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Potential of silvicultural measures for stabilising stand productivity and mitigating tree drought susceptibility of Scots pine (*Pinus sylvestris* L.) and oak (*Quercus petraea* (Matt.) Liebl., *Quercus robur* L.)

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“One of the penalties of an ecological education is that one lives alone in a world of wounds. Much of the damage inflicted on land is quite invisible to laymen. An ecologist must either harden his shell and make believe that the consequences of science are none of his business, or he must be the doctor who sees the marks of death in a community that believes itself well and does not want to be told otherwise.”

– Aldo Leopold, A Sand County Almanac

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ba	tree basal area (m^2)
BA	stand basal area (m^2 ha^{-1})
bai	tree basal area increment (cm^2 yr^{-1})
C	“composition” (fixed effect, see Eq. 15)
cbh	crown base height (m)
cl	crown length (m)
cpa	crown projection area (m^2)
CV	coefficient of variation
d (= dbh)	tree diameter at breast height (1.3 m) (cm)
d_{100}	dominant tree diameter (mean diameter at breast height of 100 largest trees per ha) (cm)
dbh (= d)	tree diameter at breast height (1.3 m) (cm)
DL	stand density level
DMI	De Martonne aridity index (De Martonne, 1926) (mm °C^{-1})
d_q	quadratic mean tree diameter (cm)
e	equivalence coefficient (oak: e_{oa}, Scots pine: $e_{S.pi}$)
E	elevation (m. a.s.l.)
GC	Gini coefficient (Gini, 1912)
h	tree height (m)
h_{100}	dominant tree height (mean height of 100 largest trees per ha) (m)
h_{100}/d_{100}	dominant tree height-diameter ratio
ha	hectare
h_q	quadratic mean tree height (m)
h_q/d_q	quadratic mean tree height-diameter ratio
I_A	Global Aridity Index by the United Nations Environmental Programme (UNEP)
IBA	stand basal area increment (m^2 ha^{-1} yr^{-1})
iv	tree volume increment (m^3 yr^{-1})
IV	stand volume increment (m^3 ha^{-1} yr^{-1})
m	mixing proportion (oak: m_{oa}, Scots pine: $m_{S.pi}$)
M	“meteorological variable” (T, P or DMI) (fixed effect, see Eq. 13)
MBA	periodical mean basal area level according to Assmann (1970)
MIX	mixture
MONO	monoculture (also used as variable to indicate composition, see Eq. 11)
MP	mixing proportion (%)

MRBA	mean relative stand basal area
N	number of trees (trees ha^{-1})
OLS	Ordinary Least Squares
P	precipitation total (mm)
PAIBA	mean periodic stand basal area increment (m^{2} ha^{-1} yr^{-1})
PAIV	mean periodic stand volume increment (m^{3} ha^{-1} yr^{-1})
PET	potential evapotranspiration (mm)
PM	parent material (geology)
P_{oa}	productivity (IV) of oak monoculture (m^{3} ha^{-1} yr^{-1})
$pp_{(S.pi), oa}$	productivity (IV) proportion of oak in the mixture (m^{3} ha^{-1} yr^{-1})
$pp_{S.pi,(oa)}$	productivity (IV) proportion of Scots pine in the mixture (m^{3} ha^{-1} yr^{-1})
$P_{S.pi}$	productivity (IV) of Scots pine monoculture (m^{3} ha^{-1} yr^{-1})
$P_{S.pi,oa}$	productivity (IV) of mixture as a whole (m^{3} ha^{-1} yr^{-1})
$\widehat{P}_{S.pi,oa}$	expected productivity (IV) of mixture as a whole (m^{3} ha^{-1} yr^{-1})
$P_{(S.pi),oa}$	productivity (IV) of oak in mixture upscaled to one hectare (m^{3} ha^{-1} yr^{-1})
$P_{S.pi,(oa)}$	productivity (IV) of Scots pine in mixture upscaled to one hectare (m^{3} ha^{-1} yr^{-1})
Rc	drought recovery index according to Lloret et al. (2011)
RP	relative productivity (ratio of productivity in mixture versus monoculture)
RPP	relative volume productivity on the basis of the proportions of volume growth
RRY	relative mixing effect (MIX/MONO−1) regarding response variable Y
Rs	drought resilience index according to Lloret et al. (2011)
Rt	drought resistance index according to Lloret et al. (2011)
RY	relative mixing effect (MIX/MONO) regarding response variable Y
S	“species” (fixed variable, see Eq. 14)
SD	standard deviation
SDI	Stand Density Index by Reineke (1933) (trees ha^{-1})
SE	standard error
SPEI	Standardised Precipitation Evapotranspiration Index by Vicente-Serrano et al. (2009)
T	temperature (°C)
V	standing volume (m^{3} ha^{-1})
yr/yrs	year/years

Abstract

Tree species mixing has become increasingly popular as an adaptation measure in European forest management. Complementarity effects between tree species may result in stabilised and enhanced stand productivity, as well as reduced tree drought susceptibility. However, mixing effects have proven to be highly context-dependant and only a limited number of species combinations have been studied in detail, revealing inconsistent results. In addition, a higher frequency of increasingly severe drought events and associated detrimental effects on forest ecosystems urgently call for short-term measures to adapt existing forests that are still far from rotation age. In this context, the maintenance of reduced stand densities has been proposed as a promising option. Yet, the relationship between stand density and tree drought susceptibility remains poorly understood, especially across ecological gradients.

This dissertation focuses on mixed forests of Scots pine (*Pinus sylvestris* L.) and oak (*Quercus petraea* (Matt.) Liebl., *Quercus robur* L.), which are likely to become increasingly important for balancing wood production and other ecosystem services under climate change. Furthermore, monospecific stands of both species, exhibiting different levels of stand density, were studied. To learn more about the interaction of stand density and drought responses under more extreme growing conditions, the investigation was extended by inclusion of chronically water-stressed ponderosa pine (*Pinus ponderosa* Douglas ex C. Lawson) stands in the U.S. Southwest. The main objective of this dissertation was to assess the potential of species mixing and stand density reduction as expedient long- and short-term silvicultural measures to mitigate the adverse effects of climate change on forest growth, health and functioning.

Using 20-year growth data from newly established triplets in Germany and Denmark, this dissertation investigated how mean tree and stand state characteristics, as well as productivity, in mixed Scots pine-oak stands compared with adjacent monocultures and how stable the observed productivity relation (mixed versus monospecific) was, considering inter-annual variations in local climate (Steckel et al. 2019, Appendix B.1). Species mixing on average resulted in 15 % higher standing volume and 14 % higher volume productivity compared with the weighted mean of adjacent monocultures. Oak was seen as the main driver of the observed stand-level overyielding, showing a 19 % higher productivity in mixed compared with monospecific stands. In mixture, standing volume of Scots pine was 25 % higher than in monocultures. Overyielding on the stand and species level increased in years with higher water supply. Both Scots pine and oak were found to modify their morphology in mixture, Scots pine growing higher and displaying smaller crowns and oak showing longer and wider crowns. Furthermore, oak in mixture showed a significantly higher inequality in stem volume compared with oak in monocultures.

Based on increment cores sampled along a comprehensive ecological gradient through Europe, spanning 33 sites in 12 countries, tree growth responses to episodic drought in mixtures and monocultures of Scots pine and oak were compared (Steckel et al. 2020a, Appendix B.2). Drought response indices ‘resistance’ (the ability to maintain growth levels during drought), 'recovery' (the ability to restore a level of growth after drought) and 'resilience' (the capacity to recover to pre-drought growth levels) were investigated, involving multiple site-specific drought events that occurred between 1976 and 2015. In monocultures, oak showed a higher resistance and resilience than Scots pine, while recovery was lower. Scots pine in mixed stands exhibited a higher resistance, but also a lower recovery compared with monocultures. Mixing increased the resistance and resilience of oak. In the case of Scots pine, resistance was on average increased by tree size, while recovery was lowered. Resistance of oak on average increased with site water supply. Positive mixing effects in terms of resistance and resilience of oak increased with site water supply, while the opposite was found regarding recovery. Site fertility moderated the positive mixing effect on the resistance of Scots pine.

The effect of reduced stand density on tree growth and growth sensitivity, as well as on short-term drought responses of Scots pine, sessile oak and ponderosa pine, was investigated using tree ring series from 409 trees, growing in monospecific stands of varying stand density, at sites with different water availability (Steckel et al., 2020b, Appendix B.3). For all species studied, mean tree growth was higher under low compared with maximum stand density. Mean tree growth sensitivity of Scots pine was higher under low compared with moderate and maximum stand density, while growth sensitivity of ponderosa pine was highest under maximum stand density. Recovery and resilience of Scots pine, as well as recovery of sessile oak and ponderosa pine, decreased with increasing stand density. Surprisingly, resistance and resilience of ponderosa pine significantly increased with increasing stand density. Higher site water availability was associated with significantly reduced average drought response indices of Scots pine and sessile oak in mixtures and monocultures, except for resistance of oak, which was not significantly affected. In ponderosa pine, higher site water availability significantly lessened recovery on average. Higher site water availability significantly moderated the positive effect of reduced stand density on drought responses in all species. Stand age had a significantly positive effect on the average resistance of Scots pine and a negative effect on the average recovery of sessile oak.

The findings of this dissertation suggest that the mixing of Scots pine and oak can stabilise and enhance stand productivity, as well as mitigate tree drought susceptibility along a wide range of growing conditions. The benefit of mixing on stand productivity appears to increase with site water supply, suggesting complementary light use as the dominant driver. Furthermore, the maintenance of reduced stand densities seems to be a suitable option for improving drought responses of Scots pine and sessile oak. However, the findings regarding ponderosa pine on xeric sites in the U.S. Southwest also point out limitations of the approach; here, higher stand densities may be favourable instead. *From a silvicultural point of view, the single-tree admixture of Scots pine and oak appears to be the most suitable option for unfolding beneficial effects on stand productivity and tree drought responses without the need for intensive silvicultural intervention. Considerable differences in rotation period of Scots pine and oak allow for continuous cover forestry using shelterwood cutting. In existing monocultures, intensive density reductions may be necessary to ensure the full beneficial effect on tree drought responses.*

Zusammenfassung

Die Mischung von Baumarten kann als wichtige Anpassungsstrategie an den Klimawandel in Europa angesehen werden. Die Komplementarität von Baumarten entscheidet über die Vorteilhaftigkeit einer bestimmten Baumartenmischung und kann im besten Fall zu einer verringerten Klimasensitivität, einer herabgesetzten Anfälligkeit gegenüber Trockenstress sowie einer stabileren und gesteigerten Bestandesproduktivität führen. Bislang zeigten sich Mischungseffekte jedoch als besonders kontextabhängig und nur wenige Baumartenmischungen wurden detailliert untersucht, oftmals mit widersprüchlichen Ergebnissen. Darüber hinaus fordert eine steigende Anzahl an zunehmend intensiveren Dürreereignissen, sowie die daraus folgenden negativen Auswirkungen auf die Waldgesundheit und Bereitstellung von Ökosystemleistungen, kurzfristige Lösungen zur Anpassung bereits bestehender Bestände, welche ihre Umtriebszeit noch nicht erreicht haben. In diesem Zusammenhang werden Bestandesdichteabsenkungen als vielversprechende waldbauliche Anpassungsstrategie angesehen. Dabei erscheint jedoch die Beziehung zwischen Bestandesdichte und Trockenstressanfälligkeit, insbesondere entlang ökologischer Gradienten, bislang nur unzulänglich erforscht.

Die vorliegende Dissertation basiert auf Untersuchungen zu Mischbeständen aus Waldkiefer (*Pinus sylvestris* L.) und Eiche (*Quercus petraea* (Matt.) Liebl., *Quercus robur* L.), welche im Kontext des Klimawandels für die Sicherung einer multifunktionalen Forstwirtschaft zusehends an Bedeutung gewinnen. Darüber hinaus wurden Reinbestände von Waldkiefer und Eiche mit unterschiedlicher Bestandesdichte untersucht. Um mehr über die Beziehung zwischen Bestandesdichte und Trockenstressreaktionen auf Extremstandorten zu erfahren, wurde die Untersuchung um ausgewählte, durch chronischen Wassermangel gekennzeichnete Bestände der Gelb-Kiefer (*Pinus ponderosa* Douglas ex C. Lawson) im Südwesten der USA erweitert. Das übergeordnete Ziel dieser Dissertation ist die Einschätzung des Potenzials von Baumartenmischungen und Bestandesdichteabsenkungen als lang- und kurzfristige waldbauliche Maßnahmen zur Verringerung negativer Auswirkungen des Klimawandels auf Wachstum, Gesundheit sowie Funktion von Waldökosystemen.

Im Rahmen dieser Dissertation wurde mittels 20-jähriger Zuwachsdaten neu angelegter Tripletts in Deutschland und Dänemark untersucht, wie sich Waldkiefer-Eiche-Mischungen hinsichtlich grundlegender Baum- und Bestandescharakteristika sowie ihrer Bestandesproduktivität von benachbarten Reinbeständen unterscheiden und wie stabil die beobachtete Produktivitätsrelation (misch zu rein) unter jährlichen Variationen meteorologischer Größen ist (Steckel et al. 2019, Appendix B.1). Es konnte gezeigt werden, dass Mischbestände durchschnittlich einen 15 % höheren Vorrat sowie eine 14 % höhere Volumenproduktivität als das gewichtete Mittel benachbarter Reinbestände aufweisen. Die Eiche profitierte am meisten von der Mischung und zeigte einen Mehrzuwachs von 19 %. In Mischung zeigte sich der Bestandesvorrat der Waldkiefer durchschnittlich um 25 % höher als in Reinbeständen. Der beobachtete Mehrzuwachs auf Bestandes- und Artenebene nahm in Jahren mit höherer

Wasserversorgung zu. Die Mischung beider Baumarten führte zu morphologischen Veränderungen der Bäume im Vergleich zu benachbarten Reinbeständen: Waldkiefern zeigten in Mischung größere Baumhöhen und kürzere Kronen, während Eichen dort längere und breitere Kronen ausbildeten. Die Eiche zeigte darüber hinaus in Mischung eine größere Ungleichverteilung der Einzelbaumvolumina.

Basierend auf Bohrkernproben, welche entlang eines umfassenden ökologischen Gradienten durch Europa gewonnen wurden (33 Standorte, 12 Länder), konnten Zuwachsreaktionen auf Trockenstress von Waldkiefer und Eiche in Rein- und Mischbeständen verglichen werden (Steckel et al. 2020a, Appendix B.2). Für standortspezifische Trockenjahre im Zeitraum 1976 bis 2015 wurden die Trockenstressindikatoren „Resistenz“ (die Fähigkeit ein bestimmtes Zuwachsniveau unter Trockenstress zu halten), „Erholung“ (die Fähigkeit ein bestimmtes Zuwachsniveau nach Trockenstress wiederherzustellen) und „Resilienz“ (die Fähigkeit zur Wiederherstellung des Zuwachsniveaus der dem Trockenereignis vorhergehenden Periode) bestimmt und analysiert. In Reinbeständen zeigte die Eiche eine höhere Resistenz und Resilienz als die Waldkiefer, obwohl die Erholung geringer ausfiel. In Mischung zeigte die Waldkiefer durchschnittlich eine höhere Resistenz und geringere Erholung als in Reinbeständen. Die Eiche wies in Mischung eine höhere Resistenz und Resilienz als in Reinbeständen auf. Die durchschnittliche Resistenz der Eiche in Rein- und Mischbeständen nahm mit zunehmender Wasserversorgung des Standortes zu. Förderliche Mischungseffekte bezüglich Resistenz und Resilienz der Eiche wuchsen mit der Wasserversorgung an, während sie für die Erholung abnahmen. Eine zunehmende Standortsproduktivität verringerte den positiven Mischungseffekt auf die Resistenz der Waldkiefer.

Basierend auf Jahrringserien von 409 Bäumen wurde der Effekt abgesenkter Bestandesdichten auf Baumzuwachs und Zuwachssensitivität sowie Trockenstressreaktionen von Waldkiefer, Eiche und Gelb-Kiefer auf Standorten mit unterschiedlicher Wasserversorgung untersucht (Steckel al., 2020b, Appendix B.3). Für sämtliche untersuchte Baumarten zeigten Bäume unter geringer Bestandesdichte höhere durchschnittliche Zuwächse als unter maximaler Bestandesdichte. Die durchschnittliche Zuwachssensitivität der Waldkiefer war unter geringer Bestandesdichte höher als unter maximaler Dichte, wobei das gegenteilige Reaktionsmuster bei der Gelb-Kiefer beobachtet wurde. Resistenz und Resilienz der Waldkiefer sowie Erholung von Eiche und Gelb-Kiefer nahmen mit zunehmender Bestandesdichte ab. Überraschenderweise nahmen bei der Gelb-Kiefer Resistenz und Resilienz mit zunehmender Bestandesdichte zu. Auf besser mit Wasser versorgten Standorten zeigten sich für Waldkiefer und Eiche, über alle Bestandesdichten hinweg, geringere Werte bei den Trockenstressindikatoren, mit Ausnahme bei der Resistenz der Eiche, welche nicht signifikant beeinflusst wurde. Die durchschnittliche Erholung der Gelb-Kiefer nahm mit höherer Wasserversorgung der Standorte ab. Der förderliche Effekt von Dichteabsenkungen war auf Standorten mit geringerer Wasserversorgung stärker ausgeprägt. Die Resistenz der Waldkiefer war in älteren Beständen höher als in jüngeren, während die Erholung der Eiche mit dem Bestandesalter abnahm.

Zusammenfassend lassen die Ergebnisse der vorliegenden Arbeit darauf schließen, dass die Mischung von Waldkiefer und Eiche zur Stabilisierung und Erhöhung der Bestandesproduktivität sowie zu einer Reduktion der Trockenstressanfälligkeit beider Baumarten entlang eines weiten Korridors an Wuchsbedingungen führen kann. Die förderliche Wirkung der Baumartenmischung auf die Bestandesproduktivität nimmt dabei mit der Wasserversorgung des Standortes zu, was auf eine komplementäre Nutzung der Ressource Licht als Haupttreiber schließen lässt. Darüber hinaus zeigt sich, dass die Bewirtschaftung reduzierter Bestandesdichten als eine vielversprechende Behandlungsoption für die Verbesserung der Trockenstressreaktion von Waldkiefer und Eiche anzusehen ist. Jedoch zeigen die Untersuchungen an Gelb-Kiefern im Südwesten der USA die Limitierung eines solchen Ansatzes auf; unter chronischem Wasserstress zeigt offenbar eine höhere Bestandesdichte Vorteile bei der Reduktion der Trockenstressanfälligkeit. *Aus waldbaulicher Sicht erscheint die einzelbaumweise Mischung von Waldkiefer und Eiche am zielführendsten, um die förderliche Wirkung der Mischung auf Bestandesproduktivität und Trockenstressreaktion abzuschöpfen, ohne dabei intensive waldbauliche Eingriffe zu erfordern. Bedingt durch deutliche Unterschiede in der Umtriebszeit ergibt sich die Möglichkeit zur zeitlich gestaffelten behutsamen Nutzung von Waldkiefer und Eiche im Schirmschlagverfahren. In bestehenden Reinbeständen sind mitunter erhebliche Reduktionen der Bestandesdichte erforderlich, um eine deutliche Verringerung der Trockenstressanfälligkeit herbeizuführen.*

Cumulative thesis – publication overview

This dissertation is based on three peer-reviewed publications (*Article I – III*). For each of these publications the original abstract, journal information and author's contribution is provided in the following. The full list of all publications and conference contributions prepared by the candidate during his doctoral studies within a more extensive framework of forest ecology and growth and yield related research is provided in Appendix A. Original versions of *Article I – III* can be found in Appendix B or be accessed via the respective DOI listed below.

Article I

Steckel, M., Heym, M., Wolff, B., Reventlow, D.O.J., Pretzsch, H., 2019. Transgressive overyielding in mixed compared with monospecific Scots pine (*Pinus sylvestris* L.) and oak (*Quercus robur* L., *Quercus petraea* (Matt.) Liebl.) stands – Productivity gains increase with annual water supply. Forest Ecology and Management 439, 81–96.

DOI: 10.1016/j.foreco.2019.02.038

Journal impact factor : 3.126 (2018)

Abstract: Tree species mixing has become a crucial tool in European forest management as positive interactions between species have been found to promote the provision of multiple ecosystem services, while at the same time reducing the risks associated with climate change. However, mixing effects have proven to be strongly context-dependant and some species combinations have still not been studied in detail. Here we focus on mixed forests of Scots pine and oak, which are likely to become increasingly popular for balancing wood production and other ecosystem services under climate change. Using 20-year growth data from newly established triplets in Germany and Denmark, this study investigates how mean tree and stand characteristics as well as productivity in mixed Scots pine-oak stands compare with adjacent monocultures and how stable the observed productivity relation is, considering inter-annual variations in local climate. Species mixing on average resulted in 15 % higher standing volume and 14 % higher volume productivity compared with the weighted mean of the adjacent monocultures. Oak profited most in mixture, showing overyielding of 19 %. Overyielding on the stand and species level increased in years with higher water supply. In mixture, standing volume of Scots pine was 25 % higher than in monocultures. Both species were found to modify their morphology in mixture. Oak in mixture showed a significantly higher inequality in stem volume compared with monocultures. We hypothesise that the observed overyielding of Scots pine-oak mixtures mainly results from complementary light use, where differences in shade tolerance, crown architecture and leaf phenology may be contributing factors.

Author's contribution: Conceptualisation: M.S., H.P.; data curation: M.S.; formal analysis: M.S.; investigation: M.S.; methodology: M.S.; resources: H.P., D.O.J.R, B.W.; software: M.S., M.H.; supervision: H.P.; validation: M.S.; visualisation: M.S.; writing – original draft preparation: M.S.; writing – review & editing: M.S., M.H., D.O.J.R., B.W., H.P.

Article II

Steckel, M., del Río, M., Heym, M., Aldea, J., Bielak, K., Brazaitis, G., Černý, J., Coll, L., Collet, C., Ehbrecht, M., Jansons, A., Nothdurft, A., Pach, M., Pardos, M., Ponette, Q., Reventlow, D.O.J., Sitko, R., Svoboda, M., Vallet, P., Wolff, B., Pretzsch, H., 2020. Species mixing reduces drought susceptibility of Scots pine (*Pinus sylvestris* L.) and oak (*Quercus robur* L., *Quercus petraea* (Matt.) Liebl.) – Site water supply and fertility modify the mixing effect. Forest Ecology and Management 461, 117908.

DOI: 10.1016/j.foreco.2020.117908

Journal impact factor: 3.126 (2018)

Abstract: Tree species mixing has been widely promoted as a promising silvicultural tool for reducing drought stress. However, so far only a limited number of species combinations have been studied in detail, revealing inconsistent results. In this study, we analysed the effect of mixing Scots pine and oak (pedunculate oak and sessile oak) trees on their drought response along a comprehensive ecological gradient across Europe. The objective was to improve our knowledge of general growth response patterns of two fundamental European tree species to drought in mixed versus monospecific stands. We focused on three null hypotheses: (HI) tree drought response does not differ between Scots pine and oak, (HII) tree drought response of Scots pine and oak is not affected by stand composition (mixture versus monoculture) and ($HIII$) tree drought response of Scots pine and oak in mixtures and monocultures is not modified by tree size or site conditions. To test the hypotheses, we analysed increment cores of Scots pine and oak sampled in mixed and monospecific stands, covering a wide range of site conditions. We investigated resistance (the ability to maintain growth levels during drought), recovery (growth increase after drought) and resilience (the capacity to recover to pre-drought growth levels), involving site-specific drought events that occurred between 1976 and 2015. In monocultures, oak showed a higher resistance and resilience than Scots pine, while recovery was lower. Scots pine in mixed stands exhibited a higher resistance, but also a lower recovery compared with corresponding monocultures. Mixing increased the resistance and resilience of oak. Ecological factors such as tree size, site water supply and site fertility were found to have significant effects on the drought response. In the case of Scots pine, resistance was increased by tree size, while recovery was lowered. Resistance of oak increased with site water supply. The observed mixing effect on the tree drought response of Scots pine and oak was in some cases modified by the site conditions studied. Positive mixing effects in terms of resistance and resilience of oak increased with site water supply, while the opposite was found regarding recovery. In contrast, site fertility lessened the positive mixing effect on the resistance of Scots pine. We hypothesise that the observed mixing effects under drought mainly result from water- and/or light-related species interactions that improve resource availability and uptake according to temporal and spatial variations in environmental conditions.

Author's contribution: Conceptualisation: M.S., H.P.; data curation: M.S.; formal analysis: M.S.; investigation: M.S. identified, established and sampled a total of six triplets himself, co-authors provided stand data and raw increment core measurements for remaining triplets; methodology: M.S.; resources: H.P.; software: M.S.; supervision: H.P.; validation: M.S.; visualisation: M.S.; writing – original draft preparation: M.S.; writing – review & editing: M.S., M.dR., M.H., J.A., K.B., et al.

Article III

Steckel, M., Moser, W.K., del Río, M., Pretzsch, H. Implications of Reduced Stand Density on Tree Growth and Drought Susceptibility: A Study of Three Species under Varying Climate. Forests 11, 627.

DOI: 10.3390/f11060627

Journal impact factor: 2.116 (2018)

Abstract: A higher frequency of increasingly severe droughts highlights the need for short-term measures to adapt existing forests to climate change. The maintenance of reduced stand densities has been proposed as a promising silvicultural tool for mitigating drought stress. However, the relationship between stand density and tree drought susceptibility remains poorly understood, especially across ecological gradients. Here, we analysed the effect of reduced stand density on tree growth and growth sensitivity, as well as on short-term drought responses (resistance, recovery, and resilience) of Scots pine (*Pinus sylvestris* L.), sessile oak (*Quercus petraea* (Matt.) Liebl.), and ponderosa pine (*Pinus ponderosa* Douglas ex C. Lawson). Tree ring series from 409 trees, growing in stands of varying stand density, were analysed at sites with different water availability. For all species, mean tree growth was significantly higher under low compared with maximum stand density. Mean tree growth sensitivity of Scots pine was significantly higher under low compared with moderate and maximum stand density, while growth sensitivity of ponderosa pine peaked under maximum stand density. Recovery and resilience of Scots pine, as well as recovery of sessile oak and ponderosa pine, decreased with increasing stand density. In contrast, resistance and resilience of ponderosa pine significantly increased with increasing stand density. Higher site water availability was associated with significantly reduced drought response indices of Scots pine and sessile oak in general, except for resistance of oak. In ponderosa pine, higher site water availability significantly lessened recovery. Higher site water availability significantly moderated the positive effect of reduced stand density on drought responses. Stand age had a significantly positive effect on the resistance of Scots pine and a negative effect on recovery of sessile oak. We discuss potential causes for the observed response patterns, derive implications for adaptive forest management, and make recommendations for further research in this field.

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1. Introduction

1.1. Motivation

European forest management has traditionally favoured monocultures dominated by one single tree species over mixed forests with several tree species. Fast- and straight-growing conifers such as Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* (L.) H. Karst.) have predominantly been promoted, often far beyond their natural distribution. In the context of climate change, these forests have proven to be particularly susceptible to abiotic and biotic disturbances (Spiecker, 2003; Goris et al., 2007; Knoke et al., 2008; Spathelf and Ammer, 2015). A recent re-evaluation of traditional forest practice has resulted in a shift towards close-to-nature forestry, a concept encompassing management strategies that promote continuous forest cover, the use of native and well adapted tree species and natural processes in forests (Schutz, 1999; Gamborg and Larsen, 2003; Brang et al., 2014). Against this background, tree species mixing has gained attention as a promising silvicultural tool for long-term adaptation and risk-reduction (Knoke et al., 2008; Reif et al., 2010). As a result, the conversion of traditional coniferous monocultures into mixed species stands with broadleaved species has been widely promoted by both forest management and forest policy (Klimo, 2000; Zerbe, 2002; Kint et al., 2006). This shift in management strategy is supported by a series of studies which suggest that species mixing can stabilise (Pretzsch, 2005; del Río et al., 2017b) and increase (Zhang et al., 2012; Pretzsch et al., 2015; Liang et al., 2016; Jactel et al., 2018) stand productivity, increase structural diversity (Pretzsch et al., 2016), promote diversity of other taxa (Dieler et al., 2017) and reduce economic risk (Knoke et al., 2008; Neuner and Knoke, 2017). Empirical evidence suggests that the productivity of Central European forest mixtures regularly exceeds the weighted mean productivity of neighbouring monocultures (overyielding) by up to 30 % (Pretzsch and Zenner, 2017). However, mixing effects with regards to productivity have often proven difficult to assess, mainly due to a dependency on multiple factors such as species composition (Lu et al., 2016; Mina et al., 2017), functional traits of the species under scrutiny (Zhang et al., 2012; Lu et al., 2016), site conditions (Forrester et al., 2013; Forrester and Albrecht, 2014), stand development stage (Cavard et al., 2011) and stand density (Condés et al., 2013; Potter and Woodall, 2014). An increasing number of studies focusing on the productivity of mixed versus monospecific forests have analysed species interactions on sites along spatial environmental gradients, reporting both increased (Pretzsch et al., 2010; Paquette and Messier, 2011; Pretzsch et al., 2013a; Toïgo et al., 2015; Jucker et al., 2016; Lu et al., 2018) and lessened (Forrester et al., 2013; Forrester and Albrecht, 2014) mixing benefits under heightened environmental stress. However, far less research has so far been devoted to examining growth performance of mixed versus monospecific stands along temporal variations in environmental growing conditions, considering short-term fluctuations in climate. This may however be crucial, as the scrutiny of mixing effects based on a single point in time only captures the net-benefits or -disadvantages and may not be sufficient to understand the intricate and highly variable species interactions over time (Forrester, 2014).

Climatic extremes, such as droughts, are expected to become more frequent and increase in intensity as a result of climate change (Spinoni et al., 2015). Forest ecosystems have proven to be particularly vulnerable to such drastic changes in growing conditions due to their slow natural adaptation rates, ultimately resulting in widespread tree mortality and decreased tree and forest growth (Allen et al., 2010; Williams et al., 2013). Drought is a particular challenge for forest managers as it affects a multitude of ecosystem responses, thereby considerably altering forest ecosystem dynamics (Floret et al., 1990; Chaves et al., 2003; Bréda et al., 2006; Rennenberg et al., 2006; Hamanishi and Campbell, 2011). Drought occurs under low levels of available water, relative to a site's mean condition, caused by reduced precipitation and/or increased atmospheric evaporative demand combined with low available soil water (Wilhite, 1993; Gleason et al., 2017). Under drought, trees may reduce stomatal conductance and photosynthesis, as well as experience carbon starvation (Irvine et al., 1998; McDowell et al., 2008), modified tree allometry (Pretzsch et al., 2012b), enhanced fine root mortality (Deans, 1979; Gaul et al., 2008) and increased defoliation (Carnicer et al., 2011; Poyatos et al., 2013). Furthermore, effects of drought include decreased tree and stand growth (Chaves et al., 2003; Leuzinger et al., 2005; Hartmann, 2011), a higher predisposition to biotic and abiotic agents (Allen et al., 2010; Griess and Knoke, 2011; Schlesinger et al., 2016) and tree die-off and mortality (McDowell et al., 2008). Growth responses of trees to drought have been found to depend on intrinsic factors, such as species (Zang et al., 2011; Eilmann and Rigling, 2012; Anderegg and HilleRisLambers, 2016; Thurm et al., 2016; Vitasse et al., 2019), provenance (Taeger et al., 2013), competitive status (Zang et al., 2012), age (Thurm et al., 2016) and size (Jucker et al., 2014; Bennett et al., 2015; Serra-Maluquer et al., 2018), as well as extrinsic factors, such as biome type (Vicente-Serrano et al., 2013; Grossiord et al., 2014b; Gazol et al., 2017), altitude (Marqués et al., 2016), soil conditions (Thurm et al., 2016), prevalent climatic conditions (Pasho et al., 2011; Dorman et al., 2013; Lévesque et al., 2014; Clark et al., 2016; Gazol et al., 2017), seasonality of the drought endured (Merlin et al., 2015; Toigo et al., 2015), stand functional diversity (Gazol and Camarero, 2016), stand competition (Dorman et al., 2015; Thurm et al., 2016) and species diversity (Grossiord, 2018). Together with the use of more drought tolerant tree species, the mixture of tree species, i.e. the increase in tree species diversity, has been widely proposed as an effective long-term silvicultural tool to counteract the adverse impacts of droughts on tree growth and vitality, thereby stabilising forest ecosystems (Kelty, 1992; Lüpke et al., 2004; Knoke et al., 2008). Some studies have shown that trees growing in mixed-species forests can be more resistant and resilient than those growing in monocultures (Lebourgeois et al., 2013; Pretzsch et al., 2013b; Merlin et al., 2015), although others have pointed out that the outcome of species mixing on tree drought responses may not always be beneficial (Grossiord et al., 2014b; Forrester et al., 2016).

Positive mixing effects are commonly explained by the 'complementary effect hypothesis', according to which, complementarity between species can be either caused by reduced competition or facilitation

(Ammer, 2019). Complementarity effects may depend on the environmental context, which affects the availability of the target resource over space and time. According to Forrester (2014), complementarity effects are generally expected to increase when the mixing of tree species improves the availability, uptake or use efficiency of the limiting resource. The influence of average site conditions on mixing effects has often been described by the stress gradient hypothesis, which states that the effect of facilitation is more pronounced on sites with stressful growing conditions, whereas under benign conditions, the effect of competition dominates (Bertness and Callaway, 1994). In addition to average growing conditions, complementarity is also expected to be present under sudden changes in environmental conditions, such as during episodic drought, when the mixing of tree species with differing ecological traits and resistance behaviours may mitigate negative effects on growth (Pretzsch et al., 2012a; del Rio et al., 2014; Thurm et al., 2016).

While the conversion of monocultures into mixed forests is often perceived as a promising long-term silvicultural adaptation tool, there is still a higher uncertainty regarding which short-term measures are feasible to mitigate the adverse effects of drought stress in existing stands that are still far from rotation age. Stand density, as a measure of tree abundance in a given area, can be seen as a primary driver of competition, with significant implications on tree growth and mortality (Bottero et al., 2017). Increasing evidence suggests that the reduction of stand density, in addition to accelerating tree growth (Pretzsch, 2019a), can be a mechanism for moderating the effects of drought-induced stress by increasing the vigour of individual trees due to increased average resource availability (Smith, 1997; Linder, 2000; Papadopol, 2000; Spittlehouse and Stewart, 2003; Thomas and Waring, 2014; Ammer, 2017). Reduced stand transpiration due to lower leaf area (Bréda et al., 1995) and the formation of more extensive root systems (Aussenac and Granier, 1988) have been considered as contributing factors that may increase tree water availability under drought in stands with reduced competition. However, several studies have also shown detrimental effects of managing lower stand densities, reporting decreased water availability resulting from increased transpiration and evaporative losses that may be caused by higher wind speeds and deeper penetration of solar radiation in recently thinned stands (Aussenac, 2000; Lagergren et al., 2008; Brooks and Mitchell, 2011), as well as increased competition for soil moisture (Nilsen et al., 2001). The inconsistency of results is likely related to several confounding factors that complicate the derivation of generalised reaction patterns. Species have for example been found to react differently to drought under varying levels of competition, as a result of differing adaptation strategies between coniferous and broadleaved species (Sohn et al., 2016b). Furthermore, the benefits of reduced competition on drought tolerance have also been found to decrease with stand age due to higher water demands of larger trees in open compared with denser stands (D'Amato et al., 2013). Furthermore, the effect of stand density on tree drought responses might be modified by climatic factors, such as site aridity (Sohn et al., 2016b). Despite a growing scientific interest in recent years, the relationship between stand density and tree drought susceptibility remains poorly quantified, especially across environmental growing conditions (van Mantgem et al., 2020).

This dissertation focuses on Scots pine and oak, the latter comprising both pedunculate oak (*Quercus robur* L.) and sessile oak (*Quercus petraea* (Matt.) Liebl.). The taxonomic status of the two "oaks" has been repeatedly reassessed (Aas, 1991). Sessile and pedunculate oak have either been described as two distinct species or, more recently, been placed within the species *Quercus robur* L. as two subspecies, *Q. r. petraea* and *Q. r. robur*, respectively (Roloff et al., 2008, pp. 506–507). To avoid any possible taxonomic pitfalls, either the generic term "oak" is used to summarise both species, or the respective colloquial names to distinguish species/subspecies, with "sessile oak" referring to the *petraea* type and "pedunculate oak" referring to the *robur* type, respectively (cf. Pretzsch et al., 2013a; Pretzsch et al., 2019b). Despite differences in ecology on marginal sites, pedunculate oak being more adapted to moist or wet sites than sessile oak, while also being more susceptible to drought stress in comparison (Annighöfer et al., 2015), both oak species grow sympatrically across most of Europe (Jones, 1959).

According to Kölling (2007), the climate envelop of Scots pine roughly encompasses mean annual temperatures of −4 to 11 °C (up to 14 °C under extreme conditions) and mean annual precipitation totals of some 400 to 1300 mm. The distribution range of oak is somewhat more limited to warmer sites (1 to15 °C) with mean annual precipitation totals similar to Scots pine (300 to 1300 mm) (Kölling, 2007). Scots pine is protected against drought due to embedded stomata and a waxy layer on the epidermis (Krakau et al., 2013), as well as a pronounced stomatal control that helps to regulate transpiration in early stages of drought (Irvine et al., 1998). However, Scots pine has recently been found to suffer growth depression and decline in some parts of its natural distribution due to increasing drought stress (Martínez-Vilalta and Piñol, 2002; Bigler et al., 2006; Kölling and Zimmermann, 2007; Galiano et al., 2010; Matías and Jump, 2012). Furthermore, past afforestation efforts have often seen the introduction of Scots pine on dry, poor and formerly degraded sites (Sohn et al., 2016a), where the adverse effects of drought may be particularly pronounced (del Río et al., 2017a). Oak on the other hand is often equipped with deep-reaching tap roots that improve the accessibility of water under drought (Praciak et al., 2013). It is found to exhibit considerable resistance and resilience to episodic drought stress in mixtures and monocultures (Pretzsch et al., 2013b). In contrast to the drought avoiding isohydric Scots pine, the anisohydric oak is found to keep its stomata open for longer during drought (Irvine et al., 1998), resulting in distinctly different drought reaction patterns of Scots pine and oak (Merlin et al., 2015). In addition, Scots pine and oak have been shown to differ in their drought response in relation to the seasonality of the drought events, Scots pine performing better under spring droughts, whereas oak shows a higher resistance under summer drought conditions (Merlin et al., 2015; Toigo et al., 2015; Vanhellemont et al., 2019). Scots pine and oak are economically important due to a wide range of end-use applications (Eaton et al., 2016; Houston Durrant et al., 2016). The ongoing transformation efforts towards mixed species forests have often seen the introduction of oak into stands traditionally dominated by Scots pine, in particular on dry sites at lower elevations (Zerbe, 2002; Schröder et al., 2007; Noack, 2011). Scots pine and oak mixtures are likely to increase in importance under adaptive forest management due to their high drought tolerance compared with other economically important tree species, such as Norway spruce and European beech (*Fagus sylvatica* L.) (Spellmann et al., 2011; Zang et al., 2011; Albert et al., 2015), which responds well to the common request for the promotion of more drought tolerant native tree species. There is also evidence that Scots pine-oak mixtures used to be more common in the past, particularly under warmer growing conditions (Björse and Bradshaw, 1998).

Contrary to the high practical relevance of Scots pine-oak mixtures and their potential role under adaptive forest management, only a limited number of studies have been devoted to analysing the productivity of this species combination in comparison to corresponding monocultures. Regional empirical evidence from England (Brown, 1992) and the Netherlands (Lu et al., 2016; Lu et al., 2018) suggests that mixed Scots pine-oak stands can be more productive than monocultures under certain site conditions. However, a French study by Toïgo et al. (2015) did not find any significant mixing effects with regard to stand productivity. Furthermore, the effect of species mixing on the ability of Scots pine and oak to withstand drought stress and to recover from it is still under much deliberation, as the small number of regional studies available reports both neutral, positive and negative effects on tree growth responses to drought (Merlin et al., 2015; Toigo et al., 2015; Bello et al., 2019b; Nothdurft and Engel, 2019).

In Europe, Scots pine and oak mostly endure acute drought stress under episodic water shortage. However, current climate projections indicate that many parts of Europe, in particular southern and western Europe, will exhibit a much lower water supply (higher temperature, lower or constant precipitation) by the end of the twenty-first century (Jacob et al., 2014). Therefore, forest managers now face the overwhelming task of adapting existing forests, which are still far from rotation age, to unprecedented climatic growing conditions. To broaden the view on the interaction of competition and tree growth under varying climatic conditions, ponderosa pine (*Pinus ponderosa* Douglas ex C. Lawson) was included in the analysis. In Arizona, USA, ponderosa pine typically incurs more chronic drought stress conditions and less constant precipitation than Scots pine and oak in Europe. Ponderosa pine is one of the most important timber species in the western United States and also used for a wide range of other applications, including erosion control and ethnobotanic use (Wennerberg, 2004). Ponderosa pine is able to survive hot and dry conditions, exhibiting a high drought tolerance, which can largely be attributed to the formation of deep reaching tap roots from an early age (Schütt et al., 2007).

Findings of regional studies suggest beneficial effects of reduced stand density on drought responses of Scots pine (Giuggiola et al., 2013; Fernández-de-Uña et al., 2015; Sohn et al., 2016a), sessile oak (Trouvé et al., 2017) and ponderosa pine (Fernández et al., 2012; Kerhoulas et al., 2013a; Thomas and Waring, 2014; Bottero et al., 2017). However, drought has also been reported to have more negative impacts on radial growth of larger ponderosa pines growing under low stand densities (McDowell et al., 2006).

So far, a comprehensive picture of mixing effects on stand productivity and tree drought responses, as well as stand density effects on tree drought responses, is lacking. Previous research is mainly anecdotal in nature and the results often inconsistent, which can largely be attributed to considerable variations in methodology and environmental growing conditions. Against this background it becomes paramount to form a strong empirical foundation that is based on broad overviews of different tree species, in particular such with a considerable practical relevance, under different ecological growing conditions, using consistent and comprehensible modelling approaches.

1.2. Objectives and outline

The overarching objective of this dissertation is to investigate the potential of two silvicultural adaptation measures (species mixing and stand density reduction) to stabilise and enhance stand productivity, as well as to mitigate tree drought susceptibility in two fundamental commercial European tree species (Scots pine and oak). This work aims to provide generalisable and easily transferrable knowledge that supports today's forest professionals in their challenging endeavour of adapting forest ecosystems to climate change and providing sustainable forest production systems for future generations.

To contribute to the growing body of knowledge on mixed-species forest growth and management, stand growth and structure of Scots pine and oak were scrutinised in mixtures and adjacent monocultures under variations in annual climate. Furthermore, the effect of species mixing on tree growth responses to episodic drought stress was studied along a comprehensive ecological gradient across Europe. Finally, the effect of reduced stand density and inter-individual competition on mean tree growth and short-term drought responses was scrutinised in monocultures at sites with different water availability. To learn more about the interaction of drought responses and stand density under more extreme growing conditions, the investigation was further extended by inclusion of chronically water-stressed ponderosa pine stands in the U.S. Southwest.

All studies within this dissertation rely on commonly used linear mixed-effects models and metrics that are easy to replicate and can serve as expedient starting points for further expansion of this important topic.

Three main research questions constitute the framework of this dissertation:

QI: How does stand growth and structure of mixed stands differ from adjacent monocultures and how is any over- or underyielding affected by variations in annual climate?

QII: How does species mixing influence tree growth responses to episodic drought under different ecological growing conditions?

QIII: How does the maintenance of reduced stand density influence tree growth responses to episodic drought under different levels of site water availability?

Each research question *QI – QIII* led to an individual study whose results were reported separately in peer-reviewed research articles (*Article I – Article III*). Figure 1 provides a graphical representation of the overarching theme complex of the dissertation and the research questions embedded within.

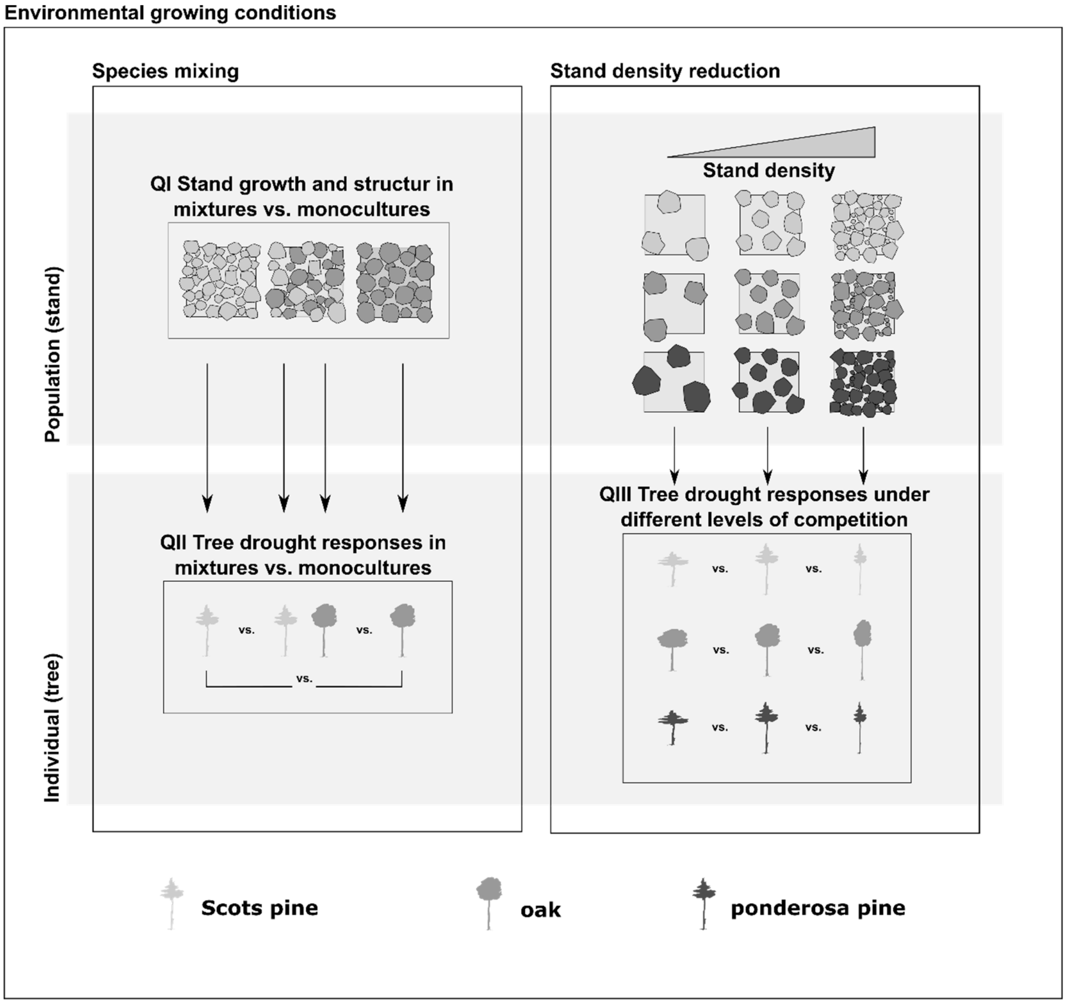

Fig. 1. Overarching theme complex of the dissertation. The analysis is carried out at the population (stand) and individual (tree) level and encompasses variations in environmental growing conditions. *QI* relates to the analysis of stand growth and structure in mixed versus monospecific stands of Scots pine and oak under annual variations in local climate. *QII* scrutinises tree drought responses in mixtures versus monocultures, considering variations in ecological growing conditions. *QIII* relates to tree drought responses in relation to variations in stand density under different levels of site water availability.

2. Material and methods

2.1. Material

2.1.1. Triplet data

Article I and *II* are based on temporary research plots in form of newly established triplets. Each triplet consists of three rectangular plots, one plot representing a mixed Scots pine-oak stand and two plots representing monospecific stands of each species respectively (Fig. 2). The plots represent even-aged stands that exhibit a more or less mono-layered structure. Only plots in fully stocked stands were included that approximately represent the site-specific maximum stand density. In all cases, the stand history was investigated as far back in time as possible in order to ensure that only unmanaged, or at most slightly managed, stands were sampled. Mixed plots were selected based on the criteria single-tree mixture and equal mixing proportion. Plots within each triplet were selected to ensure maximum similarity in site conditions, genetic material and stand age in order to avoid any residual effects. Plots were located in close proximity to each other, mostly in the same management compartment. Similarity of soil conditions was confirmed by use of boring rods and the study of soil maps.

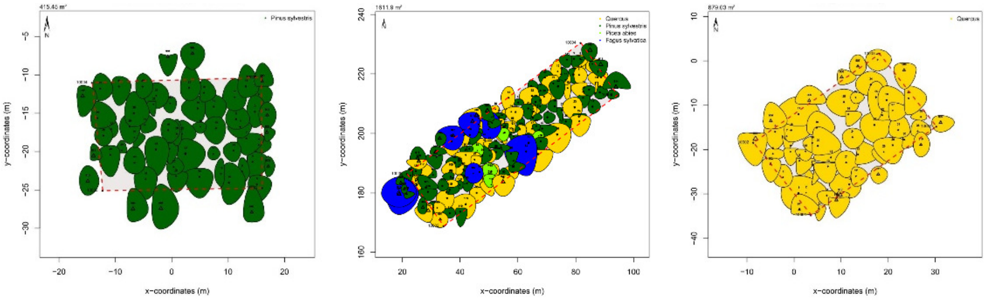

Fig. 2. Exemplary crown map of a Scots-pine oak triplet. Monospecific Scots pine (green, left) and oak (yellow, right) plots as well as a mixed-species plot with Scots pine and oak in single-tree mixture (middle). Coniferous and deciduous admixture species were assigned to Scots pine and oak respectively (in this case Norway spruce (light green) and European beech (blue)).

In total, 33 triplets were sampled along a comprehensive ecological gradient through Europe, reaching from nutrient-poorer and drier to nutrient-richer and moister sites. Some triplets were replicated to allow for the examination of thinning responses, which are the subject of a separate study. To account for this spatial clustering in the subsequent statistical analysis, each triplet was assigned to one of 24 triplet groups, based on its relative location. The study area represents the common natural European distribution of Scots pine and oak well, reaching from the south-western region in northern Spain to the northern and eastern regions in Sweden and Latvia respectively (Fig. 3). The highest concentration of study sites is found in Central Europe, covering Austria, Czechia, Germany, Poland and Slovakia.

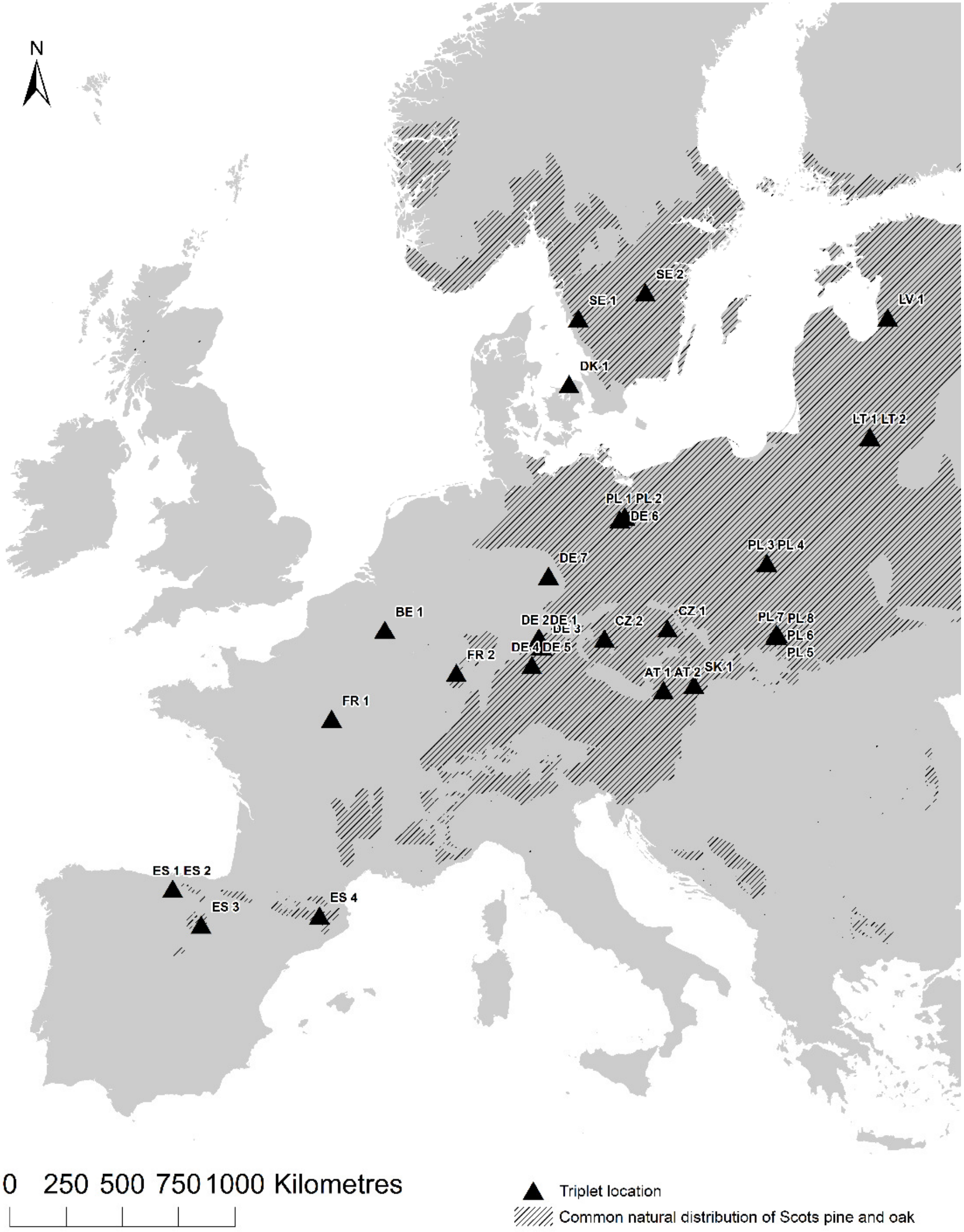

Fig. 3. Location of all 33 Scots pine-oak triplets (black triangles) across the common natural distribution of Scots pine and oak in Europe (hatched area). Reprinted from Steckel et al. (2020a).

Table 1 gives an overview of the prevalent site characteristics of each triplet. The variation in site fertility is reflected by the species-specific site index (Scots pine: $SI_{S.pi}$, oak: SI_{oa}), here quantified by the height h_q (m) of the tree with the quadratic mean diameter (hereinafter referred to as quadratic mean height) at age 100. Site indexing was performed by use of common yield tables (Wiedemann, 1948; Jüttner, 1955), which appear suitable, as they represent a broad range of site conditions. On the sampled sites, the site index ranged from 17.5 to 36.9 m (mean = 28.1 m) for Scots pine and from 14.8 to 36.0 m (mean = 25.8 m) for oak. The mean annual temperature ranged from 6.6 to 10.8 °C (mean = 8.4 °C) and the mean annual precipitation total ranged from 493 to 1267 mm (mean = 694 mm) (Tab. 1, Fig. 4).

Field sampling was carried out at the end of the growing season of 2017, using a uniform sampling protocol. For all living and dead trees the diameter at breast height (1.3 m) dbh (cm) was measured. All trees with a $dbh \geq 7.0$ cm were included in the analysis. On a sub-sample of living trees, tree height h (m) and crown base height cbh (m) were measured in each plot. These sample trees were selected to represent the entire diameter distribution in order to allow for a sufficient coverage of the actual stand height conditions for subsequent fitting of species-specific height-growth curves. Crown radii were measured on all living trees in at least all of the four cardinal directions (N, E, S, W). Crown length cl (m) was calculated by subtracting crown base height from tree height ($cl = h - cbh$). The crown projection area cpa (m^2) was computed for each tree as $cpa = \pi * \bar{r}^2$, where $\bar{r}$ is the tree's arithmetic mean crown radius.

In addition, increment cores were taken from at least 20 dominant trees per species and plot. Where available, 10 additional trees per species and plot were sampled, covering the rest of the diameter distribution. For each tree sampled in this way, two increment cores reaching from bark to pith were taken from north and east cardinal directions. Annual ring widths were subsequently measured from each core, using standardised dendrochronological techniques (Speer, 2010). Crossdating of the raw ring width series was performed for each plot, guided by narrow ring widths in species-specific pointer years (Schweingruber et al., 1990). A total of 4,175 trees was sampled this way.

Article I is based on a sub-sample of 7 triplets, encompassing a smaller research area, spanning from southern Germany to north-eastern Denmark (research sites DE 1–6, DK 1), while *Article II* covers the full data set encompassing all 33 triplets.

Tab. 1. Site characteristics of all 33 Scots-pine oak triplets sampled.

Site	Country	E	T	P	DMI	PM	Soil	Texture	$SI_{S.pi}$	SI_{oa}
AT 1	Austria	450	7.3	543	31.5	Sand/loam over granite	Cambisol	Loamy sand	24.3	22.6
AT 2	Austria	450	7.9	548	30.8	Sand/loam over granite	Cambisol	Loamy sand	18.6	17.8
BE 1	Belgium	187	9.7	861	43.9	Shale/loess	Cambisol	Clay loam	29.4	24.2
CZ 1	Czechia	265	9.0	619	32.8	Marlstone	Arenosol	Loamy sand	26.4	20.6
CZ 2	Czechia	400	8.5	567	30.7	Fylite	Cambisol	Loamy sand	27.5	25.2
DE 1	Germany	330	8.9	716	38.0	Sandstone	Cambisol	Loamy sand	21.2	21.1
DE 2	Germany	330	8.9	716	38.0	Sandstone	Cambisol	Loamy sand	21.4	19.7
DE 3	Germany	335	9.0	715	37.7	Sandstone	Cambisol	Loamy sand	24.4	23.1
DE 4	Germany	467	8.3	749	41.1	Sandstone	Stagnosol	Silt/clay loam	30.7	28.7
DE 5	Germany	467	8.3	749	41.1	Sandstone	Stagnosol	Silt/clay loam	30.9	30.8
DE 6	Germany	27	9.2	548	28.6	Sand	Cambisol	Loamy sand	28.9	30.8
DE 7	Germany	347	9.2	493	25.7	Sandstone	Cambisol	Loam	20.7	27.5
DK 1	Denmark	40	7.8	658	36.9	Sand	Arenosol	Sand	25.8	28.0
ES 1	Spain	780	7.3	966	56.2	Sandstone	Cambisol	Sandy loam	25.1	24.7
ES 2	Spain	785	7.3	966	56.2	Sandstone	Cambisol	Sandy loam	27.1	22.7
ES 3	Spain	1635	7.2	556	32.5	Sandstone	Leptosol/Cambisol	Loam	24.2	16.3
ES 4	Spain	1149	9.9	1267	63.9	Limestone/marl/sandstone	Regosol	Silty loam	17.5	16.5
FR 1	France	149	10.8	730	35.2	Sand	Planosol	Sandy loam /clay	27.9	26.0
FR 2	France	270	9.7	910	46.2	Sandstone	Cambisol	Loamy sand	29.5	30.3
LT 1	Lithuania	76	7.0	636	37.6	Sandstone	Arenosol	Loamy sand	30.3	29.0
LT 2	Lithuania	80	7.0	636	37.6	Sandstone	Arenosol	Loamy sand	36.9	26.6
LV 1	Latvia	60	7.0	870	51.2	Sand	Retisol	Loamy sand	35.8	28.9
PL 1	Poland	128	8.9	518	27.5	Sandstone	Arenosol	Loamy sand/sand	33.8	27.3
PL 2	Poland	114	8.9	518	27.5	Sandstone	Arenosol	Loamy sand/sand	33.8	26.3
PL 3	Poland	211	7.81	561	31.6	Sandstone	Luvisol	Sand/sandy loam	32.0	29.8
PL 4	Poland	209	7.8	561	31.6	Sandstone	Luvisol	Sand/sandy loam	34.5	29.5
PL 5	Poland	220	8.6	688	37.1	Sand	Arenosol	Loamy sand	34.4	32.0
PL 6	Poland	220	8.6	688	37.1	Sand	Arenosol	Loamy sand	35.9	31.3
PL 7	Poland	200	8.6	688	37.1	Sand	Arenosol	Loamy sand	33.4	29.6
PL 8	Poland	200	8.6	688	37.1	Sand	Gleysol	Loamy sand	32.8	36.0
SE 1	Sweden	110	7.7	782	44.1	Granite	Cambisol	Sandy loam	19.5	24.8
SE 2	Sweden	120	6.6	618	37.4	Granite	Cambisol	Sandy loam	23.6	14.8
SK 1	Slovakia	223	9.6	578	29.6	Sand	Arenosol	Loamy sand	27.7	28.3

E: elevation (m a.s.l.). T: mean annual temperature (°C). P: mean annual precipitation total (mm). DMI: De Martonne aridity index (De Martonne, 1926) (mm $°C^{-1}$). PM: parent material (geology). $Soil$: key reference soil group according to FAO WRB classification (IUSS Working Group WRB, 2015). $Texture$: soil texture class according to FAO WRB classification (IUSS Working Group WRB, 2015). SI: site index (m) for Scots pine ($SI_{S.pi}$) and oak (SI_{oa}) monocultures, referring to quadratic mean height, h_q, at age 100. Reference period for climate data: 1976–2015.

