

Local neighborhood affects stem rehydration under drought: evidence from mixtures of European beech with two different conifers

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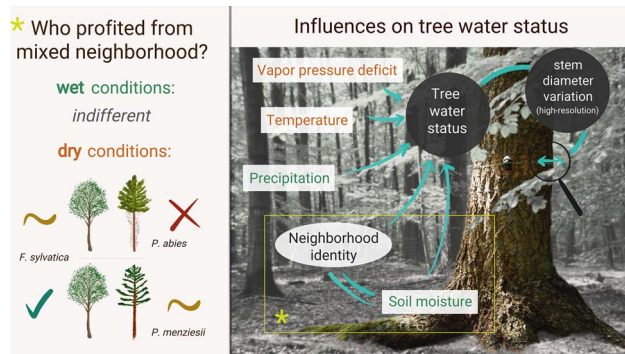
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Mixed-species forests are, for multiple reasons, promising options for forest management in Central Europe. However, the extent to which interspecific competition affects tree hydrological processes is not clear. High-resolution dendrometers capture subdaily variations in stem diameter; they can simultaneously monitor stem growth (irreversible changes in diameter) and water status (reversible changes) of individual trees. Using the information on water status, we aimed to assess potential effects of tree species mixture, expressed as local neighborhood identity, on night-time rehydration and water stress. We deployed 112 sensors in pure and mixed forest stands of European beech, Norway spruce and Douglas fir on four sites in the northwestern Germany, measuring stem diameter in 10-min intervals for a period of four years (2019–2022). In a mixture distribution model, we used environmental variables, namely soil matric potential, atmospheric vapor pressure deficit, temperature, precipitation and neighborhood identity to explain night-time rehydration, measured as the daily minimum tree water deficit (TWD_{min}). TWD_{min} was used as a daily indicator of water stress and the daily occurrence of sufficient water supply, allowing for stem growth (potential growth). We found that species and neighborhood identity affected night-time rehydration, but the impacts varied depending on soil water availability. While there was no effect at high water availability, increasing drought revealed species-specific patterns. Beech improved night-time rehydration in mixture with Douglas fir, but not in mixture with spruce. Douglas fir, however, only improved rehydration at a smaller share of beech in the neighborhood, while beech dominance tended to reverse this effect. Spruce was adversely affected when mixed with beech. At species level and under dry conditions, we found that night-time rehydration was reduced in all species, but beech had a greater capacity to rehydrate under high to moderate soil water availability than the conifers, even under high atmospheric water demand. Our study gives new insights into neighborhood effects on tree water status and highlights the importance of species-specific characteristics for tree-water relations in mixed-species forests. It shows that drought stress of European beech can be reduced by admixing Douglas fir, which may point towards a strategy to adapt beech stands to climate change.

Graphical Abstract



Key words: dendrometer, Douglas fir, interspecific competition, mixed forest, Norway spruce, tree water deficit.

Introduction

Mixed-species forests are a promising option for forest management in Central Europe (Knoke et al. 2008). On average, they harbor greater biodiversity (Ampointer et al.

2020), and are less susceptible to pest outbreaks (Jactel et al. 2021), are more productive (Pretzsch et al. 2015; Baeten et al. 2019; Pretzsch et al. 2020b), more resilient to drought (Pardos et al. 2021; Liu et al. 2022) and more stable against

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disturbances than monocultures (Tilman et al. 2014; Bauhus et al. 2017). Mixed forests provide both structural (Juchheim et al. 2019) and functional diversity and thus grant multiple ecosystem goods and services (Gamfeldt et al. 2013). It is known that the occurrence, direction and extent of these mixture effects depend on site conditions and species-specific traits (Forrester 2014; Ammer 2019). For instance, it has been shown that diverse hydraulic plant traits at a given forest site can buffer ecosystem response to drought (Anderegg et al. 2018). Positive mixture effects have been ascribed to reduced competition and/or facilitation occurring between different species, summarized as complementarity effects (Forrester 2014).

In light of climate change, which is projected to further increase both the frequency and intensity of extreme weather events in Europe (IPCC 2023), managing forests for resilience and biodiversity rather than for productivity alone has become a central goal of European policymakers (Simons et al. 2021; Lier et al. 2022). Drought-induced tree mortality has increased greatly in recent decades (Etzold et al. 2019; George et al. 2022). One way to counteract this detrimental development is to consider non-native, presumably particularly drought-resistant tree species in mixed stands. Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco), originally from the western North America, is a prominent candidate in this context. It is currently the second most widespread non-native conifer in Europe (van Loo and Dobrowolska 2019) and a potential alternative to native, but drought-sensitive Norway spruce (*Picea abies* (L.) H.Karst) (Vitali et al. 2017). Both conifers are grown in mixture with European beech (*Fagus sylvatica* L.), the most widespread, natural deciduous tree species in Europe (Antonucci et al. 2021). However, while foresters have already begun to increase the establishment of such stands, assuming that a certain share of Douglas fir in beech stands could reduce the risk of drought stress, the physiological processes underlying drought responses in mixed forests are still not understood (see reviews by Grossiord (2020) and Haberstroh and Werner (2022)). Even though overall mixture effects are mostly positive, the magnitude and direction of the effects depend on the selected species and may also vary with the investigated trait (Forrester 2014; Ammer 2019; Grossiord 2020). Furthermore, diversity effects may interact with resource availability, as suggested by the stress gradient hypothesis (Bertness and Callaway 1994; Maestre et al. 2009). According to this theory, more favorable conditions could lead to stronger interspecies competition and weaker complementarity effects.

An integrated and nondestructive way of monitoring both individual stem growth and tree water status is to measure stem diameter variation at high temporal resolution. Stem diameter variation as an indicator of plant water status has been established for decades, and has gained momentum in recent years (Klepper et al. 1971; De Swaef et al. 2015; Nal-evanková et al. 2018; Salomón et al. 2022; Leštianska et al. 2023; Peters et al. 2023). Commonly, this approach is based on the zero-growth concept (Zweifel et al. 2016), with two important assumptions: (i) growth (i.e., cell formation and enlargement) does not occur during periods of stem shrinkage (Lockhart 1965) and (ii) tree water deficit (TWD, μm) is defined as reversible stem shrinkage due to depletion of internal water reserves. Thus, higher TWD indicates more severe stem shrinkage. During the day, when transpiration is drawing

water from the stem to the canopy, TWD commonly increases. The critical period that determines whether or not growth can occur is usually during the night (Steppe et al. 2015; Zweifel et al. 2021), when stem water reserves are refilled from the soil and TWD reaches its daily minimum (TWD_{min}). Thus, TWD_{min} indicates the point of maximum nighttime rehydration. If TWD becomes zero, the tree is fully rehydrated and growth is possible. While the realized, absolute daily growth is constrained by additional factors, the condition TWD_{min} = 0 serves as an indicator for the absence of water stress and thus the potential occurrence of stem growth at least once during a given day (in the following named ‘potential growth conditions’). TWD_{min} is therefore a powerful measure of tree water stress and growth conditions on a daily scale (Dietrich et al. 2018; Salomón et al. 2022). Previous studies have already identified soil water potential and vapor pressure deficit (VPD) as the most important drivers of TWD (Zweifel et al. 2005; Salomón et al. 2022).

