2017; Hammond et al., 2019; Huang et al., 2018; Irvine et al., 1998; Rehschuh et al., 2020). Consequently, short-term recovery has been observed for tree water deficit, water potential, sap flow, transpiration and photosynthesis (Cregg and Zhang, 2001; Dietrich and Kahmen, 2019; Irvine et al., 1998; Lüpke et al., 2016, 2017). However, the short-term recovery potential of water relations may also depend on the species and the strength of previous water stress (Ruehr et al., 2019). The hydraulic system of gymnosperms generally has a lower

recovery ability, but in terms of their more isohydric behavior, also a lower risk of dysfunction than that of angiosperms (Klein et al., 2018). Whereas a medium (25%) impairment of water relations of Norway spruce saplings resulted in the total recovery of the hydraulic system to pre-drought conditions (Tomasella et al., 2017), Scots pine and loblolly pine did not fully recover after more severe drought stress of 50% and 35% loss of hydraulic conductivity, respectively (Hammond et al., 2019; Rehschuh et al., 2020). Long-term effects have been frequently observed for radial increment, canopy cover (shoot growth) as well as for whole vegetation growth (Galiano et al., 2011; Guada et al., 2016; Irvine et al., 1998; Jiang et al., 2019; Wu et al., 2018) and have been shown for multiple tree species and time scales (Becker, 1989; Bréda et al., 2006; Orwig and Abrams, 1997; Stribley and Ashmore, 2002). Most of these experimental and observational field studies on long lasting negative drought impacts did not report soil moisture conditions during recovery or report climatic measures and drought indices (Becker, 1989; Guada et al., 2016; Huang et al., 2018; Irvine et al., 1998; Jiang et al., 2019; Orwig and Abrams, 1997; Wu et al., 2018). In these cases, we have to be careful about the ultimate causes of negative carryover effects since they could be due to intrinsic constraints or due to lacking recovery of the environment (e.g. soil moisture) to pre-drought conditions (Huang et al., 2018).

Long-term carryover effects of drought can also be mediated by temperature as determined for height growth (chapter 3.3). This can be caused by a temperature-induced intensification of the stress itself that exceeds the thresholds of physiological acclimation and adaptation potentials as well as of phenotypic plasticity and therefore having long lasting impact on tree and forest vigor (Allen et al., 2015). But this cannot be the reason in our experiment, since we observed the long-lasting growth decline under ambient conditions. It is therefore more likely that temperature shifted the sensitive phase of bud development into periods of stress that may have altered the strength of carryover effects (Strømme et al., 2016; Wareing, 1956). This may be particularly true for the bi-phasic process of shoot increment that can be influenced by temperature and water availability during bud formation in the previous year as well as during shoot elongation in the following year (Jansons et al., 2015; Junttila and Heide, 1981).

Beside a direct and persistent impairment of performance by drought extending into periods of favorable conditions, drought impacts can be amplified or can only be apparent after repeated water stress as observed for annual diameter and needle growth (chapter

3.3). Bose et al. (2020a) showed on a continental-scale that resistance and recovery of Scots pine tree ring growth is indeed a function of drought frequency.

4.4. Positive carryover effects

Contrary to prevailing negative carryover effects reported in literature we also observed positive carryover effects. These positive responses buffered negative effects and were even able to mask direct drought impacts on an annual scale. Additionally, drought was able to stimulate growth in the subsequent year (chapter 3.3).

Although Huang et al. (2018) reported frequent positive carryover effects of drought on the tree width index on a continental scale, they did not give an explanation of this finding. Kannenberg et al. (2020) explained an increased performance of trees after drought with a higher water availability that is mediated by a suppression of competing vegetation or hydraulic redistribution of water. However, this cannot explain the observations in our studies with potted plants. Additionally, extreme wetness compensated drought-induced decline of vegetation and tree growth (Jiang et al., 2019), but the authors did not demonstrate how wetness interacts with previous drought events. Therefore, physiological responses that directly explain the positive carryover effects on inter- and intra-annual scale are not yet to be found in literature. However, inter-annual growth enhancement after drought years might be due to an extension of the growing season, since oak and beech can show an advance of spring phenology and oak also a delay of autumn phenology after previous year drought (Čehulić et al., 2019; Kuster et al., 2014; Spieß et al., 2012; Yonekura et al., 2004). Otherwise, also a delay of oak spring phenology after drought year is possible (Vander Mijnsbrugge et al., 2016).

During drought there is a trade-off between growth and carbohydrate storage (Bachofen et al., 2017; Piper et al., 2017). Physiological carbon sources, e.g. photosynthesis, have higher drought stress thresholds than carbon sinks, e.g. growth (Körner, 2015; Muller et al., 2011). This can lead to an accumulation of carbohydrates during water shortage (Bachofen et al., 2017). The carbon pool that has been accumulated during drought might stimulate increased growth rates during subsequent favorable conditions and thus mitigate immediate drought effects. Consistently, the ability of Scots pine to recover after drought events has been shown to depend on carbon reserves (Galiano et al., 2011). If the source threshold is also exceeded, carbohydrate accumulation may be hampered what may affect post-drought performance. Consequently, drought frequency and severity influences Scots pine recovery (Bose et al., 2020a). Moreover, we have to keep in mind that severe

drought stress can be either induced by long and low water deficits as well as by short and intense drought conditions (McDowell et al., 2008). Thus, the influence on post drought performance also has a time component (Gao et al., 2018).

