Abschlussbericht

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Mischbestände aus Douglasie und Rotbuche

Zuwachs- und Wertleistung von Buchen - Douglasien - Mischbeständen in Abhängigkeit von den Standortbedingungen (W 44)

ZENTRUM WALD FORST HOLZ
WEIHENSTEPHAN

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Projektinterne Zusammenfassung

Zusammenfassung des Abschlussberichtes W44
aus den Partner-Projekten

„Zuwachs- und Wertleistung von Buchen - Douglasien - Mischbeständen in Abhängigkeit von den Standortbedingungen“ (W 44)

Lehrstuhl für Waldwachstumskunde, Technische Universität München

Projektleiter: Prof. Dr. Hans Pretzsch

Projektbearbeiter: Eric Andreas Thurm

„Vergleichende Analyse wichtiger ökologischer Kenngrößen von Buchen-Douglasien-Misch- und Reinbeständen auf unterschiedlichen Standorten Bayern“ (B 74)

Lehrstuhl für Bodenkunde, Technische Universität München

Projektleiter: Prof. Dr. Jörg Prietzel

Projektbearbeiter: Maike Cremer

Die Projekte wurden gefördert durch die Bayerische Forstverwaltung

Inhaltsverzeichnis

Einleitung

Mischbestande und Mischungseffekt

Den wachsenden Ansprüchen an den Wald durch die Gesellschaft versucht man in vielen Forstverwaltungen mit der Umwandlung von Rein- in Mischbestände gerecht zu werden. Mehrere Meta-Analysen zeigten, dass Mischbestände Ökosystemleistungen, wie die Bereitstellung von Holz oder Erhöhung der Biodiversität, besser erfüllen können als Reinbestände (Zhang et al. 2012; Gamfeldt et al. 2013; van der Plas et al. 2016). Trotz dieses generellen Trends, zeigen mehr und mehr Studien, dass bei verschiedenen Arten-Kombinationen unterschiedliche Mischungseffekte zu erwarten sind und diese auch unterschiedlich stark ausfallen. Es ist daher wichtig, die gewünschte Artenkombination gesondert zu untersuchen, um so abschätzen zu können, welche positive Mehrleistung von der Mischung zu erwarten ist.

Hinzu kommt, dass - wie schon von Bertness und Callaway (1994) prognostiziert - die Interaktionen von zwei Arten auf unterschiedlichen Standorten auch unterschiedlich ausfallen kann. Bertness und Callaway (1994) vermuteten auf schlechten Standorten eine Begünstigung beider Arten voneinander („Faszilitation“). Auf mittleren Standorten sollten aber die Konkurrenzstärke beider Arten dazu führen, dass es in der Artmischung eher zu einer Minderleistung kommt - die Basis der Stress-Gradienten-Hypothese. Diese Hypothese wurde bei vielen Untersuchungen aufgegriffen und dort zum Teil abgelehnt, aber auch in vielen Studien bestätigt (Maestre et al. 2009). Unteranderem zeigte sich bei der Mischung Rotbuche und Eiche, dass besonders auf ungünstigen Standorten bei der Mischung ein Mehrzuwachs gegenüber dem Reinbestand zu erwarten ist (Pretzsch et al. 2013). Dies veranlasste das aktuelle Projekt dazu, die Stress-Gradienten-Hypothese in ihre Ausgangshypothesen mit einzubeziehen.

Ein weiterer Faktor, welcher die Interaktion von Mischbeständen beeinflusst, ist das Alter. Über die Lebensdauer verändert sich der Baum in seiner Form, in seiner Allometrie, aber auch in seinen physiologischen Eigenschaften. So ist beispielsweise die Douglasie in ihrem frühsten Jugendstadium recht schattentolerant und wird dann immer schattenintoleranter. Mit solchen Anpassungen ändert sich auch das Interaktionsgefüge zwischen den Baumarten. Dennoch gingen das Alter erst in wenigen Studien mit ein (Forrester et al. 2006; Zhang et al. 2012; Forrester et al. 2006). In dem vorliegenden Projekt wurde daher das Alter auch als Faktor integriert.

Die Basis der Studie waren somit ein Alters- und ein Standortsgradient. Die Auswertungen wurden immer in Abhängigkeit zu diesen Gradienten gesetzt.

Douglasie und Buche

Die Umwandlung von Nadelholz-Monokulturen zu Mischbeständen ist in vielen Forstrichtlinien verankert. Trotzdem besteht seitens der Holzindustrie großer Bedarf an Nadelholz. Aktuelle Technologie ermöglichen zwar teilweise die ursprünglichen Nadelholzwerkstoffe mit neuartigen Laubholzverarbeitungsmethoden zu kompensieren. Dennoch sind dem Laubholzeinsatz auf nicht absehbare Zeit Grenzen gesetzt, welche eine kontinuierlich hohe Nadelholzversorgung notwendig machen. Die in Deutschland am häufigsten vorkommende Baumart Fichte scheint aber im Zuge des Klimawandels diesen Leistungsansprüchen nicht mehr gerecht zu werden. Sowohl Waldeigentümer als auch die verarbeitende Sägeindustrie sprechen sich vermehrt für den Ersatz von Fichte durch Douglasie aus. Einerseits sind gute Holzqualität und hohe Masseleistung von der Baumart (Pretzsch 2005; Kleinschmit und Bastien 1992) zu erwarten, andererseits zeigt die Douglasie eine bessere Resistenz gegen Trockenstress als einheimische Nadelbaumarten (Eilmann und Rigling 2012; Weigt et al. 2015; Bréda et al. 2006). Weiterhin besitzt sie ein breites Standortspotential.

Gleichwohl soll es nicht zu einer Überführung von Fichten- zu Douglasie-Reinbeständen kommen. Die Douglasie als nicht-einheimische Baumart steht seitens des Naturschutzes unter der Kritik invasiv zu sein (Nehring et al. 2013). Die FSC-Zertifizierung gestattet daher den Douglasienanbau nur bei gemischter Baumart. Und auch der Deutsche Forstwirtschaftsrat empfiehlt den Anbau der Douglasie als Mischbaumart.

Die Optionen der Mischung sind aufgrund des starken Höhenwachstums der Douglasie jedoch nicht uneingeschränkt möglich. Neben dem Anbau mit anderen Nadelhölzern, hat sich aber besonders die Mischung mit der Buche als besonders erfolgsversprechend dargestellt (Göhre 1958; Kownatzki und Kriebitzsch 2011; Röhrig et al. 2006; Huss 1996).

Ziel dieser Arbeit soll es nun sein, diese Artenkombination zu untersuchen und das bis dato hauptsächlich aus Beobachtungen begründete Wissen mit Daten zu unterlegen.

Methodik

Zur Untersuchung der Mischungseffekte in Buchen-Douglasien-Mischbeständen wurden Versuchsflächen auf sieben unterschiedlichen Standorten (7 Versuche) in Bayern und Rheinland- Pfalz angelegt (siehe Tabelle 1).

Tabelle 1: Standortseigenschaften der 7 Versuchsstandorte

Versuchs-Nummer	Versuch	Wuchsgebiet	Geografische Position		Höhe	Jahresniederschlag (1981 - 2014)	Jahresmitteltemperatur (1981 - 2014)	Basenausstattung basenreich(1) basenarm (5)	Wasserversorgung sehr frisch (1) zu sehr trocken(6)
			O-Breite	N-Länge					
1001	Walkertshofen	Tertiäres Hügelland	10°44'49.15"	48°15'18.33"	556 (523 - 597)	961 (890 - 1011)	8.2 (8.1 - 8.4)	3	6
1002	Würzburg	Fränkische Platte	9°56'17.51"	49°56'10.05"	310 (272 - 343)	749 (718 - 792)	8.8 (8.5 - 9.2)	2	2
1003	Spessart	Spessart	9°27'56.62"	49°50'37.96"	384 (279 - 384)	1001 (878 - 1070)	8.5 (7.9 – 9.0)	3-4	3-6
1004	Ebersberg	Schwäbisch-Bayerische Schotterplatten- und Altmoränenlandschaft	11°51'09.88"	48°07'16.78"	532	1044	8.5	2	6
1005	Daun	Osteifel	6°44'36.33"	50°10'23.86"	486 (471 - 500)	978 (880 - 1066)	7.9 (7.5 - 8.2)	3	5
1006	Hirschwald	Frankenalb und Oberpfälzer Jura	11°54'34.98"	49°20'34.74"	474 (462 - 482)	821	8.0	3	4
1007	Pfälzerwald	Pfälzerwald	7°48'23.27"	49°19'10.67"	445 (416 - 457)	967 (894 – 832)	8.6 (8.3 - 8.8)	4	4

Ziel war es, neben dem Standortsgradienten einen Altersgradienten abzubilden. Daher wurden auf vier Standorten Plots im jungen (ca. 30 Jahre), mittlerem (50 -70 Jahr) und hohem Alter (90+ Jahre) angelegt. Insgesamt kommt das Projekt somit auf eine Flächenanzahl von 54 Plots. Diese wurden als Triplets angelegt und verfügen über einen reinen Buchenbestand, einen reinen Douglasienbestand und einen Mischbestand aus den beiden Baumarten. Es existiert insgesamt 18 Triplets für die Analyse (siehe Abbildung 1), wovon sich zwölf in Bayern befinden.

Das Triplet ist der wesentliche Bestandteil des Projektes und der Mischbestandsforschung. Es ermöglicht den direkten Vergleich von Baumeigenschaften unter Rein- und Mischbestandsbedingungen bei sonst gleichbleibenden Umwelteinflüssen.

Alle Triplets eines Versuchs befinden sich im gleichen Wuchsbezirk bzw. Wuchsgebiet. Fünf der insgesamt 18 Triplets wurden gemeinsam mit dem Parallelprojekt B74 (Prof. Prietzel) ausgewählt und werden von beiden Lehrstühlen gemeinschaftlich für ihre Untersuchungen genutzt.

Abbildung 1: Übersicht aller angelegten Triplets (schwarze Kästchen) aus Buchen-Douglasien-Mischbeständen und dazugehörigen Reinbeständen im süddeutschen Raum mit Bezeichnung der entsprechenden Wuchsgebiete.

Struktur

Thurm, Eric Andreas; Pretzsch, Hans (2016): ***Improved productivity and modified tree morphology of mixed versus pure stands of European beech (Fagus sylvatica) and Douglas-fir (Pseudotsuga menziesii) with increasing precipitation and age.*** *In: Ann. For. Sci. 73 (4), S. 1047–1061. DOI: 10.1007/s13595-016-0588-8.*

Pretzsch, Hans; Schütze, Gerhard (2016): ***Effect of tree species mixing on the size structure, density, and yield of forest stands.*** *In: Eur J Forest Res 135 (1), S. 1–22. DOI: 10.1007/s10342-015-0913-z.*

Pretzsch, Hans; Biber, Peter (2016): ***Tree species mixing can increase maximum stand density.*** *In: Can. J. For. Res., S. 1–15. DOI: 10.1139/cjfr-2015-0413.*

Es hat sich gezeigt, dass es zu einer deutlichen Höhenstratifizierung zwischen Buche und Douglasie im Mischbestand kommt (Thurm und Pretzsch 2016). Diese kann im Alter 100 knapp 10 m betragen (siehe Abbildung 2). Das bedeutet, dass die Douglasie auf den obersten 10 m ihres Kronenbereiches einen nahezu solitären Lichtgenuss besitzt. Die Douglasie bildet im Vergleich zum Reinbestand signifikant breitere Stammdurchmesser aus. Die Höhenleistung bleibt leicht gegenüber dem Reinbestand zurück, jedoch nicht signifikant. Letztlich bilden so die Stämme im Mischbestand ein deutlich geringeres H/d – Verhältnis aus.

Das Höhenwachstum der Buche ist im Mischbestand mit dem des Reinbestandes vergleichbar. Im höheren Alter zeigt die Buche jedoch, dass sie im Dickenwachstum dem Mischbestand gegenüber zurückbleibt. Folglich zeigen die Buchen im Mischbestand mit steigendem Alter eine schlankere Stammform als im Reinbestand.

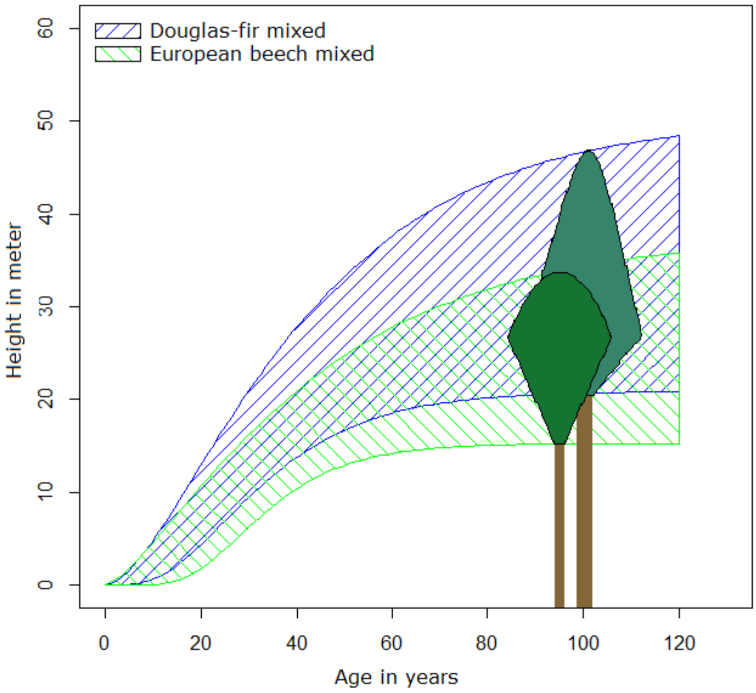

Abbildung 2: Verlauf der Baumhöhe und des Kronensansatzes der höchsten Douglasien und Buchen im Mischbestand über dem Bestandesalter.

Die wachstumskundlichen Daten wurden für zwei weiter Publikationen genutzt, welche ebenfalls die Durchmesser- und Höhenstruktur (Pretzsch und Schütze 2016) und die Bestandesdichte (Pretzsch und Biber 2016) von Rein- und Mischbeständen beschreiben. Die Studien erfassen dabei neben der Baumarten-Mischung Buche-Douglasie, noch weitere Baumartenkombinationen (Buche-Fichte, Buche-Kiefer, Kiefer-Fichte, etc.).

Zuwachsleistung

Thurm, Eric Andreas; Pretzsch, Hans (2016): ***Improved productivity and modified tree morphology of mixed versus pure stands of European beech (Fagus sylvatica) and Douglas-fir (Pseudotsuga menziesii) with increasing precipitation and age.*** *In: Ann. For. Sci. 73 (4), S. 1047–1061. DOI: 10.1007/s13595-016-0588-8.*

Die Auswertung der 18 Triplets ergab, dass die Zuwachsleistung im Mischbestand über der des Reinbestandes liegt. Dabei erreichte der Mischbestand einen jährlichen Zuwachs von $PAIV_{df,be}$ = 21.08 m³/ha/a und somit einen absoluten Mehrzuwachs ($MEAV_{df,be}$) von 1.63 m³/ha/a und relativ von rund ($MERV_{df,be}$) 8% ($p = 0.017$) (Thurm und Pretzsch 2016). Der Reinbestand Buche erreichte einen jährlichen Zuwachs von $PAIV_{be}$ = 13.59 m³/ha/a, der Reinbestand Douglasie von $PAIV_{df}$ = 26.12 m³/ha/a. Es handelt sich somit nicht um einen höheren Zuwachs als die leistungsstärkste Baumart („transgressiver Mehrzuwachs“), sondern einen höheren Zuwachs verglichen mit der Zuwachsleistungen die erreicht würde wenn man beide Baumarten anhand ihr Mischungsanteile aufsummiert.

Dieses Ergebnis gleicht sich mit Erkenntnissen von Huss (1996), Bartelink (1998) und Thomas et al. (2015).

Der Mehrzuwachs wird dabei hauptsächlich durch die Mehrleistung der Douglasie getragen. Hier ist es vor allem das Einzelbaum-Dickenwachstum was zu einer höheren Produktivität führt. Wir vermuten, dass er durch den besonderen Lichtgenuss der herausragenden Kronen der Douglasien generiert wird.

Der Mehrzuwachs (bzw. Minderzuwachs) der Mischbestände ($MEAV_{df,be}$) schwankt dabei von einem Minderzuwachs von -7,79 m³/ha/a ($MERV_{df,be} = 0.45$) bis zu einem Mehrzuwachs von +16.73 m³/ha/a ($MERV_{df,be} = 1.73$). Zu erklären ist diese Schwankung zum Teil durch den Alters- und Standortseinfluss. Auf besseren Standorten kann ein höherer Mehrzuwachs erwartet werden, da die Baumarten sich noch stärker in ihrer Höhe strukturieren können. Im höheren Alter zeigen die Mischbestände ebenfalls einen größeren Mehrzuwachs. Der Einfluss des Alters ist dabei wahrscheinlich höher zu bewerten als der des Standortes, weil erst das Alter die Differenzierung von Buche- und Douglasien-Kronendach ermöglicht (siehe auch Abbildung 2).

Verhalten unter Trockenstress

Thurm, Eric Andreas; Uhl, Enno; Pretzsch, Hans (2016): ***Mixture reduces climate sensitivity of Douglas-fir stem growth****. In: Forest Ecology and Management (376), S. 205–220. DOI: 10.1016/j.foreco.2016.06.020.*

Das Trockenstressverhalten der Bäume wurde mit Hilfe von Stamm-Bohrkernen (Jahrring-Chronologien) untersucht. Ein Abgleich des Jahrringbreiten-Niveaus von drei Jahren vor einem Trockenereignisses mit der Jahrringausbildung danach, soll Aussagen über die Resistenz und die Erholungszeit geben. Die Resistenz beschreibt das Abfallen der Jahrringbreite zum Zeitpunkt des Trockenstresses (nach Lloret et al. 2011). Im Rahmen dieses Projektes wurde die Trockenstressreaktion von Bäumen tiefergehend betrachtet als es zu Projektbeginn geplant war. Es wurde eine neue Berechnungsmethode entwickelt, welche die Erholungszeit („Growth recovery time“) der Bäume beschreibt. Sie ergibt sich aus einer Zeitspanne, ab derer die Bäume das gleiche Jahrringwachstum zeigen, wie vor dem Trockenstress (nach Thurm et al. 2016). Abbildung 3 zeigt den Verlauf dieser beiden Indizes unter Trockenstressereignissen von 1950 – 2010.

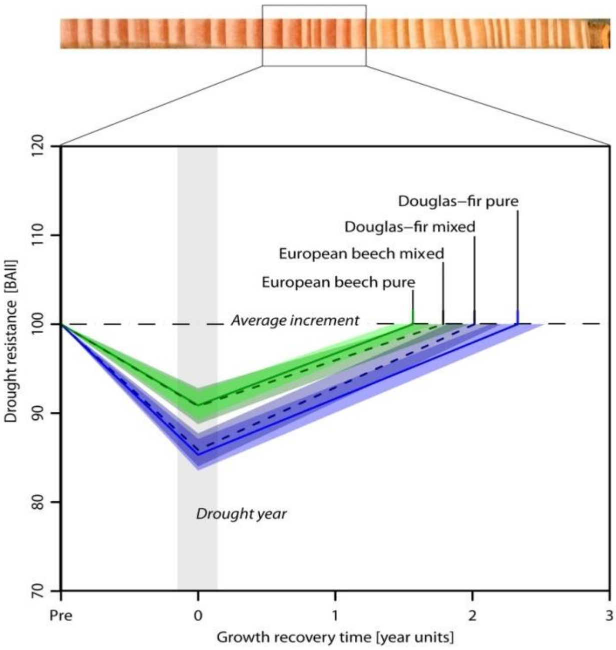

Abbildung 3: Relativer Einbruch des Grundflächenzuwachses (Einzelbaum) im Trockenjahr (*Resistance*) und die Dauer der Erholung (*Growth recovery time*) für Buche und Douglasie im Rein- und im Mischbestand. Die gestrichelt Linie symbolisiert das durchschnittliche Wachstumsniveau. Die eingefärbten Bereiche um die Linien stellen das 95%- Konfidenzintervall dar.

Im Mischbestand lassen beide Baumarten im Trockenjahr einen vergleichbaren Zuwachseinbruch wie im Reinbestand erkennen. Die Regenerationszeit von Douglasie im Mischbestand ist jedoch verkürzt, während sich die Regenerationszeit von der Rotbuche verlängert. Es wird vermutet, dass sich die Douglasien ein Jahr nach dem Trockenstress im Mischbestand schneller regenerieren, weil sie als immergrüne Pflanzen frühzeitig mit der Transpiration und der Auffüllung ihrer Reserven beginnen. Dies geschieht ohne Konkurrenz der Rotbuche, die erst nach dem Blattaustrieb transpirieren kann. Das belegen auch die Bodenwassergehaltsmessungen vom Parallelprojekt (B 74). Im Jahresverlauf fällt hier der Bodenwassergehalt im Douglasien-Reinbestand als erster ab. Zeitverzögert folgt dann der Mischbestand und als letzter der Buchen-Reinbestand (siehe Thurm 2017).

Neben dieser Einzelbaumanalyse wurde das Trockenstressverhalten der Baumarten auch auf Bestandesebene für das Jahr 2003 analysiert. Auf diese Weise sollte erstmals eine Einschätzungshilfe für die Forstpraxis entstehen, welche über die Phase der relativen Einzelbaum-Abschätzung hinausgeht und den Verlust durch ein Trockenjahr pro Hektar und Bestandestyp angibt. Hier bestand bei vorherigen Auswertungen stets eine Überführungslücke von Wissenschaft und Praxis. Die sonst gebohrten Bäume bestehen ausschließlich aus dominanten Bäumen, um die Entwicklung von Wachstumstrends durch Konkurrenz in den Jahrringchronologien zu vermeiden. Dadurch lässt sich aber nicht das Bestandesverhalten unter Trockenstress widerspiegeln, insbesondere vor dem Hintergrund einer variablen Durchmesserverteilung im Rein- und Mischbestand.

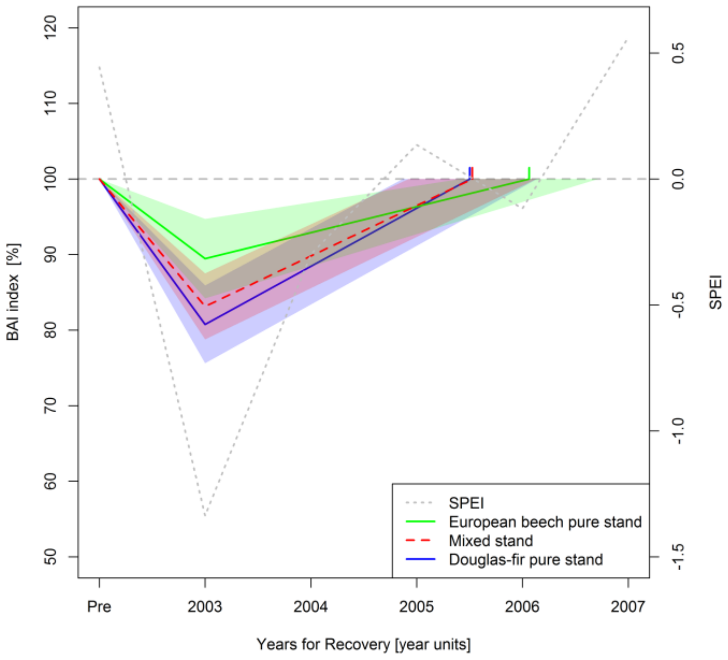

Abbildung 4: Relativer Einbruch des Grundflächenzuwachses (Bestand) im Trockenjahr (*Resistance*) und die Dauer der Erholung (*Growth recovery time*) für Buche und Douglasie im Rein- und im Mischbestand im Jahr 2003. Die gestrichelt Linie symbolisiert das durchschnittliche Wachstumsniveau. Die eingefärbten Bereiche um die Linien stellen das 95%- Konfidenzintervall dar. Die gepunktete graue Linie zeigt den Verlauf des Trockenheitsindexes SPEI mit dem deutlichen Einbruch 2003.

Die Abbildung 4 zeigt das relativen Trockenstressverhalten der Bestandestypen für das Extremjahr 2003. Eine Betrachtung von vorherigen Trockenereignissen kann jedoch mit den vorhandenen Daten nicht erfolgen. Die Ursache liegt in der Stammzahlreduktion der Bestände im Bestandesverlauf. Sie verhindert das komplette Durchmessergefüge vor mehr als 20 Jahren zu rekonstruieren.

Das Resistenzverhalten der Bestandestypen 2003 ist so, wie man es aus den Einzelbaumdaten prognostizieren würde. Der Mischbestand fügt sich zwischen den Buchen-Reinbestand mit besserer Resistenz und dem Douglasien-Reinbestand mit schlechterer Resistenz ein. Bei der Erholungszeit schneidet der Buchen-Reinbestand jedoch überraschend schlechter ab als der Douglasien-Reinbestand und der Mischbestand. Höchstwahrscheinlich hängt dies mit einem auf das Trockenjahr folgendem Mastjahr (2004) zusammen, welches für viele Regionen Deutschlands beobachtet werden konnte. Die aufgebrachte Energie zur Bucheckernproduktion geht zulasten eines deutlichen Zuwachsverlustes (Burschel 1966). Dieser Zuwachsverlust konnte von Eichhorn et al. (2008) auch an Buchen in Norddeutschland beobachtet werden.

Ein dritter Index („Loss due to drought“), welcher die Verluste durch eine Trockenjahr bis zu seiner kompletten Regeneration aufsummiert, ist in Tabelle 2 dargestellt.

Tabelle 2: Absoluter und relativer Verlust des Grundflächenzuwachses auf Bestandesebene für das Trockenjahr 2003. SD repräsentiert die Standardabweichung. Die Signifikanzunterschiede werden durch die Buchstaben widergegeben. In Klammern ist das durchschnittliche Zuwachsniveau der Bestandestypen angegeben.

Mischungstyp	**Verlust Grundflächenzuwachs ($m^2\ ha^{-1}$)**	**SD**		**Relativer Verlust des Grundflächenzuwachs (%)**	**SD**		**Relativer Verlust des Volumenzuwachs ($m^3\ ha^{-1}$)**	**SD**
Douglasie Reinbestand (1.60 $m^2\ ha^{-1}\ a^{-1}$)	0.82	0.49	a	0.52	0.29	a	15.13	11.11
Mischbestand (1.29 $m^2\ ha^{-1}\ a^{-1}$)	0.65	0.35	ab	0.50	0.25	a	11.12	6.10
Buche Reinbestand (0.91 $m^2\ ha^{-1}\ a^{-1}$)	0.45	0.44	b	0.50	0.32	a	6.54	5.48
Total	0.64	0.45		0.50	0.28		10.93	7.56

Das Jahr 2003 stellt im Douglasien-Reinbestand einen Zuwachseinbruch von 0.82 $m^2\ ha^{-1}$, im Mischbestand von 0.65 und im Buchen-Reinbestand von 0.45 dar. Damit bricht der Douglasien-Reinbestand am stärksten ein, besitzt aber auch das höchste Zuwachsniveau. Relativ zum durchschnittlichen Zuwachs unterscheiden sich die Zuwachsverluste der drei Bestandestypen nicht.

Spross-Wurzel Allometrie

Thurm, Eric Andreas; Biber, Peter; Pretzsch, Hans (2017): ***Stem growth is favored at expenses of root growth in mixed stands and humid conditions for Douglas-fir (Pseudotsuga menziesii) and European beech (Fagus sylvatica).*** *In: Trees 31 (1), S. 349–365. DOI: 10.1007/s00468-016-1512-4.*

Um die die Ressourcenverteilung zwischen Stamm und Wurzel zu beschreiben, wurden die Jahrringchronologien auf BHD-Ebene mit den Jahrringchronologien verglichen, welche an zwei Hauptwurzeln des jeweiligen Baumes genommen wurden. Das Verhältnis des Dickenwachstums von Wurzel und Stamm wurde mithilfe der allometrischen Funktion nach Peters (1983) beschrieben:

$$\log Y_1 = \log \beta + \alpha \log Y_2.$$

Vorherige Untersuchungen von Keyes und Grier (1981) und Comeau und Kimmins (1989) an Douglasie und Murraykiefer (*Pinus contorta* (Dougl. ex. Loud)) konnten zeigen, dass sich das Spross-Wurzel-Verhältnis auf schlechteren Standorten langfristig zugunsten der Wurzel verschiebt. Untersuchungen der Allometrie der Murraykiefer gegenüber kurzfristigen Trockenperioden zeigten, dass sich auch hier das Verhältnis zugunsten der Wurzel verschiebt (Pretzsch et al. 2012). Lavelle und Spain (2005) vermuten, dass die Pflanze auf Trockenstress mit Wurzelexpansion reagiert, in dem Versuch, noch kurzfristig unerschlossene Wasserreserven im Boden zu erschließen.

Ein weiteres Reaktionsmuster ist, dass sich mit zunehmender Bestandesdichte die Wachstums-Allometrie ebenfalls zugunsten der Wurzel verschiebt (Poorter et al. 2012). Es scheint ein Allokationsmuster zu existieren zwischen ungünstigen Wuchsbedingung (Trockenstress, erhöhte Konkurrenz) und einer stärkeren Allokation des Wachstums in den Bereichen der Wurzel.

Dieses Muster war auch in den Projektuntersuchungen widerfinden (Thurm et al. 2017a). Auf den schlechteren Standorten zeigte sich eine stärkere Investition des Baumwachstums in die Wurzel, ebenso wie unter Trockenstress und unter größerer Konkurrenz (beschrieben durch lokale Grundfläche) bei den untersuchten Bäumen.

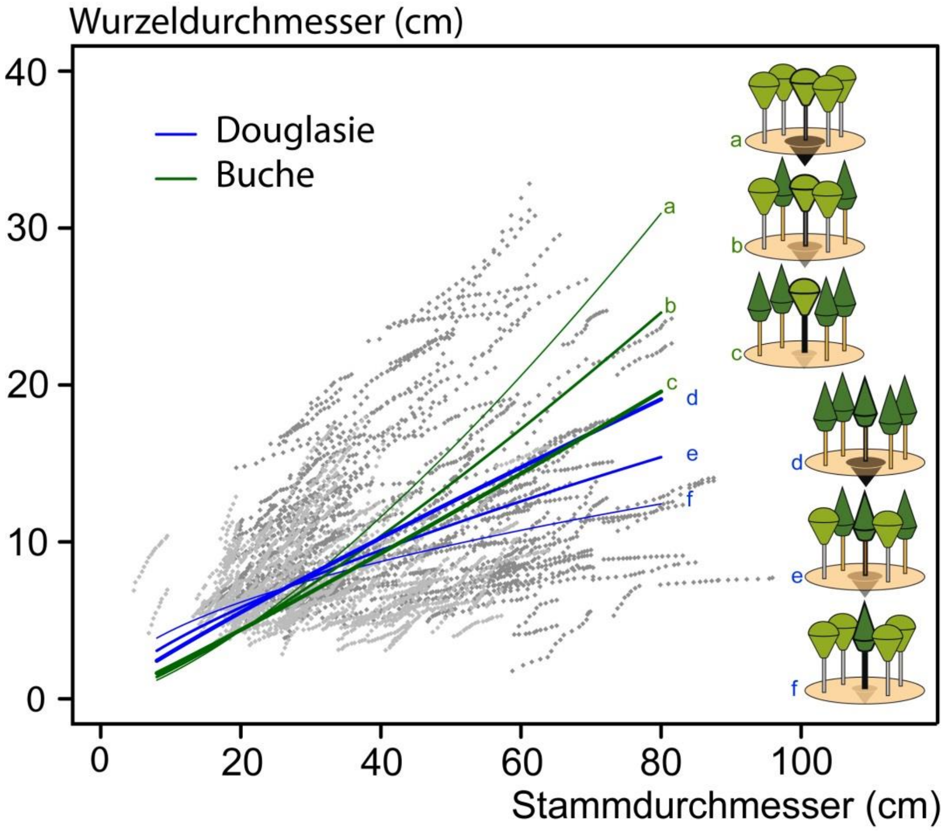

Abbildung 5: Allometrie zwischen Wurzel und Stamm in Abhängigkeit der umgebenden Mischung von Buche und Douglasie. (a,d) 100 % intraspezifische Konkurrenz für den Baum; (b,e) 50 % intraspezifische Konkurrenz für den Baum; (c,f) 100 % interspezifische Konkurrenz für den Baum.

Erstaunlicherweise war jedoch erkennbar, dass eine Verschiebung von interspezifischer zu intraspezifischer Konkurrenz zu einer verstärkten Allokation des Wachstums in den Stamm führt (siehe Abbildung 5). Die Mischung der Baumarten scheint auf die Spross-Wurzel-Allometrie somit einen ähnlichen Effekt zu haben, wie eine Verringerung der Bestandesdichte oder Verbesserung der Wasserversorgung.

Schlussfolgerung

Anhand der Untersuchung konnte feststellt werden, dass die Mischung Buche-Douglasie eine geeignete Baumartenkombination für mitteleuropäische Verhältnisse ist. Ihre Höhenstrukturierung schafft eine Waldstruktur, die mit heimischen Hölzern nicht zu erreichen ist und die in besondere Weise in der Lage ist, das zur Verfügung stehende Licht auszunutzen. Die Mischung der Arten fördert vor allem das Wachstumsverhalten der Douglasie, wobei die Buche dadurch aber keine signifikanten Nachteile erfährt. In Trockenzeiten wird das hohe Zuwachsniveau der Douglasie unterstützt durch die Mischung und zeigt außerdem, dass das Bestandesleben eine geringere Sensitivität als im Mischbestand hat.

Waldbauliche Einschätzung

Waldbaulich scheint es sich zu empfehlen, den Mischbestand in hohe Bestandesalter zu überführen (120 Jahre), da die Baumarten in der Lage sind das Standortsvermögen lange auszufüllen. Während die Douglasie im mittleren Alter (60 – 80 Jahre) den Mehrzuwachs besonders durch ihre hohe Einzelbaumleistung treibt, ist die Buche im höherem Alter in der Lage Bestandeslücken zufüllen und das Standortsvermögen weiterhin voll auszunutzen. Dabei ist zu beachten, dass die Douglasie auch im hohen Altern noch sehr hohe Wuchsleistungen am einzelbaum leistet.

Im Jungendalter muss auf die Douglasie im Bestandesgefüge geachtet werden. In dieser Phase ist die Buche durchaus in der Lage sie zu überwachsen. Durch eine gezielte Konkurrenz entstehen jedoch günstige Bedingungen für die Qualifizierung der Stämme. Sie sorgt für hohe H/d-Werte bei der Douglasie in der Jungend, die für deren spätere Holzqualität entscheidend sind. Sobald die Douglasien aus dem Kronendach der Buche herausgewachsen sind, kommt es zur raschen Dimensionierung der Stämme. Dieser biologische Automatismus erzeugt so im Mischbestand eine höhere Douglasien-Holzqualität, die in Reinbestand nur mit aufwendiger Pflege erreicht werden könnte.

Bei der Mischungsform ist darauf zu achten, dass es im Altbestand zu einer intensiven Vermischung beider Arten kommt um die Vorteile der Baumartenkombination in Bezug auf Licht, Boden und Wasser voll auszuschöpfen. Ideal ist daher eine anteilige 50:50 Mischung an der Bestockungsfläche, einzelbaumweise oder in Gruppen von zwei bis drei Bäumen. Die ausladenden Kronen beider Baumarten im Alter ermöglichen es aber dennoch die Bäume truppweise in der Jugend zu erziehen.

Die Baumartenmischung stellt eine gute waldbauliche Option dar, weil sie Produktions- und Qualitätsziele besser erreichen kann als Reinbestände und das bei einer Risikominimierung im Hinblick auf sich häufenden, zukünftige Trockenereignisse.

Zusammenfassung

Die Arbeit untersuchte die Mischung von Buche und Douglasie anhand von Triplets. Ein Triplet weist in sich homogene Alters- und Standortsbedingung auf und besteht aus einem Buchen-Reinbestand, einem Douglasien-Reinbestand und einem Mischbestand beider Baumarten. 18 dieser Triplets wurden in Deutschland in verschiedenen Altersklassen und unter verschiedenen Standortsbedingungen angelegt. Es hat sich gezeigt, dass die Mischung eine höhere Produktivität erreicht, als man von der reinen gewichteten Zusammenfassung der Reinbestände hätte erwarten können, besonders im höheren Alter und unter besseren Standortsbedingungen. Die Mischung wirkt sich günstig auf die Baumallometrie aus, was in einen verstärkten Stamm gegenüber Wurzelwachstum bemerkbar wird. Die Trockenstressreaktion der Douglasie ist im Mischbestand ebenfalls gemildert (Zusammenfassung sie auch Thurm et al. 2017b). Insgesamt interagieren die Baumarten in Kombination komplementär und eignen sich sehr gut für einen Anbau in Mischbestand.

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Anhang

A- Douglasie: eine leistungsstarke und klimarobuste Mischbaumart (LWF aktuell)

B- Die Mutter des Waldes und die Fremde (LWF aktuell)

C- Improved productivity and modified tree morphology of mixed versus pure stands of European beech (Fagus sylvatica) and Douglas-fir (Pseudotsuga menziesii) with increasing precipitation and age

D- Mixture reduces climate sensitivity of Douglas-fir stem growth

E- Stem growth is favored at expenses of root growth in mixed stands and humid conditions for Douglas-fir (Pseudotsuga menziesii) and European beech (Fagus sylvatica)

F- Soil organic carbon and nitrogen stocks under pure and mixed stands of European beech, Douglas fir and Norway spruce

G- Soil acidity and exchangeable base cation stocks under pure and mixed stands of European beech, Douglas fir and Norway spruce

Douglasie: eine leistungsstarke und klimarobuste Mischbaumart

Buchenbeimischung steigert Wachstum und Stabilität der Douglasie

Eric Andreas Thurm, Enno Uhl und Hans Pretzsch

Der Umgang mit der Douglasie als nichtheimische Art wird seit geraumer Zeit kontrovers diskutiert. So wird sie beispielsweise vom Bundesamt für Naturschutz (BfN) aufgrund eines möglichen Invasionspotenzials auf der Schwarzen Liste geführt. Der Deutsche Verband Forstlicher Forschungsanstalten (DVFFA) hat sich hingegen bewusst für einen Anbau der Douglasie ausgesprochen, denn sie zeichnet sich durch ihre hohe Zuwachsleistung und ihre höhere Trockenheitstoleranz im Vergleich zur Fichte aus.

1 Deutlich überragt die Douglasienkrone die Buchen. So kann die Douglasie ihre hohe Lichtnutzungseffizienz voll ausspielen. Die Buche als Schattbaumart hingegen kann immer noch das einfallende Streulicht in spürbares Wachstum umsetzen. Foto: B. Tuerk

Die Empfehlung des Deutschen Verbands Forstlicher Forschungsanstalten DVFFA richtet sich auf die Beteiligung der Douglasie in Mischung mit anderen Baumarten, insbesondere mit der Buche. Die Baumartenmischung Buche-Douglasie ist zwar schon seit einiger Zeit in geringem Anteil in den deutschen Wäldern zu finden, dennoch ist bisher wenig über das Zuwachsverhalten der beiden Baumarten in Mischung veröffentlicht worden. In den vergangenen drei Jahren hat sich der Lehrstuhl für Waldwachstumskunde im Rahmen eines von der Bayerischen Forstverwaltung geförderten Projekts intensiv mit Mischbeständen aus Buche und Douglasie auseinandergesetzt. Ziel dieser Forschungsarbeit war es, die Wechselwirkungen zwischen Douglasie und Rotbuche und ihre Effekte auf Zuwachsverhalten und Resilienz zu beleuchten, die Ergebnisse zu interpretieren und Möglichkeiten für waldbauliche Behandlungsprogramme aufzuzeigen.

Nachdem sich für einige Baumarten (z. B. Buche-Fichte oder Buche-Eiche) gezeigt hat, dass in Mischbeständen ein höherer Zuwachs als in Reinbeständen zu erwarten ist (Pretzsch et al. 2013; Pretzsch et al. 2010), wurde dies zunächst auch für die Mischung aus Buche und Douglasie angenommen. Um dies zu verifizieren, legte der Lehrstuhl für Waldwachstumskunde an verschiedenen Standorten in Bayern und Rheinland-Pfalz temporäre Versuchsflächen an und analysierte den Zuwachs von Buchen und Douglasien in Rein- und Mischbeständen. Auch bei dieser Baumartenkombination stellte sich ein höherer Volumenertrag von rund 8 % ein (Thurm und Pretzsch 2016). Abbildung 2 zeigt den Verlauf des Zuwachses in Abhängigkeit des Mischungsanteils

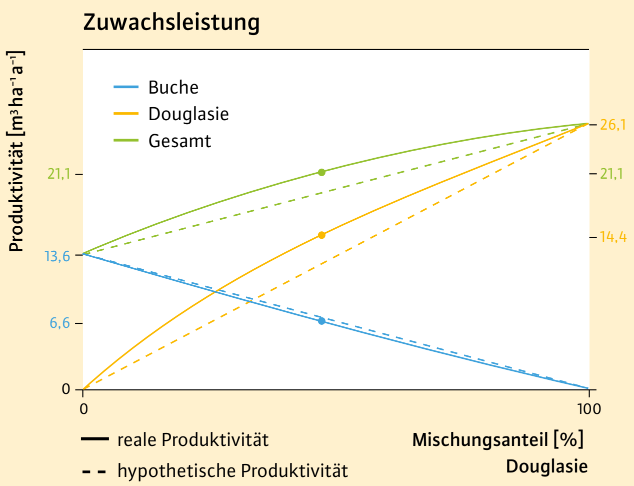
der Douglasie. Der Douglasien-Anteil von 0 % spiegelt den Buchen-Reinbestand mit 13,6 Vorratsfestmetern (Vfm) Zuwachs pro Jahr wider, 100 % Douglasien Anteil steht für den Douglasie-Reinbestand mit 26,1 Vfm Zuwachs. Der Mischbestand (dickere, obere Linie) in der aktuellen Untersuchung besaß einen durchschnittlichen Mischungsanteil von 47 % Douglasien und produzierte 21,1 Vfm, was einem Mehrzuwachs von 8 % bzw. 1,63 Vfm entspricht. Die gestrichelten Linien zeigen die rechnerische Produktivität, welche sich aus den Reinbeständen ergeben würden. Die dünneren Linien stellen die Leistung von Buche und Douglasie am Mischbestandszuwachs dar.
Beim Zustandekommen des Mehrzuwachses zeigte die Mischung beider Baumarten jedoch einige Besonderheiten.

Zuwachssteigerung durch Mischung

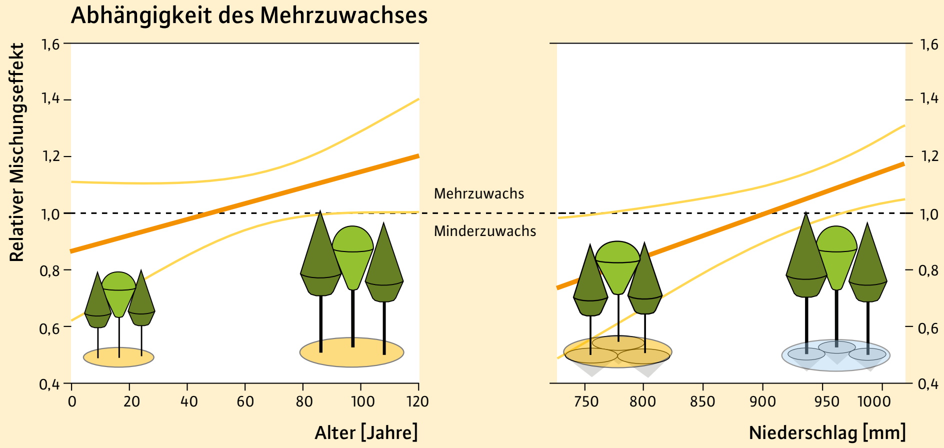
Ausgangspunkt der Untersuchung waren sogenannte Tripletts. Diese bestehen aus Untersuchungseinheiten mit jeweils einem Douglasien-Reinbestand, einem Buchen-Reinbestand und einem Mischbestand beider Arten. Die Bestände standen in unmittelbarer Nähe zueinander (rund 200 m Entfernung) und waren dem Bestandsalter und dem Standort nach identisch. Somit konnte für jedes Triplett verglichen werden, wie sich die jeweilige Baumart im Rein- und im Mischbestand verhält.

Mehrzuwachs

Der Mehrzuwachs ist eine rechnerische Größe, die aus dem Vergleich des Zuwachses eines hypothetischen Mischbestandes (zusammengesetzt aus der Leistung der beiden Reinbestände, gewichtet mit den Baumartenanteilen) mit dem tatsächlich gemessenen Zuwachs im Mischbestand abgeleitet wird. Es hat sich bewährt, diese Mehr- oder auch Minderzuwächse durch ein Kreuzdiagramm darzustellen (Abbildung2). Bei gegebenem Mischungsanteil (x-Achse) kann dort der gemessene Zuwachs im Mischbestand abtragen (grüne Kurve) und mit dem hypothetischen Mischbestand (grün gestrichelte Linie) verglichen werden. Wenn der Mischbestandszuwachs den zuwachsstärksten Reinbestand übertrifft, wird dies als transgressiver Mehrzuwachs bezeichnet. Besonders bei Buche und Douglasie sind aber die Leistungsdifferenzen der Baumarten so groß, dass dies kaum zu erwarten ist.



