Schlussbericht des Projektes

Drought Vulnerability of Conifers in Switzerland: a Multiproxy Approach

im Forschungsprogramm «Wald und Klimawandel»

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Februar, 2015

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Ein Projekt-Schlussbericht aus dem Forschungsprogramm «Wald und Klimawandel» von BAFU und WSL (www.wsl.ch/wald_klima)

Projektlaufzeit: 01.04.2011 bis 31.3.2013

Zitierung

Siegwolf R., Rigling A., Lévesque M. 2015. Drought Vulnerability of Conifers in Switzerland: a Multiproxy Approach. PSI. 19 S.

Die drei im Bericht enthaltenen Kapitel wurden in internationalen Journals publiziert. Daher steht dieser Bericht nur für den internen Gebrauch zur Verfügung.

DANK

We would like to thank Pascale Weber and Roger Köchli for their help with the soil analyses and Francesca Carnesecchi for her help in sample preparation. We thank Giorgio Vacchiano for helping us with the site selection, Corrado Letey for the coring permission, and Fabio Brunier (Department of Soil Conservation and Water Resources, Autonomous Region of Valle d'Aosta, Italy) for providing the climate data for the site in Aosta Valley. We are grateful to Bernhard Hadorn for the coring permission for the site near Biel. We also thank people in the dendro sciences groups at WSL for help in the laboratory and discussions. This research was supported by the Swiss State Secretariat for Education and Research under the COST action FP0703 and by the BAFU/WSL Research Program 'Forests and Climate Change'.

Inhalt

Zusammenfassung

(Auszug aus Lévesque, M. 2013. Drought response of five conifers along an ecological gradient in Central Europe: A multiproxy dendroecological analysis. PhD Dissertation. ETH Zurich, Switzerland.)

Trockenheit kann durch das Auslösen von Baumsterben starke Auswirkungen auf Waldökosysteme haben. Weltweit wurde über eine Zunahme der Fälle trockenheitsbedingten Waldsterbens berichtet, und solche Phänomene werden höchstwahrscheinlich in der Zukunft noch an Bedeutung gewinnen, da zu erwarten ist, dass Dürren häufiger und stärker werden. Vermehrte Baummortalität als Folge des globalen Klimawandels könnte bisherige Methoden der Waldbewirtschaftung in Frage stellen und die Versorgung mit Gütern und Dienstleistungen aus Waldökosystemen gefährden. Allerdings sind die langfristigen Auswirkungen von Trockenheit auf das Wachstum und die physiologische Reaktion der Bäume noch immer wenig erforscht. Deshalb war das Hauptziel dieser Dissertation, die Trockenheitsanfälligkeit fünf zentraleuropäischer Baumarten zu ermitteln: der endemischen *Picea abies* (L.) Karst., *Pinus sylvestris* L. und *Larix decidua* Mill. Im Vergleich zu den nicht einheimischen *Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii* und *Pinus nigra* Arn. Zu diesem Zweck wurde ein grosser ökologischer Gradient erforscht, wobei eine Kombination dendroökologischer und stabiler Isotopen-Methoden benutzt wurde. Besondere Schwerpunkte wurden gelegt auf (1) die Dauer und Saisonabhängigkeit von Bodenwasserdefiziten, welche sich am stärksten auf das Baumwachstum und die Baumphysiologie auswirken, (2) Veränderungen der Wachstumsraten und der intrinsischen Wassernutzungs-Effizienz unter steigender atmosphärischer CO_2 Konzentration (c_a) und steigender Wasserverfügbarkeit, und (3) die Auswirkungen klimatischer Schwankungen und schwerer Dürren auf das Baumwachstum.

Im ersten Kapitel wurde der Einfluss klimatischer Schwankungen und schwerer Dürren auf das radiale Stammwachstum entlang eines grossen ökologischen und klimatischen Gradienten analysiert. Es wurden Jahrringdaten von 770 Baumen an 14 Standorten innerhalb vier verschiedener biogeografischer Regionen erfasst: in den nördlichen Schweizer Alpen (nass), im Schweizer Mittelland (feucht), in den Ausläufern des Schweizer Jura (feucht) und in den Zentralalpen (trocken). Response-Funktionen, Weiserjahre und „Superposed Epoch Analysis“ wurden benutzt, um das Klima und die Trockenheitsreaktionen der Bäume zu untersuchen. Entlang des Gradienten stellten sich *P. abies*, *L. decidua* und *P. sylvestris* als am anfälligsten auf Bodenwasserdefizite heraus. An trockenen Standorten reagierte *L. decidua* sehr empfindlich auf extreme Trockenperioden. Im Gegensatz dazu waren *P. menziesii* und *P. nigra*, unabhängig von den Feuchtigkeitsbedingungen am Standort, nur wenig durch Wassermangel und schwere Trockenperioden beeinträchtigt.