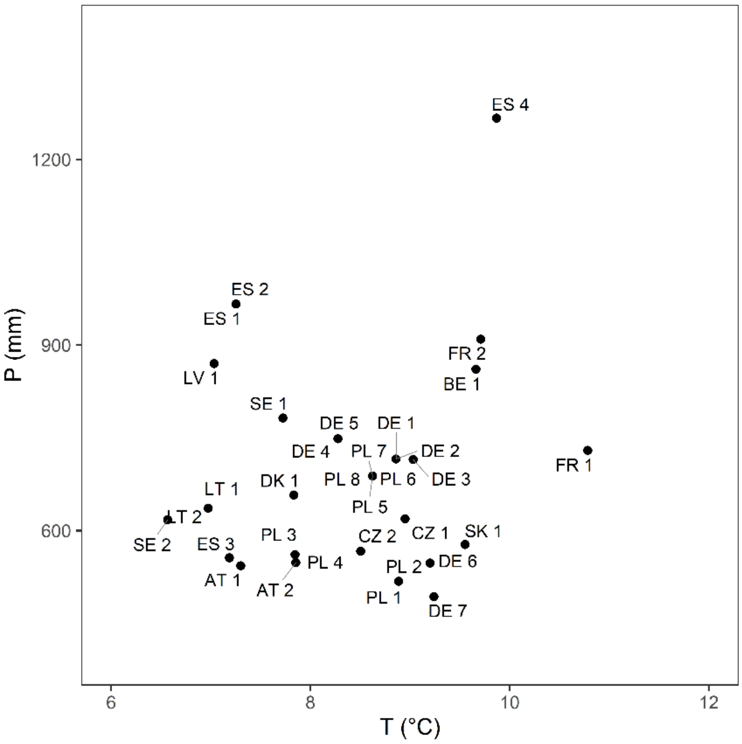

Fig. 4. Location of the 33 Scots pine-oak triplets within the climatic gradient covered. *T*: mean annual temperature (°C). *P*: mean annual precipitation total (mm). Reference period for climate data: 1976–2015. Reprinted from Steckel et al. (2020a).

2.1.2. Stand density trial data

Article III is based on tree sampling carried out in monospecific, even-aged and more or less mono-layered Scots pine and sessile oak stands in southern Germany (Bavaria) and ponderosa pine stands in the U.S. Southwest (Arizona) (Fig. 5). Trees on each site were sampled from one untreated control stand, exhibiting the site-specific maximum stand density, as well as from two adjacent stands, growing under same site conditions, but providing moderate and low stand densities respectively. For each species studied, study sites reflect different levels of site water availability, spanning the range of typical growing conditions in the respective study regions. In Bavaria, trees were sampled within the framework of existing long-term thinning and spacing trials, maintained by the Chair of Forest Growth and Yield Science at the Technical University of Munich (Preuhsler et al., 1993; Utschig et al., 1993; Klemmt, 2007; Nickel et al., 2007; Pretzsch et al., 2014b; Uhl, 2015). In Arizona, trees were sampled in stands located within the research areas of Fort Valley and Long Valley Experimental Forests, managed by the U.S. Forest Service (Olberding and Moore, 2008).

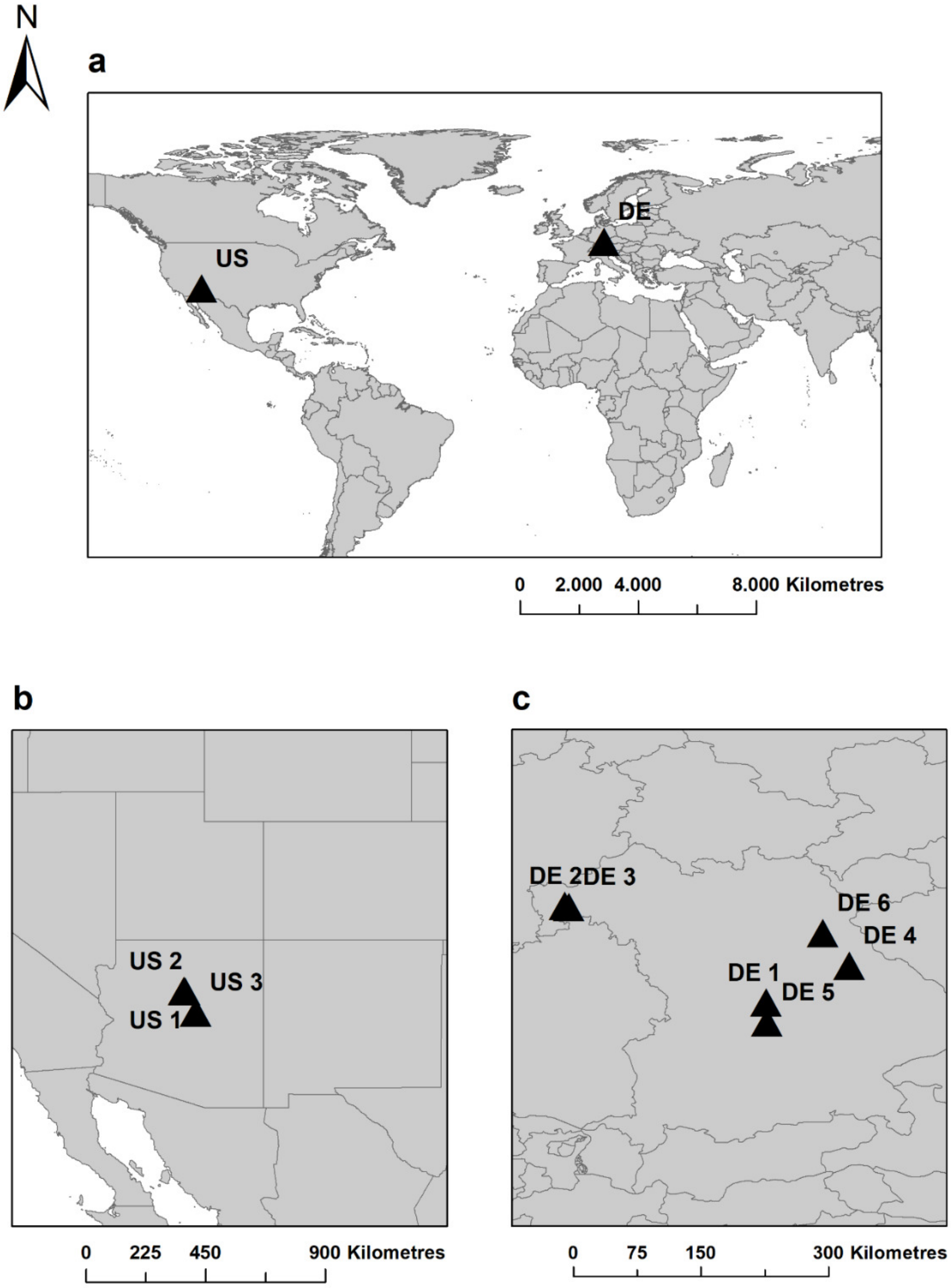

Fig. 5. Overview of study regions and sites covered in *Article III*. a) Study regions (black triangles) in Arizona, USA (US) and Bavaria, Germany (DE). b) Detailed location (black triangles) of ponderosa pine study sites in Arizona (US 1–US 3). c) Detailed location (black triangles) of sessile oak (DE 1–DE 3) and Scots pine study sites (DE 4–DE 6) in Bavaria. Reprinted from Steckel et al. (2020b).

In the sampled stands, stand density levels have been maintained over many decades by thinning intervention at certain time intervals (Tab. 2). Table 3 gives an overview of site and stand characteristics for all nine locations. The Bavarian sites are located at elevations of between 380 and 495 m a.s.l. (mean = 433 m a.s.l.). Sites in Arizona are found at elevations of 2079 to 2280 m a.s.l. (mean = 2203 m a.s.l.). Stand age varied from 47 to 68 years (mean = 60 years) in Scots pine, from 34 to 153 years (mean = 93 years) in sessile oak and from 100 to 105 years (mean = 102 years) in ponderosa pine. The geological parent material was identical within each species-group. Sampled stands grow on soils originating from sand (Bavaria) and basalt (Arizona). The mean annual temperature ranged from 8.3 to 8.9 °C (mean = 8.5 °C) on study sites of Scots pine, from 8.1 to 8.3 °C (mean = 8.2 °C) in the case of sessile oak and from 7.1 to 9.0 °C (mean = 7.7 °C) in the case of ponderosa pine. The mean annual precipitation total ranged from 714 to 756 mm (mean = 731 mm) on study sites of Scots pine and from 767 to 1021 mm (mean =923 mm) for sessile oak, while on study sites of ponderosa pine it ranged from 575 to 728 mm (mean = 638 mm). Supplement material 1 (Appendix C) provides information on the average climatic growing conditions throughout the calendar year (climate diagrams according to Walter and Lieth (1967) based on the reference period 1978–2017). In Bavaria, precipitation and temperature patterns generally show a significant peak in July. However, throughout a typical year, there is a rather constant relationship between temperature and precipitation without any water deficit. In contrast, the study sites in Arizona exhibit a bimodal precipitation pattern that peaks in winter (December–March) and the summer monsoonal season (July–August). A considerable water deficit is common prior to the start of the monsoonal season (June). According to Kerhoulas et al. (2013b), winter precipitation can be considered to be the dominant water source for ponderosa pine trees growing in the studied region.

Tab. 2. Thinning history and investigated episodic drought events.

Site	Thinning history (year of thinning and sampling)	Drought years (SPEI)
DE 1	2004, 2009, 2014	2015 (−1.5)
DE 2	1981, 1986, 1991, 1996, 2002, 2010	2003 (−1.6), 2015 (−1.8)
DE 3	1934, 1942, 1952, 1958, 1966, 1976, 1986, 1996, 2006, 2013	2003 (−1.6), 2015 (−1.8)
DE 4	1977, 1986, 1993, 1998, 2003, 2008, 2015	1976 (−1.2)
DE 5	2002	2003 (−2.1), 2015 (−1.4)
DE 6	1987, 1992, 1997, 2002, 2007, 2014	2003 (−1.7), 2015 (−1.6)
US 1	1925, 1934	1989 (−1.4), 2002 (−2.1), 2009 (−1.3)
US 2	1924, 1935, 1946, 1967-68, 1988, 1997	2002 (−2.2), 2009 (−1.3)
US 3	1925, 1936	1989 (−1.0), 2002 (−2.2), 2009 (−1.3)

SPEI: Standardised Precipitation Evapotranspiration Index (Vicente-Serrano et al., 2009) (mean monthly value for the site-specific growing season shown)

Tab. 3. Site and stand characteristics for all nine locations studied in Bavaria and Arizona (*Article III*).

Site	ID	Country	Species	Age	E	T	P	I_A	PM
DE 1	GEI 649	Germany	sessile oak	34	495	8.3	767	1.26	sand, loess
DE 2	ROB 620	Germany	sessile oak	91	440	8.1	1021	1.70	sand
DE 3	ROB 90	Germany	sessile oak	153	470	8.3	981	1.62	sand
DE 4	BOD 610	Germany	Scots pine	65	400	8.5	722	1.17	sand
DE 5	GEI 335	Germany	Scots pine	68	380	8.9	756	1.20	sand
DE 6	WEI 611	Germany	Scots pine	47	410	8.3	714	1.16	sand
US 1	FV U1	USA	ponderosa pine	105	2250	7.1	575	1.07	basalt
US 2	FV U2	USA	ponderosa pine	100	2280	7.1	612	1.14	basalt
US 3	LV	USA	ponderosa pine	100	2079	9.0	728	1.24	basalt

Age: stand age (yrs). E: elevation (m a.s.l.). T: mean annual temperature (°C). P: mean annual precipitation total (mm): I_A: Global Aridity Index. PM: parent material (geology). Reference period for climatic variables: 1978–2017.

Field sampling was carried out following the growing season of 2017. On all sites the same sampling protocol was followed. A minimum of 15 dominant to co-dominant living trees were each selected randomly in stands representing three different levels of stand density (low, moderate and maximum; $\geq 3 \times 15 = 45$ trees per site). A total of 139 Scots pine trees, 135 sessile oak trees and 135 ponderosa pine trees (409 trees combined) were sampled. To confirm local stand density and inter-individual competition levels of selected trees in the field, stand basal area BA (m² ha^{-1}) was measured via angle count sampling (Lindsey et al., 1958) at each tree, by use of a level relascope (Spiegel-Relaskop, Relaskop-Technik, Vetriebsges. m.b.H., Salzburg, Austria). For each tree, dbh and h were measured. In addition, increment cores were sampled from each tree and ring widths subsequently measured and analysed in the same fashion as described in 2.1.1.

2.1.3. Meteorological data

Monthly meteorological data (monthly mean temperature and monthly precipitation total) were sourced from national meteorological services. Local weather station data was preferably used and supported by interpolated grid data (CRU (Climatic Research Unit) 0.5° gridded dataset (Harris et al., 2014)) where required. CRU data has been used in similar research contexts and has proven reliable when local weather station data is not available (Sitko et al., 2016). This assessment was supported by exemplary comparisons of historical national weather station data and CRU grid data, which never yielded differences of any practically relevant orders of magnitude (results not presented). Monthly meteorological data was used to calculate annual values (T: annual mean temperature (°C); P: annual precipitation total (mm)), which were subsequently averaged over longer periods to derive long-term means for characterisation of average climatic site conditions (mean annual temperature and mean annual precipitation total are also referred to as T and P respectively in the following).

2.2. Methods

2.2.1. Measures of site aridity

To characterise water supply/availability, two different aridity indices were employed: a) the De Martonne aridity index DMI (mm °C^{-1}) (De Martonne, 1926) (Eq. 1), used in *Article I – II*, and b) the Global Aridity Index (I_A) by the United Nations Environmental Programme (UNEP) (Middleton and Thomas, 1993) (Eq. 2), used in *Article III*. Both indices were computed annually and averaged over longer time frames. In *Article I*, T, P and DMI were used to characterise annual climate conditions.

$$DMI = P/(T + 10) \tag{1}$$

$$I_A = P/PET \tag{2}$$

While the DMI is generally valued for its simple yet highly informative nature (Pretzsch et al., 2015), providing information on the meteorological water supply of a given site, the I_A provides a more sophisticated estimate of the relationship between the local meteorological moisture supply and moisture demand (i.e., meteorological water availability). I_A is computed as the ratio of P and the potential evapotranspiration (PET). The PET was computed from monthly meteorological data, using the Thornthwaite equation (Thornthwaite, 1948). The greater DMI and I_A become, the better the meteorological water supply/availability for plant growth (Middleton and Thomas, 1993; Pretzsch et al., 2015).

For the analysed triplets, the DMI ranged from 25.7 to 63.9 mm °C^{-1} (mean = 37.9 mm °C^{-1}) (Tab. 1).

For the studied stand density trials, the I_A ranged from 1.16 to 1.20 (mean = 1.18) for Scots pine, from 1.26 to 1.70 (mean = 1.53) for sessile oak and from 1.07 to 1.24 (mean = 1.16) for ponderosa pine (Tab. 3).

2.2.2. Stand growth and structure in mixed versus monospecific stands (*Article I*)

Reconstruction of past tree and stand growth

The comparison of stand growth and structure in mixed versus monospecific stands was based on a reconstruction of past tree and stand growth on an annual basis over a 20 year time frame (1998 – 2017) by use of increment cores, following the approach described by Heym et al. (2018), briefly outlined in the following.

For all trees, the mean year ring width was computed for every year from both increment cores sampled (see 2.1.1.). Stand age was determined from year ring counts of increment cores reaching the pith. Measured height-diameter pairs were employed to parameterise common height curves (Korsun, 1935; Michailoff, 1943; Prodan, 1951; Petterson, 1955; Freese, 1964), which were used to estimate missing individual tree heights and to calculate the quadratic mean height (h_q) for each plot and species. For cored trees, retrospective annual dbh was derived from increment cores, while plot- and species-specific regression analysis was employed to derive corresponding dbh values for non-cored trees and standing dead wood (Eq. 3).

$$id_i = a * d_{i\_end}^{b} \tag{3}$$

In Equation 3, the cumulative diameter at breast height increment for year i (id_i) is calculated as a function of the diameter at breast height at the end of the year i ($d_{i\_end}^{b}$). Parameters a and b are estimated by linear OLS (Ordinary Least Squares) regression after log-transformation. The equation assumes a typical allometric relationship between diameter and diameter growth, where a represents the scaling parameter and b the allometric exponent.

Height-age curves were selected for each plot and species from common yield tables, based on age and quadratic mean height as provided by the survey. For Scots pine and oak, the yield tables by Wiedemann (1948) and Jüttner (1955) were used respectively. Retrospective annual height growth of individual trees was estimated based on a uniform height curve system first developed by Kennel (1972) for European beech and later parameterised for other tree species by Franz et al. (1973).

Evaluation of mean tree and stand state characteristics

Mean tree and stand state characteristics were evaluated according to the DESER-Norm 1993 by Johann (1993), using evaluation software developed by the Chair of Forest Growth and Yield Science at the Technical University of Munich (Biber, 2013). Characteristics covered include mean and dominant (100 largest trees per ha) tree dimensions, such as quadratic mean height h_q (m), dominant height h_{100} (m), quadratic mean diameter d_q (cm), dominant diameter d_{100} (cm), quadratic mean height-diameter ratio h_q/d_q and dominant height-diameter ratio h_{100}/d_{100}, as well as area related sum values, such as number of trees N (trees ha^{-1}), stand density index by Reineke (1933) SDI (trees ha^{-1}), stand basal area BA (m^2 ha^{-1}) and standing volume V (m^3 ha^{-1}). Coniferous and deciduous admixture species were assigned to Scots pine and oak respectively. Table 4 provides an overview of mean tree and stand characteristics of the sub-sample of triplets used in *Article I*. Corresponding characteristics for all 33 triplets used in *Article II* are outlined in Appendix C (Supplement Material S2).

Productivity

The tree basal area ba (m²) was computed for each tree and year as $ba = \frac{\pi}{4} * d^2$, where d is the tree's diameter at breast height. Using the corresponding measured or estimated tree height h and the species-specific form factor f by Franz (1971), individual tree volume v (m³) was computed as $v = \ ba * h * f$. Tree volume increment iv_i (m³ yr^{-1}) was derived for every year i as $iv_i = v_i - v_{i-1}$. Annual stand volume increment IV_i (m³ ha^{-1} yr^{-1}) was subsequently computed from the summation of single tree values and upscaling to one hectare. Analogously, stand basal area increment IBA (m² ha^{-1} yr^{-1}) was computed by an upscaling of single tree basal area increments. As a measure of stand productivity, the focus was on IV, as it is a more relevant area measurement for forest practice and reflects tree basal area and height development, which both may be affected by species mixing.

Size and growth partitioning

To quantify size and growth partitioning of trees in mixtures versus monocultures the Gini coefficient (GC) (Gini, 1912) (Eq. 4) was employed. This metric was originally developed for quantifying the inequality of income distribution, but has since become popular for quantifying size and growth partitioning of trees in forest stands (Camino, 1976; Binkley et al., 2006; Pretzsch and Schütze, 2014; Pretzsch and Schütze, 2016).

$$GC_x = \frac{\sum_{i-1}^{n} \sum_{j=1}^{n} |x_i - x_j|}{2n(n-1) * \bar{x}} \tag{4}$$

In Equation 4 the terms x_i and x_j represent size or growth of the ith, respectively the jth tree in a stand with i=1…n trees. GC can take values between 0 and 1. In case of GC=0.0 all trees are equal in size or growth. The higher GC, the stronger the inequality of tree size or growth between the trees. When applied to mixed and monospecific stands, the Gini coefficient can show whether species mixing modifies size and growth partitioning between trees in a population, e.g. if species mixing favours small understory trees compared with monocultures (Pretzsch and Schütze, 2016). In this study, the Gini coefficient was applied to stem volume (GC_v) and stem volume increment (GC_{iv}) in mixed and monospecific stands.

Tab. 4. Mean tree and stand characteristics of the 7 triplets of mixed and monospecific stands covered in *Article I*. Stand characteristics are given for the mixed stand as a whole (S. pine + oak), for the species in the mixed stands (S. pine mixed, oak mixed), as well as for the monospecific stands (S. pine mono, oak mono). The means of all 7 triplets are given in plain text, as well as ranges (min–max) in italics.

	MP	**Age**	**d_q**	**h_q**	**N**	**SDI**	**BA**	**V**	**IBA**	**IV**
S. pine + oak					806	816	40.1	437	0.8	12.2
					411–1169	*630–1000*	*32.5–48.5*	*353–502*	*0.5–1.3*	*8.3–18.4*
S. pine mixed	58	78	28.1	24.0	432	482	24.1	264	0.4	6.5
	48–70	*50–105*	*20.2–34.0*	*20.9–28.3*	*224–665*	*346–580*	*17.8–29.3*	*181–344*	*0.1–0.8*	*2.6–10.6*
oak mixed	42	78	24.1	20.7	374	335	16.0	173	0.4	5.7
	30–52	*50–105*	*20.5–32.4*	*17.8–23.0*	*187–554*	*252–420*	*11.8–20.2*	*131–249*	*0.2–0.7*	*3.3–9.1*
S. pine mono		78	26.1	21.3	902	829	38.8	375	0.9	11.3
		45–110	*18.7–35.3*	*17.1–27.6*	*421–1602*	*670–1006*	*29.3–44.0*	*291–503*	*0.3–1.5*	*4.8–18.7*
oak mono		79	25.3	21.9	853	785	35.7	403	0.8	11.9
		40–115	*16.8–35.3*	*17.5–28.5*	*576–1371*	*629–1010*	*30.4–42.6*	*267–510*	*0.5–1.2*	*8.1–15.9*

MP: mixing proportion based on weighted SDI (%). Age: stand age (yrs). d_q: quadratic mean diameter (cm). h_q: quadratic mean height (m). N: number of trees (trees ha^{-1}). SDI: stand density index (trees ha^{-1}) (Reineke, 1933). BA: stand basal area (m² ha^{-1}). V: standing volume (m³ ha^{-1}). IBA: stand basal area increment (m² ha^{-1} yr^{-1}), five-year average (2013–2017). IV: stand volume increment (m³ ha^{-1} yr^{-1}), five-year average (2013–2017).

Quantification of mixing effects

The quantification of mixing effects on the stand and species level was performed according to the approach outlined in Pretzsch et al. (2015) and based on the nomenclature used by del Río et al. (2016) (see Figure 6 for a visualisation of the concept).

The observed (measured) productivity in the mixed Scots pine-oak stand is denoted as $P_{S.pi,oa}$ and the corresponding proportions of Scots pine and oak in this mixture are denoted $pp_{S.pi,(oa)}$ and $pp_{(S.pi),oa}$ respectively ($P_{S.pi,oa} = pp_{S.pi,(oa)} + pp_{(S.pi),oa}$). The expected productivity is calculated as the sum of the weighted means of the neighbouring pure stand as $\hat{P}_{S.pi,oa} = P_{S.pi} * m_{S.pi} + P_{oa} * m_{oa}$, where $P_{S.pi}$ and P_{oa} are the observed productivities in the monospecific Scots pine and oak stands respectively and $m_{S.pi}$ and m_{oa} are the corresponding species-specific mixing proportions. The calculation of mixing proportions is explained in the following section. The productivity of each species in the mixture upscaled to one hectare is calculated as $P_{S.pi,(oa)} = pp_{S.pi,(oa)}/m_{S.pi}$ and $P_{(S.pi),oa} = pp_{(S.pi),oa}/m_{oa}$.

At the stand level, a positive mixing effect (overyielding) is evident when the observed productivity of the mixture is higher than the expected productivity ($P_{S.pi,oa} > \hat{P}_{S.pi,oa}$). Positive mixing effects on the species level are present, when $P_{S.pi,(oa)} > P_{S.pi}$ and $P_{(S.pi),oa} > P_{oa}$. Transgressive overyielding occurs when the observed productivity in the mixed-species stand exceeds the productivity of either monospecific stand ($P_{S.pi,oa} > \max(P_{S.pi}, P_{oa})$). Analogously, underyielding ($P_{S.pi,oa} < \hat{P}_{S.pi,oa}$) and degressive underyielding ($P_{S.pi,oa} < \min(P_{S.pi}, P_{oa})$) can occur.

As a simple metric to quickly report any over- or underyielding, the relative productivity RP was used. For every triplet and year the ratio $RP_{S.pi,oa} = P_{S.pi,oa}/\hat{P}_{S.pi,oa}$ was computed. Analogously to the stand level evaluation, the corresponding ratio was computed for Scots pine and oak as $RP_{S.pi,(oa)} = P_{S.pi,(oa)}/ P_{S.pi}$ and $RP_{(S.pi),oa} = P_{(S.pi),oa}/P_{oa}$ respectively. The comparison of other stand characteristics, such as for example BA and V, in mixed versus monospecific stands was performed analogously; the relative performance of mixtures in relation to monocultures regarding any variable Y was therefore universally labelled RY.

To visualise the mixing effects regarding productivity, cross diagrams according to Harper (1977) and Kelty (1992) were used, displaying the relative volume productivity on the basis of the proportions of volume growth (RPP) on the species ($RPP_{S.pi,(oa)} = pp_{S.pi,(oa)}/P_{S.pi}$; $RPP_{(S.pi),oa} = pp_{(S.pi),oa}/P_{oa}$) and on the stand level ($RPP_{S.pi,oa} = RPP_{S.pi,(oa)} + RPP_{(S.pi),oa}$).

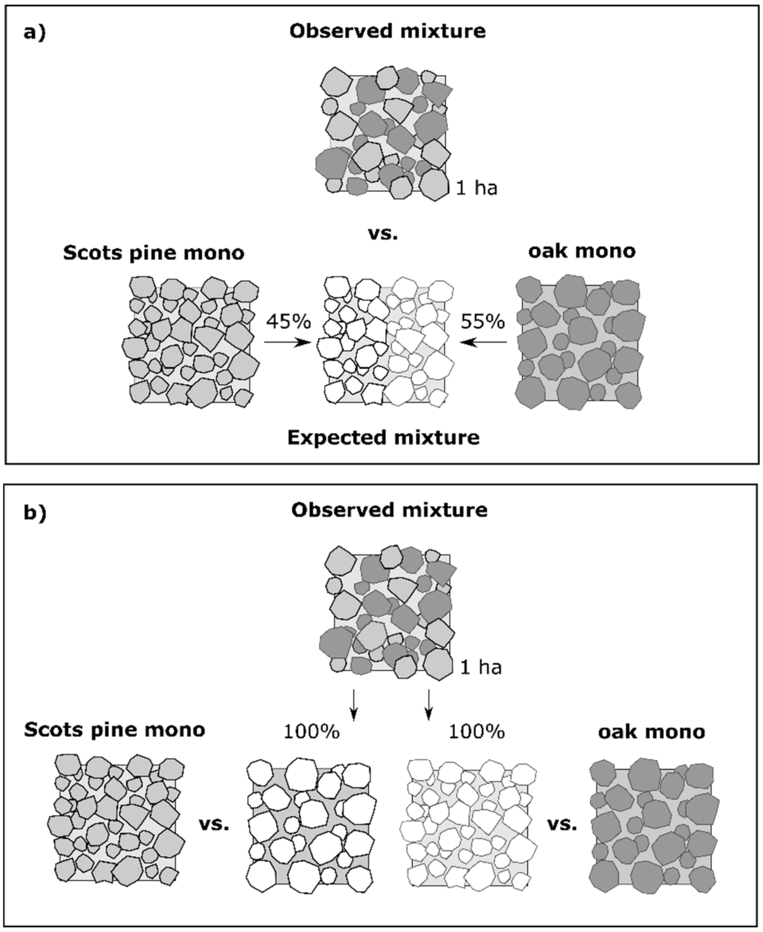

Fig. 6. Visualisation of the conceptual framework to quantify mixing effects on the level of the stand as a whole (a) and on the species level (b). The observed mixture is compared to the expected mixture, which constitutes the sum of the weighted mean values of both monocultures (a). Both observed monocultures are individually compared to the corresponding expected monoculture, calculated from the respective species' contribution in the mixture upscaled to one hectare (b). Adapted by Wellhausen and Pretzsch (2016).

Determination of mixing proportions

As proposed by Dirnberger and Sterba (2014) and Sterba et al. (2014), the mixing proportion (m) was calculated based on the weighted stand density index (SDI) by Reineke (1933) ($SDI = N * (25/\, d_q)^{-1.605}$). With this approach, differences in growing space requirements of each species were accounted for by adjusting the measured SDI values by an equivalence coefficient e, which for Scots pine was calculated as the ratio between the SDI of Scots pine ($SDI_{S.pi}$) and oak (SDI_{oa}) in the respective fully stocked monocultures. Thus, $e_{S.pi} = SDI_{S.pi}/SDI_{oa}$ indicates the growing space requirements of Scots pine in relation to oak. Subsequently, the proportion of Scots pine in mixture with oak ($m_{S.pi}$) can be calculated according to Equation 5. The mixing proportion of oak (m_{oa}) is calculated analogously.

$$m_{S.pi} = \frac{SDI_{S.pi,(oa)}}{SDI_{S.pi,(oa)} + SDI_{(S.pi),oa} * e_{S.pi}} \qquad (5)$$

2.2.3. Investigation of tree growth responses to episodic drought (*Article II – III*)

Dendrochronological evaluation

The basal area increment bai (cm² yr^{-1}) was used as the basis for assessing tree growth responses to episodic drought. It was calculated from the arithmetic mean annual ring width of both increment cores as $bai\ _i = \left(d_i^2 - d_{i-1}^2\right) * \pi/4$, where d_i is the tree's diameter at breast height for year i in cm. The basal area increment was preferably used as it is known to better reflect the growth of the whole tree rather than the one-dimensional stem diameter or stem radius increment (Biondi and Qeadan, 2008).

In order to remove long-term trends due to age, size and stand dynamics, a double detrending procedure (Holmes et al., 1986) was applied to each bai series. Firstly, a Hugershoff function (Hugershoff, 1936) was applied, which was found to adequately reflect the mainly longer time spans covered, encompassing all the typical phases of tree growth development over time. The Hugershoff function is often more suitable than commonly used negative exponential functions as it is able to imitate the accelerated growth of tree rings close to the pith (Warren, 1980). In a second step, a smoothing cubic spline was applied with a frequency cutoff of 50 % at 2/3 of the curve length (Cook and Peters, 1981). The detrending procedure resulted in dimensionless series of bai indices, calculated as the ratio between the measured increment and the fitted values. The resulting index series contained only year-to-year variability associated with fluctuations in climate (Fritts, 2001; Esper et al., 2002). To assess the signal strength of group chronologies, two standard statistics were calculated based on the bai index series, the inter-series correlation ($Rbar$) and the expressed population signal (EPS) (Wigley et al., 1984). $Rbar$ is the mean correlation coefficient among individual tree ring or bai series in a chronology. EPS assesses the degree to which a given chronology represents a hypothetical chronology based on an infinite number of cores. For descriptive statistics of bai series and detrending procedures, the package $dplR$ (Bunn, 2008) from the statistical environment R, version 3.6.1 (R Core Team, 2019), was used.

Identification of drought events and quantification of drought intensity

To identify suitable episodic drought events and to quantify the drought intensity, the Standardised Precipitation Evapotranspiration Index ($SPEI$) (Vicente-Serrano et al., 2009) was employed. The $SPEI$ is a multi-scalar drought index that is based on a monthly balance of P and PET. The $SPEI$ is a proven metric of acute water stress and has been used in a series of similar studies (Sohn et al., 2016a; Thurm et al., 2016; Perkins et al., 2018; Bose et al., 2020). Site-specific episodic drought events were only investigated when at least one month during the growing season was characterised by a $SPEI$ value of ≤ -1.0, potentially encompassing moderate to extreme drought conditions according to the classification by Potop et al. (2014) (Tab. 5). The growing season was determined for each site as months exhibiting a mean temperature of ≥ 10 °C (Winkler, 1980).

Tab. 5. Seven classes of $SPEI$ (Standardised Precipitation Evapotranspiration Index) categories according to Potop et al. (2014).

SPEI value	Category
≥ 2.00	Extreme wet
1.50 to 1.99	Severely wet
1.49 to 1.00	Moderately wet
0.99 to -0.99	Normal
-1.00 to -1.49	Moderate drought
-1.50 to -1.99	Severe drought
≤ -2.00	Extreme drought

In *Article II* a two-step approach for identifying drought events was used that not only considered the $SPEI$, but also took into account negative pointer years (Schweingruber et al., 1990), in which at least 50 % of the trees of at least one of the two species in monocultures at a given site showed a negative event with a growth reduction of > 0.75 standard deviation (SD) below the mean (Fig. 7).

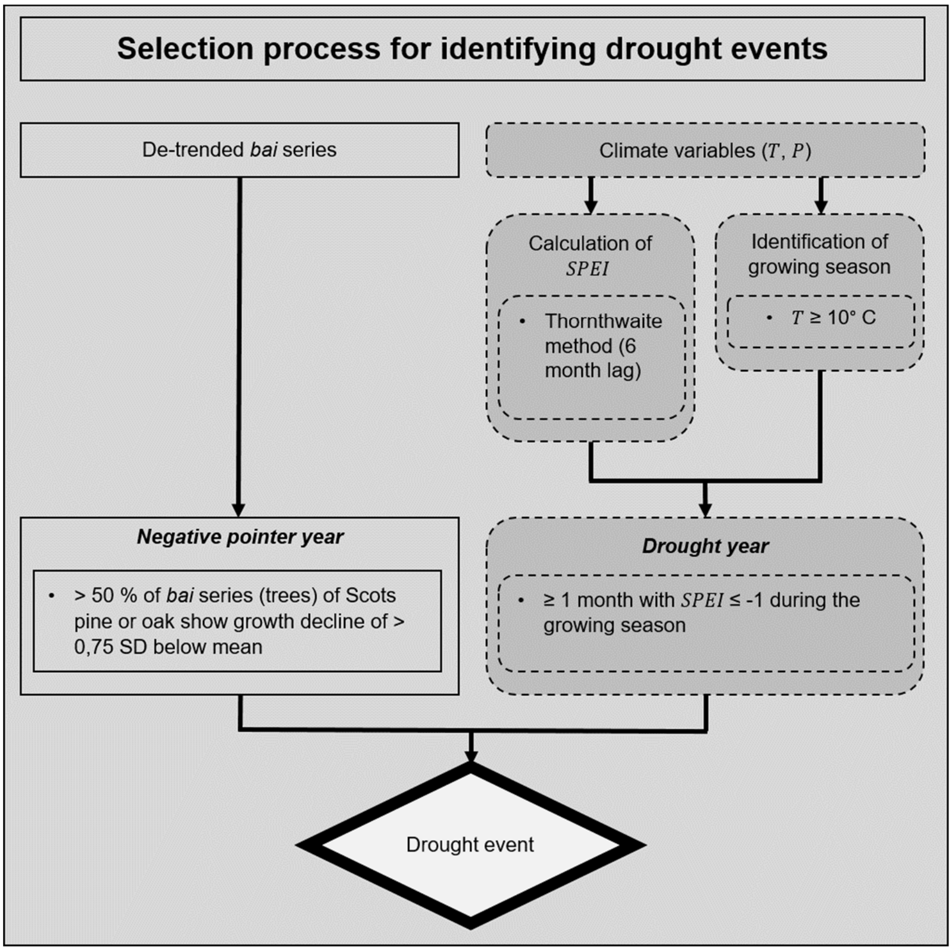

Fig. 7. Flow chart depicting the process for identifying drought events in *Article II*. Reprinted from Steckel et al. (2020a).

An overview of initially identified and finally selected drought events used in *Article II* is given in Supplement Material S3 (Appendix C). In *Article III* the analysis focused on a series of well-reported droughts, which occurred in 1976, 2003 and 2015 in Bavaria and in 1989, 2002 and 2009 in Arizona. These droughts were characterised by average monthly $SPEI$ values ranging from -1.0 to -2.2 during the growing season (moderate to extreme drought) (Tab. 2).

Quantification of tree growth in response to drought

Short-term tree growth responses to episodic drought stress were assessed using drought response indices as proposed by Lloret et al. (2011). 'Resistance' (Rt) (Eq. 6) is the ratio between tree growth during drought (G_{Dr}) and the average growth during a defined pre-drought period (G_{PreDr}). 'Recovery' (Rc) (Eq. 7) is the ratio between the average growth during the post-drought period (G_{PostDr}) and G_{Dr}. 'Resilience' (Rs) (Eq. 8) is defined as the ratio between G_{PostDr} and G_{PreDr}. Resistance highlights the tree's ability to maintain growth levels during drought. Rt = 1.0 indicates complete resistance. Recovery can be seen as the ability to restore a level of growth after drought. Rc = 1.0 indicates persistence of the drought growth level, Rc < 1.0 indicates a further decline and Rc > 1.0 indicates a recovery from the growth level during drought. Resilience exhibits the tree's capacity to recover to pre-drought growth levels. $Rs \geq 1.0$ indicates a full recovery or increased growth after the drought event, while Rs < 1.0 indicates growth decline. In *Article II* drought response indices were multiplied by 100 and therefore reported in percent (%).

$$Rt = \frac{G_{Dr}}{G_{PreDr}} \tag{6}$$

$$Rc = \frac{G_{PostDr}}{G_{Dr}} \tag{7}$$

$$Rs = \frac{G_{PostDr}}{G_{PreDr}} \tag{8}$$

Different lengths of pre- and post-drought periods were used. In *Article II* the standard three-year period according to Lloret et al. (2011) was chosen, with the exception of the drought year 2015, for which a two-year post-drought period was computed. In *Article III* a two-year period was generally used to better reflect the local climatic conditions, which saw a high frequency of drought events, especially in Arizona. In each case, the time frame chosen was based on a trade-off between a sufficiently long period, to ensure a good estimation of the mean growth before and after the drought event, and the risk of an overlap of pre- and post-drought periods with adjacent drought events. Every drought event was considered as a single stress event for each site. To minimise bias, drought events that showed any overlap of pre- and post-drought periods with adjacent drought events were excluded from the analysis. Drought events that coincided with thinning interventions in the same year were not considered in the analysis (*Article III*).

2.2.4. Quantification of population density

To study the effect of stand density and inter-individual competition on tree drought responses, the weighted mean relative stand basal area ($MRBA$) (Eq. 9) was used as a continuous measure of population density (*Article III*).

$$MRBA = MBA_{obs}/MBA_{max} \tag{9}$$

In Equation 9, MBA_{obs} and MBA_{max} represent Assmann's periodical mean basal area level (Assmann, 1970) in m² ha^{-1} for the observed treated stand and the corresponding untreated control stand respectively. MBA was determined as the mean of the stand basal area between the beginning (BA_b) and the end (BA_e) of the $1 \ldots n$ survey periods, weighted by the length of the survey period (m) (Eq. 10).

$$MBA = \frac{\frac{BA_{1b}+BA_{1e}}{2} * m_1 + \cdots + \frac{BA_{nb}+BA_{ne}}{2} * m_n}{m_1 + \cdots + m_n} \tag{10}$$

As an example, $MRBA$ = 0.7 indicates that the stand under scrutiny was on average kept at a level of 70 % of the local maximum during the entire survey time.

2.2.5. Modelling approach

In this dissertation, linear mixed-effects models (Pinheiro and Bates, 2004) were used to consider nesting in the data, thereby accounting for pseudo-replication, potentially resulting in too progressive significances (Crawley, 2013). Random effects included in the models address the inter-correlation of samples caused by spatial and temporal clustering. In *Article I* and *II* all triplets were assigned to a triplet group based on their relative location (i.e., replicated triplets located in close proximity to each other were assigned to the same triplet group) (see 2.1.1.). All statistical testing was conducted by use of the R-function lme from the package $nlme$ (Pinheiro et al., 2019).

In the following, models are described in accordance with the main research questions (*QI – QIII*) outlined in chapter 1.2. These models were formulated to test specific hypotheses in the associated publications (*Article I – III*).

QI: How does stand growth and structure of mixed stands differ from adjacent monocultures and how is any over- or underyielding affected by variations in annual climate? (Article I)

To substantiate possible causal explanations for mixing effects on stand growth and structure, the effect of mixing on tree morphology was analysed. For this, species-specific allometric relationships between h and dbh, between cl and h and between cpa and dbh were investigated, based on tree measurements carried out during the field campaign. Log-transformed expressions of the general allometry function

($\log(Y) = b_0 + b_1 * \log(x)$) were used to test for significant differences between mixed and monospecific stands. The expression of the fitted model is outlined in Equation 11.

$$\log(Y_{ijkl}) = a_0 + a_1 * \log(X_{ijkl}) + a_2 * MONO_{ijk} + a_3 * \log(X_{ijkl}) * MONO_{ijk} + b_i + b_{ij} + b_{ijk} + \varepsilon_{ijkl} \quad (11)$$

Here, Y_{ijkl} is the response variable h, cl or cpa on the level of triplet group (i), triplet (j), plot (k) and tree (l). X_{ijkl} is the corresponding explanatory variable dbh or h. $MONO_{ijk}$ is a dummy-coded binary variable, indicating the species composition (monoculture = 1, mixture = 0). Terms a_0– a_3 represent the coefficients of fixed effects. Terms b_i, b_{ij} and b_{ijk} represent random effects on the level of triplet group ($b_i \sim N(0, \tau_1^2)$), triplet ($b_{ij} \sim N(0, \tau_2^2)$) and plot ($b_{ijk} \sim N(0, \tau_3^2)$). Finally, ε_{ijkl} is an independent and identically distributed error ($\varepsilon_{ijkl} \sim N(0, \sigma^2)$). The interaction term of the explanatory variable under scrutiny with $MONO_{ijk}$ was only included in case it was significant. If either a_2 or a_3 are significantly different from 0, this indicates a significant mixture effect on tree allometry.

To test for significant mixing effects on stand growth and structure, the ratio RY was used as computed according to the approach described in chapter 2.2.2. To receive direct information on the relative mixing effect, the value of 1 was subtracted ($RRY = RY - 1$). Using Equation 12, significant differences between mixed and monospecific stands were tested on the stand ($RRY_{pi,oa}$) and species ($RRY_{S.pi,(oa)}$, $RRY_{(S.pi),oa}$) level.

$$RRY_{ijk} = a_0 + b_i + b_{ij} + \varepsilon_{ijk} \quad (12)$$

In Equation 12, the term a_0 (intercept) represents the fixed effect parameter estimate. If a_0 is significantly different from 0, this indicates a significant mixture effect. The indices i, j and k represent triplet group, triplet and the observation year respectively. The terms b_i and b_{ij} represent random effects on the level of triplet group ($b_i \sim N(0, \tau_1^2)$) and triplet ($b_{ij} \sim N(0, \tau_2^2)$) respectively. Finally, ε_{ijk} is an independent and identically distributed error ($\varepsilon_{ijk} \sim N(0, \sigma^2)$).

To analyse the influence of annual climate on relative productivity on the stand ($RP_{S.pi,oa}$) and species ($RP_{S.pi,(oa)}$, $RP_{(S.pi),oa}$) level, Equation 13 was used.

$$RP_{ijk} = a_0 + a_1 * M_{ijk} + b_i + b_{ij} + \varepsilon_{ijk} \quad (13)$$

Here, M_{ijk} is the annual meteorological variable under investigation (T, P or DMI). The indices i, j and k represent triplet group, triplet and the observation year respectively. Terms a_0 and a_1 are the fixed effect parameters and terms b_i and b_{ij} represent random effects on the level of triplet group ($b_i \sim N(0, \tau_1^2)$) and triplet ($b_{ij} \sim N(0, \tau_2^2)$) respectively. ε_{ijk} is an independent and identically distributed error ($\varepsilon_{ijk} \sim N(0, \sigma^2)$). If a_1 is significantly different from 0, a significant effect of the scrutinised meteorological variable on the relative productivity can be assumed.

QII: How does species mixing influence tree growth responses to episodic drought under different ecological growing conditions? (Article II)

Equation 14 was used to test whether Scots pine and oak differed in their growth response to episodic drought stress. For this first step in the analysis, only monospecific plots were used in order to exclude any potential mixing effects, which were specifically studied in the next step.

$$Y_{ijklm} = a_0 + a_1 * S_{ijkl} + b_i + b_{ij} + b_{ijk} + \mathcal{E}_{ijklm} \qquad (14)$$

In Equation 14, Y_{ijklm} represents the response variable, i.e., the drought response index in question (Rt, Rc or Rs) on the level of country (i), triplet group (j), triplet (k), tree (l) and drought event (m). Terms a_0 and a_1 represent the coefficients of fixed effects. Coefficient a_1 is the fixed effect parameter for the dummy-coded binary variable S_{ijkl} (species) which becomes 1 for oak and 0 for Scots pine. If a_1 is significantly different from 0, a significant species effect on the scrutinised response variable can be assumed. The terms b_i, b_{ij} and b_{ijk} represent the random effects on the level of country, triplet group and triplet respectively (($b_i \sim N(0, \tau_1^2)$), ($b_{ij} \sim N(0, \tau_2^2)$) and ($b_i \sim N(0, \tau_3^2)$)). The inclusion of a random effect on the individual tree level did not yield any advantages when comparing models based on the AIC (Akaike Information Criterion) (Akaike, 1981) and was therefore not considered. The term ε_{ijklm} represents an independent and identically distributed error ($\varepsilon_{ijklm} \sim N(0, \sigma^2)$).

Equation 15 was used to test the general influence of stand composition (mixture versus monoculture) on the species-specific tree growth response to drought. This model was fitted separately for each species.

$$Y_{ijklm} = a_0 + a_1 * C_{ijkl} + b_i + b_{ij} + b_{ijk} + \mathcal{E}_{ijklm} \qquad (15)$$

In Equation 15, terms a_0 and a_1 represent the coefficients of fixed effects. Coefficient a_1 is the fixed effect parameter for the dummy-coded binary variable C_{ijkl} (composition) which is 1 for monoculture and 0 for mixture. If a_1 is significantly different from 0, a significant composition effect on the scrutinised response variable can be assumed. The remaining notation is to be understood in the same way as for Equation 14.

To investigate any potential effects of the ecological growing conditions on the species-specific tree growth response to drought in mixtures and monocultures, Equation 15 was further expanded by adding a series of tree- and site-specific ecological variables and their respective interactions with the composition effect (C_{ijkl}). This led to Equation 16 which constitutes the full model that comprises the complete set of possible fixed effects.

$$Y_{ijklm} = a_0 + a_1 * C_{ijkl} + a_2 * ba_{ijklm} + a_3 * SI_{ijk} + a_4 * DMI_{ijk} + a_5 * C_{ijkl} * ba_{ijklm} + a_6 * C_{ijkl} * SI_{ijk} + a_7 * C_{ijkl} * DMI_{ijk} + b_i + b_{ij} + b_{ijk} + \mathcal{E}_{ijklm} \qquad (16)$$

In Equation 16, tree size is represented by the tree basal area (ba_{ijklm}) at the time of the drought event. Site-specific information comprises the species-specific site index ($SI_{S.pi}$ or SI_{oa}, denoted as S_{ijk} in the model) and the De Martonne aridity index (DMI_{ijk}). Terms a_0– a_7 represent the coefficients of the fixed effects. The remaining notation is to be understood in the same way as for Equations 14 and 15. If coefficients a_1– a_7 are significantly different from 0, a significant effect of the associated explanatory variable can be assumed. Selection of potentially less complex final models nested in Equation 16 was based on the Akaike Information Criterion (AIC) (Akaike, 1981) and biological plausibility of the results. The selection was made with additional help by an automated AIC-based model selection procedure (function $dredge$ from the R-package $MuMIn$ (Barton, 2019)). To answer the research question at hand, C_{ijkl} was kept in all final models.

QIII: How does the maintenance of reduced stand density influence tree growth responses to episodic drought under different levels of site water availability? (Article III)

Equation 17 was used to test the general influence of different stand density levels, represented by the categorial variable DL (DL_{low}: low stand density; DL_{mod}: moderate stand density; DL_{max}: maximum stand density), on the species-specific mean growth level ($Mean$) and the mean tree growth sensitivity, here represented by the mean coefficient of variation of the standardised bai index (CV). The covariate tree size was included in form of the tree basal area (ba) at the time of sampling.

$$Y_{ijk} = a_0 + a_1 * ba_{ijk} + a_2 * DL_{mod_{ij}} + a_3 * DL_{max_{ij}} + b_i + \varepsilon_{ijk} \tag{17}$$

In Equation 17, Y_{ijk} is the species-specific response variable, i.e., $Mean$ or CV. The indices represent site (i), stand (j) and tree (k) respectively. Terms a_0– a_3 represent the coefficients of fixed effects. The term b_i represents the random effect on the level of site ($b_i \sim N(0, \tau_1^2)$). The term ε_{ijk} represents an independent and identically distributed error ($\varepsilon_{ijk} \sim N(0, \sigma^2)$). Tukey HSD multiple comparison (R-package $lsmeans$ (Lenth, 2016)) was performed for contrasting all levels within DL, as obtained from the linear mixed model, against each other.

Equation 18 constitutes the full model to test the influence of the weighted mean relative basal area ($MRBA$) on the species-specific short-term growth responses to episodic drought stress and to analyse how any such influence may be modified by site water availability, represented by the Global Aridity Index (I_A), and stand age (Age). In addition, the covariate tree size (ba) at the time of the drought event was included.

$$Y_{ijkl} = a_0 + a_1 * ba_{ijkl} + a_2 * MRBA_{ij} + a_3 * I_{A_i} + a_4 * Age_{ij} + a_5 * MRBA_{ij} * I_{A_i} + a_6 * MRBA_{ij} * Age_{ij} + b_{ijk} + \varepsilon_{ijkl} \tag{18}$$

In Equation 18, Y_{ijkl} represents the species-specific growth response to drought in form of the drought response indices resistance (Rt), recovery (Rc) and resilience (Rs) on the level of site (i), stand (j), tree

(k) and drought event (l). Terms $a_0 - a_6$ represent the coefficients of fixed effects. The term b_{ijk} denotes the random effect on the level of tree ($b_{ijk} \sim N(0, \tau_1^2)$). The term ε_{ijkl} represents an independent and identically distributed error ($\varepsilon_{ijkl} \sim N(0, \sigma^2)$). Selection of potentially less complex final models nested in Equation 18 was based on the same criteria as described for Equation 16.

3. Results

3.1. Stand growth and structure in mixed versus monospecific stands (*Article I*)

Tree allometry

Fitted allometry functions according to Equation 11 for Scots pine and oak, growing in mixtures and monocultures are presented in Fig. 8. For Scots pine, tree height of measured trees was significantly higher in mixtures compared with monocultures (Fig. 8a, Tab. 6). For oak, the parameter a_3 of the fitted height model differed significantly (Tab. 6), although resulting height curves for oaks growing in mixed and monospecific stands did not appear to differ in practically relevant orders of magnitude (Fig. 8b). Scots pines in mixture exhibited significantly shorter crowns than in monocultures (Fig. 8c, Tab. 6). Regarding the crown projection area of Scots pine, both parameters a_2 and a_3 differed significantly (Tab. 6); fitted curves indicated slightly larger crown projection areas in monocultures for most of the diameter range up to approximately 40 cm, after which tree crowns in mixtures exhibited larger projections (Fig. 8e). Oak was found to significantly increase both crown length (Fig. 8d, Tab. 6) and crown projection area (Fig. 8f, Tab. 6) in mixtures compared with monocultures.

Mean tree and stand state characteristics

The mixing of Scots pine and oak had significant effects on mean tree and stand state characteristics. Table 7 reports the mean mixture effects in form of the fixed effect parameter estimate a_0 from Equation 12. Quadratic mean and dominant height of Scots pine were on average 14 % and 13 % higher respectively in mixed compared with monospecific stands ($p < 0.01$). The height-diameter relationship of dominant oak trees was 8 % lower in mixed compared with monospecific stands ($p < 0.001$). Standing volume was 15 % higher in mixtures compared with the weighted mean of the neighbouring monocultures ($p < 0.05$). Standing volume of Scots pine was 25 % higher in mixture than in monoculture ($p < 0.01$).

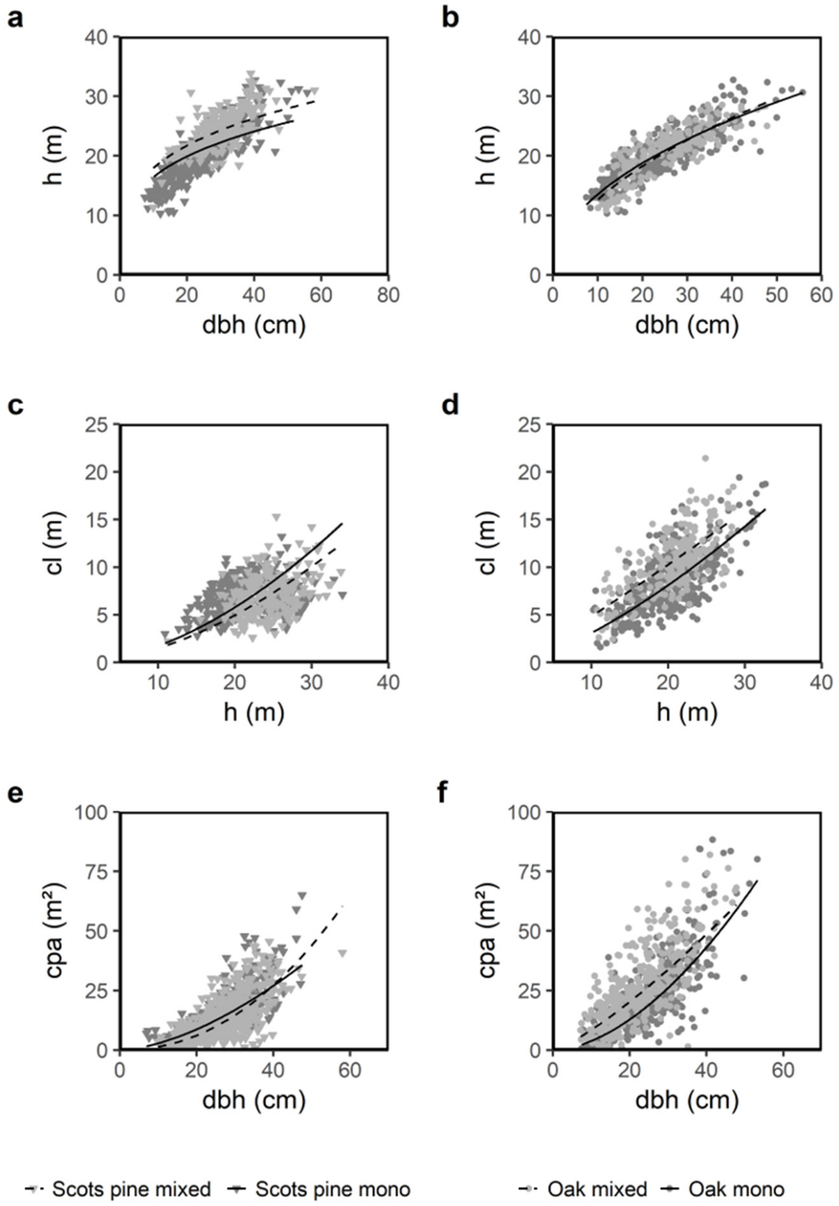

Fig. 8. Individual tree characteristics in 2017 for Scots pine and oak in monocultures and mixed-species stands on the seven triplets studied. Tree height (h, m) versus diameter at breast height (dbh, cm) (a, b), crown length (cl, m) versus h (c, d) and crown projection area (cpa, m²) versus dbh (e, f). The lines represent the results of a linear mixed-effects model (Eq. 11). Dashed lines represent trees growing in mixed stands, solid lines represent trees growing in monocultures. Reprinted from Steckel et al. (2019).

Tab. 6. Results of linear mixed-effects model regressions from Equation 11.

Species	**Response variable**	**Explanatory variable**	**n**	**Statistic**	**Intercept**	**Log(X)**	**MONO**	**Log(X)*MONO**
					a_0	**a_1**	**a_2**	**a_3**
Scots pine	h	dbh	560	Value	**2.25*** **	**0.28*** **	**-0.09*** **	-
				SE	0.07	0.01	0.01	
	cl	h	560	Value	**-3.64*** **	**1.75*** **	**0.15* **	-
				SE	0.36	0.10	0.06	
	cpa	dbh	844	Value	**-4.66*** **	**2.16*** **	**1.90** **	**-0.52*** **
				SE	0.33	0.10	0.45	0.14
oak	h	dbh	620	Value	**1.31*** **	**0.53*** **	0.20	**-0.06* **
				SE	0.07	0.02	0.08	0.03
	cl	h	620	Value	**-0.93*** **	**1.09*** **	**-1.17* **	**0.31** **
				SE	0.25	0.08	0.32	0.11
	cpa	dbh	815	Value	**-0.80*** **	**1.27*** **	**-1.92*** **	**0.49*** **
				SE	0.20	0.06	0.30	0.10

h: tree height (m). cl: crown length (m). cpa: crown projection area (m²). dbh: diameter at breast height (cm). n: number of observations. $MONO$: fixed composition effect (monoculture = 1, mixture = 0). Bold values are significant at level $p < 0.001$ (***), $p < 0.01$ (**), $p < 0.05$ (*). Only fixed effects are reported.

Tab. 7. Results of linear mixed-effects model regressions from Equation 12.

Response variable	**Mixture ($RRY_{S.pi,oa}$)**		**Scots pine ($RRY_{S.pi,(oa)}$)**		**oak ($RRY_{(S.pi),oa}$)**	
	a_0	**SE**	**a_0**	**SE**	**a_0**	**SE**
d_q (cm)			0.16	0.14	-0.01	0.13
d_{100} (cm)			0.12	0.08	0.08	0.08
h_q (m)			**0.14****	0.05	-0.03	0.09
h_{100} (m)			**0.13****	0.04	-0.00	0.07
h_q/d_q			0.02	0.06	-0.00	0.04
h_{100}/d_{100}			0.03	0.05	**-0.08*****	0.02
GC_v			-0.10	0.06	**0.18****	0.06
GC_{iv}			-0.07	0.05	0.12	0.08
N (trees ha^{-1})	0.01	0.18	-0.10	0.15	0.20	0.25
SDI (trees ha^{-1})	0.02	0.09	0.02	0.09	0.02	0.09
BA (m^2 ha^{-1})	0.08	0.06	0.10	0.07	0.07	0.06
V (m^3 ha^{-1})	**0.15***	0.06	**0.25****	0.08	0.05	0.10
IBA (m^2 ha^{-1} yr^{-1})	0.07	0.04	-0.03	0.10	0.24	0.13
IV (m^3 ha^{-1} yr^{-1})	**0.14*****	0.04	0.10	0.07	**0.19***	0.09

RRY: relative mixing effect. d_q: quadratic mean diameter (cm). d_{100}: dominant diameter (cm). h_q: quadratic mean height (m). h_{100}: dominant height (m). h_q/d_q: quadratic mean height-diameter ratio. h_{100}/d_{100}: dominant height-diameter ratio. GC_v: Gini coefficient of tree volume. GC_{iv}: Gini coefficient of tree volume increment. N: number of trees (trees ha^{-1}) SDI: stand density index (trees ha^{-1}) (Reineke, 1933). BA: stand basal area (m^2 ha^{-1}). V: standing volume (m^3 ha^{-1}). IBA: stand basal area increment (m^2 ha^{-1} yr^{-1}). IV: stand volume increment (m^3 ha^{-1} yr^{-1}). The number of observations was always n = 140. Bold values are significant at level $p < 0.001$ (***), $p < 0.01$ (**), $p < 0.05$ (*). Results are reported for the mixed stand as a whole (Mixture) and the individual species level (Scots pine, oak). Only fixed effects are reported.

