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Interannual radial growth response of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) to severe droughts: an analysis along a gradient of soil properties and rooting characteristics

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Abstract

Key message We analyzed stem growth responses of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) to severe drought in 2003/04 and 2018. The results showed high drought tolerance in sandy, loamy, and most silty soils, with limitations on clayey soils. This study indicates the susceptibility of Douglas-firs with shallow root systems to extreme drought and the importance of deep rooting for high drought resilience.

Context Although Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) is considered a more drought-tolerant substitute for Norway spruce (*Picea abies* (L.) Karst.) in Europe, there is considerable uncertainty about the drought tolerance of Douglas-fir under climate change, specifically concerning soil properties.

Aims This study aimed to assess the influence of soil texture, plant-available water capacity, and rooting characteristics on the interannual stem growth response of Douglas-fir when exposed to severe drought.

Methods Along a soil texture gradient from sand to clay, we selected seven closely spaced sites at elevations of approximately 500 m a.s.l. in southern Germany. Mixed-effects models were used to analyze the effects of soil physical and rooting characteristics on growth response indices (resistance, recovery, resilience) related to the severe to extreme droughts in 2003/04 and 2018.

Results Douglas-fir showed high drought tolerance in sandy, loamy, and most silty soils. However, the results suggest a higher drought stress risk on clayey soils, as well as at specific silty sites with shallow root systems. A higher effective rooting depth increased the resilience of Douglas-fir during the extreme drought in 2018.

Conclusion Douglas-fir demonstrated its drought tolerance in most soil textures. In addition, this study supports the need for combined above- and below-ground investigations on factors influencing drought tolerance and the importance of rooting for drought resilience.

Keywords Drought tolerance, Resilience, Extreme drought stress, Soil texture, Rooting depth, Comparison with Norway spruce

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1 Introduction

Weather extremes, such as severe droughts and heat waves, are increasing worldwide in both frequency and severity as a result of climate change (IPCC 2023). These disturbances are expected to intensify as global warming increases (IPCC 2023; Samaniego et al. 2018). Periods of severe drought can have significant impacts on forests. Wood production and carbon storage may decrease (Anderegg et al. 2015; Hanewinkel et al. 2013; Kannenberg et al. 2019), whereas forest disturbance, including large-scale forest dieback, may increase (Bréda et al. 2006; McDowell et al. 2008). The subsequent recovery of forest ecosystems and forest dynamics may also be altered (McDowell et al. 2008, 2020; Thurm et al. 2019).

These consequences of severe droughts are increasingly evident in large parts of European forests. The extreme drought in 2018 caused unprecedented mortality in many tree species in Central Europe (Schuldt et al. 2020; Senf and Seidl 2021). Severe soil water deficits and massive tree mortality persisted in some areas of Europe until 2020 (Bolte et al. 2021; Peters et al. 2020; Senf and Seidl 2021). The widespread and economically important coniferous species Norway spruce (*Picea abies* (L.) Karst.) and the deciduous species European beech (*Fagus sylvatica* L.) were most affected by dieback (Rukh et al. 2023; Schuldt et al. 2020). In Germany, 277,000 ha of forest were severely damaged mainly by the drought and heat period from 2018 to 2020 and subsequent bark beetle calamities so reforestation has become necessary (BMEL 2021). In addition, this extreme and prolonged drought brought many other forest species and ecosystems to the edge of their stress limits, particularly in Central and Eastern Europe (Schuldt et al. 2020; Senf and Seidl 2021). If such extreme drought events occur more frequently, tipping points like accelerated mortality of forests might be reached, causing profound changes in the structure and function of forest ecosystems (Haberstroh et al. 2022; McDowell et al. 2020; Rukh et al. 2023; Senf and Seidl 2021). The need for forest conversion to adapt to these climatic changes has been identified in many forest types (Jandl et al. 2019). This conversion is a major challenge for the coming decades (Bolte et al. 2021), in which different silvicultural strategies and measures can be applied (e.g., Brang et al. 2014; Coşofreţ and Bouriaud 2019; Nagel et al. 2017). One increasingly used silvicultural strategy for European forests is the plantation of specific non-native tree species that are considered to be more drought-tolerant (Kunz et al. 2018).

Under future climate change conditions, Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) is considered an important substitute for Norway spruce (Da Ronch et al. 2016; Spiecker et al. 2019) due to the high sensitivity of Norway spruce to drought (Bottero et al. 2021;

Krejza et al. 2021; Thurm et al. 2019; Vitali et al. 2017; Vitasse et al. 2019; Zang et al. 2011). Originating in North America, Douglas-fir was introduced to Europe in the 19th century. Today, it covers around 0.4% of the European forest area (van Loo and Dobrowolska 2019). Douglas-fir has been assessed as more drought-tolerant and less climate-sensitive than Norway spruce (Nadezhdina et al. 2014; Thurm et al. 2019) because it is adapted to low summer precipitation in its area of origin (Felixsik and Wilczyński 2009; Lavender and Hermann 2014; Nicolescu 2019).

Several studies, however, point to certain limits in the drought tolerance of Douglas-fir and shifts in its distribution range due to climate change. Increased damage and mortality were observed in Douglas-fir in France after the severe summer drought of 2003 (Sergent et al. 2014a, b). A study from the Czech Republic evaluated the suitability of Douglas-fir as a substitute for Norway spruce at lower elevation sites with caution because stem growth decreased abruptly in drought years after 2003 (Vejpustková and Čihák 2019). Based on pan-European and French datasets, modeling studies on climate change have found higher mortality in Douglas-fir with increasing temperatures and decreasing precipitation (Brandl et al. 2020; Taccoen et al. 2022). Due to expected climate changes in Douglas-fir's natural range of origin in North America, a significant change in climatically suitable areas for Douglas-fir will occur, and a shift towards higher elevations and more northern areas are projected (Flower et al. 2013; Littell et al. 2010). These studies also indicate that some areas where Douglas-fir grows successfully today are expected to have markedly higher drought risks in the future. With higher drought risks, site factors will become increasingly important criteria for assessing the drought tolerance of Douglas-fir.

However, the tolerance of Douglas-fir to extreme drought events in relation to soil properties has not been fully explored. More specifically, a systematic study of drought tolerance along a soil texture gradient is lacking. Previous studies have included very few sites (Rais et al. 2014) or only specific soil textures, such as sandy soils (Huang et al. 2017), while other studies have focused on soil nitrogen fertility (Sergent et al. 2014b) or yield classes (Vitali and Bauhus 2016). Soil texture essentially determines the soil water balance, rooting depth, and vertical and horizontal root distribution of Douglas-fir (Andrews et al. 2012; Curt et al. 2001; Köstler et al. 1968; Kutschera and Lichtenegger 2013; Lwila et al. 2021; Warren et al. 2005). Thus, soil texture affects both the magnitude of soil water storage capacity and the tree's access via its roots to the plant-available soil water and is therefore essential for assessing drought stress tolerance (Bréda et al. 2006). Well-aerated, deep soils are considered

optimal for Douglas-fir cultivation (Da Ronch et al. 2016; Lavender and Hermann 2014; Nicolescu 2019), whereas clay-dominated soils are considered less productive (Eckhart et al. 2019). There is an indication that clayey soils might also reduce drought tolerance. An increased occurrence of drought damage to young Douglas-fir on clay soils has been reported in North America (Lavender and Hermann 2014). Thus, there is a need for research on the influence of soil texture on the drought tolerance of Douglas-fir.

In addition, it is important to enhance our knowledge of the influence of soil water balance and rooting characteristics on the drought tolerance of Douglas-fir. Plant-available water capacity (PAWC), the water content between field capacity and wilting point (Cousin et al. 2022; Silva et al. 2014; Veihmeyer and Hendrickson 1927), is an important site factor. This capacity indicates the size of the water reservoir that trees can use (Cousin et al. 2022). A high PAWC could have a positive effect on the soil water content during a drought and thus on the relatively extractable soil water (see Bréda et al. 2006), as a larger reservoir reduces the risk of fast water depletion. However, a requirement for this is that the soil water reservoir was sufficiently filled with water before the drought. The few studies conducted thus far on the influence of PAWC on the drought tolerance of Douglas-fir did not show a clear pattern. While Sargent et al. (2014b) found partially positive effects of higher PAWC, there was no clear effect of water storage capacity observed by Huang et al. (2017). Roots absorb the water needed by trees and, depending on the rooting depth, enable the use of deeper water reserves in the soil. Thus, rooting characteristics are important factors in our understanding of reductions in soil water content and the related drought effects on trees. A reduced rooting depth was found for Douglas-fir in soils with a high clay content (Köstler et al. 1968). Studies on several tree species have indicated that deeper rooting increases drought tolerance (Brinkmann et al. 2019; Kahmen et al. 2022; Nardini et al. 2016). However, Douglas-fir has been less investigated in this context. Therefore, the effects of PAWC and rooting characteristics on drought tolerance should be further investigated.

