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Tree growth responses to severe droughts for assessment of forest growth potential under future climate

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ABSTRACT

More frequently occurring droughts, related to climate change, lead to reduced growth and loss of vitality in trees. The recent drought of 2018 was extreme, long-lasting and resulted in high evaporative demands due to the concurrent high temperatures. The aim of this study was to compare the drought resilience of nine temperate tree species in the Netherlands, and to determine their responses to the severe drought of 2018 in comparison with five earlier drought events since 1970. To assess drought effects on tree species, we analysed tree-ring series of 678 trees in 45 plots throughout the Netherlands. Resilience indices were calculated based on growth reactions and growth recovery after drought. Furthermore, the impact of drought events on species productivity was quantified. We observed species-specific differences in growth responses to drought timing. All species in nearly all sites responded with growth reductions to drought, except sessile oak (*Quercus petraea* (Matt.) Liebl.). The most productive species in our study were found to be drought sensitive, with productivity losses of up to 30 % during drought in some sites. Productivity losses were highest on the driest soils. Resilience to the 2018 drought did not differ significantly from other drought years for six out of the nine studied species. However, 77.5 % of the individual trees of all studied species did not fully recover in growth within the following two years. Low post-drought growth remains poorly understood and should be taken into account in future studies to safeguard the health and productivity of the forest under climate change. We consider sessile oak a promising species for future forests in the Netherlands. Based on our results, we provide an outlook on future resilience and growth potential of the species studied under projected climate change for the Netherlands.

1. Introduction

1.1. *Climate change & growth resilience*

Climate change is a major threat to forest ecosystems. Over the past decades, droughts and other disturbances have impacted forests worldwide, resulting in deprived growth, vitality loss and eventually mortality (Allen et al., 2010, Anderegg et al., 2015, Hammond et al., 2022). The occurrence of frequent and intense droughts is expected to increase in the future (Spinoni et al., 2018, IPCC, 2021, KNMI 2023a). A large number of tree species is vulnerable to vitality loss in dry periods, as many operate with narrow hydraulic safety margins (Choat et al., 2012).

Radial growth is a sensitive indicator of whole-tree vitality as it is directly affected by water deficits (Barbaroux and Bréda, 2002, Zweifel et al., 2006) and reduced carbon uptake (Van der Woude et al., 2023). Therefore, radial growth performance, typically captured by tree-ring analyses, may provide information on the drought-sensitivity of trees and the ability to withstand and recover from drought events.

Numerous studies have been carried out to determine the resilience to drought, defined by Lloret et al. (2011) as the ability to regain pre-drought growth levels, of different species under different local conditions and management regimes. These include large-scale studies on many species (Gazol et al., 2017, DeSoto et al., 2020), on one or few species along a latitudinal or other gradient (Cavin and Jump, 2017, Bose et al., 2020, Harvey et al., 2020, Bose et al., 2021), regional studies

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comparing several species and/or site conditions (Hoffmann et al., 2018, Fuchs et al., 2021, Stolz et al., 2021) or species at the edge of their distribution (Rubio-Cuadrado et al., 2018). In addition, these include studies on presumed drought-mitigating management regimes, such as thinning (Sohn et al., 2016) and mixtures (Merlin et al., 2015, Thurm et al., 2016, Pardos et al., 2021).

1.2. Impact of 2018 drought on tree species in Europe

The 2018 summer drought in Europe was exceptional, breaking long-term records in large parts of central and northern Europe including the Netherlands (Brakkee et al., 2021). Regions were affected that are seldomly confronted with such high temperatures and water deficits (Peters et al., 2020) and in several parts the drought continued until 2020 (Brakkee et al., 2021). Since then, several studies have been carried out to give first insights in the impacts on temperate forests, mainly in Germany. Buras et al. (2020a) conclude that the 2018 “hot drought”, a combination of drought and warmer temperatures (Allen et al., 2015), affected forests more than the extreme drought of 2003. Effects of the 2018 drought were found in many species, including silver fir (*Abies alba* Mill.), Scots pine (*Pinus sylvestris* L.), European beech (*Fagus sylvatica* L.), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), sycamore maple (*Acer pseudoplatanus* L.), pedunculate oak (*Quercus robur* L.) and sessile oak (*Quercus petraea* (Matt.) Liebl.) (Scharnweber et al., 2020, Schuldt et al., 2020, Larysch et al., 2021, Obladen et al., 2021, Rohner et al., 2021, Süßel and Brüggemann, 2021, Haberstroh et al., 2022, Enderle et al., 2024).

1.3. Forests in the Netherlands – native and exotic species on sandy soils

Scots pine, pedunculate oak, European beech, Japanese larch (*Larix kaempferi* (Lamb.) Carr.) and Douglas-fir are among the most common and commercially most important tree species in the Netherlands (Schelhaas et al., 2022). Their growth responses to drought have been described extensively in literature, though to a lesser extent for Japanese larch, and certainly less frequent on sandy soils in the Netherlands (Van der Werf et al., 2007, Eilmann et al., 2013, Buras et al., 2020b). Sessile oak and black pine (*Pinus nigra* Arn.) are less common species in Dutch forestry (Schelhaas et al., 2022), but are potentially more drought-tolerant (Cochard et al., 1992, Friedrichs et al., 2009a, Eilmann and Rigling, 2012, Martin-Benito et al., 2013). Silver fir is suggested to be an alternative for Norway spruce (*Picea abies* (Karst.) L.) under climate change (Vitali et al., 2017) and sycamore maple is a rich-litter species that is increasingly used in Dutch forests to improve the conditions of acid sandy soils (Thomassen et al., 2020, Verbeek et al., 2021).

Forests in the Netherlands are mostly situated on poor sandy soils with limited water holding capacity, where rainwater percolates through the soil rapidly and groundwater level is, in most cases, below ten meters (Van der Werf et al., 2007, Hengeveld et al., 2015). Trees on high-nutrient sites are often found to suffer more from drought-stress than those on nutrient-deprived soils (DeSoto et al., 2020, Obladen et al., 2021, Schmied et al., 2023a) and this was also observed for trees growing on moister compared to dry soils (Martínez-Vilalta et al., 2012, Cavin and Jump, 2017, Trouvé et al. 2017). Gaining knowledge on species-specific vulnerabilities to drought in relation to edaphic conditions and drought seasonality (Vitali et al., 2018, Bose et al., 2021) is urgently needed in forest management in the face of climate change (Lévesque et al., 2016).

In this study, we analyzed the growth responses of nine tree species in Dutch forests to severe and extreme droughts, with a focus on the 2018 drought, because of its severity and the fact that these droughts are expected to become more frequent and intense (KNMI 2023a). This was done by analyzing tree-ring widths of tree species growing under different site conditions during, before and after drought episodes. Multiple analyses, including commonly used resilience indices (Lloret et al., 2011), were used to highlight various aspects of drought tolerance of trees in Dutch forests. Our research questions were: (1) How do tree-growth responses to drought differ between species and what is the impact on productivity? (2) How are growth responses to drought driven by drought dimensions and edaphic conditions? (3) Did the impact of the recent drought year 2018 on growth differ from that of earlier droughts? We expected that sessile oak and black pine would show the highest drought-tolerance and the smallest productivity losses and that growth responses to drought timing would be species-specific. Finally, we expected that the impact of the 2018 drought on tree growth would be more severe than during the five previous drought years.

2. Methods

2.1. Study area and field sampling

This study was carried out on 45 plots located throughout the middle and eastern part the Netherlands where most sandy forest areas are located (Fig. 1). The climate is mild maritime with moderately warm summers and mild winters. The mean annual temperature since 1970 was 10.2 °C, and annual precipitation, generally evenly distributed throughout the year, was on average 814 mm per year (KNMI 2023b).

A field sampling campaign was carried out in autumn and winter 2020 to collect tree-ring samples. For some sites, data were collected between 2018 and 2022 (Table A1). Two 5-mm cores per tree were extracted from, on average, 15 dominant trees per site with a 40–60 cm long Haglöf increment borer. The cores were taken at a stem height between 80 and 130 cm. Diameters at breast and sample height (DBH and DSH respectively) were measured with diameter tapes. Height of the sampled trees was measured using a Nikon Forestry Pro Rangefinder. A total of 678 individual trees belonging to nine temperate species was sampled (Table A1).

2.2. Dendrochronological data

Increment cores were air dried, glued on wooden holders and prepared by using a core microtome (Gärtner and Nievergelt, 2010). Cores were either scanned at a resolution of 2400 dpi with an Epson Expression 10000XL scanner and ring widths were measured with CooRecorder 9.4 (Larsson, 2020), or measured with a LINTAB digital positioning table using the software TSAP-Win (version 4.81j, RINNTECH, Germany). Cross-dating was done both visually with TSAP-Win and statistically using COFECHA (Holmes, 1983, Grissino-Mayer, 2001). Before further processing, the individual times series were detrended to eliminate age and management related trends (Fritts, 1976, Cook et al., 1990). A flexible cubic smoothing spline with a 50 % frequency cut-off at 25 years was used to obtain dimensionless ring indices (Cook and Peters, 1981, Speer, 2010). Although series lengths differ, spline stiffness was fixed for all series, to avoid frequency bias as described by Klesse (2021). Then chronologies were built per species and site using Tukey’s bi-weight robust mean to dampen individual tree variation and thus strengthen the common climatic signal in each site. Finally, first-order autocorrelation was removed by autoregressive modelling. The quality of the chronologies was statistically checked, the strength of the common signal was assessed by means of the series intercorrelation (Rbar) (Table S1).

Basal area increment (BAI) was calculated following Biondi (1999) using individual tree ring-width measurements and diameters at sample heights, with the function bai.out in the ‘dplR’ package (Bunn et al., 2023). Afterwards, basal area chronologies were built per species and site using Tukey’s bi-weight robust mean and autoregressive modelling. The term BAI, by definition at breast height, is technically not correct here, since in the most recent campaigns trees were sampled at 80 cm height to obtain longer chronologies. For convenience, the term BAI is used throughout this study. Detrending, BAI calculations and statistical analysis of the chronologies were done with R package ‘dplR’ (Bunn et al., 2023).

