TECHNISCHE UNIVERSITÄT MÜNCHEN
Wissenschaftszentrum Weihenstephan für Ernährung, Landnutzung und Umwelt

Fachgebiet für Waldernährung und Wasserhaushalt

Dendroökologische Untersuchungen zum Einfluss der Klimaänderung auf Bergwälder der Nördlichen Kalkalpen

Claudia Theresia Martina Hartl-Meier

Vollständiger Abdruck der von der Fakultät Wissenschaftszentrum Weihenstephan für Ernährung, Landnutzung und Umwelt der Technischen Universität München zur Erlangung des akademischen Grades eines

Doktors der Naturwissenschaften

genehmigten Dissertation.

Vorsitzender:		Univ.-Prof. Dr. S. Pauleit
Prüfer der Dissertation:	1.	Univ.-Prof. Dr. A. Göttlein
	2.	Prof. Dr. A. Rothe (Hochschule Weihenstephan-Triesdorf)
	3.	Univ.-Prof. Dr. H. Roehle (Technische Universität Dresden)

Die Dissertation wurde am 26.11.2014 bei der Technischen Universität München eingereicht und durch die Fakultät Wissenschaftszentrum Weihenstephan für Ernährung, Landnutzung und Umwelt am 06.03.2015 angenommen.

INHALTSVERZEICHNIS

ABBILDUNGSVERZEICHNIS

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PUBLIKATIONSLISTE ZUM FORSCHUNGSVORHABEN

Die vorliegende Studie wurde im Rahmen des Projektes „SICALP – Standortsicherung im Kalkalpin“, gefördert durch das EU-Programm INTERREG BY/Ö (J00183) und das Bayerische Staatsministerium für Ernährung, Landwirtschaft und Forsten, durchgeführt. Das Projekt war eine Kooperation des Fachgebiets für Waldernährung und Wasserhaushalt der Technischen Universität München, der Fakultät Wald und Forstwirtschaft der Hochschule Weihenstephan-Triesdorf (HSWT) sowie des Instituts für Waldökologie der Universität für Bodenkultur Wien. Die Arbeit wurde an der HSWT erstellt und beschäftigt sich mit der Zuwachsreaktion kalkalpiner Bergwälder auf die Klimaänderung. Innerhalb des Promotionsverfahrens „Dendroökologische Untersuchungen zum Einfluss der Klimaänderung auf Bergwälder der Nördlichen Kalkalpen“ wurden folgende Publikationen in wissenschaftlichen Fachzeitschriften mit *Peer-Review* Verfahren veröffentlicht:

Publikation I) Hartl-Meier C, Zang C, Dittmar C, Esper J, Göttlein A, Rothe A (2014) ‘Vulnerability of Norway spruce to climate change in mountain forests of the European Alps’ ist in der Zeitschrift *Climate Research* (doi: 10.3354/cr01226) erschienen.

Publikation II) Hartl-Meier C, Dittmar C, Zang C, Rothe A (2014) ‘Mountain forest growth response to climate change in the Northern Limestone Alps’ ist in der Zeitschrift *Trees – Structure and Function* (doi: 10.1007/s00468-014-0994-1) erschienen.

Publikation III) Zang C, Hartl-Meier C, Dittmar C, Rothe A, Menzel A (2014) ‘Patterns of drought tolerance in major European temperate forest trees: climatic drivers and levels of variability’ ist in der Zeitschrift *Global Change Biology* (doi: 10.1111/gcb.12637) erschienen.

Publikation IV) Hartl-Meier C, Zang C, Büntgen U, Esper J, Rothe A, Göttlein A, Dirnböck T, Treydte K (*in press*) ‘Uniform climate sensitivity in tree-ring stable isotopes across species and sites in a mid-latitude temperate forest’ wird in der Zeitschrift *Tree Physiology* (doi: 10.1093/treephys/tpu096) erscheinen.

ZUSAMMENFASSUNG

Bergwälder erfüllen eine Vielzahl sozio-ökonomischer und ökologischer Funktionen, wobei eine der wichtigsten Ökosystemleistungen der Schutz vor Bodenerosion und anderen Naturgefahren (z.B. Hochwasser, Muren, Steinschlag und Lawinen) ist. Allerdings stehen die Bergwälder der Alpen in vielerlei Hinsicht unter dem Einfluss des Klimawandels, welcher erhebliche Auswirkungen auf die Funktionen dieser Ökosysteme haben kann. Eine wesentliche Rolle spielt dabei der generelle Temperaturanstieg sowie eine erhöhte Intensität und Frequenz von Trockenereignissen. Dies kann schwerwiegende Konsequenzen für die Vitalität von Bäumen mit sich bringen, doch bestehen bislang noch erhebliche Unsicherheiten wie die Bergwaldbaumarten in den Nördlichen Kalkalpen auf die Klimaänderung reagieren werden. Für ein zukunftsorientiertes Schutzwaldmanagement sind jedoch Kenntnisse über die Sensitivität und Toleranzen der heimischen Bergwaldbaumarten unabdingbar.

Ziel dieser Arbeit ist deshalb, die Eignung der wichtigsten Bergwaldbaumarten Fichte, Tanne, Lärche und Buche in den bayerischen und österreichischen Nördlichen Kalkalpen unter den sich ändernden klimatischen Bedingungen zu beurteilen. Mittels dendroökologischer Untersuchungen wurde in vier Einzelstudien die Vulnerabilität der Fichte auf die Klimaänderung (*Studie 1*), baumartenspezifische Reaktionsmuster in Abhängigkeit von Höhenlage und Hangexposition (*Studie 2*), die Persistenz und Variabilität von Trockenstressreaktionen (*Studie 3*) sowie art- und standortsspezifische physiologische Trockenstressreaktionen (*Studie 4*) retrospektiv analysiert. Hierfür wurde ein umfangreiches und für die Nördlichen Kalkalpen einzigartiges Jahrringnetzwerk bestehend aus 1140 Bäumen (500 Fichten, 210 Tannen, 130 Lärchen und 300 Buchen) aufgebaut. Mit den insgesamt 50 untersuchten Standorten umfasst diese Studie eine Region der Nördlichen Kalkalpen mit einer West-Ost-Ausdehnung von 250 km und einem Höhengradienten von 1200 m (~500-1700 m ü. NN).

Innerhalb *Studie 1* wurden 50 Fichten-Standorte untersucht. Mittels Klima-Zuwachs-Beziehungen konnte festgestellt werden, dass sich unterhalb von 1200 m ü. NN hohe Temperaturen negativ, hohe Niederschläge jedoch positiv auf die Zuwächse auswirken. Hingegen beeinflusst oberhalb dieser Höhenlage ein steigendes Wärmeangebot den Zuwachs der Fichte positiv. Bei der Trockenjahranalyse zeigt sich ein ähnliches Bild: In Tieflagen kann es zu Zuwachseinbrüchen von bis zu 40 % kommen, jedoch treten über 1400 m ü. NN sogar Zuwachsgewinne auf. Trotz der erhöhten Trockensensitivität der Fichte unterhalb von 1200-1400 m ü. NN hat sich die langfristige Temperaturerhöhung um 1 °C (in der Vegetationsperiode) seit den 1990er-Jahren bisher nicht negativ auf die Zuwächse ausgewirkt.

Im Rahmen der *Studie 2* wurden im Berchtesgadener Land die Reaktionsmuster von Fichte, Tanne, Lärche und Buche in Abhängigkeit von Höhenlage und Hangexposition untersucht. Durch Klima-Zuwachs-Beziehungen konnte nur für die Fichte in Tieflagen eine Trockensensitivität abgeleitet werden. Auch während des Hitzesommers 2003 weist einzig die Fichte in tieferen Lagen Zuwachsrückgänge auf. Bei den Baumarten Tanne, Lärche und Buche waren keine signifikanten Zuwachsreaktionen festzustellen. Diese Baumarten zeigen somit in allen untersuchten Höhenstufen und Hangexpositionen eine hohe Toleranz gegenüber sommerlicher Trockenheit. Da sich auch in dieser Studie keine Effekte der Temperaturerhöhung seit den 1990er-Jahren belegen lassen, sind alle Baumarten gegenüber dem bisherigen Temperaturanstieg als robust einzustufen.

In *Studie 3* wurde die Trockenstressreaktion von Fichte, Tanne und Buche durch verschiedene Toleranzindizes detaillierter untersucht, welche unter anderem die Resilienz der Baumarten berücksichtigen. Dabei weist die Tanne die höchste Trockentoleranz als auch Resilienz auf. Die Fichte konnte erneut als trockensensitivste Baumart identifiziert werden, jedoch übertrifft sie die Buche an kühl-feuchten Standorten in ihrem Erholungspotential. Generell sind die Zuwachsrückgänge aufgrund von Trockenheit bei allen Baumarten in den drei Folgejahren nach dem Extremereignis nur noch gering. Zudem ist die Variabilität der Stressreaktionen auf Bestandsebene insbesondere bei Fichte und Tanne sehr hoch, was ein mögliches Anpassungspotential der Baumarten durch genetische Selektion im Wege der Naturverjüngung aufzeigt.

Zur genaueren Untersuchung von art- und standortsspezifischen physiologischen Trockenstressreaktionen wurden in *Studie 4* neben der Jahrringbreite zusätzlich die Kohlenstoff- und Sauerstoffisotope von Fichte, Lärche und Buche an drei verschiedenen Standorten mit unterschiedlicher Wasserverfügbarkeit getestet.

Hierdurch konnte nachgewiesen werden, dass stabile Isotope umfassende Einblicke in die physiologischen Strategien der verschiedenen Baumarten ermöglichen. Buche und Lärche zeigen standortsspezifische Anpassungsmechanismen bei Trockenheit und können im Vergleich zu Fichte tiefere Bodenbereiche effizienter ausnutzen. Bei Buche kann dies jedoch zu negativen Effekten auf den Zuwachs in den Folgejahren führen, weshalb Fichte auf den untersuchten Standorten eine höhere Resilienz aufwies als Buche.

Zusammenfassend ist festzuhalten, dass sich bislang keine langfristigen negativen Effekte auf die Radialzuwächse der Bergwaldbaumarten in den Nördlichen Kalkalpen aufgrund der bisherigen Klimaänderung nachweisen lassen. Unterhalb von ~1200 m ü. NN reagiert die Fichte am empfindlichsten auf Trockenheit. Angesichts der prognostizierten Zunahme der Frequenz von extremen Trockenereignissen wird zur Steigerung der Stabilität der Bergwälder empfohlen, neben der in den Nördlichen Kalkalpen vielerorts vorherrschenden Fichte, verstärkt andere heimische Baumarten (insbesondere Tanne) zu beteiligen, was zugleich Borkenkäferbefall und Sturmwurf vorbeugen würde. Im Rahmen der bisherigen Klimaänderung sollte in den montanen Höhenlagen der Nördlichen Kalkalpen der natürliche Bergmischwald, bestehend aus den Hauptbaumarten Fichte, Tanne und Buche, und in subalpinen Höhenlagen die Fichte gemeinsam mit der Lärche weiterhin die Sicherung der Ökosystem-Funktionen ermöglichen.

ABSTRACT

Mountain forests offer a range of socio-economic and ecological services, such as protection from soil erosion and natural hazards (e.g. flooding, debris flow, rock falls and avalanches). However, the functions of these ecosystems can be significantly impacted by climate change. In particular, warmer temperature and an increased intensity and frequency of drought events may seriously impact the vitality of trees, but there are considerable uncertainties how the mountain forest tree species in the Northern Limestone Alps will respond to a changing climate. More detailed knowledge about the sensitivity and tolerance of native mountain forest tree species is required for a future-oriented forest management.

The aim of this dendroecological study is to assess the suitability of the most important mountain forest tree species spruce, fir, larch and beech, under changing climatic conditions in the Bavarian and Austrian Northern Limestone Alps. Within this objective, four individual studies were performed to retrospectively analyse *1)* the vulnerability of spruce to climate change, *2)* the tree species-specific response patterns as a function of altitude and slope exposure, *3)* the persistence and variability of drought stress responses, and *4)* species- and site-specific physiological drought stress responses. For this purpose, a comprehensive and unique tree-ring network for the Northern Limestone Alps was compiled consisting of 1,140 trees (500 spruces, 210 firs, 130 larches and 300 beeches). With a total of 50 studied sites, the investigation area covers a region of the Northern Limestone Alps with a west-east extension of 250 km and an altitudinal gradient of 1,200 m (~500-1,700 m a.s.l.).

Within *Study 1,* 50 spruce sites were studied. Climate/growth relationships indicated a negative effect of high temperatures, but a positive effect of high precipitation on tree growth below 1,200 m a.s.l. Above this altitude, growth of spruce is positively affected by higher temperatures. The results are similar for the drought event analysis: in lower elevations, a growth decline up to 40 %, but above 1,400 m a.s.l. a potential growth increase. Despite the high drought sensitivity of spruce below 1,200-1,400 m a.s.l., no negative growth response could be associated with the long-term temperature increase of 1 °C (during the growing season) since the 1990s until present.

Study 2 examines the response pattern of spruce, fir, larch and beech as a function of altitude and slope exposure in the Berchtesgaden region. The climate/growth relationships show a drought sensitivity for spruce only. For example, during the 2003 summer heatwave, the growth declined for spruce in the lower elevations while no significant growth reactions were found for fir, larch and beech. Thus, these tree species show a high tolerance to summer drought in all examined elevation belts and slope aspects. Since no effect could be observed associated with the rising temperatures since the 1990s, the tree species can be recognized as robust within the recent temperature increase.

The drought stress response of spruce, fir and beech was studied in more detail within *Study 3*, by using different tolerance indices that take the resilience of the tree species into account. Highest drought tolerance and resilience was found in fir. Spruce was again identified as the most drought sensitive species, though its recovery potential in cool-moist conditions exceeds that of beech. In general, growth suppressions within the three years following the drought event were small for all tree species. Furthermore, spruce and fir show a high variability in their stress reaction at the stand level, indicating a possible adaptation potential through natural regeneration by genetic selection.

For a more detailed examination of species- and site-specific physiological drought stress reactions in *Study 4*, carbon and oxygen isotopes were measured additionally to tree-ring width for spruce, larch and beech at three sites with differing water availability. This showed that stable isotopes provide comprehensive insights into the physiological strategies of the different tree species. During drought, beech and larch show site-specific adaptation mechanisms, and take better advantage of the access to deeper soils compared to spruce. For beech, however, this can lead to negative effects on growth in the following years, which results in a higher resilience of spruce at these sites.

In summary, this study shows no negative long-term effects of current climate change on mountain forest tree growth in the Northern Limestone Alps. However, drought vulnerability was found in spruce below 1,200 m a.s.l., and due to the predicted increase in frequency of extreme drought events, it is recommended to promote other native tree species (especially fir) in the spruce dominated Northern Limestone Alps. This would increase the stability of the mountain forests and also prevent bark beetle attacks and wind throw. Ecosystem functions resilient to current climate change, are thus likely to be found in a natural mixed mountain forest consisting of spruce, fir and beech in montane elevations, and spruce together with larch in the subalpine belt.

1 EINFÜHRUNG UND PROBLEMSTELLUNG

1.1 Bergwälder und Klimaänderung

In Europa sind 41 % der Gebirge bewaldet und die gesamten Alpen betreffend sogar über die Hälfte (McMorran & Price 2011). Mit rund 250.000 ha ist knapp die Hälfte des Bayerischen Alpenraums mit Bergwäldern bedeckt (StMELF 2014a). Der Stabilität dieser Ökosysteme kommt eine hohe Bedeutung zu, da sie eine Vielzahl wichtiger Funktionen erfüllen. Aus sozio-ökonomischer Sicht liefern sie beispielsweise den nachwachsenden Rohstoff Holz und bieten Raum für Erholung und den damit verbundenen Tourismus (Bugmann et al. 2005, McMorran & Price 2011). Doch auch die ökologischen Funktionen des Bergwaldes als größter terrestrischer Kohlenstoffspeicher, Biodiversitäts-Hotspot und grundlegender Bestandteil der Trinkwasserversorgung sind von großer Relevanz (Björnsen et al. 2005, Bugmann et al. 2005, Lindner et al. 2010). Eine der wichtigsten Ökosystemleistungen des Bergwaldes ist die Schutzfunktion, welche den Schutz vor Bodenerosion sowie vor anderen Naturgefahren, wie Hochwasser, Muren, Steinschlag und Lawinen, mit einschließt (Lindner et al. 2010, Schumacher & Bugmann 2006). In Bayern erfüllen beispielsweise 60 % des Bergwaldes vorrangig Schutzfunktionen (StMELF 2014a).

Die Bergwälder der Alpen stehen jedoch in vielerlei Hinsicht unter dem Einfluss des *„global change”*, welcher voraussichtlich gravierende Auswirkungen auf die Funktionen dieser Ökosysteme haben wird (Hofer 2005, Lindner et al. 2010). Aspekte des *„global change“* sind beispielsweise die anthropogen induzierten atmosphärischen Stoffeinträge, wie Stickstoff- und Schwefelverbindungen, die in den letzten Jahrzehnten markanten Einfluss auf die Zuwächse der Wälder ausübten (vgl. Elling et al. 2009, Kahle et al. 2008). Nach dem „Waldsterben-Diskurs“, insbesondere der 1980er-Jahre (vgl. Elling et al. 2012), liegt in den letzten Jahren der Fokus des öffentlichen und forstlichen Interesses zunehmend auf den Auswirkungen des *„climate change“*. Einerseits sind hier die indirekten Effekte des Klimawandels von Bedeutung, die biotischer sowie abiotischer Natur sein können: Eine erhöhte Frequenz und Intensität von Insektenausbrüchen (z.B. Esper et al. 2007, Seidl et al. 2008) und großen Sturmereignissen (Lindroth et al. 2009) können Waldökosysteme massiv beeinflussen. Doch auch die direkten Effekte des Klimawandels, wie die steigenden CO_2-Konzentrationen der Atmosphäre (Lindner et al. 2010), als auch Änderungen der Temperatur und der Niederschläge, können erhebliche Konsequenzen für die Bergwälder der Europäischen Alpen mit sich bringen (Schumacher & Bugmann 2006).

Im aktuellen IPCC-Bericht (2013) wurde erneut eine eindeutige Erwärmung des Klimasystems bestätigt. Als globale Temperaturänderung wird eine Erhöhung von 0,85 °C (linearer Trend von 1880 bis 2012) angegeben (IPCC 2013). In den Alpen wird dieser Temperaturanstieg sogar noch deutlich übertroffen und liegt im 20. Jahrhundert bei 1,2 °C, wobei die stärkste Erwärmung insbesondere in den letzten Jahrzehnten stattfand (Auer et al. 2007). Klimamodelle prognostizieren einen weiteren Temperaturanstieg (IPCC 2013) und in Kombination mit möglichen Niederschlagsreduktionen (zumindest in den Ostalpen) wird der Klimawandel eine wichtige Rolle bei der Entwicklung der zukünftigen Bergwaldvegetation spielen (Engler et al. 2011) sowie die Funktionen von Waldökosystemen erheblich beeinflussen (Elkin et al. 2013). In diesem Zusammenhang sind jedoch nicht nur Änderungen der durchschnittlichen klimatischen Bedingungen von Relevanz. Insbesondere Extremereignisse, wie Trockenperioden können schwerwiegende Konsequenzen für die Vitalität der Bäume mit sich bringen (Fuhrer et al. 2006). Für Europa wurde bereits eine Zunahme der Frequenz und Intensität von Hitzewellen festgestellt (EEA 2012) und eine weitere Häufung von extremen Witterungsereignissen, wie im Jahrhundertsommer 2003, wird prognostiziert (Luterbacher et al. 2004, Rebetez et al. 2006, Schär et al. 2004).

Aufgrund ihrer langen Lebensdauer gelten Bäume und Wälder gegenüber dem Klimawandel als besonders empfindlich. Ob ihre Anpassungsfähigkeit mit dem sich rapide ändernden Klima Schritt halten kann, ist ungewiss (Lindner et al. 2010), denn die Auswirkungen des Klimawandels sind abhängig von der Sensitivität des ökologischen und biologischen Systems selbst und zudem von artspezifischen Toleranzen (Elkin et al. 2013). Im Allgemeinen gelten flachgründige Böden auf karbonatischem Untergrund aufgrund ihrer Wasserlimitierung als sehr sensitive Standorte, speziell in montanen Höhenlagen. Auf solchen Standorten ist mit zunehmendem Trockenstress zu rechnen, was Ertragsverluste und eine erhöhte Anfälligkeit gegenüber Störungen bedingen kann (Seidl et al. 2011). Da diese Standortseigenschaften für die Nördlichen Kalkalpen charakteristisch sind, ist es fraglich, ob die kalkalpinen Bergwälder ihre zahlreichen Funktionen, insbesondere die Schutzfunktionen, auch unter den geänderten klimatischen Rahmenbedingungen erfüllen können. Für ein zukunftsorientiertes Schutzwaldmanagement sind deshalb Kenntnisse über die Klimatoleranz der heimischen Bergwaldbaumarten sehr wichtig.

1.2 Baumwachstum, Jahrringe und Klima

Die Begriffe „Wachstum“ und „Zuwachs“ von Bäumen implizieren im forstwissenschaftlichen Sinne verschiedene Komponenten. In der forstlichen Waldertragslehre sind insbesondere die „Volumenzuwächse“ von großer Bedeutung, wobei für deren Abschätzung sowohl die „Höhenzuwächse“ als auch die „Radialzuwächse“ relevant sind. Der Radialzuwachs bietet gegenüber dem Höhenzuwachs den enormen Vorteil, dass sich der annuelle Zuwachs durch Zuwachsbohrungen mit vergleichsweise geringem Aufwand retrospektiv erfassen lässt. Zudem werden im Radialzuwachs bzw. den Jahrringsequenzen eines Baumes vergangene Umweltinformationen archiviert (Schweingruber 1996), wodurch es möglich ist, die Reaktion von Bäumen auf vergangene klimatische Bedingungen sowie spezifische Extremereignisse (z.B. sommerliche Trockenheit) retrospektiv zu analysieren. Dies bietet die Möglichkeit mittels dendroökologischer Studien, das Potential bzw. die Eignung verschiedener Baumarten im Hinblick auf den Klimawandel aus ihrem retrospektiven Verhalten abzuschätzen. Demnach basiert die vorliegende Arbeit auf Jahrringmessungen und entsprechend beziehen sich die folgenden Ausführungen bei der Verwendung der Begriffe „Zuwachs“ oder „Wachstum“ ausschließlich auf den Radialzuwachs bzw. daraus abgeleitete Größen wie Jahrringindizes oder Grundflächenzuwächse.

Grundsätzlich wird der Radialzuwachs und damit die **Jahrringbreite** von verschiedenen exogenen und endogenen Faktoren in einem komplexen Zusammenspiel beeinflusst. Einer der wesentlichsten Umweltfaktoren ist jedoch das Klima, wobei sich dies an klimatisch limitierten Standorten bzw. artspezifischen Verbreitungsgrenzen am deutlichsten zeigt (Fritts 1976): An Waldgrenzstandorten in Hochlagen und in den nördlichen Breiten wird der Radialzuwachs insbesondere von den Temperaturverhältnissen der Vegetationszeit limitiert (Frank & Esper 2005). Hingegen wird der Zuwachs in Tieflagen in erster Linie von den Niederschlagsvariationen bzw. der Wasserverfügbarkeit beeinflusst (Luckman 2007). Während an den klimatischen Verbreitungsgrenzen von Baumarten zumeist ein spezifischer Limitierungsfaktor identifiziert werden kann, ist dies in Waldökosystemen der gemäßigten Breiten häufig schwieriger, da sich der Einfluss verschiedener Klimavariablen überlagern kann (Friedrichs et al. 2008, Kress et al. 2010).

Dennoch lässt sich der generelle Einfluss des Klimas auf die Jahrringbreite mit **Klima-Zuwachs-Beziehungen**, d.h. einfachen Korrelationsanalysen zwischen Klimaparameter und Jahrringbreite, ableiten. Prinzipiell ist dies eine Methode der Dendroklimatologie und dient in erster Linie der Identifikation von spezifischen Monaten bzw. Jahreszeiten, in denen statistisch signifikante Beziehungen zur Jahrringbreite existieren. Entsprechend erfolgt im Nachgang mittels Regressionsmodellen eine Kalibration der Jahrringzeitreihen mit den instrumentellen Klimadaten, um schließlich nach einer Verifikation des Modells eine Klimarekonstruktion durchzuführen (vgl. Cook & Kairiūkštis 1990 und Schweingruber 1996 für Details). Dessen ungeachtet lassen sich anhand von Klima-Zuwachs-Beziehungen auch für ökologische Fragestellungen wichtige Informationen über die Sensitivität der Bäume auf die generellen klimatischen Verhältnisse ableiten. Neben diesen tendenziellen Effekten der durchschnittlichen klimatischen Gegebenheiten eines Standortes können mittels **Extremjahranalysen** spezifische Ereignisse (z.B. Trockenperioden) und deren Wirkung auf die Bäume untersucht werden (Schweingruber 1996). In diesem Zusammenhang kann die Jahrringbreite im und nach dem Extremjahr als Zeichen der Vitalität eines Baumes angesehen werden (Dobbertin 2005). Die Jahrringbreite bzw. die Zuwachsrate bietet demnach bereits wichtige Einblicke über die Reaktion von Bäumen auf klimatische Bedingungen.

In Jahrringen sind jedoch in Form von **stabilen Isotopen** noch zusätzliche Informationen über die physiologischen Prozesse eines Baumes enthalten (Gessler et al. 2014). Dabei können anhand von Kohlenstoffisotopen ($\delta^{13}C$) Rückschlüsse auf die stomatäre Leitfähigkeit und die Photosyntheseraten eines Baumes gezogen werden (Farquhar et al. 1989) und mittels Sauerstoffisotopen ($\delta^{18}O$) Informationen über die Transpirationsleistung eines Baumes abgeleitet werden (Barbour et al. 2004, Yakir & DeNiro 1990). Im Grunde werden die $\delta^{13}C$-Werte ($^{13}C/^{12}C$-Verhältnis) in Jahrringen durch Fraktionierungsprozesse während der Photosynthese bzw. CO_2-Aufnhame beeinflusst: Bei weit geöffneten Stomata wird bei der Carboxylierung bevorzugt das leichtere ^{12}C-Isotop verarbeitet. Bei enger bzw. geschlossenen Stomata und damit geringerem CO_2 Angebot ist die Auswahl gewissermaßen reduziert, wodurch auch das schwerere ^{13}C-Isotop umgesetzt wird, was in einem höheren $\delta^{13}C$-Verhälnis resultiert (Farquhar et al. 1989). Die $\delta^{18}O$-Werte ($^{18}O/^{16}O$-Verhältnis) in Jahrringen werden insbesondere von der Isotopensignatur des Niederschlag- bzw. Bodenwassers beeinflusst (Roden et al. 2000). Beim Transport des Wassers von der Wurzel zum Blatt findet keine nennenswerte Fraktionierung statt, doch kommt es bei der Transpiration zu einer evaporativen Anreicherung des schwereren ^{18}O-Isotops. Da das Blattwasser die Isotopenwerte der Kohlenhydrate bestimmt, können $\delta^{18}O$-Variationen in Jahrringen Aufschluss über die Transpiration eines Baumes geben, die wiederum abhängig von Temperatur und relativer Luftfeuchtigkeit ist (Barbour et al. 2004, Yakir & DeNiro 1990). Mit der Kombination von Kohlenstoff- und Sauerstoffisotopen ist es demnach möglich, während Extremereignissen detailliertere Einblicke in die physiologische Trockenstressreaktion der Bäume zu erlangen.

1.3 Bergwaldbaumarten und erwartete Effekte der Klimaänderung

Zu den wichtigsten bestandsbildenden Baumarten des Bergwaldes des nördlichen Alpenrandes zählen die Fichte (*Picea abies* (L.) Karst.), die Weißtanne (*Abies alba* Mill.), die Rotbuche (*Fagus sylvatica* L.), der Berg-Ahorn (*Acer pseudoplatanus* L.), die Waldkiefer (*Pinus sylvestris* L.) und die Europäische Lärche (*Larix decidua* Mill.). Die Baumarten Berg-Ahorn und Waldkiefer wurden nicht in dieses Forschungsvorhaben einbezogen, da eine dendroökologische Analyse des Berg-Ahorns äußerst diffizil und mit großen Schwierigkeiten behaftet ist (siehe Hartl-Meier & Rothe 2013a, Rothe & Hartl-Meier 2014) und die Kiefer nur auf wenigen Standorten vertreten war, sodass das Datenmaterial keine tiefergehende statistische Auswertung zuließ (Hartl-Meier & Rothe 2013b).

Während für das Flachland Bayerns eine umfangreiche Studie zur Reaktion von Fichte, Tanne und Buche auf sommerliche Trockenheit vorliegt (Zang 2011), ist die Datenlage für den Alpenraum deutlich geringer. Für die Alpen existieren Untersuchungen zur Trockentoleranz koniferer Baumarten (u.a. Lärche und Fichte), doch konzentrieren sich diese auf trockene Standorte bzw. inneralpine Trockentäler (cf. Lévesque et al. 2013, 2014 und Schuster & Oberhuber 2013). Die Vergleichbarkeit mit den klimatischen Gegebenheiten (und der damit verbundenen Wasserverfügbarkeit) in den Nördlichen Kalkalpen ist somit schwieriger. Dennoch liefern oben genannte Studien bereits Hinweise über die generelle Vulnerabilität der Bergwaldbaumarten auf sommerliche Trockenheit, die im Folgenden neben weiteren Artcharakteristika kurz dargestellt wird:

Die Fichte ist mit 44 % der Waldfläche die häufigste Baumart Bayerns (StMELF 2014b). Im bayerischen Alpenraum macht sie sogar ~60 % des Flächenanteils aus (Binder 2007) und in den österreichischen Schutzwäldern ist sie mit 52 % ebenfalls die häufigste Baumart (Niese 2011). Natürlicherweise ist die Fichte nur in hochmontanen und subalpinen Höhenlagen bestandsbildend, doch durch anthropogene Förderung wurde sie im gesamten Bereich des Bergmischwaldes zur dominanten Baumart (Ellenberg 2009, Ewald 1997, Oberdorfer 2001). Die Fichte zeichnet ein Senkerwurzelsystem mit einem hohen Anteil von oberflächennahen Feinwurzeln aus. Deshalb erfolgt die Wasseraufnahme im Vergleich zu anderen Baumarten eher oberflächennah (Köstler et al. 1968, Rothe 1997), wodurch die Fichte eine Empfindlichkeit gegenüber sommerlichen Wasserdefiziten aufweist (Lévesque et al. 2013, 2014, Pretzsch et al. 2013, Zang 2011). Zudem reagiert die Fichte aufgrund ihres isohydirschen Charakters bereits in einer frühen Phase von Trockenheit mit einer Schließung der Stomata. Dies führt zu einer Reduktion der Photosyntheseraten und folglich zu geringeren Zuwächsen (Matyssek et al. 2013, McDowell et al. 2008, Pretzsch et al. 2013). Insgesamt gilt die Fichte im Hinblick auf die Klimaänderung und vor allem in Bezug auf sommerliche Trockenheit als besonders gefährdet (Lévesque et al. 2013, 2014, Zang 2011).

Mit nur 7 % nimmt die Tanne im bayerischen Alpenraum einen weitaus geringeren Flächenanteil ein als die Fichte (Binder 2007). In den letzten Generationen hat sich die Fichte insbesondere zu Lasten der Tanne im ursprünglichen Bergmischwald ausgebreitet (StMELF 2014b). Vitalitätsschäden bei der Tanne, v.a. in den 1960-1980er-Jahren, ließen sich insbesondere auf erhöhte SO_2-Emissionen zurückführen (Elling et al. 2009). Gegenüber Sommerdürre gilt die Weißtanne jedoch nur an Standorts-Grenzlagen als gefährdet (Oberdorfer 2001). Doch aufgrund ihres Pfahlwurzelsystems (Oberdorfer 2001) kann sie auch während Trockenperioden Bodenwasservorräte effizienter ausnutzen und weist dadurch eine größere Trockentoleranz auf als die Fichte (Zang 2011).

Die Buche ist mit 12 % der Waldfläche die häufigste Laubbaumart Bayerns (StMELF 2014b) und ist im bayerischen Alpenraum mit ~14 % (Binder 2007) und im österreichischen Schutzwald mit 13 % vertreten (Niese 2011). In den hochmontanen Lagen erreicht die Rotbuche ihre ökologische Verbreitungsgrenze, die im bayerischen und österreichischen Alpenraum in etwa bei 1500 m ü. NN liegt (Ewald 2012, Oberdorfer 2001). Aufgrund ihres tiefen Herzwurzelsystems gilt die Buche generell als weniger trockensensitiv – zumindest im Vergleich zur Fichte (Pretzsch et al. 2013, Zang 2011). Zudem folgt die Buche bei Trockenheit eher einer anisohydrischen Strategie: Im Vergleich zur Fichte kann sie ihre Stomata länger geöffnet halten und ihre physiologischen Prozesse aufrechterhalten, was sich in vergleichsweise geringen Zuwachsreduktionen im Trockenjahr äußern kann (Hartmann 2011, Matyssek et al. 2013, Pretzsch et al. 2013).

Der Anteil der Europäischen Lärche liegt in Bezug auf die Gesamtwaldfläche Bayerns nur bei 2 % (StMELF 2014b). Im österreichischen Schutzwald ist sie mit 17 % weitaus häufiger vertreten (Niese 2011). Sie ist von Natur aus insbesondere eine Baumart der subalpinen Höhenlagen und bevorzugt als schatten-intolerante Pionierbaumart sommerwarme und lufttrockene Klimalagen (Ellenberg 2009, Oberdorfer 2001). Zuwachsreduktionen bei der Lärche lassen sich in den Alpen insbesondere auf den Lärchenwickler zurückführen (Büntgen et al. 2009, Esper et al. 2007). Allerdings wurde in inneralpinen Trockentälern bereits eine Sensitivität der Lärche gegenüber sommerlichen Wasserdefiziten festgestellt (Lévesque et al. 2013, 2014, Schuster & Oberhuber 2013).

Unabhängig von der Baumart werden in Folge der Klimaänderung höhenlagenspezifische Zuwachsreaktionen erwartet. In den Schweizer Alpen konnten beispielsweise während des Hitzesommers 2003 negative Zuwachsänderungen in montanen Höhenlagen, jedoch gesteigerte Zuwächse in höheren Regionen nachgewiesen werden (Jolly et al. 2005). Weitere Studien aus der Tatra (Savva et al. 2006) und der Schweiz (Bugmann et al. 2014) bestätigen ebenso, dass höhere Temperaturen voraussichtlich Zuwachsanstiege in Hochlagenstandorten, jedoch aufgrund von zunehmenden Trockenstress, Zuwachseinbrüche in tieferen Lagen verursachen werden. Deshalb wird vermutet, dass ein allmählicher Temperaturanstieg mit zunehmender Höhenlage positive Effekte auf die Radialzuwächse haben wird (Körner 2012). An Waldgrenzstandorten in den Europäischen Alpen (Paulsen et al. 2000, Rolland et al. 1998) als auch in Nordamerika (Salzer et al. 2009) wurden derartige Zuwachssteigerungen bereits belegt.

1.4 Zielsetzung und Fragestellungen

Bislang bestehen noch erheblich Unsicherheiten wie die Bergwaldbaumarten Fichte, Tanne, Lärche und Buche in den Nördlichen Kalkalpen auf die Klimaänderung reagieren. Die derzeitige Datenlage erlaubt für diese Region noch keine klaren Aussagen über die art- und auch höhenlagenspezifischen Reaktionsmuster.

Ziel dieser Arbeit ist deshalb, die Zuwachsreaktionen der Bergwaldbaumarten auf Karbonatstandorten der bayerischen und österreichischen Nördlichen Kalkalpen in Abhängigkeit von Klima und Standortfaktor retrospektiv zu analysieren, um daraus deren Eignung unter der prognostizierten Klimaveränderung abzuschätzen. Hierfür wurde ein umfangreiches und für die Region einzigartiges Jahrringnetzwerk erstellt und darauf aufbauend vier Einzelstudien (vgl. Tabelle 1 zur Übersicht und Publikationen im Appendix) durchgeführt. Im Fokus der Untersuchungen standen folgende Fragestellungen:

1. **Wie ist die Vulnerabilität der Fichte im Hinblick auf die Klimaänderung einzustufen? (*Studie 1*)**

   Entlang eines Höhentransekts wurde die Reaktion der Fichte auf sommerliche Trockenheit sowie die generelle Temperaturerhöhung der letzten Jahrzehnte untersucht. Davon ausgehend soll die Vulnerabilität der Fichte entlang des Höhengradienten abgeschätzt werden und zudem die künftige Eignung der Fichte in Abhängigkeit von der Höhenlage definiert werden. Konkret werden für *Studie 1* folgende Hypothesen formuliert:

   H1A. Während Trockenjahren zeigt die Fichte in tieferen Lagen deutliche Zuwachseinbrüche und in Hochlagen Zuwachsgewinne.

   H1B. Die Temperaturerhöhung der letzten Dekaden spiegelt sich bereits in höhenlagenspezifischen Zuwachsänderungen wider.

2. **Können baumartenspezifische Reaktionsmuster in Abhängigkeit von Höhenlage und Hangexposition abgeleitet werden? (*Studie 2*)**

   Im direkten Baumartenvergleich (Fichte, Tanne, Lärche und Buche) sollen die Zuwachsreaktionen auf den Hitzesommer 2003 sowie die langfristigen Effekte der Temperaturerhöhung seit den 1990er-Jahren in verschiedenen Höhenstufen untersucht werden. Damit kann abgeschätzt werden, welche Baumart in der jeweiligen Höhenlage Trockenheit und höhere Temperaturen besser tolerieren kann. Zudem werden die Effekte der Hangexposition untersucht, da der Trockenstress an Sonnhängen durch die Hangneigung und Exposition bedingte intensivere Sonneneinstrahlung verschärft werden kann (Weis & Göttlein 2009). Mit diesem Hintergrund lauten die Hypothesen für *Studie 2* wie folgt:

   H2A. Alle Baumarten weisen höhenspezifische Zuwachsreaktionen auf, doch reagieren in Tieflagen die Fichte und die Lärche am empfindlichsten, sowie die Tanne und die Buche am geringsten.

   H2B. Zwischen Sonn- und Schatthängen sind signifikante Unterschiede bei den Zuwachsreaktionen festzustellen, wobei an südexponierten Standorten die größten Zuwachseinbrüche auftreten.

3. **Wie persistent und variabel sind die Trockenstressreaktionen auf Bestandsebene und entlang eines klimatischen Gradienten? (*Studie 3*)**

   Um die Vulnerabilität der wichtigsten Bergmischwaldbaumarten (Fichte, Tanne und Buche) auf sommerliche Trockenheit umfassend beurteilen zu können, sind neben der Zuwachsreaktion im Trockenjahr auch Kenntnisse über deren Erholungspotential bzw. deren Resilienz notwendig. Weiterhin kann auch die Variabilität der Reaktionen wichtige Hinweise über das *in situ* Anpassungspotential der Baumarten geben (Jump et al. 2006). Um baumartenspezifische Verhaltensmuster deutlicher herauszustellen, wird der klimatische Gradient für diese Studie durch die Einbeziehung von Flachlandstandorten aus Bayern (Jahrringnetzwerk von Zang 2011) ausgedehnt. Darauf aufbauend werden innerhalb der *Studie 3* folgende Hypothesen getestet:

H3A. Die Persistenz der Negativeffekte von Trockenjahren ist bei Fichte am größten, wohingegen Buche und Tanne eine höhere Toleranz und Resilienz aufweisen.

H3B. Die Variabilität der Trockenstressreaktion ist von den klimatischen Rahmenbedingungen des Standortes abhängig und nimmt mit zunehmender Trockenheit ab.

4. **Welche zusätzlichen Informationen liefern stabile Isotope über art- und standortspezifische physiologische Trockenstressreaktionen? *(Studie 4)***

Die Kombination von Kohlenstoff- und Sauerstoffisotopen erlaubt detailliertere Einblicke in die physiologische Trockenstressreaktion von Bäumen (vgl. Kapitel 1.2). In *Studie 4* sollen deshalb die artspezifischen physiologischen Strategien in Abhängigkeit von Standortsfeuchtebedingungen untersucht werden, um zusätzliche Informationen über die standortsspezifische Eignung von Fichte, Lärche und Buche unter den künftig geänderten klimatischen Bedingungen zu erhalten. Dabei wurden für *Studie 4* folgende Hypothesen formuliert:

H4A. Alle Baumarten zeigen am trockenen Standort die größte, am feuchten Standort die geringste physiologische Trockenstressreaktion.

H4B. Anhand der Isotopensignaturen lassen sich artspezifische Strategien im Umgang mit Trockenperioden ableiten.

Tabelle 1 Übersicht über die Fragestellungen und Hypothesen der Einzelstudien sowie der jeweils verwendeten Datensätze und Methoden (**JRB** = Jahrringbreiten, **δ^{13}C** = Kohlenstoffisotope, **δ^{18}O** = Sauerstoffisotope, *EB* = Einzelbäume, *JBI* = Jahrringbreitenindex, *GFZ* = Grundflächenzuwachs)

	Studie 1	***Studie 2***	***Studie 3***	***Studie 4***
Fragestellung	Wie ist die **Vulnerabilität der Fichte** im Hinblick auf die Klimaänderung einzustufen?	Können **baumartenspezifische Reaktionsmuster** in Abhängigkeit von Höhenlage und **Hangexposition** abgeleitet werden?	Wie **persistent und variabel sind die Trockenstressreaktionen** auf Bestandsebene und entlang eines klimatischen Gradienten?	Welche zusätzlichen Informationen liefern stabile Isotope über **art- und standortspezifische physiologische Trockenstressreaktionen**?
Hypothesen	***H1A.*** Während Trockenjahren zeigt die Fichte in tieferen Lagen deutliche Zuwachseinbrüche und in Hochlagen Zuwachsgewinne. ***H1B.*** Die Temperaturerhöhung der letzten Dekaden spiegelt sich bereits in höhenlagenspezifischen Zuwachsänderungen wider.	***H2A.*** Alle Baumarten weisen höhenspezifische Zuwachsreaktionen auf, doch reagieren in Tieflagen die Fichte und die Lärche am empfindlichsten, sowie die Tanne und die Buche am geringsten. ***H2B.*** Zwischen Sonn- und Schatthängen sind signifikante Unterschiede bei den Zuwachsreaktionen festzustellen, wobei an südexponierten Standorten die größten Zuwachseinbrüche auftreten.	***H3A.*** Die Persistenz der Negativeffekte von Trockenjahren ist bei Fichte am größten, wohingegen Buche und Tanne eine höhere Toleranz und Resilienz aufweisen. ***H3B.*** Die Variabilität der Trockenstressreaktion ist von den klimatischen Rahmenbedingungen des Standortes abhängig und nimmt mit zunehmender Trockenheit ab.	***H4A.*** Alle Baumarten zeigen am trockenen Standort die größte, am feuchten Standort die geringste physiologische Trockenstressreaktion. ***H4B.*** Anhand der Isotopensignaturen lassen sich artspezifische Strategien im Umgang mit Trockenperioden ableiten.
Datensatz	**JRB-Chronologien:** Fichte: 50 (500 *EB*)	**JRB-Chronologien:** Fichte: 18 (180 *EB*) Tanne: 9 (90 *EB*) Lärche: 11 (110 *EB*) Buche: 12 (120 *EB*)	**JRB-Chronologien:** Fichte: 39 (390 *EB*) Tanne: 21 (210 *EB*) Buche: 30 (300 *EB*)	**δ^{13}C, δ^{18}O & JRB-Chronologien:** Fichte: 3 (30 *EB*) Lärche: 2 (20 *EB*) Buche: 3 (30 *EB*)
Methodik	**Klima-Zuwachs-Beziehungen** (*JBI*)**:** Temperatur, Niederschlag **Trockenjahranalyse** (*JBI*)**:** 1947, 1992, 2003 **Einfluss Temperaturerhöhung** (*JBI*)	**Klima-Zuwachs-Beziehungen** (*JBI*)**:** Temperatur, Niederschlag, Sonnscheindauer **Trockenjahranalyse** (*GFZ*)**:** 2003 **Einfluss Temperaturerhöhung** (*GFZ*)	**Trockenjahranalyse** (*GFZ*)**:** 1947, 1976, 2003 **Variabilität der Reaktionen** (*GFZ*)	**Korrelationen mit Klima** (*δ^{13}C, δ^{18}O, JBI*)**:** Sonnenscheindauer, Temperatur, Feuchte-Index, Niederschlag, Wolkenbedeckung **Trockenjahranalyse** (*δ^{13}C, δ^{18}O, JBI*)**:** 1983, 1992, 1994, 2003

2 MATERIAL UND METHODEN

2.1 Untersuchungsgebiet

Im Fokus der Untersuchungen stehen die bayerischen und österreichischen Nördlichen Kalkalpen (vgl. Abb. 1). Entsprechend sind hier triassische Kalke und Dolomite vorherrschend (Bayerisches Geologisches Landesamt 1996). Konkret stehen auf den Untersuchungsflächen Dachsteinkalk, Hauptdolomit oder Wettersteinkalk an. In den Nördlichen Kalkalpen weisen die Böden reliefbedingt häufig eine hohe Heterogenität bezüglich der Mächtigkeit und Entwicklung auf (Weis et al. 2014). Um die standörtliche Variabilität möglichst gering zu halten, konzentriert sich diese Arbeit auf die flächenmäßig vorherrschenden flachgründigen und karbonatreichen Böden, wie Fels-Humus-Böden und Rendzinen. Aufgrund ihres Nährstoffmangels (insbesondere Phosphor, Eisen, Kalium, teilweise auch Stickstoff) und zeitweilig auftretendem Trockenstress werden solche Standorte auch als Extremstandorte charakterisiert (Weis et al. 2014).

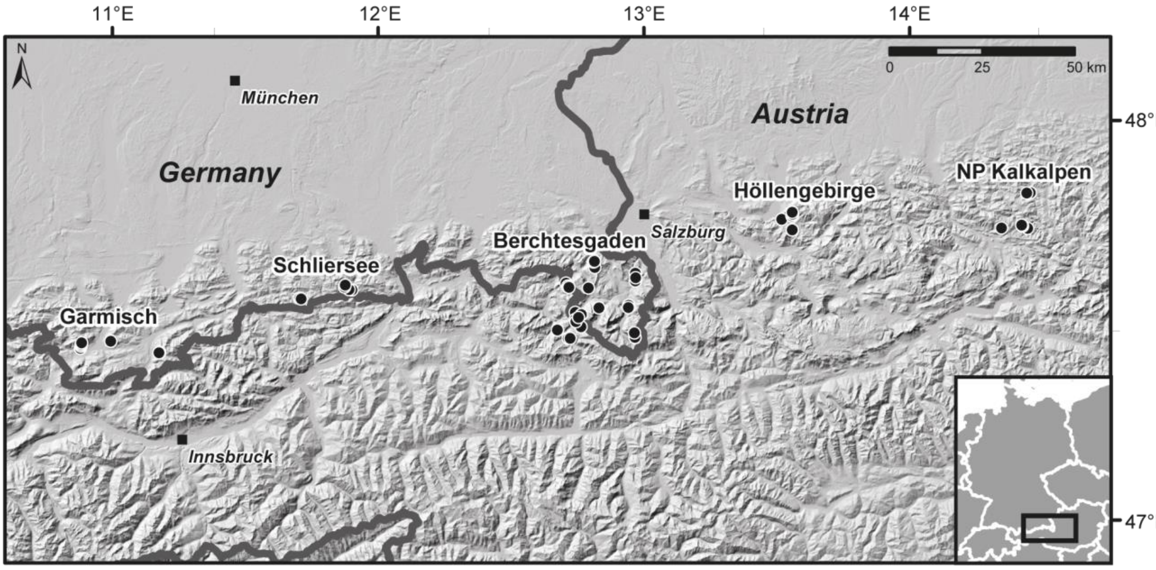

Abbildung 1 Untersuchungsgebiet mit beprobten Einzelstandorten (schwarze Punkte) (Kartengrundlage: SRTM X-band data, DLR/ASI).

Klimatisch zählt der Alpennordrand zu den niederschlagsreichsten Regionen Mitteleuropas (Weischet & Endlicher 2000). Zusammengefasst für das gesamte Untersuchungsgebiet liegen die Jahresniederschlagssummen bei ca. 1600 mm und die Jahresdurchschnittstemperaturen bei ~6 °C. Das Niederschlagsmaximum tritt deutlich im Sommer auf, wodurch in den Monaten Mai bis September mit rund 800 mm etwa die Hälfte des gesamten Jahresniederschlags fällt (Abb. 2). Die durchschnittlichen Temperaturen in der Vegetationszeit liegen bei ~12 °C (alle Angaben basieren auf HISTALP-Daten (Auer et al. 2007) und beziehen sich auf die Klimanormalperiode 1961-1990).

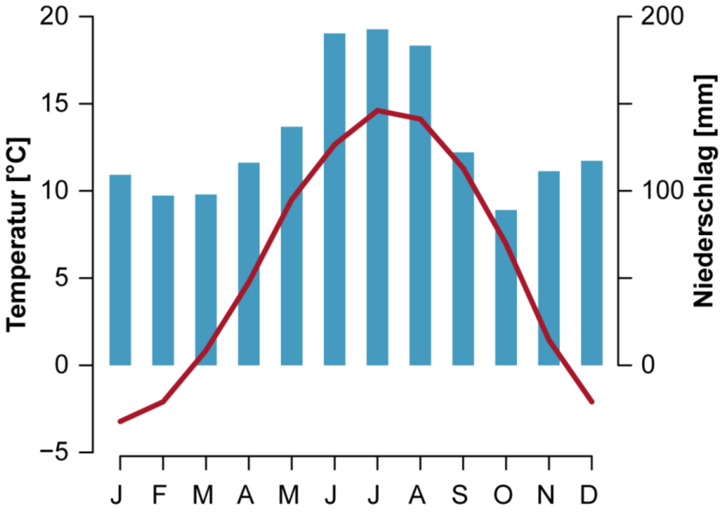

Abbildung 2 Durchschnittliche monatliche Temperaturen (rot) und Niederschläge (blau) des gesamten Untersuchungsgebiets (Bezugsperiode: 1961-1990, Datengrundlage: HISTALP (Auer et al. 2007)).

2.2 Probenahme und Messung der Jahrringbreiten

Insgesamt wurden für das vorliegende Forschungsvorhaben 50 Standorte in den bayerischen und österreichischen Kalkalpen beprobt (Abb. 1). Auf den Standorten wurden die verschiedenen Baumarten Fichte, Tanne, Lärche und Buche je nach Vorkommen parallel beprobt.

