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Acclimation of mature spruce and beech to five years of repeated summer drought – The role of stomatal conductance and leaf area adjustment for water use

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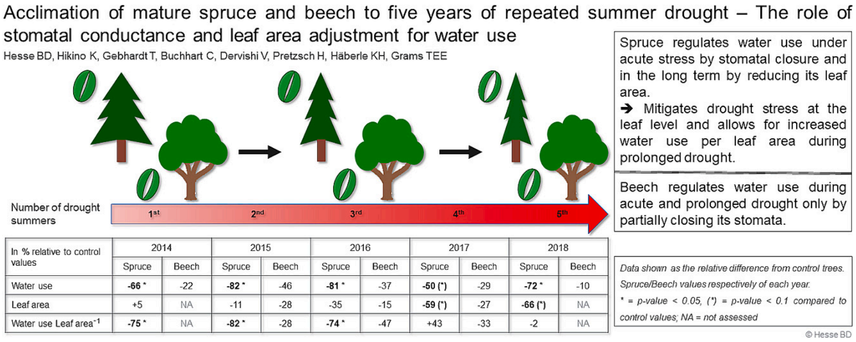
HIGHLIGHTS

- Beech and spruce survived five years of summer drought with distinct strategies.
- Beech mainly relies on stomatal regulation to control water use.
- Spruce, first controls water use by stomatal closure by up to 80 %.
- Second, over the years spruce decreases its leaf area by reducing growth.
- Third, reduced leaf area of spruce mitigates drought stress at the leaf level.

GRAPHICAL ABSTRACT



Acclimation of mature spruce and beech to five years of repeated summer drought – The role of stomatal conductance and leaf area adjustment for water use

Hesse BD, Hikino K, Gebhardt T, Buchhart C, Dervishi V, Pretzsch H, Häberle KH, Grams TEE

Spruce regulates water use under acute stress by stomatal closure and in the long term by reducing its leaf area.
➔ Mitigates drought stress at the leaf level and allows for increased water use per leaf area during prolonged drought.

Beech regulates water use during acute and prolonged drought only by partially closing its stomata.

In % relative to control values	2014		2015		2016		2017		2018	
	Spruce	Beech	Spruce	Beech	Spruce	Beech	Spruce	Beech	Spruce	Beech
Water use	**-66 ***	-22	**-82 ***	-46	**-81 ***	-37	**-50 (*)**	-29	**-72 ***	-10
Leaf area	+5	NA	-11	-28	-35	-15	**-59 (*)**	-27	**-66 (*)**	NA
Water use Leaf area^{-1}	**-75 ***	NA	**-82 ***	-28	**-74 ***	-47	+43	-33	-2	NA

Data shown as the relative difference from control trees. Spruce/Beech values respectively of each year.
** = p-value < 0.05, (*) = p-value < 0.1 compared to control values; NA = not assessed*

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ABSTRACT

Forests globally are experiencing severe droughts, leading to significant reductions in growth, crown dieback and even tree mortality. The ability of forest ecosystems to acclimate to prolonged and repeated droughts is critical for their survival with ongoing climate change. In a five-year throughfall exclusion experiment, we investigated the long-term physiological and morphological acclimation of mature Norway spruce (*Picea abies* [L.] KARST.) and European beech (*Fagus sylvatica* L.) to repeated summer drought at the leaf, shoot and whole tree level. Throughout the drought period, spruce reduced their total water use by 70 % to only 4–9 L per day and tree, while beech was less affected with about 30 % reduction of water use. During the first two summers, spruce

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achieved this by closing their stomata by up to 80 %. Additionally, from the second drought summer onwards, spruce produced shorter shoots and needles, resulting in a stepwise reduction of total leaf area of over 50 % by the end of the experiment. Surprisingly, no premature leaf loss was observed. This reduction in leaf area allowed a gradual increase in stomatal conductance. After the five-year drought experiment, water consumption per leaf area was the same as in the controls, while the total water consumption of spruce was still reduced. In contrast, beech showed no significant reduction in whole-tree leaf area, but nevertheless reduced water use by up to 50 % by stomatal closure. If the restriction of transpiration by stomatal closure is sufficient to ensure survival of Norway spruce during the first drought summers, then the slow but steady reduction in leaf area will ensure successful acclimation of water use, leading to reduced physiological drought stress and long-term survival. Neighboring beech appeared to benefit from the water-saving strategy of spruce by using the excess water.

1. Introduction

Forests cover approximately 30 % of the global terrestrial area and their conditions have a direct impact on global climate and human society (Alkama and Cescatti, 2016; Foley et al., 2005; IPCC, 2019). Recently, global forests have been experiencing immense canopy dieback and tree mortality due to severe drought (Allen et al., 2010; Hammond et al., 2022; Hartmann et al., 2022; Schuldt et al., 2020), and the frequency and duration of drought events are predicted even to increase (IPCC, 2021). Tree survival and productivity depend thereby not only on the extent of drought impacts on tree function but also on the ability to adjust to prolonged and frequent water-limiting conditions (Choat et al., 2018).

It is well known that limited water supply negatively affects tree functions by disturbing cell metabolism and reducing carbon uptake (Ciais et al., 2005; Hartmann et al., 2018; Peñuelas et al., 2011; Pretzsch et al., 2014b). Stomatal closure is the first tree responses to deal with a drought (Choat et al., 2018; Cochard et al., 1996; Limousin et al., 2009). Stomatal behavior lies along a continuum between isohydric and anisohydric drought responses (Hartmann et al., 2021; Klein, 2014; Meinzer et al., 2016). Isohydric species close stomata already at the early phase of drought to maintain midday plant water potential, while soil water potential decreases. In contrast, anisohydric species keep stomata longer open, tolerating midday water potentials to decrease more strongly (Martínez-Vilalta and Garcia-Forner, 2017). While the early stomatal closure of isohydric species minimizes the risk of hydraulic failure, this response restricts C uptake and may cause carbon depletion under prolonged drought (McDowell et al., 2008). A more anisohydric strategy on the contrary allows plants to continuously assimilate carbon but at a higher risk of hydraulic failure (McDowell et al., 2008, 2022). Accordingly, a stronger decrease in xylem sap flow density and tree water use was observed under drought in more isohydric species than in more anisohydric species (Li et al., 2019). The extent to which species-specific stomatal behavior change under repeated drought is not well understood, as tree responses to long-term and repeated drought seem to be non-linear due to their acclimation to new environmental conditions (Barbeta et al., 2013; Beier et al., 2012; Feichtinger et al., 2014; Leuzinger et al., 2011; Liu et al., 2015). In addition to the stomatal regulation, morphological and/or anatomical acclimations are expected, as revealed by greenhouse and field analyses in mostly juvenile plants (e.g. Brodribb et al., 2020; Brunner et al., 2015; Rowland et al., 2023), whereas the corresponding acclimation of mature trees to repeated drought is less intensively studied (e.g. Grossiord et al., 2017; Guérin et al., 2018; Laoué et al., 2023; Leuschner, 2020; Moreno et al., 2021).