Das zweite Kapitel beschäftigt sich mit der Frage, wie sich Bodenwasserdefizite unterschiedlicher Dauer und Saisonalität auf das radiale Stammwachstum, den Wasser und Gasaustausch sowie die Kohlenhydratdynamik der Nadelhölzer an zwei Standorten auswirken, nämlich unter sehr trockenen (Zentralalpen) und feuchten (Schweizer Mittelland) Bedingungen. Die Breiten von Frühholz, Spätholz und des gesamten Jahrrings sowie $\delta^{13}C$ und $\delta^{18}O$ wurden in den Jahrringen gemessen und statistisch mit einem multiskalaren Index des Bodenwasserdefizits für den Zeitraum von 1961 bis 2009 korreliert. *Picea abies* und *L. decidua* waren in Bezug auf Trockenheit die empfindlichsten Arten, unabhängig vom Wasserhaushalt des Standorts. Am feuchten Standort reduzierte Sommertrockenheit die Photosynthese und das Wachstum aller Arten erheblich, wogegen am trockenen Standort die Wasserverfügbarkeit im Winter und

Frühling für alle Arten kritisch war. Am feuchten Standort reagierten die Bäume auf Wasserdefizite von kürzerer Dauer anfälliger als am trockenen Standort. Demzufolge dürfte der Zuwachs am feuchten Standort erheblich abnehmen, wenn die Sommer trockener werden. Im Gegensatz dazu konnte am trockenen Standort die langfristige Leistung und das Überleben der hochsensiblen *P. abies* und *L. decidua* gefährdet sein, falls die Wasserverfügbarkeit vor dem Beginn der Vegetationsperiode zurückgeht.

Im dritten Kapitel wurden an denselben zwei Standorten das langfristige Wachstum und die Gasaustauschreaktionen von Bäumen auf Synergieeffekte von steigendem c_a, zurückgehender Wasserverfügbarkeit und Erwärmung untersucht. Veränderungen in der intrinsischen Wassernutzungseffizienz und der Wachstumsraten wurden aus jährlich aufgelösten Werten von $\delta^{13}C$ und $\delta^{18}O$ sowie des Grundflächenzuwachses abgeleitet. Es zeigte sich, dass trotz der langfristigen Zunahme der intrinsischen Wassernutzungseffizienz der radiale Stammzuwachs der meisten Arten seit den 1980er Jahren erheblich abgenommen hatte, übereinstimmend mit einem abnehmenden Trend der Wasserverfügbarkeit. Der zweifache Isotopen-Ansatz, der auf einer simultanen Bewertung von Veränderungen von $\delta^{13}C$ und $\delta^{18}O$ basiert, ergab, dass zwar der trockenheits-induzierte Stomataschluss den Wasserverlust durch Verdunstung bei Bäumen reduzierte, gleichzeitig aber die Photosynthese und das Baumwachstum hemmte. Somit erbringt diese Studie den ersten Beweis, dass temperaturbedingter Trockenheitsstress den möglichen CO_2-Düngungseffekt bei Bäumen in zentraleuropäischen Wäldern kompensierte.

Insgesamt tragen die Ergebnisse dieser Dissertation dazu bei, Wachstum und Gasaustauschreaktionen verschiedener Nadelbaumarten an Standorten mit unterschiedlicher Feuchtigkeit in Zentraleuropa besser zu verstehen. Die hohe Anfälligkeit von *P. abies* and *L. decidua* auf Trockenheit entlang des ganzen ökologischen Gradienten bedeutet, dass ihre langfristige Leistungsfähigkeit und ihr Überleben gefährdet sein könnten, wenn das Klima trockener wird, so wie es für das 21. Jahrhundert und darüber hinaus projiziert wird. Die Arten *P. nigra* und *P. menziesii* reagierten bezüglich Wasserdefiziten entlang des ökologischen Gradienten am wenigsten empfindlich. Dies konnte für ein adaptives Waldmanagement von Relevanz sein, da diese zwei fremdländischen Arten in einem trockeneren Klima die trockenheitsempfindlicheren *P. sylvestris* und *P. abies* teilweise ersetzen konnten.