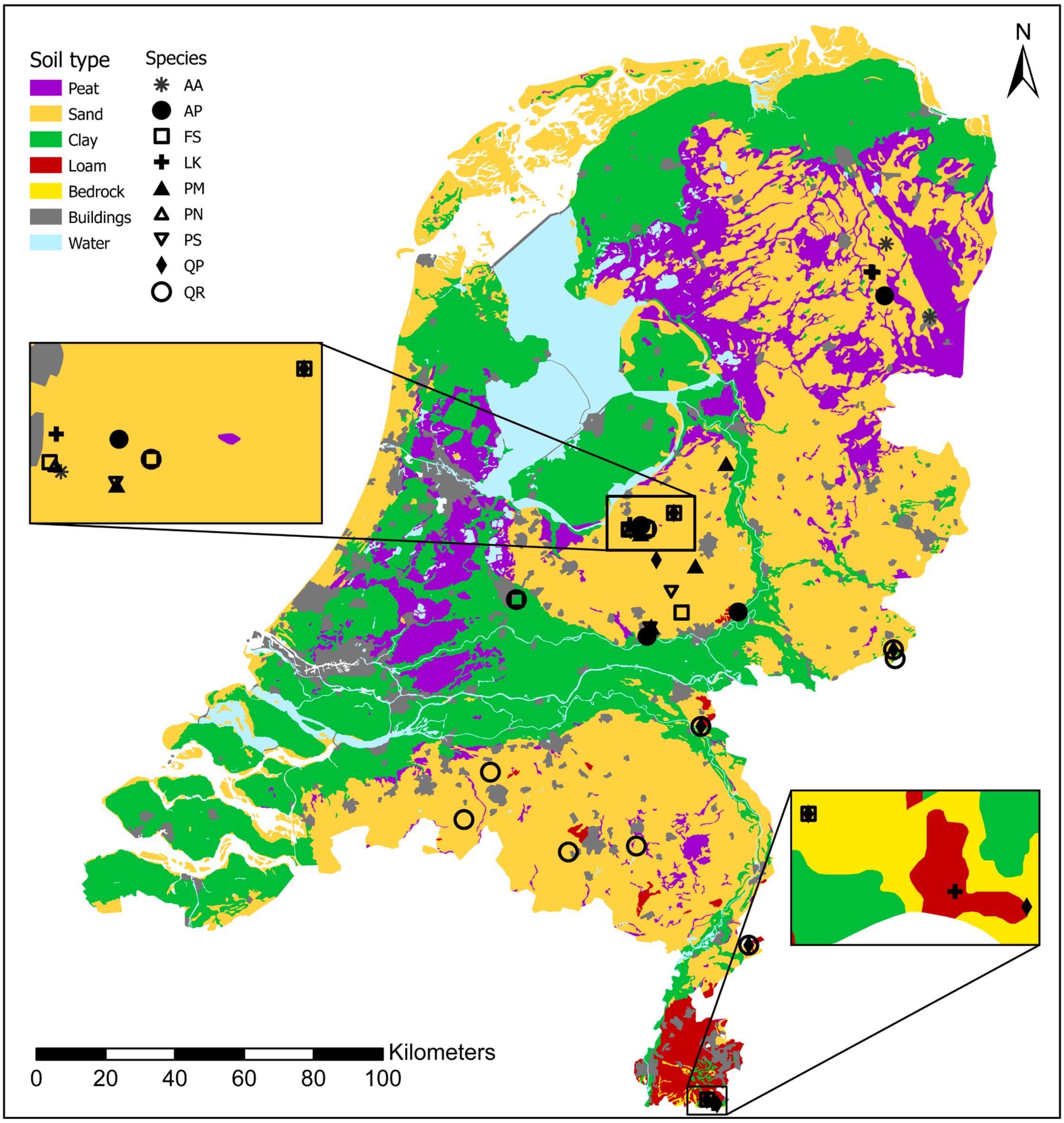

Fig. 1. Distribution of the 45 studied sites and 9 species throughout the Netherlands (AA=Silver fir, AP=Sycamore maple, FS=European beech, LK=Japanese larch, PM=Douglas-fir, PN=black pine, PS=Scots pine, QP=sessile oak and QR=pedunculate oak, Source WENR).

2.3. Climate data

To assess the influence of climatic factors on tree growth, climate data of the nearest weather station was used (KNMI 2023b), which was often in close proximity (up to 25 km) and in a few cases up to 45 km from the forest site (Table A1). Bootstrapped Pearson's correlation coefficients between climatic variables and BAI chronologies were calculated with R package 'treeclim' (Zang and Biondi, 2015). As an indicator for the climatic water balance and proxy for water availability, the Standardised Precipitation-Evapotranspiration Index (SPEI) was used (Vicente-Serrano et al., 2010). This is a scaled index, with an average value of 0 and standard deviation of 1. To obtain SPEI values, we first calculated potential evapotranspiration (PET), based on the method of Penman-Monteith, with R package 'SPEI' (Beguería and Vicente-Serrano, 2023). Therefore, we used monthly meteorological data for temperature, precipitation, solar radiation and wind speed (KNMI 2023b). Hereafter, based on precipitation minus PET, we calculated standardized SPEI indices for timescales from 1 to 24 months (Beguería and Vicente-Serrano, 2023). When information on solar radiation and/or wind speed, needed for PET calculation, was lacking for early years in some sites, the Global SPEI database (https://spei.csic.es/database.html) was used to fill in the lacking SPEI data. Long-term means of temperature, precipitation and SPEI were computed for the period 1970–2022 and averaged over all weather stations. Mean growing season temperature increased with 1.5 degrees in the study period, while growing season SPEI showed a slightly decreasing trend from positive towards negative values (Fig S1).

2.4. Selection of drought years

Drought years were identified independently from observed growth reductions, to avoid biases that may result from (1) including years of growth reduction due to other factors than drought, and (2) excluding droughts that did not have large impacts on growth (Schwarz et al., 2020). We based our selection on a growing season SPEI (SPEIgrowing), at a 6 month time scale, from April to September, reflecting the main vegetation period for the species studied. Thresholds values for SPEI values to classify droughts were based on McKee et al. (1993) and

Danandeh Mehr et al. (2020). Negative SPEI values, indicating dry conditions, were classified with the thresholds values −1.0 to −1.42, −1.43 to −1.82 and ≤−1.83 for moderate, severe and extreme drought conditions, respectively. Only severe and extreme droughts were included, selected from average SPEI values for all sites in the study region. SPEI values varied slightly between climatic stations, but for 1976, 2018 and 2020 they were below the severe drought threshold for all cases, and for 1976 and 2018 even below the extreme drought threshold of −1.83. 2020 was the main sampling year and was excluded, as no recovery after drought could be calculated. In addition, we included two typical spring droughts, in 1996 and 2011, and two summer droughts, in 1983 and 2003, based on the May and August SPEI (SPEIspring and SPEIsummer respectively) at a 3-month time scale. These do not exactly match the entire growing season, but reflect the conditions experienced at the start and in the middle of the growing season. Averaged over all climatic stations, the 1996 SPEIspring was not below −1.43, but 1996 showed a severe spring drought in proximity of many of the study sites, justifying inclusion of 1996 as drought year. Thus, in the period from 1970 until 2020, in total 6 severe or extreme drought years were selected for analysis (1976, 1983, 1996, 2003, 2011 and 2018).

Each drought year was further characterized by calculating the cumulative water balance during the growing season (Fig. S2). For the three most severe droughts, 1976, 2018 and 2003, the water balance was still negative at the end of the growing season. This was also the case for 1996, but this drought was less severe than the other three.

2.5. *Growth response to drought*

2.5.1. *Resistance, Recovery & Resilience to drought*

For the selected six drought years, resilience indices as defined by Lloret et al. (2011) were computed in order to quantify individual tree-growth responses to drought events. *Resistance* is defined as the ability of an individual to withstand a disturbance event, in this case a drought. It can be calculated as the ratio between growth in the drought year and in the years before drought (Eq. 1). *Recovery* is the ability of an individual to recover from the disturbance event; it is expressed as the ratio between growth in the years after the disturbance and during the drought event (Eq. 2). Finally, *resilience* is the ability to regain growth similar to the level before drought (Eq. 3).

$$\text{Resistance (Rt)}=\text{Dr}/\text{PreDr} \tag{1}$$

$$\text{Recovery (Rc)}=\text{PostDr}/\text{Dr} \tag{2}$$

$$\text{Resilience (Rs)}=\text{PostDr}/\text{PreDr} \tag{3}$$

where PreDr, Dr and PostDr indicate growth before, during and after disturbance, respectively. New resilience indices, following Thurm et al. (2016) and Schwarz et al. (2020), were also calculated (Van der Maaten-Theunissen et al., 2021), with a reference period of 4 years before and 4 and 2 years after the drought. As 2018 is the year of main interest, the period of 2 years post-drought had to be chosen to compare 2018 with the other years. The sites that were sampled before 2020 could not be included in the analysis of the year 2018. We calculated the resilience indices with raw ring widths, detrended ring width indices (RWI) and basal area increments (BAI). Since the results of all series were very similar, only BAI data are reported here. Resilience indices were computed with R package pointRes 2.0 (Van der Maaten-Theunissen et al., 2021).

2.5.2. *Regaining full resilience*

The framework proposed by Schwarz et al. (2020) was used to allow the comparison of resilience indices between species or treatments. Different species may have different strategies resulting in comparable resilience: a certain species may exhibit low resistance and high recovery, resulting in the same resilience as a species with high resistance but low recovery. Thus, this approach allows to interpret the resilience of individual trees for any combination of resistance and recovery.

We fitted the relationship of values of resistance and recovery using the NLS function in R:

$$\text{Recovery} = \text{a} * \text{Resistance}^{\text{b}} \tag{4}$$

where a and b are constants calculated for different subsets (i.e. species and drought year) (Eq. 4). The relationship between the indices can be expressed as (Lloret et al., 2011):

$$\text{Recovery} = \frac{\text{Resilience}}{\text{Resistance}} \tag{5}$$

Next, we assumed a hypothetical relationship representing full resilience of value 1. To calculate recovery at any given value of resistance which allows trees to fully recover we used:

$$\text{Recovery} = \frac{1}{\text{Resistance}} \tag{6}$$

Comparison of both lines (Eq. 4 and Eq. 6) was done to asses species growth responses to drought and to compare years with different drought timing. Using Spearman correlations, measurements were compared with the fitted line (Eq. 4). Confidence intervals around the fitted line were calculated based on bootstrapping with 10,000 replications.

