Less pronounced drought responses in ring-porous than in diffuse-porous temperate tree species

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**A R T I C L E   I N F O**

**A B S T R A C T**

Keywords: Water deficit Drought stress Transpiration Vapor pressure deficit Radial growth

Tree species differ in their physiological responses to drought, but the underlying causes are often unclear. Here we explored responses of radial growth to centennial drought events and sap flow ($F_s$) to seasonal drought in four mixed forests on either moist or drier sites in northwestern Switzerland. While the diffuse-porous species (Fagus sylvatica, Prunus avium, Tilia platyphyllos) showed marked growth reductions in 1976 and 2003, two known marker years for severe drought, growth of the two ring-porous species (Quercus petraea and Fraxinus excelsior) was less severely affected. During a dry early to midsummer, diffuse-porous species strongly reduced $F_s$ at the two drier sites but not (or less so) at the two moister sites. Regardless of soil moisture availability, the deep-rooting, ring-porous trees invariably down-regulated $F_s$ to 60–70\% of their maxima in response to vapour pressure deficit (VPD) and maintained similar fluxes across sites, irrespective of upper soil moisture conditions. A generalised additive model of normalised $F_s$ as a function of VPD and soil matric potential yielded a drought-sensitivity ranking of $F_s$ led by the two insensitive ring-porous species followed by the diffuse-porous trees (ordered by increasing sensitivity: Fraxinus excelsior $<$ Quercus petraea $<$ Prunus avium $<$ Acer pseudoplatanus $<$ Fagus sylvatica $<$ Tilia platyphyllos). In conclusion, ring-porous tree species exhibited stronger VPD-driven stomatal control over $F_s$, and tree-ring formation was less sensitive to severe drought than in their neighbouring diffuse-porous species. The $F_s$ regulation explained the greater drought tolerance of the ring-porous trees.

1. Introduction

Central Europe’s forests are facing a dry outlook over the next few decades as the region is projected to experience declining summer precipitation and more frequent periods of extended drought (Schuldt et al., 2020; Spinoni et al., 2018). In Switzerland, average summer temperatures are predicted to increase by up to 4.5 K with 25\% less summer rainfall until 2060 (CH2018, 2018). In a warmer and drier future, higher evaporative demand will increase evaportranspiration while reduced precipitation will hinder the replenishment of these water losses from the soil. These climatic changes are well underway as evidenced by the increase in summer temperatures, and recurrent droughts.

Given the large variation in root and crown architecture and physiological traits among trees, it is not surprising that their responses to drought are highly species-specific, and this differential behaviour can rapidly translate into stand-level effects (Dietrich et al., 2019; Leuzinger et al., 2005; Leuzinger and Körner, 2007; Scherrer et al., 2011; Zweifel et al., 2009). Therefore, shifts in forest community composition are likely to occur as water becomes an increasingly limiting resource in the future (Bader et al., 2014; Dulamsuren et al., 2009; Hoffmann et al., 2011; Johnson et al., 2018), with implications for forest management (Weemstra et al., 2013). The long-standing beech dominance across much of Europe is expected to wane as a result of its greater drought sensitivity in comparison to competitors such as sessile oak (Quercus petraea) or Scots pine (Pinus sylvestris; Brinkmann et al., 2016; Friedrichs et al., 2009). Since most forests in Central Europe are managed for timber production and recreation, future changes in forest dynamics are not only ecologically relevant but will also have socio-economic impacts (Lindner et al., 2010). Even if the species composition of forest communities will be retained under an altered climate regime, changes in wood quality (e.g., density) and yield reductions are likely and stands may become more sensitive to storm damage (Meyer et al., 2008; Pretzsch et al., 2018). A mechanistic understanding of tree species-specific responses to moisture supply can help substantiating...
Sap flow provides an integrative signal of canopy water consumption, which is controlled by stomatal conductance ($g_s$), canopy aerodynamics and atmospheric forcing (vapour pressure deficit, VPD, and wind), hydraulic traits, and the availability of water in the soil. When drought becomes severe, current theory assumes that stomata control transpiration in such a way that xylem embolism is prevented. It has long been known that ambient moisture affects stomata in two ways: (1) directly and irrespective of high soil moisture via ambient air humidity (VPD) and (2) under declining soil moisture, via a negative pressure signal in the leaf (a critical reduction in turgor pressure) and phyto-hormone signalling from roots in dry soil (for an early review see Körner, 1995). The VPD-driven stomata response starts somewhere between 0.8 and 1.5 kPa, followed by a nearly linear decline in $g_s$ with rising VPD (Grossiord et al., 2020; Körner, 2013), leading to a steady flux. In contrast to this ‘hydro-active’ response, drought losses in the leaf epidermis reduce $g_s$ ‘hydro-passively’, with the response tuned in such a species-specific way that a critical water potential is not crossed (often around ~2 MPa) (Franks, 2013). Some species are more conservative in their water spending and exert a tighter control over $\Psi$ (leaf water potential; isohydric species, such as most pines), while others permit deeper cycle fluctuations in $\Psi$ (ansisohydric species, e.g., Klein et al., 2013; McDowell, 2011; Roman et al., 2015; Skelton et al., 2015; Taneda et al., 2008). The latter are commonly deep-rooted species that are less likely cut off from water supply under receding soil moisture conditions in the upper soil profile. Hence, the stomatal response and ensuing sap flow signals obtained in the tree trunk may pass through three different daily phases: (1) light-driven stomatal opening in the morning, at high air humidity and no soil water shortage (flux proportional to VPD); (2) an active reduction of $g_s$ which prevents flux from further rising (flux deviates from VPD); (3) should soil dehydrate to a critical state and step (2) be unable to maintain $\Psi$ above a critical level, hydro-passive stomatal closure leads to an almost complete decoupling of sap flux from atmospheric conditions (Körner et al., 1985). It is important to recall these various influences on sap flow to understand the (sometimes large) variation in sap flow signals seen in diurnal courses or when plotted against only one of the involved controls (e.g., VPD).

Stomatal aperture and hence transpiration in trees exposed to (moderate) drought is largely controlled by changes in guard cell turgor (Rodriguez-Dominguez et al., 2016). Turgor pressure also provides the motive force for cell growth and therefore needs to be maintained above a certain threshold in the cambium to safeguard cell formation and expansion (Peters et al., 2021). Annual tree-ring increments thus integrate various environmental and internal controls, but low moisture supply only produces a distinct drought signal in tree-rings if the drought occurs during a certain critical phase of wood formation (e.g., Eilmann et al., 2011). So, in the Northern Hemisphere, a meteorological drought will commonly exert a direct tree-ring signal only when it occurs between April and late June/early July before the ring has reached its final width, with wood maturation occurring during the remainder of the growing season (Ertzold et al., 2022). There is also the possibility of legacy effects of a preceding, late-season drought when buds, and thus forthcoming nodes and internodes are formed in primordial tissue (Zweifel et al., 2020; Zweifel and Sterck, 2018). Such late-growing season stress may also leave hormonal fingerprints, while the often-assumed after-effect of variable carbon stores would affect growth only if trees were carbon limited, for which we have no evidence (Bader et al., 2015). Contrary to expectations, cambial reserves remained quite invariable throughout the year in various temperate forest tree species studied at one of the current study sites (Hoch et al., 2003), and across moisture conditions in an experiment with pine (Schaub et al., 2018). It is not precipitation or the precipitation/evaporation ratio or extreme VPD that ultimately determines ring width, but the turgor pressure in the cambium (Lockhart, 1965; Peters et al., 2021). However, the main drivers for turgor pressure are soil water availability and VPD, as both have a direct influence on tree water relations (Grossiord et al., 2020, 2018). While changes in soil water potential occur gradually depending on the soil type, VPD rises rapidly on every sunny day to such an extent that the transpirational water loss cannot be covered simultaneously by root water uptake. The plant water potential and the associated turgor pressure in the cambium drop rapidly and first reach the threshold value for growth cessation and somewhat later also that for incipient stomatal closure. Zweifel et al. (2021) demonstrated that air dryness acts as a key environmental driver of radial stem growth in seven temperate tree species. Already a VPD of 0.2–0.5 kPa no longer permits growth, regardless of soil water availability (Zweifel et al., 2021). Trees consequently grow mainly at night. Growth processes clearly come to a halt before the onset of stomatal closure (VPD > 0.8 kPa) and the photosynthetic output coupled to it, which was recently confirmed by Krejza et al. (2022). However, if the soil water potential sinks too low during a dry period, even high air humidity (low VPD) can no longer initiate growth.