Summary

(Extract from Lévesque, M. 2013. Drought response of five conifers along an ecological gradient in Central Europe: A multiproxy dendroecological analysis. PhD Dissertation. ETH Zurich, Switzerland.)

Drought can strongly impact forest ecosystems by triggering tree mortality. Cases of drought-induced forest decline have been reported to increase worldwide, and such phenomena are most likely to further gain importance in the future as the frequency and intensity of drought events are expected to increase. Amplified tree mortality in response to global climate change may challenge forest management practices and compromise the provision of forest ecosystem goods and services. However, the long-term impacts of drought on growth and physiological responses of trees are still poorly understood. Hence, the main goal of this dissertation was to determine the drought vulnerability of five Central European tree species, i.e., the native *Picea abies* (L.) Karst., *Pinus sylvestris* L. and *Larix decidua* Mill. in contrast to the non-native *Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii* and *Pinus nigra* Arn. To this end, a wide ecological gradient was investigated using a combination of dendroecological and stable isotope methods. Particular emphasis was put on (1) the duration and seasonality of soil water deficits that most strongly impact tree growth and physiology, (2) changes in growth rates and intrinsic water-use efficiency under rising atmospheric CO_2 concentration (c_a) and decreasing water availability, and (3) the impacts of climatic variability and severe droughts on tree growth.

In the first chapter the influence of climatic variability and severe droughts on tree radial growth was analyzed along a wide ecological and climatological gradient. Tree-ring data from 770 trees were sampled at 14 sites within four distinct biogeographic regions: the northern Swiss Alps (wet), the Swiss Plateau (moist), the foothills of the Jura Mountains (moist), and the Central Alps (dry). Response functions, pointer years and Superposed Epoch Analysis were used to study the climate and drought responses of trees. Along the gradient, *P. abies*, *L. decidua* and *P. sylvestris* turned out to be most vulnerable to soil water deficits. At dry sites, *L. decidua* was very vulnerable to extreme drought events. In contrast, irrespective of site moisture conditions, *P. menziesii* and *P. nigra* were little affected by water deficits and severe drought events.

The second chapter focuses on the duration and seasonality of soil water deficits that most strongly impact radial growth, water relations, gas exchange and carbohydrate dynamics of conifers at two sites, i.e., under xeric (dry inner-Alps) and mesic (Swiss moist lowlands) conditions. Earlywood, latewood and total ring widths, as well as the $\delta^{13}C$ and $\delta^{18}O$ in tree rings were measured and statistically related to a multiscalar soil water deficit index for the period 1961‑2009. *Picea abies* and *L. decidua* were the most vulnerable species to drought irrespective of site moisture conditions. At the mesic site, summer drought significantly impeded photosynthesis and growth of all species, whereas at the xeric site, winter and spring water availability was critical for all species. Trees at the mesic were more vulnerable to water deficits of shorter duration than at the xeric site. Thus, if summers become drier, tree growth at the mesic site will be significantly reduced. In contrast, at the xeric site, the long-term performance and survival of the highly sensitive *P. abies* and *L. decidua* may be at risk if water availability prior to the start of the growing season decreases.

The third chapter explores further the long-term growth and gas exchange responses of trees to the synergetic effects of rising ca, decreasing water availability and warming at the same two sites. Changes in intrinsic water-use efficiency and growth rates were

inferred from annually resolved $\delta^{13}C$ and $\delta^{18}O$ values and measurements of basal area increment. The results showed that despite the long-term increases in intrinsic water-use efficiency, radial growth has significantly declined for most species since the 1980s, coinciding with a decreasing trend in water availability. The dual-isotope approach, based on the simultaneous assessment of changes in $\delta^{13}C$ and $\delta^{18}O$, indicated that drought-induced stomatal closure has reduced transpirational water loss of trees, but has simultaneously impeded photosynthesis and tree growth. Thus, this study provides the first evidence that temperature-induced drought stress has offset the potential CO_2 "fertilization" of trees in Central European forests.