Recent observations highlight the importance not only of stomata but also of leaf morphology and leaf area for controlling water loss (Adams et al., 2015; Guérin et al., 2018; Limousin et al., 2009; Pritzkow et al., 2021; Schönbeck et al., 2018; Zweifel et al., 2020). Modification in leaf thickness (Flexas et al., 2006; Meier and Leuschner, 2008; Reich et al., 1997) and/or reduction in total leaf area (LA), mostly induced by leaf shedding (Ambrose et al., 2018; Barbeta and Peñuelas, 2016; Galiano et al., 2011; Limousin et al., 2009; Poyatos et al., 2013), can balance the reduced water uptake and transpiration loss under drought (Bréda et al., 2006; Pritzkow et al., 2021; Schönbeck et al., 2018; Trugman et al., 2018). To what extent modifications of the morphology occur in other tree organs (e.g. branch or stem) has rarely been studied under repeated drought (Petit et al., 2022). Barbeta and Peñuelas (2016) suggest that reduction in LA are not necessarily reflected in the sapwood area of the stem (SA), therefore impacting the leaf area to sapwood area ratio (LA/SA) (Limousin et al., 2012; McBranch et al., 2019; Moreno et al., 2021). However, reductions in stem growth under repeated drought (Pretzsch et al., 2020a) might maintain LA/SA, as suggested by allometric relationships (Forrester et al., 2017). Yet, a large part of the studies so far was conducted under either short-term/seasonal drought or using precipitation gradients (Rowland et al., 2023). To date, there are only a few experiments investigating morphological responses of the canopy of mature trees under a multi-year drought, mostly with throughfall exclusion systems (Fisher et al., 2007; Grossiord et al., 2017; Guérin et al., 2018; Laoué et al., 2023; Limousin et al., 2009; Moreno et al., 2021).

In Central European forest ecosystems, Norway spruce (*Picea abies* [L.] KARST.) and European beech (*Fagus sylvatica* L.) are two important tree species, accounting for 30 % of the forest areas (Pretzsch et al., 2014a). While evergreen spruce deploys a more isohydric strategy and closes stomata earlier (Hartmann et al., 2013; Oberhuber et al., 2015), deciduous beech shows a more anisohydric strategy (Leuschner, 2020; Magh et al., 2019), showing less decrease in C assimilation under drought. Although saplings and/or young trees of both species were affected by short-term drought in photosynthesis and transpiration (Gallé and Feller, 2007; Goisser et al., 2013; Kurjak et al., 2012; Střelcová et al., 2013), long-term observations of leaf/tree physiology/morphology and water use under prolonged drought are still scarce in mature forest stands in central Europe (Schönbeck et al., 2022).

To fill this knowledge gap, the Kranzberg Forest Roof (KROOF) project with throughfall exclusion started in 2014 in Kranzberg Forest in Southern Germany (Grams et al., 2021). Beech and spruce trees were subjected to prolonged droughts during entire growing seasons for five consecutive years from 2014 to 2018, aiming at moderate to high drought stress according to the definition of Walthert et al. (2021). Both species showed strong impairments not only in the carbon (e.g. NSC reserves or phloem transport) but also in the water (e.g. hydraulic conductivity, sap flow density profile, or osmotic acclimations) related physiology (Gebhardt et al., 2023; Hesse et al., 2019, 2021; Tomasella et al., 2018) but also in stem growth (Motte et al., 2023) and mycorrhization (Nickel et al., 2018). Taking advantage of this unique precipitation manipulation experiment we investigated the long-term physiological, i.e. xylem sap flow density and gas exchange, and morphological, i.e. shoot length, leaf size, and total leaf area, responses to prolonged and repeated summer droughts. Given the above-mentioned reports, we tested the following hypotheses.

H1. Mature spruce reduces water use more than beech under acute summer drought due to stronger stomatal control in line with their more isohydric and anisohydric strategies, respectively.

H2. Under repeated summer drought, water use of both species is regulated not only by stomatal control but additionally by morphological modifications, i.e. leaf quality (SLA) and quantity (total leaf area).

2. Materials & methods

2.1. Experimental site and climate data

This study was conducted in a mixed forest with c. 70-year-old Norway spruce (*P. abies* [L.] KARST.) and c. 90-year-old European beech trees (*F. sylvatica* L.), located in southern Germany/Bavaria (11°39′42″E, 48°25′12″N; 490 m a.s.l.). The long-term mean precipitation (1971–2010) was 720 mm/a (with 503 mm during the growing season), and mean air temperature was 7.9 °C (12.9 °C during growing season Apr–Oct) according to DWD data (Deutscher Wetterdienst, https://opendata.dwd.de/climate_environment/CDC/). On this site, a long-term throughfall exclusion experiment (Kranzberg forest roof project, KROOF) was initiated in 2014, which has been described in detail in Grams et al. (2021) including soil, weather data and stand structure. Briefly, this experimental site consists of 12 plots (110–220 m^2) with 3–7 beech trees on one side and 3–7 spruce trees on the other side of each plot. In 2010, all plots were trenched to 1 m of soil depth to prevent trees from taking up the water outside the plots (Pretzsch et al., 2014b). Furthermore, after about 1 m of soil a dense clay layer reduced root growth to a minimum into deeper soil (Häberle et al., 2012). Most fine roots have been found in the top soil layers down to 50 cm for beech and 30 cm for spruce respectively (Zwetsloot et al., 2019; Zwetsloot and Bauerle, 2021). Six plots were equipped with roofs positioned underneath the canopy at a height of 2–3 m to exclude the throughfall of precipitation (throughfall exclusion plots, TE) and the other six plots were without roofs and defined as control plots (CO). Both tree species in the TE plots were exposed to complete throughfall exclusion during the entire growing seasons between April and October for five consecutive years from 2014 to 2018, except for 2017, in which the roofs were only closed from the beginning of May until the end of the growing season (Grams et al., 2021). Due to the mortality of spruce trees in 2015 through bark beetle attack, two TE plots were removed from the analyses. The roofs were kept open between November and March, even during precipitation events Each summer an intensive measurement campaign was conducted in late July/early August for 2–3 consecutive days, presumably the peak of summer drought. A canopy crane next to the plots allowed detailed analyses of physiology and morphology in the canopy of four CO and three TE plots, which were not affected by the bark beetle attack. Diameter at the breast height (DBH) and height of beech trees were c. 33 cm and around 30 m, whereas those of spruce trees were c. 36 cm and 32 m, respectively (Table 1). Air temperature and relative humidity, global solar radiation and precipitation were measured on an on-site climate tower above the canopy (Table 2). The climate of the July + August 2014, 2016 and 2017 were slightly warmer (+3 °C on average) and equally moist (+4 mm on average) compared to the long-term mean of the experimental site, with 17.0 °C daily mean temperature and 89 mm of monthly precipitation. However, in the year 2015 a short but severe natural drought occurred in late summer (+7 °C and −56 mm) and the year 2018 was exceptionally hot but not dry (+6 °C and −12 mm) compared to the long-term mean of August/July. For more details on the climate refer to Grams et al. (2021).

Table 2
Relative extractable water in the soil (%) of CO and TE plots and climate parameters given as the daily mean, i.e. air temperature in °C (Temp), vapour pressure deficit in kPa (VPD) global solar radiation in W m^{-2} (Rad) and monthly mean precipitation in mm (Precip), of July and August in each year. Asterisks indicate differences comparing CO and TE of REW within each year, *** = $p < 0.001$, ** = $p < 0.01$; * = $p < 0.05$; (*) = $p < 0.1$; n.s. = not significant.