Productivity

Average overyielding of the stand as a whole amounted to 14 % ($p < 0.001$) (Tab. 7). Both species contributed to the observed positive mixing effect, although oak appeared to be the main driver, showing an average overyielding of 19 % ($p < 0.05$) (Tab. 7). For Scots pine, overyielding was less pronounced (10 %) and not statistically significant (Tab. 7). In absolute terms, Scots pine grew at a rate of 11.2 m^3 ha^{-1} yr^{-1} in mixture compared with 10.0 m^3 ha^{-1} yr^{-1} in monospecific stands (Fig. 9a). The volume increment amounted to 12.5 m^3 ha^{-1} yr^{-1} for oak growing in mixture and 10.9 m^3 ha^{-1} yr^{-1} for oak growing in monoculture (Fig. 9b). The absolute productivity of the mixture as a whole was 11.6 m^3 ha^{-1} yr^{-1} compared with 10.3 m^3 ha^{-1} yr^{-1} for the weighted mean of the neighbouring monospecific stands (Fig. 9c). The mean annual volume increment of the mixed stands exceeded the most productive monoculture (oak) by 0.7 m^3 ha^{-1} yr^{-1}, thereby confirming transgressive overyielding. Nearly all observations were located above the reference line (1.0-line) (Fig. 9d) and even small mixing proportions resulted in a positive mixing effect. The estimated optimum was reached when both species showed approximately equal mixing proportions.

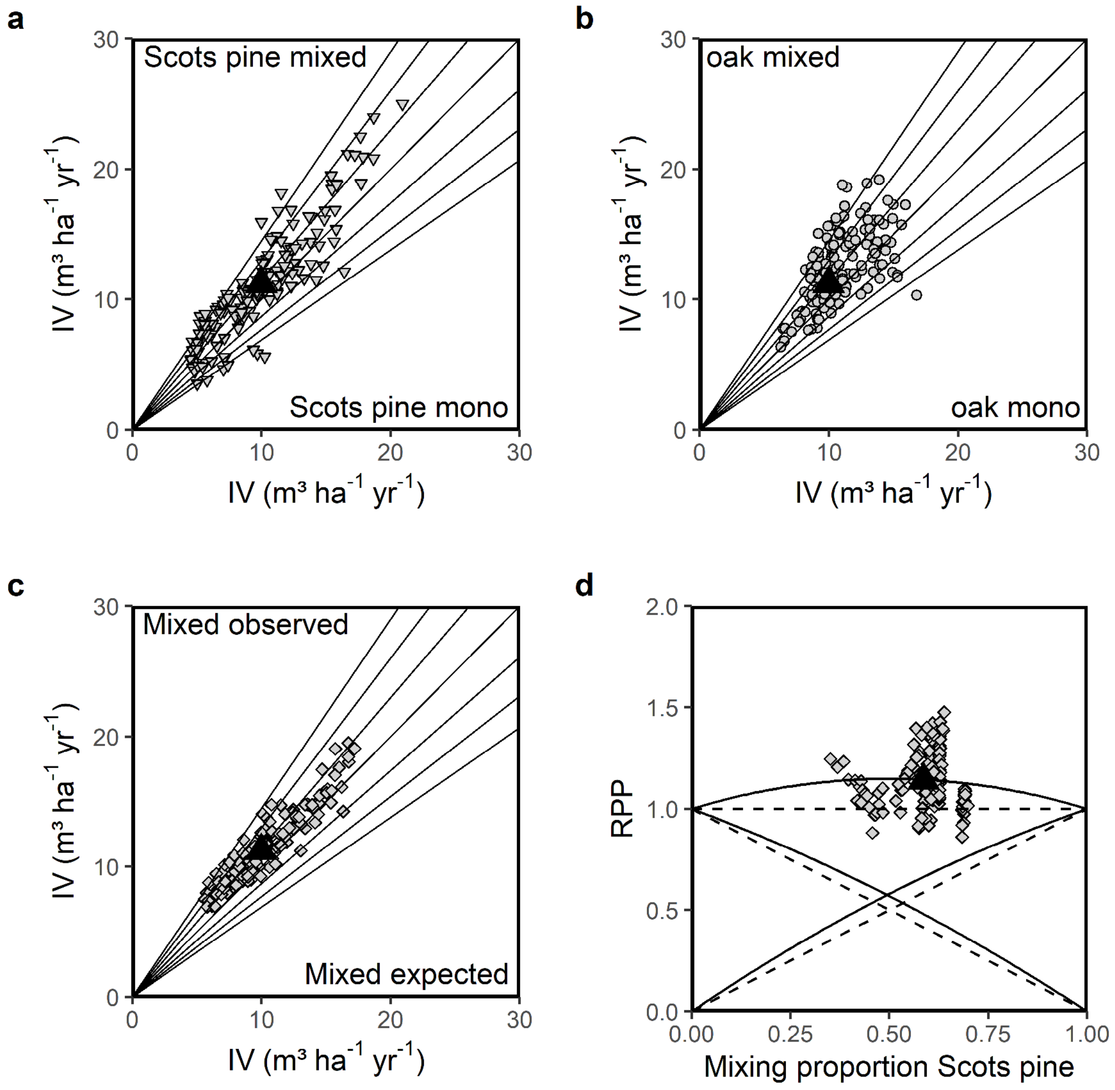

Fig. 9. Relationship between volume productivity (*IV*, m³ ha^{-1} yr^{-1}) in mixed stands and monocultures. Solid black triangles indicate the mean mixing effect, based on all 140 observations. Illustrations (a) and (b) show the expected productivity of Scots pine and oak respectively based on their performance in the mixed stand compared to the observed species-specific productivity in the monospecific stands. In (c) the observed productivity of both species in the mixture is compared with the weighted mean productivity of the adjacent monospecific stands. In (d) a cross diagram is displayed, showing the relative productivity on the basis of the proportions of volume growth (*RPP*) of Scots pine, oak and the mixed stand as a whole in relation to the productivity of the neighbouring pure stands. The abscissa shows the mixing proportion of Scots pine. The points represent the observed relative volume productivity of mixed versus pure stands. The curves indicate the average mixing reaction of Scots pine, oak and total stand. Broken reference lines represent the productivity expected for neutral mixing effects on the total stand and species levels. Adapted by Steckel et al. (2019).

Partitioning of size and growth

For oak, the Gini coefficient of tree volume (GC_v) was 18 % higher in mixtures compared with monocultures ($p < 0.01$) (Tab. 7). The Gini coefficient for tree volume increment of oak was 12 % higher in mixture but did not differ significantly (Tab 7). No statistically significant effect of species mixing on size and growth partitioning of Scots pine was evident, although Gini coefficients for tree volume and volume increment appeared to be lower in the mixtures (−10 % and −7 % respectively) (Tab. 7).

Influence of annual climate on the mixing effect

According to regression analysis based on Equation 13, the annual De Martonne aridity index was found to have a significantly positive effect on the relative productivity on the stand and species level (Fig. 10, Tab. 8). The same effect was found regarding annual precipitation total (Tab. 8). In contrast, annual mean temperature had a significantly negative effect on the stand level and for Scots pine, while the influence was not significant for oak (Tab. 8). The productivity relation of mixtures versus monocultures was overall more stable for the stand as a whole than for the individual species (Fig. 9, Fig. 10).

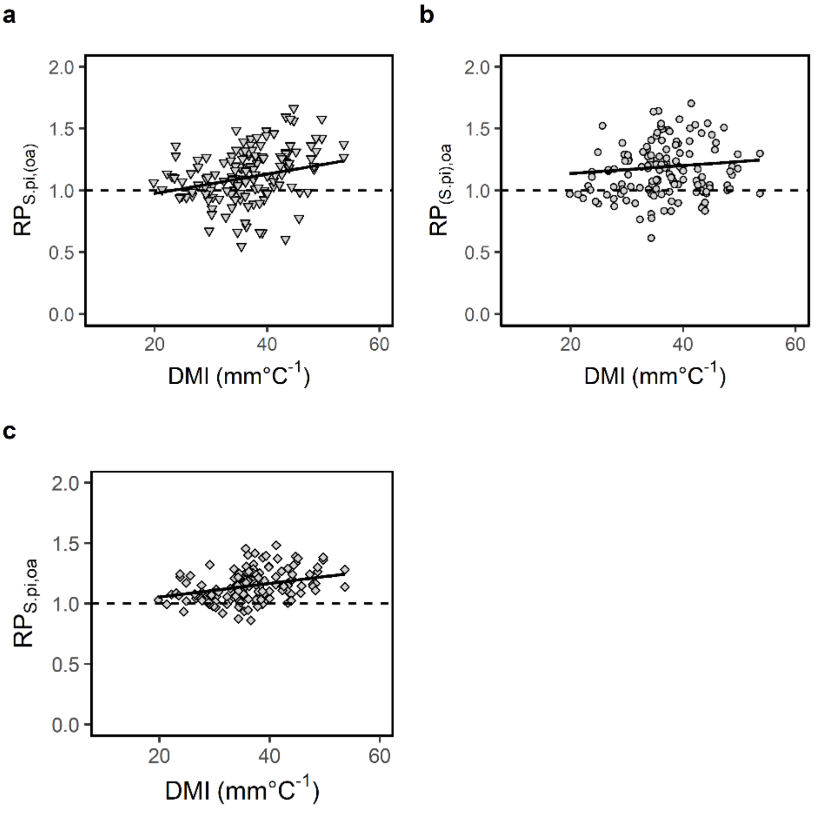

Fig. 10. Relative annual volume productivity in the years 1998–2017 at the species level for Scots pine (a) and oak (b), as well as for the stand as a whole (c) on the seven analysed triplets (ordinate) plotted against the De Martonne aridity index (DMI) (abscissa). Analysing this relationship by fitting linear mixed effect models (Eq. 13) yielded the solid lines. Adapted from Steckel et al. (2019).

Tab. 8. Results of linear mixed-effects model regressions from Equation 13.

Variable	Statistic	DMI		T		P	
		a_0	a_1	a_0	a_1	a_0	a_1
$\mathrm{RP}_{\mathrm{S.pi,oa}}$	Value	**0.9410*****	**0.0056*****	**1.4684*****	**-0.0352***	**0.9366*****	**0.0003*****
	SE	0.0598	0.0015	0.1624	0.0172	0.0629	0.0001
$\mathrm{RP}_{\mathrm{S.pi,(oa)}}$	Value	**0.8185*****	**0.0078*****	**1.5897*****	**-0.0530***	**0.8159*****	**0.0004****
	SE	0.1031	0.0023	0.2554	0.0268	0.1082	0.0001
$\mathrm{RP}_{\mathrm{(S.pi),oa}}$	Value	**1.0719*****	**0.0032***	**1.3214*****	-0.0145	**1.0653*****	**0.0002***
	SE	0.1083	0.0016	0.1946	0.0184	0.1100	0.0001

RP: relative productivity. DMI: De Martonne aridity index (mm °C^{-1}). T: annual mean temperature (°C). P: annual precipitation total (mm). The number of observations was always $n = 140$. Bold values are significant at level $p < 0.001$ (***), $p < 0.01$ (**), $p < 0.05$ (*). Only fixed effects are reported.

3.2. Tree growth responses to episodic drought in mixtures versus monocultures (*Article II*)

Tree ring series and basic statistics

Tree ring series were successfully cross-dated, converted into basal area increment series and detrended, ultimately resulting in chronologies for each species-specific composition group (Tab. 9). Mean $Rbar$ values of between 0.42 and 0.44 indicated a good common signal on average among the individuals sampled in each group (Speer, 2010). Mean EPS was > 0.90 for Scots pine and oak in all groups, which is well above the threshold of 0.85 introduced by Wigley et al. (1984).

Influence of tree species and stand composition (mixture versus monoculture) on the tree drought response

According to Equation 14, oak showed a significantly greater resistance and resilience than Scots pine, while recovery was significantly lower in the monocultures studied (Fig. 11a, Tab. 10). Under drought, growth of Scots pine and oak in monocultures was on average estimated to be reduced to 84 % and 85 % of the mean growth during the three-year pre-drought period respectively (Fig. 11a, Tab. 10). Both species recovered from the growth depression, growing on average 29 % and 26 % more in the post-drought period than during the drought event (Tab. 10). Scots pine and oak were resilient to drought, even exhibiting slightly greater average growth after than before the drought event (Rs = 101 % for Scots pine and Rs = 102 % for oak) (Fig. 11a, Tab. 10).

According to Equation 15, Scots pine and oak differed in their drought reaction patterns depending on the stand composition (mixture versus monoculture). Scots pine trees showed a significantly greater resistance in mixtures compared with monocultures, although in mixture they took significantly longer to recover (Fig. 11b, Tab. 11). Oak trees growing in mixtures showed a significantly greater resistance and resilience compared to monocultures (Fig. 11c, Tab. 11).

Tab. 9. Descriptive statistics for cored Scots pine and oak trees and their respective bai index chronologies by species in mixtures and monocultures.

Composition	Statistic	n	dbh	Rbar	EPS
S. pine mixture	Mean	27	33.1	0.44	0.93
	SD	6	8.7	0.10	0.06
	Min	7	10.0	0.23	0.69
	Max	36	62.0	0.66	0.98
S. pine monoculture	Mean	26	31.3	0.44	0.94
	SD	5	7.8	0.08	0.02
	Min	14	8.0	0.26	0.87
	Max	32	61.8	0.66	0.98
Oak mixture	Mean	26	28.0	0.42	0.91
	SD	7	9.8	0.15	0.08
	Min	7	7.4	0.13	0.68
	Max	40	63.3	0.74	0.98
Oak monoculture	Mean	27	30.5	0.43	0.92
	SD	4	9.7	0.16	0.08
	Min	16	7.3	0.08	0.60
	Max	33	70.0	0.72	0.98

n: number of cored trees. dbh: diameter at breast height (cm). $Rbar$: mean inter-series correlation. EPS: expressed population signal.

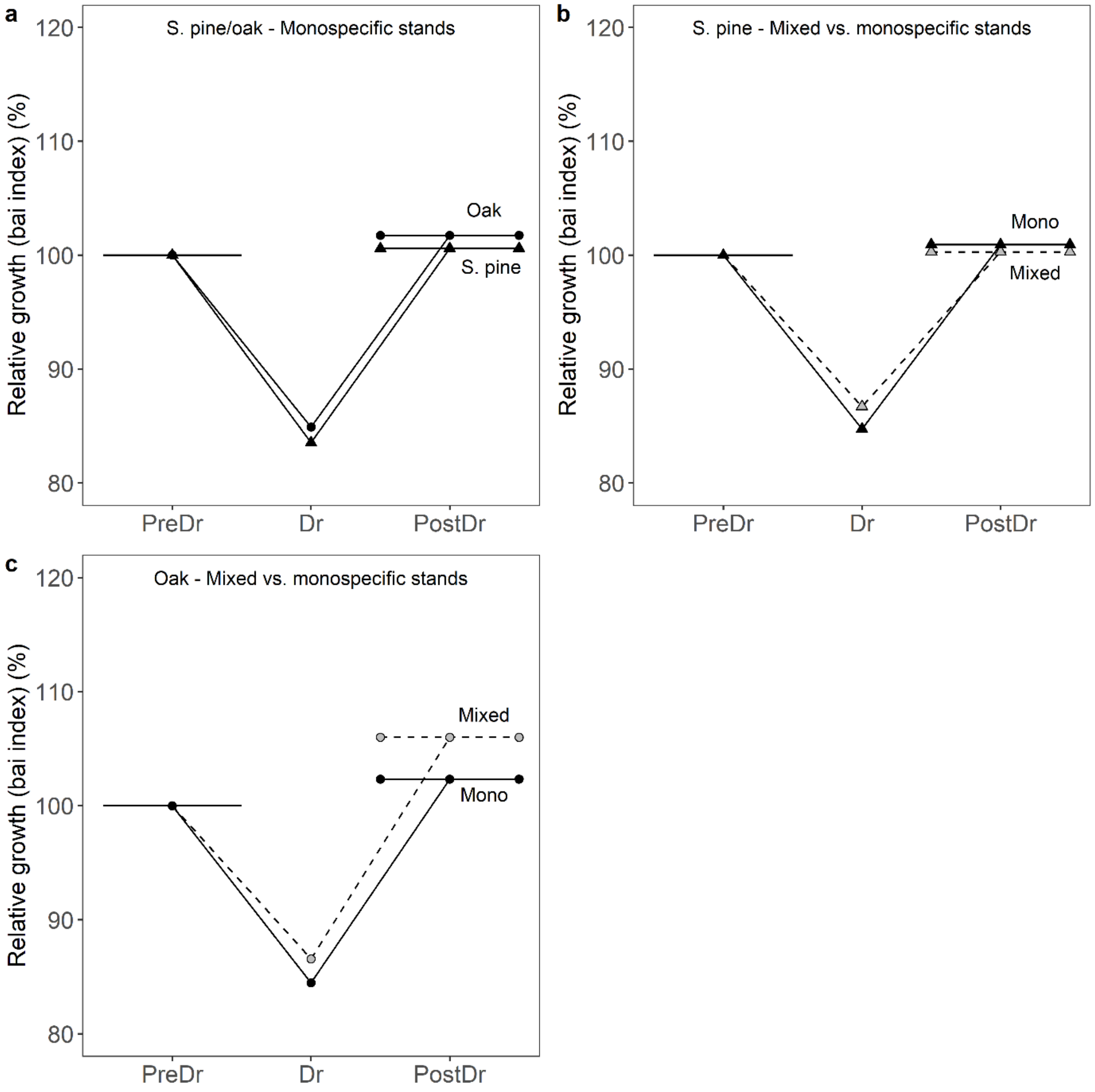

Fig. 11. Estimated growth reactions during drought (Dr) and after ($PostDr$) in relation to the mean growth level in the period before the drought event ($PreDr$) ($reference\ line$ = 100 %) for Scots pine (triangles) and oak (circles) in mixed (grey symbols, dashed lines) and monospecific stands (black symbols, solid lines) according to Equations 14 (a) and 15 (b–c). Due to the relation to growth before drought, relative growth during and after drought equals the resistance (Rt) and resilience index (Rs) respectively. a) Comparison of Scots pine and oak monocultures. b–c) Comparison between mixed and monospecific stands for Scots pine and oak respectively. Adapted by Steckel et al. (2020a).

Tab. 10. Results of the linear mixed-effects model regressions from Equation 14.

Response variable	**Statistic**	**Intercept** **a0**	**S** **a1**
Rt	Estimate	**83.5*****	**1.4***
	SE	1.8	0.7
Rc	Estimate	**129.1*****	**-2.8****
	SE	2.3	1.0
Rs	Estimate	**100.6*****	**1.2***
	SE	1.6	0.6

Rt : resistance (%). Rc: recovery (%). Rs: resilience (%). S: fixed species effect (oak = 1, Scots pine = 0). The number of observations was always n = 5,086. Bold values are significant at level p < 0.001 (***), p < 0.01 (**), p < 0.05 (*). Only fixed effects are reported.

Tab. 11. Results of the linear mixed-effects model regressions from Equation 15.

Species	**Response variable**	**Statistic**	**Intercept** **a0**	**C** **a1**
Scots pine	Rt	Estimate	**86.7*****	**-2.0****
		SE	2.4	0.7
	Rc	Estimate	**123.7*****	**4.9*****
		SE	2.7	1.0
	Rs	Estimate	**100.3*****	0.6
		SE	1.9	0.7
oak	Rt	Estimate	**86.6*****	**-2.1*****
		SE	2.6	0.6
	Rc	Estimate	**129.8*****	-1.6
		SE	3.7	1.0
	Rs	Estimate	**106.0*****	**-3.7*****
		SE	1.6	0.6

Rt: resistance (%). Rc: recovery (%). Rs: resilience (%). C: fixed composition effect (monoculture = 1, mixture = 0). The number of observations was always n = 5,167 for Scots pine and n = 5,120 for oak. Bold values are significant at level p < 0.001 (***), p < 0.01 (**), p < 0.05 (*). Only fixed effects are reported.

Influence of ecological growing conditions on tree growth responses in mixtures and monocultures

According to Equation 16, tree size (ba) and DMI had significant effects on the growth responses to drought in mixtures and monocultures (Tab. 12). On average, larger Scots pine trees were found to be significantly more resistant to drought than smaller individuals but they took longer to recover. The De Martonne aridity index (DMI) was associated with significantly greater resistance to drought in oak on average, but not in Scots pine. In addition to average effects in mixtures and monocultures, significant interaction terms indicate that the mixing effect on tree drought responses was not constant along the ecological gradient studied. For oak the advantage of admixture with Scots pine in terms of resistance and resilience significantly increased with DMI (Tab. 12, Fig. 12b,f). Contrastingly, species mixing was not beneficial for increasing recovery of oak on sites with higher DMI (Tab 12, Fig. 12d). The mixture benefit regarding the resistance of Scots pine decreased significantly with site fertility, represented by the species-specific site index ($SI_{S.pi}$) (Tab. 12, Fig. 13a).

Tab. 12. Results of the linear mixed-effects model regressions from Equation 16.

Species	**Response variable**	**Statistic**	**Intercept** **a_0**	**C** **a_1**	**ba** **a_2**	**SI** **a_3**	**DMI** **a_4**	**C*ba** **a_5**	**C*SI** **a_6**	**C*DMI** **a_7**
Scots pine	Rt	Estimate	**65.910*** **	**-9.858***	**0.007*** **	0.594	-	-	**0.301***	-
		SE	10.887	4.075	0.001	0.382			0.143	
	Rc	Estimate	**132.641*** **	**3.849*** **	**-0.014*** **	-	-	-	-	-
		SE	2.910	1.042	0.002					
	Rs	Estimate	**100.289*** **	0.633	-	-	-	-	-	-
		SE	1.872	0.677						
Oak	Rt	Estimate	**69.294*** **	**14.517*** **	-	-	**0.450** **	-	-	**-0.433*** **
		SE	5.637	2.827			0.131			0.072
	Rc	Estimate	**144.004*** **	**-11.668***	-	-	-0.372	-	-	**0.261***
		SE	12.016	4.581			0.298			0.117
	Rs	Estimate	**98.742*** **	**9.985*** **	-	-	0.190	-	-	**-0.355*** **
		SE	6.961	2.774			0.179			0.071

Rt: resistance (%). Rc: recovery (%). Rs: resilience (%). C: fixed composition effect (monoculture = 1, mixture = 0). ba: reconstructed tree basal area (cm²). SI: species-specific site index (m) ($SI_{S.pi}$, SI_{oa}). DMI: De Martonne aridity index (De Martonne, 1926) (mm $°C^{-1}$). The number of observations was always n = 5,167 for Scots pine and n = 5,120 for oak. Bold values are significant at level $p < 0.001$ (***), $p < 0.01$ (**), $p < 0.05$ (*). Only fixed effects are reported.

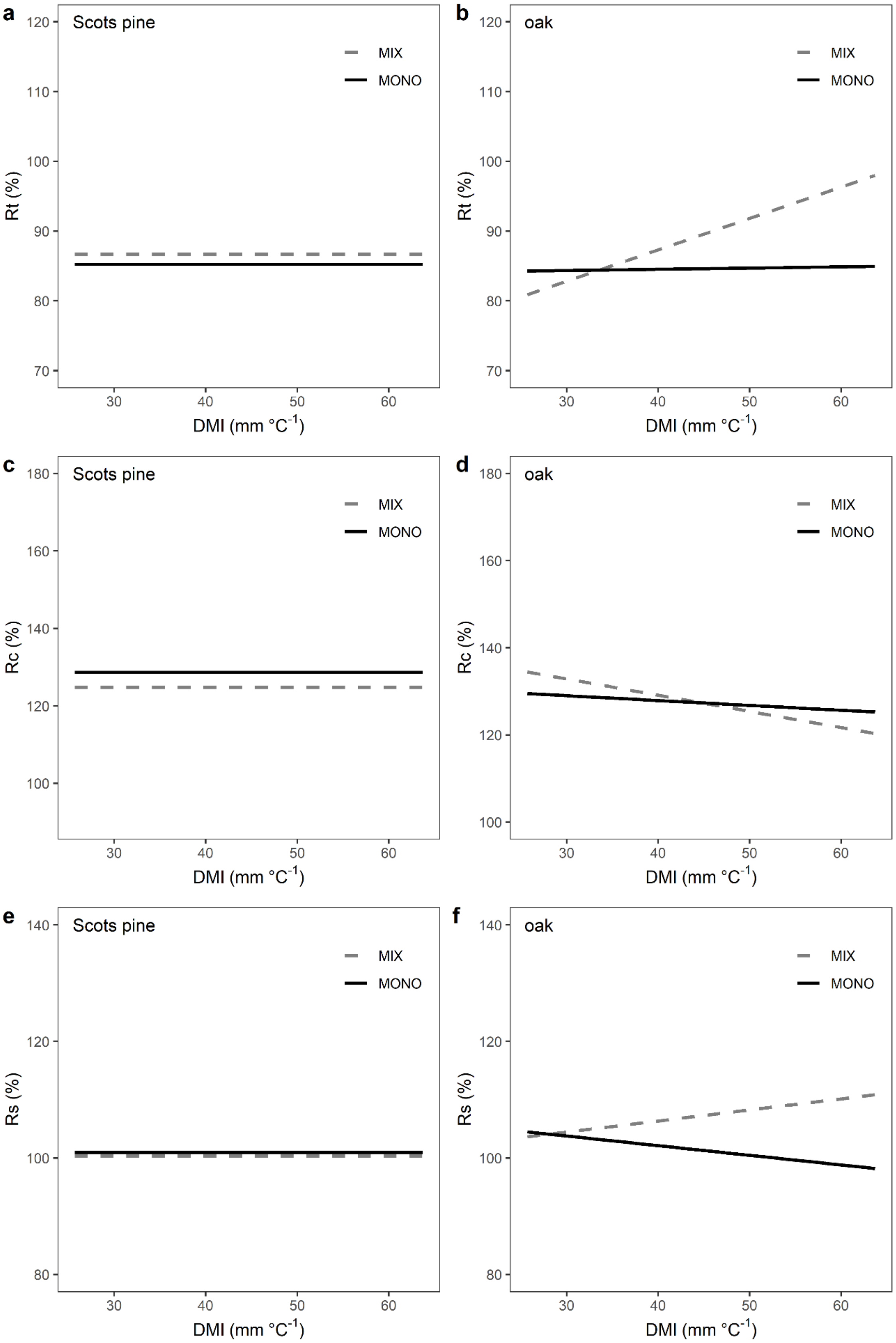

Fig. 12. Effect of the De Martonne aridity index (DMI) on the drought response of Scots pine and oak in mixed (dashed grey line) and monospecific stands (solid black line). Lines represent the fixed effect terms from Equation 16. Variables other than DMI were set at the respective means as obtained from the data. a–b) Rt: resistance index. c–d) Rc: recovery index. e–f) Rs: resilience index. Adapted from Steckel et al. (2020a).

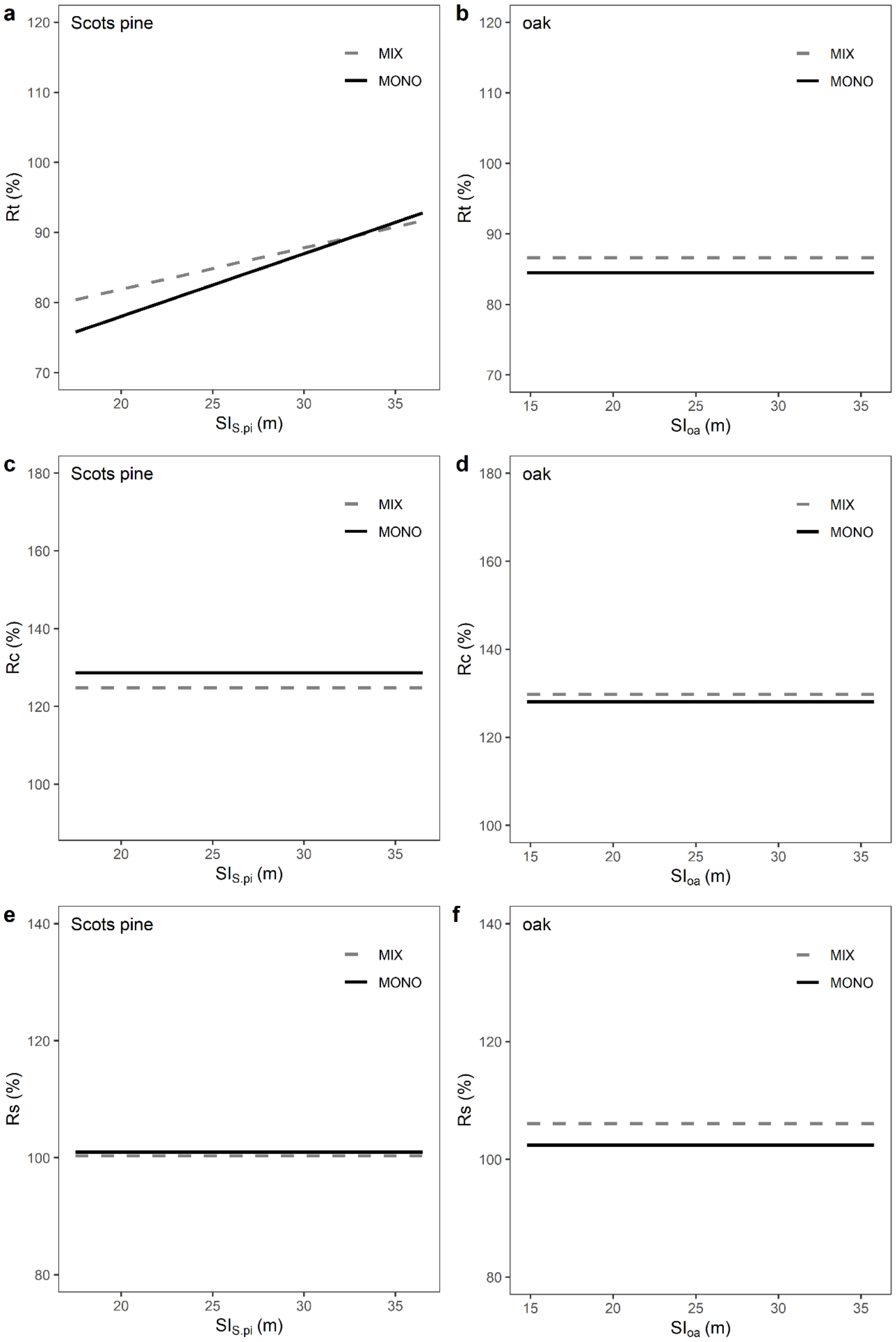

Fig. 13. Effect of the species-specific site index ($\mathrm{SI}_{\mathrm{S.pi}}$, $\mathrm{SI}_{\mathrm{oa}}$) on the drought response of Scots pine and oak in mixed (dashed grey line) and monospecific stands (solid black line). Lines represent the fixed effect terms from Equation 16. Variables other than SI were set at the respective means as obtained from the data. a–b) Rt: resistance index. c–d) Rc: recovery index. e–f) Rs: resilience index. Adapted by Steckel et al. (2020a).

3.3. Tree growth responses to episodic drought in relation to stand density and site water availability (*Article III*)

Tree ring series and basic statistics

Tree ring series were successfully cross-dated, converted into bai series and detrended, resulting in the establishment of chronologies for each site-specific competition level. For each group chronology, the basic statistics are shown in Table 13. In almost all cases, EPS was well above the critical value of 0.85 introduced by Wigley et al. (1984). $Rbar$ values of 0.46 on average indicated a good common signal across the individuals sampled (Speer, 2010).

Tab. 13. Mean tree and chronology characteristics by species, site and stand density level (DL).

Species	Site	DL	n	dbh	h	MRBA	Rbar	EPS
sessile oak	DE 1	Low	15	21.8	18.5	0.44	0.55	0.95
		Mod	15	18.5	18.3	0.65	0.45	0.92
		Max	15	18.3	19.0	1.00	0.56	0.95
	DE 2	Low	15	38.4	26.2	0.60	0.54	0.94
		Mod	15	34.8	27.2	0.73	0.56	0.94
		Max	15	28.2	28.3	1.00	0.52	0.94
	DE 3	Low	15	48.7	31.1	0.80	0.50	0.92
		Mod	15	44.0	30.5	0.86	0.59	0.95
		Max	15	35.5	29.0	1.00	0.54	0.94
Scots pine	DE 4	Low	15	30.4	20.8	0.47	0.41	0.90
		Mod	16	25.5	20.7	0.58	0.44	0.92
		Max	15	28.1	24.7	1.00	0.43	0.91
	DE 5	Low	17	38.3	23.5	0.30	0.40	0.91
		Mod	15	37.0	24.7	0.56	0.44	0.91
		Max	15	30.6	24.9	1.00	0.52	0.94
	DE 6	Low	15	24.1	18.2	0.50	0.57	0.95
		Mod	15	15.6	13.7	0.70	0.48	0.93
		Max	17	14.9	14.5	1.00	0.49	0.94
ponderosa pine	US 1	Low	15	40.8	17.1	0.30	0.47	0.93
		Mod	15	35.1	19.2	0.52	0.29	0.84
		Max	15	27.6	19.4	1.00	0.33	0.88
	US 2	Low	15	31.3	14.0	0.32	0.55	0.90
		Mod	15	27.4	13.4	0.61	0.58	0.95
		Max	15	22.3	12.7	1.00	0.44	0.92
	US 3	Low	15	36.8	13.8	0.31	0.32	0.84
		Mod	15	33.6	17.9	0.56	0.35	0.88
		Max	15	23.7	15.6	1.00	0.18	0.74

n: number of trees sampled. dbh: mean diameter at breast height (cm). h: tree height (m). $MRBA$: mean relative stand basal area. $Rbar$: mean inter-series correlation. EPS: mean expected population signal.

Mean tree growth and mean tree growth sensitivity

The investigation of mean tree growth ($Mean$) and mean tree growth sensitivity in form of the mean coefficient of variation of the detrended bai index series (CV) revealed significant differences between stands of differing stand density according to Equation 17 (Fig. 14, Tab. 14). Mean tree growth of Scots pine was significantly higher in low density stands (17.3 cm^2 yr^{-1}) compared with the untreated control (14.8 cm^2 yr^{-1}), but not significantly different from moderately dense stands (15.6 cm^2 yr^{-1}). Mean tree growth of sessile oak was significantly higher under low (17.5 cm^2 yr^{-1}) compared with moderate (15.1 cm^2 yr^{-1}) and maximum stand density levels (14.2 cm^2 yr^{-1}). In ponderosa pine, there was a particularly pronounced significant difference between mean growth under low (15.5 cm^2 yr^{-1}) versus moderate (8.6 cm^2 yr^{-1}) and maximum (7.6 cm^2 yr^{-1}) stand densities.

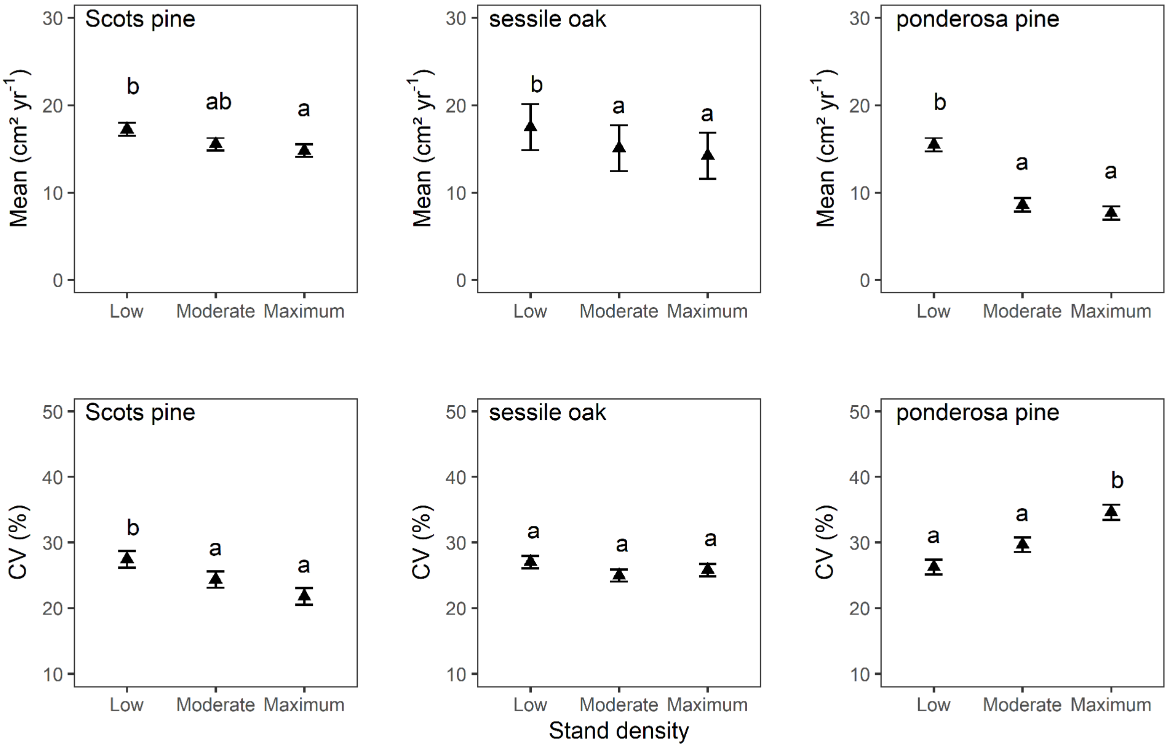

Fig. 14. Estimated least-squares means of mean tree basal area increment ($Mean$, cm^2 yr^{-1}) and mean coefficient of variation (CV, %), representing mean tree growth sensitivity, according to Equation 17 for Scots pine, sessile oak and ponderosa pine growing under different stand density levels (low, moderate, maximum) based on 409 trees (Scots pine: 139; sessile oak: 135, ponderosa pine: 135). $Mean$ was calculated on raw basal area increment series, while CV was calculated on detrended bai index series. Significant differences between the means are indicated by upper case letters. Reprinted from Steckel et al. (2020b).

Mean tree growth sensitivity of Scots pine was found to be significantly higher in stands with low stand densities (27 %) compared with moderate (24 %) and maximum (22 %) stand densities. In contrast, CV of ponderosa pine was significantly higher under maximum stand density (35 %) compared with low (26 %) and moderate (30 %) stand density levels. No significant differences in CV were observed for sessile oak trees growing in stands exhibiting low (CV = 27 %), moderate (CV = 25 %) and maximum (CV = 26 %) stand density.

Tab. 14. Results of the linear mixed-effects model regressions from Equation 17.

Species	**Response variable**	**Statistic**	**Intercept** **a₀**	**ba** **a₁**	**DL$_{mod}$** **a₂**	**DL$_{max}$** **a₃**
Scots pine	Mean	Estimate	1.45	**0.02*****	-1.73	**-2.48***
		SE	1.70	0.00	0.98	1.01
	CV	Estimate	**31.59*****	**-0.01*****	**-3.09***	**-5.65*****
		SE	2.64	0.00	1.19	1.23
sessile oak	Mean	Estimate	3.93	**0.01*****	**-2.41****	**-3.27*****
		SE	4.85	0.00	0.80	0.92
	CV	Estimate	**27.68*****	-0.00	-2.03	-1.21
		SE	2.30	0.00	1.30	1.46
ponderosa pine	Mean	Estimate	**9.24*****	**0.01*****	**-6.87*****	**-7.84*****
		SE	1.69	0.00	0.83	0.96
	CV	Estimate	**27.91*****	-0.00	**3.40***	**8.38*****
		SE	2.74	0.00	1.62	1.87

$Mean$: mean growth level (cm^2 yr^{-1}). CV: coefficient of variation of the detrended bai index series (%). ba: tree basal area (cm^2). DL: stand density level (low: DL_{low}, moderate: DL_{mod}, maximum: DL_{max}). The number of observations was always n = 139 for Scots pine, n = 135 for sessile oak and n = 135 for ponderosa pine. Bold values are significant at level $p < 0.001$ (***), $p < 0.01$ (**), $p < 0.05$ (*). Only fixed effects are reported.

Growth responses to episodic drought in relation to stand density and water availability

On average, tree growth decreased during the drought events studied in all species as indicated by resistance values of below 1.0 (Tab. 15). Average recovery and resilience values of more than 1 indicate a full recovery to above average pre-drought conditions within the time frame of two years. On average, sessile oak seemed only little affected by the drought events studied (1 % average growth reduction) compared with Scots pine (18 % average growth reduction) and ponderosa pine (11 % average growth reduction). Average recovery of oak (4 %) was much lower than for Scots pine (34 %) and ponderosa pine (41 %).

Tab. 15. Mean values (Mean) and standard deviation (SD) of drought indices.

Species	**n**	**Statistic**	**Rt**	**Rc**	**Rs**
Scots pine	229	Mean	0.82	1.34	1.07
		SD	0.16	0.34	0.27
sessile oak	225	Mean	0.99	1.04	1.02
		SD	0.20	0.28	0.32
ponderosa pine	359	Mean	0.89	1.41	1.10
		SD	0.37	0.68	0.35

n = number of observations. Rt: resistance. Rc: recovery. Rs: resilience. Means are calculated for each species over selected site-specific drought events based on basal area increment indices.

Species-specific tree drought responses according to Equation 18 are outlined in Table 16. Mean relative stand basal area ($MRBA$) was found to significantly lessen recovery and resilience of Scots pine. Site water availability, represented by the Global Aridity Index (I_A), had a significantly negative effect on the resistance, recovery and resilience of Scots pine on average. The effect of stand density on drought responses of Scots pine was significantly modified by site water availability; the advantage of reduced stand density in terms of drought recovery and resilience decreased with site water availability (Tab. 16, Fig. 15d,g). Furthermore, stand age increased the resistance of Scots pine. In the case of oak, $MRBA$ was found to significantly lessen recovery. In addition, average recovery and resilience of sessile oak significantly decreased with site water availability. Analogously to Scots pine, site water availability gradually decreased the advantage of reduced stand density in terms of drought recovery of sessile oak (Tab. 16, Fig. 15e). Furthermore, stand age significantly lessened the average drought recovery of sessile oak. In contrast to Scots pine and oak, resistance and resilience of ponderosa pine significantly increased with $MRBA$, while recovery decreased. In addition, average recovery of ponderosa pine significantly decreased with site water availability. In line with Scots pine and sessile oak, the advantage of reduced stand density in terms of recovery of ponderosa pine significantly decreased with site water availability (Tab. 16, Fig. 15f).

Tab. 16. Results of the linear mixed-effects model regressions from Equation 18.

Species	**Response variable**	**Statistic**	**Intercept**	**ba**	**MRBA**	**I_A**	**Age**	**MRBA*I_A**	**MRBA*Age**
			a_0	**a_1**	**a_2**	**a_3**	**a_4**	**a_5**	**a_6**
Scots pine	Rt	Estimate	**5.47*** **	-	-	**-4.34** **	**0.01** **	-	-
		SE	1.44			1.33	0.00		
	Rc	Estimate	**16.09*** **	-	**-15.29** **	**-12.42*** **	-	**12.85* **	-
		SE	4.29		5.86	3.62		4.95	
	Rs	Estimate	**12.31*** **	-	**-9.92* **	**-9.45** **	-	**8.30* **	-
		SE	3.39		4.62	2.86		3.91	
sessile oak	Rt	Estimate	**0.74*** **	-	-	0.16	-	-	-
		SE	0.13			0.08			
	Rc	Estimate	**3.41*** **	-	**-1.29* **	**-1.38*** **	**-0.00*** **	**0.82* **	-
		SE	0.45		0.60	0.30	0.00	0.39	
	Rs	Estimate	**2.33*** **	-	-	**-0.82*** **	-	-	-
		SE	0.19			0.12			
ponderosa pine	Rt	Estimate	**0.71*** **	-	**0.30*** **	-	-	-	-
		SE	0.04		0.07				
	Rc	Estimate	**4.76*** **	-	**-4.32* **	**-2.72* **	-	**3.45* **	-
		SE	1.37		2.01	1.18		1.73	
	Rs	Estimate	**0.97*** **	-	**0.20** **	-	-	-	-
		SE	0.04		0.06				

Rt: resistance. Rc: recovery. Rs: resilience. ba: tree basal area (cm²). $MRBA$: weighted mean stand basal area. I_A: Global Aridity Index. Age: stand age (yrs). The number of observations was always n = 229 for Scots pine, n = 225 for sessile oak and n = 359 for ponderosa pine. Bold values are significant at level $p < 0.001$ (***), $p < 0.01$ (**), $p < 0.05$ (*). Only fixed effects are reported.

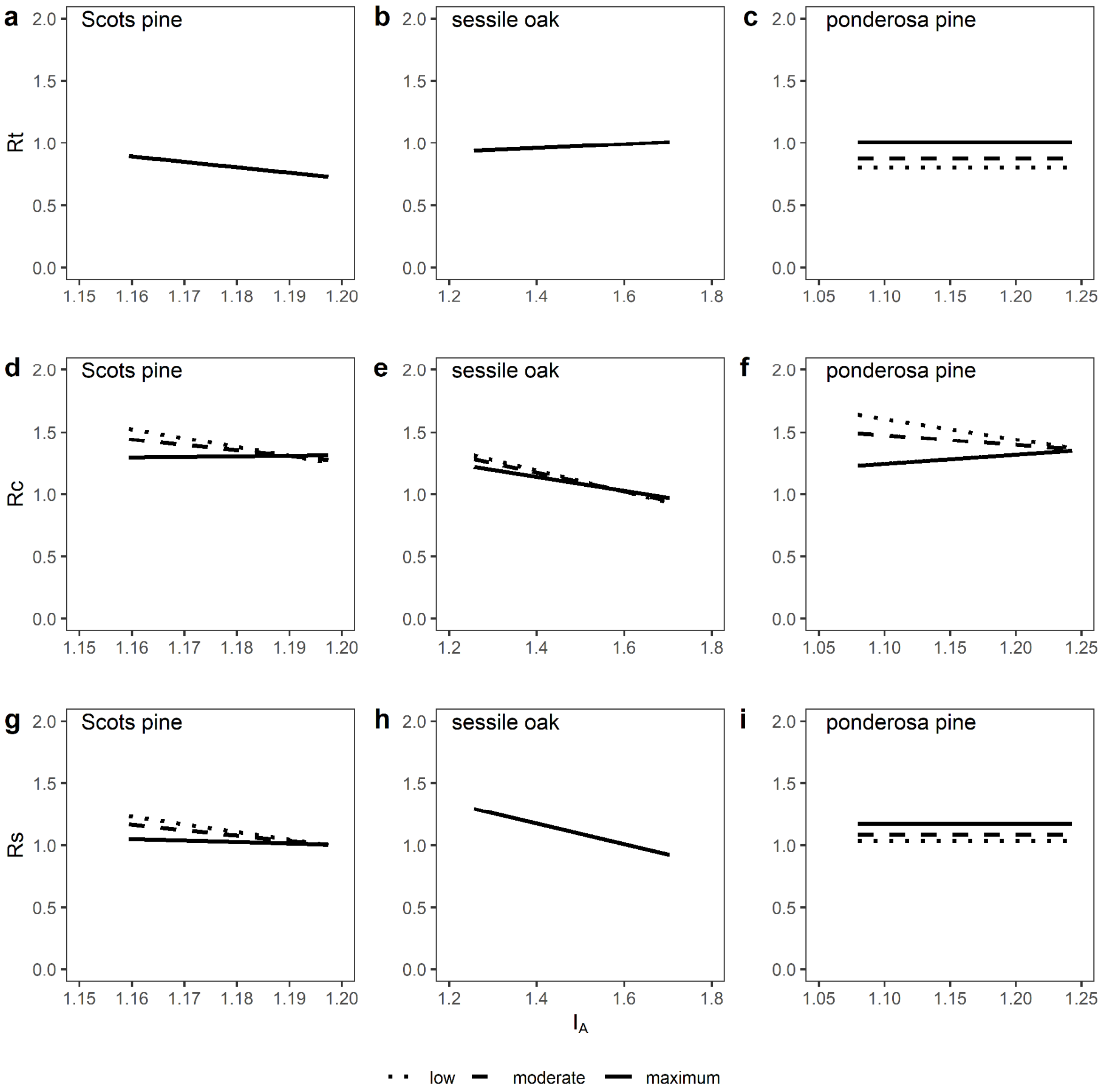

Fig. 15. Effect of site water availability (I_A) on drought response indices (Rt, Rc, Rs) of Scots pine, sessile oak and ponderosa pine under different stand density levels (low, moderate, maximum). Lines represent the fixed effect terms from Equation 18. Explanatory variables other than I_A were set at the respective means of each stand density level as obtained from the data. Reprinted from Steckel et al. (2020b).

4. Discussion

4.1. QI: How does stand growth and structure of mixed stands differ from adjacent monocultures and how is any over- or underyielding affected by variations in annual climate? (*Article I*)

Triplet plots sampled in this dissertation represent fully stocked stands and exhibit same site and stand conditions within each triplet. It can therefore be assumed that the observed differences between mixed and monospecific stands result from actual mixing effects that stem from interactions between Scots pine and oak. Such inter-specific interactions may cause changes in growth allocation between radial and height growth, thereby resulting in altered tree allometry (Pinto et al., 2008; Barbeito et al., 2014; Pretzsch, 2014a). Indeed, species mixing resulted in significantly higher Scots pine trees that exhibited significantly shorter crowns (Fig. 8). In the case of oak, mixing did not alter tree height, but significantly promoted longer and wider crowns (Fig. 8). Corresponding to changes in individual tree allometry, Scots pine exhibited significantly larger quadratic mean and dominant tree heights (h_q, h_{100}) in mixed compared with monospecific stands, while quadratic mean and dominant tree heights of oak were not significantly affected by species composition (Tab. 7). These findings indicate that mixing of Scots pine and oak can lead to a modification in stand structure towards a vertically more stratified overstory, which could highlight differences in shade tolerance and growth patterns between both species studied. Differing light compensation points of 27 to 17 μmol $m^{-2} s^{-1}$ for Scots pine and oak respectively substantiate the higher shade tolerance of oak (Ellenberg and Leuschner, 2010, pp. 103–105). In line with the current findings, del Río et al. (2018) also reported an increased height growth of Scots pine in mixture with oak. Furthermore, Lu et al. (2018) observed a two-layered stand structure in Scots pine-oak mixtures, with Scots pine growing above oak. The development of multi-layered canopies, where more shade-tolerant species grow under taller, more light-demanding species, are common and have also been reported for other coniferous-deciduous species mixtures (Hardiman et al., 2011; Pretzsch et al., 2015; Thurm and Pretzsch, 2016). In mixture, oak also exhibited a significantly lower height-diameter ratio of dominant trees compared with monocultures. This could indicate a lower level of competition for light, as these trees can allocate more carbon to diameter growth, while still being able to keep their crown in the canopy. Similar observations have been made for Douglas fir in mixture with European beech (Thurm and Pretzsch, 2016).

Standing volume was significantly higher in mixtures compared with adjacent monocultures. This effect appeared mainly to be driven by significantly higher standing volume of Scots pine in mixtures compared with monocultures. Whereas the slightly, but not significantly, increased standing volume of oak in mixture may be the result of higher tree numbers, the higher standing volume of Scots pine in mixture compared with monoculture seems more closely related to individual tree growth. Similar results were reported by Pretzsch et al. (2015) for Scots pine growing in mixture with European beech.

One of the most important findings of the current investigation is that the mixing of Scots pine and oak can result in significant positive effects on volume productivity and even transgressive overyielding (Fig. 9, Tab. 7). Furthermore, the interaction of both species was found to stabilise productivity (Fig. 9, Fig. 10). This can be seen as an indication of reduced vulnerability to biotic and abiotic disturbances, which over time may have contributed to the average overyielding observed. In line with the current results, overyielding of Scots pine-oak mixtures has also been reported for other regions in Europe. Brown (1992), using an experimental design in Gisburn, England, reported positive mixing effects on productivity in young Scots pine-oak stands. Studies on permanent field plots in the Netherlands also revealed overyielding of mixed Scots pine-oak stands, which increased on poor soils (Lu et al., 2016; Lu et al., 2018). Furthermore, a modelling approach study for one site in France revealed similar results (Perot and Picard, 2012). In contrast, Toïgo et al. (2015) did not find any significant overyielding for Scots pine-oak mixtures based on French inventory data, although oak did show a positive mixing effect on the species level, which was also confirmed in a later study (Toïgo et al., 2017). Reasons for contrasting results could be found in the differing basis of assessment; Toïgo et al. (2015) used stand basal area increment as a measure for stand performance, while the current investigation and other studies used volume increment (Lu et al., 2016; Lu et al., 2018) or yield (Brown, 1992), metrics that encompass both height growth and radial growth. For Scots pine in particular, the results of the current study clearly show that positive mixing effects on productivity may result from an accelerated height growth, which therefore should be viewed as a necessary component of the analysis. Positive mixing effects on productivity have also been reported for other pine and oak species (del Río and Sterba, 2009; Nunes et al., 2013; Jucker et al., 2014) as well as other coniferous-deciduous mixtures (Bartelink, 1998; Pretzsch and Schütze, 2009; Condés et al., 2013; Dirnberger and Sterba, 2014; Pretzsch et al., 2015; Thomas et al., 2015; Toïgo et al., 2015; Lu et al., 2016; Thurm and Pretzsch, 2016). In a subsequent study, encompassing a larger ecological gradient across Europe, the observed trend of increased tree dimensions in Scots pine was confirmed (Pretzsch et al., 2019b). Here, Scots pine showed a 10 % larger quadratic mean diameter and a 7 % larger dominant diameter in mixed compared with monospecific stands. Furthermore, in line with *Article 1*, Pretzsch et al. (2019b) found that species mixing increased the mean periodical growth of stand basal area and stand volume by 9 %. In the current study, the main driver of the positive mixture effect on the stand level seems to be the more shade tolerant oak, while for Scots pine the positive mixing effect was not as strong and remained statistically insignificant. A more pronounced positive effect for oak compared with Scots pine was also observed by other studies (Perot and Picard, 2012; Toïgo et al., 2015; Lu et al., 2018). The observed transgressive overyielding is typical for combinations of tree species that show similar productivities, as the reduction in growth area of one species is compensated for by the increased growth of both species in the mixed stand (del Río and Sterba, 2009).

A key hypothesis explaining positive relationships of biodiversity and productivity is the 'complementary effect hypothesis' (Aarssen, 1997; Loreau, 2000; Loreau and Hector, 2001; Fargione et al., 2007). According to this school of thought, complementary effects can occur under either reduced competition or facilitation. Reduced competition is relevant when inter-specific competition in the mixture is lower than intra-specific competition in the monoculture. It is often caused by niche differentiation where two or more species use the resources available in complementary ways (Fargione et al., 2007). Niche differentiation may occur due to differences in shade tolerance, phenology, crown architecture or root system (Kelty, 1992; Man and Lieffers, 1999). On the other hand, facilitation is a form of interaction where one species improves the environmental conditions for another species (Callaway, 2007; Brooker et al., 2008). Facilitation may for example be associated with an increase in available nitrogen, resulting from increased litter decomposition rates or the introduction of nitrogen-fixing species (Kelty, 1992), the sheltering of one species by the other, resulting in reduced abiotic and biotic damage (Man and Lieffers, 1999), or increased soil water availability due to hydraulic lift (i.e., upward hydraulic redistribution) (Caldwell et al., 1998). As reduced competition and facilitation are often inter-dependent and therefore difficult to separate, the combination of the two mechanisms is commonly referred to as complementarity (Forrester and Bauhus, 2016).

A reduction in competition for light can be considered a crucial factor in compositions consisting of tree species that differ in shade tolerance (Zhang et al., 2012). Mechanisms that promote niche differentiation and reduce inter-specific competition for light can be classified in three groups (Forrester and Bauhus, 2016; Pretzsch, 2017a): a) spatial complementarity as a result of vertical stratification caused by differences in shade tolerance, b) temporal complementarity caused by differences in leaf phenology of evergreen and deciduous species and c) morphological complementarity as a result of inter-specific differences in crown shape or intra-specific changes in crown architecture and allometry. In the following, all three mechanisms are discussed as potential causes of the observed overyielding in mixed Scots pine-oak stands.

a) Spatial complementarity as a result of vertical stratification caused by differences in shade tolerance

Differences in physiology, such as shade tolerance, may increase the vertical stratification of a given mixed-species stand. Spatial complementarity through canopy stratification may arise in mixtures where fast-growing species with a high light-use efficiency overtop slower growing and more shade tolerant species (Binkley et al., 1992; Forrester et al., 2012). The ability of more shade-intolerant species to overtop more shade-tolerant species can be crucial for positive diversity effects in forest mixtures (Forrester et al., 2006; Forrester et al., 2011). The findings of this investigation suggest that height growth of Scots pine is accelerated in mixture with oak, resulting in a more stratified crown space. This may result in reduced competition for light as indicated by the unaltered tree height of oak and its reduced dominant height-diameter ratio. In mixture, Scots pine is likely to transmit more light through the canopy for oak to grow underneath compared with oaks growing in adjacent monocultures (cf. Grossiord et al., 2014a). This could result in an elongated leaf life span, improving light use throughout the year, as reported for European beech growing in mixture with Scots pine (Forrester et al., 2017).

b) Temporal complementarity caused by differences in leaf phenology of evergreen and deciduous species

In mixture with oak, Scots pine is likely to receive more light in spring before the leaf-break of oak compared with growing amongst conspecific neighbours. Such differences in leaf phenology have been highlighted as one of the main drivers of overyielding in evergreen-deciduous forest mixtures (Sapijanskas et al., 2014; Lu et al., 2016).

c) Morphological complementarity as a result of inter-specific differences in crown shape or intra-specific changes in crown architecture and allometry.

Inter-specific differences in crown architecture between Scots pine and oak may cause a larger and more efficient utilisation of crown space, thereby potentially increasing the light absorption of the whole stand (cf. Pretzsch et al., 2014c; Sapijanskas et al., 2014; Jucker et al., 2015). Furthermore, the findings of this study suggest that oak in particular is able to significantly change its crown morphology (longer and wider crowns) in mixture with Scots pine, thereby potentially further increasing its ability to absorb light (cf. Forrester and Albrecht, 2014; Jucker et al., 2014; Pretzsch et al., 2014c; Sapijanskas et al., 2014; Jucker et al., 2015). The ability to plastically adapt the shape and size of the crowns is seen as crucial for increasing the light use efficiency in mixed stands (Jucker et al., 2015). The reduction of crown abrasion, defined as the physical loss of terminal buds and branches by the overlap during wind sway (Rudnicki et al., 2001), may explain some of these positive interactions. Mechanical crown abrasion resulting in crown shyness (Putz et al., 1984) can lead to a decline in crown closure, leaf area and productivity (Meng et al., 2006). In cases where the combined species fill different canopy layers, this effect may be mitigated (Pretzsch et al., 2014c). Increased crown dimensions of oak in mixture with Scots pine are likely to be the result of the observed increase in canopy stratification and indicate reduced competition and an optimised utilisation of canopy space, which oak is able to exploit due to its comparatively high crown plasticity (Longuetaud et al., 2013).