Overall, the results of this dissertation contribute to a better understanding of growth and gas exchange responses of different coniferous tree species under contrasting site moisture conditions in Central Europe. The high vulnerability of *P. abies* and *L. decidua* to drought across the ecological gradient implies that their long-term performance and survival may be compromised if the climate becomes drier, as projected for the 21st century and beyond. *Pinus nigra* and *P. menziesii* were the least sensitive species to water deficits along the ecological gradient. This may be of relevance for adaptive forest management since these two non-native species could partly substitute the more drought sensitive *P. sylvestris* and *P. abies* under a drier climate.

Synthesis

(Shortened synthesis extracted from Lévesque, M. 2013. Drought response of five conifers along an ecological gradient in Central Europe: A multiproxy dendroecological analysis. PhD Dissertation. ETH Zurich, Switzerland.)

This dissertation aimed at assessing the drought vulnerability of *P. abies*, *P. sylvestris*, *L. decidua*, *P. menziesii* and *P. nigra* in Central Europe by investigating retrospectively their growth and gas exchange responses to soil water deficits. Particular emphasis was placed on (1) the identification of the duration and seasonality of the soil water deficits that most strongly impact tree growth and physiology, (2) the assessment of changes in growth rates and intrinsic water-use efficiency ($_{i}$WUE) under rising atmospheric CO_2 concentration and decreasing water availability, and (3) the analysis of the impacts of climatic variability and severe droughts on growth of these five co-occurring conifers along a wide ecological gradient.

Key findings from this dissertation

Seasonality and duration of water deficits that impact tree growth

This dissertation shows that the seasonality and duration of water deficit significantly influence drought vulnerability of conifers in Central Europe. At dry sites, growth and physiology of trees were mainly affected by previous year and winter water deficits, whereas summer water availability was critical at moist sites. Spring and summer water deficits significantly impeded photosynthesis and growth of *P. abies* and *L. decidua* irrespective of site conditions. Therefore, if summers become drier as projected, a reduction of soil water availability will likely reduce growth and vigor of these species at moist sites in the Swiss lowlands, whereas at dry sites in the Central Alps they may undergo severe decline. Overall, trees on sites with high water holding capacity were less vulnerable to drought, indicating that the capacity of a soil to retain water is more important than the amount of precipitation *per se* as soil moisture storage allows for the buffering of short-term dry periods.

Photosynthesis and growth of trees at mesic sites were more vulnerable to water deficits of shorter duration than at xeric sites. Under mesic conditions, trees have large crowns with high foliage mass and large trunks that lead to a high metabolic demand and turnover regarding carbon and water. These characteristics make those trees quite sensitive to even small changes in water availability and droughts of short duration. In contrast, under xeric conditions, trees usually have a low stature, small canopy, and short needles with high stomatal density (Dobbertin *et al.*, 2010), which leads to an efficient control of water loss and a reduced sensitivity to droughts of short duration. Still, the limited carbon reserves, which are characteristic for trees under xeric environments, make them very vulnerable to carbon depletion under long-lasting drought conditions (McDowell *et al.*, 2008; Breshears *et al.*, 2009; Eilmann *et al.*, 2010). Therefore, irrespective of moisture conditions, the expected increase in drought duration in Central Europe will likely reduce growth and vigor of trees, and ultimately compromise their survival, particularly under currently dry conditions.

Effects of rising atmospheric CO_2 and drought on growth and physiology of conifers

Higher c_a can under certain conditions enhance photosynthetic activity, $_{i}$WUE and ultimately the growth of trees (Ainsworth and Rogers, 2007; Leakey *et al.*, 2012; Keenan *et al.*, 2013). However, contrary to this expectation, this dissertation shows that for most species tree growth has declined despite of the long-term increase in $_i$WUE. In fact, this dissertation provides first evidence that warming-induced drought stress since the 1980s has overridden the potential CO_2 fertilization effect on tree growth under both dry and moist conditions in Central Europe. These findings contradict the CO_2 'fertilization' effect observed under xeric (Huang *et al.*, 2007) and mesic conditions (McMahon *et al.*, 2010; Keenan *et al.*, 2013), but agree with the growth reductions observed at the dry-edge distribution limit of some species in the Iberian Peninsula (Penuelas *et al.*, 2008; Andreu-Hayles *et al.*, 2011). The dissertation results indicate that drought-induced stomatal closure has reduced transpirational water loss at the cost of a decrease in photosynthesis and growth of tree. Assuming that these results can be extrapolated to similar sites in the moist Swiss lowlands and in the dry inner-Alps, changes in tree growth and transpiration over large areas may have strong consequences on forest functioning, and on the terrestrial carbon and water cycle via vegetation feedbacks to the atmosphere (Bonan, 2008; Keenan *et al.*, 2013). However, these impacts and their interactions are still poorly understood, and further studies are needed (Anderegg *et al.*, 2013b; Medlyn and De Kauwe, 2013).