An jedem Standort wurden je Baumart an zumeist 14 vitalen Bäumen der Baumklasse 2 nach Kraft (1884) Bohrkerne mit einem Zuwachsbohrer nach Preßler entnommen. Pro Baum wurden auf Brusthöhe (1,30 m) zwei Bohrkerne in unterschiedlichen Himmelsrichtungen gezogen, meist an der Hangoberseite des Stammes um 45 ° in beiden Richtungen zur Hanglinie versetzt (Dittmar et al. 2003). Neben dem Brusthöhendurchmesser wurden auch die GPS-Koordinaten der einzelnen Probebäume erfasst.

Die Messung der Jahrringbreite erfolgte mittels eines LINTAB 6 Messtisches und dem Programm TSAP-Win (RINNTECH, Heidelberg) mit einer Präzision von 1/100 mm.

Nach der visuellen Kreuzdatierung der Zuwachskurven am Bildschirm wurde die Korrektheit der Daten mit dem Programm COFECHA (Holmes 1983) statistisch überprüft. Für die weiteren Auswertungen wurden die sicher synchronisierten Einzelradien von je 10 Bäumen pro Art und Standort verwendet. Insgesamt wurden 3192 Einzelserien gemessen, wovon letztlich 2280 nach bestandener Qualitätsprüfung für die weiteren Auswertungen herangezogen wurden. Insgesamt wurden für die vorliegende Arbeit 114 Chronologien, bestehend aus 50 Fichten- (à 500 Bäumen), 21 Tannen- (à 210 Bäumen), 13 Lärchen- (à 130 Bäumen) und 30 Buchen-Chronologien (à 300 Bäumen), aufgebaut. In den verschiedenen Einzelstudien wurden je nach Fragestellung nur Teile des Gesamtdatensatzes mit einbezogen (siehe Tabelle 1).

2.3 Statistische Auswertung

Generell werden Rohwertmessungen der Jahrringbreite (in mm) von nicht-klimatisch bedingten Einflussfaktoren überlagert. Insbesondere der Alterstrend, ein langfristig abnehmender Trend der Jahrringbreite, muss vor einer klimatischen Begutachtung eliminiert werden. Erst die Trendbereinigung bzw. Standardisierung ermöglicht eine klimatische Interpretation des Baumwachstums (Fritts 1976). Mittels eines geeigneten Trendbereinigungsverfahrens ist es möglich, den Alterstrend zu beseitigen und gleichzeitig klimatisch bedingte langfristige bzw. niederfrequente Wachstumssignale zu betonen. Dabei werden die in mm gemessenen Jahrringbreiten in dimensionslose Jahrringindices umgerechnet. Je nach Fragestellung wurden in den folgenden Einzelstudien verschiedene Trendbereinigungsverfahren (z.T. auch parallel) verwendet, um ein möglichst breites Spektrum abzudecken und keine verzerrten Schlussfolgerungen zu treffen.

In den folgenden Kapiteln wird ein kurzer Überblick über den verwendeten Datensatz sowie die angewendeten statistischen Methoden der einzelnen Studien gegeben (vgl. auch Tabelle 1 für einen Überblick). Für eine genauere Datenübersicht sowie methodische Details sei auf die jeweilige Publikation verwiesen (*Studie 1*: Publikation I, *Studie 2*: Publikation II, *Studie 3*: Publikation III, *Studie 4*: Publikation IV).

2.3.1 Datensatz und Methodik *Studie 1*

Datensatz: *Studie 1* basiert auf dem gesamten Fichten Datensatz, bestehend aus 50 Einzelstandorten und entsprechend 500 Bäumen. Das untersuchte Gebiet umfasst eine West-Ost-Ausdehnung von ca. 250 km (Abb. 1) und einen Höhengradienten von rund 1200 m (~500 bis 1700 m ü. NN).

Klima-Zuwachs-Beziehungen: Um den generellen Einfluss des Klimas auf das Baumwachstum abzuschätzen, wurden Pearsonsche Korrelationskoeffizienten zwischen den trendbereinigten Standorts-Chronologien und den räumlich korrespondierenden Temperatur- und Niederschlagsdaten der Vegetationsperiode (Mai-September) berechnet. Die Abhängigkeit von der Höhenlage wurde mit einem generalisierten additiven Modell (GAM) beschrieben.

Trockenjahranalyse: Über einen regionalen Feuchte-Index wurden die Sommer 1947, 1992 und 2003 als die drei extremsten Trockenjahre für das Untersuchungsgebiet identifiziert (vgl. hierfür Publikation I, u.a. Fig. 2). Für diese Jahre wurden anhand der trendbereinigten Jahrringindizes die prozentualen Zuwachsreaktionen im Vergleich zu den fünf vorhergehenden Jahren berechnet. Der Zusammenhang von Höhenlage und Zuwachsreaktion wurde anschließend mit einem linearen Regressionsmodell bestimmt.

Einfluss der Temperaturerhöhung der letzten Dekaden auf den Zuwachs: Hierfür wurden anhand trendbereinigter Jahrringindizes die prozentualen Zuwachsänderungen im Vergleich zur Referenzperiode 1941-1970 ermittelt. Da die Standardisierung von Jahrringzeitreihen verschiedene Langzeittrends – die möglicherweise von Interesse sind – eliminieren kann, wurde die Berechnung der Zuwachsänderung mit drei verschiedenen Trendbereinigungsverfahren durchgeführt. Weiterhin wurde die Persistenz des Zusammenhangs zwischen Zuwachsänderung und Klimaänderung mittels gleitenden Korrelationen überprüft.

2.3.2 Datensatz und Methodik *Studie 2*

Datensatz: Für die Untersuchung von baumartenspezifischen Reaktionsmustern wurden ausschließlich Daten aus der Region Berchtesgaden verwendet (vgl. Abb. 1). Insgesamt beinhaltet diese Studie 18 Fichten-, 9 Tannen-, 11 Lärchen- und 12 Buchen-Chronologien, was zusammengefasst 500 Bäumen entspricht. Die

Untersuchungen schließen sowohl Schatt- als auch Sonnhänge mit ein und umfassen einen Höhentransekt von knapp 1000 m (680-1670 m ü. NN).

Klima-Zuwachs-Beziehungen: Zur Beschreibung des Zusammenhangs zwischen Zuwachs und Klima wurden die Korrelationskoeffizienten nach Pearson zwischen den einzelnen trendbereinigten Chronologien und der Temperatur, dem Niederschlag und der Sonnenscheindauer verschiedener Jahreszeiten berechnet.

Trockenjahranalyse: Die prozentuale Zuwachsreaktion auf das Hitzeextrem im Jahr 2003 wurde im Vergleich zu den Jahren 1998-2002 untersucht, basierend auf den zuvor ermittelten Grundflächenzuwächsen und auf Einzelbaumebene.

Einfluss der Temperaturerhöhung der letzten Dekaden auf den Zuwachs: Auf Basis der Grundflächenzuwächse und von Einzelbaumdaten wurde die Zuwachsänderung seit 1990 im Vergleich zur Referenzperiode 1961-1990 berechnet.

Mittels des Studentschen t-Tests wurde die Signifikanz der Zuwachsreaktion bzw. –änderung überprüft. Signifikante Unterschiede zwischen den Höhenstufen und Expositionen wurden mit einer Varianzanalyse (ANOVA) gefolgt von einem Tukey-HSD *post hoc* Test bestimmt.

2.3.3 Datensatz und Methodik *Studie 3*

Datensatz: In die Studie zur Untersuchung der Persistenz und Variabilität der Trockenstressreaktionen von Fichte, Tanne und Buche fließen die Daten aus zwei Jahrringnetzwerken ein: 90 Chronologien (39 Fichten, 21 Tannen, 30 Buchen), von 39 Standorten in den Nördlichen Kalkalpen stammen aus dem für diese Arbeit erstellten Jahrringnetzwerk, 86 Chronologien von 43 Standorten (davon 4 in den Nördlichen Kalkalpen und 39 in Tieflandlagen Bayerns) stammen aus dem Jahrringnetzwerk von Zang (2011). Der aus 82 Standorten und 176 Chronologien bestehende Gesamtdatensatz deckt einen breiten klimatischen Gradienten von warm trocken bis kühl feucht ab. Zur Charakterisierung der jeweiligen klimatischen Verhältnisse wurde für alle Standorte der Ariditäts-Humiditäts-Index nach De Martonne (1926) für die Monate Juni bis August (= DMI-JJA) berechnet und für die weiteren Analysen verwendet. Da sich die Alpen klimatisch deutlich von den Tieflandlagen unterscheiden, können die kalkalpinen Untersuchungsstandorte anhand des Index klar von den Tieflandstandorten differenziert werden (DMI-JJA > 1,5 entsprechen Standorten in den Nördlichen Kalkalpen; vgl. Abb. 3).

Trockenjahranalyse: Auf Basis von Grundflächenzuwächsen wurden die Toleranzindizes *resistance*, *recovery* und *resilience* nach Lloret et al. (2011) für die Trockenjahre 1947, 1976, 2003 auf Standorts- sowie Einzelbaumebene berechnet. Dabei beschreibt *resistance* den Zuwachs im Trockenjahr im Vergleich zu den drei vorhergehenden Jahren, *recovery* die Zuwächse der folgenden drei Jahre im Vergleich zum Trockenjahr selbst und *resilience* den Zuwachs der drei Folgejahre im Vergleich zu den drei Jahren vor dem Trockenjahr. Um den generellen Einfluss des Klimas auf die Toleranzen der Baumarten zu bestimmen, wurde der Zusammenhang zwischen Toleranzindizes (Standortsmittel) und DMI-JJA mit einem linearen Regressionsmodell dargestellt.

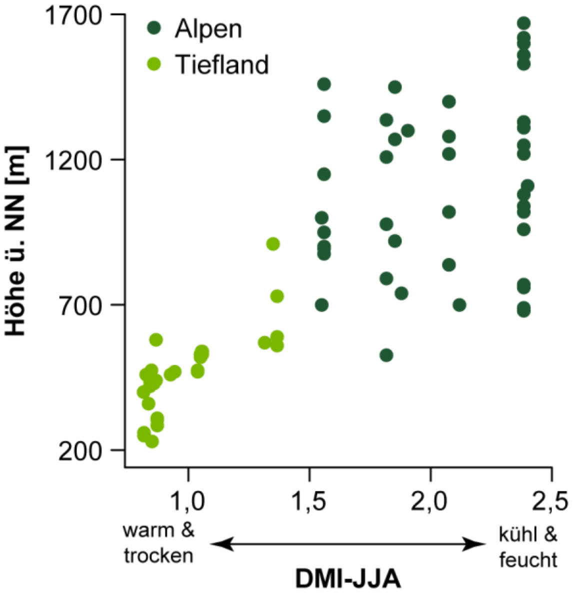

Abbildung 3 Klimabedingungen der Standorte in *Studie 3*, basierend auf dem De Martonne Index für Juni, Juli und August (DMI-JJA), in Abhängigkeit von der Höhenlage.

Variabilität der Zuwachsreaktionen innerhalb eines Bestandes: Hierfür wurde der Variationskoeffizient für die jeweiligen Toleranzindizes je Standort berechnet. Um diese Variabilität in Relation zu einer Basislinie zu setzen, wurde der Variationskoeffizient mit der „Hintergrund-Variabilität“ verglichen. Dabei entspricht die Hintergrund-Variabilität dem innerhalb einer Population auftretenden Variationskoeffizienten während klimatischen Durchschnittsbedingungen und wurde durch die wiederholte Auswahl (n = 1000) von drei Zufallsjahren berechnet (für Details siehe Publikation III). Die Signifikanz der Unterschiede zwischen der Variabilität in/nach den Trockenjahren und der jeweiligen Hintergrundvariabilität wurde anschließend mit einem gepaart einseitigem Wilcoxon-Rangsummen-Test geprüft. Der Zusammenhang der Variationskoeffizienten mit den klimatischen Gegebenheiten des Standortes (DMI-JJA) wurde mit einem linearen Regressionsmodell bestimmt.

2.3.4 Datensatz und Methodik *Studie 4*

Datensatz: Die Isotopenstudie wurde am Langzeituntersuchungsstandort „LTER Zöbelboden“ (http://www.umweltbundesamt.at/im) im Nationalpark Kalkalpen durchgeführt. An drei Einzelstandorten (Südhang, Nordhang und Plateau) wurden in annähernd gleicher Höhenlage (~900 m ü. NN) und enger horizontaler Distanz (max. 900 m zwischen den Standorten) Fichten, Lärchen und Buchen beprobt. An allen drei Standorten wurden die drei Baumarten parallel beprobt, abgesehen vom Südhang, wo Lärche absent war. Neben der Exposition variieren die Standorte insbesondere in der Bodenmächtigkeit und –feuchte (Süd: flach & trocken; Nord: mittel; Plateau: tief & feucht; für Details siehe Publikation IV, u.a. Table 2 und Fig. 1). Bei drei Fichten-, drei Buchen- und zwei Lärchen-Chronologien wurden von je acht Bäumen die δ^{13}C- und δ^{18}O-Isotope mit der Poolmethode (Mischen der im selben Jahr gebildeten Ringe je Art und Standort) für den Zeitraum 1970-2010 gemessen. Die detaillierte Messmethodik ist in Publikation IV beschrieben.

Deskriptive Analysen: Standorts- und artspezifische Unterschiede in den mittleren δ^{13}C- und δ^{18}O-Signaturen sowie der Jahrringbreite wurden mittels ANOVA und Tukey-HSD *post hoc* Test überprüft. Die Ähnlichkeiten der Jahr-zu-Jahr Variationen der Chronologien innerhalb der Standorte und Arten wurde mit der *inter-chronology correlation* (d.h. mittlere Pearsonsche Korrelationskoeffizienten) bestimmt.

Korrelation von δ^{13}C, δ^{18}O und Jahrringbreite mit dem Klima: Der Zusammenhang zwischen Sommerklima (Juni, Juli und August) und den drei Jahrringparametern wurde für die Klimavariablen Sonnenscheindauer, Temperatur, Feuchte-Index, Niederschlag und Wolkenbedeckung mit der Korrelationsanalyse nach Pearson berechnet.

Trockenjahranalyse: Die Trockenjahre 1983, 1992, 1994 und 2003 wurden durch eine Überlappung der 10 Extremwerte von Temperatur, Niederschlag und Feuchte-Index im Zeitraum 1970-2010 definiert (vgl. Publikation IV, Fig. 2). Mittels *superposed epoch analysis* (SEA) (Panofsky & Brier 1958) wurde die physiologische Reaktion auf diese Extremjahre untersucht. Dabei werden die Zeitreihen unter der Einbeziehung der vier Jahre vor und nach dem Trockensommer, zentriert auf die Trockenjahre, übereinander gelegt und die Abweichungen, basierend auf den vier Jahren vor dem Ereignis, dargestellt (für Details siehe Publikation IV).

3 DISKUSSION DER ERGEBNISSE

3.1 Vulnerabilität der Fichte gegenüber der Klimaänderung *(Studie 1)*

Als häufigste Baumart der bayerischen und österreichischen Bergwälder ist die Eignung der Fichte unter künftig geänderten Klimabedingungen von besonderem forstlichem Interesse. Deshalb wurde über eine Region mit einer West-Ost-Ausdehnung von 250 km und einem Höhengradienten von ~1200 m ein sehr umfangreiches, aus 500 Fichten bestehendes, Jahrringnetzwerk erstellt und untersucht.

Die **Klima-Zuwachs-Beziehungen**, die den generellen Einfluss des Klimas der Vegetationsperiode auf die Zuwächse der Fichte beschreiben, zeigen deutliche Zusammenhänge mit der Höhenlage (Publikation I, Fig. 4). In den tieferen Lagen korrelieren die Zuwächse negativ mit den Durchschnittstemperaturen. Bei ca. 1200 m ü. NN kommt es zu einem Vorzeichenwechsel der Korrelationskoeffizienten und ab ca. 1400 m ü. NN sind die Zusammenhänge zwischen Temperatur und Zuwachs sogar signifikant positiv ($p < 0{,}05$) (Publikation I, Fig. 4a). In einem GAM lassen sich 76 % ($p < 0{,}001$) der Varianz der Temperatur-Zuwachs-Beziehungen mit der Höhe erklären. Auch der Zusammenhang zwischen Niederschlag und Jahrringbreite zeigt eine Abhängigkeit zur Höhenlage, doch ist das Bild im Vergleich zur Temperatur invers (Publikation I, Fig. 4b). Hohe Niederschläge in der Vegetationsperiode haben in Tieflagen positive, in Hochlagen hingegen negative Effekte auf die Zuwächse der Fichte, wobei der Schwellenwert hier bei ca. 1300 m ü. NN liegt. Der Zusammenhang mit der Höhe ist für den Niederschlag nicht ganz so deutlich wie für die Temperatur, doch erklärt die Höhe in einem GAM immer noch 59 % ($p < 0{,}001$) der Varianz. Generell bestätigen auch andere Studien einen Zusammenhang zwischen Klima-Zuwachs-Beziehungen und Höhenlage (cf. Dittmar & Elling 1999, Frank & Esper 2005, Leal et al. 2007, Mäkinen et al. 2002, Savva et al. 2006, Wilson & Hopfmüller 2001). In einigen der Studien wurden auch Schwellenwerte für den Übergang von negativen zu positiven Effekten der Temperatur auf den Radialzuwachs bestimmt. Diese liegen beispielsweise bei Dittmar

& Elling (1999) in einer Höhe von ~800 m ü. NN, bei Wilson & Hopfmüller (2001) auf ~900 m ü. NN und bei Frank & Esper (2005) auf ~1500 m ü. NN. Jedoch ist ein direkter Vergleich der Höhen aufgrund der unterschiedlichen klimatischen Bedingungen der Untersuchungsgebiete (Bayerischer Wald und Schweizer Alpen) schwieriger und nicht auf die Nördlichen Kalkalpen übertragbar.

Die **Trockenjahranalyse** verdeutlicht, dass Extremereignisse wie die Jahre 1947, 1992 und 2003 auch in den humiden Klimaregionen der Alpen Zuwachseinbrüche auslösen können (Publikation I, Fig. 3). Diese beschränken sich jedoch auf Höhenlagen unter 1400 m ü. NN und liegen in den tiefmontanen Lagen bei maximal ~40 %. Damit sind die Zuwachseinbußen deutlich niedriger als in Flachlandlagen, wo für Bayern Zuwachseinbrüche von mehr als 60 % festgestellt wurden (Zang 2011). Die Bedeutung der Höhenlage im Hinblick auf die Zuwachsreaktion in Trockenjahren stimmt gut mit Untersuchungen aus den Schweizer Alpen überein. Hier wurden im Hitzesommer 2003 in Tieflagen reduzierte, jedoch in Hochlagen gesteigerte Zuwächse festgestellt (Jolly et al. 2005). Auch in den Nördlichen Kalkalpen konnten in den Hochlagen Zuwachsgewinne von bis zu ~18 % nachgewiesen werden. Zudem besteht ein eindeutiger Zusammenhang zwischen der Höhenlage und der Zuwachsreaktion im Trockenjahr (vgl. ***H1A***), wobei die Höhe in einem linearen Regressionsmodell 62 % ($p < 0{,}001$) der Varianz erklärt. Demnach kann ***H1A*** bestätigt werden. Zusammenfassend lässt sich festhalten, dass die Fichte in den bayerischen und österreichischen Kalkalpen unterhalb von 1200-1400 m ü. NN von warm-trockenen Bedingungen in ihrem Zuwachs eingeschränkt wird und oberhalb dieses Schwellenwerts von solchen klimatischen Verhältnissen profitieren kann, was letztlich auch die Ergebnisse aus den Klima-Zuwachs-Beziehungen widerspiegelt.

Nach diesen Ergebnissen wäre zu erwarten, dass die **Temperaturerhöhung der letzten Jahrzehnte** (liegt für die Monate Mai-September seit 1990 im Vergleich zu 1941-1970 bei ~1 °C für das gesamt Untersuchungsgebiet; vgl. Publikation I, Fig. S1) bereits Zuwachsreduktionen in Tieflagen und Zuwachssteigerungen in Hochlagen ausgelöst hat (vgl. ***H1B***). Dieser Aspekt wurde durch die Untersuchung der langfristigen Zuwachsänderungen jedes einzelnen Fichtenstandorts geprüft. Dabei konnten zunächst innerhalb verschiedener Höhenstufen sehr ähnliche Zuwachstrends festgestellt werden (vgl. Publikation I, Fig. S3). Dies deutet darauf hin, dass der Einfluss der Standortsbedingungen, der Untersuchungsregion (z.T. Distanzen von 250 km zwischen den Fichtenstandorten) und des Forstmanagements (Bayern vs. Österreich) auf die langfristigen Zuwachsvariationen dieser Fichten nur gering ist und in erster Linie das Klima als primärer Einflussfaktor anzusehen ist. Erstaunlicherweise lassen sich jedoch in den letzten Jahrzehnten in keiner Höhenlage gerichtete Zuwachsänderungen nachweisen (Publikation I, Fig. 5). Bei der Analyse von langfristigen Trends in Jahrringdaten muss allerdings darauf geachtet werden, dass durch die vorhergehende Trendbereinigung – die in jedem Fall zur Eliminierung des Alterstrends erforderlich ist (Fritts 1976) – möglicherweise niederfrequente Trends entfernt werden, die eigentlich von Interesse sind. Um diese potentielle Fehlerquelle zu umgehen und keine verzerrten Schlussfolgerungen zu treffen, wurden die Zuwachsänderungen basierend auf drei verschiedenen Trendbereinigungsverfahren berechnet. Bei der Betrachtung und Gegenüberstellung der Ergebnisse lassen sich jedoch für keines der Trendbereinigungsverfahren außergewöhnliche Zuwachsänderungen oder deutliche Tendenzen in den letzten Dekaden feststellen (Publikation I, Fig. 5). Die Auswirkungen der Temperaturerhöhung um 1 °C waren bislang weder in den Tieflagen negativ noch in den Hochlagen deutlich positiv, womit ***H1B*** nicht verifiziert werden kann. Im Laufe der Zeit sind jedoch durchaus Schwankungen mit Phasen über- bzw. unterdurchschnittlichen Zuwächsen festzustellen. Dabei lassen sich die Phasen verminderten Zuwachs in Höhen < 1400 m ü. NN wiederum mit den Trockenjahren 1947, 1992 und 2003 in Verbindung bringen. Demnach zeigt die Fichte auch nach Trockenjahren noch reduzierte Zuwächse, wie es auch in Flachlandlagen Bayerns bereits festgestellt wurde (Zang 2011). Dennoch werden in den Nördlichen Kalkalpen 5-10 Jahre nach dem Ereignis wieder deutlich überdurchschnittliche Zuwächse erreicht, was für ein hohes Erholungspotential der Fichte spricht.

Obwohl bei den Klima-Zuwachs-Beziehungen für diese Höhenlagen typische Klimasignale (d.h. signifikant positive Korrelationen mit der Temperatur > 1400 m ü. NN) nachgewiesen werden konnten (Babst et al. 2013), zeichnen die Hochlagen-Fichten die Temperaturerhöhung nicht in ihrem Zuwachs nach. Zur genaueren Untersuchung dieser asynchronen Trends wurde die temporäre Stabilität des Zusammenhangs zwischen Temperatur- und Zuwachsänderung mittels gleitender Korrelation überprüft (Publikation I, Fig. 6). In der subalpinen Höhenstufe (> 1400 m ü. NN) ist der Zusammenhang mit der Temperatur seit ~1900 relativ stabil und positiv. Zuvor sind die Korrelationen negativ, wie es auch Büntgen et al. (2006) für den Zusammenhang zwischen Juni-Temperatur und Zuwachs in den Alpen belegen konnte. Allerdings wurde in Büntgen et al. (2006) zusätzlich eine generelle Abschwächung des Einflusses der Temperatur nachgewiesen, was sich für die Hochlagen der Nördlichen Kalkalpen nicht zeigt. Im Gegensatz dazu sind die Korrelationen für die Temperatur in den Tieflagen wesentlich instabiler und die Koeffizienten deutlich niedriger. Hier scheint das Niederschlagssignal etwas stabiler zu sein (vgl. Publikation I, Fig. S4).

Trotz der relativ stabilen Zusammenhänge der Temperatur- und Zuwachsänderung zeigen die subalpinen Fichten keine gesteigerten Radialzuwächse aufgrund der Temperaturerhöhung um 1 °C. Jedoch konnten in anderen Regionen der Europäischen Alpen oder in Nordamerika bereits positive Zuwachstrends nachgewiesen werden (Paulsen et al. 2000, Rolland et al. 1998, Salzer et al. 2009). Bei diesen Untersuchungen handelt es sich allerdings um Baumgrenzstandorte, während sich in diesem Forschungsvorhaben auch die subalpinen Fichten immer noch im dichten Waldbestand befinden. Die höchste Verbreitung der Fichte liegt im bayerischen Alpenraum bei 1900 m ü. NN (Ewald 2012), sodass in solchen Höhenlagen möglicherweise deutlichere Signale festzustellen wären. Die „fehlenden“ Zuwachsrückgänge in den tieferen Standorten sind möglicherweise dadurch zu erklären, dass am Alpennordrand – als einer der niederschlagsreichsten Regionen Mitteleuropas (Weischet & Endlicher 2000) – immer noch ausreichend Niederschlag zur Verfügung steht. Zudem befindet sich die Fichte in den Nördlichen Kalkalpen trotz der Temperaturerhöhung um 1 °C gegenwärtig noch innerhalb ihrer Klimahülle (Kölling 2007).

Zusammenfassende Fakten *Studie 1*:

- **Hohe Temperaturen wirken sich unterhalb von 1200 m ü. NN negativ und oberhalb davon positiv aus; hohe Niederschläge beeinflussen den Zuwachs unter 1300 m ü. NN eher positiv und darüber negativ.**
- **Auf Trockenjahre reagiert die Fichte unter 1400 m ü. NN mit Zuwachseinbrüchen (max. ~40 %) und darüber mit Zuwachsgewinnen.**

➔ **Die Fichte ist unterhalb von 1200-1400 m ü. NN trockensensitiv, zeigt jedoch hohes Erholungspotential.**

- **Die bisherige Temperaturerhöhung um 1 °C wirkte sich weder negativ in den Tieflagen noch positiv in den Hochlagen aus, wodurch eine Gefährdung der Fichte bislang noch nicht festzustellen ist.**

3.2 Baumartenspezifische Reaktionsmuster und Expositionseffekte *(Studie 2)*

Die Reaktion der Fichte auf die Klimaänderung wurde in *Studie 1* bereits intensiv behandelt. Zur umfassenden Beurteilung der Stabilität der Bergwälder für künftige Klimabedingungen sind jedoch auch Kenntnisse über die weiteren bestandsbildenden Baumarten des Bergwaldes notwendig. Im Rahmen der *Studie 2* wurden deshalb im Berchtesgadener Land neben Fichte auch die Baumarten Buche, Tanne und Lärche intensiver untersucht. Zudem wurde die Hangexposition berücksichtigt, da in den Nördlichen Kalkalpen insbesondere südexponierte Standorte als Extremstandorte und damit als besonders gefährdet gelten (Weis et al. 2014).

Die **Klima-Zuwachs-Beziehungen** (Publikation II, Fig. 4) zeigen für Fichte ein sehr ähnliches Bild wie in *Studie 1*. Aufgrund des überwiegend negativen Effekts der Temperatur und Sonnenscheindauer und des positiven Effekts des Niederschlags kann die Sensitivität der Fichte auf warm-trockene Bedingungen in Höhen unter ~1300 m ü. NN bestätigt werden. Expositionsunterschiede sind nur schwach ausgeprägt, lediglich beim Niederschlag sind die Korrelationskoeffizienten an Sonnhängen tendenziell etwas höher als an Nordhängen. Für Buche und Lärche ist der Zusammenhang zwischen Klima-Zuwachs-Beziehungen und Höhenlage weniger ausgeprägt als bei Fichte. Bei beiden Baumarten ist auch in den Tieflagen keine deutliche Trockensensitivität erkennbar. Die Buche wird an fast allen Standorten (auch in Tieflagen) positiv von hohen Temperaturen beeinflusst. Für die Nördlichen Kalkalpen konnten Dittmar & Elling (1999) negative Temperatureffekte für Buchenstandorte < 600 m ü. NN nachweisen. Eine höhere Sensitivität der Buche gegenüber warm-trockenen Klimabedingungen scheint sich demnach erst im submontanen Bereich auszubilden (Zang 2011). Die Lärche kann in allen Höhenstufen (am deutlichsten in den Hochlagen) von hohen Temperaturen und viel Strahlung (insbesondere an Schatthängen) profitieren. Das Niederschlagsignal ist negativ, sodass hier, anders als bei Lévesque et al. (2013, 2014), keine Vulnerabilität gegenüber sommerlicher Trockenheit abgeleitet werden kann. Die Tanne zeigt ebenfalls keine konsistenten Zusammenhänge mit der Temperatur oder dem Niederschlag (weder negativen noch positiv). Dies spricht für die Robustheit der Tanne gegenüber Trockenheit, womit sich auch für die Nördlichen Kalkalpen die Einschätzung von Elling et al. (2009), van der Maaten-Theunissen et al. (2013) und Zang (2011) aus Regionen nördlich der Alpen bestätigt. Eine erhöhte Sensitivität der Tanne gegenüber Trockenheit konnte bislang nur in trockeneren Regionen Europas nachgewiesen werden, wie beispielsweise in Italien (Battipaglia et al. 2009), den südlichen Ostalpen (Maxime & Hendrik 2011) oder Frankreich (Lebourgeois et al. 2010).

Um die Robustheit der Baumarten auf spezifische Extremereignisse zu überprüfen wurde im Rahmen der **Trockenjahranalyse** die Zuwachsreaktion im Hitzesommer 2003 untersucht. Mit ~3,8 °C höheren Sommertemperaturen (Mai-August) und ~20 % geringerem Niederschlag (im Bezug zu 1961-1990) in den tieferen Lagen des Berchtesgadener Landes, ist dieser Sommer als Extremereignis einzustufen. Im Allgemeinen konnten mit den tatsächlichen Zuwachsreaktionen der Bäume im Jahr 2003 die Erkenntnisse aus den Klima-Zuwachs-Beziehungen weitgehend bestätigt werden. Die Fichte reagierte zum Teil mit signifikanten ($p < 0,05$) Zuwachseinbußen bis in Höhen von ca. 1200 m ü. NN (Publikation II, Fig. 5). An nordexponierten Standorten in 1300 m Höhe traten allerdings Zuwachsgewinne auf, wodurch sich aufgrund der Hangexposition signifikante ($p < 0,01$) Unterschiede bei der Zuwachsreaktionen in dieser Höhenstufe ergeben. Die positiven Zuwächse im subalpinen Bereich unterscheiden sich somit ebenfalls signifikant ($p < 0,0001$) von den andern Höhenlagen. Demnach bestätigt sich erneut, dass die Zuwachsreaktionen in Extremjahren von der Höhenlage abhängig sind (vgl. z.B. Desplanque et al. 1999, Jolly et al. 2005, Neuwirth et al. 2004). Desplanque et al. (1999) und Lebourgeois et al. (2010) stellten auch für die Tanne eine höhenlagenabhängige Zuwachsreaktion auf Trockenheit fest, doch lässt sich dies im Berchtesgadener Land nicht nachweisen. Wie oben bereits dargestellt, kann die Tanne sommerliche Trockenheit gut tolerieren (Elling et al. 2009, van der Maaten-Theunissen et al. 2013, Zang 2011), da sie auch im Hitzesommer 2003 keine signifikanten Zuwachsreaktionen zeigt. Gleiches gilt für die Lärche, was erneut den Erkenntnissen von Lévesque et al. (2013, 2014) aus inneralpinen Trockentälern widerspricht. Doch im Gegensatz zu den Nördlichen Kalkalpen sind die Niederschlagsverhältnisse in inneralpinen Trockentälern generell angespannter, wodurch die Lärche dort womöglich schneller an ihr Toleranzlimit stößt als am Alpennordrand. Für die Buche konnten im Berchtesgadener Land nur an den höheren Standorten (~1200-1300 m ü. NN) leichte (nicht signifikante) Zuwachseinbußen festgestellt werden. Dies widerspricht den Ergebnissen aus den Klima-Zuwachs-Beziehungen, und an südexponierten Tieflagenstandorten treten sogar Zuwachsgewinne auf. Vermutlich ist die Zuwachsreduktion auf andere Einflussfaktoren in diesem Jahr zurückzuführen. Da bei Buche die Häufigkeit von Spätfrost initiierten Zuwachseinbrüchen mit zunehmender Höhenlage steigt (Dittmar et al. 2003), könnte solch ein Ereignis als mögliche Erklärung herangezogen werden. Insgesamt weisen die Reaktionsmuster der Lärche und Buche zwischen den Hangexpositionen oder Höhenstufen keine signifikanten Unterschiede auf. Die breite Spannweite bzw. Variabilität der Reaktionen (Publikation II, Fig. 5) verdeutlicht zudem ein hohes Anpassungspotential dieser Baumarten auf solche Extremereignisse, jedoch wird die Variabilität von Zuwachsreaktionen auf Trockenheit im Kapitel 3.3 detaillierter untersucht.

Im Berchtesgadener Land ist seit 1990 eine **Temperaturerhöhung** von rund 1,4 °C (bezogen auf 1961-1990 in den Monaten Mai-August) zu verzeichnen. Offenbar war diese noch nicht hoch und lange genug, um signifikante Zuwachsänderungen auszulösen (Publikation II, Fig. 6). Wie in Kapitel 3.1 bereits für die Fichte festgestellt wurde, sind auch bei den anderen Baumarten seit 1990 weder deutliche Zuwachseinbrüche in den Tieflagen (eher sogar Steigerungen, v.a. bei Tanne) noch Zuwachsgewinne in den Hochlagen zu verzeichnen. Als Erklärung kann erneut aufgeführt werden, dass sich die untersuchten Standorte nicht an den artspezifischen

Höhenverbreitungsgrenzen befinden, weshalb in den Hochlagen keine Zuwachssteigerung festzustellen ist. Die höchsten hier untersuchten Fichten- und Lärchen-Standorte liegen auf 1670 m ü. NN, wohingegen sich im bayerischen Alpenraum die höchste Verbreitung der Fichte bei 1900 m ü. NN und der Lärche bei 1820 m ü. NN befindet (Ewald 2012). Mit ca. 1300 m ü. NN sind auch die Tannen- und Buchen-Standorte weit von ihrer Höhenverbreitungsgrenze entfernt, die für Tanne im bayerischen Alpenraum bei 1650 m ü. NN und für Buche bei 1500 m ü. NN liegt (Ewald 2012). Allerdings muss hier ergänzt werden, dass ein südexponierter Buchen-Standort auf 1250 m ü. NN bereits signifikante ($p < 0{,}05$) Zuwachsgewinne aufweist.

Mit den hier aufgeführten Ergebnissen konnte ***H2A*** nicht umfassend nachgewiesen werden, da nur die Fichte höhenlagenspezifische Reaktionsmuster (und dies auch nur im Trockenjahr) zeigt, sowie Tanne, Lärche und Buche keinerlei spezifische Reaktionen/Vulnerabilitäten aufweisen. Aufgrund der kaum vorhandenen unterschiedlichen Zuwachsreaktionen zwischen Sonn- und Schatthängen konnte auch ***H2B*** nicht eindeutig verifiziert werden.

Zusammenfassende Fakten *Studie 2*:

- **Im Hitzesommer 2003 zeigt nur die Fichte klare höhenspezifische Zuwachsreaktionen; Buche, Lärche und Tanne weisen in allen Höhenlagen eine hohe Toleranz auf.**
- **Die Temperaturerhöhung seit den 1990er-Jahren wirkte sich bisher nicht negativ auf die Radialzuwächse der Bäume aus, wodurch alle untersuchten Bergwaldbaumarten bislang als robust einzustufen sind.**
- **Generell sind keine signifikanten Effekte der Hangexposition auf die Zuwachsreaktionen festzustellen (abgesehen von Fichten im Sommer 2003 auf ~1200-1300 m ü. NN).**

3.3 Persistenz und Variabilität der Trockenstressreaktionen *(Studie 3)*

Zur Beurteilung der Folgeeffekte von Trockenheit auf die wichtigsten Baumarten des Bergmischwaldes wurden die Toleranzindizes *resistance*, *recovery* und *resilience* für Fichte, Tanne und Buche bestimmt (Lloret et al. 2011). Zur Erweiterung des klimatischen Gradienten wurde der Datensatz mit trockeneren Flachlandstandorten (Zang 2011) ergänzt. Anders als in den vorherigen Studien wurden in *Studie 3* die Trockenstressreaktionen nicht in Relation zur Höhenlage, sondern zu den tatsächlichen klimatischen Rahmenbedingungen des Standorts (DMI-JJA) gesetzt.

Bei der **Trockenstressreaktion** auf die Jahre 1947, 1976 und 2003 ist bei allen Baumarten für die Toleranzindizes *resistance* und *recovery* eine Abhängigkeit zu den jeweiligen klimatischen Bedingungen des Standorts festzustellen (Publikation III, Fig. 2). Demnach ist der Zuwachseinbruch umso höher je warm-trockener die klimatischen Rahmenbedingungen des Standorts sind. Bei Fichte ist der Zusammenhang zwischen Zuwachsreaktion im Trockenjahr (= *resistance*) und DMI-JJA mit 69 % erklärter Varianz ($p < 0{,}001$) am höchsten. Bei Tanne und Buche erklärt der DMI-JJA nur 37 % bzw. 23 % der Varianz ($p < 0{,}001$), da bei diesen Baumarten (v.a. Tanne) zum Teil sogar an warm-trockenen Standorten Zuwachsgewinne auftraten. Insgesamt sind die Zuwachseinbrüche in den Alpen (DMI-JJA > 1,5) bei allen Baumarten (am deutlichsten bei Fichte) wesentlich geringer als in den trockeneren Tieflagen Bayerns. Für *recovery*, welche den Zuwachs in den drei Folgejahren im Vergleich zum Trockenjahr repräsentiert, ist der Zusammenhang zum DMI-JJA umgekehrt. Dies bedeutet, dass sich die Bäume am warm-trockenen Ende des Gradienten, relativ gesehen, nach stärkeren Zuwachseinbrüchen schneller erholen. Nur an wenigen Standorten treten in den Jahren nach dem Trockenereignis noch geringere Zuwächse auf als im Trockenjahr selbst. Dieses Reaktionsmuster ist insbesondere bei Buche am kühl-feuchten Ende des Gradienten festzustellen.

Ein direkter Vergleich der Toleranzindizes der drei Baumarten bestätigt die Ergebnisse aus Kapitel 3.2: Die Fichte zeigt die größten Zuwachseinbußen in Trockenjahren, hingegen weist die Tanne keine bzw. nur am warm-trockenen Ende des Gradienten leichte Einbrüche auf (Publikation III, Fig. 3). Auch bezüglich der *resilience* (Zuwachs der drei Folgejahre in Relation zu den drei Jahren vor dem Ereignis) schneidet die Tanne im Vergleich zu Fichte und Buche am besten ab, wodurch ***H3A*** zumindest zum Teil bestätigt werden konnte. Die Fichte kann wiederholt als sensitivste Baumart gegenüber sommerlicher Trockenheit identifiziert werden. Nichtsdestotrotz liegen die Zuwächse (bei allen Baumarten) nach dem Ereignis maximal 25 % unterhalb des Zuwachses vor dem Trockenjahr (Publikation III, Fig. 2 & 3). Zudem übertrifft die Fichte die Buche am kühl-feuchten Ende des

Gradienten sogar in ihrer Resilienz, wodurch ***H3A*** diesbezüglich nicht vollständig nachgewiesen werden konnte. Zwar hat die Buche im Trockenjahr selbst zumeist geringere Zuwachseinbrüche, doch kann sich die Fichte in kühl-feuchten Standortsbedingungen wieder besser erholen. Eine höhere Regenerationsfähigkeit der Fichte gegenüber der Buche konnte auch Pretzsch et al. (2013) beim Vergleich von Fichten- bzw. Buchenreinbeständen nachweisen. Die pflanzenphysiologischen Strategien, die zu solchen Reaktionsmustern führen können, werden im Kapitel 3.4 detaillierter erörtert. Insgesamt haben Fichte und Buche auf dem Großteil der Standorte in den Jahren nach dem Trockenereignis noch geringere Zuwächse als vor den Trockenjahren. Dies verdeutlicht, dass die Persistenz der Trockenstressreaktion sehr häufig mehr als drei Jahre beträgt. Bei Tanne lässt sich das nur am warm-trockenen Ende des Gradienten, also außerhalb der Nördlichen Kalkalpen, feststellen.

In Kapitel 3.2 wurde bereits die große Streuung der Trockenstressreaktion auf Bestandsebene angedeutet. Der Variationskoeffizient in Trockenjahren unterscheidet sich für alle Toleranzindizes und alle Baumarten signifikant ($p < 0,05$) von der Hintergrund-Variabilität (Publikation III, Fig. 4). Dies bedeutet, dass sich die **Variabilität der Zuwachsreaktionen** innerhalb eines Bestandes durch Trockenheit erhöht. Die größte Steigerung der Variabilität aufgrund von Trockenheit ist bei Buche für alle Toleranzindizes festzustellen. Betrachtet man den Variationskoeffizienten wieder in Abhängigkeit zum DMI-JJA wird deutlich, dass bei Fichte und Tanne ein Zusammenhang zwischen der Variabilität in der Trockenstressreaktion und den klimatischen Rahmenbedingungen des Standorts besteht (Publikation III, Fig. 5). Dabei sind die höchsten Variationen in der Zuwachsreaktion am warm-trockenen, und die geringsten am kühl-feuchten Ende des Gradienten festzustellen, womit ***H3B*** falsifiziert wurde. Damit sind also die Variationen in der Trockenstressreaktion umso höher, je extremer der Trockenstress ist. Denn an den trockenen Standorten sind die Trockenereignisse als wesentlich extremer einzustufen als an kühl-feuchten Standorten (in Hochlagen wirken sich diese positiv aus). Prinzipiell widerspricht dieses Reaktionsmuster der generellen dendroklimatologischen Annahme, dass das gemeinsame Klimasignal in Jahrringen umso höher ist, je höher der klimatische Stress ist (Fritts 1976). Allerdings bezieht sich diese Theorie weniger auf Extremereignisse als vielmehr auf die durchschnittlichen klimatischen Gegebenheiten des Standorts, wie beispielsweise in ariden Regionen, wo ein dauerhaftes Wasserdefizit vorherrscht (vgl. Kapitel 1.2). In *Studie 3* sind auch die trockensten Standorte in Bezug auf die langjährigen Klimabedingungen noch als Optimumstandorte anzusehen. Dessen ungeachtet stellten Metsaranta & Lieffers (2008) eine zunehmende Ungleichheit der Zuwächse innerhalb eines Bestandes während Phasen mit geringen Zuwächsen fest. Dabei wurde die Variabilität insbesondere von einzelnen, schneller wachsenden Individuen ausgelöst (Metsaranta & Lieffers 2008).

Zusammenfassend konnte aufgezeigt werden, dass Trockenjahre die regulären Zuwachsreaktionen, wie sie bei durchschnittlichen Klimabedingungen auftreten, erweitern können und somit zu einem heterogeneren und variableren Reaktionsmuster in Waldbeständen führen können. Demnach könnten spontane Selektions- und Adaptionseffekte im Wege der Naturverjüngung die Anpassung der Wälder an zukünftige Klimabedingungen erhöhen und somit eine zukunftsorientierte Option des Forstmanagements darstellen (Bolte et al. 2009). Um dies abschließend beurteilen zu können, sind jedoch detailliertere Untersuchungen erforderlich.

Zusammenfassende Fakten *Studie 3*:

- **Tanne weist die höchste Trockentoleranz und Resilienz auf; Fichte ist gegenüber Trockenheit am sensitivsten, zeigt aber an kühl-feuchten Standorten eine schnellere Erholung als Buche.**
- **Bei allen Baumarten ist die Persistenz der Zuwachsreduktion nach dem Trockenereignis vergleichsweise gering.**
- **Innerhalb eines Bestandes besteht eine hohe Variabilität in den Trockenstressreaktionen. Bei Fichte und Tanne ist die Variabilität an warm-trockenen Standorten am höchsten.**

3.4 Art- und standortsspezifische physiologische Trockenstressreaktionen *(Studie 4)*

Zum besseren Verständnis der art- und standortsspezifischen physiologischen Prozesse bei Trockenstress wurden neben den Jahrringbreiten die $\delta^{13}C$- und $\delta^{18}O$-Signaturen von Fichte, Lärche und Buche an drei verschiedenen Standorten im Nationalpark Kalkalpen (Österreich) analysiert. Erste Hinweise über die unterschiedlichen physiologischen Strategien der Baumarten geben bereits die

Gesamtzeitreihen bzw. die mittleren Isotopensignaturen (Publikation IV, Fig. 3 & 4, Table 2). Generell sind die Kohlenstoffsignaturen von Laubbäumen im Vergleich zu Koniferen leichter, was auf ein effizienteres Wassertransportsystem der Laubbäume hinweist (Stuiver & Braziunas 1987). Die δ^{13}C-Werte der Buche sind dabei 2-3 ‰ niedriger als die der Fichte (vgl. auch Leavitt 1993, Saurer et al. 1995, 1997, Stuiver & Braziunas 1987) und interessanterweise liegen die Signaturen der Lärche genau dazwischen (Publikation IV, Fig. 4a). Neben den Artunterschieden sind bei den δ^{13}C-Isotopen auch innerhalb einer Art zumeist hochsignifikante ($p < 0{,}001$) Unterschiede zwischen den Standorten festzustellen, die auf die verschiedenen Bodenfeuchtebedingungen zurückzuführen sind (Leavitt 1993, Saurer et al. 1995, 1997). Auf dem trockensten Standort (Südhang) werden bei allen Arten die höchsten Werte erreicht, was darauf hinweist, dass die Bäume auf trockene Bedingungen mit häufiger geschlossenen Stomata reagieren (Saurer et al. 1995). Für die δ^{18}O-Isotope ist nur bei Buche eine deutliche Standortsabhängigkeit zu erkennen (Publikation IV, Fig. 4b). Ursache hierfür ist die Isotopensignatur des Bodenwassers, die mit den Bodentiefen variieren kann, da die oberen Bereiche zumeist evaporativ mit dem schwereren ^{18}O angereichert sind (Roden et al. 2000, Sarris et al. 2013, Treydte et al. 2014). Am tiefgründigen Plateau Standort kann die Buche durch ihr intensives Herzwurzelsystem weniger ^{16}O-abgereichertes Bodenwasser erreichen, wodurch hier die niedrigsten δ^{18}O-Werte auftreten. Für Fichte sind keine deutlichen Standortseffekte zu erkennen. Da die Fichte, im Gegensatz zur Buche, ein Senkerwurzelsystem mit einem hohen Anteil von oberflächennahen Feinwurzeln hat (Köstler et al. 1968), konzentriert sich die Wasseraufnahme, selbst auf gut durchwurzelbaren Standorten, auf die oberen (evaporativ mit ^{18}O angereicherten) Bodenbereiche (Rothe 1997).

Obwohl bei den mittleren Isotopensignaturen zum Teil sehr deutliche Unterschiede auftreten, sind die Jahr-zu-Jahr Variationen der Standorte und Arten sehr ähnlich, was in sehr hohen *inter-chronology correlations* resultiert (Publikation IV, Fig. 5a & 5b). Diese hohe Gleichläufigkeit, auch zwischen den Arten, weist darauf hin, dass die Isotopensignaturen unabhängig vom Standort von einem gemeinsamen Umweltfaktor – dem Klima – beeinflusst werden (Leavitt 1993). Dies lässt sich durch die **Korrelationen mit den Klimaparametern** anschaulich bestätigen (Publikation IV, Fig. 6 & Table S2). Die Zusammenhänge mit den Klimavariablen zeigen eine deutliche Sensitivität beider Isotope auf Trockenheit: Die Korrelationskoeffizienten für Sonnenscheindauer und Temperatur sind positiv, die für den Feuchte-Index, Niederschlag und Wolkenbedeckung negativ. Demnach führen warm-trockene Bedingungen zu geschlossenen Stomata und hohen δ^{13}C-Werten (Eilmann et al. 2010, Lévesque et al. 2013, Saurer et al. 1995), bzw. gesteigerter Transpiration und hohen δ^{18}O-Werten (Barbour et al. 2004, Marshall & Monserud 2006, Yakir & DeNiro 1990). Etwas überraschend sind die fehlenden Standortseffekte, da an trockeneren Standorten, mit geringerer Wasserspeicherkapazität, deutlichere Niederschlagssignale zu erwarten wären (Saurer et al. 1995). Beim Vergleich der in den Isotopen enthalten Klimasignale mit den Jahrringbreiten, wird eine wesentlich höhere Sensitivität der Isotope deutlich (Andreu et al. 2008, Mölder et al. 2011). Für die Jahrringbreite kann anhand der Klima-Zuwachs-Beziehungen nur bei Fichte eine Trockensensitivität abgeleitet werden, wohingegen die Signale bei Lärche und Buche weniger ausgeprägt sind, wie es in Kapitel 3.2 für solche Höhenlagen ebenfalls festgestellt wurde.

Die Sensitivität der Isotopensignatur auf Trockenheit spiegelt sich in der **Trockenjahranalyse** mittels SEA (Publikation IV, Fig. 7) deutlich wider. Insbesondere die δ^{13}C-Isotope zeigen signifikante ($p < 0{,}05$) Abweichungen während der Trockenjahre 1983, 1992, 1994 und 2003, unabhängig von Standort oder Baumart. Demnach bilden Kohlenstoffisotope sommerliche Trockenheit sehr präzise ab (Andreu et al. 2008, Mölder et al. 2011), allerdings scheinen sie keine standörtlichen Unterschiede bezüglich der erhöhten Sensitivität an trockenen Standorten aufzuzeigen (Eilmann et al. 2010, Saurer et al. 1995, Weitner et al. 2007). Bei den δ^{18}O-Isotopen sind ebenfalls höhere Werte festzustellen, jedoch sind diese nicht so konsistent wie bei den Kohlenstoffisotopen (Jansen et al. 2013, Kress et al. 2010). Erstaunlicherweise werden bei Buche und Lärche die höchsten Abweichungen an den feuchteren Standorten (Plateau und Nordhang) erreicht. Dies deutet darauf hin, dass eine höhere Wasserverfügbarkeit das Öffnen der Stomata zulässt, was allerdings Wasserverlust durch Transpiration zur Folge hat. Gleichzeitig hat dies aber den Vorteil, weiter CO_2 aufzunehmen, Photosynthese zu betreiben und Assimilate zu produzieren. Die neu produzierten Assimilate weisen schließlich durch evaporative Anreicherung des ^{18}O höhere δ^{18}O-Werte auf (Gessler et al. 2013, Offermann et al. 2011, Treydte et al. 2014). Damit reflektieren die Assimilate während Trockenjahren weniger die Bodenwasser-Effekte (siehe oben) als vielmehr das Transpirations-Signal. Da die δ^{13}C-Abweichungen in Trockenjahren standortsunabhängig sind, deutet dies darauf hin, dass auf feuchteren Standorten die Diskriminierung gegen das ^{13}C-Isotop aufgrund der erhöhten Photosyntheseraten vermindert ist und somit der eigentliche Effekt einer erhöhten Diskriminierung durch geöffnete Stomata überlagert wird (Farquhar et al. 1982, Leavitt & Long 1989).