In addition to complimentary light use, the ability to exploit underground resources in complementary ways by contrasting rooting patterns has been pointed out as an important factor in many mixtures (Schume et al., 2004; Forrester et al., 2010; Reyer et al., 2010; Brassard et al., 2012; Pretzsch et al., 2013b; Schwendenmann et al., 2014). In Scots pine-oak mixtures, this form of complementarity is likely, as the root morphology of both species differs considerably. The root system of Scots pine is often rather shallow without distinct tap roots, but can also exhibit a deeper rooting system if the site conditions require it (Carlisle and Brown, 1968). Oak on the other hand, generally produces a strong tap root, particularly in younger years, which is accompanied by, and in higher ages even replaced by, deep reaching lateral roots that gradually descend and form a dense system of heart-roots (Jones, 1959). Oaks are therefore commonly found to be capable of using deeper soil resources than pines (Kolb and Stone, 2000). In addition, Scots pine and oak in mixture have been reported to exhibit complementary water uptake depths during drought as a result of root plasticity, with oak in particular shifting to deeper water resources under drought stress (Bello et al., 2019a). Complementarity of Scots pine and oak may also be the result of seasonal differences in fine root development (Konôpka et al., 2005), or accelerated nutrient cycling due to greater nutrient contents and decomposition rates, as reported for other pine-oak mixtures (Kaneko and Salamanca, 1999; Conn and Dighton, 2000) and other species mixtures (Elmer et al., 2004; Cornwell et al., 2008; Jonard et al., 2008; Weedon et al., 2008).

Size and growth partitioning of trees may be altered by species mixing (Binkley et al., 2003; Pretzsch and Schütze, 2014; Pretzsch and Schütze, 2016). This response was also observed in the current investigation, where the Gini coefficient of tree size (GC_v) was significantly higher for oak growing in mixed compared with monospecific stands. Furthermore, there was a tendency towards a higher Gini coefficient of volume increment (GC_{iv}) of oak in mixtures, although the difference to monocultures was not statistically significant. The significantly larger size inequality and the observed tendency towards a larger growth inequality in mixture could be attributed to the higher vertical structuring and increased crown space, which could have improved light availability and thereby facilitated the survival of subdominant and understorey trees. This is a likely explanation, as mixtures are often understood to hold more small trees, while at the same time stem size and stem growth may be concentrated on a restricted number of tall trees (Pretzsch and Schütze, 2016). In contrast to oak, Scots pine showed a tendency towards reduced partitioning of tree size and growth in mixture, which would suggest a more equal tree size and growth distribution compared with monocultures. Mixing resulted in an increased size inequality of oak that is comparable to the effect of thinning from above. The opposite effect is indicated for Scots pine, where species mixing seems to rather have resulted in a size distribution found in stands thinned from below. Such differing reactions can be seen as typical for combinations of tree species that differ in shade tolerance, highlighting differences in self- and alien thinning (Pretzsch and Schütze, 2014). Structural diversity in mixed Scots pine-oak stands can increase productivity of tall oak trees in particular (Vanhellemont et al., 2018). Similar results were found in the studied stands, which was indicated by the slightly higher diameter and the corresponding significantly lower height-diameter relation for dominant oaks growing in mixed compared with monospecific stands.

Annual climate was found to significantly alter the observed mixing effect on productivity. Overyielding at the stand and species level significantly increased with the annual De Martonne aridity index and annual precipitation total (Fig. 10). In line with these findings, Jucker et al. (2014), studying Iberian pine-oak mixtures, also reported a higher overyielding in wet compared with dry years. Under the assumption that temporal responses to environmental conditions resemble those reported along spatial environmental gradients, our results are in line with a global meta-analysis by Jactel et al. (2018), who reported a generally positive correlation of overyielding with precipitation. A positive effect of water supply on overyielding is typical for species interactions that improve light absorption or light-use efficiency and can be explained by the framework developed by Forrester (2014), which states that under rich growing conditions (i.e., high nutrient and water availability), where competition for light increases due to larger leaf areas, light related interactions may be more relevant than under poor growing conditions, where the limiting factor is rather related to soil conditions. A similar relation has also been reported for mixtures of Silver fir (*Abies alba* Mill.) and Norway spruce (Forrester and Albrecht, 2014). Overyielding of oak was less sensitive to annual water supply than Scots pine. This finding is in line with the results by Jucker et al. (2014) and could be attributed to oak's better ability to compete for below-ground resources (Bello et al., 2019a). In contrast to the current findings, Lu et al. (2018) found that overyielding of Scots pine-oak mixtures was stronger on poor than on rich soils, which is perceived as in line with the stress-gradient hypothesis. These seemingly conflicting results could indicate, that the effect of spatial and temporal changes in growing conditions on the diversity-productivity relationship may not always be closely related and may instead be context-dependent (e.g. influenced by the type of limiting factor at a given site (Forrester, 2014)). Also, in the current study the environmental conditions were not very harsh. However, in a subsequent investigation along a wider ecological gradient, including the seven studied triplets reported in this dissertation, but also encompassing more extreme growing conditions, it was able to solidify a generally positive effect of water availability on the overyielding of Scots pine-oak mixtures (Pretzsch et al., 2019b). Here, mean periodic overyielding was found to increase with long-term site water supply over a wide range of growing conditions.

4.2. QII: How does species mixing influence tree growth responses to episodic drought under different ecological growing conditions? (*Article II*)

Tree drought responses differed significantly between Scots pine and oak in the studied monocultures (Fig. 11a). Resistance and resilience of oak were greater than for Scots pine, suggesting that oak had a greater capacity to withstand water stress during the drought events studied and to return to average pre-drought growth. The results confirm previous studies that report a more pronounced sensitivity of Scots pine to increased temperatures and drought, suggesting a higher vulnerability compared with oak species (Kölling and Zimmermann, 2007; Galiano et al., 2010; Zang et al., 2011; Bello et al., 2019b). Differing drought response patterns of Scots pine and oak are likely related to contrasting water uptake strategies under drought, Scots pine being characterised as isohydric and oak as anisohydric (Irvine et al., 1998; Zang et al., 2011; Zang et al., 2012; Poyatos et al., 2013; Martínez-Sancho et al., 2017). Under acute drought stress, isohydric species are found to immediately reduce water consumption and growth by closure of stomata and reduced photosynthesis, while anisohydric species continue transpiring until water resources are depleted (McDowell et al., 2008; Domec and Johnson, 2012; Kumagai and Porporato, 2012). Under prolonged water stress, maintenance of transpiration flow may require leaf area control in anisohydric species (Maseda and Fernández, 2006). Thus, twig abscission is rather common in oak and enables the trees to avoid runaway embolism (Klugmann and Roloff, 1999). The preventive strategy of isohydric species on the other hand can reduce stress damage such as defoliation, loss of fine roots or cavitation of xylem tissue, therefore often resulting in a higher recovery following drought compared with anisohydric species (Hartmann, 2011). These differences in drought response strategy seem plausible for explaining oak's higher drought resistance (i.e., higher productivity during drought), but lower recovery compared with Scots pine (Tab. 10). Differences in drought responses between Scots pine and oak may also be caused by contrasting seasonal growth dynamics. Oak attains about half of its annual radial growth during spring, when wide earlywood vessels are formed based on reserves carried over from the previous growing season (Zweifel et al., 2006). These newly formed vessels are at high risk of cavitation, which may result in water deficit and reduced cell enlargement (Tardif and Conciatori, 2006). The growth of Scots pine on the other hand is concentrated on the summer and early autumn months, following needle formation and expansion (Zweifel et al., 2006). Consequently, oak has been found to be more susceptible to spring droughts, whereas Scots pine is more affected by summer droughts (Weber et al., 2007; Merlin et al., 2015; Toigo et al., 2015; Vallet and Perot, 2018; Vanhellemont et al., 2019). The observed results may therefore also be related to a generally higher vulnerability of Scots pine to increasingly longer summer drought periods and higher mean temperatures (Weber et al., 2007). Indeed, many of the drought years analysed in the current study represent well-documented summer droughts (e.g. 1993 (European Drought Centre, 2019), 1996 (Carnicer et al., 2011), 2003 (Ciais et al., 2005; Rebetez et al., 2006; Pichler and Oberhuber, 2007; van der Werf et al., 2007; Lebourgeois et al., 2010; Merlin et al., 2015), 2006 (Merlin et al., 2015) and 2015 (Ionita et al., 2017)), which would, in part, explain the observed average response pattern of Scots pine in relation to oak.

One of the key findings of this dissertation is that species mixing can reduce tree drought susceptibility of Scots pine and oak. Resistance of Scots pine, as well as resistance and resilience of oak, were significantly enhanced by mixing. While it can be proposed that complementary light use may be the main driver of positive mixing effects under average growing conditions (see 4.1), water-related complementarity may increase in importance under episodic drought (Forrester and Bauhus, 2016). Under such acute drought stress, oak may profit from Scots pine's more conservative water stress response strategy (Loreau and Hector, 2001; Pretzsch et al., 2013b). In addition, spatial stratification of admixed tree species due to differences in root distribution, architecture or activity, can improve the exploitation of underground water resources (Schume et al., 2004; Forrester et al., 2010; Schwendenmann et al., 2014). This is a plausible explanation of the observed response patterns, as the root morphology of Scots pine and oak differs significantly (see 4.1). Most importantly however, oak is known to perform hydraulic lift (i.e., upward hydraulic redistribution) under both moderate and severe drought conditions (Caldwell et al., 1998; Jonard et al., 2011; Zapater et al., 2011; Hafner et al., 2017) and may therefore in mixture have increased water availability for Scots pine during the drought events studied. This form of facilitation is well-studied (Ryel, 2004; Neumann and Cardon, 2012; Prieto et al., 2012) and can be seen as one of the most important advantages of mixing oak with other tree species (Pretzsch et al., 2013b). The negative relationship between resistance and recovery of Scots pine suggests a trade-off between both indices, which has previously been reported for a wide range of forest types (Gazol et al., 2017; Hoffmann et al., 2018; Schwarz et al., 2020) and could be attributed to a higher depletion of non-structural C pools during drought, which subsequently results in reduced recovery (Galiano et al., 2011). Furthermore, the more growth and thereby soil nutrient consumption is limited during drought, the more soil nutrients may be available for recovery in the following years (Pretzsch et al., 2013b). In the case of Scots pine, this means that in monocultures more nutrients may have been available following low growth episodes than in mixtures. Under improving growing conditions (i.e., during post-drought periods), the relationship between Scots pine and oak may on average have changed from complementarity to competition, as suggested by the stress gradient hypothesis (del Rio et al., 2014) and by the complementary inter-specific recovery and resilience pattern observed. For Scots pine, inter-specific competition would then have been greater than intra-specific competition during the post-drought period. In contrast, oak may have experienced a competitive release in mixture compared with monoculture. One can assume that when soil water is not the limiting factor, competition for light may become more relevant again, resulting in a more asymmetric mode of competition (Schwinning and Weiner, 1998; Pretzsch and Biber, 2010; Pretzsch et al., 2018). Under these conditions, oak is more likely to receive a competitive advantage against Scots pine, owing to its high crown plasticity. The stronger resilience of oak in mixtures compared with monocultures could also be caused by a more continuous mineralisation (Pretzsch et al., 2013b).

In line with the findings of this dissertation, several previous studies have reported improved tree drought responses in mixed compared with monospecific stands (Lebourgeois et al., 2013; Pretzsch et al., 2013b; Metz et al., 2016; Gazol et al., 2017; Mölder et al., 2019; Palandrani et al., 2020). Furthermore, the results are supported by previous studies that have reported a positive effect of species mixing on drought stress reduction in oak (del Rio et al., 2014; Bello et al., 2019b) and those who have highlighted the advantages for other species that are admixed with oak, such as European beech (Pretzsch et al., 2013b). In contrast to our findings, neutral (Merlin et al., 2015; Toigo et al., 2015; Bello et al., 2019b) and negative (Bello et al., 2019b; Nothdurft and Engel, 2019) mixing effects with regard to drought resistance and resilience have also been reported for Scots pine-oak mixtures. However, previous studies are based on rather small samples of environmental growing conditions, whereas the current study reflects the growth behaviour of Scots pine-oak mixtures across a large portion of the natural distribution in Europe. Methodological differences, such as limiting the sampling to dominant trees, may also explain why these results differ from those reported in the current investigation.

Based on the observations made in this dissertation, it can be concluded that ecological factors, such as tree size and site conditions, can significantly influence tree drought responses in mixtures and monocultures and, more importantly, may also significantly modify the mixing effect. Larger Scots pine trees were significantly more resistant than smaller ones, while the opposite relationship was found regarding recovery. The greater growth reduction of smaller Scots pine is likely an effect of dominance, as small Scots pine trees growing in an understory canopy position may have to compete more fiercely for valuable resources. Larger trees may have more extensive root systems, increasing the competitive performance under drought conditions (Zang et al., 2014). Consistent with the current findings, other studies have also reported more pronounced growth reductions under drought in understory compared with overstory trees in Scots pine (Pichler and Oberhuber, 2007) and other tree species (Vose and Swank, 1994; Orwig and Abrams, 1997; Martín-Benito et al., 2008). In contrast, other studies have failed to find any significant influence (Bello et al., 2019b), or have instead reported a negative effect of tree size on drought resistance, arguing that larger trees exhibit a greater vulnerability to hydraulic stress and experience higher radiation and evaporative demand due to exposed crowns than smaller trees (Zang et al., 2012; Bennett et al., 2015; Merlin et al., 2015; Serra-Maluquer et al., 2018). Methodological differences in the definition of tree size classes and the measures for quantifying growth responses to drought may explain the conflicting results as well as the variability in soil and climatic conditions. Contrary to some studies (Jucker et al., 2014; Ledo et al., 2014), the current findings do not suggest that tree size may modify the effect of stand composition on tree drought responses. Long-term site conditions significantly modified the average drought responses of both species. Resistance of oak increased with the De Martonne aridity index. This result confirms a previous study by Pretzsch et al. (2013) that reported increased resistance along the gradient of water supply for Norway spruce, European beech and sessile oak. Most interestingly, the current findings show that site water availability significantly enhanced the positive effect of species mixing regarding resistance and resilience of oak. Consistent with these findings, a strong dependence of drought stress reduction on site conditions in mixtures has been reported from different regions in Europe (Forrester et al., 2016; Streel et al., 2019). As reported by Nothdurft and Engel (2019), resistance of Scots pine and oak can also be negatively affected through mixing within certain climate ranges. As observed on the studied sites, species mixing increased resistance and resilience of oak over most of the aridity gradient. However, on the driest sites, resistance of oak was estimated to be lower in mixtures compared with monocultures. This may be seen as indicative of the fact that trees may be more acclimated to drought stress on dry sites, resulting in less pronounced growth reactions (Lévesque et al., 2013), thereby limiting complementarity effects. However, in drought prone environments, the complementary advantage may also be replaced by competition (González de Andrés et al., 2018), unless net water-use partitioning or water-related facilitation take place (Grossiord et al., 2014b). Following Forrester and Bauhus (2016), it can be hypothesised that in the case of oak, complementary light use may be important, in particular on moister sites, where water is not the limiting resource. In contrast, the negative influence of site fertility on the mixing effect regarding resistance of Scots pine suggests a stronger dependency on water-related complementarity effects.

4.3. QIII: How does the maintenance of reduced stand density influence tree growth responses to episodic drought under different levels of site water availability? (*Article III*)

The findings of this dissertation highlight significant differences in mean tree growth and mean tree growth sensitivity in stands exhibiting different levels of stand density. It was found that mean tree growth was higher under low compared with maximum stand density in all species studied (Fig. 14). For Scots pine and oak this meant a 17 % and 23 % higher mean basal area increment respectively, when compared with fully stocked controls. In ponderosa pine the impact was even more pronounced, resulting in a 104 % higher mean tree growth in stands with low compared to maximum stand density. These findings are consistent with the general view that tree population density reductions accelerate tree growth and that the magnitude of growth increase is directly related to the intensity of the stand density reduction (Pretzsch, 2019a). Correspondingly, previous studies have also reported increasing diameter growth with stand density reductions in Scots pine (Mäkinen and Isomäki, 2004a; Mäkinen and Isomäki, 2004b; Nickel et al., 2007; Giuggiola et al., 2013; Fernández-de-Uña et al., 2015; Sánchez-Salguero et al., 2015; Stone, 2019), sessile oak (Bréda et al., 1995; Kerr, 1996; Štefančík, 2012) and ponderosa pine (Gaines and Kotok, 1954; Myers, 1967; Barrett, 1982; McDowell et al., 2003; Skov et al., 2004; McDowell et al., 2006; Miesel, 2012; Thomas and Waring, 2014; Stone, 2019). Stand density reductions are found to improve the growth of remaining trees by release from inter-individual competition for above and belowground resources, such as light, water and nutrients (Aussenac and Granier, 1988; del Río et al., 2017a; Pretzsch, 2020) and are often used as a silvicultural measure to maximise diameter growth and tree value on relatively short rotation (Pretzsch, 2019a).

Tree growth sensitivity can be seen as an indicator of the responsiveness to environmental conditions, such as high-frequency fluctuations in climate (Fritts, 2001). In the current investigation it was found that mean tree growth sensitivity, represented by the coefficient of variation of the detrended basal area increment index series, was 23 % higher for Scots pines in low compared with maximum stand density levels (Fig. 14). This response of growth sensitivity to stand density reductions was also observed by Sánchez-Salguero et al. (2015), who reported a higher growth responsiveness to climate under low competition levels for Scots pine along an altitudinal gradient in Spain. Correspondingly, Guillemot et al. (2015) found higher inter-annual growth sensitivity with increasing thinning intensity of Atlas cedar (*Cedrus atlantica* (Endl.) Manetti) in the southern French Alps. In the studied Scots pine stands in Bavaria, where water is not the limiting factor under average growing conditions, competition for light may be more relevant. Therefore, the mean climate signal may not be as pronounced in fully stocked stands, while the responsiveness of trees to show a growth reaction in response to annual climate is higher in stands with lower stand densities. This is consistent with findings by Pérez-de-Lis et al. (2011), who reported increasing climate sensitivity of Canary pine (*Pinus canariensis* Sweet ex Spreng.) with thinning intensity on wet, but not on dry sites. Surprisingly, the current findings show that mean tree growth sensitivity of ponderosa pine, in contrast with Scots pine, increased with stand density and was 35 % higher in the untreated controls compared with low stand densities. In the case of ponderosa pine, growing under chronically water stressed conditions with a more irregular seasonal water supply and a higher frequency of drought events, water can be seen as the principle limiting factor for tree growth. Thus, larger trees in the more heavily thinned stands may suffer more from hydraulic constraints and water/nutrient limitations may become more important and competition for below-ground resources might be higher due to larger average tree size and associated root systems (Martínez-Vilalta et al., 2009; Sánchez-Salguero et al., 2015). Growth sensitivity of sessile oak was not significantly influenced by stand density, which might indicate that inter-individual competition for resources was comparatively low under average growing conditions.

Not surprisingly, studied drought events on average caused a tree growth reduction in all species (Tab. 15). Differences in the drought responses between sessile oak and both pine species could be attributed to different water uptake strategies under drought (anisohydric versus isohydric behaviour) (Irvine et al., 1998; Zang et al., 2011; Zang et al., 2012; Voelker et al., 2018) (see 4.2). The results reflect the often reported high drought resistance of oak (Zang et al., 2011; Zang et al., 2012; Pretzsch et al., 2013b), which appears to come at the expense of a comparatively low recovery. According to the linear mixed-effect models used, tree growth responses to drought were significantly improved by reduced stand density. However, the effect was not always beneficial and varied between the species. The results suggest that the effect of stand density on drought responses might be correlated with climate sensitivity – the higher the climate signal in tree growth, the higher the potential for reduced drought susceptibility. Drought responses of Scots pine were significantly improved by the maintenance of reduced stand density, as recovery and resilience were higher under lower compared with higher stand densities (Tab. 16). A similar effect was observed in sessile oak, which also exhibited significantly higher recovery under lower compared with higher stand densities. In accordance with these findings, previous studies have reported beneficial effects of reduced stand density on post-drought growth responses of Scots pine. For example, studying long-term thinning experiments in Germany, Sohn et al. (2016a) found that the thinning of Scots pine significantly improved growth recovery and resilience. Correspondingly, Giuggiola et al. (2013) reported an increase in leaf area to sapwood ratio in response to thinning in a xeric Scots pine forest in Switzerland, indicating reduced competition for water. The positive effects of reduced stand density on Scots pine drought responses could be attributed to decreased transpiration rates and increased hydraulic resistance, as reported for a Scots pine spacing trial in north-eastern Scotland by Whitehead et al. (1984). In the case of sessile oak, only little research has been devoted to studying density effects on growth responses to drought. However, based on a long-term experiment in France, Trouvé et al. (2017) found that resilience was significantly lower for suppressed trees in higher density stands. In the current study, ponderosa pine showed a distinctly different response pattern in relation to drought under different stand densities compared with Scots pine and oak. Here, resistance and resilience increased with increasing stand density. In accordance with these findings, McDowell et al. (2006) showed that ponderosa pine trees growing in open stands in Arizona, USA, were bigger and exhibited a greater relative growth decline under drought than trees growing at a slower rate in high competition environments under high stand densities. The authors concluded that trees growing in highly competitive environments were less likely to benefit from wet or average growing conditions, but also less vulnerable under drought conditions. In addition, strong reductions in stand density, such as those observed on the low density ponderosa pine plots of the current study ($MRBA$ = 0.30–0.32), have been reported to counteract generally positive effects of reduced stand density on drought resistance and resilience over time (D'Amato et al., 2013). This was attributed by the authors to the significantly greater tree sizes being attained within the lower-density stands throughout stand development, resulting in higher hydraulic constraints and water demand compared with smaller trees. It is also likely that smaller trees and regeneration, which, under more favourable average growing conditions may not be a significant factor for larger trees growing in the canopy, can constitute a considerable competition for limited water resources on chronically water stressed sites, where large ponderosa pine trees may be more reliant on deep soil water than smaller trees (Kerhoulas et al., 2013b). It is also likely that increased evaporation and stand transpiration following stand density reductions (Aussenac, 2000; Lagergren et al., 2008; Brooks and Mitchell, 2011) may be particularly disadvantageous under such xeric growing conditions. An explanation of the observed beneficial drought responses of ponderosa pine under higher stand densities may also be found in facilitative interactions that may have overridden intraspecific competition, a pattern also observed in Lenga beech (*Nothofagus pumilio* (Poepp. & Endl.) Krasser) in Patagonia, Chile (Fajardo and McIntire, 2010; McIntire and Fajardo, 2011), and confirmed for ponderosa pine regeneration in Arizona (Owen, 2019), USA, and for Stone pine (*Pinus pinea* L.) in Spain (Calama et al., 2019). Fajardo and McIntire (2010) proposed habitat amelioration via wind shelter and reduced radiation as facilitative processes between conspecific individuals that reduce evapotranspiration and improve water retention. Studying Stone pine at its ecological limit in the arid Spanish Northern Plateau, Calama et al. (2019) also reported a positive effect of higher stand density on radial growth under episodic drought. As potential causes for such facilitative effects Calama et al. (2019) proposed root fusion by spontaneous graftage (anastomosis) of close conspecific neighbours, permitting an exploration of deeper ground layers and favouring mycorrhizal activity, as well as a maximisation of light interception by the formation of umbrella like deep crowns, reducing irradiance and evapotranspiration. In contrast to our findings, a number of studies have reported positive effects of reduced stand density on the tree drought resistance of ponderosa pine within its natural distribution range (Kerhoulas et al., 2013a; Thomas and Waring, 2014) and beyond (Fernández et al., 2012). The conflicting results could be related to methodological differences, such as the rationale for selecting trees, drought events and pre- and post-periods, or differences in stand structure and site conditions.

On average, higher site water availability was found to negatively influence drought resistance, recovery and resilience of Scots pine. In sessile oak, increasing site water availability lessened recovery and resilience, but had no significant effect on resistance. In addition, recovery of ponderosa pine was, on average, negatively influenced by increasing site water availability. In line with these findings, a previous study reported that Scots pine populations on wetter sites were more impacted by drought than on drier sites (Martínez-Vilalta et al., 2012). However, other studies have also reported higher growth reductions on drier when compared with wetter sites (Pasho et al., 2011; Pretzsch et al., 2013b), or no significant effect (Serra-Maluquer et al., 2018). A recent synthesis for a wide range of forest types in the Northern Hemisphere reported significant effects of water availability on resistance (positive) and recovery (negative), but not resilience (Gazol et al., 2017). Furthermore, the legacy effects of drought have been reported to be more pronounced on dry when compared with wet sites (Anderegg et al., 2015). Differences in methodological approaches may partially explain these contrasting findings, as many previous studies focused on general growth responses to climate, while the current study focused on tree growth responses to specific severe to extreme drought events.

The impacts of drought on tree growth are understood to be more detrimental in environments with limited water availability (Fritts, 2001; Ciais et al., 2005; Bréda et al., 2006). Thus, the effects of reduced stand density on growth performance are expected to be more positive on sites with scarcer water supply (Sohn et al., 2016b). Consistent with this framework, the results of this dissertation show that, in cases where site water availability significantly influenced the density effect, benefits of reduced stand density decreased with increasing site water availability (Tab. 16, Fig. 15). Based on a meta-regression of a series of mostly regionally focused studies, including investigations of Scots pine, sessile oak and ponderosa pine, Sohn et al. (2016b) reported that growth resistance increased with site aridity in heavily thinned and unthinned stands, whereas site aridity had no or even a negative effect in moderately thinned stands. The lack of uniform results in this study was attributed by the authors to an imbalanced distribution of studies across taxonomic groups, thinning intensities and climatic regions, which is not comparable with the investigation carried out in the framework of this dissertation. More pronounced effects might certainly be possible for the analysed tree species when considering the full range of potential growing conditions. In the current study no indication was found that tree size had any effect on the studied species-specific short-term drought responses. This result is likely associated with the fact that only information on codominant and dominant trees was available, which did not provide a broad range of tree sizes. Stand age was found to significantly increase the resistance of Scots pine and reduce the recovery of oak (Tab. 16). Similar to these findings, Sohn et al. (2016a) reported a generally positive effect of stand age on the resistance of Scots pine. While it was not able to confirm a significant influence of stand age on the density effect in the current study, Sohn et al. (2016a) reported that thinning helped to prevent an age-related decline in growth resistance and recovery following drought. Differences in the methodological approach relating to the selection of drought events and the quantification of stand density may explain the contrasting results.

5. Conclusion

According to the findings of this dissertation, the mixing of Scots pine and oak can significantly stabilise and enhance stand productivity (*Article I*). Overyielding was found across varying levels of annual water supply, indicating a lower overall climate sensitivity compared with monocultures, although overyielding increased with annual site water supply. These findings indicate a high level of complementarity of both species under most growing conditions and suggest a high suitability of this mixture for increasing diversity and ensuring a stable provisioning of biomass within the framework of adaptive forest management. Furthermore, the results provide support for species mixing as a valuable silvicultural option for reducing tree drought susceptibility (*Article II*). This is of considerable practical relevance as mixing may help to reduce drought-induced mortality, increase the vigour and reduce the predisposition of trees to biotic and abiotic agents (Allen et al., 2010; Chmura et al., 2011). Over time, this can ultimately result in average overyielding at the stand level, such as reported in *Article I*. The findings also highlight the facilitative effect of oak on admixed species, promoting its use as a stabilising component in mixed-forest management. The current study corroborates previous regional evidence that highlights a good complementarity of Scots pine and oak but goes even further by confirming the validity of positive mixing effects on drought responses over a comprehensive range of growing conditions across Europe. In addition, the findings provide evidence that the maintenance of reduced stand densities can significantly increase mean tree growth, while at the same time reducing tree drought susceptibility of Scots pine and oak (*Article III*). However, the results also highlight the need for consideration of local climatic conditions when deciding on the suitability of stand density reductions as an adaptation measure; positive effects of reduced stand density were much stronger on sites with higher aridity, while the effect was reduced or even lost on sites with higher water availability. This finding is new, and the results appear promising under current climate scenarios. However, it also prompts further questions as to what effects can be expected under more extreme climatic conditions. The investigation of tree drought responses in ponderosa pine on xeric sites confirms that, in contrast to Central Europe, where extreme drought events still occur less frequently and average water availability still seems sufficient, the observed relation of stand density and drought susceptibility may be reversed under more adverse growing conditions.

Despite already being considered important for the European forest sector, mixtures of Scots pine and oak hold a considerable development potential. So far only roughly 4 % of the potential common distribution of both species is actually managed as mixtures (Pretzsch et al., 2019b). Owing to the economic importance and the beneficial ecology, which allows for a higher drought tolerance compared with other commercial European tree species, Scots pine-oak mixtures are likely to become even more important in the near future. Beyond the range of European beech, oak can currently be seen as the best option for the establishment of economically and ecologically viable mixtures of Scots pine with broadleaves (Pretzsch et al., 2019b). Similar height development and light ecology allow for a balanced competition of Scots pine and oak, which becomes apparent from the sampled stands, where both species were present in the canopy even at higher stand ages. *This indicates that both species are suitable for management in mixture without intensive silvicultural intervention.* This is a real advantage compared with other compositions, such as the combination of Scots pine and European beech, where the more shade tolerant European beech will naturally outcompete the more light-demanding Scots pine. *Intimate single-tree mixing seems to be the most favourable option to ensure the positive mixing effects observed in the current investigation.* However, oak was found to exhibit significantly lower height-diameter ratios and larger crowns in mixtures, factors that are typically associated with lower timber qualities (Rais, 2015; Pretzsch and Rais, 2016). This is consistent with previous studies that have reported decreased timber quality of oak in mixtures with Scots pine as a result of crown enlargement and increased branching (Bäucker et al., 2007; Bäucker and Bues, 2009; Schröder, 2009). Increased productivity, resilience and diversity in single tree mixtures of Scots pine and oak may therefore come at the expense of timber quality of oak. This is important to notice, as in many European regions oak is still predominantly managed for the production of high-value timber for construction and furniture manufacture (Praciak et al., 2013). The focus on higher value ensures the profitability of oak production, which is generally hampered by high turnover times and investment costs for stand establishment and forest-sanitary monitoring and control. The resulting conflict of objectives may be more or less pronounced, depending on the strategic objectives of the forest owner. The management of Scots pine-oak mixtures also has to address considerable differences in rotation period, which typically ranges from 80 to 130 years for Scots pine (Egnell, 2000) and from 150 to 200 years for oak (Pretzsch et al., 2019b). *The difference in rotation period provides the option to avoid clear-cuts during final harvest by use of a temporally separated tree removal in the form of shelterwood cuttings.* One example of this has been reported by Ebeling and Hanstein (1989) for Scots pine-oak stands in northern Germany. The authors were able to show that the natural regeneration of both Scots pine and oak was able to establish under canopy and could be further promoted by the increased light availability following careful and extended removal of mature Scots pine and suppressed oaks. High-quality oaks were kept in the canopy and transferred into the next generation to be felled at a later stage. The findings of this dissertation also demonstrate that the maintenance of reduced stand densities is a suitable approach to improve tree growth and drought responses in Scots pine and oak. *Density reductions by thinning in existing stands should therefore be considered as elements of active adaptation in forest management under climate change. The results indicate that higher density reductions may be particularly beneficial.* The kind of intervention intensity required to achieve the stand densities studied may be considered extreme and certainly more intensive than the comparatively moderate thinning intensities found in most existing management guidelines. High costs associated with harvesting of small stems in young stands and a potentially detrimental effect of heavy thinning on stand level yield can be seen as the main reason for a less intensive approach to thinning (Sohn et al., 2016a; Pretzsch, 2020). Trade-offs between improved tree drought responses and possibly reduced revenues have to be considered by the forest manager.

6. Methodological considerations and research perspectives

Triplet sampling design and quantification of mixing effects

The triplet sampling design (Pretzsch et al., 2014c) used in this dissertation for answering *QI* and *QII* (*Article I* and *Article II*), provides an alternative to long-term experiments that are not yet available for the systematic research into the effects of species mixing on a broader scale (Heym et al., 2018; Ruiz-Peinado et al., 2018). When based on the direct comparison of mixed and monospecific stands at the same site with the same treatment history, triplets allow the analysis of mixing effects under *ceteris paribus* conditions. This is for example not necessarily the case for studies that rely on inventory data, which may require modelling techniques to account for site variability (del Río and Sterba, 2009). Despite the usefulness of such temporal research plots, long-term experiments have to be considered the indisputable "gold standard" for studying long-term growth dynamics in forest stands under controlled conditions. However, only very few such experiments are available for the scrutiny of mixing effects (e.g. Forrester et al., 2004; Amoroso and Turnblom, 2006), none of which cover native European tree species. Due to the considerable scientific interest in mixed forests and the widespread establishment and management of such stands in forest practice under the premise of multifunctional forestry, there is an obvious need for long-term experiments that encompass mixed stands. One example of such an experiment is the trial concept 2100 (W046) in Bavaria (FISA, 2020), which has recently been established under the scientific chairmanship of the Chair of Forest Growth and Yield Sciences at the Technical University of Munich.

It has been shown, that mixing effects can be strongly influenced by the way in which the mixing proportion is calculated (Dirnberger and Sterba, 2014; Huber et al., 2014). Some studies have determined mixing proportion based on tree number (Forrester et al., 2004; Amoroso and Turnblom, 2006), basal area (Puettmann et al., 1992; Condés et al., 2013), volume weighted by dry mass (Pretzsch et al., 2010; Pretzsch et al., 2013a), biomass and leaf area (Dirnberger and Sterba, 2014) or SDI (Lu et al., 2018). In this dissertation, the species proportion was calculated based on the weighted SDI, following the recommendations by Dirnberger and Sterba (2014) and Sterba et al. (2014) who defined species proportion by area, where the reference is the area each species would occupy in a fully stocked monoculture. As the maximum stand density levels at a given site are unknown, the selected untreated or only slightly treated monocultures were used as reference. The selection of these reference stands is of major importance for the validity of the concept and was conducted with great care. Studied monospecific stands exhibited SDI values that are at or above the range of maximum stand densities commonly reported for Scots pine (600–750 trees ha^{-1}) and oak (500–600 trees ha^{-1}) (Pretzsch, 2009, p. 272).

As pointed out above, so far mixing effects have mainly been studied in fully stocked stands and in single-tree mixtures. Such studies have yielded considerable knowledge on causes and effects of species mixing and contributed significantly to the scientific discourse. However, it has been shown that mixing effects may often be explained by density effects (Pretzsch, 2017b) and that tree interactions at the local neighbourhood scale may play a fundamental role in regulating biodiversity–productivity relationships (Fichtner et al., 2018). How tree species mixing affects the growth and structure of stands as well as drought stress reactions of trees in cultivated and continuously managed stands that do not exhibit maximum stand density and may show different types of mixing patterns (e.g. tree groups or patches) is therefore an important question that has so far not been answered adequately. As a natural progression of the current state of knowledge, including the findings of this dissertation which highlight the suitability of reduced stand densities for improved tree drought responses, future studies should aim at scrutinising the interaction of species mixing and stand density. An important step to do so has been made with the establishment of the comprehensive network of triplets used in this dissertation. The replication of triplets (see 2.1.1.) on many of the sites and a subsequent thinning campaign undertaken in autumn of 2019 allows the site-specific comparison of fully stocked and heavily thinned stands. Furthermore, recent developments such as the establishment of the before mentioned trial concept 2100 (W046) is set to allow the future analysis of growth dynamics in stands exhibiting varying species proportions and stand densities. Finally, alternative approaches of combining different tree species in the same management unit is an area worthy of further examination and discussion. For example, concepts that abandon single admixture systems in favour of spatially separated (Schröder, 2009) or spatially and temporally separated (Bilke, 2004) monospecific groups or patches, appear promising for ensuring good timber quality in oak, but still require a broader scientific basis to allow statements regarding other ecosystem services such as biomass production. Furthermore, modelling results have shown that single-tree mixtures may economically outperform block mixtures (i.e., trees planted in large blocks) under a range of climate scenarios (Paul et al., 2019).

Quantification of tree growth responses

To answer *QII* and *QIII* (*Article I* and *Article II*), short-term tree growth responses to drought were assessed using drought response indices as proposed by Lloret et al. (2011). These metrics have become highly popular in dendro-ecological analyses due to their simple yet highly informative quantification of tree responses to disturbance (Schwarz et al., 2020). The Lloret concept relates to the concept of ‘engineering resilience’ with a focus on episodic impacts of disturbance and the subsequent recovery of an ecosystem, as opposed to ‘ecological resilience’, which relates to resilience as the ability of an ecosystem to withstand a shift to an alternative state under disturbance, and ‘social-ecological’ resilience, referring to the capacity to adapt or transform in the face of change in social-ecological systems (Holling, 1996; Folke et al., 2016). In a recent review on the use of resilience concepts in forest sciences, Nikinmaa et al. (2020) point out that all three concepts should be considered as complementary rather than contradictory. Interestingly, a clear majority of studies included in this review, in line with the approach used in this dissertation, applied the concept of engineering resilience, quantifying resilience as the recovery after a disturbance. Nikinmaa et al. (2020) provide guidance on which of the three resilience concepts is applicable depending on the system studied, the stressor or disturbance impacting the system and the temporal scale considered. According to the authors' suggestions, engineering resilience appears most suitable in accessing short-term resilience in tree growth to specific drought events, such as intended by the use of Lloret drought response indices. However, the concept of engineering resilience can only be applied in cases where a pre-disturbance state can actually still be achieved. In this dissertation, great care was taken to ensure that pre- and post-drought years used in the analysis did not encompass drought or any other influence that may have reduced growth, therefore ensuring the validity of the approach. However, it is likely that future studies may encounter prolonged or multiyear drought events that may hamper the quantification of drought resilience, as prevailing drought in the pre- and post-drought periods may leave trees more vulnerable to drought in following years (Anderegg et al., 2013). Correspondingly, Bose et al. (2020) reported a lower resistance of Scots pines which experienced more frequent droughts over the long-term. The authors concluded that the physiological resilience to extreme droughts might be constrained by growth prior to drought and that more frequent and longer drought periods may overstrain the potential for acclimation. Ecological resilience may be a more convincing concept if alternative states of a system are known or changes in disturbance frequency are evident (Nikinmaa et al., 2020).

Shortcomings of the Lloret concept, such as possible biases that can arise if fixed reference periods are used, can be addressed using alternative approaches to assess growth responses to drought. This for example includes drought indices by Thurm et al. (2016) that account for the time needed to reach pre-drought levels ('growth recovery time') and the cumulative growth reduction during this time ('increment loss due to drought'). In addition, Schwarz et al. (2020) recently proposed the indices 'average growth reduction' and 'average recovery rate' that allow the quantification of average annual drought impacts and an estimation of how much of the growth reduction could be recovered within one year. Furthermore, Schwarz et al. (2020) proposed a new framework for the interpretation of tree ring-based resilience indices that compares the relationship of observed values of resistance and recovery to a hypothetical function, which represents full resilience at any given value of resistance. These alternative approaches may allow for an improved understanding of tree drought responses under climate change and could therefore be considered in future studies.

There is currently no standardised procedure to identify drought events in tree-ring chronologies. This can be considered as one of the greatest limitations to comparing results of studies that are based on the Lloret concept (Schwarz et al., 2020). Drought years have previously been either identified from climatic records (e.g. Merlin et al., 2015; Thurm et al., 2016), by significant reductions in tree ring width (e.g. Marqués et al., 2016; Rubio-Cuadrado et al., 2018) or a combination of both (e.g. Riofrío, 2018). Drawbacks exist for either approach. By relying on climatic variables alone for identifying drought events, there is a risk that climate and water availability at a particular site might have differed from a regional drought signal gathered from the comparatively coarse meteorological provided by nearby weather stations or interpolated grid data (Zang et al., 2019). On the other hand, when the response variable that is used for subsequent analysis is already used for the identification of drought years, this could have an effect on the analysis (Schwarz et al., 2020). In addition, radial growth may be reduced through other causes, such as mass seed production. In *Article II* a combination of growth reductions (i.e., negative pointer years) and climatic records was used, relying on the metric $SPEI$. As the $SPEI$ was used for selecting drought events, it was ensured that only growth responses associated with drought conditions were considered and not with any other confounding factors such as masting, frost events, insect and disease outbreaks or forest pasture. By considering negative pointer years in the identification process, it was ensured that the effect of the observed meteorological anomaly on the system level was reflected by actual drought stress suffered by the individuals studied. By identifying drought events based on the reaction of at least one of the two species, the selection process also accounted for differences in species-specific drought coping mechanisms. This is important, as lagged or delayed drought responses are possible in *Quercus sp*. (Meinardus and Bräuning, 2011). Furthermore, the approach for selecting drought events used in this dissertation captures a wide variation in drought seasonality and intensity, which is crucial for comparative drought tolerance analyses between species (Schwarz et al., 2020).

It has to be noted, that tree growth is only one of several possible measures of drought response. The consideration of additional wood characteristics, such as for example the relation of early- to latewood, the number and size of vessels as well as ring density may also improve the informative value of future studies (Merlin et al., 2015). To improve estimates of tree-level responses to drought, future studies should also consider growth data from different stem heights. This may be important, as growth responses to drought have been shown to vary along the tree trunk, which may lead to biased estimates of the whole-tree response (Schwarz et al., 2020). Furthermore, without the consideration of mortality and reproduction, the tree-level investigation of drought responses is not necessarily indicative of stand or ecosystem-level resilience (DeSoto et al., 2020; van Mantgem et al., 2020). All trees sampled to answer *QII* and *QIII* by default survived the drought events studied. Studies aiming at population-level growth responses to drought, will have to consider dead trees and trees from all size and vitality classes.

Based on the findings of *Article III*, future studies should address the need for further research into the interactions between stand density and microclimate, which might help to better understand the causes for negative effects of stand density reductions on drought responses, particularly with respect to ponderosa pine. Furthermore, facilitative effects among conspecific neighbours with overlapping ecological niches may, in part, explain the drought response patterns that were observed in ponderosa pine. This constitutes a rather novel view on individual tree interactions under drought with potentially considerable implications for techniques currently employed by forest managers and silviculturists, therefore warranting further examination.

In the framework of this dissertation, possible sub-species variation due to local evolutionary adaptation induced by drought related selection (Hampe and Petit, 2005) were not addressed. This aspect should be considered when interpreting the results and might also be analysed in future studies, in particular when considering larger ecological gradients encompassing extreme growing conditions.

Quantification of drought intensity and meteorological water supply/availability

In this dissertation detailed information on soil moisture was not consistently available for all sites studied. Therefore, meteorological data was used to derive a drought index ($SPEI$) and information on site water supply/availability (DMI, I_A). However, such an approach neglects the crucial importance of local soil characteristics such as the capacity to hold plant available soil water. In future studies, information on water stress estimated from the climatic water deficit should therefore preferably be complemented by data on soil moisture wherever possible (Zang et al., 2019).

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Appendix

A List of publications

A.1. Lead-authorship

1. Steckel, M., del Río, M., Heym, M., Aldea, J., Bielak, K., Brazaitis, G. Černý, J., Coll, L., Collet, C., Ehbrecht, M., Jansons, A., Nothdurft, A., Pach, M., Pardos, M., Ponette, Q., Reventlow, D.O.J., Sitko, R., Svoboda, M., Vallet, P., Wolff, B., Pretzsch, H. 2020. Species mixing reduces drought susceptibility of Scots pine (*Pinus sylvestris* L.) and oak (*Quercus robur* L., *Quercus petraea* (Matt.) Liebl.) – Site water supply and fertility modify the mixing effect. Forest Ecology and Management 461, 117908. https://doi.org/10.1016/j.foreco.2020.117908.
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A.3. Conference contributions

A.3.1. Presentations

1. Pretzsch, H., Steckel, M., 2019. Silver fir in pure and mixed-species stands – growth trends, mixing effects and silvicultural potential. IUFRO 1.01.09 Ecology and Silviculture of Fir conference, Prospects for fir management in a changeable environment, Krakow, 28.-30. May 2019.
2. Steckel, M., 2018. Kiefer und Eiche in Mischung und Reinbestand. Erste Befunde zur Untersuchung von Struktur und Produktivität. Forstwissenschaftliche Tagung, Göttingen, 24.-26. September 2018.

A.3.2. Scientific posters

1. Steckel, M., 2018. Kiefer und Eiche in Mischung und Reinbestand. Zuwachs unter Trockenstress entlang eines ökologischen Gradienten. Forstwissenschaftliche Tagung, Göttingen, 24.-26. September 2018

B. Original research articles (*Article I – III*)

B.1. Article I

Title: Transgressive overyielding in mixed compared with monospecific Scots pine (*Pinus sylvestris* L.) and oak (*Quercus robur* L., *Quercus petraea* (Matt.) Liebl.) stands – Productivity gains increase with annual water supply

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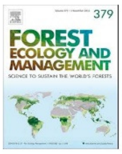

Transgressive overyielding in mixed compared with monospecific Scots pine (*Pinus sylvestris* L.) and oak (*Quercus robur* L., *Quercus petraea* (Matt.) Liebl.) stands – Productivity gains increase with annual water supply

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ABSTRACT

Tree species mixing has become a crucial tool in European forest management as positive interactions between species have been found to promote the provision of multiple ecosystem services, while at the same time reducing the risks associated with climate change. However, mixing effects have proven to be strongly context-dependant and some species combinations have still not been studied in detail. Here we focus on mixed forests of Scots pine and oak, which are likely to become increasingly popular for balancing wood production and other ecosystem services under climate change. Using 20-year growth data from newly established triplets in Germany and Denmark, this study investigates how mean tree and stand characteristics as well as productivity in mixed Scots pine-oak stands compare with adjacent monocultures and how stable the observed productivity relation is, considering inter-annual variations in local climate. Species mixing on average resulted in 15% higher standing volume and 14% higher volume productivity compared with the weighted mean of the adjacent monocultures. Oak profited most in mixture, showing overyielding of 19%. Overyielding on the stand and species level increased in years with higher water supply. In mixture, standing volume of Scots pine was 25% higher than in monocultures. Both species were found to modify their morphology in mixture. Oak in mixture showed a significantly higher inequality in stem volume compared with monocultures. We hypothesise that the observed overyielding of Scots pine-oak mixtures mainly results from complementary light use, where differences in shade tolerance, crown architecture and leaf phenology may be contributing factors.

1. Introduction

Forest management in Central and Northern Europe has traditionally favoured monocultures dominated by one single tree species over mixed forests with several tree species. Fast- and straight-growing conifers such as Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* (L.) H. Karst.) have been promoted, often far beyond their natural distribution. Over time, these stands have proven to be particularly susceptible to abiotic and biotic disturbances (Spiecker, 2003; Goris et al., 2007; Knoke et al., 2008; Spathelf and Ammer, 2015). Re-evaluating traditional forest practice and risk-management has more recently resulted in a noticeable shift towards close-to-nature forestry, a concept encompassing management strategies that promote continuous forest cover, the use of native and well adapted tree species and natural processes in forests (Schütz, 1999; Gamborg and Larsen, 2003; Brang et al., 2014). In this context, species mixing has gained attention as a crucial forest management tool for adaptation and risk-reduction (Knoke et al., 2008; Reif et al., 2010). As a result, the conversion of coniferous monocultures into mixed species stands with broadleaved species has been widely promoted by forest management and policy alike (Klimo et al., 2000; Zerbe, 2002; Kint et al., 2006; Knoke et al., 2008). Often, the conversion of coniferous monocultures has been initiated by the introduction of European beech (*Fagus sylvatica* L.) or oak (*Quercus* sp.) (Pretzsch et al., 2015). This change in management strategy has been supported by a series of studies, focusing on the effects of species mixing on forest productivity and other ecosystem functions. These studies show that forest mixtures can be more resilient and resistant to abiotic disturbances (Loreau et al., 2001; Pretzsch et al.,

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2013b; Thurm et al., 2016), can show a higher structural diversity (Pretzsch et al., 2016), may better promote diversity of other taxa (Dieler et al., 2017; but see Heinrichs et al., 2019) and can be better for the provisioning of multiple ecosystems goods and services (Nadrowski et al., 2010; Gamfeldt et al., 2013; Schuler et al., 2017) compared with monocultures. Furthermore, the productivity of Central European forest mixtures is found to regularly exceed the weighted mean productivity of neighbouring monospecific stands (overyielding) by up to 10–30% (Pretzsch and Zenner, 2017). On a broader scale, a series of global studies have confirmed a generally positive biodiversity-productivity relationship in forests (Zhang et al., 2012; Liang et al., 2016; Jactel et al., 2018), which has also been reported for other plant communities (Marquard et al., 2009). Despite an increasing interest in the topic, the underlying processes that cause mixing effects are still not well understood. Mixing effects with regards to productivity have been found to depend on multiple factors such as species composition (Lu et al., 2016; Mina et al., 2017), functional traits of the species under scrutiny (Zhang et al., 2012; Lu et al., 2016), site conditions (Forrester et al., 2013; Forrester and Albrecht, 2014), stand development stage (Cavard et al., 2011) and stand density (Condés et al., 2013; Potter and Woodall, 2014).

An increasing number of studies focusing on the productivity of mixed versus monospecific forests have analysed species interactions on sites along spatial environmental gradients, reporting stronger (Pretzsch et al., 2010; Paquette and Messier 2011; Pretzsch et al., 2013a; Toïgo et al., 2015; Jucker et al., 2016; Lu et al., 2018) and weaker (Forrester et al., 2013; Forrester and Albrecht 2014) overyielding under heightened environmental stress. Far less research has so far been devoted to examining growth performance of mixed versus monospecific stands along temporal environmental gradients within sites, considering short-term fluctuations in abiotic growing conditions. This may however be crucial, as the scrutiny of mixing effects based on a single point in time may not be sufficient to capture the actual mixing effects, as species interactions may be highly variable and can change over time (Forrester, 2014). Furthermore, species interactions that influence mixed versus monospecific stand performance in the long term (i.e. along spatial environmental gradients) can also be assumed to be relevant when considering short-term growth performance e.g. in single years. In this context, some studies have examined the temporal variability of species interactions in single years in relation to abiotic stress factors such as drought, reporting both stronger (del Río et al., 2014) and weaker (Jucker et al., 2014b) overyielding in stressful years as well as reduced climate sensitivity (Lebourgeois et al., 2013; Pretzsch et al., 2013b; Jucker et al., 2014a; Metz et al., 2016; Thurm et al., 2016). Jucker et al. (2016) studied a time series of 15 years and did not find any consistent effect of inter-annual fluctuations in climate on the strength of the diversity-productivity relationship. Due to the inconclusive nature of these results, further research into the effect of inter-annual variations in climate conditions seems crucial for understanding the underlying causes and effects of diversity-productivity relationships and may provide a basis for the evaluation of forest vulnerability under climate change.

In this study we focus on the combination of Scots pine and oak, the latter consisting of pedunculate oak (*Quercus robur* L.) and sessile oak (*Quercus petraea* (Matt.) Liebl.). Both Scots pine and oak are some of the most economically important tree species in Europe and highly valued for a variety of applications (Praciak et al., 2013). As climate change is expected to promote increased stress due to rising summer temperatures and precipitation shifts towards the winter months (IPCC, 2014), mixed Scots pine and oak forests are likely to gain further importance due to their high drought tolerance compared with other economically important native tree species such as Norway spruce and European beech (Spellmann et al., 2011; Albert et al., 2015). Scots pine is protected against water loss by imbedded stomata and a pronounced waxy layer on the epidermis (Krakau et al., 2013). Oak is able to withstand drought due to its deep-reaching taproots that increase the accessibility of water (Praciak et al., 2013). Both Scots pine and oak are considered light demanding species, although oak is more shade tolerant than Scots pine (Niinemets and Valladares, 2006).

Despite the high practical relevance of Scots pine-oak mixtures and their potential role under climate change, only a limited number of studies have been devoted to analysing the productivity of this species combination in comparison to corresponding monocultures. Empirical evidence from England (Brown, 1992) and the Netherlands (Lu et al., 2016, 2018) suggests that mixed Scots pine-oak stands can overyield under certain site conditions. However, a French study by Toïgo et al. (2015) did not find any significant mixing effects with regard to stand productivity.

The aim of this study is to contribute to the growing body of knowledge on mixed-species forest growth and management, by analysing mixing effects in mixed Scots pine and oak stands. Based on seven triplets and a reconstructed 20-year time series, we investigated how mean tree and stand characteristics as well as productivity in mixed-species stands compare with adjacent monocultures. To explain the observed mixing effects, we analysed on the tree, species and stand level and examined the productivity relation between mixed and monospecific stands along a temporal gradient in local climate.

In this study we tried to answer the following research question: How does the growth and yield of mixed Scots pine-oak stands differ from adjacent corresponding monocultures and how is any over- or underyielding affected by inter-annual changes in environmental conditions?

Based on the research question, we developed the following hypotheses:

HI: *Mean tree and stand characteristics do not differ between mixed and neighbouring monospecific stands.*

HII: *Productivity in mixed stands is equivalent to the weighted mean productivity in neighbouring monospecific stands.*

HIII: *Size and growth partitioning among trees within the stand is independent of species mixing.*

HIV: *The productivity relation of mixed* versus *monospecific stands does not change with inter-annual fluctuations in local climate.*

2. Material and methods

2.1. Material

2.1.1. Study sites and sampling design

This study is based on seven Scots pine-oak triplets in Germany and Denmark, established at the end of the growing season in 2017. Each triplet entails three rectangular plots, one plot representing a mixed Scots pine-oak stand and two plots representing monospecific stands of each species respectively.

Despite differences in ecology on marginal sites, pedunculate oak being more adapted to moist or wet sites and more susceptible to drought stress than sessile oak (Annighöfer et al., 2015), both oak species grow together across most of Europe (Jones, 1959; Annighöfer et al., 2015) and are known to hybridise (Kremer et al., 2002; Jensen et al., 2009). As it is difficult to distinguish the ecological traits of crossbred individuals based on observations alone, we decided to pool the data for both oak species.

The triplets examined in this study are located in southern Germany (Baunach, Oesdorf, Triesdorf) in north-eastern Germany (Neuendorf) and in eastern Denmark (Tisvilde) (Fig. 1). All sites lie within the natural distribution area of Scots pine and oak. In the case of Baunach and Triesdorf, triplets were replicated to allow for a subsequent examination of thinning responses, which are the subject of a separate study. In total, seven triplets were sampled, containing 21 plots.

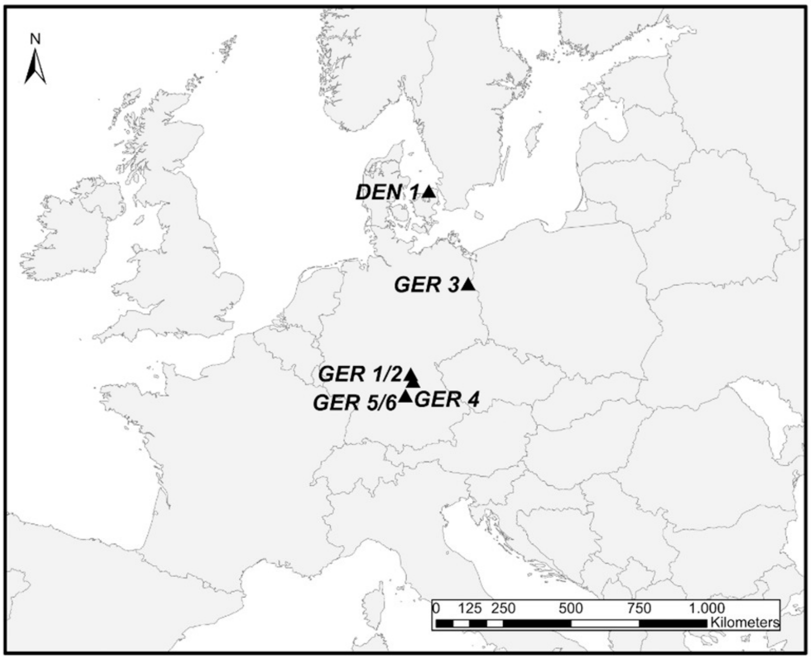

Fig. 1. Location of the seven Scots pine-oak triplets Tisvilde (DEN 1), Baunach (GER 1/2), Neuendorf (GER 3), Oesdorf (GER 4) and Triesdorf (GER 5/6).

Geographical information and site characteristics are presented in Table 1. The stands observed are located at an altitude of between 30 and 470 m a.s.l. (average = 293 m a.s.l.). The mean annual temperature ranges from 8.8 to 9.7 °C (average = 9.2 °C), with an annual precipitation of between 564 and 734 mm (average = 698 mm). This study includes a range of climatic conditions from drier and warmer (Neuendorf) to moister and colder sites (Triesdorf). Stands under scrutiny grow on base-poor Arenosols (Tisvilde), on Cambisols with a moderate base status (Baunach, Neuendorf, Oesdorf) as well as on base-rich Stagnosols (Triesdorf). Site productivity is reflected in the site index, here defined as the quadratic mean tree height at age 100, which ranges from 19.3 to 31.3 m (mean = 25.9 m) in the monocultures observed.

Plots within each triplet were selected to ensure maximum similarity in site conditions and stand age, minimising residual effects such as soil, microclimate, tree genetic and management effects. Individual plot sizes range from 0.04 to 0.35 ha (mean = 0.12 ha) and stand age from 40 to 115 years (mean = 78 years). Most triplets consist of plots located in close proximity to each other, mainly within the same management compartment. The similarity of soil conditions within each triplet was confirmed by comparing soil maps. In cases where plots were not inside the same compartment, the similarity of soil conditions was verified using a soil sample boring rod.

To establish the triplets, we focused on finding even-aged, monolayered stands that are fully stocked and approximately represent maximum density. The plots represent sections of anthropogenically

Table 1
Geographical information and site characteristics of the seven Scots pine-oak triplets.

Location	Code	Coordinates		Site characteristics				SI	
		N lat.	E lon.	A	T	P	Soil	Pi_{mono}	Oa_{mono}
Tisvilde	DEN 1	56° 02′ 18″	12° 04′ 57″	40	8.9	681	Arenosol	25.8	28.2
Baunach	GER 1	49° 56′ 52″	10° 50′ 38″	360	9.4	728	Cambisol	19.8	20.9
Baunach	GER 2	49° 56′ 53″	10° 50′ 37″	360	9.4	728	Cambisol	19.9	19.3
Neuendorf	GER 3	52° 53′ 38″	14° 03′ 49″	30	9.7	564	Cambisol	29.3	31.3
Oesdorf	GER 4	49° 42′ 07″	10° 56′ 19″	320	9.6	715	Cambisol	24.4	23.4
Triesdorf	GER 5	49° 13′ 42″	10° 33′ 32″	470	8.8	734	Stagnosol	30.8	28.6
Triesdorf	GER 6	49° 13′ 41″	10° 33′ 32″	470	8.8	734	Stagnosol	30.5	30.3

A: altitude (m a.s.l.).*T*: mean annual temperature (°C). *P*: annual precipitation (mm). *Soil*: soil type based on the nomenclature of FAO (IUSS Working Group WRB, 2015). *SI*: site index (m) for Scots pine (Pi_{mono}) and oak (Oa_{mono}) monocultures, referring to quadratic mean height at age 100. Climate data is shown as the quadratic mean of the reference period 1998–2017 (Scharling, 2012; Danmarks Meteorologiske Institut (DMI), 2018; Deutscher Wetterdienst (DWD), 2018a, 2018b). Information on soil properties is based on Adhikari et al. (2014) and Bayerische Landesanstalt für Wald und Forstwirtschaft LWF (2018) and complemented by control samples taken in the field.

regenerated stands (planted or naturally regenerated) with the management goal of promoting Scots pine and oak. Therefore, the proportion of additional tree species was low in mixed and monospecific plots (on average < 5% of total basal area) and if present, mainly constituted suppressed trees. When defining the boundaries of each plot we tried to include a buffer zone of at least one tree length, to exclude edge effects or mixing effects with other tree species. In all cases, neighbouring trees continued the species composition of the plot.

Mixed plots were selected based on the criteria single-tree mixture and equal mixing proportion. Building on the considerations of Dirnberger and Sterba (2014) and Sterba et al. (2014), the mixing proportion (m) was calculated based on the stand density index (SDI) by Reineke (1933). Differences in stand density between the species are adjusted by an equivalence coefficient e_1 computed for each triplet and year by the ratio between the SDI of species 1 in monoculture (SDI_1) and species 2 in monoculture (SDI_2). The ratio $e_1 = SDI_1/SDI_2$ reflects the growing space requirement of species 1 in relation to species 2. Using Scots pine as an example, the mixing proportion is calculated as:

$$m_{pi,(oa)} = \frac{SDI_{pi,(oa)}}{SDI_{pi,(oa)} + SDI_{(pi),oa} \times e_{pi}} \tag{1}$$

The proportions of Scots pine and oak in the mixture are abbreviated with $_{\mathrm{pi,(oa)}}$ and $_{\mathrm{(pi),oa}}$ respectively. On average over all triplets and years, the equivalence factor e_{pi} was 1.12. The mixing proportions of Scots pine ranged from 48 to 70% (mean = 58%) and those of oak from 30 to 52% (mean = 42%) correspondingly.