Drought vulnerability of conifers in Central Europe

Information on species-specific response to drought is essential for the elaboration of adaptive forest management strategies in the face of a warmer and drier climate in Central Europe (Lindner *et al.*, 2010). This dissertation contributes to a better understanding of the climate and drought responses of five conifer species in four distinct biogeographic regions in Central Europe: the northern Swiss Alps, the Jura Mountains, the Swiss Plateau and the Central Alps. Of all investigated species, *P. abies* and *L. decidua* were most vulnerable to summer drought across the four regions. Spring and summer water deficits significantly reduced the carbon assimilation and fixation, as well as the growth of these species. The radial growth of *P. abies* and *L. decidua* strongly decreased during extremely dry years, but recovered to the pre-drought level within a year. This fast recovery implies a strong coupling between carbon assimilation and growth for these species, which is supported by the stable isotope analysis. However, long-lasting water deficit periods may strongly reduce carbon assimilation and carbohydrates of *P. abies* and *L. decidua*, which, in return, may reduce their vigor, prolong their growth recovery and increase their vulnerability to pests and pathogens. Thus, the long-term performance and survival of these species in Central Europe may be at risk under a drier climate. Still, species-specific growth and physiological responses to drought and rising c_a were not uniform in space, indicating a high variability at the population level and potential local adaptations to mitigate the negative effects of climate change (Aitken *et al.*, 2008). Among the five species studied here, *P. sylvestris* showed an intermediate response in its drought tolerance along the gradient. At the driest sites, our findings and those from other studies (e.g., Eilmann *et al.*, 2010; Voltas *et al.*, 2013) indicate that the physiological capacity of *P. sylvestris* to withstand periodic drought is limited, thus suggesting that this species is highly prone to drought induced mortality (Bigler *et al.*, 2006). Across the ecological gradient, the growth and gas exchange of *P. menziesii* and *P. nigra* were little affected by drought, indicating that these species have the potential to withstand moderate water deficits without difficulty.

Methodological aspects

Study sites (dry edge vs. moist sites, tree-ring network)

In this dissertation, an effort was made to cover a wide spectrum of environmental conditions in Central Europe, i.e., from the dry edge of the species distribution in the dry inner-Alps to wet conditions of the northern Swiss Alps. Particular emphasis was placed on sampling sites near the dry distribution limit of *P. abies*, *P. sylvestris* and *L. decidua* in the dry inner-Alps where recent rapid climate change has caused drought-induced mortality and a shift in species distribution (Rigling *et al.*, 2013). Still, one challenge of this dissertation was to find stands were non-native and native tree species co-occur. Often, for management and financial reasons, non-native tree species occur in pure, even-aged stands and on moist sites, and are rather rare under xeric conditions where productivity is too low to justify the return on the investment of plantings. Despite this methodological problem, this multiproxy study is one of the most comprehensive dendroecological analysis conducted in Central Europe so far (cf. Zang, 2011).

For his dissertation, Zang (2011) investigated the growth reactions of *P. abies*, *P. sylvestris*, *Abies alba* Mill., *Fagus sylvatica* L., *Quercus robur* L. and *P. menziesii* to summer drought all over Bavaria by comparing tree-ring width series with climate. He found that *P. abies* was the least tolerant species to summer drought. However, his study did not cover the full spectrum of environmental conditions encountered in Central Europe since he did not sample trees near their dry distribution limits, e.g., in the Central Alps. Further, Zang (2011) did not assess simultaneously the long-term growth and gas exchange responses of co-occurring tree species. This dissertation covered a much wider range of conditions and used a multiproxy approach. It provided additional and even new evidence that drought strongly impedes growth and gas exchange of conifers, particularly of *P. abies* and *L. decidua*, below 1300 m a.s.l. in Central Europe. However, this study did not allow to assess species-specific response to warming and rising c_a at high elevation sites (e.g., at the treeline) where trees may benefit from higher temperature and c_a (Dawes et al., 2011). In fact, species-specific response to global climate change along wide elevation gradients (i.e., from valley bottoms to treeline) are still poorly understood and further studies are needed.