Die hier aufgezeigten physiologischen Strategien lassen sich schließlich mit den Radialzuwächsen in Verbindung bringen. Bei Fichte ist der Zusammenhang zwischen ^{13}C-Diskriminierung und Zuwachsraten nicht nur in Trockenjahren sehr direkt (was auch durch negative Korrelation der C-Isotopen- und Ringbreitenchronologien repräsentiert wird, vgl. Publikation IV, Fig. 5c) (Stuiver & Braziunas 1987). Dies verdeutlicht den isohydrischen Charakter der Fichte: Bei Trockenheit werden die Stomata geschlossen, die Photosyntheseaktivität wird damit eingeschränkt und als Folge schmälere Jahrringe gebildet (Publikation IV, Fig. 7). Jedoch beugt dies stressbedingte Schädigung vor, womit sich die Fichte innerhalb von drei Jahren nach dem Ereignis wieder vollständig erholen kann (Matyssek et al. 2013, McDowell et al. 2008, Pretzsch et al. 2013). Im Gegensatz dazu kann die Buche von einer höheren Wasserverfügbarkeit profitieren und auch bei Trockenheit ihre Photosynthese-aktivität aufrechterhalten. Somit wird weiter Holz produziert, wodurch im Trockenjahr selbst keine Zuwachseinbrüche auf den beiden feuchten Standorten auftreten. Jedoch kann diese anisohydrische Strategie der Buche zu hohem Wasserverlust (durch geöffnete Stomata) während der Trockenjahre und folglich zu Xylemembolismus führen (Gessler et al. 2007). Um dies zu kompensieren, müssen die in den Folgejahren gebildeten Assimilate zunächst zur Wiederherstellung des geschädigten Gewebes verwendet werden (Hartmann 2011, Matyssek et al. 2013, Pretzsch et al. 2013). Damit zeigt die Buche erst im Jahr nach dem Ereignis die größten Zuwachsreduktionen und braucht bis zu 4 Jahre, um sich vollständig zu erholen. Es scheint als ob die Lärche wie die Buche einer anisohydrischen Strategie folgt (Anfodillo et al. 1998, Lévesque et al. 2013), da im Trockenjahr keine markanten Zuwachseinbrüche auftreten. Allerdings sind auch in den Folgejahren keine negativen Effekte festzustellen. Insgesamt stimmen die Ergebnisse der SEA für die Standorte im Nationalpark Kalkalpen gut mit den Ergebnissen von *Studie 2* und *Studie 3* überein: Unabhängig vom Standort reagiert die Fichte im Trockenjahr mit markanten Zuwachsrückgängen während die Buche nur am trockensten Standort reagiert; die Fichte übertrifft jedoch die Resilienz der Buche.

Zusammenfassend kann ***H4A*** nicht direkt verifiziert werden, da die Baumarten auf allen Standorten deutliche physiologische Reaktionen zeigen, die jedoch unterschiedlich zu interpretieren sind. Damit erlauben sie allerdings umfassende Einblicke in die verschiedenen Strategien der Baumarten mit Trockenheit umzugehen. Demnach kann ***H4B*** schließlich bestätigt werden und zudem zeigen stabile Isotope die artspezifische physiologische Anpassungsfähigkeit in Bezug zu unterschiedlichen Standortsbedingungen auf.

Zusammenfassende Fakten *Studie 4*:

- **Stabile Isotope bieten umfassende Einblicke in die physiologischen Prozesse bei Trockenstress und zeigen deutliche art- und standort-spezifische Strategien auf.**
- **Buche und Lärche können während Trockenheit tiefere/feuchtere Böden effizienter ausnutzen als Fichte und weisen geringere Zuwachsrückgänge auf. Dies kann bei Buche zu negativen Effekten in den Folgejahren führen, wodurch die Resilienz der Fichte an diesen Standorten höher ist.**

4 SCHLUSSFOLGERUNGEN

Die Bergwaldbaumarten der Nördlichen Kalkalpen sind im Rahmen der bisherigen Klimaänderung als robust einzustufen. Der markante Temperaturanstieg der letzten Jahrzehnte hat sich bislang noch nicht auf die Zuwächse der Bäume ausgewirkt. Im Allgemeinen wird davon ausgegangen, dass höhere Temperaturen eine Verlängerung der Vegetationsperiode bewirken und damit die Zuwächse in den Hochlagen ansteigen (Lindner et al. 2010). Dies konnte im Rahmen dieses Forschungsvorhabens bei keiner Baumart eindeutig nachgewiesen werden. Phänologische Studien aus dem Berchtesgadener Land zeigten bereits, dass Bäume generell weniger sensitiv auf Temperaturerhöhungen reagieren als andere mehrjährige Pflanzen, was zu einer langsameren Reaktion von Bäumen auf den Klimawandel führen könnte (Cornelius et al. 2013). Da auch in tiefmontanen Lagen und auf den als Extremstandorte geltenden südexponierten Hängen in den letzten Dekaden keine Zuwachsreduktionen festzustellen sind, kann von einem gewissen Anpassungspotential der Bergwaldbaumarten hinsichtlich einer langfristigen Temperaturerhöhung ausgegangen werden. Trotz der erhöhten Temperaturen befinden sich alle untersuchten Bergwaldbaumarten im Bereich der Nördlichen Kalkalpen immer noch innerhalb ihrer jeweiligen Klimahülle (Kölling 2007). Die bisherige Temperaturänderung war möglicherweise noch zu gering und zu kurz, um eine signifikante Veränderung des Wuchsverhaltens hervorzurufen.

Dessen ungeachtet werden Extremereignisse wie Trockenjahre vermutlich schwerwiegendere Konsequenzen auf die Vitalität von Bäumen haben als allmähliche Änderungen der klimatischen Durchschnittsbedingungen (Fuhrer et al. 2006). Bei Fichte konnte dies bestätigt werden, da während Trockenjahren in Tieflagen deutliche Zuwachseinbußen von bis zu 40 % auftreten. Mit zunehmender Höhenlage werden die Zuwachsrückgänge geringer und ab 1200-1400 m ü. NN kann die Fichte sogar von warm-trockenen Klimabedingungen profitieren. Obwohl die Fichte unter den untersuchten Baumarten zumeist die größten Zuwachsreduktionen aufgrund sommerlicher Trockenheit zeigt, weist sie auch ein hohes Regenerationspotential sowie eine große Variabilität in der Zuwachsreaktion (insbesondere an sehr trockenen Standorten) auf. Insgesamt ist die Fichte in den Nördlichen Kalkalpen bezüglich ihrer Vitalität noch nicht von den direkten Effekten der Klimaänderung gefährdet. Nichtsdestotrotz können auch die indirekten Folgen des Klimawandels die Stabilität der Fichte beeinflussen, denn nach Trockenereignissen kommt es zumeist zu einem erhöhten Borkenkäferbefall und zudem gilt die Fichte in der Forstpraxis als besonders empfindlich gegenüber Sturmwurf. Ein zentrales Ziel einer zukunftsorientierten Forstwirtschaft ist die Erhöhung der Stabilität von Wäldern im Hinblick auf Trockenheit, Sturm und sekundären Einflussfaktoren (Bolte et al. 2009). Deshalb sollten zur Risikovorsorge in den Bergwäldern der Nördlichen Kalkalpen andere Baumarten wie Tanne, Lärche und Buche gefördert werden. Insbesondere die Tanne zeigt sich im Rahmen dieser Studie als robust gegenüber Trockenheit. Im Bergwald sind nur geringe sowie wenig persistente negative Zuwachsreaktionen festzustellen, zudem weist sie eine hohe Resilienz auf. Durch ihr tiefes Wurzelsystem erreicht die Tanne während Trockenperioden tiefere Bodenwasservorräte (Zang 2011) und ist gegenüber Sturmwurf stabiler. Deshalb sollt die Tanne im Hinblick auf den Klimawandel im Bergwald verstärkt beteiligt werden. Die Lärche wurde wiederholt als empfindlich gegenüber Trockenheit beschrieben (cf. Lévesque et al. 2013, 2014, Schuster & Oberhuber 2013), doch konnte dies für die Nördlichen Kalkalpen nicht bestätigt werden. Auf den untersuchten Standorten reagiert de Lärche kaum auf Trockenjahre und zeigt somit eine hohe Trockentoleranz. Die Sensitivität der Buche ist nicht so eindeutig zu definieren wie bei Fichte, da weniger die Höhenlage oder Hangexposition als vielmehr der Standort bzw. die Tiefgründigkeit des Bodens eine große Rolle bei der Zuwachsreaktion spielt. Die physiologischen Mechanismen sowie das intensive Herzwurzelsystem erlauben bei Trockenheit, tiefere Bodenwasservorräte effizienter auszunutzen, wodurch im Trockenjahr selbst nur geringe Zuwachsrückgänge auftreten. Allerdings können durch diese Strategie die Zuwächse in den Folgejahren reduziert sein, womit die Erholungsphase in den Nördlichen Kalkalpen zum Teil länger andauert als bei der Fichte.

Insgesamt bleibt festzuhalten, dass die Klimaänderung der letzten Dekaden bislang keinen langfristigen negativen Effekt auf die Zuwächse der Bergwaldbaumarten in den Nördlichen Kalkalpen hat. Nichtsdestotrotz wird eine erhöhte Frequenz von extremen Trockenereignissen prognostiziert. Da die Fichte (unterhalb von 1200 m ü. NN) als trockensensitivste Baumart identifiziert wurde und mehr als die Hälfte des Waldflächenanteils in den bayerischen und österreichischen Nördlichen

Kalkalpen ausmacht, sollten zur Steigerung der Stabilität der Bergwälder verstärkt andere heimische Baumarten (insbesondere Tanne) beteiligt werden. Trotz der bisherigen Klimaänderung scheinen Fichte, Tanne, Lärche und Buche in montanen Lagen sowie Fichte und Lärche in subalpinen Lagen geeignet, um die Ökosystem-Funktionen der kalkalpinen Bergwälder zu sichern.

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DANKSAGUNG

Dieses Promotionsvorhaben wäre ohne die vielfältige Unterstützung sehr vieler Personen nicht möglich gewesen.

Ein herzliches Dankeschön gebührt:

Prof. Dr. Axel Göttlein für die Betreuung und Unterstützung sowie wertvolle Ratschläge und gleichzeitigen Freiraum beim Durchführen dieser Arbeit.

Prof. Dr. Andreas Rothe für die Betreuung und umfassende Unterstützung, die Diskussionen sowie sehr viel Vertrauen und Freiheiten, die zum Gelingen dieser Arbeit geführt haben.

Dr. Christoph Dittmar für die Einführung in die Jahrringforschung bzw. Dendroökologie.

Dr. Christian Zang für die Einführung in die „R-Welt".

Dr. Kerstin Treydte für die Einführung in die Isotopenanalysen und deren Durchführung.

Prof. Dr. Jan Esper für sehr viel Geduld und Unterstützung.

PD Dr. Ulf Büntgen für sehr viel Unterstützung und Förderung.

Klaus Limmer und allen Studentischen Hilfskräften für die Hilfe im Bergwald und im Labor.

Meinen „Förster-Kollegen" Toni Brumer, Robert Bauer, Thomas Buchmann, Benjamin Fischer, Josef Gangkofer, Christian Genser, Peter Gruber, Martin Heckner, Harald Meschendörfer, Birgit Reger, Michael Schwemmer, Bernhard Thalhammer und Matthias Wilnhammer für ihre Herzlichkeit, uneingeschränkte Hilfsbereitschaft sowie viele schöne und lustige Momente an der HSWT und im Bergwald.

Meinen „Mainzer Kollegen" für viele Jahrring-Diskussionen und Jenny Lindén for the English-language support.

Meiner Familie Johanna und Elmar Hartl sowie Katharina und Luisa Eder für die jahrelange Unterstützung und ihrer Akzeptanz für die geringe Präsenz.

Meinem Ehemann Daniel Meier für unfassbar viel Geduld, sehr umfassende Unterstützung sowie die stetige Motivation und dafür, dass er immer an mich glaubt! Ihm ist diese Arbeit gewidmet.

APPENDIX

Publikation I

Hartl-Meier C, Zang C, Dittmar C, Esper J, Göttlein A, Rothe A (2014) Vulnerability of Norway spruce to climate change in mountain forests of the European Alps. *Climate Research* 60 (2):119-132, doi: 10.3354/cr01226.

Publikation II

Hartl-Meier C, Dittmar C, Zang C, Rothe A (2014) Mountain forest growth response to climate change in the Northern Limestone Alps. *Trees – Structure and Function* 28 (3): 819-829, doi: 10.1007/s00468-014-0994-1.

Publikation III

Zang C, Hartl-Meier C, Dittmar C, Rothe A, Menzel A (2014) Patterns of drought tolerance in major European temperate forest trees: climatic drivers and levels of variability. *Global Change Biology* 20 (12):3767-3779, doi: 10.1111/gcb.12637.

Publikation IV

Hartl-Meier C, Zang C, Büntgen U, Esper J, Rothe A, Göttlein A, Dirnböck T, Treydte K (*in press*) Uniform climate sensitivity in tree-ring stable isotopes across species and sites in a mid-latitude temperate forest. *Tree Physiology*, doi: 10.1093/treephys/tpu096.

Publikation I

Hartl-Meier C, Zang C, Dittmar C, Esper J, Göttlein A, Rothe A

(2014)

Vulnerability of Norway spruce to climate change in mountain forests of the European Alps

Climate Research 60 (2):119-132

doi: 10.3354/cr01226

CR 60:119-132 (2014) - doi:10.3354/cr01226

Vulnerability of Norway spruce to climate change in mountain forests of the European Alps

Claudia Hartl-Meier[1,2,]*, Christian Zang[3], Christoph Dittmar[4], Jan Esper[1], Axel Göttlein[2], Andreas Rothe[5]

[1]Department of Geography, Johannes Gutenberg University, Johann-Joachim-Becher-Weg 21, 55128 Mainz, Germany
[2]Forest Nutrition and Water Resources, Technische Universität München, Hans-Carl-von-Carlowitz-Platz 2, 85354 Freising, Germany
[3]Ecoclimatology, Technische Universität München, Hans-Carl-von-Carlowitz-Platz 2, 85354 Freising, Germany
[4]Environmental Research and Education (UFB), Am Sandacker 25, 95511 Mistelbach, Germany
[5]Faculty of Forestry, University of Applied Sciences Weihenstephan-Triesdorf, Hans-Carl-von-Carlowitz-Platz 3, 85354 Freising, Germany
*Corresponding author: c.hartl-meier@geo.uni-mainz.de

ABSTRACT: Mountain forests offer a range of socio-economic and ecological services, e.g. providing wood harvest products, serving as hotspots of biodiversity and fulfilling protective functions. In the European Alps, where these environments are dominated by drought-sensitive Norway spruce, it has been questioned whether these services can be secured in the substantially warmer and drier climates predicted for the mid-to-late 21st century. Here, we compile a tree-ring width network of 500 spruce trees from the Northern Limestone Alps to assess growth reactions to drought events and evaluate the long-term impact of the recent temperature shift through analyses along elevational transects. Our dataset covers a larger region in the Northern European Alps extending 250 km from west to east and encompassing an altitudinal range of 1200 m (from 500 to 1700 m a.s.l.). Climate–growth analyses reveal spatially varying drought sensitivities within this spruce network, with elevation (along with associated hydrothermal changes) being the key drivers behind the varying responses. Trees at lower elevations are affected negatively by drought and high temperatures, but at higher altitudes, spruce benefits from warmer climatic conditions. However, despite a sharp temperature increase of ~1°C since the 1990s, we observed neither growth suppression at the lower elevation sites nor growth increase at higher elevation sites. These findings reveal the ability of mountain forests to adapt to an unprecedented temperature shift, suggesting that adaptation to forthcoming climate changes might not require a shift in tree species composition in the Northern Limestone Alps.

KEY WORDS: Drought · Extreme events · Tree-ring width · Dendroecology · Northern European Alps · *Picea abies*

1. INTRODUCTION

Mountain forests cover over 9 million km^2 worldwide and compose 23% of the Earth's forest-covered surface (Price et al. 2011). These ecosystems fulfil a multitude of functions because they provide important goods, such as timber and fuelwood, and cultural services such as tourism (Bugmann et al. 2005, McMorran & Price 2011). In addition, they provide ecological services, e.g. as a major terrestrial carbon pool, diversity hot-spots, and provision of fresh water through their function as a component of the fresh water cycle (Björnsen et al. 2005, Bugmann et al. 2005, Lindner et al. 2010). One of the fundamental ecosystem services is a protective function involving the attenuation of soil erosion and protection from natural hazards (e.g. flooding, debris flow, landslides, rock falls and avalanches) (Schumacher & Bugmann 2006, Lindner et al. 2010). For example, the prime function of 20% of Austrian forests is protection against natural hazards, and in Bavaria (Germany), 63% of the forests are for prevention of soil erosion, and 42% are for protection against avalanches (Duguma & Gratzer 2011).

Mountains are fragile regions, and global change is likely to seriously impact these habitats, including effects on the protective function of mountain forests (Hofer 2005, Lindner et al. 2010). One aspect of global change is the atmospheric nitrogen and sulphur deposition that has been a major factor influencing forest growth over the last decades (Kahle et al. 2008, Elling et al. 2009). However, in recent years, more attention has been focused on the changes in climate. Climate change may exert indirect biotic effects, such as a higher frequency and intensity of insect outbreaks (cf. Esper et al. 2007, Seidl et al. 2008), and abiotic disturbances, such as changes in wind storm frequency and intensity (cf. Lindroth et al. 2009). The direct effects of rising CO_2 concentrations in the atmosphere (Lindner et al. 2010), as well as changes in temperature and precipitation, are likely to have major consequences for mountain forests in the European Alps (Schumacher & Bugmann 2006). In particular, a distinct temperature increase was observed in the Alps (1.2°C in the 20th century), with a pronounced warming in the last 30 yr (Auer et al. 2007), which doubled the global average temperature shift (Lindner et al. 2010). The projected continuing warming, in combination with more frequent and severe drought events, may play an important role in the future development of mountain vegetation (Engler et al. 2011). Anomalous meteorological conditions, such as those during the heat-wave of 2003, may occur more often (Luterbacher et al. 2004, Schär et al. 2004, Rebetez et al. 2006).

Thus, the question of whether mountain forests can adapt to climate change and maintain their protective functions is of pivotal interest. Due to their long lifespans and turnover times, trees and forests are considered to be particularly vulnerable to climate change, and not as readily adaptable as this occurs (Lindner et al. 2010). Water-limited sites with shallow soils on calcareous bedrock are the most sensitive, particularly in the montane elevation belt. Drought stress at such sites is expected to increase, followed by productivity losses and increased susceptibility to disturbances (Seidl et al. 2011). Furthermore, these sites are dominated by Norway spruce *Picea abies* (L.) Karst., a species described as particularly sensitive to summer drought (Oberdorfer 2001, Zang et al. 2011). Norway spruce is the most prominent tree species in the European Alps (Ellenberg 1996), comprising ~60% of the Bavarian mountain forest area (Binder 2007) and ~52% of Austrian protection forest area (Niese 2011). Although it is predominantly indigenous to montane and subalpine forests (Ellenberg 1996, Oberdorfer 2001, Büntgen et al. 2006), spruce has also become the dominant species of the naturally mixed mountain forests in this region through human impact. Its presence there has been supported for centuries because spruce is economically the most important species (Ewald 1997).

Previous studies investigating the growth response of plants to the 2003 heat-wave indicated growth suppressions in montane forests and growth increases in high elevation sites in the Swiss Alps (Jolly et al. 2005). Similar findings were reported from treeline environments in other regions of the European Alps (Rolland et al. 1998, Paulsen et al. 2000) and North America (Salzer et al. 2009). Savva et al. (2006) also concluded that rising temperatures will likely cause increased growth at high elevation Norway spruce sites in the Tatra Mountains but negative effects at lower elevation sites due to increased drought stress. Moreover, studies with different (i.e. dendroclimatological) approaches exist, which use tree growth as a proxy archive for temperature reconstructions (see Frank et al. 2010 for an overview). Trees from high latitudes and altitudes are used because growth in these environments is sensitive to temperature variations (Frank & Esper 2005). Several studies have, however, detailed a disassociation of mid-20th century tree growth and temperature trends, the so-called 'divergence phenomenon', where tree growth does not parallel the warming trend (D'Arrigo et al. 2008, Esper & Frank 2009 for an overview). Although this phenomenon is especially observed in tree line sites at high northern latitudes (Esper et al. 2010 and citations therein), Büntgen et al. (2008) did not identify unusual late 20th century divergence in the European Alps. Therefore, a growth enhancement at high elevation sites throughout the 20th century warming period is expected.

Common to all of the dendroclimatological studies mentioned above is a primary focus on singular events and/or on the tree growth–climate relationship. There is a lack of ecological interpretation in terms of the adaptability of species to future climate conditions.

In this study, we apply a dendroecological approach to a larger tree-ring width (TRW) network that integrates 500 spruce trees. Spruce is the dominant conifer species, and economically the most important tree species in the Northern Limestone Alps. We hypothesize that spruce responds to increasing drought events and rising temperatures with a growth decline at lower elevations and growth increase at higher altitudes. TRWs were measured and subsequently detrended using different techniques to emphasize variance at lower to higher frequencies. The short-term impact of extreme climatic events is analysed with respect to site elevation. General growth–climate relationships are determined, and lower frequency growth trends are compared with temperature trends during recent decades. These assessments of higher and lower frequency covariance are considered for estimating the robustness of Norway spruce, and thus extrapolating the future vigour of the mountain forests in the Northern Limestone Alps.

2. DATA AND METHODS

2.1. Study design

Five hundred Norway spruce trees (2 cores per tree) were sampled at 50 sites (10 trees per site) in the Northern Limestone Alps. The 1000-series TRW network encompasses the Bavarian and Austrian Limestone Alps reaching from 11°01' to 14°28'E and 47°29' to 47°50'N (Fig. 1, Table 1). The study sites are typically comprised of stands on shallow soils with calcareous bedrock, predominantly on southexposed slopes. Samples were taken at different altitudes between ~500 and 1700 m above sea level (a.s.l.), thereby covering a region with a west–east extension of ca. 250 km and an altitudinal gradient of ~1200 m. The dataset was categorized into 4 elevational belts including lower montane (<950 m), montane (950 to 1200 m), altimontane (1200 to 1400 m) and subalpine (>1400 m).

2.2. Climate data

Monthly homogenized temperature and precipitation data representative of each site and elevation belt (see Table 2 for locations and annual means/sums) were obtained from the HISTALP database (Grid mode 2, 5’ × 5’ grid) (Auer et al. 2007, Böhm et al. 2009).

To identify ‘drought events’ in a precipitation-rich region like the Alps (see annual precipitation sums in Table 2), a region-specific humidity index was calculated derived from the mean precipitation and temperature of the vegetation period (May to September):

$$\text{Humidity index} = \frac{\text{Precipitation}}{(\text{Temperature x } 10)} \qquad (1)$$

Humidity index values < 1 represent warm and dry ‘extreme events’, equal to a temperature/precipitation factor of 1:10, similar to the climate diagram scheme by Walter & Lieth (1960−1967) (Fig. 2). Through this, 1947, 1992 and 2003 were identified as the 3 most extreme events in every region and elevation level.

The long-term climatic trends, i.e. mean temperatures and precipitation sums of the vegetation period, are expressed as anomalies with respect to the 1941−1970 mean.

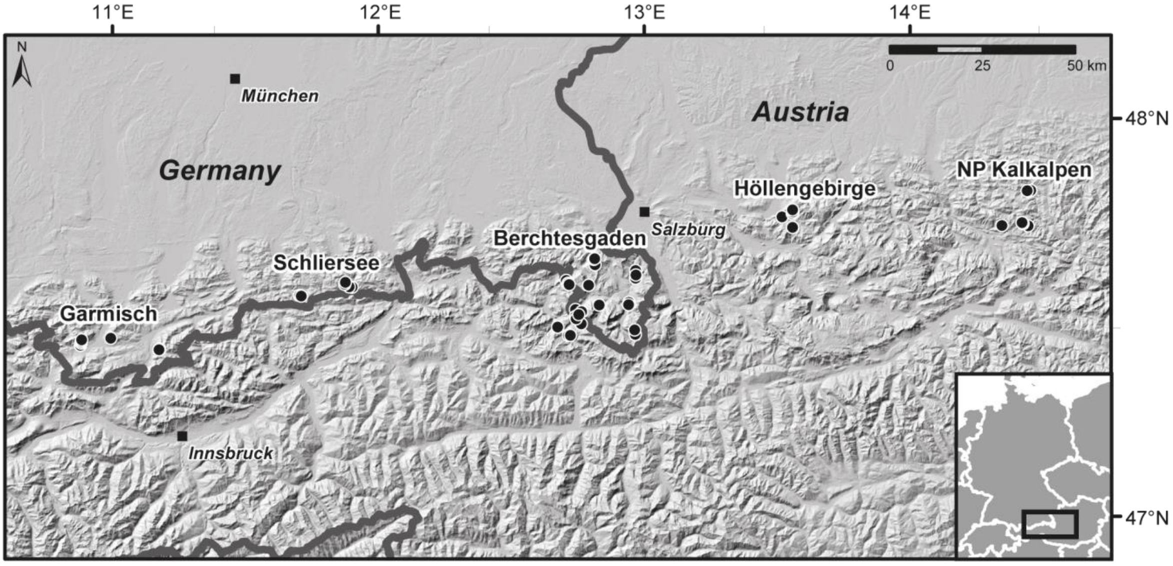

Fig. 1. Location of the 50 spruce sites in the Northern Limestone Alps

2.3. Tree-ring data

TRW was measured with a LINTAB 6 (RINNTECH, Heidelberg) system and TSAP-Win Scientific software (Rinn 2003). The TRW series were cross-dated visually and confirmed statistically using the software COFECHA (Holmes 1983). For further analyses, non-climatic trends related to age and size trends, stand dynamics and internal and external disturbances were removed from the raw ring widths (Fritts 1976). Ring width indices (RWI) were obtained using 3 different detrending techniques: (1) A cubic smoothing spline with a frequency cut-off of 50% at 67 yr (RWI_{67}) to preserve inter-annual and multidecadal scale variability, (2) a stiffer spline with a frequency cut-off of 50% at 300 yr (RWI_{300}) to preserve centennial scale variability (Cook & Peters 1981), and (3) regional curve

Table 1. Characteristics of the 50 spruce sites sorted by elevation within a region and statistics referring to RWI_{67}-chronologies. MSL: mean segment length (yr), AGR: average growth rate (mm), Rbar: inter-series correlation (calculated over 30 yr windows lagged by 15), EPS: expressed population signal (calculated over 30 yr windows lagged by 15), lag-1: first order autocorrelation

No.	Site code	Lat. (N)	Lon. €	Elevation (m a.s.l.)	Period	MSL	AGR	Rbar	EPS	Lag-1
Oberammergau										
1	OGLD	47° 29.1'	11° 01.6'	838	1840-2010	146	1,43	0,22	0,84	0,81
2	OGLC	47° 29.4'	11° 01.7'	1020	1823-2007	165	1,12	0,24	0,85	0,79
3	OGLB	47° 29.7'	11° 01.8'	1220	1807-2010	181	1,11	0,28	0,89	0,83
4	TZSZ	47° 28.6'	11° 18.6'	1240	1954-2010	52	2,68	0,37	0,92	0,7
5	TZSB	47° 28.6'	11° 18.5'	1240	1814-2010	183	0,77	0,31	0,89	0,83
6	OGWB	47° 30.2'	11° 08.1'	1280	1804-2010	173	0,64	0,27	0,88	0,83
7	OGLA	47° 29.9'	11° 01.8'	1400	1797-2010	177	1,11	0,32	0,89	0,82
Schliersee										
8	SSHU	47° 37.8'	12° 00.0'	920	1813-2009	177	0,9	0,34	0,91	0,84
9	SLHB	47° 36.6'	11° 48.7'	1060	1851-2010	147	1,25	0,24	0,84	0,83
10	SLHI	47° 36.5'	11° 49.1'	1050	1835-2010	154	1,34	0,35	0,9	0,81
11	SLLS	47° 36.5'	11° 49.1'	1015	1853-2010	148	1,53	0,42	0,93	0,74
12	SSHO	47° 02.7'	11° 15.6'	1110	1825-2009	177	0,83	0,37	0,92	0,72
13	SSAK	47° 38.2'	11° 58.5'	1270	1932-2009	73	1,76	0,43	0,93	0,82
14	SSMS	47° 38.6'	11° 58.6'	1450	1874-2009	127	1,11	0,38	0,9	0,81
Berchtesgaden										
15	NGML	47° 35.0'	12° 59.7'	680	1901-2008	97	1,92	0,43	0,93	0,75
16	TSSW	47° 35.3'	12° 59.7'	690	1934-2008	62	2,95	0,4	0,92	0,68
17	SAGB	47° 31.9'	12° 44.3'	700	1874-2008	104	1,84	0,25	0,78	0,76
18	BGBS	47° 40.0'	13° 01.3'	760	1857-2008	128	1,36	0,24	0,85	0,81
19	BGOB	47° 38.9'	13° 01.2'	770	1880-2008	115	1,63	0,31	0,89	0,78
20	BGAA	47° 38.7'	12° 46.3'	920	1879-2010	126	1,26	0,45	0,94	0,79
21	NGEW	47° 34.4'	12° 48.2'	960	1870-2008	125	1,64	0,27	0,84	0,8
22	BGOA	47° 39.4'	13° 01.3'	1020	1882-2008	117	1,67	0,33	0,9	0,77
23	BGGP	47° 37.9'	12° 51.1'	1040	1885-2008	111	1,83	0,26	0,84	0,71
24	BGPA	47° 40.9'	12° 52.5'	1040	1926-2010	83	2,34	0,35	0,91	0,7
25	SAMA	47° 30.6'	12° 46.7'	1080	1879-2008	100	1,89	0,34	0,86	0,82
26	NGLS	47° 30.7'	13° 01.0'	1220	1820-2008	171	1,3	0,4	0,93	0,81
27	BGAB	47° 38.2'	12° 46.7'	1220	1761-2010	215	0,96	0,47	0,95	0,88
28	SAMG	47° 30.6'	12° 47.0'	1250	1871-2008	125	1,73	0,37	0,91	0,74
29	NGMW	47° 33.4'	12° 48.2'	1310	1794-2008	191	1,04	0,38	0,92	0,8
30	NGMK	47° 35.0'	12° 53.3'	1330	1849-2008	139	1,7	0,31	0,9	0,76
31	BGPB	47° 41.7'	12° 52.2'	1330	1815-2010	181	1,03	0,37	0,92	0,79
32	BGAC	47° 38.1'	12° 46.9'	1420	1781-2010	193	1,2	0,43	0,93	0,84
33	BGPC	47° 41.8'	12° 52.5'	1520	1830-2010	166	1,19	0,5	0,95	0,84
34	SAKK	47° 32.3'	12° 49.4'	1530	1851-2008	142	1,38	0,41	0,92	0,78
35	NGMA	47° 33.1'	12° 48.3'	1560	1879-2008	100	2,2	0,3	0,84	0,69
36	NGSB	47° 34.1'	12° 49.5'	1600	1684-2008	265	0,87	0,36	0,91	0,79
37	NGHS	47° 33.7'	12° 48.9'	1620	1848-2008	138	1,48	0,42	0,92	0,71
38	NGKS	47° 31.3'	13° 00.9'	1670	1836-2008	159	1,5	0,48	0,94	0,78
Höllengebirge										
39	MWSE	47° 47.5'	13° 33.1'	527	1826-2010	173	0,99	0,37	0,92	0,79
40	MWSD	47° 48.0'	13° 35.3'	791	1771-2010	212	0,88	0,38	0,92	0,79
41	MWSC	47° 48.1'	13° 35.5'	978	1770-2010	218	0,97	0,36	0,91	0,79
42	MWSB	47° 48.5'	13° 35.5'	1209	1782-2010	214	1,1	0,42	0,93	0,83
43	MWSA	47° 48.6'	13° 35.4'	1337	1797-2010	197	0,84	0,41	0,93	0,73
NP Kalkalpen										
44	NKZS	47° 50.3'	14° 26.7'	876	1781-2010	211	1,13	0,48	0,94	0,76
45	NKZP	47° 50.4'	14° 27.1'	894	1917-2010	88	2,03	0,29	0,89	0,68
46	NKZN	47° 50.4'	14° 26.3'	901	1838-2010	116	1,7	0,28	0,86	0,82
47	NKRB	47° 45.4'	14° 20.6'	950	1827-2009	162	1,17	0,37	0,92	0,79
48	NKSK	47° 45.2'	14° 26.3'	1150	1792-2009	188	0,98	0,38	0,92	0,84
49	NKGU	47° 45.6'	14° 25.2'	1350	1868-2009	124	1,53	0,36	0,91	0,87
50	NKGO	47° 45.7'	14° 25.0'	1460	1858-2009	146	1,29	0,43	0,94	0,84

standardization (RCS) to retain potential multi-centennial variance in the resulting chronologies (RWI_{RCS}). RCS was applied on a site-by-site basis and considering the pith offset of each sample (see Esper et al. 2003 for details). The site chronologies were obtained by averaging the detrended single series using a robust mean (Mosteller & Tukey 1977). Chronologies were corrected for lag-1 autocorrelation and truncated at a minimum sample replication of 5 series. Standard parameters, such as the inter-series correlation (Rbar) and expressed population signal (EPS), were calculated for RWI_{67} using 30 yr windows, lagged by 15 yr, over the common 1900−2004 period (shorter period for 6 sites, see Table 1) to estimate the internal coherence of the site chronologies (Table 1) (Wigley et al. 1984). Furthermore, the mean segment length (MSL, i.e. an estimate of mean tree age within 1 chronology), average growth rate and lag-1 autocorrelation (raw ring widths) are presented in Table 1 for the different sites.

Table 2. Annual temperature and precipitation from the gridded HISTALP dataset representative of regions and elevation belts in the study area from 1941 to 1970

Elevation belt	Lat. (N)	Lon. €	Temp. (°C)	Precip. (mm)
Oberammergau				
< 950 m	47° 30.0'	11° 05.0'	7,2	1455
950-1200 m	47° 25.0'	10° 55.0'	5,9	1406
1200-1400 m	47° 30.0'	11° 10.0'	4,1	1468
> 1400 m	47° 30.0'	10° 55.0'	1,7	1452
Schliersee				
< 950 m	47° 45.0'	11° 55.0'	6,5	1494
950-1200 m	47° 45.0'	12° 00.0'	6,6	1425
1200-1400 m	47° 40.0'	12° 00.0'	6,7	1474
> 1400 m	47° 40.0'	11° 55.0'	3,7	1542
Berchtesgaden				
< 950 m	47° 35.0'	13° 00.0'	7,2	1703
950-1200 m	47° 35.0'	12° 50.0'	6,3	1739
1200-1400 m	47° 35.0'	12° 55.0'	6,5	1735
> 1400 m	47° 35.0'	12° 45.0'	5,4	1750
Höllengebirge				
< 950 m	47° 50.0'	13° 35.0'	6,7	1543
950-1200 m	47° 45.0'	13° 45.0'	5	1850
1200-1400 m	47° 40.0'	13° 40.0'	5,4	1759
> 1400 m	47° 40.0'	13° 30.0'	4,2	1672
NP Kalkalpen				
< 950 m	47° 50.0'	14° 30.0'	6,3	1458
950-1200 m	47° 45.0'	14° 35.0'	5,4	1497
1200-1400 m	47° 45.0'	14° 25.0'	4,8	1495
> 1400 m	47° 40.0'	14° 25.0'	4,7	1451

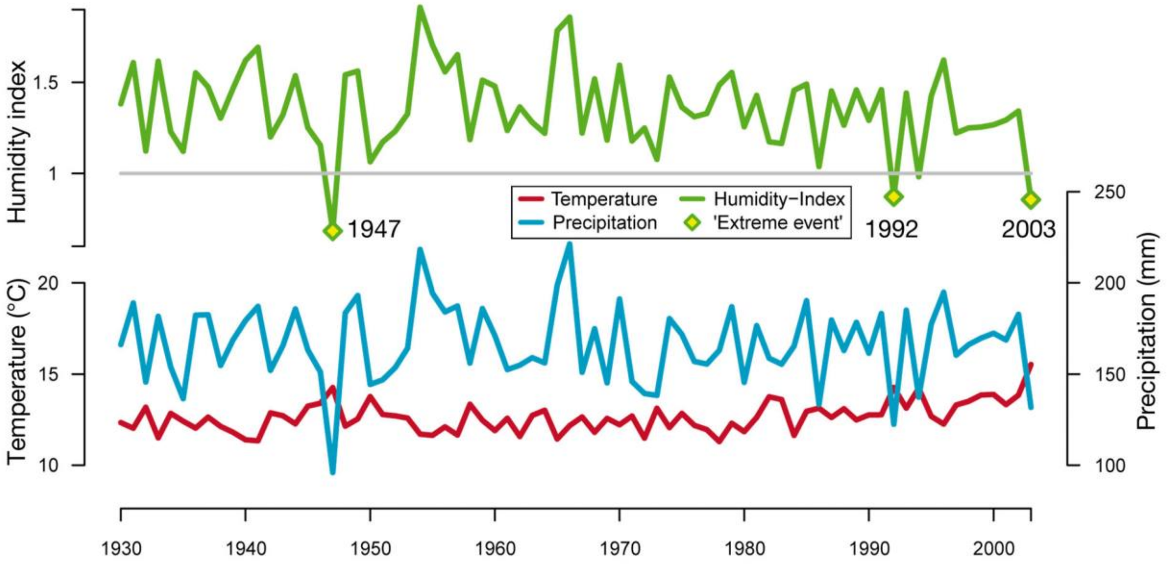

Fig. 2. Vegetation period (May to September) temperature, precipitation and humidity index averaged for the entire study

2.4. Statistical analyses

The short-term impact of relative drought events on the radial growth of Norway spruce was analysed by calculating the percentage growth reaction. Here, the RWI_{67} data were used, because the inter-annual variability was the primary interest when calibrating against the humidity index. The growth in warm and dry years was related to the average growth of the 5 previous years:

$$\text{Growth Reaction } = \left(\frac{1}{3}\sum_k \frac{RWI_{67_k}}{\frac{1}{5}\sum_{j=1}^{5} RWI_{67_{k-j}}} - 1\right) * 100; \quad \text{with } k = 1947, 1992, 2003 \tag{2}$$

The growth reaction was calculated for each individual series and then summarized at the site level.

To investigate the influence of climate elements on tree growth, Pearson's correlation coefficients (r) were computed between the RWI_{67} site chronologies and the mean temperatures and precipitation sums of the vegetation period over the common 1900 −2003 period (shorter for 6 sites, see Table 1). The relationship between elevation and growth/climate response was represented by a generalized additive model (GAM) using a penalized thin plate regression spline as the spline base (Wood 2006). To study the response of Norway spruce to 20th century climate trends, particularly the long-term increase in temperature, we calculated the relative growth change of each individual series to a reference period (1941 to 1970) for every tree-ring in the year *i* and each detrending procedure separately as follows:

$$\text{Growth Change}_i = \left(\frac{RWI_i}{\frac{1}{30}\sum_{j=1}^{30} RWI_{m+j}} - 1\right) * 100; \text{ with } m = 1940 \tag{3}$$

The results of the individual series were combined for each site and elevation belt using a robust mean.

Associations between climate and growth change were assessed using moving 31 yr correlations calculated between the elevational belt growth change curves and temperature, precipitation and humidity index anomalies. All statistical procedures were performed using R 3.0.1 (R Development Core Team 2013) and the packages dplR (Bunn et al. 2012) and mgcv (Wood 2006).

3. RESULTS

3.1. Long-term climatic trends

Vegetation period climate data reveal a long-term temperature increase but no clear change in precipitation compared to the 1941−1970 reference period (see Fig. S1 in the Supplement at www.int-res.com/articles/suppl/c060p119_supp.pdf). The average temperature rise is similar across the study region, i.e. since the 1990s, temperatures are 0.97 to 1.08°C higher than the 1941−1970 reference period. Some precipitation differences were observed between the sub-regions, the western section indicating increased (+13 to 31 mm) and eastern section decreased (−52 mm) vegetation period rainfall since the 1990s.

3.2. Chronology characteristics

The EPS values exceed the widely accepted threshold of 0.85 (Wigley et al. 1984), indicating sufficient internal signal strength in most sites (except for Site 17). EPS reaches 0.84 in Sites 1, 9, 21, 23 and 35 (Table 1). Rbar values range from 0.22 (Site 1) to 0.50 (Site 33), indicating substantially changing internal coherences among the chronologies. Lag-1 autocorrelation fluctuates between 0.68 (Sites 16 and 45) and 0.88 (Site 27), and the average growth rate varies between 0.64 mm (Site 6) and 2.95 mm (Site 16) (Table 1). Ring widths over the common first 60 yr of the tree's lifespan do not significantly decrease with elevation, but growth rates over the entire chronology lengths correlate with the MSL (r^2 = 0.75, $p < 0.001$), indicating that distinct age trends are inherent to the data (see Fig. S2 in the Supplement).

3.3. Short-term impact of drought events

The impact of relative drought events on tree growth resulted in distinct growth reductions at 43 of 50 sites (Fig. 3). The strongest decline was recorded at low-elevation Site 16 in the Berchtesgaden region, with 42.6% less growth compared to the 5 yr preceding the drought event. Nine sites exhibited an increase in growth. The strongest increase of 17.9% was detected at a high elevation Site 33 in the Berchtesgaden region. The subalpine sites at 1400 m and higher predominantly displayed growth releases during warm and dry years. In contrast, all sites below 1300 m a.s.l. showed a growth decline, so that overall a significant association between growth decline and elevation in warm and dry years was observed that can be approximated by a linear regression model explaining 62% ($p < 0.001$) of the variance (Fig. 3).

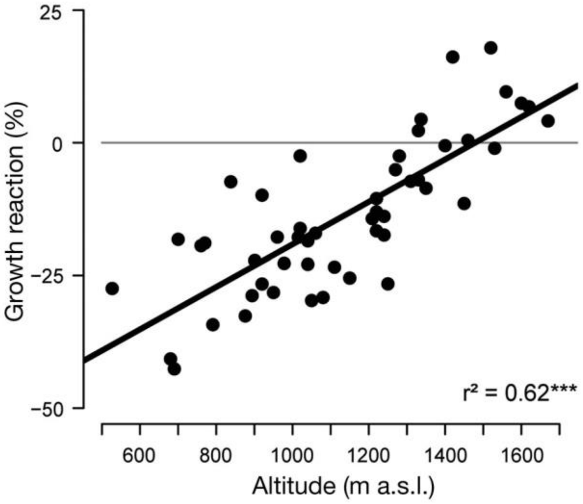

Fig. 3. Relationship between altitude and the percentage growth reaction of spruce to drought events (***$p < 0.001$)

3.4. Growth–climate response

Spruce growth and temperature during the vegetation period are consistently negatively correlated at the lower elevation sites; in contrast, at the high elevation sites, growth is significantly ($p \leq 0.05$) positively correlated with temperature (Fig. 4a). An altitude of ~1200 m a.s.l. seems to be a turning point from predominantly negative to positive growth/temperature correlations. A trend along the altitudinal gradient was observed, where the effects of high temperatures on radial growth gradually changed from negative to positive with increasing elevation. This relationship can be represented by a GAM explaining 76% ($p < 0.001$) of the temperature response variance (Fig. 4a). An inverse pattern was observed for precipitation (Fig. 4b). Whereas positive correlations between tree growth and vegetation period precipitation are predominant at lower altitudes, this association weakens and turns negative toward the higher elevation belts. The turning point for precipitation is less obvious, compared to temperature, but might lie between 1300 and 1500 m a.s.l., where correlations turn negative and reach significance ($p \leq 0.05$). The general association between precipitation signal and elevation is less tight, but the GAM function still explains 59% of the variance ($p < 0.001$; Fig. 4b). The overall highest absolute r values were observed at the higher elevation belts for both temperature and precipitation (Fig. 4).

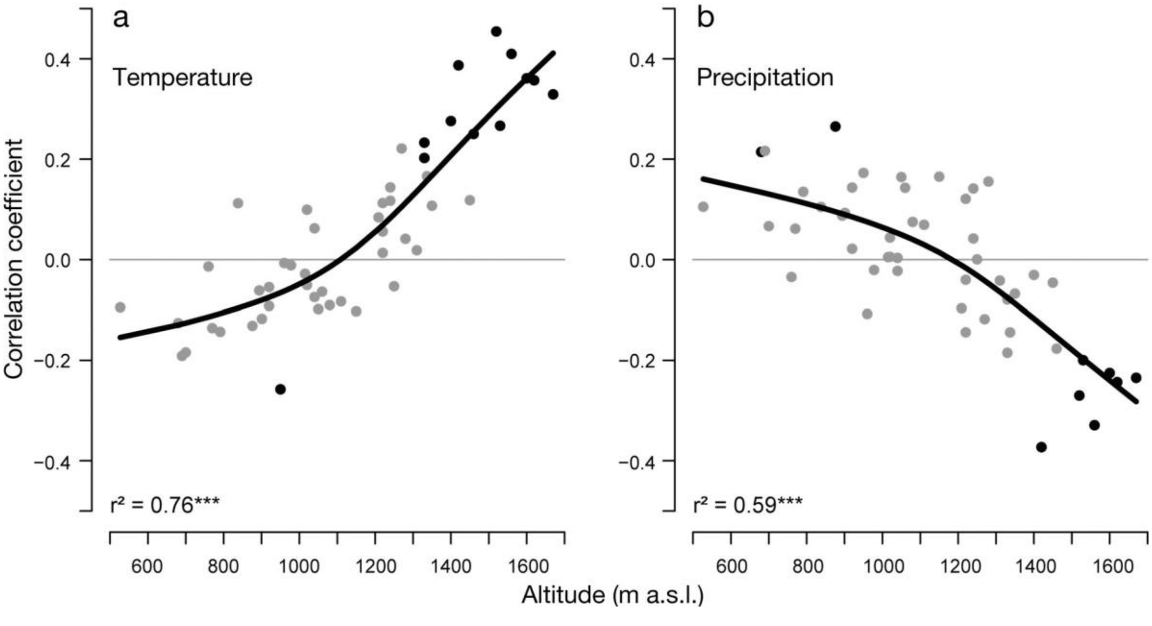

Fig. 4. Comparison of seasonal correlations as a function of elevation for RWI_{67}-chronologies and (a) temperature and (b) precipitation. Black dots indicate significant correlations ($p \leq 0.05$). Non-linear fits and adjusted r^2 (***$p < 0.001$) are based on generalized additive models

3.5. Impact of 20th century climatic trends

To quantify a potential long-term impact of the observed temperature increase on tree growth, the percentage growth change of the RCS detrended data, in which lower frequency variance is preserved (Esper et al. 2003), is considered. Extremely similar growth changes within the different altitudinal belts were observed, especially since 1900 and independent of the location of the site (e.g. west or east, Bavaria or Austria) (see Fig. S3 in the Supplement). Rbar values range from 0.45 in the lower montane and montane belts to 0.46 in the altimontane and 0.48 in the subalpine belts. Overall, no clear pattern of negative or positive growth change trends was observed, either in the lower or in the higher elevational belts (Fig. S3).

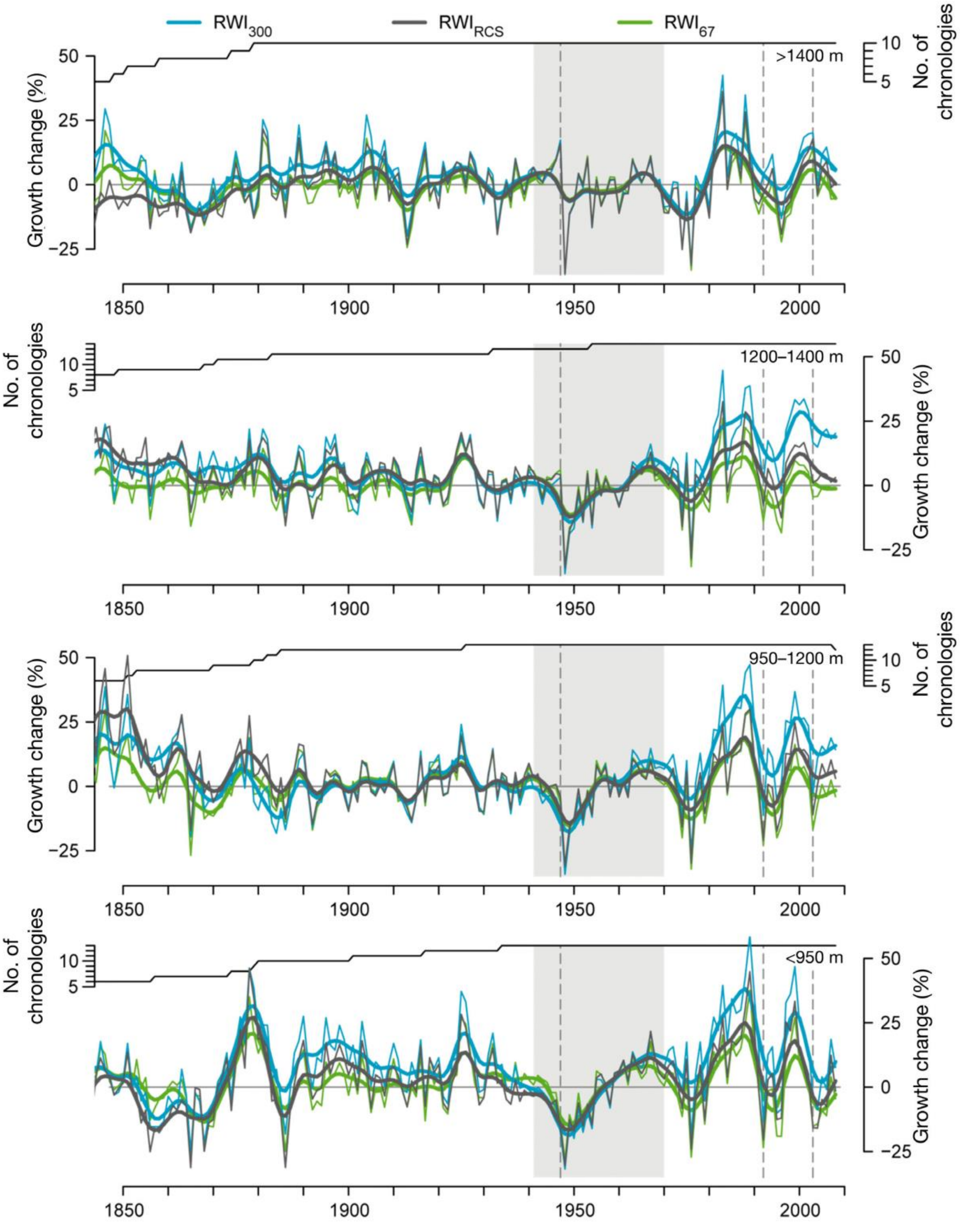

Fig. 5. Comparison of mean percentage growth change curves (with reference to 1941−1970, grey bar) based on different detrending techniques (blue = RWI_{300}, grey = RWI_{RCS}, green = RWI_{67}) for different elevation belts. Smoothed curves are 45 yr lowpass filters. The dashed lines mark relative drought events in 1947, 1992 and 2003

To evaluate potential influences of the detrending technique on the results, the elevational mean growth change curves of the different detrendings are juxtaposed to each other (Fig. 5). The different detrending procedures yielded approximately equivalent trends. Whereas the RWI_{67} chronology indicates smaller values during recent decades, the RWI_{300} chronology indicates increased growth toward the present. The RWI_{RCS} curve lies in most cases between the other detrendings. Distinct growth fluctuations over the entire period were found for all detrendings and elevation belts (Fig. 5). Some periods indicate negative growth patterns, e.g. at the end of the 1940s until the 1950s. In the 1990s and in the mid-2000s, no negative growth pattern was observed except for a downward trend compared to previous years. These periods of growth decline can be compared to the identified drought events in 1947, 1992 and 2003 (grey dashed lines in Fig. 5). The results confirm the findings of the short-term impact assessment: trees at the subalpine elevation belt respond positively in these extreme years, but growth reactions below 1400 m are negative. Furthermore, an after-effect of these events becomes apparent, suggesting that drought influences spruce growth over multiple years.