2.1.2. *Data collection and preparation*

For all living and dead trees on a given plot, diameter at breast height (dbh) was measured using a girth tape. All trees with a $dbh \geq 7.0$ cm were included in the analysis and investigated further (living trees: 2187, dead trees: 179). Tree height (h) and crown base height (cbh), the latter being defined as the height of the crown's lowest primary branch at the stem, were measured for a sub-sample of living trees on each plot using a VERTEX IV hypsometer (Haglöf Sweden AB, Långsele, Sweden). Height measurements were carried out along the entire diameter distribution to ensure sufficient coverage of the actual stand height conditions for subsequent fitting of species-specific and strata-specific height growth curves. Crown radii were measured on all living trees in at least all of the four cardinal directions (N, E, S, W). The crown length (cl) was computed for every measured tree by subtracting crown base height from tree height ($cl = h - cbh$). The crown projection area for every measured tree (cpa) was computed as $cpa = \pi \times \bar{r}^2$, where $\bar{r}$ is the quadratic mean crown radius of the tree under scrutiny.

Increment cores were taken from at least 20 dominant trees per species and plot. Where available, 10 additional trees per plot were sampled, covering the rest of the diameter distribution. This ensured an adequate representation of each plot́s size distribution. Two increment cores reaching from bark to pith were taken from the north and east direction of each sampled tree, using a 5.15 mm diameter increment borer (Haglöf Sweden AB, Långsele, Sweden). Increment cores were stored in wooden boxes covered with glass lids and air dried for two weeks before being mounted on wooden carriers for subsequent sanding. Using a Type II digital positiometer after Johann (1977) (Biritz and Hatzl GmbH, Vienna, Austria), the annual radial growth increments were measured for every increment core with an accuracy of 0.01 mm. Tree chronologies were subsequently cross-dated and synchronised. Broken and otherwise unreadable cores were neglected. In total, 1722 increment cores were used for further analysis.

2.2. *Methods*

2.2.1. *Tree allometry*

Based on trees measured in 2017, we analysed how species mixing affects tree allometry of Scots pine and oak. We compared species-specific tree height and crown dimensions (cl, cpa) in mixed versus monospecific stands over all seven triplets sampled.

2.2.2. *Historical development – reconstruction of tree and stand productivity*

To compare mean tree and stand characteristics as well as productivity of mixed versus monospecific stands of Scots pine and oak, annual tree and stand growth was reconstructed for a period of 20 years (1998–2017) based on a modelling approach described in the following:

For each sampled tree, the quadratic mean year ring width was calculated for every year from both cores sampled. Precise stand age was determined based on the year ring count of increment cores reaching the pith.

Measured height-diameter pairs were used to parameterise common height curves (Korsun, 1935; Michailoff, 1943; Prodan, 1951; Petterson, 1955; Freese, 1964). These functions were then used to derive missing individual tree heights and to calculate the height of the tree with the quadratic mean diameter (hereinafter referred to as quadratic mean height) for each plot and species.

Retrospective annual diameters at breast height for cored trees were derived directly from increment cores. Plot-specific and species-specific regression analysis was carried out to derive annual diameter at breast height for non-cored trees and standing dead wood (Eq. (2)).

$$id_i = a \times d_{i\_end}^{b} \tag{2}$$

In Eq. (2) the cumulative diameter increment in mm for year i (id_i) is calculated as a function of the diameter at breast height at the end of the year i ($d_{i\_end}^{b}$). Parameters a and b are estimated by linear OLS regression after log-transformation. The equation assumes a typical allometric relationship between diameter and diameter growth, where a represents the scaling parameter and b the allometric exponent.

Plot- and species-specific height-age curves were selected from yield tables (e.g. Wiedemann (1943) and Jüttner (1955) for Scots pine and oak respectively) based on age and quadratic mean height provided by the survey. Individual tree heights were estimated annually based on a uniform height curve system first developed by Kennel (1972) for European beech and later parameterised for other tree species by Franz et al. (1973).

For a detailed description of the modelling approach please refer to Heym et al. (2018).

2.2.3. *Mean tree and stand characteristics*

Quadratic mean and dominant (100 largest trees per ha) tree dimensions (quadratic mean height: h_q (m), dominant height: h_{100} (m), quadratic mean diameter: d_q (cm), dominant diameter: d_{100} (cm), quadratic mean height-diameter ratio: h_q/d_q and dominant height-diameter ratio: h_{100}/d_{100}) as well as area related sum values (number of trees: N (trees ha^{-1}), stand density index: SDI (trees ha^{-1}), stand basal area: BA (m^2 ha^{-1}) and standing volume: V (m^3 ha^{-1})) were evaluated for each plot, target species (Scots pine, oak) and year, based on the DESER-Norm 1993 by Johann (1993), using evaluation software developed by the Chair of Forest Growth and Yield Science, TU Munich (Biber, 2013). Coniferous and deciduous admixture species were assigned to Scots pine and oak respectively.

2.2.4. *Productivity*

The individual tree basal area for year i (ba_i) was computed as $ba_i = \frac{\pi}{4} * d_i^2$, where d_i is the tree's diameter at breast height. Using the corresponding tree height (h_i) and species-specific form factor f_i by Franz (1971), individual tree volume (v_i) was derived from $v_i = ba_i \times h_i \times f_i$. Tree specific volume increment (iv_i) and basal area increment (iba_i) were derived for every year i from $iv_i = (v_i - v_{i-1})$ and $iba_i = (iba_i - iba_{i-1})$ respectively. Annual stand volume increment (IV, m^3 ha^{-1} year^{-1}) and annual stand basal area increment (IBA, m^2 ha^{-1} year^{-1}) were subsequently computed from the summation of single tree values and upscaling to one hectare. As a measure of stand productivity, we focused on IV as it is a more relevant area measurement for forest practice and reflects both tree basal area and height development, which both may be affected by species mixing.

2.2.5. *Comparing tree size and growth partitioning in mixed versus monospecific stands*

The Gini coefficient, originally developed by Gini (1912) for measuring the inequality of income distribution, can be used for quantifying size and growth partitioning between trees in forest stands (de Camino, 1976; Binkley et al., 2006; Pretzsch and Schütze, 2014; Pretzsch and Schütze, 2016). The Gini coefficient (GC_x) is computed as:

$$GC_x = \frac{\sum_{i-1}^{n} \sum_{j=1}^{n} |x_i - x_j|}{2n(n-1) \times \bar{x}} \tag{3}$$

Here the variables x_i and x_j represent the size or growth of the ith, respectively the jth tree in a stand with $i = 1 \ldots \text{n}$ trees. GC can take values between 0 and 1. In cases where $GC = 0.0$, all trees are equal in size or growth. The higher the GC, the stronger the inequality of tree size or growth between the trees. When applied to mixed and monospecific stands, the Gini coefficient can show whether species mixing modifies size and growth partitioning between trees in a population, e.g. if species mixing favours small understory trees compared with monocultures (Pretzsch and Schütze, 2016). We applied the Gini coefficient to stem volume (GCv) and stem volume growth ($GCiv$) of mixed and monospecific stands.

2.2.6. *Quantification of mixing effects*

Mixing effects at the stand and species level were analysed by comparison of mixed versus monospecific stands according to the approach outlined in Pretzsch et al. (2015).

The observed productivity in the mixed stand is $P_{pi,oa}$ and the absolute shares of Scots pine and oak are $pp_{pi,(oa)}$ and $pp_{(pi),oa}$ respectively ($P_{pi,oa} = pp_{pi,(oa)} + pp_{(pi),oa}$). The expected productivity $\widehat{P}_{pi,oa}$ is calculated from the weighted mean of the neighbouring pure stand as $\widehat{P}_{pi,oa} = P_{pi} \times m_{pi} + P_{oa} \times m_{oa}$, where P_{pi} and P_{oa} are the observed productivities in the monospecific Scots pine and oak stands respectively and m_{pi} and m_{oa} are the corresponding mixing proportions. The productivity of both species in the mixture $P_{pi,(oa)}$ and $P_{(pi),oa}$, upscaled to one hectare, are calculated as $P_{pi,(oa)} = pp_{pi,(oa)}/m_{pi}$ and $P_{(pi),oa} = pp_{(pi),oa}/m_{oa}$ respectively. At the stand level, a positive mixing effect (overyielding) is evident when the observed productivity in the mixture is higher than the expected productivity ($P_{pi,oa} > \widehat{P}_{pi,oa}$). Positive mixing effects on the species level are present, when $P_{pi,(oa)} > P_{pi}$ and $P_{(pi),oa} > P_{oa}$. Transgressive overyielding occurs when the observed productivity in the mixed-species stand exceeds the productivity of the respective monospecific stands ($P_{pi,oa} > \max(P_{pi}, P_{oa})$). Analogously, underyielding ($P_{pi,oa} < \widehat{P}_{pi,oa}$) and degressive underyielding ($P_{pi,oa} < min(P_{pi}, P_{oa})$) can occur. The same nomenclature and algorithm are used for all other stand variables (e.g. SDI, V). In the following, all the tree and stand variables analysed are therefore simply referred to as Y.

For every triplet and year, we computed the ratio $RY_{pi,oa} = Y_{pi,oa}/\widehat{Y}_{pi,oa}$ to quantify the mixing effect for each stand variable under scrutiny. Analogously to the stand level evaluation, the ratio was also computed on the species level for Scots pine and oak as $RY_{pi,(oa)} = Y_{pi,(oa)}/Y_{pi}$ and $RY_{(pi),oa} = Y_{(pi),oa}/Y_{oa}$ respectively.

To display the observed over- or underyielding, we used cross diagrams according to Harper (1977) and Kelty (1992), showing the relative volume productivity on the basis of the proportions of volume growth (RPP) on the species ($RPP_{pi,(oa)} = \frac{PP_{pi,(oa)}}{P_{pi}}$; $RPP_{(pi),oa} = \frac{PP_{(pi),oa}}{P_{oa}}$) and stand ($RPP_{pi,oa} = RPP_{pi,(oa)} + RPP_{(pi),oa}$) level (Pretzsch et al., 2013a).

2.2.7. *The influence of annual climate conditions on the mixing effect*

To analyse the influence of annual climate conditions on the mixing effect, we compared the relative volume productivity at the stand ($RP_{pi,oa} = P_{pi,oa}/\widehat{P}_{pi,oa}$) and species ($RP_{pi,(oa)} = \frac{P_{pi,(oa)}}{P_{pi}}$, $RP_{(pi),oa} = \frac{P_{(pi),oa}}{P_{oa}}$) level with the annual mean temperature (T) and annual precipitation (P) as well as their combination in form of the de Martonne aridity index (dMI) (de Martonne, 1926) (Eq. (4)).

$$dMI = P/(T + 10) \tag{4}$$

The de Martonne aridity index characterises the water supply of a given site and is valued due to its minimal data requirement and high explanatory strength (e.g. Bielak et al., 2014; Pretzsch et al., 2015). The higher the index, the better the water supply for plant growth. We tested the relationship between relative productivity and the presented meteorological variables using pooled data for all triplets and years.

Meteorological data (T, P) was obtained in the form of annual values covering the full time series (1998–2017) for each of the seven triplets (Scharling, 2012; Danmarks Meteorologiske Institut (DMI), 2018; Deutscher Wetterdienst (DWD), 2018a, 2018b).

2.2.8. *Statistical testing*

Because of nesting in the data (spatial, temporal), we used linear mixed-effects regression models (LME) to compare the performance of mixed and monospecific stands. To account for any possible spatial autocorrelation, all triplets were assigned to a triplet group, based on their relative location (i.e. triplets located in close proximity to each other were assigned the same triplet group). All calculations were carried out with R version 3.4.3 (R Core Team, 2017); the mixed effects models were fitted with methods available in the R-package nlme (Pinheiro et al., 2018); graphs were made with the R-package ggplot2 (Wickham, 2016).

To scrutinise the effect of species mixing on the tree allometry of Scots pine and oak, we considered species-specific allometric relationships between h and dbh, cl and h as well as cpa and dbh, based on tree measurements carried out in 2017. To test for significant differences between mixed species stands and monocultures, we fitted log-transformed expressions of the general allometry function $\log(Y) = b_0 + b_1 \times \log(X)$, considering random effects on the triplet group, triplet and plot level. The expression of the fitted model by species is outlined in Eq. (5):

$$\begin{aligned}\log(Y_{ijkl}) = a_0 + a_1 \times \log(X_{ijkl}) + a_2 \times MONO_{ijk} + a_3 \times \log(X_{ijkl}) \\ \times MONO_{ijk} + b_i + b_{ij} + b_{ijk} + \varepsilon_{ijkl}\end{aligned} \tag{5}$$

In Eq. (5) Y_{ijkl} is the response variable h, cl or cpa for tree l in plot k of the triplet j of the triplet group i and X_{ijkl} the corresponding explanatory variable dbh or h. $MONO_{ijk}$ is a dummy-coded variable indicating the species composition (monoculture = 1, mixture = 0). The parameters a_0, a_1, a_2 and a_3 are the fixed effect parameters. The interaction term of the explanatory variable and $MONO_{ijk}$ was only included in case it was significant. If either a_2 or a_3 are significantly different from 0, this indicates a significant mixture effect. The parameters b_i, b_{ij} and b_{ijk} are random effects at the triplet group (i), triplet (j) and plot (k) level ($b_i\ N(0, \tau_1^2)$, $b_{ij}\ N(0, \tau_2^2)$, $b_{ijk}\ N(0, \tau_3^2)$), while ε_{ijkl} are identically and independently distributed errors ($\varepsilon_{ijkl}\ N(0,\sigma^2)$).

Below, we present model equations used to test the hypotheses HI-HIV:

HI-HIII: Mean tree and stand characteristics do not differ between mixed and neighbouring monospecific stands. Productivity in mixed stands is equivalent to the weighted mean productivity in neighbouring monospecific stands. Size and growth partitioning among trees within the stand is independent of species mixing.

To test for significant differences between mixed and monospecific stands we used the ratios calculated according to the method given in subchapter 2.2.6 and subtracted the value of 1 ($RRY = RY - 1$). This modification provided us with direct information on the relative mixing effect. Using Eq. (6), we tested for significant differences between mixed stands and monocultures on the stand ($RRY_{pi,oa}$) and species level ($RRY_{pi,(oa)}$, $RRY_{(pi),oa}$).

$$RRY_{ijk} = a_0 + b_i + b_{ij} + \varepsilon_{ijk} \tag{6}$$

In Eq. (6) the parameter a_0 (intercept) is the fixed effect parameter; if a_0 is significantly different from 0, this indicates a significant mixture effect. The indices i, j and k represent the triplet group, the triplet and the observation year respectively. The parameters b_i and b_{ij} are random effects on triplet group and triplet level respectively (b_i $N(0, \tau_1^2)$ and b_{ij} $N(0, \tau_2^2)$). Finally, ε_{ijk} represents identically and independently distributed errors (ε_{ijk} $N(0,\sigma^2)$).

HIV: *The productivity relation of mixed* versus *monospecific stands does not change with inter-annual fluctuations in local climate.*

To analyse the relationship between the annual relative productivity and local climate conditions on a stand ($RP_{pi,oa}$) and species ($RP_{pi,(oa)}$, $RP_{(pi),oa}$) level, we used Eq. (7).

$$RP_{ijk} = a_0 + a_1 \times M_{ijk} + b_i + b_{ij} + \varepsilon_{ijk} \tag{7}$$

Here RP_{ijk} is the relative productivity and M_{ijk} the annual meteorological variable under investigation (T, P or dMI). Parameters a_0 and a_1 are the fixed effects and b_i and b_{ij} the random effects (b_i $N(0, \tau_1^2)$ and b_{ij} $N(0, \tau_2^2)$), while ε_{ijk} are identically and independently distributed errors (ε_{ijk} $N(0,\sigma^2)$). Indices are identical to Eq. (6). If a_1 is significantly different from zero we can assume a significant effect of the scrutinised meteorological variable on the relative productivity.

3. Results

Table 2 shows descriptive growth and yield characteristics for all seven triplets at the time of the survey in 2017, separately for monospecific stands, as well as the mixture in total and the absolute shares of both species in the mixture. On average, the *SDI* was 6% higher in monospecific Scots pine (829 trees ha^{-1}) than in monospecific oak stands (785 trees ha^{-1}) and 2% higher than in the mixed stands (816 trees ha^{-1}). With regard to quadratic mean height, monospecific oak (21.9 m) was only 3% ahead of monospecific Scots pine (21.3 m). In mixture, Scots pine was 13% taller (24.0 m) than in monoculture and overtopped adjacent oaks (20.7 m), which were slightly shorter than in monoculture. Standing volume was higher in mixed stands (437 m^3 ha^{-1}) compared with monocultures of Scots pine (375 m^3 ha^{-1}) and oak (403 m^3 ha^{-1}).

Fitted allometry functions (Eq. (5)) are reported in Fig. A1 and Table A1. Tree height was significantly higher for Scots pine growing in mixture compared with monocultures. For height growth of oak, the interaction parameter a_3 differed significantly; however, resulting curves for trees growing in mixed and monospecific stands did not differ in relevant orders of magnitude. Scots pine growing in mixture exhibited shorter crowns than in monospecific stands. Considering *cpa* of Scots pine, both parameters a_2 and a_3 differed significantly; fitted curves for mixed and monospecific stands indicated a slightly larger *cpa* for most of the diameter range up to approximately 40 cm, after which *cpa* in monocultures was estimated to be smaller than in mixtures. Oak significantly increased its *cl* and *cpa* in mixture compared with monocultures.

3.1. Comparison of mean tree and stand characteristics 1998–2017

In Table 3, we report the mean mixture effect in form of the fixed-effect parameter estimate a_0 from Eq. (6).

In mixed stands, the quadratic mean and dominant height of Scots pine were respectively 14 and 13% higher compared with monospecific stands. The quadratic mean and dominant diameter of Scots pine were on average also increased by 16% and 12% respectively, although not significantly. Slightly, but not significantly higher height-diameter ratios were observed for Scots pine growing in mixtures compared with monocultures (h_q/d_q: +2%, h_{100}/d_{100}: +3%). Tree heights and diameters of oak were not significantly influenced by mixing, although the height-diameter relationship of dominant oaks in mixture was significantly lower (−8%) than in monospecific stands.

While *SDI* and stand basal area were not significantly influenced by species mixing, standing volume was significantly higher in mixtures compared with the weighted mean of the neighbouring monospecific stands (+15%). Standing volume of Scots pine was even 25% higher in mixture than in monocultures. Oak also showed slightly, but not significantly, higher standing volume in mixtures than in monocultures (+5%). Stem number was on average 20% higher for oak and 10% lower for Scots pine in mixture compared with monospecific stands, although not significantly.

3.2. productivity in mixed versus monospecific stands 1998–2017

Mean overyielding at the stand level amounted to 14% (Table 3). Both species contributed to the observed mixing effect, although oak was the main driver, showing a significant overyielding of 19%. For Scots pine, overyielding was less pronounced (+10%) and not significant. In absolute terms, Scots pine on average grew at a rate of 11.2 m^3 ha^{-1} year^{-1} in mixture compared with 10.0 m^3 ha^{-1} year^{-1} in monospecific stands (Fig. 2a). The absolute volume increment on average amounted to 12.5 m^3 ha^{-1} year^{-1} for oak growing in mixture

Table 2

Mean tree and stand characteristics of the seven triplets of mixed and monospecific stands in 2017.

	N trees ha^{-1}	SDI trees ha^{-1}	dq cm	hq m	BA m^2 ha^{-1}	V m^3 ha^{-1}	IBA m^2 ha^{-1} year^{-1}	IV m^3 ha^{-1} year^{-1}
Mixture	806	816			40.1	437	0.8	12.2
	411–1169	*630–1000*			*32.5–48.5*	*353–502*	*0.5–1.3*	*8.3–18.4*
Pine$_{mix}$	432	482	28.1	24.0	24.1	264	0.4	6.5
	224–665	*346–580*	*20.2–34.0*	*20.9–28.3*	*17.8–29.3*	*181–344*	*0.1–0.8*	*2.6–10.6*
Oak$_{mix}$	374	335	24.1	20.7	16.0	173	0.4	5.7
	187–554	*252–420*	*20.5–32.4*	*17.8–23.0*	*11.8–20.2*	*131–249*	*0.2–0.7*	*3.3–9.1*
Pine$_{mono}$	902	829	26.1	21.3	38.8	375	0.9	11.3
	421–1602	*670–1006*	*18.7–35.3*	*17.1–27.6*	*29.3–44.0*	*291–503*	*0.3–1.5*	*4.8–18.7*
Oak$_{mono}$	853	785	25.3	21.9	35.7	403	0.8	11.9
	576–1371	*629–1010*	*16.8–35.3*	*17.5–28.5*	*30.4–42.6*	*267–510*	*0.5–1.2*	*8.1–15.9*

Stand characteristics are given for the mixed stand as a whole (*Mixture*), for the species in the mixed stands (*Pine$_{mix}$*, *Oak$_{mix}$*) as well as for the monospecific stands (*Pine$_{mono}$*, *Oak$_{mono}$*). The means of all seven triplets are given in plain text as well as ranges (*min-max*) in italics. *N*: number of trees (trees ha^{-1}). *SDI*: stand density index (trees ha^{-1}). d_q: quadratic mean diameter (cm). h_q: quadratic mean height (m). *BA*: stand basal area (m^2 ha^{-1}). *V*: standing volume (m^3 ha^{-1}). *IBA*: stand basal area increment (m^2 ha^{-1} year^{-1}, average of last 5 years). *IV*: stand volume increment (m^3 ha^{-1} year^{-1}, average of last 5 years).

Table 3
Results of linear mixed-effects model regressions from Eq. (6).

Variable	Mixture ($RRY_{pi,oa}$)						Scots pine ($RRY_{pi,(oa)}$)						Oak ($RRY_{(pi),oa}$)					
	Fixed effects			Random effects			Fixed effects			Random effects			Fixed effects			Random effects		
	a_0	SE	p	τ_1^2	τ_2^2	σ^2	a_0	SE	p	τ_1^2	τ_2^2	σ^2	a_0	SE	p	τ_1^2	τ_2^2	σ^2
d_q (cm)							0.16	0.14	0.255	0.299	0.056	0.036	**−0.01**	0.13	0.929	0.280	0.075	0.032
d_{100} (cm)							0.12	0.08	0.130	0.163	0.059	0.022	0.08	0.08	0.300	0.173	0.048	0.034
h_q (m)							**0.14**	0.05	0.008	0.115	0.020	0.015	−0.03	0.09	0.748	0.158	0.136	0.027
h_{100} (m)							**0.13**	0.04	0.001	0.085	0.004	0.019	−0.00	0.07	0.977	0.114	0.113	0.030
h_q/d_q							0.02	0.06	0.788	0.139	0.037	0.037	−0.00	0.04	0.977	0.081	0.061	0.031
h_{100}/d_{100}							0.03	0.05	0.567	0.096	0.066	0.033	**−0.08**	0.02	< 0.001	< 0.001	0.052	0.028
GC_v							−0.10	0.06	0.082	< 0.001	0.153	0.067	**0.18**	0.06	0.002	0.116	0.067	0.064
GC_{iv}							−0.07	0.05	0.143	< 0.001	0.124	0.105	0.12	0.08	0.113	0.139	0.107	0.130
N (trees ha^{-1})	0.01	0.18	0.971	0.363	0.167	0.031	−0.10	0.15	0.503	0.321	0.125	0.051	0.20	0.25	**0.421**	0.505	0.276	0.042
SDI (trees ha^{-1})	0.02	0.09	0.848	0.182	0.064	0.030	0.02	0.09	0.848	0.182	0.064	0.030	0.02	0.09	0.848	0.182	0.064	0.030
BA ($m^2\ ha^{-1}$)	0.08	0.06	0.209	0.133	0.043	0.025	0.10	0.07	0.186	0.156	0.049	0.021	0.07	0.06	0.240	0.122	0.039	0.037
V ($m^3\ ha^{-1}$)	**0.15**	0.06	0.016	0.140	0.025	0.040	**0.25**	0.08	0.003	0.180	0.049	0.034	0.05	0.10	0.587	0.197	0.106	0.065
IBA ($m^2\ ha^{-1}\ year^{-1}$)	0.07	0.04	0.092	0.083	0.043	0.130	−0.03	0.10	0.772	0.201	0.076	0.197	0.24	0.13	0.060	0.249	0.147	0.146
IV ($m^3\ ha^{-1}\ year^{-1}$)	**0.14**	0.04	< 0.001	0.075	< 0.001	0.110	0.10	0.07	0.140	0.140	0.040	0.171	**0.19**	0.09	0.048	0.201	0.061	0.115

The fixed effect parameter estimate a_0 represents the mean mixture effect, resulting from the triplet-specific division of the characteristic of the mixed stand by the respective monospecific stand. Results are reported for the mixed stand as a whole (*Mixture*) and the individual species level (*Scots pine*, *Oak*). The number of observations is 140. Values in bold are significant at $p < 0.05$.

and 10.9 $m^3\ ha^{-1}\ year^{-1}$ for oak growing in monoculture (Fig. 2b). The absolute productivity of the mixture as a whole was on average 11.6 $m^3\ ha^{-1}\ year^{-1}$ compared with 10.3 $m^3\ ha^{-1}\ year^{-1}$ for the weighted mean of the neighbouring monospecific stands (Fig. 2c). The absolute annual volume increment of the mixed stands on average exceeded the most productive monoculture (oak) by 0.7 $m^3\ ha^{-1}\ year^{-1}$, thereby confirming transgressive overyielding for the analysed species mixture. Fig. 2d displays the relative mixing effect on the stand level and the corresponding contribution of each species. We can see that the mixture results in considerable productivity gains and that nearly all observations lie above the reference line (1.0-line). Even small mixing proportions result in a positive mixing effect. The optimum is reached, when both species show approximately equal mixing proportions.

3.3. The influence of species mixing on size and growth partitioning in mixed versus monospecific stands

The Gini coefficient for tree volume (GC_v) was significantly higher for oak in mixture compared to monocultures (+18%) (Table 3). The Gini coefficient for tree volume growth of oak was on average +12% higher, although not significantly. No significant effect of species mixing on size and growth partitioning of Scots pine was evident, although both the Gini coefficient for tree volume and volume growth on average appeared to be lower in the mixture than in monoculture (−10 and −7% respectively).

3.4. The influence of annual climate conditions on the mixing effect

Fig. 3 shows the relative productivity (i.e. the relative overyielding in terms of annual stand volume growth) on the species (Scots pine: a, oak: b) and stand (c) level in relation to the de Martonne aridity index over the entire 20-year investigation period. The straight lines depicted in Fig. 3 represent the average linear relationship as fitted by Eq. (7). The de Martonne aridity index had a significantly positive effect on the relative productivity on the stand and species levels (Fig. 3, Table A2). Analogously, annual precipitation had a significantly positive effect on relative productivity (Table A2) on the stand and species level. In contrast, annual mean temperature had a significantly negative effect on relative productivity on the stand level and Scots pine, while the relationship was not significant for oak (Table A2).

4. Discussion

4.1. Mean tree and stand characteristics

As the plots analysed in this study were selected to represent fully stocked stands and to ensure same site conditions within each triplet, we can assume that the observed differences between mixed and monospecific stands result from true mixing effects that occur due to interactions between both species observed (Pretzsch and Biber, 2016). Such inter-specific interactions can cause changes in growth allocation between radial growth and height growth, thereby influencing tree morphology (Pinto et al., 2008). In this study, we observed significantly larger quadratic mean and dominant tree heights for Scots pine growing in mixture with oak compared to monocultures. The height growth of oak on the other hand, was on average not significantly influenced by mixing. Our results indicate that species mixing can lead to a modification in stand structure towards a vertically more stratified overstory, highlighting differences in shade tolerance and growth patterns between Scots pine and oak. These findings are in line with del Río et al. (2018) who showed that Scots pine increased its height in mixture with oak and Lu et al. (2018) who observed a two layered stand structure in Scots pine-oak mixtures, with Scots pine growing above oak. The development of multi-layered canopies, where more shade-tolerant species grow under taller, more light-demanding species, have also been reported for other mixtures (Hardiman et al., 2011; Pretzsch et al.,

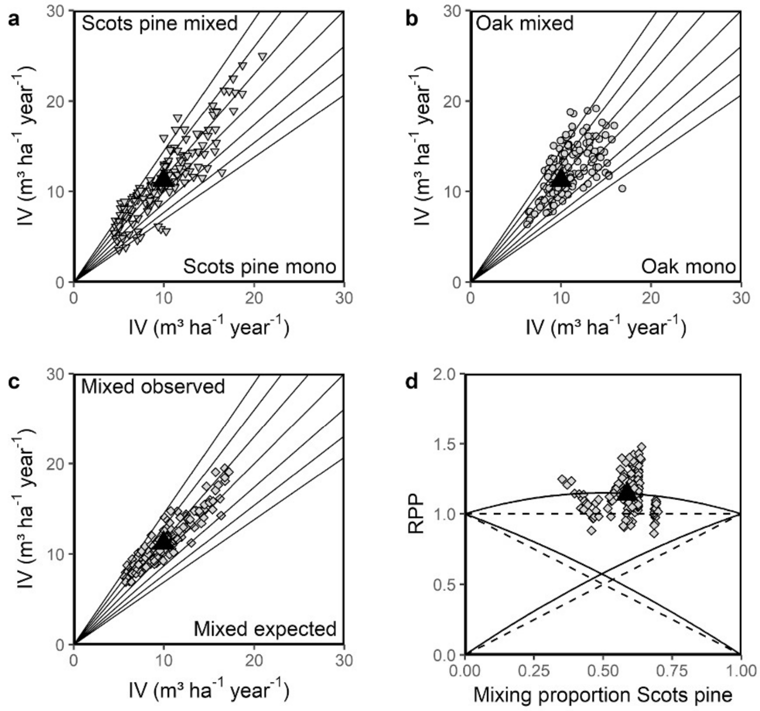

Fig. 2. Relationship between volume productivity (*IV*) in mixed stands and monocultures. Solid black triangles indicate the mean mixing effect, based on all 140 observations. Illustrations (a) and (b) show the expected productivity of Scots pine and oak respectively based on their performance in the mixed stand compared to the observed species-specific productivity in the monospecific stands. In (c) the observed productivity of both species in the mixture is compared with the weighted mean productivity of the adjacent monospecific stands. In (d) a cross diagram is displayed, showing the relative productivity on the basis of the proportions of volume growth (*RPP*) of Scots pine, oak and the mixed stand as a whole in relation to the productivity of the neighbouring pure stands. The abscissa shows the mixing proportion of Scots pine. The points represent the observed relative volume productivity of mixed versus pure stands. The curves indicate the average mixing reaction of Scots pine, oak and total stand. Broken reference lines represent the productivity expected for neutral mixing effects on the total stand and species levels (Pretzsch et al., 2013a).

2015; Thurm and Pretzsch, 2016). In our study, oak displayed a significantly lower height-diameter ratio of dominant trees in mixture with Scots pine compared with monocultures. This could indicate a lower level of competition for light, as these trees can allocate more carbon to diameter growth, while still being able to keep their crown in the canopy. Similar observations have been made for Douglas fir in mixture with European beech (Thurm and Pretzsch, 2016). It should be pointed out that the observed stand structure may change over time. Our focus was on younger to medium aged stands with a mean age of 78 years. Therefore, structural characteristics in older, more mature stands are not reflected in this study. However, the competitive relationship in mixture has been shown to change with increasing age, pointing at a shift in competitive power from Scots pine to oak (Schröder, 2009).

On average, standing volume was significantly higher in mixtures compared with adjacent monocultures. This effect was mainly driven by significantly higher standing volume of Scots pine in mixtures compared with monocultures. Whereas the slightly, but not significantly increased standing volume of oak in mixture may be the result of higher stem numbers, the higher standing volume of Scots pine in mixture compared with monoculture seems more closely related to individual tree growth. Similar results were reported by Pretzsch et al. (2015) for the mixture of Scots pine and European beech.

Based on our observations, we can reject HI as there is clear evidence that species mixing alters mean tree and stand characteristics.

4.2. Productivity

We found evidence that inter-specific interactions can have a positive effect on the volume productivity of mixed Scots pine-oak stands and that transgressive overyielding can occur in these stands. We therefore reject HII. Overyielding of Scots pine-oak mixtures has also been reported for other regions in Europe. For an experimental design in Gisburn, England, Brown (1992) reported positive mixing effects in young Scots pine-oak stands. Recent studies on permanent field plots in the Netherlands (Lu et al., 2016, 2018) showed overyielding of mixed Scots pine-oak stands, which increased on poor soils. A modelling approach study for one site in France revealed similar results (Pérot and Picard, 2012). In contrast, Toïgo et al. (2015) did not find any significant overyielding for Scots pine-oak mixtures based on French inventory data, although oak did show a positive mixing effect on the species level, which was also confirmed in a later study (Toïgo et al.,

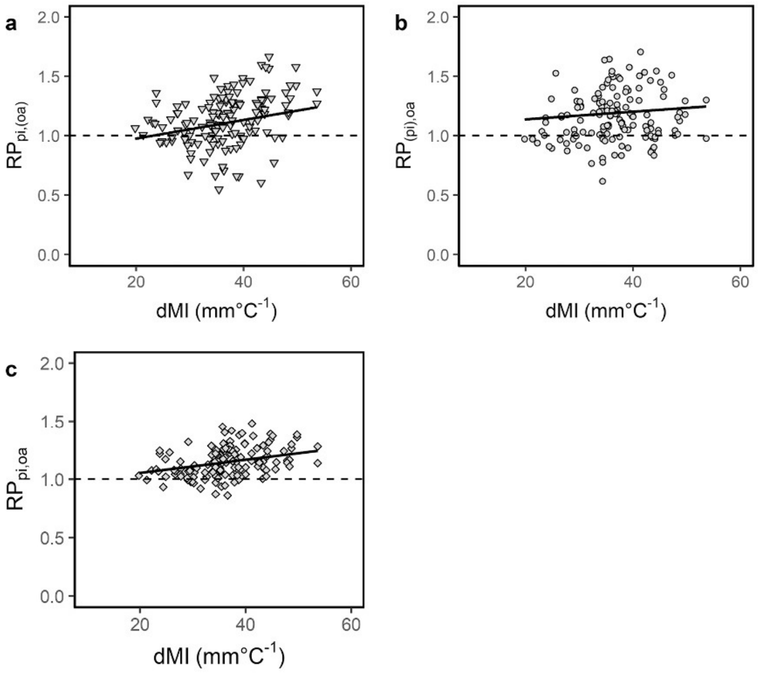

Fig. 3. Relative volume productivity in the years 1998–2017 at the species level for Scots pine (a) and oak (b) as well as for the total stand level (c) on the seven analysed triplets (ordinate) plotted against the de Martonne aridity index (dMI) (abscissa). Analysing this relationship by fitting linear mixed effect models (Eq. (7)) yielded the added straight lines.

2017). A possible reason for these contrasting results could be that the study by Toïgo et al. (2015) included a wider range of stand conditions compared with our and other aforementioned studies, therefore covering a larger ecological context. Another possible reason for this discrepancy may be the differing basis for assessment. While Toïgo et al. (2015) use basal area increment as a measure for stand performance, our and other empirical studies rely on volume increment (Lu et al., 2016, 2018) or yield (Brown, 1992) for quantifying mixing effects, encompassing both diameter and height growth. As our results suggest, positive mixing effects of Scots pine in particular may result from an accelerated height growth, which therefore should be viewed as a necessary component of the analysis. Positive mixing effects have also been confirmed for mixtures of different pine and oak species (e.g. del Río and Sterba, 2009; Nunes et al., 2013; Jucker et al., 2014b) as well as other coniferous-deciduous mixtures (e.g. Bartelink, 1998; Pretzsch and Schütze, 2009; Condés et al., 2013; Dirnberger and Sterba, 2014; Pretzsch et al., 2015; Thomas et al., 2015; Toïgo et al., 2015; Lu et al., 2016; Thurm and Pretzsch, 2016).

In our study, the more shade tolerant oak profited strongly from the admixture of Scots pine and can be seen as the main driver of the observed stand-level overyielding. For Scots pine, the positive mixing effect was not as strong and not significant. A stronger mixing effect for oak compared with Scots pine has also been observed in some of the studies mentioned before (Pérot and Picard, 2012; Toïgo et al., 2015; Lu et al., 2018) and could be attributed to a higher reduction of competition for oak compared with Scots pine. In general, transgressive overyielding is likely to occur when the combined tree species show similar productivities, as the reduction in growth area for one species is compensated for by the increased growth of both species in the mixed stand (del Río and Sterba, 2009). This is also the case for the studied monospecific Scots pine and oak stands, thus explaining the transgressive overyielding observed.

4.3. *Causal explanation of mixing effects*

In this study, we did not analyse any eco-physiological processes. However, using the results derived on the tree, species and stand level, we are able to provide indications on the underlying mechanisms and causes that may drive the observed overyielding.

A key hypothesis explaining the positive relationship between biodiversity and productivity is the "complementarity effect hypothesis" (Aarssen, 1997; Loreau, 2000; Loreau and Hector, 2001; Fargione et al., 2006). The complementarity effect can be caused by reduced competition or facilitation (Ammer, 2019). Reduced competition occurs when inter-specific competition in the mixture is lower than intra-specific competition in the monospecific stands (Bauhus et al., 2017) and is often caused by niche differentiation where two or more species use the resources available in complementary ways (Fargione et al., 2006). This can be due to differences in shade tolerance, phenology, crown architecture or root system (Kelty, 1992; Man and Lieffers, 1999; Pretzsch et al., 2015). Facilitation is a form of interaction where one species improves the environmental conditions for another species (Callaway, 2007; Brooker et al., 2008; Bauhus et al., 2017). Competitive reduction and facilitation can be inter-dependant and therefore difficult to separate. As a result, the combination of the two mechanisms is commonly referred to as complementarity (Forrester and Bauhus, 2016).

wAmong the possible causes of complementarity in mixed forests stands, the reduction in competition for light has been viewed as a crucial factor in compositions consisting of tree species with differing shade tolerance (Zhang et al., 2012; Jucker et al., 2014b;

Toïgo et al., 2017). Building on the considerations of Forrester and Bauhus (2016) and Pretzsch (2017), mechanisms that promote niche differentiation and increase light capture can be classified in three groups: (i) spatial complementarity as a result of vertical stratification caused by differences in shade tolerance, (ii) temporal complementarity caused by differences in leaf phenology of evergreen and deciduous species and (iii) morphological complementarity as a result of inter-specific differences in crown shape or intra-specific changes in crown architecture and allometry. In the case of the studied Scots pine-oak triplets it is likely that all three mechanisms may be causing the observed positive mixing effect and will therefore be discussed further.

Differences in physiology, namely shade tolerance and height growth pattern, may influence the vertical stratification of a given stand. Spatial complementarity through canopy stratification may arise in mixtures where fast-growing species with a high light-use efficiency overtop slower growing and more shade tolerant species (Binkley et al., 1992; Forrester et al., 2012). It has even been shown, that positive diversity effects in mixtures may depend on the ability of the shade-intolerant species to overtop the more shade-tolerant species (Forrester et al., 2006, Forrester et al., 2011). In our study, the height growth of Scots pine is clearly accelerated in mixture with oak, resulting in a more stratified crown space (Table 2, Table 3). Reduced competition for light through spatial complementarity is indicated by the unaltered tree heights for oak and its reduced height to diameter relationship. Scots pine may transmit sufficient light through the canopy to allow for oak to grow underneath (Jucker et al., 2014b). This could result in an elongated leaf life span, improving light use throughout the year, as reported for European beech growing in mixture with Scots pine (Forrester et al., 2017).

Differences in leaf phenology are likely to play a large role in the positive mixing effect of Scots pine, as in mixture it receives more light in spring before the leaf-break of oak compared with growing in monocultures. Differences in leaf phenology have been highlighted as one of the main drivers of overyielding in evergreen-deciduous stands (Sapijanskas et al., 2014; Lu et al., 2016).

It is likely that the inter-specific differences in crown architecture between Scots pine and oak cause a larger and more efficient utilisation of crown space, thereby potentially increasing the light absorption of the whole stand (Pretzsch, 2014; Sapijanskas et al., 2014; Jucker et al., 2015). Moreover, our results suggest that oak in particular is able to significantly change its crown morphology in mixture with Scots pine, thereby potentially further increasing its ability to absorb light (Forrester and Albrecht, 2014; Jucker et al., 2014b; Pretzsch, 2014; Sapijanskas et al., 2014; Jucker et al., 2015). The ability to plastically adapt the shape and size of the crowns is seen as crucial for increasing the light use efficiency in mixed stands (Jucker et al., 2015). The reduction of crown abrasion, defined as the physical loss of terminal buds and branches by the overlap during wind sway (Rudnicki et al., 2001), may explain these positive interactions. Mechanical crown abrasion resulting in crown shyness (Putz et al., 1984) can lead to a decline in crown closure, leaf area and productivity (Meng et al., 2006). In cases where the combined species fill different canopy layers, this effect may be mitigated (Pretzsch, 2014). The crown expansion of oak in mixture with Scots pine is likely to be the result of the observed increase in canopy stratification and indicates reduced competition and an optimised utilisation of canopy space, which oak is able to exploit due to its high crown plasticity (Longuetaud et al., 2013). Scots pine on the other hand, shows slightly shorter crowns in mixture and, although the results indicate significant biological differences between mixed and monospecific stands, the difference in *cpa* seems to be of small practical relevance.

In addition to reduced competition for light, other mechanisms may also attribute to the observed mixing effect. It has for example been shown that tree species in mixture are able to exploit underground resources in a complementary way by differing rooting patterns (e.g. Schume et al., 2004; Forrester et al., 2010; Reyer et al., 2010; Brassard et al., 2012; Pretzsch et al., 2013b; Schwendenmann et al., 2014). The root system of Scots pine is found to be highly dependent on the prevailing soil conditions. It is frequently shallow with no distinct tap root, but can also exhibit a deeper rooting system with tap roots (Carlisle and Brown, 1968). Oak produces a strong tap root in younger years, which is accompanied by, and with increasing age even replaced by, deep-reaching lateral roots that gradually descend and form a dense system of heart-roots (Jones, 1959). Oak trees are commonly believed to be capable of using deeper soil resources than pine trees (Kolb and Stone, 2000). Both Scots pine and oak have in mixture been shown to exhibit complementary water uptake depths during droughts as a result of root plasticity, with oak in particular shifting to deeper water resources (Bello et al., 2019). Complementarity between Scots pine and oak may also arise from seasonal differences in fine root development (Konôpka et al., 2005). Additional benefits could result from accelerated rates of nutrient cycling due greater nutrient contents and decomposition rates reported for different pine-oak mixtures (Kaneko and Salamanca, 1999; Conn and Dighton, 2000) and other species mixtures (Elmer et al., 2004; Cornwell et al., 2008; Jonard et al., 2008; Weedon et al., 2009).

4.4. The effect of species mixing on size and growth partitioning

GC_v was significantly higher for oak growing in mixture than in monospecific stands. In addition, for oak there was a tendency towards a higher GC_{iv} in mixtures compared with monocultures, albeit not significant. Increased GC_v and GC_{iv} could be a result of the higher vertical structuring of the crown space in mixture compared with monospecific stands, which improves light availability and thereby facilitates the survival of subdominant and understorey trees. In mixtures usually more small trees exist, but at the same time stem size and growth is concentrated on a restricted number of tall trees (Pretzsch and Schütze, 2016). In contrast, Scots pine showed a tendency towards lower G_v and G_{iv} in mixture compared with monoculture. This could indicate a more equal tree size and growth distribution in mixture. The admixture of Scots pine resulted in an increased size inequality of oak, comparable to the effect of thinning from above. The opposite effect is indicated for Scots pine, where the admixture of oak seems to result in a size distribution found in stands that have been thinned from below. These different reaction patterns are typical for combinations of tree species differing in shade tolerance and highlight differences in self- and alien-thinning (Pretzsch and Schütze, 2014). For uneven-aged mature Scots pine-oak forests in the Netherlands and northern Belgium Vanhellemont et al. (2018) showed that structural diversity had a positive effect on the basal area increment of tall oaks. Similar results were found in our study, as indicated by the slightly higher diameter and corresponding significantly lower height-diameter relation for dominant oaks growing in mixed stands compared with monocultures.

Our observations let us reject HIII and support the assertion that the observed overyielding is driven by reduced competition for light.

4.5. The influence of annual climate conditions on the mixing effect

We found evidence that the annual climate conditions can have a significant effect on the observed overyielding and therefore reject HIV. Overyielding at the species and stand level was increased in years with high water supply and precipitation. For Iberian pine-oak mixtures, Jucker et al. (2014b) also showed that overyielding was higher in a wet year and lower in a dry year. Under the assumption that temporal responses to environmental stress resemble those reported along spatial environmental gradients, our results are in line with a global meta-analysis by Jactel et al. (2018), which found a general positive correlation of overyielding with precipitation. The observed dependency of overyielding on water supply is typical for species interactions that improve light absorption or light-use efficiency and can be explained by the framework presented by Forrester (2014); as water and nutrient availability increases, competition for light may increase due to the development of larger leaf areas, thereby enhancing effects that are based on complementary use of resources. This relationship has also been reported for mixtures of Silver fir and Norway spruce (Forrester and Albrecht, 2014). In our study, the overyielding of oak was less sensitive to water supply than Scots pine. This could be the result of oak's better ability to compete for below-ground resources (Bello et al., 2019), meaning that in particularly dry years Scots pine in mixture could have less access to water than in monocultures. The same reaction patterns were observed in the study by Jucker et al. (2014b) and attributed to an increase in below-ground competition for water in dry years in mixed stands versus monocultures as reported by Grossiord et al. (2014). Our findings support the idea that in Scots pine-oak mixtures complementarity for light may be the key factor driving the observed diversity-productivity relationship and that this effect is more relevant under benign environmental conditions as indicated by years with higher water supply. Under harsh growing conditions, light related interactions are less likely to result in positive mixture effects on stand productivity, as growth is more limited by other resources such as water or nutrients (Forrester and Bauhus, 2016). However, Lu et al. (2018) found that overyielding of Scots pine-oak mixtures was stronger on poor than on rich soils, which is perceived as in line with the stress-gradient hypothesis (Bertness and Callaway, 1994). These seemingly conflicting results could indicate, that the effect of spatial and temporal changes in growing conditions on the diversity-productivity relationship may not always be closely related and may instead be context-dependent (e.g. influenced by the type of limiting factor at a given site (Forrester, 2014)). In our study the environmental conditions were not very harsh. Further research should therefore extend the environmental gradient to extreme sites, in order to provide the full range of potential species interactions.

4.6. Comparison of mixed versus monospecific stands – methodological considerations

While long-term experimental plots are the indisputable "gold standard" for studying long-term growth dynamics in forest stands under controlled conditions, today there are only very few such experiments available for the scrutiny of mixing effects (e.g. Forrester et al., 2004; Amoroso and Turnblom, 2006), none of which cover native European tree species. Temporary research plots such as those analysed in this study therefore make a substantial contribution to the scientific discourse by permitting fast reactions to upcoming topics not yet covered by existing long-term experiments (Heym et al., 2018). The triplet design has in this context proven its worth for quantifying mixing effects in forest stands (Ruiz-Peinado et al., 2018). When based on the direct comparison of mixed and monospecific stands at the same site with the same treatment history, triplets allow the analysis of mixing effects under *ceteris paribus* conditions. This is not necessarily the case for studies that rely on large-scale inventory data, which may require modelling techniques to account for site variability (e.g. del Río and Sterba, 2009; Vallet and Pérot, 2011).

It has been shown, that overyielding can be strongly influenced by the way in which the mixing proportion is calculated (Dirnberger and Sterba, 2014; Huber et al., 2014; Thurm and Pretzsch, 2016). The comparability of results from studies using different approaches to calculating mixing proportion may therefore be impeded. Other studies have based mixing proportion on stem number (Forrester et al., 2004; Amoroso and Turnblom, 2006), basal area (Puettmann et al., 1992, Condés et al., 2013), volume weighted by dry mass (Pretzsch et al., 2010; Pretzsch et al., 2013a), biomass and leaf area (Dirnberger and Sterba, 2014) or absolute *SDI* (Lu et al., 2018). In this study, we use the adjusted *SDI* as a basis for determining the mixing proportions, which follows the recommendations made by Dirnberger and Sterba (2014) and Sterba et al. (2014) for defining species proportion by area, where the reference is the area each species would occupy in a fully stocked monospecific stand. As these maximum density values are unknown, we assume that the monocultures selected in this study represent maximum density at a given site. By selecting fully stocked stands and ensuring similar site conditions of the monospecific and mixed stands in each triplet, we were able to exclude the most important confounding factors that might have impaired our results. The selected monospecific stands exhibit *SDI* values (Table 2) that are well above the range of maximum stand densities commonly reported for Scots pine (600–750 trees ha^{-1}) and oak (500–600 trees ha^{-1}) (Pretzsch, 2009, p. 272).

4.7. Conclusions

Our results show that the mixture of Scots pine and oak can have a positive effect on stand productivity and that transgressive overyielding can occur in these stands. Overyielding was present under varying levels of water supply, indicating a lower long-term climate sensitivity compared with monocultures, although the relative productivity increased with annual water supply. These findings underline a good complementarity of both species and suggest a high suitability for increasing the diversity and productivity of temperate forests within the framework of adaptive forest management. However, the mixing of Scots pine and oak has in the past often been shown to be detrimental for timber quality of oak (e.g. Bäucker et al., 2007; Bäucker and Bues, 2009; Schröder, 2009). Our results point in the same direction, with oak exhibiting significantly lower height-diameter ratios and larger crowns in mixture, factors that are typically associated with lower timber qualities (Rais, 2015; Pretzsch and Rais, 2016). Increased productivity and diversity in single tree mixture of Scots pine and oak may therefore come at the expense of timber quality of oak and thus ultimately at the expense of profitability. The resulting conflict of objectives may be more or less pronounced, depending on the strategic objectives of the forest owner. For future stand development, concepts that abandon single admixture systems in favour of spatially separated (Schröder, 2009) or spatially and temporally separated (Bilke, 2004) monospecific groups or patches, appear promising for balancing productivity and timber quality in mixed Scots pine and oak stands.

Conflict of interest

None.

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Appendix A

See Fig. A1 and Tables A1–A2.

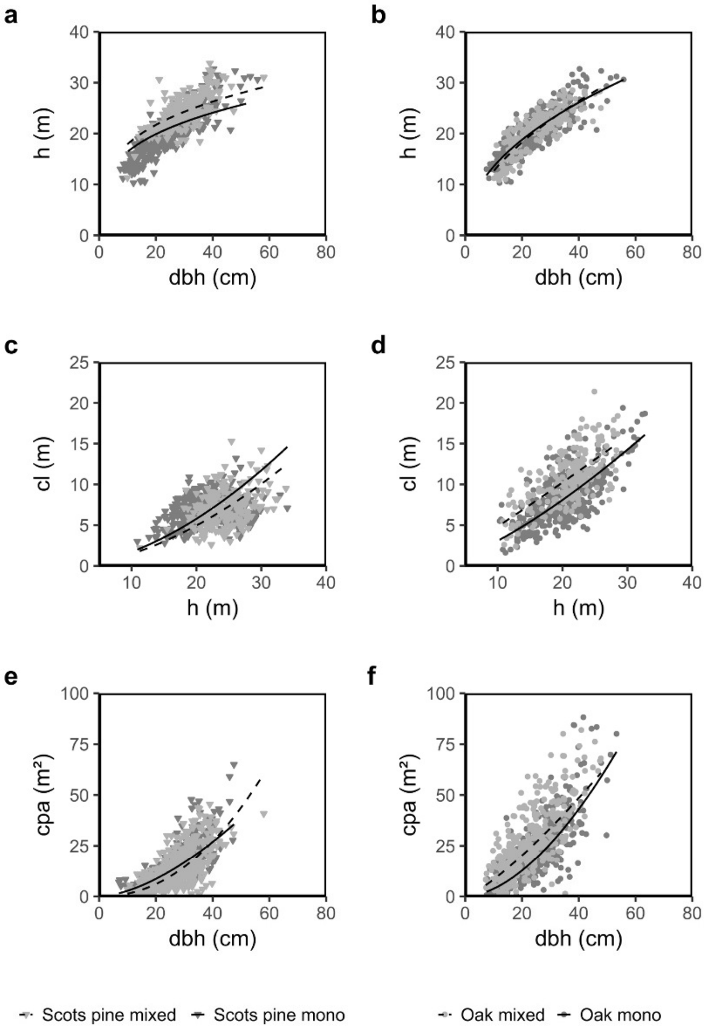

Fig. A1. Individual tree characteristics in 2017 for Scots pine and oak in monocultures and mixed species stands on the seven sampled triplets: tree height versus diameter at breast height (a, b), crown length versus tree height (c, d) and crown projection area versus diameter at breast height (e, f). The lines represent the results of a linear mixed-effects model (Eq. (5)) with nesting effects on the triplet group, triplet and plot level. Dashed lines represent trees growing in mixed stands, solid lines represent trees growing in monocultures.

Table A1
Results of linear mixed-effects model regressions from Eq. (5).

Species	Response variable	Explanatory variable	Statistic	Fixed effects				Random effects			
				a_0	a_1	a_2	a_3	τ_1^2	τ_2^2	τ_3^2	σ^2
Scots pine	h	dbh	Value	**2.248**	**0.277**	**−0.088**	n.s.	0.115	< 0.001	0.023	0.069
			SE	0.070	0.014	0.014					
			p	< 0.001	< 0.001	0.001					
	cl	h	Value	**−3.638**	**1.748**	**0.154**	n.s.	0.302	< 0.001	0.097	0.221
			SE	0.359	0.103	0.057					
			p	< 0.001	< 0.001	0.036					
	cpa	dbh	Value	**−4.662**	**2.158**	**1.904**	**−0.518**	< 0.001	< 0.001	0.175	0.483
			SE	0.326	0.096	0.453	0.135				
			p	< 0.001	< 0.001	0.006	< 0.001				
Oak	h	dbh	Value	**1.309**	**0.532**	0.199	**−0.057**	0.062	< 0.001	0.033	0.096
			SE	0.068	0.019	0.083	0.025				
			p	< 0.001	< 0.001	0.053	0.024				
	cl	h	Value	**−0.928**	**1.086**	**−1.169**	**0.311**	0.085	0.068	< 0.001	0.258
			SE	0.249	0.081	0.319	0.106				
			p	< 0.001	< 0.001	0.011	0.003				
	cpa	dbh	Value	**−0.791**	**1.267**	**−1.917**	**0.487**	< 0.001	0.085	< 0.001	0.510
			SE	0.198	0.064	0.298	0.096				
			p	< 0.001	< 0.001	< 0.001	< 0.001				

h: tree height (m). *cl*: crown length (m). *cpa*: crown projection area (m^2). *dbh*: diameter at breast height (cm). Values in bold are significant at $p < 0.05$

Table A2
Results of linear mixed-effects model regressions from Eq. (7).

Variable	Statistic	Fixed effects						Random effects								
		dMI		T		P		dMI			T			P		
		a_0	a_1	a_0	a_1	a_0	a_1	τ_1^2	τ_2^2	σ^2	τ_1^2	τ_2^2	σ^2	τ_1^2	τ_2^2	σ^2
$RP_{pi,oa}$	Value	**0.9410**	**0.0056**	**1.4684**	**−0.0352**	**0.9366**	**0.0003**	0.0612	0.0011	0.1056	0.0722	< 0.0001	0.1091	0.0612	0.0002	0.1061
	SE	*0.0598*	*0.0015*	*0.1624*	*0.0172*	*0.0629*	*0.0001*									
	p	*< 0.0001*	*0.0002*	*< 0.0001*	*0.0424*	*< 0.0001*	*0.0003*									
$RP_{pi,(oa)}$	Value	**0.8185**	**0.0078**	**1.5897**	**−0.0530**	**0.8159**	**0.0004**	0.1300	0.0415	0.1646	0.1294	0.0400	0.1693	0.1328	0.0414	0.1652
	SE	*0.1031*	*0.0023*	*0.2554*	*0.0268*	*0.1082*	*0.0001*									
	p	*< 0.0001*	*0.0009*	*< 0.0001*	*0.0497*	*< 0.0001*	*0.0016*									
$RP_{(pi),oa}$	Value	**1.0719**	**0.0032**	**1.3214**	−0.0145	**1.0653**	**0.0002**	0.1970	0.0614	0.1139	0.2011	0.0613	0.1153	0.1964	0.0614	0.1139
	SE	*0.1083*	*0.0016*	*0.1946*	*0.0184*	*0.1100*	*0.0001*									
	p	*< 0.0001*	*0.0462*	*< 0.0001*	*0.4325*	*< 0.0001*	*0.0472*									

RP: relative volume productivity. dMI: de Martonne aridity index. T: mean annual temperature. P: annual precipitation. Values in bold are significant at $p < 0.05$.

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B.2. Article II

Title: Species mixing reduces drought susceptibility of Scots pine (*Pinus Sylvestris* L.) and oak (*Quercus robur* L., *Quercus petraea* (Matt.) Liebl.) – Site water supply and fertility modify the mixing effect

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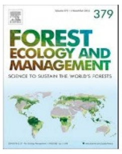

Species mixing reduces drought susceptibility of Scots pine (*Pinus sylvestris* L.) and oak (*Quercus robur* L., *Quercus petraea* (Matt.) Liebl.) – Site water supply and fertility modify the mixing effect

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ABSTRACT

Tree species mixing has been widely promoted as a promising silvicultural tool for reducing drought stress. However, so far only a limited number of species combinations have been studied in detail, revealing inconsistent results. In this study, we analysed the effect of mixing Scots pine and oak (pedunculate oak and sessile oak) trees on their drought response along a comprehensive ecological gradient across Europe. The objective was to improve our knowledge of general drought response patterns of two fundamental European tree species in mixed versus monospecific stands. We focused on three null hypotheses: (*HI*) tree drought response does not differ between Scots pine and oak, (*HII*) tree drought response of Scots pine and oak is not affected by stand composition (mixture versus monoculture) and (*HIII*) tree drought response of Scots pine and oak in mixtures and monocultures is not modified by tree size or site conditions. To test the hypotheses, we analysed increment cores of Scots pine and oak, sampled in mixed and monospecific stands, covering a wide range of site conditions.

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We investigated *resistance* (the ability to maintain growth levels during drought), *recovery* (the ability to restore a level of growth after drought) and *resilience* (the capacity to recover to pre-drought growth levels), involving site-specific drought events that occurred between 1976 and 2015. In monocultures, oak showed a higher resistance and resilience than Scots pine, while recovery was lower. Scots pine in mixed stands exhibited a higher resistance, but also a lower recovery compared with Scots pine in monocultures. Mixing increased the resistance and resilience of oak. Ecological factors such as tree size, site water supply and site fertility were found to have significant effects on the drought response. In the case of Scots pine, resistance was increased by tree size, while recovery was lowered. Resistance of oak increased with site water supply. The observed mixing effect on the tree drought response of Scots pine and oak was in some cases modified by the site conditions studied. Positive mixing effects in terms of resistance and resilience of oak increased with site water supply, while the opposite was found regarding recovery. In contrast, site fertility lessened the positive mixing effect on the resistance of Scots pine. We hypothesise that the observed positive mixing effects under drought mainly result from water- and/or light-related species interactions that improve resource availability and uptake according to temporal and spatial variations in environmental conditions.