Year	2014	2015	2016	2017	2018
CO REW [%]	28.2 ± 3.3 **	31.5 ± 2.9 ***	34.7 ± 3.0 ***	37.0 ± 2.7 **	23.1 ± 3.3 *
TE REW [%]	13.2 ± 3.7 **	8.1 ± 2.3 ***	11.0 ± 2.4 ***	18.3 ± 2.7 **	11.9 ± 3.3 *
Temp [°C]	18.3 ± 0.5	23.7 ± 0.8	21.2 ± 0.6	21.5 ± 0.6	22.8 ± 0.6
VPD [kPa]	0. ± 0.05	1.10 ± 0.09	0.64 ± 0.06	0.65 ± 0.07	0.87 ± 0.08
Rad [W m^{-2}]	209 ± 13	250 ± 13	237 ± 13	230 ± 13	252 ± 13
Precip [mm]	107 ± 34	33 ± 15	75 ± 15	98 ± 27	77 ± 5

2.2. Measurement of volumetric soil water content and leaf water potential

Soil water content (SWC in vol.-%) was recorded weekly using Time Domain Reflectometry (TDR100, Campbell Scientific, Logan, CT, USA). The sensors are installed at three positions per plot in four depths: 0–7 cm, 10–30 cm, 30–50 cm, and 50–70 cm (for details see Grams et al., 2021). Relative extractable soil water (REW) was calculated using soil water content at saturation (Hesse et al., 2023) and permanent wilting point (Grams et al., 2021) from the same experimental site. The permanent wilting point was assessed for each sensor during the natural dry summer of 2015, when SWC was on a stable level for several weeks and plants could no longer take up water from the respective layer (for details see Grams et al., 2021). Predawn leaf water potential (Ψ_{PD} in MPa) of sun-exposed twigs was assessed before sunrise (3 am–5 am CET) with a Scholander pressure bomb (mod. 1505D, PMS Instrument Co., Albany, OR, USA) on one twig on 6 to 8 individuals per species and treatment (Table 1).

2.3. Measurement of mean daily xylem sap flow density

Xylem sap flow density per unit sapwood area was measured with custom-built Granier-type heat dissipation sensors and calculated as suggested in Granier (1987) in 10 min intervals (144 values per day). At breast height, sap flow was measured in the outer xylem sapwood (0–2 cm depth) with two sensors (north and south exposure) and each sensor was sheltered with an aluminum foil cap. Each spring the sensor were exchanged and re-installed in the same measurement trees as the year before. Individual missing values of the 10-min interval data were filled with the "Fill missing" function (Method: PCA with scaled data) and smoothed with a Gaussian filter (7 points) in software "The Unscrambler" (Aspentech, Bedford, USA). Missing data of daily xylem sap flow (less that 5 %) was calculated via the correlation between the remaining data at the same time with VPD and radiation. Data from both sensors were averaged and the mean sap flow density per day (average sap flow over 24 h) and tree was calculated (u_{daily} in L dm^{-2} d^{-1}). The xylem sap flow density was analyzed for approx. 2 weeks around each

Table 1
Tree diameter at breast height [cm] and tree height of 2014 at the start of the experiment and the Number of replicates (number of plots) for each measurement parameter.

Year	DBH of 2014 [cm]	Height of 2014 [m]	Xylem sap flow density, water use	Water potential, leaf gas exchange	Leaf/shoot morphology	Total leaf area
CO Beech	32.2 ± 3.0	29.2 ± 0.9	12 (6)	8 (4)	8 (4)	(6)
TE Beech	34.5 ± 3.1	30.1 ± 0.9	8 (4)	6 (3)	6 (3)	(4)
CO Spruce	36.5 ± 1.4	32.4 ± 0.4	12 (6)	8 (4)	8 (4)	3 (3)
TE Spruce	37.2 ± 2.8	32.5 ± 0.7	8 (4)	6 (3)	6 (3)	6 (3)

measurement campaign on 8–12 individuals per species and treatment (Table 1). Because of the focus on transpiration differences between CO and TE, all days with precipitation have been excluded from the analysis (<3 days for each year).

2.4. Calculation of the whole-tree daily water use

Whole tree water use (Table 1) was calculated using the xylem sap flow density and the xylem sap flow density profiles measured on 4–6 trees per species and treatment of the same experiment and experimental trees (see Gebhardt et al., 2023). U_{daily} data were weighted following the xylem sap flow profile for each 1 cm ring of sapwood (e.g. 0–1 cm, 1–2, …, 7–8 cm), multiplied with the respective sapwood area annulus and summed up over all 8 cm to calculate the whole tree daily water use (in L day^{-1}). For spruce trees, the xylem sap flow profile changed during the course of the experiment and was adapted for each summer following the work of Gebhardt et al. (2023), which assessed the xylem sap flow profile at the same experimental site. Additionally, for the measured trees the conducting sapwood depth was around 8 cm (Gebhardt et al., 2023) and did not change during the five summers of the recurrent drought event.

2.5. Measurements of stomatal conductance

Stomatal conductance to water vapour (g_s) at 400 ppm CO_2 were determined on sun-exposed twigs using the open gas exchange systems LI-6800 (for the measurements in 2018) and LI-6400 (for the measurements in the other years) (Li-Cor Inc., Lincoln, NE, USA). Spruce trees were not measured in 2016. During the measurements, the light intensity (PPFD) was set to 1500 μmol m^{-2} s^{-1} to saturate photosynthesis and the leaf temperature was kept at 25 °C. The relative humidity was set around 60–65 %. We limited the measurement time between around 9 and 15 (CET). To minimize the effect of VPD change over the day time, CO and TE trees were measured by turn. For beech, 3–5 intact sun-exposed leaves were randomly chosen from each tree for the measurements. For spruce, 2–3 one-year-old twigs per tree were randomly selected. In TE spruce, however, annual shoot growth was not always sufficiently long (i.e. <4 cm) to cover the gas exchange chamber, so needles from the previous year sometimes had to be taken into account. Gas exchange measurements were performed on 6 to 8 individuals per species and treatment (Table 1).

Needles of spruce used for the gas exchange measurements were collected at the end of each growing season and immediately scanned (Epson Perfection 4990 Photo, Epson Deutschland GmbH, Meerbusch, Germany). The projected leaf area of the needles was determined using software Image J (version 1.53a, National Institute of Health, USA), which was then multiplied by a factor of 3.2 to calculate the total needle surface area (Goisser et al., 2016; Homolová et al., 2013). The g_s data measured was then corrected by the total needle surface area to calculate the area-based g_s in mmol m^{-2} s^{-1}.

2.6. Measurements of leaf/needle and shoot morphology

Specific leaf area (SLA in cm^2 g^{-1}), and shoot length growth of sun crowns were recorded annually at the end of the growing seasons for both species from the same trees as used for leaf stomatal conductance measurements (Table 1). For SLA, 5–10 beech leaves or c. 150 spruce needles from 3 to 5 branches in sun crowns were randomly harvested, scanned (Epson Perfection 4990 Photo), dried for 72 h at 64 °C, and weighed. The projected leaf area was determined using the software Image J. The projected area (leaf size hereafter) of each beech leaf was thereby also recorded.

For shoot length growth, 4–6 branches per tree in sun crowns were randomly selected and measured. For spruce, needle length (mm) and density (n cm^{-1}) were additionally measured from the same branches in sun crowns used for the shoot length measurements. Needle length was recorded with randomly selected 4–6 needles. Needle density was determined by counting the needles and shoot length. All measurements were performed on 6 to 8 trees per species and treatment (Table 1).

2.7. Estimation of beech leaf biomass

To evaluate the total leaf biomass of beech trees, litter bags were installed below the canopy about 10 m above ground at two positions per plot (4 plots per treatment), in the middle of spruce and beech tree groups. Five litter bags (0.25 m^2 each) were arranged in each tree group. The bags were collected every 1–4 months for the purpose of another study and the sum of the whole growing season each year were used for this study. The collected beech leaves were sorted, dried and weighed. Beech leaves found in the bags below the spruce tree groups were considered to derive from the beech trees in the same plot. The litter biomass was then expressed in dry weight per forest ground area (g m^{-2}).