3.6. Temporal variability of climate signals

To assess the temporal patterns of climate–growth change associations, moving 31 yr correlations were calculated. Consistently positive growth–temperature-change relationships since 1900 were observed at the subalpine elevation belt (Fig. 6a). The growth change correlates clearly with the temperature change, though the growth trend does not entirely track the rising temperatures after 1990. In contrast, the lower montane belt exhibited changing correlation coefficients and no clear relationship with temperature (Fig. 6b). A distinct negative relationship since the 1980s that suggested an increase in a temperature-driven growth reduction could not be confirmed. Spruce growth in the subalpine belt also revealed no clear relationship with precipitation (see Fig. S4a in the Supplement). The coefficients are negative from 1900 to 1960 and fluctuate around zero thereafter. In the lower montane belt, spruce growth correlates positively with precipitation before 1900, but this association weakens thereafter (Fig. S4b). Comparison with the humidity index data indicates that cool and moist conditions negatively affected growth since 1900 in higher altitudes (Fig. S5a). In the lower montane belt, the correlation coefficients did not stabilize and adjust to zero with time (Fig. S5b). This indicates that even in the lower elevation belts, cool and moist (warm and dry) conditions do not exert distinct positive (negative) effects on tree growth.

4. DISCUSSION AND CONCLUSIONS

We compiled a TRW network of 500 Norway spruce trees from the Northern Limestone Alps covering a region extending 250 km from west-to-east and including an altitudinal gradient of ~1200 m. We performed this investigation to assess the impact of climate change on mountain forests and to estimate the performance of these forests and the persistence of their protective function. As ring width has been identified as a key parameter to assess a tree's vitality (Dobbertin 2005), we used this parameter to evaluate the species vulnerability. Because Norway spruce is the dominant species in the Alps (Ellenberg 1996, Oberdorfer 2001, Büntgen et al. 2006) and is among the most drought-sensitive mountain forest species (Kölling 2007), it was chosen in our dendroecological approach.

Our findings suggest that the growth reaction of spruce to drought depends on altitude. An elevation of ~1400 m seems to be the break point between growth decline and increase. Plants at higher elevations benefit from exceptionally warm and dry conditions but suffer at lower elevations. These findings confirm results of a study on the 2003 drought event in the Swiss Alps (Jolly et al. 2005). Comparable dependencies were also reported in other studies on annual extremes from the Swiss and French Alps (e.g. Desplanque et al. 1999, Neuwirth et al. 2004). Although we observed a distinct growth decline at lower elevations (max. ~40%), this is a minor reduction compared to the reaction in lowland spruce sites in southern Germany (up to ~60%; Zang et al. 2011, Zang 2012), indicating that an extended transect would further emphasize the elevational dependence of drought signals in this species.

The seasonal growth–climate response also demonstrated a significant relationship with altitude. In lower montane and montane elevations, tree growth correlated negatively with temperature but positively with precipitation during the vegetation period, indicating these sites may be sensitive to drought. At higher altitudes, the coefficients were inverse; hence, warm and dry conditions have a positive effect on tree growth, while cold and wet conditions have a negative influence. The dependency of the growth–climate relationship on elevation has been demonstrated in other studies of Norway spruce (e.g. Dittmar & Elling 1999, Wilson & Hopf - müller 2001, Mäkinen et al. 2002, Frank & Esper 2005, Savva et al. 2006, Leal et al. 2007). The switch from negative to positive correlation coefficients at ~1200 m a.s.l. as revealed here differs from thresholds reported in previous studies based on fewer spruce sites: ~800 m a.s.l. in Dittmar & Elling (1999), ~900 m a.s.l. in Wilson & Hopfmüller (2001) and ~1500 m a.s.l. in Frank & Esper (2005). However, a direct comparison of critical altitudes for this conversion is difficult due to the varying seasons of the growth–climate relationships as well as the differing regions in the European Alps and Southern Germany considered in these studies.

The growth–climate relationship showed a significant sensitivity of spruce to temperature, particularly at higher altitudes, thus confirming the ‘common knowledge’ of distinct temperature signals at high elevations (and latitudes) (Babst et al. 2013). However, the growth change trends do not follow the temperature increase. To examine this disassociation in more detail, long-term climate data were combined with growth change results. We identified relatively stable (and since ~1900, consistently positive) relationships between the temperature change and growth change at the subalpine elevation belt. Previously, the coefficients were negative, similar to the results of the June growth–temperature relationship demonstrated by Büntgen et al. (2006). Nonetheless, Büntgen et al. (2006) observed a recent decreasing growth–temperature response that we could not confirm in our study. Indeed, no direct tracking of the rising temperatures could be observed in the growth change data; instead spruce growth seemed to remain constant. In contrast to the higher altitudes, the temporal stability of the relationship between the temperature change and growth change at the lower montane belt is much lower, as could be expected for the generally weaker connections between tree growth and climate at this elevation. At the lower montane belt, the precipitation signal appeared more stable. The humidity index represents a fairly good combination of temperature and precipitation conditions and illustrates that a cool and wet climate negatively affects growth at higher sites but has a rather positive effect at lower elevations.

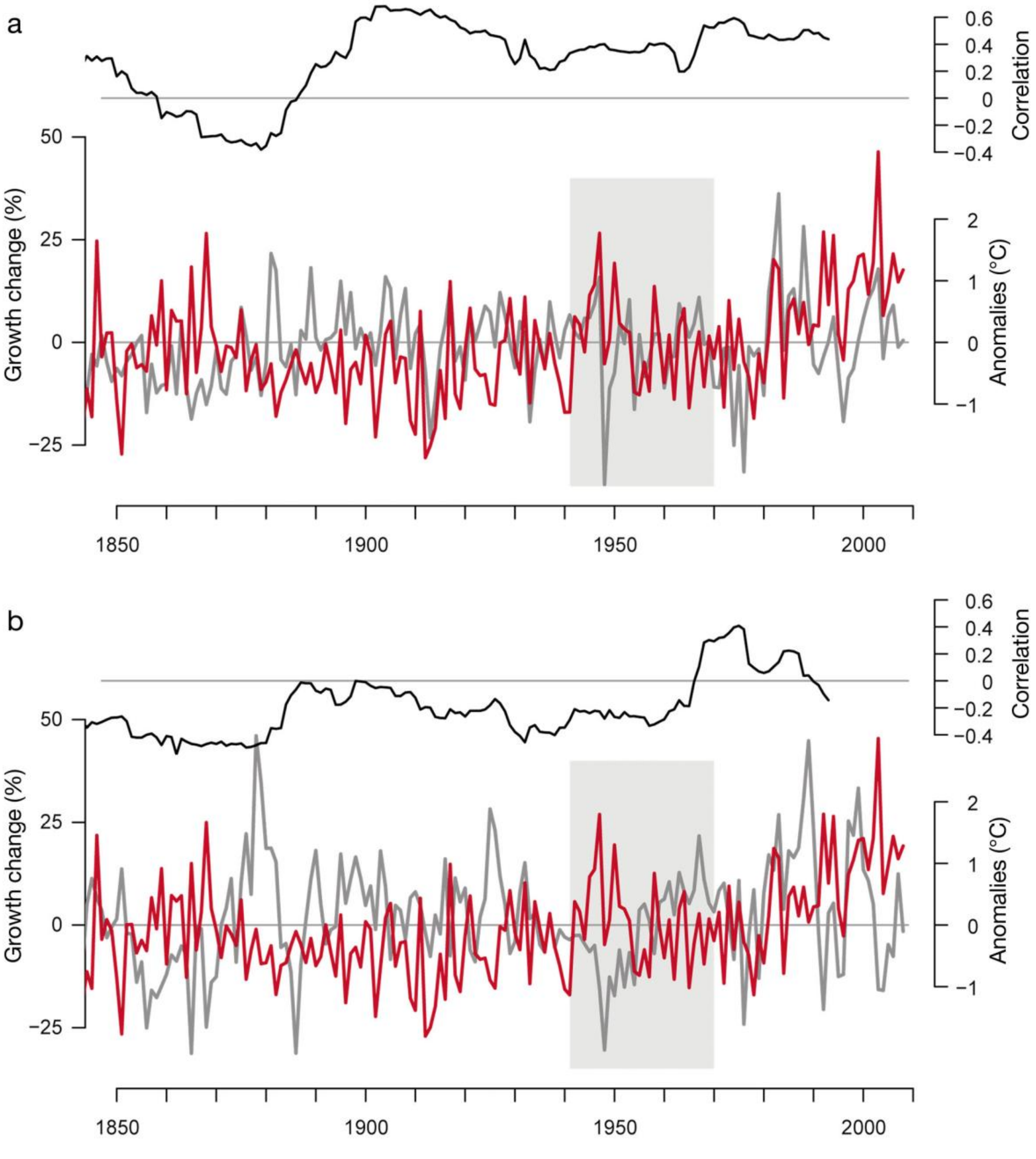

Fig. 6. Comparison of the RCS-detrended percentage growth change (grey curves) and temperature anomalies (red curves), both with reference to 1941–1970 (grey bars), in the (a) subalpine and (b) lower montane belts. Top panels show running 31 yr correlations (black lines) between the tree-ring and instrumental data

Although the growth change pattern does not indicate a positive or negative effect of rising temperatures, the effect of drought events is more apparent. The spruce growth pattern contains fluctuations connected to drought events, at least at the lower elevation sites. After a drought event, we observed downwards growth trends over several years, which, after about 5 to 10 yr, changed toward wider rings again. In southern Germany, prolonged growth suppression after drought events was also reported for spruce by Zang et al. (2011).

However, our results also reflect the ability of Norway spruce to successfully recover from drought, indicating this tree species to be resilient to recent temperature changes.

Since we did not observe a growth increase associated with rising temperatures at subalpine elevations, our results could be interpreted as evidence for the divergence phenomenon. However, Büntgen et al. (2008) did not find an unusual divergence in growth in the European Alps. Because we dedicated special care to the detrending of tree-ring series in the present study, we can exclude a divergence phenomenon detection by mistake. For the northern latitudes, Esper et al. (2010) demonstrated that the preservation of low-frequency variance in tree-ring series can prevent the spurious detection of divergence phenomena. In addition, studies from the European Alps (Rolland et al. 1998, Paulsen et al. 2000) and North America (Salzer et al. 2009) identified positive growth trends at high elevation sites. A possible explanation may be that our study does not comprise trees from tree-line sites (at ~1800 to 1900 m in the Northern Alps; Ellenberg 1996). Even trees from the subalpine sites were growing in closed canopy conditions, and the tree temperature sensitivity studied is generally weaker in these sites. Higher temperatures are also expected to extend the growing season (Lindner et al. 2010), which could potentially lead to increased tree growth at higher elevations. Cornelius et al. (2013) observed, in a phenological study of our investigation area, that trees were less sensitive to temperature changes than herbs; thus, the tree response to climate change should be less pronounced. However, Hasenauer et al. (1999) observed an incremental increase in Norway spruce growth in the 1980s in the Austrian Alps and explained this as being the result of warmer climatic conditions and the associated prolonged vegetation period. We also identified above-average growth in this period, but a growth decline occurred thereafter due to the drought events in 1992 and 2003. At lower elevations, the missing growth suppression might be due to the general climatic conditions of the Northern Limestone Alps, where the precipitation sums are commonly high (between 740 and 980 mm for 1941– 1970 in the vegetation period only), so the temperature trend may actually have a small effect. Furthermore, despite the temperature shift of 1°C, all of the study sites are still in the recognized Norway spruce climate envelope (Kölling 2007).

Spruce is the dominant species of mountain forests (Ellenberg 1996, Oberdorfer 2001, Büntgen et al. 2006), but mountain forests also contain other species, so it is not possible to assess the vulnerability of these forests in their totality from other results. Although spruce is regarded as being sensitive to summer drought (Oberdorfer 2001), it displayed a high potential to successfully recover from a growth decline after drought events; nevertheless, lag effects can occur in the years following an event. Additionally, if drought events appear more often, and with a higher intensity, the lower elevations might be negatively affected in the long term. In addition to this pattern, the effects of climate change are not restricted to temperature and precipitation. A higher frequency and intensity of wind storms (Lindroth et al. 2009) and insect outbreaks (Seidl et al. 2008) can also occur. Norway spruce is again considered the most vulnerable species of the mountain forests to such disturbances, and it would be ecologically valuable to mix other species with deeper roots, especially in the montane elevation belts.

Our results suggest that up to the present climate change has not had an adverse effect on Norway spruce in the European Alps. Norway spruce is still robust in the existing conditions, and can thrive in the mountain forests of the Northern Limestone Alps; however, our hypothesis of increased growth at high elevations and growth suppression in low elevation sites could not be verified. The mountain forests of the Northern Limestone Alps seem to have the capability to respond and adapt to unprecedented temperature shifts.

Acknowledgements. We thank Klaus Limmer and Harald Meschendörfer for field assistance as well as the concerned forest and national park administrations and their foresters for kind support. The present work was supported by the Bavarian State Ministry for Food, Agriculture and Forestry and the EU program INTERREG within the project SICALP (J00183). C.Z. acknowledges funding by the European Research Council under the European Union’s Seventh Framework Programme (FP7/2007-2013)/ERC grant agreement no. (282250).

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Editorial responsibility: Nils Chr. Stenseth,
Oslo, Norway

Submitted: November 29, 2013; Accepted: March 24, 2014
Proofs received from author(s): May 30, 2014

The following supplement accompanies the article

Vulnerability of Norway spruce to climate change in mountain forests of the European Alps

Claudia Hartl-Meier[1,2,*], Christian Zang[3], Christoph Dittmar[4], Jan Esper[1], Axel Göttlein[2], Andreas Rothe[5]

[1]Department of Geography, Johannes Gutenberg University, Johann-Joachim-Becher-Weg 21, 55128 Mainz, Germany
[2]Chair of Forest Nutrition and Water Resources, Technische Universität München, Hans-Carl-von-Carlowitz-Platz 2, 85354 Freising, Germany
[3]Chair of Ecoclimatology, Technische Universität München, Hans-Carl-von-Carlowitz-Platz 2, 85354 Freising, Germany
[4]Environmental Research and Education (UFB), Am Sandacker 25, 95511 Mistelbach, Germany
[5]Faculty of Forestry, University of Applied Sciences Weihenstephan-Triesdorf, Hans-Carl-von-Carlowitz-Platz 3, 85354 Freising, Germany

*Corresponding author: c.hartl-meier@geo.uni-mainz.de

Climate Research: 60: 119–132 (2014)

Supplement. Additional data

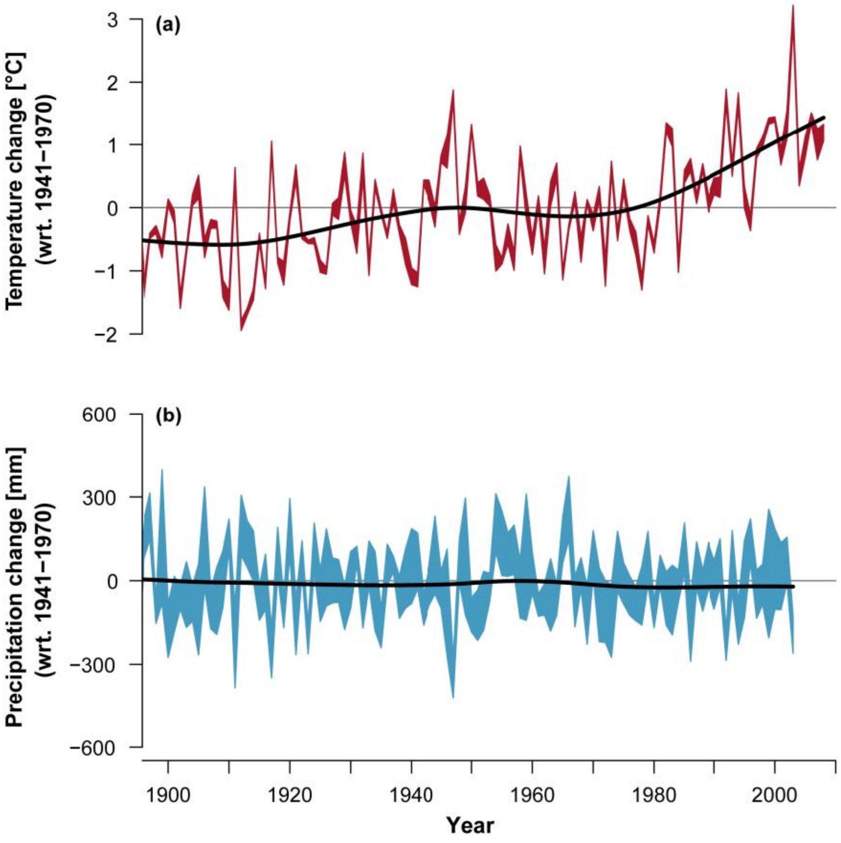

Fig. S1. Range of vegetation period (May to September) temperature (a) and precipitation (b) anomalies (w.r.t. 1941 to 1970) for the entire study region. Smoothed curves are 10 yr low-pass filters

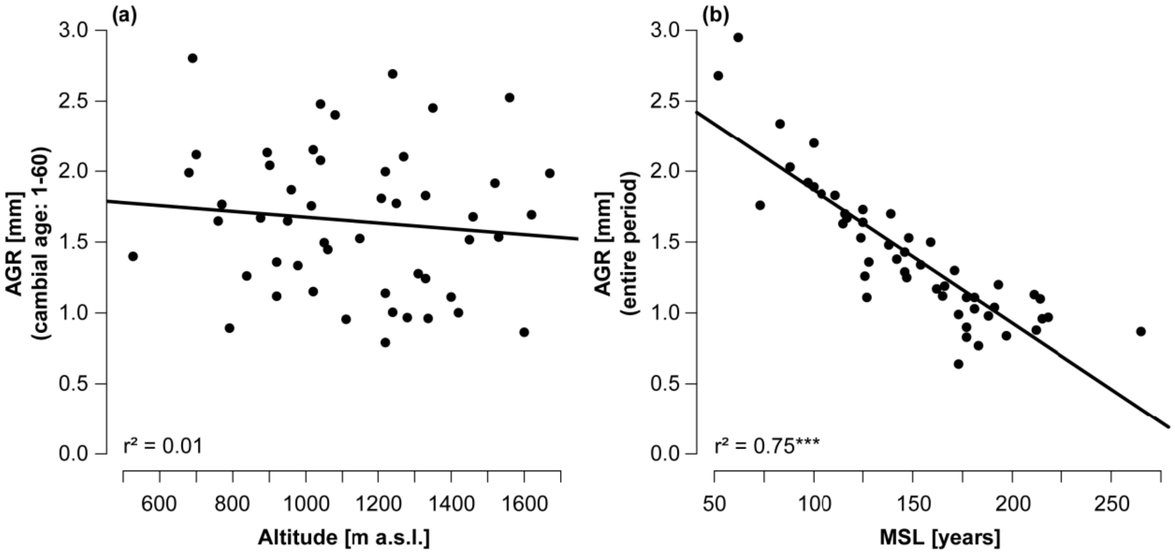

Fig. S2. Relationship (a) between average growth rate (AGR) calculated over the common first 60 yr of the trees' lifespans (cambial age 1 to 60) and site elevation and (b) between AGR calculated over the full individual lifespans and mean segment length (MSL) at each site (***p < 0.001)

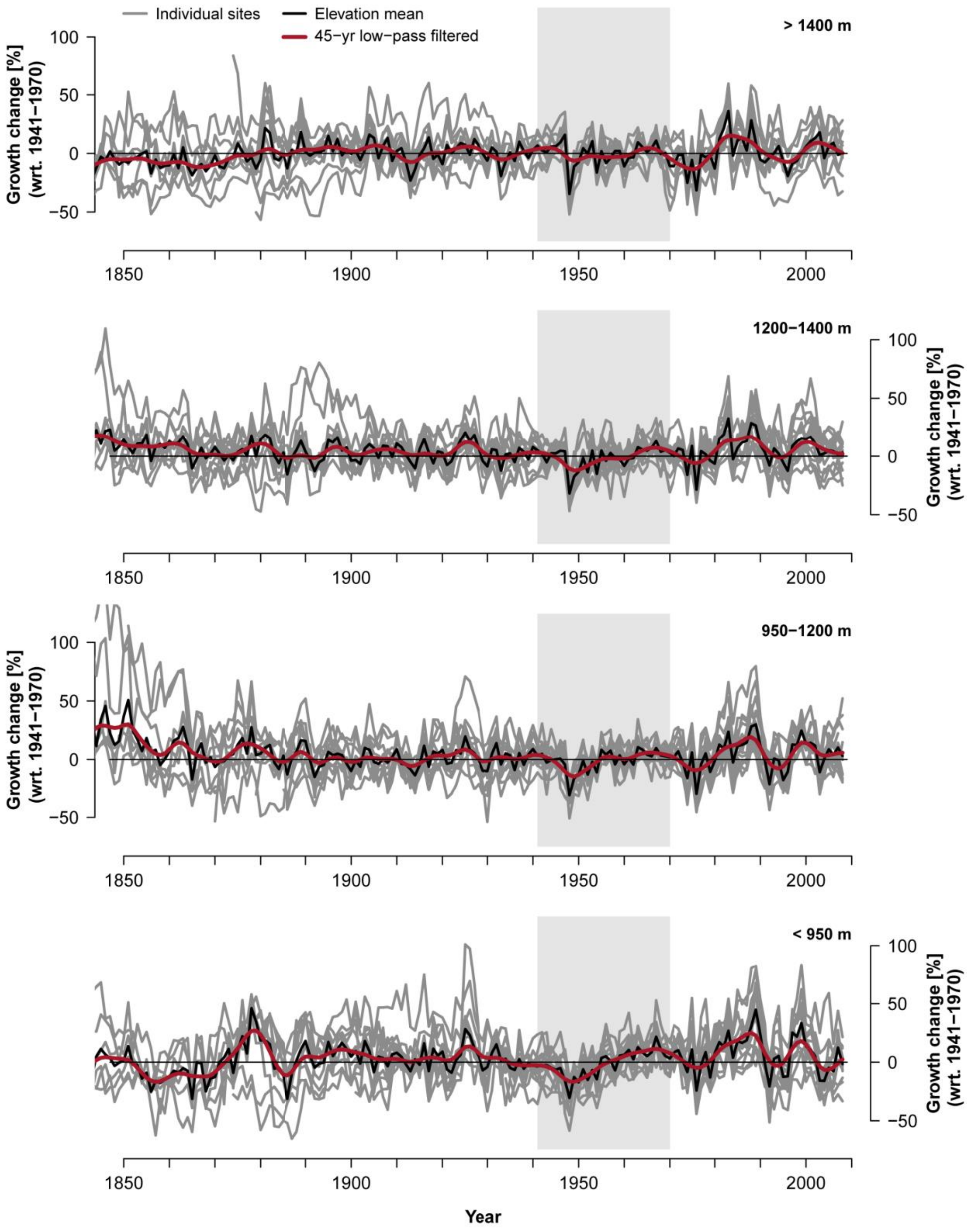

Fig. S3. Percentage growth change (RWI_{RCS} chronologies) of the individual spruce sites (grey) and their elevation means (black). Red curves are 45 yr low-pass filters. Grey bars indicate the 1941–1970 reference period

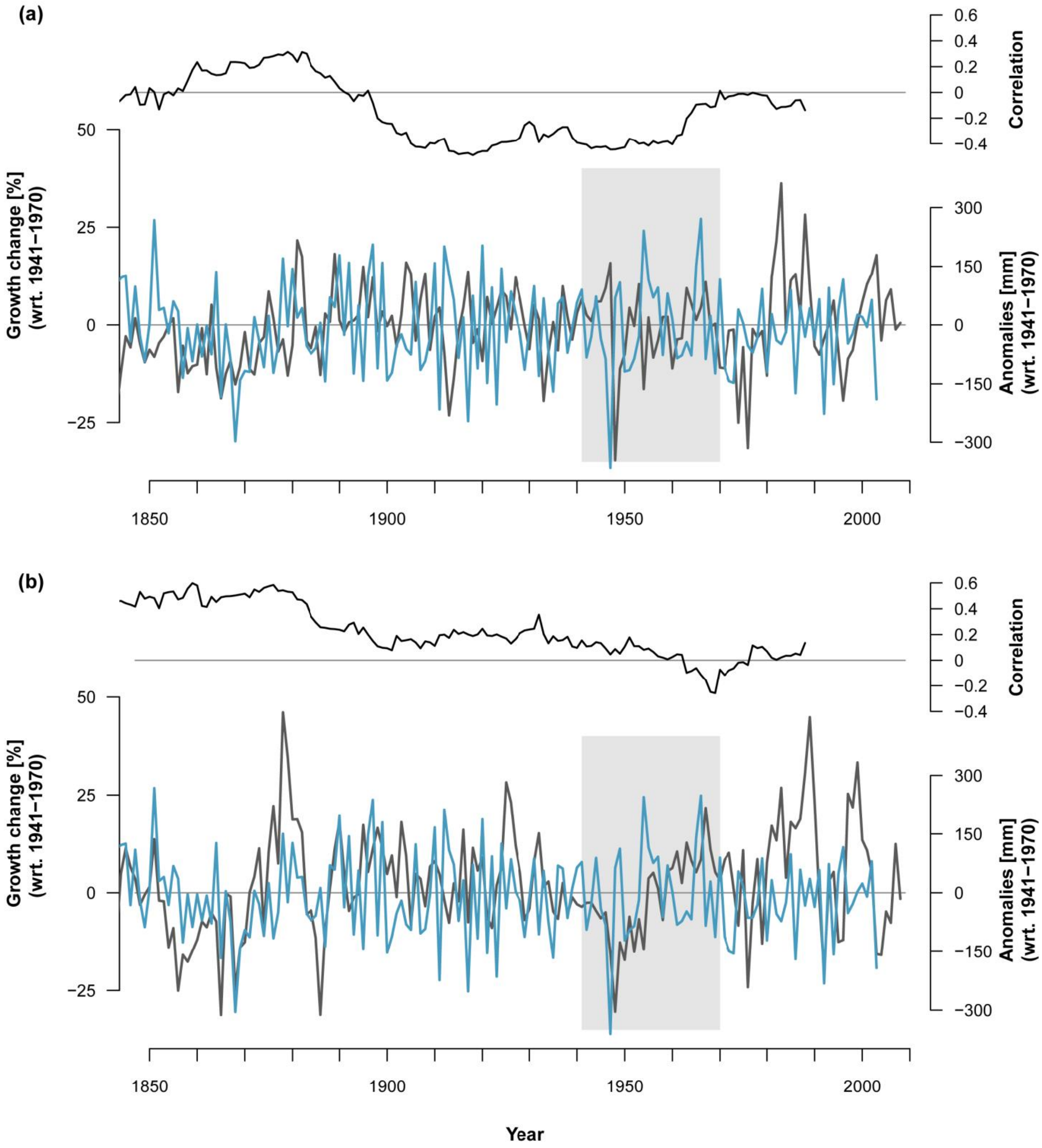

Fig. S4. Comparison of RCS-detrended percentage growth change (grey curves) and precipitation anomalies (blue curves) in the (a) subalpine and (b) lower montane belts. Top panels show running 31 yr correlations (black lines) between the tree-ring and instrumental data. Grey bars indicate the 1941–1970 reference period

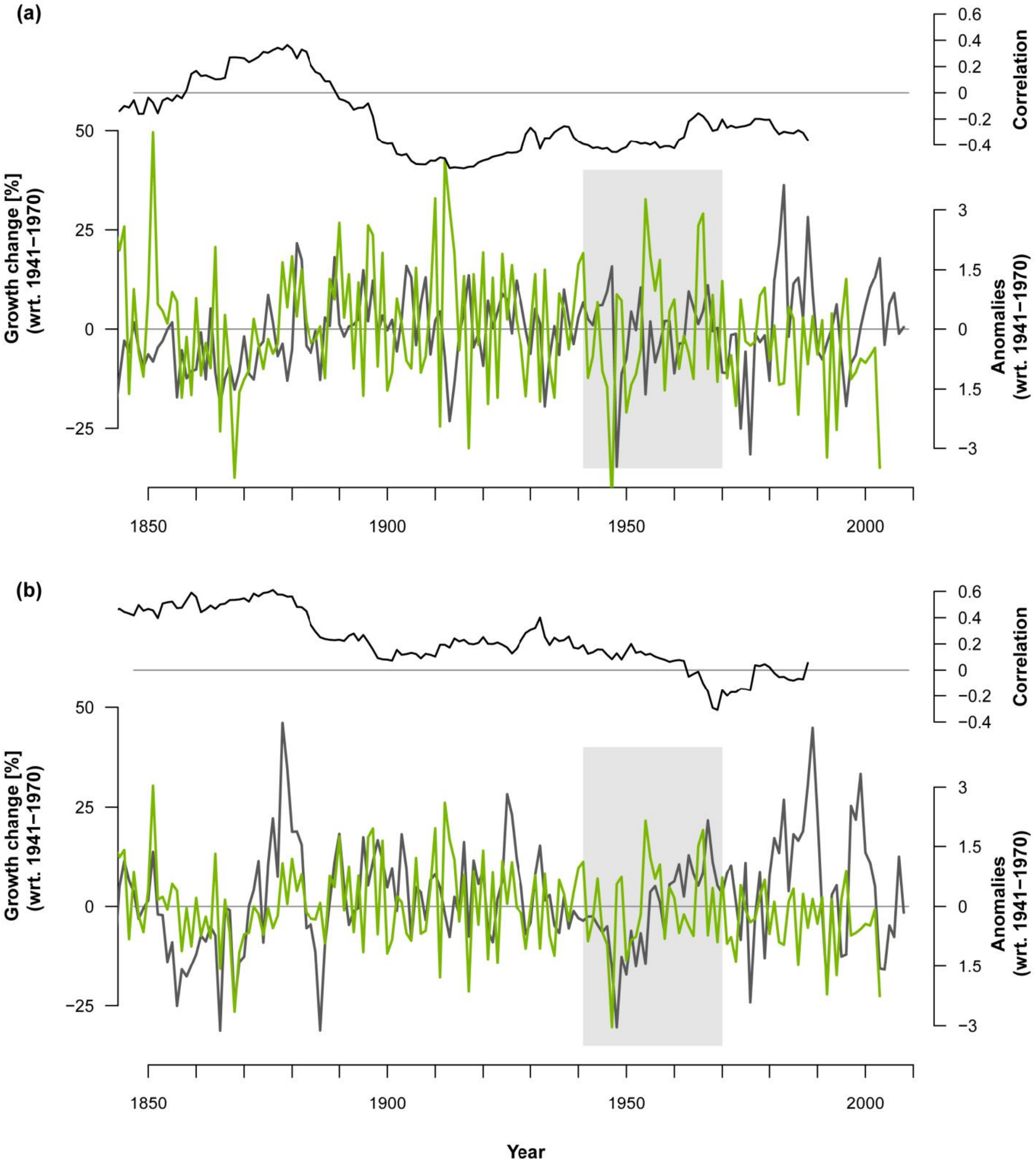

Fig. S5. Comparison of the RCS-detrended percentage growth change (grey curves) and Humidity Index anomalies (green curves) in the (a) subalpine and (b) lower montane belts. Top panels show running 31 yr correlations (black lines) between the tree-ring and instrumental data. Grey bars indicate the 1941–1970 reference period

Publikation II

Hartl-Meier C, Dittmar C, Zang C, Rothe A

(2014)

Mountain forest growth response to climate change in the Northern Limestone Alps

Trees – Structure and Function 28 (3):819-829

doi: 10.1007/s00468-014-0994-1

Trees Structure and Function
© Springer-Verlag Berlin Heidelberg 2014
10.1007/s00468-014-0994-1

Original Paper

Mountain forest growth response to climate change in the Northern Limestone Alps

Claudia Hartl-Meier[1], Christoph Dittmar[2], Christian Zang[3] and Andreas Rothe[4]

(1) Department of Geography, Johannes Gutenberg University, Johann-Joachim-Becher-Weg 21, 55099 Mainz, Germany

(2) Environmental Research and Education (UFB), Am Sandacker 25, 95511 Mistelbach, Germany

(3) Chair of Ecoclimatology, Technische Universität München, Hans-Carl-von-Carlowitz-Platz 2, 85354 Freising, Germany

(4) Faculty of Forestry, University of Applied Sciences Weihenstephan-Triesdorf, Hans-Carl-von-Carlowitz-Platz 3, 85354 Freising, Germany

Claudia Hartl-Meier
Email: c.hartl-meier@geo.uni-mainz.de

Received: 9 November 2013 / **Revised:** 30 January 2014 / **Accepted:** 6 February 2014

Communicated by G. Wieser.

Abstract

Key message **Growth response to climate differs between species and elevation. Fir is the most drought-tolerant species. The mountain forests are robust to the climatic changes until now.**

Abstract Alpine mountain forests provide a wide range of ecological and socio-economic services. Climate change is predicted to challenge these forests, but there are still considerable uncertainties how these ecosystems will be affected. Here, we present a multispecies tree-ring network of 500 trees from the Berchtesgaden Alps (Northern Limestone Alps, Southeast Germany) in order to assess the performance of native mountain forest species under climate change conditions. The dataset comprises 180 spruce, 90 fir, 110 larch and 120 beech trees from different elevations and slope exposures. We analyse the species with respect to: (1) the general growth/climate response; (2) the growth reaction (GR) during the hot summer in 2003 and (3) the growth change (GC) resulting from increasing temperatures since the 1990s. Spruce is identified as the most drought-sensitive species at the lower elevations. Fir shows a high drought tolerance and is well suited with regard to climate change. Larch shows no clear pattern, and beech remains unaffected at lower elevations. The unprecedented temperature increase of the last decades did not induce any distinct GC. The mountain forests of the Berchtesgaden Alps appear to be robust within the climatic changes until now.

Keywords Tree-rings – Climate signal – Radial growth – Elevational belts – Dendroecology – Berchtesgaden Alps

Electronic supplementary material
The online version of this article (doi:10.1007/s00468-014-0994-1) contains supplementary material, which is available to authorized users.

Introduction

Forests cover 1.02 billion Ha of Europe's total land area (FOREST EUROPE UaF 2011) and 41 % of Europe's mountain area (Mc Morran and Price 2011). Mountain forests offer a wide range of socio-economic and ecological services, e.g. by providing timber, serving as a hotspot of biodiversity and fulfilling protective functions (Björnsen et al. 2005; Bugmann et al. 2005; Lindner et al. 2010; Mc Morran and Price 2011; Schumacher and Bugmann 2006). Global change is likely to impact these ecosystems and their functions (Hofer 2005; Lindner et al. 2010). However, there is still a high degree of uncertainty and the effects will depend both on the sensitivity of the ecological and biological system itself and on species-specific tolerances (Elkin et al. 2013).

The IPCC (2013) reports an unequivocal warming of the climate system in the last decades and a further warming is likely. Additionally, likeliness and duration of heat waves have increased in Europe over the last century and are projected to increase even more in the future (EEA 2012). The extraordinary summer in 2003 for example was very likely the hottest summer with respect to the past 500 years (Luterbacher et al. 2004). And the frequency of events such as the heat wave of 2003 has been projected to increase substantially in the near future (Schär et al. 2004).

An unprecedented warming of 1.2 °C was observed in the Alps in the twentieth century (Auer et al. 2007), which even doubles the global temperature shift (Lindner et al. 2010). This temperature rise occurred especially within the past 30 years (Auer et al. 2007), and in general, the late twentieth and early twenty-first century decades were the warmest periods since 1500 or even longer (Luterbacher et al. 2004). A continuing warming in combination with a possible precipitation decrease may play an important role in the future development of mountain vegetation (Engler et al. 2011) and may have substantial impacts on forest ecosystems and the services they provide (Elkin et al. 2013). But the consequences of drought events on tree vitality might be more severe than changes in average conditions (Fuhrer et al. 2006). Due to their long lifespans, trees and forests are considered to possess only limited adaptability and therefore to be particularly vulnerable to climate change (Lindner et al. 2010).

For trees, an elevation-dependent growth response to climate change is expected; e.g. the heat wave in 2003 caused growth suppression in montane forests but growth enhancement at high elevation sites in the Swiss Alps (Jolly et al. 2005). At high altitudes global warming is assumed to increase radial growth (Körner 2012), as observed in the European Alps (Paulsen et al. 2000; Rolland et al. 1998) or in North America (Salzer et al. 2009). A study from the Tatra Mountains reveals a positive growth effect of Norway spruce to increasing temperatures at higher elevations, but a negative influence at lower sites due to drought stress (Savva et al. 2006). At the colline and submontane belt Norway spruce is expected to be more sensitive to climate change than other native tree species (Bolte et al. 2009; Zang et al. 2011; Zang 2012), but current knowledge is insufficient for a clear assessment of the behaviour of different tree species at higher elevations. Dendroecological studies offer a high potential to analyse the possible effects of climate change on trees since the tree-ring width (TRW) is assumed to reflect a tree's vitality (Dobbertin 2005). Several TRW networks in the Greater Alpine Region have been analysed with a dendroclimatological approach aiming at the reconstruction of temperature, precipitation or drought events (e.g. Affolter et al. 2010 and citations herein). However, only few Alpine studies deal with the ecological interpretation of the response to changing climate conditions (e.g. Lévesque et al. 2013; Schuster and Oberhuber 2013; Weber et al. 2007 for inner-Alpine dry valleys), and especially in the Northern Limestone Alps dendroecological information is scarce.

In this study, we compile a multispecies TRW network in the Northern Limestone Alps (Berchtesgaden, Southeast Germany) in order to assess the aptness of native mountain forest species, i.e. Norway spruce [*Picea abies* (L.) Karst.], silver fir (*Abies alba* Mill.), European larch (*Larix decidua* Mill.) and common beech (*Fagus sylvatica* L.) under conditions of climate change. Using a dendroecological approach we analyse the vulnerability of the different species to climate change through: (1) the long-term growth/climate response; (2) the GR to the unprecedented heat wave in 2003 and (3) the potential GC due to the exceptional twentieth century warming. The results contribute to the assessment of tree species suitability in mountain forests under changing climate.

Materials and methods

Study area and sampling design

Five hundred trees (180 Norway spruce, 90 silver fir, 110 European larch, 120 common beech) were sampled at 18 sites in the Berchtesgaden National Park and the surrounding forest districts (Northern Limestone Alps/Southeast Germany) (Fig. 1; Table 1). Sampling was performed in closed, mixed stands (without any visible natural and human disturbances or recent harvesting) resembling the natural forest types as far as possible. The whole investigation area was influenced by humans since the early medieval age due to salt mining, and tree species composition was strongly altered in favour of spruce (current proportion 50 %) and larch (28 %). The originally dominating species beech and fir nowadays cover only 8, 1 % of the area, respectively (Konnert and Siegrist 2000).

Table 1 Site description and chronologies

#	Site code	Lat.	Lon.	m a.s.l.	Slope exposure	Onset of chronologies[a]			
						S	F	L	B
1	NGML	N47°35.0′	E12°59.7′	680	su	1901			1897
2	SAGB	N47°31.9′	E12°44.3′	700	su	1874			1902
3	BGOB	N47°38.9′	E13°01.2′	770	su	1880	1869		
4	TSSW	N47°35.3′	E12°59.7′	690	sh	1934	1869		1915
5	BGBS	N47°40.0′	E13°01.3′	760	sh	1857	1878	1850	1855
6	BGOA	N47°39.4′	E13°01.3′	1,020	su	1882	1868		1848
7	SAMA	N47°30.6′	E12°46.7′	1,080	su	1879	1871	1889	1818
8	NGEW	N47°34.4′	E12°48.2′	960	sh	1870	1860		1864
9	BGGP	N47°37.9′	E12°51.1′	1,040	sh	1885	1830	1838	1811
10	NGLS	N47°30.7′	E13°01.0′	1,220	su	1820			1817
11	SAMG	N47°30.6′	E12°47.0′	1,250	su	1871	1837	1803	1817
12	NGMW	N47°33.4′	E12°48.2′	1,310	sh	1794	1850	1832	1840
13	NGMK	N47°35.0′	E12°53.3′	1,330	sh	1849		1806	1825
14	SAKK	N47°32.3′	E12°49.4′	1,530	su	1851		1782	
15	NGHS	N47°33.7′	E12°48.9′	1,620	su	1848		1747	
16	NGKS	N47°31.3′	E13°00.9′	1,670	su	1836		1781	
17	NGMA	N47°33.1′	E12°48.3′	1,560	sh	1879		1780	
18	NGSB	N47°34.1′	E12°49.5′	1,600	sh	1684		1706	

su sunny, *sh* shady, *S* spruce, *F* fir, *L* larch, *B* beech

[a] End of chronologies = 2008

Sampling sites cover an altitudinal gradient of 680–1,670 m a.s.l. and comprise sunny and shady slopes. The dataset was categorised into four elevational belts: lower montane (<950 m), montane (950–1,200 m), altimontane (1,200–1,400 m) and subalpine (>1,400 m) belt. At each site, ten healthy dominant trees per species (termed collective further on) were sampled by taking two increment cores per tree at breast height parallel to the contour. On the whole a TRW network of 50 collectives and 1,000 individual series was compiled.

Climate data

Monthly climate data (temperature, precipitation) representative for different elevation belts (grid mode 2, 5 in. × 5 in. grid) (Table S1; Fig. 1) and monthly sunshine duration data as deviation of long-term means (CRMS data, Region NE and summits) were obtained from the HISTALP database (Auer et al. 2007). Climatic conditions of the study area are characterised by high precipitation sums, and most of the precipitation falls during summer months (June, July, August) (Table S1; Fig. S1). Average temperatures decrease with altitude and maximum temperatures are reached in July (Table S1; Fig. S1). The yearly temperature amplitude is 18.6 °C in the lower montane and 17.7 °C in the subalpine elevation belt.

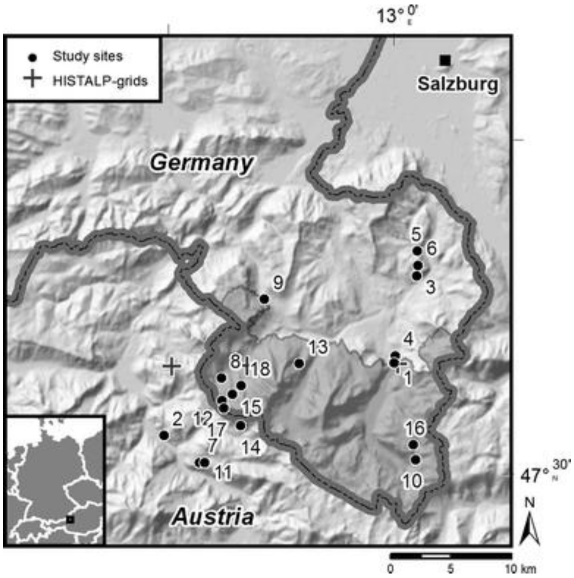

Fig. 1 Study area and sampling sites in Southeast Germany. The National Park Berchtesgaden is *shaded* (base map: SRTM X-band data, DLR/ASI)

Tree-ring data and statistical analyses

TRW was measured to the nearest 0.01 mm with a LINTAB 6 system (RINNTECH, Heidelberg, Germany) and TSAP-Win Scientific software (Rinn 2003). Cross-dating was confirmed both visually and statistically using the program COFECHA (Holmes 1983). Standard parameters such as average growth rate (AGR), mean sensitivity (MS) and first-order autocorrelation (lag-1) were calculated for the 50-year period 1959–2008.

Detrended chronologies were used for long-term growth/climate response. For reducing non-climatic trends related to age and size, or internal and external disturbances from the raw ring widths (Fritts 1976), negative exponential curves were applied to the individual series. The ring width index (RWI)-chronologies were obtained by averaging the detrended single series collective-wise based on a robust mean (Mosteller and Tukey 1977). Chronologies were corrected for lag-1 autocorrelation, i.e. resulting in residual chronologies, and truncated at a minimum sample replication of five series. For signal strength estimation, inter-series correlation (Rbar) and expressed population signal (EPS) were calculated based on the residual chronologies for the 50-year period 1959–2008. To assess the common climatic control along the elevational gradient, bootstrapped correlation coefficients were computed for the individual residual chronologies and the corresponding mean temperatures, precipitation and sunshine duration sums of six different current year seasons (May/June = MJ, June/July = JJ, July/August = JA, May/June/July = MJJ, June/July/August = JJA and May/June/July/August = MJJA) within the common period 1934–2003. The climate response of two previous years' late summer seasons (July/August = pJA and August/September = pAS) is shown in Fig. S3 and Table S2.

For further analyses, TRW series from one tree were averaged and transformed to basal area increment (BAI) according to the formula:

$$\mathrm{BAI}=\pi(R_t^2 - R_{t-1}^2)$$

where R is the radius of the tree inside the bark and t the year of tree-ring formation. The radius of a tree was derived through measured diameter at breast height and bark thickness. Converting TRW to BAI removes age-related trends but maintains other growth trends (Speer 2010). Using this standardisation method preserves low- and mid-frequency growth variance—e.g. caused by climate change what is of special interest here—which might be removed through conservative detrending techniques.

To study the percentage GR of each tree to the heat wave in 2003, BAI of this year was compared to the mean BAI of the five previous years (1998–2002). For assessing the tree response to twentieth century temperature trends, the percentage GC since 1990, compared to the 30-year reference period 1961–1990, was calculated for each tree. A Student's t test was performed for testing the significance of mean growth deviation on collective level for GR and GC. To estimate the differences in GR and GC between elevation belts and/or slope exposures, analyses of variance (ANOVA) followed by a Tukey-HSD *post hoc* test was applied. Elevation and species-specific GC was finally averaged based on a robust mean (Mosteller and Tukey 1977).

All statistical procedures were performed using R 3.0.1 (R Development Core Team 2013) and the packages dplR (Bunn et al. 2012) and bootRes (Zang and Biondi 2013).

Results

Climate change and the extreme event 2003

The study area is characterised by mild temperatures and high precipitation during the growing season (Fig. S1). Since 1990 temperature increased by 1.43 °C and precipitation decreased by 30 mm at all altitudinal belts (Fig. 2). The sunshine duration (data not shown) increased by 37 h in the montane elevations and by 55 h in the high mountains during growing season. In summary, climate change induces warmer and drier growing seasons with increased radiation.

The temperature of the growing season in the exceptional hot summer in 2003 was ~3.8 °C higher compared to the 1961–1990 reference period throughout all the elevations (Fig. S1). Furthermore, a precipitation reduction of 150 mm at the lower montane belt (montane/altimontane 120 mm, subalpine 165 mm), equal to a reduction of ~20 % (montane/altimontane 16 %, subalpine 21 %) was observed (Fig. S1).