2 **Verlauf des Zuwachses anhand des Mischungsanteils der Douglasie**

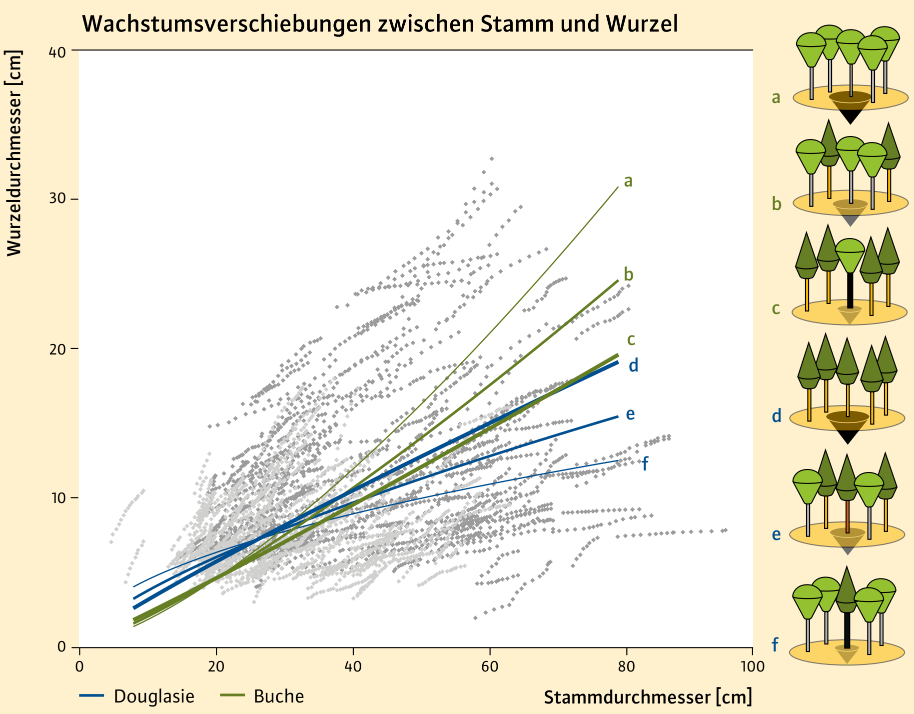


3 **Verlauf des Mehrzuwachses in Douglasien-Buchen-Mischbeständen gegenüber Reinbeständen in Abhängigkeit a) Bestandsalter (li.) und b) Jahresniederschlag (re.)**

Die Anlage dieser Tripletts erfolgte auf unterschiedlichen Standorten und in verschiedenen Altersklassen. Es spannten sich so ein Standortsgradient vom Feuchten zum Trocknen und ein Altersgradient von 30 bis 120 Jahre auf. Mit Hilfe der Gradienten konnte neben dem generellen Mehrzuwachs im Mischbestand aufgezeigt werden, dass der Mehrzuwachs insbesondere auf Standorten mit höherem Niederschlag und bei höherem Bestandsalter auftritt (Abbildung 3). Diese Zuwachssteigerung wird dabei im Wesentlichen durch ein stärkeres Dickenwachstum der Douglasie getragen. Die Buche zeigte ein verhältnismäßig gleiches Wachstumsverhalten im Rein- und im Mischbestand. Sie trägt erst im hohen Alter zum Mehrzuwachs im Mischbestand bei.

Die Struktur macht den Unterschied

Warum verbessert aber nun die Mischung der Baumarten den Zuwachs? Hierzu bestehen unterschiedliche Theorien, wie die einzelnen Baumarten von der Mischung profitieren: Ist es eine Verbesserung (Faszilitation) des Nährstoffangebots wie bei Douglasie und Roterle *(Alnus rubra)*? Oder ist es eine bessere Ausnutzung von Licht oder Wasser wie bei Buche und Kiefer *(Pinus sylvestris)* (Komplementarität)?
Grundsätzlich zeigt sich in der aktuellen Mischbestandsforschung, dass es einen einzigen Mischungseffekt, der für alle Baumartenkombinationen zutrifft, nicht gibt. Die Eigenschaften der jeweils gemischten Baumarten führen zu unterschiedlichen Mischungseffekten und verbessern bzw. verschlechtern die Ressourcenaufnahme der Baumindividuen. Die limitierend wirkende Ressource bestimmt letztlich auch die Abhängigkeit des Mehrzuwachses vom Standort.



4 **Verschiebung des Wachstums zwischen Stammdurchmesser und Wurzeldurchmesser in Abhängigkeit der umgebenden Mischung von Buche und Douglasie; (a,d) 100 % intraspezifische Konkurrenz für den Baum – Reinbestand, (b,e) 50 % intraspezifische Konkurrenz für den Baum – Baum ist von eigenen Arten und der anderen Art umgeben, (c,f) 100 % interspezifische Konkurrenz für den Baum**

Douglasie gewinnt im Licht, Buche ist im Schatten stark

Bei der Mischung von Buche und Douglasie hat sich gezeigt, dass besonders die Höhenstrukturierung den Mischungseffekt bestimmt (Thurm und Pretzsch 2016). So finden sich im Alter von 100 Jahren problemlos Bestände, in denen die Douglasie (h_{100} = 46 m) die Buche (h_{100} = 36 m) um 10 m überragt. Die Douglasie als Baumart mit einer sehr hohen Lichtnutzungseffizienz kann diese »Freistellung« des oberen Kronenbereiches effektiv nutzen. Die Buche mit ihrem niedrigen Lichtkompensationspunkt ist dennoch in der Lage, auch das einfallende Streulicht noch effizient umzusetzen. Das Licht ist bei dieser Mischung offenbar der limitierende Faktor beider Baumarten. Damit erklärt sich, dass mit höherem Alter und größerer Höhenstrukturierung der Mischungseffekt zunimmt. Der Standort hat einen ähnlichen Effekt: Auf einem besseren Standort gewinnt die Douglasie an Wuchsvorsprung und durch die somit stärkere Strukturierung stellt sich ein höherer Mehrzuwachs ein.

Die biologisch getriebene Strukturierung bietet neben der besseren Lichtausnutzung einen weiteren Vorteil: Die in Mischbeständen auftretende horizontale Struktur führt zu einer Qualifizierung der Stämme, die in Reinbeständen nur durch aufwendige Pflegemaßnahmen zu erreichen ist (Pretzsch und Rais 2016).

Wenn das Licht im Mischbestand limitierend wirkt, stellt sich die Frage, wie die beiden Baumarten im Boden interagieren. Allgemein wird gelehrt, dass sich die Streu verbessert, wenn ein Nadelbaum mit einem Laubbaum gemischt wird. Fakt ist, dass die Douglasie keine so ungünstige Streu hat (Edmonds 1980; Augusto et al. 2002). Auch der positive Effekt der höheren Struktur der gemischten Nadel-Laub-Streu ist bei weitem nicht so ausgeprägt, wie es häufig vermutet wird. Es sind vielmehr die veränderten Umweltbedingungen und die faunistische Zusammensetzung, die im Mischbestand für eine schnellere Umsetzung sorgen (Berger und Berger 2014) (Prietzel in diesem Heft).

Mehr Stamm-, weniger Wurzelwachstum

Ein wichtiger Aspekt bei Buche und Douglasie ist vielmehr, dass sich beide Baumarten in der Nährstoffaufnahme ergänzen, weil unterschiedliche Nährstoffe für ihre Versorgung wichtig sind (Pretzsch et al. 2014). Diese Konkurrenzminderung im Boden ermöglicht es, dass die Bäume verstärkt in das oberirdische Wachstum investieren können.

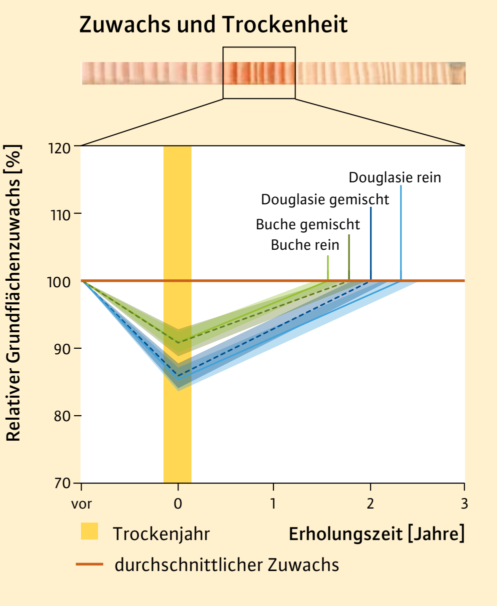
Bei unseren Untersuchungen an Wurzel und Stamm der Bäume (Abbildung 4) konnten wir feststellen, dass im Vergleich zum Reinbestand Bäume im Mischbestand eher in das Dickenwachstum des Stammes und weniger in das Dickenwachstum der Grobwurzeln investieren (Thurm et al. in Bearbeitung). Im Reinbestand, wo die intraspezifische Konkurrenz 100 % beträgt, ist der Wurzeldurchmesser im Verhältnis zum Stammdurchmesser stets größer als in Mischungssituationen, wo der untersuchte Baum von Individuen der eigenen und der anderen Art umgeben ist (50 % intraspezifische Konkurrenz). Am geringsten ist jeweils der Wurzeldurchmesser, wenn der untersuchte Baum ausschließlich von der anderen Art (100 % interspezifische Konkurrenz) umgeben ist. Demnach zeigt ein höherer Mischungsanteil bei beiden Baumarten eine Verschiebung der Kurve zugunsten des Stammwachstums.

Dieses veränderte Spross-Wurzel-Verhältnis zugunsten des Stammwachstums war auch im Hinblick auf andere Einflussfaktoren festzustellen. So zeigen Douglasien auf besseren Standorten ein geringeres Wurzelwachstum als auf schlechteren Standorten. Eine geringere Bestandsdichte beeinflusst die Stamm-Wurzel-Relation ähnlich zu Gunsten des Stammes. Dass die Mischung den gleichen positiven Einfluss auf das Stammwachstum hat, konnte mit der aktuellen Studie jedoch zum ersten Mal festgestellt werden. Der Vergleich von Standortgüte und Bestandsdichte zeigt jedoch, welche positive Wirkung die Mischung von Buche und Douglasie auf die Bäume ausübt.

Mischung verkürzt die Erholungszeit

Ein weiterer Teil unserer Arbeit befasste sich mit dem Einfluss von Trockenstress auf das Zuwachsverhalten (Thurm et al. 2016). Dazu untersuchten wir die Jahrringzuwächse der Stämme mit Hilfe von Bohrkernen. Betrachtet wurden die stärksten Trockenereignisse zwischen 1950 und 2010 und dahingehend analysiert, wie stark der Grundflächenzuwachs des Einzelbaumes im Trockenjahr einbricht und wieviel Zeit die Baumarten benötigen, um sich wieder auf ihr Niveau vor dem Trockenereignis einzufinden.

Dabei stellte sich heraus, dass die Mischung keinen Einfluss auf den Zuwachseinbruch im Trockenjahr hat. Abbildung 5 beschreibt den relativen Zuwachseinbruch innerhalb der Jahrringe von Buche und Douglasie im Rein- und Mischbestand in Trockenjahren und die anschließende Erholungsphase. Der Einbruch zeigt den Zuwachsverlust gegenüber dem durchschnittlichen Zuwachs an (orange Linie). Die aufstrebenden Linien stellen dar, wann sich die Bäume wieder von einem Trockenjahr erholt haben und sich auf dem Wachstumsniveau vor dem Trockenstress befinden. Die Douglasien brechen im Reinbestand prozentual etwas mehr ein, besitzen aber auch ein generell höheres Wachstumsniveau als die Buchen. In der Erholungsphase regenerierten sich die Douglasien im Mischbestand jedoch etwas schneller als die Douglasien im Reinbestand. Die Buchen benötigten im Mischbestand eine längere Erholungszeit. Wir vermuten, dass eine zeitlich verzögerte Wassernutzung im Folgejahr die Ursache ist. Die Douglasie als immergrüne Baumart fängt mit der Transpiration an, sobald es die Witterungsbedingungen erlauben. Die Buche beginnt erst wieder mit der Transpiration ab Laubaustrieb. Das bedeutet: Im Mischbestand kann die Douglasie bei günstigen Bedingungen im Frühjahr frühzeitig ihre Reserven wieder auffüllen, das jedoch ohne Konkurrenz der noch nicht ausgetriebenen Buche. In den jeweiligen Reinbeständen beginnen die beiden Baumarten jeweils gleichzeitig zu transpirieren. Die Douglasie, die im Vergleich zur Fichte generell eine bessere Trockenheitsresistenz hat, profitiert also zusätzlich von der Buchenmischung nach Trockenphasen.



5 **Relativer Zuwachseinbruch innerhalb der Jahrringe von Buche und Douglasie im Rein- und Mischbestand in Trockenjahren**

Schlussfolgerungen für die Bewirtschaftung

Unsere Studie hat gezeigt, dass die Mischung von Buche und Douglasie positive Effekte nach sich zieht. Das Wachstum der Douglasie wird gesteigert und das Wachstum der Buche bleibt mindestens konstant. Einen durchschnittlichen Bestandszuwachs von 21 Vorratsfestmetern je Hektar und Jahr (Vfm $\text{ha}^{-1}\ \text{a}^{-1}$) im Alter von 60 Jahren auf guten Standorten erreichen sicherlich nur wenige Bestandstypen in Mitteleuropa. Im Hinblick auf eine prognostizierte Nadelholzverknappung stellt die Douglasie damit eine sinnvolle Alternative zur Fichte dar. Hohe Niederschläge fördern dabei den Mischungseffekt zusätzlich. Im besonderen Maße ist es das Alter, das zu einem Mehrzuwachs von Mischbeständen gegenüber Reinbeständen führt. Die Mischung braucht Zeit, um einen Mischbestandseffekt auszubilden (unabhängig davon, wie der Mischungseffekt zustande kommt).

Eine weitere waldbauliche Konsequenz ist, dass Buchen-Douglasien-Mischbestände aufgrund der besseren Lichtausnutzung in höheren Bestandsdichten gehalten werden können, ohne dass dadurch Zuwachsverluste verursacht werden. Diese höheren Dichten erlauben auch im späteren Bestandsalter zusätzliche waldbauliche Spielräume. Aufgrund der starken Dominanz der Buche im Jugendalter empfiehlt es sich, die Douglasie truppweise in die Buche einzubringen. Somit erhält man im Altbestand die gewünschte Durchmischung von ein bis maximal drei starken Douglasien, die von Buchen umfasst werden.

Mit Blick auf künftige klimatische Veränderungen zeigt sich die Douglasie ohnehin resistenter als die wichtige einheimische Nadelbaumart Fichte. Die Mischung mit der Buche verschafft ihr noch einen weiteren Stabilitätsvorteil für die Zukunft.

Zusammenfassung

In Rein- und Mischbeständen von Douglasie und Buche wurden die Wechselwirkungen zwischen diesen beiden Baumarten hinsichtlich Zuwachsverhalten und Resilienz untersucht. Vor allem das Wachstum der Douglasie ist im Mischbestand deutlich höher als im Reinbestand. Der Zuwachs der Buche bleibt in Rein- und Mischbeständen weitgehend gleich. Wegen der besseren Lichtausnutzung sind in Mischbeständen höhere Bestandsdichten möglich, ohne dass es zu Zuwachsverlusten kommt. Nach Zuwachseinbrüchen in Trockenjahren erholen sich Douglasien in Mischbeständen schneller als in Reinbeständen.

Projekt

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1 **Douglasien-Buchen-Bestand in der Abteilung Tännig – die Mischung steht für gesunden Boden, starkes Wachstum und hohe Stabilität.** Foto: J. Prietzel

Die Mutter des Waldes und die Fremde

Douglasien-Buchen-Mischbestände: aus bodenkundlicher Sicht eine attraktive Mischungsoption

Maike Cremer und Jörg Prietzel

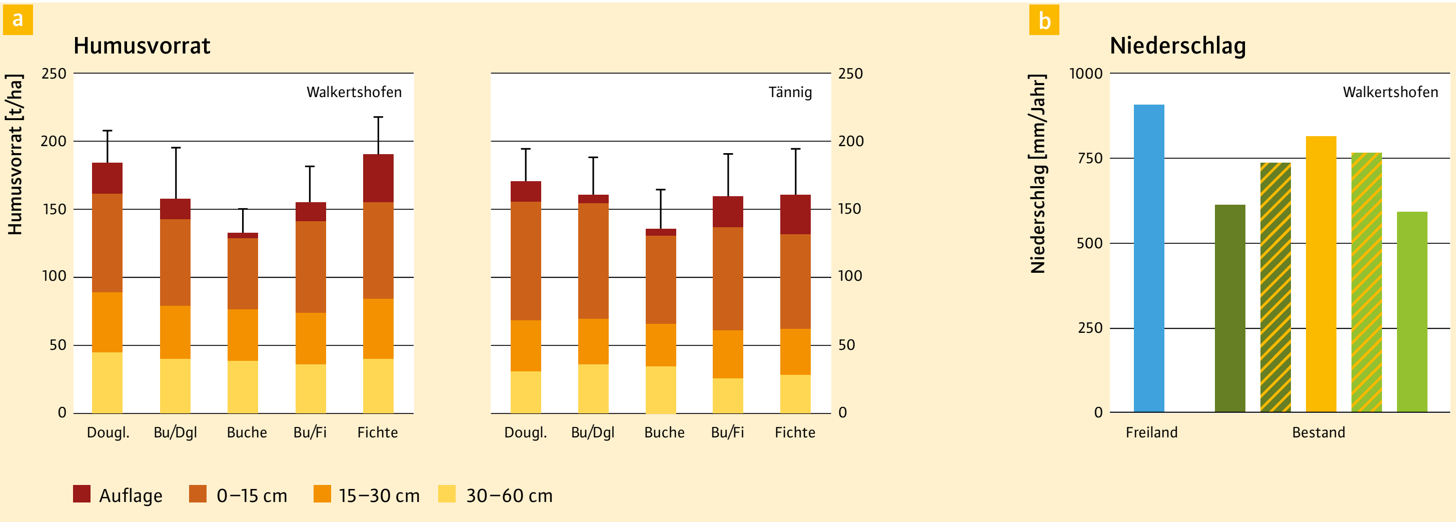
Die Anpassung der Wälder Bayerns an den Klimawandel ist ein Kernelement der waldbaulichen Planung. Eine wesentliche Rolle hierbei spielen standortsgerechte, stabile und strukturreiche Mischbestände aus Laub- und Nadelbäumen. In diesem Kontext ist auch die Douglasie – vorzugsweise in Mischung mit der Buche – eine wirtschaftlich attraktive Ersatzbaumart für die Fichte, die in zahlreichen Regionen Bayerns durch die Folgen des Klimawandels zunehmend geschwächt wird. Während für Mischbestände von Buche und Fichte mittlerweile eine Fülle an Informationen über deren ökologische Eigenschaften existiert, fehlen derartige Informationen über Mischbestände von Buche und Douglasie bislang fast völlig.

Im Rahmen eines von der Bayerischen Forstverwaltung geförderten Forschungsprojektes untersuchte der Lehrstuhl für Bodenkunde der TU München wichtige ökologische Kenngrößen von Rein- und Mischbeständen aus Buche und Douglasie auf unterschiedlichen Standorten Bayerns und verglich diese mit jenen von Rein- und Mischbeständen aus Buche und Fichte. Die untersuchten Waldorte unterscheiden sich deutlich hinsichtlich ihrer Wasser- und Nährstoffverfügbarkeit. Sie repräsentieren sowohl reiche (Südbayern, Lösslehm; z. B. Waldort Walkertshofen) als auch ärmere Standorte (Spessart, Buntsandstein; z. B. Waldort Tännig). In allen Beständen wurden unter anderem das C/N-Verhältnis, der pH-Wert und die Basensättigung der Böden bestimmt sowie die Bodenvorräte an organischem Kohlenstoff (Humus) und Stickstoff quantifiziert. Im monatlichen Rhythmus wurden darüber hinaus die Menge und die Qualität des Bestandesniederschlags und des Unterbodensickerwassers über zwei Jahre hinweg untersucht.

Mischungseffekte auf den Boden sind standortsabhängig

Die untersuchten bodenchemischen Kenngrößen der Rein- und Mischbestände von Buche, Douglasie und Fichte sind sowohl vom Standort als auch vom Bestockungstyp abhängig. Die geringmächtigen Humusauflagen unter Buchenreinbeständen sind weniger sauer und haben höhere Basensättigungen als die mächtigeren Auflagen unter reiner Douglasie und insbesondere unter reiner Fichte. Auf reichen Standorten weist die Humusauflage unter reiner Douglasie im Vergleich zum jeweiligen Fichtenreinbestand ein engeres C/N-Verhältnis auf, welches vergleichbar mit jenem unter reiner Bu-

2 **Humusvorräte, Niederschlagssummen und Nitratkonzentrationen unter Reinbeständen sowie Mischbeständen an den Waldorten Walkertshofen (Lösslehm) und Tännig (Buntsandstein)**



3 **Traumpaar Douglasie und Buche: Douglasienzapfen (li.) und Bucheckern (re.) sorgen für den Fortbestand dieses Waldtyps.** Foto: conny-wr, A. Ströbel, pixelio.de

che ist. Im Spessart ist die Humusauflage unter reiner Douglasie weniger sauer und reicher an austauschbaren Basenkationen (Ca^{2+}, Mg^{2+}, K^{+}) als unter reiner Fichte (Cremer und Prietzel 2017). Bezüglich Auflagemächtigkeit und bodenchemischen Eigenschaften sind die Buchen-Nadelholz-Mischbestände meist zwischen jenen der entsprechenden Reinbestände einzuordnen; die Buchen-Douglasien- und Buchen-Fichten-Mischbestände unterscheiden sich diesbezüglich kaum voneinander. Die Bodenhumusvorräte der Buchen-Nadelholz-Mischbestände sind im Vergleich mit den Buchenreinbeständen signifikant erhöht (Abbildung 2a): Am Waldort Walkertshofen spiegeln sie die Baumartenanteile wider, am Waldort Tännig liegen sie auf dem Niveau der Humusvorräte unter den Nadelholzreinbeständen.

Wasserhaushalt spiegelt Baumartenanteile wider

Aufgrund des ganzjährig dicht belaubten Kronendachs der Nadelholzreinbestände ist der Bestandesniederschlag unter reiner Douglasie oder reiner Fichte um etwa ein Viertel geringer als jener unter reiner Buche (Abbildung 2b) und auch die Sickerwassermenge ist unter den Nadelholzreinbeständen deutlich geringer als unter reiner Buche. In den Nadelholz-Buchen-Mischbeständen führt die im Winter im Vergleich zu den Nadelholzreinbeständen deutlich reduzierte Evapotranspiration zu einer Erhöhung von Bestandesniederschlag, Sickerwasserspende und Grundwasserneubildung. Dabei wird allerdings nicht das hohe Niveau der Buchenreinbestände erreicht.

Buchen-Douglasien-Mischwälder reichern Stickstoff im Boden an

Unabhängig vom Standort ist den Untersuchungen zufolge in Mischbeständen von Buche und Douglasie der Stickstoffeintrag aus der Luft im Vergleich zu Reinbeständen dieser Baumarten erhöht. Mit ihrer großen Blattoberfläche filtern diese i. d. R. sehr ausgeprägt strukturierten Mischbestände offenbar Stickstoffverbindungen besonders intensiv aus der Luft (deutlich stärker als Mischbestände von Buche und Fichte) und erhöhen somit den N-Eintrag in den Bestand. Die Nitratkonzentrationen im Sickerwasser (Abbildung 2c) und auch die Nitratausträge sind unter den Douglasien-Buchen-Mischbeständen hingegen ausnahmslos sehr niedrig und vergleichbar mit jenen unter Buche. Den Ergebnissen zufolge reichert sich der Waldboden unter Buchen-Douglasien-Mischungen derzeit besonders stark mit Stickstoff an.

Zusammenfassung

Vor allem unter dem Aspekt der Humuspflege sind Buchen-Douglasien-Mischbestände sehr positiv zu bewerten. Sie speichern mehr organischen Kohlenstoff in stabiler Form im Mineralboden als Nadelholz- oder Buchenreinbestände und ihre Gesamt-Bodenhumusvorräte sind nur unwesentlich niedriger als jene unter benachbarten Nadelholzreinbeständen, aber deutlich höher als unter Buchenreinbeständen. Auch die Nitratbelastung des Grundwassers ist deutlich geringer als unter Douglasien- oder Fichtenreinbeständen und nur wenig höher als unter reiner Buche. Im »Normalbetrieb« reichern diese Mischbestände offenbar besonders effizient organischen Kohlenstoff (Humus) und Stickstoff in stabiler Form im Mineralboden an. Zudem sind in Buchen-Douglasien-Mischbeständen das Kalamitätsrisiko und die damit verbundene Gefahr einer schlagartigen Freisetzung von z. B. Nitrat in Bodensicker-, Grund- und Oberflächenwasser deutlich geringer als in Reinbeständen von Buche, Douglasie oder Fichte. Buchen-Douglasien-Mischbestände sind demnach für die ökochemische Qualität von Wasser und Boden vorteilhafter als Douglasien- oder Fichtenreinbestände und oftmals nicht schlechter als Buchenreinbestände auf gleichem Standort. Zusammenfassend kann gesagt werden, dass die Mischung von Douglasie und Buche zumindest im Hinblick auf die Qualität des Bodens und des Bodensickerwassers eine attraktive Option darstellt.

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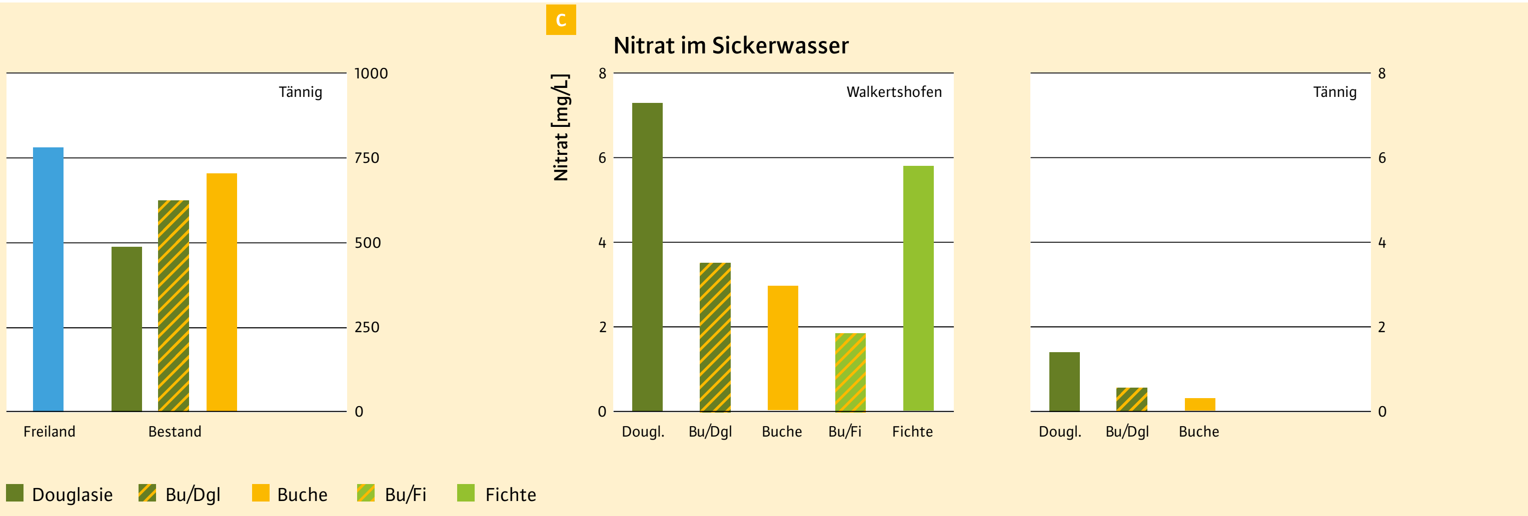

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ORIGINAL PAPER

Improved productivity and modified tree morphology of mixed versus pure stands of European beech (*Fagus sylvatica*) and Douglas-fir (*Pseudotsuga menziesii*) with increasing precipitation and age

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Abstract

- ***Key message*** **The mixture of Douglas-fir and European beech produced more biomass compared to what would have been expected from a weighted average of pure stands. Overyielding of the mixed stands improved with increasing stand age and under better site conditions.**
- ***Context*** The mixture of Douglas-fir and European beech has the intrinsic potential to be one of the most productive forest types in Central Europe.
- ***Aims*** The study investigated how the structure and productivity of mixed stands changed in comparison to pure ones. It analyzed whether there is overyielding in mixed stands and if it was modified due to stand development or along an ecological gradient.
- ***Methods*** Throughout Germany, 18 research plot triplets with 1987 trees were established in seven different ecological regions from dry to moist site conditions at ages 30 to 120 years. To investigate the growth of the stands, tree cores were collected from 1293 stems.
- ***Results*** The study revealed significant overyielding of biomass in mixed stands of 6 % or 0.81 Mg ha^{-1} year^{-1}. It was found that: (i) Overyielding in mixed stands was driven by an increase in Douglas-fir growth. (ii) Both species modified their morphology in mixture. Compared to the species in pure stands, Douglas-fir diameters in mixed stands were significantly larger, whereas European beech had a smaller diameter at breast height in the mixture. The effect increased with the age. (iii) The analyses revealed more pronounced overyielding in older stands and on better sites.
- ***Conclusion*** The findings show that overyielding of Douglas-fir and European beech in mixed stands results from a higher light interception by complementary space occupation.

Keywords Mixing effect · Overyielding · Triplet experimental setups · Age gradient · Ecological gradient · Height stratification

1 Introduction

Recently, the mixture of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and European beech (*Fagus sylvatica* L.) has greatly increased in relevance (Thünen-Institut 2012). Silviculture with Douglas-fir is a very controversial topic in Germany. On the one hand, it is considered as one of the most successfully introduced tree species in Europe because it is known for its high wood quality, growth, and adaptability to heterogeneous environments (Kleinschmit and Bastien 1992). Douglas-fir is superior in its productivity in comparison to other species in Central Europe (Pretzsch 2005). Therefore,

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Contribution of the co-authors
Eric A. Thurm: running field work and data analysis and writing the paper.
Hanz Pretzsch: initiating the project, contributing to study conception and design, and reviewing the manuscript.

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the high productivity of this tree species offers the potential to counteract the expected wood supply gaps in the future (Mantau et al. 2008). On the other hand, it is often criticized that Douglas-fir, as a neophyte, leads to a floristic and faunistic impoverishment in European forests (Knoerzer and Reif 1996; Meyer 2011). It is known that introducing additional tree species in pure stands can increase overall biodiversity (Felton et al. 2010; Cavard et al. 2011) and decrease the risk of pest outbreaks (Kelty 1992; Montagnini et al. 1995; Jactel and Brockerhoff 2007). Thus, a practical compromise might be the management of Douglas-fir in mixed stands.

Due to its specific growing behavior, there are not many candidate species to mix with Douglas-fir to get an even-aged, single-tree mixture (Göhre 1958). Its slow growth after planting places it in danger of being overgrown by other species. After it is established, its vigorous growth can easily drive other species into suppression. So, the species considered for admixture should be both vigorous in growth and shade-tolerant at the same time.

In its natural North American range, Douglas-fir is a subclimax species. Natural pure stands mainly arise as a result of forest fires (Hermann 2007). Over the course of stand development, the Douglas-firs are joined by shade-tolerant species like western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and Western red cedar (*Thuja plicata* Donn ex D. Don) in the understory. These mixtures might also work in Central Europe but considering biodiversity issues, indigenous species are mostly preferred to mix with Douglas-fir in Europe.

European beech is often considered an appropriate Central European deciduous species to mix with Douglas-fir (Göhre 1958; Otto 1987). The climatic requirements of both species overlap in Central Europe (Kölling 2007). Given the shade-tolerance of European beech, it is able to build a second stand layer below the predominant Douglas-fir. European beech retains its vitality and fills developing gaps in the canopy in older stands (Göhre 1958). The horizontal structure and resulting tree size pattern seems to be an important issue to understand mixing effects (del Río et al. 2016).

With regard to the known high productivity potential of Douglas-fir in pure stands and the relevance of its mixture with European beech, it is important to improve knowledge about the growth and yield of such mixed stands. While there are many studies dealing with the question of over- or underyielding in mixed stands (e.g., Kelty 1992; Piotto 2008; Pretzsch et al. 2013), there are, to our knowledge, only two extensive studies dealing with Douglas-fir and European beech (Bartelink 1998, Thomas et al. 2015). Both studies showed a higher increment in mixed stands compared to what would have been expected from a weighted average of pure stands. Bartelink (1998) included an age gradient in his study, but did not analyze the impact of the age on overyielding. Studies with other mixtures pointed out that age influenced overyielding (Binkley 2003; Forrester et al. 2004; Amoroso and Turnblom 2006). That is why the current study analyzes if it is possible that over- or underyielding in Douglas-fir–European beech stands changes with stand age.

Studies on mixed stand effects revealed that, independent of tree species, over- or underyielding is dependent on site conditions (Binkley 2003; Pretzsch et al. 2010; Forrester et al. 2013). The shift of facilitation to competition along an improving environmental gradient (Callaway and Walker 1997) leads to overyielding on poorer sites in some studies (Pretzsch et al. 2010; Binkley 2003; Toïgo et al. 2014). In other studies, complementary effects were especially evident on better sites and resulted in a higher yield with improving site conditions (Forrester et al. 2013; Forrester and Albrecht 2014).

Based on previous studies, the following questions were investigated: (i) How does the structure change in mixed stands compared to pure stands? (ii) Does overyielding arise in mixed stands? How does this overyielding change along an (iii) age and (iv) productivity gradient?

2 Material and methods

2.1 Study sites

2.1.1 Site characteristics

In Southern Germany, seven ecological regions—five in Bavaria and two in Rhineland-Palatinate—were selected for experimental setup (Fig. 1). Table 1 summarizes important climate and soil characteristics. The experiment collection was concentrated in the colline level (330–580 m a. s. l.) and covered a span of 430 km. The mean annual temperature ranged from 7.5 to 9.3 °C (average = 8.4 °C) with an annual mean precipitation between 718 and 1070 mm (average = 935 mm) (Deutscher Wetterdienst 2015). The experiment included drier, warmer sites in the ecological region of *Fränkische Platte* and moister, colder sites like the *Schwäbisch-Bayerische Schotterplatten- und Altmoränenlandschaft*. The base supply of the soil ranged from base-rich to base-poorer sites. The water supply of the established plots, described by the combination of water-holding capacity, precipitation, and transpiration, ranged from very fresh (equate with much moisture) to moderate dry (Landesforst Rheinland-Pfalz 2014; Bayerische Landesanstalt für Wald und Forstwirtschaft 2013).

2.1.2 Experimental design of plots

The samples were subdivided into stands of three age levels per ecological region: young (around 30 years), mature (around 60 years) and old (older than 90 years). The age levels of the ecological regions were used to build chronosequences

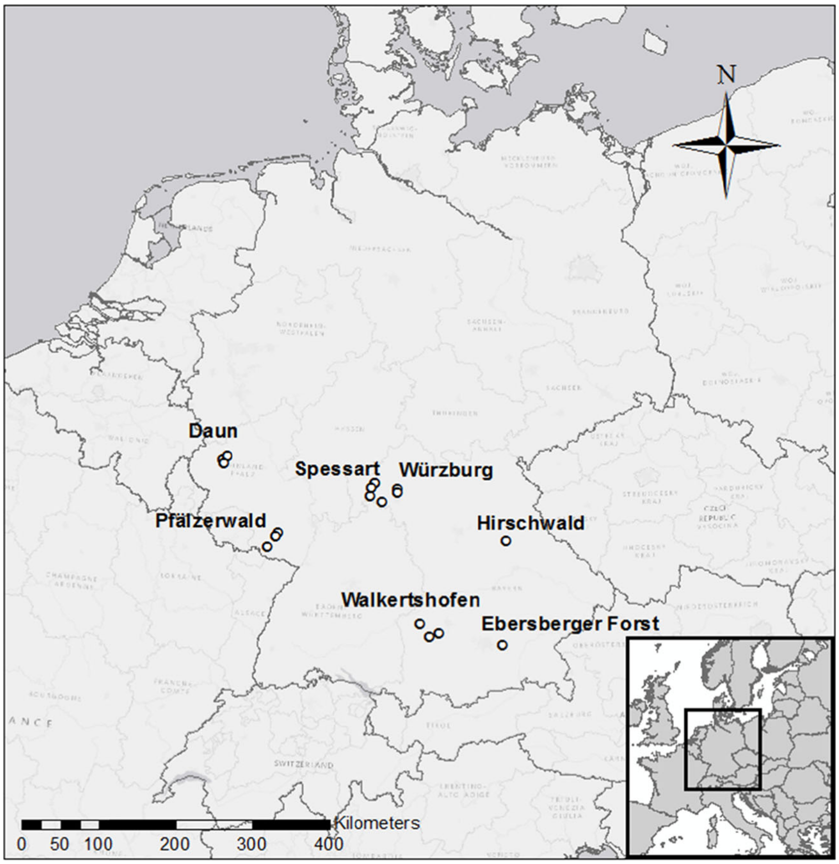

Fig. 1 Geographic location of the 18 triplets at seven different ecological regions in Germany; each of the 18 sites (*black points*) include three plots: a pure stand of Douglas-fir, a pure stand of European beech, and a mixed stand of both species

(also see de Wall et al. 1998). In two of the seven ecological regions, only one age level was established. In the ecological region *Spessart*, we sampled four triplets because mature triplets were already installed. Altogether, 18 triplets were analyzed (open circles in Fig. 1). The triplet setup is a well-established method for mixture research (e.g., Amoroso and Turnblom 2006, Pretzsch et al. 2010) and consisted of a pure stand of Douglas-fir ($_{\mathrm{Df}}$), a pure stand of European beech ($_{\mathrm{Eb}}$), and a mixed stand of both species($_{\mathrm{Df,Eb}}$). The selection of the triplets was made in managed forest stands without experimental background. The plots of a triplet were located in close proximity. The median distance from the center of the pure to the center of the mixed plot was 86 m for Douglas-fir and 260 m for European beech. In the majority of triplets, the three plots were inside the same compartment. They were more or less even-aged (see Online Resource 1) and had similar site conditions (also seen in Online Resource 2). The soil similarity of the triplets was checked by a comparison of the site map. When the plots were not inside the same compartment, the similarity of the soil was visually checked by a sample with a boring rod. The distances between the plots of a triplet were not great enough to have a significant influence on climate. Minor climatic differences might result from the intersection of the plots with the gridded climate data. For the analyses, we used the average site conditions of a triplet. Overall, 54 plots were part of the study. All site conditions from all plots within an ecological region are assumed to be similar (also seen in Online Resource 2).

In the selection of the plots, we tried to select only fully stocked stands with low thinning intensity. The maximum stand density should ensure that all stands produce their maximum yield and enables a comparison between the different mixing types. Because we investigated backwards a time period of 20 years, the mechanism of self-thinning and thinning took effect in the development of the stands. Therefore, we also collected the dead trees and the stumps of the felled trees and their time point of death and reconstructed fully stocked stands for the whole time period.

We selected the plots with the requirement to include only the two investigated species. The plots were sections of planted stands or anthropogenic initiated natural regeneration. Therefore, pure stands consisted completely of one species. The proportion of foreign tree species in pure and mixed stands was 1.2 % of the overall basal area. These individual trees were only suppressed trees. We added them to the stand productivity of Douglas-fir or European beech, depending on whether they were broadleaf or coniferous species.

When selecting the plots, we tried to consider a buffer zone of more than one tree length, to exclude edge effects or mixing effects with other tree species. The minimum requirement was that the neighboring trees continued the species composition of the plot.

Table 1 Site characteristics of the seven experimental locations in their ecological regions (Gauer and Kroiher 2012), climate data (Deutscher Wetterdienst 2015), base-richness, and water supply (Landesforst Rheinland-Pfalz 2014; Bayerische Landesanstalt für Wald und Forstwirtschaft 2013)

Experimental location	Ecological region	Geographic position		Elevation	Mean annual precipitation (1981–2014) mm $year^{-1}$ (min–max)	Mean annual temperature (1981–2014) °C (min–max)	Base-richness from base-poor (1) to base-rich (5)	Water supply from very dry (1) to very fresh(7)
		N latitude	E longitude	m above sea level (min-max)				
Walkertshofen	Tertiäres Hügelland	48° 15′ 18.33″	10° 44′ 49.15″	556 (523–597)	961 (890–1011)	8.2 (8.1–8.4)	3	7
Würzburg	Fränkische Platte	49° 56′ 10.05″	9° 56′ 17.51″	310 (272–343)	749 (718–792)	8.8 (8.5–9.2)	4	3
Spessart	Spessart	49° 50′ 37.96″	9° 27′ 56.62″	384 (279–384)	1001 (878–1070)	8.5 (7.9–9.0)	3–4	4–7
Ebersberger Forst	Schwäbisch-Bayerische Schotterplatten-und Altmoränen-landschaft	48° 07′ 16.78″	11° 51′ 09.88″	532	1044	8.5	4	7
Daun	Osteifel	50° 10′ 23.86″	6° 44′ 36.33″	486 (471–500)	978 (880–1066)	7.9 (7.5–8.2)	3	6
Hirschwald	Frankenalb und Oberpfälzer Jura	49° 20′ 34.74″	11° 54′ 34.98″	474 (462–482)	821	8.0	3	5
Pfälzerwald	Pfälzerwald	49° 19′ 10.67″	7° 48′ 23.27″	445 (416–457)	967 (894–832)	8.6 (8.3–8.8)	2	5

The mixed plots were selected by the criterion of single-tree mixture. The mixing proportion (m) was calculated using the stand density index (SDI) introduced by Reineke (1933). The stand density differences between the species were adjusted by an equivalence coefficient e_1 computed by the ratio between the SDI of pure Douglas-fir stands ($\mathrm{SDI_{Df}}$) and pure beech stands ($\mathrm{SDI_{Eb}}$) (Sterba et al. 2014; Pretzsch et al. 2015). The equivalence coefficient (average 1.63) was computed for every triplet. Douglas-fir and European beech in mixed stands were abbreviated with $_{\mathrm{Df,(Eb)}}$ and $_{\mathrm{(Df),Eb}}$.

$$m_{\mathrm{Df,(Eb)}} = \frac{\mathrm{SDI_{Df,(Eb)}}}{\mathrm{SDI_{Df,(Eb)}} + \mathrm{SDI_{(Df),Eb}}\cdot \mathrm{e1}} \tag{1}$$

The mean ratio of mixture was 0.47:0.53 (Douglas-fir/European beech) and ranged between 0.22 and 0.76 for Douglas-fir.

The 54 plots comprised a span of size between 0.01 and 0.24 ha (mean = 0.06 ha). The sizes of the plots were dependent on the age of the trees. Each pure stand contained 20 dominant trees and each mixed stand contained 20 dominant trees per species. For all of the 1987 trees, diameter at breast height (DBH), positions of the crown and tree height (h) were measured (Online Resource 1). Two cores were taken from all dominant trees and, when available, from five suppressed trees. Altogether, cores of 1293 trees (2586 cores) were gathered (Online Resource 3) and measured with a digital positiometer (Biritz GmbH, Gerasdorf bei Wien, Austria). Cross-dating of the year rings was undertaken with the software TSAPWin Scientific 4.69d (Rinntech, Heidelberg, Germany).

In addition to the standing trees, all stumps on the plots were registered. Their diameters were measured in order to comprehend the thinning in the past and thus to not underestimate the increment of the whole stands. With the root collar diameters from the living trees and their DBHs, the DBHs from the stumps could be reconstructed. We estimated the approximate date of tree felling by visual attribution of the decay. The assessment of the stumps was carried out in five decay classes based on the classification by Krüger (2013).

2.2 Stand history—increment calculation

The annual diameter increment (i_d) of stumps and undrilled trees were calculated by fitting the function $\ln(id) = a + b\cdot\ln(\mathrm{DBH})$. The reconstruction time span was usually 20 years. For young trees of an age of less than or equal to 30 years, the time span was 10 years. The current tree heights and the positions of the crowns were measured with a Vertex IV (Haglöf, Långsele, Sweden). Previous height developments were described by the Michailov height curve system, which was parametrized by measured tree heights of the chronosequences. Wherever no chronosequences were available, height development was calculated by yield tables (Bergel 1985; Schober 1987). With the given size and tree number per plot, the volume of the plots could be extrapolated by the reconstructed diameters and heights. The increment results from the difference in the volume from one period to the previous period plus removal stand (thing and self-thinning).

For each of the 18 triplets, the most common growth and yield parameters were computed according to the DESER Norm (Johann 1993) in 5-year periods for the last three decades using standard software of the Chair for Forest Growth and Yield Science (Biber 2013). In the end, a data pool of 66 survey periods of the triplets periods existed.

The aboveground biomass was calculated by functions based on Pretzsch et al. (2014). The biomass of the individual tree (B_it) was calculated by the diameter at breast height (DBH) and the tree height (h):

$$B_{\mathrm{it}} = e^{a_0}\cdot \mathrm{DBH}^{a_1}\cdot h^{a_2}, \tag{2}$$

with $a_0 = -2.996$, $a_1 = 2.123$, and $a_2 = 0.694$ for European beech and $a_0 = -3.211$, $a_1 = 2.008$, and $a_2 = 0.730$ for Douglas-fir.

The biomass increment was obtained by the biomass of a tree in the current period subtracted by the previous period. The increment of the stand arose from all trees of a plot scaled up to 1 ha.

2.3 Structure

The height (h), diameter at breast height (DBH), and the ratio between both (h/d ratio) showed the structural differences between trees in pure and mixed stands. They were included in the analysis as the quadratic mean diameter tree of the plots, backwards in 5-year intervals.

To characterize the species-specific dynamics along the age gradient, we fitted height growth curves for both species in mixed stands (also described by del Río et al. 2016). For this, we used the tree heights and positions of crowns in mixed stands in the year of sampling. The fitting was done by means of the Chapman-Richard growth function.

2.4 Mixing effects

The description of the mixing effect has often been considered and is commonly accepted (Huber et al. 2014). So, here only, the formulas are presented. For a more detailed overview, see Pretzsch et al. (2010). As already used by Pretzsch et al. (2010), periodic mean annual increment of volume (PAIV) and aboveground biomass (PAIW) were used as a measure of productivity in this study. The description of over- or underyielding the mixing effect was made by the comparison of expected mixed stand $\hat{p}_{\mathrm{Df,Eb}}$ based on pure stand versus observed mixed stand $p_{\mathrm{Df,Eb}}$. So, absolute (MEA) and relative (MER) mixing effect was quantified by

$$\mathrm{MEA}_{\mathrm{Df,Eb}} = p_{\mathrm{Df,Eb}} - p_{\mathrm{Df,Eb}} \text{ and } \mathrm{MER}_{\mathrm{Df,Eb}} = \frac{p_{\mathrm{Df,Eb}}}{p_{\mathrm{Df,Eb}}} \qquad (3)$$

and was calculated for increment of volume (MEAV, MERV) and aboveground biomass (MEAW, MERW). The absolute mixing effect is defined as cubic meters (MEAV) or tons (MEAW) per hectare and year. The expected mixed stand productivity (Eq. 4) if there were no mixture effects is calculated by weighting the pure stands' productivities by the species' proportions in the mixed stands.

$$p_{\mathrm{Df,Eb}} = p_{\mathrm{Df}} \cdot m_{\mathrm{Df,(Eb)}} + p_{\mathrm{Eb}} \cdot m_{\mathrm{(Df),Eb}} \qquad (4)$$

To compare the intraspecific differences of Douglas-fir and European beech between pure and mixed stands (Eq. 5), the productivity in mixed stands ($\mathrm{pp}_{\mathrm{Df,(be)}}$, $\mathrm{pp}._{\mathrm{(Df),be}}$) was scaled up to 1 ha.

$$\begin{aligned} p_{\mathrm{Df,(Eb)}} &= pp_{\mathrm{Df,(Eb)}} \cdot m_{\mathrm{Df,(Eb)}} \text{ and } p_{\mathrm{(Df),Eb}} \\ &= pp_{\mathrm{(Df),Eb}} \cdot m_{\mathrm{(Df),Eb}} \end{aligned} \qquad (5)$$

The ratio of the scaled-up productivity in the mixed stand and the productivity in the pure stand of the same species (Eq. 6) identified the species-specific over- and underyielding in the mixed stand.

$$\mathrm{MER}_{\mathrm{Df,(Eb)}} = \frac{p_{\mathrm{Df,(Eb)}}}{p_{\mathrm{Df}}} \text{ and } \mathrm{MER}_{\mathrm{(Df),Eb}} = \frac{p_{\mathrm{(Df),Eb}}}{p_{\mathrm{Eb}}} \qquad (6)$$

2.5 Statistics

This study was based on measured and reconstructed data. Because of this nesting in data, we used linear mixed-effects regression models. The nesting levels of experiment location and triplet within the experiment location could be included as random effects.