2.8. Estimation of spruce total leaf area

The leaf area of spruce was calculated for all summers on 3 (for CO) and 6 (for TE) trees (for details see "Method S1" in supporting information and Gebhardt et al. (2023)). Briefly, the total number of needles of each needle age (N_n) was calculated based on the measured data in the field, separately for sun and shade crowns. Sun and shade crowns were visually separated on site according to the clear differences in the needle morphology (SLA, length, and density).

$$N_n = N_s \times L_b \times L_s \times D,$$

where N_s represents the number of shoots of each needle age (in n cm^{-1} needled branch length), L_b the total length of the needled branches (in cm), L_s the length of each shoot (in cm), and D the needle density in each shoot (in n cm^{-1}). Then, the total leaf area of each needle age (A_n in m^2) was estimated with needle length (L_n in mm), following Riederer et al. (1988).

$$A_n = \frac{N_n \times (3.279 \times L_n - 16.31)}{1000000} \ (\textit{for current year needles})$$

$$A_n = \frac{N_n \times (4.440 \times L_n - 24.78)}{1000000} \ (\textit{for older needles})$$

Finally, A_n of each needle age was summed up to determine the total leaf area (LA). Based on the 2020 data, LA between 2014 and 2018 was calculated retrospectively (see Methods S1, Gebhardt et al. (2023).

2.9. Statistics

Data were analyzed using R (version 4.0.3) in R studio (version 1.3.1093). Ψ_{PD}, xylem sap flow density, daily water use, leaf gas exchange, and morphology were tested with a mixed effect model using the year (2014–2018) and the treatment (CO and TE) as fixed and the tree number and the plot (1–8) as a random effect (package: nlme, version: 3.1-151). Relationships between u_{daily} and Ψ_{PD} were compared between beech and spruce using ANCOVA, after logarithmic transforming of u_{daily}. Normality of the residuals (Shapiro test/qq-plots) and homogeneity of variances (Levene test) were tested for every model. If any fixed factor was significant, post-hoc test with Tukey correction (package: emmeans, version: 2.30-0) was performed. All the errors in the text and graphics refer to the standard error of the mean (SE) unless otherwise noted.

3. Results

3.1. Relative extractable soil water (REW) and predawn leaf water potential (Ψ_{PD})

Relative extractable soil water (REW) averaged over the upper 70 cm soil depths significantly decreased under TE already in the first drought summer and remained significantly lower over all summer droughts compared to CO (Table 1). The mean REW under TE trees averaged over all summers was 12.5 ± 1.3 % and under CO trees 30.1 ± 1.6 %.

In the first drought summer (2014), Ψ_{PD} of TE beech (−0.62 ± 0.04 MPa) was by 40 % lower than that of CO (−0.44 ± 0.02 MPa, Fig. 1). Ψ_{PD} of TE beech decreased significantly in the second drought summer 2015 to −1.28 ± 0.06 MPa, and was 60 % lower Than that of CO beech with −0.80 ± 0.05 MPa. This indicates moderate to high drought stress in 2014 and 2015 according to the definition of Walthert et al. (2021) for beech trees. In 2016, Ψ_{PD} of TE beech remained significantly (2016, with −0.67 ± 0.02 MPa) and in 2017 (−0.40 ± 0.05 MPa) plus 2018 (−0.54 ± 0.06 MPa) insignificantly lower than that of CO beech (2016: −0.35 ± 0.02 MPa, 2017: −0.25 ± 0.03 MPa, 2018: −0.41 ± 0.02 MPa, Fig. 1).

In contrast, already in the first drought summer of 2014, TE spruce had significantly lower Ψ_{PD} (by 56 %) with −1.39 ± 0.05 MPa compared to CO spruce with −0.89 ± 0.06 MPa (Fig. 1). In the second drought summer, the difference between treatments increased to 66 % (CO: −0.96 ± 0.04, TE: −1.60 ± 0.05 MPa). In 2016 and 2018, Ψ_{PD} of TE spruce increased to −0.94 ± 0.06 and −0.89 ± 0.07 MPa, which were yet still significantly lower than that of CO spruce with −0.56 ± 0.02 and −0.58 ± 0.04 MPa, respectively. In 2017, even no significant differences were found between CO (−0.51 ± 0.02 MPa) and TE (−0.81 ± 0.21 MPa) spruce in the predawn water potential (Fig. 1).

3.2. Xylem sap flow density at outer 2 cm sapwood

In 2014, the daily mean sap flow density (u_{daily}) in TE beech was 6.6 ± 0.3 L dm^{-2} d^{-1}, which was slightly lower than in CO beech with 8.9 ± 0.4 L dm^{-2} d^{-1} (Fig. 2a). In the two following drought summers, TE beech showed significantly lower u_{daily} (7.6 ± 0.2 and 7.6 ± 0.4 L dm^{-2} d^{-1}) by about 40 to 50 % than CO beech with 14.8 ± 0.2 and 13.7 ± 0.4 L dm^{-2} d^{-1} in 2015 and 2016, respectively. In 2017 and 2018, u_{daily} was still reduced by about 20 to 30 % in TE beech (6.3 ± 0.7 and 7.8 ± 0.2 L dm^{-2} d^{-1}) compared to CO beech (9.9 ± 07 and 9.6 ± 0.3 L dm^{-2} d^{-1}), but no longer significantly (Fig. 2a). In contrast, already in the first drought summer of 2014, u_{daily} of TE spruce with 1.7 ± 0.2 L dm^{-2} d^{-1} was about 60 % lower than that of CO spruce with 4.4 ± 0.3 L dm^{-2} d^{-1}. In the following drought summers (2015, 2016), u_{daily} of TE spruce was reduced by about 75 % (1.3 ± 0.1, 1.4 ± 0.1 L dm^{-2} d^{-1}, Fig. 2a) compared to that of CO spruce (6.1 ± 0.2, 5.1 ± 0.2 L dm^{-2} d^{-1}, respectively). Although still strongly reduced by about 30 to 60 % in 2017 and 2018, no significant difference in u_{daily} was found between treatments in the last two summers.

There were significant relationships between u_{daily} and Ψ_{PD} in both species (Fig. 2b), i.e. stomatal responses to changing Ψ_{PD} did not differ between CO and TE trees. The slop of spruce was significantly steeper than that of beech, indicating that spruce showed a stronger decrease with decreasing Ψ_{PD}. The decrease of u_{daily} per Ψ_{PD} [MPa] was 0.79 ± 0.19 log L dm^{-2} d^{-1} in beech, while spruce showed larger decrease with 1.31 ± 0.25 log L dm^{-2} d^{-1}.

3.3. Daily whole-tree water use

Daily whole-tree water use of spruce trees during summer was more strongly reduced under drought than that of beech (Fig. 3). TE spruce already significantly reduced their water use in 2014 to 6.6 ± 0.6 L day^{-1}, by >60 % compared to CO spruce with 19.4 ± 1.5 L day^{-1}. In the following drought summers, water use of TE spruce was reduced up to 82 % and remained constantly very low (4.8 ± 0.2, 4.1 ± 0.3, 8.9 ± 0.9 and 6.2 ± 0.3 L day^{-1} in 2015, 2016, 2017 and 2018) and significantly lower, except for 2017, than that of CO spruce (26.5 ± 0.8, 21.7 ± 1.0, 17.9 ± 1.3 and 22.1 ± 0.8 L day^{-1}, respectively) by 50 to 80 % (Fig. 3). In contrast, TE beech reduced their daily water use throughout the drought summers by 10–46 % (not significant, Fig. 3) with TE beech consuming 28.2 ± 1.7, 33.1 ± 1.1, 36.0 ± 3.4, 29.4 ± 4.8 and 35.6 ± 1.5 in 2014, 2015, 2016, 2017 and 2018, compared to CO beech (36.3 ± 2.3, 61.8 ± 1.7, 57.0 ± 3.4, 41.6 4.2 and 39.7 ± 1.6 L day^{-1}, respectively).