Drought stress tolerance of trees can be assessed by different methods, such as studying mortality rates (Allen et al. 2010) or growth responses to drought. Often, retrospective or current growth data of radial stem growth are used since trees under drought stress typically reduce photosynthesis and carbon allocation to the stem (Bréda et al. 2006; McDowell et al. 2008; Waring 1987). In this context, a frequently used method to analyze the growth response to drought is the framework of the resilience concept, according to Lloret et al. (2011). Thereby, the

indices resistance (R_t), recovery (R_c), and resilience (R_s) are derived from radial stem growth data before, during, and after severe drought events (for more details, see Section 2.5). They quantify the ability of trees to maintain stem growth during a stress event, such as drought (R_t), how well stem growth can recover after drought (R_c), and the extent to which the tree can return to pre-disturbance growth after drought (R_s) (Elfstrom and Powers 2023; Lloret et al. 2011; Pretzsch 2019).

In this study, we analyzed the interannual radial stem growth responses of Douglas-fir for selected severe to extreme drought events over the past two decades (2003/04 and 2018) along gradients of two site characteristics: soil texture (seven sites, dominated by sand, silt, loam, or clay) and PAWC. In addition, the influence of selected rooting characteristics (rooting depth and fine root density) on Douglas-fir was examined. For sites where both Douglas-fir and Norway spruce were present, we compared the growth responses of both species.

We tested the following four hypotheses:

Interannual stem growth responses of Douglas-fir to severe drought are less resistant, recovering, and resilient (1) on clayey soil compared to sandy, loamy, and silty soils, (2) with decreasing PAWC, and (3) with decreasing rooting depth and fine root density. (4) Douglas-fir is more tolerant to severe drought than Norway spruce in terms of resistance, recovery, and resilience.

2 Material and methods

2.1 Study sites

Stand and site selection were based on the following criteria: (i) Douglas-fir stands or Douglas-fir–Norway spruce stands, (ii) similar age of stands, and (iii) comparable previous management in the form of crop tree-oriented thinning. The criteria for site conditions were (iv) soil texture gradient from sand to clay and (v) spatial proximity and comparable elevation (comparable weather conditions). Thus, the drought responses of Douglas-fir at sites with different soil textures and PAWC can be compared with each other.

All study sites are located in southern Germany (Baden-Württemberg) in the Rammert Growth District, a mountain range of the Triassic “Keuperbergland” in the Tübingen Forest District (48°27'N, 8°58'E). Site conditions vary considerably in this region. To minimize the influence of different site climates on tree growth, all study sites were chosen in close proximity within a radius of 1 km at an elevation of 500–520 m above sea level. The area is characterized by a warm, temperate climate with warm summers and no recurrent dry season (Rubel et al. 2017). The mean annual temperature from 1991 to 2020

was 9.3 °C, recorded at the nearest weather station of the German Meteorological Service (Hechingen, elevation 517.5 m a.s.l.), with a mean annual precipitation of 806.4 mm (DWD 2021).

In total, seven sites were studied, located in four forest stands (FS1 to FS4) and differing in soil types and textures (gradient from sand to clay), as well as water balance (Table 1). Stands FS2 to FS4 contained one site each. Stand FS1 had four sub-areas, each with a different site. At each site, one soil profile was dug to determine the soil's physical and rooting characteristics. The profile wall was located at the border of the outer to the middle third of the crown radius of an investigated Douglas-fir at a location representative of the site (Arbeitskreis Standortskartierung 2016). For this purpose, preliminary exploration was carried out using areal soil coring.

At the soil profile wall, soil physical characteristics such as soil texture, bulk density, and skeletal content were determined for each soil horizon down to a depth of 1 m according to the Arbeitskreis

Standortskartierung (2016) and Ad-hoc-AG Boden (2005). The PAWC (mm) for the horizons was calculated according to Ad-hoc-AG Boden (2005) based on soil texture, bulk density, and humus content. For this calculation, PAWC values derived from samples of the forest soil survey in Baden-Württemberg were used (Arbeitskreis Standortskartierung 2016; Puhlmann and von Wilpert 2011). The total PAWC for the site was determined by considering the thickness of the soil horizons and the respective skeletal content. In addition, coarse and fine roots were counted at the soil profile wall using counting squares (5×5 cm), with fine roots defined by diameters <2 mm (Böhm 1979). The PAWC was calculated down to the effective rooting depth, where the threshold of three fine roots per dm² was reached (Arbeitskreis Standortskartierung 2016). Superordinate soil texture information was attributed to soil depth from 0 to 1 m (sand, silt, clay, and loam). Soil types were classified according to the World Reference Base for Soil Resources (IUSS Working Group WRB 2015) (Table 1).

Table 1 Soil and rooting characteristics of the seven study sites

Site abbreviation ^a	Sand	Loam	Silt1	Silt2	Silt3	Clay1	Clay2
Number of forest stand	FS1	FS4	FS1	FS1	FS2	FS1	FS3
Relief	Plain	SE-upper slope	Plain	NNE-middle slope	NNE-middle slope	N-middle slope	SE-lower slope
Slope (°)	2	7	3	9	6	12	5
Aspect (°)	343	143	4	24	20	354	144
Sites^b							
Soil type (classification according to WRB)	Cambisol (epidystric, endoskeletal)	Planosol (albic, ruptic, epidystric)	Stagnic cutanic Luvisol (ruptic, epidystric, endosiltic)	Cambisol (endoeutric, ruptic)	Cutanic Luvisol (ruptic, hyperdystric, episiltic)	Vertic Cambisol (eutric, ruptic, epiclayic)	Vertic stagnic Cambisol (eutric, ruptic)
<i>Main soil texture</i>	<i>Sand</i>	<i>Loam</i>	<i>Silt</i>	<i>Silt</i>	<i>Silt</i>	<i>Clay</i>	<i>Clay</i>
Soil textures	0–40 cm: loamy sand deeper than 40 cm: sandstone slabs (parent material)	0–41 cm: sandy loam 41–100 cm: silt clay loam (parent material)	0–40 cm: silt loam 40–70 cm: silt clay loam 70–100 cm: clay (parent material)	0–41 cm: loam 41–100 cm: silt loam (parent material)	0–38 cm: silt loam 38–100 cm: silt clay loam	0–20 cm: loam 20–75 cm: clay 75–100 cm: clay (parent material)	0–34 cm: loam 34–82 cm: clay 82–100 cm: clay (parent material)
<i>PAWC (mm)</i>	<i>50</i>	<i>88</i>	<i>67</i>	<i>101</i>	<i>85</i>	<i>44</i>	<i>90</i>
<i>PAWC-level</i>	<i>Very low</i>	<i>Low</i>	<i>Low</i>	<i>Medium</i>	<i>Low</i>	<i>Very low</i>	<i>Low</i>
<i>Effective rooting depth (cm)</i>	<i>30</i>	<i>65</i>	<i>50</i>	<i>95</i>	<i>45</i>	<i>35</i>	<i>50</i>
<i>Fine root density (n/dm²)</i>	<i>6.8</i>	<i>10.0</i>	<i>4.7</i>	<i>14.6</i>	<i>6.4</i>	<i>11.1</i>	<i>9.2</i>

The four predictors whose influence on growth response indices to drought for Douglas-fir were primarily investigated are written in italics

^a Site abbreviations according to main soil texture for soil depth from 0 to 1 m

^b WRB World Reference Base for Soil Resources (IUSS Working Group WRB 2015), soil textures according to FAO (2006), main soil texture in the range of 0–1 m soil depth, PAWC Plant-available water capacity, PAWC-level according to Arbeitskreis Standortskartierung (2016), effective rooting depth: up to the limit of three fine roots per dm² (Arbeitskreis Standortskartierung 2016), mean fine root density in 0–40 cm soil depth

2.2 Identification and characterization of drought years

To identify drought years, two drought indices were applied. The de Martonne aridity index (DMI) (DeMartonne 1926) considers the sum of precipitation (P [mm]) and mean temperature (T [°C]) of a period