While the response of European beech and Norway spruce to drought and (to a limited degree) also their mixture has been researched extensively (Neuner et al. 2015; Leuschner 2020; Pretzsch et al. 2020a), Douglas fir and its mixture with European beech has received less attention. Applying a framework of indices for resistance, resilience and recovery to yearly ring data from stem cores, Thurm et al. (2016) found that compared with pure stands, Douglas fir performed better in mixture with European beech, the latter tending to be more drought sensitive. However, we are not aware of any study that has focused on tree water status in mixtures of mature European beech and Douglas fir at high temporal resolution. Considering daily and seasonal scales of physiological variables (such as tree water deficit) and environmental conditions will allow for a deeper understanding of the drivers of mixture effects.

In this study, we assessed daily TWD_{min} of European beech, Norway spruce and Douglas fir in mixed and pure stands in response to atmospheric demand and soil water availability. We first investigated species-specific responses, and then expanded our analysis to assess potential mixture effects. Mixture was determined at tree level; by applying a continuous measure of the local con- or allospecific competitive environment (‘neighborhood identity’), we aimed to capture the spatial scale most relevant for species interactions. Considering common forest management practice, we investigated only mixed stands of European beech with either of the conifers, and neglected the mixture of Norway spruce and Douglas fir as well as the mixture of all three species. With a unique data set of 112 trees and the corresponding time series of high-resolution stem diameter measurements covering four years, we addressed the following hypotheses:

- (1) The sensitiveness of TWD to dry conditions differs between the studied species and increases in the order: Douglas fir, European beech, Norway spruce.
- (2) Trees in allospecific neighborhoods are less likely to experience TWD than trees in conspecific neighborhoods (positive neighborhood identity effects).
- (3) Positive neighborhood identity effects are less pronounced (or absent) at high water availability.

The approach and methodology of the study are illustrated in a conceptual figure (Fig. 1).

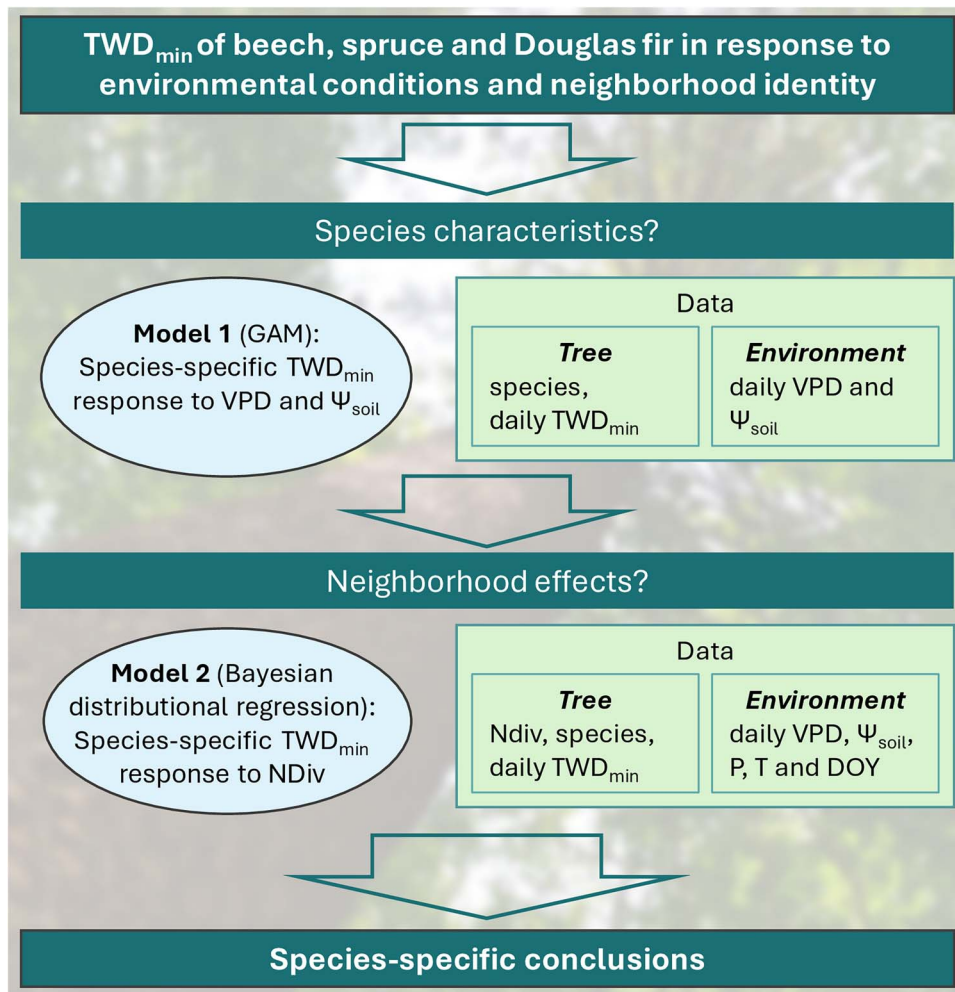


Figure 1. Conceptual figure summarizing the approach and methodology of the study. Variables used to explain standardized daily minimum tree water deficit (TWD_{min}) include, in model 1, atmospheric water VPD (kPa), Ψ_{soil} (soil matric potential, MPa) and in model 2 additionally neighborhood identity (NDiv), precipitation (P), temperature (T) and day of year (DOY).

Materials and methods

Study sites

The study was conducted in mature temperate forests of the northern Germany (federal state of Lower Saxony), where experimental plots of 50×50 m were established in 20 different forest stands, grouped into four quintets (Table 1). Each quintet comprised three pure stands and two mixed stands: pure native European beech (*Fagus sylvatica*, ‘beech’), pure Norway spruce (*Picea abies*, ‘spruce’; a native conifer cultivated outside its natural range) and pure non-native Douglas fir (*Pseudotsuga menziesii*), as well as mixed beech-spruce, and mixed beech-Douglas fir. Mixed stands of spruce and Douglas fir or of all three species were not considered. These mixtures do not represent viable economic or ecological options for forest management practice in Germany and thus are extremely rare. All stands were even-aged, whereas in the mixtures, beech was often established first (Table 2). Ground vegetation was largely absent in pure beech stands and in the mixed stands. In pure spruce stands, some moss and herb species were present, and in pure Douglas fir stands, there was often a sparse layer of *Rubus*. Since the ground vegetation was a typical ecological element of the studied stands that does not represent a strong competitor for water

compared with mature trees, we did not consider them in the analysis.

According to their geographical location, the quintets were clustered into two regions: ‘North’—sites ‘Unterlüß’ ($52.836752^{\circ}\text{N}$, $10.330936^{\circ}\text{E}$) and ‘Göhrde’ ($53.201222^{\circ}\text{N}$, $10.800878^{\circ}\text{E}$)—characterized by sandy soil and lower precipitation in the lowland of Lower Saxony, and ‘South’—sites ‘Winnefeld’ ($51.664759^{\circ}\text{N}$, 9.571193°E) and ‘Nienover’ ($51.696624^{\circ}\text{N}$, 9.528585°E)—located on loamy soil in the Solling mountain range with higher precipitation (Table 1). None of the sites provides access to a groundwater body within the rooting zones of the trees. An overview of stand attributes is given in Table 2. The plots were established in 2018. However, three stands were affected by windthrow and/or bark beetle infestation and were replaced by similar stands nearby in April 2021. The corresponding dendrometers were moved to new trees and entered the analysis as separate series. More details on the overall study design can be found in Ammer et al. (2020).