2.5.3. *Intensity of growth reaction to drought*

Finally, a Superposed Epoch Analysis (SEA) for each full BAI chronology was executed, to test the significance of the mean tree response to drought years (Lough and Fritts, 1987). SEA calculates departures from the mean growth performance for each year in a chosen period from the mean of all analyzed periods per chronology. Bootstrap resampling (10000 times) was used to randomly select similar periods from the dataset to calculate significance and confidence intervals of the departures. A period of 11 years was used, with the drought year in the center of the period (Kunz et al., 2018). All drought years were used, but for 2018 in most cases only 2 years post-drought could be included in the epoch. Although this might have reduced the statistical power of the years 3–5 post-drought, the analysis of the remaining 8 years remained robust. Afterwards, unscaled mean deviations from the chronologies during drought (year 0) were compared with the average mean pre-drought deviation (year −5 until −1), to calculate the percental loss in BAI during drought.

2.6. *Edaphic conditions*

For each drought year, site-specific daily cumulative water balance (P-PET) was calculated for the growing season (April-September). In cases where this water balance was negative, soil texture determined water availability and water uptake (assuming no direct influence of groundwater table). For soil characteristics, we used soil data from the ISRIC-World Soil Information SoilGrids250m version 2.0 database (https://soilgrids.org) (de Sousa et al., 2020). These include predictions of sand, silt and clay content, bulk density (BD), cation-exchange capacity (CEC), soil organic carbon (SOC), pH (in H_2O), total nitrogen content (N) and coarse fragments (CRF). We used the predictions for 6 interval depths (0–15, 15–30, 30–60, 60–100 and 100–200 cm) for all properties. Assuming that average rooting depth did not exceed 120 cm, we multiplied the values for each layer until 120 cm with the thickness of each depth interval to obtain weighted means. Bulk density and soil texture data were then used to estimate the Van Genuchten-Mualem soil hydraulic parameters with the module ROSETTA Lite version 1.1 (Schaap et al., 2001). These hydraulic pedo-transfer parameters were implemented in the software RETC, version 6.02 (Van Genuchten et al., 1991), to model water retention curves. Plant available water was then estimated as the difference of the soil water content at field capacity (-0.033 MPa) and the permanent wilting point (-1.5 MPa). Available soil water (ASW in mm) was calculated per layer and added until 1.20 m, assuming an average rooting depth of 1.20 m (Table A1).

To determine the major soil gradients at the sites, a principal component analyses (PCA) was carried out, based on the weighted averages of all soil properties, except SOC and CEC. For those properties, the weighted average of the first two layers was used, since the majority of the organic matter is located in the topsoil. Soils were classified, depending on PCA values (Table A1). Although we qualitatively classified these soils, it is important to note that most sites in our study are located on acidified sandy soils, with acidification resulting from high nitrogen deposition leading to cation loss (Van der Eerden et al., 1998). For the statistical analysis the values of the first and second principle components PCA 1 and 2 were used, instead of the soil classification. The first principle component PCA 1 explained 45 % of the variance and the second principle component PCA 2 20 % (Fig. S3). PCA 1 was interpreted as a water availability gradient driven by soil texture, from acidified sandy soils towards increased clay and silt content, while PCA 2 reflected a gradient of decreasing nutrient and water availability; from soils with higher organic matter, nitrogen and cation-exchange capacity, towards soils with low water availability due to higher bulk density and coarse fragments (Table S2).

2.7. Statistical analyses

Linear mixed-effects models were fitted with R package "lme4" (Bates et al., 2015) to test for significant differences in the resilience indices between species. Full models include all species and variables for direct comparison of the resilience indices between species. Indices were transformed with the natural logarithm to obtain normal distributions. The full model included species, soil variables (PCA1, PCA2, ASW), estimated age at the drought year, drought variables (DOY, WB, SPEI, timing) and their relevant interactions as fixed effects, and site and year within site as random effects on the intercept (Eq. 7):

$$\mathrm{Ln(Y)} \sim \mathrm{species} + \mathrm{age} + \mathrm{SPEI} + \mathrm{WB} + \mathrm{DOY} + \mathrm{timing} + \mathrm{PCA1} + \mathrm{PCA2} + \mathrm{ASW} + \mathrm{species{:}SPEI} + \mathrm{species{:}WB} + \mathrm{species{:}ASW} + \mathrm{species{:}age} + \mathrm{species{:}DOY} + \mathrm{species{:}timing} + \mathrm{species{:}PCA1} + \mathrm{SPEI{:}PCA1} + \mathrm{SPEI{:}DOY} + \mathrm{SPEI{:}timing} + (1|\mathrm{site}) + (1|\mathrm{site{:}year}) \quad (7)$$

in which DOY is the day when cumulative P-PET was below 0, WB the minimal cumulative P-PET (positive values; higher values reflecting drier conditions) during the growing season and timing a factor with categories "growing", "spring" and "summer". To test the differences between years, the following full model is applied, with site as random effect on the intercept (Eq. 8):

$$\mathrm{Ln(Y)} \sim \mathrm{species} + \mathrm{age} + \mathrm{SPEI} + \mathrm{WB} + \mathrm{DOY} + \mathrm{year} + \mathrm{PCA1} + \mathrm{PCA2} + \mathrm{ASW} + \mathrm{species{:}SPEI} + \mathrm{species{:}WB} + \mathrm{species{:}age} + \mathrm{species{:}DOY} + \mathrm{species{:}ASW} + \mathrm{species{:}year} + \mathrm{species{:}PCA1} + \mathrm{SPEI{:}PCA1} + \mathrm{SPEI{:}DOY} + \mathrm{SPEI{:}year} + (1|\mathrm{site}) \quad (8)$$

Tree was not included in the random part, as the effect of tree in combination with site in the random part was negligible. To test the impact of drought years (D) versus non-drought years (ND) on BAI growth, the following full model is applied, with site and tree within site as random effect on the intercept (Eq. 9):

$$\mathrm{Ln(BAI)} \sim \mathrm{DND} + \mathrm{species} + \mathrm{PCA1} + \mathrm{PCA2} + \mathrm{ASW} + \mathrm{species{:}DND} + \mathrm{PCA1{:}DND} + \mathrm{species{:}\ PCA1} + \mathrm{species{:}ASW} + \mathrm{ASW{:}DND} + \mathrm{PCA2{:}DND} + \mathrm{species{:}\ PCA2} + (1|\mathrm{site}) + (1\ |\ \mathrm{site{:}tree}) \quad (9)$$

in which DND is a factor with two levels: drought or non-drought year. To avoid legacy effects of drought years in non-drought years, the 2 post-drought years were excluded from the model, i.e. for drought year 1976, 1977 and 1978 were excluded from the analysis.

For direct comparison of the relative importance of the fixed variables, all continuous explanatory variables were standardized, by subtracting the mean and dividing by the standard deviation. Significant differences were identified using the R package "lmerTest" (Kuznetsova et al., 2017) that calculates p-values with degrees of freedom based on Satterthwaite's approximation. Following Zuur et al. (2009), model selection was based on Akaike's information criterion (AIC). Normality and homogeneity of the residuals were checked by visual inspections of the diagnostic plots, and variance inflation factors (VIF) were inspected to check collinearity among the variables. Variables with VIF larger than 3 were excluded (Zuur et al., 2010). Marginal means for species in combination with timing; for species with drought year; and for species with DND, were estimated with the R package "emmeans" (Lenth, 2021). Pairwise comparisons were performed using Tukey correction to adjust for multiple testing. All statistical analyses were executed in R version 4.3.3 (R Core Team, 2024).

3. Results

3.1. Growth resilience to drought

3.1.1. Species and trees within species differ in growth resilience

Comparison of the observed values of the relationship between resistance and recovery with a hypothetical line where resilience is 1, assuming full recovery after drought, showed that drought reduced radial growth of the studied trees, but that individual variation was large (Fig. 2 and Fig. 3).

At the species level, European beech trees exhibited very low resistance values, indicating strong growth reduction during the drought year. However, the fitted line showed minimal deviation from the line of full resilience, suggesting full growth resilience for trees with resistance values above 0.45 (Fig. 2, Table S3). The curves of other species showed greater deviation. Many trees were within reach of full resilience if their resistance values were not too low, such as silver fir with resistance values above 0.76. However, individual variation was large, with many trees not experiencing growth depressions at all, demonstrated by resistance values above 1. This was observed in European beech (21 %), sycamore maple (31.4 %), silver fir (37.3 %), Japanese larch (22.8 %), Douglas-fir (27.1 %), black pine (32.7 %), Scots pine (32.7 %), sessile oak (31.4 %), and pedunculate oak (29.9 %) of the individual trees.

3.1.2. High impact of 2018 on individual trees

The comparison of growth reactions of all nine tree species to different drought years showed the impact of the 2018 drought, with most trees (77.5 %) having resilience values below the line of full resilience (Fig. 2, orange dots). For the other drought years, more individual trees reached full recovery after 2 years (Fig. 3, Table S4). Thus, in 2018 the fitted relationship between resistance and recovery deviated largely from the hypothetical line of full resilience, even at resistance values around 1. For the two spring droughts (1996 and 2011), and for the severe 1976 drought, the observed relationships showed a close fit to the line of full resilience (Fig. 3). As an example: a tree that had a resistance value of 0.45 in 1976 experienced full recovery within 2 years, whereas a tree in 2018 had to have a resistance value above 1.08 to experience recovery within that period.

The same analysis executed with detrended ring width series (Fig. S4, S5) and raw ring widths (Fig. S6, S7) revealed similar patterns for species and years, although the fitted lines were closer to full resilience for the detrended series. Increasing the recovery period from 2 to 4 years resulted in higher resilience values of the studied trees, but for that analysis it was not possible to include the year 2018, since final sampling was carried out in 2020. Therefore, only the recovery after 2 years is reported here.