1. Introduction

Climate change is characterised by increased temperatures and modified precipitation patterns (Schär et al., 2004; Della-Marta et al., 2007; Jacob et al., 2014). Correspondingly, extreme climate events, such as severe droughts, have increased in frequency and intensity, a trend that is predicted to continue in the future (IPCC, 2014). Drought is a particular challenge for forest managers, as it may affect a multitude of ecosystem responses from the molecular, through organ and individual, to the stand level, thereby altering forest ecosystem dynamics (Floret et al., 1990; Chaves et al., 2003; Bréda et al., 2006; Rennenberg et al., 2006; Hamanishi and Campbell, 2011). Drought occurs under low levels of available water, caused by reduced precipitation and/or increased atmospheric evaporative demand combined with low available soil water (Wilhite, 1993). Under drought, trees may reduce stomatal conductance and photosynthesis, and experience carbon starvation (Irvine et al., 1998; McDowell et al., 2008), modified tree allometry (Pretzsch et al., 2012b), enhanced fine root mortality (Deans, 1979; Gaul et al., 2008) or increased defoliation (Carnicer et al., 2011; Poyatos et al., 2013). Possible effects include decreased tree and stand growth (Chaves et al., 2003; Leuzinger et al., 2005; Hartmann, 2011), a higher susceptibility to biotic and abiotic agents (Allen et al., 2010; Griess and Knoke, 2011; Schlesinger et al., 2016) and, ultimately, even tree die-off and mortality (McDowell et al., 2008). The large extent of drought and heat-induced mortality currently observed, pays witness to a global vulnerability of trees and forests to climate change (Allen et al., 2010).

Droughts, such as those reported for the years 1976, 2003 and 2015 throughout Europe (Bréda et al., 2006; Rebetez et al., 2006; Ionita et al., 2017), have had a detrimental effect on tree and stand growth and show that the natural adaptive ability may be overstrained by sudden changes in growing conditions. Growth responses of trees to drought may depend on intrinsic factors, such as species (Zang et al., 2011; Eilmann and Rigling, 2012; Anderegg and HilleRisLambers, 2016; Thurm et al., 2016; Vitasse et al., 2019), provenance (Taeger et al., 2013), competitive status (Zang et al., 2012), age (Thurm et al., 2016) and size (Jucker et al., 2014; Bennett et al., 2015; Serra-Maluquer et al., 2018); as well as extrinsic factors, such as biome type (Vicente-Serrano et al., 2013; Grossiord et al., 2014; Gazol et al., 2017), altitude (Marqués et al., 2016), soil conditions (Thurm et al., 2016), prevalent climatic conditions (Pasho et al., 2011; Dorman et al., 2013; Lévesque et al., 2014; Clark et al., 2016; Gazol et al., 2017), seasonality of the endured drought event (Merlin et al., 2015; Toigo et al., 2015), stand functional diversity (Gazol and Camarero, 2016), stand competition (Dorman et al., 2015; Thurm et al., 2016) and species mixing (Grossiord, 2018).

The mixture of tree species, i.e. the increase in tree species diversity, has been widely proposed as an effective silvicultural tool to counteract the adverse impacts of droughts on tree growth and vitality, thereby stabilising forest ecosystems (Kelty, 1992; Lüpke et al., 2004; Knoke et al., 2008). Empirical evidence suggests that species mixing can improve resource utilisation within stands, thereby reducing tree climate sensitivity (Thurm et al., 2016), as well as stabilising (Pretzsch, 2005; del Río et al., 2017) and increasing stand productivity (Zhang et al., 2012; Pretzsch, 2017). In this light, the conversion of traditional coniferous monocultures into mixed stands of coniferous and broadleaved species has been widely promoted in European forest policy and management (Klimo, 2000; Zerbe, 2002; Kint et al., 2006; Knoke et al., 2008).

Positive mixing effects are commonly explained by the complementary effect hypothesis, according to which complementarity between species can be either caused by reduced competition or facilitation (Ammer, 2019). Complementarity effects depend on the environmental context, which affects the availability of the target resource over space and time. According to the conceptual framework by Forrester (2014), complementarity effects are expected to increase when the mixing of tree species improves the availability, uptake or use efficiency of the limiting resource. Under rich growing conditions (i.e., high nutrient and water availability), where competition for light increases due to larger leaf areas, light related interactions may be more relevant than under poor growing conditions, where the limiting factor is rather related to soil conditions. The influence of average site conditions on mixing effects has often been described by the stress gradient hypothesis, which states that the effect of facilitation is more pronounced on sites with stressful growing conditions, whereas under benign conditions, the effect of competition dominates (Bertness and Callaway, 1994). Complementarity is also expected to be present under temporal changes in environmental conditions, such as during annual drought (Pretzsch et al., 2012a; del Rio et al., 2014; Thurm et al., 2016), when the mixing of tree species with differing ecological traits and resistance behaviours may mitigate negative growth effects.

Despite a rapidly growing interest from the scientific community and a clear trend towards implementing mixed forest management (Knoke et al., 2008; Messier et al., 2013), the effect of tree species diversity on the drought responses of trees and stands is still under debate. A recent review by Grossiord (2018) showed that positive, negative or neutral effects occur, depending on tree species and ecosystems. This inconsistency across studies may be explained by the often limited scope in terms of geographical extent and number of scrutinised species. The apparent lack of generalisable results makes it difficult to develop silvicultural guidelines for forest mixtures. It rather highlights the need for further studies into the effect of species mixing under drought for different species combinations across various site conditions.

In this study we focus on the drought stress behaviour of Scots pine (*Pinus sylvestris* L.) and oak (*Quercus* spp.) in mixtures and monocultures. The latter comprises both pedunculate oak (*Q. robur* L.) and sessile oak (*Q. petraea* (Matt.) Liebl.), which are considered together to avoid possible taxonomic pitfalls due to potential cross-breeding (Roloff et al., 2008, pp. 506–507). Following Pretzsch et al. (2019), we use "oak" as a generic term summarising both oak species, or their colloquial names "pedunculate oak" or "sessile oak". Despite differences in ecology on marginal sites, pedunculate oak being more adapted to moist or wet sites than sessile oak, while also being more susceptible to drought stress in comparison (Annighöfer et al., 2015), both oak species grow sympatrically across most of Europe (Jones, 1959). Scots pine is known to be well protected against drought due to its imbedded stomata and pronounced waxy layer on the epidermis (Krakau et al., 2013), although its sensitivity to increased temperatures and drought has been a cause for concern regionally (Kölling and Zimmermann, 2007; Galiano et al., 2010). Oak is able to withstand drought due to its deep-reaching taproots that increase the accessibility of water (Praciak et al., 2013). Scots pine is able to regulate its transpiration in an early stage of drought, whereas oak keeps its stomata open for a longer period of time (Irvine et al., 1998). Pronounced stomatal control (Scots pine) and deep reaching rooting systems (oak) generally allow for a high drought avoidance capacity (Levitt, 1980; Aubin et al., 2016). Scots pine and oak have been shown to differ in their drought response in relation to the seasonality of the drought events (Merlin et al., 2015; Toigo et al., 2015; Vanhellemont et al., 2019); Scots pine performs better under spring drought, whereas oak shows a higher resistance under summer drought conditions. Scots pine and oak are economically important due to a wide range of end-use applications (Eaton et al., 2016; Houston Durrant et al., 2016) and the ongoing transformation efforts towards mixed species forests have often seen the introduction of oak into stands traditionally dominated by Scots pine, in particular on

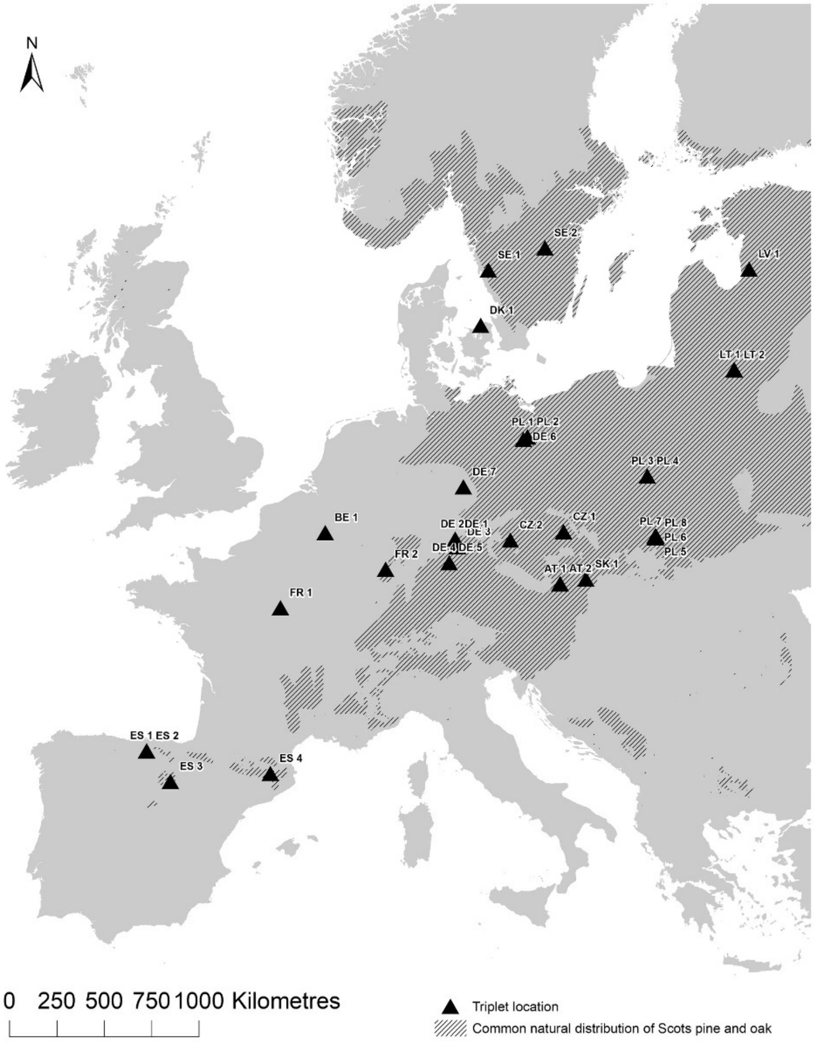

Fig. 1. Location of the 33 Scots pine-oak triplets (black triangles). The hatched area represents the common natural distribution of Scots pine and oak according to EUFORGEN (www.euforgen.org) (EUFORGEN, 2009a–c).

dry sites at lower elevations (Zerbe, 2002; Schröder et al., 2007; Noack, 2011).

Scots pine and oak mixtures are likely to increase in importance under adaptive forest management due to their high drought resistance compared with other economically important tree species, such as Norway spruce (*Picea abies* (L.) H. Karst.) and European beech (*Fagus sylvatica* L.) (Spellmann et al., 2011; Zang et al., 2011; Albert et al., 2015). However, there is also evidence that this mixture used to be more common in the past, particularly under warmer growing conditions (Björse and Bradshaw, 1998). Empirical studies suggest productivity gains resulting from the mixture of Scots pine and oak (Brown, 1992; Toïgo et al., 2015; Lu et al., 2016; Lu et al., 2018; Pretzsch et al., 2019; Steckel et al., 2019), providing additional incentive for forest owners to establish and manage such forests.

Despite the growing importance of Scots pine-oak mixtures for European forest management under climate change, only a limited number of regional studies (Merlin et al., 2015; Toigo et al., 2015; Bello et al., 2019b; Nothdurft and Engel, 2019) have tried to shed some light on their actual ability to withstand drought stress, reporting both neutral, positive and even negative mixing effects.

The objective of this study was to improve our knowledge of general drought response patterns of two fundamental European tree species in mixed versus monospecific stands. By focusing on the mixture of Scots pine and oak across a comprehensive ecological gradient, covering 33 study sites across 12 European countries, we hope to contribute to a more robust and transferable understanding of the general growth responses under drought stress. For assessing tree drought responses, we considered basic components of tree growth stability (McCann, 2000), as quantified by drought response indices proposed by Lloret et al. (2011): '*resistance*' (Rt), '*recovery*' (Rc) and '*resilience*' (Rs).

To address the research objective, we tested the following null hypotheses:

HI: *Tree drought response does not differ between Scots pine and oak.*
HII: *Tree drought response of Scots pine and oak is not affected by stand composition (mixture versus monoculture).*
HIII: *Tree drought response of Scots pine and oak in mixtures and monocultures is not modified by tree size or site conditions.*

2. Material and methods

2.1. Study area and sites

This study is based on 33 triplets located along a comprehensive ecological gradient through Europe, reaching from nutrient-poorer and drier sites, to nutrient-richer and moister sites (Table A1). A more detailed description of the site selection process and experimental design is outlined in previous studies, focusing on stand structure and productivity (Pretzsch et al., 2019; Steckel et al., 2019).

Each triplet entails three rectangular plots, representing a mixed Scots pine-oak stand and two monospecific stands of each species respectively. The plots represent even-aged, fully stocked stands that exhibit a more or less mono-layered structure (see Table A2 for an overview of the stand characteristics).

The study area covers the overlap of the natural distribution of Scots pine and oak well, reaching from the south-western region in northern Spain to the northern and eastern regions in Sweden and Latvia respectively (Fig. 1). The highest concentration of study sites is found in Central Europe, covering Austria, Czechia, Germany, Poland and Slovakia. Table A1 gives an overview of the prevalent site characteristics for each triplet. The triplets are located at elevations of between 27 and 1635 m a.s.l. (mean = 334 m a.s.l.). The stands mainly grow on cambisols or arenosols, originating from sand or sandstone, but also from fylite, granite, limestone, marlstone or shale/loess. The variation in site fertility is reflected by the species-specific site index (Scots pine: $SI_{S.pi}$, oak: SI_{oa}), quantified by the height, hq (m), of the tree with the quadratic mean tree diameter at age 100. Site indexing was carried out by use of common yield tables (Wiedemann, 1948; Jüttner, 1955), which appear suitable, as they are based on long-term experiments, encompassing a broad range of site conditions (Pretzsch et al., 2019). These hq values range from 17.5 to 36.9 m (mean = 28.1 m) for Scots pine and from 14.8 to 36.0 (mean = 25.8 m) for oak in the analysed monocultures. The mean annual temperature ranges from 6.6 to 10.8 °C (mean = 8.4 °C) and the annual precipitation total from 493 to 1267 mm (mean = 694 mm) (Fig. A1).

2.2. Data collection and preparation

All field work was carried out at the end of the growing season in 2017 using a standardised protocol (Steckel et al., 2019). All living and dead trees with a diameter at breast height (dbh, cm) ≥7 cm were included in the survey (see Table A2 for mean tree characteristics). Two increment cores were taken from at least 20 dominant living trees per species and plot, from north and east cardinal directions. Where available, 10 additional living trees per plot were sampled, covering the rest of the diameter distribution (see Table A3 for an overview of cored trees).

Annual ring widths were measured from each increment core using standardised dendrochronological techniques (Speer, 2010). Cross-dating of the raw ring width series was performed for each plot, guided by narrow ring widths in species-specific pointer years (Schweingruber et al., 1990). Broken and otherwise unreadable cores were neglected.

2.3. Calculation of basal area increment

For the analysis of tree growth responses to drought, the tree basal area increment (bai, cm^2) was used. It was calculated based on the mean annual ring width of both increment cores as $bai_n = (d_n^2 - d_{n-1}^2) * \pi/4$, where d_n is the tree diameter at breast height (dbh) for year n, calculated from the cumulative ring widths for each year. The bai was used as basis of assessment, as it is a two-dimensional measure that is known to better reflect tree growth of the whole tree (volume) rather than the one-dimensional growth of tree ring width (Biondi and Qeadan, 2008).

2.4. De-trending procedures

To remove the long-term trends dependent on age as well as the medium-term oscillations due to past thinning activities, we standardised the bai series using a double de-trending procedure (Thurm et al., 2016). For this, the individual raw bai series were first standardised using the Hugershoff function (Hugershoff, 1936) to eliminate any age-related trends. In a second step, the resulting index values were further de-trended by applying a smoothing cubic spline, fixed by 15 years with a 50% frequency-response cut-off to remove any thinning effects. The detrended bai series were subsequently used to quantify tree drought responses.

To assess the reliability of the de-trended bai series, the appropriate descriptive statistics were computed by use of the R-package dplR (Bunn, 2008) (Table A3). The mean interseries correlation (Rbar) is commonly used to measure the strength of the common growth signal within each chronology (Wigley et al., 1984). In our case, mean Rbar values of between 0.42 and 0.44, indicated a good common signal on average among the individuals sampled in each species-composition group (Table A3). The Expressed Population Signal (EPS) was used to measure the reliability of chronologies (Lindholm et al., 1999). On average, EPS was >0.90 for Scots pine and oak in the studied mixtures and monocultures (Table A3). These values are well above the threshold of EPS > 0.85 introduced by Wigley et al. (1984), indicating that the sampled trees accurately represented the hypothetical population.

2.5. Climate data and identification of drought events

Local meteorological data (monthly mean temperature and monthly precipitation total) were obtained from meteorological stations nearby each triplet. In cases where suitable local station data were not available, gridded data were used as provided by national meteorological services or the CRU (Climatic Research Unit) 0.5°-gridded dataset (Harris et al., 2014).

To characterise the climatic site conditions, we calculated the mean annual meteorological variables (mean annual temperature (T, C°) and annual precipitation total (P, mm)) over a time period of 40 years (1976–2015), based on the acquired monthly data. The De Martonne aridity index (De Martonne, 1926) (DMI, mm $C^{\circ -1}$) (Eq. (1)) characterises the climatic water supply of a given site. It is valued due to its minimal data requirement and high explanatory strength (Bielak et al., 2014; Pretzsch et al., 2015). The greater the index, the better the water supply for plant growth.

$$DMI = \frac{P}{(T + 10)} \tag{1}$$

On the analysed sites, DMI ranged from 25.7 to 63.9 mm $C^{\circ -1}$ (mean = 37.9 mm $C^{\circ -1}$) (Table A1), which translates into a range of semi-humid to very humid growing conditions according to the classification by Baltas (2007).

For analysing tree growth response to drought, we selected site-specific drought events that had a negative effect on tree growth. For this purpose, we developed a selection approach outlined in Fig. A2 and briefly described here:

First, we identified negative pointer years (Schweingruber et al., 1990) (i.e., years with remarkable negative growth responses), using the normalisation in a moving window method (Cropper, 1979) as implemented in the R-package pointRes (van der Maaten-Theunissen et al., 2015). For this analysis, we used the default window width of five years. Years were considered when at least 50% of the de-trended bai series of one of the two species in monocultures at a given site showed a negative event that indicated a growth reduction of >0.75 standard deviation below the mean. Secondly, these negative pointer years were compared to drought years, identified by means of the Standardised Precipitation and Evapotranspiration Index (SPEI) (Vicente-Serrano et al., 2010). This procedure should guarantee that only growth depressions associated with drought conditions were considered, rather than those associated with masting, frost events, insect and disease outbreaks or forest pasture. Additionally, it ensures that the observed meteorological anomaly, evident on the system level, is reflected by actual drought stress, suffered by the studied individuals. The SPEI is a multi-scalar drought index that is based on a monthly balance of precipitation and the potential evapotranspiration (PET). In our study, PET was calculated using the Thornthwaite equation (Thornthwaite, 1948). The SPEI was derived for a time scale of six months. Site-specific drought years were selected based on the approach outlined in Potop et al. (2014), i.e., we considered years that displayed at least one month with a SPEI ≤ -1.0 during the growing season, potentially encompassing moderate to extreme drought conditions. The growing season was determined for each site by selecting months with a minimum mean temperature of ≥ 10 °C (Winkler, 1980). Years which were classified as both negative pointer years and drought years, were considered as drought events and used as a basis for the subsequent analysis.

2.6. Measures of growth in relation to drought

Growth responses to selected drought events were assessed based on tree drought response indices proposed by Lloret et al. (2011), calculated from the detrended bai series. To improve readability of the results, we multiplied the indices with 100 and thus, report them in percent (%).

$$Rt = \frac{G_{Dr}}{G_{PreDr}} * 100 \tag{2}$$

$$Rc = \frac{G_{PostDr}}{G_{Dr}} * 100 \tag{3}$$

$$Rs = \frac{G_{PostDr}}{G_{PreDr}} * 100 \tag{4}$$

The resistance index Rt (Eq. (2)) is the ratio between tree growth during the drought event (G_{Dr}) and the mean growth during the pre-drought period (G_{preDr}). It shows the capacity of trees to buffer drought stress; Rt = 100 indicates complete resistance.

The recovery index Rc (Eq. (3)) is the ratio between the mean growth during the post-drought period (G_{postDr}) and G_{Dr}. It describes the tree's ability to restore a level of growth after disturbance; Rc = 100 indicates persistence of the drought growth level, Rc < 100 indicates a further decline and Rc > 100 indicates a recovery from the growth level during drought.

The resilience index Rs (Eq. (4)) is the ratio between the average growth after (G_{postDr}) and before (G_{preDr}) the drought event, thereby measuring the capacity of trees to return to growth rates as experienced before drought; Rs ≥ 100 indicates a full recovery or increased growth after the drought event, while Rs < 100 indicates growth decline.

Growth during pre- and post-drought periods (G_{preDr}, G_{postDr}) was calculated as the average growth during the three years before, or after, respectively, the studied drought event. This time frame was used as it represents the best trade-off between a sufficiently long period, to ensure a good estimation of the mean growth before and after the drought event, and the risk of an overlap of pre- and post-drought periods with adjacent drought events.

The analysis of tree drought response was restricted to a 40-year time window (1976 – 2015). This time frame is suitable to ensure low variations in stand structure and composition and to consider a sufficient number of site-specific drought events. As a small number of relatively young stands was included in the data set, we introduced an age threshold of 10 years, i.e. drought events were only considered when the stand age at a specific site was 10 years or above. We considered every drought event as a single stress event for each site. To minimise bias, we excluded drought events that showed an overlap of pre- and post-drought periods with adjacent drought events. The final number of site-specific event years ranged from one to five and is outlined in Supplement material 1. The selected drought events include well-reported European droughts as presented by Spinoni et al. (2015). The year 2015 was considered a remarkable drought event and therefore included in the analysis. Due to the fact that trees were sampled in 2017, the post-drought period was reduced to two years in this specific case.

2.7. Modelling approach

In this study, we applied linear mixed-effects models (Pinheiro and Bates, 2004) to account for nesting in the data. By including not only fixed, but also random effects, we were able to account for pseudo-replication, potentially resulting in false, i.e. too progressive, significances (Crawley, 2013). The random effects included in our models address the inter-correlation of samples caused by spatial clustering of trees within the country, triplet group (each triplet is assigned to one of 24 triplet groups, based on its relative location) and triplet. The inclusion of a random effect on the individual tree level did not yield any advantages when comparing models based on the AIC (Akaike Information Criterion) (Akaike, 1981) and was therefore not considered. A separate model was fitted to each of the analysed drought response indices Rt, Rc and Rs. All fitted models were visually checked for homoscedasticity and normal distribution of the residuals. Statistical analyses were conducted in the statistical environment R, version 3.6.0 (R Core Team, 2019), in particular relying on the function lme from the

Table 1
Results of the linear mixed-effects model regressions from Eq. (5). We test a_1, the fixed effect parameter for the dummy-coded binary variable S (species), which becomes 0 for Scots pine and 1 for oak.

Response variable	Statistic	Intercept a_0	S a_1
Rt (%) – Resistance	Estimate	**83.5*****	**1.4***
	SE	1.8	0.7
Rc (%) – Recovery	Estimate	**129.1*****	**−2.8****
	SE	2.3	1.0
Rs (%) – Resilience	Estimate	**100.6*****	**1.2***
	SE	1.6	0.6

S: fixed species effect. Values in bold are significant at level $p < 0.001$ (***), $p<0.01$ (**), $p<0.05$ (*). Non-significant values are denoted by " ns". The number of observations was always n = 5086.

package nlme (Pinheiro et al., 2019).

Below, we present the model equations used to test the hypotheses HI–HIII:

HI: *Tree drought response does not differ between Scots pine and oak.*

Eq. (5) was used to test the general influence of tree species (Scots pine versus oak) on the tree growth response to drought. For this analysis, we only considered monospecific stands in order to exclude any potential confounding effects resulting from the mixture of both species.

$$Y_{ijklm} = a_0 + a_1 * S_{ijkl} + b_i + b_{ij} + b_{ijk} + \varepsilon_{ijklm} \tag{5}$$

In Eq. (5), Y_{ijklm} is the response variable, i.e. the analysed drought response index (Rt, Rc or Rs). The indices represent country (i), triplet group (j), triplet (k), tree (l) and drought event (m) respectively. Coefficient a_1 is a fixed effect parameter for the dummy-coded binary variable S_{ijkl} (species) which becomes 0 for Scots pine and 1 for oak. The terms b_i, b_{ij} and b_{ijk} represent the random intercept effects on the level of country, triplet group and triplet respectively ($b_i \sim N(0, \tau_1^2)$, $b_{ij} \sim N(0, \tau_2^2)$ and $b_{ijk} \sim N(0, \tau_3^2)$). Finally, ε_{ijklm} is an independent and identically distributed error ($\varepsilon_{ijklm} \sim N(0,\sigma^2)$).

HII: *Tree drought response of Scots pine and oak is not affected by stand composition (mixture versus monoculture).*

We used Eq. (6) to test the general influence of stand composition (mixture versus monoculture) on the species-specific tree growth response to drought. This model was fitted for Scots pine and oak separately.

$$Y_{ijklm} = a_0 + a_1 * C_{ijkl} + b_i + b_{ij} + b_{ijk} + \varepsilon_{ijklm} \tag{6}$$

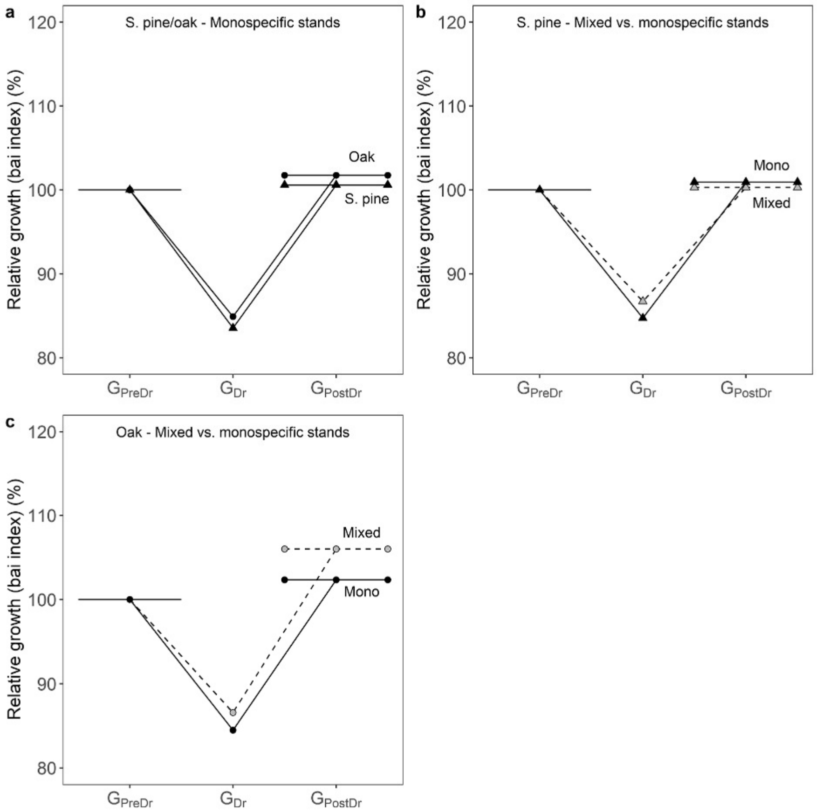

Fig. 2. Estimated growth response to drought (G_{Dr}) as well as growth levels before (G_{PreDr}) and after drought (G_{PostDr}) for Scots pine (triangles) and oak (circles) in mixed (grey symbols, dashed lines) and monospecific stands (black symbols, solid lines) according to Eqs. (5) and (6). Due to the relation to growth before drought, G_{Dr} and G_{PostDr} equal the resistance (Rt) and resilience index (Rs) respectively. a) Comparison of Scots pine and oak trees in monocultures. b-c) Comparison of Scots pine and oak trees growing in mixed versus monospecific stands.

Here, a_1 is a fixed effect parameter for the dummy-coded binary variable C_{ijkl} (stand composition) which is 0 for mixture and 1 for monoculture. The remaining notation is to be understood in the same way as for Eq. (5).

HIII: *Tree drought response of Scots pine and oak in mixtures and monocultures is not modified by tree size or site conditions.*

To analyse the influence of ecological growing conditions on the species-specific tree growth response to drought in mixed and monospecific stands, we expanded Eq. (6) further by adding a collection of tree and site-specific ecological variables and their respective interactions with the mixture effect. This leads to the following saturated model that comprises the complete set of possible fixed effects together with the respective interactions (Eq. (7)).

$$\begin{aligned} Y_{ijklm} = {} & a_0 + a_1 * C_{ijkl} + a_2 * ba_{ijklm} + a_3 * SI_{ijk} + a_4 * DMI_{ijk} \\ & + a_5 * (C_{ijkl} * ba_{ijklm}) + a_6 * (C_{ijkl} * SI_{ijk}) \\ & + a_7 * (C_{ijkl} * DMI_{ijk}) + b_i + b_{ij} + b_{ijk} + \varepsilon_{ijklm} \end{aligned} \tag{7}$$

In Eq. (7), tree size is represented by the tree basal area (ba_{ijklm}) at the time of the drought event m. Site-specific information comprises the species-specific site index ($SI_{S.pi}$, SI_{oa}, denoted as SI_{ijk} in the model), representing site fertility, and the De Martonne aridity index (DMI_{ijk}), representing site water supply. The remaining notation is to be understood in the same way as for Eqs. (5) and (6).

Selection of potentially less complex final models nested in Eq. (7) was based on the AIC (Burnham and Anderson, 1998) and biological plausibility of the results. The selection was made with additional help by an automated AIC-based model selection procedure (function dredge from the R-package MuMIn (Barton, 2019)). To address the research question at hand, C_{ijkl} (stand composition) was included a priori in all final models.

3. Results

3.1. *Influence of tree species (Scots pine versus oak) and stand composition (mixture versus monoculture) on the tree drought response*

Oak trees in monocultures on average showed a greater resistance and resilience compared to Scots pine trees ($p < 0.05$), while recovery was lower ($p < 0.01$) (Table 1, Fig. 2a). Under drought, growth of Scots pine and oak in monocultures was on average reduced to 84% and 85% of the pre-drought period respectively (Table 1, Fig. 2a). Both Scots pine and oak recovered from drought, growing 129% and 126% respectively compared with the growth during drought (Table 1). Scots pine and oak were both resilient to drought, indicated by greater growth after compared to before the stress event, (Rs = 101% for Scots pine and Rs = 102% for oak) (Table 1, Fig. 2a).

Scots pine and oak differed in their reaction patterns depending on stand composition. Scots pine trees showed a greater resistance in mixtures compared with monocultures ($p < 0.01$), although they took longer to recover ($p < 0.001$) (Table 2, Fig. 2b). Oak trees growing in mixtures showed a significantly greater resistance and resilience compared to those in monocultures ($p < 0.001$) (Table 2, Fig. 2c).

3.2. *Influence of ecological growing conditions on the species-specific tree growth response to drought*

Tree size and site water supply had a significant effect on the growth responses to drought in mixtures and monocultures (Table 3). Larger Scots pine trees were more resistant to drought than smaller ones ($p < 0.001$), but took longer to recover ($p < 0.001$). Site water supply, represented by the De Martonne aridity index (DMI), was associated with greater resistance to drought in oak ($p < 0.01$), but not Scots pine (n.s.). Significant interactions between site variables and the composition effect (C) indicate that the general mixing effect on tree drought response presented in 3.1 was not constant along the studied ecological gradient. In particular, for oak the mixture-advantage in terms of resistance and resilience increased with site water supply ($p < 0.001$) (Table 3, Fig. A3b,f). In contrast, species mixing was not favourable for increasing recovery of oak on sites with higher site water supply ($p < 0.05$) (Table 3, Fig. A3d). Furthermore, the mixture benefit regarding resistance of Scots pine decreased with increasing site fertility ($SI_{S.pi}$) ($p < 0.05$) (Table 3, Fig. A4a).

4. Discussion

Our results indicate that the drought responses were species specific (Scots pine versus oak) (Table 1, Fig. 2a) and depended on stand composition (mixture versus monoculture) (Table 2, Fig. 2b-c). Moreover, we found that the analysed ecological factors influenced the general growth response to drought, while also modifying the observed mixing effect (Table 3, Fig. A3, Fig. A4).

The revealed growth responses to drought are well substantiated, owing to the meticulous identification process of independent site-specific drought events, the comprehensive study area as well as the detailed information on tree- and site-specific characteristics. Although no physiological or hydrological measurements were available for this study, our results provide indications for inferring the underlying mechanisms and causes that drive the observed reaction patterns.

During the studied drought events, neither Scots pine nor oak were resistant to drought, as indicated by growth reductions of 16% and 15% respectively in monocultures (Table 1, Fig. 2a). This result was expected, as drought events were identified by negative pointer years. However, the observed magnitude of growth reduction can be seen as representative of the average drought intensity experienced during the selected drought events and allows a comparison of drought responses between species and composition types. The observed reductions in growth were only slightly less than reported by Merlin et al. (2015) for Scots pine and oak, but considerably lower than found for other economically relevant tree species such as European beech and Norway Spruce (Pretzsch et al. 2013, Metz et al., 2016), thereby confirming a relatively high drought resistance of both species studied. However, because we used a double stage detrending that was independently applied in an extra step prior to regression modelling, it is possible that our smooths led to an underestimation of the magnitude of possible climate-related effects. Furthermore, differing criteria for selection of drought events may explain differences between the studies.

Table 2

Results of the linear mixed-effects model regressions from Eq. (6). We test a_1, the fixed effect parameter for the dummy-coded binary variable C (stand composition), which becomes 0 for mixture and 1 for monoculture.

Species	Response variable	Statistic	Intercept a_0	C a_1
Scots pine	Rt (%) – Resistance	Estimate	**86.7*****	**−2.0****
		SE	2.4	0.7
	Rc (%) – Recovery	Estimate	**123.7*****	**4.9*****
		SE	2.7	1.0
	Rs (%) – Resilience	Estimate	**100.3*****	0.6 ^{ns}
		SE	1.9	0.7
Oak	Rt (%) – Resistance	Estimate	**86.6*****	**−2.1*****
		SE	2.6	0.6
	Rc (%) – Recovery	Estimate	**129.8*****	−1.6 ^{ns}
		SE	3.7	1.0
	Rs (%) – Resilience	Estimate	**106.0*****	**−3.7*****
		SE	1.6	0.6

C: fixed composition effect. Values in bold are significant at level $p < 0.001$ (***), $p < 0.01$ (**), $p < 0.05$ (*). Non-significant values are denoted by " ns". The number of observations was always $n = 5167$ for Scots pine and $n = 5120$ for oak.

Table 3
Results of the linear mixed-effects model regressions from Eq. (7). We test the effect of ecological factors on the studied tree drought responses in mixtures and monocultures (fixed effect parameters a_1-a_7).

Species	Response variable	Statistic	Intercept	C	ba	SI	DMI	C*ba	C*SI	C*DMI
			a_0	a_1	a_2	a_3	a_4	a_5	a_6	a_7
Scots pine	Rt (%) – Resistance	Estimate	**65.910*****	**−9.858***	**0.007*****	0.594 ^{ns}	–	–	**0.301***	–
		SE	10.887	4.075	0.001	0.382			0.143	
	Rc (%) – Recovery	Estimate	**132.641*****	**3.849*****	**−0.014*****	–	–	–	–	–
		SE	2.910	1.042	0.002					
	Rs (%) – Resilience	Estimate	**100.289*****	0.633 ^{ns}	–	–	–	–	–	–
		SE	1.872	0.677						
Oak	Rt (%) – Resistance	Estimate	**69.294*****	**14.517*****	–	–	**0.450****	–	–	**−0.433*****
		SE	5.637	2.827			0.131			0.072
	Rc (%) – Recovery	Estimate	**144.004*****	**−11.669***	–	–	-0.372^{ns}	–	–	**0.261***
		SE	12.017	4.581			0.298			0.117
	Rs (%) – Resilience	Estimate	**98.742*****	**9.985*****	–	–	0.190^{ns}	–	–	**−0.355*****
		SE	6.961	2.774			0.179			0.071

C: fixed composition effect. *ba*: reconstructed tree basal area (cm^2). SI: species-specific site index (m) ($SI_{S.pi}$, SI_{oa}). *DMI*: De Martonne aridity index (De Martonne, 1926) (mm °C^{-1}). Values in bold are significant at level $p < 0.001$ (***), $p < 0.01$ (**), $p < 0.05$ (*). Non-significant values are denoted by " ns". The number of observations was always $n = 5167$ for Scots pine and $n = 5120$ for oak.

4.1. Scots pine and oak respond differently to drought

In the studied monocultures, the tree growth response pattern of Scots pine and oak to drought differed significantly. Thus, we reject HI. Resistance and resilience of oak were greater than for Scots pine, suggesting that oak on average had a greater capacity to withstand water stress during the drought events studied and to return to average growth rates as experienced before drought. This finding contradicts Niinemets and Valladares (2006), who assigned greater drought tolerance to Scots pine compared with oak. However, our results confirm a growing body of regional studies that report a more pronounced sensitivity of Scots pine to increased temperatures and drought, suggesting a higher vulnerability compared with pedunculate and sessile oak (Kölling and Zimmermann, 2007; Bello et al., 2019b; Zang et al., 2011) as well as other *Quercus* species (Galiano et al., 2010).

The observed differences in drought response between Scots pine and oak can be attributed to their differing water uptake strategies under drought. Scots pine is characterised by an isohydric strategy, whereas oak is characterised by an anisohydric strategy (Irvine et al., 1998; Zang et al., 2011; Zang et al., 2012; Poyatos et al., 2013; Martínez-Sancho et al., 2017). Under drought, isohydric species are found to reduce water consumption and growth at an early stage by closure of stomata (reduced photosynthesis), whereas anisohydric species continue transpiring until water resources are depleted (McDowell et al., 2008; Domec and Johnson, 2012; Kumagai and Porporato, 2012). Under prolonged water stress, maintenance of transpiration flow in anisohydric plants often requires leaf area control, which reduces water demand (Maseda and Fernández, 2006). Twig abscission is common in oak and enables the trees to avoid runaway embolism (Klugmann and Roloff, 1999). The preventive strategy of isohydric species can reduce stress damage, such as defoliation, loss of fine roots or cavitation of xylem tissue, thereby often resulting in a higher recovery following drought compared with anisohydric species (Leuschner, 1998; Hartmann, 2011). These patterns can be seen as a plausible explanation of the observed species-specific drought reaction, oak exhibiting a significantly higher resistance (i.e., higher productivity), but also a lower recovery than Scots pine.

Differences in resistance behaviour of Scots pine and oak may also arise due to differing seasonal growth dynamics. Oak attains about half of its annual radial growth during spring (Zweifel et al., 2006), when wide earlywood vessels are formed based on reserves carried over from the last growing season. These newly formed vessels are at high risk of cavitation, which may result in water deficit and reduced cell enlargement (Tardif and Conciatori, 2006). In contrast, the growth of Scots pine is concentrated on the summer and early autumn months following needle formation and expansion (Zweifel et al., 2006). Consequently, oak has been found to be more susceptible to spring droughts, whereas Scots pine is more affected by summer droughts (Weber et al., 2007; Merlin et al., 2015; Toigo et al., 2015; Vallet and Perot, 2018; Vanhellemont et al., 2019). Our results may therefore also be related to the generally higher vulnerability of Scots pine to longer summer drought periods and higher mean temperatures, as observed in many regions (Weber et al., 2007). This idea is substantiated by the fact that many of the drought years covered in this study represent well-documented summer droughts, such as for example endured in 1993 (European Drought Centre, 2019), 1996 (Carnicer et al., 2011), 2003 (Ciais et al., 2005; Rebetez et al., 2006; Pichler and Oberhuber, 2007; van der Werf et al., 2007; Lebourgeois et al., 2010; Merlin et al., 2015), 2006 (Merlin et al., 2015) and 2015 (Ionita et al., 2017).

4.2. Stand composition affects drought response of Scots pine and oak

Our results suggest that species mixing can have a significantly positive effect on drought response of scots pine and oak. The resistance of Scots pine was greater in mixture with oak than in corresponding Scots pine monocultures, while recovery was lower. At the same time, resistance and resilience of oak were greater under mixed compared with monospecific stand conditions. Based on these observations, we reject HII. Positive mixing effects are commonly explained by the complementary effect hypothesis (Aarssen, 1997; Loreau, 2000; Loreau and Hector, 2001; Fargione et al., 2007), under which complementarity arises from either facilitation, where one species improves the environmental conditions for another species (Callaway, 2007; Brooker et al., 2008), or reduced competition as a result of niche differentiation (Kelty, 1992; Man and Lieffers, 1999). Both interaction types may be present at the same time and can be difficult to distinguish (Forrester and Bauhus, 2016). Complementary light use, driven by differences in shade tolerance, crown architecture and leaf phenology, can be seen as the prevalent driver of positive mixing effects in Scots pine and oak mixtures under average growing conditions, when water is not the limiting resource (Pretzsch et al., 2019; Steckel et al., 2019). However, as pointed out by Forrester and Bauhus (2016), under periodic drought stress water-related complementarity effects may become more important than under average growing conditions. In this context, oak in mixtures may profit from Scots pine's more conservative stress response strategy, which results in a higher water availability compared to oaks growing with conspecific neighbours (Loreau and Hector, 2001; Pretzsch et al., 2013). Furthermore, spatial stratification of mixed tree species, due to differences in root distribution, architecture or activity, have been shown to improve the exploitation of underground water resources (Schume et al., 2004; Forrester et al., 2010; Schwendenmann et al., 2014). These patterns are likely in the case of Scots pine and oak, as the root morphology differs considerably. The root system of Scots pine is frequently shallow, with no distinct tap root, while oak produces a strong tap root which eventually is replaced by a deep reaching dense system of "heart-roots" (Jones, 1959; Carlisle and Brown, 1968). Furthermore, both Scots pine and oak have been reported to utilise deeper water resources in mixtures compared with monocultures and to exhibit partial niche complementarity for limited water resources (Bello et al., 2019a). Additional complementarity between Scots pine and oak could also arise from seasonal differences in fine root development (Konôpka et al., 2005). Moreover, oak has been shown to exhibit hydraulic lift (i.e., upward hydraulic redistribution) under moderate and severe drought conditions (Caldwell et al., 1998; Jonard et al., 2011; Zapater et al., 2011; Hafner et al., 2017), thereby potentially increasing water availability in the upper soil layers for the admixed species. This form of facilitation is well understood (Neumann and Cardon, 2012; Prieto et al., 2012; Ryel, 2004) and has been hypothesised to be one of the main advantages of mixing oak with other tree species for increased drought resistance (Pretzsch et al., 2013). The admixture of oak may therefore have increased the water availability for Scots pine under drought, resulting in higher radial growth in mixed compared with monospecific stands. The negative relationship between the resistance and recovery of Scots pine suggests a trade-off between both indices, which has also been reported by Gazol et al. (2017) for a wide range of forest types in the Northern Hemisphere and could be attributed to differences in nutrient supply following drought events. Building on Körner (2002), Pretzsch et al. (2013) hypothesise that the more growth and thereby soil nutrient consumption is limited during drought, the more soil nutrients may be available for recovery in the following years. In the case of Scots pine, this means that in monocultures more nutrients may have been available following low growth episodes than in mixtures. Under improving growing conditions (i.e., during post-drought periods), the relationship between Scots pine and oak may on average have changed from complementarity to competition, as suggested by the stress gradient hypothesis (del Rio et al., 2014) and by the complementary inter-specific recovery and resilience pattern observed. For Scots pine, inter-specific competition would then have been greater than intra-specific competition during the post-drought period. In contrast, oak may have experienced a competitive release in mixture compared with monoculture. We assume that when soil water is not the limiting factor, competition for light may become more relevant, resulting in a more asymmetric mode of competition (Hara, 1988; Schwinning and Weiner, 1998; Pretzsch and Biber, 2010; Pretzsch et al., 2018). Under these conditions, oak is more likely to receive a competitive advantage owing to its high crown plasticity (Longuetaud et al., 2013). The stronger resilience of oak in mixtures compared with monocultures could also be caused by a more continuous mineralisation (Pretzsch et al., 2013).

Our findings of an average positive effect of mixing Scots pine and oak are in line with several studies reporting positive diversity effects in terms of tree growth response under drought stress for other species combinations (Lebourgeois et al., 2013; Pretzsch et al., 2013; Metz et al., 2016; Gazol et al., 2017; Mölder et al., 2019). Furthermore, our results are supported by previous studies that reported a positive effect of species mixing on drought stress reduction in oak (del Rio et al., 2014; Bello et al., 2019b) and those who highlight the advantages of admixing oak with other tree species, such as European beech (Pretzsch et al., 2019). In contrast to our findings, neutral (Merlin et al., 2015; Toigo et al., 2015; Bello et al., 2019b) and negative mixing effects (Bello et al., 2019b; Nothdurft and Engel, 2019) have also been reported in Scots pine-oak stands. However, spatial variations in the interactions between tree species regarding growth have been reported for many forests, suggesting that the use of data from limited parts of the species distribution for deriving general mixing effects may be misleading (Forrester, 2014). The before mentioned Scots pine-oak studies are based on a rather small sample of environmental growing conditions, whereas our results reflect the growth behaviour of Scots pine-oak mixtures across a large portion of the natural distribution area. Furthermore, methodological differences, such as limiting the sampling to dominant trees, may explain why these results differ from ours.

4.3. Tree size and site conditions modify species-specific drought responses in mixed and monospecific stands

Based on our observations, we can reject HIII as there was clear evidence that tree size and site conditions significantly affected the growth response to drought in the analysed mixtures and monocultures. Larger Scots pine trees were significantly more resistant than smaller trees, while the opposite pattern was found with regard to recovery (Table 3). The greater growth reduction of smaller Scots pine is likely an effect of dominance, as small Scots pine trees growing in an understory canopy position may compete for light, water and nutrients. In particular, larger trees may have more extensive root systems, increasing the competitive performance under drought conditions (Zang et al., 2014). Our findings are in line with other reports for Scots pine (Pichler and Oberhuber, 2007) and other tree species (Orwig and Abrams, 1997; Vose and Swank, 1994; Martín-Benito et al., 2008), where growth reductions due to drought were greater for understory than for overstory trees. In contrast, other studies have failed to find any significant influence (Bello et al., 2019b), or have reported a negative effect of tree size on drought resistance, arguing that larger trees show a greater vulnerability to hydraulic stress and experience higher radiation and evaporative demand due to exposed crowns than smaller trees (Zang et al., 2012; Bennett et al., 2015; Merlin et al., 2015; Serra-Maluquer et al., 2018). Methodological differences in the definition of tree size classes and the measures for quantifying growth responses to drought may explain the conflicting results as well as the variability in soil and climatic conditions. Contrary to some studies (Jucker et al., 2014; Ledo et al., 2014), we did not find any indication that tree size modified the effect of stand composition on the tree growth response to drought.

Site conditions modified the drought response of both species. We found that the resistance of oak increased with site water supply. This result confirms a previous study by Pretzsch et al. (2013) that reported increased resistance along the gradient of water supply for Norway spruce, European beech and sessile oak. More importantly however, we found that site water supply significantly increased the positive effect of species mixing regarding resistance and resilience of oak (Fig. A3b,f). Consistent with our results, a strong dependence of drought stress reduction on site conditions in mixtures has been reported from different regions in Europe (Forrester et al., 2016; de Streel et al., 2019). Such as demonstrated by Nothdurft and Engel (2019), resistance of Scots pine and oak can also be negatively affected through mixing within certain climate ranges. As observed on the studied sites, species mixing increased resistance and resilience of oak over most of the water supply gradient. However, on the driest sites, resistance of oak was estimated to be lower in mixtures compared with monocultures. This may be seen as indicative of the fact that trees may be more acclimated to drought stress on dry sites, resulting in less pronounced growth reactions (Lévesque et al., 2013), thereby limiting complementarity effects. However, in drought prone environments, the complementary advantage may also be replaced by competition (González de Andrés et al., 2018), unless net water-use partitioning or water-related facilitation take place (Grossiord et al., 2014). Following the conceptual framework by Forrester and Bauhus (2016), we can hypothesise that in the case of oak, complementary light use may be important, in particular on mesic and moist sites, where water is not the limiting resource. Previous studies along the analysed transect (Pretzsch et al., 2019; Steckel et al., 2019) solidify the importance of reduced light competition as the main driver of stand-level overyielding. In these studies, oak was found to exhibit significantly longer and wider crowns in mixtures versus monocultures, thereby promoting light capture. In contrast, the negative influence of site fertility on the mixing effect regarding resistance of Scots pine under drought (Fig. A3a) suggests a stronger dependency on water-related complementarity effects (Forrester and Bauhus, 2016). Our results confirm studies which report that species mixing does not always improve the response to drought stress, but instead varies in its effect in accordance with temporal and spatial variations in environmental conditions (Grossiord et al., 2014; Forrester et al., 2016; Bonal et al., 2017; de Streel et al., 2019).

The findings of our study are of importance for forest managers seeking to mitigate adverse effects of climate change. By being able to predict under which conditions the mixture of two given tree species is favourable and under which conditions it may be disadvantageous, forest management strategies can be optimised. Current climate projections indicate that sites in Southern Europe and large parts of Western Europe will have lower water supply (higher temperature, lower or constant precipitation) by the end of the 21st century, while conditions are likely to remain more constant in Northern Europe and parts of Central Europe (higher temperature, higher precipitation) (Jacob et al., 2014). These scenarios foresee that a substantial proportion of European forests will be located on sites with an annual water supply of less than 30 mm $^{\circ}C^{-1}$. The climate is also likely to become increasingly variable, meaning more frequent and severe droughts in many parts of Europe (Spinoni et al., 2018). These projections, combined with the results from our study, seem to indicate that mixing of Scots pine and oak might especially be recommendable on many sites in Northern Europe and parts of Central Europe, where future average water supply is not expected to decrease severely, but drought events may still increase in frequency and intensity.

5. Conclusions

Our study provides support for species mixing as a valid management option to reduce the drought vulnerability of European forest ecosystems. Based on our results, mixtures of Scots pine and oak can play a considerable role in shaping climate-smart forests along a wide range of ecological growing conditions. We were able to consolidate previous findings that emphasise the facilitative effect of oak on admixed species. It should therefore be considered as a stabilising component under adaptive forest management. However, oak also benefitted significantly from the admixture of Scots pine over most of the studied ecological gradient, in particular on sites with higher average site water supply. Our research highlights the importance of considering a broad range of environmental growing conditions when comparing the performance of mixtures versus monocultures and demonstrates the possibilities and limitations of the ecological concept of complementarity. The results corroborate previous works that report a good complementarity of Scots pine and oak, proposing this species mixture as a promising option under climate change. However, both species are currently pressured in many European regions due to close-to-nature management schemes that promote more competitive shade tolerant species such as European beech. Silvicultural intervention to increase light availability may often be required to ensure the continuance of oak in particular.

Authors' contribution

M. Steckel initiated the study, performed field and increment core measurements, managed the data, carried out the analysis and wrote the manuscript. H. Pretzsch and M. del Río initiated the study and reviewed the manuscript. All authors provided field data and increment core measurements and improved the manuscript.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A

See Figs. A1–A4
See Tables A1–A3

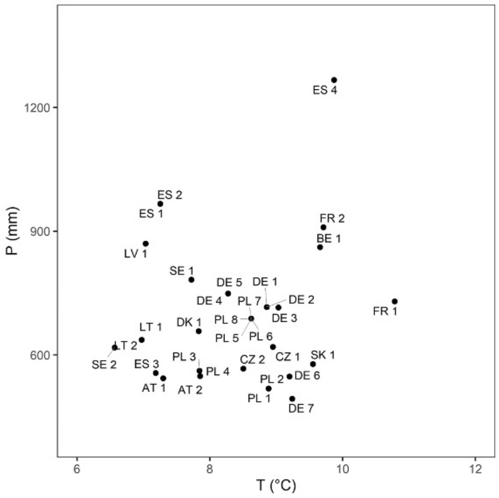

Fig. A1. Location of the 33 Scots pine-oak triplets within the climatic gradient covered. *T*: mean annual temperature (°C). *P*: annual precipitation total (mm). Reference period climate data: 1976–2015.

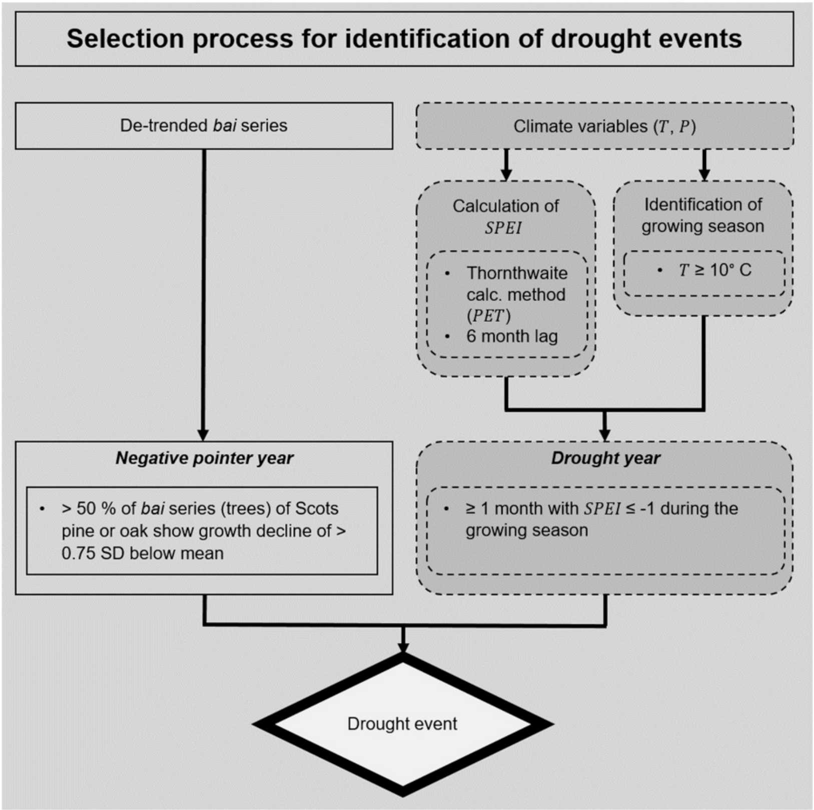

Fig. A2. Flow chart depicting the process for identifying drought events.

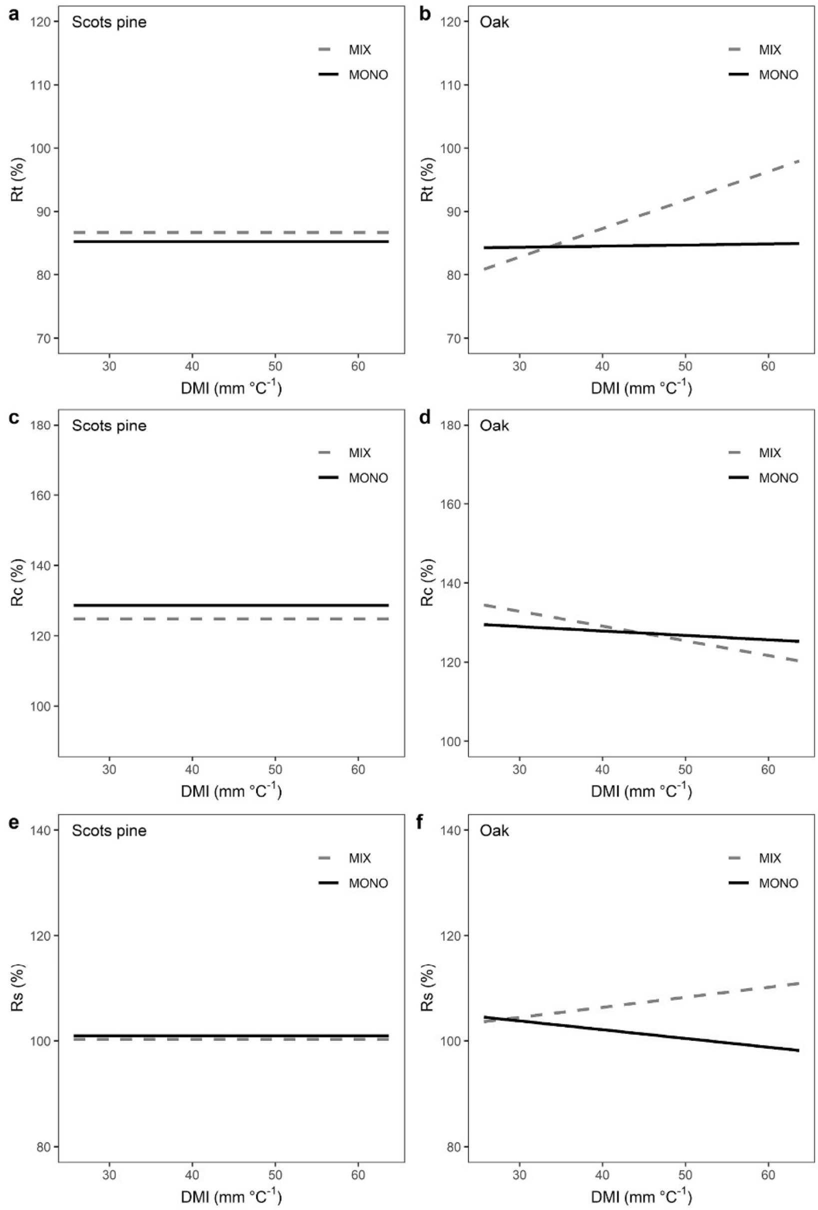

Fig. A3. Effect of the De Martonne aridity index (*DMI*) on the drought response of Scots pine and oak in mixed (dashed grey line) and monospecific stands (solid black line). Lines represent the fixed effect terms from Eq. (7). Variables other than *DMI* were set at the respective means as obtained from the data. a-b) Resistance (*Rt*). c-d) Recovery (*Rc*). e-f) Resilience (*Rs*).

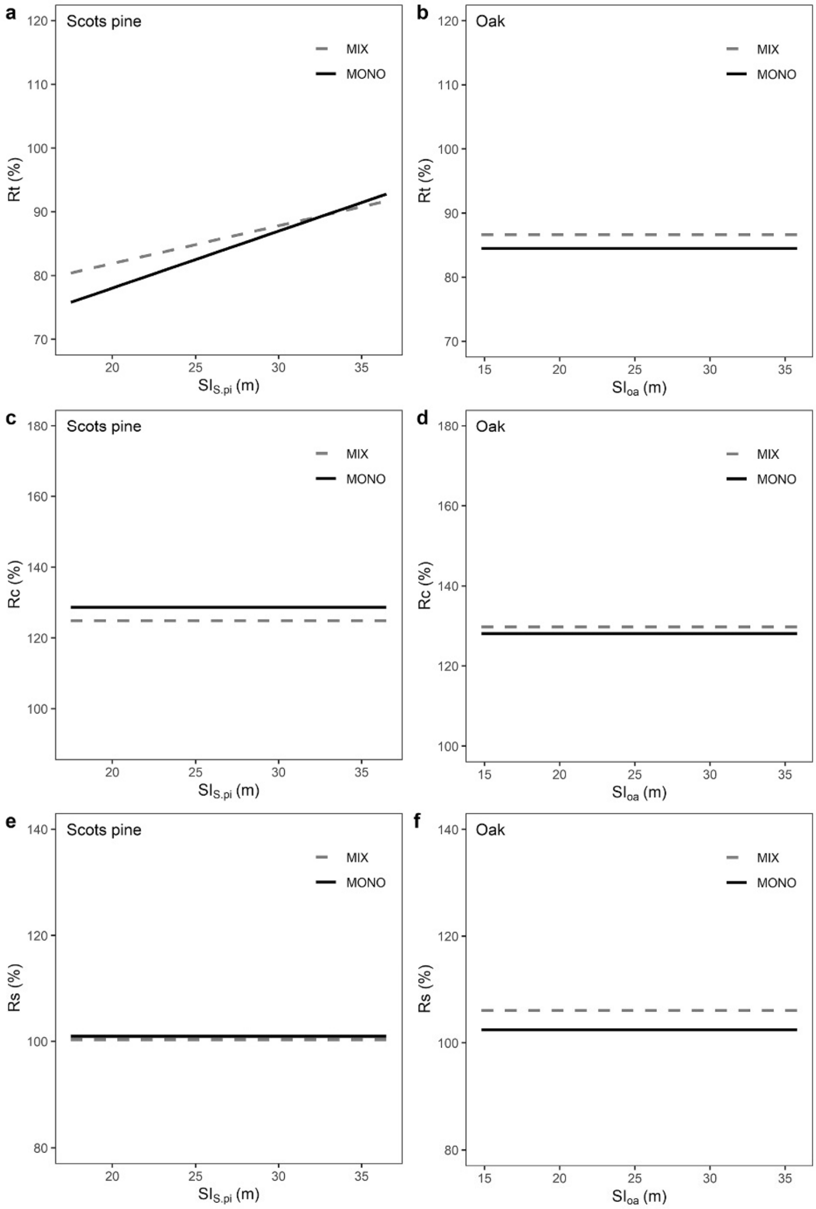

Fig. A4. Effect of the species-specific site index ($SI_{S.pi}$, SI_{oa}) on the drought response of Scots pine and oak in mixed (dashed grey line) and monospecific stands (solid black line). Lines represent the fixed effect terms from Eq. (7). Variables other than SI were set at the respective means as obtained from the data. a-b) Resistance (Rt). c-d) Recovery (Rc). e-f) Resilience (Rs).