Environmental conditions

Air temperature (T, $^{\circ}\text{C}$), relative humidity (RH, %), solar radiation (SR, MJ m^{-2}), wind speed (WS, m s^{-1}) and open

Table 1. Location and characteristics of the study sites. Long-term climatic averages (MAP, mean annual precipitation and MAT, mean annual temperature) are based on elevation-sensitive interpolations from weather stations of the German weather service (DWD). Modified from Foltran et al. (2023) and Lwila et al. (2021).

Region	Quintet	Location (Lat., Long.)	Elevation (m.a.s.l.)	MAP (mm)	MAT (°C)	Soil type
South	Winnefeld	51.664759, 9.571193	345–402	839	8.8	Dystric Cambisol
	Nienover	51.696624, 9.528585	273–405	895	8.8	Dystric Cambisol
North	Unterlüß	52.836752, 10.330936	149–167	747	9.0	Haplic Podzole
	Göhrde	53.201222, 10.800878	113–126	673	9.2	Spodic Arenosol

Table 2. Stand attributes of the study sites, including mean tree height (m), mean diameter at breast height (DBH) \pm standard deviation (cm), age (years) and basal area ($\text{m}^2 \text{ha}^{-1}$). In mixed stands, the value for beech is followed by the value for the respective conifer in parentheses. Tree height was estimated from diameter measurements. Modified from Foltran et al. (2023) and Lwila et al. (2021).

Region (Quintet)	Stand type	Mean height (m)	Mean DBH \pm SD (cm)	Age (years)	Basal area ($\text{m}^2 \text{ha}^{-1}$)	Stem density (N ha^{-1})
South (Winnefeld)	Beech	29.3	33.6 \pm 12.9	89	26	248
	Douglas fir	34.0	42.2 \pm 11.3	73	29	199
	Spruce	23.3	27.7 \pm 8.1	59	48	475
	Beech (Douglas fir)	31.4 (40.9)	36.9 \pm 11.9 (64.5 \pm 17.6)	90 (80)	21 (12)	162 (31)
	Beech (Spruce)	30.3 (33.7)	36.3 \pm 14.6 (52.5 \pm 4.2)	94 (86)	18 (7)	158 (35)
South (Nienover)	Beech	23.4	21.7 \pm 12.8	86	27	599
	Douglas fir	32.0	38.3 \pm 12.2	44	26	192
	Spruce	26.5	34.5 \pm 9.7	55	38	363
	Beech (Douglas fir)	31.6 (48.0)	32.6 \pm 17.1 (81.0 \pm 22.0)	73 (58)	12 (13)	260 (52)
	Beech (Spruce)	27.9 (31.3)	18.5 \pm 10.4 (49.4 \pm 10.4)	85 (83)	15 (29)	336 (124)
North (Unterlüß)	Beech	22.1	20.0 \pm 12.2	85	24	527
	Douglas fir	32.6	40.0 \pm 15.8	70	43	263
	Spruce	26.7	36.1 \pm 10.8	111	27	232
	Beech (Douglas fir)	25.1 (36.3)	21.4 \pm 12.7 (62.6 \pm 15.4)	85 (82)	16 (14)	335 (39)
	Beech (Spruce)	23.9 (33.1)	25.7 \pm 14.0 (47.4 \pm 11.4)	122 (122)	17 (12)	240 (72)
North (Göhrde)	Beech	22.4	26.4 \pm 16.2	130	23	348
	Douglas fir	35.3	40.8 \pm 11.6	53	35	232
	Spruce	30.4	32.8 \pm 12.8	61	43	404
	Beech (Douglas fir)	28.6 (37.2)	25.3 \pm 16.8 (45.1 \pm 11.6)	74 (53)	11 (28)	175 (155)
	Beech (Spruce)	24.5 (29.0)	20.4 \pm 11.6 (39.8 \pm 9.0)	80 (80)	10 (14)	287 (107)

sky precipitation (P , mm) were measured and stored at 15-min resolution intervals (Campbell CR300) at four climate stations (MET300; DMS, Dundee, UK) close to the respective quintets. VPD (kPa) was determined from T and RH according to Jones (1992) using the *plantecophys* R package (Duursma 2015).

Soil matric potential (Ψ_{soil} , MPa) was measured hourly at 5, 20, 50 and 100 cm depths in the center of each study plot, using dielectric water potential sensors (TEROS 21, METER Group). Ψ_{soil} was corrected for temperature according to Walthert and Schleppi (2018) and screened for outliers with the *datacleanr* R package (Hurley et al. 2022). While it has been shown that soil moisture within a forest stand can vary horizontally (Schume et al. 2003), changes over time of the environmental variables are more relevant than absolute values for the statistical analyses in this study. Considering the limited size of the study plot, the closed tree canopy in combination with a widely spread root system of the individual trees in all stands (Lwila et al. 2021), and the relatively homogeneous soil conditions within the stands, it is assumed that a single measurement point results in a representative time series for the entire plot.

We included environmental variables in our statistical models to explain TWD_{min} (see Statistical analyses section), using daily averages (T , RH, VPD, Ψ_{soil} at 20 cm depth) and sums (P).

The monthly standardized precipitation evapotranspiration index (SPEI) was calculated for each quintet from monthly sums of precipitation and potential evapotranspiration, using the *SPEI R* package (Vicente-Serrano et al. 2010; Beguería and Vicente-Serrano 2023). Potential evapotranspiration was calculated from climate data using the ICID Penman-Monteith method (Allen et al. 1994), implemented in the *SPEI R* package.

Long-term climatic averages of the sites (as listed in Table 1) were based on elevation-sensitive interpolations from weather stations of the German Weather Service (DWD).

Dendrometer measurements and tree selection

We measured stem diameter at 10-min intervals with high-resolution band dendrometers (DC2 and DC3; Ecomatik, Munich, Germany). Similar to the setup in Metz et al. (2020), glide rings minimized friction between wire and bark, and tree bark was slightly smoothed where necessary (mainly on conifers), to ensure solid contact with the stem and to reduce bark influence on diameter variations. The installations took place in June 2018, but only full growing seasons (2019–2022) were used for the analysis. The dendrometers were installed at breast height (1.3 m above ground) on a total of 112 trees, distributed over the 20 stands. In each stand, four mature trees were selected per species, resulting in four trees in the pure and eight trees in the mixed stands. Thus, the analysis

is based on $n = 48$ beech, $n = 32$ Douglas fir and $n = 32$ spruce trees. This comprises $n = 16$ trees per species in conspecific neighborhoods, and another $n = 16$ trees in allospecific or mixed neighborhoods, for each species combination: beech (with Douglas fir), beech (with spruce), Douglas fir (with beech) and spruce (with beech). Only vital, dominant trees of comparable diameters, and in the mixed stands, with a mixed neighborhood were selected. An overview of the stand attributes, including average tree dimensions and stem density, is given in Table 2.