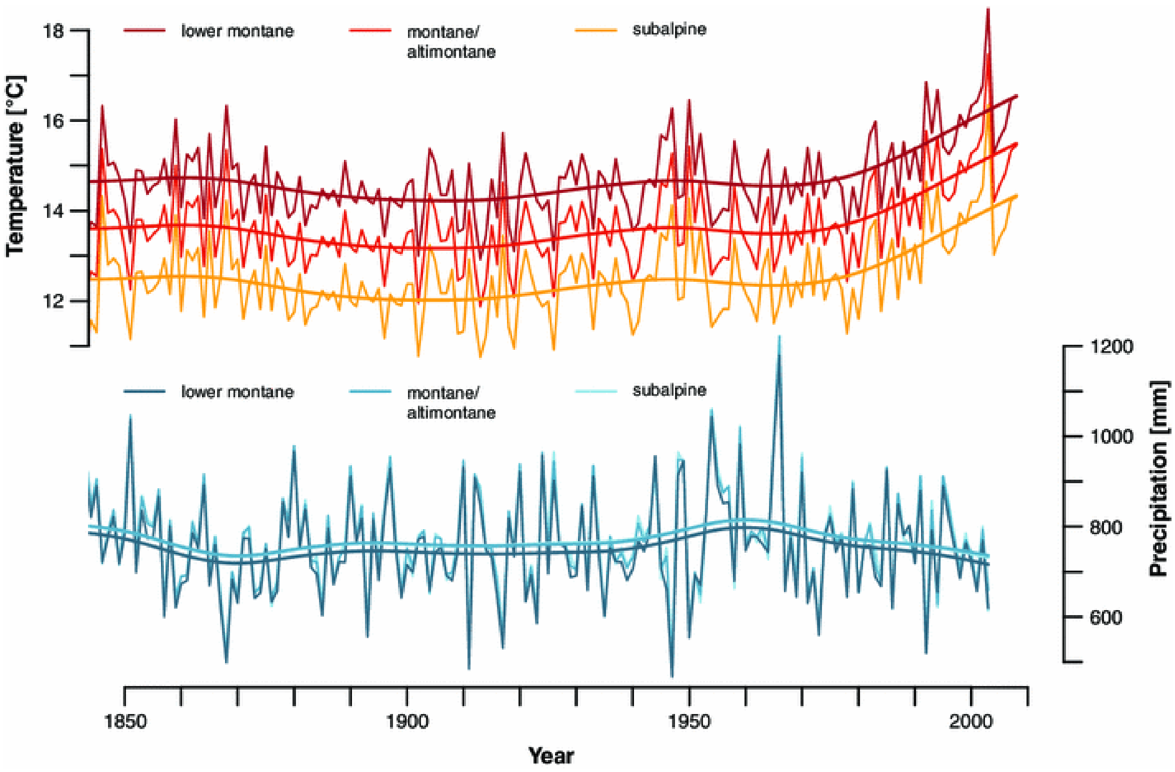

Fig. 2 Long-term temperature (mean) and precipitation (sum) records of the growing season (May–August) in different elevational belts. The *smooth curves* are 10-year low-pass filters (data basis HISTALP)

Chronology characteristics

AGR decreases with elevation for all species. The maximum ring width (3.1 mm) was found for spruce at the lower montane belt (site 4) (Fig. 3). The minimum radial growth rates (0.4 mm) were observed for larch at the subalpine belt (site 15 and 18). MS is low for spruce and fir (0.15–0.24) and decreases with elevation. In contrast, MS for larch and beech is higher (0.19–0.38) and increases with altitude (Fig. S2a). Lag-1 is generally high and fluctuates between 0.34 and 0.78 (Fig. S2b). Rbar values range from 0.16 to 0.69 and the EPS statistics indicate sufficient internal signal strength for nearly all sites, since EPS is above the widely accepted quality threshold of 0.85 (Wigley et al. 1984) (Fig. S2c).

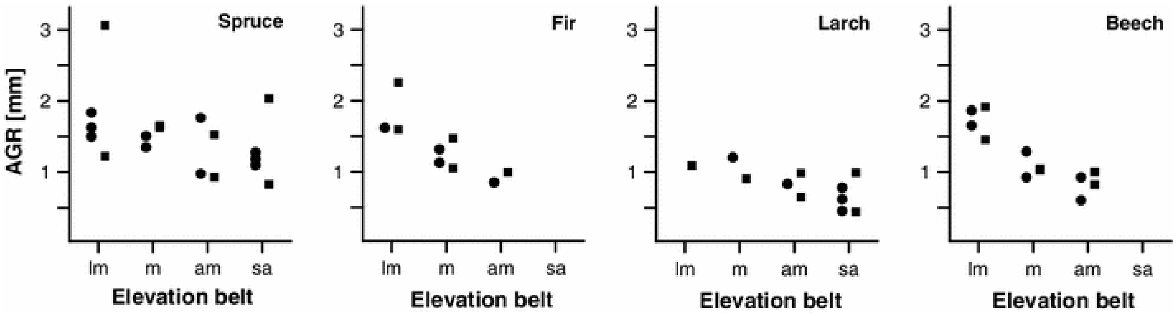

Fig. 3 Average growth rate (AGR) of spruce, fir, larch and beech at different elevation belts in the 1959–2008 period. *Circles* denote sunny and *squares* shady slopes (*lm* lower montane, *m* montane, *am* altimontane, *sa* subalpine belt)

Long-term growth/climate response

Distinct differences were observed in the long-term growth/climate response between tree species and elevation belt (Fig. 4, Fig. S4). The assessment of shorter (and variable) seasons generally does not change the response pattern along the elevational gradient (Fig. S4; Table S3). The growth/climate response for the whole growing season (MJJA) results in most frequent significant relationships (Table S3).

Spruce growth at the lower montane and montane belt is rather negatively correlated with temperature during the growing season. At the altimontane belt a switch to positive correlation coefficients occurs and at the subalpine belt spruce growth is significantly positively correlated with temperature (Fig. 4a; Fig. S4a; Table S3). Fir growth correlates positively with temperature, especially from June to August (Table S3). For larch, the response is positive at almost all belts and seasons. The coefficients increase with altitude and become significant at the subalpine belt. Only at one site beech growth is negatively correlated with temperature during the growing season. Even at the montane belt significant positive correlations were observed (Fig. 4a; Table S3).

The precipitation/growth response is inverted compared to the temperature/growth response (Fig. 4b; Fig. S4b). High amounts of precipitation during the growing season affect spruce growth (significant) positively at the lower altitudes but (significant) negatively at the subalpine belt. Fir does not show a clear dependence on precipitation at any elevation belt. The negative effect of high precipitation on larch growth increases with altitude. Beech growth at shady slopes at the montane belt is (significantly) negatively affected by high precipitation, but beech trees at sunny slopes do not show clear correlations with precipitation (Fig. 4b).

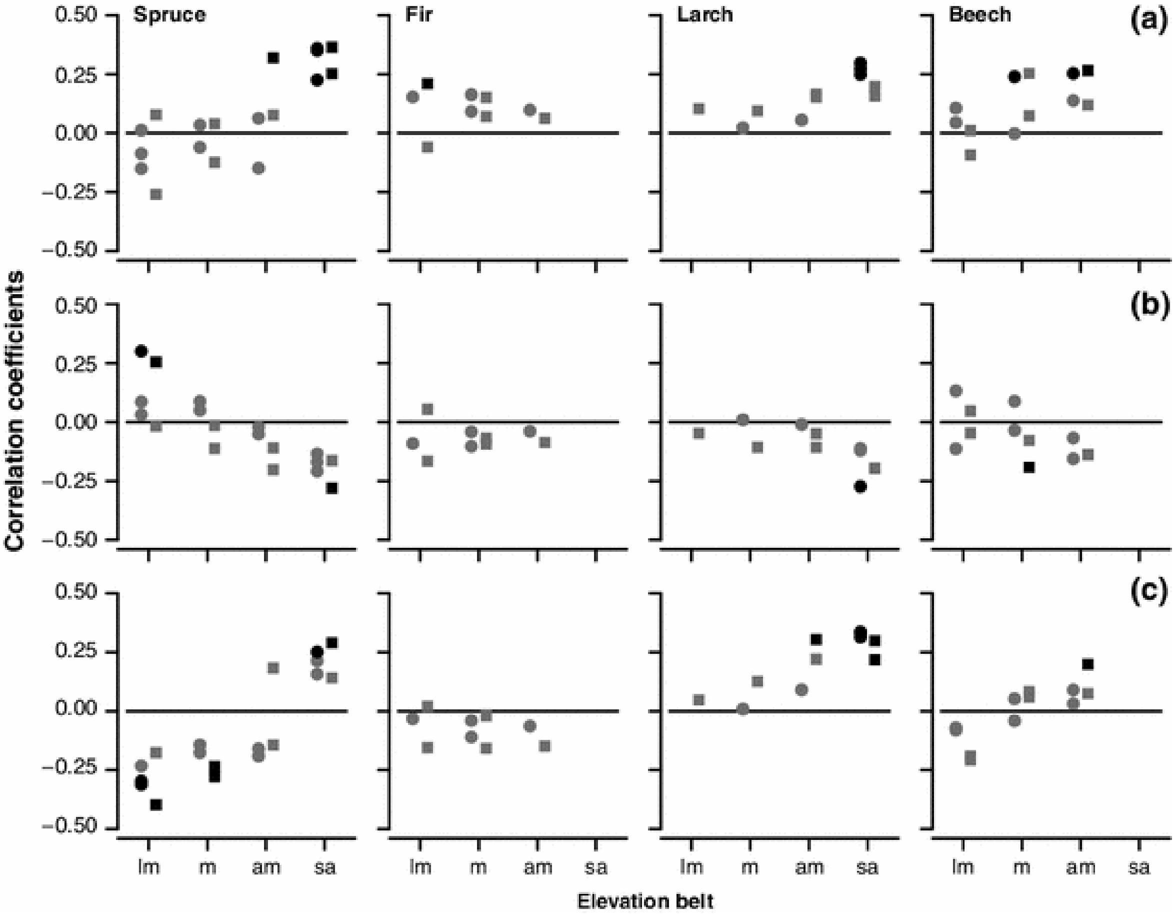

Fig. 4 Correlations between spruce, fir, larch and beech growth (residual chronologies) and seasonal (May–August) **a** temperature, **b** precipitation and **c** sunshine duration. *Circles* denote sunny and *squares* shady aspects. *Black symbols* indicate $p \leq 0.05$ significant correlations (*lm* lower montane, *m* montane, *am* altimontane, *sa* subalpine belt)

Growth response to sunshine duration compares to the temperature response (Fig. 4c; Fig S4c). For spruce, the correlation is significantly negative at the lower elevations but significantly positive at the subalpine belt. Fir does not show any significant relationships. High sunshine duration has significantly positive effects on larch tree growth at the altimontane and subalpine belt and there is a clear effect of slope exposure at the montane belt. At the lower montane belt beech responds negatively to high sunshine duration, but the correlation coefficients get positive with increasing elevation (Fig. 4c; Fig. S4c).

Growth reaction to the 2003-heat wave

For spruce a negative GR was observed in the lower montane and montane elevations independent of the slope exposure (Fig. 5). Four sites (one even at the altimontane belt) showed significant ($p < 0.05$) growth reductions in 2003 (Fig. 5). At the altimontane belt trees at sunny slopes still show growth decline while growth increased at the subalpine belt (Fig. 5). The shady slopes at the altimontane belt and the subalpine sites differ significantly from the other sites (Table S4). Fir, larch and beech do not show a clear GR to this drought event, but a high tree-to-tree variability within one site. There are no clear effects in relation to altitude or slope exposure (Fig. 5; Table S4). For beech, there is a tendency towards a growth reduction at the altimontane elevation belt (Fig. 5).

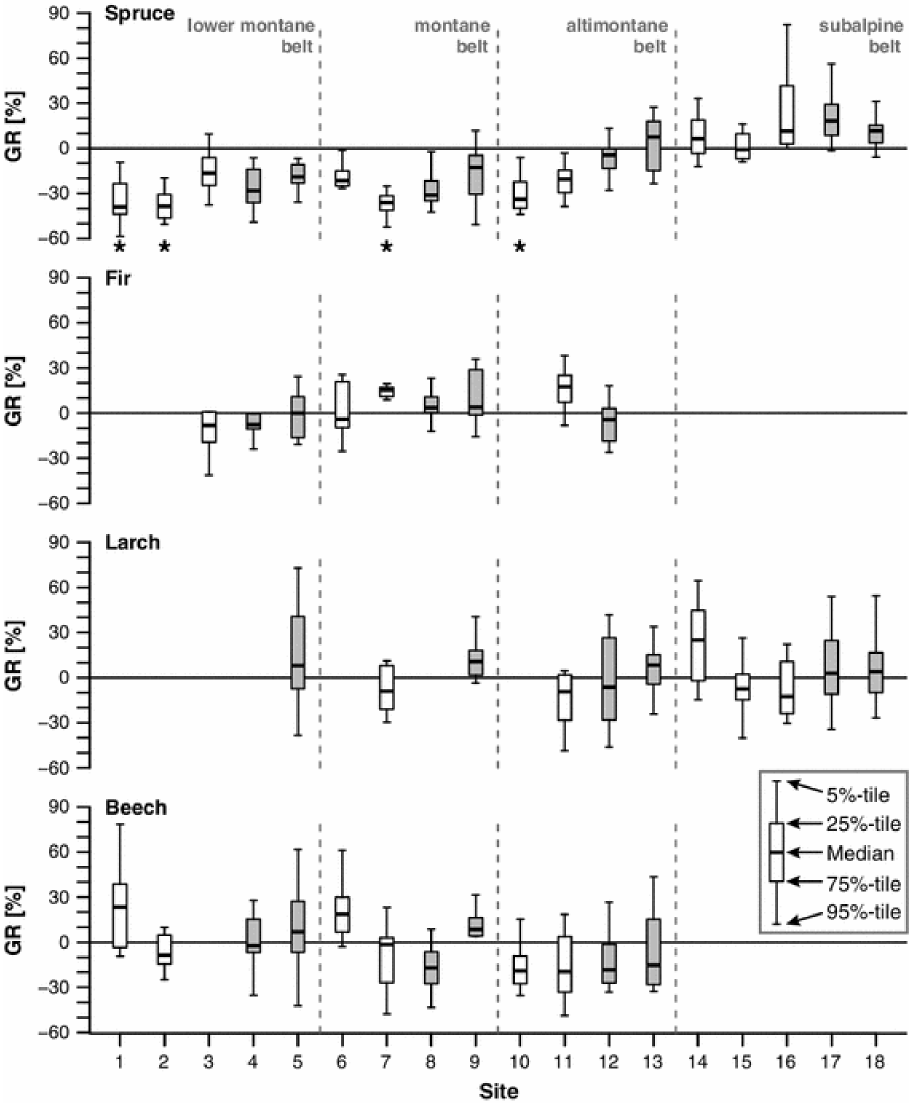

Fig. 5 Percentage growth reaction (GR) to the extreme event in 2003 for spruce, fir, larch and beech at the different sites. *White boxes* denote sunny, *grey boxes* shady slopes (*significant difference at $p < 0.05$)

Growth change due to twentieth century warming

There was no clear growth trend induced by the temperature increase since 1990, except for one beech collective which showed significant growth increase (Fig. 6), and for neither species significant differences ($p < 0.01$) within the elevation belts were detected (Table S5). Tree-to-tree variability within one site is high for all species (Fig. 6). On average, among all sites there is a tendency towards increased growth rates for spruce, beech and fir (Table S6). For spruce, radial growth increased by ~10 % compared to the reference period. This GC is highest in the lower montane belt (15 %), about 10 % in the altimontane and subalpine belt and lowest with about 7 % in the montane belt (Table S6). Average growth increase was 22 % for fir with the strongest effects at higher altitudes (Table S6). For beech, the positive growth effect at the different elevations ranged from 3 to 14 %, with an average of 8 % (Table S6). For larch, a slight growth decline in the lower montane and montane belt was balanced by a slight positive GC in the altimontane and subalpine belt (Table S6).

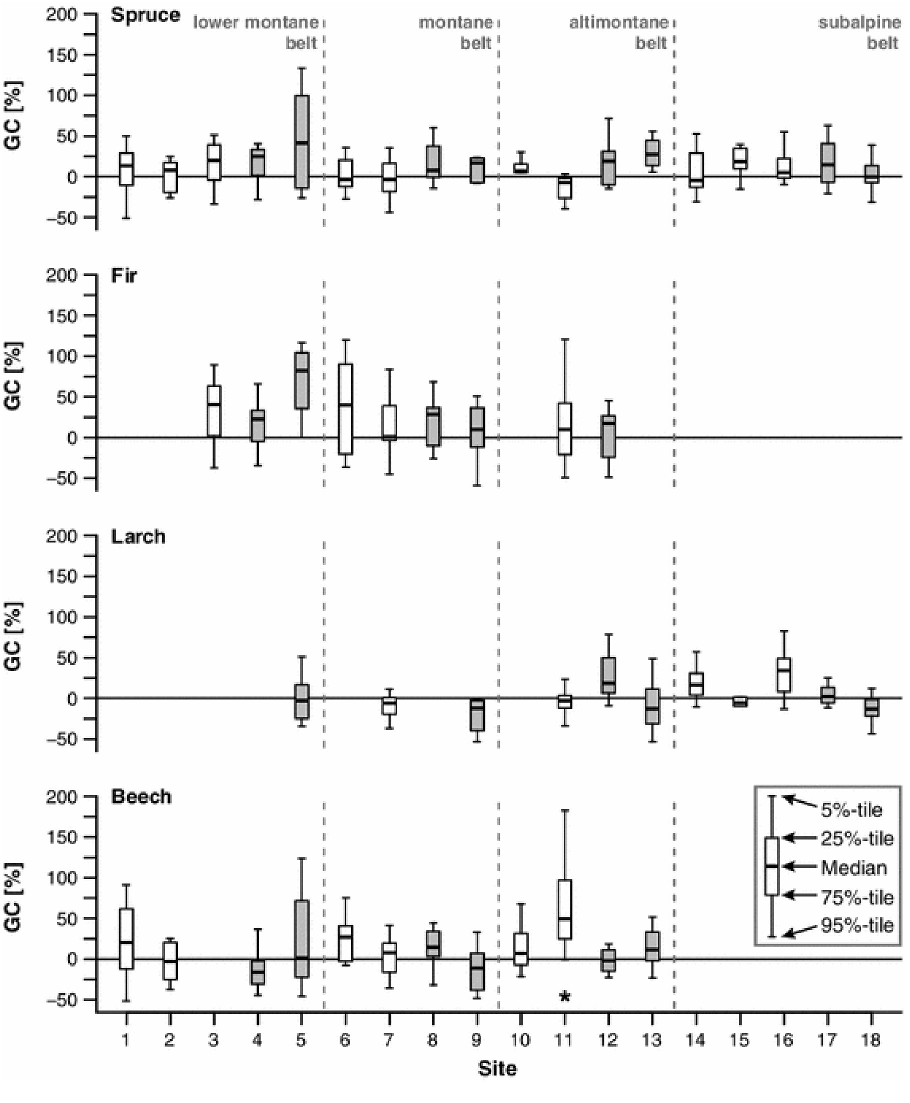

Fig. 6 Percentage growth change (GC) since 1990 compared to the 1961–1990 reference period, for spruce, fir, larch and beech at the different sites. *White boxes* denote sunny, *grey boxes* shady slopes (*significant difference at $p < 0.05$)

Discussion

Mountain forests are of critical ecological and economic importance in the European Alps, but there is still a high degree of uncertainty how these ecosystems will be affected by climate change (Elkin et al. 2013). In our investigation area a distinct temperature increase is unequivocal, but still there are high amounts of precipitation (Fig. 2). Based on these humid climatic conditions the notion of summer drought remains a relative term in this area. Nonetheless, even in the Berchtesgaden Alps the heat wave in 2003 was an exceptional extreme event and remarkably divergent from average conditions (Fig. 2; Fig. S1).

Our findings concerning the long-term growth/climate response of spruce confirm the ‘common knowledge’ that trees growing at higher elevations are sensitive to temperature variations (Babst et al. 2013) and have distinct temperature signals, while trees growing at lower elevations are more sensitive to moisture (Luckman 2007). Spruce is drought sensitive at the lower montane and montane belt with a negative growth response to temperature/sunshine duration and a positive response for precipitation. We found inverse relationships at the altimontane and subalpine belt indicating that these sites will benefit from higher temperatures. Similar patterns for spruce were reported in several other studies (e.g. Dittmar and Elling 1999; Frank and Esper 2005; Leal et al. 2007; Mäkinen et al. 2002; Savva et al. 2006; Wilson and Hopfmüller 2001). For larch and beech, the growth/climate response also depended on altitude, but there was no clear drought sensitivity (in terms of negative/positive correlations to temperature/precipitation) at low elevation sites. At high altitudes, higher temperatures during growing season favour growth of larch and beech. For beech, Dittmar and Elling (1999) found a distinct negative temperature response at low elevation sites but their sites were located at much lower elevations compared to our study. At the higher elevations in their study, Dittmar and Elling (1999) also found a positive temperature effect. Larch seems to benefit from higher temperatures or increased sunshine duration at the montane and altimontane belt especially at shady sites. The positive (negative) correlation between growth of fir and temperature (precipitation) of the growing season, and especially from June to August, in our study indicates that fir is less sensitive to drought. This is well in line with findings of, e.g. Elling et al. (2009), van der Maaten-Theunissen et al. (2013) or Zang et al. (2011) from regions north of the Alps. Studies which contradict the drought tolerance of fir are located in drier climates of Europe like Southern Italy (Battipaglia et al. 2009), the south-eastern Alps (Maxime and Hendrik 2011) or France (Lebourgeois et al. 2010), where water consistently is a limiting factor. This is not the case in our humid investigation area and moreover, fir might originate from different provenances.

The drought sensitivity derived from the long-term growth/climate response can be verified by the reaction of the tree species during the 2003-heat wave. Spruce growth significantly decreased in 2003 at some lower elevation sites. At the altimontane belt there is a switch from a negative to a positive GR. Trees at sunny slopes show growth reduction, while trees at shady slopes benefit from high temperatures. At the subalpine belt the growth response is generally positive. Similar altitudinal effects in extreme years were found for spruce in other studies (e.g. Desplanque et al. 1999; Jolly et al. 2005; Neuwirth et al. 2004). Contrary to our findings, Desplanque et al. (1999) and Lebourgeois et al. (2010) observed an elevation-dependent growth decline caused by drought events for fir as well. In other studies (Elling et al. 2009; van der Maaten-Theunissen et al. 2013; Zang et al. 2011) fir showed no significant reaction in drought years, which agrees well with our findings. Also larch and beech showed no consistent reaction during 2003 indicating a high resistance against such events. Only the growth decline of beech in 2003 at the altimontane belt contradicts the long-term growth/climate response at this belt and the findings from other studies (e.g. Dittmar et al. 2003). Since no growth decline was obvious for beech at lower elevations (even at sunny slopes), we assume that the growth reduction of beech at the altimontane belt results from other causes in this specific year. A possible explanation might be a late frost event, which could also explain the high MS values of beech at this belt. Dittmar et al. (2006) found a higher frequency of frost-related growth reductions with increasing altitude.

Due to their long lifespan, trees are considered to be particularly vulnerable to changing climate, since they are not able to adapt as rapidly (Lindner et al. 2010). Fuhrer et al. (2006) suggests that extreme events, such as drought may have more severe effects on tree vitality than changes in average conditions, but a long-term increase in temperatures may also have substantial consequences for forest ecosystems (Elkin et al. 2013). Average temperatures during the growing season were ~1.4 °C higher since 1990 compared to the 1961–1990 period in our investigation area. The strength and duration of this temperature signal was not enough to cause a significant growth response of the trees investigated. There were neither clear signals for growth reduction at the lower elevations (rather a slight growth increase) nor for growth increase in the altimontane or subalpine belt. At high elevation sites, positive growth trends of different tree species were found in the European Alps (Paulsen et al. 2000; Rolland et al. 1998) or North America (Salzer et al. 2009). These investigations were located at the respective timberline and in our study area, stronger growth signals might be present at the timberline as well. But the subjects of this study are mountain forests, i.e. closed canopy stands, since these forests fulfil important ecological, economic and protection functions in the region. Hasenauer et al. (1999) explained an increased growth of, e.g. Norway spruce since 1980 (including different elevations) with warmer climatic conditions and an associated prolonged vegetation period. In general, higher temperatures are expected to increase the growing season (Lindner et al. 2010) and we can approve the sensitivity of our examined species to the duration of the growing season since the AGR decreases with altitude. But a recent phenological study in our investigation area showed that trees are generally less sensitive to temperature changes than plants with shorter lifespans indicating that trees may react more slowly to climate change than perennial herbs (Cornelius et al. 2013). The missing growth effect—despite the temperature shift since 1990—was not expected and somehow contradicts the findings of the long-term growth/climate response and the growth response during the 2003 event. However, in spite of the strong warming, all of our study sites and analysed species are still well within their bioclimatic envelopes (Kölling 2007). While Norway spruce and European larch were found to be at their dry distribution and physiological limits in inner-Alpine dry valleys (Lévesque et al. 2013; Schuster and Oberhuber 2013), the temperature signal may not have been strong and/or long enough in the Berchtesgaden Alps in order to cause significant growth effects.

Conclusion

Both the heat wave in 2003 and the temperature increase since 1990 had only minor effects on growth patterns of the main tree species in the Berchtesgaden area. The mountain forests seem to be vital and can tolerate a certain shift in climate. On the other hand, climate change is not restricted to rising temperatures or drought events. It is accompanied by other biotic or abiotic impacts (Bolte et al. 2009), e.g. a higher frequency and intensity of insect outbreaks (Seidl et al. 2008), and wind storms (Lindroth et al. 2009). Norway spruce is considered to be the most vulnerable tree species of the mountain forests to such disturbances and it was also the most drought-sensitive species in the lower elevations in our investigation. The ultimate ambition of silvicultural measure has to be the improvement of the stand stability against drought, storms and secondary factors (Bolte et al. 2009), especially in mountain forests, where the protection function is of critical importance. Therefore, we recommend the conversion of spruce monocultures at the montane belts into mixed mountain forests with beech and fir in the long term. Due to the higher drought tolerance of fir compared to spruce this will increase the climatic stability of mountain forests.

Acknowledgments We thank the staff from the Berchtesgaden National Park and the adjacent forest districts, in particular M. Vogel, V. Konnert, R. Baier, M. Hofbeck, H. Neubauer, W. Vogel, M. Gröll., D. Müller, P. Renoth and C. Dinger for supporting site selection and sampling. L. Ma, J. Riepl and F. Forster helped with field and laboratory work, and J. Esper with refining the climate response analysis. We are grateful to the Berchtesgaden National Park for funding this study. C.Z. acknowledges funding by the European Research Council under the European Union's Seventh Framework Programme (FP7/2007-2013)/ERC grant agreement no. [282250].

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Supplementary Material

Mountain forest growth response to climate change in the Northern Limestone Alps

Trees – Structure and Function

Claudia Hartl-Meier*, Christoph Dittmar, Christian Zang, Andreas Rothe

* corresponding author:

Address:	Department of Geography, Johannes Gutenberg University, Johann-Joachim-Becher-Weg 21, 55099 Mainz, Germany
Phone:	+49 6131 39 23183
Fax:	+49 6131 39 24735
Email:	c.hartl-meier@geo.uni-mainz.de

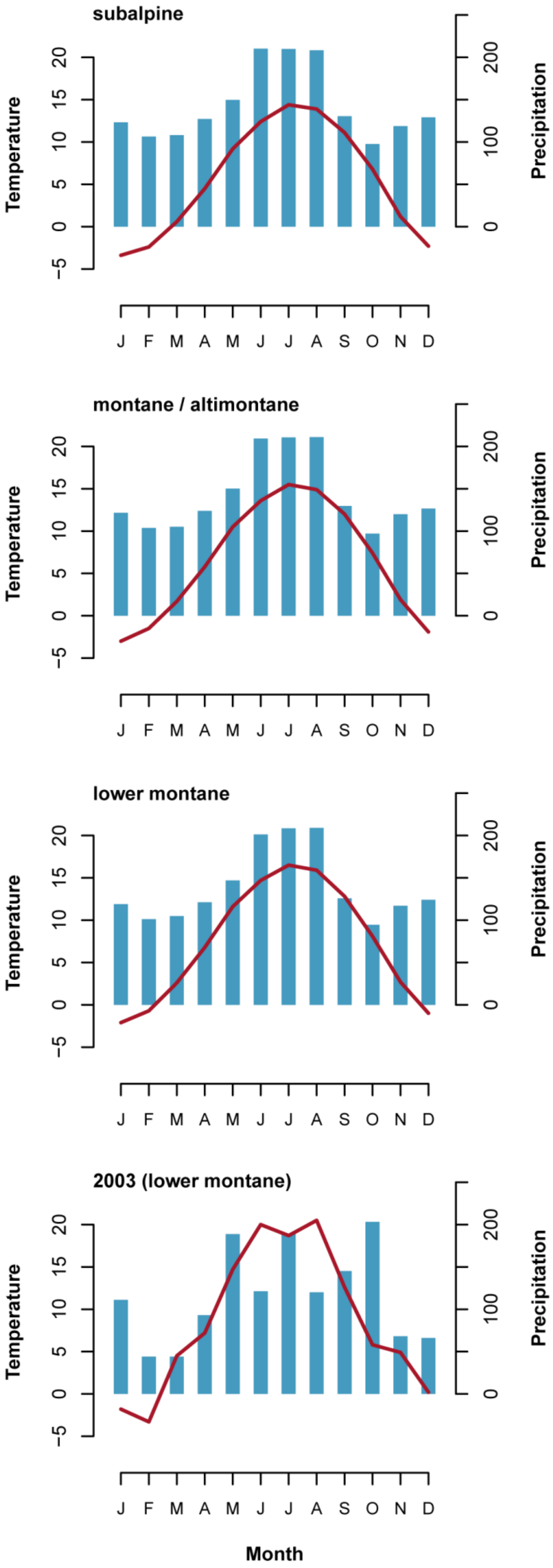

Fig. S1 Climate diagrams of the elevation belts and the exceptional year 2003 (data basis: HISTALP).

Table S1 Selected grid points of the HISTALP database representative for elevation belts, annual mean temperature and precipitation sum with relation to 1961-1990 period.

Elevation belt	Lat.	Lon.	Temp. [°C]	Prec. [mm]
lower montane	N47°35'	E13°0'	7.3	1673
montane / altimontane	N47°35'	E12°50'	6.4	1708
subalpine	N47°35'	E12°45'	5.5	1719

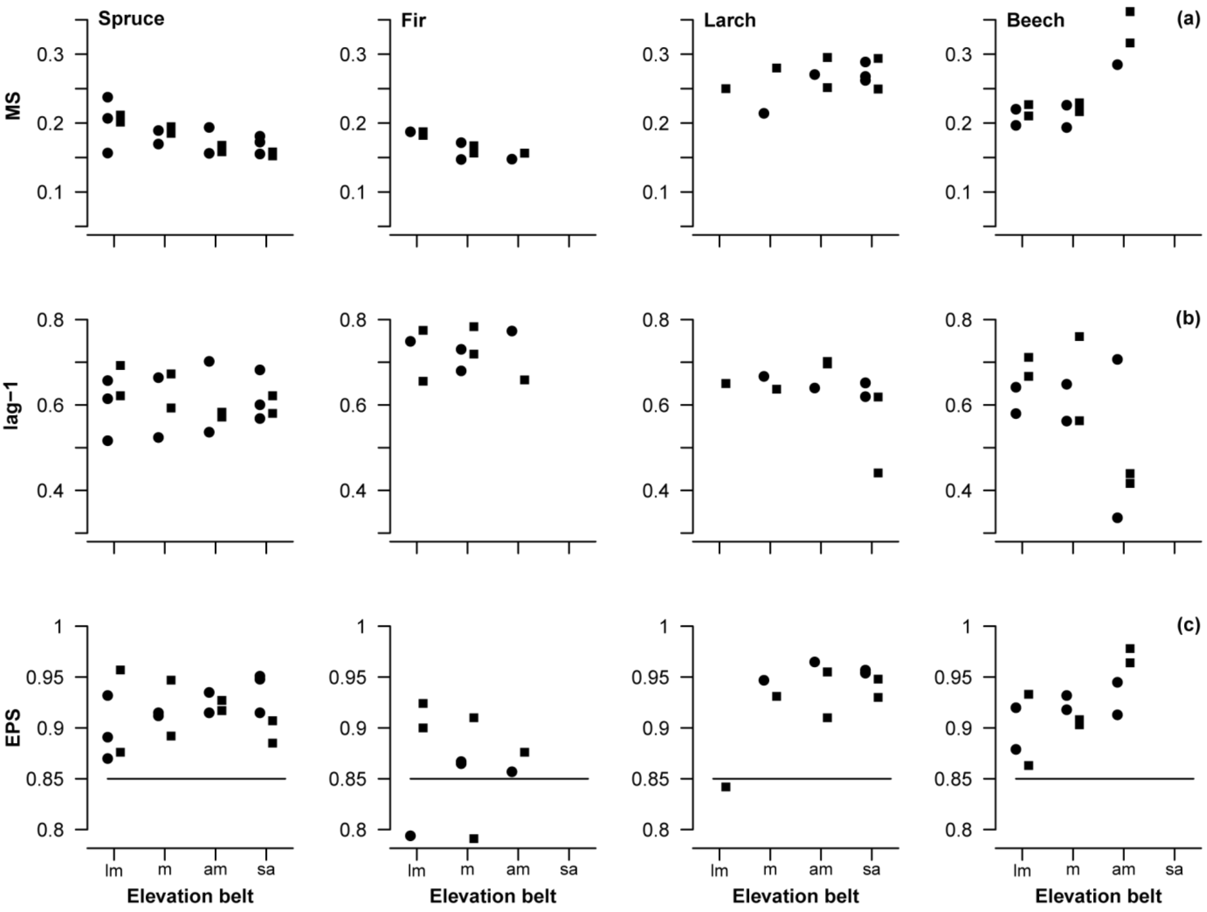

Fig. S2 (a) Mean sensitivity (MS), (b) first order autocorrelation (lag-1) and (c) EPS for spruce, fir, larch and beech at different elevation belts in the 1959-2008 period. Circles denote sunny and squares shady slopes (lm = lower montane, m = montane, am = altimontane, sa = subalpine belt).

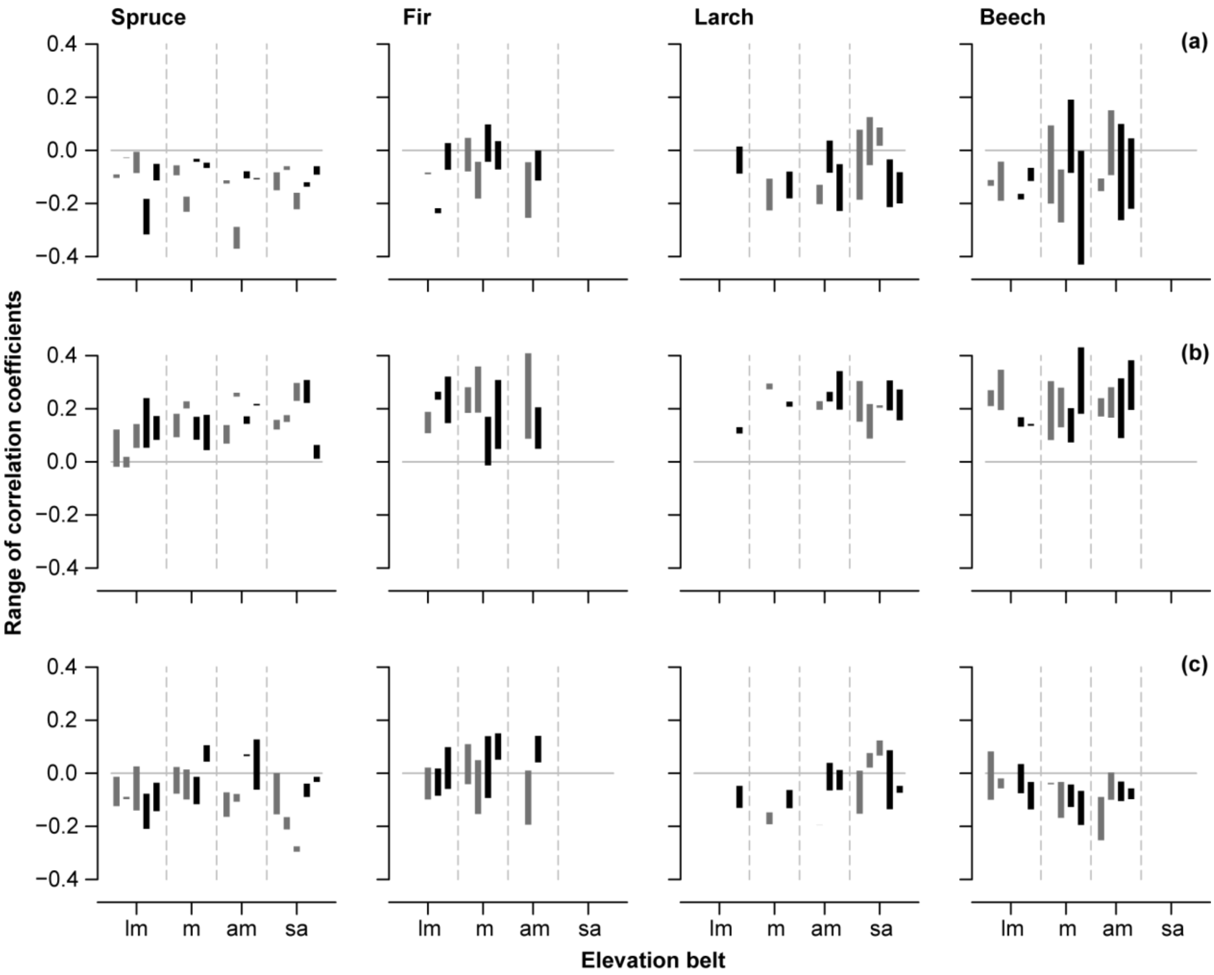

Fig S3 Range of correlation coefficients for the growth/climate response of different previous year seasons (pJA, pAS (see Table S2) for (a) temperature, (b) precipitation and (c) sunshine duration. Grey bars denote sunny and black bars shady slopes. Sequence of the sites within an elevation level follows Table 1 (lm = lower montane, m = montane, am = altimontane, sa = subalpine belt).

Table S2 Correlation coefficients for the growth/climate response of different previous year seasons (pJA = previous year July/August, pAS = previous year August/September) for temperature, precipitation and sunshine duration. Bold numbers indicate p ≤ 0.05 significant correlations.

			Site #																	
			1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**
SPRUCE	**Temp.**	pJA	-0,09	-0,03	-0,01	-0,18	-0,05	-0,06	-0,23	-0,04	-0,07	-0,12	**-0,37**	-0,11	-0,11	-0,15	-0,07	**-0,22**	-0,14	-0,09
		pAS	-0,10	-0,03	-0,09	**-0,32**	-0,11	-0,09	-0,17	-0,03	-0,05	-0,11	**-0,29**	-0,08	-0,11	-0,08	-0,06	-0,16	-0,12	-0,06
	Prec.	pJA	-0,02	0,02	0,05	0,05	0,08	0,09	0,20	0,08	0,04	0,14	**0,25**	0,17	0,21	0,12	0,18	0,23	0,22	0,01
		pAS	0,12	-0,02	0,14	0,24	0,17	0,18	0,23	0,17	0,18	0,07	0,26	0,14	0,22	0,16	0,15	**0,30**	**0,31**	0,06
	Sun.	pJA	-0,01	-0,10	0,03	-0,08	-0,04	0,02	0,01	-0,01	0,11	-0,07	-0,08	0,07	0,13	-0,15	-0,17	**-0,29**	-0,09	-0,01
		pAS	-0,12	-0,09	-0,14	-0,21	-0,14	-0,08	-0,10	-0,12	0,04	-0,16	-0,11	0,07	-0,06	0,00	**-0,21**	**-0,28**	-0,04	-0,03
FIR	**Temp.**	pJA			-0,08	**-0,24**	0,03	0,05	-0,04	0,10	0,03		-0,05	0,00						
		pAS			-0,09	-0,22	-0,07	-0,08	-0,18	-0,04	-0,07		**-0,25**	-0,11						
	Prec.	pJA			0,11	**0,23**	0,15	0,18	0,19	-0,01	0,05		0,09	0,05						
		pAS			0,19	**0,26**	**0,32**	**0,28**	**0,36**	0,17	**0,31**		**0,41**	0,21						
	Sun.	pJA			0,02	0,02	0,10	0,11	0,05	0,14	0,15		0,01	0,14						
		pAS			-0,10	-0,08	-0,06	-0,04	-0,15	-0,09	0,05		-0,19	0,04						
LARCH	**Temp.**	pJA					-0,09		-0,23		-0,18		-0,20	-0,08	-0,23	-0,19	-0,06	0,02	-0,21	-0,20
		pAS					0,01		-0,11		-0,08		-0,13	0,04	-0,05	0,08	0,13	0,09	-0,03	-0,08
	Prec.	pJA					0,11		**0,29**		0,23		0,20	**0,26**	**0,34**	**0,30**	0,22	0,20	**0,31**	0,27
		pAS					0,13		**0,27**		0,21		0,23	**0,23**	**0,20**	0,15	0,09	**0,21**	0,19	0,16
	Sun.	pJA					-0,13		-0,15		-0,13		-0,20	-0,06	-0,06	-0,15	0,02	0,12	-0,14	-0,07
		pAS					-0,05		-0,19		-0,06		-0,20	0,04	0,01	0,01	0,08	0,07	0,09	-0,05
BEECH	**Temp.**	pJA	-0,13	-0,19		-0,16	-0,12	-0,20	**-0,27**	-0,08	**-0,43**	-0,15	-0,09	**-0,26**	-0,22					
		pAS	-0,11	-0,04		-0,18	-0,07	0,09	-0,07	0,19	0,00	-0,11	0,15	0,10	0,04					
	Prec.	pJA	0,21	**0,35**		0,13	0,14	**0,30**	**0,28**	**0,20**	**0,43**	**0,24**	**0,28**	**0,31**	**0,38**					
		pAS	**0,27**	0,20		0,17	0,14	0,08	0,13	0,07	**0,18**	0,17	0,17	0,09	0,20					
	Sun.	pJA	0,08	-0,02		0,03	-0,03	-0,04	-0,03	-0,04	-0,19	-0,09	0,00	-0,10	-0,10					
		pAS	-0,10	-0,06		-0,07	-0,14	-0,04	-0,17	-0,13	-0,07	-0,25	-0,10	-0,03	-0,06					

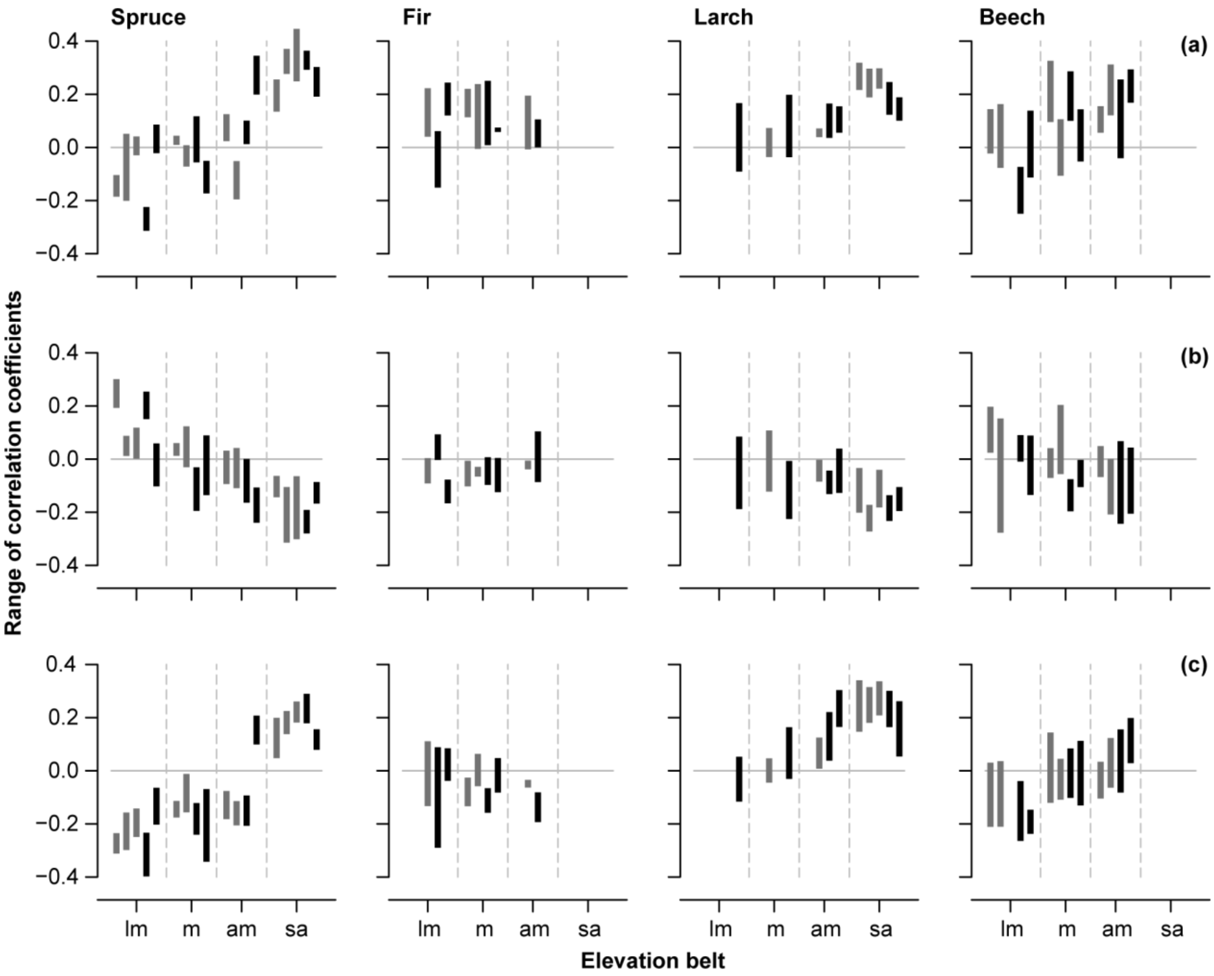

Fig S4 Range of correlation coefficients for the growth/climate response of different current year seasons (MJ, JJ, JA, MJJ, JJA, MJJA (see Table S3)) for (a) temperature, (b) precipitation and (c) sunshine duration. Grey bars denote sunny and black bars shady slopes. Sequence of the sites within an elevation level follows Table 1 (lm = lower montane, m = montane, am = altimontane, sa = subalpine belt).

Table S3 Correlation coefficients for the growth/climate response of different current year seasons (MJ = May/June, JJ = June/July, JA = July/August, MJJ = May/June/July, JJA = June/July/August, MJJA = May/June/July/August) for temperature, precipitation and sunshine duration. Bold numbers indicate p ≤ 0.05 significant correlations.