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

and has often been used in studies for this purpose (Rais et al. 2014; Vitali et al. 2017). We calculated the DMI using data from the nearby weather station of the German Meteorological Service in Hechingen (DWD 2021). The DMI only considers the drought, which refers to climate. However, soils have different PAWC and thus different abilities to store plant-available water. This can result in different soil water deficits even under the same weather conditions. We have therefore also evaluated the soil moisture index (SMI). SMI values are determined and provided for Germany by the Helmholtz Centre for Environmental Research–UFZ (UFZ 2021). Based on meteorological data from the German Meteorological Service the local soil moisture for the entire root zone is estimated by the UFZ using the mesoscale hydrological model (mHM) (Samaniego et al. 2010, 2013). Hydrological processes such as interception, snow accumulation, soil water dynamics, groundwater recharge and storage are comprised (Zink et al. 2016). The modeled daily soil moisture data are transformed into the SMI, which varies between 0 and 1. The SMI represents the percentile of the simulated soil moisture value (moving average of the preceding 30 days) compared to a 60-year soil moisture reconstruction (1954–2013) (Zink et al. 2016). Decreasing SMI values indicate an increase in drought (Samaniego et al. 2013). This index is determined for all regions of Germany as interpolated grid data with a resolution of 4×4 km². The SMI is provided for the topsoil (uppermost 25 cm) and for the total soil (down to approximately 180 cm, depending on the soil properties) (Zink et al. 2016). We evaluated both SMI indices for the area of our study sites to identify drought years. Soil drought, but also rewetting of soils after drought, is more quickly noticeable in the topsoil. However, deeper soil layers and thus the SMI for the total soil are crucial for the survival of trees during severe drought periods because deeper roots then take up a significantly higher proportion of the required water (Warren et al. 2005).

Drought indices were derived for the study period from 2000 to 2020. We analyzed the mean values of growth-determining periods, in particular the period from May to August (Vitali et al. 2017; Zang et al. 2011) and the course over that year. In the overall analysis of the drought indices (DMI, SMI topsoil, and SMI total soil) (Fig. 1a), the years 2003, 2004, and 2018 proved to be pronounced drought

years. Drought during the growing season was more severe in 2018 than in 2003/04 in the study area (Figs. 1 and 2) but also in almost all regions of Central Europe (Bolte et al. 2021; Schuldt et al. 2020). In 2003, severe to extreme drought occurred at our sites from August to September. After a slight recovery during winter 2003/04, the subsequent summer of 2004 was again very dry. In contrast, 2018 was characterized by several months of extreme drought, starting at the beginning of summer and continuing into the winter of 2018/19 (Fig. 2).

2.3 Genetic analysis

For the study of drought tolerance, information on the provenances of the Douglas-fir trees examined is important. Significant growth differences among those with different origins have been documented by studies in North America, as well as by various Douglas-fir provenance trials in Europe (Klesse et al. 2020; Kownatzki et al. 2011; Lavender and Hermann 2014). Tree ring growth in response to drought, tolerance to drought periods, and water-use efficiency is influenced by provenance (Eilmann et al. 2013; Hintsteiner et al. 2018; Jansen et al. 2013; Lavender and Hermann 2014; Martinez Meier et al. 2008; Sergent et al. 2014a). Therefore, we performed a genetic analysis of Douglas-fir in all studied stands and thus in all study sites.

Depending on the size of the sampled stands, 20–36 Douglas-fir trees per stand were genetically tested to determine their origin. For this purpose, we collected cambium samples at the base of the trunk using a punch with a diameter of 2 cm. The samples were genetically analyzed in the molecular genetic laboratory of the Institute of Silviculture at the University of Natural Resources and Life Sciences (BOKU) in Vienna, Austria. Overall, 13 highly variable microsatellite loci were used to investigate the origin of Douglas-fir. These 13 loci, as well as primers for their amplification by PCR, were developed by Slavov et al. (2004). Details of the analytical procedure used can be found in Neophytou (2019), Hintsteiner et al. (2018), and van Loo et al. (2015). A population genetic analysis was carried out based on the genotypes identified and the genotypic data of 38 reference populations from the area of origin (Neophytou 2019).

All genotyped trees of all four studied stands comprising the seven study sites could clearly be assigned to the coastal variety of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*). Douglas-fir trees in the four studied stands were genetically very similar at the 13 microsatellite loci analyzed. No significant genetic differentiation was detected among the four stands (Neophytou 2019). Therefore, Douglas-fir trees from the seven study sites were pooled for all subsequent analyses.

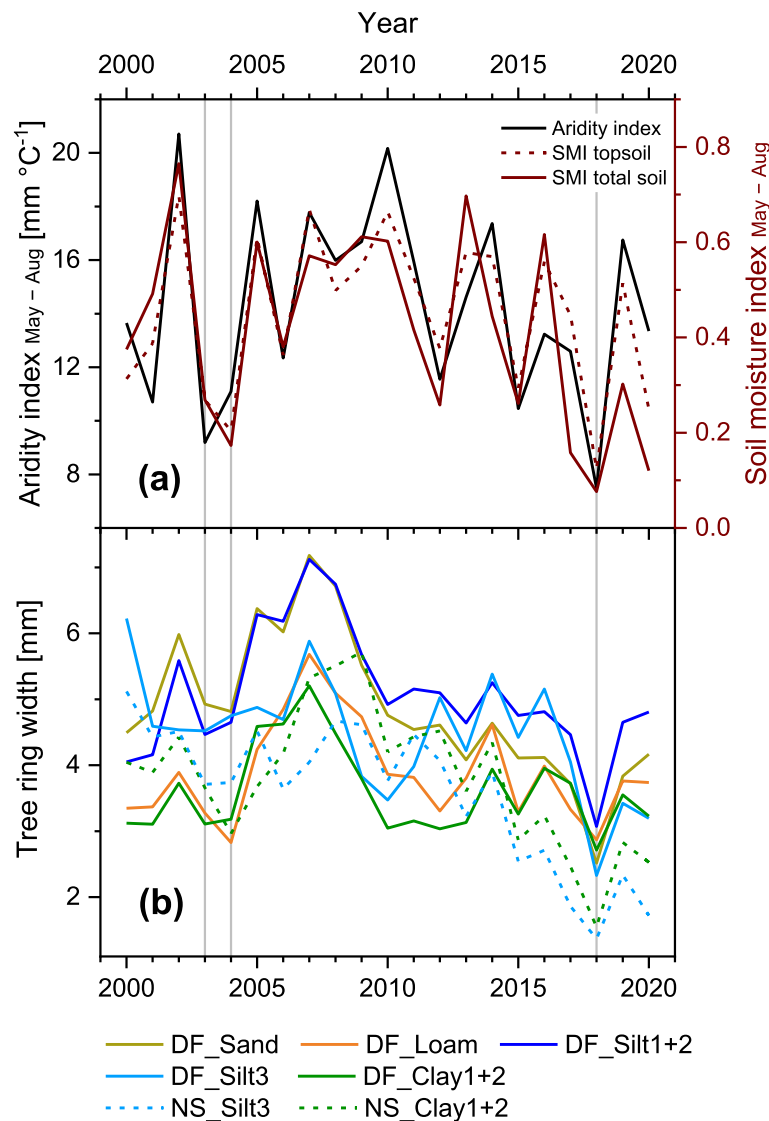


Fig. 1 **a** De Martonne aridity index and soil moisture index (SMI) for the region of the study sites calculated from May to August in each year. They indicate severe drought years. **b** Mean raw tree ring width chronologies of Douglas-fir (DF) and Norway spruce (NS), classified according to the main soil texture. Vertical gray lines mark the severe drought years 2003, 2004, and 2018

2.4 Tree ring data

The studied stands were 40–55 years old. At each of the seven sites, we sampled and measured 15 healthy Douglas-fir trees of social tree classes 1 or 2 (predominant or dominant trees) (Kraft 1884). At site Clay1, we sampled only 12 trees. At three of the seven sites, 15 healthy Norway spruce trees of social tree classes 1 or 2 were sampled. Both tree species were spatially separated at Clay1 and Clay2 and presented in the group mixture or the individual tree mixture at Silt3. From each tree, two cores with a diameter of 5 mm were collected with increment borers (Haglöf, Sweden) at a breast height of 1.3 m, vertical to the slope direction on opposite sides. A total of

294 cores were collected from 147 trees (102 Douglas-fir and 45 Norway spruce trees). The tree height and height of the crown base of each tree were determined with a Vertex (Haglöf, Sweden), and the diameter at breast height (DBH) was measured (Table 2). In addition, we determined stand characteristics (stand density, stand basal area, DBH and tree height refer to the tree with quadratic mean diameter). These stand data are based on a DBH-full inventory of a representative stand area for each site. Yield classes were derived from the growth tables for Baden-Württemberg (Forstliche Versuchs- und Forschungsanstalt BW 2001). Input parameters for this were the measured heights and the age (determined from