Neighborhood identity

As a continuous measure of tree-level neighborhood identity, we applied the NDiv index (Glatthorn 2021). The NDiv is a simple indicator for the extent of interspecific interaction. It ranges from 0 (conspecific neighborhood) to 1 (allospecific neighborhood) of a target tree and equals to the relative proportion to which its ‘area potentially available’ (APA) borders with that of allospecific neighbors. The APA of a target tree, in turn, represents its main growing space and is calculated based on the diameter at breast height (DBH) of the target tree and its neighbors, and the distance between them. Since our study investigated two-species mixtures, the NDiv represented only the proportion of the second species in the tree neighborhood; it is not a measure of species diversity. Accordingly, trees in monospecific stands always have an NDiv of 0. Our data set included beech trees with a maximum NDiv of 0.6 when growing in mixture with Douglas fir, and a maximum NDiv of 0.8 in mixture with spruce. Thus, there were no beech trees exclusively surrounded by Douglas fir or Norway spruce. The NDiv of the conifers covered the entire range from 0 to 1.

High-resolution diameter data processing

For the analysis of the dendrometer data, we excluded the winter months (December–March) from the time series, and only considered the individual growing season of each tree (i.e., the period when 99% of annual growth was completed), typically between April and September.

We applied the zero-growth concept (Zweifel et al. 2016), which distinguishes between irreversible diameter growth and reversible swelling and shrinking of the stem due to changes in stem water content (Fig. 2). Only values that exceed the previous all-time diameter maximum were considered as diameter growth (GRO, μm), while values below this previous maximum expressed a tree water deficit (TWD, μm , >0) (Fig. 2a and b). Potential growth at the cell level, that is, cell division without subsequent cell enlargement by water inflow and cell wall thickening, is not covered by this approach.

Tree water deficit typically occurs during the day when transpiration is drawing stem water upwards. In contrast, water reserves are restored during the night and TWD decreases. During dry conditions, however, stem water reserves may not be refilled completely during the night, leading to periods where the daily minimum TWD is still >0 . Thus, TWD and, on a daily basis, daily minimum TWD (TWD_{\min}), serve as proxies for the drought stress of a tree (Zweifel et al. 2001).

We extracted TWD and TWD_{\min} from the dendrometer data using the *treenetproc* R package (Haeni et al. 2020; Knüsel et al. 2021). Similar to Peters et al. (2023), we standardized TWD_{\min} by dividing it by the tree-specific greatest daily shrinkage, calculated as the 99th percentile of maximum daily shrinkage across the measurement period

(Fig. 2c), which compensates for differences in TWD magnitude due to stem size, wood architecture or bark thickness. Standardization changes the unit of TWD_{\min} from μm to $\mu\text{m} \mu\text{m}^{-1}$.

Some trees were not measured for the entire period of 2019–2022 because of technical issues, physical disturbance and/or re-establishment of a plot. In these cases, only full growing seasons were considered in the analysis. To perform the standardization comparably to the trees that were measured during all years, we premodeled the 99th percentile of the tree-specific annual maximum daily shrinkage of the missing years. For this, we used a Bayesian generalized linear model within the *brms* R package (Bürkner 2017; 2018), with Gamma-distributed response (logarithmic link-function) and grouping terms (‘random intercepts’) for the combination of measurement year, tree species, and quintet ID, plot ID and tree ID. We then used the maximum across years (either modeled or measured) for standardization.

All data processing, analyses and modeling were performed using the R programming environment, version 4.3.1 (R Core Team 2023).

Statistical analyses

Species comparison. We used generalized additive models (GAMs) as implemented by the *mgcv* R package (Wood 2011) to assess the response of TWD_{\min} to VPD and Ψ_{soil} for each tree species. Since this analysis aimed to identify species-specific traits, we included all trees of a species into the analysis, irrespective of neighborhood identity. To account for potential mixture effects, plot type (mixed, pure) was included as a random effect. TWD_{\min} was standardized as described in High-resolution diameter data processing section, and then scaled to the range 0–1 for each species, improving comparability between species. The beta regression family was used. Details on the formulation and model summaries can be found in Supplementary Methods S1 available as Supplementary data at *Tree Physiology* Online.

Neighborhood effects and environmental conditions. Neighborhood identity was included as covariate in a distributional regression with TWD_{\min} as response variable, using the *brms* R package (Bürkner 2017; 2018). We used a hurdle Gamma mixture distribution, which extends the Gamma distribution (that is applied for strictly positive response variables) by adding a subprocess that models responses with the value zero. This differentiation mirrors the characteristics of tree water deficit data, where $\text{TWD} = 0$ indicates possible growth, while $\text{TWD} > 0$ reflects the intensity of stem dehydration. The probability mass and density function of our hurdle Gamma distribution is thus given by

$$f_{\pi, \alpha, \mu}(\text{TWD}_{\min}) = \begin{cases} \pi, & \text{if } \text{TWD}_{\min} = 0, \\ (1 - \pi) \cdot f_{\alpha, \mu}(\text{TWD}_{\min}), & \text{if } \text{TWD}_{\min} > 0, \end{cases}$$

where α is the positive shape parameter and μ is the expectation (both of the Gamma distribution for TWD_{\min} if $\text{TWD}_{\min} > 0$), and π models the probability for $\text{TWD}_{\min} = 0$.

We modeled the parameters μ and π conditional on covariates, using a logarithmic link function for μ , and a logit link function for π . In addition to NDiv, we included VPD, Ψ_{soil} , P, T and day of year (DOY, by year) as covariates that characterize water demand, water availability and seasonality, respectively, as well as tree and stand ID as random effects. Due to the correlation with VPD (Figure S1

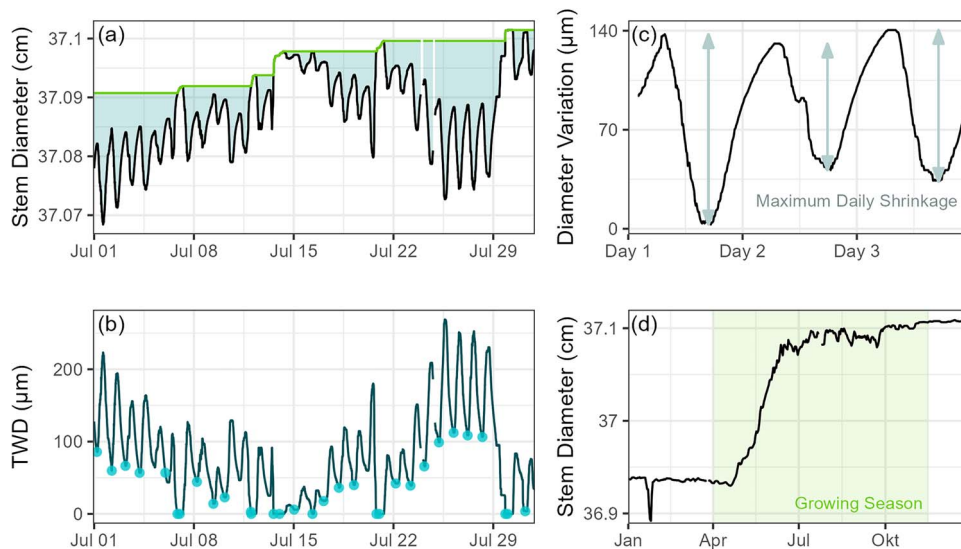


Figure 2. Variables derived from high-resolution stem diameter data as extracted with the *treenetproc* R package (Haeni et al. 2020; Knüsel et al. 2021), illustrated by the example of a beech tree in 2019. (a) One month of stem diameter variations with characteristic daily cycles. The upper line indicates irreversible growth, the shaded area represents tree water deficit. (b) Tree water deficit of the same time period (solid line), by definition corresponding to the difference between the two lines in panel (a). Light points mark the daily minimum tree water deficit (TWD_{min}). Note that if $TWD_{min} = 0$, irreversible growth is possible. (c) Maximum daily shrinkage (light gray arrows) of stem diameter (black line) on three consecutive days. (d) Annual course of stem diameter (daily averages). Note the frost event in late January, the main growth period from April to June and extended phases of stem shrinkage during July and August in that year.