3.4. Stomatal conductance at the leaf level

TE spruce significantly reduced g_s in the first two drought summers by 66 % in 2014 and 84 % in 2015). In the fourth and fifth drought

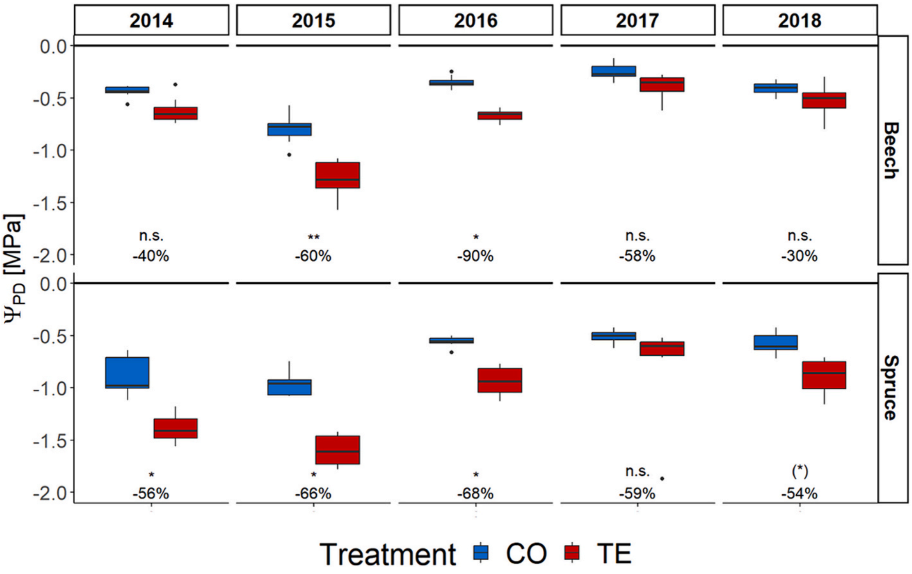

Fig. 1. Predawn leaf water potential (Ψ_{PD}) of beech (top) and spruce (bottom) during the experiments in control (CO, blue) and throughfall exclusion (TE, red) plots. Asterisks indicate differences comparing CO and TE trees, *** = $p < 0.001$, ** = $p < 0.01$; * = $p < 0.05$; (*) = $p < 0.1$; n.s. = not significant. Percentages give the relative reduction in the mean of the TE trees compared to the mean of the CO trees. Data taken from Grams et al. (2021).

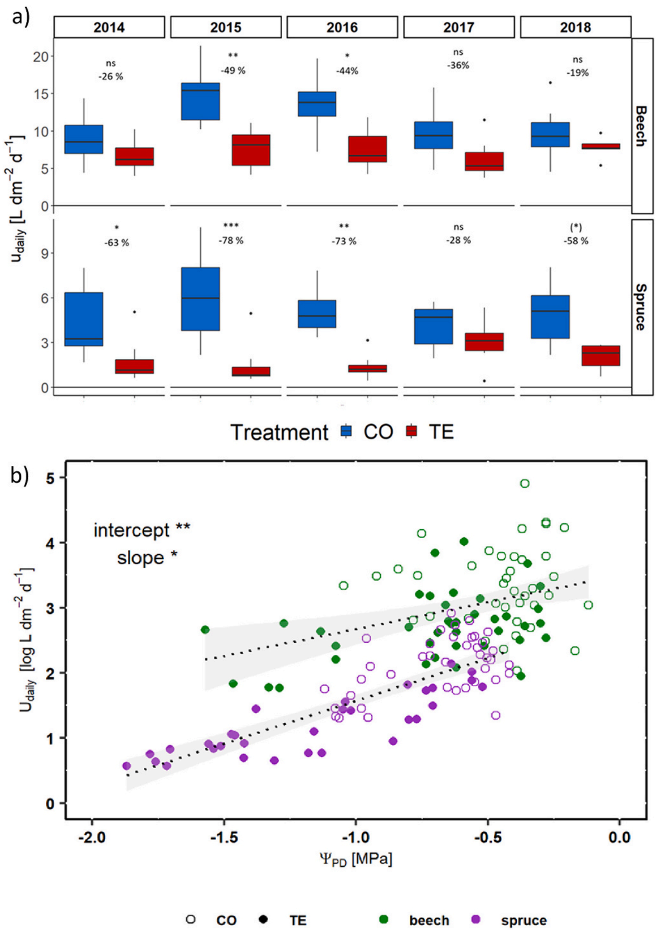

Fig. 2. a) Daily xylem sap flow density (u_{daily}) in control (CO, blue) and throughfall exclusion (TE, red) beech (top) and spruce (bottom) trees. b) Relationship between u_{daily} (logarithmic transformed) and predawn leaf water potential (Ψ_{PD}) in beech (green) and spruce (purple). The data from five growing seasons were pooled for each species. Asterisks in the Fig. 2a indicate significant differences comparing CO and TE trees and asterisks in the Fig. 2b indicates the difference between species according to ANCOVA, *** = $p < 0.001$, ** = $p < 0.01$; * = $p < 0.05$; (*) = $p < 0.1$; n.s. = not significant. Percentages give the relative reduction in the mean of the TE trees compared to the mean of the CO trees.

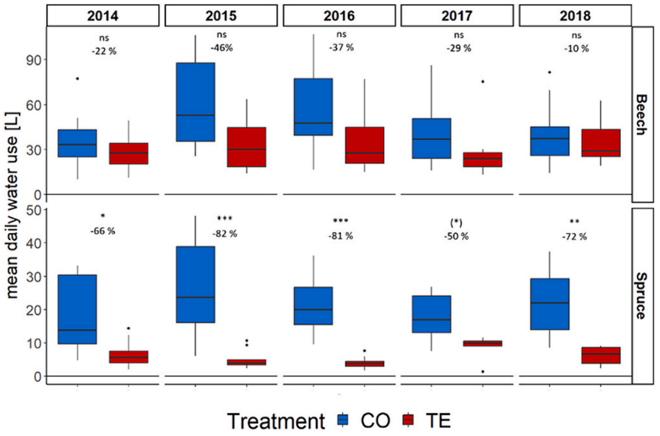

Fig. 3. Whole-tree daily water use (in L) of beech and spruce trees in control (CO) and throughfall exclusion (TE) plots. Asterisks indicate significant differences comparing CO and TE trees, *** = $p < 0.001$, ** = $p < 0.01$; * = $p < 0.05$; (*) = $p < 0.1$; n.s. = not significant. Percentages give the relative reduction in the mean of the TE trees compared to the mean of the CO trees.

summer (2017 & 2018), the differences between CO and TE spruce were still significant but much smaller (g_s: by28% and 63 %, Fig. 4). In 2014 in comparison, TE beech significantly lowered stomatal conductance only by 36 % compared to CO beech (192 ± 16 mmol m^{-2} s^{-1}). In the next drought summers (2015 & 2016), the difference in g_s between CO and TE increased to 49 % and 46 %. In the last two drought summers, g_s increased close to the level of CO trees, resulting in non-significant treatment effects in 2017 and 2018.

3.5. Morphology at the shoot and leaf level

3.5.1. Shoot length growth

In the first drought summer (2014), TE beech trees still showed similar shoot length growth as CO (CO: 32.3 ± 2.1 cm, TE: 29.3 ± 1.1 cm, Fig. 5a). However, a treatment effect was observed after the second drought summer with TE beech significantly reducing shoot length growth by 42 % (CO: 30.5 ± 2.9 cm, TE: 17.7 ± 1.6 cm). In the last three drought summers, TE beech shoot length growth remained significantly shorter with relative reductions of 40 to 70 % (13.3 ± 1.1, 11.8 ± 1.5, and 15.8 ± 3.0 cm) than in controls (29.0 ± 1.8, 35.9 ± 0.9, and 27.1 ± 2.1 cm), respectively.