3.1.3. Climate-growth relationships

Climate-growth relationships show that hot and dry summers reduced radial growth of most species, although the correlation is generally low and not always significant (Fig. S8). Correlations with SPEI reveal that growth of both oak species and Japanese larch was

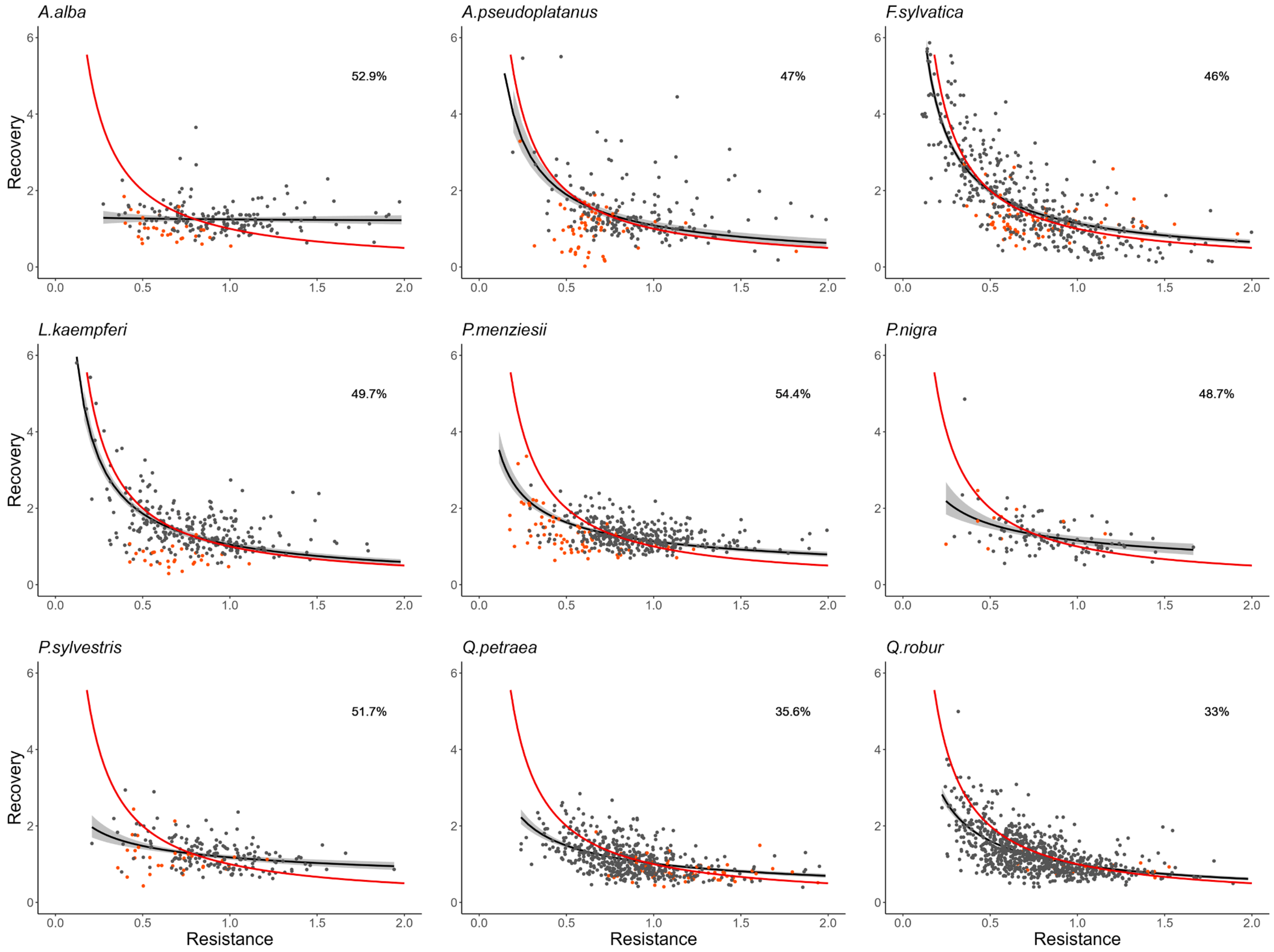

Fig. 2. Comparisons of the relationships between the observed resistance and recovery values calculated with BAI series per species for all drought years, and the hypothetical line of full resilience (red), in which resilience equals 1 at any given value of resistance (see Eq. 6). The black line represents the fitted relationship (Eq. 4) for the observed values (estimates, coefficients and residual standard error in Table S3), in grey the confidence interval around the fitted relationship based on 10.000 times bootstrapping. Observed values for 2018 are indicated in orange, the other drought years in dark grey. The numbers in the right upper corner indicate the % of individual tree-drought year combinations with resilience values above the line of full resilience (n=204 (AA), n=264 (AP), n=504 (FS), n=312 (LK), n=432 (PM), n=113 (PN), n=205 (PS), n=567 (QP), n=812 (QR)).

mainly influenced by previous summer SPEI, which was significant for two-third of the sites of those species (Fig. S9). Other species showed positive correlations with the growing season and/or summer SPEI of the year of ring formation, indicating sensitivity to droughts occurring in the current growing season.

3.1.4. *Different effect of spring, summer and growing season drought on species*

Timing of drought was included in all final linear mixed-effects models and had species-specific effects on resistance, resilience and recovery (Fig. 4, S10). Resistance and recovery of both pine species was highly variable, which was also the case, though to a lesser extent, for silver fir. European beech showed low resilience to summer droughts but relatively high resilience to spring droughts. Resilience of pedunculate and sessile oak was significantly lower to spring droughts, compared to European beech, and sycamore maple had lowest resilience values during growing season droughts, compared to all other species (Fig. 4).

3.1.5. *Low resilience to 2018 drought*

Resilience to the 2018 drought was generally low in all species. However, in most cases, differences with other years were not significant, except for 1976 for silver fir, 1983 and 2003 for sycamore maple and 2003 for Japanese larch (Fig. 5). Recovery from the 2018 drought was lower than from other years for European beech, sycamore maple and Japanese larch (Fig. S11).

All final linear mixed effect models explaining resilience, resistance and recovery to drought included age, which had a negative effect on resilience, although not for all species. For the longer chronologies of both oak species and, to a lesser extent, European beech, older trees did not show lower resilience to drought events compared to younger trees (Table S5, Fig. S12). Soil fertility (PCA1) was included in the final resistance and recovery models only and did not significantly affect resilience, but more severe droughts, in terms of soil water balance (WB), resulted in lower resilience for Japanese larch, Scots pine and sycamore maple (Table S5, Fig. S13).

3.2. *Growth reductions during drought*

Superposed Epoch Analysis (SEA) demonstrated reduced radial growth during drought years (Fig. 6). This was observed for all species and at nearly all sites, although it was not significant for sessile and pedunculate oak at the more moist sites. European beech, pedunculate oak, Douglas-fir and Japanese larch showed the highest growth reductions. The length of the recovery period differed per species and site,

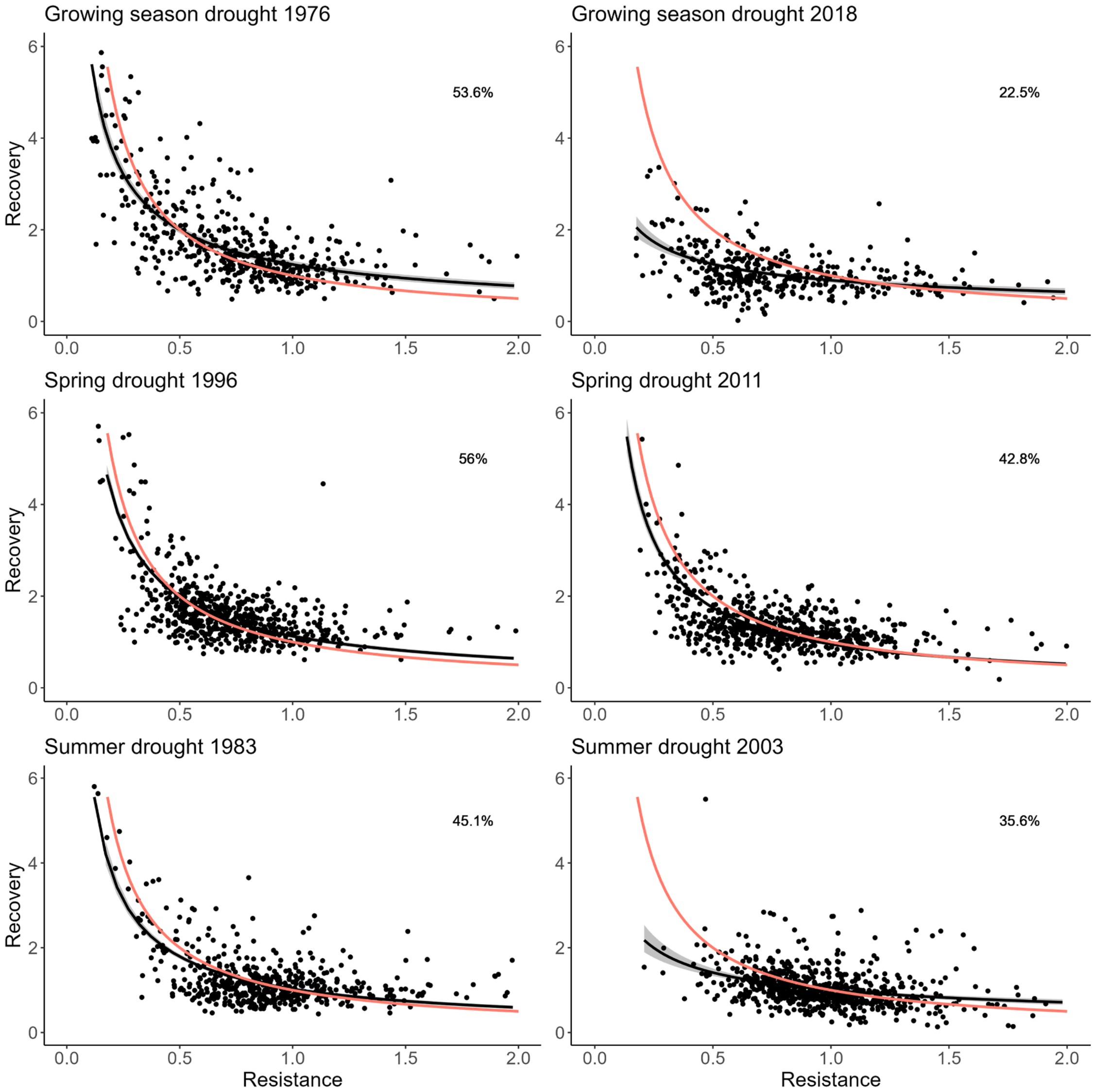

Fig. 3. Comparisons of the relationships between the observed resistance and recovery values calculated with BAI series for all studied species and sites per drought year, and the hypothetical line of full resilience (red), in which resilience equals 1 at any given value of resistance (see Eq. 6). The black line represents the fitted relationship (Eq. 4) for the observed values (estimates, coefficients and residual standard error in Table S4), in grey the confidence interval around the fitted relationship based on 10.000 times bootstrapping. The numbers in the right upper corner indicate the % of individual trees with resilience values above the line of full resilience (n=481 (1976), n=383 (2018), n=655 (1996), n=676 (2011), n=543 (1983), n=675 (2003)).