Native and non-native tree species

In this dissertation, emphasis was put on in situ assessments and comparisons of the drought vulnerability of native and non-native conifers along a moisture gradient. Of special interest was the comparison of *P. menziesii* with *P. abies*, a species of high economic importance in Central Europe where its economic share is expected to decrease under climate change (Hanewinkel et al., 2013). This study also focused on the comparison of the drought tolerance of *P. sylvestris* and *P. nigra* along contrasting sites conditions. Furthermore, *L. decidua*, a species of high ecological and economic importance in the Alps, was included in the analysis since little is known about its drought vulnerability. Thus, this dissertation offers one of the first detailed assessments and comparisons of growth-climate relationships and gas exchange responses of native and non-native species in Central Europe. However, it did not consider deciduous species such as *Quercus spp*. and *F. sylvatica*, two ecologically and economically important tree species in Central Europe. This was motivated by several considerations. First, suitable sites where *Quercus spp*. or *F. sylvatica* co-occur with native and non-native conifers were rather rare along the ecological gradient and consisted of uneven-aged stands. Second, the sampling design, which aimed at the comparison of the drought response of *P. abies* vs. *P. menziesii* and *P. sylvestris* vs. *P. nigra* and the inclusion of *L. decidua*, as well as the time constraints limited our analysis to five species. Third, detailed assessments of the growth-climate relationships of *Quercus spp*. (Zang, 2011; Rohner, 2012) and *F. sylvatica* (Lebourgeois et al., 2005; Zang, 2011; Weber et al., 2013) in Central Europe already exist.

Multiproxy and multiscalar analysis

Very often dendroecological studies focus on variations of tree-ring width alone to elucidate the vulnerability of trees to drought and changing climate (e.g., Martin-Benito et al., 2008; Lebourgeois et al., 2010), without being able to consider the physiological responses of trees in a more comprehensive manner. Here, growth and physiological responses of trees to rising ca and drought were assessed by investigating early- and latewood widths as well as the carbon and oxygen isotopic composition in early- and latewood. This provided novel insights on the water-use efficiency, photosynthesis and stomatal conductance of trees under changing climatic conditions at the annual and intra-annual scales. A remarkable finding of this dissertation was the higher sensitivity to drought of the $\delta^{13}C$ and $\delta^{18}O$ than the radial growth variables of all species. This indicates that the stable isotope proxies yield valuable growth and physiological information that would otherwise remain undetected with standard tree-ring width analysis.

One of the main aims of this dissertation was to identify the duration and seasonality of soil water deficits that most strongly impact growth and physiology of conifers in Central Europe. For this, earlywood, latewood and total ring width as well as the $\delta^{13}C$ and $\delta^{18}O$ in early- and latewood were measured and statistically related to a multiscalar soil water deficit index. This analysis considered the seasonality and duration (month to year) at which water deficits impact trees, as well as the lags between drought occurrence and tree response. Thus, this approach provided novel information on drought characteristics that affect physiological and growth response patterns of trees, which, in return, influence their resistance and resilience to drought. This is of high importance, since standard correlation or response function analyses based on monthly climatic variables (temperature and precipitation) ignore the seasonality, duration and lag characteristics of drought phenomena.

Outlook

Recommendations for forest managers

Based on the results of this dissertation, we conclude that the projected decrease in water availability is likely to become a major threat for the productivity of Central European forests and may trigger major changes in forest composition and the provision of ecosystem goods and services. Thus, adaptive forest management strategies are required to maintain forest productivity and the provision of ecosystem goods and services (Temperli et al., 2012).