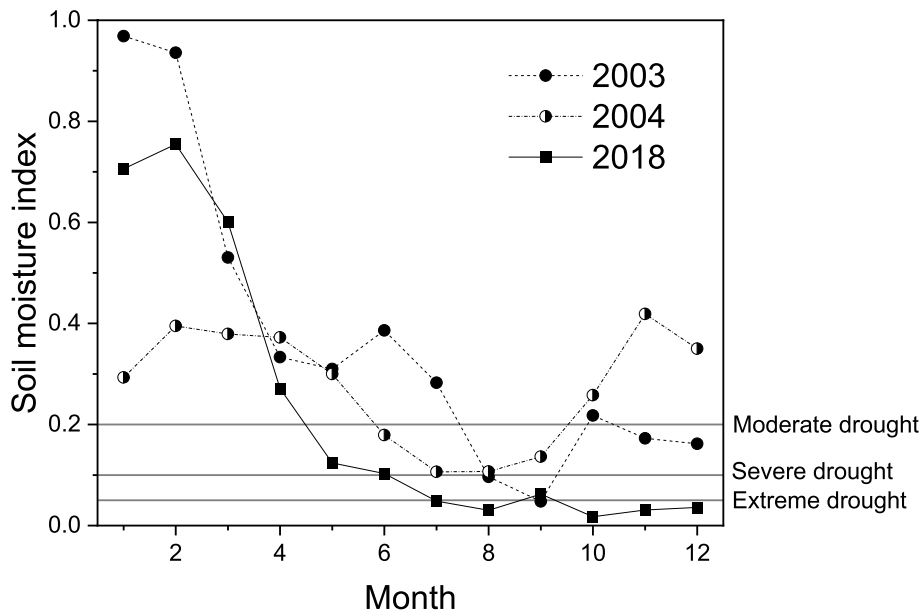


Fig. 2 Annual course of soil moisture index for the total soil (down to approximately 1.8 m) in the studied severe drought years; drought classes (moderate to extreme) according to Zink et al. (2016)

Table 2 Tree and stand characteristics of the study sites. At three of the seven sites, in addition to Douglas-fir, Norway spruce was also present

Site abbreviation	Sand	Loam	Silt1	Silt2	Silt3	Clay1	Clay2
Sampled trees: Douglas-fir (DF)^a							
N _{Tree}	15	15	15	15	15	12	15
DBH _{Tree} (cm)	48.6 (0.14)	35.0 (0.12)	44.9 (0.16)	54.1 (0.12)	59.4 (0.19)	37.5 (0.13)	33.5 (0.15)
H _{Tree} (m)	30.9 (0.57)	25.7 (0.48)	28.3 (0.65)	32.4 (0.65)	35.1 (0.39)	27.9 (0.54)	26.1 (0.61)
Crown length _{Tree} (m)	18.2 (0.62)	14.7 (0.47)	17.0 (0.62)	19.0 (0.76)	19.3 (0.59)	14.8 (0.55)	14.6 (0.54)
Age _{Tree} based on cores	42	35	40	42	49	42	37
Sampled trees: Norway spruce (NS)^a							
N _{Tree}					15	15	15
DBH _{Tree} (cm)					44.1 (0.14)	34.5 (0.12)	36.7 (0.16)
H _{Tree} (m)					31.0 (0.52)	26.5 (0.38)	27.1 (0.57)
Crown length _{Tree} (m)					15.4 (0.84)	13.3 (0.52)	14.8 (0.53)
Age _{Tree} based on cores					51	47	49
Stand characteristics^b							
N (ha ⁻¹)	326	840	379	392	300	416	770
BA (m ² ha ⁻¹)	26.0	29.5	35.5	33.0	35.8	26.6	29.8
DBH _g DF (cm)	41.4	32.8	41.3	49.7	56.1	36.0	28.7
H _g DF (m)	26.7	24.6	26.6	31.6	33.5	25.5	24.0
Yield class DF (m ³ a ⁻¹ ha ⁻¹)	18–19	17	17–18	19	19	16	17
DBH _g NS (cm)					38.4	31.6	36.5
H _g NS (m)					28.1	24.9	26.3
Yield class NS (m ³ a ⁻¹ ha ⁻¹)					18–19	17	17

^a N Number of cored trees, DBH Stem diameter at breast height, H Tree height, Crown length Length of green tree crown (Crown base: height of the first living primary branch), values for these characteristics: arithmetic means (in brackets: standard error SE), based on measurement 3/2021; Age Number of years derived from the oldest annual tree ring in the cores per site until 2020 (actual tree age is higher due to sampling at breast height)

^b N or BA Number of trees or basal area per hectare, DBH_g Diameter at breast height and H_g Tree height refer to the tree with quadratic mean diameter, Yield class Mean total volume production per year up to age 100, based on Forstliche Versuchs- und Forschungsanstalt BW (2001), DF Douglas-fir, NS Norway spruce

the number of years derived from the cores plus 5 years, because the cores were taken at 1.3 m). Cores were prepared with a core-microtome (WSL, Switzerland) (Gärtner and Nievergelt 2010), and ring widths were measured with WinDENDRO 2019 (Regents Instruments Inc., Canada). Cross-dating accuracy was checked visually. This method ensured a high quality of our tree chronologies with drought years that were clearly pronounced in radial growth. In addition, the quality of the chronologies was assessed by calculating the Gleichläufigkeit (Schweingruber 1988).

2.5 Growth responses to drought

The indices resistance (R_t), recovery (R_c), and resilience (R_s), according to Lloret et al. (2011), were used to study growth responses to drought. These indices allow quantification of the effects of stress events, such as severe drought, on radial stem growth. Calculations were based on tree ring width data (mean chronologies of single trees) using the following formulae.

$$\text{Resistance } R_t = \frac{Dr}{PreDr} \quad (2)$$

$$\text{Recovery } R_c = \frac{PostDr}{Dr} \quad (3)$$

$$\text{Resilience } R_s = \frac{PostDr}{PreDr} \quad (4)$$

“ Dr ” is the tree ring width during a stress period (drought period in this study), which, in our calculations, included the increment of 2018 and the mean increment of 2003 and 2004. “ $PreDr$ ” includes the mean tree ring width in the period before the drought period, and “ $PostDr$ ” the mean after the drought period. The following results are based on calculations with a 2-year “ $PreDr$ ” (2016/17 and 2001/02) or “ $PostDr$ ” (2019/20 and 2005/06) period length (in accordance with, e.g., Bottero et al. 2021; Ding et al. 2017; Heklau et al. 2019; Keyser and Brown 2016; Vitali et al. 2017; Vitasse et al. 2019). There are several reasons for this: (i) Disturbing events, such as the drought year 2015 (Fig. 1a) (Zink et al. 2016) would be included in the calculation if the reference period length was longer. (ii) With the accumulation of drought years, as occurred in Central Europe in recent years (Bolte et al. 2021), the ability of trees to recover rapidly is important. A relatively short reference period length of 2 years represents this better than longer periods, whereas a shorter reference period of 1 year is not sufficiently representative. (iii) To validate our results, we calculated other frequently used “ $PreDr$ ” and “ $PostDr$ ” period lengths (4, 6, and 8 years) in addition to the 2-year

reference period for the 2003/04 drought (Schwarz et al. 2020). Calculations with longer reference periods led to the same conclusions. The analyses presented in Section 3 are based on calculations with raw data in accordance with other studies (Lloret et al. 2011; Vitali et al. 2017; Zang et al. 2014). In comparable studies with a 2-year reference period, the use of detrended data led to similar results as calculations with raw data (Bottero et al. 2021; Vitali et al. 2017).

2.6 Statistical analysis

Linear mixed-effects models (LMM) were used to evaluate the effects of soil and rooting characteristics on growth response indices to drought. LMM allows for the estimation of possible random effects and thus accounts for the non-independence of the data. Statistical analyses using LMMs were conducted with R packages “lme4” (Bates et al. 2015), “lmerTest” (Kuznetsova et al. 2017), and “performance” (Lüdtke et al. 2021). Model optimization was performed using the maximum likelihood method. First, a null model containing only random effects was tested. Then, the fixed effects of the respective model equation were included and the best-fitting model was determined using a model simplification procedure. For this model selection, the Akaike Information Criterion (AIC) was used to evaluate the relative goodness of fit of the models (Akaike 1974). Possible problems with collinearity in the models were checked using the variance inflation factor (VIF) (Zuur et al. 2010). $VIF > 10$ was used as the threshold for critical collinearity (Dormann et al. 2013). If a model showed high collinearity, biological reasons for the removal of predictors from the model played a decisive role (Harrison et al. 2018; Zuur et al. 2010). Normality and homoscedasticity were checked visually using plots of residuals vs. fitted values (Zuur et al. 2010).