Likewise, spruce showed the first drought effect in the second drought summer (Fig. 5b) with 41 % shorter shoot growth (8.0 ± 1.4 cm) than that of CO spruce (13.6 ± 1.0 cm). During the following three drought summers, shoot length growth of TE spruce remained significantly shorter (4.2 ± 0.9, 5.4 ± 0.8 and 7.0 ± 0.9 cm) than in CO spruce (13.5 ± 0.9, 17.2 ± 1.5 and 14.1 ± 1.1 cm), by 69 %, 69 % and 51 % respectively.

3.5.2. Leaf morphology

SLA of beech was not affected by drought treatments, although the values varied between 102 ± 4 and 117 ± 3 cm^2 g^{-1} among summers (Fig. S1a). Leaf size was similar between treatments in the second and fifth drought summers (Fig. 5c) but in 2016 somewhat smaller under TE than CO beech (13 ± 1 and 19 ± 1 cm^2, respectively).

Similarly, spruce did not change SLA throughout the drought summers, although the TE spruce showed somewhat higher SLA in 2015 (32.5 ± 2.6 cm^2 g^{-1}) than CO spruce (29.0 ± 0.4 cm^2 g^{-1}, Fig. S1b). In the other summers, SLA varied between 27 and 32 cm^2 g^{-1} in both treatments. In contrast, needle lengths of TE spruce significantly decreased by 35 % in the second drought summer (9 ± 1 mm) and remained significantly smaller in the following drought summers (10 ± 1, 11 ± 1 and 11 ± 1 mm in 2016, 2017 and 2018) than those of CO spruce (remained constant around 15 ± 1 mm, Fig. 5d).

3.5.3. Beech litter biomass and spruce total leaf area (LA)

Litter dry biomass of beech was similar between TE and CO trees. The values varied between 350 and 450 g m^{-2} from 2015 to 2017 (Fig. 5e), thus indicating no significant reduction (Fig. 5e) (not assessed in 2014 and 2018).

In contrast, modification in leaf and shoot growth led to a significant reduction in the total leaf area of spruce (LA, Fig. 5f). In the first drought summer, the total leaf area of TE spruce trees was 468 ± 54 m^2 tree^{-1}, similar to that of CO trees with 447 ± 146 m^2 tree^{-1}. In subsequent summers (2015 & 2016), TE spruce gradually reduced its total LA by 11 % and 35 % compared to controls. In the last two drought summers (2017 & 2018) leaf area of TE spruce was reduced by 60–70 % compared to CO, i.e. 188 ± 30 and 172 ± 32 m^2 tree^{-1} under TE compared to 458 ± 136 and 501 ± 139 m^2 tree^{-1} for CO in 2017 and 2018, respectively.

3.5.4. Daily water use per leaf area in spruce

To estimate the daily water use per leaf area at the canopy level (in mL m^{-2} day^{-1}), we divided the daily water use of spruce by their total leaf area. Similar to the whole-tree water use, TE spruce consumed significantly (by >70 %) less water per leaf area in the first three drought summers (9 ± 2, 11 ± 2, and 12 ± 2 mL m^{-2} day^{-1} in 2014,

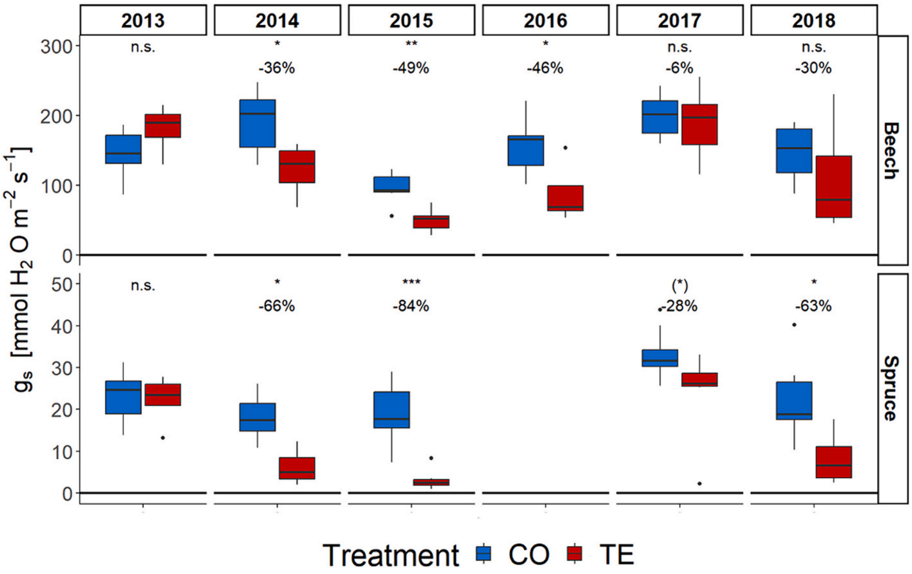

Fig. 4. Stomatal conductance to water vapour (g_s), of control (CO, blue) and throughfall exclusion (TE, red) beech (top) and spruce (bottom) trees. The drought treatment started in 2014. Asterisks indicate significant differences comparing CO and TE trees, *** = $p < 0.001$, ** = $p < 0.01$; * = $p < 0.05$; (*) = $p < 0.1$; n.s. = not significant. Percentages give the relative reduction in the mean of the TE trees compared to the mean of the CO trees.

2015, and 2016) than CO spruce with 36 ± 6, 58 ± 9, and 47 ± 4 mL m^{-2} day^{-1}, respectively (Fig. 6). However, in 2017 and 2018, water use per leaf area in TE spruce increased to the same level as CO spruce (41 ± 9 and 43 ± 12 versus 29 ± 3 and 45 ± 6 mL m^{-2} day^{-1} in 2017 and 2018, respectively).

4. Discussion

The present study investigates the acclimation of the water use of mature beech and spruce trees to repeated, experimentally induced summer drought. The more isohydric and shallow rooting spruce was more strongly affected by the drought treatment than the more anisohydric and deeper rooting beech. Both tree species were able to strongly reduce their water use by reducing their stomatal conductance. In the long term (>3 summers), spruce in particular acclimated to drought by more than halving its leaf area, which reduces the intensity of drought stress for the trees.

4.1. Greater reduction in water use of spruce than beech under acute drought through stronger stomatal regulation

During the drought period, relative extractable soil water (REW) was significantly lower in soils of TE plots compared to controls (Table 2). Correspondingly, TE trees of both species experienced a predawn leaf water potential lower than −1.0 MPa (Fig. 1), i.e. moderate to high drought stress according to Walthert et al. (2021). As a first response to the drought, both species regulated stomatal aperture and reduced sap flow density (Figs. 2a, 4), which is in line with previous reports under acute drought in beech (Lüttschwager and Jochheim, 2020; Nalevanková et al., 2020; Peiffer et al., 2014) and spruce forests (Baumgarten et al., 2019; Gartner et al., 2009; Lagergren and Lindroth, 2002). Compared to beech, spruce trees reduced their water use more strongly under repeated drought (Fig. 3), confirming H1 that spruce would show a stronger response under acute drought than beech. This is further supported by the significantly steeper decrease of u_{daily} in spruce compared to beech in parallel with the decrease of Ψ_{PD} (Fig. 2b). These findings are consistent with the contrasting drought response strategies of more anisohydric beech and more isohydric spruce (Hartmann et al., 2021; Leuschner, 2020). Compared to the 20–50 % decrease in beech (g_s, and u_{daily}), the drought effect on spruce was higher (60–85 %). Thus, the greater reduction in water use by spruce, compared to beech, is primarily attributed to stronger stomatal control at the leaf level, reflecting a more isohydric strategy.