The first questions, the differences of structure and productivity between pure and mixed stands, were tested by:

$$\begin{aligned} Y_{\mathrm{ijkt}} = a_0 &+ a_1 \cdot \mathrm{mixture}_{ijk} + a_2 \cdot \ \mathrm{age}_{\mathrm{ijkt}} \\ &+ a_3 \cdot \mathrm{mixture}_{ijk} \cdot \ \mathrm{age}_{\mathrm{ijkt}} + b_i + b_{ij} + b_{ijk} \\ &+ \left(c_i + c_{ij} + c_{ijk}\right) \cdot \ \mathrm{age}_{\mathrm{ijkt}} + \varepsilon_{\mathrm{ijkt}}. \end{aligned} \qquad (7)$$

Y_{ijt} stands for the structural and productivity variables (height, DBH, *h*/*d* ratio, mean periodic increment of volume and aboveground biomass) to be tested. The differences of pure and mixed stands were included by the explanatory variables of mixture. We added an interaction of mixture and age to consider changing behavior of the variables along the stand age gradient. The indexes *i*, *j*, *k*, and *t* represent an experimental location, a triplet, a plot, and a point in time, respectively. The fixed-effect coefficient is represented by *a*. Random effects of experimental location, triplet, and plot level were included in *b* for the intercept and *c* for the age. Differences in height and *h*/*d* ratio were not based on reconstructed data. Therefore, we excluded the random-effect plot *k* in these models. The symbol ε represents the independent and identically distributed random error. Model selection was based on the Akaike Information Criterion (Burnham and Anderson 1998) and biological plausibility of the results.

The question about the influence of age and site conditions on overyielding was investigated by the relative periodic mean annual increment of aboveground biomass (MERW). It was used instead of the mean annual increment of volume (MERV) because aboveground biomass is closer to the biological explanation approach.

To verify the influence of age and ecological conditions on MERW, the following explanatory variables were included into linear mixed models: age, site index, water supply, base-richness, mean annual temperature, and mean annual precipitation (also seen in Table 1). Site index was the dominant top height at the age of 100 years of Douglas-fir in pure stands. Interactions of explanatory variables were expected between site index and age and between precipitation and water supply. The analysis was split into two approaches. The first one included the ecological conditions via the site index (SI) of Douglas-fir as one single variable:

$$\mathrm{MERW}_{ijt} = a_0 + a_1 \cdot \mathrm{age}_{ijt} + a_2 \cdot \mathrm{SI}_{ij} + a_3 \cdot \mathrm{age}_{ijt} \cdot \mathrm{SI}_{ij} + b_i + b_{ij} + \varepsilon_{ijt} \qquad (8)$$

The second model included the ecological conditions in more detail:

$$\begin{aligned} \mathrm{MERW}_{ijt} = a_0 &+ a_1 \cdot \mathrm{age}_{ijt} + a_2 \cdot \mathrm{precipitation}_{ij} \\ &+ a_3 \cdot \mathrm{temperature}_{ij} + a_4 \cdot \mathrm{base{-}richness}_{ij} \\ &+ a_5 \cdot \mathrm{water\ supply}_{ij} \\ &+ a_6 \cdot \mathrm{water\ supply}_{ij} \cdot \mathrm{precipitation}_{ij} + b_i \\ &+ b_{ij} + \varepsilon_{ijt} \end{aligned} \qquad (9)$$

This model was fitted with MERW for the whole stand ($\mathrm{MERW}_{\mathrm{Df,Eb}}$) as well as for both species separately ($\mathrm{MERW}_{\mathrm{Df,(Eb)}}$, $\mathrm{MERW}_{\mathrm{(Df),Eb}}$).

All models were processed with the *lmer* function in the R package *lme4* (Bates et al. 2015). Model selection from the extensive model of the gradients was made with the additional help of automated model selection (*dredge*) from the R package *MuMln* (Barton 2015). The significances of the fixed effects were tested by an *F* test with Satterthwaite's approximation (Kuznetsova et al. 2015). To calculate the marginal coefficient of determination for the mixed-effect models, *r.squaredGLMM* from the *MuMln* package was used. The command is based on the coefficient of determination calculation of Nakagawa and Schielzeth (2013). All statistical analyses were performed in the statistical environment R version 3.2.1 (R Core Team 2015).

3 Results

3.1 Structure

By comparing the species tree height (h) and diameter at breast height (DBH), it could be determined that Douglas-fir, regardless of whether mixed or pure, was generally taller (h = 33.1 m, p < 0.001) and thicker (DBH = 46.1 cm, p < 0.001) than European beech (h = 23.8 m; DBH = 23.6 cm) (Online Resource 1). The species-specific height difference also becomes evident in terms of the site index in pure stands: At age 100, Douglas-fir had a dominant top height of 47.2 m while European beech was only 36.9 m (Online Resource 4).

Figure 2 shows the structural comparison between pure and mixed stands by height, DBH, and the ratio of height and diameter (h/d ratio). The significances and how the structural parameters react along the age gradient can also be seen in Online Resource 5. The data indicated that the height of Douglas-fir in mixed stands (32.5 m) was similar to in pure stands (33.3 m, p > 0.05) (Fig. 2a), whereas the DBH was significantly larger (42.6 to 37.1 cm, p < 0.001)(Fig. 2b). So, the taper which was described here by the h/d ratio (Fig. 2c) showed a higher taper for Douglas-fir in mixture (87.4 to 75.0, p < 0.05). A contrary picture for European beech could be observed. The DBH was significantly smaller (19.5 to 23.7 cm, p < 0.001) (Fig. 2e) and slender in mixed stands (105.3 to 113.4, p < 0.05) (Fig. 2f). The tree height of mixed stands was also similar to pure stands (23.3 to 24.3 m, p > 0.05) (Fig. 2d).

Figure 3 shows the height development of the highest trees in mixed stands along an age gradient. It shows the large height difference between Douglas-fir and European beech in mixed stands. At younger ages, the differences between European beech and Douglas-fir were marginal, with European beech slightly leading. After 20 years, the differences increased in favor of Douglas-fir until its maximum of 11.4 m at the age of 90 years.

3.2 Overyielding

The species-specific mean volume increment in pure stands differs greatly in the present study. A mean volume increment ($PAIV_{Df}$) of 26.12 m^3 ha^{-1} $year^{-1}$ for pure Douglas-fir and ($PAIV_{Eb}$) 13.59 m^3 ha^{-1} $year^{-1}$ for pure European beech (see Online Resource 4) was found. The mixed stand lay with 21.08 m^3 ha^{-1} $year^{-1}$ between the two. Important for the analysis of overyielding was the comparison between the productivity which would be expected in mixed stands with the weighted average of the neighboring pure stands and the observed productivity in mixed stands (MEA). Overall, the mixing effect of annual volume increment ($MEAV_{Df,Eb}$) was spread from 73 % above to 55 % below the expected productivity. On average, the mixed stands produced 1.63 m^3 ha^{-1} $year^{-1}$ (p < 0.05) more than expected from pure stands (Fig. 4a, see also Online Resource 4). This means a mixture leads to overyielding, which amounts to a significant, positive mixing effect of 8 %.

In detail, there was a significant difference in how overyielding in mixed stands arose. The cross diagrams (Fig. 5, see also Online Resource 6) show that overyielding was contributed to by Douglas-fir. It produced 20 % more volume in mixed than in pure stands (5.09 m^3 h^{-1} $year^{-1}$, p < 0.05) (Fig. 4b), whereas European beech in mixed stands tended to lose increment compared to pure stands (p > 0.05) (Fig. 4c). It produced 8 % less volume than in pure stands, which means an inferiority of 1.25 m^3 ha^{-1} $year^{-1}$ (Fig. 4c). The large productivity differences between Douglas-fir and European beech in pure stands ($PAIV_{Df}/PAIV_{Eb}$ 1:2.09) increased even in mixed stands. Douglas-fir grew 2.97 times more than European beech (Online Resource 4), which showed that productivity overyielding was determined by the increment of Douglas-fir.

It was shown that the productivity differences of volume increment between the two species reduced in the calculation with the aboveground biomass production. Douglas-fir grew 1.39 times more in pure stands ($PAIW_{Df}/PAIW_{Eb}$) and 1.59 times more in mixture ($PAIW_{Df,(Eb)}/PAIW_{(Df),Eb}$). The absolute annual growth of aboveground biomass in pure stands was 15.6 Mg ha^{-1} $year^{-1}$ for Douglas-fir ($PAIW_{Df}$) and 12.4 Mg ha^{-1} $year^{-1}$ for European beech ($PAIW_{Eb}$). Nevertheless, at 14.73 Mg ha^{-1} $year^{-1}$, an average overyielding in biomass production of 6 % or 0.81 Mg ha^{-1} $year^{-1}$ (p < 0.05) was established in mixed stands (Fig. 4d, see also Online Resource 4). Overyielding was driven in general by Douglas-fir, but we found that higher age also leads to additional overyielding for European beech in mixed stands, while lower ages are connected to underyielding (p < 0.05). However, in the average age span of our triplets (60–80 years), there were no differences in increment whether European beech occurs in pure or in mixed stands.

3.3 Dependency of overyielding on age and site conditions

The explanatory variables remaining in the final models are shown in Table 2. The first model (model 1) contains all explanatory variables that were initially chosen. Age and site index were positively correlated with overyielding. The

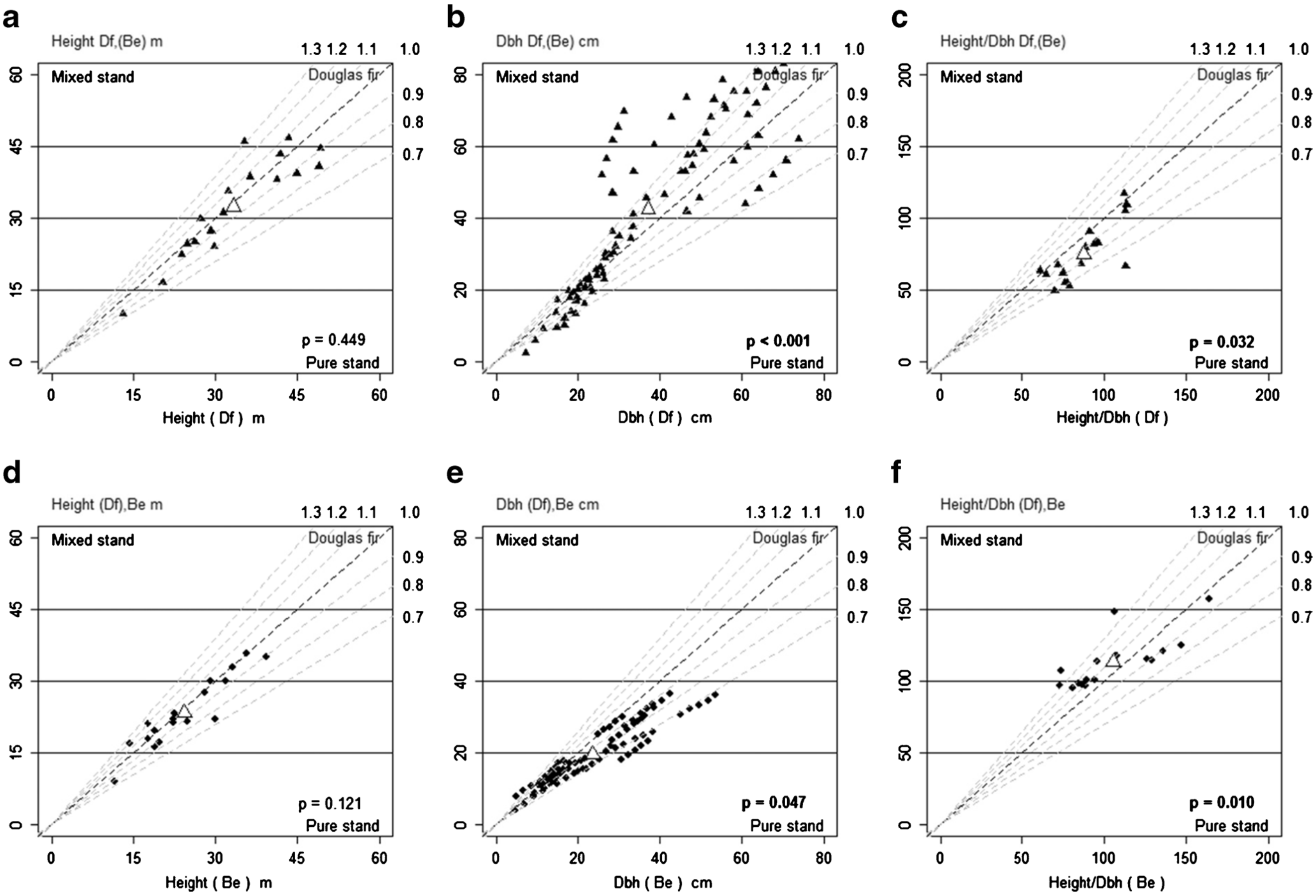

Fig. 2 Comparison between pure and mixed stand of height (**a**, **d**); diameter at breast height (**b**, **e**); and h/d ratio(**c**, **f**) of Douglas-fir—*triangles* (*above*) and European beech—*circles* (*below*). *White symbols* describe the mean value. Listed is the decisive significant in connection with the mixture (mixture or correlation of mixture and age). The values represent the measured and reconstructed data of the quadratic mean diameter tree. The whole descriptive statistic for significance is given in Online Resource 5

negative interactions between age and site index results from the decreasing influence of age with improving site index. The second model was based on stand description by site characteristics. It shows slightly more variance ($R^2 = 0.34$) than the first model ($R^2 = 0.26$). In the second model, the main explanatory variables are precipitation and temperature. Rising precipitation and temperature improved the mixing effect. Age was incorporated into the model but was not significant. Nevertheless, the AIC (−14.536) indicated that the age gave a benefit to the model compared to model without age (AIC −13.889). In both models it was shown that improving site conditions, in the first one by site index and in the second one by mean annual precipitation and temperature, led to a greater relative mixing effect.

In addition to the explanation of the relative mixing effect of the stand, models three and four try to explain how Douglas-fir ($\mathrm{MERW}_{\mathrm{Df,(Eb)}}$) and European beech ($\mathrm{MERW}_{\mathrm{(Df),Eb}}$) react to environmental conditions in mixed stands. The model of Douglas-fir showed no significant explanatory variables ($R^2 = 0.11$). Only the temperature was incorporated in the model. The European beech model was more insightful ($R^2 = 0.31$). The two explanatory variables of overyielding were base-richness and age. Age also correlated positively as in the whole stands. Base-richness reduced the mixing effect.

4 Discussion

4.1 Use of triplet experimental setup

The study could determine a significant average overyielding of 6 % more biomass increment per year in mixture, but this mixing effect was spread with a standard deviation of 28 % (standard error = 3.42). Besides the discussion of how ecological gradients influenced this overyielding, it must be discussed which influence the method has, especially the triplet selection, on the variance of overyielding. Triplet experimental setups have been proven in many studies to be a good method to detect the mixing effect (e.g., Dirnberger and Sterba

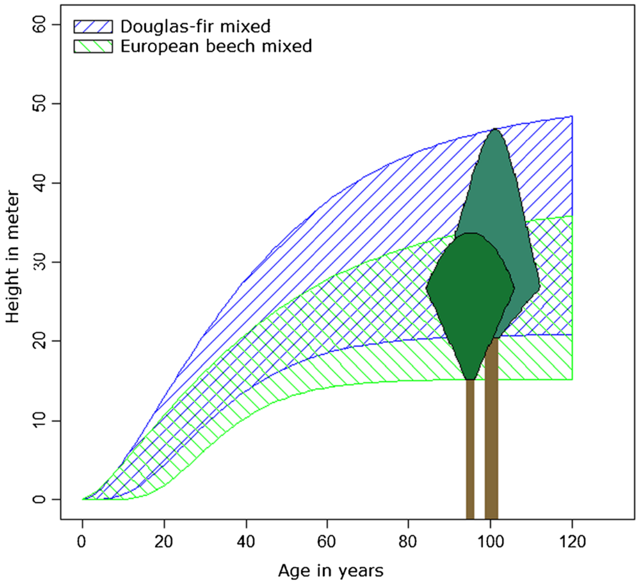

Fig. 3 Crown development from Douglas-fir and European beech of 20 % of the highest tree in mixed stand along the age gradient. The data were measured tree heights and position of crowns at the survey points, which were averaged by the Chapman-Richards model ($a(1 - \text{exp.}(-k\,t))^p$); Douglas-fir (height: $a = 53.25$, $k = 0.027$, $p = 1.57$; crown: $a = 19.27$, $k = 0.08$, $p = 8.98$); European beech (height: $a = 49.44$, $k = 0.012$, $p = 1.00$; crown: $a = 15.13$, $k = 0.08$, $p = 10.00$). Significance of the parameter can be seen in Online Resource 7

2014; Pretzsch et al. 2015). Besides the advantage of the direct comparability of species reaction in pure and mixed stands, triplets always entail the risk of heterogeneity (e.g., age, soil conditions, genetic material) inside the triplet.

The proximity of the plots inside the triplet was a main criterion for selection to minimize any heterogeneity. The soil conditions were controlled visually and by site maps. Yet, it could not be excluded that there were differences in base richness and water supply because of soil microsites. However, it cannot be assumed that the difference is systematical. Another point was the silvicultural influences. Some studies designed experimental setups which were especially established for the research of pure to mixed stands (Forrester et al. 2004; Amoroso and Turnblom 2006). This has the advantage that they can ensure the same stand history. To answer the question how age influences the mixing effect, it was necessary to cover the whole (or rather a longer) time span of the stand. Such long-term plots do not exist for Douglas-fir and European beech. That is why we used chronosequences to cover the whole rotation time.

Currently, the proportion of Douglas-fir in German forests is very low. Only 2 % of German forest is forested with Douglas-fir. It was difficult to find plots which had not been thinned over the last 20 years. Completely unthinned stands would bring the advantage that we “only” had to collect the dead trees and reconstruct their exclusion from the tree collective. In managed forests, this self-thinning mechanism is anticipated by forest management. Therefore, we also recorded the felled trees to reconstruct fully stocked stands over the whole investigation time. The thinning bore the risk of not investigating the tree response at the maximum possible stand density. Nevertheless, the growth–density relationship gives us a buffer because in high-density stands the tree collective is able to compensate for the productivity loss of the felled trees through more productivity of the remaining trees (Assmann 1970). This enabled comparable productivities of stand densities close to the maximum stand density. A comparison of yield table of fully stocked stands under given ages (Bergel 1985; Schober 1987) with our pure plots indicated that the mean SDIs are more or less equal (2 % higher SDI in selected plots). Non-experimental plot stands may be a doubtful point of reference. Nevertheless, the use of plots in managed forest is a useful benchmark as it often represents the silvicultural business as usual.

A comparable stand history was another main reason for the necessity of proximity of the stands, so that it could be expected that the same seed material was used which grows under the same forestry management system. In some cases, the current study could use plots which were less than 20 m apart. These plots were much easier to handle than plots which definitely grow on the same soil but lie 1 km apart. It can be said that for further research, the proximity of the stands is of particular importance for the selection of the triplets.

4.2 Mixing proportion

As expected, our study showed a great difference of increment between Douglas-fir and European beech. We noted that overyielding is strongly influenced by the approach of the calculation of mixing proportion. The calculation of mixing proportion was handled very differently in other studies. Mixing proportion can be calculated for example by tree number (Forrester et al. 2004; Amoroso and Turnblom 2006), basal area (Puettmann et al. 1992), volume weighted by wood dry mass (Pretzsch et al. 2013), or biomass and leaf area (Dirnberger and Sterba 2014). In this study, different approaches for mixing proportions (tree number, basal area, volume weighted by wood dry mass, adjusted SDI) were calculated and compared. In the choice of plots, the mixing proportion was estimated visually with the goal of a 50:50 proportion. It was surprising how volume shifted the mixing proportion in favor of Douglas-fir, whereas the number of trees shifted the mixing proportion in favor of European beech. Dirnberger and Sterba (2014) and Huber et al. (2014) could also show how strongly the different calculation approaches of mixing proportion influenced over- or underyielding. Finally, the adjusted SDI was taken to determine the mixing proportion, as it proved to be close to tree leaf area (Dirnberger and Sterba 2014) and results in a mixture of 0.47:0.53 (Douglas-fir/E. beech).

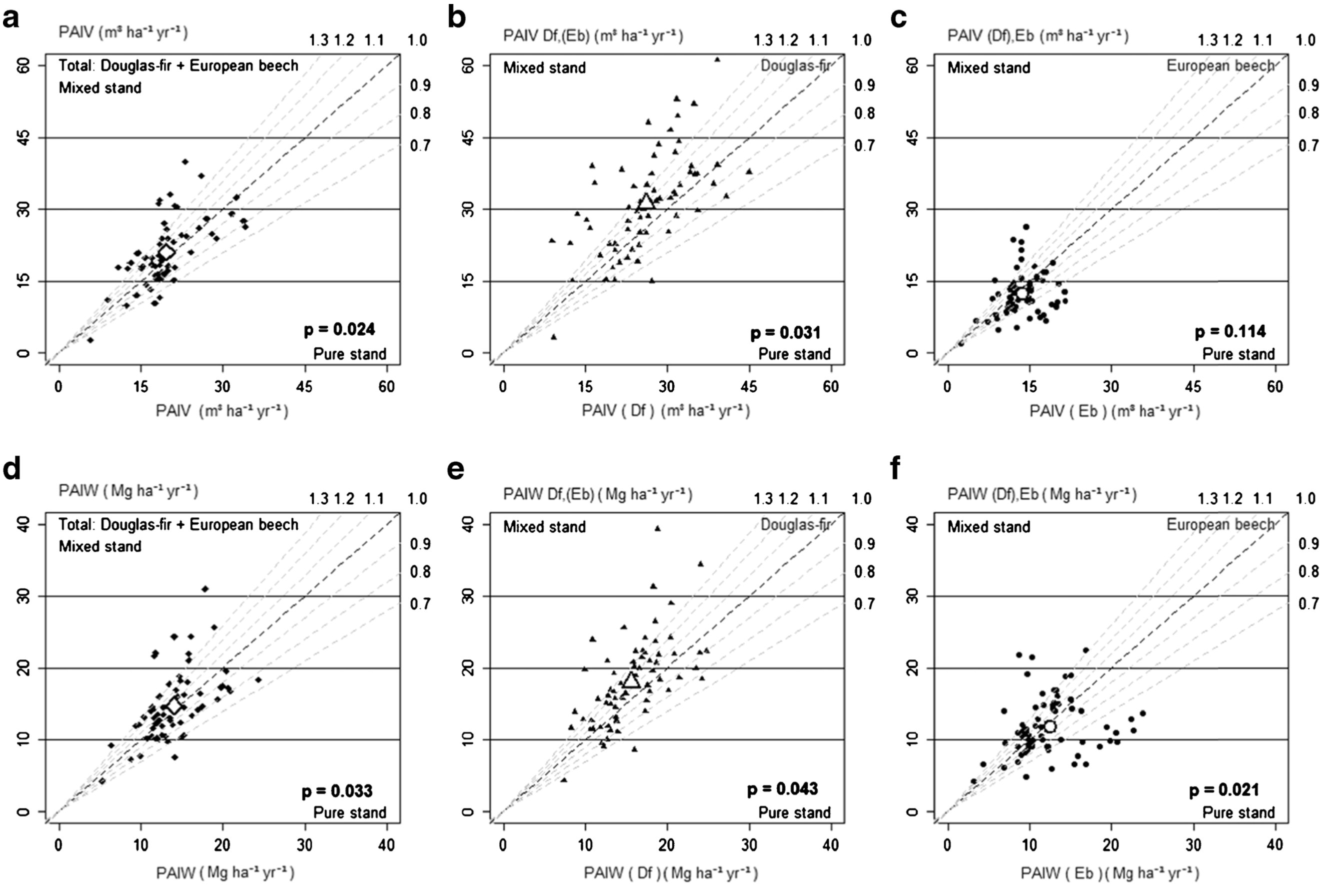

Fig. 4 Comparison between pure and mixed stands of the periodic mean annual increment of volume (*above*) and aboveground biomass (*below*) for the whole stand—*diamonds* (**a**, **d**); Douglas-fir—*triangle* (**b**, **e**); and European beech—*circle* (**c**, **f**). *White symbols* describe the mean value of pure and mixed stands. Listed is the decisive significant in connection with the mixture (mixture or correlation of mixture and age). The values represent the measured and reconstructed data. The whole descriptive statistic for significance is given in Online Resource 5

Two increment characteristics (volume and aboveground biomass) were compared in this study. It was mentioned that increasing productivity differences between the two species lead to an increasing of influence in the calculation of mixing proportion. The advantage of the aboveground biomass was that the increment ratio between Douglas-fir and European beech decreased. So, the similar overyieldings in volume (1.08) and biomass (1.06) suggest that the choice of adjusted SDI was near to reality.

4.3 Structure

The first question was whether there are any structural differences between the two species grown together compared to grown in monocultures. In the present study, the tree height–diameter ratio from mixed to pure stand differed significantly for Douglas-fir and European beech. The tree height–diameter ratio can be used as an indicator of changing competition in even-aged stands (Abetz 1976). The reason is that trees under increased competition allocate more carbon to height than to diameter growth in order to keep their crown in the canopy (Bauhus et al. 2000; Forrester et al. 2004). As a result, a higher *h*/*d* ratio indicates greater competition for light. The lower *h*/*d* ratio of Douglas-fir and greater *h*/*d* ratio of European beech in mixed stands compared to pure stands could be a sign of decreased competition for light for Douglas-fir and increased competition for European beech.

The differences of stem taper in mixed stands compared to pure stands can also be observed by the mixture of Douglas-fir and shade-tolerant western hemlock, where Douglas-fir overtopped the mixed species (Amoroso and Turnblom 2006; Erickson et al. 2009). Both could measure increasing *h*/*d* ratios for Douglas-fir and decreasing *h*/*d* ratios for the suppressed western hemlock in mixture. Erickson et al. (2009) found that the individual tree volume of Douglas-fir in mixed stands increased while the tree volume of western hemlock did not change significantly.

The reverse situation was found by Radosevich et al. (2006) in a simultaneously planted mixture of Douglas-fir with red alder (*Alnus rubra* [Bong.]). Here, Douglas-firs in mixed stands were either as small as or smaller in diameter than those trees measured in pure stands. This reverse

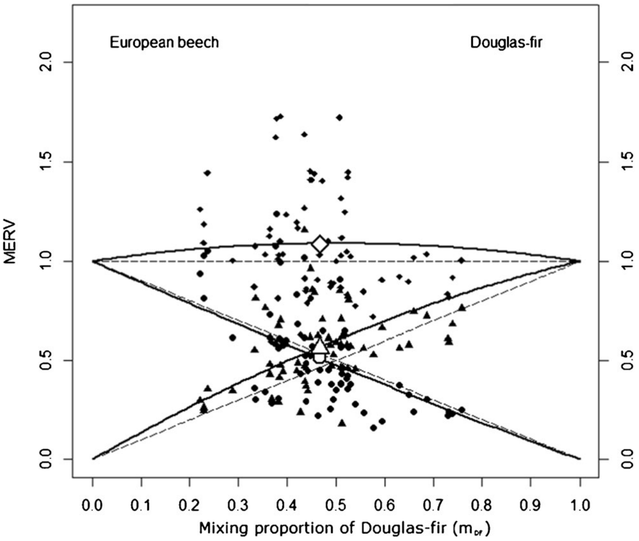

Fig. 5 Cross diagrams according to Harper (1977) and Kelty (1992) displaying the mixing effect on the productivity of Douglas-fir and European beech for volume increment. The left (European beech) and right (Douglas-fir) ordinates in the cross diagrams represent the relative productivity. The abscissa shows the mixing portion of Douglas-fir ($m_{Df,(Be)}$). *Broken lines* represent the productivity expected for neutral mixing effects on the level of the stand as a whole (horizontal 1.0 line) and on the level of the two contributing species (decreasing with respect to increasing lines). The *solid lines* show the observed productivity from whole stand (*upper bold curve*) and species-specific (*lower thin curves*). *Black symbols* represent the single observation of the whole stand (*diamond*), Douglas-fir (*triangle*), and European beech (*circle*). The *means* are marked with a *white symbol*

allocation pattern of trunk growth could be determined because Douglas-fir, at younger ages, will be suppressed by red alder. At older ages, the dominance situation changes in favor of Douglas-fir (Binkley 2003). The influence of the *h*/*d* ratio was not analyzed in this study. For European beech mixed with Norway spruce (*Picea abies* (L.) H. Karst.), Dieler and Pretzsch (2009) found that the *h*/*d* ratio of European beech increased in mixed stands, whereas the *h*/*d* ratio of Norway spruce did not change. The increased taper of European beech in mixture resulted from an increased DBH.

In addition to the dimensional change from pure to mixed stands, our study showed how large the height differences of Douglas-fir and European beech are and how they change along the stand development (Fig. 3). De Wall et al. (1998) also found similar height differences of Douglas-fir and European beech mixed stands along chronosequences. They described that the fast growth of Douglas-fir led to separation in height zones by a dominant Douglas-fir and a suppressed European beech. In the present study the highest Douglas-firs overtopped the highest beeches at the age of 90 years by 11.4 m. Therefore, the predominated Douglas-fir possessed a low lateral restriction of the crowns that increased with age. For the younger stands (around 15 years), the special situation arose that European beech outgrew Douglas-fir. This was also mentioned by Göhre (1958). It could be a critical situation for Douglas-fir because strong shading by European beech could lead to a demixing of Douglas-fir.

Table 2 Influence of the environmental gradients on the relative mixing effect based on aboveground biomass increment for the stand ($MERW_{Df,Eb}$) and separated for Douglas-fir ($MERW_{Df,(Eb)}$) and European beech ($MERW_{(Df),Eb}$)

Model/equation	Response variable:			
	$MERW_{Df,Eb}$		$MERW_{Df,(Eb)}$	$MERW_{(Df),Eb}$
	(1/8)	(2/9)	(3/9)	(4/9)
$SI_{(Df)}$	**0.083***			
47.2	(*0.033*)			
Age	**0.060***	0.003		**0.006**†
69.1	(*0.023*)	(*0.002*)		(*0.003*)
$SI_{(Df)}$ × Age	**−0.001***			
47.2 × 69.1	(*0.0005*)			
Precipitation		**0.002***		
939		(*0.001*)		
Temperature		**0.329***	**0.329**†	
8.4		(*0.143*)	(*0.180*)	
Water supply				
4.3				
Base-richness				**−0.024***
3.0				(0.012)
Constant	**−3.100.**	**−3.298***	−1.596	**1.356****
	(*1.584*)	(*1.549*)	(*1.505*)	(*0.407*)
Observations	66	66	66	66
Log Likelihood	13.501	14.268	−5.572	7.241
Akaike Inf. Crit.	−13.002‡	−14.536	21.144	−2.482
Bayesian Inf. Crit.	2.326	0.792	32.093	10.656
R^2	0. 26	0.34	0.11	0.31

The standard error are in italics and in brackets

Signif. codes: 0; ***0.001; **0.01; *0.05; † 0.1; 1

4.4 Productivity

We found overyielding in mixed stands in our study. This corresponds with the results of Bartelink (1998). Thomas et al. (2015) concluded that, for the mixture of Douglas-fir and European beech, there is no overyielding. This contrasting result arose because of a different definition of overyielding. Their aboveground biomass increment in mixed stands did not overtop the most productive pure stand, the Douglas-fir stands. This is defined as transgressive overyielding (Harper 1977). In our definition, with a comparison of the expected mixed stand from the combination of pure stands, Thomas et al. (2015) would have overyielding as well.

Similar to Bartelink (1998) and Thomas et al. (2015), the present study found that mixed stands did not exceed the absolute productivity of Douglas-fir pure stands. But why did the mixing effect not generate average transgressive overyielding? A reason could be the large differences between growth rates of Douglas-fir and European beech. A mixing effect, regardless of how it developed, had to be much stronger to compensate for these differences (Forrester 2014).

The overyielding in the present study resulted in an increased productivity of Douglas-fir. The results of Amoroso and Turnblom (2006) and Erickson et al. (2009) have also shown that overyielding contributed to Douglas-fir. In their studies, they compared Douglas-fir in mixed stands with western hemlock. The growth situation in young stands of Douglas-fir and red alder was the reverse. Radosevich et al. (2006) showed that overyielding was driven by red alder. Binkley (2003) showed that this situation can change. With increasing age and height dominance, Douglas-fir contributes more and more to overyielding in mixed stands (Binkley 2003).

For the mixture of European beech, there are studies which found overyielding driven by European beech (Pretzsch et al. 2010) or by the admixed species (Pretzsch et al. 2013). It seems to be that interaction between European beech to admixed species can vary.

4.5 Explanation of mixing effect

4.5.1 Light

As mentioned above, the height stratification in Douglas-fir–European beech mixed stands is an important factor. Thereby, a forest type developed where an intermediate shade-tolerant species like Douglas-fir (Barnes and Spurr 1998) exists beside the very shade-tolerant European beech (Ellenberg and Leuschner 2010). Normally, the shade-tolerant European beech outcompetes the native, intermediate species over the course of stand development (Thomas et al. 2015; Röhrig et al. 2006). In pure stands, Douglas-firs are surrounded in the crown stratum by individuals of the same species in the same height zones. An interspecific competition situation for light arises (“interference”), which could be seen in higher h/d ratios. In mixed stands, we found a physical exclusion of individual Douglas-firs which outgrew the closed canopy layer of European beech. Douglas-fir with its high light-saturated net photosynthetic rates (Lewis et al. 2000) could efficiently use this improved light access. European beech with a lower light compensation point (Ellenberg and Leuschner 2010) can still exist in the lower height zones. Overall, it seems to be that the two species differentiate each other by niches of different radiation intensity. It may result in maximum light interception of the available light at the site. Menalled et al. (1998) could provide evidence that the height stratifications of Douglas-fir and suppressed western hemlock resulted in sufficient radiation interception in the upper canopy. This allows higher productivity of the shade-intolerant Douglas-fir and yet adequate transmission of radiation to the shade-tolerant western hemlock. Thomas et al. (2015) measured the relative fraction of sun leaves of European beech mixed with Douglas-fir. They also concluded a more efficient usage of incoming light. Vandermeer (1989) called this interaction complementarity.

4.5.2 Soil

In the present study, it was asked how site quality influenced the mixture. Due to the fact that the belowground situation was not directly measured, the assumptions about the belowground competition in the present study were only speculative. Improving site fertility was detected in both models as a driver of increasing overyielding. This was in line with findings of a global biodiversity study based on forest inventory data (Liang et al. 2016). In the first model of the study at hand (Eq. 8), site fertility was determined by the site index. In the second model (Eq. 9), increasing precipitation and temperature drove overyielding. Case and Peterson (2005) found that precipitation and temperature (model 2) mainly drove the growth variation of Douglas-fir. Therefore, we interpreted the site index of Douglas-fir as a proxy for precipitation and temperature. The improved site conditions probably led to increased height differences, which reinforced the complementary effect between Douglas-fir and European beech.

Studies on Douglas-fir–red alder (Binkley and Greene 1983; Binkley 2003) and European beech–Norway spruce (Pretzsch et al. 2010) mixtures found that under poor site conditions, the mixing effect declined. These studies assumed that the mixing effect arose because one species, the “facilitator,” improved soil conditions for the other species. In the case of Douglas-fir mixed stands, it is well-researched that the presence of nitrogen-fixing red alder on nitrogen-poor sites improved soil conditions and ecosystem productivity (Tarrant and Miller 1963; Binkley and Greene 1983; Binkley 2003). Tree litter in mixed stands of Douglas-fir and red alder decomposed faster than in pure stands (Fyles and Fyles 1993). In the case of European beech–Norway spruce mixtures, Norway spruce benefited from the improved decomposition conditions and turnover of the mixed litter (Berger and Berger 2014). The influence of litter and its decomposition on mixtures of Douglas-fir and European beech has not been researched yet. Whether this positive reaction would also occur for Douglas-fir–European beech mixtures is doubtful. This is because Douglas-fir already has intermediate decomposable litter (Edmonds 1980; Augusto et al. 2002).

Another facilitative effect in Douglas-fir–European beech mixtures could be that the soil profile has been “opened” for European beech by decreasing Douglas-fir root density in older ages (Hendriks and Bianchi 1995). However, this rooting strategy needs much more replication to be accepted (Rothe and Binkley 2001). Besides this facilitation between the two species, Hendriks and Bianchi (1995) showed that root density in deeper soil strata was higher in mixed than in pure stands. They conclude that nutrient and water uptake is more efficient in mixed stands. Therefore, complementary effects are not only present in the canopy, but in the soil as well.

Our analyses of the influence of the ecological parameters on the productivity of European beech showed a significant increase in productivity with reduced base-richness. Thomas et al. (2015) found a competitive superiority of Douglas-fir over European beech at root level. Their site fertility is comparable to our average site fertility. It might be that European beech reinforces competitive strength in root stratum on base-poor sites. Hendriks and Bianchi (1995) confirmed the importance of the belowground competition in addition to the aboveground competition for Douglas-fir–European beech mixtures. Their study showed the shift of competition strength between the two species only along an age gradient. The influence of changing site conditions on belowground competition is still unknown. Pretzsch et al. (2010) already stated that along a site gradient, competitive strength can shift from one species to the other.

Nevertheless, the present study assumed that overyielding was less influenced by declined base-richness for European beech because Douglas-fir was mainly responsible for productivity.

The limiting resource for our study seems to be light, rather than soil. Forrester (2014) concluded that the major growth-limiting resource determines the mixing effect. Other studies which showed that different factors, such as poorer sites (e.g., Pretzsch et al. 2010; Toïgo et al. 2014), increased overyielding did not contradict our results. They only show the influence of the present factors under given locations and tree species mixtures.

The selected study sites represent average and best climate conditions (Table 1) in comparison to climate conditions in Germany (Deutscher Wetterdienst 2015). This could be seen by the site indices of top height as well (Online Resource 4). In the study, there was a lack of poorer, arid sites to embrace a complete ecological gradient for the whole of Central Europe. A facilitative effect might have appeared more under poor site conditions. The present study assumed that along a greater ecological site gradient, positive interactions in mixed stands are rather quadratic than linear, as Bertness and Callaway (1994) predicted.

4.5.3 Age

Our findings show that the age had a relevant influence on overyielding. This was shown by the steep rise of age in models one and two (Table 2). Although not all explanatory variables were significant, like age in model 2, the AIC indicated that their presence in combined effect with the other variables was important. In addition, all parameters (DBH and increment), which included an interaction of age and mixture showed that positive mixing effects arise only in older stands (Online Resource 5).

The present study and also de Wall et al. (1998) came to the conclusion that the increasing age of Douglas-fir–European beech stands leads to a vertical separation of the species in the canopy zone. As mentioned above, we suspected that structuring leads to overyielding. So higher stand ages could have a positive effect on productivity. Other studies also concluded that overyielding increases with increasing age (Zhang et al. 2012). Independent of the reason for overyielding, it might be that the positive mixing effect takes time to appear. In our study, the break-even point of mixture seems to be 60 years.

5 Conclusion

The mixture of Douglas-fir and European beech emerges as a stable mixture type, which does not lead to the loss of one of the species without silvicultural intervention. That is noteworthy because it is a species composition of a native with an introduced species. This mixture creates considerable height stratification, which is unusual for native Central European forest types. The accrued overyielding in mixture was determined by the age dynamics of the stands. Failing to consider the age dynamics could lead to a miscalculation of the mixing effect. Further mixture research should consider the influence of age.

The gradient of the site conditions shows that overyielding is particularly expected in favorable locations. Further research should extend the gradient to extreme sites. That would enable a more comprehensive site conclusion about the whole site spectrum.

Douglas-fir–European beech mixed stands can be recommended for forest management. It is an option that combines the demand for mixed stands with the need for coniferous wood production. The benefits that come with increasing age of the mixture should be brought into the focus of silviculture.

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Mixture reduces climate sensitivity of Douglas-fir stem growth

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ABSTRACT

Due to possible positive and compensatory interaction between species, mixed stands are a commonly accepted silvicultural response to reduce risks arising from climate change. Nonetheless, only a few species combinations have been studied more detailed so far revealing variable mixing effects. Here, we analyze the effect of the mixture of Douglas fir and European beech with regard to the species-specific climate sensitivity of growth. We focus on three hypotheses: (i) Species-specific long term growing performance and climate sensitivity do not differ between monocultures and mixed stands, (ii) species-specific growth reactions to severe drought events do not differ between monocultures and mixed species stands and (iii) species-specific growth reactions on severe drought events are not influenced by differing ecological growing conditions.

To scrutinize the hypothesis we analyzed tree cores from both species taken from pure and mixed stands covering different site conditions and age classes. Tree ring characteristics were used to analyze the differences in climate related long-term growth responses in pure and mixed stands. Short-term responses were investigated by growth reaction indices on individual tree and stand level involving drought events during the years 1950–2010. Linear mixed models were applied to detect effects of ecological co-variables on the indices.

Results reveal that Douglas-fir in mixed stands exhibit a significant improved growing performance compared to pure stands. European beech seems to react indifferently concerning its performance in mixture compared to pure stands.

Differences in drought stress resistance and growth recovery time mainly arose between the species. Douglas-fir showed a significantly lower resistance and required more time to reach again its initial growth level compared to European beech. In mixture we found a trend that Douglas-fir growth recovery time is shortened and extended for European beech.

The analysis along the ecological gradients showed that base-limited soils systems are more drought-tolerant during drought events. Lower basal area as a proxy for reduced stand competition decreased the relative growth loss by drought.

We hypothesize that mainly spatial differentiation in height trigger enhanced diameter growth of Douglas-fir in mixture. Temporal differentiation expressed by deferred phenology attenuates climate sensitivity of this conifer. We conclude that in mixed Douglas-fir and European beech stands the former species is stabilized against climatic impacts. On the contrary, climate sensitivity of European beech is increased.

1. Introduction

An increase in frequency and intensity of ecosystem disturbances such as severe drought events have been observed in many regions of the world (IPCC, 2014) challenging forest management to deal with adaptation issues. In this context species mixing seems to be an effective way to stabilize forests against such impacts (Kelty, 1992; Knoke et al., 2008; Lüpke, 2004). Previous studies focusing on productivity (Forrester, 2014; Toïgo et al., 2014; Vallet and Pérot, 2011) provide evidence, that mixing species modifies resource utilization within a stand. Generally, interactions between combined species seem to be responsible for a change in resource partitioning. Larocque et al. (2013) separate these into interactions resulting in positive (through facilitation and complementarity) or negative (through competition) outcomes. Mainly processes of facilitation and niche differentiation improve the utilization of available resources in mixed stands. Mixing effects are not a constant phenomenon but depend on

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developmental stage of a stand (Binkley and Greene, 1983; Zhang et al., 2012) and on site conditions (Toïgo et al., 2014). According to the stress gradient hypothesis the effect of facilitation is more pronounced on sites with stressful growing conditions whereas under benign conditions competition dominates (Bertness and Callaway, 1994; Callaway and Walker, 1997).

When considering drought events as temporal setbacks of growing conditions it is assumable that in mixed stands comprised by species exhibiting different functional traits and resistance behavior negative growth reactions may also be attenuated. Growth loss or dramatic drop out of one species by a disturbance may be mitigated or even compensated by the second species (Kelty, 1992). Some studies provide evidence that mixture has a positive effect during drought events for at least one species (Lebourgeois et al., 2013; Pretzsch et al., 2013).

In Central Europe forest managers aim at reducing the share of conifer monocultures, mainly dominated by the highly vulnerable Norway spruce (*Picea abies* (L.) H. Karst.) by establishing mixed stands of conifers and broadleafed species (Klimo et al., 2000; Zerbe, 2002). In this context, mixed stands of Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) and European beech (*Fagus sylvatica* L.) receive increasing attention (Reyer et al., 2010). European beech is one of the most competitive species and would dominate the potential natural vegetation in Central Europe (Bolte et al., 2007; Ellenberg and Leuschner, 2010). Douglas-fir as a non-indigenous species in Europe provides the advantages of having high growth rates and good wood quality and being very adaptable to various site conditions (Kleinschmit and Bastien, 1992). Its growth rates outperform Scots pine (*Pinus sylvestris* L.) and Norway spruce (Hermann and Lavender, 1999; Pretzsch, 2005). Additionally, its drought tolerance seems to be more accomplished compared to other European conifers (Bréda et al., 2006; Eilmann and Rigling, 2012). Complementary characteristics of both species have been described by Hendriks and Bianchi (1995) concerning below ground space occupation and by Thomas et al. (2015) concerning crown stratification.

To enhance knowledge about the effect of mixing Douglas-fir and European beech concerning their resistance against drought, the study analyzed the respective past growth responses of both species. We tested three null hypotheses: (i) Species-specific long term growing performance and climate sensitivity do not differ between monocultures and mixed stands, (ii) species-specific growth reactions to severe drought events do not differ between monocultures and mixed species stands and (iii) species-specific growth reactions on severe drought events are not influenced by differing ecological growing conditions.

Our analyses of the tree growth performance make use of the comparison of two stand types (pure and mixed) growing on similar site conditions. This enables to detect possible mixing effects on tree chronology characteristics by contrasting intra- and interspecific competition situations.

In a first step, we use tree ring characteristics to analyze the long term climate response of the trees. Fritts (1976) described the changes of tree chronology characteristics under a gradient from forest interior to semiarid forest border. Trees under harsher conditions built *sensitive* tree rings, with higher mean sensitivity, lower autocorrelation and smaller ring width. In contrast, trees under benign conditions built *complacent* year rings with opposite characteristics. Additionally, Biondi and Qeadan (2008b) showed that tree ring variability computed by the Gini-coefficient varied between different species and between different time periods.

Tree ring chronologies are further used to analyses the short term growth reaction of the species during past droughts event. Pretzsch et al. (2013) could show that resistance of trees is modified in mixture compared to pure stands. We introduce growth recovery time and loss of increment as measure of growth reaction due to drought, whereas the pre drought growth level serves as reference. Several studies suggest that subsequent years with unfavorable water supply have to be considered when looking at growth recovery time (Eilmann and Rigling, 2012; Hartmann, 2011; McDowell et al., 2008). Therefore, we also take a look at the climate condition after a drought year and link it with the growth recovery time.