We used models that included the predictors of soil texture, PAWC, effective rooting depth, and fine root density, and thus data on the site level. In addition, covariates at the tree level (DBH, height, and crown length) were also included as predictors to estimate their influence (Eq. (6)). Soil texture was a categorical variable with four levels (clay, loam, sand, silt). The other predictors were quantitative variables. The predictor soil texture was analyzed in a separate model without integrating the other predictors (Eq. (5)). The reason for this was the high collinearity between soil texture and other variables. If soil texture was integrated as an additional predictor in Eq. (6), the VIF would be > 10 for four predictors (soil texture, effective rooting depth, fine root density, height). This led to implausible results. In the models we used (Eqs. (5) to (7)), the VIF is below 10 for all predictors.

In the Eqs. (5) to (7), R (i.e., R_t , R_c , or R_s) indicate the response variables, a_0 is the overall intercept, b_1 to b_5 are the coefficients to be estimated of the fixed effect predictors at site level s (explanatory variables), and c_1 to c_3 are the coefficients to be estimated for the fixed effect predictors at tree level t (covariates). In addition, possible random effects were considered. In the Eqs. (5) to (7), α indicates the random effects at site level s (seven sites) and ε is the independent error term. The variances

$$R = a_0 + b_2PAWC_s + b_3RDepth_s + b_4RDens_s + c_1DBH_{st} + c_2Height_{st} + c_3CL_{st} + \alpha_s + \varepsilon_{st} \tag{6}$$

of these random effects were estimated during model fitting.

The model for estimating the influence of soil texture (ST) on the growth response of Douglas-fir to drought (hypothesis 1) was

$$R = a_0 + b_1ST_s + \alpha_s + \varepsilon_{st} \tag{5}$$

To study the influence of PAWC and rooting characteristics (effective rooting depth (RDepth) and mean fine root density in 0–40 cm soil depth (Rdens)) on the growth response of Douglas-fir to drought (hypotheses 2 and 3) we used Eq. (6). In addition to these predictors at the site-level s , covariates at the tree level t (DBH, height, and crown length (CL)) were also included as predictors. With this model, we only analyzed the drought of 2018, as values for the tree and rooting parameters for 2003/04 were not available.

To analyze the influence of tree species (SP: categorical variable, Douglas-fir or Norway spruce) on the growth response to drought depending on soil texture (hypothesis 4) we used Eq. (7). The three sites where both tree species occurred were considered.

$$R = a_0 + b_5ST_s * SP_{st} + \alpha_s + \varepsilon_{st} \tag{7}$$

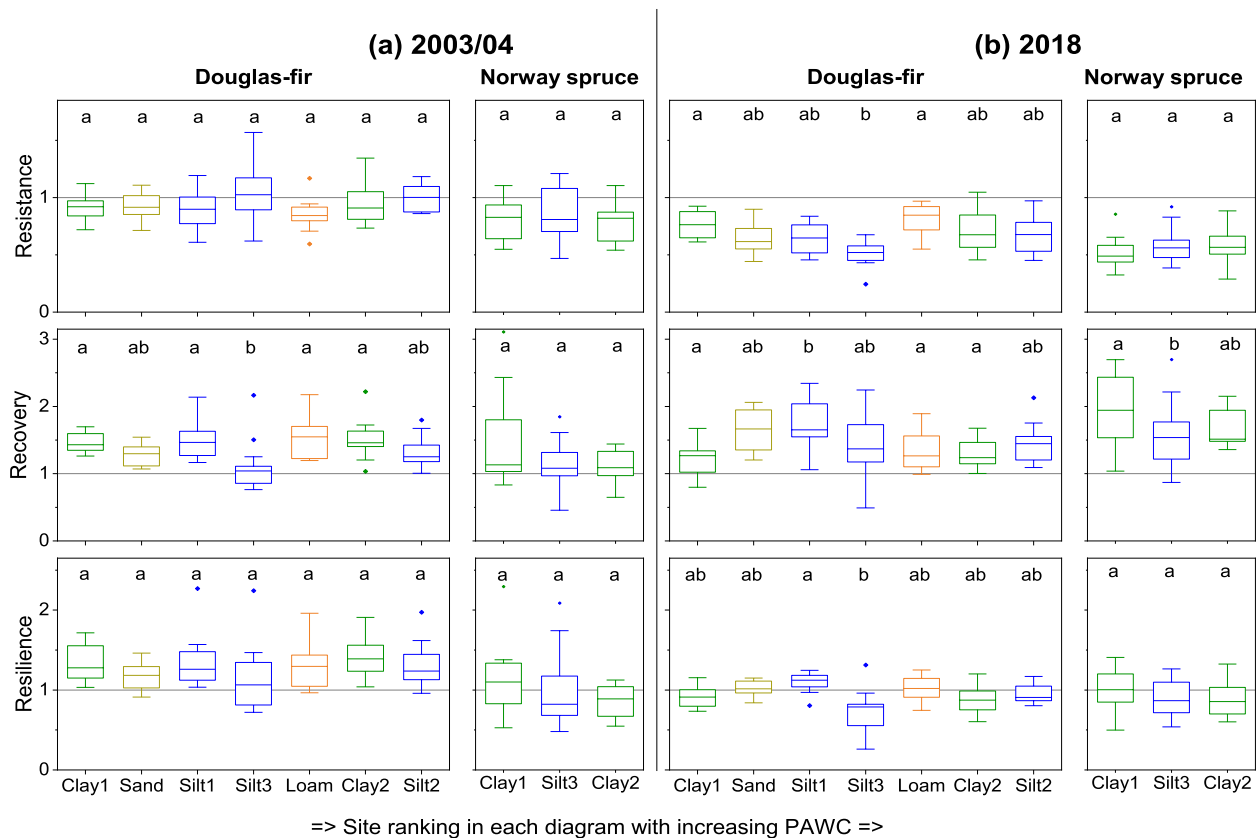


Fig. 3 Site-dependent growth responses of Douglas-fir and Norway spruce in terms of resistance, resilience, and recovery (see Section 2) to drought periods 2003/04 and 2018. Boxplot colors indicate different main soil textures (green: clay, yellow: sand, orange: loam, blue: silt). Different lowercase letters indicate a significant difference among sites (same tree species, same drought year), $p < 0.05$. R -values of 1 (gray line) indicate unchanged tree ring widths during the drought period. Length of reference periods: 2 years before and after the drought period. Ring growth in the drought years 2003 and 2004 are averaged. Box plots are drawn with whiskers within 1.5 IQR values

Growth response indices to drought shown in Fig. 3 were tested for significant differences between several sites separately for each drought event in multiple comparisons by an analysis of variance (ANOVA) and a subsequent post-hoc test ($p < 0.05$). A Games–Howell test with a p-value correction according to Holm was used as post-hoc test. Pairwise comparisons between the droughts of 2003/04 and 2018 were performed using Welch's t -test ($p < 0.05$). The three sites with Douglas-fir and Norway spruce were evaluated together. All statistical analyses were carried out using R version 4.2.1 (R Core Team 2022). The data on which the analyses were based are available in a repository (Spangenberg et al. 2024).

3 Results

3.1 Growth responses depending on soil texture

In Douglas-fir, during the drought years 2003 and 2004, the sandy site had a significantly lower R_s compared to the clay-dominated sites (Table 3). There were no other significant influences of the soil texture compared to the reference soil texture clay for 2003/04. For the drought year 2018, the influence of soil texture was more pronounced. Silt-dominated sites had significantly lower R_t than clayey sites. In addition, a significantly higher R_c was found on sandy and silty sites compared to clayey sites. There were no significant differences in R_s values between soil textures for 2018.

When comparing the seven individual sites, Douglas-fir at the silt-dominated site Silt3 differed significantly from other sites in some of the growth response indices (Fig. 3). There, during the drought event in 2003/04 mean R_t , R_c , and R_s values for Douglas-fir were close to 1. At the other sites, with the exception of Silt2, Douglas-fir showed a slight decrease in radial increment during the drought in 2003/04, and at four sites significantly higher R_c values after this drought compared to Silt3. In contrast, in 2018, the R_t and R_s values of Douglas-fir at site Silt3 were lowest during this drought year compared to the other six sites (in a few cases, significantly lower). In addition, Douglas-firs at Silt3 showed high variability in some of the growth response indices for 2003/04 and 2018.

3.2 Growth responses depending on PAWC and rooting

Significant influences of PAWC and rooting on growth response indices of Douglas-fir during the drought 2018 were found for the R_t and R_s values (Table 4). Higher PAWC resulted in lower R_t and R_s . Higher effective rooting depth increased R_s . Mean fine root density in 0–40 cm soil depth had no significant influence on growth response indices for the drought year 2018.