available as Supplementary data at *Tree Physiology Online*), temperature at a site on a given day was included as the premodeled probability (p_{temp})—conditional on the value of the VPD measurement at that site on the given day—for seeing this or a higher temperature value. Thus, a high p_{temp} indicates comparably high temperature for the given VPD, while a low p_{temp} indicates comparably low temperature (see Supplementary Method S2 available as Supplementary data at *Tree Physiology Online*, for details).

Tree water deficit and environmental data were organized in a daily measurement time-series structure. Here, we assumed that the response on a given day was influenced not only by the values of a covariate on the same day, but also by the values on preceding days. In other words: it seemed possible that there were meaningful lagged covariate effects. For Ψ_{soil} , there was comparably little variation between days (Figure S2 available as Supplementary data at *Tree Physiology Online*). Therefore, we included only the Ψ_{soil} value of the previous day (lag 1). For VPD, p_{temp} and P, we included lags of 0, 1, 2 and 3 days. Additionally, we included an autoregressive error model component to get valid inference statements. Further details on the model formulation and underlying equations can be found in Supplementary Methods S3 available as Supplementary data at *Tree Physiology Online*.

We set a length of at least 14 consecutive days with non-missing measurements (in TWD outcomes and covariates) per series in order to include a series into our analysis. This was done to split the data into training and test-data (described below) and left us with $n = 815$ series totaling 50,174 daily measurements. Construction of lagged covariates generates missing covariates at the beginning of a series, since for the first days of a series, the information on previous days is unknown. Removing those days with incomplete lagged information further reduced the data set to 46,099 measurements.

The respective last 7 days of each series were kept as external test-data—for checking the predictive performance

of our models, such that series of at least 7 days entered the estimation of the model parameters. This left us with 5705 measurements for testing, and 40,394 for estimation.

The final model formulation was selected using leave-one-out cross-validation (LOO) and posterior predictive checks. Models were checked for Markov chain convergence using the Gelman-Rubin diagnostic (Rhat) (Gelman and Rubin 1992); all Rhat values were ≤ 1.05 .

Results

Weather conditions during the study years

Compared with the long-term (20 years) annual mean (Table 1), all study years exhibited higher mean temperatures and lower precipitation, but in different magnitudes. The year 2021 was the most humid year of the study period; it was 0.3 to 1.1 °C warmer (depending on the quintet) and showed 28–100 mm less precipitation than average. The year 2022 was remarkably hot and dry, being on average 1.2 to 2.2 °C warmer and having 110–214 mm less precipitation (equivalent to a reduction of up to 30%) compared with the long-term mean. The years 2019 and 2020 showed intermediate values. Accordingly, 2022 had the highest VPD (Fig. 3c), long phases of low Ψ_{soil} (Fig. 3d) and a negative SPEI drought index throughout most of the growing season (Fig. 3b), while 2021 had opposite tendencies. In all study years except 2021, several sites exceeded a Ψ_{soil} of -1.5 MPa, which is considered an estimate of the permanent wilting point (Chesworth 2008) and indicates that the study trees were temporarily exposed to severe drought stress.

Tree water deficit response to weather conditions

We aimed to assess if there were neighborhood effects on TWD_{min} , as well as environmental influences or interactions

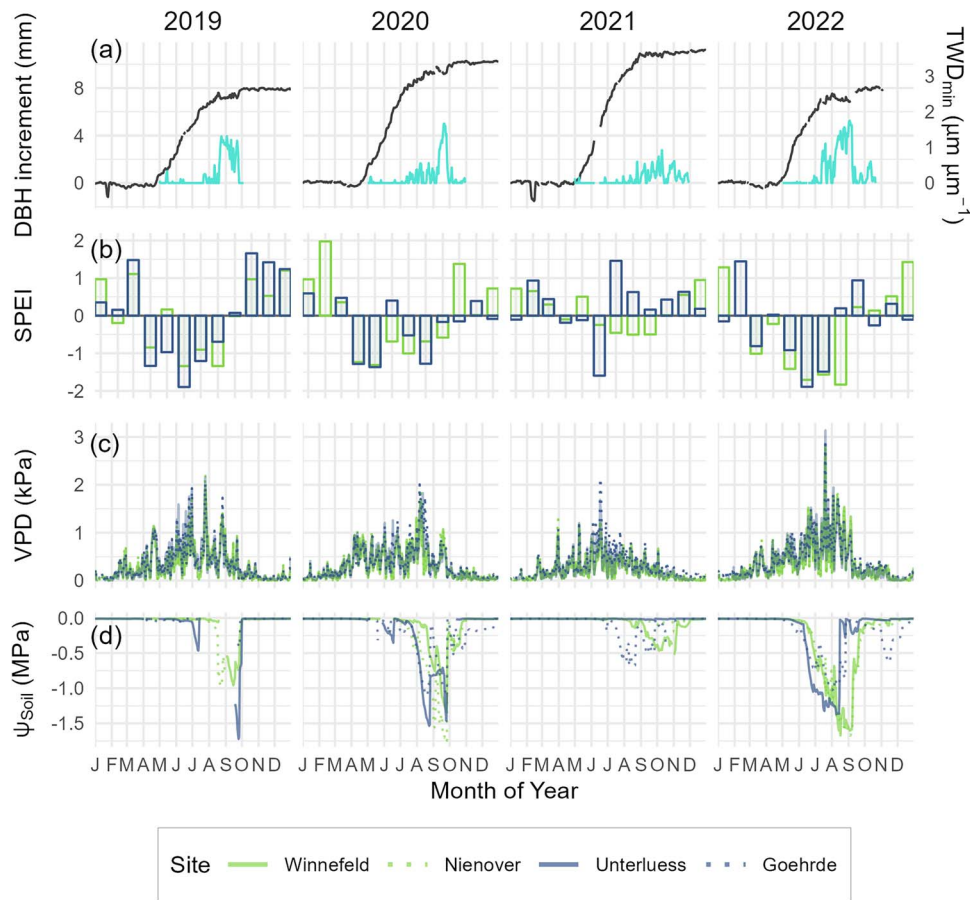


Figure 3. Environmental conditions and dendrometer measurements during the study period (2019–2022). (a) Daily mean diameter at breast height, reset to zero each year (DBH increment, mm, dark line) and standardized daily minimum tree water deficit (TWD_{min} , $\mu m \mu m^{-1}$, light line) for one sample tree, a Douglas fir on site Nienover. (b) Monthly SPEI (–) for the sites Winnefeld (light) and Unterluess (dark), displaying drought severity. Positive values indicate humid conditions, negative values dry conditions. (c) Daily mean VPD (kPa) for each year on the four study sites (solid light line = Winnefeld, dotted light line = Nienover, solid dark line = Unterluess, dotted dark line = Goehrde. Sites of the same color are geographically closer to each other and have similar soil characteristics.). (d) Daily mean soil matric potential (MPa) at 20 cm soil depth, averaged for the five plots in each study site (same legend as in (c)). Lower (more negative) values indicate drier soil.