We look at both, growth reaction on individual tree and stand level. As growth reaction to drought may be dependent on tree size individual reaction do not allow to scale up to stand level without considering tree size distribution (Mérian and Lebourgeois, 2011). This is even more relevant when comparing pure and mixed stands as tree size distribution may differ between stand types (Pretzsch and Schütze, 2016). By providing relative reaction values, it is possible to explain the biological response patterns of the trees during drought. Absolute growth values on stand level enable a link to forest management.

2. Materials and methods

2.1. Study site and plot set-up

The study was conducted in Central Europe and covered a range of 430 km. Seven different ecological regions were included from "Osteifel" (N 6°44′36.33″, O 50°10′23.86″) in the north west to "S chwäbisch-Bayerische Schotterplatten- und Altmoränenlandschaf t" (N 11°51′09.88″, E 48°07′16.78″) in the south east (Fig. 1). The study made use of a triplet experimental setup. Each triplet is composed of a mono-specific stands of Douglas-fir and European beech, respectively and a mixed stand of both species, growing on identical site conditions and exhibiting similar stand age. The plots of a triplet were selected in direct proximity, mostly in the same compartment, to minimize residual effects like soil, tree genetic and management effects. When the plots were not in inside the same compartment, the similarity of the soil was visually checked by a sample with a boring rod. All triplets represented more or less fully stocked and mono-layered forest stands (see Supplementary material 1). General differences in stand density resulted from species-specific, tree size related space occupation (Reineke, 1933) and from mixing effect (Pretzsch and Biber, 2016). By this, comparisons of growth reactions in pure stands of Douglas-fir and European beech as well as in mixed stands of both species under similar growing conditions are enabled. The climate response of the species in mono-specific stands is used to reference possibly deviating response of the species in mixed stands.

The mean annual temperatures between the triplets range from 7.0 to 9.5 °C and from 13.7 to 15.7 °C during the growing period. The mean annual precipitations range from 733 to 1066 mm, and to 322–576 mm in the growing period, respectively (multi annual values from 1981 to 2010) (Deutscher Wetterdienst, 2015). The soil water supply of the triplets, described by a combination of water holding capacity, precipitation and transpiration, ranged from dry to very fresh. The base equipment of the soils ranged from base-poor to base-rich. The age gradient covers three classes: young (approx. 30 years), mature (approx. 60 years) and old stands (approx. 90–120 years). Table 1 gives an overview of the triplet's site conditions and stand parameters.

2.2. Sampling and standardization of tree rings

During the years 2012–2014, in total 1279 trees were sampled by extracting two increment cores from northern and eastern direction from each tree at breast height (1.30 m). Ring widths were measured with digital positiometer (Biritz GmbH, Gerasdorf bei Wien, Austria) with an accuracy of 0.01 mm. Cross-dating

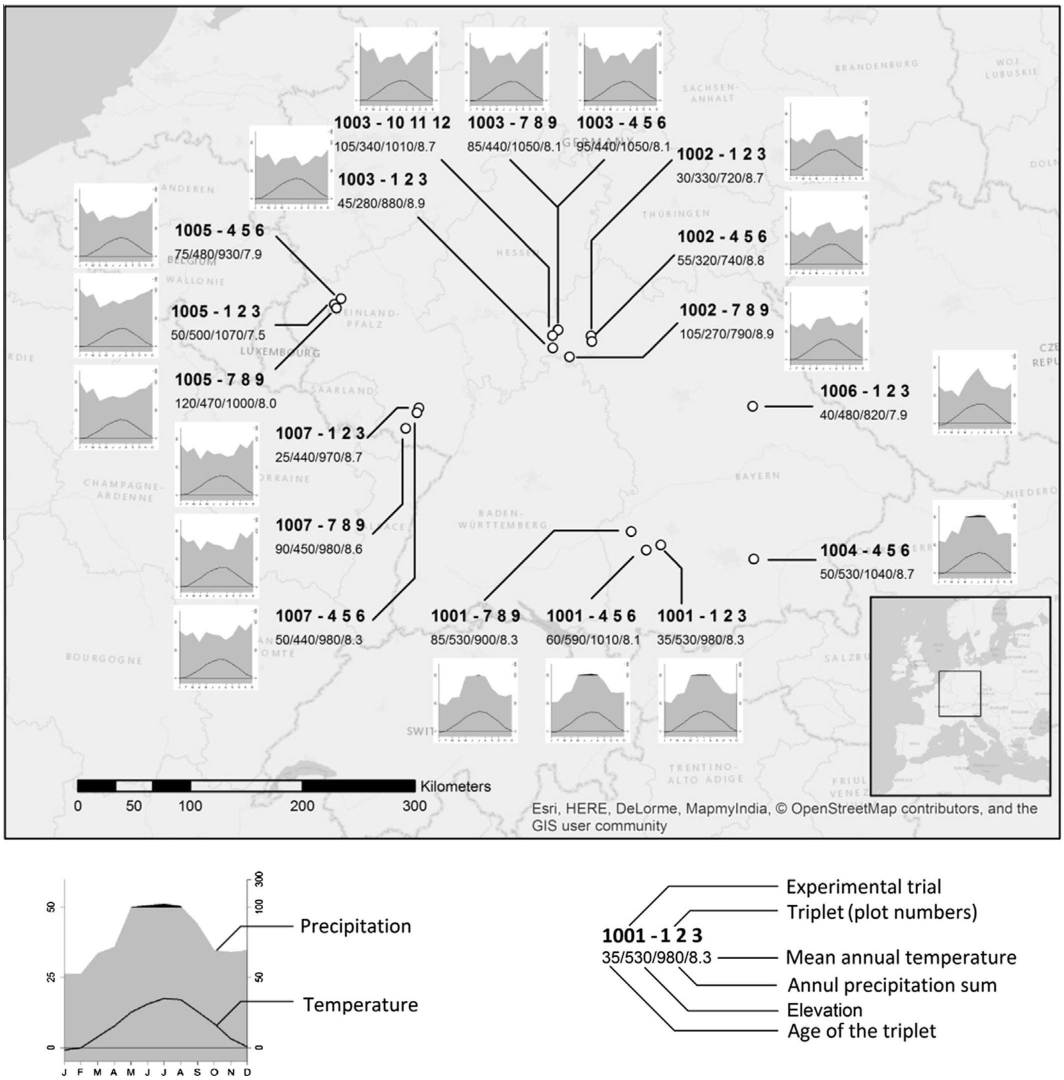

Fig. 1. Location of the 18 triplets in Central Europe (dots) with the associated climate charts according to Walter and Lieth (1967). The experimental trial number results from a four-digit experimental number and a three-digit triplet number. Beneath the experimental trial number, plot information concerning stand age of the triplet, elevation above sea level, annual precipitation sum and mean annual temperature is given.

and synchronization of the tree chronologies were conducted using the software platform TSAP-Win (Rinntech, Heidelberg, Germany). We measured diameter at breast height (DBH) and tree height from all cored tree and from the remaining trees of each plot (n = 1987, see Table 1).

In order to extract the climate related growth reaction from the chronologies the individual tree core series were standardized. Here, we use basal area increment (BAI) series instead of ring width series for detrending and statistical analyses, because the BAI as a two-dimensional measurement, better reflects three-dimensional growth of the whole tree (volume) than the one-dimensional growth of tree ring width (Biondi and Qeadan, 2008a; LeBlanc, 1990). The BAI for each individual tree was calculated using the mean radial increment of both cores. A double detrending procedure was applied to standardize BAI time series (Holmes et al., 1986). This two-stage curve fitting (see example in Appendix A) was used to eliminate the deterministic age trend at first. Due to the nature of BAI age trend we applied a Hugershoff function (1936) instead of a negative exponential function or linear regression, usually used for detrending. For the second detrending procedure, a cubic spline was applied because residual growth trends from forest trees strongly depend on competition and release of competition through thinning. The wavelength of the cubic spline was fixed by 15 years with a frequency response of 0.5. A 15 year window was used as it covers a usual time interval of thinning activities.

To quantify the long-term growth behavior of both species in pure and in mixed stands, we used five standard tree ring characteristics (Biondi and Qeadan, 2008b; Fritts, 1976; Speer, 2010). The mean basal area increment (Mean), calculated as mean value for each tree chronology, provides a measure of the general growth potential. The Gleichlaeufigkeit (GLK) describes the intra-specific conformity of the tree chronologies within a sample stand. The first-order autocorrelation (AC) indicates to what extent the increment of year n correlated with year n−1. In terms of sensitivity we calculated mean sensitivity (MS), which quantifies the year-to-year variability. AC indicates the existence of low frequency variability in tree ring chronologies which is triggered for instance by physiological processes leading to a lag in response to climate conditions. MS is a measure of high frequency variability and is regulated by short term shifts in climate related growing conditions (Fritts, 1976). Lastly, the Gini coefficient (GINI) represents a quantitative measure of the heterogeneity of increment in tree ring chronologies. GINI, MS and GLK where calculated based on index

Table 1

Stand and site characteristics of the 18 triplets sampled between 2012 and 2014 (Survey) indicating ecoregions (Gauer and Kroiher, 2012) and climate data (Temp - mean annual temperature, Prcp - mean annual precipitation sum) (Deutscher Wetterdienst, 2015), base-richness (Base), water supply (Water) and plant available water capacity (PAWC) (Landesforst Rheinland-Pfalz, 2014a; Taegger and Kölling, 2016), diameter at breast height (DBH) and tree height (Height) refer to the quadratic mean diameter tree, number of cored trees. Base-richness is ranked from very base-poor (1) to very base-rich (5) and water supply is ranked from very dry (1) to very fresh (7).

Experimental trial	Triplet	Ecoregion	Temp [°C]	Prcp [mm]	Base	Water	PAWC [mm]	Stand age [year]	Survey	Douglas-fir						European beech					
										Pure			Mixed			Pure			Mixed		
										DBH [cm]	Height [m]	Cored trees	DBH [cm]	Height [m]	Cored trees	DBH [cm]	Height [m]	Cored trees	DBH [cm]	Height [m]	Cored trees
1001	1 2 3	Tertiäres Hügelland	8.3	977	3	7	192	33	2013	26.2	23.8	19	24.7	22.4	22	13.9	18.9	26	13.5	16.3	17
	4 5 6	Tertiäres Hügelland	8.1	1011	3	7	130	60	2013	45.1	32.3	20	53.1	35.7	14	23.3	22.3	37	19.3	22.0	18
	7 8 9	Tertiäres Hügelland	8.3	898	3	7	214	85	2013	74.0	44.9	18	62.0	39.4	17	38.3	28.1	20	25.8	27.7	13
1002	1 2 3	Fränkische Platte	8.7	718	4	3	210	29	2013	18.2	20.3	22	14.0	16.5	16	8.7	14.3	19	10.7	16.9	23
	4 5 6	Fränkische Platte	8.8	740	4	3	200	54	2013	28.3	27.3	24	36.2	29.9	17	15.2	22.3	19	17.0	21.2	30
	7 8 9	Fränkische Platte	8.9	792	4	3	210	103	2013	58.0	43.4	17	75.4	46.8	9	53.6	39.3	14	36.2	35.2	17
1003	1 2 3	Spessart	9	878	2	7	144	43	2013	32.9	29.2	19	34.2	27.3	16	15.4	19.8	24	15.1	17.3	27
	4 5 6	Spessart	8.1	1054	3	4	154	95	2013	64.1	49.2	8	63.1	44.7	5	35.6	35.6	16	29.7	35.8	20
	7 8 9	Spessart	8.1	1054	3	4	154	85	2013	55.2	41.2	10	78.6	38.2	5	30.9	31.8	17	29.9	29.9	19
	10 11 12	Spessart	8.7	1012	2	6	144	105	2013	63.9	41.8	13	80.8	43.5	4	42.4	29.1	17	36.4	30.2	11
1004	4 5 6	Schwäbisch-Bayerische Schotterplatten und Altmoränenlandschaft	8.5	1044	4	7	132	49	2013	27.6	26.2	18	29.9	25.0	14	21.3	22.6	21	15.6	23.2	18
1005	1 2 3	Osteifel	7.5	1066	3	6	171	49	2014	36.7	31.4	28	45.7	31.2	14	16.4	17.7	21	15.2	18.0	25
	4 5 6	Osteifel	7.9	926	3	6	155	75	2014	46.4	36.4	16	73.7	38.7	5	28.1	24.8	25	22.1	21.5	23
	7 8 9	Osteifel	8	1000	3	6	155	119	2014	70.3	49.0	12	83.2	40.9	4	37.0	29.9	18	23.2	22.0	16
1006	1 2 3	Frankenalb und Oberpfälzer Jura	7.9	821	3	5	156	37	2013	26.6	24.9	25	30.2	24.7	23	17.9	19.0	22	17.2	19.7	8
1007	1 2 3	Pfälzerwald	8.7	974	2	5	146	26	2012	11.5	13.0	22	9.1	10.0	15	9.0	11.4	20	7.8	9.0	15
	4 5 6	Pfälzerwald	8.3	980	2	5	193	51	2012	26.4	29.8	20	23.0	24.1	16	16.6	17.7	23	17.9	21.0	18
	7 8 9	Pfälzerwald	8.6	981	2	5	172	92	2012	62.5	43.4	20	69.8	46.2	15	38.2	33.1	20	33.6	32.9	20
		Total (min-max)	8.4 (7.5–9.0)	940 (718–1066)				66 (25.7–119.0)		41.2 (11.5–74.0)	33.3 (13.0–49.2)	331 (8.0–28.0)	49.3 (9.1–83.2)	32.5 (10.0–46.8)	231 (4.0–23.0)	25.7 (8.7–53.6)	24.3 (11.4–39.3)	379 (14.0–37.0)	21.5 (7.8–36.4)	23.3 (9.0–35.8)	338 (8.0–30.0)

values, whereas AC were calculated based on measured raw ring width.

The basal area of the stands was calculated by summing up the basal area of all individual trees per plot and afterwards scaled up to 1 ha. Missing basal area increments of not drilled trees were calculated by fitting a function that relates DBH and previous growth rates of drilled trees ($\ln(i_d) = a + b \cdot \ln(DBH)$). All in all, not drilled trees represented less than 15 percent of the whole basal area.

By the calculation for the drought response of the whole stands, the stand increment was detrended by a Hugershoff function.

For the descriptive core statistics and the calculation of the cubic spline we used the package *dplR* (Bunn, 2008, 2010).

2.3. Weather data

The climatic characterization of the sites and the calculation of the drought indices are based on 1 ∗ 1 km grid of multi annual and monthly precipitation and temperature data (Deutscher Wetterdienst, 2015). The plots of a triplet were mostly located closer than 200 m together, so that climate data were aggregated only for the mixed stand but also used for the whole triplet (for a more detailed view of experimental setup see Thurm and Pretzsch, submitted for publication). The standardized precipitation-evapo transpiration index (SPEI) was used to identify drought years (Vicente-Serrano et al., 2010). The SPEI was calculated for a time scale of 5 month using a Gaussian kernel function. The length of the timescale was deduced from a comparison of drought events and BAI response. Thereafter, the mean SPEI of the growth period from May to September was calculated. As drought years, the seven years (10th percentile) with lowest SPEI during 1950–2010 per triplet were selected (see Supplementary material 2). Thereby, we investigated tree response during extreme drought years as well as during moderate drought years.

To consider different drought stress behaviors of Doulas-fir and European beech, e.g. isohydric or anisohydric traits (Hartmann, 2011; Tardieu and Simonneau, 1998), drought years were classified into three groups. The classification depended on the climate conditions after a drought year. If after a drought year a year with above average dry climate conditions was following, it was classified as *good post-year*. Respectively average conditions after a drought year were classified as *average post-year* and below-average conditions as *adverse post-year*. The selection was done individually for every triplet. Classification concerning a specific drought year may thus vary between sites.

2.4. Drought year analyses

The *drought year analyses* focused on short-term individual trees' response to drought weather events. Secondly, the drought year analysis was performed for the whole stand. Lloret et al. (2011) introduced three indices (resistance, resilience and recovery) describing the performance of trees under drought stress. Here, beside resistance, we used two new indices characterizing the growth reactions (growth recovery time, increment loss due to drought) of individual trees and stands to drought.

The *resistance* (Rt) quantifies the ability of plants to withstand a disturbance. Lloret et al. (2011) defined Rt as the ratio between growth during the drought event and a mean growth level of a reference period prior to the drought event.

For the resilience (Rs), we found different definitions in the literature. Lloret et al. (2011) described the resilience as the ratio of post-disturbance growth level to pre-disturbance growth level. Pimm (1984) refers to resilience as the time a system needs to return to an equilibrium following disturbance. Here, we used resilience in terms of the duration starting in the drought year until reaching the pre-drought growth level again (Fig. 2). To avoid confusion of ideas the index is named *growth recovery time* (GRT). The index's unit is year units, as possible decimal figures do not represent ratios of a full year.

The index *increment loss due to drought* (Loss) describes the loss of stand growth due to drought in relation to the pre-drought growth level. It is the cumulated loss during the time of recovery.

To provide a value more common in forest practice, basal area increment loss due to drought was transformed into volume loss. Therefore, we fitted a stand volume function (Eq. (1)) for each mixture (*m*, Douglas-fir pure stand, mixed stand, European beech pure stand) at survey point (*p*) with basal area and stand age as independent variables, including their interaction. The coefficients $a_0 \ldots a_3$ of the fixed effect from the single models are shown in Appendix B.

$$\ln(Volume_{mp}) = a_0 + a_1 \cdot \ln(Basal\ area_{mp}) + a_2 \cdot \ln(Stand\ age_{mp}) + a_3 \cdot \ln(Basal\ area_{mp} \cdot Stand\ age_{mp}). \qquad (1)$$

As mentioned in chapter 2.2, deterministic age trend that may influence pre- and post-drought growth rates can be removed by double detrending procedures. Additionally, specific weather conditions prior and after drought events, may also affect the index values. To cope with this problem, all indices for drought event identified along the chronologies were pooled assuming to average possible differences in pre- and post-drought weather conditions.

2.5. Statistics

2.5.1. Tree chronology characteristics

Species-specific chronologies characteristics were used to test for differences of long-term growth behavior between Douglas-fir and European beech in mixed and in pure stands. Therefore, we applied a linear mixed model (Eq. (2)), *lmer* from the R-package *lme4* (Bates et al., 2015). Y_{ij} refers to the mean tree chronology characteristics per plot and species. The mixing types (mixed Douglas-fir, pure European beech and mixed European beech) were included as fixed effects and coded as binary variables, which switch between 1 and 0, depending on which mixing type is fitted.

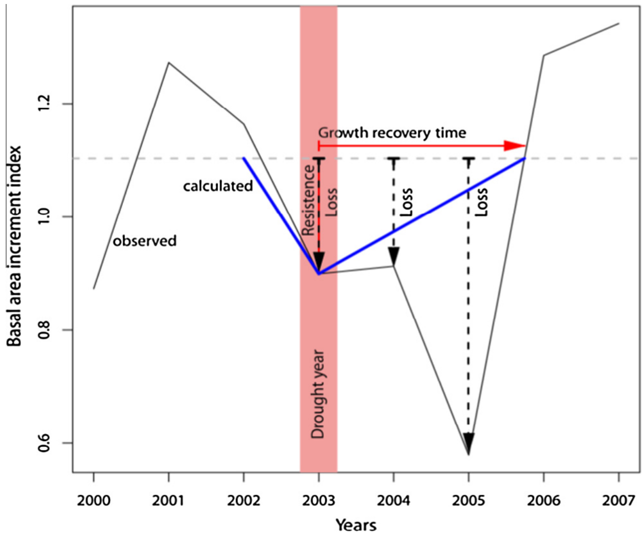

Fig. 2. Schematic illustration of the growth reaction indices used in the analyses (resistance, growth recovery time and increment loss due to drought). The solid black line represents the detrended basal area increment. The bold solid blue line shows the drought response calculated by resistance and growth recovery time, also used in Figs. 5 and 6. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

$$Y_{ij} = a_0 + a_1 \cdot mixed\ Douglas\text{-}fir_{ij} + a_2 \cdot pure\ E.\ beech_{ij} + a_3 \cdot mixed\ E.\ beech_{ij} + b_i + b_{ij} + \varepsilon_{ij} \quad (2)$$

The indexes i and j represent experimental location and the triplet. a_0 and a_1 represent the coefficients of fixed effects. Random effects are considered with b on experimental location and plot level. The symbol ε represents the independent and identically distributed random error. Results were checked for homoscedasticity and normal distribution. A generalized linear hypothesis test was used for contrasting all mixing type effects, as obtained by the linear mixed model, against each other. We applied the R-package "multcomp" (Hothorn et al., 2008).

In a second step a multivariate analysis of tree chronology characteristics was performed by a Principal Component Analysis (PCA) using the packages "FactomineR" (Husson et al., 2015). It was applied to identify patterns in tree characteristics which are linked to the species, mixing types, age and experimental trial. The four mixing types (pure and mixed Douglas-fir, pure and mixed European beech) of each triplet were addressed individually within the analysis. Mean tree characteristics (mean basal area increment, autocorrelation, mean sensitivity, Gini coefficient and Gleichlaeufigkeit) were included as quantitative variables. Ellipses corresponding to 95% confidence intervals were calculated, based on the coordinates of mixing types, species, age and experimental location.

2.5.2. Drought year analyses

A linear mixed model approach was applied to analyze possible effectors on resistance and growth recovery time and increment loss due to drought on individual tree and stand level. The effectors were separated into two types: plot specific (species, mixing type, post-year conditions) and overarching ecological factors.

With Eq. (3), we tested the effect of plot specific variables at the individual tree level for the resistance and the growth recovery time (YI).

$$\begin{aligned} YI_{ijkt} = {} & a_0 + a_1 \cdot species_{ij} + a_2 \cdot mixture_{ij} + a_3 \cdot species_{ij} \cdot mixture_{ij} \\ & + a_4 \cdot post\text{-}years_{ij} + a_4 \cdot species_{ij} \cdot post\text{-}years_{ij} \\ & + a_4 \cdot mixture_{ij} \cdot post\text{-}years_{ij} \\ & + a_4 \cdot species_{ij} \cdot mixture_{ij} \cdot post\text{-}years_{ij} \\ & + b_i + b_{ij} + b_{ijk} + \varepsilon_{ijkt} \end{aligned} \quad (3)$$

In addition to Eq. (2), the indexes k and t represent individual tree and drought event, respectively. Additionally, the tree number was considered as random effect. In case of resistance, the dependent effect of post-year and its respective interactions were omitted.

To test the resistance, the growth recovery time and the increment loss due to drought at stand level (YS) we used Eq. (4). The two stand types, European beech pure stand and the mixed stand, are considered as binary variables like in Eq. (2). The Douglas-fir pure stand is represented by the intercept. The post-year factor was omitted on this level completely, because in most cases the weather conditions in 2004 were below average.

$$YS_{ijt} = a_0 + a_1 \cdot pure\ E.\ beech\ stand_{ij} + a_1 \cdot mixed\ stand_{ij} + b_i + b_{ij} + \varepsilon_{ijt} \quad (4)$$

To verify the influence of the ecological factors on resistance and growth recovery time, the following independent variables were taken into account: age, DBH (in case of stand level model the basal area per hectare), relative DBH (ratio of DBH to DBH of the quadratic mean diameter tree per plot), water supply, base-richness, mean annual temperature, annual precipitation sum and in case of stand level model the proportion of European beech (proportion$_{(\mathrm{Eb})}$)(Table 1).

Individual tree level:

$$\begin{aligned} YI_{ijkt} = {} & a_0 + a_1 \cdot age_{ijkt} + a_2 \cdot DBH_{ijkt} + a_3 \cdot age_{ijkt} \cdot DBH_{ijkt} \\ & + a_4 \cdot relative\ DBH_{ijkt} + a_5 \cdot base\text{-}richness_{ij} \\ & + a_6 \cdot temperature_{ij} + a_7 \cdot precipitation_{ij} \\ & + a_8 \cdot water\ supply_{ij} + a_9 \cdot precipitation_{ij} \cdot water\ supply_{ij} \\ & + b_i + b_{ij} + b_{ijk} + \varepsilon_{ijt} \end{aligned} \quad (5)$$

Stand level:

$$\begin{aligned} YS_{ijt} = {} & a_0 + a_1 \cdot age_{ijt} + a_2 \cdot proportion_{(\mathrm{Eb})_{ijt}} + a_3 \cdot basal\ area_{ijt} \\ & + a_4 \cdot base\text{-}richness_{ij} + a_5 \cdot temperature_{ij} + a_6 \cdot precipitation_{ij} \\ & + a_7 \cdot water\ supply_{ij} + a_8 \cdot precipitation_{ij} \cdot water\ supply_{ij} \\ & + b_i + b_{ij} + \varepsilon_{ijt} \end{aligned} \quad (6)$$

Model selection was based on the Akaike Information Criterion (Burnham and Anderson, 1998) and biological plausibility of the results. The selection was made with additionally help of automated model selection (*dredge*) from the R package *MuMln* (Barton, 2015), which consider all possible variable combinations.

All statistical analyses were performed in the statistical environment R version 3.2.2 (R Core Team 2015).

3. Results

3.1. Tree chronology characteristics

The analysis of the tree characteristics revealed considerable differences between the mixing types (Fig. 3). In general, the mean basal area increment of Douglas-fir (29.0 $\mathrm{cm}^2\ \mathrm{a}^{-1}$) was significantly larger than European beech (9.6 $\mathrm{cm}^2\ \mathrm{a}^{-1}$). Douglas-fir in mixed stands (33.5 $\mathrm{cm}^2\ \mathrm{a}^{-1}$) showed a significantly higher increment than in pure stands (26.0 $\mathrm{cm}^2\ \mathrm{a}^{-1}$). Between the increments of European beech in mixture (8.7 $\mathrm{cm}^2\ \mathrm{a}^{-1}$) and pure stands (10.5 $\mathrm{cm}^2\ \mathrm{a}^{-1}$) no significant differences were observed. The autocorrelation of tree ring chronologies of Douglas-fir in pure stands (0.68) was highest compared to Douglas-fir in mixed stands as well as to European beech in both stands types. The autocorrelation of European beech in pure stand (0.60) did not differ significantly from Douglas-fir (0.58) or European beech in mixture (0.61).

The patterns of the mixed stands concerning mean sensitivity and Gini coefficient were similar. European beech in mixed stands showed the highest sensitivity (MS = 0.28, Gini = 0.14) whereas Douglas-fir in mixture (MS = 0.24, Gini = 0.12) showed the lowest sensitivity. Douglas-fir in pure (MS = 0.25, Gini = 0.13) and in mixed stands did not differ significantly. The sensitivity of European beech in pure stands (MS = 0.26, Gini = 0.13) did not differ from any mixing type. Concerning Gleichlaeufigkeit a significant interspecific variation was found; Douglas-fir having a higher Gleichlaeufigkeit (pure = 0.63, mixed = 0.64) than European beech (pure = 0.58, mixed = 0.57).

The principal component analyses (Fig. 4) showed, that the two axes (PC1 and PC2) performed on tree chronology characteristics explained 53.0% and 23.5%, respectively of the total variance. The descriptive statistic of the PCA can be seen in Supplementary material 3. The similar trend of mean sensitivity (MS) and Gini coefficient (Gini) is evident by the correlation of first dimension (Fig. 4a). Autocorrelation (AC1) was negative correlated to sensitivity. Mean basal area increment (Mean) and Gleichlaeufigkeit showed same correlation on both dimensions. Each of the five tree chronology characteristics were significant correlated to the first

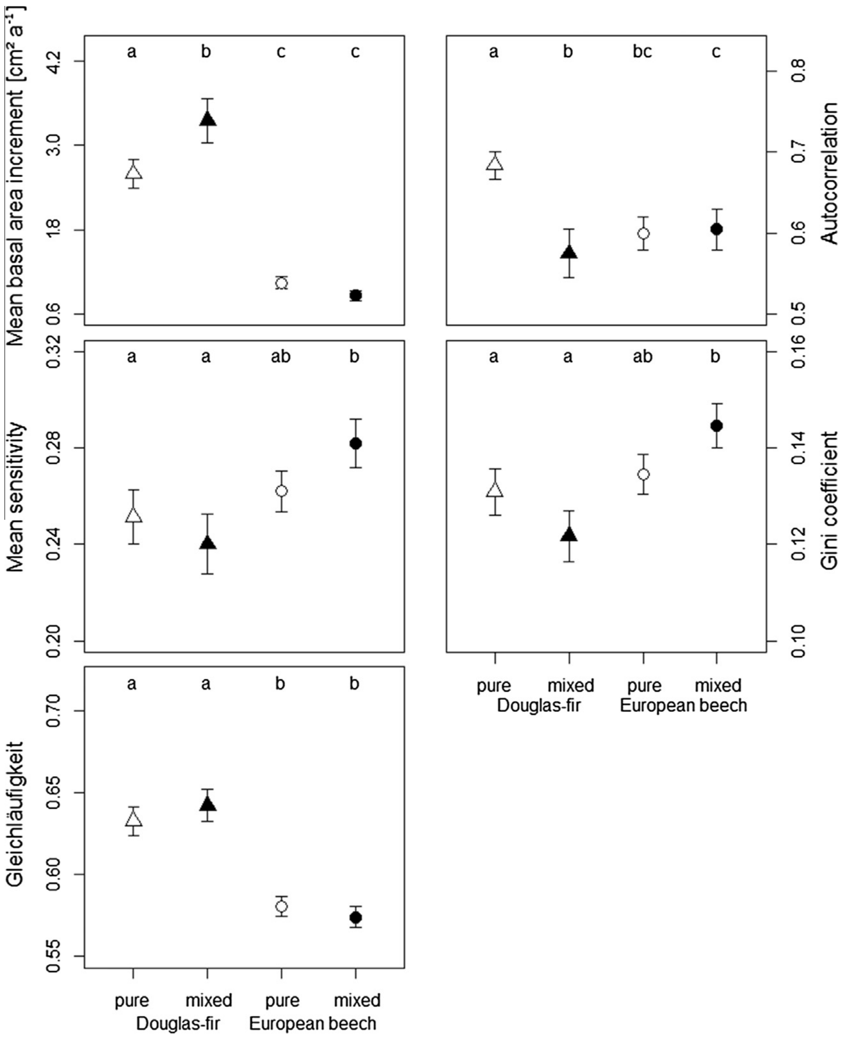

Fig. 3. Statistics of growth series of Douglas-fir (triangle) and European beech (circle) in pure (white) and mixed stand (black) based on 1279 cores. Autocorrelation was calculated on ring width. Mean sensitivity, Gini coefficient and Gleichläufigkeit calculated on double detrended basal area increment indices. Significant differences between the mixing types are indicated by different upper case letters.

dimension and to the second dimension, except for the Gini coefficient.

Each qualitative variables (species Fig. 4d) explained significant differences in tree chronology characteristics, mainly concerning experimental location ($R^2 = 0.57$, $p < 0.001$) and mixing type ($R^2 = 0.35$, $p < 0.001$). The qualitative variables species (Fig. 4b) and mixing type (Fig. 4c) mainly differ by mean basal area increment and Gleichlaeufigkeit. Fig. 4b shows that Douglas-fir and European beech differ significantly in their characteristics. Douglas-fir offered higher mean basal area increment, Gleichlaeufigkeit and autocorrelation; whereas European beech is characterized by lower mean basal area increment, higher sensitivity (MS), and heterogeneity (GINI). Same can be seen in mixing types (Fig. 4c). It is remarkable, that Douglas-fir and European beech differ significantly more in their characteristics in mixed than in pure stands. Young stands differ significantly in their tree chronology characteristics from mature and old stands ($R^2 = 0.08$, $p < 0.05$). They exhibited higher sensitivity, heterogeneity and lower mean basal area increment (Fig. 4d). The PCA showed that younger stands revealed a higher sensitivity. The experimental location was strongly determined by the shift from high autocorrelation to high sensitivity (Fig. 4e).

3.2. Drought year analyses

3.2.1. Individual tree level

The general response of the Douglas-fir and European beech to drought years is illustrated in Fig. 5. The appendant results from the multi comparisons of the linear mixed models are summarized in Table 2. The increment of European beech (resistance = 90.8%) during the drought years dropped significantly less than of Douglas-fir (Rt = 85.5%, $p < 0.001$). No significant mixing effect was existent for both Douglas-fir and European beech. The resistance of both species either in pure or in mixed stands was nearly equal (European beech pure = 90.9, mixed = 90.8, $p > 0.05$; Douglas-fir pure = 85.3, mixed = 85.9, $p > 0.05$). The analysis of plot specific and overarching factors on growth reaction due to drought indicated that the resistance of Douglas-fir was negatively influenced by the DBH and positive by the age (Table 3). This contradiction is solved by the fact that smaller DBH at same age showed a higher resistance for Douglas-fir. The resistance of European beech seemed to be influenced by the social position. Trees with smaller DBH than the basal area tree per plot tended to have a better resistance. Higher base-richness of soils seemed to reduce resistance of both species.

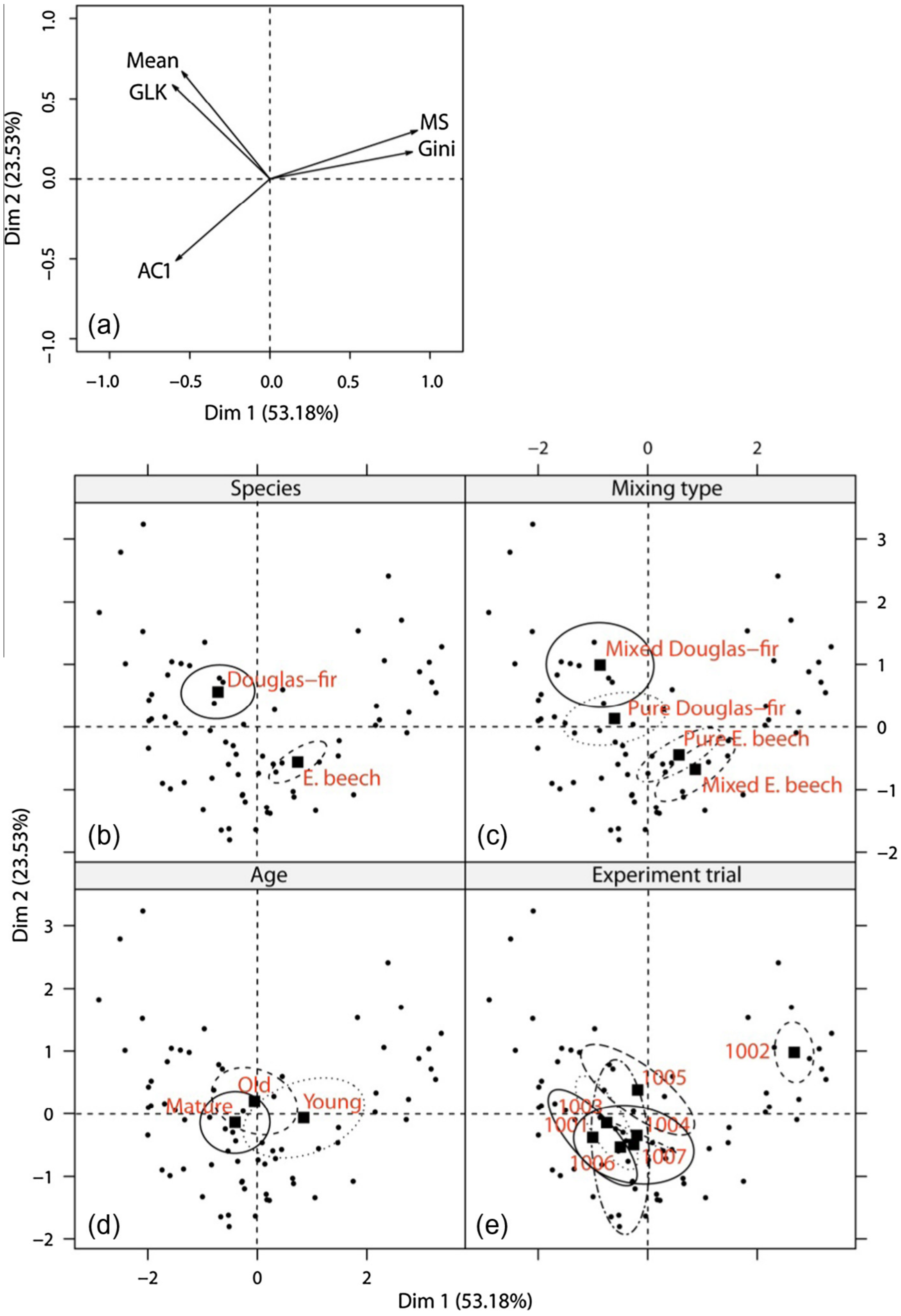

Fig. 4. Principal component analysis (PCA) applied on tree chronologies characteristics for 72 mixing types (Douglas-fir pure and mixed, European beech pure and mixed). (a) The variables factor map indicates correlation and contribution of tree chronology characteristics on the first two axes. (b…e) 95% confidence intervals for average coordinates of species, mixing type, age and experimental trial was depicted by ellipses.

Concerning growth recovery time the analysis showed that European beech (GRT = 1.67) recovered significantly faster than Douglas-fir (GRT = 2.21, $p < 0.01$) (Fig. 5, Table 2). Mixing species affected the growth recovery time but not significantly. The growth recovery time in mixed stands was shortened for Douglas-fir (pure = 2.33, mixed = 2.01, $p > 0.05$) and extended for European beech (pure = 1.57, mixed = 1.79, $p > 0.05$). The growth recovery times of European beech and Douglas-fir in mixed stand range between growth recovery times of both species in pure stand.

The condition of the post-years showed a clear signal for both species; improved weather situation one year after drought, lead to a significant reduction of the growth recovery time (Rs; good = 1.48, average = 2.01, adverse = 2.25, $p < 0.01$). In case of adverse post-years the differences of the growth recovery time between European beech (GRT = 1.94) and Douglas-fir (GRT = 2.67) increased ($p < 0.001$). European beech needed significantly more time to return to its initial yield in mixed stands (GRT = 2.33) than in pure stands (GRT = 1.64, $p < 0.05$) if dry weather conditions followed a drought event.

Concerning the ecological co-variables only tree age showed a significant effect on growth recovery time for Douglas-fir. Progressive tree age extended growth recovery time (Table 3).

3.2.2. Stand level

Analysis of the stand level reaction showed that the resistance of the European beech pure stands (Rt = 89.5) on drought event

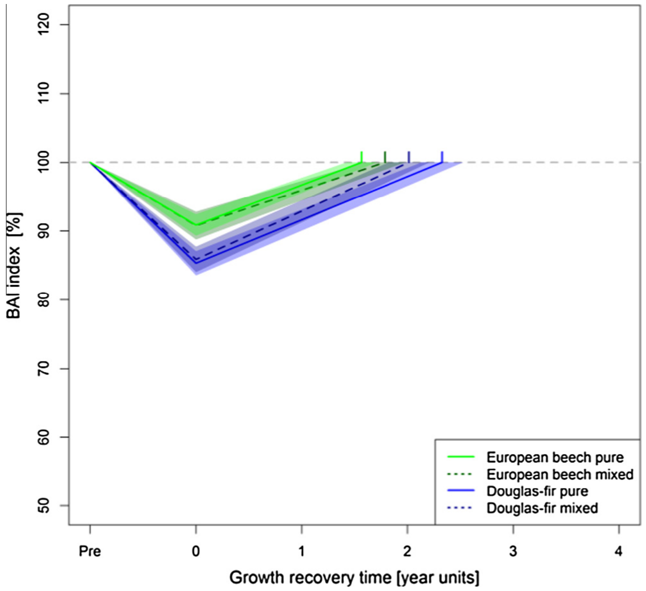

Fig. 5. Mean drought response on individual tree level for all drought events represented by the indices resistance and growth recovery time for European beech (green) and Douglas-fir (blue) in pure (solid) and mixed stands (dashed). The colored bands behind the lines show the respective 95% confidence interval. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

were significantly greater than in mixed stands (Rt = 83.1, $p < 0.05$) and that of Douglas-fir in pure stands (Rt = 80.8, $p < 0.01$) (Table 2, see also Fig. 6). The mixed stands range between the European beech and the Douglas-fir pure stands. The analysis of the effect of co-variables indicated an increasing resistance with increasing age and with decreasing proportion of European beech (Table 3). Also base-poorer sites appeared to bear higher resistance.

The climate specification of 2003 represented an extreme drought year for all triplets and an adverse post-year in 2004 for most of the triplets. Only in case of four triplets a year with good or average weather conditions followed 2003. Concerning the drought year 2003 growth recovery time did not differ significantly between the stands. Douglas-fir pure (GRT = 2.50) and mixed stands (GRT = 2.53) tended to recover relatively faster, whereas European beech pure stands (GRT = 3.06) needed more time to return to their initial level. In contrast to the positive influence of age on resistance, a higher age extended the growth recovery time. Also improved water supply characteristics of soils extended growth recovery time.

The loss of increment caused by the drought year 2003 was on average 50% of the long-term growth level, independent of species or mixture (Table 4). But reflecting the general growth levels absolute basal area increment loss due to drought was highest in Douglas-fir pure stands. The loss increased in plots with higher stand density (basal area per hectare) (Table 3). Additionally, base-poverty, higher precipitation and warmer temperatures led to a lower increment loss due to drought.

Table 2
Mean values, estimates and significance levels of the multiple comparison of the parameters used in the models (Eqs. (3) and (4)) to estimate resistance and growth recovery time. As independent variable we used species, mixture and post-year (effect of the weather condition on year after drought year). Minor differences between the measured and estimated data arose, because of the random effects. Significant pairs are printed in bold.

	Variables	Pairs (A - B)	Mean		Multiple comparison	
			A	B	Estimate	P-value
Individual tree level (1950–2010)						
Resistance	**Species**	**Douglas-fir - E. beech**	**85.5**	**90.8**	**−5.27**	**0.00*****
	Mixture	Mixed - pure	89.0	88.4	−0.30	0.88
	Species:Mixture	Douglas-fir mixed - Douglas-fir pure	85.9	85.3	−0.66	0.79
	Species:Mixture	E. beech mixed - E. beech pure	90.8	90.9	0.07	0.98
Growth recovery time	**Species**	**Douglas-fir - E. beech**	**2.2**	**1.7**	**0.41**	**0.00****
	Mixture	Mixed - pure	1.9	1.9	−0.05	0.80
	Post-years	**Average - adverse**	**2.0**	**2.2**	**−0.38**	**0.01****
	Post-years	**Average - good**	**2.0**	**1.5**	**0.46**	**0.00*****
	Post-years	**Adverse - good**	**2.2**	**1.5**	**0.85**	**0.00*****
	Species:Mixture	Douglas-fir mixed - Douglas-fir pure	2.0	2.3	−0.22	0.37
	Species:Mixture	E. beech mixed - E. beech pure	1.8	1.6	0.12	0.60
	Species:Post-years	Douglas-fir good - E. beech good	1.8	1.3	0.30	0.11
	Species:Post-years	Douglas-fir average - E. beech average	2.2	1.9	0.31	0.14
	Species:Post-years	**Douglas-fir adverse - E. beech adverse**	**2.7**	**1.9**	**0.63**	**0.00*****
	Mixture:Post-years	Mixed good - pure good	1.5	1.5	0.05	0.85
	Mixture:Post-years	Mixed average - pure average	1.8	2.2	−0.32	0.24
	Mixture:Post-years	Mixed adverse - pure adverse	2.3	2.2	0.12	0.61
	Species:Mixture:Post-years	Douglas-fir mixed good - Douglas-fir pure good	1.7	1.8	0.10	0.75
	Species:Mixture:Post-years	E. beech mixed good - E. beech pure good	1.4	1.3	−0.01	0.97
	Species:Mixture:Post-years	Douglas-fir mixed average - Douglas-fir pure average	1.9	2.4	−0.41	0.24
	Species:Mixture:Post-years	E. beech mixed average - E. beech pure average	1.8	2.0	−0.22	0.50
	Species:Mixture:Post-years	Douglas-fir mixed adverse - Douglas-fir pure adverse	2.4	2.9	−0.35	0.27
	Species:Mixture:Post-years	**E. beech mixed adverse - E. beech pure adverse**	**2.3**	**1.6**	**0.60**	**0.04***
Stand level (2003)						
Resistance	Species:Mixture	Douglas-fir pure stand - Mixed stand	80.8	83.1	−2.40	0.45
		Douglas-fir pure stand - E. beech pure stand	**80.8**	**89.5**	**−8.70**	**0.00****
		Mixed stand - E. beech pure stand	**83.1**	**89.5**	**−6.30**	**0.05***
G. recovery	Species:Mixture	Douglas-fir pure stand - Mixed stand	2.5	2.5	0	0.9
		Douglas-fir pure stand - E. beech pure stand	2.5	3.1	−0.6	0.1
		Mixed stand - E. beech pure stand	2.5	3.1	−0.5	0.2

Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1.

Table 3
Estimates for ecological parameters with effect on resistance, growth recovery time and increment loss due to drought separated for individual tree level and stand level. Signifcant estimates are in bold. Hyphens indicate that the respective independent variable was neglected in the model (Eqs. (5) and (6)). The lower part of the table provides information about the quality of the model.

	Dependent variables						
	Individual tree level (1950–2010)				Stand level (2003)		
Independent variables:	Resistance (%)		Growth recovery time (year units)		Resistance (%)	Growth recovery time (year units)	Loss due to drought (%)
	Douglas-fir	E. beech	Douglas-fir	E. beech			
DBH	**−0.415***** *(0.064)*				–	–	–
Rel DBH		**−0.131***** *(0.019)*			–	–	–
Basal area per hectare							**0.004*** *(0.002)*
Mixing proportion of E. beech	–	–	–	–	**8.150*** (3.016)		
Age	**0.164**** *(0.054)*		**0.017***** *(0.004)*		**0.135*** *(0.056)*	**0.022**** *(0.007)*	
Base-richness	**−4.407*** *(0.203)*	**−4.016 .** *(1.775)*			**−4.225 .** *(2.196)*		0.012 *(0.007)*
Water supply						**0.378*** *(0.135)*	
Precipitation							**0.001*** *(0.001)*
Temperature							0.132 *(0.124)*
Intercept	**106.288***** *(6.494)*	**114.199***** *(5.728)*	**1.579***** *(0.198)*	**1.658***** *(0.144)*	**85.394***** *(7.545)*	−0.18 *(0.755)*	−2.241 *(1.444)*
Observations	1556	2242	1556	2242	54	54	54
Log Likelihood	−7237.847	−10805.140	−3827.272	−5502.645	−195.076	−90.51	−21.146
Akaike Inf. Crit.	14491.690	21624.280	7666.543	11015.290	404.152	193.019	58.293
Bayesian Inf. Crit.	14534.490	21664.280	7698.642	11043.860	418.075	204.953	74.204

Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1.