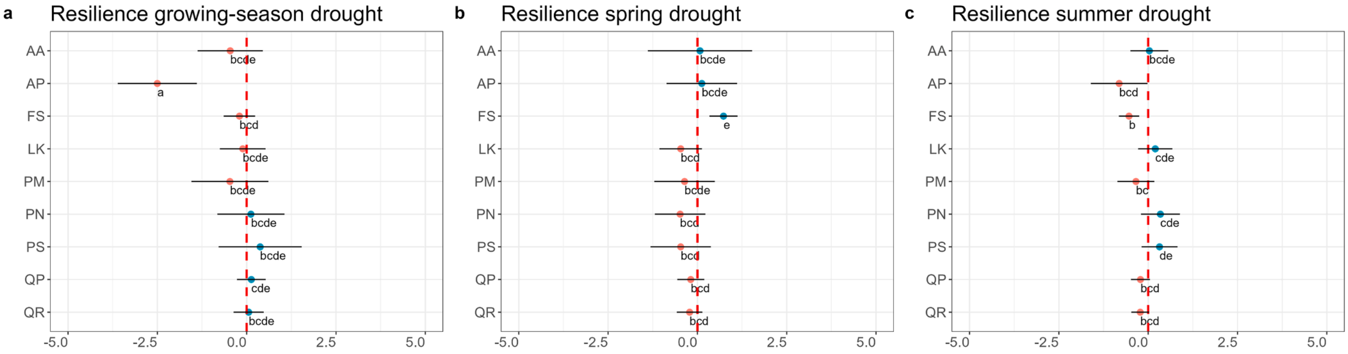

Fig. 4. Species-specific effects of timing of drought episodes on BAI growth resilience. Estimated means were calculated with linear mixed effect models based on Eq. 7, using age, drought and edaphic variables as fixed effects, and site and year within site as random factors (note different scale on X-axis). Estimated marginal means and 95 % confidence intervals are shown, with red circles indicating negative and blue circles indicating positive means. Letters indicate, per resilience index, significant differences between each combination of species and timing. For species abbreviations refer to Table A1.

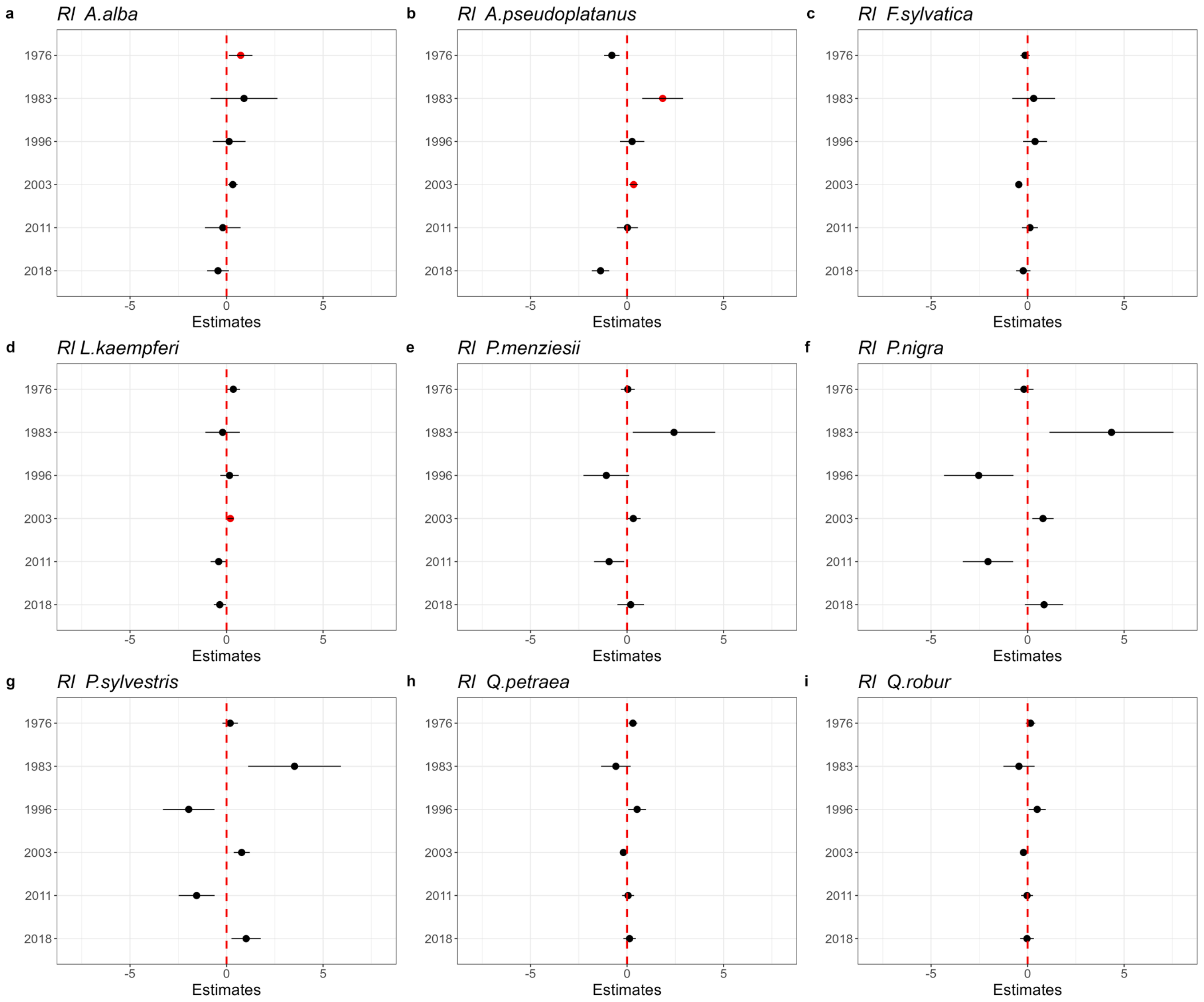

Fig. 5. Species-specific estimations of growth resilience (Rl) indicated per drought year. Parameter estimates were calculated with linear mixed effect models based on Eq. 8, using age, drought and edaphic variables as fixed effects, and site as random factors. Models were fitted with resilience indices based on BAI series. Estimated marginal means and 95 % confidence intervals are shown. Only contrasts between 2018 and the other years were tested. Significant contrasts between 2018 (bottom, in black) and the other years are shown in red, significant contrasts between other years are not indicated.

with recovery generally occurring within 3 years.

Likewise, a comparison of drought and non-drought years revealed that drought impacted basal area growth significantly for all species except silver fir, with highest BAI losses for European beech, Japanese larch and pedunculate oak (28.5 %, 24.6 % and 21.6 %, respectively, Fig. 7, Table S6). In drier sites (lower ASW), the impact of drought on growth was larger than in moister sites (Fig. 7, Table S6).

4. Discussion

4.1. Drought tolerance - all species but sessile oak are affected by drought

Among the four broadleaved and five conifer species, sessile oak was the only species that did not respond to drought with significant growth reductions on most sites (Fig. 6) and generally showed a low sensitivity to variation in (summer) climate (Fig. S8 and S9). This high drought-tolerance is in line with other studies (Cochard et al., 1992, Bréda et al., 1993, Friedrichs et al., 2009b, Scherrer et al., 2011, Cavin et al., 2013, Zimmermann et al., 2015, Kunz et al., 2018, Steckel et al., 2020, Fuchs et al., 2021, Kasper et al., 2022). Oaks are relatively well protected against severe embolism (Tyree and Cochard, 1996, Lobo et al., 2018). As anisohydric species, they keep their stomata open and can maintain photosynthesis for longer periods under a successively low leaf-water potential (Zang et al., 2012, Steckel et al., 2020). However, in contrast to sessile oak and European beech, pedunculate oak had slower recovery to pre-drought growth levels (Zang et al., 2012, Vanhellemont et al., 2019).

Resilience to the 1983 summer drought was lower for both oak species compared to other broadleaved species (Fig. 5), which likely resulted from late frost events in May, during earlywood vessel formation, and defoliation by winter moth larvae that were highly abundant in 1983 (Oosterbaan and Nabuurs, 1991). In addition, also the previous year (1982) was dry, which is relevant since both oak species were found to be sensitive to conditions in the year previous to ring formation, especially in the driest sites (Fig. S8 and S9).

European beech is often found to be plastic in traits regarding hydraulic safety, water loss control and phenology (Leuschner, 2020), and high plasticity may lead to high drought-tolerance. However, in our study European beech expressed a low growth resilience and high sensitivity to summer droughts (Fig. 4, S8 and S9). It is found that high