In this study, we compared the drought responses of six co-occurring hardwood species (Acer pseudoplatanus, Fagus sylvatica, Fraxinus excelsior, Prunus avium, Quercus petraea, Tilia platyphyllos) across sites that differ in local moisture regime under otherwise similar atmospheric conditions over short (few km) distances in NW Switzerland. We first explore the a priori site selection as ‘dry’ versus ‘moist’ by comparing soil moisture data and tree vigour (tree-ring chronologies) including pointer years of known centennial drought events. We then employ sap flow data collected during a midsummer drought event to explain the observed tree-ring responses. We used a generalised additive modelling approach to evaluate the response of sap flow to the combined effects of topsoil matric potential and VPD. We also introduce a new metric termed the critical VPD (VPD$^{crit}$), which pinpoints the shift from predominantly environmental control of sap flow to strong stomatal control (Fig. 1). The well-known greater vulnerability of ring-porous trees to xylem embolism linked to their wide earlywood vessels (Hacke and Sperry, 2001), led us to assume an earlier onset of stomatal control of sap flow reflected in lower VPD$^{crit}$ values for ring-porous compared to diffuse-porous species.

The work presented here is a companion study to the one by Scherrer et al. (2011). In their study, thermal imaging during summer drought had been used to infer the canopy energy balance in the same species and sites. The data showed persistent transpirational canopy cooling in both ring-porous species, while the other species, especially Acer pseudoplatanus and Tilia platyphyllos, warmed significantly during the dry summer period (more so on the drier sites) indicating restricted transpiration. Here we present the associated sap flow data and long-term tree-ring responses, in order to establish a drought-sensitivity ranking of these major forest tree species. The important point in our study design is that all species co-occur at all study sites and are thus exposed to the same environmental conditions.

2. Material and methods

2.1. Study sites and tree species

The study area in NW Switzerland comprised two neighbouring lowland regions in the provinces of Solothurn and Basel-Landschaft, hereafter referred to as West (WM and WD) and East (EM and ED; M for moister, D for drier; Table 1, Fig. 2). With support from the regional Swiss forestry authorities, we selected four near-natural and highly diverse, closed-canopy forest stands, two of which were assumed to be drier and two moister, but all hosting the same tree species. All sites were located on nearly flat terrain between 300 and 550 m elevation. The criteria to rank the sites as moist or dry included floristic composition in the understory, stand- or crown density, maximum tree height (more stunted versus taller), micro-topographic setting (raised plain or outcrop versus embedded/adjacent to draining slopes) and soil features (gravel or rock debris versus clay beds or deep loess). Taken individually, these are soft criteria, but in combination they permitted a clear site
differentiation, with the hard criteria such as depth of soil profile and rooting depth remaining unknown (Table 1). All stands have been extensively managed for decades. The ED stand is managed for recreational purposes, the EM stand is a high-value forest managed for precious timber, the WD stand lies within a nature reserve (Hofstetter Chöpfl) and the WM stand is situated in a near-natural forest area which is part of the Swiss Canopy Crane research facility run by the University of Basel.

All stands were dominated by *Fagus sylvatica* L. and *Quercus petraea* (Matt.) Liebl., interspersed with *Fraxinus excelsior* L., *Acer pseudoplatanus* L., *Prunus avium* L., *Tilia platyphyllos* Scop., *Acer campestre* L., and *Carpinus betulus* L. Conifers occurred only in small numbers (*Abies alba* Mill., *Larix decidua* Mill., *Picea abies* L., *Pinus sylvestris* L.). We focussed on *Acer pseudoplatanus*, *Fagus sylvatica*, *Fraxinus excelsior*, *Prunus avium*, *Quercus petraea* and *Tilia platyphyllos*, which were present at all sites with at least three large canopy-forming individuals. Wood anatomy information was obtained from the ‘Wood anatomy of Central European species’ database (Schoch et al., 2004).

*Fagus sylvatica* forms diffuse-porous wood under average meteorological conditions but under extremely dry summer conditions, reductions in vessel area cause a slight tendency towards a seemingly semi-ring porous vessel distribution (Arnič et al., 2021; Schweingruber, 2007). However, early-wood vessel diameters of *Fagus* wood (ca. 100 µm) never reach the values seen in truly ring-porous species like *Fraxinus excelsior* (250–300 µm) or *Quercus petraea* (200–400 µm) (Schweingruber, 2007), meaning that *Fagus* does not share the typically high vulnerability to stem embolism. Also, in contrast to truly ring-porous species whose water relations heavily rely on current-year xylem, *Fagus* employs older xylem contributing to differences in leaf out phenology between ring- and diffuse porous trees.
We will refer to *Fraxinus* and *Quercus* as ‘ring-porous’ throughout the paper although this actually refers to a syndrome of traits, including greater maximum vessel diameter, restriction of conducting sapwood to the last tree ring, greater rooting depth and associated canopy traits such as less crown density and more intense gas-exchange per unit leaf area.

All study sites lie within 15 km distance and hence share the same temperate zone climate, characterised by mild winters and moderately warm summers. The growing season usually lasts from end of April to the end of October, i.e., roughly 180 days. The long-term annual precipitation in the region is 791 mm and the mean January and July temperatures are 2.1 and 19.1 °C (Fig. 3). In the study year 2010 the precipitation during the growing season (May – October) was 512 mm.

2.2. Meteorological data and soil matric potential

Long-term meteorological data were obtained from an official weather station (Binningen, 316 m a.s.l., Federal Office of Meteorology and Climatology MeteoSwiss) located close to our two eastern study sites. In addition, we had collected climate data near the moist western site, above the forest canopy at the Swiss Canopy Crane research facility (Vantage Pro2 Plus equipped with a solar radiation sensor; Davis Instruments, Hayward, CA, USA). For each site, vapour pressure deficit (VPD) was calculated based on relative humidity and air temperature data (Buck, 1981, 1996). To highlight severe drought events, the Standardised Precipitation-Evapotranspiration Index (SPEI) was calculated on a 12-month time scale for the period 1864–2010 (Beguería and Vicente-Serrano, 2017). Soil matric potential (Ψsoil) at 10 cm depth was recorded at 5-min intervals using three dielectric permittivity sensors per site (MPS-1, Decagon Devices Inc, Pullman, WA, USA).

2.3. Radial stem increment

We collected two wood cores per tree using a standard 5-mm diameter, stainless steel increment borer (two tree individuals per species and site, except for *Fagus sylvatica* at the Swiss Canopy Crane site where tree-ring series of seven individuals were available from a concomitant dendrochronological study). Tree-ring widths were measured using an automated bench equipped with a stereomicroscope (Lintab™ and TSAP-Win™, Rinntech, Heidelberg, Germany). Dendrochronological data processing and analyses were performed using the dplR package (Bunn, 2008) within the R software environment (R Core Team, 2019). For each tree species, we created a mean chronology based on Tukey’s biweight robust mean across the raw tree-ring series.