			Site #																	
			1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**
SPRUCE	**Temperature**	MJ	-0,12	-0,20	0,02	-0,22	0,04	0,04	-0,06	-0,06	-0,16	0,02	-0,20	0,03	**0,20**	0,14	**0,28**	**0,25**	**0,29**	**0,19**
		JJ	-0,12	-0,06	-0,01	**-0,29**	-0,02	0,01	0,01	-0,04	-0,17	0,12	-0,16	0,01	**0,29**	**0,26**	**0,30**	**0,45**	**0,31**	**0,30**
		JA	-0,14	0,05	0,01	-0,23	0,09	0,03	-0,04	0,12	-0,05	0,08	-0,05	0,10	**0,35**	0,25	**0,32**	**0,35**	**0,32**	**0,24**
		MJJ	-0,10	-0,08	0,04	**-0,25**	0,06	0,04	0,01	0,03	-0,13	0,08	-0,14	0,06	**0,29**	**0,22**	**0,37**	**0,37**	**0,36**	**0,27**
		JJA	-0,19	-0,08	-0,03	**-0,31**	0,02	0,01	-0,07	0,00	-0,15	0,09	-0,17	0,05	**0,34**	**0,25**	**0,30**	**0,40**	**0,33**	**0,27**
		MJJA	-0,15	-0,09	0,01	-0,26	0,08	0,03	-0,06	0,04	-0,12	0,06	-0,15	0,08	**0,32**	**0,23**	**0,36**	**0,35**	**0,36**	**0,25**
	Precipitation	MJ	0,24	0,01	0,00	0,15	-0,10	0,01	0,00	-0,15	-0,14	-0,09	0,04	-0,16	**-0,20**	-0,06	-0,20	**-0,21**	**-0,24**	-0,17
		JJ	0,19	0,09	0,11	0,19	-0,06	0,06	-0,03	-0,17	-0,05	0,03	-0,11	0,00	-0,23	-0,14	-0,21	-0,26	-0,26	-0,13
		JA	0,21	0,04	0,12	**0,22**	0,06	0,06	0,12	-0,03	0,09	0,02	-0,06	-0,01	-0,11	-0,14	-0,12	-0,06	-0,19	-0,09
		MJJ	0,22	0,01	0,07	0,20	-0,10	0,04	-0,02	**-0,19**	-0,07	-0,05	-0,05	-0,05	**-0,24**	-0,14	**-0,31**	**-0,30**	**-0,28**	-0,16
		JJA	**0,28**	0,09	0,11	**0,24**	0,02	0,06	0,10	-0,07	0,01	0,02	-0,06	-0,07	-0,18	-0,14	-0,11	-0,11	-0,26	-0,14
		MJJA	**0,30**	0,03	0,09	**0,25**	-0,02	0,05	0,09	-0,11	-0,01	-0,05	-0,02	-0,11	-0,20	-0,13	-0,21	-0,17	**-0,28**	-0,16
	Sunshine duration	MJ	**-0,25**	**-0,30**	-0,14	**-0,38**	-0,20	-0,16	-0,08	**-0,24**	**-0,34**	-0,08	-0,18	-0,09	0,10	0,05	0,14	0,18	0,18	0,14
		JJ	-0,24	-0,21	-0,17	**-0,30**	-0,18	-0,12	-0,01	-0,19	**-0,23**	-0,09	-0,20	**-0,21**	0,14	0,13	0,14	**0,26**	0,19	0,12
		JA	-0,24	-0,16	-0,24	-0,23	-0,06	-0,11	-0,16	-0,12	-0,07	-0,18	-0,11	-0,15	0,21	0,20	0,19	0,20	**0,27**	0,08
		MJJ	**-0,26**	**-0,28**	-0,17	**-0,38**	-0,18	-0,15	-0,07	**-0,22**	**-0,32**	-0,10	-0,17	-0,15	0,13	0,11	**0,22**	**0,26**	**0,24**	0,16
		JJA	**-0,30**	-0,24	-0,25	**-0,34**	-0,18	-0,16	-0,12	-0,20	-0,19	-0,17	-0,21	-0,18	0,20	0,18	0,15	**0,25**	**0,27**	0,11
		MJJA	**-0,31**	**-0,30**	-0,23	**-0,40**	-0,18	-0,18	-0,14	**-0,23**	**-0,28**	-0,16	-0,19	-0,14	0,18	0,16	0,21	**0,25**	**0,29**	0,14
FIR	**Temperature**	MJ			0,04	-0,15	0,12	0,11	-0,01	0,01	0,06		-0,01	0,00						
		JJ			0,12	-0,07	0,14	0,22	0,24	**0,23**	0,06		0,19	0,08						
		JA			**0,22**	0,06	**0,24**	0,17	0,17	**0,25**	0,07		0,18	0,11						
		MJJ			0,13	-0,09	0,18	0,18	0,12	0,15	0,07		0,09	0,05						
		JJA			0,15	-0,04	0,20	0,19	0,17	0,21	0,06		0,18	0,10						
		MJJA			0,15	-0,06	**0,21**	0,16	0,09	0,15	0,07		0,10	0,06						
	Precipitation	MJ			-0,04	0,09	-0,15	-0,08	-0,03	0,01	-0,12		-0,03	-0,06						
		JJ			0,00	0,03	-0,08	-0,01	-0,05	0,00	0,00		-0,01	0,10						
		JA			-0,09	0,00	-0,11	-0,08	-0,03	-0,10	-0,02		-0,03	-0,07						
		MJJ			-0,05	0,05	-0,14	-0,07	-0,03	-0,04	-0,08		-0,02	0,03						
		JJA			-0,05	0,04	-0,12	-0,06	-0,07	-0,04	-0,03		-0,03	-0,04						
		MJJA			-0,09	0,05	-0,17	-0,10	-0,04	-0,07	-0,10		-0,04	-0,09						
	Sunshine duration	MJ			-0,13	**-0,29**	-0,04	-0,13	-0,06	-0,13	-0,06		-0,06	-0,08						
		JJ			-0,07	-0,19	-0,04	-0,08	0,06	-0,07	-0,08		-0,04	-0,19						
		JA			0,11	0,09	0,08	-0,03	0,00	-0,11	0,05		-0,03	-0,17						
		MJJ			-0,06	**-0,25**	0,00	-0,11	-0,02	-0,13	-0,04		-0,06	-0,16						
		JJA			-0,03	-0,08	0,00	-0,09	0,02	-0,12	-0,04		-0,05	-0,17						
		MJJA			-0,03	-0,16	0,02	-0,11	-0,04	-0,16	-0,02		-0,06	-0,15						

Continuation Table S3

			Site #																	
			1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**
LARCH	**Temperature**	MJ					0,17		0,07		**0,20**		0,05	0,14	0,15	**0,22**	0,19	**0,26**	0,17	0,17
		JJ					-0,09		0,03		0,00		0,07	0,04	0,06	**0,26**	**0,28**	0,22	0,15	0,15
		JA					0,00		-0,04		-0,04		0,04	0,13	0,11	**0,25**	0,23	0,24	0,15	0,10
		MJJ					0,09		0,05		0,14		0,06	0,12	0,11	**0,23**	0,22	**0,25**	0,12	0,12
		JJA					-0,02		0,00		-0,01		0,06	0,12	0,13	**0,32**	**0,30**	**0,29**	**0,25**	0,19
		MJJA					0,10		0,02		0,09		0,06	0,17	0,15	**0,27**	**0,25**	**0,30**	0,20	0,16
	Precipitation	MJ					-0,19		-0,11		-0,17		0,00	-0,13	-0,13	-0,16	-0,17	-0,12	-0,14	-0,11
		JJ					-0,09		-0,12		**-0,23**		-0,08	-0,09	-0,10	-0,20	**-0,27**	-0,18	-0,21	-0,16
		JA					0,08		0,11		-0,01		-0,01	-0,04	0,04	-0,03	**-0,23**	-0,04	-0,17	-0,17
		MJJ					-0,16		-0,09		**-0,22**		-0,03	-0,11	-0,12	-0,19	**-0,27**	-0,14	-0,16	-0,16
		JJA					0,01		0,00		-0,09		-0,06	-0,09	-0,03	-0,11	**-0,26**	-0,14	-0,23	**-0,19**
		MJJA					-0,05		0,01		-0,11		-0,01	-0,11	-0,05	-0,12	**-0,27**	-0,11	-0,20	-0,20
	Sunshine duration	MJ					0,05		0,05		0,16		0,12	0,19	**0,25**	**0,34**	**0,30**	**0,29**	**0,28**	**0,26**
		JJ					-0,12		0,02		-0,03		0,05	0,04	0,17	**0,25**	**0,29**	0,21	0,18	0,17
		JA					0,02		-0,04		0,01		0,01	0,14	0,22	0,15	0,18	0,21	0,16	0,05
		MJJ					0,05		0,03		0,15		0,12	0,18	**0,28**	**0,30**	**0,31**	**0,27**	0,21	0,21
		JJA					-0,07		0,00		-0,02		0,03	0,12	**0,22**	**0,29**	**0,30**	**0,30**	**0,30**	0,19
		MJJA					0,05		0,01		0,13		0,09	0,22	**0,30**	**0,33**	**0,31**	**0,34**	**0,30**	**0,22**
BEECH	**Temperature**	MJ	0,03	-0,08		-0,09	-0,11	0,10	-0,11	0,15	-0,01	0,09	0,13	-0,04	0,17					
		JJ	-0,02	-0,06		**-0,25**	-0,02	0,12	-0,04	0,10	-0,05	0,06	0,12	0,03	0,17					
		JA	0,14	0,16		-0,07	0,14	**0,33**	0,11	**0,29**	0,14	0,15	**0,31**	**0,26**	**0,28**					
		MJJ	0,06	0,00		-0,14	-0,02	0,15	-0,05	0,19	0,00	0,08	0,19	0,02	0,18					
		JJA	0,06	0,02		-0,16	0,02	**0,26**	0,02	0,21	0,07	0,15	0,23	0,17	**0,29**					
		MJJA	0,11	0,04		-0,09	0,01	**0,24**	0,00	0,25	0,07	0,14	**0,25**	0,12	**0,27**					
	Precipitation	MJ	0,20	0,15		0,09	0,09	0,04	0,20	-0,09	0,00	-0,04	0,00	0,07	0,02					
		JJ	0,09	-0,03		0,08	-0,03	0,04	0,00	-0,08	-0,09	0,05	-0,12	-0,01	0,04					
		JA	0,02	**-0,28**		-0,01	-0,14	-0,07	-0,06	-0,18	-0,11	-0,06	-0,21	**-0,24**	**-0,21**					
		MJJ	0,08	-0,06		0,05	-0,07	-0,01	0,04	**-0,20**	-0,10	-0,05	-0,14	-0,04	-0,05					
		JJA	0,15	-0,10		0,07	-0,01	0,01	0,06	-0,09	-0,06	0,01	-0,14	-0,12	-0,07					
		MJJA	0,13	-0,11		0,05	-0,05	-0,03	0,09	**-0,19**	-0,08	-0,07	-0,16	-0,14	-0,14					
	Sunshine duration	MJ	-0,12	-0,14		-0,24	-0,18	-0,04	-0,09	0,07	-0,01	0,03	0,03	-0,02	0,13					
		JJ	-0,21	-0,21		**-0,26**	**-0,24**	-0,12	-0,11	-0,10	-0,13	-0,10	-0,06	-0,08	0,03					
		JA	0,03	0,04		-0,04	-0,15	0,14	0,04	0,05	0,11	0,01	0,12	0,16	0,20					
		MJJ	-0,13	-0,12		**-0,25**	-0,20	-0,03	-0,07	0,06	-0,02	0,00	0,04	-0,02	0,12					
		JJA	-0,11	-0,13		-0,18	**-0,23**	0,02	-0,05	-0,03	0,00	-0,03	0,03	0,06	0,15					
		MJJA	-0,07	-0,08		-0,19	-0,21	0,05	-0,04	0,08	0,06	0,03	0,09	0,08	**0,20**					

Table S4: Statistical significance of differences between GR of the different elevation belts and respective slope exposures for spruce, fir, larch and beech (lm = lower montane, m = montane, am = altimontane, sa = subalpine belt; su = sunny, sh = shady slope; *p<0.05, **p<0.01, ***p<0.001, ****p<0.0001, n.s. = not significant, - = not available).

Spruce	lm su	lm sh	m su	m sh	am su	am sh	sa su
lm sh	n.s.						
m su	n.s.	n.s.					
m sh	n.s.	n.s.	n.s.				
am su	n.s.	n.s.	n.s.	n.s.			
am sh	**	*	**	*	**		
sa su	****	****	****	****	****	n.s.	
sa sh	****	****	****	****	****	n.s.	n.s.

Fir	lm su	lm sh	m su	m sh	am su	am sh	sa su
lm sh	n.s.						
m su	n.s.	n.s.					
m sh	n.s.	n.s.	n.s.				
am su	n.s.	n.s.	n.s.	n.s.			
am sh	n.s.	n.s.	n.s.	n.s.	n.s.		
sa su	-	-	-	-	-	-	
sa sh	-	-	-	-	-	-	-

Larch	lm su	lm sh	m su	m sh	am su	am sh	sa su
lm sh	-						
m su	-	n.s.					
m sh	-	n.s.	n.s.				
am su	-	n.s.	n.s.	n.s.			
am sh	-	n.s.	n.s.	n.s.	n.s.		
sa su	-	n.s.	n.s.	n.s.	n.s.	n.s.	
sa sh	-	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

Beech	lm su	lm sh	m su	m sh	am su	am sh	sa su
lm sh	n.s.						
m su	n.s.	n.s.					
m sh	n.s.	n.s.	n.s.				
am su	*	n.s.	*	n.s.			
am sh	n.s.	n.s.	n.s.	n.s.	n.s.		
sa su	-	-	-	-	-	-	
sa sh	-	-	-	-	-	-	-

Table S5: Statistical significance of differences between GC of the different elevation belts and respective slope exposures for spruce, fir, larch and beech (lm = lower montane, m = montane, am = altimontane, sa = subalpine belt; su = sunny, sh = shady slope; *p<0.05, **p<0.01, ***p<0.001, ****p<0.0001, n.s. = not significant, - = not available).

Spruce	lm su	lm sh	m su	m sh	am su	am sh	sa su
lm sh	n.s.						
m su	n.s.	*					
m sh	n.s.	n.s.	n.s.				
am su	n.s.	**	n.s.	n.s.			
am sh	n.s.	n.s.	n.s.	n.s.	n.s.		
sa su	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	
sa sh	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

Fir	lm su	lm sh	m su	m sh	am su	am sh	sa su
lm sh	n.s.						
m su	n.s.	n.s.					
m sh	n.s.	n.s.	n.s.				
am su	n.s.	n.s.	n.s.	n.s.			
am sh	n.s.	n.s.	n.s.	n.s.	n.s.		
sa su	-	-	-	-	-	-	
sa sh	-	-	-	-	-	-	-

Larch	lm su	lm sh	m su	m sh	am su	am sh	sa su
lm sh	-						
m su	-	n.s.					
m sh	-	n.s.	n.s.				
am su	-	n.s.	n.s.	n.s.			
am sh	-	n.s.	n.s.	n.s.	n.s.		
sa su	-	n.s.	n.s.	n.s.	n.s.	n.s.	
sa sh	-	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

Beech	lm su	lm sh	m su	m sh	am su	am sh	sa su
lm sh	n.s.						
m su	n.s.	n.s.					
m sh	n.s.	n.s.	n.s.				
am su	n.s.	*	n.s.	*			
am sh	n.s.	n.s.	n.s.	n.s.	*		
sa su	-	-	-	-	-	-	
sa sh	-	-	-	-	-	-	-

Table S6 Percentage growth change (GC) for spruce, fir, larch and beech since 1990 compared to the 1961-1990 reference period averaged for elevation belts based on a robust mean.

Elevation belt	Spruce	Fir	Larch	Beech
Lower montane	15 %	38 %	-2 %	3 %
Montane	7 %	17 %	-13 %	9 %
Altimontane	10 %	8 %	4 %	14 %
subalpine	10 %		4 %	

Publikation III

Zang C, Hartl-Meier C, Dittmar C, Rothe A, Menzel A

(2014)

Patterns of drought tolerance in major European temperate forest trees: climatic drivers and levels of variability

Global Change Biology 20 (12):3767-3779

doi: 10.1111/gcb.12637

Global Change Biology (2014), **20**, 3767–3779, doi: 10.1111/gcb.12637

Primary Research Article

Patterns of drought tolerance in major European temperate forest trees: climatic drivers and levels of variability

CHRISTIAN ZANG[1] , CLAUDIA HARTL-MEIER[2] , CHRISTOPH DITTMAR[3], ANDREAS ROTHE[4] and ANNETTE MENZEL[1, 5]

[1]Chair of Ecoclimatology, Technische Universität München, Hans-Carl-von-Carlowitz-Platz 2, Freising 85354, Germany, [2]Department of Geography, Johannes Gutenberg University, Johann-Joachim-Becher-Weg 21, Mainz 55128, Germany, [3]Environmental Research and Education (UFB), Am Sandacker 25, Mistelbach 95511, Germany, [4]Faculty of Forestry, University of Applied Sciences Weihenstephan-Triesdorf, Hans-Carl-von-Carlowitz-Platz 3, Freising 85354, Germany, [5]Institute for Advanced Study, Technische Universität München, Lichtenbergstr 2a, Garching 85748, Germany

Abstract

The future performance of native tree species under climate change conditions is frequently discussed, since increasingly severe and more frequent drought events are expected to become a major risk for forest ecosystems. To improve our understanding of the drought tolerance of the three common European temperate forest tree species Norway spruce, silver fir and common beech, we tested the influence of climate and tree-specific traits on the inter and intrasite variability in drought responses of these species. Basal area increment data from a large tree-ring network in Southern Germany and Alpine Austria along a climatic cline from warm-dry to cool-wet conditions were used to calculate indices of tolerance to drought events and their variability at the level of individual trees and populations. General patterns of tolerance indicated a high vulnerability of Norway spruce in comparison to fir and beech and a strong influence of bioclimatic conditions on drought response for all species. On the level of individual trees, low-growth rates prior to drought events, high competitive status and low age favored resilience in growth response to drought. Consequently, drought events led to heterogeneous and variable response patterns in forests stands. These findings may support the idea of deliberately using spontaneous selection and adaption effects as a passive strategy of forest management under climate change conditions, especially a strong directional selection for more tolerant individuals when frequency and intensity of summer droughts will increase in the course of global climate change.

Keywords: climatic extremes, common beech, intrasite variability, Norway spruce, populations, resilience, silver fir, tree ring

Received 10 September 2013 and accepted 12 May 2014

Introduction

With the human influence on climate becoming increasingly apparent (IPCC, 2013), the consequences of altered temperature and precipitation regimes for trees and thus for forest ecosystems are vividly discussed. In Europe, the rise in mean annual temperature by already more than 1.1 °C compared to the preindustrial average exceeds the global mean increase of 0.78 °C (IPCC, 2007, 2013). At the same time, the average length of summer heat waves over Western Europe has doubled and the frequency of hot days has almost tripled (EEA, 2012). In forests, drought is a major constraint to plant growth and productivity, as it is for most terrestrial plant communities (e.g. Churkina & Running, 1998; Luyssaert *et al*., 2010). The direct consequences of drought and secondary damages for forests range from losses in productivity and increased mortality rates on stand level to regional forest die-offs covering several million hectares (Ciais *et al*., 2005; Allen *et al*., 2010). Accordingly, increasing frequency and intensity of summer drought is generally understood as one of the major challenges for forest ecosystems associated with anthropogenic climate change (Bolte *et al*., 2009; Lindner *et al*., 2010).

Uncertainties due to climatic risks have always affected forestry decisions. However, the projected changes, which will exceed past variability (Luterbacher *et al*., 2004) and frequency of extremes (Schär *et al*., 2004; IPCC, 2013) by far, challenge current heuristics of forest management and call for integrative concepts. A core element of any alternative management strategy is the profound knowledge about the tree species' responses to altered climatic conditions (Bolte *et al*., 2009). One of the most prominent approaches toward assessing the future potential of a species are studies on its retrospective performance, in terms of growth, mortality and reproduction (Bolte *et al*., 2009).

Dendroecological studies usually rely on a strong common growth signal of a population of trees, which is achieved by averaging the individual trees' series of radial increment growth to a chronology (Fritts, 1976). This procedure removes large parts of tree-specific variability in increment growth stemming from differences in social class (Martin-Benito *et al*., 2008; Zang *et al*., 2012), age (Carrer & Urbinati, 2004; Dorado Liñán *et al*., 2011), genotype, and other factors that are comparably hard to quantitate, such as microsite differences and small-scale exogenous and endogenous disturbance pulses (Cook, 1990). Consequently, the large body of tree-ring studies on growth response to increasing temperatures and drought episodes predominantly promotes insights about general, population-wide responses, but less so about the bandwidth of responses of individual trees in terms of intrasite variability. Typically, biogeographical patterns of drought responses are revealed by chronology-based studies, and their intersite variability is mainly explained by macro-climate and local modifications of large-scale drought events (e.g., Huang *et al*., 2010; Zang *et al*., 2011; Subedi & Sharma, 2013).

More recently, the bandwidth of responses within populations has gained increasing interest with the demonstration of adaptive climatic differentiation among individuals of the same population (Jump & Penuelas, 2005; Jump *et al*., 2006; Eveno *et al*., 2008; Sthultz *et al*., 2009). With selection pressures on populations altered by rapid climate change, more frequent drought episodes will favor directional selection for drought-resistance (Hoffmann & Sgrò, 2011), especially since intrapopulation variability in the response to climate has been connected to different water use strategies on the level of individuals (Morán-López *et al*., 2014). In this context, the distribution of different response types within a population sample can give further insight regarding the adaptability of a local population, and is – additionally to the information about the averaged, species-specific response – of pivotal interest for assessing a species' adaptability in general.

Tree growth can be a first estimate for the selection for drought adapted species and genotypes. The growth decline in response to drought is generally used as a measure for the loss in vitality (Dobbertin, 2005), with prolonged, drought-induced episodes of reduced growth increasing mortality (Bigler *et al*., 2004, 2006, 2007). The potential consequences of a directional selection process are complex, and include declines in general plant fitness through loss of chromosomal diversity (Jump & Penuelas, 2005), or adverse effects due to variations in the susceptibility to other climate extremes (Reusch *et al*., 2005) and perturbations (Sthultz *et al*., 2009). Furthermore, provenance studies have frequently identified higher drought tolerance in trees to be associated with lower relative growth rates (Rose *et al*., 2009; Taeger *et al*., 2013). This is confirmed by the generally lower growth rates at the warm and dry margins of the species' distributions (Loehle, 1998), where populations are directionally selected for drought tolerance. Fast growing trees within a population reveal a higher susceptibility to drought stress (Morán-López *et al*., 2014). Since most provenance studies focus on populations as a whole, the current knowledge about the relationship of drought tolerance and growth rates within populations is rather limited.

In Europe, three of the major temperate forest tree species are Norway spruce [*Picea abies* (H.) Karst.], silver fir (*Abies alba* Mill.) and common beech (*Fagus sylvatica* L.). The isohydric Norway spruce belongs to the economically most important and widest distributed species in Europe and has repeatedly been described as particularly vulnerable to drought (Zang *et al*., 2011, 2012; Pretzsch *et al*., 2013; Boden *et al*., 2014). In contrast, the more anisohydric common beech as the most abundant broad-leaved forest tree in Central Europe (Dittmar *et al*., 2003) is characterized as more drought-resistant than spruce (Zang *et al*., 2011; Pretzsch *et al*., 2013). In direct comparison with Norway spruce, silver fir is described as considerably less vulnerable to drought stress (Becker, 1989; Desplanque *et al*., 1999; Kölling, 2007; Bouriaud & Popa, 2009), and therefore discussed as a possible alternative for spruce under changing climate conditions (Zang *et al*., 2011).

This study assesses the variability in tolerance of tree growth against drought events using a comprehensive dendroecological investigation comprising 1760 trees from 86 sites in Southern Germany and Austria. We aim to improve our understanding of the drought tolerance of the three major European temperate forest tree species spruce, fir and beech based on past drought events at multiple sites on a climate cline and to analyze more specifically how variability on the individual level contributes to the tolerance of populations. The data set used in this study is compiled aiming at reducing the variability among the individual trees at a site stemming from site differences and small-scale disturbance pulses. This allows for testing the hypotheses that (i) climate and species drive general patterns in drought tolerance; (ii) drought events amplify the regular variability in growth responses to climate; (iii) individuals with higher drought tolerance are characterized by specific traits, such as smaller relative growth.

Material and methods

Tree-ring data

We used a comprehensive tree ring data set from Southern Germany and Austria (Table S1, Hartl-Meier *et al*., 2014a,b; Zang *et al*., 2011), consisting of 1760 trees (750 Norway spruce, 460 silver fir, 550 common beech) from 86 sites. The study area covers the region 47–51°N and 9–15°E, and includes lower mountain ranges as well as Alpine sites. An overview of the sampling locations is given in Fig. 1.

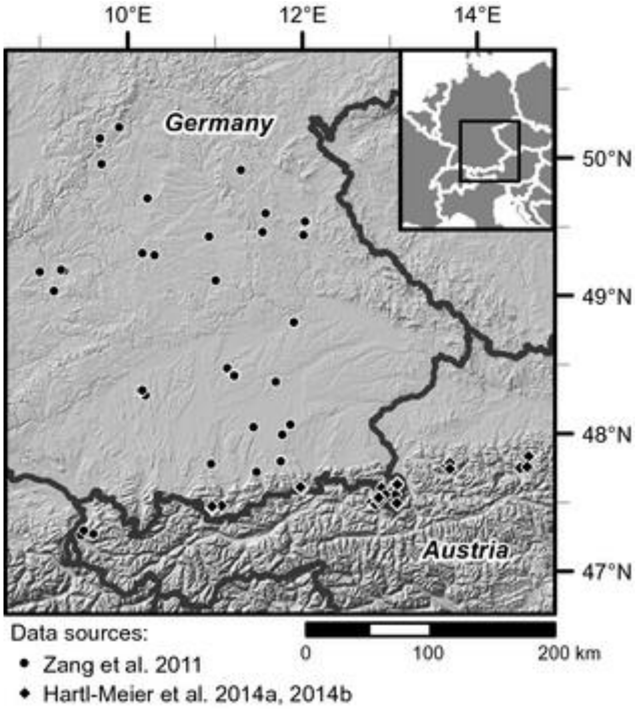

Fig. 1 Map of the investigation area comprising southern Germany and the Alpine area of Austria. The points on the map show the sites where tree-ring data was collected and correspond to the site codes in Table S1.

At each site, we selected ten healthy (co)dominant trees per species (hereafter termed population sample) for coring. To reduce variability due to small-scale differences in site conditions, we sampled only in areas where we could either assume approximately homogenous soil conditions throughout, or where we could confirm, following standardized procedures, uniform substrate by repeated soil coring to at least 1 m in depth followed by *in situ* assessment of soil texture. We cored each tree twice at 1.3 m breast height in opposite directions using 5 mm increment borers (Haglöf, Sweden; Suunto, Finland). Using LINTAB series 5 and 6 measuring tables and the TSAP-Win software package (all Rinntech, Heidelberg, Germany), ring widths were measured to the nearest 0.01 mm on each core. We checked cross-dating accuracy both visually and statistically using program cofecha (Holmes, 1983). The two series of tree-ring widths from one tree were averaged and transformed to basal area increment (BAI) according to Biondi & Qeadan (2008). Lacking a complete record of diameter at breast height, the total basal area for a tree (BA) was approximated as the sum of its annual BAIs.

The tree-ring data were characterized on the level of population samples in terms of mean series length (MSL), expressed population signal (EPS), mean interseries correlation (Rbar), mean sensitivity (MS), and mean BAI (MBAI). EPS, Rbar, and MS were computed for the common time span of 1940–2008 based on raw tree-ring widths, while MBAI was calculated from the BAI series for fixed tree ages of 30–60 years. For each tree, the individual tree age was approximated as the number of rings counted in direction from pith to bark. Real tree age is (partly) underestimated since the pith of the tree was not reached by all cores and the age at which trees reach breast height is varying.

Climatic data

We used temperature and precipitation data from the observational CRU TS 3.2 worldwide data set available on a 0.5° grid (Mitchell & Jones, 2005). Monthly mean temperatures and monthly precipitation sums are available from 1901 and have been aggregated to seasonal means and sums, respectively, corresponding to the summer months of June, July, and August (JJA). Site-specific time series of temperature and precipitation have been constructed by interpolation of the four nearest grid points using inverse distance weighting (Shepard, 1968). The quality of this interpolation from gridded data could be validated for 45 sites using station data and for 39 sites using the HISTALP data set (Auer *et al.*, 2007, see supporting methods M1).

June, July, and August mean temperature and precipitation are highly negatively correlated across the sites for the time span 1939–2008 ($r = -0.88$), indicating that the sampling took place along a distinct climatic gradient from warm and dry to cool and wet. To simplify further climate-related analyses, JJA temperature, and precipitation along the gradient were aggregated into the De Martonne aridity-humidity index (DMI-JJA, De Martonne, 1926) by calculating precipitation sum (in cm)/(temperature (in °C) + 10). The climatic gradient is then characterized by 70 year long-term means (1939–2008) of DMI-JJA. Note that DMI-JJA values increase from warm-dry to cool-wet conditions. Characterization of drought conditions was validated by the SPEI drought index (Standardized Precipitation and Evapotranspiration Index) using CRU, HISTALP, and local climate station data (see next paragraph).

Tree tolerance

Ratios of growth in drought years to growth during reference periods can be used to describe the impact of these events and the subsequent recovery (Fekedulegn *et al.*, 2003; Zang *et al.*, 2011). Lloret *et al.* (2011) presented a unified framework of tolerance components to describe those growth responses. Here, we used the tolerance components resistance (Rt, the ratio between growth during drought and growth prior to drought), recovery (Rc, the ability to recover relative to the growth reduction experienced during drought) and resilience (Rs, the after-drought ability to reach performance levels observed prior to drought). All three measures were calculated based on the individual BAI series, namely BAI during drought (Dr), BAI in the respective predrought period (PreDr), and BAI in the respective postdrought period (PostDr) (Figure S2, Lloret *et al*., 2011) as:

$$\mathrm{Rt} = \mathrm{Dr}/\mathrm{PreDr}$$

$$\mathrm{Rc} = \mathrm{PostDr}/\mathrm{Dr}$$

$$\mathrm{Rs} = \mathrm{PostDr}/\mathrm{PreDr}$$

A three-year period was chosen for both PreDr and PostDr reference (Pretzsch *et al*., 2013). We selected the pan-European drought years of 1947, 1976, and 2003 with extremely dry summers based on the current literature (Beniston, 2004; Fink *et al*., 2004; Vautard *et al*., 2007) as Dr, and pooled the respective tolerance indices for further analyses except for testing ontogenetic effects (see below). Drought conditions were confirmed at all sites for the chosen years using the Standardized Precipitation and Evapotranspiration Index SPEI (Vicente-Serrano *et al*., 2010; see Figure S1 and Data S1). For characterization of the climate cline, we preferred DMI to SPEI, because due to its standardization the SPEI yields meaningless values close to zero for long-term means. Using common drought years across different sites has the advantage that conditions before and after the drought events are similar, which is crucial for the comparison of tolerance indices. This would not necessarily be the case when, e.g. the driest years on each site were chosen (Martínez-Vilalta *et al*., 2012).

To assess the general climatic influence on tree tolerance, population sample means of the individual tolerance components were regressed against DMI-JJA using linear regression.

The relationship between the three tolerance components Rt, Rc, and Rs and the predictors PreDr, BA, and tree age at the level of individual trees were tested with linear mixed effects models. We chose a linear mixed effects approach, because the incorporation of random site effects allows interpreting the fixed effect model parameters regardless of a possible large-scale gradient across the investigation area due to climatic differences. Furthermore, we formulated the models with the maximal random effects structure justified by the sampling design to optimize their generalization performance (Barr *et al*., 2013). We used the site as grouping variable and obtained the general model structure.

$$\begin{aligned}\tilde{T}_{ij} &= \beta_0 + \beta_1 \times \mathrm{PreDr}_{ij} + \beta_2 \times \mathrm{BA}_{ij} + \beta_3 \times \mathrm{age}_{ij} + u_{0j} \\ &\quad + u_{1j} \times \mathrm{PreDr}_{ij} + u_{2j} + \mathrm{BA}_{ij} + u_{3j} \times \mathrm{age}_{ij} + \varepsilon_{ij}\end{aligned}$$

where $\tilde{T}_{ij}$is the vector containing a tolerance index (Rt, Rc, or Rs) for tree *i* and site *j*, *β*0……,*β*3 are fixed effects associated with the standardized tree-level covariates PreDr, BA and age, *u*0j…*u*3j denote the random population sample effects associated with the intercept and PreDr, BA and age slopes, and *ε*ij corresponds to the residuals. The intercept was kept in the model despite standardized variables, since standardization is carried out globally and not on the level of individual population samples.

The influence of PreDr on PostDr was investigated using simpler linear mixed effects models of the form

$$\widetilde{\mathrm{PostDr}}_{ij} = \beta_0 + \beta_1 \times \mathrm{PreDr}_{ij} + u_{0j} \times u_{1j} \times \mathrm{PreDr}_{ij} + \varepsilon_{ij}$$

with fixed effects $\beta 0 \ldots\ldots \beta 1$ and random effects $u0\mathrm{j} \ldots u1\mathrm{j}$ A model with the same mixed effects structure was used to identify a possible relation between tree age and BA.

Assessment of variability in growth response

The variability in growth response to severe drought was assessed using the coefficient of variation (CV) of the individual tree tolerance indices. Since for non-log-normally distributed data the CV does not necessarily correspond to the inequality of the distribution as indicated by e.g. the Gini coefficient (Bendel *et al*., 1989), all tolerance indices for the individual population samples were tested for log-normality using the Shapiro–Wilk test for normality on the log-transformed data. All distributions displayed log-normal or nearly log-normal distributions at the level of individual population samples, and the close relation of CV to the Gini coefficient of inequality was further approved by their close correlation across all population samples ($r = 0.99$, $P < 0.001$).

Since differently aged stands were assembled in this study, with older stands prominently sampled in higher altitudes and thus under relatively more favorable climatic conditions in severe drought years (Table S1), effects of ontogeny on the CV of tolerance indices might mask the effects of regional climate characteristics. Accordingly, the frequent coincidence of older stands and higher altitudes prevented from testing the influence of tree age on the CV by using MSL as factor. To assess a potential ontogenetic bias, we calculated the CV of tolerance indices separately for each drought year. Thus mean tree ages differed by 27 years (between the events of 2003 and 1976), 29 years (between 1976 and 1947), and 56 years (between 2003 and 1947), respectively.

Two different baselines for assessing the variability in tolerance metrics were established: one to compare the individual within-population variability in drought response to the respective background variability (i.e. comparing variability during drought events to variability under average conditions), and a second one to compare the within-population variability to a between-population baseline, i.e. the variability expected when taking all population samples into account.

For the first case, the baseline variability was computed by resampling ($n = 1000$) three random years as Dr for the calculation of tolerance indices and respective CV values for all population samples. Paired (according to populations) one-sided Wilcoxon signed rank test were used to globally test the set of all CV of the tolerance indices for the original three drought years for differences from the corresponding medians of all 1000 intrapopulation baseline CV.

For the second case, we used the relationship between geographical distance and CV of tolerance indices. We randomly selected each ten trees across all population samples of a species, calculated the CV of the tolerance indices and recorded their respective mean geographic distance. For each tolerance index, a distance-CV-relation was constructed on 1000 random samples of ten trees. The effect of mean geographic distance on CV of the tolerance indices was tested using linear regression on the distance-CV-relations, and proved in all cases to be positive and significant at the $P < 0.05$ level (an example is given in Figure S4). The expected variability in a given tolerance index for an average population sample was then derived from the linear fit on the respective distance-CV-relation and its parametric 95% prediction interval for the mean distance of 20 m, assumed to represent a good approximation of the mean distance of the trees in a population sample at a given site.

Linear regression models were used to test for relationships between the CV of the tolerance indices of the individual population samples and DMI-JJA. All computations were performed using R version 3.0.1 (R Development Core Team, 2013) with packages *lme4* (Bates *et al*., 2014), *lmerTest* (Kuznetsova *et al*., 2013), *reldist* (Handcock, 2011) and *dplR* (Bunn *et al*., 2013).

Results

General characteristics of tree-ring data

Mean chronology length was 129 years (spruce 122, fir 131, beech 135), with MSL increasing with altitude (Table S1). The overall quality of the chronologies was high, with a mean EPS of 0.90 (spruce 0.89, fir 0.88, beech 0.93), and 82% of all chronologies reaching the critical value of 0.85 (Wigley *et al*., 1984) (spruce 79%, fir 74%, beech 95%). Chronologies below the 0.85 threshold were not excluded from further analyses, since our analyses focus on three drought years and their preceding/subsequent years, and the dating of these years was assumed to be accurate due to the generally negative deflection of growth associated with these years.

DMI-JJA and altitude were strongly positively correlated ($r = 0.78$, $P < 0.001$), i.e. colder and wetter summers were expected at higher altitudes. For all species, EPS decreased significantly with increasing DMI-JJA, with the weakest relation observed for spruce (spruce: $r = -0.33$, $P = 0.003$; fir: $r = -0.60$, $P < 0.001$; beech: $r = -0.59$, $P < 0.001$). MBAI decreased with DMI-JJA for all species, with the strongest decrease depicted by beech (spruce: $r = -0.50$; fir: $r = -0.48$; beech: $r = -0.53$; all $P < 0.001$). Spruce and fir showed a strong decrease in MS with increasing DMI-JJA (spruce: $r = -0.80$; fir: $r = -0.90$; both $P < 0.001$), while there was no effect of DMI-JJA on MS for beech ($r = 0.00$). No significant correlation between tree age and BA could be observed for fir ($r = 0.03$) and beech ($r = -0.09$), for spruce a significant positive correlation could be detected ($r = 0.31$, $P < 0.001$).

Drought tolerance in relationship with climate

Indices of tolerance to extreme drought events showed clear and consistent relationships to summer climate for Rt and Rc on the population sample level (Fig. 2). For all species, Rt decreased toward the warm and dry end of the gradient (positive correlation with DMI-JJA), with the strongest relation observed for spruce. Since only very few population samples of spruce displayed Rt values above 1.0, a consistent growth decline associated with summer drought was observed, regardless of the regional climatic conditions. For fir and beech, a few population samples displayed Rt values above 1.0, indicating a relative growth increase under summer drought. Population samples with Rt values above 1.0 were distributed rather evenly over the climatic gradient for the latter two species (Fig. 2).

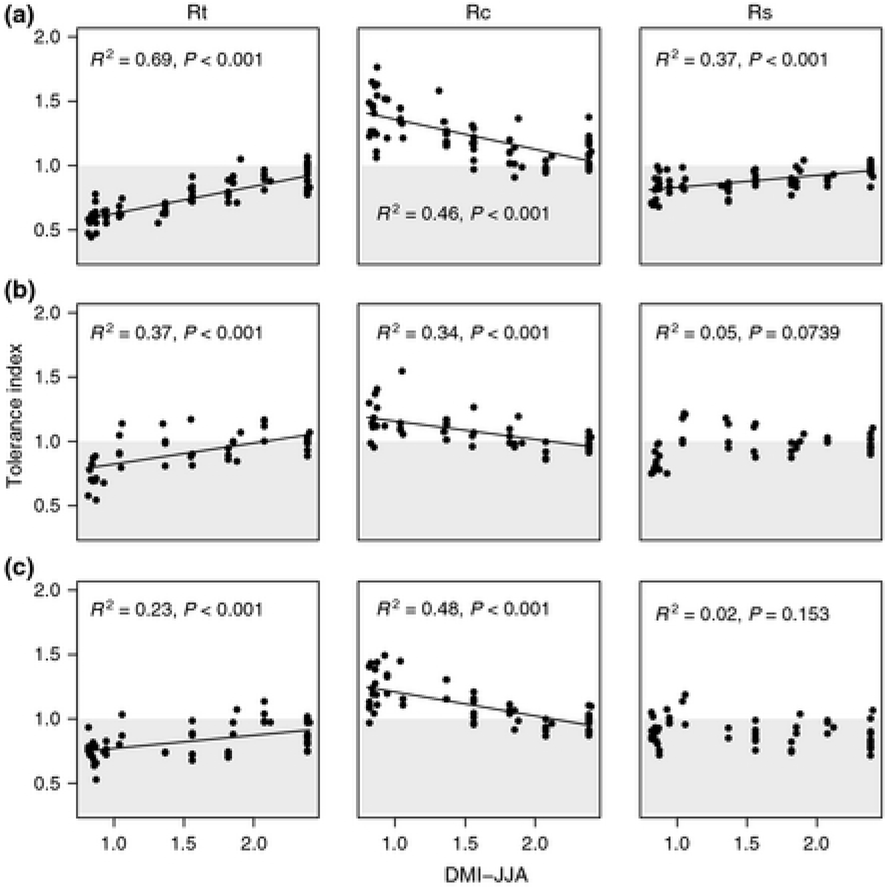

Fig. 2 Correlation of the tolerance indices resistance (Rt), recovery (Rc), and resilience (Rs) in spruce (a), fir (b), and beech (c) on population sample level with DMI-JJA. Coefficients of determination and significance values correspond to the respective linear model fits. The light gray area represents a relative growth decline (index values < 1).

The relation of summer climate and Rc was inverted, with higher Rc values observed toward the warm and dry end of the gradient (Fig. 2). This indicated a quick recovery from the more severe effects in Rt by a relatively faster growth rate after the drought event. The majority of population samples displayed Rc values above 1.0. This means, that only a few population samples displayed progressing growth decline after the drought event.

We did not find a significant correlation of Rs and DMI-JJA for fir and beech, whereas spruce depicted a relatively strong positive correlation of Rs and DMI-JJA implying long-lasting drought effects at the warm-drier end of the gradient (Fig. 2).

A direct comparison of the species along the climatic gradient (Fig. 3) showed generally higher Rt and Rs in silver fir in comparison to Norway spruce and common beech. Spruce consistently showed lower Rt and higher Rc than beech and fir. Furthermore, spruce had the smallest Rs at the warm and dry end of the gradient.

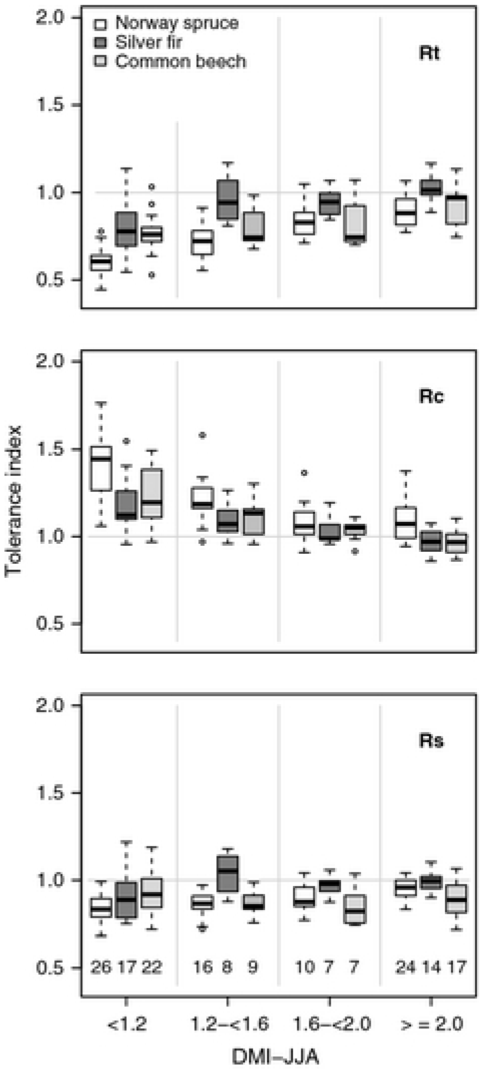

Fig. 3 Comparison of the tolerance indices resistance (Rt), recovery (Rc), and resilience (Rs) in spruce, fir, and beech along the climatic gradient characterized by DMI-JJA. The numbers under the boxes in the lowest panel indicate the number of observations in each group.

PreDr and PostDr growth were highly positively correlated for all species, with fixed effects estimates of 0.90 for spruce, 0.81 for fir, and 0.88 for beech (all $P < 0.001$). The different components of tolerance were surprisingly differently controlled by PreDr, BA and tree age (Table 1). The strongest influence on Rt was exerted by PreDr in all species, resulting in throughout negative correlations between Rt and PreDr. In spruce and fir, age had no influence on Rt, while BA had a positive effect on Rt, resulting in higher Rt for larger trees. For beech, BA also had a positive effect on Rt, while age had a negative effect, leading to smaller Rt for older trees. In spruce and fir, Rc was predominantly controlled by age, with older trees showing smaller Rc. In beech, age was also negatively associated with Rc, but equally strong effects were exerted by PreDr (negative) and BA (positive). Consequently, this led to an influence of all three parameters on Rs, with PreDr displaying the strongest effect in all species, resulting in trees with low predrought growth rates exhibiting higher Rs. BA was positively, and age was negatively associated with Rs in all species (Table 1).

Table 1 Parameters for fixed effects ($\beta 1\ldots$, $\beta 3$) in the linear mixed effects models relating tolerance indices resistance (Rt), recovery (Rc) and resilience (Rs) to predrought growth level (PreDr), basal area (BA), and tree age. Reported are the parameter values and the significance of the fixed effects (coded as: *** for $P < 0.001$, **for $P < 0.01$, and *for $P < 0.05$) for the species-wise models (sample size for spruce was 750, 460 for fir, and 550 for beech)

Species	Fixed effects	Rt	Rc	Rs
Norway spruce	PreDr	−0.35***	−0.11	−0.74***
	Age	0.05	−0.50***	−0.44***
	BA	0.29***	0.11	0.66***
Silver fir	PreDr	−0.33***	−0.21*	−0.50***
	Age	0.00	−0.55***	−0.27*
	BA	0.16**	0.19*	0.31***
Common beech	PreDr	−0.48***	−0.36***	−0.92***
	Age	−0.25**	−0.37***	-0.64***
	BA	0.29**	0.29**	0.60***

Intrapopulation variability in drought years vs. background variability

For all species, the variability in Rt, Rc, and Rs in drought years was significantly higher than the background variability calculated by random selection of event years from the same population samples ($P < 0.05$ in all cases, Fig. 4). The strongest increase from background variability to variability under severe drought conditions was depicted by beech and the weakest increase was found for Rs of spruce.

In spruce and fir, MS, as an integrative measure over all series of a population sample, could explain the variability in the tolerance metrics under drought conditions quite well (Table 2).

Table 2. Summary of the linear regression models relating the variability in tolerance indices resistance (CV of Rt), recovery (CV of Rc), and resilience (CV of Rs) to the chronology characteristic mean sensitivity (MS) (see text for explanation). Reported are the coefficients of determination ($R2$, numeric), and the significance of the ordinary least squares regression (coded as: ***for $P < 0.001$, **for $P < 0.01$, and *for $P < 0.05$) for the species-wise models (sample size was 75 for spruce, 46 for fir, and 55 for beech). All correlations between CV and MS are negative

Species		CV of Rt	CV of Rc	CV of Rs
Norway spruce	MS	0.32***	0.42***	0.36***
Silver fir	MS	0.34***	0.41***	0.37***
Common beech	MS	0.01	0.01	0.01

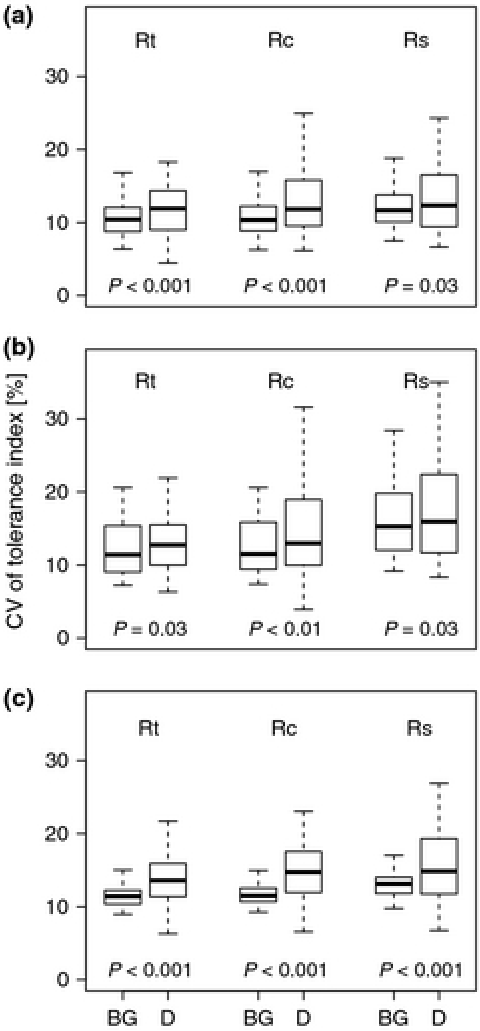

Fig. 4 Comparison of intrapopulation background variability (BG) with variability in drought years 1947, 1976, and 2003 (D) for resistance (Rt), recovery (Rc), and resilience (Rs) in spruce (a, sample size $n = 75$ for all groups), fir (b, $n = 46$), and beech (c, $n = 55$). Significance levels correspond to one-sided paired Wilcoxon signed rank tests.

Since the study employed differently aged stands, we also tested for systematic ontogenetic effects on the variability in tolerance metrics using the individual drought years separately. Due to the lack of consistent differences in the coefficient of variation in tolerance indices (CV) related to increasing mean tree age (Figure S3), we can discard a potential ontogenetic effect on CV at the population level.

Climatic drivers of variability in tolerance

For spruce and fir, DMI-JJA could explain the variability in tolerance indices at the population sample level (Fig. 5). The variability in all tolerance indices increased with warmer and drier conditions. For beech, only the variability in Rc showed a weak negative correlation with increasing DMI-JJA (Fig. 5).

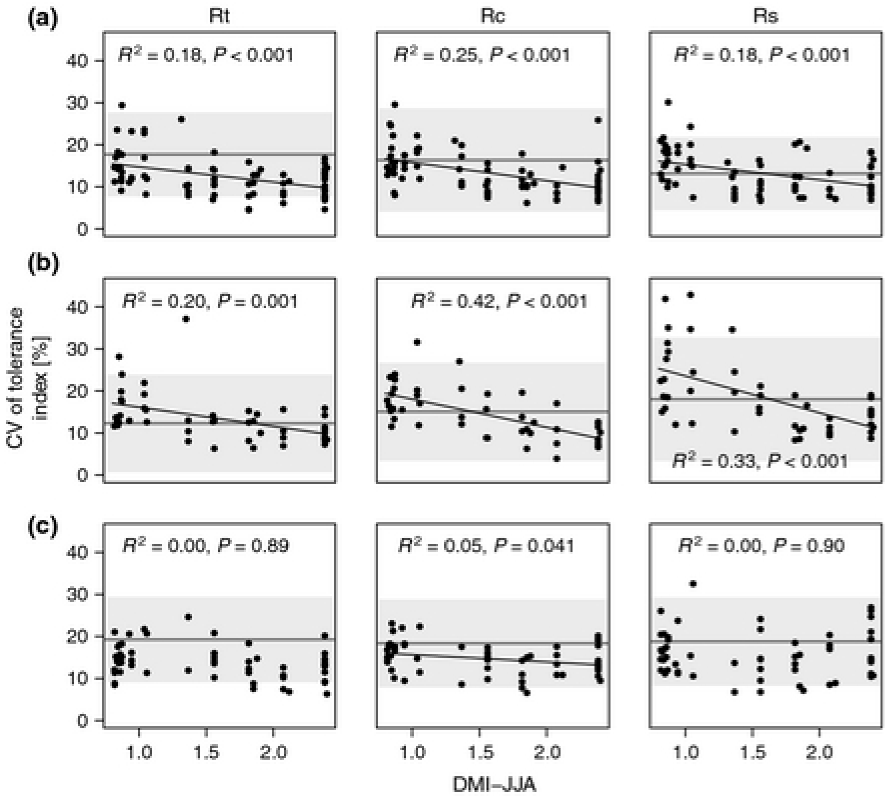

Fig. 5 Correlation of variability in tolerance indices resistance (Rt), recovery (Rc), and resilience (Rs) in spruce (a), fir (b), and beech (c) with DMI-JJA. Coefficients of determination and significance values correspond to the respective linear model fits. The dark gray line corresponds to the expected CV at a distance of 20 m, the area shaded in light gray signifies its parametric prediction interval.

Relation to expected variability

Most population samples displayed intrapopulation variabilities in tolerance metrics inside the prediction interval for the expected variability based on the intraspecific range (Fig. 5). This means that only few populations displayed either higher or lower variability than would be expected from treating the whole data set as one population.

Higher than expected variability occurred only at the warm and dry end of the gradient, most prominently for Rs of fir (Fig. 5), but also for the other tolerance indices of spruce and fir. In beech, higher than expected variability was not observed for Rt and Rc, and only one population showed higher than expected variability in Rs (Fig. 5).

Discussion

Chronology characteristics

Observed reduced mean sensitivity (MS) at wet-cool summer conditions (higher DMI-JJA) for spruce and fir points at decreasing climatic constraints on the year-to-year variability in tree growth (Fritts, 1976). In cool-wet summers, non-climatic factors contribute stronger to year-to-year variability in tree growth, and the common growth signal of the population samples (EPS) is reduced. A decrease in MS with altitude (and thus climatic constraints) in closed stands of Norway spruce and silver fir was also observed by Dittmar *et al*. (2012) in Southern Germany. This is in contrast to well-established relationships between MS and altitude as the basis for climate reconstruction from tree rings where sensitivity and climate signal strength increases with altitude. However, our findings were retrieved at sites from lowlands to below the tree line.

Species-specific tolerance to drought

All three species compared in this study displayed strong relations between resistance and recovery (tolerance indices Rt and Rc) and summer climate (Fig. 2). The strongest relation was found for Rt in spruce, with a particularly large part of the variance explained by the climatic gradient. In all species, Rt and Rc behaved reciprocal and low Rt values were generally linked to higher Rc values. This resulted in a relatively weak climatic differentiation of the integrating factor of resilience (Rs) in silver fir and common beech (Fig. 3), while for Norway spruce, Rs still followed the climatic gradient notably well (Fig. 2). Most spruce population samples showed a prolonged growth reduction after the three drought years of 1947, 1976, and 2003 as indicated by low Rs (Fig. 2). This confirms the rating of Norway spruce as a particularly drought intolerant species as previously indicated by complementary approaches, such as climatic envelopes (Kölling, 2007), simulation studies (Pretzsch & Dursky, 2002), ecophysiological studies (Cochard, 1992), and other dendroecological assessments (Kahle & Spiecker, 1996; Mäkinen *et al*., 2002; Pretzsch *et al*., 2013).

The even distribution of resilience (Rs) along the climatic gradient in fir and beech (Fig. 2) indicates full recoveries from the initial impact of drought independent from general climate conditions. Following Galiano *et al*. (2011), a strong growth reduction (in terms of a low Rt) which was also observed toward the warm and dry end of the climatic gradient for the majority of fir and beech populations, is only compensated if Rc is not exclusively dependent on stored carbon reserves, but profits from rebuilt photosynthetic tissue.

The different response patterns of spruce and beech along the climatic gradient (Fig. 3) agree with the findings of Pretzsch *et al*. (2013). According to literature, the isohydric spruce reduces water consumption and growth already in an early stage of drought stress through stomata closure (Dobson *et al*., 1990; Maier-Maercker, 1998), a strategy that avoids damages and allows for a relatively quick recovery. However, our study suggests, that due to resilience varying with site, spruce is only competitive with beech at the cooler and wetter half of the climatic gradient. This insufficient recovery in stem growth from drought stress can be explained by a strong preconditioning of growth through previous-year climate (Zang *et al*., 2011) and changes in the root-shoot allometry as a direct response to dry conditions (Nikolova *et al*., 2011). In contrast, the more anisohydric beech maintains a higher stomatal conductivity throughout the drought period, and can thus continue to grow for longer. This strategy risks the hydraulic integrity of the xylem, e.g. by xylem embolism (Geßler *et al*., 2007). Considerable investments of assimilates into the restoration of the conducting pathway result in slow recovery rates after-drought stress (Pretzsch *et al*., 2013).