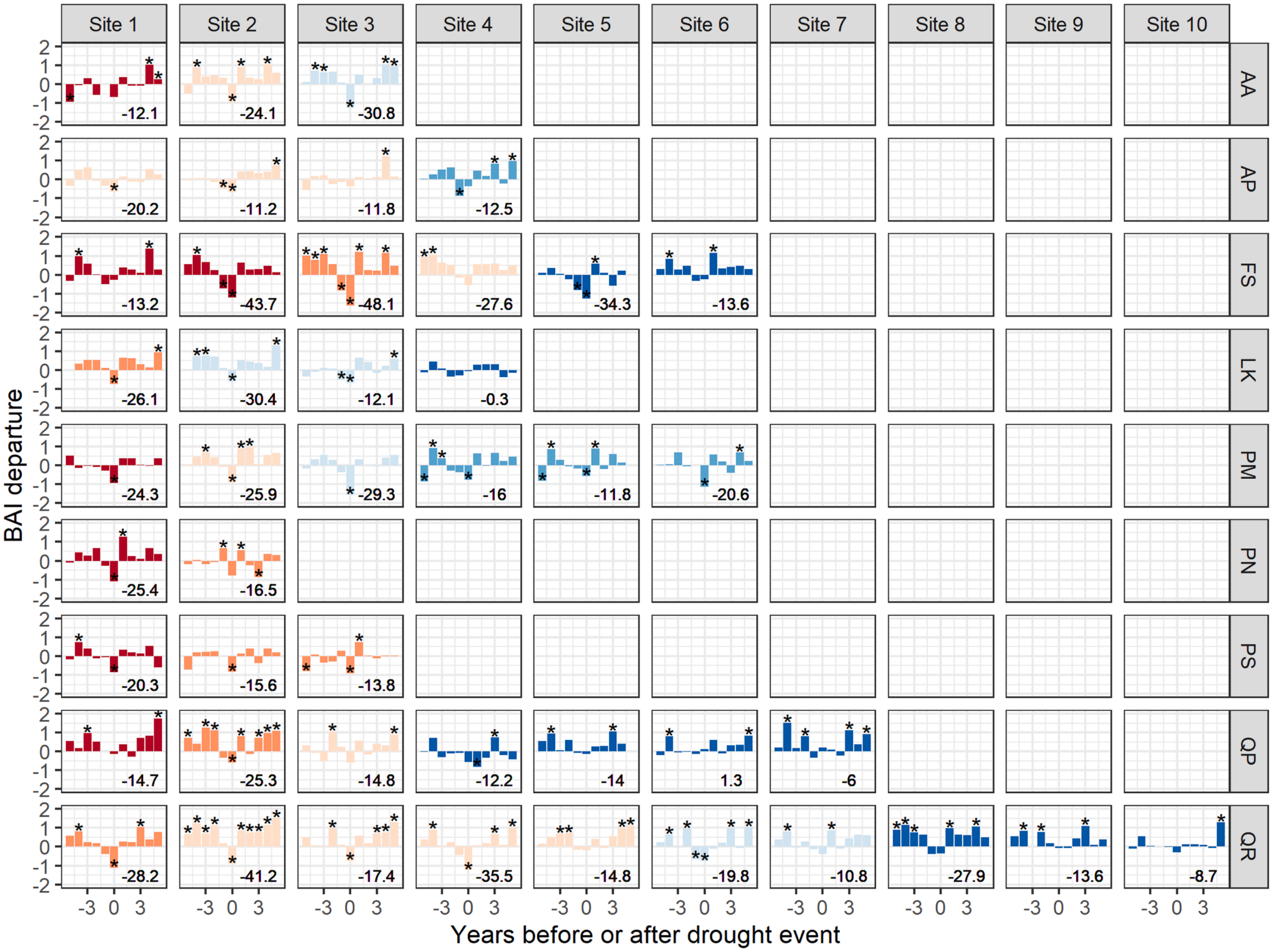

Fig. 6. Results of the Superposed Epoch Analysis (SEA) on the growth deviation during drought years from the mean BAI in an 11 year period, indicated per species and site. Scaled departures from the mean chronology of the BAI during all studied drought years are shown in the centre (lag 0), with the 5 years before and after each event left and right of the centre, respectively. Asterisks indicate a significant departure ($p<0.05$). The numbers in the graphs indicate the loss in BAI (in %) in the drought year compared with the mean of the 5 years before, calculated per site and species. The sites are arranged from dry (left) to moist (right) per species, with the colouring based on the available soil water (ASW), ranging from red (dry, 0–50 mm) to blue (moist, 181–220 mm). Intermediate ASW levels are from 51 to 75; 76–109; 110–145 and 146–180 mm. See Table A1 for species and site order.

light intensity and high leaf-temperatures during summer expose the canopy to critical stress (Leuschner, 2020). At some sites in Europe, recent (hot) droughts even led to substantial European beech mortality (Archambeau et al., 2020, Schuldt et al., 2020, Obladen et al., 2021, Rukh et al., 2023).

Sycamore maple had low index values compared to the other species (Fig. 4), although the spread in resilience was large for individual trees (Fig. 2) and growth reduction was not significant for all sites (Fig. 6). This low drought-tolerance is in agreement with earlier findings (Heklau et al., 2019) but in contrast with Scharnweber et al. (2020).

We conclude that of the broadleaved species, sessile oak is most drought-tolerant, considering its smallest growth reductions during drought and its relative low sensitivity to summer climate. This species is followed by pedunculate oak, European beech and sycamore maple. However, the growth reaction of oak to the successive occurrence of years with low water availability (Bose et al., 2024) combined with late frost and defoliation by winter moth, points out the risk of combinations of disturbances impacting future forests.

4.1.1. *Lowest drought-resilience ranking for most productive conifers*

In contrast to broadleaved species, reduced radial growth after drought was observed in all studied conifer species. This was most prominent for Japanese larch and Douglas-fir (Fig. 6). Low drought resilience of Japanese larch was also observed in other studies (Huang et al., 2017, Song et al., 2022). However, variation between individual trees was large (Fig. 2). The relatively young stand age may have led to higher resilience in two out of four Japanese larch sites. The analyzed dominant individuals survived the first two droughts as saplings and seedlings, which may have resulted in overestimated resilience values. The driest site of the study, Schovenhorst, lies within a couple of kilometers from the site of Song et al. (2022) and here resilience was comparable.

Douglas-fir was found to be drought sensitive, as significant growth depressions during drought occurred (Fig. 6), a large number of trees had resilience values below 1 (Fig. 2) and estimated means were relatively low (Fig. 4). This confirms findings of Sergent et al. (2014), though Huang et al. (2022) observed that Douglas-fir remained productive even during drought. Combinations of variations in short-term phenotypical and long-term genetic traits related to drought tolerance, as found between Douglas-fir populations in provenance trials, may explain these differences (Bansal et al., 2015, Chauvin et al., 2019).

Silver fir showed considerable growth reductions during drought, but absolute growth remained high, comparable to other findings (George et al., 2015, Schwarz and Bauhus, 2019, Serra-Maluquer et al.,

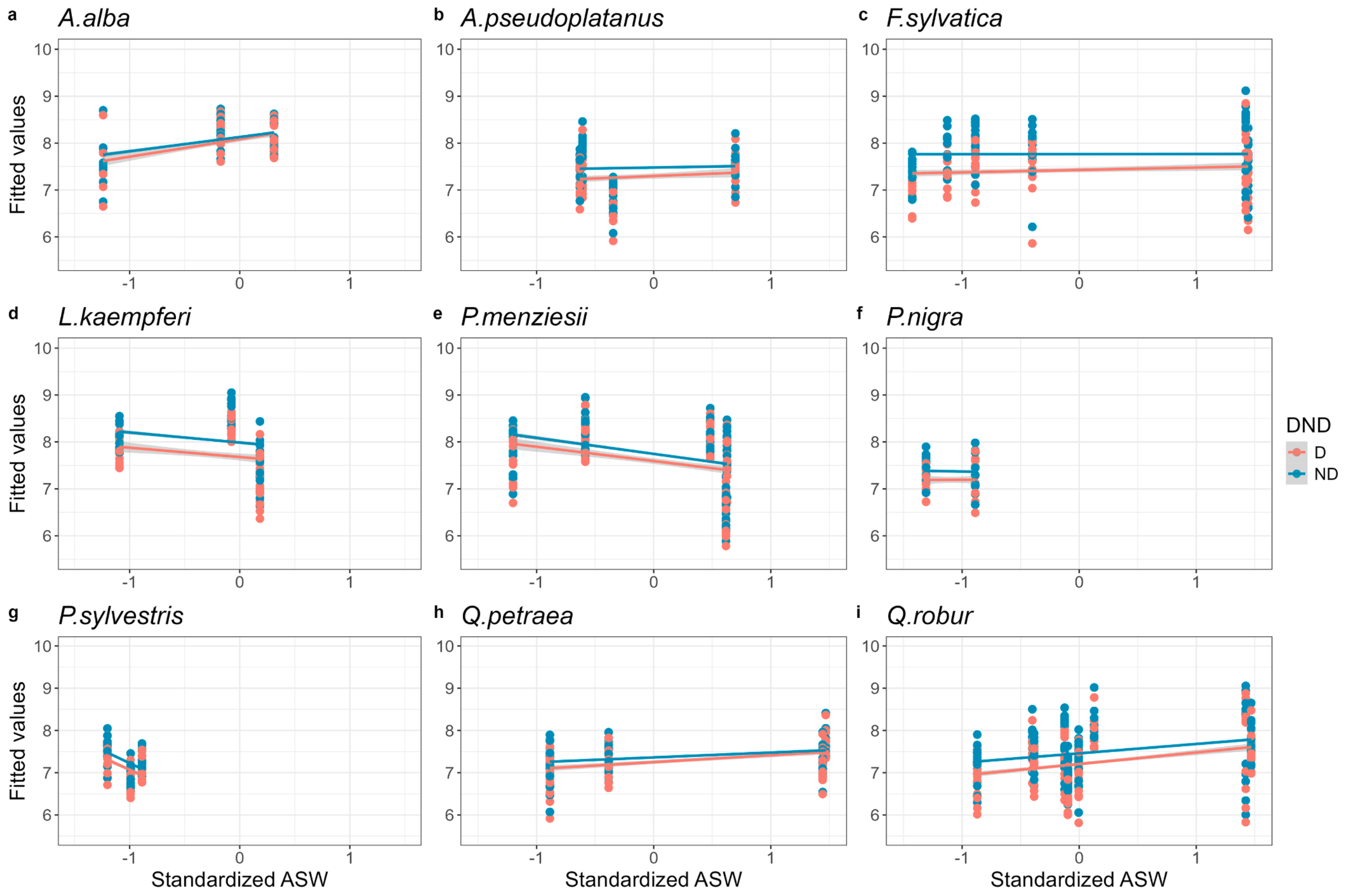

Fig. 7. Model predictions of log-transformed BAI in drought (D, red lines) and non-drought (ND, blue lines) years per standardized available soil water (ASW). Linear predictions are based on Eq. 9, using species, drought or non-drought year, edaphic variables and their relevant interactions as fixed effects, and site and tree within site as random factors. Model predictions and confidence intervals (in grey) are shown per species.

2021). At the individual tree level, resilience was highly variable, showing an overshoot in the fitted line at resistance values above 1 (Fig. 2), demonstrating that for a large proportion of silver fir trees the analyzed droughts did not limit growth. This confirms the findings of earlier studies (Zang et al., 2014, Vitali et al., 2017, Vitasse et al., 2019a, Gillerot et al., 2021).

Black pine was not more drought-tolerant than Scots pine, as was observed in some studies (Eilmann and Rigling, 2012, Martin-Benito et al., 2013), but not in others (Serra-Maluquer et al., 2018). However, with only two sites, black pine is underrepresented in the dataset and there is a lot of variation in the final linear models for both pine species (Figs. 4 and 5). Therefore, the analysis needs to be extended with a direct comparison of both species on more sites.