A first measure could be the selection of drought-adapted species or provenances that are productive also under drought (Thiel et al., 2012; Eilmann et al., 2013). For instance, this dissertation highlighted the superiority of *P. menziesii* and *P. nigra* to withstand periodic water stress over *P. abies*, *L. decidua* and *P. sylvestris*. Thus, *P. menziesii* and *P. nigra* could be regarded as alternative species at sites prone to soil water deficit where the long-term performance or even survival of native species is likely to be compromised under drier conditions. However, before promoting non-native species, forest managers should consider native species that are drought tolerant such as *Quercus spp*. (Weber et al., 2007; Zang, 2011). If the introduction of non-native species is necessary to maintain the provision of ecosystem goods and services under climate change (cf. Temperli et al., 2012), this should be done at very low scale to limit potential ecological consequences (e.g., loss of biodiversity and natural habitats, and invasiveness).

A second measure could be the promotion of species mixtures. Although this study did not test inter-specific interactions, there is evidence that species mixtures reduce drought vulnerability of species through interspecific facilitation (Lebourgeois et al., 2013; Pretzsch et al., 2013). In this dissertation, we showed that the seasonality and duration of water deficits impact the species differently since not all species responded to water deficits simultaneously (Chapter I and II). These asynchronous speciesspecific responses to water deficits may increase water use efficiency at the stand level by reducing competition for water and enhancing hydraulic lift, hence reducing drought experienced by trees (Pretzsch et al., 2013). Further, mixed stands tend to have higher productivity (Morin et al., 2011) and less variability of productivity over time (Morin et al., submitted), thus reducing the risk of financial loss (Knoke et al., 2008) under climate change.

Recommendations for further research

Specific research gaps were discussed and research recommendations were made within each chapter of the dissertation. Here, we describe some general recommendations for further research that would enhance our understanding of the growth and physiological mechanisms of trees to cope with drought.

- *Competition:* Intra- and inter-specific competition were not directly considered in this dissertation. Possible bias due to competition was minimized by sampling and averaging many trees per species (i.e., site chronologies of tree-ring width and stable isotope were used in the analysis). Thus, this sampling procedure yielded a mean site-specific response of a species and minimized the influence of competition, but ignored the whole range of individual responses among sample trees (Carrer, 2011). Nevertheless, there is evidence that inter-tree competition can influence the response and vulnerability of trees to drought (Linares et al., 2010; Ruiz-Benito et al., 2013). Trees experiencing a high degree of competition usually have lower growth rates and intrinsic water-use efficiency, and a greater vulnerability to drought than trees subjected to less competition (Linares et al., 2009; Moreno-Gutierrez et al., 2012). However, it is still poorly understood how competition at the stand level, rising c_a and drought interact to influence growth and gas exchange of trees. The use of retrospective dynamic competition indices, which consider a temporal and a spatial component (Weber et al., 2008), combined with a detailed assessment of growth and $_i$WUE of individual trees would provide novel information on how competition influences the vulnerability of trees to drought.

- *Age and size classes*: In this study, the influence of tree age and size on the drought response was not taken into account. Tree age and size effects were minimized by sampling even-aged stands. Still, this sampling strategy did not allow for assessing the influence of ontogeny and size on the growth and physiological responses of conifers to drought. Several studies indicate that the climate response of trees changes with age (Carrer and Urbinati, 2004), size (Zang et al., 2012) and social status (Martin-Benito et al., 2008). Age- and size-related tree responses to climate change are still poorly understood, and studies are needed to disentangle the relative contribution of ageing, tree size and social status on the physiological and growth responses of trees to drought.

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Abstract

Lévesque, M., M. Saurer, R. Siegwolf, B. Eilmann, P. Brang, H. Bugmann, and A. Rigling. 2013. Drought response of five conifer species under contrasting water availability suggests high vulnerability of Norway spruce and European larch. Global Change Biology 19:3184–3199.

The ability of tree species to cope with anticipated decrease in water availability is still poorly understood. We evaluated the potential of Norway spruce, Scots pine, European larch, black pine, and Douglas-fir to withstand drought in a drier future climate by analyzing their past growth and physiological responses at a xeric and a mesic site in Central Europe using dendroecological methods. Earlywood, latewood, and total ring width, as well as the $\delta^{13}C$ and $\delta^{18}O$ in early- and latewood were measured and statistically related to a multiscalar soil water deficit index from 1961 to 2009. At the xeric site, $\delta^{13}C$ values of all species were strongly linked to water deficits that lasted longer than 11 months, indicating a long-term cumulative effect on the carbon pool. Trees at the xeric site were particularly sensitive to soil water recharge in the preceding autumn and early spring. The native species European larch and Norway spruce, growing close to their dry distribution limit at the xeric site, were found to be the most vulnerable species to soil water deficits. At the mesic site, summer water availability was critical for all species, whereas water availability prior to the growing season was less important. Trees at the mesic were more vulnerable to water deficits of shorter duration than the xeric site. We conclude that if summers become drier, trees growing on mesic sites will undergo significant growth reductions, whereas at their dry distribution limit in the Alps, tree growth of the highly sensitive spruce and larch may collapse, likely inducing dieback and compromising the provision of ecosystem services. However, the magnitude of these changes will be mediated strongly by soil water recharge in winter and thus water availability at the beginning of the growing season.