2.4. Sap flow measurements

Sap flow ($F_s$) was continuously recorded on two trees per species and site (2 trees × 6 species × 4 sites = 48 trees in total) from day of year (DOY) 150 to 225 in 2010. We used ‘Granier-type’ sap flow gauges consisting of two 20 mm long and 2 mm diameter probes, which were inserted into aluminium sleeves previously fitted into the north-facing sapwood at breast height (1.5 m) with a vertical spacing of 15 cm (SFS2, UP Umweltanalytische Produkte GmbH, Ibbenbüren, Germany). Sensors were protected against environmental water and thermal fluctuations using styrofoam guards and foil-faced bubble wrap insulation. Readings were taken at 10 s intervals and aggregated as 5 min means using a wireless multichannel data logging system (DecentNet, Dübendorf, Switzerland). The $F_s$ raw data measured as temperature difference ($\Delta T$; °C) between the two device needles were processed to sap flow (g h$^{-1}$) according to Granier (1985) but using a dynamically changing baseline ($\Delta T_{max}$) to define the zero flow. $\Delta T_{max}$ was calculated.
as a moving window over four days but using the averaged $\Delta T$ between 2:00 and 4:00 only.

Each of the $F_s$ time series spanning June to mid-August was standardised using feature scaling (min-max normalisation): normalised $F_s = (F_s - F_s\text{ min}) / (F_s\text{ max} - F_s\text{ min})$ resulting in relative sap flow rates between 0 and 1.

### 2.5. Statistical analysis

All statistical analyses and graphics were performed using the free software R version 3.6.1 (R Core Team, 2019). In all analyses, we applied a significance level of $\alpha = 0.05$, with marginal significance indicated by $0.05 < P \leq 0.1$. Sap flow and radial growth responses of the WM and EM sites were lumped together and are henceforth referred to as the moist habitat. In the same vein, the WD and ED sites were pooled and are henceforward referred to as the dry habitat. In a mixed model context, ‘habitat’ (moist and dry) was used as a fixed effect and ‘site’ as a random term.

#### 2.5.1. Tree-ring analysis

We examined species-specific radial growth responses in each habitat in relation to the two pointer years 1976 and 2003. Sparse data coverage during the 1940–1950 period, precluded an analysis of the severe drought events in the 1940s (no data available for Prunus avium and Fraxinus excelsior at the dry sites and incomplete tree-ring series for the remaining species at least at one of the study sites). We used a superposed epoch analysis approach to determine whether a statistically significant departure from the mean raw tree-ring width had occurred as a result of the two extreme drought years, using the default 5 lagged years and 1000 bootstrap resamples (Bunn, 2008, R package dplR).

#### 2.5.2. Seasonal patterns of sap flow

We applied generalised additive mixed models (GAMMs) to the daily maximum normalised sap flow ($F_s$) which allowed us to incorporate a random term for species and site to account for the repeated measures nature of the data (Wood, 2011, R package mgcv). Separate GAMMs for each habitat (moist vs. dry) were created which contained ‘species’ as sole parametric term and a smoothing term (based on thin plate regression splines) for ‘day of year’ including ‘species’ as a by-variable to allow a factor-smooth interaction, i.e., separate smoothers for each tree species. Given the 0–1 range of $F_s$, the beta error distribution is appropriate but not yet available in the GAMM framework (currently only available in ordinary generalised additive models, see below). Therefore, we ran the GAMMs with a gaussian error distribution and applied a logit transformation to the $F_s$ values to ensure the model predictions and their 95% confidence limits stay within the bounds of 0 and 1.

#### 2.5.3. Relationship between normalised sap flow, VPD and $\Psi_{soil}$

We applied a binned aggregation approach for data reduction by grouping VPD and $\Psi_{soil}$ values into equal range bins of 0.05 kPa and 25 kPa intervals, respectively. Within each bin we derived the 95th percentile of $F_s$. For plotting purposes, multilevel B-splines were applied to interpolate the $F_s$ percentiles across the range of VPD and $\Psi_{soil}$ values (R package MBA, Finley et al., 2017). Generalised additive models (GAM) were used to analyse the relationship between $F_s$ and the two environmental drivers VPD and $\Psi_{soil}$ (Wood, 2011, R package mgcv). To account for the normalisation of the $F_s$ data in the 0 to 1 range, the GAMs employed a beta error distribution with logit link function. The explanatory variables comprised ‘species’, ‘habitat’ and their interaction in the parametric term and the nonparametric component comprised smoothers based on cubic regression splines for VPD and $\Psi_{soil}$ in the simplest model. More complex GAMs additionally contained a tensor product interaction between these two continuous predictors and the most complex model also included a factor-smooth interaction allowing separate smooths by species and habitat. Likelihood-based comparisons of a set of four candidate GAMs identified the most complex model as the superior one (supplementary Table 1). Subsequently, two types of post-hoc analyses based on likelihood ratio tests were performed: i) habitat-wise comparisons were done for each species by contrasting a GAM allowing separate smoothers for each habitat (dry vs. moist) to a simpler GAM with a common smoother for both habitats, ii) to compare the six tree species among each other within a habitat, two species were pooled in turn resulting in 15 unique combinations to test. Each of these species combinations translated into a GAM where the two pooled species were assumed to share a common smoother (effectively testing the null hypothesis of no difference in the $F_s$ patterns between the two species that were lumped). Each of these GAMs was compared to a GAM allowing separate smoothers for each tree species. The $P$-values resulting from this post-hoc procedure were multiplicity-adjusted using the Benjamini & Hochberg (1995) method.

#### 2.5.4. Relationship between $F_s$ slopes and VPD

We applied a cubic spline to emulate the normalised daily $F_s$ traces and derived the associated slopes with the built-in R function splinefun (using the timestamp as x-variable). We then binned the concomitant VPD values in 0.05 kPa intervals and extracted the 95th percentile of the slope values in each VPD bin for each tree species and site (Fig. 1). GAMs were applied to this data using the slope percentiles of the normalised $F_s$ as response variable and a smoother for the midpoints of the VPD bins as predictor. Derivatives of the smooths and their 95% confidence bounds were calculated to determine their maxima. We defined the VPD corresponding to this peak of the GAM smoother as the critical VPD ($VPD_{crit}$), that marks the transition from environmental to stomatal control of tree water use (Fig. 1).

### 3. Results

#### 3.1. Weather and soil matric potential

Due to the geographical proximity, the meteorological differences between sites are quite small (Fig. 3). The main site differences result from topography and soil conditions. Since the depth of the rooted soil profile and the moisture dynamics below the topsoil were unknown, we relied on the indicators listed in the material and methods (see also Table 1) and some of our results below justify the a priori classification of the four sites into two drier and two moister sites.