Table 3 Results of the mixed-effects model using Eq. (5): Effect of soil texture on growth response indices to drought for Douglas-fir (see hypothesis 1)

	Resistance		Recovery		Resilience	
	R_t		R_c		R_s	
Drought 2003/04						
Fixed effects	Estimate	<i>P</i> value	Estimate	<i>P</i> value	Estimate	<i>P</i> value
a_0 (Intercept)	0.934	< 0.001	1.487	< 0.001	1.379	< 0.001
b_1 (Loam) ^a	−0.079	0.122	0.034	0.814	−0.084	0.341
b_1 (Sand) ^a	−0.013	0.793	−0.212	0.165	−0.212	0.018
b_1 (Silt) ^a	0.040	0.295	−0.178	0.125	−0.125	0.062
Random effects	Variance		Variance		Variance	
α_s	< 0.001		0.008		< 0.001	
ε_{st}	0.024		0.063		0.075	
Drought 2018						
Fixed effects	Estimate	<i>P</i> value	Estimate	<i>P</i> value	Estimate	<i>P</i> value
a_0 (Intercept)	0.728	< 0.001	1.258	< 0.001	0.895	< 0.001
b_1 (Loam) ^a	0.069	0.322	0.057	0.673	0.129	0.340
b_1 (Sand) ^a	−0.084	0.233	0.375	0.022	0.129	0.342
b_1 (Silt) ^a	−0.114	0.048	0.278	0.023	0.028	0.776
Random effects	Variance		Variance		Variance	
α_s	0.002		0.004		0.009	
ε_{st}	0.018		0.100		0.025	

The estimated coefficients for the respective comparison with the reference soil texture clay and the variance of the random effects are listed. Significant fixed effect estimates ($p < 0.05$) are printed in bold

^a Reference is soil texture clay

Table 4 Results of the mixed-effects model using Eq. (6): Effect of plant-available water capacity (PAWC), rooting, and tree characteristics on growth response indices to the drought 2018 for Douglas-fir (see hypotheses 2 and 3)

Drought 2018		Rt (Resistance)		Rc (Recovery)		Rs (Resilience)	
Fixed effects		Estimate	<i>P</i> value	Estimate	<i>P</i> value	Estimate	<i>P</i> value
Predictors at site level	a_0 (Intercept)	1.089	< 0.001	0.206	0.326	1.785	< 0.001
	b_2 (PAWC)	-0.002	0.037			-0.006	< 0.001
	b_3 (effective rooting depth)	0.003	0.085			0.006	0.002
	b_4 (fine root density)	0.007	0.297			-0.014	0.096
Covariates at tree level	c_1 (DBH)	-0.006	0.022	0.028	< 0.001	0.007	0.031
	c_2 (height)	-0.005	0.436			-0.051	< 0.001
	c_3 (crown length)					0.036	< 0.001
Random effects		Variance		Variance		Variance	
	α_s	<0.001		0.054		<0.001	
	ε_{st}	0.015		0.067		0.023	

The estimated coefficients for fixed-effect predictors in the best-fit LMM and the variance of random effects are listed. Significant fixed effect estimates ($p < 0.05$) are printed in bold

3.3 Growth responses depending on DBH

Predictors at the tree level, especially the DBH, had a significant influence on all three growth response indices of Douglas-fir to the drought in 2018 (Table 4). Thicker trees had a significantly lower Rt but higher Rc and Rs values. In contrast, tree height and crown length only had a significant influence on Rs. Lower tree height and higher crown length increased Rs.

3.4 Growth responses depending on tree species

A comparison between Douglas-fir and Norway spruce was possible at the two clayey sites (Clay1 and Clay2) and at one of the silty sites (Silt3). At the clay-dominated sites, Rt, Rc, and Rs for Norway spruce were significantly lower than for Douglas-fir during the drought in 2003/04 (Table 5). The extreme drought year 2018 led to a significantly stronger growth decrease for

Table 5 Results of the mixed-effects model using Eq. (7): Effect of tree species on growth response indices to drought depending on soil texture (see hypothesis 4)

		Resistance		Recovery		Resilience	
Drought 2003/04		Rt		Rc		Rs	
Soil texture		Estimate	<i>P</i> value	Estimate	<i>P</i> value	Estimate	<i>P</i> value
Clay	Fixed effects						
	a_0 (Intercept)	0.934	< 0.001	1.488	< 0.001	1.379	< 0.001
	b_5 (Norway spruce) ^a	-0.121	0.014	-0.232	0.022	-0.390	< 0.001
Silt	Fixed effects						
	a_0 (Intercept)	1.039	< 0.001	1.101	< 0.001	1.126	< 0.001
	b_5 (Norway spruce) ^a	-0.172	0.011	0.027	0.842	-0.136	0.270
Random effects		Variance		Variance		Variance	
	α_s	< 0.001		< 0.001		< 0.001	
	ε_{st}	0.033		0.140		0.112	
Drought 2018		Rt		Rc		Rs	
Soil texture		Estimate	<i>P</i> value	Estimate	<i>P</i> value	Estimate	<i>P</i> value
Clay	Fixed effects						
	a_0 (Intercept)	0.726	< 0.001	1.260	< 0.001	0.893	< 0.001
	b_5 (Norway spruce) ^a	-0.191	< 0.001	0.561	< 0.001	0.056	0.325
Silt	Fixed effects						
	a_0 (Intercept)	0.511	< 0.001	1.406	< 0.001	0.718	< 0.001
	b_5 (Norway spruce) ^a	0.070	0.154	0.162	0.239	0.162	0.041
Random effects		Variance		Variance		Variance	
	α_s	< 0.001		< 0.001		< 0.001	
	ε_{st}	0.018		0.139		0.046	

Only the three sites where both tree species occurred were considered (Clay1, Clay2, Silt3). The estimated coefficients for the comparison of Norway spruce with the reference tree species Douglas-fir and the variance of the random effects are listed. Significant fixed effect estimates ($p < 0.05$) are printed in bold

^a Reference is Douglas-fir

Norway spruce at the clayey sites compared to Douglas-fir. Subsequent recovery, however, was significantly higher for Norway spruce. At the silt-dominated site Silt3, Norway spruce showed significantly lower R_t in 2003/04 and significantly higher R_s in 2018 compared to Douglas-fir. Thus, the differences in growth response indices between the two tree species were more pronounced at the clayey sites than at the silty sites.

When comparing the growth responses of Douglas-fir and Norway spruce between the drought years 2003/04 and 2018, there were similarities and differences (Welch's t -test ($p < 0.05$), Figs. 1 and 3). At the three sites with both tree species, the mean R_t was significantly lower for both tree species in 2018 than in 2003/04 (−33% for Douglas-fir, −34% for Norway spruce, $p < 0.001$). Because the mean R_c of Douglas-fir after 2018 at these three sites was comparable to that of 2003/04 ($p > 0.05$), this resulted in a significantly lower mean R_s for Douglas-fir in 2018 compared to 2003/04 (−36%, $p < 0.001$). The R_c of Norway spruce was higher after 2018 than after 2003/04 (+43%, $p < 0.001$), and therefore, the mean R_s in 2018 was not significantly lower than that in 2003/04 ($p > 0.05$). Thus, the effects of drought on radial growth were mostly stronger in 2018 than in 2003/04.

4 Discussion

This study focused on the influence of two site characteristics (soil texture, PAWC) and two rooting characteristics (effective rooting depth, fine root density in the upper 40 cm of soil) on the annual radial stem growth of Douglas-fir exposed to severe drought events in 2003/04 and 2018. Hypothesis 1, namely lower growth response indices of Douglas-fir on clayey soils compared to sandy, loamy, and silty soils, was found for recovery after the extreme drought in 2018. In contrast, Douglas-fir showed high drought tolerance at the sandy and loamy sites and at two of the three silty sites. One silty site with a comparably low rooting depth showed high drought susceptibility during the extreme drought in 2018. In contrast to hypothesis 2, a higher PAWC reduced the resistance and resilience of Douglas-fir related to the drought in 2018. Hypothesis 3 was confirmed for one of the rooting characteristics; a higher effective rooting depth increased the resilience of Douglas-fir during the 2018 drought. Hypothesis 4 was that Douglas-fir would show higher resistance, recovery, and resilience than Norway spruce. This hypothesis was confirmed for the clayey sites during the severe drought in 2003/04. In contrast, the advantages of Douglas-fir in terms of drought tolerance were less or not provable at the silty site Silt3 for both droughts and for the clayey sites in 2018.

This study confirms the high drought tolerance of Douglas-fir at most sites (Rais et al. 2014; Schwarz et al.