In Europe and the Netherlands, different coniferous species were planted in monocultures with a focus on productivity. But productivity comes at a cost, since traits that enlarge the photosynthetic capacity, e.g. the amount of foliage area, also increase the transpiration surface (Bansal et al., 2015). The studied coniferous species have an effective stomatal control mechanism (Irvine et al., 1998, Zweifel et al., 2009, Bansal et al., 2015, Vitasse et al., 2019b, Bhusal et al., 2020, Sasani et al., 2021), but this is considered to substantially reduce photosynthesis during drought (Granier et al., 2007). The most productive species considered here, Douglas-fir, Japanese larch and, to a lesser extent, silver fir, were found to be drought sensitive, with relatively low resilience and productivity losses of up to 30 % during drought (Fig. 6). This is comparable with other findings (Jiang et al., 2024). At least for Douglas fir, drought-tolerance relates to provenance selection, with a trade-off between productivity and drought resilience (Montwé et al. 2015, Spiecker et al., 2019). Despite the fact that many individual silver fir trees did not show growth reductions at all, the low resilience of silver fir to the 2018 drought suggests susceptibility to a changing climate. Still, in areas with Norway spruce mortality, like southern Germany, both silver fir and Douglas-fir were found to be more drought tolerant than the widely planted Norway spruce (Vitali et al., 2017). In the Netherlands, where Scots pine is the dominant coniferous species, both pine species showed relatively high resilience values, even to 2018, but also high variation, due to the small number of especially black pine trees, of which one site was sampled in 2019, so that no reliable resilience to 2018 could be yielded from the models. Yet, for the Netherlands, we consider both pine species the most drought-tolerant conifers, followed by silver fir, Douglas-fir and Japanese larch.

Among the nine studied conifer and broadleaved species in the Netherlands, we found sessile oak to be the least drought-sensitive species. When comparing conifer species, largely planted in monocultures, Japanese larch turned out to be most vulnerable. These results support conclusions from research on the benefits of mixed forests, where susceptible coniferous species are combined with broadleaved tree species such as oak and European beech to mitigate effects of a future climate with more frequent and intense drought events (Pretzsch et al., 2013, Thom et al., 2023).

4.2. *Drought impact on growth is higher on water-limited sites*

Soil fertility did not affect drought resilience, similar to earlier findings (Fuchs et al., 2021), but not to others (Schmied et al., 2023a, Schmied et al., 2023b). Significant effects of soil parameter PCA1 and drought intensity (WB) on resilience indices were observed only in interaction with species. In a review paper, Gessler et al. (2017) describe in a conceptual model the mechanisms how trees on sites with high nutrient availability can suffer more from drought-stress and eventually mortality than those on nutrient-deprived soils. As most of the Dutch forests are situated on acidified sandy soils, without access to groundwater, nutrient and water availability in these sites is generally low. It is plausible that the range in soil fertility covered by the sites was generally too small to pick up such soil-fertility effects for a larger range of species in our study.

Growth reductions in drought compared to non-drought years were larger in drier than moister sites (Fig. 7, Table S6), suggesting more drought-stress on the driest sites. Available water is often a limiting resource for growth (Bréda et al., 2006) and soil moisture storage can compensate for xeric periods (Mellert et al., 2018). Our results are in agreement with several studies that found larger drought responses on xeric than moist soils (Fritts et al., 1965, Weber et al., 2007, Rehschuh et al., 2017, Chakraborty et al., 2021), but in contrast with others (Cavin and Jump, 2017, Trouvé et al. 2017). In addition, some studies did not highlight clear soil moisture effects (Lévesque et al., 2014, Schmied et al., 2023a). The disagreement between findings are likely caused by local (drought) conditions and species studied, impacting stomatal control and water use efficiency (Bréda et al., 2006). Soil water status, which determines the actual drought trees experience, was not measured directly but estimated using a simplified model, with soil water holding capacity calculated from gridded soil data. Although these numbers may be less accurate than when measured in the field, they reflect a gradient from the driest sandy soils towards more moist soils. In addition, by taking only the most severe droughts in our study area, we ensured to analyze conditions that were experienced as droughts. How trees would perform under less severe conditions requires a different experimental set-up, including time-series of local soil water status.

The effects we found on timing of drought on growth reactions were species-specific (Fig. 4) and in agreement with the climate-growth relationships (Fig. S8 and S9).

4.3. Lower resilience to 2018 drought than to earlier droughts

The results reported here show that resilience to the 2018 drought was lower than to other droughts, as most individual trees (77.5 %) did not experience full resilience (Fig. 3). This was also supported by the results of linear models, showing lower resilience to the 2018 drought, although differences with other years were not significant in most cases (Fig. 5).

Two aspects are relevant when discussing the reasons for this lower growth resilience after the 2018 drought: (1) the timing and intensity of the drought, resulting in growth responses of tree species growing in a certain context, and the possible combination with other disturbances, which leads to legacy effects; and (2) the fact that detrimental climate conditions can prevail after an extreme drought year and delay the growth recovery.

It is likely that, in addition to the extreme drought intensity in 2018, rising temperatures since the beginning of the study period (Fig. S1) have led to higher evaporative demand, herewith partly explaining these low resilience values. In a recent European-wide dendrometer study on several common temperate tree species, no consistent growth reductions were found in 2018, but a significant stem shrinkage, due to depletion of water reserves, was observed (Salomón et al., 2022). In other studies, the growth reductions were more severe in 2019 than in 2018 (Scharnweber et al., 2020, Schnabel et al., 2021, Mathes et al., 2023). Throughout Europe, several species showed clear growth reductions to the 2018 drought, and higher mortality rates than normal (Schuldt et al., 2020, Obladen et al., 2021, Mathes et al., 2023, Rukh et al., 2023, Thom et al., 2023). Species that were most affected were Norway spruce, European larch, European beech, silver fir, Scots pine, pedunculate oak and, to a lesser extent, sessile oak. Causes of this higher mortality are largely related to the combination of extreme climate events and subsequent disturbances (Patacca et al., 2023). But also delayed effects of the 2018 hot drought, like premature leaf senescence in European beech as observed in Switzerland was suggested to serve as an indicator for tree mortality in the following years (Frei et al., 2022).

Drought effects on growth may last several years (Peltier et al., 2016). Legacy effects of previous droughts on growth and vitality of trees have been discussed in numerous studies in the past years (Anderegg et al., 2015, Buras et al., 2018, Kannenberg et al., 2019, Schuldt et al., 2020, Obladen et al., 2021, Sangüesa-Barreda et al., 2023). It has been observed that individuals that were less resilient in previous droughts had higher changes to die during actual droughts (Camarero et al., 2015, Cailleret et al., 2017, Camarero et al., 2018, DeSoto et al., 2020), but also abrupt growth decline after 2018 has been reported for previously good-growing individuals (Schmied et al., 2023b).

Yet, not only drought effects may last several years and cause legacy effects, but also drought conditions may prevail longer than a single year. In the Netherlands, unlike previous drought years, 2018 was followed by drier and warmer than average years (Fig. S1). Long-term, multi-year droughts not only intensify the effects of water deficits on tree physiology and growth (Moravec et al., 2021), but obviously also delay the recovery process, hence affecting growth resilience (Gessler et al., 2020).

Therefore, recovery and resilience indicators as calculated from growth in pre- and post-drought periods should be thoroughly interpreted, as they do not take climate effects in these periods into account. Attempts have been made to cope with this by introducing additional indices, that take into account the recovery period, which is the time needed to reach pre-drought growth levels, and herewith avoid a predetermined post-drought period (Schwarz et al., 2020). Although in the present study all additional indices (Schwarz et al., 2020, Van der Maaten-Theunissen et al., 2021) have been calculated, determining the recovery period was not possible for the year 2018, the main year of interest, since most of the sampling was executed in 2020. Therefore, it was not possible to unravel legacy effects from effects due to hot and dry post-drought years. The question if and when growth would return to growth levels prior to 2018, similar to earlier droughts, remains unanswered here, even when using multiple approaches. Nevertheless, under future climate, longer hot drought periods, as observed in 2018 and afterwards, are expected to become more frequent (Van der Wiel et al., 2022), stressing the relevance of the findings of this study for forest management to make informed decisions.

In addition, it can be considered that “negative drought legacy”, in terms of low post-drought growth rates, is a way to secure future growth and survival by acclimation (Galiano et al., 2017, Gessler et al., 2020). It is therefore crucial to better understand the physiological mechanisms behind drought legacy effects (Leifsson et al., 2023). Due to the sample-bias of only including (co-)dominant surviving trees, it remains uncertain if impaired productivity indicates a potential higher mortality risk in coming years. Including mortality records to compare the growth of trees that died and those that survived (Dobbertin, 2005), will be needed to unravel acclimation from growth impairment and eventually mortality. Overall, intra-specific variation in drought response in our study is large. It is likely that factors that were not addressed, e.g. stand structure, microclimate and genetic variability, underlay the individual variation found here (Thom et al., 2023).

4.4. Conclusions

Our study highlights major growth reductions during drought in both coniferous and broadleaved tree species growing under various site conditions in the Netherlands. Drought impact varied across species and site, and was most prominent on the driest soils and for the most productive conifers. Productivity loss was smallest for sessile oak. On water-limited soils, growth of pedunculate oak was more reduced than for most other species-site combinations, indicating a risk for future forests on those soils. This is relevant under climate change, since prolonged and repeated climatic droughts are expected to increase soil moisture drought (Samaniego et al., 2018).

Many individual trees of all tree species had fully recovered growth two years after previous drought, whereas this was not the case after the more severe and longer-lasting recent 2018 (-2020) drought. Nearly all years after 2018 were drier than normal (KNMI 2023b) and multi-year droughts as seen in 2018–2020, are expected to increase in probability and in duration (Van der Wiel et al., 2022). Thus, it can be expected that drought-legacy effects in terms of carbohydrate depletion and hydraulic impairment have a negative effect on tree growth and vitality in the post-drought years (Cailleret et al., 2017). As tree growth is directly related to carbon sequestration, growth reductions due to climate change may affect carbon mitigation potential, as was observed in the extreme drought year 2022, when reduced net carbon uptake by forests was found in large parts of Europe (Van der Woude et al., 2023). Decreased productivity in temperate forests is also suggested by a study from central Europe, which found that in 2022 the growing season not only started, but also ended earlier than normal (Matula et al., 2023). This resulted in a shorter growing season and reduced growth. Others observed diverging trends in European forest growth over the past decades, with slightly increasing growth in the Western part of Europe from 1975 until 2015, i.e. not including recent dry years (Pretzsch et al., 2023).