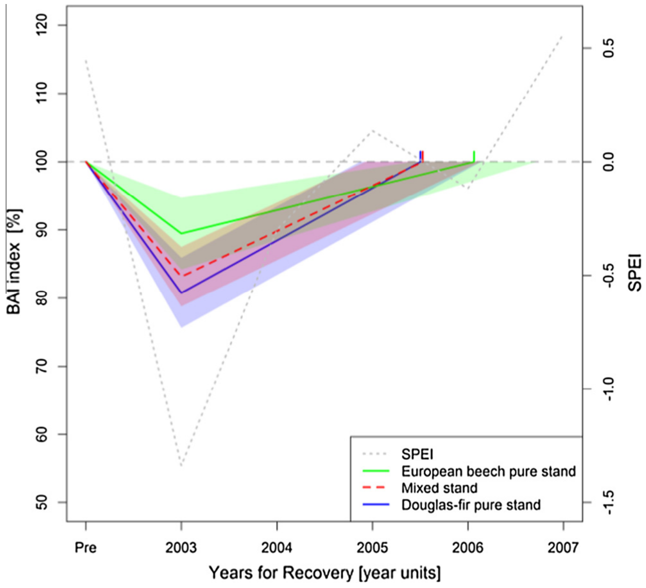

Fig. 6. Mean drought response on stand level to drought event 2003. The response is represent by the indices resistance and growth recovery time for European beech (green solid line) and Douglas-fir (blue solid line) pure stands and for the mixed stands (red dashed line).The grey dashed line represents the average standardized precipitation-evapotranspiration index (SPEI) for all triplets. The colored bands behind the lines show the respective 95% confidence interval. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

4. Discussion

4.1. Tree chronology characteristics

As expected, mean basal area increment of Douglas-fir was higher than for European beech. Individual growth of Douglas-fir in mixture overtopped the increment of Douglas-fir in pure stands. This is conform with the results of a previous study, based on the same sample plots (Thurm and Pretzsch, submitted for publication). The authors reported that overyielding in Douglas-fir – European beech stands is realized mainly by Douglas-fir. They assumed that higher productivity of Douglas-fir in mixture results from an improved growth on individual tree level. Niche complementarity, fostered by improved resource utilization, may lead to accelerated growth of species in mixture (Vandermeer, 1989). Structural diversification, through dominant Douglas-fir and inferior European beech, as observed here in mixed stands (Thurm and Pretzsch, submitted for publication), enables an increasing utilization of incoming light (Thomas et al., 2015). Studies of Hendriks and Bianchi (1995) and Thomas et al. (2015) supposed that roots of Douglas-fir dominate in the top soil, whereas those of European beech spread into deeper soil layers. This may promote Douglas-fir by better access to nutrient because the uppermost soil layer is the dominant area of decomposition and mineralization of organic matter (Thomas et al., 2015). Species-specific basal area increment varied stronger between European beeches in pure mixed stands than for Douglas-firs, as indicated by the pattern of Gleichlaeufigkeit. This may result from a higher variation in diameter and tree heights for European beech compared to Douglas-fir (Pretzsch and Schütze, 2016).

Table 4
Absolute and relative loss of increment at stand level for the drought year 2003. SD represents the standard deviation. The significant differences were tested by a multiple comparison of the linear mixed models and are indicated by letters. The loss of volume increment was calculated on the independent variables basal area increment, age and their interaction (Eq. (1)).

Mixing type	Loss of basal area increment ($m^2\ ha^{-1}$)	SD		Relative loss of basal area increment (%)	SD		Loss of volume increment ($m^3\ ha^{-1}$)	SD
Douglas-fir pure stand ($1.60\ m^2\ ha^{-1}\ a^{-1}$)	0.82	0.49	a	0.52	0.29	A	15.13	11.11
Mixed stand ($1.29\ m^2\ ha^{-1}\ a^{-1}$)	0.65	0.35	ab	0.50	0.25	A	11.12	6.10
E. beech pure stand ($0.91\ m^2\ ha^{-1}\ a^{-1}$)	0.45	0.44	b	0.50	0.32	A	6.54	5.48
Total	0.64	0.45		0.50	0.28		10.93	7.56

Growth responses of large trees, who dominated the stand, are less influenced by competition. Their growing performance is stronger connected with the weather conditions than the suppressed trees (Chhin et al., 2008; Piutti and Cescatti, 1997). The calculation of the Gleichlaeufigkeit with a conglomeration of large and small trees results in a declined Gleichlaeufigkeit.

Autocorrelation is assumed to indicate the existence of low frequency variation in tree chronologies and a higher persistency of growth level from year to year. Here, Douglas fir in pure stands showed highest values of autocorrelation but contrasting low values in mixed stands. LaMarche and Stockton (1974) analyzed the link between autocorrelation in tree ring growth series and needle growth. They showed that needle growth by bristlecone pines (*Pinus longaeva* D.K. Bailey and *Pinus aristata* Engelm.) decreased under negative weather conditions. Consequently, the photosynthetic potential of a tree with perennial needles declined resulting in declined current year ring growth. The influence of the previous year's needles still increase by the fact that the photosynthetic rate of previous year needles can be greater than current year needles (Clark, 1961; Hébert et al., 2011; Hom and Oechel, 1983). In summary, autocorrelation in growth series of conifers having perennial needles should be higher than that of broadleaved species. This can also be seen in a study of silver fir (*Abies alba* Miller) and European beech by Lebourgeois et al. (2014). The low autocorrelation of Douglas-fir which we found in mixed stands might be related to improved resource supply. Douglas-fir seems to be less influenced by the resource store of previous years. Annual variation of the photosynthetic leaf area may be stabilized by higher resource use efficiency in mixed stands.

Sensitivity, here measured by the mean sensitivity and the Gini-coefficient tend to be greater on sites with harsher conditions (Fritts et al., 1965). We observed that European beech showed an increased sensitivity in mixed stands compared to pure stands whereas for Douglas-fir an opposing trend was revealed. This positive mixing effect on sensitivity was also observed by silver fir which growing together with European beech (Lebourgeois et al., 2013). In contrast, the same study could not detect similar effects in a mixture of silver fir and Norway spruce. It might be that the partitioning of water resources varies between pure stands and mixed stands of coniferous and broad-leave trees. Douglas-fir as a coniferous species transpires nearly throughout the whole year (Waring and Running, 1978). The transpiration time of European beech is restricted to the growing period, where the trees carry leaves. During spring times, Douglas-fir in mixed stands profits from higher water availability in spring due to less intra-specific competition than in pure stands. When European beech starts to transpire, water supply is already reduced by Douglas-fir. Moore et al. (2011) observed this temporal partitioning of water utilization by Douglas-fir and red alder. We assume that this is a main reason for the differences in sensitivity between Douglas-fir and European beech in mixed stands. This is also in accordance with the hypothesis that the lower autocorrelation of Douglas-fir in mixed stands is related to a higher independency of previous year resources, which would reflect a facilitation effect by European beech.

4.2. Drought year analyses

4.2.1. Individual tree level

Resistance to drought events of Douglas-fir was generally lower than that of European beech. This is in line with the results of Weigt et al. (2015), who also examined the resistance of European beech and Douglas-fir. But the species-specific differences must be reflected in the context of generally higher absolute increment rates of Douglas-fir, especially in mixed stands. An analysis with the absolute increment values was not appropriate here, because tree age and residual trends may obscure possible responses (also mentioned in chapter 2.4). Resistance in our study did not differentiate between the mixing types. This consists with findings of resistance for European beech admixed to other species (Metz et al., 2016).

Concerning growth recovery time there was also a significant species-specific difference, with longer growth recovery time for Douglas-fir. The growth recovery time was reduced for Douglas-fir in mixed stands compared to pure stands and extended for European beech, but not on a significant level. These trends are in line with the findings for autocorrelation and mean sensitivity. We assume that trees in pure stands start simultaneously to grow in the subsequent year. In mixed stands Douglas-fir may have an advantage by starting to grow earlier than European beech, providing the chance to replenish its reserves more quickly. Douglas-fir in mixed stands starts to deplete water resources earlier during the growing season and this better access to water may shorten the growth recovery time in the years after drought. In cases where a year with below average water supply follows a dry year the effect of growth recovery time extension for European beech becomes more pronounced and significant. This supports the hypothesis that in mixed stands water resources are temporally more partitioned to Douglas-fir. This would lead to a stabilization effect for this coniferous species. As mentioned in chapter 4.1, a spatially different utilization of water resource by diverging rooting patterns between both species is also possible, but current studies do not enable general statements.

Anderegg et al. (2015) examined the recovery of stem growth after drought on a huge amount of forest sites across the globe and several genera. They found a general recovery time between 1 and 4 years after drought. During the drought year 2003, comparable to the stress conditions considered by Anderegg et al. (2015) the reaction of the trees examined here showed an average growth recovery time of 2.7 years and lies within the reported range.

Our data reveal, that the inter-specific differences of the growth recovery time between single drought event and extended drought periods (adverse post-year) increase. This would lead to the conclusion that Douglas-fir is disadvantaged by extended dryer weather conditions, whereas European beech is better capable to compensate this situation. We suggest, that growth recovery time is a good measure to distinguish between iso- or anisohydric traits of tree species.

Anderegg et al. (2015) drew the conclusion that species with lower safety margin of leaf water potential (isohydric species) tend to slower growth recovery after drought. Similar features were hypothesized by McDowell et al. (2002) stating greater suffering for isohydric species during extended drought periods. From this, Douglas-fir tends to have a more isohydric character than European beech.

Klein and Niu (2014) recommended to differ iso- and anisohydric characteristics by the stomatal conductance of leaf water potential at 50% of the maximum ($\Psi g_s 50$). According to Woodruff et al. (2008), $\Psi g_s 50$ for Douglas-fir provinces from Wind River Basin of southwestern Washington (USA) range between from −0.75 to −1.25. Stout and Sala (2003) measured a $\Psi g_s 50$ of −4.83 for Douglas-fir var. *glauca.* In the current paper we investigated Douglas-fir var. *viridis*. European beech had a $\Psi g_s 50$ from −2.12 to −3.17 (Aranda et al., 2000; Köcher, 2013). This would strengthen the assumption that Douglas-fir has isohydric and European beech anisohydric traits. The anisohydric strategy and the greater cross section of xylem predisposed European beech for hydraulic failure (McDowell et al., 2008). Nevertheless, several additional factors influenced the risk of hydraulic failure, like tree height, crown disposition and root system which were not all measured here.

The hydric characteristics might also be a reason for the unchanged resistance in mixed stands versus pure stands. In drought years, Douglas-fir stomatal safety margin leads to an earlier stop of water consumption than that of European beech. This enables European beech to use free water resources and prevent a more drastic drop of increment compared to pure stands (Pretzsch et al., 2013).

4.2.2. Stand level

During the drought year 2003 the stand level resistance concerning basal area increment followed the species specific single tree pattern being higher in European beech than in Douglas-fir stands. Mixed stands showed an intermediate response, being only significantly different from European beech stands. Due to the high proportion of Douglas-fir in mixed stands, the value for resistance was closer to the reaction of Douglas-fir pure stands. When comparing the measured resistance in mixed stands with the expected value from pure stands, weighted by the mixing proportion no deviation occurred (Appendix C). Because of the responses of both species (Jucker et al., 2014) no compensatory mixing effect concerning resistance was detectable.

In contrast to the general pattern of the growth recovery time for European beech, in 2003 European beech needed much longer to recover. In this case initial growth level was reached even later than for Douglas-fir. This might be a consequence of the subsequent year 2004 when European beech had a high fructification rate (Konnert et al., 2014; Landesforst Rheinland-Pfalz, 2014b). Eichhorn et al. (2008) observed a decreased stem wood production for European beech in 2004 in North Germany. They detected a shift of biomass production from stem wood to fruits. Heavy ‘mast’-years generally lead to a high consumption of reserve stores (Burschel, 1966). This might be a reason for the extended growth recovery time for European beech.

Nevertheless, the relative loss due to drought amounted to around 50% for both species and mixing types. The variation in loss of absolute basal area increment was a result of the diverging levels of increment rates between Douglas-fir and European beech. When reflecting stand volume growth a loss due to drought of 15.1 $m^3\,ha^{-1}$ was found for Douglas-fir pure stands, 11.1 $m^3\,ha^{-1}$ for mixed stands and 6.5 $m^3\,ha^{-1}$ for European beech stands (Table 4). Concerning the loss of volume increment, the absolute differences between mixing types is more pronounced compared to the loss of basal area increment. This bias might be induced by the applied volume estimation function (Appendix B), but is presented here to provide a dimension for the forest management. The presentation of relative and absolute drought responses is a major issue of our study. Relative values provide a biological understanding, whereas absolute values take differences in productivity of tree species into account.

4.3. Changing patters along ecological gradients

The applied statistical models revealed that several ecological variables influence drought response of trees. The response of ecological system to ecological conditions is inherently nonlinear (Burkett et al., 2005). Therefore, we additionally checked the courses of independent variables with generalized additive mixed models. Because crucial variables showed linear or almost linear courses we decided to use linear mixed models for better interpretation.

The observed linear course may result because our study covering as well the current planting area of Douglas-fir and European beech pure and mixed stands in Germany but the potential growing area would be greater. So a greater gradient may show a nonlinear course.

It seems that on fertile sites drought has a more severe impact on growth. Higher base richness reduces resistance of Douglas-fir and European beech at individual tree and at stand level. It is assumed that base limited systems are less influenced by short-term water restriction than water limited systems (Mitscherlich, 1909). On sites with higher water supply the impact of drought events also seems to have a more severe impact in terms of growth recovery time and relative growth loss at stand level. Sergent et al. (2014b) investigated Douglas-fir on different fertile sites and found a better recovery on the more fertile ones. The influence of nutrients can have variable effects (Rennenberg et al., 2006) and is less well understood. Additionally, different proveniences response variable on drought stress (Eilmann et al., 2013; García-Plazaola and Becerril, 2000; Sergent et al., 2014a) and may compensate drought stress an different ways.

Tree age was also a significant co-variable in most models. It seems to trigger a twofold pathway of reaction concerning Douglas-fir. On the one hand resistance is higher with progressive tree age on the other hand growth recovery time is extended. An age-related increase of drought stress sensitivity was found for European larch (*Larix decidua* Mill.) and Swiss stone pine (*Pinus cembra* L.) by Carrer and Urbinati (2004). They supposed that hydraulic constraints increase with tree age and tree height. The assumption is that the gravitation potential in the hydraulic pathways of plants increases with the height (Matyssek et al., 2010; McDowell et al., 2008). The height growth dynamic of Douglas-fir and its huge hydraulic path length may explain such age-dependent drought sensitivity. We additionally performed a drought year analysis on a small collective of sample trees for which we reconstructed tree heights (not shown in the method and result section). The results reveal a significant interaction between increasing height and decreasing resistance and increasing growth recovery time. We assume that the tree height is a major driver of drought response. This interaction of increasing size and increasing sensitivity could also observed for European beech and silver fir (Mérian and Lebourgeois, 2011) and for Scots pine (Merlin et al., 2015). For Douglas-fir in our study, tree age correlates very closely with tree height. This is not the case for European beech. Because of their shade-tolerant traits, European beech forms a wider range of tree heights at similar age (Pretzsch and Schütze, 2016). Therefore, no correlation of tree age with resistance was found for European beech. The negative correlation of the relative DBH with resistance indicates that trees in lower social classes with lower heights and smaller tree rings have a better resistance. This is conform to the findings concerning size dependent patterns of resistance.

The mentioned contradiction of the age effect of Douglas-fir at individual tree level is explained when considering the DBH effect. We suggest that the older trees with smaller DBH had higher wood density and form stronger hydraulic pathways bearing better resistance against hydraulic pressure under drought (Hacke et al., 2001).

The PCA indicated a general higher climate sensitivity of younger compared to older stands. As tree chronologies have been analyzed throughout the entire tree age this may reveal a climate change effect on trees' sensitivity. Young stands have faced a greater share of time under recent climate change conditions than older ones. Biondi and Qeadan (2008b) also reported from a species-unspecific change in sensitivity over a time period of 400 years.

Increment loss to drought was linked with stand density. With increasing basal area the stand level loss also increased. This outcome is in line with the findings of Rais et al. (2014), who found higher resistance in Douglas-fir plantation with lower stand density. Lebourgeois et al. (2014) confirmed a negative impact on sensitivity with increasing stand density for European beech and silver fir, as well. Rais et al. (2014) concluded that lower stand density is associated with better availability of soil space and a larger root system of the individual tree.

5. Conclusions

Our study of mixing effects between Douglas-fir and European beech on individual tree and stand level comprised a wide range of site conditions, stand ages, and mixing proportions in Central Europe. The results give evidence that Douglas-fir profits from being mixed with European beech in terms of productivity, drought stress release, and time of growth recovery. The stabilized growth of Douglas-fir seems to be on the expense of European beech. Nevertheless, mixed stands with European beech contribute to risk mitigation for the high productive coniferous Douglas-fir.

The study indicate that base limited systems are less affected by drought events and that taller trees have less resistance, both facts are independent from species and mixing type.

The study focused on tree ring information at DBH height. Although the trunk represents a major share of total tree biomass (Pretzsch et al., 2014), resource allocation pattern between above and below ground organs (Nikolova et al., 2011; Pretzsch et al., 2012) or wood density (Toïgo et al., 2015) may also change during drought periods. Considering these aspects in future analyses may refine the picture of mixing effect between Douglas-fir and European beech.

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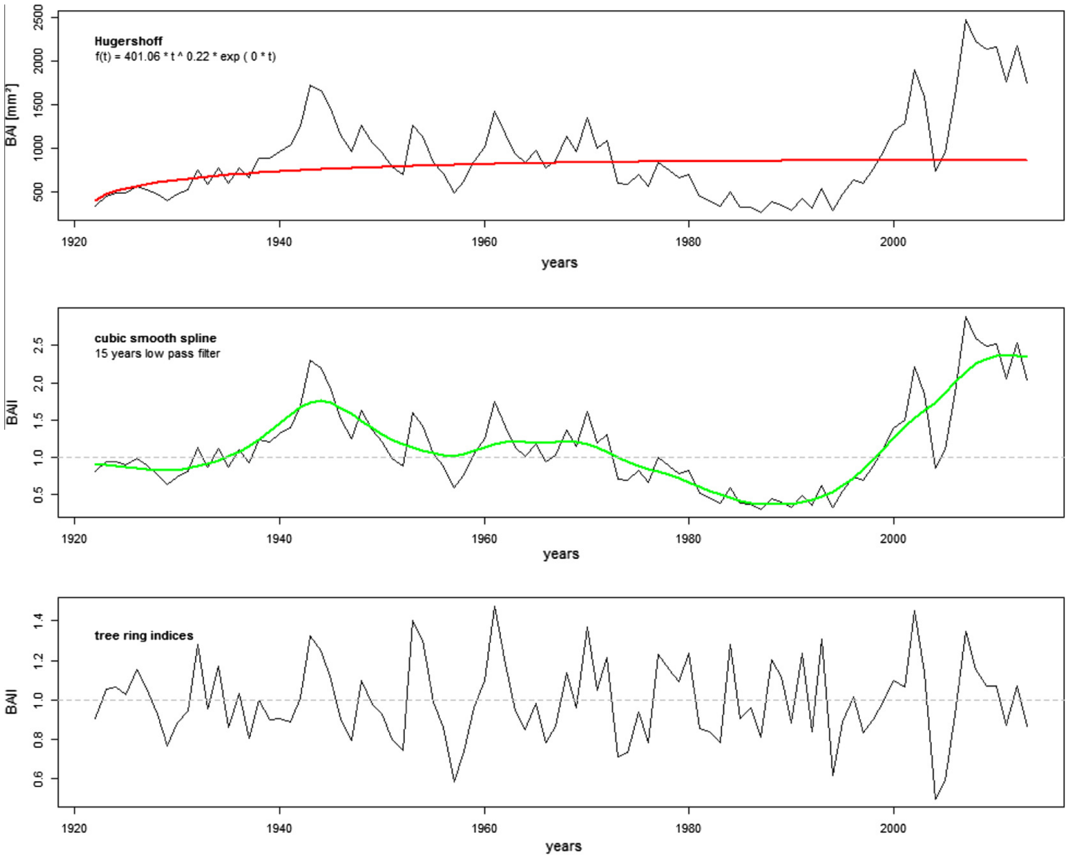
Appendix A. Exemplary illustration of the double detrending method for a single European beech tree chronology



The figures show the individual European beech No. 1003_11_1 and the steps of double detrending applied to all series of the study. (A) Original basal area increment course (BAI) calculated on the mean of two cores per tree (black line) Growth trend estimated according to Hugershoff equation (red line). (B) Index Series (BAII) (black line) as basal area increment index (BAII) and trend estimated by cubic spline of 15-year wavelength (green line). (C) Resulting basal area increment indices after two step detrending (black line).

Appendix B. Estimates of the regression coefficients (Eq. (1)) and model quality for calculating volume area loss due to drought

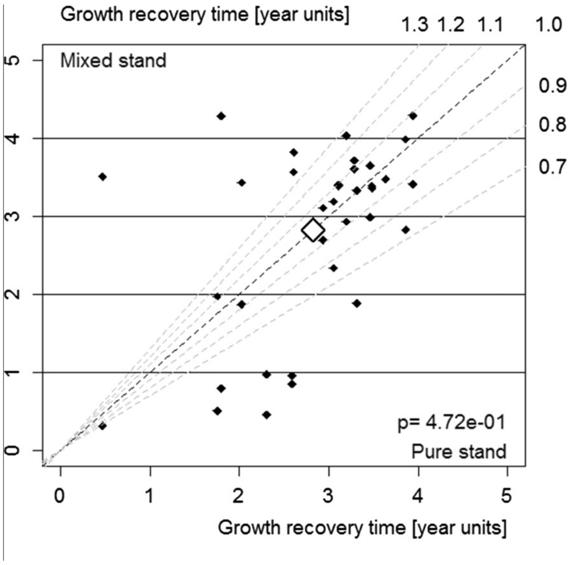
The table contains the coefficients a1…a3 of the fixed effects from the model which estimated volume by basal area increment loss. The last row represents the coefficient of determination (R^2).

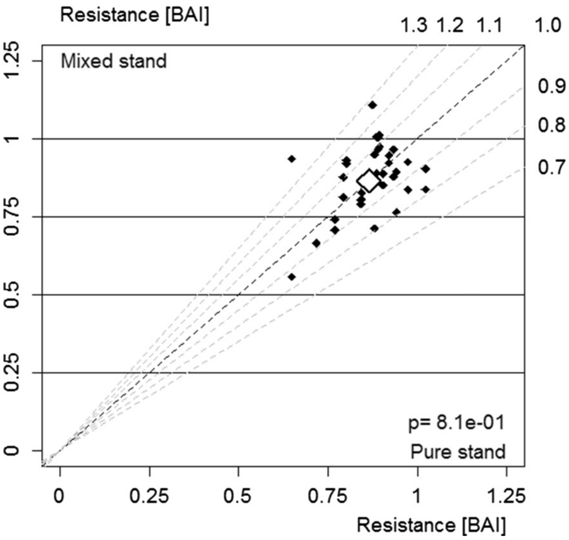
Mixing type	a0	a1	a2	a3	R^2
Douglas-fir pure stand	0.50	1.78	0.57^{**}	−0.16	0.81
Mixed stand	0.75	−2.58 .	0.50^{**}	0.89^{*}	0.80
European beech pure stand	−0.75	1.31	0.86^{***}	−0.04	0.82

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1.

Appendix C. Comparison of pure and mixed stands resistance and growth recovery time

This figure shows the comparison of the observed parameter value for mixed stand ($p1.2$ – y-axis) and expected value derived from pure stands ($\hat{p}1.2$ –x.axis). The resistance and growth recovery time of the expected mixed stand was calculated by summarizing the species-specific values of pure stands ($p1, p2$) weighted by the species-specific mixing proportion in mixed stand ($m1, m2$); $\hat{p}1.2 = p1 * m1 + p2 * m2$ (for a more detailed view see Pretzsch et al. (2010)).





Appendix D. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2016.06.020.

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ORIGINAL ARTICLE

Stem growth is favored at expenses of root growth in mixed stands and humid conditions for Douglas-fir (*Pseudotsuga menziesii*) and European beech (*Fagus sylvatica*)

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Abstract

Key message **The study found an increased investment into stem growth (compared to root growth) if trees were surrounded by a complementary species. This response is consistent with known patterns about root–stem allometry under favorable conditions (humidity and stand density).**

Abstract The study investigated partitioning of resources between roots and stems in mono-species and mixed-species stands of Douglas-fir and European beech at four different sites. We combined tree ring analyses of stems and coarse roots to scrutinize root–stem allometry with a focus on how it is influenced by species mixture and humidity. The results show that allometry in mixed stands changed in favor of stem growth for both species. The greatest relative allocation into stem growth was observed for individual trees which were completely surrounded by trees of the other species. The data indicate that a decrease of stand density, which was used as a proxy for tree competition, has the same effect on allocation. To analyze the influence of humidity, we used a long- and short-term index. Based on these, we can show that allocation changes with general site conditions and annual humidity variations. We found that on both time scales, both species increase resource investment into stem growth if conditions are more humid. Under harsher conditions, allocation shifts into root growth. The findings contribute to understanding the overyielding in mixed stands. Mixing Douglas-fir and European beech leads to the same allocation patterns as an improvement of site conditions. We suggest that for both species, mixture is equivalent to growing on a better site.

Keywords Mixed stands · Root–stem allometry · Density · Site gradient · Complementarity

Introduction

Since long, species mixture is deemed to be a standard measure for improving productivity and stability of forest stands in the practice of silviculture (Liang et al. 2016). The underlying mechanisms behind such mixing effects and the conditions, under which they occur, however, are only partly understood so far. Many studies were conducted to analyze the above-ground overyielding (Binkley and Greene 1983; Bartelink 1998; Amoroso and Turnblom 2006) and the reduced climate sensitivity of stem growth in mixed stands (Pretzsch et al. 2013; Lebourgeois et al. 2013; Jucker et al. 2014). However, for a holistic understanding of the mixing effect, it is essential to investigate the whole system, the aboveground as well as the belowground production.

Several studies could show that an increased resource uptake of the involved species is responsible for the higher productivity often found in mixed stands (Binkley 2003; Forrester et al. 2006b; Thomas et al. 2015). Two mechanisms lead to this increasing uptake, facilitation, and species complementary (Larocque et al. 2013). Facilitation may, i.a., modify resource availability, whereas complementarity means a more efficient use of resources which result from niche differentiations.

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Changes of resource uptake in mixed stands imply shifts of resource allocation among tree compartments (Dieler and Pretzsch 2013). This can be observed by measuring the size of tree compartments or investigating tree allometry (Amoroso and Turnblom 2006; Erickson et al. 2009; Radosevich et al. 2006). The allometry between root and stem size is of particular interest and has been repeatedly examined (Nikolova et al. 2011; Shainsky et al. 1992). Nevertheless, the results about the influence of intraspecific competition show diverse patterns (Poorter et al. 2012) and species-specific analyses, especially for woody plants, seems to be advisable.

In our context of interest, two theories have been advanced to describe the allocation in plants. The first one is the allometric biomass partitioning theory (APT). It describes how organismal attributes change with plant size according to the allometric equation (Peters 1983):

$$\log Y1 = \log \beta + \alpha \log Y2. \qquad (1)$$

The variables $Y1$ and $Y2$ in the equation represent the sizes of two interdependent tree compartments, in our case (coarse) root and stem diameter. The parameter α represents the allometric exponent, while β is a scaling parameter. The constancy of α is the major statement of APT. The second theory differs in this assumption. The optimal partitioning theory (OPT) states that plants allocate additional biomass to the organ that takes up the most limiting resource (Bloom et al. 1985; Thornley 1972). Thereby, the allometric exponent α must be variable. Several studies could show plastic responses of tree compartments beyond the predetermined allometric development (Schall et al. 2012; Meier and Leuschner 2008; Nikolova et al. 2011).

From a methodological point of view, the allocation between belowground and above-ground tree compartments can be scrutinized in different ways. The destructive approach excavates whole trees and weighs above-ground and below-ground biomass. Especially for mature trees, this method is extremely laborious and difficult to realize at a large number of trees, which is required for statistical evidence as only one observation per tree is possible. For this reason, we applied a method which compares coarse root and stem diameter growth based on increment borings. The method has already been successfully applied in studies about relationships of site and tree allometry (Nikolova et al. 2011; Pretzsch et al. 2012a, b). It allows for sampling a larger number of trees and to obtain retrospective time series per tree.

In the study at hand, the species mixing effect on root–stem allometry is investigated for Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and European beech (*Fagus sylvatica* L.) under mixed and monospecific settings. Previous studies identified an overyielding in mixed stands of both species compared to mono-species stands (Bartelink 1998; Thurm and Pretzsch 2016). Notwithstanding, while complementarity of both species in the crown layer was considered a major effect, there was evidence for additional effects in the root zone. Thurm and Pretzsch (2016) supposed that under harsher conditions, species complementary shifts from the crown stratum into the soil stratum. Drought year analyses, which could show a complementary water use between Douglas-fir and European beech, confirm this assumption (Thurm et al. 2016). In this context, the study at hand intends to supplement the understanding of mixing effects by investigating root–stem allometry and its possible differences due to species mixing.

Based on the existing knowledge, we start from the hypothesis that (1) Douglas-fir and European beech have different root–stem allometry and (2) that mixing both species modifies their allocation into coarse roots and stems compared to their growth in monospecific environments. In this context, we also scrutinize the impact of stand density on allometry. In addition, we formulated the hypotheses that (3) unfavorable general site conditions (low humidity) influence the allocation in favor of root growth, and that (4) short-term droughts have an analogous effect.

Materials and methods

Study area and experimental setup

The study was conducted in spring 2014 on several locations in Southern Germany, which belongs to the warm temperate climate zone. We made use of a triplet experimental setup which has meanwhile turned out an effective method for detecting the mixed stands effects in many studies (e.g., Dirnberger and Sterba 2014; Pretzsch et al. 2015). Each triplet is composed of a pure Douglas-fir stand, a pure European beech stand, and a mixed stand of both species (Table 1). The plots consisted of around 20 individuals in pure stand and 20 individual per species in mixed stands (mean plot size 660 m^2). Each triplet is characterized by homogenous site conditions, and both species have the same age in the respective pure and the mixed stand. Beside these two requirements, the proximity of the plots was a crucial factor. The distance of the plots inside a triplet is on median 90 m (maximum 570 m). Another requirement of the triplet was the structural comparability. The proximity of the plots should ensure the same management regime. Selected were fully stocked stands with very low thinning intensity as confirmed by stump counting. The sampling was made in a managed forest, so totally, unthinned situations could not be found. However, we deemed thinning intensity of the selected stands close to self-thinning, maximum stand density

Table 1 Site characteristics of the four triplets indicating ecoregions (Gauer and Kroiher 2012), climate data (Deutscher Wetterdienst 2015), soil data (Taegger and Kölling 2016) and age

Experimental number	Plot	Ecological region	Geographic position		Elevation	Mean annual Temperature (1981–2014) (°C)	Mean annual Precipitation (1981–2014) (year mm^{-1})	Base-richness from base-poor (1) to base-rich (5)	Water supply from very dry (1) to very fresh (7)	Sand (%)	Clay (%)	Silt (%)	Soil types by LUFA	Age (years)	Skeleton section between 60 and 90 cm (%)
			N-longitude	E-latitude	m above sea level										
1001	4	Tertiäres Hügelland	4393914.11	5343070.81	597	8.1	1011	3	7	55	22	22	Sandy loam	56	48.1
	5	Tertiäres Hügelland	4393968.08	5343012.33	597	8.1	1011	3	7	55	22	22	Sandy loam	64	48.1
	6	Tertiäres Hügelland	4393923.63	5342981.38	588	8.1	1011	3	7	55	22	22	Sandy loam	61	48.1
1002	4	Fränkische Platte	4352612.71	5529925.84	312	8.9	727	4	3	16	59	24	Clay	51	0.6
	5	Fränkische Platte	4352830.72	5530457.12	319	8.8	740	4	3	16	59	24	Clay	54	0.6
	6	Fränkische Platte	4352743.94	5530469.82	319	8.8	740	4	3	16	59	24	Clay	51	0.6
	7	Fränkische Platte	4332272.39	5517554.27	293	8.9	792	4	3	12	56	32	Clay	98	1.8
	8	Fränkische Platte	4332385.63	5517503.25	285	8.9	792	4	3	12	56	32	Clay	102	1.8
	9	Fränkische Platte	4332372.5	5517593.21	272	8.9	792	4	3	12	56	32	Clay	100	1.8
1003	4	Spessart	4323073.04	5541828.39	439	8.1	1054	3	4	31	36	34	Clay loam	85	8.3
	5	Spessart	4322988.25	5542160.09	447	8.1	1054	3	4	31	36	34	Clay loam	88	8.3
	6	Spessart	4323072.25	5542183.9	449	8.1	1054	3	4	31	36	34	Clay loam	87	8.3
Total					410	9	895	4	4	29	43	28		75	

conditions (for a more detailed description of the setup and stand level growth parameter, see Thurm and Pretzsch 2016).

In total, four triplets comprising 12 plots altogether were established. The four triplets were set up in three different ecological regions which range from drier, warmer sites in the ecological region of *Fränkische Platte* to moister, colder sites in the ecoregion *Schwäbisch-Bayerische Schotterplatten- und Altmoränenlandschaft* (see Gauer and Kroiher (2012) for an overview of the German forest ecoregions). The long-term mean annual temperature covers a span of 8.1–8.9 °C with an annual mean precipitation between 727 and 1054 mm. Multiannual and monthly temperature and precipitation data were obtained along a 1 × 1 km grid of the German Weather Service (Deutscher Wetterdienst 2015). The profundity of soil was always deeper than 1 m (for the skeleton section in soil depth 60–90 cm and the soil type, see Table 1).

Long and short-term humidity indices

For scrutinizing short-term weather effects on root–stem allometry, we used the standardized precipitation–evapotranspiration index SPEI (Vicente-Serrano et al. 2010). It was summarized as an annual value based on the average of monthly SPEI values in the growing period (May–September). The SPEI uses the monthly differences between precipitation and the climatic water balance after Thornthwaite (1948). The input variables of the climatic water balance are monthly mean temperature and geographic latitude. We calculated the climatic water balance at a time scale of 5 months using a Gaussian kernel function, respective for every triplet. The SPEI indexed a time period from 1950 to 2010, whereas the mean weather conditions in this period represent by the index zero and dry conditions represent by negative indices.

As a measure of long-term climate-induced site productivity, the CVP index by Paterson (1956) was brought to bear (Eq. 2):

$$\mathrm{CVP} = \frac{\mathrm{Tv} \cdot P \cdot G \cdot E}{\mathrm{Ta} \cdot 12}. \tag{2}$$

The CVP index is designed to indicate the growth potential of plants just by climate parameters. Greater CVP indices mean better growing conditions. We calculated it for a time span of 30 years (1980–2010). The variable Tv is the mean monthly temperature of the warmest month (°C); P is the sum of the annual rainfall (mm a^{-1}); and G represents the length of the growing period (number of months). Growing season length in Central Europe is mainly determined by temperature (Vitasse et al. 2009). According to Paterson (1956), we attributed months with an average temperature equal to or higher than 3 °C to the growing period. Ta is the difference between the mean maximum temperature of the warmest month and the mean minimum temperature of the coolest month (°C). The variable E is the so-called evapotranspiration reducer, which Paterson (1956) suggested to calculate by relating the solar radiation at the poles to the radiation at the site of interest. While this is meaningful for differentiating potential plant productivity on a global scale as originally intended by Paterson, we used a modification *E*' introduced by Gandullo and Serrada (1977) which better reflects the comparably small spatial scope of our study. *E*' considers the real insolation at the plots by using the local annual sunshine hours per year n_{sun} (Eq. 3):

$$E' = \frac{2500}{n_{sun} + 1000}. \tag{3}$$

The sunshine hours were derived from 1 × 1 km grid data from the German Weather Service (Deutscher Wetterdienst 2016). In this study, the values of *E*' fluctuated around 0.97, which represent an average sunshine duration of 1583 h per year.

Sampling and measurement

For this study, we sampled approximately ten dominant trees per species at each plot. At these trees, we measured tree height, DBH, and diameter of the cored root at the position of coring (see below). To quantify the competitive situation of such a tree, we determined the basal area (m^2/ha) in the tree's vicinity with an angle count sampling using a relascope (Bitterlich 1952) with the tree of interest in the center of the sampling spot. The local basal area (local BA) was used as a tree individual competition index. For the counted trees, we recorded also their affiliation to the groups of coniferous (Douglas-fir) and broadleaved trees (European beech). This enabled us to tell whether competition for a given tree of interest was more inter- or intraspecific (cf. Pretzsch 2009) and we get and individual tree mixing proportion (mixing proportion doug, based on proportion of surrounding Douglas-firs). Finally, we adjusted the mixing proportion of European beech with an equivalence coefficient (1.6). Douglas-fir and European beech have different patterns of spatial occupation. Douglas-fir reached greater stand densities, European beech lower. To avoid a spatial overestimation of one species, it was applied the mentioned coefficient. The equivalence coefficient results from the ratio of stand density index from pure Douglas-fir and a pure European beech stand. It was detected in a mixed study of 18 triplets which also used the triplets of the study at hand (for further information, see Thurm and Pretzsch 2016).

For taking stem cores, we applied long-term standard procedures (Pretzsch 2002; Cook and Kairiūkštis 1990).

For the selection and the drilling of the roots, we were geared to a pilot study from Nikolova et al. (2011) which has been successfully applied in several other studies later (Pretzsch et al. 2012a, b). All cores were sampled with a Haglöf increment borer. The stem was cored twice at breast height in North and East directions. The root cores were taken at two tall, lateral structural roots which were excavated. The root coring position was about 60–80 cm from their offset at the trunk. This distance range was chosen a compromise between having the lowest number of missing or discontinuous root growth rings (Krause and Morin 1995) and avoiding strongly eccentric cross-sectional shapes which result from root growth response to wind load (Nicoll and Ray 1996). Nevertheless, many sampled roots show elliptic shapes with the largest radius from the upper edge to the downmost edge and the smallest parallel to the soil surface. To obtain the mean annual growth of the roots, one core was taken from the root's top edge to the center (largest radius) and another one perpendicularly from one lateral root edge to the center (smallest radius). This method also minimizes the amount of year rings which are not hit perpendicularly with the borer. This procedure provided six cores for every tree (two from the stem, two from the first root, and two from the second root). All in all, the data set comprises 175 trees (see Table 2; Fig. 1).

Ring width measurements were made using a digital positiometer after Johann (1977) (Biritz GmbH, Gerasdorf bei Wien, Austria) with an accuracy of 0.01 mm. Measurements of cores stops when tree rings run non-perpendicular. For cross-dating and synchronization of the tree chronologies, we used the software platform TSAP-Win (Rinntech, Heidelberg, Germany). The analyses of root–stem allometry base on relating diameter change between roots and stem. Diameters were calculated backwards by subtracting the measured increments from the diameter at survey time. This annual backward diameter calculation was only done for the time span which was covered by both increment cores per sampling point.

To extract the climate signal in root and stem growth, we detrended the basal area increment of the tree compartments in two steps, as described in detail Thurm et al. 2016). In a nutshell, the first detrending step relied on fitting a Hugershoff increment function (1936). For the second step, we fitted a cubic spline with a wavelength of 15 years.

Statistical analyses

The basic allometric model (cf. Eq. 1) we used for relating root and stem diameter (droot and dstem) can be written as follows:

$$\ln(\text{droot}) = a_0 + a_1 \cdot \ln(\text{dstem}). \tag{4}$$

The coefficient a_0 represents the scaling parameter, and a_1 is the allometric exponent.

To answer our research questions, this model was extended to incorporate several explanatory variables of interest (see below) and fitted to the data. For taking into account the nested data structure (triplet, plot, tree, and root), we applied linear mixed models. Model selection was based on the Akaike Information Criterion (Burnham and Anderson 1998, 2004) and biological plausibility of the results.

At first, we tested for a general difference in the root–stem allometries of Douglas-fir and European beech. To this end, the fixed effect *species* coded as binary variable (1: European beech, 0: Douglas fir) was introduced:

$$\begin{aligned}\ln\left(\text{droot}_{ijklt}\right) = a_0 &+ a_1 \cdot \ln\left(\text{dstem}_{ijklt}\right) + a_2 \cdot \text{species} + a_3 \\ &\cdot \ln\left(\text{dstem}_{ijklt}\right) \cdot \text{species} + b_i + b_{ij} + b_{ijk} \\ &+ b_{ijkl} + \varepsilon_{ijklt}\end{aligned} \tag{5}$$

where $a_0 \ldots a_n$ represent the coefficients of the fixed effects. Random effects b are considered triplet i, plot j, tree k, and root level l. The index t stands for the year a measurement belongs to. The symbol ε represents i.i.d. errors. If the estimate of a_2 differs significantly from zero, this suggests species-specific allometric scaling factors. If, however, a_3 differs significantly from zero, we have to assume species-specific allometric slopes.

Further models were fitted separately for Douglas-fir and European beech. Related to the second research question, the influence of the mixture on allometry, we applied the Eq. 6. The fixed effect *mixture* was included as a binary variable (0: pure stand, 1: mixed stand):

$$\begin{aligned}\ln\left(\text{droot}_{ijklt}\right) = a_0 &+ a_1 \cdot \ln\left(\text{dstem}_{ijklt}\right) + a_2 \cdot \text{mixture}_{ij} + a_3 \\ &\cdot \ln\left(\text{dstem}_{ijklt}\right) \cdot \text{mixture}_{ij} + b_i + b_{ij} + b_{ijk} \\ &+ b_{ijkl} + \varepsilon_{ijklt}.\end{aligned} \tag{6}$$

Similar to the binary variable species in Eq. 5, the parameters a_2 and a_3 indicate mixture effects on the scaling factor and the allometric slope, respectively.

In addition, to refine the view on species mixing effects, we investigate the shift of allocation by introducing the individual mixing proportion doug as a continuous variable. The proportion ranged between 0 and 1. The value 0 means the individual tree is completely surrounded by European beech and 1 surrounded by Douglas-fir:

$$\begin{aligned}\ln\left(\text{droot}_{ijklt}\right) = a_0 &+ a_1 \cdot \ln\left(\text{dstem}_{ijklt}\right) + a_2 \\ &\cdot \text{mixing proportion doug}_{ijk} + a_3 \\ &\cdot \ln\left(\text{dstem}_{ijklt}\right) \\ &\cdot \text{mixing proportion}(df)\text{doug}_{ijk} + b_i + b_{ij} \\ &+ b_{ijk} + b_{ijkl} + \varepsilon_{ijklt}.\end{aligned} \tag{7}$$

To investigate, whether there is also a pattern of stand density, we fitted a model with local BA:

$$\ln\left(\mathrm{droot}_{ijklt}\right) = a_0 + a_1 \cdot \ln\left(\mathrm{dstem}_{ijklt}\right) + a_2 \cdot \mathrm{local\ BA}_{ijk} + a_3 \cdot \ln\left(\mathrm{dstem}_{ijklt}\right) \cdot \mathrm{local\ BA}_{ijk} + b_i + b_{ij} + b_{ijk} + b_{ijkl} + \varepsilon_{ijklt}. \tag{8}$$

The short- and long-term climatic influences on root–stem allometry were analyzed based on Eqs. 9 and 10. Fixed effects are the standardized precipitation–evapotranspiration index *SPEI* and the Paterson index CVP, respectively. Because the influence of mixture turned out non-significant on long-term scale, we omitted it in Eq. 10:

$$\ln(\mathrm{droot}_{ijklt}) = a_0 + a_1 \cdot \ln\left(\mathrm{dstem}_{ijklt}\right) + a_2 \cdot \mathrm{SPEI}_{ijt} + a_3 \cdot \mathrm{mixture}_{ij} + a_4 \cdot \ln\left(\mathrm{dstem}_{ijklt}\right) \cdot \mathrm{SPEI}_{ijt} + a_5 \cdot \ln\left(\mathrm{dstem}_{ijklt}\right) \cdot \mathrm{mixture}_{ij} + a_6 \cdot \mathrm{SPEI}_{ijt} \cdot \mathrm{mixture}_{ij} + a_7 \cdot \ln\left(\mathrm{dstem}_{ijklt}\right) \cdot \mathrm{SPEI}_{ijt} \cdot \mathrm{mixture}_{ij} + b_i + b_{ij} + b_{ijk} + b_{ijkl} + \varepsilon_{ijklt} \tag{9}$$

$$\ln(\mathrm{droot}_{ijklt}) = a_0 + a_1 \cdot \ln\left(\mathrm{dstem}_{ijklt}\right) + a_2 \cdot \mathrm{CVP}_{ij} + a_3 \cdot \ln\left(\mathrm{dstem}_{ijklt}\right) \cdot \mathrm{CVP}_{ij} + b_i + b_{ij} + b_{ijk} + b_{ijkl} + \varepsilon_{ijklt}. \tag{10}$$

All statistical analyses and graphics were conducted with the statistical environment R version 3.2.2 (R Core Team 2015). Linear mixed models were fitted with *lmer* from the R-package *lme4* (Bates et al. 2015). The significances of the coefficients were tested with an F Test with Satterthwaite's approximation (Kuznetsova et al. 2015) from the R-package *lmerTest*.

Results

Species-specific root–stem allometry

The average age of the sampled trees was approximately 59 years (Table 2). However, Douglas-fir was on average 7 year younger, it was 4.4 m higher in pure stands than European beech in pure stands. In mixed stands, the height difference was amounted to even 7.9 m between Douglas-fir and European beech. Douglas-fir had a 9.2 cm greater diameter in pure stands and a 21.5 cm greater diameter in mixed stands than European beech. Overall, the DBH ranged from 19.6 to 95.9 cm and from 9.5 to 63.9 cm for Douglas-fir and European beech, respectively. We found the same pattern of size differences for the root diameters. The average coarse root diameter of Douglas-fir was 13.1 cm (pure = 12.2 cm; mixed = 14.0 cm) and 8.9 cm for European beech (pure = 9.3 cm; mixed = 8.4 cm).