4.5. Acclimation

Besides the immediate and carryover effects, seedlings in our experiments also showed responses that suggest some degree of acclimation to drought. In general, acclimation by drought results in a reduced impact of a subsequent drought or even a lack of impairment (Niinemets, 2010). Accordingly, intra-annual diameter and intra- as well as inter-annual needle growth were less affected, and survival was longer during a second drought episode (chapter 3.2, 3.3).

The seedlings in our experiments may have been basically acclimated by structural and hydraulic adjustment. Indeed, height and needle growth were smaller during drought which has been frequently shown for Scots pine (Dobbertin et al., 2010; Sterck et al., 2008; Taeger et al., 2015). Lower growth rates before water shortage generally favour drought resistance (Bose et al., 2020a). Smaller trees have a smaller needle area that reduces water loss (Morán-López et al., 2014), thus extending the time during drought till a critical threshold for growth and survival is reached. Furthermore, drought mortality rates increase with tree size (Etzold et al., 2019; Stovall et al., 2019) that is probably caused by size-mediated hydraulic failure (McDowell and Allen, 2015). Moreover, Garcia-Forner et al. (2016) observed superior survival of seedlings when concentrations of glucose and fructose were high prior to drought. Consequently, an accumulation of carbohydrates during the previous drought (Bachofen et al., 2017) could explain a lower mortality hazard during a repeated drought.

Although Bose et al. (2020a) stated that mature Scots pine may not be able to acclimate to future more severe and more frequent droughts, this might be able for seedlings developing during these limiting conditions and therefore in the long run for mature trees that arise from these seedlings. Mature trees have a low ratio of current year growth to total biomass that might diminish the effect of structural acclimation as explained above. Young trees have to sustain a lower proportion of carbon sinks and have higher assimilation rates in relation to their biomass (Niinemets, 2010). Moreover, the accumulation of carbohydrates during drought, that might be used in subsequent recovery periods, is found in seedlings but not in mature trees (Bachofen et al., 2017; Gruber et al.,

2011). Thus, acclimation of seedlings might be possible if drought does not exceed mortality thresholds.

4.6. Temperature effects on growth and drought impacts

Higher temperatures in our experiments advanced phenophases (chapter 3.3). That is a common observation and linked to the accumulated temperature sum needed for the onset of phenophases (Fu et al., 2015; Menzel et al., 2006) and partly affected provenance-specific biomass production as well as inter-annual growth in our study. Overall growth of seedlings was almost comparable between ambient and warmer growing conditions with the exception of higher annual diameter growth under increased temperature. Nevertheless, growth during cooler periods of the year at the beginning and the end of the growing season were favored under increased temperatures, but summer growth was higher under ambient temperature conditions (chapter 3.3).

In Mediterranean and temperate climates, Scots pine radial increment shows a negative relationship with summer temperatures (Martínez-Vilalta et al., 2008; Michelot et al., 2012; Misi et al., 2019). Temperatures might directly constrain summer growth by exceeding specific temperature thresholds (Niinemets, 2010). Contrary, warmer temperatures can induce an earlier onset, delayed cessation and a higher rate of xylogenesis; thus, extending the growing season as well as increasing radial growth (Antonucci et al., 2019; Balducci et al., 2016; Begum et al., 2016, 2018; Rahman et al., 2020; Rossi et al., 2014b). Actually, autumn radial growth and drought-induced compensation growth in our study was higher under warmer temperatures that mitigated drought effects on an annual time scale. Scots pine can respond very plastically and translate favorable temperature conditions into longer growing seasons (Martinez del Castillo et al., 2016). A longer growing season is typically observed in regions with higher temperatures (Rötzer and Chmielewski, 2001) and growing season length positively influences the productivity of Scots pine forests (Danielewska et al., 2015). Thus, temperature changes that extend the growing season might counteract drought impacts. But the extension of the growing season can also impose new challenges to plants such as a higher risk to experience frost at the beginning and at the end of the growing season (Liu et al., 2018). However, Scots pine has a wide safety margin at least to late frost events (Bachofen et al., 2016).

Besides the direct impact on tree performance, temperature can influence the strength of drought responses. We mainly observed stronger effects of warmer droughts on biomass

production and shoot elongation as well as negative carryover effects on summer radial growth (chapter 3.3). Higher temperatures increase the atmospheric demand for water and thus exacerbate the impacts of soil drought (Allen et al., 2015). Drought intensity is an important factor for Scots pine drought resistance and recovery (Bose et al., 2020a). Therefore, higher temperatures may affect resistance, resilience and recovery. Based on our experimental setup, we cannot evaluate if the temperature effects after drought stress release are caused by an intensification of the drought itself or by an alteration of post-drought reactions.