between the two; thus, the regression model also included several other covariates (see Neighborhood effects and environmental conditions section). Since our study was focused on (i) species-specific differences (see below) and (ii) neighborhood effects, we do not discuss the other covariates in depth, but display the results in Figures S5–S8 available as Supplementary data at *Tree Physiology Online*. In general, moist conditions (low VPD, high precipitation, high soil matric potential) were associated with low or no tree water deficits, while dry conditions (high VPD, low to no precipitation, low soil matric potential) led to higher tree water deficits. Recent conditions (current or previous day) had a stronger effect than conditions 2–3 days before. On an annual scale, TWD_{min} exhibited a strong seasonality (Figures S5–S8 available as Supplementary data at *Tree Physiology Online*, inner right column). Potential growth ($TWD_{min} = 0$) was more likely in spring and early summer (around May to July, i.e., days of year 120–220). An increase in TWD_{min} occurred throughout summer and autumn (around July to October, i.e., days of year 220–300). Beyond these general patterns, there were clear differences between the study years. For instance, the probability for potential growth conditions ($TWD_{min} = 0$) decreased earlier in 2022. As shown in Fig. 3a, a Douglas fir tree reached its highest annual growth in 2021, and the lowest in 2019 and

2022, with notably higher and earlier peaks of tree water deficit in 2022.

Stand ID was included as a random effect and explained some additional variation in TWD_{min} (Figures S5–S8, Table S5 available as Supplementary data at *Tree Physiology Online*, central column). Generally, the loamy sites in the southern study region with higher annual precipitation were more likely to reach potential growth conditions than the sandy sites of the northern study region. However, stand ID effects were mostly not significant, indicating that the differences most relevant for TWD_{min} were already included in the set of covariates.

Species-specific tree water deficits as a function of atmospheric water demand and soil water availability

We used generalized additive models to study the response of TWD_{min} particularly to Ψ_{soil} and VPD at species-level, including tree species mixture as a random effect. TWD_{min} was transferred to a relative scale between 0 and 1 to improve the comparability between the three species. As could be expected, TWD_{min} increased with increasing VPD and decreasing soil matric potential for all species, indicating more severe stem

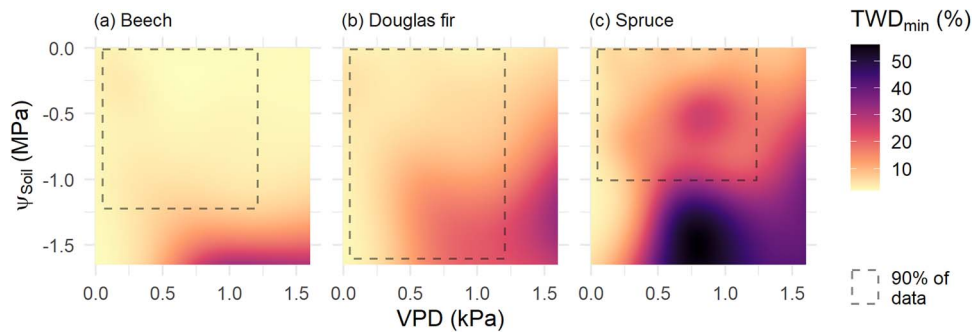


Figure 4. Standardized daily minimum tree water deficit (TWD_{min} , scaled from 0 to 1 for each species) as it occurred with atmospheric drought (x-axis: Previous day mean VPD (kPa)) and soil drought (y-axis: Previous day mean soil matric potential (MPa)) for beech (a), Douglas fir (b) and spruce (c). Both atmospheric and soil drought conditions can be found at the bottom right of each graph, while wet conditions are at the top left. The dashed rectangles enclose the inner 90% of the weather data. TWD_{min} visualization is based on a generalized additive model (see Materials and methods section).

dehydration with increasing drought (Fig. 4). TWD_{min} of Douglas fir (Fig. 4b) increased slower with rising VPD and decreasing Ψ_{soil} than spruce (Fig. 4c), but faster than beech (Fig. 4a). In contrast to the conifers, beech TWD_{min} barely responded to VPD on moist to moderately dry soil. The sensitiveness of TWD_{min} to drying did thus not increase in the order Douglas fir, beech, spruce (as expected in our Hypothesis 1), but instead in the order beech, Douglas fir, spruce. Continuing from this, we extended the analysis to explore potential neighborhood identity effects on each of the species.

Tree water deficit response to neighborhood identity

We used environmental variables (VPD, precipitation, temperature, soil matric potential) and neighborhood identity (NDiv) to explain standardized daily minimum tree water deficit (TWD_{min}) in a species-specific Bayesian regression model. Following a mixture-distribution approach, we modelled the probability $TWD_{min} = 0$ (potential growth conditions) separately from $TWD_{min} > 0$ (higher tree water deficit, no growth). We ran one model per species combination: beech (with Douglas fir), beech (with spruce), Douglas fir (with beech) and spruce (with beech). For each of these, we show the model summaries in Tables S1–S4 available as Supplementary data at *Tree Physiology Online*, and example series with model predictions and measured training and test data in Figures S9–S20 available as Supplementary data at *Tree Physiology Online*.

Neighborhood identity influenced TWD_{min} significantly in interaction with soil water availability (Fig. 5). At high Ψ_{soil} , effects of NDiv on TWD_{min} were low or absent. However, with increasingly dry soil, we found species-specific neighborhood identity effects. Beech in pure stands (NDiv = 0) was less likely to reach growth conditions than beech in neighborhood of Douglas fir (Fig. 5a) and had higher TWD_{min} (Fig. 5e). For beech in mixture with spruce, the picture was less clear: growth conditions were more likely in mixed than in conspecific neighborhood for most soil conditions (Fig. 5b), but this seemed to reverse under extremely dry conditions (this prediction relies on few data points). Furthermore, beech in conspecific neighborhood exhibited similar or lower TWD_{min} than beech with a spruce neighborhood (Fig. 5f). Douglas fir responded more sensitively to the mixture gradient. While a small proportion of beech in its neighborhood made growth conditions more likely than in conspecific neighborhood,

a high proportion of beech was associated with impaired growth conditions (Fig. 5c). Furthermore, Douglas fir in beech neighborhood exhibited higher TWD_{min} (Fig. 5g). Spruce was less likely to reach growth conditions (Fig. 5d) and had higher TWD_{min} with increasing beech proportion in the neighborhood (Fig. 5h). Figure 5 does not include uncertainties, however, as shown by narrow credibility intervals (Figure S3 available as Supplementary data at *Tree Physiology Online* for $TWD = 0$, Figure S4 available as Supplementary data at *Tree Physiology Online* for $TWD > 0$) and successful prediction of test-data (Figures S9–S20 available as Supplementary data at *Tree Physiology Online*), model estimates for TWD_{min} and the direction and strength of neighborhood identity effects proved to be reliable.