Table 2 Characteristics of the sampled trees

Species	Mixture	Number	DBH (cm)			Height (m)			H/d ratio			Root diameter (cm)			Age (years)			LocalBA ($m^2\ ha^{-1}$)		
			Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max
Douglas-fir	Pure	49	47.4	19.6	87.5	35.4	23.0	46.8	72	50	100	12.2	5.7	29.8	56	24	89	52.9	27.6	90.8
	Mixed	41	52.3	28.5	95.9	35.8	26.5	49.2	96	66	181	14.0	5.1	33.6	54	28	96	49.8	28.8	86.4
European beech	Pure	40	38.3	17.0	63.9	31.0	23.9	43.7	81	50	127	9.3	4.9	18.4	65	35	110	44.2	10.4	74.0
	Mixed	45	30.8	9.5	55.4	28.0	17.2	43.2	87	52	148	8.4	5.0	17.5	61	23	108	52.8	36.0	92.2
Total		175	42.2			32.6			72			11.0			59			52.9		

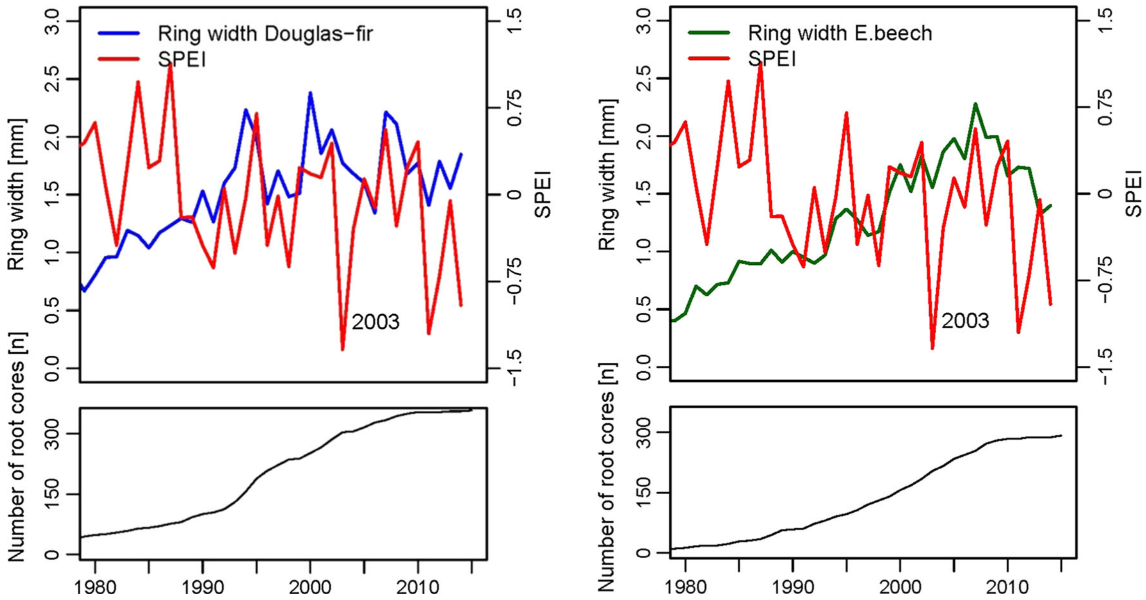

Fig. 1 Ring width chronologies of the lateral roots for Douglas-fir (*blue line*, *left*) and European beech (*green line*, *right*) and the standardized precipitation–evapotranspiration index SPEI (*red line*). *Labeled* is the extreme drought year 2003. The *black line* shows the number of available cores in the respective year

The fit results of all linear mixed models shown above are summarized in Table 3. The species-specific model (Eq. 5) indicates that Douglas-fir and European beech significantly differ in their root–stem allocation. European beech has a significantly lower allometric scaling factor but a significantly steeper slope than Douglas fir. We illustrate this result in Fig. 2; up to a DBH of about 26, cm, a typical Douglas-fir invested more resources into coarse roots growth than European beech, at greater diameters, and European beech shows a greater root growth. The inclusion of stand level mixing (dichotomous variable mixture) into the allometric model (Eq. 6, Fig. 3) indicates that Douglas-fir in pure stand has a significant smaller scaling factor than in mixed stands but a significant greater slope. Same effect can be seen for European beech but much it is more pronounced. Both species in pure stands allocate higher biomass portions to the roots if they have DBH beyond about 30 cm (Douglas-fir) and 45 cm (European beech), respectively.

Including mixing proportion at individual tree level gives a clearer view on the shift between root and stem allocation (Table 3, Eq. 7). As shown in the methods section, the proportion of Douglas-fir in the local BA is the variable which was used to this end in the models for both species. Therefore, the highest interspecific competition presented in Fig. 4 is 0.8 for European beech and 0.2 for Douglas-fir. Both species exhibit a significantly higher allocation to stem growth compared to root growth if they compete more against the other species than against their own.

Influence of competition

The 95% of the local BA's arranged between 26.0 m^2/ha and 82.6 m^2/h. Figure 5 shows by means of the fitted Eq. 8, how the trees partitioned resource between root and stem under increasing stand density. The analyses aggregate all trees, independent if mixed or not. The sampled trees in mixed stands show a little bit higher local BA (50.8 m^2/ha) than pure stands (49.1 m^2/ha), but the difference was not significant. The data exhibited that with increasing competition allocation favors root growth relative to stem growth. This pattern was significant for both species but more pronounced for Douglas-fir.

Influence of short-term humidity variation

As shown in the "Methods", the short-term variation of humidity was represented by the SPEI. In the measuring period, the SPEI ranged between −1.58, which was reached in the drought year 2003, and 1.14, which was reached 2002. The SPEI index for all triplets existed from 1998 to 2010 which results in a lower observation account in Table 3. As mentioned in the "Methods", the triplet specific SPEI enables to calculate site-specific minimum and maximum SPEI values. Figure 6 illustrates the allocation pattern of Douglas-fir and European beech in pure and mixed stands. Under humid weather conditions, both species allocate resources in favor of stem growth compared to root growth (Eq. 9). This reaction could be found in pure as well as in mixed

Table 3 Estimated fixed effects for the extended root–stem allometry models (Eqs. 5–10)

Equation	Dependent variable:										
	log(droot)										
	Tree allometry pattern			Competition/density/mixing proportion				Humidity response			
Independent variable:	5 EB - DF	6 Douglas-fir	6 E.beech	7 Douglas-fir	7 E.beech	8 Douglas-fir	8 E.beech	9 Douglas-fir	9 E.beech	10 Douglas-fir	10 E.beech
log(dstem)	0.726*** (0.013)	0.633 (0.015)	1.149*** (0.028)	0.506*** (0.027)	1.416*** (0.033)	0.282*** (0.04)	1.501*** (0.087)	0.608*** (0.018)	1.078*** (0.032)	−0.825*** (0.114)	0.058 (0.176)
Species E.beech	−1.990*** (0.109)										
Log(dstem)*species E.beech	0.608*** (0.024)										
SPEI								−0.075** (0.028)	−0.074* (0.031)		
Mixture(pure)		−0.904*** (0.194)	−1.889*** (0.378)					−1.096*** (0.205)	−1.979*** (0.38)		
Log(dstem)*SPEI								0.020** (0.007)	0.025** (0.01)		
Log(dstem)*mixture(pure)		0.267*** (0.025)	0.490*** (0.045)					0.315*** (0.031)	0.522*** (0.052)		
Mixing proportion doug				−1.279*** (0.247)	1.025 (0.549)						
Log(dstem)*Mixing proportion doug				0.390*** (0.043)	−0.338** (0.108)						
Local BA						−0.032*** (0.004)	0.014* (0.007)				
Log(dstem)*local BA						0.009*** (0.001)	−0.003 (0.002)				
SPEI*mixture(pure)								0.072* (0.036)	0.045 (0.045)		
Log(dstem)*SPEI*mixture(pure)								−0.019* (0.01)	−0.016 (0.013)		
CVP										−0.016*** (0.002)	−0.022*** (0.003)
log(dstem)*CVP										0.003*** (0.0002)	0.002*** (0.0003)
Constant	−0.471 (0.144)	−0.104 (0.253)	-1.809*** (0.26)	0.300 (0.277)	−2.773*** (0.215)	1.105*** (0.288)	−3.290*** (0.384)	−0.019 (0.264)	−1.590*** (0.259)	8.403*** (1.259)	10.091** (2.000)

Table 3 continued

Equation											
Dependent variable:	log(droot)										
	Tree allometry pattern			Competition/density/mixing proportion				Humidity response			
	5	6	6	7	7	8	8	9	9	10	10
Independent variable:	EB - DF	Douglas-fir	E.beech	Douglas-fir	E.beech	Douglas-fir	E.beech	Douglas-fir	E.beech	Douglas-fir	E.beech
Number of observations	4433	2512	1921	2512	1929	2512	1929	1994	1482	2512	1929

The numbers in brackets represented the standard deviation of the independent variables (*EB* E. beech, *DF* Douglas-fir, *SPEI* Standardized precipitation-evapotranspiration index, *Local BA* Local basal area, *CVP* Paterson index)

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

stands. The response of Douglas-fir to SPEI in Fig. 6 is almost invisible but this is a problem of scale. However small, the model shows a significant relationship between SPEI and root stem allometry. Obviously, the reaction to short-term humidity fluctuations is very small, but existent. It is all the more surprising that one can separate the reaction to short-term humidity from other effects.

The linear mixed models of the short-term humidity variation (Eq. 9) were significant as well as the models of mixture and local BA (Eqs. 7, 8). Nevertheless, it can be seen that mixture and local BA had a stronger influence on allocation than the SPEI. Only for European beech in mixed stands, a variation of humidity seems to have a large effect.

To clarify, if drought causes contrary responses in root and stem growth or if the allocation of resource is more reduced for one than for the other, we pictured the course of detrended root and stem growth (Fig. 7). A dendrochronological parameter which compared the course of two chronologies against each other is the 'Gleichläufigkeit' (Eckstein and Bauch 1969). The Gleichläufigkeit respects the direction of index (ups and downs) and not the strength of deflection. The Gleichläufigkeit for the mean root and stem growth index was 0.76 between 1990 and 2013. This means 76% of the ups and downs are equal. The year-to-year agreement of root and stem reduced with 1990 because of the decreased number of root chronologies (see also Fig. 1). The 'Gleichläufigkeit' let us suggest that root and stem growth do not have a contrary course.

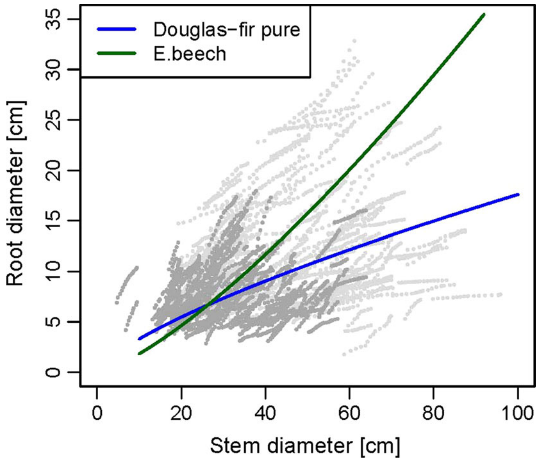

Fig. 2 Root–stem allometry from fitted models according to Eq. 5, and the related, measured, and reconstructed diameter for Douglas-fir (*grey*) and European beech (*dark grey*). Model coefficients can be seen in Table 3

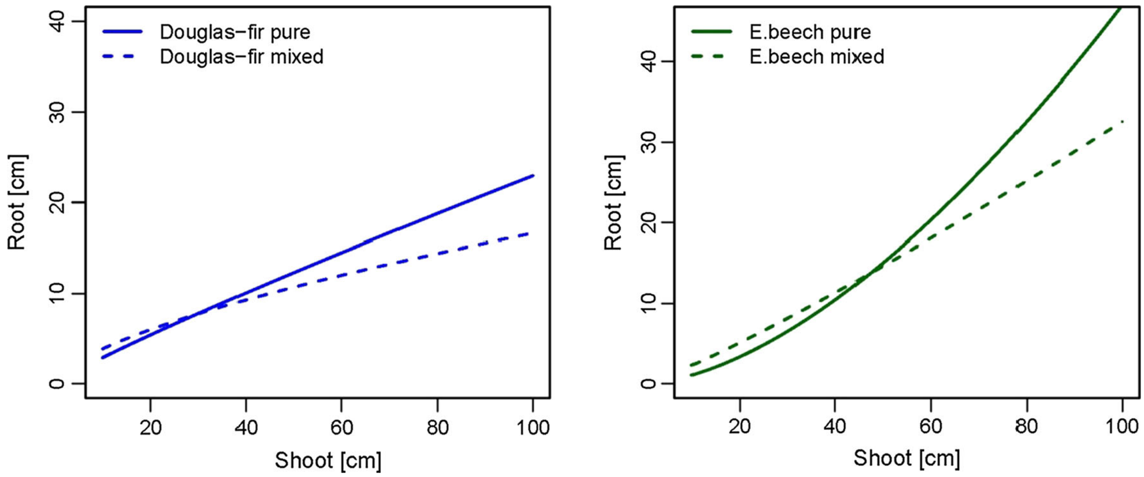

Fig. 3 Root–stem allometry in dependence of stand level mixing type for Douglas-fir (*left*) and European beech (*right*). Model coefficients can be seen in Table 3 and Eq. 6

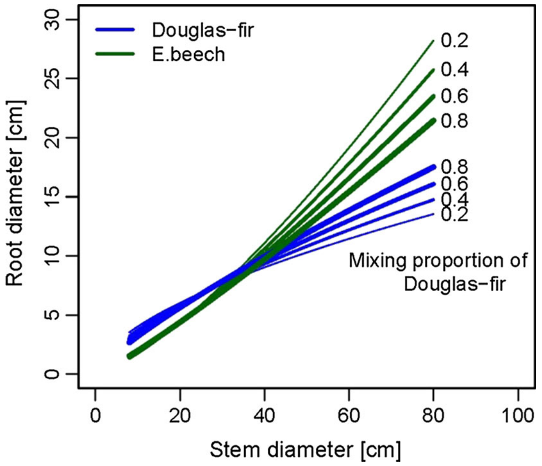

Fig. 4 Root–stem allometry in dependence of interspecific competition represented by mixing proportion of the own species for Douglas-fir (*blue*) and European beech (*green*) related to Eq. 7. Mixing proportions are to be understood as shares of Douglas fir in the local BA. Model coefficient are shown in Table 3

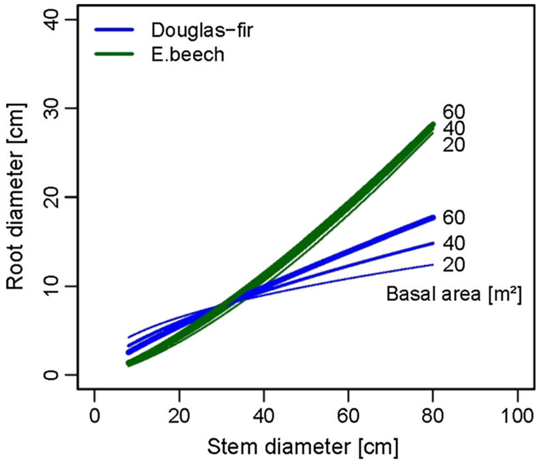

Fig. 5 Root–stem allometry in dependence of local stand density for Douglas-fir (*blue*) and European beech (*green*) according to Eq. 8. Density is represented by local BA which is defined as surrounding basal area of a individual tree. Model coefficients are shown in Table 3

Influence of long-term humidity variation

In comparison with the influence of short-term humidity, the effect of site conditions, expressed through the CVP index, on tree allometry was much more pronounced. The CVP index at the driest site was 497 (ecoregion 'Fränkische Platte'). The site with the most favorable growing conditions (ecoregion 'Spessart') had a CVP index of 676. The models of both species indicate that the allometry of trees is strongly determined by the site-specific growth conditions (Fig. 8, Eq. 10). Douglas-fir as well as European beech invests in root growth under harsher conditions at the expense of stem growth compared to more favorable sites. This response was especially pronounced for European beech.

Discussion

Patterns in root–stem allometry

The study investigated the allometric relationship of root and stem growth. We could show that the allometric exponent was influenced by tree species mixture, mixture proportion, stand density, short-term humidity variation, and long-term site-specific humidity. Thereby, the strength of the influence differed strongly among these variables. The finding of a general variability of the allometric exponent supports the optimal partitioning theory (OPT). This is consistent with results for root–stem allometry from several other studies (Nikolova et al. 2011; Pretzsch et al. 2012b; McConnaughay and Coleman 1999).

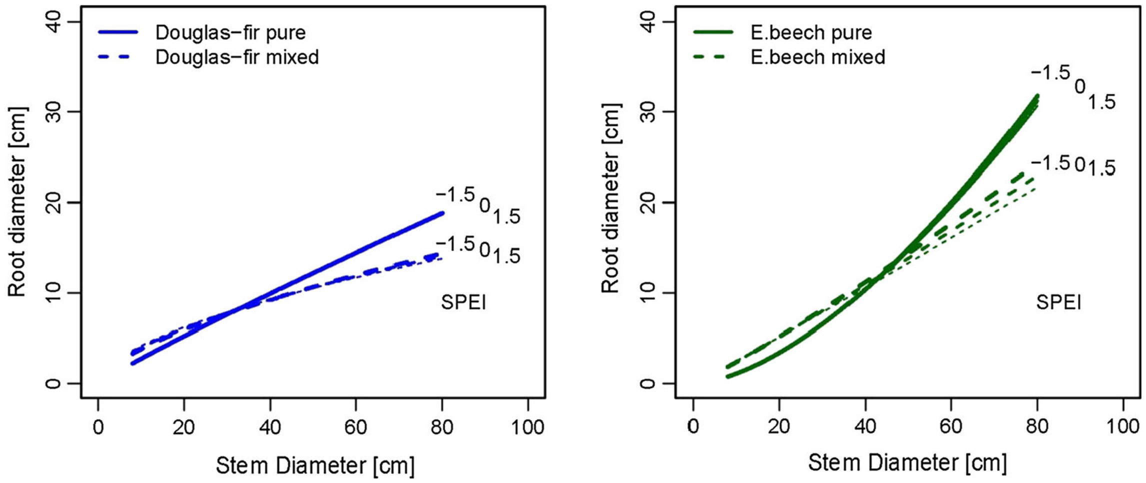

Fig. 6 Root–stem allometry in dependence of humidity in growing period for Douglas-fir (*left*, *blue*) and European beech (*right*, *green*) according to the fitted Eq. 9 Humidity is represented by standardized precipitation-evapotranspiration index SPEI (model predictions shown for SPEI = −1.5, 0, 1.5, corresponding SPEI values et the ends of the lines), although the SPEI effects are very small they turned out significant nevertheless. Model coefficients are shown in Table 3

The pattern of allocation between root and stem was similar for mixture, density and humidity. More favorable conditions lead to a pronounced growth of stem, whereas unfavorable conditions increase growth of roots (see Fig. 9).

Methodological restrictions

Basis of the study is the comparison of stem diameter in breast height and two prominent coarse roots per tree. This method has several advantages to total tree excavation (non-destructive, less resource-demanding, allows sampling mature trees). Nonetheless, the results are diameter comparisons. They cannot be equated with the measured biomasses of above and belowground tree compartments, because in contrast to biomass, they describe resource allocation only indirectly. Another related problem is that we do not know the total number of roots. Therefore, it might be that some of the observed effects are only shifts from individual root increment to a number of roots. This would, however, presuppose that trees changed the structure of their root system. Studies about Douglas-fir where entire root systems were excavated, found out that for this species the number of coarse roots per tree is nearly equal (Mauer and Palátová 2012), going along with a uniform structure of the root system (McMinn 1963). It seems

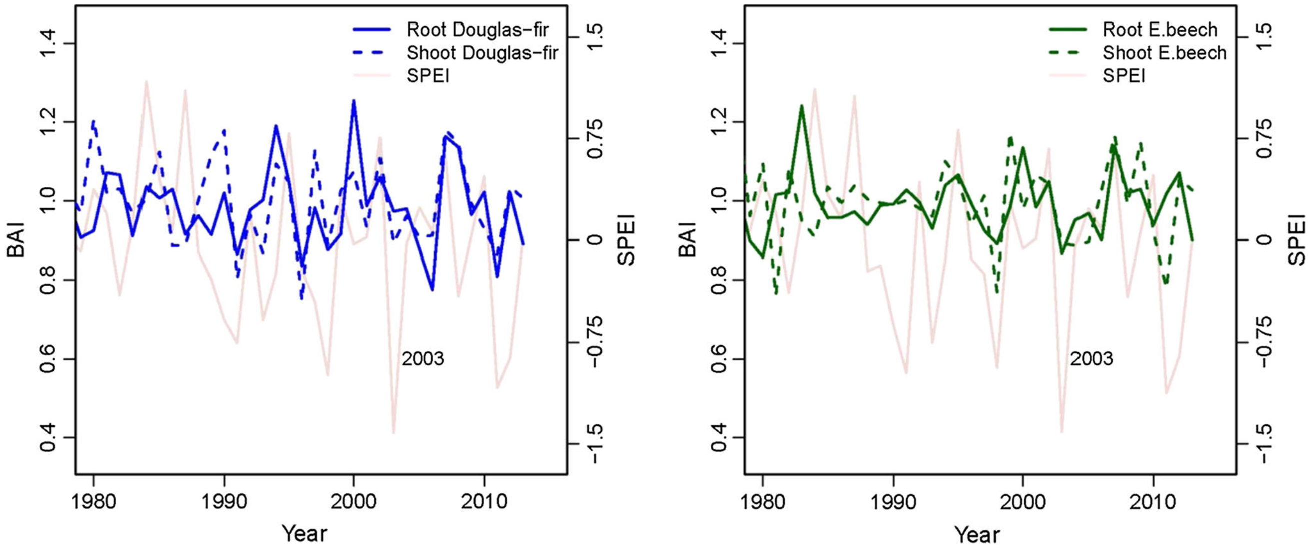

Fig. 7 Detrended root and stem chronologies for Douglas-fir (*blue line*, *left*) and European beech (*green line*, *right*). The standardized precipitation-evapotranspiration index SPEI is added as *red line*. *Labeled* is the extreme drought year 2003

plausible that trees can modify their structural composition within certain limits only. Therefore, we assume that tree species mixing does not lead to significantly different of root numbers.

Several authors found a species-specific, vertical stratification of root systems in mixed stands (Kelty 2006; Forrester et al. 2006a; Bolte and Villanueva 2005). The stratification could be seen in a displacement of fine roots. Two options for this displacement of fine roots in deeper soils are possible: (1) a displacement, realized by sinker roots which branch from the horizontal roots. We should have observed such a reaction when sampling horizontal roots in this study. (2) A greater stratification, in which one species displaces their nutrient uptake into deeper soil layers. This displacement would be generated by an increased growth in heart or tap roots. Douglas-fir as well as European beech feature a heart-root system (Matyssek et al. 2010). Therefore, both species are potentially capable to form a secondary root layer by increase heart-root growth and decrease the growth of the horizontal roots. This would mean that the results we obtained with horizontal roots have to be interpreted in another way, namely, that the mixing effect is not an allocation between roots and stems, but an allocation inside the root system. The retreating species would shift the nutrient transport, respectively, fine root production on these types of roots. Root growth is preferentially favored near the soil surface, because nutrients, soil strength, aeration, and temperature are more favorable there than at depth (Sands and Mulligan 1990). Therefore, stratification without a struggle seems to be not expedient.

A study which was made on a part of our plots found out that out that mixing effects on soil organic carbon and nitrogen concentrations were restricted to the forest floor and the uppermost mineral soil (Cremer et al. 2016). A mixture-induced stratification into deeper soil horizons would cause a change of carbon and nitrogen concentrations in these soil layers compared to pure stands. Hendriks and Bianchi (1995) measured root density and biomasses in pure and mixed stands of Douglas-fir and European beech. Their data indicate that both species did not extend their fine root growth pattern in a soil layer, but they have lower root density in mixed stands in the uppermost soil layer (down to 30 cm) compared to pure stands. This would strengthen the assumption of reduced struggle for resources. The data of Hendriks and Bianchi (1995) show a considerable drop of belowground biomass in the mixed stands (25–50%) below what would have been expected from pure stands. This is consistent with our findings of reduced investment into root growth in mixed stands.

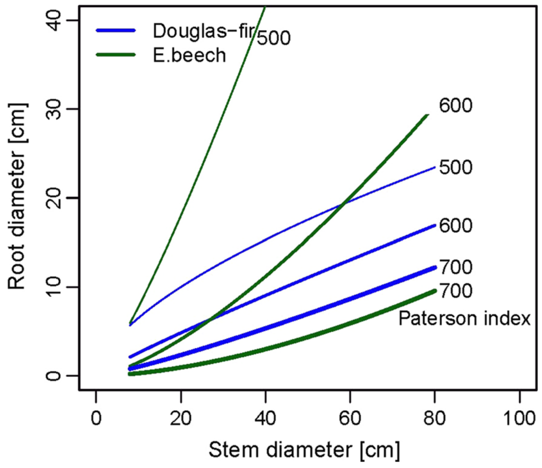

Fig. 8 Root–stem allometry in dependence of long-term site-specific humidity for Douglas-fir and European beech, according to the fitted model after Eq. 10. Humidity at the site is represented by the CVP index by Paterson (1956)

Bolte and Villanueva (2005) bring evidence for a root stratification of mixed stands from European beech and Norway spruce. In contrast to our species of interest, European beech and Norway spruce have different root systems which may trigger the stratification. Nevertheless, they also found a reduced fine root biomass in mixed stands.

Humidity

The sensitivity of root–stem allometry to site conditions was pointed out for lodgepole pine *Pinus contorta* (Dougl. ex. Loud) and Douglas-fir by Comeau and Kimmins (1989) and Keyes and Grier (1981). These studies provided evidence that conifers increase stem growth at the expense of root growth under favorable soil moisture conditions. This is a tree individual adaption to site conditions which develops over decades and may explain the great pronounced influence of humidity on root–stem allometry in our results.

The influence of short-term humidity fluctuations was much weaker but also significant in our data. Plants under short-term water-stress may proliferate roots into unexplored regions of soil to unlock water resources and avoid rapid water depletion (Lavelle and Spain 2005). The short allometry response in the current study accords with results from Pretzsch et al. (2012b) for lodgepole pine. They found a more pronounced root growth in a climatically unfavorable period. Nevertheless, growth potential is not excessive in such short periods. Therefore, the reaction cannot compare with a long-term adaptation of allometry (Fig. 8, Eq. 10) to site conditions. In addition, the possibility for unexplored root space in existing stands is not boundless. Easy accessible and favorable root strata are just occupied. The individual trees are restricted in their ability to respond by hardly variable neighbor constellations. That is, another reason why there is only a small possibility to root

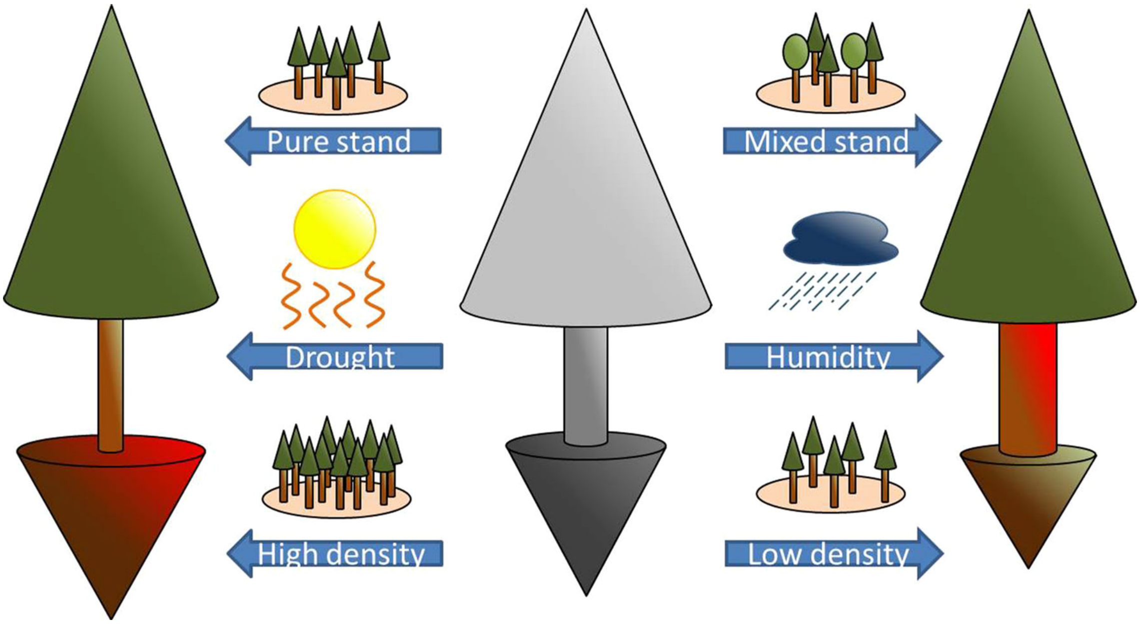

Fig. 9 Comparsion of the factors mixing type, humidity and stand density and their influence on root–stem allometry in schematic representation. A gradient from unfavorable conditions to favorable conditions went from *left* to *right* and shift growth allocation from root to stem. The *schematic trees* represents Douglas-fir as well as European beech

extension. In this context, it is interesting that this effect was most pronounced in European beech mixed stands. In a previous study on the same plots, it was found that European beech had limited access only to the soil water storage (Thurm et al. 2016).

Nevertheless, the general patterns of improved root growth in dryer growing periods do not mean that lateral roots get a growth spurt. Stem increment and root increment show a contrary course. Under unfavorable weather conditions, both tree compartments exhibited a loss of growth but absorbed resources will mainly be invested into root growth. This is conformed with the findings of Nikolova et al. (2011) who worked with Norway spruce (*Picea abies* [L.] Karst.).

Mixture and density

Our data showed that an increasing proportion of the admixed species comes with a higher investment in stem growth. Pretzsch and Biber (2016) provide evidence that maximum tree density is higher in mixed stands. Such a more intense crowding might be possible because of a better or complementary nutrient utilization. Pretzsch et al. (2014) showed significant differences in the nutrient content of Douglas-fir and European beech on the whole-tree level. European beech accumulate more potassium and Douglas-fir more phosphor. The combination of different, species-specific nutrient requirements per hectare enables greater supply for the individual. The mixing of complementary species, such as Douglas-fir and European beech, can likely be seen as an improved resource availability (Bartelink 1998; Thurm and Pretzsch 2016; Thomas et al. 2015). However, an increasing density increased the root–stem ratio in general as also highlighted by Pearson et al. (1984). Species mixing seems to attenuate the competition situation (Piotto 2008).

Our data indicate that increasing age augmented the mixing effect on root–stem allometry. The finding that the mixing effect takes time to appear was also confirmed in other studies (Zhang et al. 2012; Cavard et al. 2011). An increased investment into stem growth with increasing shares of interspecific competition was well pronounced for both species. However, the general comparison of European beech in pure and mixed stands (Eq. 6, Fig. 3) shows that the allocation of stem growth in smaller DBH classes is more pronounced in pure stands than in mixed stand. This allometry first differs when stem size of European beech passes the mean DBH in our plots. Interestingly, we could observe an analogous response in a previous investigation on the same plots, which deals with above-ground biomass productivity (Thurm and Pretzsch 2016). Overyielding of European beech likewise begins when the species reach greater DBH values, in other words, with some delay. Although these responses do not directly match with this study because the study at hand deals with individual tree level data whereas the previous study deals with stand level data, this analogy remains remarkable. When comparing tree allometry in pure and mixed stands, it should be taken into account that DBH distributions in pure and mixed stands might be different (Pretzsch and Schütze 2016).

A previous study about Douglas-fir and European beech in mixture (Thurm and Pretzsch 2016) and studies about mixing other species (Moore et al. 2011; Pretzsch et al. 2016) could show that overyielding and above-ground structural diversity enhanced soil water availability. Due to partitioning of water resources (Jonard et al. 2011; Forrester et al. 2010), mixed stands may not reach a limit of sufficient water supply, while mono-species stands already do. Therefore, the limiting factor, which drives the overyielding, respectively, the height stratification, shifts from soil to light (Forrester 2014; Pretzsch et al. 2016) and root growth can be reduced in mixed stands.

Seemingly, there is a connection between increasingly differing allometry in pure and mixed stands and overyielding in mixed stands with increasing age. Keyes and Grier (1981) found out that total stand net biomass production (above plus belowground) did not change significantly under a varying site condition gradient but only the partitioning between above and belowground biomass. Maybe, the measured overyielding in mixed stands is partly a partitioning of growth into above-ground biomass with comparable total biomass to pure stands. This is of particular interest because carbon-balance based forest models might overestimate the overyielding in mixed stands.

A physiological adaption against drought is likely to shift allocation in favor of the roots (Bréda et al. 2006). This was clearly confirmed in our study. However, this fact alone would also suggest a declined drought tolerance of mixed stands where we found a decreased root–stem ratio. However, it was found in several studies that mixing tree species can improve their drought tolerance (Lebourgeois et al. 2013; Thurm et al. 2016; Pretzsch et al. 2013). Maybe, the complementary water partitioning between the species in mixed stands (Jonard et al. 2011; Forrester et al. 2010; Thurm et al. 2016) or water pumping property of trees (Aranda et al. 2012) improved the drought sensitivity of mixed species by enhancing the general water supply. But these mechanisms in mixed stands are not well understood so far. In addition, the role of mycorrhizae in the water uptake of trees keeps our interpretation open. Lehto and Zwiazek (2011) mentioned that this could also have an effect on water uptake under stress.

We are aware that there might be complex interactions of stand density, mixture and humidity that influence root stem allometry (Elkin et al. 2015; Guillemot et al. 2015). However, this was not the main focus of the study and we refrained from including them in order to avoid over-complex statistical models.

Wind load and root–stem allometry

Wind stability is another reason for trees to change their root–stem ratio (Coutand et al. 2008; Reubens et al. 2009; Gardiner et al. 2016). In general, stronger wind loads result in a shift in favor of the roots. The decreased investment in roots in mixed stands could suggest a higher risk of windthrow in mixed stands. However, a positive influence of species mixture on wind stability of trees was confirmed by several studies (Mayer et al. 2005; Schütz et al. 2006; Schelhaas 2008). Schelhaas (2008), who investigated the influence of wind on European beech and Douglas-fir found out that a lower height-stem diameter ratio (h/d) of Douglas-fir in mixed stands decreased the risk of wind damage. This different h/d ratio results from a changed competition situation in mixed compared to pure stands (Schelhaas 2008; Thurm and Pretzsch 2016). Abetz (1976) concluded that the predominant species in mixture decreased their h/d ratio whereas suppressed species increased their h/d ratio. Reason is the necessity to grow to light. Thurm and Pretzsch (2016) also observed this pattern of predominant Douglas-fir and suppressed beech with modified h/d ratios in mixed stands. Nevertheless, there seems to be no direct link between h/d ratio and root stem allometry, because the response in h/d went contrary, whereas the allometry pattern based on root stem diameters in mixed stands for both species is similar.

A contrasting point should not go unmentioned in this context: e.g., Röhrig et al. (2006) point out, stand canopy roughness strengthens wind turbulences, and increase the risk of wind damages. In mixed stands as covered by our plots, the great tree height difference between Douglas-fir and European beech would thus predispose Douglas-fir.

Conclusions

The morphological plasticity and adaptability of tree stems and crowns to a given competitive status is rather easy to measure and well known. It affects, among others, growth resilience of the stand, stand stability, and wood quality. Compared with this, the plasticity of the stem in relation to roots is much more difficult to access and, therefore, rather unknown. However, of course, it is also highly relevant, for, many important tree and stand traits, e.g., tree and stand stability against wind, below and above-ground carbon storage, resource use, and tree and stand productivity. Although based on rather rough sampling, we could show a high plasticity and adaptability of the root–stem relationship. Further detailed analyses seem desirable, as they might show to what extent this partitioning affects overyielding in mixed stands, as well as their susceptibility to windthrow or drought compared to pure stands.

Author contribution statement ET collected and analyzed data and wrote the manuscript; PB contributed to data analysis and manuscript writing; HP initiated the study, developed the concept, and contributed to writing the paper.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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Soil organic carbon and nitrogen stocks under pure and mixed stands of European beech, Douglas fir and Norway spruce

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ABSTRACT

Numerous studies have addressed tree species effects on forest soil carbon (C) and nitrogen (N); however, knowledge of how and to what extent specific tree species and species mixtures impact forest soil C and N stocks is scarce and inconsistent across soil types. Therefore, we studied three forest sites in Southern Germany differing in parent material, soil properties as well as nutrient and water supply. Each site comprises adjacent groups of pure mature European beech (*Fagus sylvatica*), Douglas fir (*Pseudotsuga menziesii*) and Norway spruce (*Picea abies*) as well as single-tree mixtures of beech with Douglas fir or Norway spruce. To account for tree-species-specific spatial heterogeneity, we sampled the forest floor and mineral soil to a depth of 60 cm at different distances from the trees.

Significant tree species and species mixing effects on soil organic carbon (OC) and N concentrations, C/N ratios and soil OC and N stocks were mainly found in the forest floor and in the uppermost (0–15 cm) mineral soil. Forest floor OC and N stocks and total soil OC stocks were higher under Douglas fir and Norway spruce compared with beech. While tree species effects on soil OC and N were present across sites, the influence of soil type induced variations in their magnitude. The forest floor C/N ratio under Douglas fir was low and comparable with beech in soils developed from nutrient-rich parent material, whereas it was higher and similar to spruce in the soil formed from sandstone. Tree species-specific differences in foliar nutrient concentrations between beech and conifer stands might influence litter decomposition rates among the species and thus modify soil OC and N stocks.

Forest floor OC stocks were significantly higher in mixed beech–conifer stands compared with pure beech, and most often smaller than or similar to pure conifer stands. Forest floor N stocks showed the same tendency, but differences were inconsistent and not always significant across sites. Admixture of beech with Douglas fir or Norway spruce reduced the share of OC and N stored in the forest floor compared with the pure conifer stands and significantly increased mineral topsoil (0–15 cm) OC stocks compared with pure beech stands. Hence, the vertical distribution of OC and N in the soil profile varied depending on the tree species composition. Total soil (forest floor + mineral soil) OC and N stocks of mixtures were similar to pure beech, pure conifers or intermediate depending on site and soil type.

1. Introduction

Forest management in general and tree species choice in particular have various impacts on soil OC and N dynamics and sequestration (Jandl et al., 2007; Vesterdal et al., 2008). Such effects of tree species and species mixtures on forest soil OC and N are thought to be caused by differences in litter decomposition behaviour among tree species, which in turn is affected in large part by soil moisture, soil biological activity and species-specific nutrient contents of foliar litter (Hobbie et al., 2006; Vesterdal et al., 2013). Higher soil moisture, soil biological activity and nutrient contents in aboveground litter are associated with higher decomposition rates in broadleaf compared to conifer forests, the former forming forest floors higher in base cations and pH (Binkley, 1995; Augusto et al., 2015). In contrast, lower nutrient contents and less easily decomposable components in conifer litter lead to the formation of thick forest floors (Hobbie et al., 2006). Prescott (2002) concluded that the more diverse canopy of a mixed stand influences the soil surface by increasing the nutritional diversity of the stand, thereby improving biological diversity and activity. Higher biological activity favours the incorporation of organic material into the mineral soil, where it is protected from external disturbance. In addition, different rooting depths and root

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turnover rates among species impact soil OC and N input and distribution (Finér et al., 2007; Spielvogel et al., 2014). While roots of shallow-rooted tree species (e.g. Norway spruce) predominantly penetrate the organic and uppermost soil layers, roots of tree species like European beech and Douglas fir, which are characterised by a heart-shaped root system, also exploit deeper soil layers (Spielvogel et al., 2014). In general, broadleaf species are characterised by higher root biomass per tree, but species-specific root biomasses vary depending on site fertility (Finér et al., 2007), with highest values for e.g. beech on poor soils and for spruce on more fertile soils. In comparison with the corresponding pure stands, altered rooting patterns in mixed stands caused by belowground interspecific competition, with higher deep-soil root density in beech–Douglas fir mixed stands (Hendriks and Bianchi, 1995) or a shift in beech fine roots towards the subsoil in mixtures with beech (Bolte and Villanueva, 2006), may modify OC and N input and distribution in the soil profile. Furthermore, root chemistry differs significantly among tree species (Thomas et al., 2013), with conifer roots containing lower lignin concentrations and lignin:N ratios than roots of broadleaves (Newman and Hart, 2006), thus promoting root decomposition and turnover in conifer stands. To account for species-specific horizontal OC and N distribution (Prietzel and Bachmann, 2012), the soil sampling design for this study took into account the soil OC and N at different distances from the tree trunks.

More frequent drought, windthrow and bark beetle infestations, induced by climate change, make the currently wide-spread use of Norway spruce (*Picea abies*) in German forestry increasingly problematic (Kölling and Zimmermann, 2007). Coastal Douglas fir (*Pseudotsuga menziesii menziesii*) is considered a suitable alternative forest tree species to Norway spruce in Central Europe. Characterised by fast growth, good wood features and a high tolerance of heat and drought, it is a highly profitable tree species at appropriate sites (Kownatzki, 2011). Thus far, little information is available regarding the ecological effects of Douglas fir cultivation on forest soils in Europe (Schmid et al., 2013), particularly with respect to soil OC and N stocks. There is some evidence that soils (forest floor + mineral soil) under pure European beech (*Fagus sylvatica*) and Douglas fir stands store less OC than soils under pure Norway spruce (Prietzel and Bachmann, 2012). Regarding only the forest floors, there is comprehensive information on smaller OC stocks in forest floors under beech and Douglas fir compared to Norway spruce (Vesterdal and Raulund-Rasmussen, 1998; Mareschal et al., 2010). However, for forest protection and ecosystem stability reasons (Knoke et al., 2008), there is no aim to cultivate pure stands of Douglas fir in Germany as realised in the past for Norway spruce, but rather to introduce it into established stands of native tree species, particularly European beech, on a small-scale (Brosinger and Baier, 2008). Compared with monocultures, the establishment of mixed stands promotes ecosystem stability by decreasing their vulnerability to adverse environmental impacts (Pretzsch, 2005; Jandl et al., 2007). Concerning their ecological characteristics, mixed stands are often believed to be intermediate in comparison with the pure stands of the respective species (Rothe and Binkley, 2001; Augusto et al., 2002); however, knowledge of above- and belowground ecological properties, e.g. productivity, litter decomposition rates, or rooting patterns of specific mixed stands on different soil types is incomplete due to a lack of corresponding studies (Rothe and Binkley, 2001; Pretzsch et al., 2013). Aboveground yield parameters of mixed stands in general (Rothe and Binkley, 2001) and of beech–Douglas fir mixtures in particular (de Wall et al., 1998) are often between those of the respective monocultures. In comparison with pure conifer stands, mixed stands of broadleaf trees with conifers are preferable in terms of C-sequestration (Wiesmeier et al., 2013). However, patterns of tree species mixtures effects on soil OC and N vary depending on climatic factors and soil type.

Thus, as a contribution to close existing knowledge gaps we (1) quantified differences in soil OC and N stocks among pure stands of European beech, Douglas fir and Norway spruce at sites with different geologic parent material, soil type and nutrient status; and (2) investigated whether the establishment of mixed beech–Douglas fir and/or beech–Norway spruce stands at different sites results in increased soil C and N stocks across sites.

2. Material and methods

2.1. Study sites

We studied three forest sites in distinct regions of Bavaria, Southern Germany, that differ in parent material, soil properties and nutrient and water supply (Tables 1 and 2). Site Walkertshofen (WAL) is situated about 30 km south-west of Augsburg, in the Tertiary uplands. According to the International Union of Soil Sciences (IUSS) Working Group World Reference Base (WRB) for Soil Resources (2015), the soil type is classified as Albic Stagnic Luvisol. It has developed from loess on glaciofluviatile gravel (Deckenschotter). Site Ebersberg (EBE) is located about 20 km east of Munich, in the Munich gravel plain. At this site, Dystric Skeletic Cambisols have formed from loess on glaciofluviatile calcareous gravel (Niederterrassenschotter). Site Tännig (TAN) is situated in the Spessart, about 50 km north-west of Würzburg. Here Dystric Endoskeletic Rhodic Cambisols have developed from triassic red sandstone (Buntsandstein). Each site comprises adjacent groups of pure mature beech, Douglas fir and Norway spruce (pure stands) as well as single-tree mixtures of beech with Douglas fir and beech with Norway spruce (mixed stands), both on a small scale. Climate conditions and soil properties of the pure and mixed stands within a site were identical.

2.2. Soil and foliage sampling

For each pure and mixed stand at sites WAL and TAN, 10 pairs of trees were chosen as sampling points (five in spruce and beech–spruce mixtures at site TAN). At site EBE, we chose six pairs of trees as sampling points. The sampling design for this study took into account the soil OC and N at different distances from the tree trunks. At each sampling point, we took soil samples at half the distance between two trees and, in pure stands, at a quarter of the distance from one tree or, in mixed stands, at a quarter of the distance from both trees. This lead to a total of 20 sampling spots in pure and of 30 sampling spots in mixed stands at site WAL. At EBE, we sampled 12 spots in pure and 18 spots in mixed stands. At TAN, we had a total of 20 sampling spots in pure stands of beech and Douglas fir (10 in pure spruce) and of 30 in mixed stands of beech and Douglas fir (15 in beech–spruce mixture). At each sampling spot, the whole organic layer (organic material above the mineral soil; referred to as forest floor) of an area within a $20 \times 20\ \text{cm}^2$ metal frame was sampled completely. Where the forest floor had been collected, samples of the mineral soil were taken with a core auger at depth increments of 0–15, 15–30 and 30–60 cm. The core with a diameter of 5 cm for 0–30 cm and of 2.5 cm for 30–60 cm mineral soil was used to determine fine earth bulk densities as well as mineral soil masses and stocks.

Half-year old needles and leaves were sampled in February 2014 (Douglas fir) and in July/August 2015 (beech) from dominant or co-dominant trees of different species at all sites. In each pure beech stand, we collected leaves from five trees serving as five individual samples for analysis per site; in each pure Douglas fir stand, needles were collected from up to 40 trees and pooled to five composite samples per site. Norway spruce needles were sampled only at site WAL.

Table 1
Important site and stand characteristics.

Site	Walkertshofen	Ebersberg	Tännig
Elevation (m a.s.l.)	602	532	447
MAT (°C)	8.1	8.5	8.1
MAP (mm)	1011	1044	1057
Atmospheric N deposition (kg ha^{-1} a^{-1})[a]	9.8	9.5	4.2
Parent material	Loess on gravel	Loess on gravel	Red Sandstone
Soil type (WRB)	Albic Stagnic Luvisol	Dystric Skeletic Cambisol	Dystric Endoskeletic Rhodic Cambisol
Soil texture	Silty/clay loam	Silty/clay loam	Loamy sand/sandy clay
C/N ratio forest floor (Beech)	21.5	21.1	23.3
Stand age	60	50	90
Tree height (m)			
D	37.1	28.4	44.5
BD	29.1(B)/36.0(D)	23.9(B)/26.5(D)	34.7(B)/40.3(D)
B	26.3	24.2	32.9
BS	27.2(B)/29.8(S)	28.9(B)/31.6(S)	33.9(B)/35.9(S)
S	28.0	30.1	34.0
Basal area (m^2 ha^{-1})			
D	68.9	47.1	85.1
BD	22.4 (B)/34.8 (D)	17.3 (B)/18.3 (D)	27.8 (B)/24.7 (D)
B	34.0	28.9	26.3
BS	23.7(B)/28.3(S)	14.7(B)/21.7(S)	23.8 (B)/25.7 (S)
S	67.7	46.3	48.0

MAT = mean annual temperature, MAP = mean annual precipitation, B = European beech, D = Douglas fir, S = Norway spruce, BD = European beech–Douglas fir mixture and BS = European beech–spruce mixture.