4.2. Long-term reduction of total leaf area in spruce attenuates drought stress

Under a prolonged and repeated drought, leaf and shoot morphology, in addition to stomatal control, may play an important role in balancing trees' water loss (Limousin et al., 2009). Thicker and smaller leaves can improve turgor maintenance (Mitchell et al., 2008), increase g_s per unit leaf area (Flexas et al., 2006; Mencuccini and Comstock, 1999; Reich et al., 1997), and simultaneously reduce water loss (Bert et al., 2021). However, neither of the species significantly adjusted SLA throughout the drought period, indicating no acclimation via leaf quality under the long-term drought. This observation is consistent with previous findings in beech (Knutzen et al., 2015; Meier and Leuschner, 2008) and conifer species (Dobbertin et al., 2010; Raison et al., 1992); however, also several other studies have shown a lower SLA under drought (e.g. Da Sois et al., 2024). Additionally, TE beech did not significantly change their litter biomass under drought (Fig. 5e), although the leaf size was reduced in 2016 (Fig. 5c), which can be explained by the severe but short natural drought in 2015 in addition to the drought treatment. Combined with no modification in the SLA, this results indicates no significant reduction in the total leaf area in beech, rejecting H2 for beech that morphological changes would regulate water use under repeated drought. However, the branches of TE beech became significantly shorter under repeated drought (Fig. 5a), leading to a smaller crown size (Jacobs et al., 2021). As a result, beech trees invested more carbon to the leaf area relative to non-green branch biomass and increased the leaf biomass per branch biomass compared to controls (Petit et al., 2022), at the expense of continuing high water loss. Potentially the drought was not high enough to trigger essential loss of hydraulic conductivity (Tomasella et al., 2018) with following up foliage reduction as seen during natural severe drought years of 2018 in other stands in Central Europe (e.g. Arend et al., 2022). During drought, beech continued to produce fine roots to compensate for root mortality (Nikolova et al., 2020; Zwetsloot and Bauerle, 2021), thus maintaining their water uptake capacity. To supply this belowground carbon sink, carbon allocation may have shifted from stem/branch to fine root

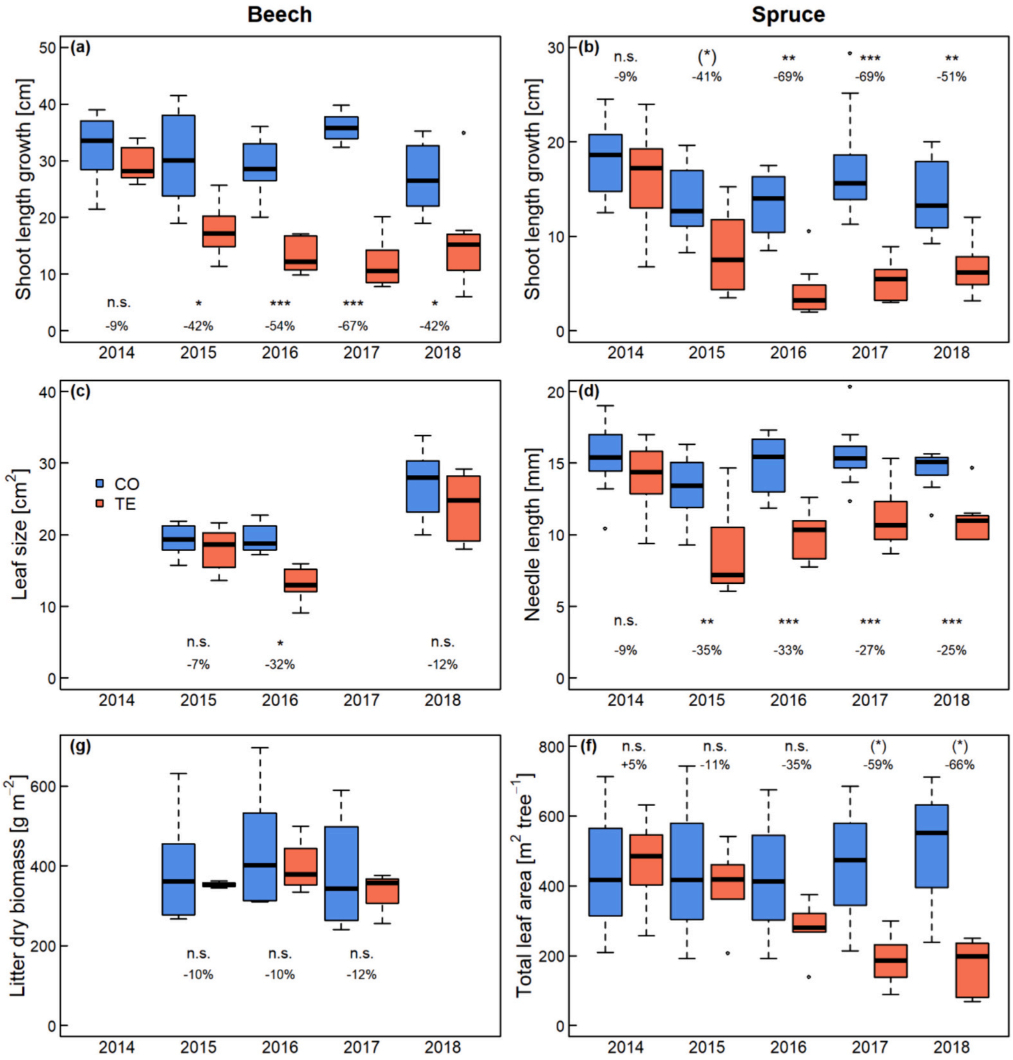

Fig. 5. Shoot length growth (a, b), leaf size (c), needle length (d), litter dry biomass (e), and total leaf area (f) of beech (left) and spruce (right) and control (CO, blue) and throughfall exclusion (TE, red). Asterisks indicate significant results based on linear-mixed model comparing CO and TE trees, ***, $p < 0.001$; **, $p < 0.01$; *, $p < 0.05$; (*), $p < 0.1$; n.s., not significant. Percentages give the relative reduction in the mean of the TE trees compared to the mean of the CO trees.

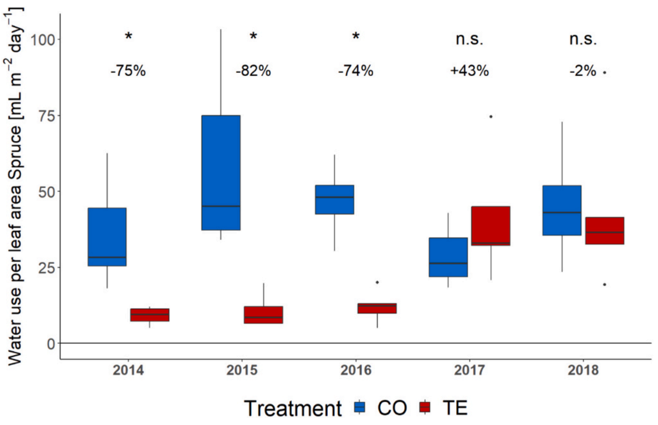

Fig. 6. Water use per leaf area (mL m^{-2} day^{-1}) of spruce trees under control (CO, blue) and throughfall exclusion (TE, red). Beech data are not shown, since total leaf area of beech trees were not assessed. Asterisks indicate significant differences comparing CO and TE trees,* = $p < 0.05$; n.s. = not significant. Percentages give the relative reduction in the mean of the TE trees compared to the mean of the CO trees.

growth, as widely observed in saplings during drought (see review by Poorter et al., 2012), without any strong reduction in leaf production.