2020; Thomas et al. 2022; Vitali et al. 2017; Zang et al. 2011). The drought intensity in 2003/04 was lower than in 2018 (see Section 2.2, Figs. 1 and 2). During the severe drought in 2003/04, the growth responses of Douglas-fir showed a high drought tolerance for all sites (e.g., the resilience of all sites > 1 , Fig. 3). In contrast, the extreme drought of 2018 led to more severe growth reductions (mean reduction of 32.5%). At most sites, however, we observed a complete or almost complete recovery of radial growth within 2 years after 2018 and, as a result, a resilience close to 1 (Fig. 3). Soil texture, PAWC, and effective rooting depth had significant impacts on the growth response indices of Douglas-fir during the extreme drought in 2018. In contrast to this finding, soil texture played a minor role during the severe drought in 2003/04 (Table 3). This suggests that site characteristics are more important for the drought tolerance of Douglas-fir when exposed to periods of extreme drought.

4.1 Douglas-fir was drought-tolerant on most soil textures—specific observations for clay and silt

There were few significant differences among the soil textures in terms of the growth response of Douglas-fir to drought, and if so, then mainly during the extreme drought year 2018. On the sandy and loamy soils, Douglas-fir returned to pre-drought growth levels within 2 years, even after the 2018 drought, and confirmed its suitability for these sites (Forstliche Versuchs- und Forschungsanstalt BW 2022; Huang et al. 2017). At the two clay-dominated sites, in terms of growth response to drought, Douglas-fir performed average to slightly above average during the drought in 2003/04 (Fig. 3 and Table 3). In contrast, recovery on the clayey soils was significantly lower than on the sandy and silty soils after the extreme drought in 2018 (Table 3). We presume that the reason for these different growth responses between the drought years is the compensation of the reduced rooting depth on clayey soils by an increased lateral expansion of the root system. In soils with a high clay content, Douglas-fir reduces rooting depth (Köstler et al. 1968). In contrast to the previous assumption of low lateral root expansion of Douglas-fir, studies have found large lateral root expansions, especially for compacted soils (Kutschera and Lichtenegger 2013). Less pronounced precipitation events can thus be efficiently absorbed. Anderegg et al. (2013) hypothesized that shallow-rooted plant communities are more vulnerable to severe or extreme drought events (such as 2018) but less susceptible to prolonged moderate drought periods (such as 2003/04). This presumption was confirmed for the clayey sites in our study. In an even more extreme drought event than in 2018, clayey sites for Douglas-fir might be more susceptible to drought compared to deeper rootable

sites. For conifers, a subsequent higher mortality risk is mainly related to reduced recovery ability after drought (DeSoto et al. 2020). Therefore, we see the significantly lower recovery on the clay-dominated soils in 2018 as a warning signal for a higher drought stress risk for possibly stronger drought periods, even though resistance and resilience on clay did not have significantly lower values than on the other soil textures. Both of the clayey sites we investigated were located on slopes. In the case of clayey soils in flat terrain, an increased risk of stagnant water should be expected. Soils with prolonged impeded gas exchange (e.g., Stagnosols) were not part of this study. They are considered critical for Douglas-fir because of the impeded penetration of roots into poorly aerated soil horizons (Köstler et al. 1968; Nicolescu 2019).

Douglas-fir behaved differently at the three silt-dominated sites. Sites Silt1 and Silt2 differed only slightly from the sand- and loam-dominated sites and were quite drought-tolerant in both studied drought periods. In contrast, Silt3 showed the lowest resistance and resilience of all seven sites to drought in 2018 (Fig. 3). The significantly lower resilience at Silt3 compared to Silt1 in 2018 is particularly remarkable. In addition to some similarities between these two silty sites, Silt3 is characterized by a higher silt content in the deeper soil layers, partially less pronounced hydromorphic properties, a higher PAWC, and a higher yield class (Tables 1 and 2). However, Silt3 showed the lowest effective rooting depth of the three silty sites and a low fine root density in the uppermost 40 cm of soil (Table 1). At the same time, the Douglas-firs on this site exhibited the greatest heights, DBHs, and lengths of green crowns (Table 2). Even though the difference of 7 years in the age of the tree must be considered, this comparison suggests that Douglas-fir trees at the productive site Silt3 have invested preferentially in aboveground biomass. This confirms other studies that have found that Douglas-fir trees on more productive sites form lower proportions of fine root biomass to total biomass (Keyes and Grier 1981; Olsthoorn 1991; Tingey et al. 2005; Vogt et al. 1983). The root-to-shoot ratio of trees is largely determined by the supply of resources (Pretzsch 2019). If resource availability changes (e.g., due to an increase in drought events), the adjustment to these changed conditions might be insufficient (Nikolova et al. 2011). In times of extreme drought stress, a comparatively small root system must supply a large canopy, and the large soil water reservoir at this site is accessible only to a limited extent due to the poorly developed root system. We hypothesize that Douglas-fir trees at specific silt-dominated productive sites with unfavorable ratios of above- to belowground biomass are particularly susceptible to extreme drought events.

4.2 Higher PAWC reduced the resilience of Douglas-fir

The positive effect of increasing PAWC on the drought responses of Douglas-fir (cf. hypothesis 2) assumed on the basis of cultivation recommendations (Jenssen 2009; Kölling 2008; Nicolescu 2019) was not confirmed. For the extreme drought in 2018, our LMM analyses showed the opposite; a higher PAWC resulted in lower resistance and resilience (Table 4). Other studies also suggest that a higher PAWC does not automatically lead to higher drought resilience. Modeling of climate change-induced mortality of Douglas-fir in France did not show a significant influence of the available soil water capacity on mortality (Taccoen et al. 2022). A Danish study showed no clear patterns of the influence of the available soil water capacity on the growth of Douglas-fir in dry years (Huang et al. 2017). During drought periods, a high PAWC has a positive effect on drought tolerance only when water is still available in the soil reservoir and when the soil is sufficiently rooted. However, it should be considered that our results are influenced by different soil textures.

4.3 Higher rooting depth increased the resilience of Douglas-fir

This study showed that soil conditions, such as soil texture, clearly affect the rooting depth and fine root density of Douglas-fir, which is in agreement with previous studies (Table 1) (Curt et al. 2001; Keyes and Grier 1981; Köstler et al. 1968; Kutschera and Lichtenegger 2013; Lwila et al. 2021). Furthermore, in our study, a higher effective rooting depth increased the resilience of Douglas-fir during the extreme drought in 2018 (Table 4). Although possible differences in rooting between trees within one site should be considered, this positive effect of rooting depth on resilience is physiologically well comprehensible. Deep and dense root systems allow trees access to larger soil water reserves and ensure higher tolerance towards severe drought events (Bréda et al. 2006). In addition, this result confirms other studies, although most of them were carried out on other tree species. Studies by Nardini et al. (2016), Kahmen et al. (2022), and Brinkmann et al. (2019) have shown that rooting depth, root water uptake depth, and the ability to shift water uptake to deeper soil layers during drought periods significantly influence the drought vulnerability of different tree species. Douglas-fir can root comparatively deeply, e.g., in deep loamy soils, and can also penetrate rock crevices (Köstler et al. 1968; Polomski and Kuhn 1998; Thomas et al. 2015), which enables it to take up larger amounts of water from deeper soil layers (Thomas et al. 2015). In addition, Douglas-fir has the ability to absorb a higher proportion of water

from deeper soil layers during drought periods (Andrews et al. 2012; Warren et al. 2005) and to take water from deeper soil layers more efficiently than Norway spruce (Nadezhdina et al. 2014). This study indicates that a high rooting depth is an important factor in the high drought tolerance of Douglas-fir. Rooting depth depends on tree species and soil conditions but is also influenced by certain silvicultural measures (Kohnle et al. 2019, 2021). Therefore, this result is an important indication of forest management in view of climate change.

In contrast, in the present study, the mean fine root density in the upper 40 cm of the soil had no significant influence on growth response indices to the drought in 2018. Fine root density is subject to stronger dynamics. Fine root propagation depends not only on soil characteristics but also on seasonal growth dynamics, weather and climate conditions, and tree species mixture (Lozanova et al. 2019; Lwila et al. 2023). In addition, Warren et al. (2005) showed that roots of Douglas-fir in the upper 60 cm of the soil take up only a smaller amount of water during drought periods. Therefore, we consider rooting depth during drought periods to be more crucial to drought tolerance than fine root density in the often severely desiccated topsoil.