[a] NO_3-N + NH_4-N in field precipitation January–December 2014.

Table 2
Important soil characteristics at the study sites (data from central soil profile within each site).

	Depth (cm)	pH ($CaCl_2$)	BS (%)	Soil texture	Organic C (mg g^{-1})	Total N (mg g^{-1})
Walkertshofen, Albic Stagnic Luvisol						
Ah	0–3	3.1	10.2	Silty loam	49.4	2.26
Eg	3–18	3.7	2.2	Silty loam	9.9	0.56
BtEg	18–43	3.8	6.2	Silty loam	5.4	0.42
Btg	43–73	4.0	36.6	Clay loam	1.9	0.35
Cg	73+	4.0	58.8	Clay loam	2.5	0.38
Ebersberg, Dystric Skeletic Cambisol						
Ah	0–4	3.7	44.7	Silty loam	85.6	5.15
BwAh	4–12	3.9	6.8	Silty loam	30.9	1.63
Bw_1	12–25	4.1	5.5	Silty loam	11.1	0.74
Bw_2	25–43	4.0	8.9	Silty loam	5.5	0.50
CBw	43–65+	3.9	7.9	Clay loam	3.2	0.37
Tännig, Dystric Endoskeletic Rhodic Cambisol						
Ah	0–5	3.1	17.6	Loamy sand	82.8	4.12
Bw	5–34	3.8	3.3	Sandy loam	9.5	0.65
CBw	34–51	3.6	3.2	Loamy clay	2.1	0.48
C	51+	3.5	3.8	Sandy clay	1.1	0.44

2.3. Sample preparation and analysis

For chemical analysis, all soil samples were dried at 40 °C until constant mass. All roots and stones were removed from mineral soil samples before the fine earth (<2 mm) was separated from bulk soil by sieving. Forest floor samples were sieved to separate organic material >2 mm (e.g. coarse roots) and stones from finer organic material. The fine earth of mineral soil samples was weighed and used for estimation of fine earth masses and bulk densities. Forest floor (<2 mm) weight was used to calculate forest floor masses. After homogenisation of all forest floor and mineral soil samples (<2 mm), one subsample each was finely ground with a swing mill for C and N analysis. Leaves and needles were dried at 40 °C for at least 24 h and also finely ground. Foliage nutrient concentrations (e.g. Ca, K, Mg, P) were analysed by ICP-OES (Spectro Genesis, Spectro, Kleve, Germany) after pressure digestion with concentrated HNO_3.

Total C and N concentrations of forest floor, soil and foliage samples were determined in duplicate by dry combustion with an elemental analyser (Euro EA, Hekatech GmbH, Wegberg, Germany). Since the pH values of all soil samples were below 5, we concluded that none of the samples contained carbonate; therefore organic C was considered identical to total C. Soil OC and N stocks in the depth increment samples were calculated from measured C and N concentrations and fine earth bulk density for individual soil depths. Total (forest floor + mineral soil 0–60 cm) soil OC and N stocks were calculated as the sum of soil OC and N stocks, respectively, of the individual soil depths for each sampling spot.

2.4. Statistical analysis

For statistical analysis, we created five groups, representing the three tree species beech, Douglas fir and Norway spruce as well as the two tree species mixtures beech–Douglas fir and beech–Norway spruce. Tree species and species mixtures means and standard deviations of the investigated variables (e.g. OC and N concentrations, OC and N stocks, C/N ratio) were calculated for each site and soil depth separately. As the sampling distance from the tree trunks did not significantly affect soil OC and N within the groups, group means were calculated from all investigated samples within each group. The variables were tested for normal distribution with the Shapiro–Wilk-test. As in some cases the assumption of normal distribution was not met, the Kruskal–Wallis-H-test, followed by pairwise Mann–Whitney-U-tests with a correction factor for multiple pairwise testing, was used to identify statistically significant differences ($p < 0.05$) between tree species and species mixtures. All statistical analyses were conducted using SPSS (Version 22, IBM, Ehningen, Germany).

3. Results

3.1. Forest floor mass and mineral soil bulk density

Tree species and species mixtures effects on forest floor mass (<2 mm) were present, but inconsistent across sites (Table 3). Pure beech stands had significantly lowest forest floor masses compared

Table 3

Forest floor[*] and mineral soil mass [t ha^{-1}; upper rows] and bulk density [g cm^{-3}, lower rows/italics; arithmetic mean value ± standard deviation] in depth increments under different tree species and tree species mixtures at the three study sites. Significant ($p < 0.05$; Kruskal–Wallis-H-test, followed by pairwise Mann–Whitney-U-test with correction factor for multiple comparisons) differences between tree species within a soil depth are marked by different letters.

	Douglas fir	Beech–Douglas fir	Beech	Beech–spruce	Spruce
Walkertshofen					
Forest floor[*]	34.3 ± 16.3**bc**	26.1 ± 14.7**b**	6.5 ± 3.1**a**	22.1 ± 14.8**b**	43.6 ± 10.6**c**
	n.d.	*n.d.*	*n.d.*	*n.d.*	*n.d.*
0–15 cm	1237 ± 196**b**	1082 ± 272**ab**	910 ± 255**a**	1149 ± 260**b**	1137 ± 282**ab**
	0.82 ± 0.13 **b**	*0.72 ± 0.18* **ab**	*0.61 ± 0.17* **a**	*0.77 ± 0.17* **b**	*0.76 ± 0.19* **ab**
15–30 cm	1744 ± 230**b**	1631 ± 218**ab**	1507 ± 240**a**	1724 ± 194**b**	1845 ± 205**b**
	1.16 ± 0.15 **b**	*1.09 ± 0.15* **ab**	*1.00 ± 0.16* **a**	*1.15 ± 0.13* **b**	*1.23 ± 0.14* **b**
30–60 cm	4163 ± 996	3599 ± 936	3585 ± 758	4079 ± 940	4075 ± 727
	1.39 ± 0.33	*1.20 ± 0.31*	*1.19 ± 0.25*	*1.36 ± 0.31*	*1.36 ± 0.24*
Ebersberg					
Forest floor	39.9 ± 14.3**b**	25.9 ± 14.2**b**	9.8 ± 3.7**a**	30.6 ± 15.1**b**	45.9 ± 26.2**b**
	n.d.	*n.d.*	*n.d.*	*n.d.*	*n.d.*
0–15 cm	850 ± 172	874 ± 164	762 ± 163	737 ± 161	777 ± 202
	0.57 ± 0.11	*0.58 ± 0.11*	*0.51 ± 0.11*	*0.49 ± 0.11*	*0.52 ± 0.13*
15–30 cm	1230 ± 232**b**	1113 ± 205**b**	937 ± 217**ab**	851 ± 235**a**	1021 ± 239**a**
	0.82 ± 0.15 **b**	*0.74 ± 0.14* **b**	*0.62 ± 0.14* **ab**	*0.57 ± 0.16* **a**	*0.68 ± 0.16* **a**
30–60 cm	2094 ± 448**ab**	2425 ± 423**b**	2181 ± 538**ab**	1896 ± 412**a**	1554 ± 481**a**
	0.70 ± 0.15 **ab**	*0.81 ± 0.14* **b**	*0.73 ± 0.18* **ab**	*0.63 ± 0.14* **a**	*0.52 ± 0.16* **a**
Tännig					
Forest floor	21.0 ± 12.6**ab**	12.8 ± 10.9**a**	11.3 ± 13.5**a**	32.0 ± 16.1**b**	37.4 ± 17.6**b**
	n.d.	*n.d.*	*n.d.*	*n.d.*	*n.d.*
0–15 cm	923 ± 160	965 ± 375	853 ± 226	819 ± 186	972 ± 186
	0.62 ± 0.11	*0.64 ± 0.25*	*0.57 ± 0.15*	*0.55 ± 0.12*	*0.65 ± 0.12*
15–30 cm	1190 ± 319**ab**	1015 ± 335**a**	1272 ± 349**ab**	1153 ± 349**ab**	1403 ± 273**b**
	0.79 ± 0.21 **ab**	*0.68 ± 0.22* **a**	*0.85 ± 0.23* **ab**	*0.77 ± 0.23* **ab**	*0.94 ± 0.18* **b**
30–60 cm	2697 ± 1013	2192 ± 1239	2559 ± 792	1975 ± 699	2074 ± 632
	0.90 ± 0.34	*0.73 ± 0.41*	*0.85 ± 0.26*	*0.66 ± 0.23*	*0.69 ± 0.21*

[*] Forest floor bulk density could not be determined (n.d.), as we did not measure forest floor depth.

Table 4

Concentrations of soil organic carbon (SOC) [mg g^{-1}; arithmetic mean value ± standard deviation] in forest floor and mineral soil depth increments under different tree species and tree species mixtures at the three study sites. Significant ($p < 0.05$; Kruskal–Wallis-H-test, followed by pairwise Mann–Whitney-U-test with correction factor for multiple comparisons) differences between tree species within a soil depth are marked by different letters.

	Douglas fir	Beech–Douglas fir	Beech	Beech–spruce	Spruce
Walkertshofen					
Forest floor	340.0 ± 54.8**b**	281.4 ± 58.9**a**	304.8 ± 55.0**ab**	293.8 ± 62.2**ab**	406.3 ± 40.4**c**
0–15 cm	29.6 ± 6.6	31.1 ± 8.9	30.3 ± 7.0	31.2 ± 9.0	32.5 ± 7.6
15–30 cm	13.1 ± 5.0	11.8 ± 3.3	12.5 ± 2.8	11.0 ± 3.0	12.1 ± 4.0
30–60 cm	5.8 ± 2.1	5.9 ± 2.6	5.8 ± 1.5	4.8 ± 1.6	5.1 ± 1.8
Ebersberg					
Forest floor	329.0 ± 51.3**bc**	290.9 ± 42.9**ab**	254.7 ± 41.1**a**	274.4 ± 69.1**ab**	374.1 ± 56.7**c**
0–15 cm	57.5 ± 17.1	48.5 ± 8.8	60.6 ± 13.9	54.9 ± 11.9	58.7 ± 21.1
15–30 cm	19.0 ± 9.6	16.2 ± 5.8	17.5 ± 4.0	17.7 ± 6.0	17.0 ± 4.5
30–60 cm	7.0 ± 2.8**ab**	5.8 ± 3.0**a**	5.9 ± 1.6**ab**	9.2 ± 4.4**bc**	14.0 ± 7.9**c**
Tännig					
Forest floor	323.0 ± 62.8**ab**	288.6 ± 66.6**a**	256.8 ± 63.5**a**	355.1 ± 61.4**b**	380.2 ± 45.1**b**
0–15 cm	49.7 ± 13.2	48.1 ± 15.3	40.3 ± 12.4	47.5 ± 11.6	36.6 ± 8.1
15–30 cm	15.9 ± 5.0**ab**	18.1 ± 7.5**a**	12.9 ± 4.7**ab**	15.2 ± 3.6**ab**	12.0 ± 2.6**b**
30–60 cm	5.9 ± 2.2	10.0 ± 8.5	6.8 ± 2.7	6.6 ± 2.5	7.5 ± 4.0

with the pure conifer and mixed beech–conifer stands at WAL and EBE (N-rich site with loamy soil). At TAN (N-poor site with sandy soil), beech was similar to Douglas fir and beech–Douglas fir, whereas pure spruce and beech–spruce mixtures forest floor masses significantly exceeded those under beech. At TAN, forest floor masses differed significantly between the mixtures, while they were similar at WAL and EBE.

Fine earth bulk densities of the mineral soil depth increments were also influenced by tree species and species mixtures, but patterns differed among sites and effects were most often non-significant.

3.2. Forest floor and mineral soil OC and N concentrations

At all sites, forest floor OC concentrations increased in the order: beech < Douglas fir < Norway spruce and were always significantly larger under Norway spruce compared with beech (Table 4). Forest floor N concentrations also increased in the order: beech < Douglas fir < Norway spruce at all sites; but differences between beech and spruce were significant only at EBE (N-rich) and TAN (N-poor) (Table 5). At EBE and TAN, forest floor OC and N concentrations under beech–Douglas fir and beech–Norway spruce mixtures were between those of the respective pure beech and conifer stands. In contrast, at WAL (N-rich), forest floor OC and N concentrations of the mixed stands were significantly lower than those under the respective pure conifer stands. At WAL and EBE, forest floor OC and N concentrations under beech–spruce mixture were similar to that under pure beech, but at the poorer site TAN, they were similar to those under pure spruce. In contrast to the forest floor, tree species and species mixtures effects on mineral soil OC and N concentrations were small and inconsistent between sites (Tables 4 and 5).

Table 5
Concentrations of total nitrogen [mg g^{-1}; arithmetic mean value ± standard deviation] in forest floor and mineral soil depth increments under different tree species and tree species mixtures at the three study sites. Significant ($p < 0.05$; Kruskal–Wallis-H-test, followed by pairwise Mann–Whitney-U-test with correction factor for multiple comparisons) differences between tree species within a soil depth are marked by different letters.

	Douglas fir	Beech–Douglas fir	Beech	Beech–spruce	Spruce
Walkertshofen					
Forest floor	14.99 ± 2.17**a**	12.48 ± 2.25**b**	14.22 ± 2.68**ab**	12.52 ± 2.10**b**	15.89 ± 1.67**a**
0–15 cm	1.53 ± 0.34	1.61 ± 0.43	1.79 ± 0.39	1.73 ± 0.44	1.55 ± 0.35
15–30 cm	0.77 ± 0.17**ab**	0.71 ± 0.19**b**	0.84 ± 0.11**a**	0.74 ± 0.22**ab**	0.70 ± 0.16**b**
30–60 cm	0.49 ± 0.11	0.48 ± 0.13	0.53 ± 0.11	0.46 ± 0.10	0.45 ± 0.10
Ebersberg					
Forest floor	14.97 ± 1.88**b**	13.59 ± 1.86**ab**	12.06 ± 1.99**a**	13.01 ± 3.20**ab**	15.17 ± 1.78**b**
0–15 cm	2.70 ± 0.85	2.48 ± 0.50	3.06 ± 0.61	2.78 ± 0.52	2.97 ± 0.89
15–30 cm	1.05 ± 0.41	0.94 ± 0.28	0.94 ± 0.20	1.01 ± 0.24	0.77 ± 0.29
30–60 cm	0.52 ± 0.10**a**	0.46 ± 0.12**a**	0.47 ± 0.08**a**	0.69 ± 0.21**b**	0.86 ± 0.34**b**
Tännig					
Forest floor	12.94 ± 2.55**ab**	12.25 ± 2.76**a**	10.97 ± 2.47**a**	16.46 ± 2.57**c**	15.55 ± 1.58**bc**
0–15 cm	2.02 ± 0.62	2.18 ± 0.79	1.92 ± 0.68	2.00 ± 0.51	1.60 ± 0.33
15–30 cm	0.75 ± 0.18	0.88 ± 0.31	0.73 ± 0.18	0.70 ± 0.13	0.65 ± 0.10
30–60 cm	0.47 ± 0.10	0.55 ± 0.35	0.54 ± 0.15	0.45 ± 0.10	0.48 ± 0.10

3.3. C/N ratio

At the N-rich sites WAL and EBE, forest floor C/N ratios were significantly larger under pure Norway spruce than under beech and Douglas fir, which did not differ significantly from each other (Fig. 1). The forest floor C/N ratio under Douglas fir was larger at TAN compared with WAL and EBE and it was similar to that of Norway spruce. With the exception of the beech–spruce mixture at TAN, forest floor C/N ratios under beech–Douglas fir and beech–Norway spruce mixtures were between those of the respective beech and conifer stands. However, while beech–spruce differed significantly from spruce at all sites, no significant differences were present between Douglas fir and beech–Douglas fir. Mineral topsoil (0–15 cm) C/N ratios did not show any systematic tree species or species mixtures effects (Fig. 1). In some cases they were similar to those of the respective beech stand, in other cases to those of the respective conifer stands.

3.4. Forest floor and mineral soil OC and N stocks

At all sites, total (forest floor + 0–60 cm mineral soil) soil OC stocks were significantly lower under pure beech compared with Douglas fir and Norway spruce, where soils stored similar OC amounts (Fig. 2a). Total soil OC stocks of beech–Douglas fir and beech–spruce mixtures were between those of the respective pure beech and conifer stands, and beech–Douglas fir mixtures stored as much soil OC as beech–Norway spruce mixtures. However, the three sites had different patterns of soil OC stock levels under mixed vs. pure stands: (1) at WAL, beech–Douglas fir as well as beech–Norway spruce mixed forests had intermediate SOC stocks compared with pure beech or pure conifer stands, which differed significantly from the SOC stocks of both the beech and conifer stands. (2) In contrast, at EBE, the SOC stock under mixed beech–conifer forests was similar to that under pure beech, while (3) at TAN, the SOC stocks under both beech–conifer mixtures were similar to those under the respective pure conifer stands.

At all sites, total soil N stocks were highest under Douglas fir and Norway spruce compared to beech (Fig. 3a). However, differences among tree species and species mixtures were significant only at WAL. At that site, the total soil N stock under the beech–spruce mixture was significantly larger than that under pure beech and similar to spruce, whereas the beech–Douglas fir total soil N stock was similar to that of beech and smaller than that under Douglas fir.

Forest floor OC stocks were always highest under Norway spruce and Douglas fir and smallest under beech (Fig. 2). At all sites, forest floor OC stocks under mixed beech–conifer stands, irrespective whether the conifer was Norway spruce or Douglas fir, always significantly exceeded those of the respective pure beech stands (exception beech–Douglas fir at site TAN). Forest floor OC stocks under

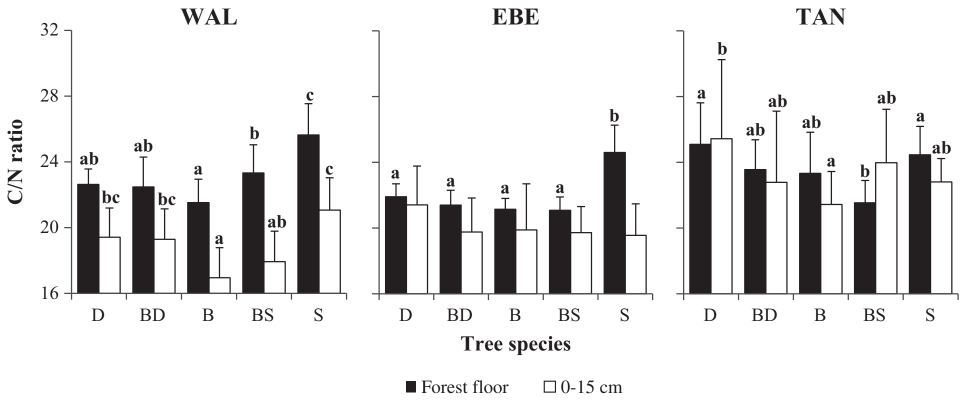

Fig. 1. C/N ratio (arithmetic mean value + standard deviation) in forest floor and mineral topsoil (0–15 cm) under different tree species and tree species mixtures at sites Walkertshofen (WAL), Ebersberg (EBE) and Tännig (TAN). Significant ($p < 0.05$; Kruskal–Wallis-H-test, followed by pairwise Mann–Whitney-U-test with correction factor for multiple comparisons) differences between tree species within a soil depth are marked by different letters. B = European beech, D = Douglas fir, S = Norway spruce, BD = European beech–Douglas fir mixture and BS = European beech–spruce mixture.

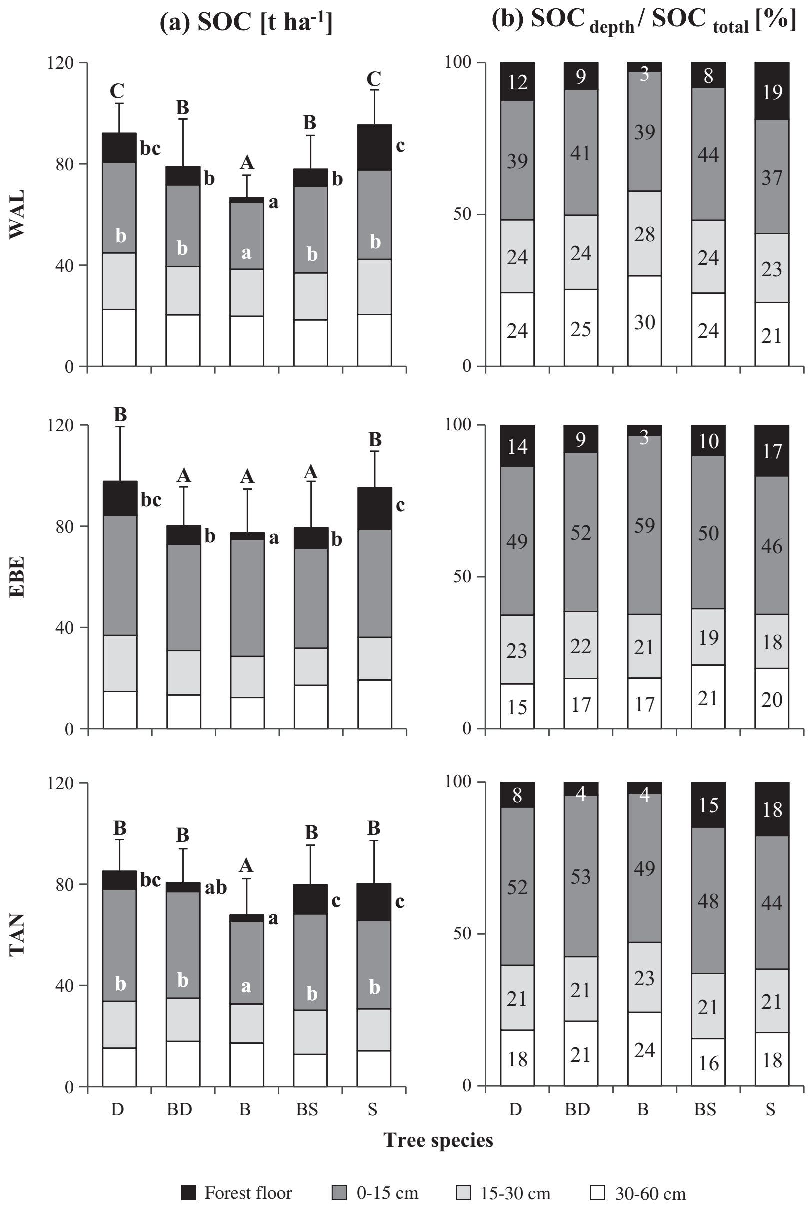

Fig. 2. (a) Stocks of soil organic carbon (SOC) [t ha^{-1}; left panel] of individual soil depths (arithmetic mean value) and total soil (arithmetic mean value + standard deviation). Significant ($p < 0.05$; Kruskal–Wallis-H-test, followed by pairwise Mann–Whitney-U-test with correction factor for multiple comparisons) differences between tree species are marked by different letters: lowercase letters for individual soil depths and capitals for total soil, (b) percentage share of SOC stocks of individual soil depths based on total SOC stock [%; right panel] under different tree species and tree species mixtures at study sites Walkertshofen (WAL), Ebersberg (EBE) and Tännig (TAN). B = European beech, D = Douglas fir, S = Norway spruce, BD = European beech–Douglas fir mixture and BS = European beech–spruce mixture.

the mixtures showed the same site-dependent patterns as reported for total SOC stocks; however, the patterns were less pronounced. Forest floor OC stocks (as well as the contribution of the forest floor to the total soil OC stock) under the mixtures were similar at WAL and EBE (N-rich sites), but were significantly higher under beech–spruce than under Douglas fir at TAN (N-poor site). Moreover, the share of OC stored in the forest floor was significantly lowest under pure beech (WAL and EBE; Fig. 2b); at site TAN, beech only differed significantly from spruce and beech–spruce and was similar to Douglas fir and beech–Douglas fir. The share of OC stored in the forest floor under Norway spruce always significantly exceeded that under the beech–Douglas fir mixture, while it was only significantly higher than beech–spruce at site WAL.

Forest floor N stocks were significantly smaller under beech than under Norway spruce and beech–Norway spruce mixture (all sites; Fig. 3a). Douglas fir and beech–Douglas fir stored significantly more N in their forest floor than pure beech (with the exception of site TAN, which showed the same tendency). A tendency for larger forest floor N stocks under spruce compared with Douglas fir as well as for larger forest floor N stocks under the conifers compared with the respective beech–conifer stands could be observed at all sites. However, in no case differences were significant. Mixed beech–Douglas fir and beech–Norway spruce stands did not differ significantly from each other, both forming almost identical forest floor N stocks. An exception was site TAN, where the beech–Douglas fir stand had smaller forest floor N stocks and, due to similar total soil N stocks, also stored proportionally less OC in the forest floor than beech–Norway spruce (Fig. 3b).

At WAL and TAN, the mineral topsoil (0–15 cm) OC stock was significantly smallest under beech compared with the pure conifer and mixed beech–conifer stands (Fig. 2a). Similarly, mineral topsoil N stocks were significantly smallest under beech compared with

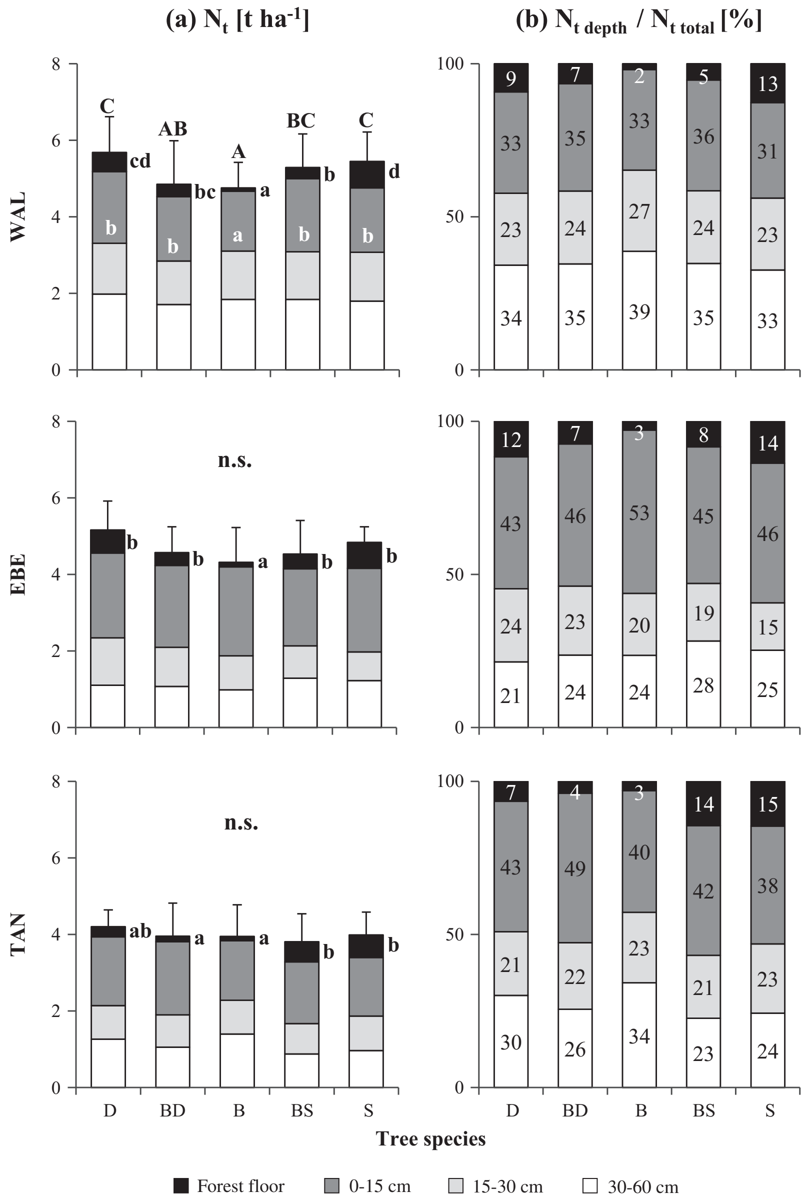

Fig. 3. (a) Stocks of total nitrogen (N_t) [t ha^{-1}; left panel] of individual soil depths (arithmetic mean value) and total soil (arithmetic mean value ± standard deviation). Significant ($p < 0.05$; Kruskal–Wallis-H-test, followed by pairwise Mann–Whitney-U-test with correction factor for multiple comparisons) differences between tree species are marked by different letters: lowercase letters for individual soil depths and capitals for total soil, (b) percentage share of SOC stocks of individual soil depths based on total SOC stock [%; right panel] under different tree species and tree species mixtures at study sites Walkertshofen (WAL), Ebersberg (EBE) and Tännig (TAN). B = European beech, D = Douglas fir, S = Norway spruce, BD = European beech–Douglas fir mixture and BS = European beech–spruce mixture.

pure conifer stands and the beech–conifers mixtures (Fig. 3a). No significant differences between mineral topsoil OC and N stocks of Douglas fir, Norway spruce and the beech–conifer mixtures were present.

3.5. Foliage nutrient concentrations

Nutrient concentrations (N, Ca, Mg, K) in half-year old needles and leaves were affected by tree species across sites, except for P concentrations, which did not differ significantly between tree species (Table 6). N concentrations in foliage of beech were significantly higher than in Douglas fir (all sites) and Norway spruce (one site) needles. Similarly, beech leaves had higher concentrations of Ca than Douglas fir needles. However, this difference was only significant at two sites. Mg and K concentrations were significantly higher in Douglas fir compared with Norway spruce needles, while concentrations of N, P and Ca were similar for both conifer species. Further tree species effects on foliage Mg and K concentrations were inconsistent across sites.

4. Discussion

4.1. Tree species effects on forest floor and mineral soil OC and N in pure stands

At all sites, forest floor OC concentrations and stocks were significantly smaller under beech compared with Norway spruce, while those of Douglas fir stands were intermediate (though not significantly different from spruce), confirming earlier results of Raulund-Rasmussen and Vejre (1995). In contrast to previous findings (Vesterdal et al., 2008, 2013), smallest forest floor OC stocks under beech were not accompanied by larger OC stocks in the

Table 6
Nutrient concentrations in half-year old needles and leaves [mg g^{-1}; arithmetic mean value ± standard deviation] in dominant or co-dominant trees of different species at the study sites. Norway spruce foliage litter was only sampled at site Walkertshofen (WAL) during previous investigations. Significant ($p < 0.05$; Kruskal–Wallis-H-test, followed by pairwise Mann–Whitney-U-test with correction factor for multiple comparisons) differences between tree species within a soil depth are marked by different letters.

	N	P	Ca	Mg	K
Walkertshofen					
Beech	22.32 ± 1.81**a**	0.99 ± 0.12**a**	3.86 ± 0.77**a**	0.93 ± 0.16**a**	4.96 ± 0.77**a**
Douglas fir	12.81 ± 0.85**b**	1.13 ± 0.30**a**	3.54 ± 0.50**a**	1.41 ± 0.24**b**	4.91 ± 0.92**a**
Norway spruce	14.16 ± 2.31**b**	1.14 ± 0.29**a**	2.98 ± 0.41**a**	0.78 ± 0.09**a**	2.96 ± 0.62**b**
Ebersberg					
Beech	20.25 ± 1.82**a**	1.05 ± 0.15**a**	7.87 ± 0.71**a**	1.61 ± 0.50**a**	3.93 ± 0.46**a**
Douglas fir	13.34 ± 0.90**b**	1.20 ± 0.13**a**	3.47 ± 0.57**b**	1.26 ± 0.22**a**	4.49 ± 0.20**a**
Tännig					
Beech	18.12 ± 2.08**a**	1.48 ± 0.21**a**	6.15 ± 1.20**a**	1.07 ± 0.24**a**	7.93 ± 1.25**a**
Douglas fir	12.61 ± 1.39**b**	1.48 ± 0.30**a**	4.12 ± 0.78**b**	1.62 ± 0.13**b**	5.34 ± 0.79**a**

mineral topsoil (0–15 cm). Similarly, forest floor N stocks were always significantly smallest under beech compared with Douglas fir (N-rich sites) and Norway spruce. In comparison with broadleaf tree species, conifers tend to store a relatively higher amount of OC in a labile form in the organic layer (Wiesmeier et al., 2013); accordingly, in our study, they also had highest forest floor N stocks at all sites. Forest floor thickness varies among tree species, being higher under spruce, intermediate under Douglas fir and lowest under beech (Augusto et al., 2003). Forest floor masses (<2 mm) in our study resemble this order, with decreasing masses from spruce over Douglas fir to beech (Table 3).

Such tree species effects on forest floor OC and N are thought to be caused by differences in decomposition behaviour among tree species (Vesterdal et al., 2013). As tree species grown at the same site hardly differ in their amount of litterfall (Augusto et al., 2002; Hansen et al., 2009), it is litter chemistry, predominantly lignin and Ca contents (Reich et al., 2005; Hobbie et al., 2006), and C/N ratio that drive litter decomposition (Vesterdal et al., 2013). Spruce litter is richer in lignin than beech litter, hampering litter decomposition; whereas Douglas fir litter contains less lignin and higher amounts of cellulose (Kubartova et al., 2009), favouring higher rates of decomposition. Mareschal et al. (2010) found that forest floor Ca concentrations increase in the order: Norway spruce < Douglas fir < European beech. In our study, forest floor exchangeable Ca concentrations, base saturation and pH increased in the same order (unpublished data; in prep.). Highest forest floor pH under beech compared with Douglas fir and Norway spruce were found across fertility gradients of sites (Raulund-Rasmussen and Vejre, 1995). They also found Ca accumulation in forest floors being higher in beech and in Douglas fir than in spruce stands on a sandy site, while spruce tended to have highest Ca accumulation on a loamy soil.

Foliage nutrient contents (*e.g.* Ca, Mg, K, N and P) of broadleaf species ecosystems can be many times higher than those of conifer species ecosystems (Augusto et al., 2002), promoting soil biological activity and accelerating litter decomposition. In our study, Ca concentrations in half-year old foliage were significantly higher under beech compared with Douglas fir (EBE and TAN) and tended to be higher than Norway spruce and Douglas fir at WAL. Highest N concentrations in foliage of beech compared with Norway spruce (site WAL) and Douglas fir probably further favoured litter decomposition under beech compared to the conifers.

Besides differences in litter chemistry, differing rooting patterns among beech, Douglas fir and Norway spruce might have caused the differentiation between beech and the conifers in terms of soil OC and N distribution in the soil profile (Spielvogel et al., 2014). Production of soil OC by (fine) root turnover and root exudates, which is dependent on rooting depth and distribution, is a major pathway for OC input to mineral soil (Rothe et al., 2002; Rumpel and Kögel-Knabner, 2011). According to Finér et al. (2007), fine root biomass in soils is higher under beech than under conifers. This was confirmed by Konopka (2009), who found less fine roots under spruce than under beech in an acidic soil, whereas root turnover was higher in spruce than in beech stands. Lower lignin concentrations and lignin:N ratios in roots of conifers compared to roots of broadleaves (Newman and Hart, 2006) might promote root decomposition and turnover in conifer stands. In contrast, Thomas et al. (2013) reported that Douglas fir roots lignin:N ratios were higher than those of beech and refer to slower decomposition of Douglas fir compared with beech roots. Additionally, the distribution of OC in the soil profile is particularly affected by tree species-specific root systems. While the fine roots of Norway spruce are almost entirely restricted to the forest floor and uppermost soil layer, beech and Douglas fir roots, forming a heart-shaped root system, also penetrate deeper soil layers (Jandl et al., 2007; Spielvogel et al., 2014), thus potentially increasing the mineral soil OC stock.

In our study, the differences in forest floor C/N ratios among species were site-dependent. In particular, the forest floor C/N ratio under Douglas fir was variable depending on the site. For example, in loamy soils developed from nutrient-rich parent material, it was similar to that of beech, whereas in the sandy soil formed from nutrient-poor sandstone, it was higher and similar to the forest floor C/N ratio under spruce. In other studies encompassing all three tree species beech, Douglas fir and Norway spruce at comparable sites, there is some evidence that Douglas fir is intermediate between beech and spruce in terms of forest floor C/N ratio (Augusto et al., 2002). Douglas fir is an exception among conifer tree species (Prietzel and Bachmann, 2012) as it produces, compared with Norway spruce (humus form mor), a more favourable humus form (moder) with lower (−10 ± 3%) C/N ratios (Thomas and Prescott, 2000; Mareschal et al., 2010).

After replacement of Norway spruce by Douglas fir, Prietzel and Bachmann (2012) reported a significant increase in total and mineral soil N stocks that did not occur after replacement by European beech. Our results are not in line with these findings, as total and mineral soil N stocks do not differ significantly between Douglas fir and Norway spruce. However, forest floor N concentrations under pure Douglas fir seemed to be more affected by the inherent N supply of the ecosystem than N concentrations under Norway spruce. Lower foliar N concentrations of beech and Douglas fir and lower field N-deposition (Table 5) compared with the other sites, indicate that TAN is characterised by a rather poor ecosystem N status. With sufficient N availability (sites WAL and EBE), Douglas fir maintains high forest floor N concentrations and stocks and a comparatively favourable C/N ratio (<25), which generally promote soil fertility. On the other hand, a combination of a low C/N ratio and high potential N mineralisation under Douglas fir (Zeller et al., 2007; Trum et al., 2011) poses an elevated risk of N output via nitrate leaching, particularly after thinning or harvesting, insect calamity or windthrow. At the N-rich sites WAL and

EBE, forest floors under pure Douglas fir were richer in N, as expressed by a lower C/N ratio (22.6 and 21.9), than forest floors under Norway spruce (⩾25). In contrast to beech, and especially spruce, the Douglas fir forest floor C/N ratio at TAN was highest (25.1). Studying Douglas fir in the US, Edmonds (1980) found that mineralisation of N from Douglas fir litter occurs when the C/N ratio is below 29, while Prescott et al. (2000) reported that net N mineralization in Douglas fir forest floors occurs with a C/N ratio below 35. In laboratory incubation experiments, Douglas fir forest floor featured the highest rates of N mineralisation and N concentrations and the lowest C/N ratio, in comparison with paper birch and lodgepole pine (Thomas and Prescott, 2000). They also found lowest lignin concentrations under Douglas fir, and suggested that mineralised N remains in its inorganic form rather than being incorporated into SOM. Inorganic N, usually in the form of nitrate, is mobile in soils. This could either promote N availability under Douglas fir or, in the case of ecosystem N saturation, result in a higher potential risk of N leaching and loss from the soil. Increasing soil nitrate concentrations with increasing clay content, reported by Callesen et al. (1999), indicate a higher risk of nitrate leaching from fine textured compared with coarse textured soils. According to Gundersen et al. (1998), conifer stands with a forest floor C/N ratio between 25 and 30 feature a "moderate risk" of nitrate leaching from soil, while values <25 are related to a "higher risk" of nitrate leaching. Prietzel and Bachmann (2011) investigated the subsoil seepage water at four sites in Southern Bavaria (comparable with our sites), observing that nitrate leaching from the soil was strongly elevated under Douglas fir compared with beech growing at the same site and almost similar to high nitrate leaching under Norway spruce. In contrast, at TAN, on a soil developed from N-poor sandstone, the risk of nitrate leaching might be smaller because of the higher C/N ratios of the forest floor (25.1 ± 2.5) and mineral topsoil (25.4 ± 4.8) and probably lower clay content, but is still not negligible as compared with the thresholds of N mineralisation and of nitrate leaching when the C/N ratio is <25 (Gundersen et al., 1998; MacDonald et al., 2002; Borken and Matzner, 2004). We therefore highlight the importance of considering site and soil characteristics to address possible consequences of tree species, and more precisely of Douglas fir, cultivation.

4.2. Tree species mixtures effects on forest floor and mineral soil OC and N

As mentioned above, pure stands of beech are characterised by relatively small total soil OC stocks, whereas conifers, which have higher total soil OC storage, accumulate it to a large extent in the forest floor. Soils under pure beech stored substantially less OC (all sites) and N (one site) than those under Douglas fir and Norway spruce at the same sites. In our study, admixture of Douglas fir or Norway spruce to beech enlarged forest floor OC (all sites) and N (N-rich sites) stocks compared to pure beech. At the same time, it reduced the share of OC and N stored in the forest floor compared with the pure conifer stands and significantly increased mineral topsoil (0–15 cm) OC stocks compared with pure beech stands. Accordingly, forest floor masses (<2 mm), but not mineral soil bulk densities and masses, were significantly higher in mixtures than in beech stands (Table 3). Storage of OC and N in the mineral soil probably leads to a higher stabilisation of these compounds due to association with soil minerals and protection within aggregates (von Lützow et al., 2006). In general, forest floor and total soil OC and N stocks under mixed beech–Douglas fir and beech–spruce were within the range spanned by the respective pure stands; they resembled beech at site EBE and reached the level for conifers at site TAN. Inconsistent (synergistic, linear and antagonistic) effects of tree species mixtures on soil OC and N stocks have been reported (as reviewed by Rothe and Binkley, 2001) and depend on the specific species and soil type. Total soil N stocks of broadleaf–conifer mixtures were intermediate between those of the respective pure stands; however, soil N partitioning into forest floor and mineral soil might deviate from that pattern. Mixed stands of, for example, European beech and Norway spruce might favour lower N storage in the forest floor and increased N storage in the mineral topsoil when compared with a pure conifer stand (Rothe, 1997). Berger et al. (2002) found SOC stocks under pure spruce stands to be higher than those under beech–spruce mixtures. The tree species effects in their study also interacted with soil type, with a larger effect observed on a nutrient-poor soil. The admixture of easily decomposable leaf litter with more recalcitrant needle litter might induce faster decomposition of the latter in mixed stands compared with pure conifer stands by providing an additional available nutrient source for soil biota (Saetre et al., 1999), thereby reducing forest floor mass. Prescott (2002) concluded that the more diverse canopy of a mixed stand influences the soil surface by increasing the nutritional diversity of the stand, thereby altering and improving biological diversity and activity. This might be a possible reason for smaller forest floor and total soil OC stocks under beech–spruce compared with pure spruce stands at N-rich sites. However, this feature was noticed for the beech–Douglas fir mixture. Furthermore, lower C/N ratios in forest floors under beech–spruce mixtures (21.1 ± 0.5–23.3 ± 1.4) might increase the risk of nitrate leaching compared with pure spruce stands (~25). Forest floor C/N ratios in beech–Douglas fir stands are similar to beech–spruce, also indicating a potential risk of nitrate leaching from their soils. Still, N mineralisation, soil nitrate concentrations and thus the risk of nitrate leaching depend on soil nutrient status and soil texture as discussed previously, and therefore cannot be predicted reliably from our data. Moreover, mixed conifer–beech forests are less susceptible to severe ecosystem distributions, like windthrow and insect calamities, than monocultures, which often result in extreme nitrate leaching (Huber et al., 2004).

Altered rooting patterns in mixed compared with pure stands can be expected to impact soil OC and N accumulation and distribution (Rothe and Binkley, 2001). The high competitive ability of beech fine roots, expressed by their capacity to also exploit the deeper soil and those soil layers less occupied by a competing species (Bolte and Villanueva, 2006), restricts Douglas fir and Norway spruce fine roots to the topsoil and produces a concomitant shift in beech fine roots towards the subsoil (Hendriks and Bianchi, 1995; Schmid and Kazda, 2002). Contrastingly, Lei et al. (2012) reported that fine-root turnover increased with species richness in young temperate forests due to higher fine root production of Douglas fir and spruce, respectively, than in pure stands. While Douglas fir roots increased penetration of deeper soil layers (15–30 cm), Norway spruce roots were translocated to the topsoil (0–15 cm). The higher production and turnover of fine-roots was attributed to high competitive strength and thus lower interspecific than intraspecific competition of the conifers. The varied and sometimes higher soil exploitation in mixed stands, as reported by Schmid and Kazda (2002) and Bolte and Villanueva (2006) can result in distinct OC and N accumulation in the mineral topsoil. The former found total (beech + spruce) fine root biomass in beech–spruce mixtures being two times higher than in pure spruce stands on a stagnic cambisol and slightly, but not significantly, higher on a podsolic cambisol. On both soil types, spruce fine root biomass was significantly reduced in comparison with the pure spruce stands. However, as we did not measure root biomass and distribution, we are not able to judge whether a shift in rooting patterns has induced site-dependent differences in soil OC and N stocks and distribution between pure and mixed stands. Still, due to the absolute increase in OC (and in tendency N) stored in the mineral topsoil

(0–15 cm) under mixtures of beech with Douglas fir or Norway spruce (compared with pure beech stands), we conclude that mixed stands possibly enhance C-sequestration in the mineral soil.

5. Conclusions

Pronounced, site dependent effects of tree species (European beech, Douglas fir and Norway spruce) on soil OC and N stocks as well as on soil OC and N allocation in different soil compartments exist. Forest floor OC and N stocks generally are smallest in pure beech stands compared with Douglas fir and Norway spruce. Total soil OC stocks show the same pattern, whereas tree species effects on total soil N stocks were only present at one out of three sites. Tree species-specific differences in foliage nutrient concentrations between beech and conifer stands might influence decomposition rates among the species and thus modify soil OC and N stocks.

Soil OC and N stocks in mixed stands of beech with Douglas fir or Norway spruce are generally between those of the respective pure stands, but patterns differ depending on the site. Compared with pure beech stands, admixture of beech with Douglas fir or Norway spruce results in increased forest floor OC and N stocks and mineral topsoil (0–15 cm) OC stocks.

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REGULAR ARTICLE

Soil acidity and exchangeable base cation stocks under pure and mixed stands of European beech, Douglas fir and Norway spruce

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Abstract
Background The establishment of mixed forest stands is nowadays seen as an opportunity to maintain forest services in the course of global climate change.
Methods Thus, we determined forest floor and mineral soil pH, base saturation (BS) as well as exchangeable base cation stocks in adjacent groups of pure mature European beech *(Fagus sylvatica)*, Douglas fir *(Pseudotsuga menziesii)* and Norway spruce *(Picea abies)* as well as single-tree mixtures of beech with either Douglas fir or spruce at two forest sites in Southern Germany that differ in site and soil properties.
Results Spruce forest floors had lowest pH and BS, while beech favoured less acidic forest floors with higher BS. The impact of Douglas fir on soils varied depending on the site. Under beech–Douglas fir and beech–spruce mixtures, forest floor and mineral soil pH and BS were higher than under the respective pure conifer stands. While beech depletes soil exchangeable Ca and Mg stocks more than Douglas fir and spruce, respectively, total soil exchangeable K stocks under beech were among the highest. Again, beech–conifer mixtures were intermediate.
Conclusions Mixed species stands might maintain forest soil fertility by mitigating soil acidification, nutrient leaching and concomitant soil base cation depletion compared to pure conifer stands.