Table A1
Site characteristics for all 33 Scots pine-oak triplets.

Triplet	Country	E	T	P	DMI	PM	Soil	Texture	SI	
									$SI_{S.pi}$	SI_{oa}
AT 1	Austria	450	7.3	543	31.5	Sand/loam over granite	Cambisol	Loamy sand	24.3	22.6
AT 2	Austria	450	7.9	548	30.8	Sand/loam over granite	Cambisol	Loamy sand	18.6	17.8
BE 1	Belgium	187	9.7	861	43.9	Shale/loess	Cambisol	Clay loam	29.4	24.2
CZ 1	Czechia	265	9.0	619	32.8	Marlstone	Arenosol	Loamy sand	26.4	20.6
CZ 2	Czechia	400	8.5	567	30.7	Fylite	Cambisol	Loamy sand	27.5	25.2
DE 1	Germany	330	8.9	716	38.0	Sandstone	Cambisol	Loamy sand	21.2	21.1
DE 2	Germany	330	8.9	716	38.0	Sandstone	Cambisol	Loamy sand	21.4	19.7
DE 3	Germany	335	9.0	715	37.7	Sandstone	Cambisol	Loamy sand	24.4	23.1
DE 4	Germany	467	8.3	749	41.1	Sandstone	Stagnosol	Silt/clay loam	30.7	28.7
DE 5	Germany	467	8.3	749	41.1	Sandstone	Stagnosol	Silt/clay loam	30.9	30.8
DE 6	Germany	27	9.2	548	28.6	Sand	Cambisol	Loamy sand	28.9	30.8
DE 7	Germany	347	9.2	493	25.7	Sandstone	Cambisol	Loam	20.7	27.5
DK 1	Denmark	40	7.8	658	36.9	Sand	Arenosol	Sand	25.8	28.0
ES 1	Spain	780	7.3	966	56.2	Sandstone	Cambisol	Sandy loam	25.1	24.7
ES 2	Spain	785	7.3	966	56.2	Sandstone	Cambisol	Sandy loam	27.1	22.7
ES 3	Spain	1635	7.2	556	32.5	Sandstone	Leptosol/Cambisol	Loam	24.2	16.3
ES 4	Spain	1149	9.9	1267	63.9	Limestone/marl/sandstone	Regosol	Silty loam	17.5	16.5
FR 1	France	149	10.8	730	35.2	Sand	Planosol	Sandy loam/clay	27.9	26.0
FR 2	France	270	9.7	910	46.2	Sandstone	Cambisol	Loamy sand	29.5	30.3
LT 1	Lithuania	76	7.0	636	37.6	Sandstone	Arenosol	Loamy sand	30.3	29.0
LT 2	Lithuania	80	7.0	636	37.6	Sandstone	Arenosol	Loamy sand	36.9	26.6
LV 1	Latvia	60	7.0	870	51.2	Sand	Retisol	Loamy sand	35.8	28.9
PL 1	Poland	128	8.9	518	27.5	Sandstone	Arenosol	Loamy sand/sand	33.8	27.3
PL 2	Poland	114	8.9	518	27.5	Sandstone	Arenosol	Loamy sand/sand	33.8	26.3
PL 3	Poland	211	7.8	561	31.6	Sandstone	Luvisol	Sand/sandy loam	32.0	29.8
PL 4	Poland	209	7.8	561	31.6	Sandstone	Luvisol	Sand/sandy loam	34.5	29.5
PL 5	Poland	220	8.6	688	37.1	Sand	Arenosol	Loamy sand	34.4	32.0
PL 6	Poland	220	8.6	688	37.1	Sand	Arenosol	Loamy sand	35.9	31.3
PL 7	Poland	200	8.6	688	37.1	Sand	Arenosol	Loamy sand	33.4	29.6
PL 8	Poland	200	8.6	688	37.1	Sand	Gleysol	Loamy sand	32.8	36.0
SE 1	Sweden	110	7.7	782	44.1	Granite	Cambisol	Sandy loam	19.5	24.8
SE 2	Sweden	120	6.6	618	37.4	Granite	Cambisol	Sandy loam	23.6	14.8
SK 1	Slovakia	223	9.6	578	29.6	Sand	Arenosol	Loamy sand	27.7	28.3

E: elevation (m a.s.l.). T: mean annual temperature (°C) (40-year average 1976–2015). P: annual precipitation total (mm) (40-year average 1976–2015). DMI: De Martonne aridity index (mm $°C^{-1}$) (De Martonne, 1926) (40-year average 1976–2015). PM: parent material. Soil: key reference soil group according to FAO WRB classification (IUSS Working Group WRB, 2015). Texture: texture class according to FAO WRB classification (IUSS Working Group WRB, 2015). SI: site index (m) for Scots pine ($SI_{S.pi}$) and oak (SI_{oa}) monocultures, referring to quadratic mean height, h_q, at age 100.

Table A2
Mean tree and stand characteristics of the 33 triplets of mixed and monospecific stands as sampled in 2017. The evaluation for each plot and species is based on the DESER-Norm 1993 by Johann (1993), using evaluation routines developed by the Chair of Forest Growth and Yield Science at the Technical University of Munich (Biber, 2013).

	MP %	Age years	d_q cm	h_q m	N trees ha^{-1}	SDI trees ha^{-1}	BA m^2 ha^{-1}	V m^3 ha^{-1}	PAIBA m^2 ha^{-1} $year^{-1}$	PAIV m^3 ha^{-1} $year^{-1}$
S. pine + oak					773	823	38.7	419	0.6	10.3
					257–2071	*450–1276*	*20.5–59.3*	*110–567*	*0.2–1.1*	*3.9–16.8*
S. pine mixed	49	74	30.9	23.7	349	440	21.9	238	0.3	5.5
	19–80	*42–132*	*19.5–48.9*	*11.9–33.2*	*51–976*	*145–837*	*7.8–36.4*	*72–475*	*0.1–0.6*	*1.6–10.7*
oak mixed	51	74	26.1	21.5	424	383	16.8	181	0.3	4.8
	20–81	*43–130*	*15.7–39.3*	*9.0–29.3*	*117–1263*	*153–769*	*5.8–29.9*	*38–307*	*0.1–0.5*	*1.5–8.2*
S. pine mono		73	28.4	23.1	795	871	41.2	431	0.7	10.4
		41–130	*18.2–39.2*	*10.8–31.2*	*327–2249*	*395–1354*	*18.3–58.6*	*99–622*	*0.3–1.3*	*3.4–15.9*
oak mono		78	27.1	22.1	774	718	32.7	363	0.6	9.1
		40–126	*14.0–40.7*	*9.1–32.3*	*181–2397*	*393–1034*	*20.3–50.6*	*110–648*	*0.2–1.1*	*4.1–14.9*

Stand characteristics are given for the mixed stand as a whole (S. pine + oak), for the species in the mixed stands (S. pine mixed, oak mixed) as well as for the monospecific stands (S. pine mono, oak mono). The means of all 33 triplets are given in plain text as well as ranges (min–max) in italics. MP: mixing proportion, based on weighted SDI (%). Age: stand age (years). d_q: quadratic mean diameter (cm). h_q: quadratic mean height (m). N: number of trees (trees ha^{-1}). SDI: stand density index (trees ha^{-1}). BA: stand basal area (m^2 ha^{-1}). V: standing volume (m^3 ha^{-1}). PAIBA: five-year (2013–2017) periodic stand basal area increment (m^2 ha^{-1} $year^{-1}$). PAIV: five-year (2013–2017) periodic stand volume increment (m^3 ha^{-1} $year^{-1}$).

Table A3
Descriptive statistics for cored Scots pine and oak trees and their respective detrended *bai* chronologies in mixtures and monocultures.

Composition	Statistic	n	dbh	Rbar	EPS
S. pine mixture	mean	27	33.1	0.44	0.93
	sd	6	8.7	0.10	0.06
	min	7	10.0	0.23	0.69
	max	36	62.0	0.66	0.98
S. pine monoculture	mean	26	31.3	0.44	0.94
	sd	5	7.8	0.08	0.02
	min	14	8.0	0.26	0.87
	max	32	61.8	0.66	0.98
Oak mixture	mean	26	28.0	0.42	0.91
	sd	7	9.8	0.15	0.08
	min	7	7.4	0.13	0.68
	max	40	63.3	0.74	0.98
Oak monoculture	mean	27	30.5	0.43	0.92
	sd	4	9.7	0.16	0.08
	min	16	7.3	0.08	0.60
	max	33	70.0	0.72	0.98

n: number of cored trees. *dbh*: diameter at breast height (1.3 m) of cored trees. *Rbar*: mean interseries correlation (average pairwise correlation between all detrended *bai* series). *EPS*: expressed population signal of detrended *bai* series.

Appendix B. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2020.117908.

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B.3. Article III

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Article

Implications of Reduced Stand Density on Tree Growth and Drought Susceptibility: A Study of Three Species under Varying Climate

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Abstract: A higher frequency of increasingly severe droughts highlights the need for short-term measures to adapt existing forests to climate change. The maintenance of reduced stand densities has been proposed as a promising silvicultural tool for mitigating drought stress. However, the relationship between stand density and tree drought susceptibility remains poorly understood, especially across ecological gradients. Here, we analysed the effect of reduced stand density on tree growth and growth sensitivity, as well as on short-term drought responses (resistance, recovery, and resilience) of Scots pine (*Pinus sylvestris* L.), sessile oak (*Quercus petraea* (Matt.) Liebl.), and ponderosa pine (*Pinus ponderosa* Douglas ex C. Lawson). Tree ring series from 409 trees, growing in stands of varying stand density, were analysed at sites with different water availability. For all species, mean tree growth was significantly higher under low compared with maximum stand density. Mean tree growth sensitivity of Scots pine was significantly higher under low compared with moderate and maximum stand density, while growth sensitivity of ponderosa pine peaked under maximum stand density. Recovery and resilience of Scots pine, as well as recovery of sessile oak and ponderosa pine, decreased with increasing stand density. In contrast, resistance and resilience of ponderosa pine significantly increased with increasing stand density. Higher site water availability was associated with significantly reduced drought response indices of Scots pine and sessile oak in general, except for resistance of oak. In ponderosa pine, higher site water availability significantly lessened recovery. Higher site water availability significantly moderated the positive effect of reduced stand density on drought responses. Stand age had a significantly positive effect on the resistance of Scots pine and a negative effect on recovery of sessile oak. We discuss potential causes for the observed response patterns, derive implications for adaptive forest management, and make recommendations for further research in this field.

Keywords: drought stress; growth sensitivity; *Pinus*; *Quercus*; recovery; resilience; resistance; stand density; thinning; water availability

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1. Introduction

Climatic extremes, such as severe droughts, are expected to become more frequent and increase in intensity as a result of climate change [1]. Drought occurs under low levels of available water, relative to a site's mean condition, being caused by reduced precipitation and/or increased atmospheric evaporative demand combined with low available soil water [2,3]. Forest ecosystems have, in the recent past, proven to be particularly vulnerable to such drastic changes in growing conditions due to their slow natural adaptation rates, ultimately resulting in widespread tree mortality and decreased tree and forest growth [4,5]. Silvicultural strategies, such as growing more drought-resistant tree species and converting monocultures into mixed, uneven aged forests, are seen as promising long-term options for adaptation, to cope with the increasing threat of climate change to forest ecosystem health and functioning [6–8]. However, there is still uncertainty regarding which short-term measures are feasible to mitigate the adverse effects of drought stress in existing stands, still far from rotation age, and to aid the transitioning into more stable forest compositions. Stand density, as a measure of tree abundance in a given area, is a primary driver of competition, with significant implications on tree growth and mortality [9]. Increasing evidence suggests that the reduction of stand density, in addition to accelerating tree growth [10] and increasing the growth responsiveness to environmental conditions [11], can be a mechanism for moderating the effects of drought-induced stress by increasing the vigour of individual trees due to increased average resource availability [12–17]. Reduced stand transpiration due to lower leaf area [18], as well as the formation of more extensive root systems [19], have been reported as contributing factors that may increase tree water availability under reduced competition. However, several studies have also shown detrimental effects of managing lower stand densities, reporting decreased water availability resulting from increased transpiration and evaporative losses that are caused by higher wind speeds and deeper penetration of solar radiation in recently thinned stands [20–22], as well as increased competition for soil moisture [23]. The inconsistency of the current body of knowledge is likely related to several confounding factors that complicate the derivation of generalized reaction patterns. For example, species have been found to react differently to drought under different levels of competition, as a result of varying adaptation strategies between coniferous and broadleaved species [24]. Furthermore, the benefits of reduced competition on drought tolerance have also been found to decrease with stand age due to higher water demands of larger trees in open compared with denser stands [25]. Finally, the effect of stand density on tree drought responses might be modified by climatic factors, such as long-term site aridity [24]. Despite a growing scientific interest in recent years, the relationship between stand density and tree drought susceptibility remains poorly quantified, especially across climatic growing conditions. In addition, under most site conditions, stand density reductions in favour of resource supply and growth of remaining trees, may ultimately cause a loss of stand productivity [26]. Thus, it appears important to know and quantify whether and how much density reductions really mitigate any growth losses that are caused by drought.

To improve the state of knowledge, this study focuses on tree growth and tree drought reactions of Scots pine (*Pinus sylvestris* L.), sessile oak (*Quercus petraea* (Matt.) Liebl.), and ponderosa pine (*Pinus ponderosa* Douglas ex C. Lawson) under different stand density levels and climatic growing conditions. Scots pine and sessile oak constitute two fundamental European tree species that are economically important [27,28] and have proven to exhibit a relatively high drought tolerance as compared with other European tree species, such as European beech (*Fagus sylvatica* L.) and Norway spruce (*Picea abies* (L.) H. Karst.) [29–31]. Scots pine is protected against drought due to embedded stomata and a waxy layer on the epidermis [32], as well as a pronounced stomatal control that helps to regulate transpiration in early stages of drought [33]. However, Scots pine has more recently been found to suffer growth depression and decline in some parts of its natural distribution due to increasing drought stress [34–38]. Furthermore, Scots pine is widely represented on dry, poor, and formerly degraded sites, where it in the past was introduced for afforestation purposes [39]. On these marginal sites, the adverse effects of drought may be particularly pronounced [40]. Sessile oak is often equipped with deep-reaching tap roots that improve the accessibility of water under drought [41] and found to exhibit considerable resistance and resilience to episodic drought stress in mixtures and monocultures [42,43]. In contrast to the drought avoiding isohydric Scots pine, the anisohydric oak is found to keep its stomata open for longer during drought [33], resulting in differing drought reaction patterns of both species [43,44]. Previous studies have revealed positive effects of mixing both species in terms of productivity and growth responses to episodic drought stress over broad ecological gradients [43,45,46]. In Europe, both species endure acute drought stress under episodic water shortage. However, current climate projections indicate that many parts of Europe, in particular southern and western Europe, will have a chronically lower water supply (higher temperature, lower or constant precipitation) by the end of the 21st century [47]. Therefore, forest managers now face the overwhelming task of adapting existing forests, which are still far from rotation age, to unprecedented climatic growing conditions. Thus, it becomes increasingly important to study indigenous tree species growing at the fringes or beyond their natural distribution (e.g.[48]), as well as comparing them with similar tree species, growing under conditions that may resemble future climate scenarios. Against this background, we analogously study ponderosa pine (*Pinus ponderosa* Douglas ex C. Lawson) in Arizona, USA, which, in this region, typically incurs more chronic drought stress conditions and less constant precipitation than Scots pine and sessile oak in Europe. Ponderosa pine is one of the most important timber species in the western United States and also used for a wide range of other applications, including erosion control and ethnobotanic use [49]. Ponderosa pine is able to survive hot and dry conditions, exhibiting a high drought tolerance that is, in part, resulting from deep reaching tap roots that are developed in early stages of tree ontogenesis [50]. Within the southern part of its distribution range, which encompasses the studied sites, it grows at higher elevations up to 3000 m. Regional evidence suggests beneficial effects of reduced stand density on drought responses of Scots pine [39,51,52], sessile oak [53], and ponderosa pine [9,16,54,55], although drought has also been reported to have more negative impacts on radial growth of larger ponderosa pines growing under low stand densities [56].

The objective of this study was to analyse the effect of reduced stand density on the species-specific mean tree growth and mean tree growth sensitivity, as well as on short-term tree growth responses (resistance, recovery, and resilience) to episodic drought stress on sites with different water availability for two of the most important commercial European tree species. We included data from chronically water stressed sites in the U.S. Southwest, analysing the growth behaviour of ponderosa pine, in order to better understand how stand density interacts with tree growth and tree growth responses to episodic drought stress.

To address the research objective, we tested the following hypotheses for each species:

Hypothesis 1 (H1): *Mean tree growth and mean tree growth sensitivity increase under reduced stand density.*

Hypothesis 2 (H2): *Reduced stand density improves tree drought responses.*

Hypothesis 3 (H3): *The benefit of reduced stand density on tree drought responses is moderated by site water availability.*

2. Material and Methods

2.1. Study Sites and Sampling Design

This study is based on individual tree sampling, carried out in monospecific, even-aged, and more or less mono-layered stands of Scots pine and sessile oak in southern Germany (Bavaria) and ponderosa pine stands in the U.S. Southwest (Arizona) (Figure 1). In order to study the influence of stand density on tree growth, trees on each site were sampled from one untreated control stand, exhibiting the site-specific maximum stand density, as well as from two adjacent stands, growing under same site conditions, but providing moderate and low stand densities, respectively. Study sites reflect different levels of site water availability, as represented by the Global Aridity Index (I_A) (cf. 2.4). In Bavaria, the trees were sampled within the framework of existing long-term thinning and spacing trials, maintained by the Chair of Forest Growth and Yield Science, Technical University of Munich. In Arizona, trees were sampled in stands located within the research areas of Fort Valley and Long Valley Experimental Forests, managed by the United States Forest Service. In the sampled stands, the density levels have mostly been maintained for many decades by thinning intervention at certain intervals (Table A1 provides information on the treatment history). Table 1 gives an overview of the site and stand characteristics for all nine study sites. The Bavarian sites are located at elevations of between 380 and 495 m a.s.l. (mean = 433 m a.s.l.), while sites in Arizona are found at elevations of 2079 to 2280 m a.s.l. (mean = 2203 m a.s.l.). The stand age varied from 47 to 68 years (mean = 60 years) in Scots pine, from 34 to 153 years (mean = 93 years) in sessile oak, and from 100 to 105 years (mean = 102 years) in ponderosa pine. The age ranges sampled can be considered to be typical for the species-specific rotation periods in the respective study regions.

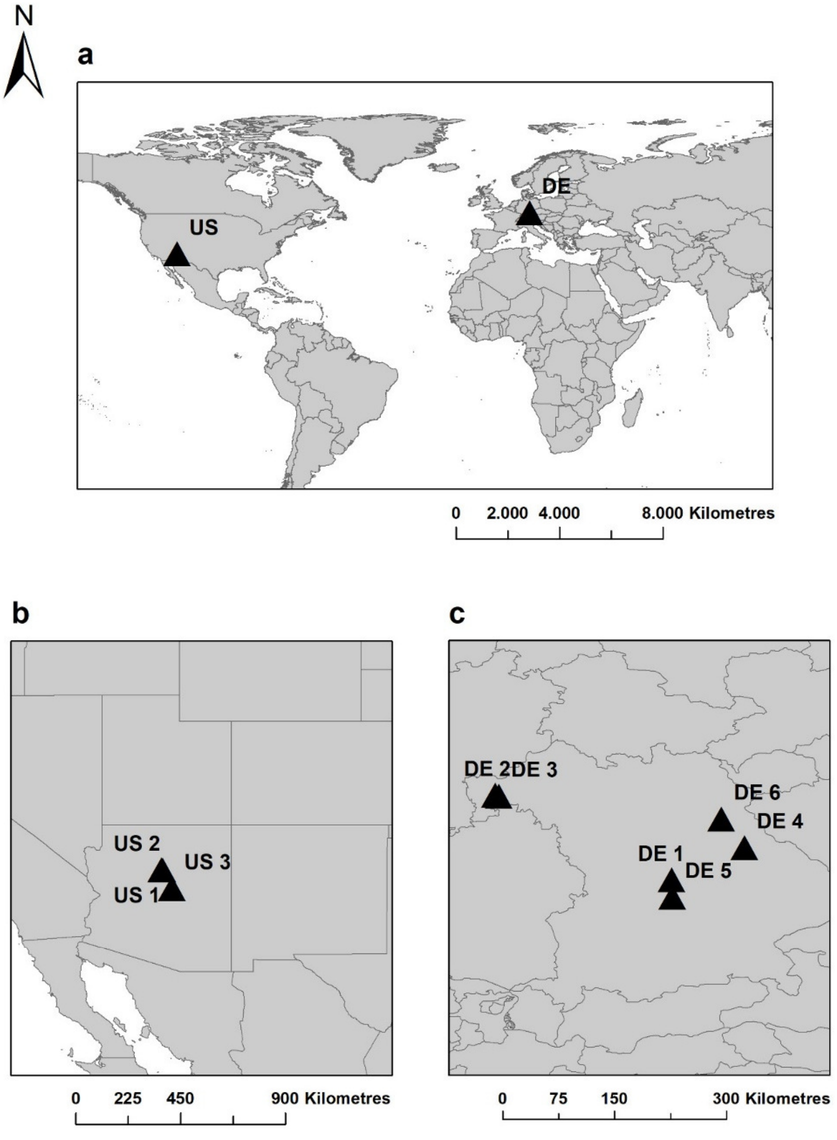

Figure 1. (**a**) Overview of study regions (black triangles) in Arizona, USA (US) and Bavaria, Germany (DE). (**b**) Detailed location (black triangles) of ponderosa pine study sites in Arizona (US 1–US 3). (**c**) Detailed location (black triangles) of sessile oak (DE 1–DE 3) and Scots pine study sites (DE 4–DE 6) in Bavaria.

Table 1. Site and stand characteristics for all nine locations studied in Bavaria, Germany (DE 1–DE 6) and Arizona, USA (US 1–US 3). Age: stand age. E: elevation. T: mean annual temperature. P: mean annual precipitation total. I_A: Global Aridity Index. PM: parent material (geology). Reference period for climatic variables: 1978–2017.

Site	ID	Country	Species	Age yrs	E m a.s.l	T C°	P mm	I_A	PM
DE 1	GEI 649	Germany	sessile oak	34	495	8.3	767	1.26	sand, loess
DE 2	ROB 620	Germany	sessile oak	91	440	8.1	1021	1.70	sand
DE 3	ROB 90	Germany	sessile oak	153	470	8.3	981	1.62	sand
DE 4	BOD 610	Germany	Scots pine	65	400	8.5	722	1.17	sand
DE 5	GEI 335	Germany	Scots pine	68	380	8.9	756	1.20	sand
DE 6	WEI 611	Germany	Scots pine	47	410	8.3	714	1.16	sand
US 1	FV U1	USA	ponderosa pine	105	2250	7.1	575	1.07	basalt
US 2	FV U2	USA	ponderosa pine	100	2280	7.1	612	1.14	basalt
US 3	LV	USA	ponderosa pine	100	2079	9.0	728	1.24	basalt

2.2. Data Collection and Preparation

All fieldwork was carried out at the end of the growing season of 2017, using a standardized protocol, described in the following. At least 15 dominant to co-dominant living trees were selected randomly in stands representing three different levels of stand density (low, moderate and maximum; ≥ 3 × 15 = 45 trees per site). Stand basal area (BA, m^2 ha^{-1}) was measured via angle count sampling [57] at each tree, by use of a level relascope (Spiegel-Relaskop, Relaskop-Technik, Vetriebsges. m.b.H., Salzburg, Austria) in order to confirm stand density levels of selected trees in the field and to gather information on local competition. For each tree, the diameter at breast height (dbh, cm) and height (h, m) were measured (see Table A2 for information on mean tree dimensions). In addition, two increment cores were taken from north and east cardinal directions at breast height, using a 5.15 mm diameter increment borer (Haglöf Sweden AB, Långsele, Sweden). The annual ring widths were measured with an accuracy of 0.01 mm from each increment core, using a Type II digital positioning table after Johann [58] (Biritz and Hatzl GmbH, Vienna, Austria). Cross-dating of the raw ring width series was visually performed for each plot, guided by narrow ring widths in species-specific pointer years [59].

2.3. Dendrochronological Evaluation

The assessment of mean tree growth, mean tree growth sensitivity, and tree growth responses to episodic drought stress was based on the tree basal area increment (bai, cm^2 yr^{-1}), which was calculated from the mean annual ring width of both increment cores as $bai_n = (d_n^2 - d_{n-1}^2) * \frac{\pi}{4}$, where d_n is the tree's dbh for year n. The two-dimensional bai is preferably used, as it better reflects the growth of the whole tree rather than the one-dimensional stem diameter or stem radius increment [60].

A double detrending procedure [61] was applied in order to standardize the bai series. In a first step, we applied a Hugershoff function [62], which was found to better reflect the nature of the observed bai age trend, as compared with a negative exponential function or linear regression, traditionally used for detrending purposes. In a second step, we applied a smoothing cubic spline with a frequency cutoff of 50% at 2/3 of the curve length [63]. This resulted in a dimensionless series of basal area indices for each series, being calculated as the ratio between the actual measured increment and the fitted values. The applied detrending procedure allowed for us to remove long-term trends due to age, size, and stand dynamics [64]. The resulting index series contained only year-to-year variability associated with fluctuations in climate [64,65]. We calculated the mean inter-series correlation ($Rbar$) and the mean expressed population signal (EPS) for each site-specific stand density level to assess the signal strength of the corresponding chronologies [66].

We employed the package $dplR$ [67] from the statistical environment R, version 3.6.1 for descriptive statistics of bai series and all detrending procedures [68].

2.4. Meteorological Data and Selection of Drought Events

Meteorological data (monthly mean temperature and monthly precipitation total) were obtained from gridded datasets provided by the German Meteorological Service (Deutscher Wetterdienst, DWD) [69,70] for the study sites in Bavaria and by PRISM (Parameter elevation Regression on Independent Slopes Model) [71] for the study sites in Arizona. We calculated the mean annual meteorological variables (mean annual temperature (T, C°) and mean annual precipitation total (P, mm)) over a period of 40 years (1978–2017) (Table 1), based on the acquired monthly data, in order to characterize the general climatic site conditions. The mean annual temperature ranged from 8.3 to 8.9 °C (mean = 8.5 °C) on study sites of Scots pine, from 8.1 to 8.3 °C (mean = 8.2 °C) in the case of sessile oak and from 7.1 to 9.0 °C (mean = 7.7 °C) in the case of ponderosa pine. The mean annual precipitation total ranged from 714 to 756 mm (mean = 731 mm) on study sites of Scots pine and from 767 to 1021 mm (mean =923 mm) for sessile oak, while on study sites of ponderosa pine it ranged from 575 to 728 mm (mean = 638 mm). We used the Global Aridity Index (I_A) by the United Nations Environmental Programme (UNEP) [72] as a measure of meteorological site water availability, which determines the relation of moisture supply versus moisture demand (Equation (1)).

$$I_A = P/PET \tag{1}$$

I_A is calculated as the ratio between P and the mean annual potential evapotranspiration (PET, mm). PET was computed from monthly meteorological data, using the Thornthwaite equation [73]. Higher I_A values indicate a better site water availability and improved growing conditions. For sampled sites of Scots pine, the I_A values ranged from 1.16 to 1.20 (mean = 1.18), while for sites of sessile oak and ponderosa pine the corresponding values ranged from 1.26 to 1.70 (mean = 1.53) and from 1.07 to 1.24 (mean = 1.16), respectively (Table 1).

Figure S1 (Supplementary Material) provides information on the average climatic growing conditions throughout the calendar year (climate diagrams according to Walter and Lieth [74] based on the reference period 1978–2017). In Bavaria, precipitation and temperature patterns showed a significant peak in July; however, throughout a typical year, there was a more or less constant relationship between temperature and precipitation without any water deficit. In contrast, the study sites in Arizona exhibited a bimodal precipitation pattern that peaked in winter (December–March) and the summer monsoonal season (July–August); a considerable water deficit was common prior to the start of the monsoonal season. According to Kerhoulas et al. [75], winter precipitation can be considered to be the dominant water source for ponderosa pine trees growing in the studied region.

Tree growth responses to episodic drought were investigated by considering a series of well-reported drought events that occurred in 1976, 2003, and 2015 across Europe [42,76–79] and in 1989, 2002, and 2009 across the U.S. Southwest [9,16,80,81]. In these years, the mean monthly Standardized Precipitation Evapotranspiration Index ($SPEI$) [82], as experienced during the growing season (all months with a mean temperature of ≥ 10.0 °C [83]), ranged from −1.0 to −2.2 (Table A1), indicating a range of moderate to extreme drought intensities according to the classification by Potop et al. [84].

2.5. Quantification of Tree Population Density

We calculated the weighted mean relative stand basal area ($MRBA$) (Equation (2)) as a continuous measure of tree population density and inter-individual competition.

$$MRBA = MBA_{obs}/MBA_{max} \tag{2}$$

Here, MBA_{obs} and MBA_{max} represent Assmann's periodical mean basal area level [85] in m^2 ha^{-1} for the observed stand and the corresponding untreated control stand, respectively. MBA was determined as the mean of the stand basal area between the beginning (BA_b) and the end (BA_e) of the $1 \cdots n$ survey periods, weighted by the length of the survey period (m) (Equation (3)).

$$MBA = \frac{\frac{BA_{1b} + BA_{1e}}{2} * m_1 + \cdots + \frac{BA_{nb} + BA_{ne}}{2} * m_n}{m_1 + \cdots + m_n} \quad (3)$$

This concept of quantifying mean relative stand density has proven useful for analysing density-growth relationships over longer time periods [26]. For example, $MRBA$ = 0.7 indicates that the stand under scrutiny was, on average, kept at a level of 70% of the local maximum during the entire survey time. Information on historic stand density development was sourced from long-term records of existing experiments (DE 1, DE 2, DE 3, DE 4, DE 6, DE 7), based on reoccurring complete inventories of research plots that are associated with the trees sampled, according to the DESER-Norm 1993 by Johann [86]. In other cases, this information was not available for the trees sampled (DE 5, US 1–US 3). Here, the relative stand basal area was derived from the angle count samples taken during the field survey. Table A2 provides information on the $MRBA$ values for each stand. In the case of Scots pine, $MRBA$ ranged from 0.6 to 0.7 (mean = 0.6) and from 0.3 to 0.5 (mean = 0.4) in stands with moderate and low stand density, respectively. Sessile oak stands exhibited $MRBA$ values of between 0.7 and 0.9 (mean = 0.7) and 0.4 to 0.8 (mean = 0.6) in stands with moderate and low stand density, respectively. Moderate stand density in ponderosa pine was characterized by $MRBA$ values of between 0.5 and 0.6 (mean = 0.6), while corresponding values under low stand density levels amounted to 0.3 on average.

2.6. Assessment of Mean Tree Growth, Mean Tree Growth Sensitivity and Short-Term Growth Responses to Episodic Drought Stress

We used two dendrochronological standard characteristics to quantify the average species-specific tree growth behaviour under different levels of stand density. Firstly, the mean raw bai ($Mean$, cm^2 yr^{-1}), which provides a measure of the general tree growth level or potential [87], and secondly, the mean coefficient of variation (CV, %) of the standardized bai index series, which provides information on the high-frequency year-on-year variability that is caused by environmental growing conditions [64,67]. $Mean$ and CV were both calculated based on a 30-year time frame (1988–2017). Short-term tree growth responses to selected drought events were individually assessed for each species by use of drought response indices as proposed by Lloret et al. [88], which were calculated from the standardized bai index series. Resistance Rt (Equation (4)) is calculated as the ratio between tree growth during the drought event (G_{Dr}) and the mean growth during the pre-drought period (G_{PreDr}). Recovery Rc (Equation (5)) is calculated as the ratio between the mean growth during the post-drought period (G_{PostDr}) and the growth during the drought event (G_{Dr}). Resilience Rs (Equation (6)) is defined as the ratio between the average growth after (G_{PostDr}) and before (G_{PreDr}) the drought event. Resistance highlights the tree's ability to maintain growth levels during drought, while recovery can be seen as the ability to restore a level of growth after drought. Resilience exhibits the tree's capacity to recover to pre-drought growth levels.

$$Rt = \frac{G_{Dr}}{G_{PreDr}} \quad (4)$$

$$Rc = \frac{G_{PostDr}}{G_{Dr}} \quad (5)$$

$$Rs = \frac{G_{PostDr}}{G_{PreDr}} \quad (6)$$

G_{PreDr} and G_{PostDr} were calculated as the average growth during the two years before, or after, respectively, the selected drought events. This time frame was used, as it represented the best trade-off between a sufficiently long time, in order to ensure a good estimation of the mean growth before and after the drought event, and the opportunity to study the year 2015, which constitutes a severe drought event in recent European history, characterized by SPEI values that range from −1.5 to −1.8 on the studied sites (Table A1). We considered every drought event as a single stress event for each site. Drought events that coincided with thinning interventions in the same year were not considered in the analysis. In cases where local angle count samples were used to determine relative stand density, the time frame was limited to a maximum of 30 years (1988–2017) and to periods without any recent thinning intervention, in order to ensure low variations in stand structure and inter-individual competition. The final number of site-specific drought events ranged from one to three, as outlined in Table A1.

2.7. Statistical Testing

In this study, we applied linear mixed-effects models to account for nesting in the data, thereby accounting for pseudo-replication, potentially resulting in too progressive significances [89]. A separate model was fitted for each species and response variable ($Mean$, CV, Rt, Rc, and Rs). All of the fitted models were visually checked for homoscedasticity and normal distribution of the residuals. We compared least-squares means of stands with different stand densities (*low*, *moderate*, *maximum*), as specified by the sampling design, to test the overall effect of stand density on mean tree growth and mean tree growth sensitivity (H1). In a next step, we used the weighted mean relative stand basal area ($MRBA$) as a continuous predictor of short-term tree growth responses to episodic drought stress (H2, H3). Statistical analyses were conducted by use of the R-function lme from the package $nlme$ [90].

In the following, we present model equations used to test H1–H3.

H1: *Mean tree growth and mean tree growth sensitivity increase under reduced stand density.*

Equation (7) was used to test the influence of different stand density levels, represented by the categorical variable SD (low stand density: SD_{low}; moderate stand density: SD_{mod}; maximum stand density: SD_{max}), as specified by the sampling design, on the species-specific mean tree growth ($Mean$) and mean tree growth sensitivity, represented by the mean coefficient of variation of the standardized bai index series (CV). The covariate tree size was included in form of the tree basal area (ba) at the time of sampling.

$$Y_{ijk} = a_0 + a_1 * ba_{ijk} + a_2 * SD_{mod\,ij} + a_3 * SD_{max\,ij} + b_i + \varepsilon_{ijk} \tag{7}$$

In Equation (7), Y_{ijk} is the species-specific response variable, i.e., $Mean$ or CV. The indices represent site (i), stand (j) and tree (k), respectively. Terms a_0, a_1, a_2, and a_3 represent the coefficients of fixed effects. The term b_i represents the random effect on the level of site ($b_i \sim N(0, \tau_1^2)$). Finally, ε_{ijk} is an independent and identically distributed error ($\varepsilon_{ijk} \sim N(0, \sigma^2)$). Tukey HSD multiple comparison (R-package $lsmeans$ [91]) was performed for contrasting all levels within SD, as obtained from the linear mixed model, against each other.

H2: *Reduced stand density improves tree drought responses.*

H3: *The benefit of reduced stand density on tree drought responses is moderated by site water availability.*

Equation (8) constitutes the full model to test the influence of the weighted mean relative basal area ($MRBA$) on the species-specific short-term tree growth responses to episodic drought stress and to analyse how this influence might be modified by site water availability, represented by the Global Aridity Index (I_A), and stand age (Age). In addition, we included the covariate tree size (ba) at the time of the drought event.

$$\begin{aligned} Y_{ijkl} = a_0 + a_1 * ba_{ijkl} + a_2 * MRBA_{ij} + a_3 * I_{A_i} + a_4 * Age_{ij} + a_5 * MRBA_{ij} * I_{A_i} \\ + a_6 * MRBA_{ij} * Age_{ij} + b_{ijk} + \varepsilon_{ijkl} \end{aligned} \tag{8}$$

In Equation (8), Y_{ijkl} represents the species-specific tree growth response to drought in form of the drought response indices resistance (Rt), recovery (Rc), or resilience (Rs) on the level of site (i), stand (j), tree (k), and drought event (l). Terms a_0–a_6 represent the coefficients of fixed effects. The term b_{ijk} denotes the random effect on the level of tree ($b_{ijk} \sim N(0, \tau_1^2)$). Finally, ε_{ijkl} is an independent and identically distributed error ($\varepsilon_{ijkl} \sim N(0, \sigma^2)$). The selection of potentially less complex final models nested in Equation (8) was based on the Akaike Information Criterion (AIC)

[92] and biological plausibility of the results. The selection was made with additional help by an automated AIC-based model selection procedure (function $dredge$ from the R-package $MuMIn$ [93]).

3. Results

3.1. Tree Ring Series and Their Basic Statistics

On the nine sites studied, the sampled Scots pine, sessile oak, and ponderosa pine trees covered a representative range of diameter at breast height and tree height (Table A2). Tree ring series were successfully cross-dated and converted into bai series, ultimately resulting in the establishment of chronologies for each site-specific stand density level. Table A2 shows the basic statistics for each chronology. In almost all cases, EPS was well above the critical value of 0.85, proposed by Wigley et al. [66], indicating that the sampled trees accurately represented a hypothetical population. $Rbar$ values of 0.46, on average, also indicate a good common signal across the individuals sampled in each group [94].

3.2. Mean Tree Growth and Mean Tree Growth Sensitivity

The analysis of tree growth characteristics ($Mean$, CV) according to Equation (7) revealed considerable differences in mean tree growth and mean tree growth sensitivity in stands of differing stand density (Figure 2, Table A3). For Scots pine trees growing under low stand density levels, the mean basal area increment (17.3 cm² yr⁻¹) was significantly higher than in the untreated controls (14.8 cm² yr⁻¹), but not significantly different from the moderately dense stands (15.6 cm² yr⁻¹). The mean tree growth of sessile oak was significantly higher under low (17.5 cm² yr⁻¹) compared with moderate (15.1 cm² yr⁻¹) and maximum stand density levels (14.2 cm² yr⁻¹). For ponderosa pine, there was a particularly pronounced significant difference between mean growth under low (15.5 cm² yr⁻¹) versus moderate (8.6 cm² yr⁻¹) and maximum (7.6 cm² yr⁻¹) stand densities.

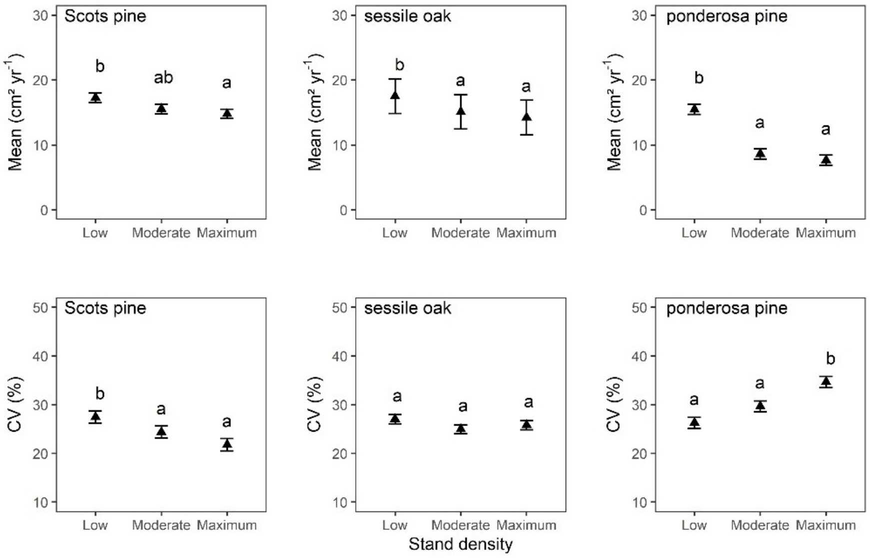

Figure 2. Estimated least-squares means of mean tree basal area increment ($Mean$, cm² yr⁻¹) and mean coefficient of variation (CV, %), representing mean tree growth sensitivity, according to Equation (7) (Table A3) for Scots pine, sessile oak and ponderosa pine growing under different stand density levels

(*low, moderate, maximum*) based on 409 trees (Scots pine: 139; sessile oak: 135, ponderosa pine: 135). $Mean$ was calculated on raw bai series, while CV was calculated on detrended bai index series. Significant differences between the means ($p < 0.05$) are indicated by upper case letters.

For Scots pine, the mean coefficient of variation of basal area increment (CV), i.e., mean tree growth sensitivity, was significantly higher in stands with low stand densities (27%) compared with moderate (24%) and maximum (22%) stand densities. In contrast, CV of ponderosa pine was significantly higher under maximum (35%) compared with low (26%) and moderate (30%) stand density. No significant differences in CV were observed for sessile oak trees growing in stands exhibiting low (CV = 27%), moderate (CV = 25%) and maximum (CV = 26%) stand density.

3.3. Growth Responses to Episodic Drought Stress

As expected, growth decreased during the studied drought events in all species, as witnessed by resistance values of less than 1 on average (Table 2). Average recovery and resilience values of more than 1 indicate a full recovery to above average pre-drought conditions within the time frame of two years. On average, sessile oak seemed only little affected by the drought events studied (1% average growth reduction) when compared with Scots pine (18% average growth reduction) and ponderosa pine (11% average growth reduction).

Table 2. Mean values and standard deviation (sd) of species-specific resistance (Rt), recovery (Rc), and resilience (Rs) indices. Means are calculated for each species over selected site-specific drought events based on standardized basal area increment indices. n = number of observations.

Species	n	Statistic	Rt	Rc	Rs
Scots pine	229	Mean	0.82	1.34	1.07
		sd	0.16	0.34	0.27
sessile oak	225	Mean	0.99	1.04	1.02
		sd	0.20	0.28	0.32
ponderosa pine	359	Mean	0.89	1.41	1.10
		sd	0.37	0.68	0.35

The estimated species-specific tree growth responses to selected episodic drought events are apparent from the results of linear mixed-effects regression modelling according to Equation (8) (Table 3). Higher weighted mean relative stand basal area ($MRBA$) significantly lessened recovery (Rc) and resilience (Rs) of Scots pine, while its resistance (Rt) increased with increasing stand age. Site water availability, represented by the Global Aridity Index (I_A), had a significantly negative effect on the resistance, recovery, and resilience of Scots pine. The effect of stand density on drought responses of Scots pine was significantly influenced by site water availability; the advantage of reduced stand density in terms of drought recovery and resilience gradually decreased with increasing site water availability (Table 3, Figure 3d,g). In the case of sessile oak, a higher $MRBA$ significantly lessened drought recovery, as did higher stand age. Furthermore, the recovery and resilience of sessile oak significantly decreased with increasing site water availability. Analogously to Scots pine, increasing site water availability gradually decreased the advantage of reduced stand density in terms of drought recovery of sessile oak (Table 3, Figure 3e). Resistance and resilience of ponderosa pine significantly increased with increasing $MRBA$, while recovery decreased. In addition, the recovery of ponderosa pine significantly decreased with increasing site water availability. In line with Scots pine and sessile oak, the advantage of reduced stand density in terms of recovery of ponderosa pine significantly decreased with increasing site water availability (Table 3, Figure 3f).

Table 3. Results of the linear mixed-effects model regressions from Equation (8). We test the effect of tree basal area (ba, cm^2), mean relative stand basal area ($MRBA$), Global Aridity Index (I_A), stand age (Age, yrs) and corresponding interactions with $MRBA$ ($MRBA$*I_A, $MRBA$*Age) on the studied species-specific tree drought responses (Rt, Rc, Rs). The number of observations was always n = 229 for Scots pine, n = 225 for sessile oak and n = 359 for ponderosa pine. Bold values are significant at level p < 0.001 (***), p < 0.01 (**), p < 0.05 (*), p < 0.1 (.).

Species	Response Variable	Statistic	Intercept	ba	MRBA	I_A	Age	MRBA * I_A	MRBA * Age
			a_0	a_1	a_2	a_3	a_4	a_5	a_6
Scots pine	Rt—Resistance	Estimate	**5.47** ***	-	-	**−4.34** **	**0.01** **	-	-
		SE	1.44			1.33	0.00		
	Rc—Recovery	Estimate	**16.09** ***	-	**−15.29** **	**−12.42** ***	-	**12.85** *	-
		SE	4.29		5.86	3.62		4.95	
	Rs—Resilience	Estimate	**12.31** ***	-	**−9.92** *	**−9.45** **	-	**8.30** *	-
		SE	3.39		4.62	2.86		3.91	
sessile oak	Rt—Resistance	Estimate	**0.74** ***	-	-	**0.16** .	-	-	-
		SE	0.13			0.08			
	Rc—Recovery	Estimate	**3.41** ***	-	**−1.29** *	**−1.38** ***	**−0.00** ***	**0.82** *	-
		SE	0.45		0.60	0.30	0.00	0.39	
	Rs—Resilience	Estimate	**2.33** ***	-	-	**−0.82** ***	-	-	-
		SE	0.19			0.12			
ponderosa pine	Rt—Resistance	Estimate	**0.71** ***	-	**0.30** ***	-	-	-	-
		SE	0.04		0.07				
	Rc—Recovery	Estimate	**4.76** ***	-	**−4.32** *	**−2.72** *	-	**3.45** *	-
		SE	1.37		2.01	1.18		1.73	
	Rs—Resilience	Estimate	**0.97** ***	-	**0.20** **	-	-	-	-
		SE	0.04		0.06				

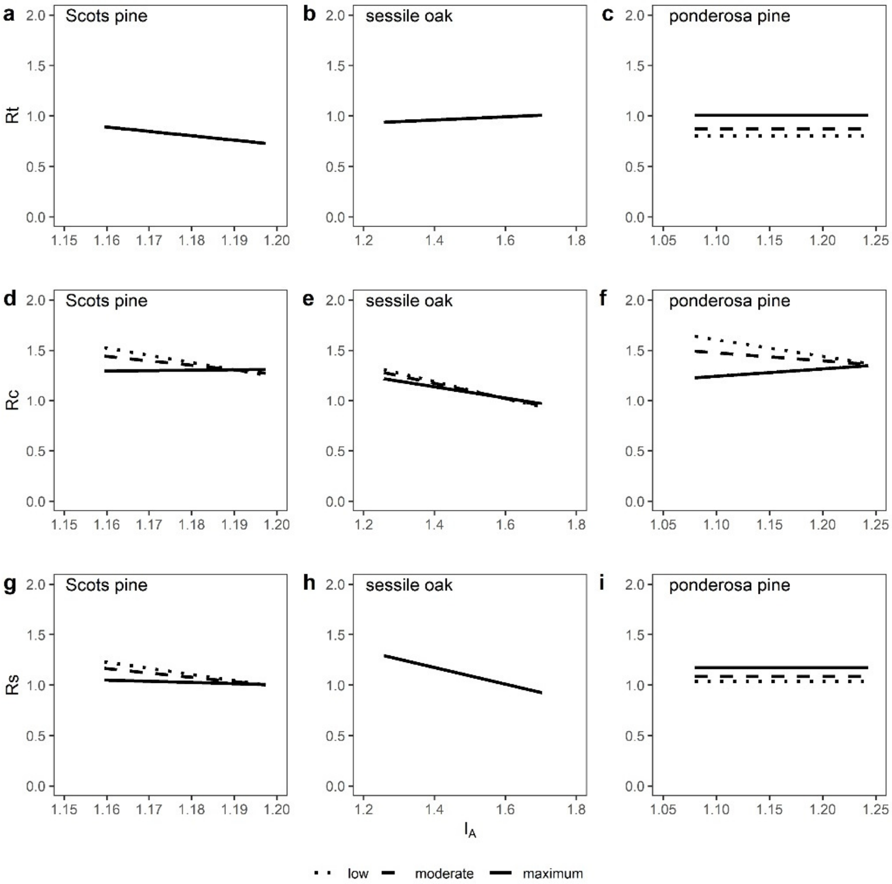

Figure 3. Effect of site water availability (I_A) on the drought responses of Scots pine (Rt (**a**), Rc (**d**), Rs (**g**)), sessile oak (Rt (**b**), Rc (**e**), Rs (**h**)) and ponderosa pine (Rt (**c**), Rc (**f**), Rs (**i**)) under different stand density levels (low, moderate, maximum). Lines represent the fixed effect terms from Equation (8). Explanatory variables other than I_A were set at the respective means of each stand density level as obtained from the data.

4. Discussion

Our study reveals significant species-specific differences in mean tree growth and mean tree growth sensitivity in accordance with prevalent stand density levels. In addition, species-specific short-term tree growth responses to episodic drought stress were found to be significantly influenced by relative stand density, site water availability, and, to a lesser degree, stand age. Of particular interest is the finding that increasing site water availability significantly moderated the positive effect of reduced stand density on drought responses in all species.

The revealed growth patterns are well substantiated, owing to the ecological gradient covered, the investigation of site-specific drought events, characterized by considerable climatic drought stress, as confirmed by the metric $SPEI$, and the detailed information on tree and site characteristics.

4.1. Stand Density Influences Mean Tree Growth and Mean Tree Growth Sensitivity

Mean tree growth was estimated to be higher under low compared with maximum stand densities for all species studied (Figure 2). Scots pine and sessile oak trees growing under low stand densities showed an estimated 17% and 23% higher mean basal area increment, respectively, when compared with fully stocked control stands. For the studied ponderosa pine trees, the stand density effect was even more pronounced, resulting in an estimated 104% higher mean basal area growth in stands with low compared with maximum stand densities. Mean growth in moderately dense stands was in no case significantly different from growth in the fully stocked control plots. Our findings are in line with the general view that tree population density reductions result in accelerated tree growth and that the magnitude of growth increase is directly related to the intensity of the density reduction [e.g.10]. Previous studies have also reported increasing diameter growth with thinning and reduced inter-individual competition in Scots pine [51,52,95–98], sessile oak [18,99,100], and ponderosa pine [16,51,56,101–106]. Stand density reductions can improve the growth of remaining trees by release from inter-individual competition for above and belowground resources, such as light, water, and nutrients [19,26,40], and are therefore often used as a silvicultural measure to maximize diameter growth and tree value on relatively short rotation [10]. At the same time, yield, defined as the entire stand biomass produced since stand establishment [107], might be lower under heavy compared with moderate stand density reductions or untreated controls [95,97,100,103], often prompting a trade-off between enhanced tree growth and stand productivity [26].

Growth sensitivity of trees can be seen as an indicator of the general responsiveness to prevailing environmental conditions, such as fluctuations in annual climate [64]. Mean tree growth sensitivity, measured here as the coefficient of variation of the detrended *bai* index series, was estimated to be 23% greater for Scots pine trees in low stand density environments as compared with fully stocked stands (Figure 2). This general response of growth sensitivity to reduced stand density was also observed by Sánchez-Salguero et al. [98], who reported a higher growth responsiveness to climate under low competition levels for Scots pine along an altitudinal gradient in Spain. Correspondingly, Guillemot et al. [11] found higher inter-annual growth sensitivity with increasing thinning intensity of Atlas cedar (*Cedrus atlantica* (Endl.) Manetti) in the southern French Alps. These and our findings underline the idea that inter-individual competition determines climate sensitivity of individual tree growth. We can hypothesize that in the studied Scots pine stands in Bavaria, where water is not the limiting factor under average growing conditions, competition for light is more relevant. Therefore, the mean climate signal may not be as pronounced in fully stocked stands, while the responsiveness of trees to show a growth reaction in response to annual climate is higher in stands with lower stand densities, where, in addition, a more asymmetric mode of competition might be present [108–110]. This idea is consistent with Pérez-de-Lis et al. [111], who reported increasing climate sensitivity of Canary pine (*Pinus canariensis* Sweet ex Spreng.) with thinning intensity on wet, but not on dry sites. In contrast to Scots pine, we found that mean tree growth sensitivity of ponderosa pine increased with stand density and was 35% higher in the untreated controls compared with low stand densities. In the case of ponderosa pine, growing under chronically water stressed conditions with a more irregular seasonal water supply and a higher frequency of drought events, water can be seen as the principle limiting factor for tree growth. Here, larger trees in the more heavily thinned stands may suffer more from hydraulic constraints and water/nutrient limitations may become more important [98,112]; competition for below-ground resources might be higher due to larger average tree size and associated root systems. Growth sensitivity of sessile oak was not significantly influenced by stand density, which might indicate that inter-individual competition for resources was comparatively low under average growing conditions.

Based on our results, we partly confirm H1, as mean tree growth was positively affected by reduced stand density in all species, but the effect on mean tree growth sensitivity was insignificant in oak and inconsistent when considering the studied pine species.

4.2. Tree Growth Reactions to Episodic Drought Stress are Shaped by Relative Stand Density, Site Water Availability and Stand Age

Water stress endured during the studied drought events on average reduced tree growth in all species (Table 2). The observed growth reductions were, on average, lower than previously reported for these species [42,44,81] and considerably more moderate than reported for other commercial European tree species, such as European beech and Norway spruce [42,113], confirming a comparatively high drought resistance of the species studied. However, it is possible that the smoothing led to and underestimation of the magnitude of possible climate-related effects due to the double detrending procedure used in our study [cf. 43]. Furthermore, differing criteria for selection of drought events may explain the differences between the studies [cf.39]. Differences in the average drought responses between sessile oak and both pine species could be attributed to different water uptake strategies under drought; while anisohydric species, such as sessile oak [30,114], are known to continue transpiration until water resources are depleted [115], isohydric species, such as Scots pine [30,33,114] and ponderosa pine [116], reduce water consumption and growth at an early stage of drought by closure of stomata and reduced photosynthesis [115]. The preventive drought response strategy of isohydric species can reduce stress damage (defoliation, fine root loss, and cavitation of xylem tissue), often resulting in a higher recovery after drought when compared with anisohydric species [117]. Our results confirm the often reported high drought resistance of oak [30,42,43,114], which, in line with the literature, seems to come at the expense of a lower recovery (Table 2).

We found evidence that tree growth responses to drought can be significantly improved by reduced stand density. However, we can only partly confirm H2, as the effect was not always beneficial and it varied between the species studied. Overall, our results suggest that the effect of stand density on drought responses might be correlated with climate sensitivity (cf. 4.1); the higher the climate signal in tree growth, the higher the potential for reduced drought susceptibility. The drought responses of Scots pine were significantly improved by the maintenance of reduced stand density, as recovery and resilience were higher under lower compared with higher stand densities (Table 3), indicating the enhanced ability of Scots pine trees under lower inter-individual competition to recover after drought and reach or exceed pre-drought growth levels. A similar effect was observed in sessile oak, which also exhibited significantly higher recovery under lower compared with higher stand densities (Table 3). In accordance with our findings, previous studies have reported beneficial effects of reduced stand density on post-drought growth responses of Scots pine and sessile oak. For example, studying long-term thinning experiments in Germany, Sohn et al. [39] found that the thinning of Scots pine significantly improved growth recovery and resilience. Accordingly, Giuggiola et al. [51] reported an increase in leaf area to sapwood ratio in response to thinning in a xeric Scots pine forest in Switzerland, indicating reduced competition for water. Based on growth models that were developed from two thinning experiments in Spain, Fernández-de-Uña et al. [52] predicted lessened impacts of climate change under low levels of competition. The positive effects of reduced stand density on Scots pine drought responses could be attributed to decreased transpiration rates and increased hydraulic resistance, as reported for a Scots pine spacing trial in north-eastern Scotland by Whitehead et al. [118]. In the case of sessile oak, only little research has been devoted to studying density effects on growth responses to drought, but, based on a long-term experiment in France, Trouvé et al. [53] found that resilience was significantly lower for suppressed trees in higher density stands. In our study, ponderosa pine showed a distinctly different response pattern in relation to drought under different stand densities; resistance and resilience increased with increasing stand density, while, in line with Scots pine and oak, recovery was reduced (Table 3). In accordance with our findings, McDowell et al. [56] showed that ponderosa pine trees growing in open stands in Arizona, USA were bigger and exhibited a greater relative growth decline under drought than trees growing at a slower rate in high competition environments under high stand densities. They concluded that trees growing in highly competitive environments were less likely to benefit from wet or average growing conditions, but also less vulnerable under drought conditions. Furthermore, particularly strong reductions in stand density, such as those observed on the low density ponderosa pine plots of our study ($MRBA$ = 0.30–0.32), have been reported to counteract generally positive effects of reduced stand density on drought resistance and resilience over time [25]. This was attributed to significantly greater tree sizes being attained within the lower-density stands through stand development, resulting in higher hydraulic constraints and water demand compared with smaller trees. It is also likely that smaller trees and regeneration, which, under more favourable average growing conditions, may not be a significant factor for larger trees growing in the canopy, can constitute considerable competition for limited water resources on chronically water stressed sites, such as those sampled in Arizona, where large ponderosa pine trees may be more reliant on deep soil water than smaller trees [75]. Among the causality mechanisms reported for explaining negative effects of reduced stand density on drought responses, it is likely that increased evaporation and stand transpiration following stand density reductions [20–22] may prove particularly disadvantageous under arid growing conditions, such as those observed on the sampled ponderosa pine sites in Arizona. An explanation of the observed beneficial drought responses of ponderosa pine under higher stand densities may be found in facilitative interactions that may have overridden intraspecific competition, a mechanism observed by Fajardo and McIntire [119] and McIntire and Fajardo [120] in Lenga beech (*Nothofagus pumilio* (Poepp. & Endl.) Krasser) in Patagonia, Chile and confirmed by Owen [121] for ponderosa pine regeneration in Arizona, USA and Calama et al. [122] for Stone pine (*Pinus pinea* L.) in Spain. Fajardo and McIntire [119] proposed habitat amelioration via wind shelter and a reduction in radiation as facilitative processes between conspecific individuals that reduce evapotranspiration and improve water retention. Studying Stone pine at its ecological limit in the arid Spanish Northern Plateau, Calama et al. [122] also reported a positive effect of higher stand density on radial growth under episodic drought, which was seen as indicative of a shift from competition to facilitation under short-term water shortage. As potential causes for such facilitative effects Calama et al. [122] proposed root fusion by spontaneous graftage (*anastomosis*) of close conspecific neighbours, permitting an exploration of deeper ground layers and favouring mycorrhizal activity, as well as a maximization of light interception by the formation of single, umbrella like deep crowns, reducing irradiance and evapotranspiration. In our case, similar mechanisms may have increased ponderosa pine growth responsiveness to climate in dense compared to more open stands and improved growth responses under episodic drought. This seems like an interesting finding, as it, in general, is expected that intraspecific competition is fiercer than inter-specific competition, due to absolute niche overlapping [79,119,123]. In contrast to our findings, a number of studies have reported positive effects of reduced stand density on ponderosa pine tree drought resistance in its natural distribution range [16,55] and beyond [54]. The conflicting results could be related to methodological differences, such as the rationale for selecting trees, drought events, and pre- and post-periods, or differences in stand structure and site conditions. In accordance with our findings, Thomas and Waring [16] reported a positive effect of reduced stand density on the recovery of ponderosa pine.