Discussion

Based on a 4-year data set of high-resolution stem diameter measurements of European beech, Douglas fir and Norway spruce, we were able to explain patterns of daily tree water status as a function of water demand and availability, species identity and tree neighborhood identity.

Species-specific responses to soil and atmospheric drought

As suggested by our results and previous research (Forrester 2014; Ammer 2019), the effects of tree species mixture need to be seen in the context of species-specific traits. We thus compared species-specific TWD_{min} depending on Ψ_{soil} and VPD (Fig. 4), the two most important drivers of tree water status (Zweifel et al. 2005; Salomón et al. 2022). Notably, night-time rehydration of spruce and also Douglas fir was impaired faster in response to VPD and Ψ_{soil} than beech. Under high to moderate water availability, beech barely responded to VPD, indicating successful night-time rehydration even under high atmospheric water demand, as long as sufficient soil moisture was available.

Species differences in the effectiveness of stem rehydration have been attributed to stomatal regulation and xylem anatomy (Borchert and Pockman 2005; Dietrich and Kahmen 2019; Peters et al. 2023). For instance, beech was shown to maintain a higher stomatal conductance and more flexible stomatal regulation under elevated soil dryness than the two conifers (Paligi et al. 2024), which could possibly facilitate rehydration. Furthermore, Peters et al. (2023)

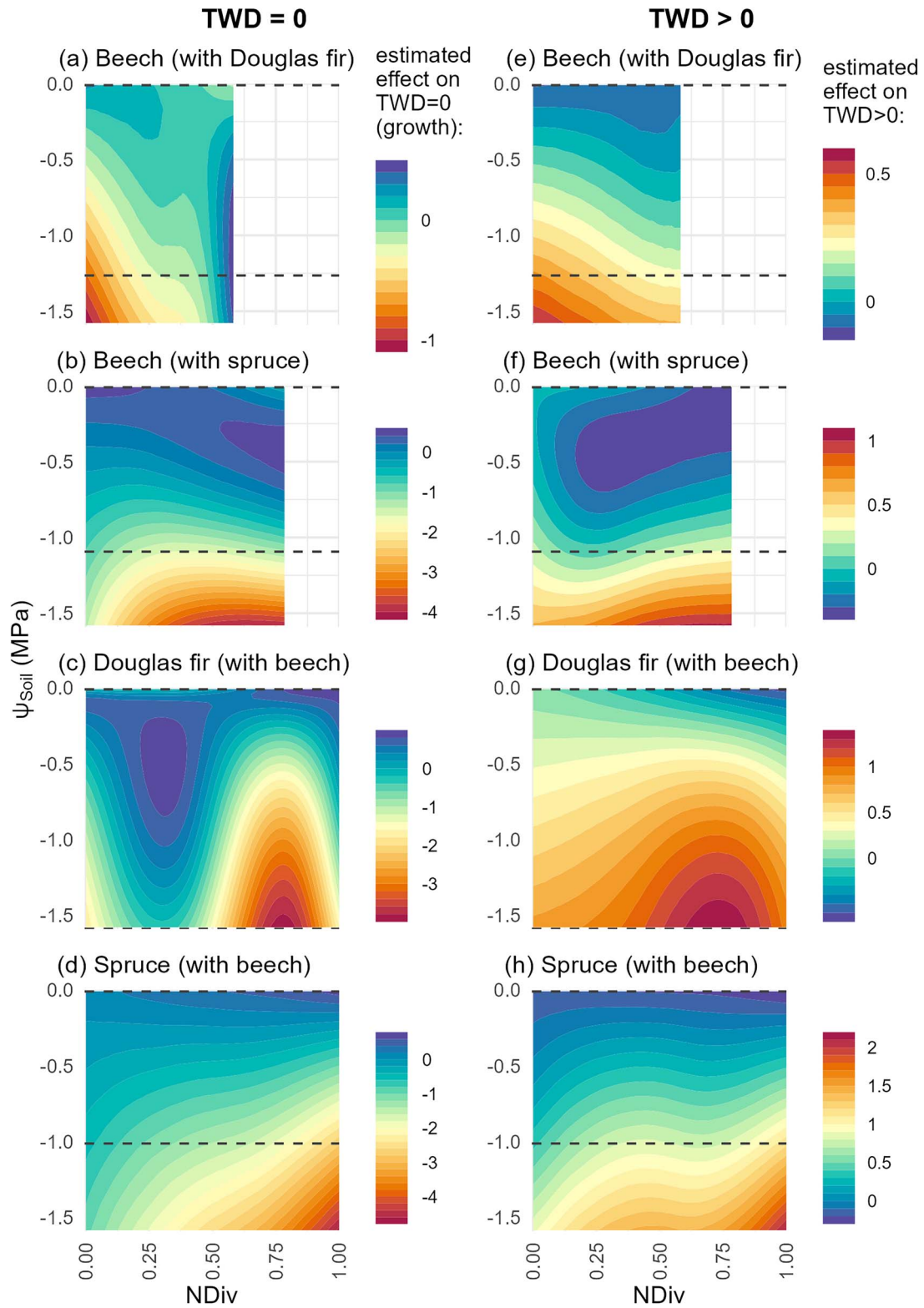


Figure 5. Estimated effect of neighborhood identity (NDiv, x-axis) and soil moisture (Ψ_{soil} , y-axis) on the probability of $TWD_{min} = 0$ (i.e., potential growth conditions) in panels a–d, and on the probability of $TWD_{min} > 0$ (i.e., more severe stem dehydration) in panels e–h. dashed lines enclose inner 90% of Ψ_{soil} data, where more negative values indicate drier soil. Panels (a) and (e) beech with increasing neighborhood proportion of Douglas fir, panels (b) and (f) beech with increasing neighborhood proportion of spruce, panels (c) and (g) Douglas fir with increasing neighborhood proportion of beech, (d) and (h) spruce with increasing neighborhood proportion of beech. Note the inverse scales: for the left column ($TWD = 0$), positive effects indicate that growth conditions are more likely; for the right column ($TWD > 0$), positive effects indicate more severe stem dehydration.

found that species with lower xylem-specific resistance, i.e., diffuse-porous broadleaf species (such as beech), were more effective at night-time rehydration than those with higher resistance, i.e., tracheid-bearing conifers (such as spruce), a pattern that also appears in our study. However, our results indicate that this ability of beech is limited by the point at which soil water availability is too low to sustain replenishment.

Species differences as discussed above could not be detected when investigating maximum TWD at midday in response to soil drying (Brinkmann et al. 2016), highlighting that nighttime rehydration provides essential information about tree drought response. Physiological responses of trees such as growth are only dependent on meteorological daytime maxima insofar as these determine the extent of dehydration. Whether the missing water can be replaced, thereby reducing TWD to zero and allowing growth, depends largely on the prevailing nocturnal conditions (Zweifel et al. 2021).