In comparison to spruce and beech, fir generally showed high values of resistance (Rt) and resilience (Rs) across the whole climatic gradient (Fig. 3). This is well consistent with the findings of Elling *et al*. (2009) that healthy fir trees (i.e. especially those not damaged by SO2 immissions) show a remarkably good drought-resistance in Central Europe.

Aside from increasing severity of drought, there might also be a genetic differentiation along the climatic gradient. Modrzyński & Eriksson (2002) found local adaptation to drought in Norway spruce from southern Poland in terms of earlier bud set and higher root biomass in high-elevational individuals. This is interpreted as a relative advantage of high-elevation ecotypes, when drought conditions will intensify with climate change. On the other hand, King *et al*. (2013) found strong evidence for gene flow in Norway spruce along an altitudinal gradient, possibly counteracting local adaption.

Variability in drought response at the population level

Literature suggests that increasing climatic stress will increase the common climatic signal in tree growth, thus EPS, since the contributions of nonclimatic effects on tree growth are reduced (Fritts, 1976). This rationale is the basis of climate reconstruction using tree-ring proxy data. Also, provenance trials indicate that variation in response pattern with genetics is smaller under generally less favorable conditions (Modrzyński & Eriksson, 2002; Taeger *et al*., 2013).

However, our study for the first time revealed that we cannot conclude from patterns of climate sensitivity under less favorable climate conditions to patterns in extreme years, since different mechanisms apply when climatic extremes are considered: instead of a more uniform response of the whole population, we found a significant increase in variability in within-population drought responses (Fig. 4). Since variability and inequality were highly correlated at the level of population samples (see Material and methods section), a higher variability in drought responses is linked to a more unequal distribution of the responses. Our finding that the more severe a drought extreme is, the more variability in response can be expected at the population sample level was also confirmed by the comparison along the climatic gradient (Fig. 5). Here, the variability in all tolerance indices (spruce and fir) or Rs (beech) at the population sample level significantly increased from favorable to less favorable conditions. This is consistent with the observation that during low-growth episodes, the inequality in size-increment is increased within stands (Metsaranta & Lieffers, 2008). In addition, this is indicated by a change from size-asymmetric to size-symmetric competition under drought stress (Zang *et al*., 2012), leading to the development of distinct size hierarchies in the long run (Metsaranta & Lieffers, 2008).

The comparison of observed vs. expected (horizontal lines in Fig. 5) individual level variability for the population samples showed a remarkable and significant increase in variability for some populations of spruce and fir at the warm and dry end of the climatic gradient. Consequently, the observed high resilience of fir under these conditions must stem from some extremely well performing trees that outweigh other, poorly performing trees in the population samples. This is supported by the observation that during low-growth episodes the increased inequality in size-increment is caused by a few, extraordinarily fast growing individuals (Metsaranta & Lieffers, 2008).

For all species and sites, growth rates prior and after-drought events were highly positively correlated. Thus, effects of disturbance or mortality of neighbor trees on observed tree tolerance should be of minor importance. Lloret *et al*. (2011) interpret such a correlation as an effect of robustness: trees that are more robust due to microsite conditions and intrinsic factors (physiological state, genetics) are able to perform better after stress periods.

Variability in drought response at the individual level

At the level of individuals, we found a considerable relationship between high tolerance against drought and low-growth rates prior to drought (Table 1). While high growth rates are intuitively associated with benefits for the fitness of trees, Bigler & Veblen (2009) showed decreased longevity of conifers connected to increased early growth rates. Martínez-Vilalta *et al*. (2012) found a link between high growth rates prior to drought and high-drought susceptibility. This is interpreted as a reduced investment in defense, and structural disadvantages such as decreased root-shoot ratio or decreased mechanical stability. Bigler & Veblen (2009) also confirm this relationship for different tree ages. Equally in our study, the average growth rate for the first 30 years of each trees' life is a similarly good predictor for tolerance to drought as the growth immediately preceding the drought event (PreDr, $P < 0.001$ for all species, data not shown). Higher PreDr growth rates can therefore be interpreted in terms of structural maladaptation to extreme drought.

The sole focus on above-ground stem growth is an important shortcoming of the tolerance indices used. Since relatively low above-ground growth rates could also be due to an increased root to shoot allocation ratio, smaller above-ground growth could consequently be linked to improved water uptake and the possibility to shut down photosynthesis later (Comeau & Kimmins, 1989; Nikolova *et al*., 2011; Pretzsch *et al*., 2012). Our finding of lower growth rates being associated with increased resistance to drought events is further confirmed by provenance studies, where highly drought-resistant origins show reduced above-ground growth rates (Rose *et al*., 2009; Taeger *et al*., 2013).

Although we sampled only (co)dominant trees, tree size had a positive effect on all tolerance indices, with the strongest influence on Rt and Rs (Table 1). Dominant trees are more likely to compete successfully for resources, such as water. These findings are well consistent with studies on Norway spruce, that demonstrate smaller growth reductions in drought years of dominant trees as compared to suppressed ones (van den Brakel & Visser, 1996; Zang *et al*., 2012).

Recovery from drought events also depended on tree age, however, opposite to the effect of tree size described above. Younger trees recovered better and thus showed higher resilience to drought. The literature on ontogenetic changes in climate sensitivity is ambiguous, pointing at either no consistent change across age classes (Carrer & Urbinati, 2004; Esper *et al*., 2008), or at a declining sensitivity with increasing tree age (Szeicz & MacDonald, 1995; Rozas *et al*., 2009). However, most of the studies relating tree age to climate sensitivity focus on long-term growth-climate relationships, but not on climatic extremes. For drought extremes, a higher tree age has been associated to lower resilience in the growth response (Martínez-Vilalta *et al.*, 2012). In the case of drought, decreasing resistance with age can be interpreted as a decreasing capability to compensate for the loss in reserves due to reduced photosynthetic capacity (Yoder *et al.*, 1994) or ontogenetic changes in root structural traits (Rozas *et al.*, 2009).

Implications for ecosystem management

The unequivocally lower drought tolerance of Norway spruce, especially at the warm-dry end of the climatic gradient suggests a rethinking of this species' suitability in future forests, especially where climate and soil conditions reinforce extreme drought episodes in the future (Boden *et al.*, 2014). Drought events amplify the regular diversity in growth responses to climate, and lead to more heterogeneous and variable response patterns in forests stands. Despite the careful sampling design, we cannot exclude microsite effects on individual tree growth interacting with possible genetic traits. But generally, trees with a (genetically or microsite derived) predisposition to lower above-ground growth rates could in the long-term be favored by directional selection under aggravating summer droughts. This is also supported by recent findings on the coupling of growth and drought susceptibility of forest trees in the Mediterranean (Martínez-Vilalta *et al.*, 2012; Morán-López *et al.*, 2014). On the other hand, rising temperatures, higher atmospheric CO2 concentrations, and increasing availability of nutrients through atmospheric deposition have led to accelerated tree growth during the 20th century in Europe (Spiecker, 1999). As indicated by our results, this trend may favor structural maladaptation to drought-induced physiological stress, and can therefore contribute to the destabilization of forest stands under climate change by lowering the resilience of growth response to drought events. Consequently, whether the idea of deliberately using spontaneous selection and adaption effects as a passive strategy in forest management (Bolte *et al.*, 2009) is supported by the strong diversity in drought response at the population level can only be decided after further investigations. A special focus on the interaction between microsite and genetic influence on the linkage between age, growth rate and resilience of tree growth to drought and other important facets of performance under drought such as regeneration and mortality on individual and population level is of primary importance in this regard.

Acknowledgements

The research leading to these results has received funding from the European Research Council under the European Union's Seventh Framework Programme (FP7/2007-2013)/ERC grant agreement n° (282250) and the Bavarian State Ministry for Food, Agriculture and Forestry (board of trustees of the Bavarian State Institute of Forestry LWF, grant E 45). C.H.-M. acknowledges funding by the Bavarian State Ministry for Food, Agriculture and Forestry and the EU program INTERREG within the project SICALP (J00183). The authors thank two anonymous reviewers for their comments on previous versions of this manuscript.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Data S1. Validation of interpolated climate data against station data and the HISTALP data set.
Data S2. Verification of drought conditions at the sampled sites.
Figure S1. SPEI values for all sites, calculated from gridded SPEI data and from local station data and the HISTALP data set.
Figure S2. Response to drought characterized by growth in the periods before the drought event, during, and after the drought event.
Figure S3. Testing for ontogenetic effects on variability in tolerance indices.
Figure S4. Exemplary distance-CV-relation for the mean geographic distance of 10 randomly selected trees and the CV for a tolerance index.
Table S1. Location and elevation for all sampling sites, and characteristics of tree-ring chronologies for the sampled species.

Patterns of drought tolerance in major European temperate forest trees: climatic drivers and levels of variability

Supporting Information

Christian Zang[1], Claudia Hartl-Meier[2], Christoph Dittmar[3],
Andreas Rothe[4], Annette Menzel[1,5]

[1]Chair of Ecoclimatology, Technische Universität München, Hans-Carl-von-Carlowitz-Platz 2, 85354 Freising, Germany

[2]Department of Geography, Johann-Joachim-Becher-Weg 21, 55128 Mainz, Germany

[3]Environmental Research and Education (UFB), Am Sandacker 25, 95511 Mistelbach, Germany

[4]Faculty of Forestry, University of Applied Sciences Weihenstephan-Triesdorf, Hans-Carl-von-Carlowitz-Platz 3, 85354 Freising, Germany

[5]Institute for Advanced Study, Technische Universität München, Lichtenbergstr. 2a, 85748 Garching, Germany

Table S1: Location and elevation for all sampling sites, and characteristics of tree-ring chronologies for the sampled species: mean segment length (MSL), expressed population signal (EPS), mean interseries correlation (Rbar), mean sensitivity (MS), and mean basal area increment (MBAI).

#	Site	Lat [°N]	Lon [°E]	Alt [m a.s.l.]	Species	MSL [a]	EPS	Rbar	MS	MBAI [mm^2]
1	QGHT	49.17	9.10	230	*P. abies*	76	0.89	0.45	0.29	2375
2					*A. alba*	80	0.96	0.70	0.31	1769
3					*F. sylvatica*	79	0.99	0.88	0.25	1883
4	HSBB	50.13	9.72	250	*F. sylvatica*	74	0.97	0.78	0.22	1208
5	HSKM	50.14	9.72	250	*F. sylvatica*	87	0.99	0.88	0.24	1833
6	ASHE	49.96	9.74	260	*F. sylvatica*	110	0.98	0.66	0.26	1002
7	HSLF	50.15	9.72	260	*P. abies*	99	0.87	0.40	0.26	1418
8					*F. sylvatica*	93	0.97	0.79	0.26	732
9	QGHK	49.19	9.33	285	*P. abies*	73	0.95	0.68	0.36	1146
10	QGHB	49.18	9.37	305	*P. abies*	76	0.94	0.62	0.29	1488
11					*A. alba*	78	0.95	0.68	0.33	1710
12					*F. sylvatica*	114	0.96	0.68	0.35	1333
13	QGHI	49.03	9.27	310	*P. abies*	45	0.86	0.43	0.30	1930
14					*A. alba*	65	0.95	0.66	0.29	2883
15					*F. sylvatica*	58	0.97	0.80	0.32	2518
16	RTAV	49.45	10.96	360	*P. abies*	97	0.94	0.61	0.33	1466
17					*A. alba*	91	0.94	0.60	0.30	1571
18					*F. sylvatica*	117	0.90	0.47	0.28	1074
19	BBOB	50.24	9.93	400	*P. abies*	65	0.89	0.48	0.28	1584
20					*A. alba*	88	0.95	0.68	0.26	915
21					*F. sylvatica*	75	0.99	0.92	0.23	912
22	RXHS	49.49	11.56	420	*P. abies*	67	0.97	0.76	0.28	3211
23					*A. alba*	95	0.91	0.51	0.27	1283
24	KNJB	49.73	10.27	430	*F. sylvatica*	123	0.91	0.51	0.28	2116
25	RTSL	49.31	10.37	440	*P. abies*	77	0.95	0.67	0.33	1597
26					*A. alba*	98	0.91	0.51	0.33	1417
27					*F. sylvatica*	87	0.98	0.81	0.27	1014
28	SNBS	49.57	12.05	440	*P. abies*	106	0.98	0.84	0.20	348
29	SNHS	49.57	12.05	440	*P. abies*	75	0.94	0.60	0.25	1771
30					*A. alba*	100	0.98	0.86	0.29	977
31	SNMG	49.63	11.59	440	*P. abies*	60	0.94	0.65	0.26	2289
32					*F. sylvatica*	89	0.97	0.79	0.21	1348
33	ALWB	49.14	11.04	460	*P. abies*	75	0.94	0.61	0.25	1742
34					*A. alba*	142	0.97	0.77	0.32	978
35					*F. sylvatica*	144	0.97	0.79	0.26	495
36	BTHK	49.94	11.32	460	*P. abies*	91	0.92	0.54	0.23	1847
37					*A. alba*	100	0.96	0.71	0.27	1294
38					*F. sylvatica*	101	0.99	0.90	0.20	704
39	KHKF	48.84	11.91	470	*P. abies*	68	0.95	0.65	0.26	1269
40					*F. sylvatica*	78	0.97	0.74	0.27	1145
41	KHKT	48.84	11.91	470	*P. abies*	67	0.95	0.67	0.27	731
42	KHLF	48.84	11.91	470	*F. sylvatica*	111	0.98	0.86	0.23	622
43	KHLW	48.84	11.91	470	*P. abies*	82	0.86	0.33	0.25	1528
44					*F. sylvatica*	111	0.94	0.62	0.25	768
45	LLSN	48.45	11.27	470	*P. abies*	102	0.95	0.67	0.23	1404
46					*A. alba*	109	0.90	0.46	0.26	1216
47	LLSR	48.45	11.25	470	*P. abies*	85	0.96	0.69	0.22	1795
48					*A. alba*	89	0.95	0.64	0.26	1253
49					*F. sylvatica*	82	0.98	0.81	0.19	2304

50	LLSS	48.45	11.26	470	*P. abies*	93	0.92	0.54	0.24	2269
51					*A. alba*	104	0.87	0.40	0.32	1174
52	ANOS	49.33	10.23	475	*P. abies*	89	0.86	0.38	0.28	1919
53					*A. alba*	97	0.88	0.43	0.27	1617
54					*F. sylvatica*	100	0.96	0.76	0.24	1157
55	FSSC	48.41	11.71	475	*P. abies*	35	0.97	0.76	0.26	484
56	WHWG	48.33	10.26	520	*A. alba*	55	0.95	0.67	0.25	4344
57	MWSE	47.79	13.55	527	*P. abies*	179	0.89	0.45	0.22	536
58					*F. sylvatica*	180	0.97	0.76	0.18	344
59	WHBK	48.29	10.30	530	*P. abies*	105	0.97	0.75	0.27	951
60	WHSB	48.32	10.25	530	*P. abies*	75	0.91	0.49	0.24	2292
61					*A. alba*	82	0.95	0.67	0.29	2015
62					*F. sylvatica*	90	0.90	0.47	0.22	1667
63	WHSG	48.32	10.25	530	*F. sylvatica*	55	0.96	0.74	0.23	3235
64	WSEF	48.09	11.87	560	*P. abies*	83	0.93	0.56	0.23	1731
65	WSEM	48.09	11.87	560	*P. abies*	80	0.90	0.46	0.23	1977
66	MCFP	48.07	11.48	570	*P. abies*	57	0.96	0.74	0.27	3388
67	SNFB	49.47	12.02	580	*P. abies*	57	0.97	0.80	0.24	2245
68					*A. alba*	70	0.96	0.73	0.29	1724
69					*F. sylvatica*	109	0.94	0.60	0.25	1066
70	WSHK	48.02	11.79	590	*P. abies*	77	0.95	0.68	0.20	1192
71					*A. alba*	68	0.94	0.60	0.23	2145
72					*F. sylvatica*	84	0.92	0.53	0.27	1642
73	NGML	47.58	12.99	680	*P. abies*	104	0.94	0.62	0.22	1022
74					*F. sylvatica*	108	0.94	0.61	0.24	827
75	TSSW	47.59	13.00	690	*P. abies*	68	0.98	0.82	0.23	2291
76					*A. alba*	122	0.93	0.58	0.20	590
77					*F. sylvatica*	89	0.89	0.45	0.23	1398
78	SAGB	47.53	12.74	700	*P. abies*	115	0.75	0.23	0.14	1278
79					*F. sylvatica*	102	0.85	0.36	0.18	1076
80	ATTI	47.30	9.68	700	*P. abies*	71	0.87	0.50	0.18	1941
81					*A. alba*	83	0.94	0.70	0.22	1111
82	SMTN	47.84	11.77	730	*P. abies*	100	0.90	0.48	0.23	1579
83					*A. alba*	105	0.90	0.49	0.22	1650
84					*F. sylvatica*	104	0.95	0.75	0.22	979
85	SMTS	47.83	11.77	730	*P. abies*	104	0.89	0.46	0.20	1944
86					*A. alba*	105	0.91	0.50	0.22	1702
87	MXUB	47.75	11.51	740	*P. abies*	74	0.96	0.71	0.20	2181
88					*A. alba*	77	0.96	0.70	0.18	2298
89					*F. sylvatica*	82	0.86	0.37	0.24	1562
90	BGBS	47.67	13.02	760	*P. abies*	134	0.89	0.45	0.19	669
91					*A. alba*	119	0.92	0.52	0.19	811
92					*F. sylvatica*	143	0.89	0.45	0.21	613
93	BGOB	47.65	13.02	770	*P. abies*	126	0.86	0.39	0.19	866
94					*A. alba*	138	0.83	0.32	0.18	689
95	MWSD	47.80	13.59	791	*P. abies*	225	0.87	0.40	0.22	166
96					*A. alba*	232	0.84	0.34	0.18	166
97					*F. sylvatica*	237	0.94	0.61	0.24	156
98	OGLD	47.48	11.03	838	*P. abies*	154	0.83	0.33	0.14	444
99					*A. alba*	183	0.89	0.46	0.18	281
100					*F. sylvatica*	171	0.92	0.54	0.20	261
101	NKZS	47.84	14.44	876	*P. abies*	217	0.92	0.52	0.20	710
102					*F. sylvatica*	207	0.92	0.53	0.25	274
103	NKZP	47.84	14.45	894	*P. abies*	94	0.96	0.69	0.16	1231
104					*F. sylvatica*	93	0.97	0.79	0.22	982

105	NKZN	47.84	14.44	901	*P. abies*	130	0.69	0.18	0.18	1089
106					*F. sylvatica*	201	0.91	0.51	0.24	384
107	OGHP	47.80	11.02	910	*P. abies*	101	0.91	0.49	0.23	1392
108					*A. alba*	107	0.96	0.72	0.26	1012
109	SSHU	47.63	12.00	920	*P. abies*	190	0.79	0.27	0.15	411
110					*A. alba*	165	0.89	0.44	0.17	142
111					*F. sylvatica*	173	0.94	0.59	0.22	75
112	NKRB	47.76	14.34	950	*P. abies*	176	0.79	0.27	0.20	794
113					*A. alba*	221	0.80	0.28	0.17	180
114					*F. sylvatica*	175	0.94	0.60	0.23	317
115	NGEW	47.57	12.80	960	*P. abies*	137	0.96	0.73	0.16	831
116					*A. alba*	146	0.78	0.26	0.15	1055
117					*F. sylvatica*	145	0.87	0.39	0.22	890
118	MWSC	47.80	13.59	978	*P. abies*	230	0.82	0.32	0.19	455
119					*A. alba*	222	0.89	0.45	0.20	352
120					*F. sylvatica*	250	0.86	0.39	0.27	162
121	ATVB	47.30	9.68	1000	*P. abies*	125	0.68	0.17	0.18	1824
122					*A. alba*	131	0.90	0.44	0.22	1585
123	BGOA	47.66	13.02	1020	*P. abies*	132	0.84	0.34	0.17	1148
124					*A. alba*	133	0.75	0.23	0.18	483
125					*F. sylvatica*	133	0.91	0.51	0.22	757
126	OGLC	47.49	11.03	1020	*P. abies*	178	0.73	0.21	0.16	350
127					*A. alba*	184	0.63	0.15	0.18	541
128					*F. sylvatica*	188	0.93	0.58	0.22	148
129	BGGP	47.63	12.85	1040	*P. abies*	121	0.90	0.47	0.18	1122
130					*A. alba*	159	0.53	0.10	0.17	1051
131					*F. sylvatica*	175	0.80	0.29	0.25	357
132	SAMA	47.51	12.78	1080	*P. abies*	115	0.76	0.24	0.18	1286
133					*A. alba*	139	0.67	0.17	0.15	842
134					*F. sylvatica*	166	0.86	0.38	0.20	433
135	SSHO	47.04	11.26	1110	*P. abies*	184	0.84	0.34	0.18	258
136					*A. alba*	180	0.99	0.91	0.16	235
137					*F. sylvatica*	171	0.92	0.52	0.18	138
138	NKSK	47.75	14.44	1150	*P. abies*	194	0.87	0.41	0.21	582
139					*A. alba*	211	0.88	0.41	0.19	421
140					*F. sylvatica*	220	0.90	0.48	0.29	254
141	MWSB	47.81	13.59	1209	*P. abies*	227	0.91	0.51	0.17	812
142					*A. alba*	231	0.94	0.62	0.15	578
143					*F. sylvatica*	233	0.93	0.56	0.28	237
144	NGLS	47.51	13.02	1220	*P. abies*	182	0.87	0.40	0.18	963
145					*F. sylvatica*	189	0.90	0.48	0.36	621
146	OGLB	47.49	11.03	1220	*P. abies*	195	0.90	0.48	0.17	385
147					*A. alba*	178	0.87	0.41	0.18	536
148					*F. sylvatica*	195	0.95	0.65	0.31	206
149	SAMG	47.51	12.78	1250	*P. abies*	141	0.90	0.49	0.15	826
150					*A. alba*	171	0.61	0.13	0.16	950
151					*F. sylvatica*	181	0.91	0.50	0.31	196
152	SSAK	47.64	11.97	1270	*P. abies*	77	0.87	0.41	0.16	964
153					*A. alba*	195	0.80	0.29	0.17	427
154					*F. sylvatica*	155	0.77	0.25	0.20	151
155	OGWB	47.50	11.14	1280	*P. abies*	201	0.79	0.28	0.15	259
156	ATBL	47.28	9.78	1300	*P. abies*	132	0.92	0.52	0.17	1967
157					*A. alba*	158	0.77	0.25	0.16	2124
158	NGMW	47.56	12.80	1310	*P. abies*	198	0.90	0.46	0.15	463
159					*A. alba*	156	0.79	0.27	0.15	1325

160					*F. sylvatica*	159	0.93	0.57	0.31	353
161	NGMK	47.58	12.89	1330	*P. abies*	147	0.91	0.50	0.15	973
162					*F. sylvatica*	173	0.95	0.67	0.38	553
163	MWSA	47.81	13.59	1337	*P. abies*	206	0.82	0.31	0.17	243
164	NKGU	47.76	14.42	1350	*P. abies*	138	0.81	0.29	0.16	1327
165					*F. sylvatica*	158	0.94	0.59	0.31	415
166	OGLA	47.50	11.03	1400	*P. abies*	197	0.88	0.42	0.15	333
167					*A. alba*	162	0.90	0.48	0.15	814
168					*F. sylvatica*	180	0.93	0.57	0.33	228
169	SSMS	47.64	11.98	1450	*P. abies*	135	0.91	0.49	0.20	612
170	NKGO	47.76	14.42	1460	*P. abies*	158	0.83	0.32	0.16	797
171					*F. sylvatica*	143	0.93	0.57	0.28	491
172	SAKK	47.54	12.82	1530	*P. abies*	153	0.88	0.43	0.16	690
173	NGMA	47.55	12.81	1560	*P. abies*	122	0.89	0.46	0.15	1495
174	NGSB	47.57	12.82	1600	*P. abies*	293	0.83	0.32	0.16	217
175	NGHS	47.56	12.82	1620	*P. abies*	148	0.93	0.57	0.15	781
176	NGKS	47.52	13.01	1670	*P. abies*	167	0.93	0.57	0.17	1009

Supporting Methods M1

Checking interpolated climate data against station data and the HISTALP data set

Since the spatial resolution of the CRU TS 3.2 data set is rather crude, with a 0.5° x 0.5° grid cell covering ca. 2700 km^2, we checked the quality of the interpolation from the CRU data against station data from the German Weather Service (Deutscher Wetterdienst, DWD), and the HISTALP (Auer et al. 2007) data set. To this end, all sites for which nearby weather stations could be identified (mainly the lowland sites, 45 sites in total), station data from climate and precipitation stations was acquired and interpolated to the site using inverse distance weighting. For the alpine sites, interpolated control series were obtained by inverse distance weighting on the four nearest grid cells from the HISTALP data set.

Agreement between interpolated CRU TS 3.2 data was assessed using Pearson's correlation coefficient for the monthly resolved climate series on a common time span from 1950 to 2007. Agreement was found to be generally high, with a mean correlation between CRU TS 3.2 temperature data and local station data of 0.98 ± 0.03, a mean correlation between CRU TS 3.2 precipitation data and local station data of 0.86 ± 0.07, a mean correlation between CRU TS 3.2 temperature data and HISTALP temperature data of 0.99 ± 0.002, and a mean correlation between CRU TS 3.2 precipitation data and HISTALP precipitation data of 0.93 ± 0.07.

Note that this is not a valid test for the general quality of the data, since the station and HISTALP data used is not independent from the data the CRU TS 3.2 is constructed from. We rather use this approach for checking the quality of the interpolation done from the 0.5° CRU grid.

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Supporting Methods M2

Verification of drought conditions on the sampled sites

To verify that all sites experienced drought in the selected years, we compared the Standardized Precipitation and Evapotranspiration Index (SPEI, Vicente-Serrano *et al.* 2010a) for these sites, both from interpolated gridded data resulting from the same grid space used for the climatic data (Vicente-Serrano *et al.* 2010b), as well as calculated for the local station data (lowland) and interpolated HISTALP data set (Auer *et al.* 2007) using *R* package *SPEI* (Beguería & Vicente-Serrano 2013).

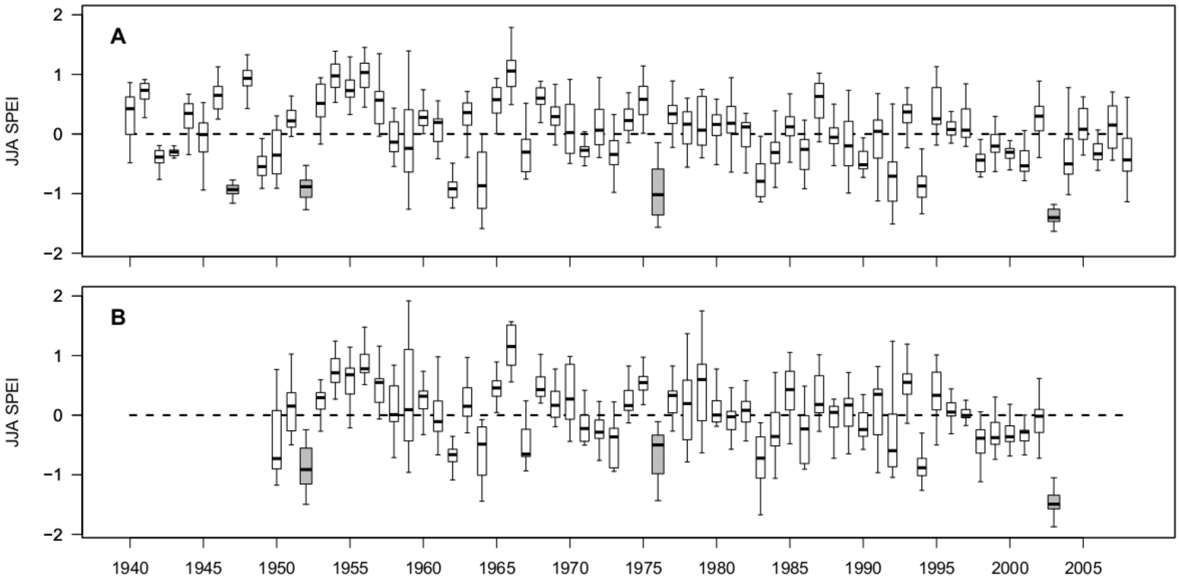

Fig. S1: SPEI values for all sites, calculated from A) gridded SPEI data, and B) from local station data and the HISTALP data set.

For the gridded data set, each site displays SPEI values for 2003 and 1947 that are in the lowest quartile of the data, confirming severe drought conditions for these years (figure S1A). The comparably dry year of 1952 was omitted from the analysis because of temporal proximity to 1947. For the SPEI calculated from station and HISTALP data, all sites are in the lowest quartile for 2003, and 64% of the sites are in the lowest quartile for 1976, with the rest located in the second quartile (figure S1B). The relative conditions for 1947 could not be assessed for station data, as reliable climatic information for all sites could only be obtained for the years 1950 and later.

Consequently, both approaches confirm the selected drought years of 1947, 1976 and 2003 to represent absolute (values below 0 in all cases) and relative drought conditions (positions in the distribution for each site).

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Figur S2: Response to drought characterized by growth in the periods before the drought event (PreDr), during (Dr), and after the drought event (PostDr) (modified after Lloret *et al.*, 2011). Indices for resistance (Rt = Dr/PreDr), recovery (Rc = PostDr/Dr), and resilience (Rs = PostDr/PreDr) are used to quantify the patterns in drought response.

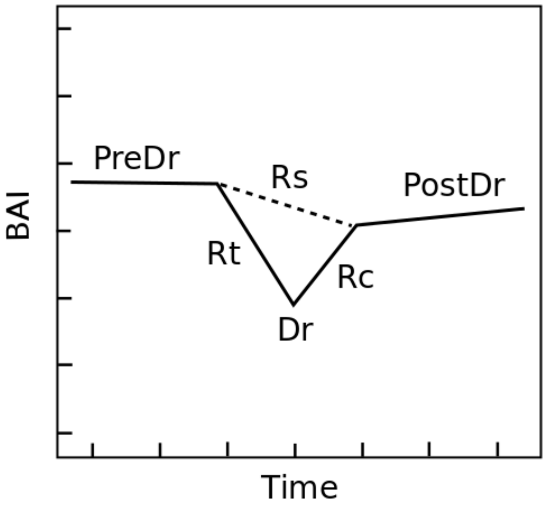


Figure S3: Testing for ontogenetic effects on variability in tolerance indices. For spruce (a), fir (b), and beech (c), the tolerance indices resistance (Rt), recovery (Rc), and resilience (Rs) have been computed separately for the drought years 1947, 1976, and 2003. Depicted are the changes in variability for the respective drought years compared to the background variability.

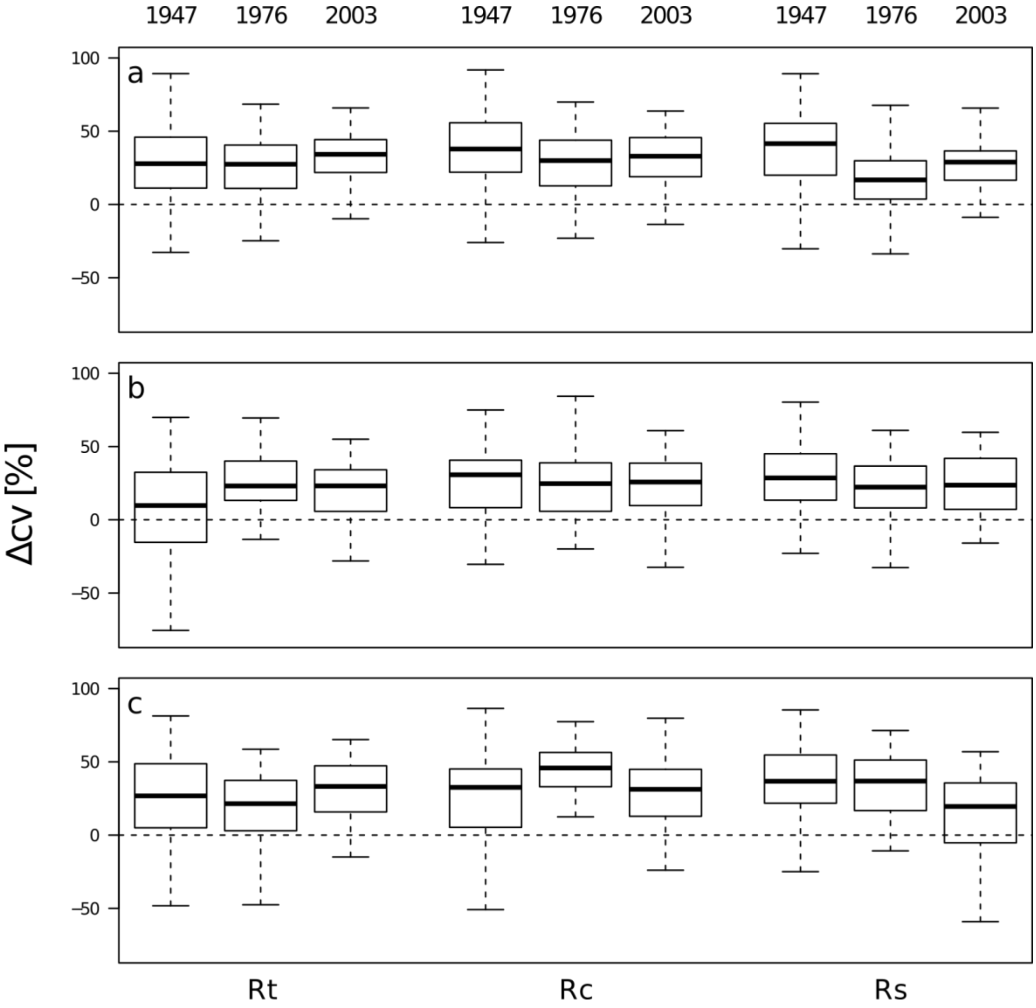
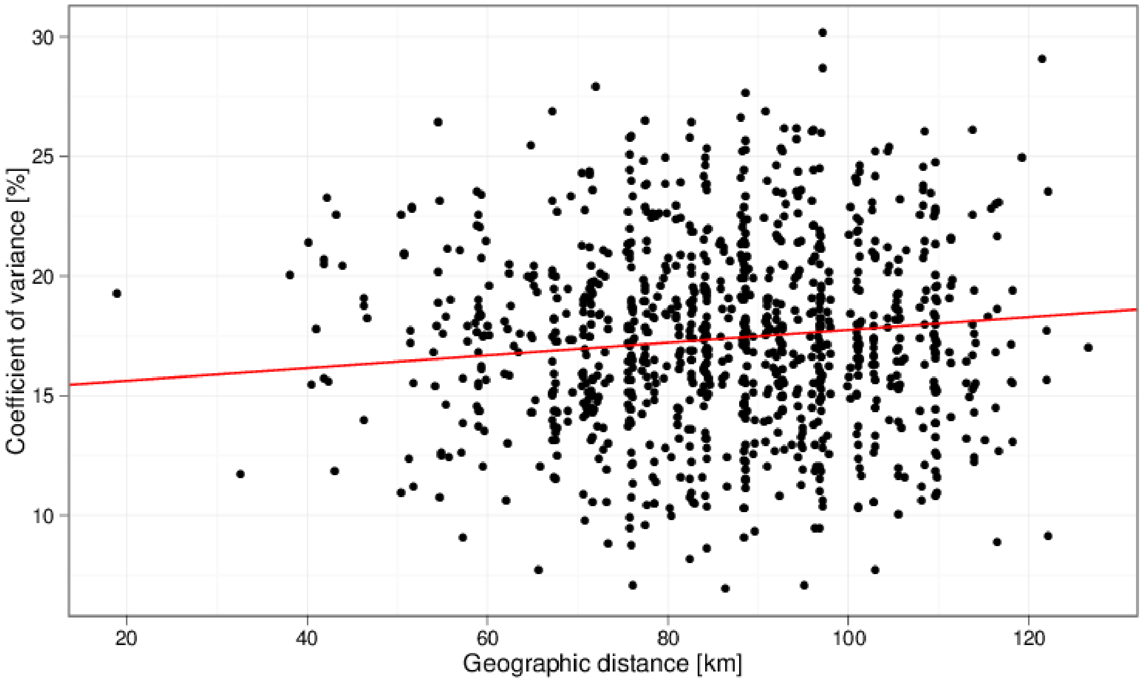


Figure S4: Exemplary distance-CV-relation for the mean geographic distance of 10 randomly selected trees and the CV for a tolerance index. Here, CV for resistance (Rt) of spruce is shown. The correlation is significant due to the high number of replicates (n = 1000), but the amount of explained variance is low (< 1%).



Publikation IV

Hartl-Meier C, Zang C, Büntgen U, Esper J, Rothe A, Göttlein A, Dirnböck T, Treydte K

(*in press*)

Uniform climate sensitivity in tree-ring stable isotopes across species and sites in a mid-latitude temperate forest

Tree Physiology

doi: 10.1093/treephys/tpu096

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Research paper

Uniform climate sensitivity in tree-ring stable isotopes across species and sites in a mid-latitude temperate forest

Claudia Hartl-Meier[1,2,8], Christian Zang[3], Ulf Büntgen[4,5], Jan Esper[1], Andreas Rothe[6], Axel Göttlein[2], Thomas Dirnböck[7] and Kerstin Treydte[4]

[1]Department of Geography, Johannes Gutenberg University Mainz, Johann-Joachim-Becher-Weg 21, 55128 Mainz, Germany; [2]Forest Nutrition and Water Resources, Technische Universität München, Hans-Carl-von-Carlowitz-Platz 2, 85354 Freising, Germany; [3]Ecoclimatology, Technische Universität München, Hans-Carl-von-Carlowitz-Platz 2, 85354 Freising, Germany; [4]Swiss Federal Research Institute WSL, Zuercherstrasse 111, 8903 Birmensdorf, Switzerland; [5]Oeschger Centre for Climate Change Research, University of Bern, 3012 Bern, Switzerland; [6]Faculty of Forestry, University of Applied Sciences Weihenstephan-Triesdorf, Hans-Carl-von-Carlowitz-Platz 3, 85354 Freising, Germany; [7]Department for Ecosystem Research and Monitoring, Environment Agency Austria, Spittelauer Lände 5, 1090 Vienna, Austria; [8]Corresponding author (c.hartl-meier@geo.uni-mainz.de)

Received July 11, 2014; accepted October 9, 2014; handling Editor Lucas Cernusak

Tree-ring stable isotopes, providing insight into drought-induced eco-physiological mechanisms, are frequently used to reconstruct past changes in growing season temperature and precipitation. Their climatic response is, however, still not fully understood, particularly for data originating from non-extreme, mid-latitude environments with differing ecological conditions. Here, we assess the response of δ^{13}C, δ^{18}O and tree-ring width (TRW) from a temperate mountain forest in the Austrian pre-Alps to climate and specific drought events. Variations in stem growth and isotopic composition of Norway spruce, common beech and European larch from dry, medium and moist sites are compared with records of sunshine, temperature, moisture, precipitation and cloud cover. Results indicate uniform year-to-year variations in δ^{13}C and δ^{18}O across sites and species, but distinct differences in TRW according to habitat and species. While the climate sensitivity of TRW is overall weak, the δ^{13}C and δ^{18}O chronologies contain significant signals with a maximum sensitivity to cloud cover changes ($r = -0.72$ for δ^{18}O). The coherent inter-annual isotopic variations are accompanied by substantial differences in the isotopic signatures with offsets up to ~3‰ for δ^{13}C, indicating species-specific physiological strategies and varying water-use efficiencies. During severe summer drought, beech and larch benefit from access to deeper and moist soils, allowing them to keep their stomata open. This strategy is accompanied by an increased water loss through transpiration, but simultaneously enables enhanced photosynthesis. Our findings indicate the potential of tree-ring stable isotopes from temperate forests to reconstruct changes in cloud cover, and to improve knowledge on basic physiological mechanisms of tree species growing in different habitats to cope with soil moisture deficits.

Keywords: dendroecology, drought, radial growth, tree physiology, carbon isotopes, oxygen isotopes

Introduction

Temperate forests are of importance to society and economies since these ecosystems constitute a large fraction of utilized biomass (FOREST EUROPE 2011). Forest ecosystem functioning and productivity, however, are expected to be affected by intensified climate anomalies such as the summer heat wave in 2003 (Luterbacher et al. 2004, Schär et al. 2004, Rebetez et al. 2006), and even more importantly by co-occurring drought events (Fuhrer et al. 2006, Straile and Stenseth 2007). More detailed knowledge about the physiological processes underlying climate-induced growth changes of different tree species, and their varying capabilities to cope with drought events, is required for the estimation of future forest adaption strategies to climate change.

At sites located at the distribution limit of forest ecosystems, tree growth is usually constrained by one climatic factor while in temperate forests, the delineation of growth responses to a single controlling factor often fails (Friedrichs et al. 2008, Kress et al. 2010). Reliable hydro-climatic reconstructions based on radial growth measures are thus mostly restricted to moisture-sensitive sites (Wilson et al. 2005, Esper et al. 2007). In the moist mid-latitudes, comprehensive dendroecological investigations based on annual stem increments have been performed to study the growth response of the most important native European tree species to climate and particularly drought events (Affolter et al. 2010, Zang et al. 2011, 2014, Hartl-Meier et al. 2014a, 2014b). While these studies have focused on radial growth only, additional information on the physiological responses of trees can be inferred from stable isotopes in tree rings (Gessler et al. 2014 and references therein).

Stable carbon ($\delta^{13}C$) and oxygen ($\delta^{18}O$) isotopes in tree rings differ from the classical dendrochronological variables as they reflect more directly the plant physiological response to climate and other environmental variables rather than net tree growth (Treydte et al. 2007, 2014, Gessler et al. 2013, 2014). $\delta^{13}C$ values depend on factors affecting the photosynthetic uptake of CO_2 and are mainly controlled by stomatal conductance and the rate of carboxylation during photosynthesis (Farquhar et al. 1989). $\delta^{18}O$ values are constrained by the isotopic ratio of the source water (Roden et al. 2000) and locally integrate the stomatal response to vapour pressure deficit via leaf water enrichment, coupled with transpiration (Yakir and DeNiro 1990, Barbour et al. 2004). These factors controlling isotopic fractionation are closely related to meteorological variables. Thus, stable isotopes can provide information on past precipitation and drought variations in regions where tree-ring width (TRW) and maximum late wood density (MXD) are mainly driven by temperature (Treydte et al. 2001, Kirdyanov et al. 2008, Kress et al. 2010), or contain information on climate variability at temperate sites with relatively weak signals recorded in TRW and MXD (Masson-Delmotte et al. 2005, Saurer et al. 2008, 2012, Haupt et al. 2011, Rinne et al. 2013).

Despite the dendroecological inferences that can be drawn from tree-ring stable isotopes, we still lack knowledge on how climatic signals, and their strengths, may vary among species growing in similar temperate climatic conditions but with varying access to soil water. Norway spruce (*Picea abies* [L.] Karst.), European larch (*Larix decidua* Mill.) and common beech (*Fagus sylvatica* L.) differ in their strategies of water uptake and, hence, in their capacity to cope with drought. Spruce is an intermediately shade-tolerant species widely distributed across the Alps and sensitive to summer water deficits (Ellenberg 2009, Lebourgeois et al. 2010, Zang et al.

2011, Zang 2012, Lévesque et al. 2013, Pretzsch et al. 2013) at least below the montane elevation belt (Hartl-Meier et al. 2014a, 2014b). As an evergreen species with a shallow root system, it relies upon internally stored and superficial soil water supplies (Tranquillini 1976, Valentini et al. 1994). European larch is a pioneer and shade-intolerant deciduous conifer in mid-to-high elevations (Ellenberg 2009) capable of tolerating summer drought in lower montane elevations (Hartl-Meier et al. 2014a). It develops deep root systems accessing soil water pools even in extended dry periods (Tranquillini 1976, Valentini et al. 1994). Common beech is the most abundant broadleaf tree species in Central Europe (Dittmar et al. 2003). It is less drought sensitive than spruce (Zang et al. 2011, 2014, Hartl-Meier et al. 2014a), as it reaches deeper soil regions containing water throughout sustained drought periods (Pretzsch et al. 2013).

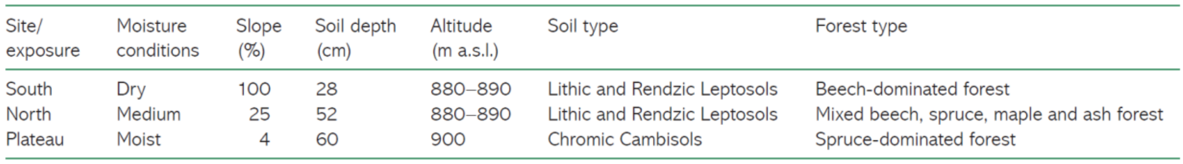
Here, we present δ^{13}C, δ^{18}O and TRW chronologies of Norway spruce, European larch and common beech from three sites in the mid-latitudes of Europe. We assess the response of these tree species to climate and severe drought events with respect to differences in site moisture and species-specific strategies to cope with drought. Our objectives are twofold: (i) testing the performance of δ^{13}C, δ^{18}O and TRW from different species growing together under different soil moisture conditions in temperate conditions to record climate information; and (ii) providing insight into the physiological mechanisms driving both the long-term response to climate and the short-term response to specific drought events. To accomplish these objectives we study: (i) site- and species-specific differences and coherences of the chronologies; (ii) the response of these chronologies to different climate variables including sunshine duration, temperature, Thornthwaite's (1948) moisture index, precipitation and cloud cover; and (iii) their response to extreme drought events. The combined information on tree growth and physiology should help to assess the potential of different tree species from temperate sites to adapt to climate change.

Materials and methods

Study area and sampling design

Our study area is the long-term ecosystem monitoring site ‘LTER Zöbelboden’ (N47°50’25”, E14°26’30”, Figure 1a) (http://www.umweltbundesamt.at/im, last accessed: July 2014) at 880–900 m above sea level in the northern part of the Austrian National Park ‘Northern Limestone Alps'. The climatic conditions are characterized by high annual precipitation (~1370 mm year−1) and a seasonal temperature range of 18.5 °C with a mean annual temperature of 7 °C (all data referring to the 1971–2000 period).

Table 1. Site characteristics.



Site/ exposure	Moisture conditions	Slope (%)	Soil depth (cm)	Altitude (m a.s.l.)	Soil type	Forest type
South	Dry	100	28	880–890	Lithic and Rendzic Leptosols	Beech-dominated forest
North	Medium	25	52	880–890	Lithic and Rendzic Leptosols	Mixed beech, spruce, maple and ash forest
Plateau	Moist	4	60	900	Chromic Cambisols	Spruce-dominated forest

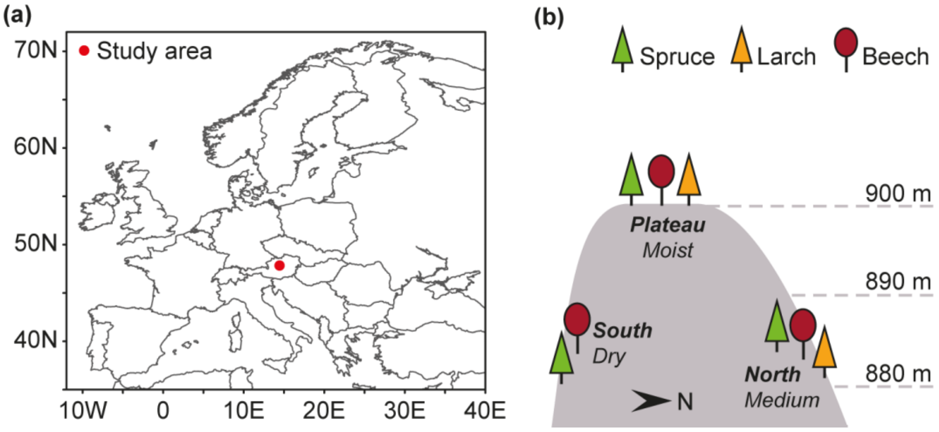


Figure 1. Study area "LTER Zöbelboden" in Austria (a) and sampling design (b). At each site ten individuals per species were sampled. All ten trees were used for TRW measurements, eight trees were used for carbon and oxygen stable isotope measurements. Micro-habitats were differentiated according to site exposure into dry, moist and medium soil conditions (see text and table 1). Note that the dry, south exposed site is composed of spruce and beech only, i.e. larch is missing here.

Ten dominant spruce, larch and beech trees were selected at a south-facing slope, a north-facing slope and a plateau site (hereafter termed South, North and Plateau; Figure 1b). Note that larch is missing on the dry, south-exposed site. We sampled two 5-mm diameter increment cores per tree at breast height. All three sites are located within a horizontal distance of 900 m and an elevational difference of ~20 m. The sampling sites differ in soil moisture and depth mainly controlled through exposure and slope differences (Table 1). South is located on a steep grade (100%) with shallow soils (28 cm), North is less steep (25%) with much deeper soils (52 cm), and the Plateau is almost flat with the deepest soils (60 cm). The soil moisture categories are supported by high-resolution (30 min) soil-water content data available for the period 2001–10 at North and Plateau (Jost et al. 2011). Although no such data are available for South, it appeared obvious that this is the driest site due to the shallow soil, steep slope, southern exposure and plant community. Tree composition at the Plateau has been influenced by a plantation early in the 20th century following a clear cut around 1910 (Hülber et al. 2008).

Sample preparation and data treatment

Tree-ring width was measured at 0.01 mm resolution using a LINTAB 6 table and the TSAP-Win software (Rinn 2003). Species- and site-specific cross-dating accuracy was checked both visually and statistically using the program COFECHA (Holmes 1983). To remove age-related growth trends and potential disturbance signals (e.g., due to forest management), the TRW measurement series were detrended individually using a cubic smoothing spline with a 50% frequency cut-off at 15 years (Cook and Peters 1981). Species-specific site chronologies were produced by averaging the detrended single series using a robust mean (Mosteller and Tukey 1977). Inter-series correlation (Rbar) and expressed population signal (EPS) statistics (Wigley et al. 1984) are used to estimate the internal coherence of each chronology.