During the study period (DOY 150–225 in 2010), mean daily air temperature varied between 12 and 27 °C at the two western sites (WM and WD) and between 10 and 27 °C at the two eastern sites EM and ED (Fig. 3). Daily variation in air temperature and vapour pressure deficit (VPD) were somewhat larger at the E-sites compared to the W-sites. During a 30-day period in July with very little rainfall, mean daily air temperature rarely dropped below 20 °C and peaked between 34 and 36 °C producing maximum VPDs of 3.6 kPa at the W-sites and 4.1 kPa at the E-sites in the afternoon. The long-term meteorological time series for the weather station near the E-sites (1864–2010), showed an average summer air temperature from June to August in 2010 of 19.3 °C. At the start of our measurements in June 2010, soil matric potential ($\Psi_{soil}$) at 10 cm soil depth was around −20 kPa at all sites. Following the onset of the midsummer drought period, $\Psi_{soil}$ initially declined at similar rates across sites (briefly interrupted by a storm event in early July at the W-sites only). At the W-sites, $\Psi_{soil}$ started diverging from DOY 195 onwards and minimum $\Psi_{soil}$ values at the WM site were somewhat lower compared to the WD site (−522 kPa vs. −452 kPa), what we attribute to either the brief, and very local summer storm, the stonier, coarser topsoil and the much denser ground cover at the WM site. Yet, $\Psi_{soil}$ declined more rapidly and generally remained at lower values in the WD habitat (except for DOY 195–205). At the E-sites, the diverging trend in $\Psi_{soil}$ started about a week earlier (from DOY 187) and $\Psi_{soil}$ decreased more rapidly at the ED site relative to the EM site, reaching minimal values between −622 and −454 kPa, respectively (Fig. 3). So, the trends in soil moisture are in line with the site distinction, but they serve as a proxy for

\[ F_s = \frac{(F_{s\text{ max}} - F_{s\text{ min}})}{(F_{s\text{ max}} - F_{s\text{ min}})} \]
the overall moisture situation only, because the actual deep soil moisture is unknown.

3.2. Radial stem increment

At times, the tree-ring series reflected our dry vs. moist habitat classification, especially around the pointer years, but a clear distinction between habitats was not always apparent (Fig. 4). In general, diffuse-porous trees showed greater variation in ring widths (particularly at the moist sites) than the ring-porous trees (Fig. 4). Annual increments in *Prunus* growing at the moister sites varied most by more than 9-fold across the chronology (7.5 mm in 1961, 70 mm in 1981), while *Quercus* trees at the dry sites showed the smallest variation (3-fold), rarely exceeding 2 mm yearly increment. At the dry sites, *Quercus* trees grew always less, *Fraxinus* showed no trend (if anything, more growth than at the moist sites), and *Fagus* grew less before 1976, while *Tilia* and *Prunus* trees grew less from 1976 onwards. Differently adjusted stand density, rooting depth or deep soil moisture are likely causes for the differences at the individual tree level to be smaller than expected. Since all species grew side-by-side in our experimental stands, a site bias seems unlikely. Note that *Acer* is missing here because its tree-rings could not be determined with certainty.

In the following we will focus on the pointer years. In central Europe, the year 1976 was characterised as a particularly dry but less hot summer compared to the 2003 extreme weather event, which showed a less severe drop in rainfall but scorched the Central European region with a record summer heat wave. In 1976, the Standardised Precipitation-Evaporation Index (SPEI) was in the normal range (±0.5) from January to May and then varied between −1.42 and −2.12 for the rest of the year (Fig. 4A). Yet, mean summer temperature (June – August) was only 1.4 K higher than the long-term average (Fig. 4B). In 2003, on the other hand, SPEI values indicated a rather humid period until May (0.94–1.49) followed by normal conditions in June/July and a drier period starting from August (−0.70 to −1.99) (Fig. 4A). However, mean summer temperature exceeded the long-term average by 5.3 K (Fig. 4B) rising evaporative forcing dramatically (heat wave summer).

A superposed epoch analysis using a back and forward lag of five years showed that the drought of 1976 caused significant (moist habitat) or marginally significant (*P* = 0.05–0.1, dry habitat) radial growth reductions in *Fagus* in the same year but not in any of the five post-drought years (Fig. 4C). The decline in tree-ring width was greater in the moist habitat (−55% relative to the average of the five pre-drought years) compared to the dry habitat (−42%). In *Fagus* trees growing at moist sites, the 2003 drought and heat wave also led to a significant and immediate growth depression (−43%) which lasted until 2006. At the dry sites, a significant reduction in tree-ring width only occurred in 2004 (−53%).

In *Prunus*, the drought of 1976 did not produce a statistically significant decline in radial increment, regardless of habitat (Fig. 4D). Instead, in both habitats a statistically significant increase in tree-ring width occurred in the wake of the drought event. During the five post-drought years, the radial increments of *Prunus* trees had more than doubled at the moist sites compared to the average tree-ring width of the five pre-drought years and returned to ‘normal’ in the mid-90s only. At the dry sites, the gain was less (<54%) and ring width was back to ‘normal’ already in 1980. During the 2003 drought, radial increment hardly decreased at the moist sites, but was significantly reduced at the dry sites by 62% (Fig. 4D).

*Tilia* showed a steady ring width decline since the late 1960s which coincided with less precipitation, a trend seen in all species except *Prunus*, reaching a statistically significant low-point in *Tilia* in 1977 (Fig. 4E), the year after the extreme drought. In the following years radial increment rose nearly 3-fold, a shorter replica of the pattern observed in *Prunus*. This post-drought gain was slower (not statistically significant) at the dry compared to the moist sites but led to an all-time peak of 4.2 mm per year in 1981 at the dry sites, which was significantly higher than any other annual increment included in the superposed epoch analysis (1971–1981).

In the ring-porous *Fraxinus* trees, the 1976 drought had no significant effect on radial increment while the 2003 drought and heat wave only caused a small, marginally significant decline under moister conditions in the same year (−16%) and also under dry conditions in the first post-event year (−23%; Fig. 4F). *Quercus* trees showed a marginally significant reduction in radial growth in 1976 at the moist sites (−35%), but not in the dry habitat (Fig. 4G). The 2003 heat wave caused a significant and sustained reduction in radial increment of ca. −46% compared to the average tree-ring width seen in the five pre-drought years at the moist sites but not at the dry sites. Yet, there was a small, but significant decrease in tree-ring width in the first post-drought year (Fig. 4G).

All in all, the growth reductions during these pointer years were not
dramatic but were more pronounced in diffuse-porous trees compared to ring-porous trees, and clearly sharper in *Fagus* at the moist sites than in any other species or site. Except for *Prunus*, all species showed a temporary, more or less pronounced decrease in ring width starting from the late 1960s, which may have reduced the power to detect statistically significant changes in the extreme drought year of 1976 or afterwards. Remarkably, all species except *Quercus* (and *Fraxinus* after 2003) showed a post-drought gain in ring width, both after the 1976 and the 2003 drought (most obvious in *Prunus* and *Tilia*). Whatever response there was in diffuse-porous species (drought reduction or post-drought gain), it was more pronounced at the moist sites.

### 3.3. Seasonal patterns of sap flow

Overall, the daily maximum sap flow ($F_s$) of the four diffuse-porous tree species responded more strongly to meteorological and soil moisture changes compared to the two ring-porous species, irrespective of habitat (Fig. 5). In the dry habitat (ED and WD), the seasonal patterns were similar among the diffuse-porous species, with $F_s$ values dropping to 0.3–0.4 towards the end of the ca. 30-day low precipitation period in summer (between DOY 170 and 203). The decline in $F_s$ during the low rainfall period became markedly steeper in those species when $Ψ_{soil}$ fell below ~200 kPa (see Figs. 3 and 5 around DOY 190). In the same habitat, $F_s$ of the ring-porous *Fraxinus* and *Quercus* showed a much more gradual decline to values of around 0.6 at the end of the low rainfall period. However, $F_s$ of *Quercus* responded more sensitively to light intensity and VPD compared to *Fraxinus* (at least in the lower VPD range) as indicated by the drop of $F_s$ at DOY 168 when solar radiation was only around 200 W m$^{-2}$ and VPD showed the lowest diurnal maximum of the season around 0.25 kPa (Fig. 5). At the presumed moister sites (WM and EM), the diffuse-porous species formed two distinct groups: *Acer* and *Tilia* displayed strikingly similar $F_s$ patterns characterised by large drops close to 0.2 in response to low solar radiation and the lowest diurnal maximum of VPD, whereas *Fagus* and *Prunus* also showed $F_s$ patterns that closely resembled each other but with less marked reductions related to low light and VPD (Fig. 5, lower panels).