On average, higher long-term site water availability was found to negatively influence drought resistance, recovery, and resilience of Scots pine. In sessile oak, increasing site water availability lessened recovery and resilience, but had no significant effect on resistance. In addition, recovery of ponderosa pine was, on average, negatively influenced by increasing site water availability. In line with these findings, a previous study reported that Scots pine populations on wetter sites were more impacted by drought than on drier sites [124]. However, other studies have also reported higher growth reductions on drier when compared with wetter sites [42,125], or no significant effect [126]. A recent synthesis for a wide range of forest types in the Northern Hemisphere reported significant effects of water availability on resistance (positive) and recovery (negative), but not resilience [127]. Furthermore, the legacy effects of drought have been reported to be more pronounced on dry when compared with wet sites [128]. Differences in methodological approaches may partially explain these contrasting findings, as many previous studies focused on general growth responses to climate, while our study focused on tree growth responses to specific severe to extreme drought events. It should also be pointed out that mean annual climate variables used in previous studies and ours may hide important seasonal differences among sites.

The impacts of drought on tree growth are understood to be more detrimental in environments with limited water availability [64,76,129]. Thus, the effects of reduced stand density on growth performance are expected to be more positive on sites with scarcer water supply [24]. Consistent with this framework, our results show that, in cases where site water availability significantly influenced the density effect, the benefits of reduced stand density decreased with increasing site water availability (Table 3, Figure 3). Therefore, we confirm H3. Based on a meta-regression of previous regional studies, including investigations of Scots pine, sessile oak, and ponderosa pine, Sohn et al. [24] reported that growth resistance increased with site aridity in heavily thinned and unthinned stands, whereas site aridity had no or even a negative effect in moderately thinned stands. The lack of uniform results in this study was attributed to an imbalanced distribution of studies across taxonomic groups, thinning intensities, and climatic regions, which is not the case in our study. More pronounced effects might be possible for the analysed tree species, especially at marginal sites, as our sites did not reflect the full range of potential growing conditions.

We did not find any indication that tree size had any effect on the studied species-specific short-term drought responses. This result is likely associated with the fact that only information on co-dominant and dominant trees was available in this study, which did not provide a broad range of tree sizes. Other studies, covering a larger part of the diameter distribution, reported significant influences of tree size or social class on drought responses of Scots pine [43], sessile oak [53,76], and ponderosa pine [55,105].

Stand age was found to significantly increase the resistance of Scots pine and reduce the recovery of oak (Table 3). Similar to our findings, Thurm et al. [87] reported a higher resistance with tree age, accompanied by a prolonged growth recovery time in Douglas fir. They proposed that these responses related to higher hydraulic constraints in older trees. In addition, Sohn et al. [39] reported a generally positive effect of stand age on the resistance of Scots pine. While we were not able to confirm a significant influence of stand age on the density effect, Sohn et al. [39] reported that thinning helped to prevent an age-related decline in growth resistance and recovery following drought. Differences in the methodological approach relating to the selection of drought events and the quantification of stand density may explain the differing results.

5. Conclusions

Our study provides empirical evidence that the maintenance of reduced stand densities over longer periods of time can significantly increase mean tree growth, while at the same time reducing tree drought susceptibility of Scots pine and oak by accelerated growth recovery and resilience in the former and increased recovery in the latter case. Therefore, silvicultural measures that reduce inter-individual competition, such as thinning, appear to be a suitable option for adapting existing stands of Scots pine and sessile oak to climate change. This is of high practical relevance, as mortality might be reduced and trees may become less susceptible to secondary pests and pathogens [24]. However, our findings also highlight the need for consideration of local climatic conditions when deciding on the suitability of such adaptation measures; the positive effects of reduced stand density were much stronger on sites with higher aridity, while the effect was reduced or even lost on sites with higher long-term water availability. This finding is new and the results appear promising under current climate scenarios that foresee higher average temperatures and lower or constant precipitation in many European regions, such as southern and western Europe [47]. However, it also prompts further questions as to what effects can be expected under more extreme climatic conditions and under higher seasonal variability in water supply. Our investigation of tree drought responses in chronically water stressed ponderosa pine confirms that, in contrast to Central Europe, where extreme drought events still occur less frequently and average water availability still seems sufficient, the observed relation of stand density and drought susceptibility may be reversed, a response pattern that was characterized by significantly decreased drought resistance and resilience in more open as compared with denser ponderosa pine stands. However, ponderosa pine growing under lower competition levels still exhibited greater recovery, higher absolute growth, and less variable growth overall. Further research should aim at studying the effect of competition on drought responses along larger continuous climatic gradients, encompassing more extreme growing conditions at marginal sites. In addition, the sampling of trees should ideally be conducted along the entire diameter range of a given stand to better account for potential effects of tree size and social class on drought responses under different levels of competition. Future studies should also address the need for further research into the interactions between stand density and microclimate, which might help to better understand the causes for negative effects of stand density reductions on drought responses, particularly with respect to ponderosa pine. Finally, facilitative effects among conspecific neighbours with overlapping ecological niches may, in part, explain the drought response patterns that were observed in ponderosa pine. This constitutes a rather novel view on individual tree interactions under drought with potentially considerable implications for techniques currently employed by forest managers and silviculturists, therefore warranting further examination.

Supplementary Materials: The following are available online at www.mdpi.com/1999-4907/11/6/627/s1, Figure S1: Climate diagrams (reference period: 1978–2017) for all nine study sites in Bavaria, Germany (DE 1–DE 6) and Arizona, USA (US 1–US 3).

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Conflicts of Interest: The authors declare no conflict of interest.

Appendix A

Table A1. Thinning history (year of thinning and subsequent sampling) and analysed episodic drought events (year of drought and corresponding mean *SPEI* value during the growing season in brackets) for each site.

Site	Species	Thinning History (Year of Thinning and Sampling)	Drought Years (SPEI)
DE 1	sessile oak	2004, 2009, 2014	2015 (−1.5)
DE 2	sessile oak	1981, 1986, 1991, 1996, 2002, 2010	2003 (−1.6), 2015 (−1.8)
DE 3	sessile oak	1934, 1942, 1952, 1958, 1966, 1976, 1986, 1996, 2006, 2013	2003 (−1.6), 2015 (−1.8)
DE 4	Scots pine	1966, 1977, 1986, 1993, 1998, 2003, 2008, 2015	1976 (−1.2)
DE 5	Scots pine	2002	2003 (−2.1), 2015 (−1.4)
DE 6	Scots pine	1987, 1992, 1997, 2002, 2007, 2014	2003 (−1.7), 2015 (−1.6)
US 1	ponderosa pine	1925, 1934	1989 (−1.4), 2002 (−2.1), 2009 (−1.3)
US 2	ponderosa pine	1924, 1935, 1946, 1967, 1968, 1988, 1997	2002 (−2.2), 2009 (−1.3)
US 3	ponderosa pine	1925, 1936	1989 (−1.0), 2002 (−2.2), 2009 (−1.3)

Table A2. Mean tree and chronology characteristics by species, site and stand density level (*SD*). *n*: number of trees sampled. *dbh*: diameter at breast height. *h*: tree height. *MRBA*: weighted mean relative stand basal area. *Rbar*: inter-series correlation. *EPS*: expected population signal.

Species	Site	SD	*n*	dbh	h	MRBA	Rbar	EPS

				cm	m			
sessile oak	DE 1	Low	15	21.8	18.5	0.44	0.55	0.95
		Mod	15	18.5	18.3	0.65	0.45	0.92
		Max	15	18.3	19.0	1.00	0.56	0.95
	DE 2	Low	15	38.4	26.2	0.60	0.54	0.94
		Mod	15	34.8	27.2	0.73	0.56	0.94
		Max	15	28.2	28.3	1.00	0.52	0.94
	DE 3	Low	15	48.7	31.1	0.80	0.50	0.92
		Mod	15	44.0	30.5	0.86	0.59	0.95
		Max	15	35.5	29.0	1.00	0.54	0.94
Scots pine	DE 4	Low	15	30.4	20.8	0.47	0.41	0.90
		Mod	16	25.5	20.7	0.58	0.44	0.92
		Max	15	28.1	24.7	1.00	0.43	0.91
	DE 5	Low	17	38.3	23.5	0.30	0.40	0.91
		Mod	15	37.0	24.7	0.56	0.44	0.91
		Max	15	30.6	24.9	1.00	0.52	0.94
	DE 6	Low	15	24.1	18.2	0.50	0.57	0.95
		Mod	15	15.6	13.7	0.70	0.48	0.93
		Max	17	14.9	14.5	1.00	0.49	0.94
ponderosa pine	US 1	Low	15	40.8	17.1	0.30	0.47	0.93
		Mod	15	35.1	19.2	0.52	0.29	0.84
		Max	15	27.6	19.4	1.00	0.33	0.88
	US 2	Low	15	31.3	14.0	0.32	0.55	0.90
		Mod	15	27.4	13.4	0.61	0.58	0.95
		Max	15	22.3	12.7	1.00	0.44	0.92
	US 3	Low	15	36.8	13.8	0.31	0.32	0.84
		Mod	15	33.6	17.9	0.56	0.35	0.88
		Max	15	23.7	15.6	1.00	0.18	0.74

Table A3. Results of the linear mixed-effects model regressions from Equation (7). We test the effect of tree basal area (ba, cm^2), and stand density level (SD_{min}, SD_{mod}, SD_{max}) on the mean tree growth ($Mean$, cm^2 yr^{-1}) and the mean growth sensitivity (CV, %). The number of observations was always n = 139 for Scots pine, n = 135 for sessile oak and n = 135 for ponderosa pine. Bold values are significant at level p < 0.001 (***), p < 0.01 (**), p < 0.05 (*), p < 0.1 (.).

Species	**Response Variable**	**Statistic**	**Intercept**	**ba**	**SD$_{\text{mod}}$**	**SD$_{\text{max}}$**
			a_0	a_1	a_2	a_3
Scots pine	Mean	Estimate	1.45	**0.02 *****	**−1.73 .**	**−2.48 ***
		SE	1.70	0.00	0.98	1.01
	CV	Estimate	**31.59 *****	**−0.01 *****	**−3.09***	**−5.65 *****
		SE	2.64	0.00	1.19	1.23
sessile oak	Mean	Estimate	3.93	**0.01 *****	**−2.41****	**−3.27 *****
		SE	4.85	0.00	0.80	0.92
	CV	Estimate	**27.68 *****	−0.00	−2.03	−1.21
		SE	2.30	0.00	1.30	1.46
ponderosa pine	Mean	Estimate	**9.24 *****	**0.01 *****	**−6.87 *****	**−7.84 *****
		SE	1.69	0.00	0.83	0.96
	CV	Estimate	**27.91 *****	−0.00	**3.40 ***	**8.38 *****
		SE	2.74	0.00	1.62	1.87

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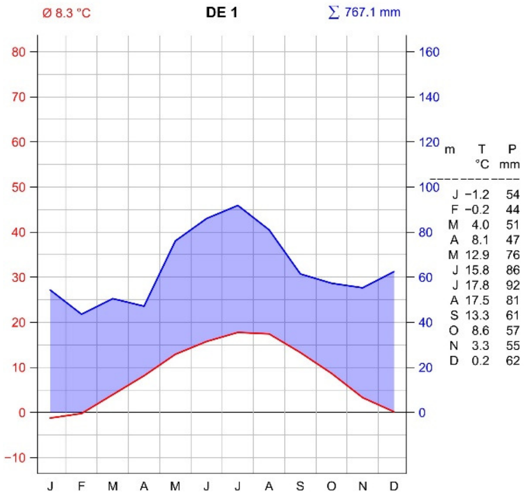
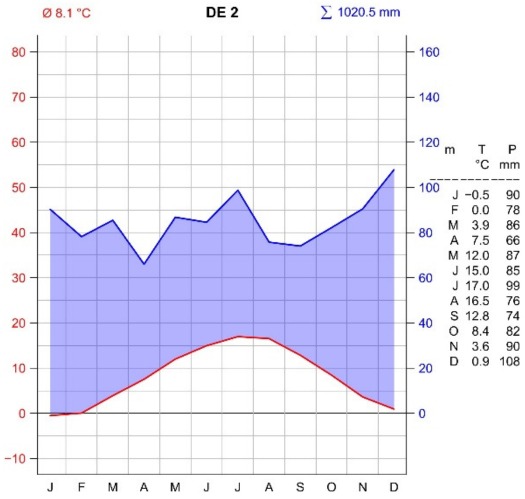
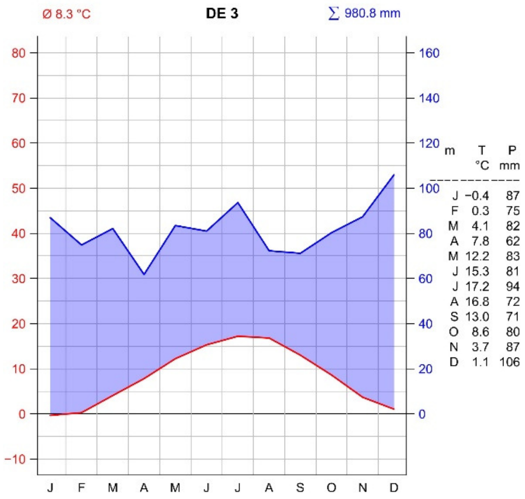
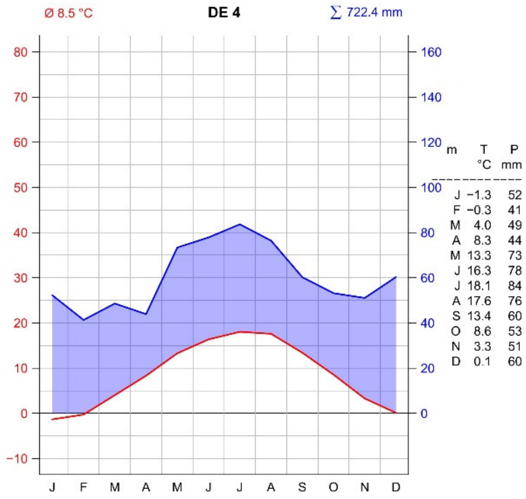
C. Supplement material

Supplement Material S1. Climate diagrams (reference period: 1978–2017) for all nine study sites in Bavaria, Germany (DE 1–DE 6) and Arizona, USA (US 1–US 3). Reprinted from Steckel et al. (2020b).

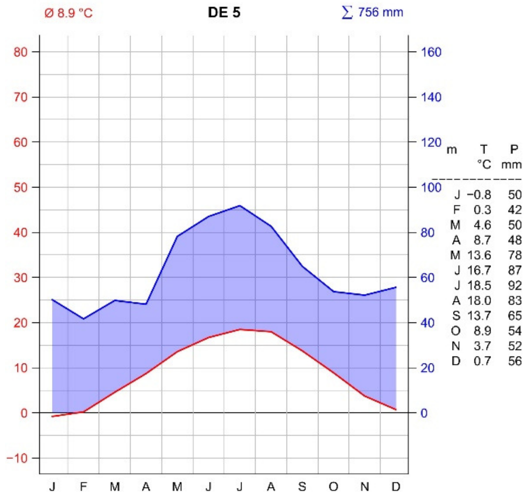




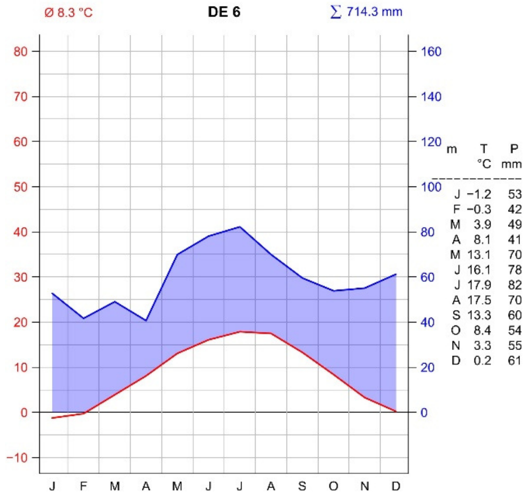




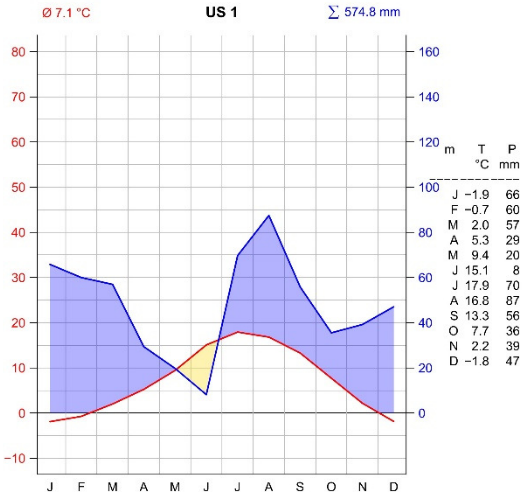
m	T °C	P mm
J	−1.3	52
F	−0.3	41
M	4.0	49
A	8.3	44
M	13.3	73
J	16.3	78
J	18.1	84
A	17.6	76
S	13.4	60
O	8.6	53
N	3.3	51
D	0.1	60



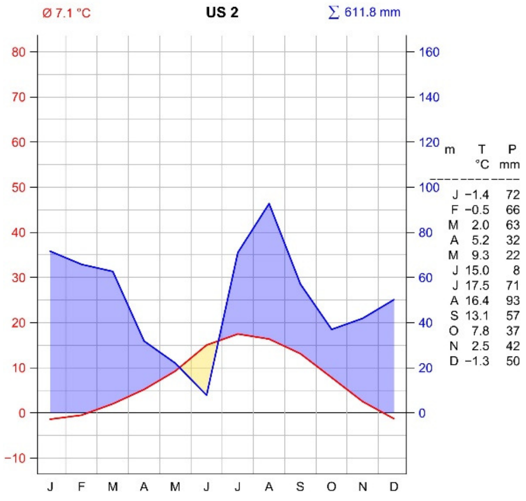
m	T °C	P mm
J	−0.8	50
F	0.3	42
M	4.6	50
A	8.7	48
M	13.6	78
J	16.7	87
J	18.5	92
A	18.0	83
S	13.7	65
O	8.9	54
N	3.7	52
D	0.7	56



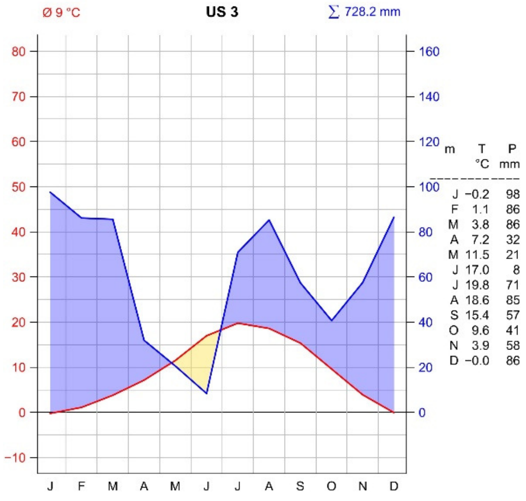
m	T °C	P mm
J	−1.2	53
F	−0.3	42
M	3.9	49
A	8.1	41
M	13.1	70
J	16.1	78
J	17.9	82
A	17.5	70
S	13.3	60
O	8.4	54
N	3.3	55
D	0.2	61



m	T °C	P mm
J	−1.9	66
F	−0.7	60
M	2.0	57
A	5.3	29
M	9.4	20
J	15.1	8
J	17.9	70
A	16.8	87
S	13.3	56
O	7.7	36
N	2.2	39
D	−1.8	47



m	T °C	P mm
J	−1.4	72
F	−0.5	66
M	2.0	63
A	5.2	32
M	9.3	22
J	15.0	8
J	17.5	71
A	16.4	93
S	13.1	57
O	7.8	37
N	2.5	42
D	−1.3	50



m	T °C	P mm
J	−0.2	98
F	1.1	86
M	3.8	86
A	7.2	32
M	11.5	21
J	17.0	8
J	19.8	71
A	18.6	85
S	15.4	57
O	9.6	41
N	3.9	58
D	−0.0	86

Supplement Material S2. Mean tree and stand characteristics of the 33 triplets of mixed and monospecific covered in *Article II*. Stand characteristics are given for the mixed stand as a whole (S. pine + oak), for the species in the mixed stands (S. pine mixed, oak mixed), as well as for the monospecific stands (S. pine mono, oak mono). The means of all 33 triplets are given in plain text, as well as ranges (*min-max*) in italics.

	MP	**Age**	**d_q**	**h_q**	**N**	**SDI**	**BA**	**V**	**PAIBA**	**PAIV**
S. pine + oak					773	823	38.7	419	0.6	10.3
					257–2071	*450–1276*	*20.5–59.3*	*110–567*	*0.2–1.1*	*3.9–16.8*
S. pine mixed	49	74	30.9	23.7	349	440	21.9	238	0.3	5.5
	19–80	*42–132*	*19.5–48.9*	*11.9–33.2*	*51–976*	*145–837*	*7.8–36.4*	*72–475*	*0.1–0.6*	*1.6–10.7*
oak mixed	51	74	26.1	21.5	424	383	16.8	181	0.3	4.8
	20–81	*43–130*	*15.7–39.3*	*9.0–29.3*	*117–1263*	*153–769*	*5.8–29.9*	*38–307*	*0.1–0.5*	*1.5–8.2*
S. pine mono		73	28.4	23.1	795	871	41.2	431	0.7	10.4
		41–130	*18.2–39.2*	*10.8–31.2*	*327–2249*	*395–1354*	*18.3–58.6*	*99–622*	*0.3–1.3*	*3.4–15.9*
oak mono		78	27.1	22.1	774	718	32.7	363	0.6	9.1
		40–126	*14.0–40.7*	*9.1–32.3*	*181–2397*	*393–1034*	*20.3–50.6*	*110–648*	*0.2–1.1*	*4.1–14.9*

MP: mixing proportion based on weighted SDI (%). Age: stand age (yrs). d_q: quadratic mean diameter (cm). h_q: quadratic mean height (m). N: number of trees (trees ha^{-1}). SDI: stand density index (trees ha^{-1}) (Reineke, 1933). BA: stand basal area (m² ha^{-1}). V: standing volume (m³ ha^{-1}). $PAIBA$: five-year (2013-2017) mean periodic stand basal area increment (m² ha^{-1} yr^{-1}). $PAIV$: five-year (2013-2017) mean periodic stand volume increment (m³ ha^{-1} yr^{-1}).

Supplement Material S3. Selected site-specific drought events. Grey bars indicate the monthly $SPEI$ (Standardised Precipitation Evapotranspiration Index) (growing season highlighted by dark grey bars). Drought events are identified according to the framework presented in Figure 7. Solid black triangles indicate selected drought events used in the analysis, while empty triangles indicate drought events that were not considered in the analysis due to overlaps of G_{Dr} with G_{PreDr} or G_{PostDr}. Grey triangles indicate drought events that were neglected as the respective stand age was <10 years. Reprinted from Steckel et al. (2020a).

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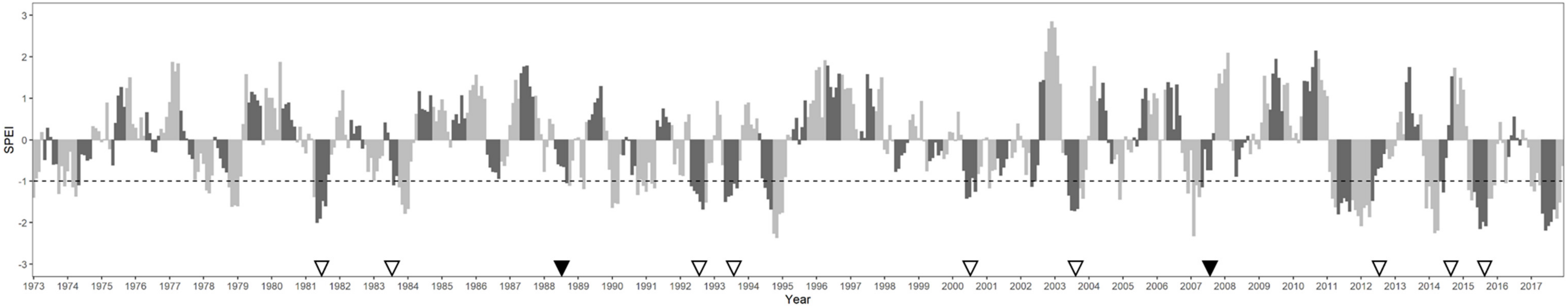

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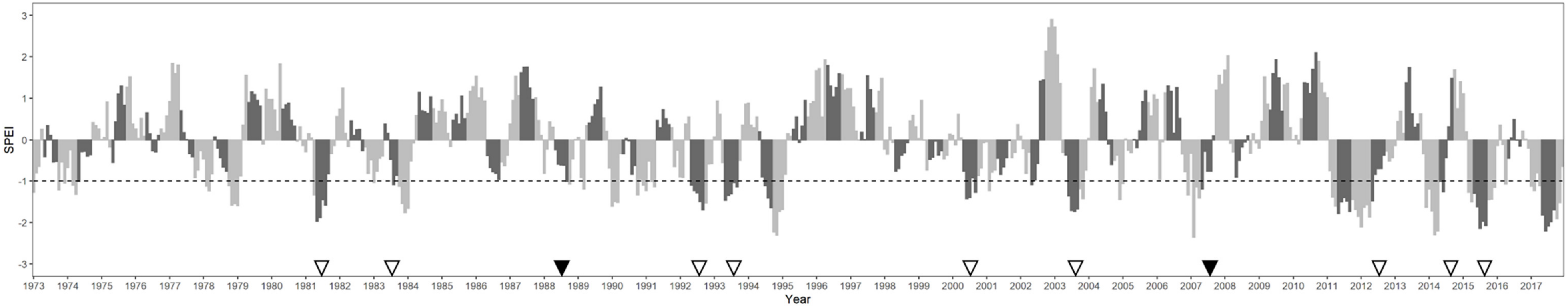

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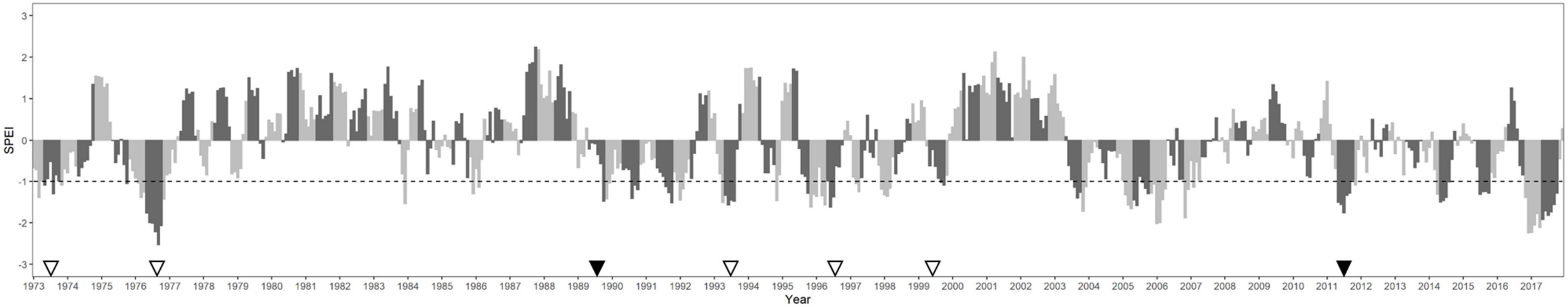
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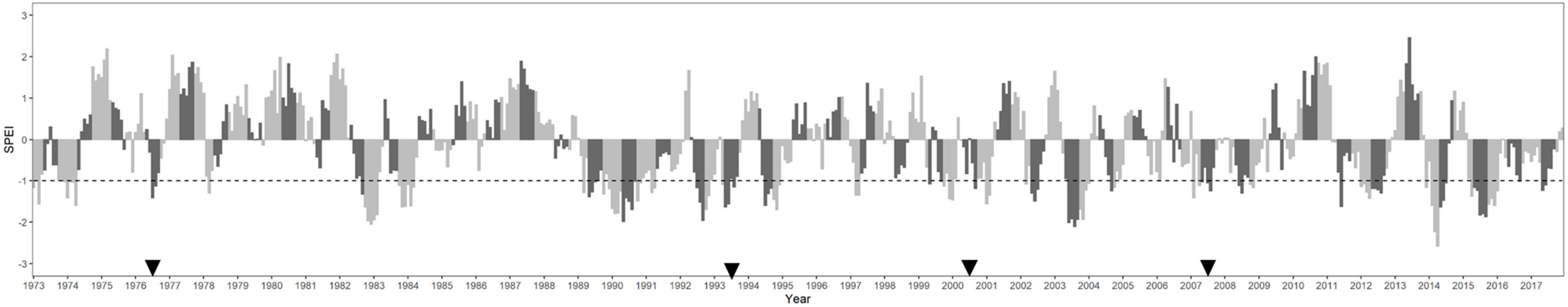
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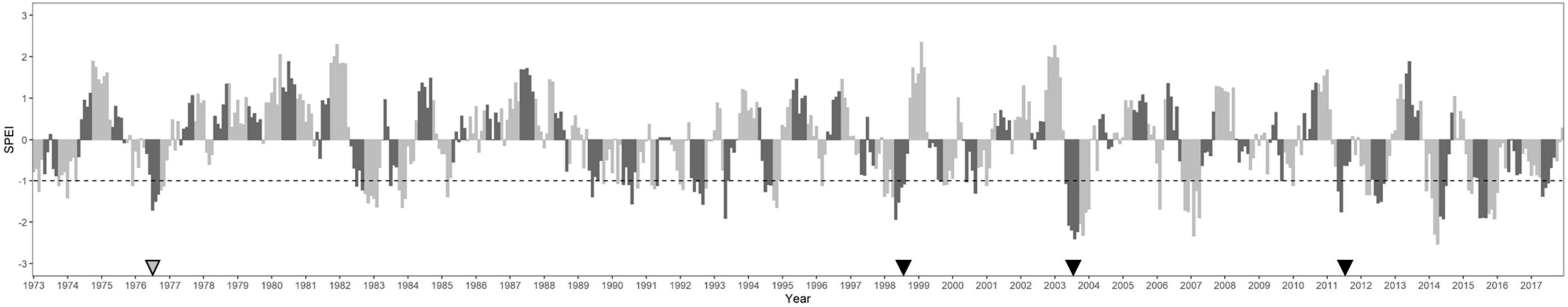
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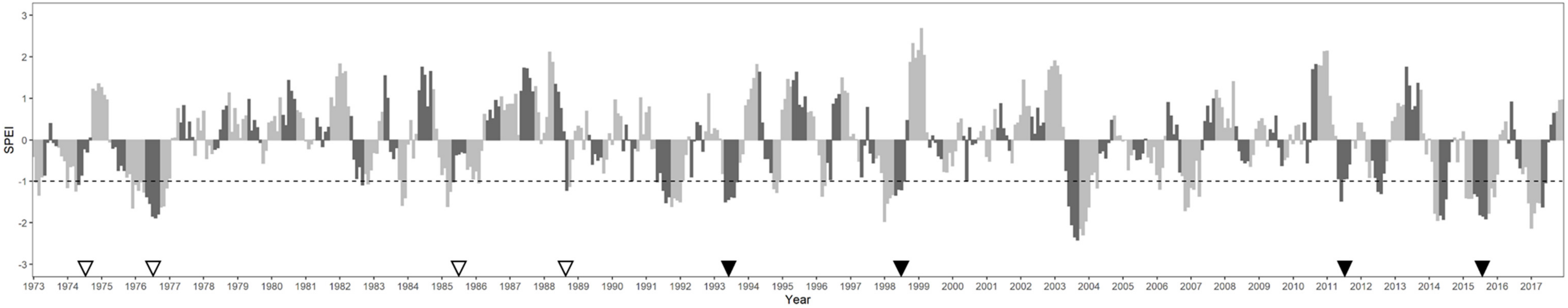
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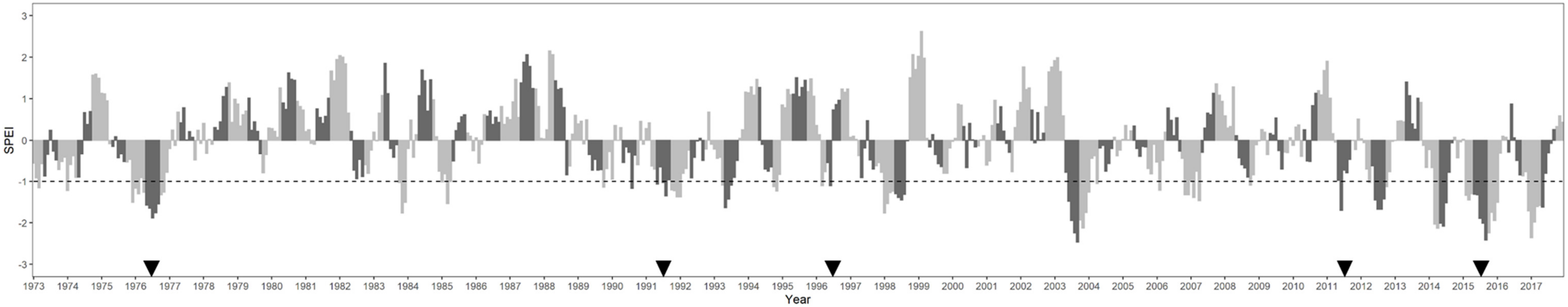
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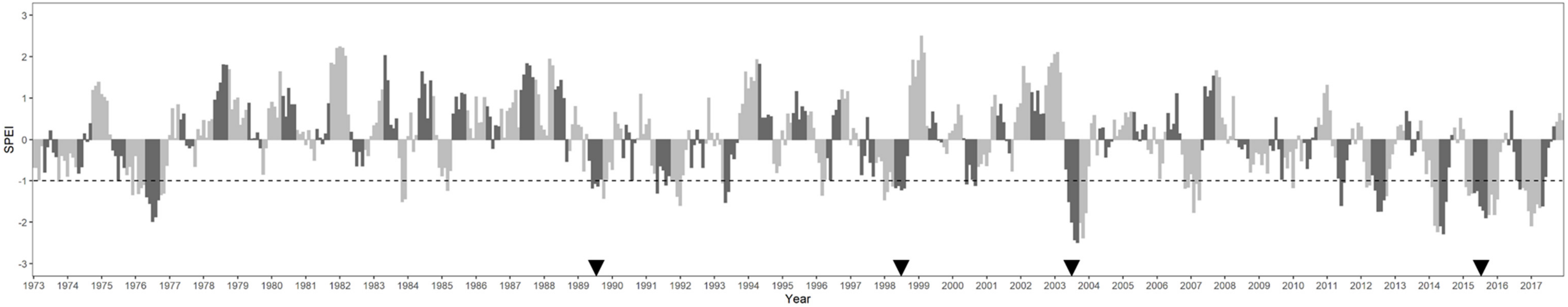
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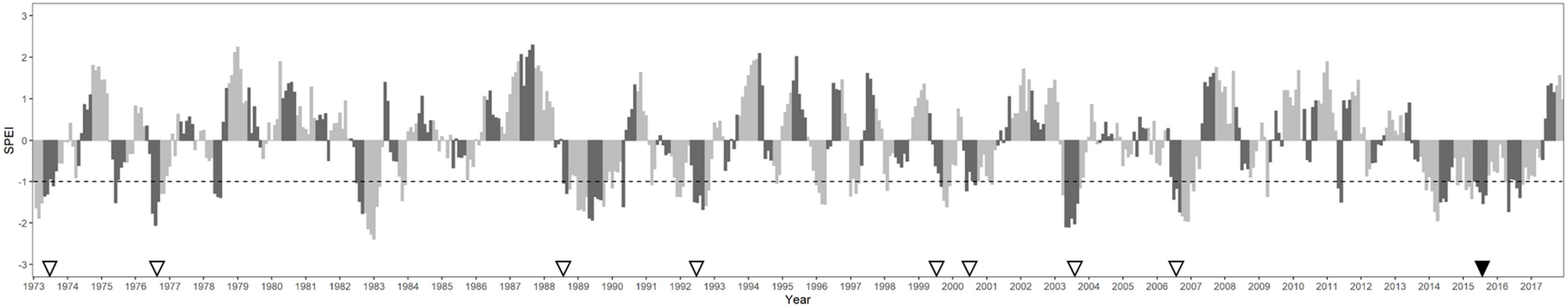
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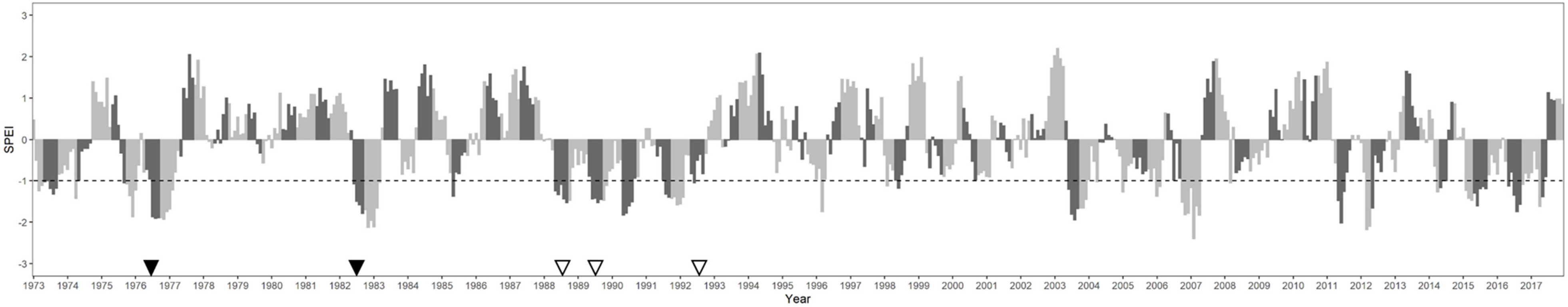
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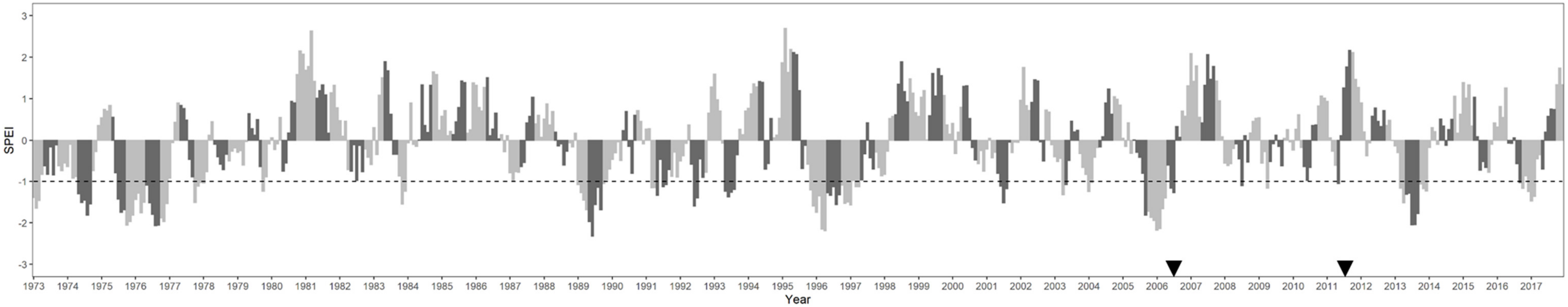
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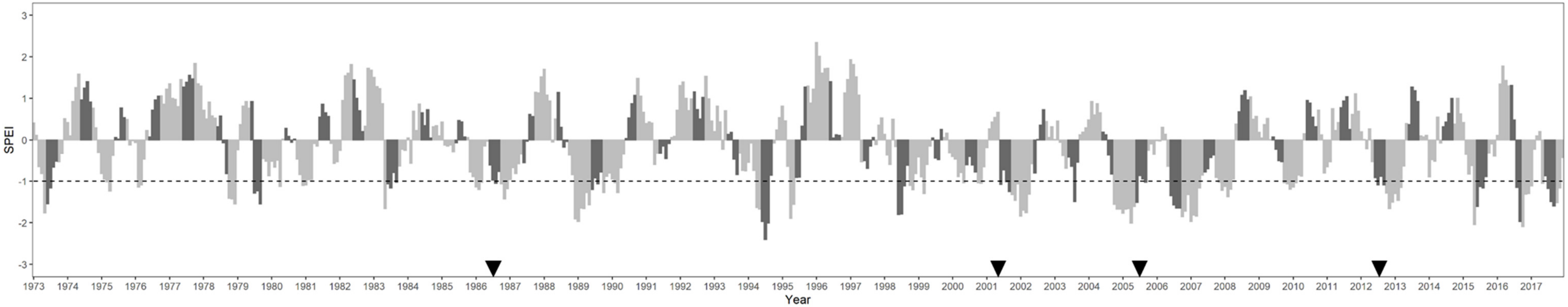
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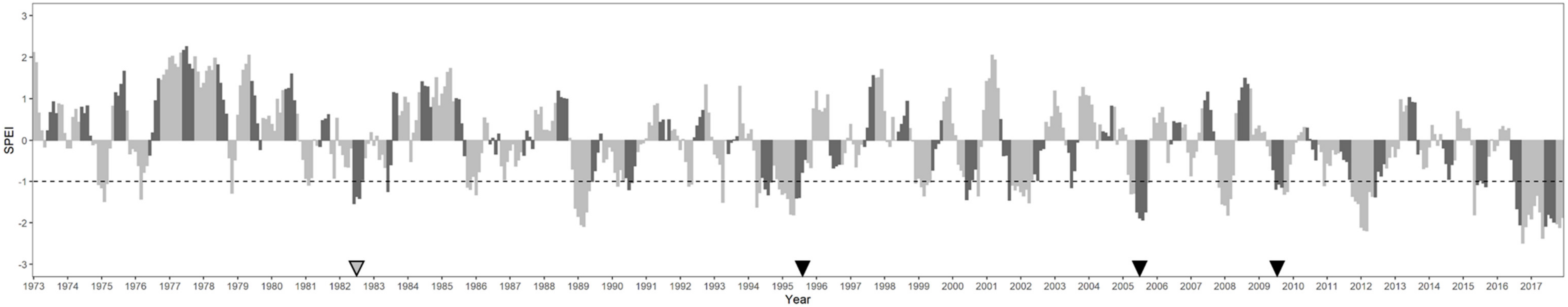

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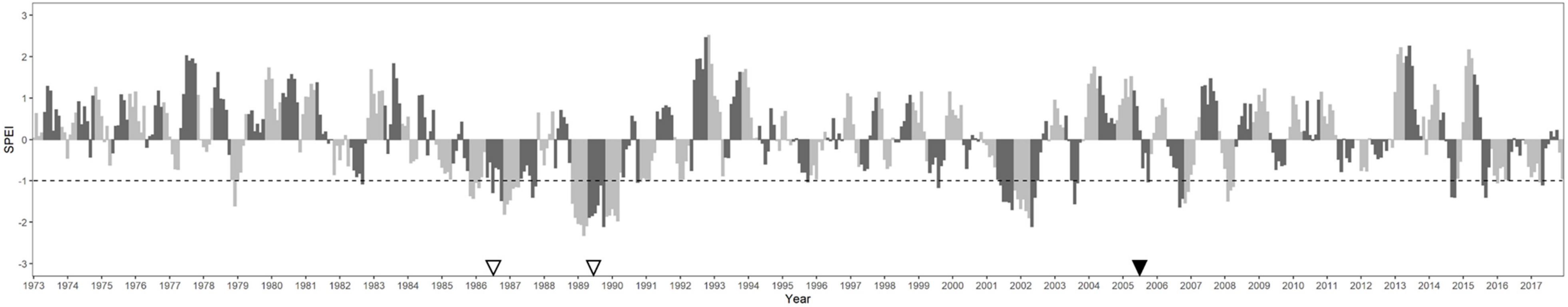

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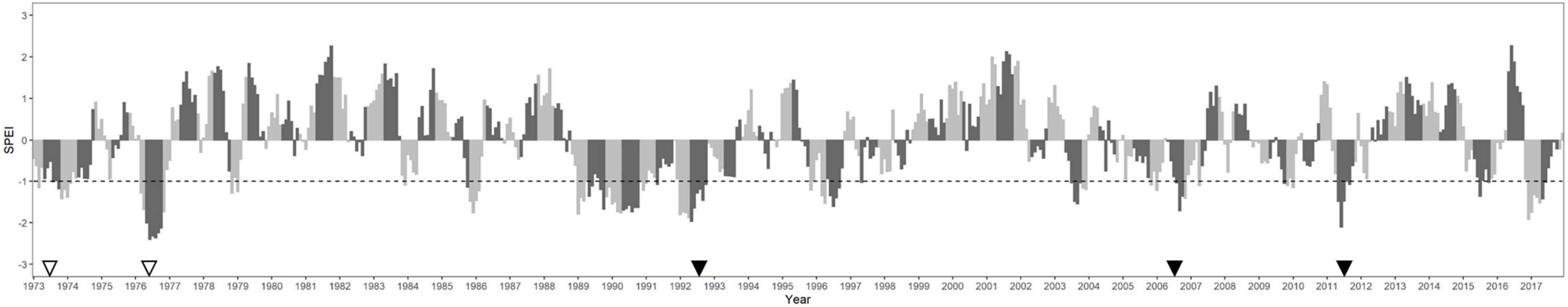
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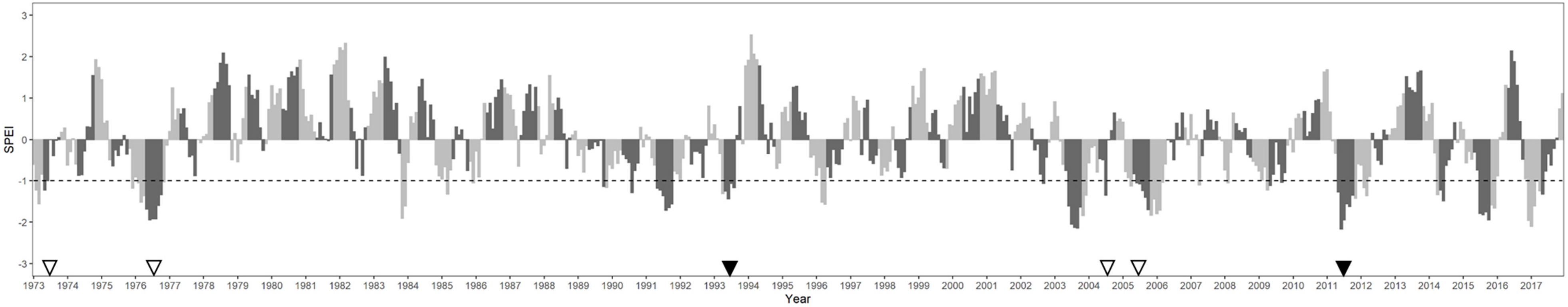
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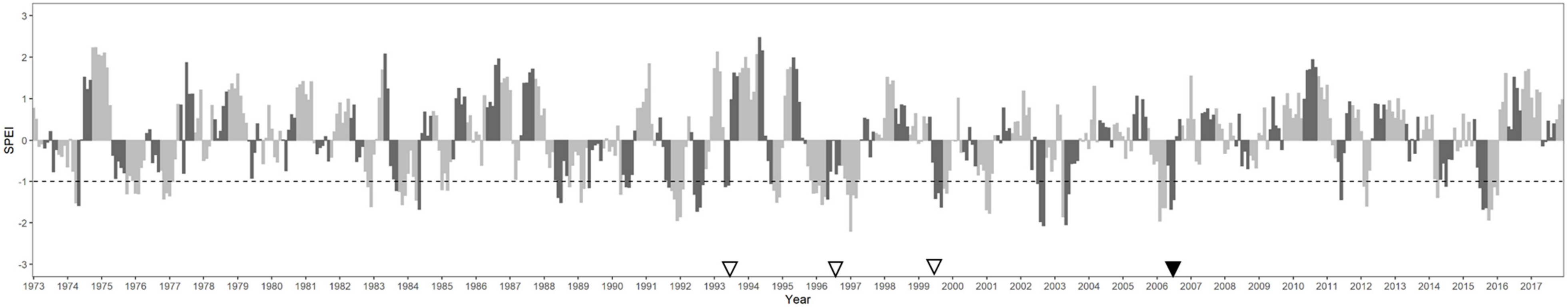

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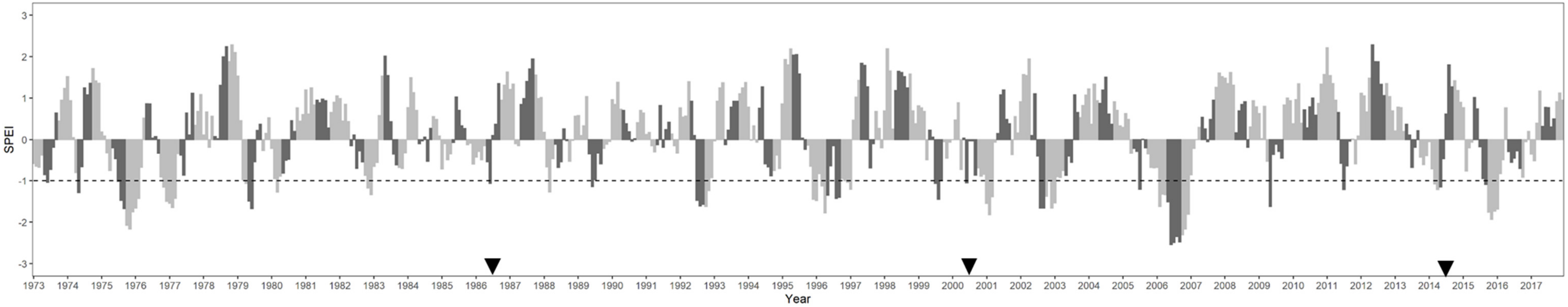

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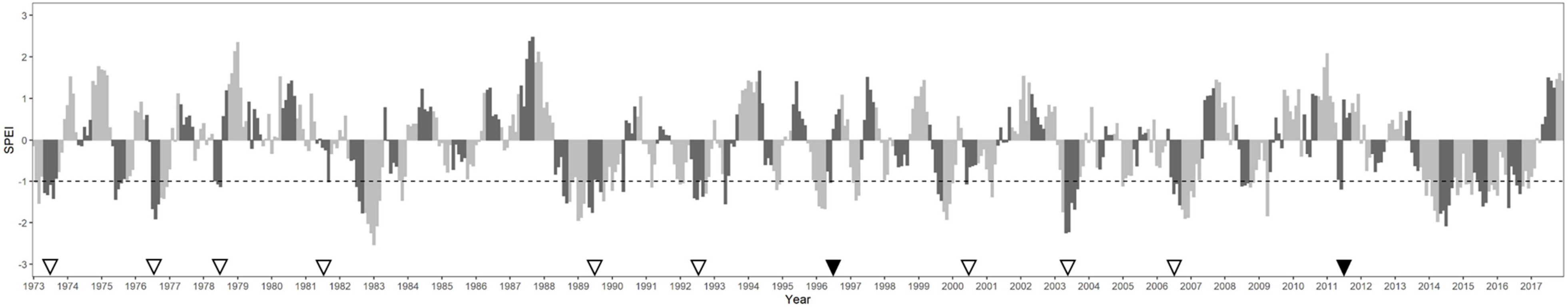
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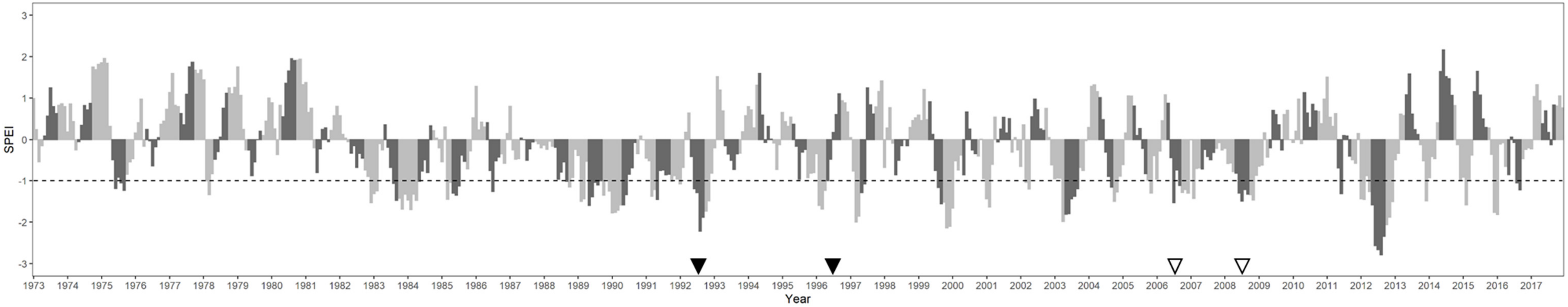
PL 3/4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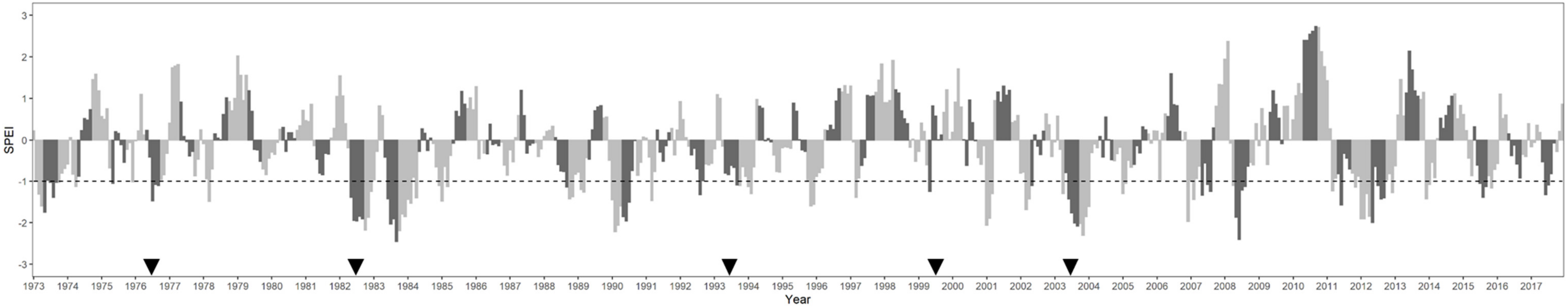
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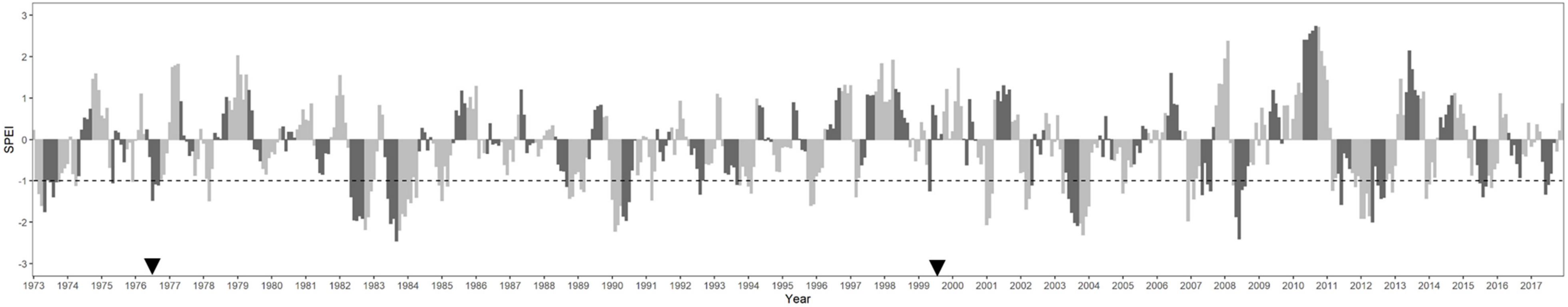
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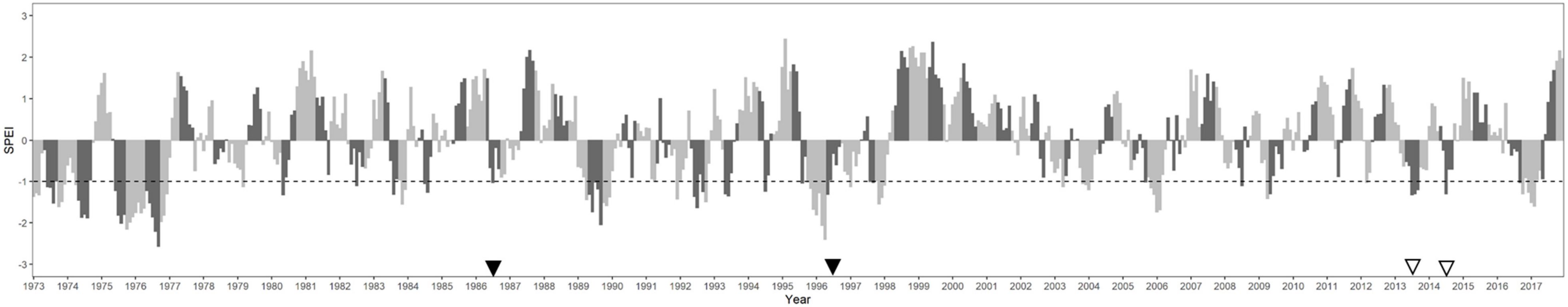

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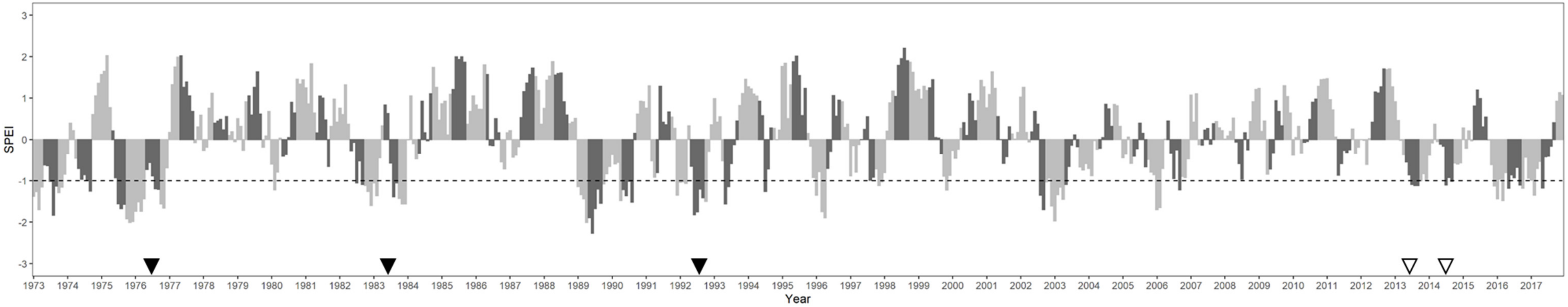

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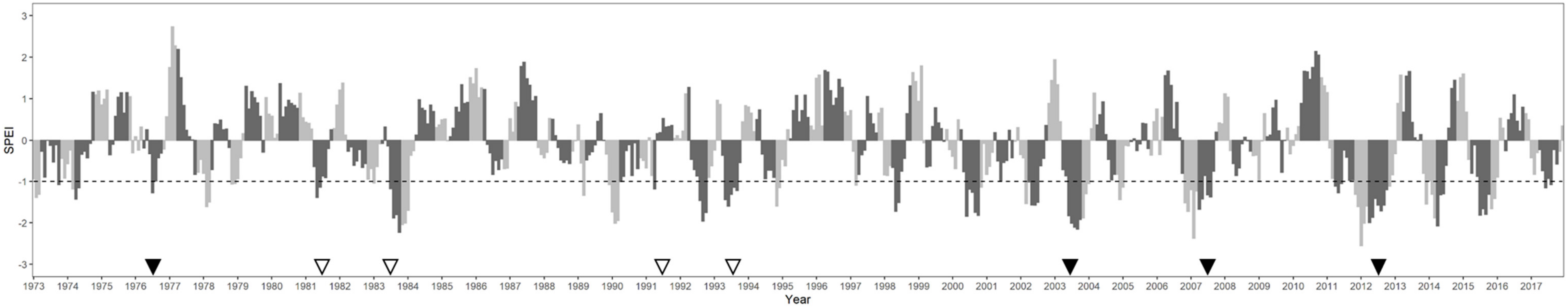
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