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Detecting the fingerprint of drought across Europe's forests: do carbon isotope ratios and stem growth rates tell similar stories?

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Abstract

Background: Understanding how trees respond to drought is critical to forecasting both short and long-term impacts of climate change on forests. The isotopic ratio of ^{13}C to ^{12}C stored in wood – referred to as $\delta^{13}C$ – is widely used as an indicator of plant water status. Yet whether changes in $\delta^{13}C$ linked to drought are also associated with declines in annual carbon assimilation and allocation to stem growth remains unclear.

Methods: Here we used tree ring data from over 3000 trees – representing 26 populations of 16 common European tree species sampled at six locations that span more than 20° in latitude – to test whether drought induces coordinated changes in carbon isotope ratios and stem basal area increments (BAI).

Results: We found that $\delta^{13}C$ is a reliable indicator of drought across a wide range of species and environmental conditions. All but one of the populations sampled in this study showed a statistically significant increase in $\delta^{13}C$ under drought conditions. However, when considering the effects of these same drought events on BAI, we found no evidence to suggest that increases in $\delta^{13}C$ were coupled with significant declines in stem growth. While BAI was 11.9% lower on average in drought years, this decline in BAI was not significant when analysed across species. In fact, only seven of the 26 populations we sampled exhibited significant declines in BAI under drought conditions – four of these from a single study site in the Carpathian Mountains of Romania.

Conclusions: While $\delta^{13}C$ responded strongly and consistently to drought across a diverse group of tree species and environmental conditions, we found that most tree species were able to sustain growth even under conditions of low soil water availability. Consequently, while $\delta^{13}C$ provides a powerful indicator of past drought occurrence, by themselves carbon isotope ratios tell us little about how carbon sequestration and allocation to wood are affected by conditions of low water availability across Europe's forests.

Keywords: Basal area increments, Climate change, $\delta^{13}C$, Dendrochronology, Plant water status, Productivity, Tree rings

Background

Forests are a key component of the terrestrial carbon cycle and play a critical role in regulating climate by removing CO_2 from the atmosphere and storing it in wood (Luyssaert et al. 2008; Beer et al. 2010; Pan et al. 2011). Over the past two decades the world's forests have functioned as a net carbon sink, sequestering as much as 30% of all carbon emissions (Pan et al. 2011). Yet whether this carbon sink will persist under future climate conditions is unclear (Friend et al. 2014), with the likelihood of increasingly frequent and severe droughts and heat waves being a major cause for concern (Allen et al. 2015). Consequently, understanding how trees respond to drought is critical to forecasting both short and long-term impacts of climate change on forests (Clark et al. 2016; Grossiord et al. 2017).

At the level of the leaf, C_3 plants (which includes virtually all tree species) respond to low soil moisture availability by closing their stomata to limit water loss through

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transpiration (Bréda et al. 2006; Grossiord et al. 2017). One consequence of reduced stomatal conductance is a drop in the intercellular concentration of CO_2 (relative to ambient concentrations outside the leaf), which in turn affects the ratio of ^{13}C to ^{12}C – known as $\delta^{13}C$ – being fixed by RuBisCO (Farquhar et al. 1982; Leary 1988; Farquhar et al. 1989). Specifically, when stomata are fully open and intercellular concentration of CO_2 are high, plants preferentially fix ^{12}C relative to ^{13}C, as the lighter isotope diffuses through stomata more rapidly and reacts with RuBisCO more readily (Farquhar et al. 1982). However, as intercellular concentrations of CO_2 decline, so too does the degree of fractionation, resulting in a greater proportion of ^{13}C being fixed and thereby an increase in the $\delta^{13}C$ of photosynthates. As a result, $\delta^{13}C$ reflects plant water status at the time of carbon fixation, and by analysing the isotopic composition of wood in tree rings we can reconstruct a picture of past drought events (Leavitt 1993; Warren et al. 2001; Gessler et al. 2014). Yet whether $\delta^{13}C$ signals obtained from tree rings also reflect rates of annual carbon assimilation and allocation to stem growth remains unclear (Ferrio et al. 2003; Peñuelas et al. 2008; Jansen et al. 2013; Belmecheri et al. 2014; Hentschel et al. 2016; Shestakova et al. 2017).

Here we provide the first comprehensive test of whether drought induces coordinated changes in carbon isotope ratios and stem growth rates across Europe's dominant tree species and main forest types, an assumption which is routinely made in the literature but has yet to be rigorously tested. Using tree ring data for 26 populations of 16 common European tree species sampled at six locations that span more than 20° in latitude, we assess the evidence for the following alternative hypotheses (Fig. 1):

H1: Under drought conditions, trees exhibit an increase in $\delta^{13}C$ linked to stomatal regulation. This increase in $\delta^{13}C$ is coupled with a decline in stem growth (Ferrio et al. 2003; Belmecheri et al. 2014).
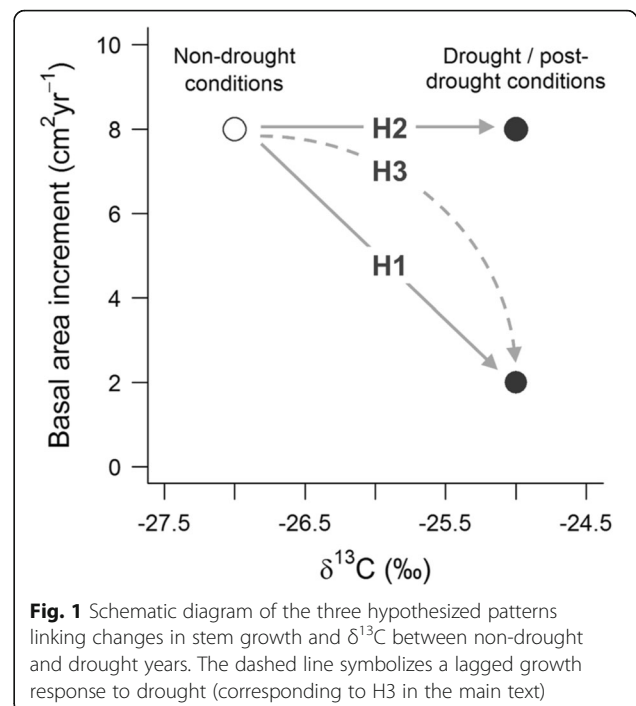
H2: Despite increases in $\delta^{13}C$ under drought conditions, stem growth varies little between drought and non-drought years (e.g., as a result of the stomatal regulation itself or access to carbon reserves that buffer against strong declines in growth; Hentschel et al. 2016).