At the moist sites, all four diffuse-porous species maintained fairly high $F_s$ between 0.8 and 0.9 during the low rainfall period (DOY 170–203, shaded), clearly supporting our site categorisation. *Fraxinus* and *Quercus* showed even less variation in $F_s$ and maintained steady levels around 0.7 during the summer drought period (Fig. 5). Peak $F_s$ values in these ring-porous species occurred slightly after rainfall on clear days with favourable VPD < 2 kPa. Remarkably, the drops in $F_s$ to minima under low daily VPD maxima and overcast conditions (DOY 168) were much sharper across the four diffuse-porous species at the moist sites (most pronounced in *Tilia* and *Acer*), perhaps because of the denser canopies (self-shading of crowns).

#### 3.4. Sap flow response to VPD and soil matric potential

Using a generalised additive modelling (GAM) approach, we detected a significant interaction between VPD and $Ψ_{soil}$ on normalised $F_s$ (tensor product interaction, $L = 1442.8$, $df = 133.35$, $P < 0.001$). We expanded this model by including a factor-smooth interaction allowing separate fits for each species in each habitat (moist habitat vs. dry habitat). A likelihood ratio test confirmed the superiority of the latter model implying that habitat- and species-specific model fits were warranted ($L = 1.89 \times 10^{7}$, $df = 155.23$, $P < 0.001$; supplementary Table 1). The GAM captured the patterns seen in the normalised $F_s$ data well (Fig. 6A, B, root mean square error: 0.26, mean absolute error: 0.18). In general, all tree species showed rather low $F_s$ values up to a VPD threshold of around 1 kPa (slightly lower in the two ring-porous species) beyond which $F_s$ started to rise more steeply (Fig. 6A, B). This trend was stronger in diffuse-porous trees and under favourable soil water conditions (Fig. 6A, B). In essence, a red/yellow color indicates low $F_s$ (because of either drought or low evaporative forcing), while a green-blue trend indicates high $F_s$ (good water supply with high evaporative forcing). A post-hoc procedure revealed that the response of $F_s$ to VPD and $Ψ_{soil}$ differed significantly between habitats for all tree species (supplementary Table 2). This effect was clearly reflected in the generally lower $F_s$ rates in the dry compared to the moist habitat when $Ψ_{soil}$ dropped below ~350 kPa and VPD exceeded 1.5 kPa. The $F_s$ response also differed significantly between tree species within the same habitat, except for the similar patterns obtained for *Fagus* and *Prunus* growing in the moist habitat ($L = 32.69$, $df = 30.81$, $P = 0.375$; supplementary Table 3). The strongest habitat-related difference in the $F_s$ response pattern was observed in *Tilia* trees which showed $F_s$ values $\leq 0.5$ throughout the entire VPD range as soon as $Ψ_{soil}$ fell below ~300 kPa in the dry habitat but maintained $F_s$ rates $> 0.7$ over a wide range of VPD values in the moist habitat (Fig. 6A, B). The smallest habitat-related differences were seen in the two ring-porous species (*Fraxinus excelsior*, *Quercus petraea*), whose $F_s$ rates only varied within a relatively narrow interval between 0.6 and 0.7 across a wide range of VPD and $Ψ_{soil}$ values once VPD exceeded around 1.5 kPa (Fig. 6B). The median differences in $F_s$ predictions between habitats under drought conditions, i.e., for the range of $Ψ_{soil} ≤ -300$ kPa and VPD $≥ 1.5$ kPa, allowed us to establish a drought-sensitivity ranking led by the two ring-porous species showing less than 12% habitat-driven reduction followed by the

![Fig. 5. Time series of daily maximum normalised sap flow ($F_s$) of four diffuse-porous and two ring-porous tree species in dry (upper panels) and moist habitats (lower panels) in northern Switzerland (grey circles eastern sites, white circles western sites). Solid lines represent generalised additive mixed model fits and the surrounding grey areas indicate the 95% confidence intervals. Grey rectangles indicate the summer drought period. The dotted vertical lines indicate the extremely overcast DOY 168 when daily peak VPD was only 0.25 kPa.](image-url)
diffuse-porous species whose $F_s$ dropped between 15 and roughly 50% (Fig. 7). The following median-based ranking from the least to the highest drought-sensitivity remained valid after normalising the median using a robust scale estimator ($Q_n$) to account for differing variances:

Fraxinus excelsior $<$ Quercus petraea $<$ Prunus avium $<$ Acer pseudoplatanus $<$ Fagus sylvatica $<$ Tilia platyphyllos.

3.5. Relationship between $F_s$ slopes and VPD

The response of the diel $F_s$ slopes (95th percentiles) plotted against VPD, showed a unimodal, right-skewed shape (Fig. 8). We defined the VPD associated with the maximum $F_s$ slope (peak of the curve) as the critical VPD ($VPD_{crit}$) that marks the transition from the predominantly abiotically-driven increase in slopes of $F_s$ to strong stomatal control of transpiration resulting in smaller slope values.

We anticipated to see markedly lower $VPD_{crit}$ values for the two ring-porous species compared to the diffuse-porous trees but this was only true for Fraxinus (Fig. 8, Table 2). In the rainless period, all trees growing at the drier sites showed $VPD_{crit}$ values of 1.00 – 1.20 kPa, apart from Fraxinus whose $VPD_{crit}$ was 0.80 kPa. At the moister sites in the absence of rain, Fraxinus showed a $VPD_{crit}$ of 0.70 kPa, while the $VPD_{crit}$ values of the remaining species ranged from 0.87 to 1.23 kPa. During the rainfall period at the drier sites, $VPD_{crit}$ ranged from 0.58 kPa in Fraxinus to 0.83 kPa in Acer. During the rainy period at the moister sites, $VPD_{crit}$ varied between 0.60 kPa in F. excelsior and 1.02 kPa in Tilia (Table 2). Taking the 95% confidence intervals into account, $VPD_{crit}$ values for the remaining species were rather similar across species and habitats and varied around 1 kPa during the rainless period but were slightly lower during the rainfall period (Fig. 8, Table 2). However, when considering
the entire pattern, then habitat-related differences in water use strategies became strikingly evident across species during the rainless period (Fig. 8, upper panels). Among the diffuse-porous trees, *Acer* and *Tilia* showed the largest variation in *F*95 slopes between habitats, *Fagus* and *Prunus* took an intermediate position while the two ring-porous species, especially *Fraxinus*, displayed only small differences in slopes between habitats. This visual impression was supported by likelihood ratio tests comparing species-specific GAMs employing either a common smoother for both habitat types and GAMs allowing separate smoothers for each species. Significant *P*-values support the more complex model providing habitat-wise fits. Note that the degrees of freedom derived from GAMs are commonly non-integers, hence the decimals in the numerator and denominator degrees of freedom of the *F*-statistic underlying the likelihood ratio test for these GAMs.

**Table 2** Critical VPD thresholds (VPD<sub>95</sub>) indicating the transition from environmental to stomatal control of sap flow.