Neighborhood identity affects tree water deficit under drought

To our knowledge, this was the first time neighborhood identity effects on species-specific tree water deficit have been determined, which expands previous findings on tree species mixture effects (Grossiord 2020) to a new scale. It had already been shown that even for a given pair of species, these effects are not similar across environmental conditions (Boyden et al. 2005; Pretzsch et al. 2010), with complementarity effects increasing under reduced resource availability (Bertness and Callaway 1994; Forrester 2014). Accordingly, the neighborhood identity effects found in our study differed between species and pronounced only at reduced water availability (Fig. 5). Herewith, our results only partly supported the second hypothesis, but confirmed Hypothesis 3.

Contrary to our second hypothesis, allospecific neighborhoods did not generally lead to lower TWD_{min} or make growth conditions more likely than conspecific neighborhoods. Instead, the response was species-specific and interacted with soil water availability. While the water supply of beech seemed to benefit from mixture with Douglas fir, there was no strong effect in its mixture with spruce. Under intense drought, pure beech stands showed even a lower TWD_{min} than in mixture with spruce. On the conifer side, Douglas fir benefited from only a small proportion of beech in the neighborhood, while beech dominance seemed to impair Douglas fir water status. Spruce was adversely affected by mixture with beech. These findings highlight the importance of species-specific traits as determinants for the magnitude and direction of tree species mixture effects, as suggested by previous research (Coates et al. 2013; Grossiord 2020; Bottero et al. 2021). The most relevant traits are likely root distribution and water uptake (Bello et al. 2019; Haberstroh and Werner 2022), as well as species-specific leaf morphology and canopy structure with its cascading effects on light and microclimate (Kovács et al. 2017; Ehbrecht et al. 2019; Richter et al. 2022).

Beech is known as a strong belowground competitor (Leuschner et al. 2001; Grams et al. 2002). In competition with beech, spruce was observed to shift its fine root system and water uptake depth to shallow soil layers (Lwila et al. 2021), which suggests a decreased soil water accessibility under drought (Goisser et al. 2016) and could explain why spruce did not profit from mixture with beech in our study.

Since root water acquisition is essential to rehydrate the stem and overcome tree water deficit, these may be relevant traits to explain our daily-based results.

Furthermore, broadleaved beech and coniferous Douglas fir and spruce differ substantially in their aboveground structure. For instance, tree height is known to impact drought response, which is attributed to increased hydraulic path length and, if a tree is taller than its neighbors, elevated exposure to solar radiation and increased evapotranspiration (Bennett et al. 2015; Grote et al. 2016; Ma et al. 2023). This could be particularly relevant in mixed stands of beech and Douglas fir, since mature Douglas firs are—on most sites—taller than mature beech trees; this was also the case on our plots (Table 2). We speculate that beech may profit from being shaded by Douglas fir under hot and dry conditions, while Douglas fir may be more drought-exposed when surrounded by many beech trees. In the case of spruce, its difference in height to beech is usually not so large, potentially weakening the stand-structure effect. A study from southern Germany found that spruce profited from mixture with beech under drought (Pretzsch et al. 2020a), which contrasts with our results. We believe that this can be attributed to site effects, since those trees were exposed to overall lower temperatures and more favorable soil conditions than in our study, where the sites can be considered outside the natural range of spruce. Very low absolute growth rates indicate decreased vitality in our spruce stands; at this stage, competitiveness against beech may be hampered. Our results emphasize the need for alternatives to spruce cultivation outside its ecological niche, even in mixed stands. Nevertheless, we did not include any additional traits in our analysis, so that the mechanisms leading to the observed effects remain elusive, opening opportunities for future research.

For the given site conditions, we conclude that under drought, competition prevailed over complementarity in beech–spruce mixtures, while beech and Douglas fir could be combined to the benefit of beech, or even mutual benefit.

Study limitations

Even though our study is based on a comprehensive data set, we cannot fully exclude confounding factors. For example, even though all measured trees were mature and part of the canopy, not all were of the same age (Table 2; minimum: Douglas fir, 44 years; maximum: beech, 130 years; median: 81 years) and diameter (minimum: beech, 25 cm; maximum: Douglas fir, 102 cm; median: 46 cm), with potential implications for water transport within the tree (Köstner et al. 2002; Mencuccini et al. 2005). To overcome this, we standardized TWD for each tree by its maximum daily shrinkage (see Materials and methods section), which yields a similar range of values for all trees within a species.

Furthermore, the studied stands were regularly thinned until the start of the measurements, which is known to affect ecohydrological processes (Del Campo et al. 2022). As indicated in Table 2, mixed stands often had a lower stem density than pure beech stands, which may benefit beech in mixture. However, stand basal area of the mixed stands was mostly similar to or even higher than in the pure beech stands, indicating (on average) bigger trees in the mixed stands, with accordingly higher resource consumption (Dawson 1996). Generally, mixture effects as investigated here need to be understood in concert with common management practices.

Finally, the study sites represent two regions and three different soil types. While a broader ecological gradient would be preferable, with Cambisol and Podzol we cover two dominant soil types in central Europe (Jones et al. 2010) for which we assume that our sample size allows robust conclusions. Different results could be expected, e.g., on sites with groundwater access, which may reduce water stress exerted by drying topsoil for deeper-rooted species (Yin et al. 2015), or under different climatic conditions, such as at higher elevations.

Conclusions

In Central Europe, diverse societal demands, past forest decline due to air pollution and, more recently, global change have led to a paradigm shift towards multifunctional forests (Borrass et al. 2017). Resilient species combinations, suitable for future climate conditions, are needed. Our study used high-resolution stem diameter measurements to take the analysis of tree drought response and species mixture effects to a daily level, filling a gap between established methods at different spatial and temporal scales.

We found that tree species mixture effects only occurred under decreased soil water availability, and the direction and intensity of the effect was species-specific: in beech–spruce mixtures, beech profited slightly, while spruce did not. Even though the two species are complementary in many traits (rooting depth, canopy structure), this did not lead to complementarity effects in a sense of mutual benefit. In beech–Douglas fir mixtures, the situation was different: beech profited, and Douglas fir as well, as long as the share of beech neighbors was not too high. Thus, we conclude that competition prevailed over complementarity in beech–spruce mixtures, but not in beech–Douglas fir mixtures.

Our results underscore the importance of tree species identity for the drought response of mixed stands, and highlight that interactions at the local neighborhood level seem to be substantial. This also has implications for the implementation of mixed stands (block-, group- or tree-wise). For the species investigated in our study, we conclude that European beech in mixture with Douglas fir is a promising option for future forest management in Central Europe as an alternative to mixture with Norway spruce.

Finally, our study shows the great potential of high-resolution stem diameter measurements as a standardized tool in ecophysiology. Further research is needed to elucidate the relation of tree species mixture, TWD_{min} and other physiological variables at different spatial and temporal scales.

Supplementary data

Supplementary data for this article are available at *Tree Physiology* Online.

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Conflict of interest

None declared.

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Data availability

The data used in this manuscript will be archived in GRO.data (<https://data.goettingen-research-online.de/>): 10.25625/SPI2C4.

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