For isotope measurements, eight trees per species and site and one core per tree were selected based on straight ring borders and absence of missing rings. Tree rings from 1970–

2010 were cut off and the corresponding years of all cores and trees per site and species pooled before isotope measurement (Leavitt and Long 1984, Treydte et al. 2001, 2006, 2007, Leavitt 2008). The wood of the pooled samples was milled using an ultra-centrifuge ZM200 (Retsch, Haan Germany) with a mesh size of 0.5 mm. Cellulose was extracted following standard procedures (Boettger et al. 2007) and packed into tin capsules for mass spectrometry. For carbon isotope measurement, cellulose samples were combusted to CO_2 using a EURO EA Elemental Analyser (EuroVector, Milan, Italy); for oxygen isotope measurements, cellulose was pyrolized to CO using a HT oxygen analyser from HEKAtech (Wegberg, Germany). Stable isotope ratios were determined with a Delta V Advantage from Thermo Scientific (Bremen, Germany). All isotope measurements were conducted at the WSL Central Lab at a precision of ±0.3‰ for oxygen and ±0.02‰ for carbon. δ^{13}C chronologies were corrected for changes in the atmospheric δ^{13}C value due to anthropogenic activities (Treydte et al. 2009). All further analyses refer to the CO_2-corrected data, termed raw δ^{13}C. Other potential non-climatic trends in both the raw δ^{13}C and δ^{18}O time series (Treydte et al. 2006, 2009, Esper et al. 2010) were accounted for by calculating residuals from linear trends.

Climate data and drought events

Monthly climate data were obtained from the HISTALP database (Auer et al. 2007). For temperature and precipitation, the grid point closest to our site (N47°50′ E14°20′, grid mode 2), and for sunshine duration and cloud cover CRMS (Coarse Resolution Subregional Means) data (region NE-Alps) were used. A simple moisture index was calculated after Thornthwaite (1948) based on monthly precipitation sums and monthly sums of potential evapotranspiration as a function of temperature and latitude (see Kress et al. 2010 for details).

Severe drought events were classified by combining the 10 most extreme values of June/July/August temperature, precipitation and moisture index. Considering the mean of all parameters indicated 1983, 1992, 1994 and 2003 as the most extreme drought events of the analysis period 1970–2010 (Figure 2).

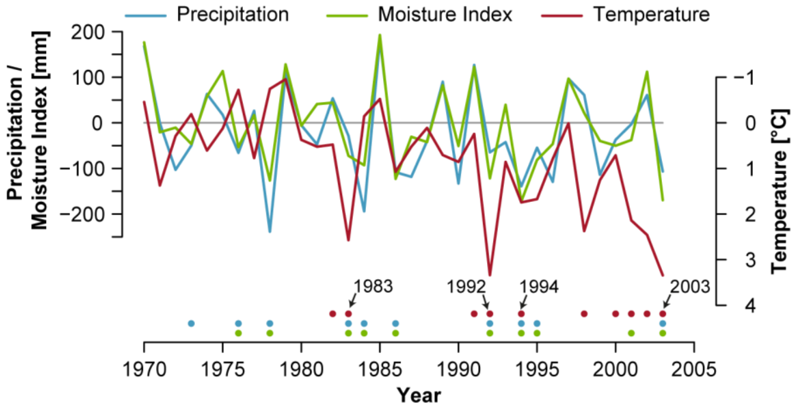


Figure 2. Precipitation, moisture index and temperature (note inverse scale) anomalies in the study area for June to August of the common period 1970-2003. Dots indicate the ten strongest extreme values of each climate parameter. The drought events 1983, 1992, 1994 and 2003 are identified by an overlap of the extremes for all climate parameter.

Statistical analyses

Chronologies were characterized considering the first year autocorrelation (lag-1) and average growth rates (AGR) (Table 2). Differences in the raw δ^{13}C, δ^{18}O and TRW chronologies, between sites and species, were assessed by analyses of variance followed by a Tukey HSD post hoc test. Coherency, here expressed as the similarity of the year-to-year variations among sites and species, was quantified using Pearson's correlation coefficients (i.e., the inter-chronology correlation).

The relationship of δ^{13}C, δ^{18}O and TRW with climate variables was calculated using bootstrapped correlations, and the statistical significance was determined at $P \leq 0.05$. Since the focus of this study is on summer drought, the climate response was determined for June/July/August averages (temperature, cloud cover) and sums (sunshine duration, precipitation, moisture index) over the 1970–2003 period.

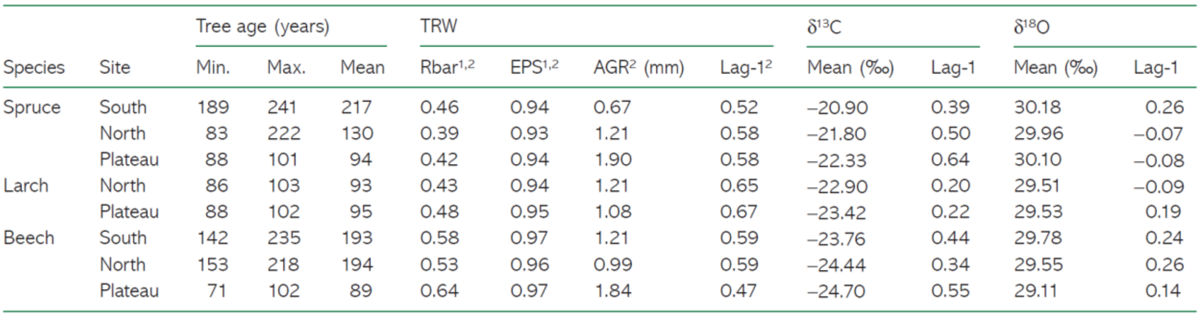
The response to drought events was assessed using superposed epoch analysis (SEA) (Panofsky and Brier 1958), by analysing the 4 years before and after the 1983, 1992, 1994 and 2003 drought events. In SEA, tree-ring parameters are expressed as scaled anomalies with respect to the mean of the 4 years preceding a drought event (years −4 to −1). All statistical procedures were performed using R 3.0.1 (R Development Core Team 2013) and the packages dplR (Bunn et al. 2012) and bootRes (Zang and Biondi 2013).

Results

Chronology characteristics

Maximum tree ages were reached at South (241 years, Table 2), trees at North were slightly younger (222 years) and trees were youngest at Plateau (102 years). Almost all species at a site were even-aged. Rbar values ranged from 0.39 to 0.64, indicating the highest internal coherency for the beech chronologies. All EPS values exceeded the widely considered threshold of 0.85 (Wigley et al. 1984), indicating sufficient internal signal strength for all chronologies (Table 2). Lag-1 autocorrelation was generally high in TRW and fluctuated between 0.47 and 0.67. The values for δ^{13}C were lower but also more variable with 0.20 to 0.64. For the δ^{18}O chronologies, serial correlations ranged between −0.07 and 0.26, indicating almost no lag effects inherent to these data (Table 2).

Table 2. Characteristics of the TRW, δ^{13}C and δ^{18}O chronologies. Rbar, inter-series correlation; EPS, expressed population signal; AGR, average growth rate; Lag-1, first year autocorrelation; ^{1}referring to detrended TRW-data; ^{2}calculated for the 1970–2010 period.



		Tree age (years)			TRW				δ^{13}C		δ^{18}O	
Species	Site	Min.	Max.	Mean	Rbar^{1,2}	EPS^{1,2}	AGR^{2} (mm)	Lag-1^{2}	Mean (‰)	Lag-1	Mean (‰)	Lag-1
Spruce	South	189	241	217	0.46	0.94	0.67	0.52	−20.90	0.39	30.18	0.26
	North	83	222	130	0.39	0.93	1.21	0.58	−21.80	0.50	29.96	−0.07
	Plateau	88	101	94	0.42	0.94	1.90	0.58	−22.33	0.64	30.10	−0.08
Larch	North	86	103	93	0.43	0.94	1.21	0.65	−22.90	0.20	29.51	−0.09
	Plateau	88	102	95	0.48	0.95	1.08	0.67	−23.42	0.22	29.53	0.19
Beech	South	142	235	193	0.58	0.97	1.21	0.59	−23.76	0.44	29.78	0.24
	North	153	218	194	0.53	0.96	0.99	0.59	−24.44	0.34	29.55	0.26
	Plateau	71	102	89	0.64	0.97	1.84	0.47	−24.70	0.55	29.11	0.14

Species- and site-specific differences

Significant differences were found between sites and species, particularly in the raw δ^{13}C chronologies (Figure 3; Table S1 available as Supplementary Data at Tree Physiology Online): at all sites, spruce consistently showed the highest, and beech showed the lowest δ^{13}C mean values. Intra-species comparisons indicated maximum δ^{13}C values at South and minimum values at Plateau (Table 2, Figure 4a). In contrast, δ^{18}O values did not change significantly among sites and species, although again spruce showed higher and beech slightly lower values (Figure 4b). Both δ^{18}O and δ^{13}C values decreased with increasing moisture conditions, most notably in beech (Figure 4c).Average growth rates showed a clear site dependency for spruce only, with the lowest growth rates at South and the highest at Plateau. Beech growth was also slightly higher at Plateau compared with the other two sites, but AGR of larch remained similar among sites.

Coherency between species and sites

Both the δ^{13}C and δ^{18}O time series were significantly coherent among species and sites (Figure 5, Table S1 available as Supplementary Data at Tree Physiology Online). The mean correlation within one species over all sites (intra-species coherency) ranged from 0.57 (δ^{13}C of beech) to 0.85 (δ^{13}C of larch). Interestingly, coherence between the mean species records, integrating all isotope records throughout the sites (inter-species coherence) was even stronger with r-values ranging from 0.52 to 0.69 for δ^{13}C and 0.83 to 0.84 for δ^{18}O. In contrast, the correlation between the TRW records of the different species over all sites was close to zero, except for spruce and beech with a relatively low r-value of 0.45.

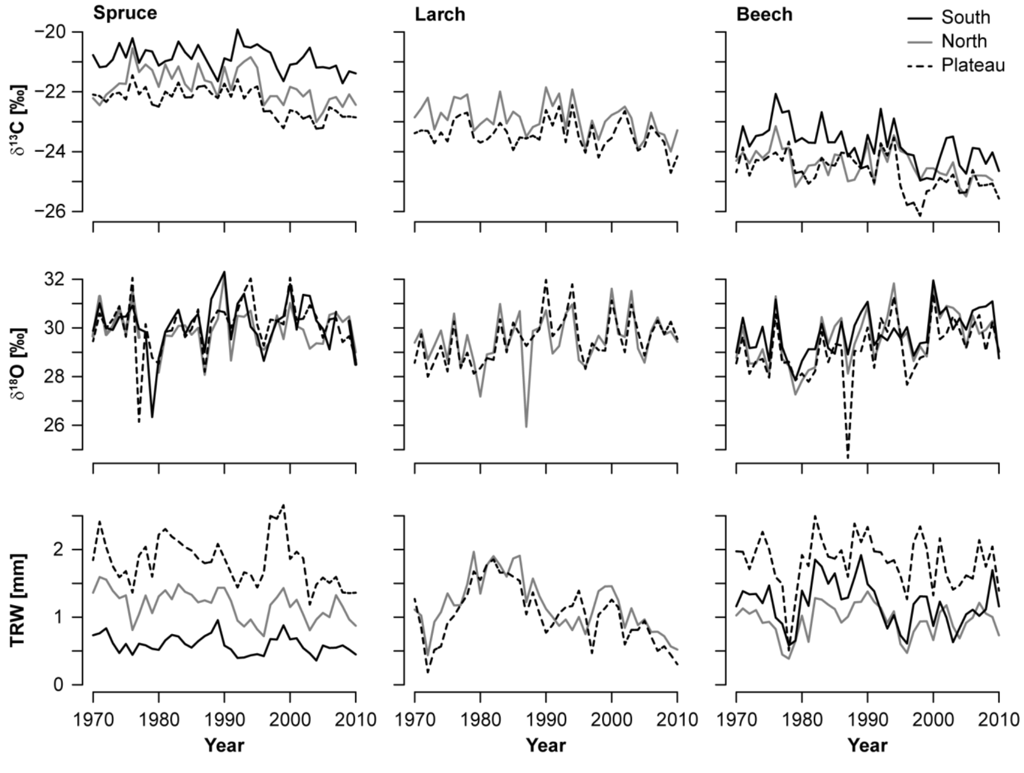


Figure 3. Raw δ^{13}C, δ^{18}O, and TRW chronologies of spruce, larch and beech at the three sites.

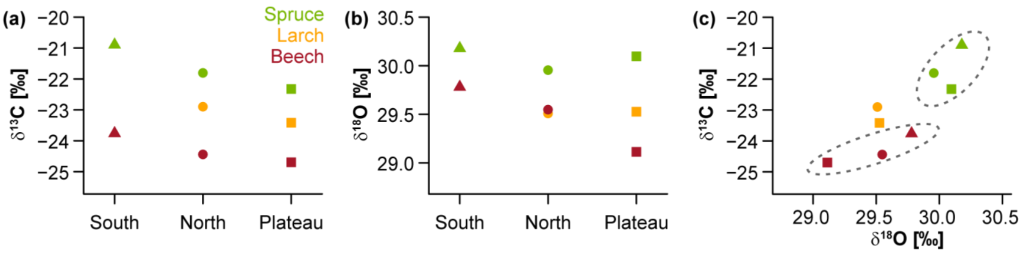


Figure 4. Mean (a) δ^{13}C and (b) δ^{18}O of spruce, larch and beech at the three sites and (c) the relationships between δ^{18}O and δ^{13}C (symbols and colour scheme in (c) are as in (a)).

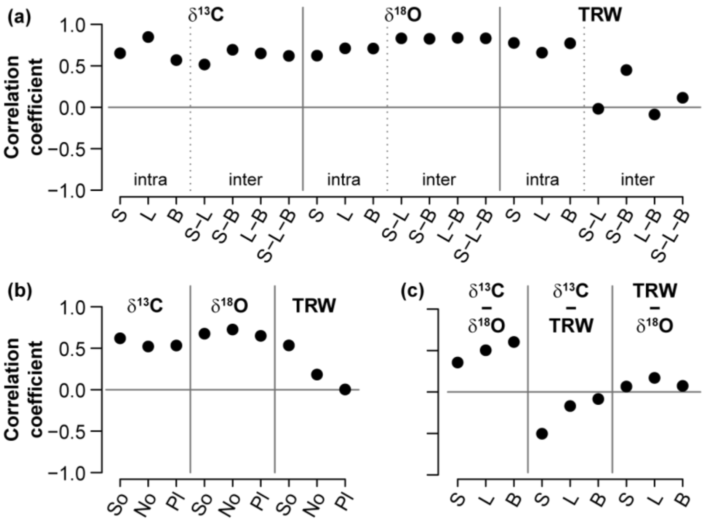


Figure 5. (a) Intra- and inter-species (mean species chronologies) correlations of detrended δ^{13}C, δ^{18}O and TRW chronologies. (b) Inter-species correlation of detrended δ^{13}C, δ^{18}O and TRW chronologies within the different sites. (c) Correlation between tree-ring parameter of the mean species chronologies. S, spruce; L, larch; B, beech; So, South; No, North; Pl, Plateau. $P < 0.01$ is reached at $r \sim 0.4$.

Within the sampling sites, the carbon and oxygen time series of the different species were again strongly correlated reaching r = 0.52–0.62 for δ^{13}C and r = 0.65–0.73 for δ^{18}O. The TRW chronologies, however, only showed common variability at the driest site South (r = 0.53) among the species and no relationship at the moist North and Plateau sites.

A comparison of the different tree-ring parameters (Figure 5c) indicated strong coherence between the δ^{13}C and δ^{18}O chronologies for beech (r = 0.58), medium coherence for larch (r = 0.48) and weak coherence for spruce (r = 0.33). Tree-ring width and δ^{13}C were negatively correlated, most significantly for spruce (r = -0.53). No association was found between TRW and δ^{18}O.

Response to summer climate

Distinct and homogenous inter-site and inter-species summer climate signals were inherent to the δ^{13}C and δ^{18}O data, while TRW showed divergent and weak relationships (Figure 6). Both δ^{13}C and δ^{18}O of all sites and species correlated positively with summer season sunshine duration and temperature, and negatively with the moisture index, precipitation and cloud cover. Relationships between the climate parameters and the stable isotopes were frequently significant ($P \leq 0.05$) (Table S2 available as Supplementary Data at Tree Physiology Online). The correlation coefficients were coherent among sites and species, without a clear species (Figure 6a) or site-dependent response pattern (Figure 6b). Highest correlations with

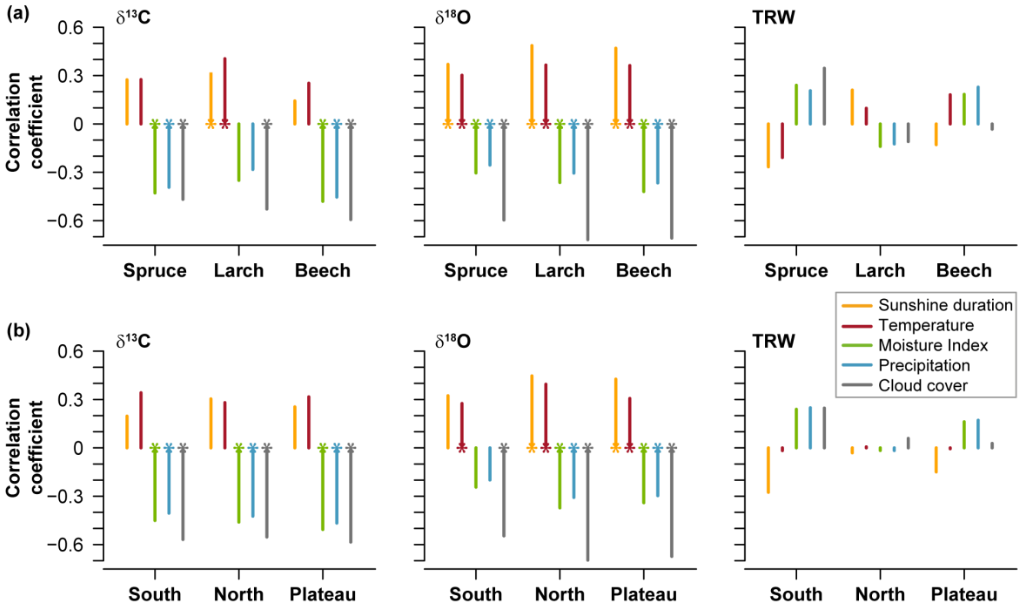


Figure 6. Relationships of (a) species and (b) sites to the climate variables of the June/July/August season. *P ≤ 0.05 significant correlations.

sunshine duration were inherent to the δ^{18}O data, with coefficients ranging from 0.37 to 0.49 for the species mean chronologies. The temperature signal was high in the δ^{18}O data (r = 0.30–0.37) as well, but the highest response was found in larch δ^{13}C (r = 0.41). The strongest moisture and precipitation signals were inherent to beech δ^{13}C with correlation coefficients of r = −0.48 and −0.45, respectively. However, the overall strongest relationships in both C and O stable isotopes were observed with cloud cover, reaching r = −0.71 for larch and r = −0.72 for beech δ^{18}O data.

The correlation coefficients between TRW and climate data were weak, reaching a maximum of r = 0.35 between spruce and cloud cover. The low correlation patterns also appeared to be influenced by species (Figure 6a) and site effects (Figure 6b). For example, spruce growth was negatively correlated with sunshine duration and temperature, but positively correlated with moisture index, precipitation and cloud cover. The climate response of larch was largely inverse to the spruce pattern. Severe site effects were seen for larch indicating no correlation with precipitation at North, but −0.24 at Plateau, for example (Table S2 available as Supplementary Data at Tree Physiology Online).

Response to drought events

The SEA revealed a distinct relationship of all δ^{13}C chronologies to drought, independent of species and site. The most significant (P ≤ 0.05) δ^{13}C deviations were always reached in the year when the drought event occurred (Year 0) with almost no lag effects (Figure 7a). However, there were noticeable positive and negative peaks in the Years −2 and −3, respectively. By comparing the species mean δ^{13}C deviations with the climate data, the strong relationship between δ^{13}C and climate, especially cloud cover, becomes apparent, indicating that δ^{13}C strongly depends on irradiance conditions (Figure 7b, Table S3 available as Supplementary Data at Tree Physiology Online).

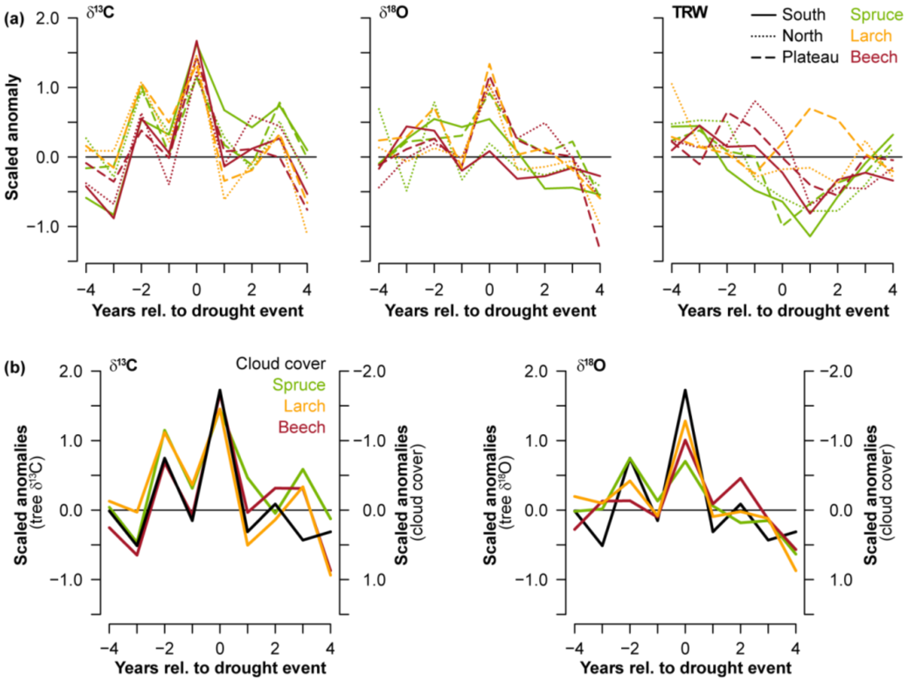


Figure 7. (a) Superposed epoch analysis for δ^{13}C, δ^{18}O and TRW site chronologies of spruce, larch and beech. Curves represent scaled time series centred on the drought events (Year 0) in 1983, 1992, 1994 and 2003, and scaled to zero mean over Years −4 to −1. (b) Comparison of the δ^{13}C and δ^{18}O mean species with cloud cover data.

For δ^{18}O, the SEA-derived relationship to drought events is less pronounced and the strength of the response varied among sites (Figure 7a). Again, no lag effects were found, and the SEA revealed significant ($P \leq 0.05$) positive deviations in δ^{18}O during drought events at both larch sites (Plateau and North) and at Plateau for spruce and beech. The δ^{18}O SEA of the species mean (Figure 7b) revealed a species-specific response including stronger deviations in larch and beech, and a weaker response of spruce. As with δ^{13}C, cloud cover seems to be the most important influencing factor of δ^{18}O.

In contrast to the coherent isotopic patterns, TRW indicated strong site- and species-dependent drought responses (Figure 7). Although a growth decline was only significant ($P \leq 0.05$) 1 year after the drought event for spruce at South, the SEA nevertheless revealed strong negative growth reactions of the other sites and species, including the following species-specific patterns: spruce growth declined sharply during drought, and the reduction persisted until Year 4; larch growth showed no obvious reaction to drought; and beech growth deviated weakly during drought, then declined more strongly in Year +1, and persisted until Year +4. Besides the species-specific growth reaction, the response pattern within a species showed only minor site-specific differences including a stronger decline in South and faster recovery in Plateau. Because of the biological persistence inherent to TRW, the SEA patterns were overall less distinct.

Discussion

Performance of δ^{13}C, δ^{18}O and TRW as climate proxies

The common variance of both the C and O isotope chronologies, among sites and species, exceeded the strength of the inter-series correlation of the TRW chronologies. This high degree of uniformity is especially conspicuous, as the compared species included an evergreen conifer, a deciduous conifer and a deciduous broadleaved species (Leavitt 1993). Our results indicate a stronger dependency of the stable isotopes on atmospheric conditions (Saurer et al. 2008) compared with TRW, while the latter seems to be controlled by species-specific and especially local soil moisture conditions.

This is also confirmed by our climate response analyses indicating a stronger sensitivity of the isotopic signatures compared with TRW, a finding also reported by Andreu et al. (2008) and Mölder et al. (2011). Particularly for $\delta^{13}C$, other studies indicated a stronger precipitation signal compared with TRW (Saurer et al. 1995, Gagen et al. 2004, Andreu et al. 2008, Kirdyanov et al. 2008). Our results reveal that also the oxygen isotope variations show a more coherent and stronger sensitivity to climate variables. Moreover, a site and species-independent precipitation signal, in both isotopic parameters, challenges the assumption that precipitation signals are stronger at locally drier sites (Saurer et al. 1995, McCarroll and Loader 2004). The absence of strong speciesspecific responses in the isotopic parameters supports the development of large-scale isotope networks from regions with weak signals in classical TRW and MXD data (Treydte et al. 2007).

Both $\delta^{13}C$ and $\delta^{18}O$ correlated best with the climate variables representing irradiance conditions (i.e., cloud cover and sunshine) with strongest relationships revealed in $\delta^{18}O$ of larch and beech. Correlations exceeding $r = -0.70$ indicate the potential for a $\delta^{18}O$-based cloud cover reconstruction also in the temperate climatic zone to accompany similar efforts using $\delta^{13}C$ in the high latitudes of Scandinavia (Young et al. 2010, 2012, Gagen et al. 2011, Loader et al. 2013) and eastern European Alps (Hafner et al. 2013).

The correlations between TRW and the climate variables are rather inconsistent. Only spruce revealed a relationship between TRW and drought, whereas the weak correlations of larch and beech are typical for such regions/elevations (Hartl-Meier et al. 2014a). In general, the strength of the climate signal in TRW depends on local site conditions rather than on species.

The response of the different tree-ring parameters to severe drought, as derived from SEA, supports this conclusion. $\delta^{13}C$ uniformly displayed drought signals across sites most precisely, again questioning expectations of increased sensitivity to drought at drier sites (Saurer et al. 1995, Weitner et al. 2007, Eilmann et al. 2010). Leavitt (1993), however, reported common $\delta^{13}C$ variations from different sites in periods with distinct moisture deficit compared with pluvial periods. This also holds for our results, since the $\delta^{13}C$ values diverge in the years following the drought event. Surprisingly, we could not detect any significant speciesspecific response to drought, although the mean values indicated different efficiency in the water use among species (see below).The O isotopes also increased during drought, though did not record the drought events as closely as $\delta^{13}C$ (Kress et al. 2010, Jansen et al. 2013). Interestingly the values particularly increased at the wet Plateau site, indicating that $\delta^{18}O$ is not necessarily associated with environmental stress conditions.

Although the SEA-derived response of radial growth is inconsistent among species and sites, it nevertheless provided insight into the recovery potential of the tree species. For spruce, we found a distinct growth decline during drought events followed by a rapid recovery. Differences in soil moisture conditions had no influence on the growth reaction of spruce, a finding in line with Hartl-Meier et al. (2014a, 2014b), reporting that the growth response of spruce to drought is rather driven by altitude, along with the corresponding hydrothermal changes. We also found growth reductions to be strongest in beech in the year following a drought event, and as indicated by Zang et al. (2014), that spruce exceeded the recovery potential of beech.

Physiological insights from the response to long-term climate and extreme drought events

Common variance and uniform climate response in both the C and O isotope data, throughout species and sites, are striking. In contrast, the mean isotope values differ substantially among species and sites, particularly for $\delta^{13}C$. It has, however, to be noted that due to the pooling procedure an estimation of the inter-tree variability cannot be provided. Leavitt (2010) summarized for a number of studies the offsets in the mean values between trees, which can be up to 3‰ for $\delta^{13}C$ and 4‰ for $\delta^{18}O$, almost independent of species. These values exceed the differences among sites in our study, though the offsets reported here are consistent and systematic supporting the interpretation of differing species- and site-specific physiological strategies: The lower carbon and oxygen isotope values of the deciduous larch and beech trees than those of the evergreen spruce indicate higher stomatal conductance in correspondence with access to deeper soil water pools that are typically depleted in ^{18}O (Barbour et al. 2004, Marshall and Monserud 2006, Lévesque et al. 2013). Besides the more efficient water transport and deeper root system of the deciduous trees (Stuiver and Braziunas 1987, Leavitt 1993, Saurer et al. 1995, 1997, Lévesque et al. 2013), both species seem to enhance their photosynthetic capacity during the short period of assimilate production (Anfodillo et al. 1998). This strategy, however, involves risking water losses through increased transpiration and subsequent cavitation and hydraulic failure. The among-site, intra-species differences of the mean isotopes seemingly point to this strategy as well as to an obvious dependence on soil moisture conditions (Leavitt 1993, Saurer et al. 1995, 1997, Treydte et al. 2001, 2014). This holds particularly for $\delta^{13}C$, where the highest values are reached at the driest sites indicating reduced stomatal conductance and decreased water-use efficiency (Saurer et al. 1995, 2014, Treydte et al. 2001, Gessler et al. 2014).

For $\delta^{18}O$, the short distances between our sites exclude an influence of varying precipitation $\delta^{18}O$ signatures. It is, however, well known that soil water close to the surface is evaporatively enriched in ^{18}O compared with the deeper soil water pools (Roden et al. 2000, Sarris et al. 2013, Treydte et al. 2014). Soils are deepest at the Plateau site and thus, specifically the deep rooting beech (Pretzsch et al. 2013) shows lower isotope values. Since water uptake in the shallow rooting spruce (Przybylski 2007, Pretzsch et al. 2013) is limited to the enriched near-surface soils, spruce $\delta^{18}O$ appears to be less site dependent, compared with larch and beech.

Despite these fundamental differences, the temporal variations of the C and O isotope records contain substantial variance in common and respond uniformly to climate. This can be explained by the fact that the relative variations in the few atmospheric variables controlling the physiological processes are similar at all sites and therefore cause similar variations in the tree-ring isotopes. Cloud cover, the variable with strongest correlation to the tree-ring isotopes, is strongly linked to irradiance (i.e., photon flux), relative air humidity and vapour pressure deficit, the most important factors controlling stomata conductance, transpiration and partly also soil water evaporation.

Interestingly, all trees with good access to soil water (North and Plateau sites) are most sensitive to cloud cover and drought events. Obviously high soil water availability allows the stomata to stay open resulting in water loss through transpiration, but offering the advantage of enhanced CO_2 uptake and increased assimilate production. Since high transpiration is associated with high evaporative leaf water ^{18}O enrichment, the isotopic values of the newly produced assimilates used for cellulose synthesis show higher isotope values (Offermann et al. 2011, Gessler et al. 2013, 2014, Treydte et al. 2014). Under moist conditions, the relative variations in leaf water enrichment, due to increased transpiration, seem to outweigh the relative variations of soil water $\delta^{18}O$. The fact that the response of $\delta^{13}C$ to drought events does not show any similar site differences to $\delta^{18}O$ supports the assumption of increased photosynthetic activity with higher soil water availability: in this case the discrimination against ^{13}C is reduced due to increased photosynthetic activity. This seems to outweigh the common effect of increased discrimination due to higher stomatal conductance (Farquhar et al. 1982, Leavitt and Long 1989). The observed $\delta^{13}C$ response to warm-dry conditions may therefore not only be a stomatal signal, but also reflect changes in the assimilation rate (Gessler et al. 2014 and references therein).

The differing physiological strategies identified here may be related to stem biomass production represented in TRW. We found significant negative correlations between $\delta^{13}C$ and TRW at least for spruce, indicating that wood production is related to stomatal conductance. By linking this relationship to climate, it appears that low soil water availability during drought periods might reduce carbon fixation and subsequently tree growth (Francey and Farquhar 1982, Saurer et al. 1995, Weitner et al. 2007). This particularly holds for Norway spruce and reveals its isohydric character: stomata closure during early phases of drought stress, resulting in low growth rates but preventing stress damage and allowing fast recovery (McDowell et al. 2008, Matyssek et al. 2013, Pretzsch et al. 2013). For the other species, the differences in physiological strategies and sensitivity to climate are less clearly linked to variations of radial growth. During drought events, beech takes advantage of the access to deeper soil horizons, increases photosynthetic activity as described above, and continues biomass production. Since this capability is associated with increased water losses, this anisohydric strategy might lead to xylem embolism (Gessler et al. 2007) that might need to be compensated by using assimilates for restoration in subsequent years (Hartmann 2011, Matyssek et al. 2013, Pretzsch et al. 2013, Zang et al. 2014). The result is a slow recovery, including a prolonged low stem biomass production following extreme drought events. It seems that larch follows an anisohydric strategy (Anfodillo et al. 1998, Lévesque et al. 2013) similar to beech, at least with respect to transpiration vs enhanced photosynthetic activity, but the next year's assimilation products may nonetheless build up stem increment.

Conclusions

Our findings reveal that the temporal patterns of carbon and oxygen isotopes show generally strong common variation, and consequently respond uniformly to short- and long-term climate variability. Tree-ring stable isotopes from this temperate forest show high climate sensitivities independent of site and species, and much stronger than radial growth. High correlations with irradiance variables demonstrate the potential of tree-ring stable isotopes for reconstructing past climatic conditions in mid-latitude, temperate environments. During drought events, tree-ring stable isotopes (particularly $\delta^{13}C$) show distinct signals. Although the growth response is inconsistent between sites and species, TRW still provides important information about future tree-species suitability, since tree performance can be inferred from the strength of growth reductions and subsequent recovery.

Despite the high temporal synchronicity and coherence of climatic signals, the isotopic signatures also allow identification of different physiological strategies of different tree species. Significant offsets inherent to the carbon and oxygen isotopes arise from differing water-use efficiencies, varying among species and with local soil moisture conditions. Our findings suggest that higher soil water availability allows high stomatal conductance in beech and larch and simultaneously enhanced photosynthetic activity, leading to continued biomass production during drought. We conclude that stable isotopes in tree rings from temperate sites do not only provide valuable proxies for climate reconstruction, but also enable the identification of drought-induced changes in physiological strategies.

Supplementary data

Supplementary data for this article are available at Tree Physiology Online.

Acknowledgments

The authors thank Klaus Limmer, Harald Meschendörfer and René Arnold for field assistance, as well as Christoph Dittmar, Kinga Jánosi, Anne Hollstein, Loïc Schneider and Ursula Graf for support in the laboratory. They also thank two anonymous reviewers and Elise Pendall for valuable comments on the manuscript.

Conflict of interest

None declared.

Funding

This work was supported by the Bavarian State Ministry for Food, Agriculture and Forestry, and the EU program INTERREG within the project SICALP (J00183). C.Z. acknowledges funding by the European Research Council under the European Union’s Seventh Framework Programme (FP7/2007-2013)/ERC grant agreement no. (282250). K.T. acknowledges the support by the Swiss National Science Foundation (200021_130112 ‘ISOPATH’, CRSII3_136295 ‘iTREE’, IZK0Z3_154157 ‘TREEPULSE’).

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The following supplement accompanies the article

Uniform climate sensitivity in tree-ring stable isotopes across species and sites in a mid-latitude temperate forest

CLAUDIA HARTL-MEIER[1,2*], CHRISTIAN ZANG[3], ULF BÜNTGEN[4,5], JAN ESPER[1], ANDREAS ROTHE[6], AXEL GÖTTLEIN[2], THOMAS DIRNBÖCK[7], KERSTIN TREYDTE[4]

1 Department of Geography, Johannes Gutenberg University Mainz, 55128 Mainz, Germany
2 Chair of Forest Nutrition and Water Resources, Technische Universität München, 85354 Freising, Germany
3 Chair of Ecoclimatology, Technische Universität München, 85354 Freising, Germany
4 Swiss Federal Research Institute WSL, 8903 Birmensdorf, Switzerland
5 Oeschger Centre for Climate Change Research, University of Bern, 3012 Bern, Switzerland
6 Faculty of Forestry, University of Applied Sciences Weihenstephan-Triesdorf, 85354 Freising, Germany
7 Department for Ecosystem Research and Monitoring, Environment Agency Austria, 1090 Vienna, Austria

*Email address: c.hartl-meier@geo.uni-mainz.de

Supplementary Material

Table S1. Statistical differences and correlation coefficients (grey) of raw δ^{13}C, δ^{18}O and TRW time series between sites and species

Table S2. Correlation coefficients of the June/July/August climate response for δ^{13}C, δ^{18}O and TRW chronologies.

Table S3. Correlation coefficients between the SEA for δ^{13}C, δ^{18}O and TRW and climate variables.

Table S1. Statistical differences and correlation coefficients (grey) of raw $\delta^{13}C$, $\delta^{18}O$ and TRW time series between sites and species (**S** = spruce, **L** = larch, **B** = beech, **So** = South, **No** = North, **Pl** = Plateau; *p<0.05, **p<0.01, ***p<0.001, ****p<0.0001, n.s. = not significant).

$\delta^{13}C$	S So	S No	S Pl	L No	L Pl	B So	B No	B Pl
S So		0.66	0.61	0.41	0.44	0.66	0.54	0.44
S No	****		0.80	0.57	0.49	0.69	0.60	0.61
S Pl	****	***		0.61	0.51	0.72	0.67	0.74
L No	****	****	****		0.86	0.66	0.64	0.58
L Pl	****	****	****	***		0.62	0.49	0.52
B So	****	****	****	****	n.s.		0.71	0.76
B No	****	****	****	****	****	****		0.56
B Pl	****	****	****	****	****	****	n.s.	

$\delta^{18}O$	S So	S No	S Pl	L No	L Pl	B So	B No	B Pl
S So		0.68	0.58	0.67	0.55	0.58	0.53	0.54
S No	n.s.		0.60	0.70	0.54	0.65	0.60	0.63
S Pl	n.s.	n.s.		0.74	0.62	0.55	0.66	0.64
L No	n.s.	n.s.	n.s.		0.72	0.62	0.78	0.83
L Pl	n.s.	n.s.	n.s.	n.s.		0.61	0.80	0.69
B So	n.s.	n.s.	n.s.	n.s.	n.s.		0.80	0.67
B No	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.		0.80
B Pl	***	**	***	n.s.	n.s.	n.s.	n.s.	

TRW	S So	S No	S Pl	L No	L Pl	B So	B No	B Pl
S So		0.75	0.69	0.34	0.13	0.57	0.31	0.36
S No	****		0.70	0.36	0.12	0.61	0.47	0.43
S Pl	****	****		0.46	0.33	0.40	0.12	0.32
L No	****	n.s.	****		0.85	0.25	0.01	0.13
L Pl	****	n.s.	****	n.s.		0.09	-0.08	0.01
B So	****	n.s.	****	n.s.	n.s.		0.73	0.75
B No	****	*	****	*	n.s.	*		0.75
B Pl	****	****	n.s.	****	****	****	****	

Table S2. Correlation coefficients of the June/July/August climate response for δ^{13}C, δ^{18}O and TRW chronologies. Bold numbers indicate $p \leq 0.05$ significant correlations. **So** = South, **No** = North, **Pl** = Plateau, **M** = mean species chronology, **Su** = sunshine duration, **Te** = temperature, **Mo** = moisture index, **Pr** = precipitation and **Cl** = cloud cover.

δ^{13}C	**Spruce**				**Larch**			**Beech**			
	So	**No**	**Pl**	**M**	**No**	**Pl**	**M**	**So**	**No**	**Pl**	**M**
Su	0,32	0,19	0,18	0,27	0,31	0,28	**0,31**	0,09	0,19	0,23	0,14
Te	**0,38**	0,18	0,16	0,28	**0,39**	**0,39**	**0,41**	0,27	0,29	0,17	0,25
Mo	**-0,38**	**-0,39**	**-0,43**	**-0,43**	-0,32	-0,35	-0,35	**-0,44**	**-0,46**	**-0,45**	**-0,48**
Pr	**-0,33**	**-0,37**	**-0,42**	**-0,39**	-0,26	-0,29	-0,28	**-0,40**	**-0,42**	**-0,44**	**-0,45**
Cl	**-0,45**	-0,30	**-0,43**	**-0,47**	**-0,56**	**-0,45**	**-0,53**	**-0,58**	**-0,51**	**-0,51**	**-0,59**

δ^{18}O	**Spruce**				**Larch**			**Beech**			
	So	**No**	**Pl**	**M**	**No**	**Pl**	**M**	**So**	**No**	**Pl**	**M**
Su	0,32	0,26	**0,37**	**0,37**	**0,42**	**0,50**	**0,49**	0,27	**0,48**	0,32	**0,47**
Te	**0,33**	0,08	**0,35**	**0,30**	**0,34**	0,33	**0,37**	0,15	**0,34**	**0,36**	**0,36**
Mo	-0,18	-0,16	**-0,28**	**-0,30**	**-0,31**	**-0,37**	**-0,36**	-0,28	**-0,38**	**-0,40**	**-0,42**
Pr	-0,11	-0,16	-0,23	**-0,25**	-0,26	**-0,32**	**-0,30**	-0,27	**-0,33**	**-0,35**	**-0,37**
Cl	**-0,51**	**-0,46**	**-0,50**	**-0,60**	**-0,65**	**-0,68**	**-0,72**	**-0,50**	**-0,71**	**-0,66**	**-0,71**

TRW	**Spruce**				**Larch**			**Beech**			
	So	**No**	**Pl**	**M**	**No**	**Pl**	**M**	**So**	**No**	**Pl**	**M**
Su	-0,26	-0,23	-0,20	-0,27	0,16	0,23	0,21	-0,23	-0,04	-0,14	-0,13
Te	-0,12	-0,17	-0,23	-0,21	0,07	0,10	0,10	0,06	0,29	0,19	0,18
Mo	0,14	0,24	0,29	0,24	0,03	-0,25	-0,14	0,26	0,16	0,16	0,18
Pr	0,12	0,22	0,25	0,21	0,04	-0,24	-0,12	0,29	0,23	0,21	0,23
Cl	0,33	0,28	0,34	0,35	-0,04	-0,14	-0,11	0,13	-0,12	0,07	-0,03

Table S3. Correlation coefficients between the SEA for δ^{13}C, δ^{18}O and TRW and climate variables. **So** = South, **No** = North, **Pl** = Plateau, **M** = mean species chronology, **Su** = sunshine duration, **Te** = temperature, **Mo** = moisture index, **Pr** = precipitation and **Cl** = cloud cover.

δ^{13}C		Spruce				Larch			Beech				Climate				
		So	**No**	**Pl**	**M**	**No**	**Pl**	**M**	**So**	**No**	**Pl**	**M**	**Su**	**Te**	**Mo**	**Pr**	**Cl**
Spruce	**So**		0,70	0,77	0,84	0,46	0,55	0,51	0,90	0,85	0,76	0,82	0,53	0,76	-0,71	-0,63	-0,67
	No			0,89	0,96	0,83	0,92	0,88	0,86	0,69	0,84	0,86	0,34	0,65	-0,61	-0,53	-0,77
	Pl				0,93	0,76	0,81	0,79	0,85	0,80	0,74	0,82	0,39	0,67	-0,76	-0,70	-0,71
	M					0,75	0,85	0,80	0,92	0,80	0,85	0,89	0,49	0,73	-0,71	-0,63	-0,81
Larch	**No**						0,96	0,99	0,77	0,65	0,84	0,84	0,32	0,65	-0,48	-0,37	-0,78
	Pl							0,99	0,83	0,65	0,83	0,85	0,38	0,71	-0,47	-0,34	-0,81
	M								0,80	0,66	0,84	0,85	0,35	0,68	-0,48	-0,36	-0,80
Beech	**So**									0,91	0,93	0,97	0,61	0,88	-0,74	-0,61	-0,89
	No										0,81	0,91	0,57	0,74	-0,81	-0,73	-0,79
	Pl											0,97	0,53	0,80	-0,71	-0,60	-0,90
	M												0,51	0,79	-0,74	-0,63	-0,88
Climate	**Su**													0,80	-0,50	-0,37	-0,79
	Te														-0,63	-0,47	-0,89
	Mo															0,98	0,70
	Pr																0,57
	Cl																

δ^{18}O		Spruce				Larch			Beech				Climate				
		So	**No**	**Pl**	**M**	**No**	**Pl**	**M**	**So**	**No**	**Pl**	**M**	**Su**	**Te**	**Mo**	**Pr**	**Cl**
Spruce	**So**		0,37	0,71	0,88	0,67	0,70	0,70	0,63	0,47	0,65	0,49	0,30	0,43	-0,11	-0,01	-0,56
	No			0,19	0,62	0,47	0,55	0,52	0,28	0,09	0,35	0,13	0,18	0,16	-0,34	-0,33	-0,53
	Pl				0,81	0,90	0,79	0,87	0,37	0,86	0,95	0,84	0,22	0,61	-0,49	-0,39	-0,65
	M					0,83	0,88	0,87	0,60	0,67	0,83	0,68	0,38	0,55	-0,44	-0,35	-0,77
Larch	**No**						0,91	0,98	0,38	0,76	0,93	0,81	0,29	0,65	-0,54	-0,44	-0,78
	Pl							0,97	0,58	0,77	0,88	0,84	0,51	0,65	-0,64	-0,55	-0,87
	M								0,48	0,78	0,93	0,85	0,40	0,67	-0,60	-0,50	-0,84
Beech	**So**									0,20	0,39	0,31	0,11	0,14	-0,15	-0,12	-0,31
	No										0,87	0,97	0,47	0,67	-0,62	-0,52	-0,72
	Pl											0,88	0,20	0,51	-0,55	-0,48	-0,67
	M												0,51	0,68	-0,61	-0,50	-0,76
Climate	**Su**													0,80	-0,50	-0,37	-0,79
	Te														-0,63	-0,47	-0,89
	Mo															0,98	0,70
	Pr																0,57
	Cl																

TRW		Spruce				Larch			Beech				Climate				
		So	No	Pl	M	No	Pl	M	So	No	Pl	M	Su	Te	Mo	Pr	Cl
Spruce	So		0,84	0,83	0,94	0,57	-0,51	0,08	0,66	0,25	0,33	0,44	-0,24	-0,32	0,30	0,26	0,31
	No			0,83	0,95	0,60	-0,44	0,14	0,75	0,39	0,62	0,65	-0,14	-0,31	0,29	0,26	0,14
	Pl				0,93	0,41	-0,50	-0,03	0,67	0,25	0,42	0,45	-0,41	-0,61	0,70	0,64	0,57
	M					0,55	-0,47	0,09	0,73	0,26	0,44	0,50	-0,31	-0,47	0,43	0,37	0,38
Larch	No						0,07	0,76	0,39	0,12	0,35	0,20	-0,47	-0,37	0,05	-0,03	0,11
	Pl							0,70	-0,53	-0,62	-0,67	-0,74	-0,10	-0,22	-0,29	-0,37	-0,04
	M								-0,07	-0,32	-0,19	-0,34	-0,40	-0,41	-0,16	-0,26	0,05
Beech	So									0,71	0,61	0,77	-0,16	-0,06	0,41	0,47	0,00
	No										0,71	0,91	0,28	0,44	0,26	0,40	-0,38
	Pl											0,88	0,06	0,17	0,16	0,22	-0,25
	M												0,29	0,34	0,20	0,31	-0,35
Climate	Su													0,80	-0,50	-0,37	-0,79
	Te														-0,63	-0,47	-0,89
	Mo															0,98	0,70
	Pr																0,57
	Cl																

VERÖFFENTLICHUNGEN

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CURRICULUM VITAE

PERSÖNLICHE INFORMATIONEN

Name	Claudia Theresia Martina Hartl-Meier
Geburtsdatum	13.05.1984
Geburtsort	Nabburg
Familienstand	verheiratet
Nationalität	Deutsch

BILDUNGSWEG

seit Apr 2011	**DOKTORANDIN** an der Technischen Universität München, Wissenschaftszentrum Weihenstephan für Ernährung, Landnutzung und Umwelt, Fachgebiet Waldernährung und Wasserhaushalt, Prof. Dr. Axel Göttlein
Okt 2003 – Okt 2009	**STUDIUM DER GEOGRAPHIE** an der Universität Regensburg Schwerpunkt: Physische Geographie Nebenfächer: Bodenkunde und Botanik Abschluss: Diplom-Geographin Univ. (Note: 1,7)
Sept 1994 – Juni 2003	**ALLGEMEINE HOCHSCHULREIFE** am Gymnasium Freyung Leistungskurse: Physik und Biologie

BERUFSERFAHRUNG

seit Sept 2013	**WISSENSCHAFTLICHE MITARBEITERIN** an der Johannes Gutenberg Universität Mainz, Geographisches Institut, Klimatologie, Prof. Dr. Jan Esper
Mär 2010 – Aug 2013	**WISSENSCHAFTLICHE MITARBEITERIN** an der Hochschule Weihenstephan-Triesdorf, Fakultät Wald und Forstwirtschaft, Prof. Dr. Andreas Rothe

Sept 2011 – Okt 2011	**GASTWISSENSCHAFTLERIN** an der Eidgenössischen Forschungsanstalt für Wald, Schnee und Landschaft WSL, Forschungseinheit Landschaftsdynamik, Gruppe Dendroklimatologie, Dr. David Frank und PD Dr. Ulf Büntgen
Nov 2010 – Dez 2010	**GASTWISSENSCHAFTLERIN** an der Eidgenössischen Forschungsanstalt für Wald, Schnee und Landschaft WSL, Forschungseinheit Landschaftsdynamik, Gruppe Dendroklimatologie, Dr. David Frank und PD Dr. Ulf Büntgen
Nov 2007 – Juli 2008	**STUDENTISCHE HILFSKRAFT** an der Technischen Universität München, Wissenschaftszentrum Weihenstephan für Ernährung, Landnutzung und Umwelt, Fachgebiet Geomorphologie und Bodenkunde, Prof. Dr. Jörg Völkel
Feb 2008 – Mär 2008	**PRAKTIKANTIN** am Wasserwirtschaftsamt Regensburg, Fachbereich Grundwasser- und Bodenschutz/Wasserversorgung
Sept 2007 – Okt 2007	**PRAKTIKANTIN** bei der Regierung der Oberpfalz, Sachgebiete Naturschutz, Wasserwirtschaft und Technischer Umweltschutz
Juni 2007	**STUDENTISCHE HILFSKRAFT** an der Universität Regensburg, Institut für Geographie, Abteilung Landschaftsökologie und Bodenkunde, Prof. Dr. Jörg Völkel

AUSZEICHNUNGEN

2012	**“ATR-AWARD – BEST ORAL PRESENTATION AT THE CONFERENCE TRACE 2012“**, TRACE conference, 09.-12.05.2012, Potsdam und Eberswalde, Deutschland.