Keywords Tree species effects · Broadleaves · Conifers · *Fagus sylvatica* · *Pseudotsuga menziesii* · *Picea abies*

Introduction

Forest management in general and tree species choice in particular have various impacts on soil biological, physical and chemical processes and characteristics (Ranger and Nys 1994; Augusto et al. 2002; Jandl et al. 2007). On the part of soil chemical properties, especially soil acidity and soil exchangeable cation concentrations and stocks may be affected by tree species composition (Binkley 1995). Different tree species grown under similar conditions, such as climate, soil type, and land use history, differ substantially from each other with respect to foliage nutrient content, root and litter chemistry, mineral weathering rates, throughfall deposition, nutrient leaching and uptake by roots as well as mineralization and nitrification rates, all of them having a large impact on soil nutrient input, output and cycling (Binkley and Giardina 1998; Guckland et al. 2009; Augusto et al. 2015) and consequently soil acidification. Differences in litter decomposition behaviour among tree species cause variation in soil chemical features (Vesterdal et al. 2013). Less easily decomposable components and lower nutrient contents in conifer litter lead

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to the formation of thick forest floors with relatively higher soil acidity in conifer ecosystems. In contrast, higher litter nutrient contents and soil biological activity are associated with higher decomposition rates in broadleaf compared to conifer forests, the former forming forest floors higher in base cations and pH (Binkley 1995; Rothe et al. 2002b; Hobbie et al. 2006; Augusto et al. 2015).

In recent decades, Central European forests have been subject to anthropogenically elevated S, N and acid deposition (de Vries et al. 2014). Also, the soil-acidifying effect of elevated N and S deposition is dependent on tree species (Augusto et al. 2002). Due to higher acid deposition rates in conifer compared to broadleaf forests (De Schrijver et al. 2007), forest soils in conifer ecosystems are more susceptible to soil acidification resulting in a decrease in and depletion of exchangeable base cation stocks. Higher N input via throughfall in spruce compared to beech forests, attributed to higher leaf area and perennial foliage, induced higher leaching of nitrate from soils under the conifer species (Rothe et al. 2002a), fostering the concomitant increased loss of soil base cations. Moreover, Legout et al. (2016) found that excessive nitrification in an acidic forest soil under pure Douglas fir strongly reinforced soil acidification primarily due to soil base cation depletion.

As an adaption of forest management to climate change, large forested areas across Europe covered with Norway spruce (*Picea abies*) monocultures have recently increasingly been replaced by mixed stands of spruce with broadleaves, e.g. European beech (*Fagus sylvatica*) (Rothe et al. 2002b). However, adverse events, e.g. more frequent drought, windthrow and bark beetle infestations, induced by climate change, impair Norway spruce forest ecosystems, making its currently wide-spread use, particularly in German forestry, increasingly problematic (Kölling and Zimmermann 2007). Douglas fir (*Pseudotsuga menziesii menziesii*) is considered a suitable alternative forest tree species to Norway spruce in Central Europe. However, for forest protection and ecosystem stability reasons (Knoke et al. 2008), there is no aim to cultivate pure stands of Douglas fir in Germany as realised in the past for Norway spruce, but rather to introduce it into established stands of native tree species, particularly European beech, on a small-scale (Brosinger and Baier 2008). Nowadays, Douglas fir is the most important foreign tree species cultivated in European forests (Prietzel and Bachmann 2012; Schmid et al. 2013) with a continuing increase of its cultivation area for the last decades. Thus far, studies regarding the ecological effects of Douglas fir cultivation on European forest soils are scarce (Schmid et al. 2013), particularly with respect to soil acidity and exchangeable base cation stocks. Ecological characteristics of mixed species stands are often intermediate in comparison with pure stands of the corresponding species (Rothe and Binkley 2001; Augusto et al. 2002); however, investigations on the impact of tree species mixtures, particularly broadleaf–conifer mixtures, on soil nutrient status and acidity and the underlying mechanisms are scarce and the few results are inconsistent (Rothe and Binkley 2001; Berger et al. 2004). Moreover, patterns of tree species and species mixtures effects on forest soil chemistry vary depending on climatic factors and soil type (Vesterdal and Raulund-Rasmussen 1998; Augusto et al. 2015).

We investigated the impact of tree species and species mixtures on soil acidity and soil base cation stocks and hypothesised that (1) beech–Douglas fir and beech–spruce mixtures have higher soil pH and base saturation than pure conifer stands, (2) soil exchangeable base cation stocks are highest in pure beech stands and (3) beech–Douglas fir mixtures are superior to beech–spruce mixtures with respect to topsoil acidification. Furthermore, we address site dependency of tree species and species mixtures effects, their relative importance for topsoil acidification and deduce recommendations for forest management. Our investigation supplements a recent study where tree species and species mixtures effects on soil organic carbon (OC) and N stocks have been assessed for the same stand types at the same sites (Cremer et al. 2016).

Material and methods

Study sites

We investigated two forest sites in distinct regions of Bavaria, Southern Germany, that differ in parent material, soil properties as well as nutrient and water supply. The sites have been described in detail in Cremer et al. (2016). Site Walkertshofen (WAL) is located about 30 km south-west of Augsburg, in the Tertiary uplands, where the soil type Albic Stagnic Luvisol (IUSS Working Group WRB 2015) has developed from nutrient-rich loess on glaciofluviatile gravel. Site Tännig

(TAN) is located in the Spessart forest, about 50 km north-west of Würzburg. It is characterised by soil type Dystric Endoskeletic Rhodic Cambisol (IUSS Working Group WRB 2015) that has developed from nutrient-poor Triassic red sandstone. Topsoils (0–30 cm) at both sites have a loamy texture with 25–27% sand, 48–49% silt and 25–26% clay. The forest sites have similar climatic conditions (mean annual temperature (~8 °C) and precipitation (1000 mm a^{-1})), but atmospheric N deposition at TAN (4.2 kg ha^{-1} a^{-1}) is less than half of that at WAL (9.8 kg ha^{-1} a^{-1}; NO3-N + NH4-N in field precipitation January – December 2014). Both sites comprise adjacent groups of pure mature European beech (*Fagus sylvatica*), Douglas fir (*Pseudotsuga menziesii menziesii*) and Norway spruce (*Picea abies)* (pure stands) as well as single-tree mixtures of beech with either Douglas fir or Norway spruce (mixed stands). Since all investigated groups at a given site occur most closely to each other, microclimatic conditions, exposition and soil properties of the different stands at a given site were identical. The uniformity of soil properties among stands within a site was ensured not only by close proximity of the different groups, but particularly by choosing groups of species that were grown on identical site units according to former site evaluations.

Soil sampling

In each pure and mixed stand at both sites, we chose ten pairs of trees as representative sampling points (five in spruce and beech–spruce mixture at TAN). The sampling design for this study took into account small scale soil heterogeneity. The sampling of soil regions between two trees with different distances from the tree trunks resulted in a total of 20 sampling spots (two per sampling point) in pure stands (10 in spruce at TAN) and of 30 sampling spots (three per sampling point) in mixed stands (15 in beech–spruce at TAN; see Cremer et al. 2016). At each sampling spot, the organic layer (organic material above the mineral soil; referred to as forest floor) of an area within a metal frame (20 × 20 cm^2) was sampled completely; all living plant material was removed on site. Where the forest floor had been collected, mineral soil samples were taken using core augers with a diameter of 5 cm for depth increments 0–15 and 15–30 cm and of 2.5 cm for 30–60 cm soil depth. The cores were used to determine fine earth bulk densities as well as mineral soil masses and stocks.

Sample preparation and analysis

All soil samples were dried at 40 °C until constant mass for chemical analysis. Roots and stones were removed by hand from mineral soil samples before the fine earth (<2 mm) was separated from bulk soil by sieving. The fine earth of mineral soil samples was weighed and used for estimation of fine earth masses and bulk densities. Forest floor samples were sieved to separate organic material >2 mm (e.g. coarse roots) and stones from finer organic material. Forest floor (<2 mm) weight was used to calculate forest floor masses. After homogenisation of all forest floor and mineral soil samples (<2 mm), subsamples were used for further chemical analyses.

For pH analysis, 50 ml of 0.01 M $CaCl_2$ was added to sieved subsamples (5 g of forest floor, and 20 g of mineral soil respectively), and the mixture was thoroughly shaken. After sedimentation of the solid phase, the pH value of the solution was determined with a glass electrode. For determination of exchangeable cation (Ca^{2+}, Mg^{2+}, Na^+, K^+, Al^{3+}, Fe^{2+}, Mn^{2+}, H^+) concentrations, sieved subsamples (1.25 g of forest floor, and 2.5 g of mineral soil) were extracted by shaking the samples with 100 ml of 0.5 M NH_4Cl solution for two hours. The suspension was left standing for another 24 h and afterwards filtrated through membrane filters with mesh size 0.45 μm (Sartorius, Göttingen, Germany). Cation concentrations of the filtrates were analysed by ICP-OES (Spectro Genesis, Spectro, Kleve, Germany). The sum of all extracted cations plus the exchangeable H^+ as determined with a pH electrode was defined as effective cation exchange capacity (CEC; $mmol_c$ kg^{-1}). Base saturation (BS; %) was defined as the share of exchangeable cations Ca^{2+}, Mg^{2+}, Na^+, K^+ in CEC. Soil base cation stocks (Ca^{2+}, Mg^{2+}, K^+) in the depth increment samples were calculated from exchangeable cation concentrations and fine earth bulk density for individual soil depths. Total (forest floor + mineral soil 0–30 cm) soil exchangeable base cation stocks were calculated as the sum of soil exchangeable base cation stocks of the individual soil depths for each sampling spot.

Statistical analysis

Tree species (beech, Douglas fir, Norway spruce) and species mixtures (beech–Douglas fir, beech–spruce) means and standard deviations of all investigated variables were calculated for each site and soil depth separately. As the sampling distance from the tree trunks did not significantly affect mean pH, BS and exchangeable (base) cations within groups (tree species and species mixtures), group means were calculated from all investigated samples within a group. As in some cases the assumption of normal distribution was not met (tested for with Shapiro–Wilk–test), the Kruskal–Wallis–H–test, followed by pairwise Mann–Whitney–U–tests with a correction factor for multiple pairwise testing, was used to identify statistically significant differences between tree species and species mixtures. Correlations between the investigated variables and C/N ratio, soil OC content and stock (cf. Cremer et al. 2016) were tested with Spearman (non-parametric) rank correlation test for individual soil depths. We ran one sample t-tests to assess whether there were additive or non-additive effects of tree species mixtures on the investigated variables. Tree species mixtures effects were referred to as non-additive, if the (observed) values of mixed stands differed significantly from the (expected) mean value of the respective pure stands. In return, if the observed values of mixed stands were not significantly different from the respective expected values, they were referred to as additive effects. All statistical analyses were conducted using SPSS (Version 22, IBM, Ehningen, Germany). Effects were considered significant when *P* was <0.05.

Results

Results on exchangeable cations, base saturation (BS) and pH are presented for forest floors and 0–60 cm mineral soils. Investigations on soil nutrients, BS and pH are often constrained to the forest floor and the uppermost mineral soil. In fact, that is where most studies found tree species having an impact on soil chemistry. In greater soil depth, confounding effects of spatial parent material inhomogeneity on soil properties become increasingly relevant and often mask tree species effects, especially regarding soil cations and pH. This was also the case in our investigation. For that reason, we did not include the lower mineral soil (30–60 cm) when calculating soil base cation stocks (data given in Online Resource 1).

Soil base saturation, pH and exchangeable cations

Tree species and species mixtures impacts on soil BS mainly occurred in the forest floor and mineral topsoil (0–15 cm, Fig. 1). Pure beech stands had forest floor and mineral topsoil with highest BS compared to pure spruce (both sites) and Douglas fir (site WAL). At TAN, BS of forest floor and mineral topsoil under Douglas fir was similar to beech and significantly higher than that under spruce. Pure beech still maintained highest BS in 15–30 cm soil depth at site TAN (not significant), while further tree species specific differences were absent in this soil depth. Soil BS in 30–60 cm soil depth was similar for all stands at site TAN, whereas at WAL, beech had significantly lowest BS compared to the conifers. BS of forest floors and all mineral soil depth increments under mixed beech–Douglas fir and beech–spruce stands was between those of the respective pure beech and conifer stands (Fig. 1); it was slightly (not statistically significant) larger for beech–Douglas fir than for beech–spruce mixtures.

Correspondingly, pH values of the forest floor and mineral topsoil (0–15 cm) were highest under pure beech stands (Fig. 1). At TAN, forest floor pH under Douglas fir was similar to beech and tended to be higher than under spruce, while there were no differences between the conifers in the mineral topsoil. Forest floor and mineral topsoil pH in the mixtures mainly were between those of the respective pure stands. As with forest floor BS, mean forest floor pH values under beech–Douglas fir and beech–spruce mixtures were significantly different from both, the pure beech and the respective conifer stands at WAL. In contrast, at site TAN, forest floor and mineral topsoil pH under beech–Douglas fir stands were similar to beech and significantly larger than those under beech–spruce stands. There were only small and non-systematic differences in pH in 15–30 cm soil depth. Tree species effects on soil pH in 30–60 cm soil depth were absent.

Effective cation exchange capacity (CEC) in forest floors was similar for beech, Douglas fir and Norway spruce at site WAL, whereas the pure beech stand had a smaller forest floor CEC at site TAN (Table 1). Mineral topsoil (0–15 cm) CEC was higher in pure conifer stands compared to beech and similar for Douglas fir and spruce. Highest BS and pH in beech forest floor at site WAL were accompanied by higher concentrations of exchangeable Ca, Mg and K compared to Douglas fir and spruce (Table 1). In contrast, at site TAN, lowest BS in spruce forest floor was associated with similar amounts of exchangeable Ca and Mg under spruce, beech and Douglas fir. Exchangeable K concentrations of beech forest floors and mineral topsoils were always significantly higher than under Douglas fir and spruce.

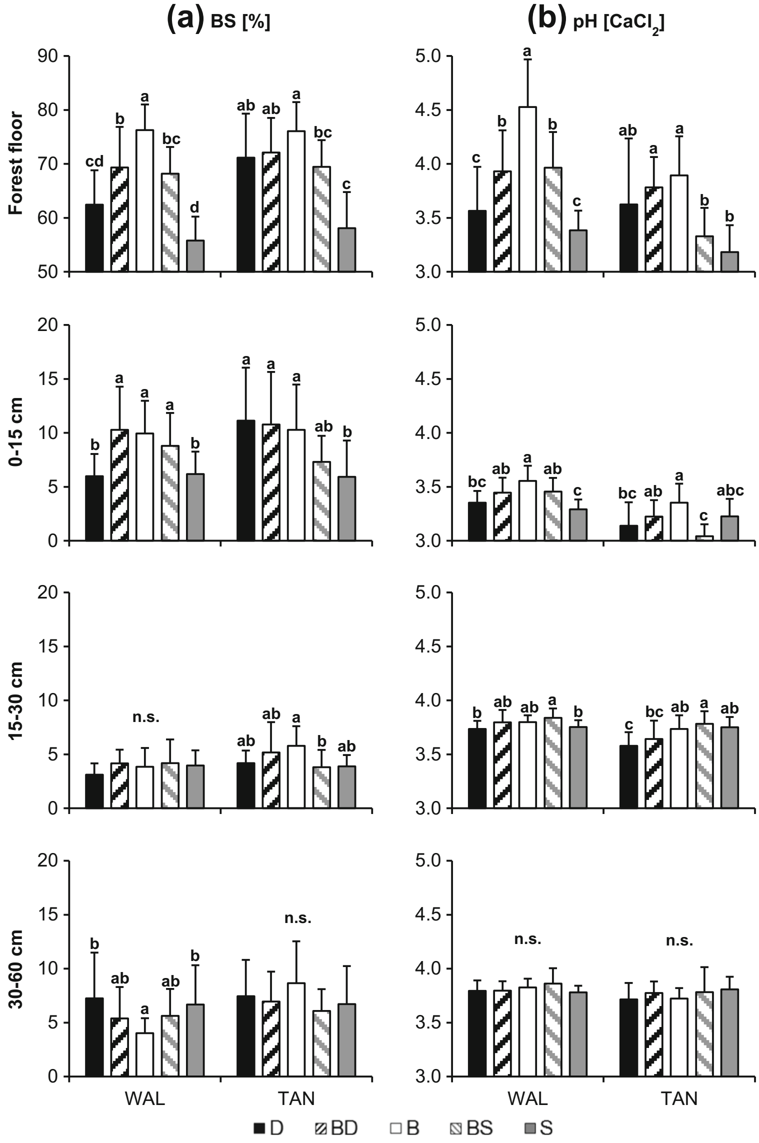

Fig. 1 **a** Base saturation [BS; %] and **b** pH [CaCl$_2$] [arithmetic mean value ± standard deviation] in forest floors and mineral soil depth increments under different tree species and species mixtures at sites Walkertshofen (WAL) and Tännig (TAN). Significant ($p < 0.05$; Kruskal-Wallis-H-test, followed by pairwise Mann-Whitney-U-test) differences between tree species for a given soil depth are marked by different letters. n.s. = not significant; B = European beech (*white bars, middle*), D = Douglas fir (black bars, left), S = Norway spruce (*grey bars, right*), BD = beech–Douglas fir mixture (*black-white bars, left*) and BS = beech–spruce mixture (*grey-white bars, right*)

Forest floor and mineral topsoil exchangeable Al concentrations at least tended to be higher under pure Douglas fir and spruce compared to beech. Tree species effects on deeper mineral soil (15–30 and 30–60 cm) were small and inconsistent at both sites. Regarding forest floor and mineral topsoil CEC as well as concentrations of different exchangeable cations, mixed beech–Douglas fir and beech–spruce stands were intermediate, not being significantly different from both, pure beech and pure conifer stands.

Particularly within the forest floor, where tree species effects were strongest, BS and pH were (significantly) negatively correlated with OC content, C/N ratio and OC stock in the respective soil depth (Table 2). In the mineral topsoil (0–15 cm), this relation was also present for pH, but not BS. In return, topsoil CEC was (significantly) positively correlated with the investigated parameters of topsoil OC. Moreover, topsoil BS, pH and exchangeable Ca, Mg and K at least tended to be negatively correlated to forest floor OC and C/N, while the opposite was the case for topsoil CEC and Al (Table 2).

Exchangeable base cation stocks

Patterns of soil exchangeable base cations stocks differed depending on site and tree species composition

Table 1 Effective cation exchange capacity and exchangeable cation concentration [mmol$_c$ $\mathbf{kg}^{-1}$; arithmetic mean value ± standard deviation] in forest floors and mineral soil depth increments under different tree species and species mixtures at the two study sites. Significant ($p < 0.05$; Kruskal-Wallis-H-test, followed by pairwise Mann-Whitney-U-test) differences between tree species for a given soil depth and variable are marked by different letters

	Douglas fir	Beech–Douglas fir	Beech	Beech–Spruce	Spruce
Walkertshofen					
Forest floor					
CEC	260 ± 37	248 ± 70	295 ± 80	261 ± 43	248 ± 31
Ca	128 ± 29ab	135 ± 48a	165 ± 56a	133 ± 29a	104 ± 20b
Mg	25 ± 6bc	26 ± 9bc	39 ± 15a	29 ± 7ab	23 ± 4c
K	10 ± 4c	14 ± 9bc	23 ± 7a	15 ± 5b	11 ± 2bc
Al	15 ± 9c	9 ± 6b	4 ± 3a	9 ± 6bc	13 ± 7bc
0–15 cm					
CEC	78 ± 12b	70 ± 12ab	67 ± 8a	72 ± 12ab	76 ± 13ab
Ca	2.4 ± 1.2bc	4.3 ± 2.6a	3.4 ± 1.5ab	3.2 ± 1.7ab	1.9 ± 1.1c
Mg	1.5 ± 0.3	1.8 ± 0.8	1.4 ± 0.5	1.7 ± 0.6	1.5 ± 0.4
K	0.5 ± 0.4c	1.1 ± 0.4ab	1.5 ± 0.8a	1.1 ± 0.3ab	0.9 ± 0.3bc
Al	60 ± 12b	50 ± 8a	49 ± 7a	53 ± 11ab	58 ± 11ab
15–30 cm					
CEC	54 ± 11	52 ± 9	54 ± 9	50 ± 11	51 ± 7
Ca	0.4 ± 0.3	0.7 ± 0.6	0.6 ± 0.3	0.5 ± 0.4	0.6 ± 0.5
Mg	0.6 ± 0.2b	0.6 ± 0.3ab	0.4 ± 0.2a	0.5 ± 0.2ab	0.5 ± 0.1ab
K	0.4 ± 0.3	0.6 ± 0.1	0.7 ± 0.5	0.7 ± 0.5	0.6 ± 0.1
Al	47 ± 10	44 ± 8	46 ± 10	43 ± 10	44 ± 7
30–60 cm					
CEC	61 ± 11	64 ± 10	64 ± 14	64 ± 15	62 ± 8
Ca	1.2 ± 1.2	1.1 ± 1.2	0.8 ± 0.5	0.9 ± 0.8	1.1 ± 1.0
Mg	2.1 ± 1.6c	0.9 ± 0.7ab	0.5 ± 0.4a	1.2 ± 0.8bc	1.4 ± 1.1bc
K	0.7 ± 0.4b	1.0 ± 0.3ab	0.9 ± 0.3ab	1.0 ± 0.2a	1.1 ± 0.3a
Al	50 ± 11	55 ± 10	55 ± 14	55 ± 14	52 ± 9
Tännig					
Forest floor					
CEC	269 ± 40ab	251 ± 57ab	227 ± 62b	288 ± 36a	282 ± 39ab
Ca	151 ± 34	139 ± 40	126 ± 43	142 ± 24	128 ± 19
Mg	27 ± 8a	27 ± 7a	28 ± 149a	36 ± 6b	26 ± 5a
K	13 ± 5c	16 ± 4bc	19 ± 6ab	21 ± 6a	13 ± 3bc
Al	12 ± 8ab	9 ± 10a	7 ± 4a	14 ± 8b	22 ± 9b
0–15 cm					
CEC	93 ± 15a	77 ± 16b	70 ± 15b	83 ± 13ab	87 ± 14ab
Ca	5.3 ± 3.4a	4.3 ± 3.3ab	3.2 ± 2.9ab	2.2 ± 1.8b	2.3 ± 2.2b
Mg	3.0 ± 1.3b	2.3 ± 1.0ab	1.9 ± 0.7a	2.1 ± 1.1ab	1.5 ± 0.6a
K	1.4 ± 0.5b	1.6 ± 0.6ab	1.8 ± 0.5a	1.5 ± 0.5ab	1.0 ± 0.3c
Al	59 ± 11bc	50 ± 11a	50 ± 11ab	54 ± 4 ac	64 ± 9c
15–30 cm					
CEC	59 ± 12a	53 ± 15ab	47 ± 11b	43 ± 6b	49 ± 9ab
Ca	0.5 ± 0.4	0.7 ± 1.2	0.7 ± 0.8	0.1 ± 0.1	0.3 ± 0.4
Mg	0.7 ± 0.2c	0.7 ± 0.5bc	0.4 ± 0.2ab	0.4 ± 0.1a	0.3 ± 0.1a

Table 1 (continued)

	Douglas fir	Beech–Douglas fir	Beech	Beech–Spruce	Spruce
K	0.8 ± 0.2ab	1.0 ± 0.9ab	1.0 ± 0.2a	0.8 ± 0.4b	0.8 ± 0.2ab
Al	50 ± 9b	43 ± 11ab	40 ± 10a	37 ± 5a	42 ± 8ab
30–60 cm					
CEC	51 ± 14a	41 ± 10ab	45 ± 7a	36 ± 5b	40 ± 5ab
Ca	0.8 ± 1.1ab	0.8 ± 1.5ab	1.1 ± 0.8a	0.3 ± 0.3b	0.5 ± 0.5ab
Mg	0.6 ± 0.2ab	0.6 ± 0.4ab	0.6 ± 0.2a	0.4 ± 0.2b	0.5 ± 0.3ab
K	1.6 ± 0.5a	1.2 ± 0.3bc	1.4 ± 0.3ab	1.0 ± 0.3c	1.2 ± 0.6abc
Al	43 ± 13b	34 ± 8ab	37 ± 7ab	31 ± 5a	33 ± 5ab

(Fig. 2). Pure beech had significantly smallest total soil (forest floor + uppermost 30 cm mineral soil) exchangeable Ca (−37%) and Mg (−45%) stocks compared to Douglas fir and spruce, while total soil exchangeable K stocks were among the highest under beech and lowest under pure Douglas fir. Differences in total soil exchangeable Ca stocks among tree species mainly originated from differences in forest floor exchangeable Ca stocks, which are up to five times higher under Douglas fir and spruce, respectively, compared to beech. In addition, total soil exchangeable Ca and Mg stocks at site TAN were highest under Douglas fir (but not significantly different from spruce) due to highest stocks of exchangeable Ca and Mg in the mineral soil. Depending on the site, more than half (WAL: 55 and 59%; TAN: 40 and 65%) of the total exchangeable Ca under Douglas fir and spruce is stored in the forest floor. In pure beech stands, both, absolute and relative (−20% (D) and −30% (S)) exchangeable Ca forest floor stocks were smallest. However, mineral soil exchangeable Ca stocks under beech were as high as under Douglas fir and spruce. In contrast, exchangeable Mg stocks under beech were smallest in both, forest floor and mineral soil compared to Douglas fir. High mineral soil exchangeable K stocks compensate for smallest forest floor exchangeable K stocks under beech. At both sites, and equally for Ca, Mg and K stocks, there was a tendency of smaller forest floor stocks under Douglas fir compared to spruce; however, no significant differences were found.

Table 2 Correlation coefficients between the investigated variables (BS = base saturation [%], pH [$CaCl_2$], CEC = effective cation exchange capacity [$mmol_c$ kg^{-1}], exchangeable cation concentrations [$mmol_c$ kg^{-1}]) and organic carbon content [mg g^{-1}], C/N ratio and organic carbon stocks [kg ha^{-1}] in and between different soil depth increments. Significant ($p < 0.05$; Spearman rank correlation test) correlations are marked by bold characters

		BS	pH	CEC	Ca	Mg	K	Al
		Forest floor						
Forest floor	OC	**–0.661**	**–0.758**	0.382	–0.273	–0.382	–0.479	**0.794**
	C/N	–0.515	–0.370	–0.370	–0.576	–0.527	–0.612	0.370
	OC stock	**–0.879**	**–0.830**	–0.030	–0.539	**–0.661**	**–0.673**	**0.842**
		0–15 cm						
0–15 cm	OC	0.515	**–0.770**	0.564	0.224	**0.758**	0.576	0.030
	C/N	0.248	**–0.952**	**0.806**	0.030	**0.697**	0.309	0.358
	OC stock	0.139	**–0.879**	**0.842**	0.067	**0.636**	0.018	0.442
		15–30 cm						
15–30 cm	OC	0.103	**–0.745**	0.309	0.079	0.394	0.394	0.030
	C/N	0.236	–0.600	–0.248	–0.152	0.042	0.612	–0.406
	OC stock	–0.479	0.382	0.479	–0.067	0.333	**–0.939**	**0.661**
		0–15 cm						
Forest floor	OC	**–0.709**	–0.442	0.576	**–0.661**	–0.382	–0.588	**0.709**
	C/N	**–0.685**	–0.479	0.539	**–0.673**	–0.176	**–0.685**	**0.794**
	OC stock	–0.042	–0.273	0.442	–0.127	0.079	–0.309	0.527

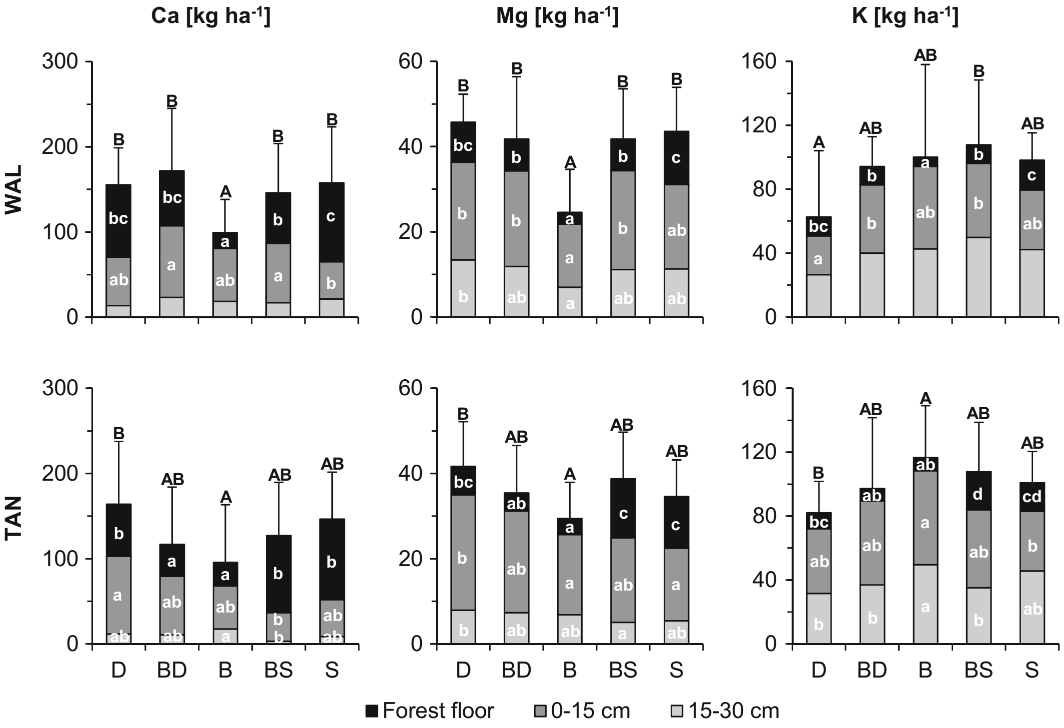

Fig. 2 Stocks of exchangeable base cations [kg ha^{-1}] of individual soil depths [arithmetic mean value] and total soil [arithmetic mean value ± standard deviation] under different tree species and species mixtures at sites Walkertshofen (WAL) and Tännig (TAN). Significant ($p < 0.05$; Kruskal-Wallis-H-test, followed by pairwise Mann-Whitney-U-test) differences between tree species for a given soil depth are marked by different letters: lowercase letters for individual soil depths and capitals for total soil. B = European beech, D = Douglas fir, S = Norway spruce, BD = beech–Douglas fir mixture and BS = beech–spruce mixture

In most cases, total soil (forest floor + uppermost 30 cm mineral soil) exchangeable Ca, Mg and K stocks of beech–Douglas fir and beech–spruce mixtures were between those of the respective pure beech and conifer stands; at a given site there were no differences between the beech–Douglas fir and beech–spruce mixtures (Fig. 2). Forest floor exchangeable Ca, Mg and K stocks were significantly higher in beech–Douglas fir stands compared to pure beech at WAL and only tended to be smaller than under pure Douglas fir. In contrast, forest floor exchangeable Ca, Mg and K stocks in beech–spruce mixtures were always significantly larger than those in beech stands; they were smaller compared to spruce forest floors at WAL and similar to spruce at TAN. Accordingly, the share of exchangeable Ca, Mg and K stored in the forest floor of beech–conifer mixtures was at least as high as in pure beech stands (but most often higher), and in most cases smaller than (never exceeding) those of the respective conifer stands. Hence, there was no difference in forest floor exchangeable base cations stocks between beech–Douglas fir and beech–spruce mixture at site WAL; but at TAN, beech–spruce mixture stored significantly more exchangeable Ca, Mg and K in its forest floor.

Discussion

Forest floor and mineral topsoil acidification under pure stands

Forest floor and topsoil acidification differs among beech and conifer species

Beech forest floors and mineral topsoils (0–15 cm) were less acidic and had higher BS than those under pure spruce. Douglas fir forest floors were either intermediate and significantly different from both, beech and spruce, or similar to beech and at least tended to be higher in pH and BS than those under spruce. Tree species composition affects forest floor and mineral topsoil acidity and soil exchangeable base cation stocks in various ways. With broadleaf species, e.g. European beech, having markedly larger foliage nutrient and lower foliage lignin contents than conifer species, particularly spruce, but also Douglas fir (Augusto et al. 2002), they accelerate litter decomposition and bioturbation and promote thin organic layers with comparable high base saturation and less acidity. The introduction of acidic and nutrient-poor litterfall in conifer stands contributes to high concentrations of exchangeable Al in forest floors under Douglas fir and Norway spruce (Hansson et al. 2011). Forest floor mass, as an (antagonistic) predictor of litter decomposition and bioturbation, increased in the order: beech < Douglas fir < spruce (Cremer et al. 2016), supporting the observed species specific patterns of soil acidification.

Though differences in pH and BS were significant also in mineral soil, their magnitude was lower. As in forest floors, highest topsoil (0–15 cm) pH and BS in pure beech stands were related to lowest exchangeable Al concentrations. The formation of thick, OC rich forest floors under spruce (and to a lesser extent Douglas fir) compared to beech can partly be ascribed to hampered litter decomposition commonly found in conifer stands (Prescott et al. 2000). Partial decomposition of litter triggers the production of organic acids (Binkley 1995), potentially contributing to topsoil (0–15 cm) acidification under spruce and Douglas fir. Forest floor organic carbon (OC) contents in beech, Douglas fir and spruce stands are negatively correlated to parameters of mineral soil fertility, particularly exchangeable Ca and pH (Vesterdal and Raulund-Rasmussen 1998), as was the case in this study (significant for BS and Ca). Both, forest floor OC content and C/N ratio were a good predictor of topsoil exchangeable Al concentrations. Thus, the significantly higher forest floor OC storage under pure conifer stands compared to pure beech (Cremer et al. 2016) can explain lower topsoil pH, Ca contents and BS as well as highest exchangeable Al contents under Douglas fir and spruce stands.

Moreover, higher CEC in mineral topsoil under Douglas fir and spruce can be attributed to higher contents and stocks of soil OC due to the importance of soil organic matter (SOM) in cation binding (Hobbie et al. 2007). Gruba and Mulder (2015) ascribed the higher CEC of SOM to conifer stands in comparison to broadleaves, supporting our findings of higher CEC in Douglas fir and spruce topsoils compared to beech. However, topsoil OC contents hardly differ among species at the present sites (Cremer et al. 2016) and are not generally higher under conifers. Though, topsoil OC contents were positively correlated with topsoil CEC ($p = 0.09$) and negatively correlated with topsoil pH, as were topsoil C/N ratio and OC stocks. Tree species impacts on CEC are likely to be indirect effects, triggered by the effect of tree species on topsoil OC parameters.

Further possible explanations to differences in soil acidification among pure stands of beech, Douglas fir and Norway spruce might be atmospheric deposition and nutrient leaching from soils as influenced differently by specific tree species. External inputs of acidifying elements, e.g. N (in the form of NH_4^+ and NO_3^-) and SO_4^{2-}, via throughfall, are many times higher in conifer than in beech forests (Ranger and Nys 1994) and in regions with high atmospheric deposition loads, they induce enhanced base cation losses via leaching (Rothe et al. 2002a; Kristensen et al. 2004; De Schrijver et al. 2007). In fact, N deposition via throughfall under pure Douglas fir (~16 kg N ha^{-1} a^{-1}) stands was more than twice as high than under pure beech (~7 kg N ha^{-1} a^{-1}) at site TAN, and 1.5 times higher under the pure conifer stands (~19 (D) or 16 (S) kg N ha^{-1} a^{-1}) at site WAL (unpublished data; in prep.). Similarly, throughfall fluxes of NO_3^- in 35-year old common garden stands in France increased in the order beech < spruce < Douglas fir, with soil solution NO_3^- concentrations increasing in the same order (Legout et al. 2016). However, apart from the relation between throughfall and leaching fluxes, highest nitrate leaching was ascribed to excessive nitrification under Douglas fir. Prietzel and Bachmann (2011) investigated the subsoil seepage water at four sites in Southern Bavaria (comparable with our sites), observing that nitrate leaching from the soil was strongly elevated under Douglas fir compared to beech growing at the same site and almost similar to high nitrate leaching under Norway spruce. High nitrate leaching from soils was associated with high losses of accompanying base cations in conifer stands in both studies, as well as with highest Al concentrations and lowest pH in Douglas fir soil solution in the French common garden stands (Legout et al. 2016).

Site dependent differences in forest floor and topsoil acidity between Douglas fir and spruce

We can only hypothesise possible causes for forest floor and topsoil differences in BS and pH among Douglas fir and spruce at site TAN. Higher Mg and K contents in Douglas fir needles compared to spruce (Pretzsch et al. 2014; Cremer et al. 2016) likely promote nutrient return into the soil under Douglas fir compared to Norway spruce stands. Moreover, differing rooting patterns among Douglas fir and spruce might have contributed to the differentiation between the conifers. The restriction of spruce roots to the forest floor and the uppermost mineral soil, while Douglas fir also penetrates deeper soil layers (Spielvogel et al. 2014), reinforces soil acidification in spruce topsoils. Calvaruso et al. (2011) found that only roots of Norway spruce, but not those of beech and Douglas fir, acidified their surrounding soil through the deposition of acid root products into the rhizosphere. However, forest floor pH differences between Douglas fir and spruce are mostly small; both species reinforce forest floor acidification compared to broadleaves (Raulund-Rasmussen and Vejre 1995).

Beech depletes soil Ca and Mg, but Douglas fir depletes soil K stocks

Despite Douglas fir and spruce stands having higher forest floor and mineral soil acidity, also total soil exchangeable Ca and Mg stocks were highest under the conifers. Soil base cation stocks depend on both, cation concentrations and bulk density within the respective soil depth. Especially forest floor mass and thickness varies among tree species, being highest under spruce, intermediate under Douglas fir and lowest under beech (Augusto et al. 2003). Forest floor masses (< 2 mm) in our study resemble this order, with decreasing masses from spruce over Douglas fir to beech (Cremer et al. 2016), thus leading to highest forest floor and in most cases highest total soil Ca and Mg stocks under the conifers. Bergkvist and Folkeson (1995) attributed higher pools of soil exchangeable base cations to faster mineral weathering rates under spruce than under beech and birch, respectively. The release of base cations through mineral weathering might compensate for high losses via soil leaching in conifer stands (Bergkvist and Folkeson 1995; Binkley and Giardina 1998). Highest total soil exchangeable Ca and Mg storage in Douglas fir and spruce stands and the trend of highest mineral soil Mg stocks under Douglas fir reflect the patterns of nutrient uptake and accumulation in tree biomass by beech, Douglas fir and spruce. Nutrient contents of wood can provide a reliable estimation of net nutrient uptake by tree species and nutrient export due to wood harvesting in managed forests. Despite of its highest biomass production, Douglas fir trees are characterised by lowest base cation contents, originating mainly from particularly low contents of Ca, Mg and K in wood and bark compared to spruce and especially beech (Augusto et al. 2000; Pretzsch et al. 2014). Overall, nutrient immobilization in aboveground biomass of fast growing Douglas fir stands with highest tree biomass (deduced from highest values of basal area and tree height; cf. Cremer et al. 2016) compared to beech or Norway spruce might still be smallest, thus preserving soil nutrient stocks more than in pure beech stands, where nutrient removal of Ca, Mg and K (kg t^{-1} biomass) was highest at selected sites (Pretzsch et al. 2014).

Depending on the site, higher external inputs of acidifying elements in conifer compared to beech forests (Ranger and Nys 1994) might be accompanied by the input of non-acidic Ca and Mg cations, promoting the storage of Ca and Mg as exchangeable base cation pools in conifer forest soils. Moreover, excessive dry deposition of Ca and Mg in conifer stands, together with acidifying elements, could foster Ca and Mg storage under Douglas fir and spruce (De Schrijver et al. 2007) but preventing the improvement of soil BS and soil pH due to confounding effects of acidifying compounds. Confirming earlier results of Mareschal et al. (2010), forest floor and mineral topsoil K concentrations and stocks, in contrast to Ca and Mg, were higher in beech compared to spruce and particularly Douglas fir stands. Under beech, high mineral soil exchangeable K stocks compensate for smallest forest floor exchangeable K stocks. Canopy exchange of base cations, as the major source for K input via throughfall deposition, is higher in deciduous stands compared to conifer forests (De Schrijver et al. 2007), compensating for higher dry deposition in the latter. Coincidentally higher K contents in beech leaves compared to Douglas fir and spruce needles (Pretzsch et al. 2014; Cremer et al. 2016) might furthermore balance K inputs between beech and the conifers.

Tree species mixtures effects on forest floor and mineral topsoil acidification

According to our results, admixture of beech to Douglas fir, and especially to spruce, counteracts soil acidification by increasing forest floor and mineral topsoil BS and pH. The same effect was found by Berger et al. (2009a), where soils in mixed beech–spruce stands tended to have higher BS and a smaller amount of exchangeable acid cations than pure spruce stands. Studying mixed stands of beech and spruce in Bavaria, Rothe et al. (2002b) found a positive relation between forest floor thickness and acidity, which is comparable to our result of smaller forest floor masses in mixed compared to pure conifer stands (Cremer et al. 2016), especially for spruce. The mixture of easily decomposable leaf litter with more recalcitrant needle litter results in faster decomposition of the latter compared to pure conifer stands, improving soil biological activity and thus reducing forest floor mass. The significantly higher storage of OC in total soil and mineral topsoil (0–15 cm) in mixed beech–conifer stands (Cremer et al. 2016) can explain lower soil pH and BS as well as higher exchangeable Al contents compared to beech, but reduced soil acidity in comparison with Douglas fir and spruce.

Our results indicate that at nutrient-poor sites, beech–Douglas fir mixtures can be superior to beech–spruce mixtures with respect to topsoil acidification. Associated with smaller forest floor mass, OC storage and C/N ratio at site TAN (Cremer et al. 2016), forest floor under beech–Douglas fir is less acidic than beech–spruce forest floor, favouring litter decomposition and bioturbation, thus reducing the amount of nutrient immobilisation (e.g. Ca and Mg) in forest floors. Present patterns of soil exchangeable base cation stocks support this theory. Similarly to pure spruce at site TAN, and in contrast to beech–Douglas fir mixtures, the beech–spruce stand tends to exploit mineral soil exchangeable Ca and Mg stocks, while translocating these nutrients into the forest floor, but preventing nutrient return to the mineral soil.

Furthermore, throughfall deposition of acidifying elements might be reduced in mixed stands compared to pure conifer stands thereby mitigating topsoil acidification especially in regions with high atmospheric deposition. In a recent study conducted in Austria by Berger et al. (2009b) the amount of acidifying elements (e.g. N and S) in throughfall increased in the order: beech < beech–spruce mixture < spruce. Reduced N input via throughfall might inhibit soil N saturation and hence reduce the risk of high N losses due to leaching. Apart from that, mixed species forests are less prone to excessive nitrate leaching, owing to their reduced susceptibility to insect infestations (Jactel and Brockerhoff 2007), which often entail extreme nitrate leaching from conifer stands (Mikkelson et al. 2013). Accordingly, soil acidification under mixed beech–spruce stands was found to be lower than in pure spruce stands due to nitrate retention in the former and nitrate leaching from the latter (Berger et al. 2009b). However, an identical magnitude of proton production in mixed compared to pure spruce stands as a result of dominating NO_3^- losses in spruce but SO_4^{2-} under mixed stands may even out the effect of nutrient leaching among spruce and beech–spruce. Similar mechanisms as those observed for beech–spruce mixtures may account for our findings in beech–Douglas fir mixtures at our study sites.

Overall, our data provides basic knowledge on beech–Douglas fir mixtures and their impact on European forest soils compared to adjacent pure stands and mixed stands of beech with Norway spruce. Generally, species mixtures effects on forest floor and mineral topsoil acidity and base cations were additive effects, meaning that beech–Douglas fir and beech–spruce mixtures were within the range spanned by the corresponding pure stands and that values of mixtures did not differ from the mean value of these respective stands (cf. Online Resource 2). There were only few and mostly inconsistent (across sites and species mixtures) deviations from this pattern, suggesting that there were hardly any non-additive effects of species mixtures. But yet, in three out of four mixtures (two sites x two mixed stands), forest floor acidity was slightly (pH +0.2 units) lower than what would have been expected from the mean of the respective pure beech and conifer stand. In return, our data indicates that topsoil (0–15 cm) pH under beech–spruce stands might be lower than expected (Online Resource 2). Though mixed stands are often assumed to be intermediate in comparison with the pure stands (additive effects) of the respective species concerning their soil chemical properties (Rothe and Binkley 2001), this strongly depends on site and the specific tree species involved (Augusto et al. 2002). Confounding effects of differing environmental and stand parameters may modify trends and magnitudes of tree species mixtures effects (Richards et al. 2010). Thus, the few existing results are ambiguous and underlying mechanisms still need to be explored in more detail (Rothe and Binkley 2001; Berger et al. 2004).

Conclusions

Our assumption that (1) mixed beech–Douglas fir and beech–spruce stands are more favourable than pure conifer stands with respect to soil acidification was confirmed by our data. However, the hypothesis that (2) beech–Douglas fir mixtures are superior to beech–spruce mixtures with respect to topsoil acidification was not strongly supported. Tree species effects among the mixtures mostly were similar with the exception of higher forest floor pH under beech–Douglas fir at one out of two sites likely arising from lower forest floor mass. Moreover, (3) soil exchangeable Ca and Mg stocks increased in the order pure beech < mixed beech–conifer stands ≤ pure conifers (reverse order as expected), while only soil exchangeable K stocks under beech were among the highest. Differences in soil acidity and exchangeable base cation stocks among stands at the given sites partly arise from species specific impacts on humus quality, litter decomposition and soil organic carbon distribution within the soil profile. Furthermore, tree species specific impacts on mineral weathering, nutrient uptake and throughfall deposition might endorse variation in soil acidification.

The cultivation of Douglas fir and Douglas fir mixtures with beech does not cause unexpected changes in soil acidity and soil exchangeable base cation reserves compared to common European tree species beech and spruce and their mixtures. Tree species mixtures overall appeared to have additive effects on soil acidity and soil base cation stocks with only few and inconsistent deviations from this pattern. In addition, the establishment of mixed beech–Douglas fir stands, similarly to beech–spruce mixtures, likely maintains forest soil fertility more than conifer monocultures. Mixed species forest ecosystems will be prevented from excessive nutrient leaching and concomitant depletion of soil base cations under regular forest management conditions (see our Results), and particularly after calamity-induced forest dieback, which is more likely to occur in monoculture compared to mixed stands. Reduced topsoil acidification under mixed–species stands compared to pure conifer stands, associated with decreased nutrient leaching from soils, might contribute to European forest ecosystems providing high quality ground- and drinking water.

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