In contrast, TE spruce significantly decreased needle and shoot length (Fig. 5b, d) but did not increase the leaf biomass per branch biomass (Petit et al., 2022), leading to a strong reduction in LA (Fig. 5f) and lower crown transparency (Jacobs et al., 2021), which is similar to the observed morphological adjustments of mature Scots pine during a long-term irrigation experiment (Bose et al., 2022; Dobbertin et al., 2010). Since spruce needle biomass collected by litterbags underneath the canopy did not differ between treatments (data not shown), the reduction in LA was caused by the production of shorter needles and shoots under repeated drought rather than pre-mature leaf shedding, in contrast to recent observations in other species (Ambrose et al., 2018; Barbeta and Peñuelas, 2016). This is likely because the water potential of TE spruce throughout the drought summers was higher than −2.1 MPa which should cause a 50 % loss of conductivity in end-twigs as determined for the same spruce trees (Tomasella et al., 2018). In contrast to leaf shedding as a quick response to a high drought, the observed decrease in LA through morphological changes started only in the second drought summer. The strong reduction in leaf area (>50 %) allowed a physiological recovery of g_s and u_{daily} while the whole-tree water use remained stable (Fig. 3). Looking at the water use per whole-tree LA, which should be an indicator for the whole-crown conductance in contrast to single-leaf measurements of g_s, TE spruce consumed significantly less water per leaf area than CO spruce in the first three drought summers (Fig. 6). After strongly reducing its whole-tree LA, TE spruce had the same water use per leaf area as CO spruce in the last two drought summers (Fig. 6). In comparison, this increase in the water use per leaf area is unlikely for TE beech with no significant reduction in the LA. Therefore, H2 is accepted for spruce, as the morphological acclimation to repeated drought reduced the whole tree water use to a similar extent as stomatal closure during the first drought summers, but also allowed an increase in water use per leaf area. In contrast to previous reports on long-term drought (Hudson et al., 2018; Limousin et al., 2012; Martin-StPaul et al., 2013), sapwood depth was not affected in the present study (Gebhardt et al., 2023). Therefore, the significant reduction in leaf area and the resulting drastically reduced ratio of leaf area to sapwood area (LA/SA) is likely responsible for the increased water use per unit leaf area in the last two drought summers.

4.3. Water use strategies of beech and spruce under 5 years of throughfall exclusion

The control of water loss by stomatal closure was the decisive mechanism to save water in the first two drought summers of the experiment. From the third drought summer on the reduction of leaf area was the important mechanism to save water for spruce. This additional mechanism of spruce enabled the partial recovery from moderate to high drought at the leaf physiology level while water use of TE spruce did not further decrease after the leaf area reduction and remained at the same level as in 2014/15. The water not used by spruce could then be used by the neighboring trees, in this case beech, not only during the drought but also during the recovery afterward. However, this would require beech to grow roots into the soil close to spruce in order to acquire the unused water. Leuschner et al. (2001) have shown that beech is indeed able to quickly occupy water- and nutrient-rich soil patches, even when growing with other competing species. Therefore, beech as a highly competitive species could potentially take up unused water of spruce (Schmid, 2002). This may also account for the absence of morphological alterations at the leaf level in beech, as the degree of drought stress was only moderate in the subsequent drought years. However, other studies have identified a high degree of plasticity in the morphology of beech trees (Schumann et al., 2024), particularly under conditions of drought (Weithmann et al., 2022). Furthermore, it can be reasonably assumed that xylem embolism does not play a pivotal role in the water relations of this experiment, as the measured water potentials are not close to the critical thresholds ($\Psi_{50/88}$, Choat et al., 2012) of −3.8 MPa and −4.5 MPa, respectively (Tomasella et al., 2018).

Compared to beech, spruce shows a more complex response pattern, from the initial physiological response, which can be quickly reversed, to more costly and longer-lasting morphological changes. The growth of shorter shoots and smaller needles to reduce the leaf area in spruce is at first somewhat surprising, as it is a very slow process that takes several years, while summer drought can be a very rapid developing stress. Other species also reduce leaf area under drought stress, but they do so by shedding parts of their leaf area (Ambrose et al., 2018; Barbeta and Peñuelas, 2016; Li et al., 2020; Nadal-Sala et al., 2021; Poyatos et al., 2013). Spruce may not be able to follow this strategy due to its original ecological distribution in boreal and mountain forests (Schmidt, 2014). Frost (drought) and other unfavorable conditions (Charra-Vaskou et al., 2012 and literature therein) are common in high altitudes and latitudes. Slow growth is a simple but effective response by spruce (Pretzsch et al., 2020b) and other species (Coomes and Allen, 2007) to these conditions. Therefore, evolutionary, spruce is potentially not able to shed older needles as a response to drought stress, but instead, it reduces overall growth in order to counteract the unfavorable conditions in the long term. This may also explain the very high mortality of planted spruce stands during recent heavy drought years in central Europe (i.e. 2018/19, Obladen et al., 2021; Schuldt et al., 2020). The rapid growth in planted spruce forests appears to counteract the natural strategy of spruce to withstand abiotic stresses. Therefore, the approach of closing stomata and minimizing transpiration to avoid drought stress was insufficient during recent high drought spells in central Europe for spruce stands growing outside their natural range. However, our results suggest that even a rather drought-sensitive species such as spruce (Zang et al., 2014) can withstand repeated droughts through a combination of physiological and morphological acclimation, if not for biotic calamities, i.e. bark beetle attacks (Netherer et al., 2015, 2019). Given the ongoing climate change and the increasing frequency of drought periods, the slow but effective strategy of spruce may prove successful for some stands. However, this includes a strong reduction in growth and productivity of the surviving spruce stands. In summary, morphology plays a crucial role in tree water use and survival under repeated drought, potentially even more so than physiology, i.e. via stomatal closure. This is achieved by mitigating the effects of drought on physiology and potentially prolonging the time until internal water reserves are depleted (Petek-Petrik et al., 2023).

5. Conclusion

While both tree species experienced the same drought treatment, beech trees regulated water use solely through stomatal control. In contrast, spruce trees showed a more comprehensive strategy, achieving a greater reduction in water use than beech through both early stomatal regulation and a strong reduction in total leaf area as a long-term response, with a parallel physiological recovery at the whole tree level. In contrast to the mere physiological regulation observed in beech, the morphological responses in spruce, in particular the reduction in leaf area, may have a lasting effect even after the drought has ended, contributing to a prolonged drought legacy effect on tree productivity. Importantly, the implications of these observed morphological responses may differ between deciduous and evergreen trees, as the former can produce new leaves in subsequent growing seasons, while the latter retains older leaves for extended periods. As the frequency and duration of drought events are projected to increase, understanding the short- and especially long-term effects of past droughts on tree performance is critical. This knowledge is essential to anticipate the effects of repeated drought events on forest health and productivity.

CRediT authorship contribution statement

Benjamin D. Hesse: Writing – original draft, Visualization, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation. **Kyohsuke Hikino:** Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation. **Timo Gebhardt:** Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Claudia Buchhart:** Writing – review & editing, Methodology, Data curation. **Vjosa Dervishi:** Writing – review & editing, Investigation. **Michael Goisser:** Writing – review & editing, Investigation, Conceptualization. **Hans Pretzsch:** Writing – review & editing, Project administration, Investigation, Funding acquisition, Data curation, Conceptualization. **Karl-Heinz Häberle:** Writing – review & editing, Supervision, Investigation, Funding acquisition, Conceptualization. **Thorsten E.E. Grams:** Writing – review & editing, Supervision, Project administration, Methodology, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Thorsten E.E. Grams, Hans Pretzsch reports financial support was provided by German Research Foundation. Benjamin D. Hesse reports financial support was provided by German Federal Environmental Foundation. Thorsten E.E. Grams reports financial support was provided by Bavarian State Ministry of the Environment and Consumer Protection. Thorsten E.E. Grams reports financial support was provided by Bavarian State Ministry of the Food, Agriculture and Forestry. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgments

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2024.175805.

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