<table>
<thead>
<tr>
<th>Species</th>
<th>Rainfall period</th>
<th>VPD&lt;sub&gt;95&lt;/sub&gt; (kPa)</th>
<th>95% CI (kPa)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Tilia platyphyllos</em></td>
<td>dry</td>
<td>1.20</td>
<td>0.96 – 1.57</td>
</tr>
<tr>
<td></td>
<td>moist</td>
<td>1.15</td>
<td>1.03 – 1.30</td>
</tr>
<tr>
<td><em>Fagus sylvatica</em></td>
<td>dry</td>
<td>1.03</td>
<td>0.89 – 1.19</td>
</tr>
<tr>
<td></td>
<td>moist</td>
<td>1.05</td>
<td>0.92 – 1.21</td>
</tr>
<tr>
<td><em>Acer pseudoplatanus</em></td>
<td>dry</td>
<td>1.19</td>
<td>1.03 – 1.37</td>
</tr>
<tr>
<td></td>
<td>moist</td>
<td>1.23</td>
<td>1.09 – 1.38</td>
</tr>
<tr>
<td><em>Prunus avium</em></td>
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<td>1.14</td>
<td>1.01 – 1.28</td>
</tr>
<tr>
<td></td>
<td>moist</td>
<td>1.07</td>
<td>0.93 – 1.24</td>
</tr>
<tr>
<td><em>Quercus petraea</em></td>
<td>dry</td>
<td>1.00</td>
<td>0.88 – 1.13</td>
</tr>
<tr>
<td></td>
<td>moist</td>
<td>0.88</td>
<td>0.74 – 1.02</td>
</tr>
<tr>
<td><em>Fraxinus excelsior</em></td>
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<td>0.80</td>
<td>0.68 – 0.91</td>
</tr>
<tr>
<td></td>
<td>moist</td>
<td>0.70</td>
<td>0.60 – 0.81</td>
</tr>
<tr>
<td><em>Tilia platyphyllos</em></td>
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<td>0.78</td>
<td>0.67 – 0.90</td>
</tr>
<tr>
<td></td>
<td>moist</td>
<td>0.84</td>
<td>0.68 – 1.02</td>
</tr>
<tr>
<td><em>Fagus sylvatica</em></td>
<td>dry</td>
<td>0.79</td>
<td>0.68 – 0.93</td>
</tr>
<tr>
<td></td>
<td>moist</td>
<td>1.02</td>
<td>0.86 – 1.20</td>
</tr>
<tr>
<td><em>Acer pseudoplatanus</em></td>
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<td>0.69 – 1.07</td>
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<td></td>
<td>moist</td>
<td>0.99</td>
<td>0.83 – 1.18</td>
</tr>
<tr>
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<td></td>
<td>moist</td>
<td>0.84</td>
<td>0.71 – 0.98</td>
</tr>
<tr>
<td><em>Quercus petraea</em></td>
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<tr>
<td></td>
<td>moist</td>
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<td>0.55 – 0.87</td>
</tr>
<tr>
<td><em>Fraxinus excelsior</em></td>
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<td>0.48 – 0.66</td>
</tr>
<tr>
<td></td>
<td>moist</td>
<td>0.60</td>
<td>0.51 – 0.68</td>
</tr>
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**Table 3** Habitat comparisons of the *F*95 slopes (95th percentiles of the slope values within each 0.05 kPa VPD bin) for the rainless period during summer drought and the following rainfall period. Results of likelihood ratio comparisons between species-specific generalised additive models (GAM) assuming a common smoother for both habitat types and GAMs allowing separate smoothers for each habitat. Significant *P*-values support the more complex model providing habitat-wise fits. Note that the degrees of freedom derived from GAMs are commonly non-integers, hence the decimals in the numerator and denominator degrees of freedom of the *F*-statistic underlying the likelihood ratio test for these GAMs.

<table>
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<tr>
<th>Species</th>
<th>Rainfall period</th>
<th>df&lt;sub&gt;num&lt;/sub&gt;</th>
<th>df&lt;sub&gt;den&lt;/sub&gt;</th>
<th><em>F</em></th>
<th><em>P</em></th>
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<td>197.042</td>
<td>0.972</td>
<td>0.447</td>
</tr>
<tr>
<td></td>
<td>moist</td>
<td>5.385</td>
<td>202.902</td>
<td>3.573</td>
<td>0.002 ***</td>
</tr>
<tr>
<td><em>Acer pseudoplatanus</em></td>
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<td>260.382</td>
<td>3.433</td>
<td>0.002 ***</td>
</tr>
<tr>
<td></td>
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<td>5.347</td>
<td>262.469</td>
<td>6.788</td>
<td>0.002 ***</td>
</tr>
<tr>
<td><em>Prunus avium</em></td>
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<td>259.932</td>
<td>2.863</td>
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<tr>
<td></td>
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<td>5.280</td>
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<td>0.001 ***</td>
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<tr>
<td><em>Quercus petraea</em></td>
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<td>6.452</td>
<td>260.382</td>
<td>2.063</td>
<td>0.050</td>
</tr>
<tr>
<td></td>
<td>moist</td>
<td>5.385</td>
<td>262.469</td>
<td>2.063</td>
<td>0.050</td>
</tr>
<tr>
<td><em>Fraxinus excelsior</em></td>
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<td>5.152</td>
<td>202.902</td>
<td>0.972</td>
<td>0.447</td>
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<tr>
<td></td>
<td>moist</td>
<td>5.337</td>
<td>260.382</td>
<td>3.805</td>
<td>0.001 ***</td>
</tr>
</tbody>
</table>

4. Discussion

We investigated the effects of historical extreme summer droughts on tree-ring width and explored potentially associated physiological mechanisms by studying *F*95 dynamics under actual summer drought in common hardwoods differing in wood anatomy and rooting depth. We aimed at establishing a drought-sensitivity ranking to support ecological risk assessments and future forest management planning. Given the close coupling between *F*95 and *g*<sub>leaf</sub> (Hernandez-Santana et al., 2016), our smoother for both habitats best described the response of the ring-porous *Fraxinus* suggesting rather habitat-independent regulation of *F*95 dynamics. Increased soil water availability after rainfall resulted in nearly identical response curves among dry and moist sites in all species apart from *Tilia*, which exerted stronger control over *F*95 at the dry sites lending support to habitat-specific smoothers in our GAM models (Fig. 8, lower panels, Table 3).
data indicate that ring-porous species regulate water flux in such a way that they are less affected by extreme drought. This response pattern is characterised by a strong VPD-driven stomatal control of $F_s$ that is maintained even under moist conditions.

4.1. Radial stem increment

Linking growth (tree-ring formation) with climate has one fundamental limitation that neither this nor most previous dendrological works resolved, namely the actual timing of tissue formation. Once the width of a ring has been established early during the season (Eitzold et al., 2022), climate has little further influence on its final width (Michelot et al., 2012b). The uncertainty of cambial phenology in the two pointer years thus complicates assessments of historical trends in tree-ring series. The smaller declines in ring width in 2003 (compared to 1976) may be related to the late drought occurrence when ring formation had already largely been completed. For both pointer years, SPEI scores only turned critical after May, suggesting that the moderate growth declines in both years and the differences among species may in part relate to the unknown fraction of annual radial increments in May versus June. In other words, the phenology of wood formation is decisive on whether drought events leave an imprint in tree-ring series (Andreu-Hayles et al., 2022; Eitzold et al., 2022; and the classical literature by Priestley (1930); Zimmermann et al. (1974).

At our WM site, dendrometer band readings during the 2003 drought revealed a 25% reduction in radial increment across 5 hardwoods, with strongest declines in Fagus and Tilia, while Quercus remained largely unaffected (Leuzinger et al., 2005). In the two previous years with normal precipitation, more than half of the annual radial growth was completed by the end of May in Tilia and Quercus (~ 90% by mid-July) (Leuzinger et al., 2005). However, radial growth of Fagus spanned a much longer period, reaching 50% on 1 July and ~ 90% by early August only. The growth of Tilia and Fagus ceased abruptly during the 2003 event by 1 June, inevitably leading to greater growth losses in Fagus (ca. 45% of previous years’ increment).