4.4 DBH as an influencing covariate

In this study, thicker Douglas-fir trees showed lower resistance but higher recovery and resilience (Table 4). Although the stands we studied had slight age differences, our results of a negative linkage of resistance with DBH in Douglas-fir are in agreement with Thurm et al. (2016) and Vernon et al. (2018). While Thurm et al. (2016) suggested a lower wood density of Douglas-fir trees with a larger diameter and thus lower pressure stability of the hydraulic pathways, Vernon et al. (2018) saw the cause in the greater leaf area and the higher water requirement of thicker trees. In these studies, the influence of DBH on recovery and resilience was not investigated. However, considering the positive impact of a lower stand density and thus thinning on DBH-increment, our results are in agreement with studies on the positive effect of thinning on recovery and resilience of conifers (e.g., Elfstrom and Powers 2023; Sohn et al. 2016). After thinning, the remaining trees can develop larger root systems and crowns. This allows these trees to recover faster and more completely, as they can benefit more from the improved water supply after a drought (Sohn et al. 2016). Thus, our result from the studied stands confirms that stem number reduction through (periodic) thinning is a silvicultural strategy to reduce drought stress and to adapt forests to increasingly severe drought periods (Bottero et al. 2017; Moreau et al. 2022; Sohn et al. 2016).

4.5 Limits of the suitability of Douglas-fir as a substitute for Norway spruce

The comparison between Douglas-fir and Norway spruce was carried out at the three sites (Clay1, Clay2, Silt3) that were found to be less drought-tolerant for Douglas-fir than the other four sites during the extreme drought in 2018 (see Section 4.1). Differences between the two species in drought tolerance varied by drought event and soil. They were particularly pronounced at the clayey sites (Table 5). During the drought in 2003/04, Norway spruce showed significantly lower values for all growth response indices at the clayey sites, while in 2018, only resistance was lower. In soils with high clay content, both tree species reduce the rooting depth (Köstler et al. 1968; Polomski and Kuhn 1998). However, the rooting intensity of Douglas-fir is greater than that of Norway spruce (Köstler et al. 1968; Kutschera and Lichtenegger 2013). This more intensive rooting of the topsoil is advantageous during prolonged moderate droughts with occasional, weak rain events, as observed in 2003/04. In contrast, Norway spruce appears to have greater problems with prolonged moderate droughts on clay. However, if the topsoil dries out completely, as may have occurred in 2018, our results suggest that the superiority of Douglas-fir in drought tolerance decreases at clayey sites.

At the silt-dominated site Silt3, Douglas-fir and Norway spruce differed less in growth responses to the droughts than at the clay-dominated sites (Table 5). This result is not consistent with the findings of Nadezhdina et al. (2014), who found that Douglas-fir took up water from deeper soil layers more efficiently than Norway spruce at a silty site. In general, Douglas-fir is able to root deeply in silty soils (Köstler et al. 1968; Kutschera and Lichtenegger 2013). However, at Silt3, only a comparably low rooting depth was found. The reason that Douglas-fir was not found to be more drought resilient than Norway spruce at Silt3 might be an unfavorable root-to-shoot ratio (cf. Section 4.1).

Thus, the finding that Douglas-fir was only partially more drought-tolerant than Norway spruce is probably due to site-specific particularities. In soils suitable for Douglas-fir, such as loam- and sand-dominated soils, it has proven to be more drought-tolerant than Norway spruce (Huang et al. 2017; Stangler et al. 2022). At sites with a high clay content, however, we consider Douglas-fir to be a suitable substitute tree species for Norway spruce only to a limited extent in view of the predicted increase in severe drought events. There, more suitable alternatives should be used.

4.6 Limitations and the need for further research

There were factors that may have influenced our study results: (i) Forest structure, especially tree species

mixture, can affect tree species-specific responses to drought (Pretzsch 2019; Thurm et al. 2016; Vitali et al. 2018). It cannot be excluded that the understory beech trees occurring mainly on sites Clay2 and Loam had an influence on the study results. However, the growth response indices of Clay1 and Clay2 were similar, despite the differences in understory and the resulting differences in the number of trees per hectare and the mean stem diameter (Table 2). (ii) Mast years can reduce the radial increment (Eis et al. 1965; Mencuccini and Piussi 1995). Within the study period, mast years occurred in 2001 and 2018 for Douglas-fir and 2003 for Norway spruce (T. Ebinger, Forst BW, seed collection station, personal communication, 15.12.2021). Our results for the comparison between Douglas-fir and Norway spruce could have been influenced by it. However, our analyses on the influence of site, rooting, and tree characteristics with Douglas-fir only (Sections 4.1, 4.2, 4.3 and 4.4) should have been less influenced by mast years because all sites were probably affected similarly. (iii) Climatic conditions and (iv) tree age have an influence on the effects of drought stress (Bréda and Brunette 2019; Thurm et al. 2016; van der Maaten-Theunissen et al. 2013; Vitali et al. 2017). (v) In addition, the drought tolerance of Douglas-fir trees in the area of origin increases towards the south (Eilmann et al. 2013; Nicolescu 2019). The assignment test to provenances from the natural distribution range showed that all four stands of our study originated from the central area of the range of the coastal variety, located between central Washington and the northern part of California (Neophytou 2019). Therefore, the results of this study should be validated with other mixture ratios, in regions with different climatic conditions, and with Douglas-fir trees of other age classes and provenances.

Further studies should also consider nutrient supply, tree mortality, and drought years recurring in short time intervals. Nutrient supply can influence rooting depth and drought tolerance (Köstler et al. 1968; Sergent et al. 2014b). Frequent drought periods give trees little time to recover and increase the risk of drought damage (Obladen et al. 2021). The effects of drought on trees also depend on the timing of the drought (Anderegg et al. 2013). Even a moderate drought stress event before a pronounced drought year might have a noticeable negative influence on tree vulnerability (Schwarz et al. 2020). Differentiation into pre-drought years, drought years, and post-drought years becomes more difficult when drought years of varying severity accumulate, as occurred in some regions of Germany after 2018 (Bolte et al. 2021). Moreover, the applied method of this study does not allow conclusions about the short-term effects of drought periods on tree growth in the course of a year. Supplementary

methods are necessary to validate the findings of this study.

5 Conclusion

The results of this study indicate that, in the context of climate change, consideration of site and rooting characteristics for high drought tolerance is increasingly important in the cultivation of Douglas-fir. Our study confirms the high drought tolerance and broad physiological amplitude of Douglas-fir (Eckhart et al. 2019). During the severe drought of 2003/04, Douglas-fir revealed only minor growth reductions and high resilience at all seven study sites. Norway spruce showed more severe growth reductions in 2003/04 in our study and in other studies (Vitali et al. 2017; Zang et al. 2014). However, the results of this study provide an important indication for forest management that with increasing severity of drought events (such as the extreme drought in 2018), drought tolerance of Douglas-fir may decrease at specific sites. The cultivation of Douglas-fir in soils with a high clay content should be considered with some caution because of the reduced rooting depth. In addition to clay content, relief is decisive; clay on slopes is less critical than in flat terrain (Nadezhkina et al. 2014). Douglas-fir stands on specific silt-dominated soils with previously sufficient water supply, and the resulting unfavorable root-to-shoot ratios might suffer particularly from a possible increase in severe drought periods. Deeply developed soils with a high plant-available water capacity only lower the risk of severe drought stress to trees when trees have developed root systems that can access available soil water resources.

There are few studies on the complex relationships among soil, rooting, and drought tolerance in Douglas-fir. Site-specific studies of tree drought tolerance that examine both above- and belowground biomass are essential for understanding the response patterns of tree species to drought. For example, drought-induced reductions in stem growth might also suggest adaptation processes in roots (Lwila et al. 2023). In addition, combined above- and below-ground studies on the effects of drought are necessary for deriving specific recommendations for silvicultural management. Our study indicates the importance of deep rooting for high drought tolerance. Therefore, silvicultural measures that promote root growth in deeper soil horizons and thus the exploitation of additional water resources are very important, especially at the critical sites mentioned above.

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Code availability

Not applicable.

Authors' contributions

Conceptualization: Göran Spangenberg, Sebastian Hein; methodology: Göran Spangenberg, in soil science issues also Jürgen Schäffer; formal analysis and investigation: Göran Spangenberg; writing—original draft preparation: Göran Spangenberg; writing—review and editing: Göran Spangenberg, Reiner Zimmermann, Manfred Küppers, Jürgen Schäffer, Sebastian Hein; supervision: Sebastian Hein. The authors read and approved the final manuscript.

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Availability of data and materials

The datasets generated and/or analyzed during the current study are available in the Zenodo repository (<https://doi.org/10.5281/zenodo.11127374>).

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

All authors gave their informed consent to this publication and its content.

Competing interests

The authors declare that they have no conflict of interest.

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