4.7. Intra-specific drought response variation

Overall, southern provenances exhibited morphological and growth traits as well as stomatal control strategies that might render them more resistant and resilient to drought. They had lower shoot growth and shorter needles (chapter 3.3). Their water relations, evaluated by needle surface temperatures (chapter 3.1) and stable carbon isotope ratio (chapter 3.3), responded less to and recovered faster from water shortage. Growth responses of provenances to drought were found to be negatively related to summer aridity suggesting local adaptations (chapter 3.3). Moreover, Mediterranean provenances had a lower hazard for drought mortality (chapter 3.2).

Provenances from origins with dry summers grew less in height. This relationship was conserved irrespectively of growing temperature conditions (chapter 3.3). Vizcaíno-Palomar et al. (2019) could show that Spanish provenances are locally very well adapted to drought conditions in terms of height growth. Smaller trees may have an advantage and higher fitness under water limiting conditions because they have a lower risk to suffer hydraulic dysfunction caused by drought-induced xylem embolism (Olson et al., 2018).

Controversially to height growth, needle growth as well as the drought responses of needle and shoot growth differed between growing temperature conditions. However, provenances originating from more moist locations showed a higher growth variability thus phenotypic plasticity (chapter 3.3). Provenances can have specific growth responses to changing growing temperatures (Reich and Oleksyn, 2008; Zhang et al., 2020). Additionally, also provenance-specific climate responses can change with temperature (Kapeller et al., 2012). Moreover, drought-response might be masked by temperature mediated changes of phenology in relation to drought occurrence as explained above.

In general, a more plastic response of shoot growth under the assumption of a drier environment in the near future might lead to a maladapted structural overshoot to drought conditions (Jump et al., 2017; Magnani et al., 2000), because plastic shoot growth might maximise tree height and thus increases the risk of hydraulic dysfunction as noted above. This is in line with the recent finding that Scots pine trees with a high growth variability are more sensitive and less resistant to drought events (Bose et al., 2020a). Opposite to northern provenances, provenances from the southern distribution range might be favoured when transplanted to cooler regions because of their specific height growth and survival ability (Reich and Oleksyn, 2008). They might thus be well suited for a northward transfer under future climate change which has been already shown for white spruce in Canada (Lu et al., 2014; Otis Prud'homme et al., 2018).

Drought stress indices derived from needle surface temperatures and needle stable carbon isotope ratios of southern provenances suggest less stomatal constraints of photosynthesis under drought conditions. Moreover, the positive relationship between growth and stable carbon isotope ratios indicates that height growth of southern provenances is not limited by stomatal control (Marguerit et al., 2014). Thus, photosynthesis of southern provenances from dry sites might be less affected by water shortage compared to northern provenances from moister sites. Drought adaptation strategies may therefore vary across the distribution range (Isaac-Renton et al., 2018). Whereas dry site populations follow a riskier strategy in terms of leaf water relations, they on the other hand reduce the risk of hydraulic dysfunction by drought adapted structural traits.

5. Conclusion

Scots pine seedlings show growth traits and ecophysiological traits to resist drought episodes. Moreover, they have the ability to recover from, to acclimate to and to compensate water shortage. Additionally, seedlings from southern provenances are better adapted to dry conditions. Scots pine will thus also be able to contribute to natural regeneration and forest persistence under future climate change. An evaluation based on climate analogues revealed that *Pinus sylvestris* still may remain an abundant tree species throughout Europe as long as appropriate forest adaptation will be conducted (Buras and Menzel, 2019). Especially provenance originating from Mediterranean climates might be of special importance in these forest adaptation programs since they have a lower growth variability and are thus less sensitive to drought (Bose et al., 2020a). Nevertheless, also provenances from temperate regions might prove climate change resilient because of the species acclimation potential that might even act, as just recently shown, across generations (Bose et al., 2020b). Drought acclimation might also be expressed by slower growth recovery rates that might be favourable in the light of more frequent droughts in the future (Gessler et al., 2020). Scots pine can also be a valuable species in climate change adapted forest conversion programs since it itself profits from species mixing and can buffer drought impacts on co-occurring species (Steckel et al., 2020).

However, the adaptability of Scots pine trees and forests is subjected to the assumption that no mortality thresholds are surpassed on a wide spatial and temporal scale by rapid and intense environmental changes (Buras et al., 2018; Schuldt et al., 2020). Favourable climatic conditions and management in the past may have generated a mismatch between the actual tree as well as forest structure and the drought resilience potential (Jump et al., 2017). The carryover effects influencing the persistence of Scots pine ecosystems are therefore important since these long-term impacts of drought are of special interest when evaluating drought consequences on biogeochemical cycles (especially of carbon, water and nutrients), vegetation dynamics and productivity (Kolus et al., 2019; van der Molen et al., 2011).

6. References

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7. Figures and Tables

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