Similarly, Härdtle et al. (2013) found a ca. 50% reduction in tree-ring width in mature Fagus sylvatica trees growing on soils with contrasting water supply during the 2003 drought. The lacking soil type effect was ascribed to stronger adaptation and thus greater drought resilience at shallow-soiled sites. This interpretation is supported by our findings for 2003, indicating an immediate and sustained growth reduction of Fagus at moister sites but a delayed growth decline in dry habitats, implying local adaptation to dry soil conditions and a resultant shift from direct impacts to carry-over effects of drought (see also Zweifel et al., 2020; Zweifel and Sterck, 2018). Michelot et al. (2012a) also reported a sudden growth cessation in Fagus sylvatica during the 1976 and 2003 droughts, contrasted by much smaller effects in Quercus petraea. The impact on oaks also emerged more gradually, seemingly linked to previous autumn rainfall, suggesting longer integration periods of the moisture regime (deep soil moisture stores), matching the slow declining trend in our oak chronologies starting in the early 2000s (Fig. 4). On productive soil, ca. 30-year-old Fagus sylvatica trees showed a 32% decline in tree-ring width during the 2003 drought, while Fraxinus excelsior and Prunus avium experienced smaller reductions of only 16% (Weemstra et al., 2013), corroborating our results. A recent dendrochronological study across 104 Swiss sites also found greater drought tolerance in Quercus petraea and Q. robur compared to Fagus sylvatica (Vitasce et al., 2019), which was lately confirmed in a pan-European survey (Bose et al., 2021).

Although growth impairments cannot be directly linked to tree vigour, drought-related water shortage usually causes lower tissue water potentials which negatively impact cell division and expansion before even affecting leaf gas-exchange and photosynthesis (Körner, 2015; Muller et al., 2011) resulting in reduced wood formation (Choat et al., 2018). In addition, drought conditions often trigger stomatal down-regulation entailing a rise in leaf temperature due to reduced transpirational cooling (Leuzinger and Körner, 2007; Scherrer et al., 2011). Commonly, drought-related reductions in $g_s$ do not (rapidly) result in carbohydrate depletion but often rather in an increase in non-structural carbohydrates due to diminished sink strength since structural sinks are far more sensitive to turgor loss than photosynthesis (Körner, 2019; Krejza et al., 2022). Even under curtailed photosynthetic supply, the maintenance of non-structural carbohydrate levels has been shown to take precedence over carbon allocation to growth across a variety of woody species (Weber et al., 2019). Hence, carbon limitation is an unlikely explanation for the observed growth restrictions under drought.

4.2. Sap flow patterns

Overall, the ring-porous trees (Fraxinus excelsior, Quercus petraea) showed a conservative water-use strategy strongly regulating $F_s$ within a narrow range over a wide span of VPD and $\Psi_{soil}$ whereas the diffuse-porous species showed more fluctuating patterns and rather profligate water consumption under favourable soil moisture conditions. The observed water-use strategies align well with our dendrological data, illustrating the trade-off between hydraulic safety and growth in ring-porous taxa and reflecting the generally more pronounced growth responses of diffuse-porous trees to abiotic changes.

The slower down-regulation of $F_s$ in the ring-porous species during summer drought in the dry habitats indicates access to a greater pool of soil water resources compared to the diffuse-porous species. However, in the moist habitats all diffuse-porous trees capitalised on the better water supply and maintained high $F_s$ (80–90% of their maximum), whereas the lower $F_s$ of around 70% seen in the ring-porous species suggests a more conservative, precautious water-saving strategy with regard to VPD, even when moisture is readily available (Figs. 5 and 6).

Most oak species, including Quercus petraea, are well-known for their deep rooting habit, facilitating long-distance transport from deep-lying soil water resources (Koestler et al., 1968). Fraxinus excelsior is also deep rooting (Koestler et al., 1968) and the presence of shallow-rooted competitors stimulates this deep-rooting habit (Rust and Savill, 2000). Indeed, the Fraxinus trees growing in our mixed stands showed little response to changes in topsoil moisture in both habitats indicating that water uptake largely relies on sinker roots tapping into deeper, moister soil horizons, when topsoil moisture declines. Similarly, in the Swiss Jura mountains, midday $F_s$ maxima of Fraxinus remained unaffected by decreasing water availability in the upper 30 cm of the soil profile while strong down-regulation of transpiration was seen in the shallow-rooting conifer Picea abies (~92%) and the broadleaves Fagus sylvatica (~53%) and Acer pseudoplatanus (~48%: Brinkmann et al., 2016). Pre-dawn leaf water potentials of drought-exposed Fraxinus excelsior seedlings can drop down to ~5.7 MPa without signs of wilting, indicating strong anisohydric behaviour (Guicherd et al., 1997). The high drought tolerance of Fraxinus partly relies on osmotic adjustment based on malate and mannitol with the former also inhibiting stomatal opening (Guicherd et al., 1997; Marigo and Pelletier, 1996).

Although osmotic adjustment also occurs in Quercus petraea (Collet and Guehl, 1997; Thomas et al., 2000), it is deemed drought-avoiding (isohydric) because of the strong stomatal control over transpiration preventing leaf water potentials from falling below threshold values around ~3 MPa in adolescent trees (Breda et al., 1995). In our study, similar patterns of downregulation of $F_s$ and thus transpiration under water-limited conditions were seen in both Fraxinus and Quercus suggesting that the pronounced isohydric and anisohydric strategies in younger trees converge towards a common water saving strategy in adult trees (Figs. 5 and 6). Even at the moist sites, both ring-porous species operated at normalised $F_s$ rates between 60 and 70% across a wide range of VPD and $\Psi_{soil}$, indicating conservative water use and stronger-than-expected decreases in $g_s$ in Fraxinus,
given its purported anisohydric nature.

The sensitivity of Tilia to $Ψ_{soil}$ at our dry sites implies stronger reliance on near-surface lateral roots for water uptake compared to moister forests, where high $P_F$ across a wide range of $Ψ_{soil}$ indicate access to deeper-lying soil water resources (Fig. 6). This suggests a strong influence of habitat on root architecture and water uptake strategies in Tilia implying high phenotypic plasticity of the root system. A comparison of five co-occurring temperate broadleaves showed drought-induced reductions in $P_F$ of 44% in Tilia cordata, 39% in Fagus sylvatica, 37% in Acer pseudoplatanus and 31% in Carpinus betulus, but no significant response in Fraxinus excelsior (Holscher et al., 2005), which aligns with our findings. This further suggests that Tilia cordata and Tilia platyphyllos are similarly sensitive to drought. In our study, $P_F$ of Fagus responded more strongly to changes in soil moisture than VPD (Fig. 6) which was also noted by Holscher et al. (2005). A study at our WM site during the severe 2015 drought, showed that $P_F$ of Fagus declined sharply by about 50% with dwindling soil moisture while Quercus responded only weakly, underpinning our multi-site results (Dietrich et al., 2019). Such a greater sensitivity of $P_F$ to soil moisture in diffuse versus ring-porous trees has also been reported for North American taxa (Meinzer et al., 2013). Recent studies have highlighted the strong sensitivity of Fagus to $Ψ_{soil}$ associated with quickly escalating stress levels (Walthert et al., 2021), but also emphasised its strong heat tolerance under favourable moisture conditions resulting in above-average growth during hot summers in areas with sufficient soil water availability (Burri et al., 2019). A recent study illustrated that the often fatal consequences of extreme drought for Fagus are related to terminal branchlet embolism and thus dehydration, with limited repair capacity (Arend et al., 2022).