It remains unclear if the growth reductions to severe to extreme droughts will result in continued growth decline and eventually higher mortality in the near future, but the immediate effects of drought on annual ring width and hence productivity are clear, with varying resilience across species, especially in successive drought years. These insights and the implications for forest management are therefore highly relevant under projected climate change for the Netherlands.

Declaration of Competing Interest

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

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Appendix

Table A1

Characteristics of stand structure and soil properties for each series. Mean height (m) and diameter at sample height (cm) of the sampled trees is given with the standard deviations indicated in parentheses. Soil properties include pH (0–1.20 m), soil texture based on the percentages of sand, silt and clay (0–1.20 m), estimated soil capacity for plant available water (ASW in mm) and soil richness (poor, intermediate, richer). Poor soils are classified as those with PCA1< -0.07 and PCA2 > -0.07, rich soils with PCA1 > 0.07 or PCA2 < -0.07, and intermediate with values of PCA1 and 2 that do not match one of both conditions. The last year of ring formation (Year), the estimated age (Age) in that year, the number of sampled trees per location (No ind) and climate station used for climate growth relationships are given (DB=De Bilt, DE=Deelen, EE=Eelde, EH=Eindhoven, MA=Maastricht, TW=Twenthe). The table is sorted by species and in ascending order of available soil water capacity per site.

	Species	Common name	Species Code	Site	No ind	Height (m)	DBH (cm)	Age	pH	Soil texture	ASW (mm)	Soil richness	Year	Climate
1	*Abies alba*	Silver fir	AA	Schovenhorst (SCH)	10	-	37.35 (11.79)	47	4.5	loamy sand	43	poor	2019	DB
2	*Abies alba*	Silver fir	AA	Emmerdennnen (EMM)	15	32.32 (1.79)	67.49 (8.49)	95	4.9	sandy loam	105	richer	2020	EE
3	*Abies alba*	Silver fir	AA	Gieten (GIE)	15	28.89 (1.68)	50.70 (7.51)	79	4.9	sandy loam	133	richer	2020	EE
4	*Acer pseudoplatanus*	Sycamore maple	AP	Dorschkamp (DOR)	15	21.24 (1.46)	37.43 (4.18)	46	4.5	sandy loam	78	poor	2021	DE
5	*Acer pseudoplatanus*	Sycamore maple	AP	Drie (DRI)	15	19.49 (1.68)	39.61 (9.79)	59	4.6	loamy sand	79	poor	2021	DB
6	*Acer pseudoplatanus*	Sycamore maple	AP	Wezuperbrug (WEZ)	15	15.21 (0.84)	23.73 (2.73)	33	5.2	loamy sand	95	richer	2021	EE
7	*Acer pseudoplatanus*	Sycamore maple	AP	Middachten (MID)	15	22.69 (2.75)	40.89 (7.44)	75	4.9	sandy loam	155	richer	2021	DE
8	*Fagus sylvatica*	European beech	FS	Hoge Veluwe (HVK)	15	20.77 (2.06)	36.74 (5.01)	65	4.6	loamy sand	32	poor	2020	DE
9	*Fagus sylvatica*	European beech	FS	Schovenhorst (SCH)	15	26.71 (3.30)	60.57 (9.12)	170	4.6	loamy sand	49	poor	2020	DB
10	*Fagus sylvatica*	European beech	FS	Elspeet (ELS)	15	25.96 (2.77)	65.77 (12.31)	193	4.5	loamy sand	63	poor	2021	DE
11	*Fagus sylvatica*	European beech	FS	Pijpebrandje (PIJ)	15	23.81 (2.56)	66.43 (8.39)	188	4.6	sandy loam	91	poor	2020	DE
12	*Fagus sylvatica*	European beech	FS	Amelisweerd (AMW)	13	28.50 (3.14)	73.13 (30.37)	119	6.2	loam	197	richer	2019	DB
13	*Fagus sylvatica*	European beech	FS	Vijlen (VIJ)	14	21.71 (2.43)	44.21 (9.66)	94	5.2	silty clay loam	198	richer	2020	MA

(continued on next page)

Table A1 (*continued*)

	Species	Common name	Species Code	Site	No ind	Height (m)	DBH (cm)	Age	pH	Soil texture	ASW (mm)	Soil richness	Year	Climate
14	*Larix kaempferi*	Japanese larch	LK	Schovenhorst (SCH)	15	26.73 (1.87)	55.93 (4.39)	82	4.5	loamy sand	51	poor	2020	DB
15	*Larix kaempferi*	Japanese larch	LK	Grolloo (GRO)	15	28.45 (1.29)	71.33 (6.86)	89	4.9	sandy loam	110	richer	2020	EE
16	*Larix kaempferi*	Japanese larch	LK	Grolloo (GRH)	20	24.56 (2.22)	32.63 (7.31)	46	4.8	sandy loam	125	richer	2019	EE
17	*Larix kaempferi*	Japanese larch	LK	Vaals (VAA)	23	-	36.93 (2.74)	46	5.1	silt loam	215	richer	2019	MA
18	*Pseudotsuga menziesii*	Douglas-fir	PM	Speulderbos (SPS)	15	33.53 (3.47)	43.21 (9.63)	58	4.5	loamy sand	45	poor	2020	DB
19	*Pseudotsuga menziesii*	Douglas-fir	PM	Zwolse Bos (ZWB)	15	39.75 (3.56)	59.89 (8.83)	78	4.9	sandy loam	81	inter	2020	DE
20	*Pseudotsuga menziesii*	Douglas-fir	PM	Het Leesten (LEE)	15	-	55.99 (7.84)	70	4.6	sandy loam	143	inter	2020	DE
21	*Pseudotsuga menziesii*	Douglas-fir	PM	Oostereng (ONG)	14	20.16 (2.39)	24.38 (5.89)	36	4.7	sandy loam	150	inter	2018	DE
22	*Pseudotsuga menziesii*	Douglas-fir	PM	Oostereng (OEN)	11	20.9 (1.94)	24.83 (3.32)	38	4.7	sandy loam	150	inter	2020	DE
23	*Pseudotsuga menziesii*	Douglas-fir	PM	Oostereng (OOS)	16	28.79 (3.13)	45.51 (9.11)	59	4.7	sandy loam	151	inter	2020	DE
24	*Pinus nigra*	Black pine	PN	Schovenhorst (SCH)	10	19.84 (1.50)	41.59 (6.27)	82	4.6	loamy sand	39	poor	2020	DB
25	*Pinus nigra*	Black pine	PN	Oostereng (OOS)	11	19.76 (1.70)	36.27 (5.94)	55	4.6	loamy sand	63	poor	2019	DE
26	*Pinus sylvestris*	Scots pine	PS	Speulderbos (SPS)	15	24.53 (2.40)	43.79 (3.28)	98	4.5	loamy sand	45	poor	2020	DB
27	*Pinus sylvestris*	Scots pine	PS	Hoge Veluwe (HVP)	15	17.16 (0.72)	25.92 (3.02)	50	4.7	loamy sand	57	poor	2020	DE
28	*Pinus sylvestris*	Scots pine	PS	Oostereng (OOS)	10	19.22 (0.69)	33.81 (4.31)	55	4.6	loamy sand	63	poor	2019	DE
29	*Quercus petraea*	Sessile oak	QP	Riemstruiken (RIE)	15	19.51 (0.91)	40.87 (7.61)	115	4.6	sand	18	poor	2020	DE
30	*Quercus petraea*	Sessile oak	QP	Elspeet (ELS)	16	23.17 (2.96)	49.34 (8.81)	211	4.5	loamy sand	63	poor	2021	DE
31	*Quercus petraea*	Sessile oak	QP	Winterswijk (WIN)	15	25.65 (1.18)	57.69 (7.58)	179	5.4	sandy loam	92	inter	2019	TW
32	*Quercus petraea*	Sessile oak	QP	Vijlen (VIJ)	15	20.77 (2.03)	52.31 (9.48)	160	5.2	silty clay loam	198	richer	2020	MA
33	*Quercus petraea*	Sessile oak	QP	Sint Jansberg (STJ)	15	15.00 (3.52)	44.49 (8.48)	88	5.3	loam	200	richer	2019	EH
34	*Quercus petraea*	Sessile oak	QP	Meinweg (MEI)	15	13.76 (0.73)	37.19 (6.46)	73	5.3	silt loam	204	richer	2019	MA
35	*Quercus petraea*	Sessile oak	QP	Vijlen (VIL)	14	20.82 (2.06)	35.89 (5.23)	90	5.2	silt loam	210	richer	2020	MA
36	*Quercus robur*	Pedunculate oak	QR	Loon op Zand (LOZ)	20	20.03 (2.88)	34.73 (6.42)	73	5.4	loamy sand	64	inter	2019	EH
37	*Quercus robur*	Pedunculate oak	QR	Pijpebrandje (PIJ)	11	23.56 (2.51)	55.91 (7.38)	188	4.6	sandy loam	91	poor	2020	DE
38	*Quercus robur*	Pedunculate oak	QR	Winterswijk (WIN)	15	24.00 (2.12)	54.57 (8.01)	179	5.4	sandy loam	92	inter	2019	TW
39	*Quercus robur*	Pedunculate oak	QR	t Zand (ZAN)	18	21.33 (1.37)	47.27 (11.75)	85	5.0	sandy loam	107	poor	2019	EH
40	*Quercus robur*	Pedunculate oak	QR	Someren (SOM)	23	18.50 (2.00)	25.74 (6.61)	82	5.7	sandy loam	109	richer	2018	EH
41	*Quercus robur*	Pedunculate oak	QR	Veldhoven (VEH)	25	22.29 (1.78)	33.70 (6.84)	80	5.2	sandy loam	114	inter	2019	EH
42	*Quercus robur*	Pedunculate oak	QR	Wooldse Veen (WOV)	12	-	64.81 (12.83)	127	5.2	sandy loam	122	inter	2022	TW
43	*Quercus robur*	Pedunculate oak	QR	Amelisweerd (AMW)	11	27.40 (3.66)	80.14 (31.46)	153	6.2	loam	197	richer	2019	DB
44	*Quercus robur*	Pedunculate oak	QR	Sint Jansberg (STJ)	16	16.67 (1.44)	42.74 (7.59)	88	5.3	loam	200	richer	2019	EH
45	*Quercus robur*	Pedunculate oak	QR	Meinweg (MEI)	15	17.47 (2.19)	40.63 (10.05)	73	5.3	silt loam	204	richer	2019	MA

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2024.122423.

Data availability

Data will be made available on request.

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