Abstract

Lévesque, M., R. Siegwolf, M. Saurer, B. Eilmann, and A. Rigling. 2014. Increased water-use efficiency does not lead to enhanced tree growth under xeric and mesic conditions. New Phytologist 203:94–109.

- Higher atmospheric CO_2 concentrations (c_a) can under certain conditions increase tree growth by enhancing photosynthesis, resulting in an increase of intrinsic water-use efficiency ($_i$WUE) in trees. However, the magnitude of these effects and their interactions with changing climatic conditions are still poorly understood under xeric and mesic conditions.

- We combined radial growth analysis with intra- and interannual $\delta^{13}C$ and $\delta^{18}O$ measurements to investigate growth and physiological responses of *Larix decidua*, *Picea abies*, *Pinus sylvestris*, *Pinus nigra* and *Pseudotsuga menziesii* in relation to rising c_a and changing climate at a xeric site in the dry inner Alps and at a mesic site in the Swiss lowlands.

- $_i$WUE increased significantly over the last 50 yr by 8–29% and varied depending on species, site water availability, and seasons. Regardless of species and increased $_i$WUE, radial growth has significantly declined under xeric conditions, whereas growth has not increased as expected under mesic conditions. Overall, drought-induced stomatal closure has reduced transpiration at the cost of reduced carbon uptake and growth.

- Our results indicate that, even under mesic conditions, the temperature-induced drought stress has overridden the potential CO_2 ‘fertilization’ on tree growth, hence challenging today’s predictions of improved forest productivity of temperate forests.

Abstract

Lévesque, M., A. Rigling, H. Bugmann, P. Weber and P. Brang. 2014. Growth response of five co-occurring conifers to drought across a wide climatic gradient in Central Europe. Agricultural and Forest Meteorology **197**:1–12.

Climate change projections indicate drier conditions and an increase in the frequency and duration of extreme drought events in the coming decades in Central Europe. However, it is not clear which tree species will be able to cope with drier climatic conditions and higher year-to-year climatic variability. We analyzed tree-growth responses of five co-occurring conifer species to past climatic variations and severe droughts across a wide climatic gradient in Central Europe, covering four distinct biogeographic regions: the northern Swiss Alps, the Swiss Plateau, the foothills of the Jura Mountains and the dry Central Alps. We studied three native tree species (*Larix decidua* Mill, *Picea abies* (L.) Karst. and *Pinus sylvestris* L.) and two non-native species (*Pinus nigra* Arn. and *Pseudotsuga menziesii* var. *menziesii* (Mirb.)Franco). Tree-ring width was measured for 770 trees from 14 sites and species-specific site chronologies were established. Response-function analysis, Principal Component Analysis (PCA), linear regressions and Superposed Epoch Analysis were used to assess the species-specific growth sensitivity to climate and severe drought along the gradient. Irrespective of the species and site conditions, high temperature sand low precipitation amounts in summer and autumn of the year prior growth significantly reduced tree growth. When evaporative demand, precipitation and soil water holding capacity were considered together, low water availability in current summer strongly reduced growth. Overall, the growth-climate relationships of the species were not or only slightly related to the site water balance per se. However, when all species-specific growth response coefficients were introduced into a PCA, a clear separation of the populations of the Central Alps (driest sites) became apparent. At these sites, soil water deficits in previous autumn and current spring strongly reduced radial growth, whereas at moist and wet sites on the Swiss Plateau, in the Jura Mountains and northern Alps summer drought impeded growth. Along the gradient, the native *P. abies*, *L. decidua* and *P. sylvestris* were the most sensitive species to drought, implying that their long-term performance and survival on nowadays dry sites can be compromised under a drier climate in Central Europe.