We devised a new approach based on the 95th percentiles of the slopes of the daily $P_F$ traces to derive the VPD threshold that indicates the shift from predominantly environmental towards stomatal control of $P_F$ and we termed this metric the critical VPD (VPDcrit, Fig. 8). The higher vulnerability to xylem cavitation of ring-porous trees linked to their large-diameter earlywood vessels (Hacke and Sperry, 2001), prompted us to hypothesise an earlier onset of stomatal down-regulation of $P_F$ and thus lower VPDcrit values for Fraxinus and Quercus compared to the diffuse-porous tree species. This hypothesis was partly confirmed by significantly lower VPDcrit values seen in Fraxinus (Table 2). Across the remaining species, VPDcrit varied narrowly around 1 kPa suggesting strong physiological convergence among tree taxa regarding the VPD-driven stomata response (Grossiord et al., 2020, 2018).

Ring-porous wood embodies the trade-off between conductivity and susceptibility to embolism but that does not necessarily translate into higher cavitation rates compared with co-occurring diffuse-porous species. For example, in a French riparian forest, Acer pseudoplatanus was much more prone to cavitation than Fraxinus excelsior, whose low vulnerability decreased even further in dry habitats (Lemoine et al., 2001). However, the role of xylem cavitation in tree responses to drought may have been overemphasised in the past (Körner, 2019) which is corroborated by another study at our WM site where hardwoods and conifers operated well above critical water potential thresholds for cavitation during the severe 2015 drought (Körner et al., 2019). There is growing evidence that tree responses to drought and drought-induced mortality are mainly driven by belowground processes, rooting depth and hydraulic redistribution rather than xylem resistance to embolism (Bleby et al., 2010; Carminati and Javva, 2020; Johnson et al., 2018). Thus, embolisms appear as a consequence of a disconnection of roots from xylem hydraulic wall to wall water potentials ($Ψ_{soil}$) rather than the primary cause of life-threatening tree dehydration under severe drought (Körner, 2019). Johnson et al. (2018) demonstrated that narrow tracheids confer extremely high resistance to embolism in Juniperus ashei which, however, suffered the greatest mortality under drought, whereas ring-porous, wide-vasculared Quercus fusiformis trees were most vulnerable to embolism but showed very little mortality. These findings were ascribed to differences in rooting depth. At the same site, Bleby et al. (2010) showed that deep roots supplied up to five times more water to transpiration and hydraulic redistribution than shallow roots during drought, but substantially reduced their contribution after rain, underpinning the conservative strategy indicated by our data. Likewise, stable isotope tracing revealed that Fraxinus excelsior, Fagus sylvatica and Acer pseudoplatanus may shift their water uptake to deeper soil horizons with increasing topsoil desiccation (Brinkmann et al., 2019). Rodriguez-Dominguez and Brodribb (2020) identified whole-root hydraulic conductance including the soil-root interface as the main driver for changes in plant hydraulic conductance and $g_L$ under moderate drought stress. Their findings demonstrate the tight link between root hydraulic conductance and the integrity of the fine root-soil connection. In a fine root study comprising five co-occurring broadleaves, Fraxinus excelsior roots had the smallest mean vessel diameter and relatively low vessel density resulting in low conductivity (Köcher et al., 2012). Nonetheless, Fraxinus roots showed the largest conductivity losses. Therefore, the rather constant $F_v$ of Fraxinus during dry spells observed by Köcher et al. (2012) and in our study, implies that the impaired conductivity must be compensated by either high fine root biomass or fast turnover, rapid embolism repair, a super-efficient mycorrhiza network (Fraxinus hosts VA mycorrhiza) or perhaps root connections with neighbours (Bader and Leuzinger, 2019). Although Fagus sylvatica fine roots had the largest vessels and conductivity, leaf water potential declined more strongly than in the other species (Köcher et al., 2012). The currently available data on conduit anatomy and drought responses holds little promise in explaining tree drought sensitivity. Once stomata are closed, and the soil-root capillary continuum has become interrupted, conduits play a marginal role in securing a tree’s water reserves (Körner, 2019; Rodríguez-Dominguez and Brodribb, 2020). Besides the increasing importance of rooting depth in a drier future, the redistribution of water resources amongst trees via the mycorrhizal pathway (Klein et al., 2016) or natural root grafts (Bader and Leuzinger, 2019) may become more important.

Our helicopter-based thermal imaging of the same four forests highlighted leaf-to-air temperature differences during the 2010 drought, which served as a proxy for drought sensitivity. These data yielded a similar ranking (by increasing sensitivity): Fraxinus excelsior < Quercus petraea < Prunus avium < Tilia platyphyllos < Fagus sylvatica < Acer pseudoplatanus (Scherrer et al., 2011). Our $F_v$-based ranking and this canopy temperature-based ranking differ only in the swapped positions for Tilia and Acer. Clearly, Tilia reduced $F_v$ and hence transpirational cooling more strongly than Acer, implying that the smaller leaf-to-air temperature difference seen in Tilia trees by Scherrer et al. (2011) is related to leaf size (aerodynamic coupling) or canopy architecture allowing more efficient convective cooling.

The known later flushing of ring-porous taxa (Hacke and Sperry, 2001; Olson, 2022; Savage et al., 2022) such as Quercus and Fraxinus, should not affect our conclusions, because flushing a few days later refers to the early spring period when soil moisture availability is commonly high. During this early period, the overlapping shallow portions of the root sphere and thus water extraction together with the generally lower canopy density and the higher gas-exchange rates (per unit leaf area) in these ring-porous taxa (e.g., Bader et al., 2010) are likely to compensate such differences in flushing date. Rooting depth comes in as a key trait, whenever drought comes into play.

From an ecophysiological perspective, adult Fraxinus and Quercus seem to be well preadapted to a drier future. Whether seedling establishment exerts a bottleneck for tree regeneration under future climate scenarios awaits to be explored. Beyond that, several existing and looming biotic issues argue against promoting Prunus as a tree for the future. Praxinus is currently threatened by ash dieback caused by the Asian ascomyete Hymenoscyphus fraxineus (Gross et al., 2014), and trees surviving infection become more vulnerable to secondary pests (Kúnc et al., 2011). We would like to emphasise that at the time of our investigation, this pathogen had not yet manifested in the study area (Gross et al., 2014).

By comparison, the biotic threats to Quercus petraea seem less fatal at
present. Regional warming favours the development of a lepidopteran defoliator complex including the thermophilic gypsy and oak processionary moths. Also, root rot causing oomycetes can trigger oak decline events and are expected to become more widespread under future climate and trade scenarios (Jung et al., 2000; Scott et al., 2019).

5. Conclusions

Our findings indicate superior drought tolerance of ring-porous compared to diffuse-porous Central European trees characterised by a higher degree of turgor maintenance during water shortage and thus less impact on tissue formation (growth) in the ring-porous species. Higher $F_t$ under drought also permits continued CO$_2$ gas-exchange. Given the relatively high sensitivity of Fagus to drought, the dominance of beech forests across Central Europe is expected to dwindle (Schuldt et al., 2013). Central European hardwood trees in a high-CO$_2$ future synthesis of an 8-year forest canopy CO$_2$ enrichment project. J. Ecol. 101, 1509–1519. https://doi.org/10.1111/1365-3020.12149.


Acknowledgements

We are grateful to Reinhard Bischoff and Jonas Meyer for technical support and thank the forest authorities of the cantons Basel-Landschaft and Solothurn for granting permission to conduct research at the Hofstetten and Münchstein forest districts. We also like to acknowledge the local foresters, particularly Fredi Hügi and Christoph Sütterlin for their support and assistance in study site selection. This work was funded through the NCCR Climate (P30.3 ECOWAT) and the research program 'Forests and climate change' of the Swiss Federal Office of the Environment (FOEN) and the Swiss Federal Institute of Forest, Snow and Landscape Research (WSL, project MATCHTREE).

Supplementary materials

Supplementary material associated with this article can be found in the online version, at doi: 10.1016/j.agrformet.2022.109184.


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