H3: Trees show a lagged growth response to drought (Babst et al. 2013; Anderegg et al. 2015). Consequently, coordinated responses in $\delta^{13}C$ and stem growth only emerge in the year following the drought.

Methods
Study design
We sampled tree cores for both carbon isotope analysis and growth estimation from permanently marked forest plots established through the FunDivEUROPE project (Baeten et al. 2013). The FunDivEUROPE plot network consists of 209 forest plots distributed among six study

Fig. 1 Schematic diagram of the three hypothesized patterns linking changes in stem growth and $\delta^{13}C$ between non-drought and drought years. The dashed line symbolizes a lagged growth response to drought (corresponding to H3 in the main text)

sites across Europe (Table 1). The network was originally designed to explore the functional significance of biodiversity in forests, but is also ideally suited to studying physiological responses of Europe's forests to global change. The six study sites span more than 20° in latitude and encompass the major forest types found in Europe (EEA 2007), including boreal forests in Finland, hemi-boreal and mixed broadleaved-coniferous forests in Poland, beech forests in Germany, mountainous beech forests in Romania, thermophilous deciduous forests in Italy and Mediterranean mixed forests in Spain. In total, the plot network includes 26 study populations belonging to 16 tree species, several of which feature at more than one site (Table 1). The species pool includes conifers (four species), deciduous broadleaves (11 species) and evergreen broadleaves (one species).

At each site, 30 × 30 m permanent plots were established in 2011. Within each plot all stems ≥7.5 cm in diameter were identified to species and permanently marked (12,939 stems in total). For each stem, we recorded the diameter at breast height (D; to the nearest 0.1 cm using diameter tape) and used the crown illumination index (CII) to characterize crown dominance by scoring stems from 1 (suppressed crown receiving no direct light) to 5 (fully exposed dominant crown; Clark and Clark 1992). CII scores effectively capture the degree to which tree crowns are exposed to light (e.g., Jennings et al., 1999), and were used to select trees for isotope analysis and to model the effects of competition for light on growth (see following sections).

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Table 1 Overview of the FunDivEUROPE plot network

	Finland	Poland	Germany	Romania	Italy	Spain
Forest type[a]	Boreal	Hemiboreal	Beech	Mountainous beech	Thermophilous deciduous	Mediterranean mixed
Coordinates	63 °N, 30 °E	53 °N, 24 °E	51 °N, 11 °E	47 °N, 26 °E	43 °N, 11 °E	41 °N, 2 °W
Number of plots	28	43	38	28	36	36
Elevation range (m.a.s.l.)	80–200	135–185	500–600	600–1000	260–525	960–1400
Mean annual temperature (°C)	2.1	6.9	6.8	6.8	13.0	10.2
Mean annual precipitation (mm)	700	625	775	800	850	500
Non-drought year	2004	2010	2002	2001	2002	2002
Drought year	2006	2002	2003	2003	2003	2001
Water stress index of the drought year (unitless)	1.5	44.6	74.2	50.6	50.1	46.4
Water stress index between May – Oct of the drought year	1.5	40.3	59.2	35.4	49.7	44.8
Number of days with REW[b] < 0.4 during the drought year	13	92	157	171	88	109
Mean basal area (m^2 ha^{-1})	22.8	37.8	35.7	51.3	27.2	22.0
Species pool	*Betula pendula*	*Betula pendula*	*Acer pseudoplatanus*	*Acer pseudoplatanus*	*Quercus ilex*	*Quercus ilex*[c]
	Picea abies	*Carpinus betulus*	*Fagus sylvatica*	*Fagus sylvatica*	*Castanea sativa*	*Quercus faginea*
	Pinus sylvestris	*Quercus robur*	*Fraxinus excelsior*	*Abies alba*	*Ostrya carpinifolia*	*Pinus nigra*
		Picea abies	*Quercus petraea*	*Picea abies*	*Quercus cerris*	*Pinus sylvestris*
		Pinus sylvestris	*Picea abies*		*Quercus petraea*	

[a]Categories of the European Environment Agency (EEA 2007)
[b]Relative extractable water in the soil, calculated across the entire calendar year
[c]*Quercus ilex* was not targeted for isotope analysis in Spain due to difficulties in distinguishing between earlywood and latewood

Selecting drought and non-drought years

To test how drought influences both carbon isotope discrimination and stem growth, we used the BILJOU water balance model (Granier et al. 1999) to characterize annual soil water availability at each site between 1997 and 2010. Using the output of the model we then identified drought and non-drought years for each FunDivEUROPE site, as is described in detail in Grossiord et al. (2014,b). Briefly, the BILJOU model uses daily meteorological data (precipitation, global radiation, air temperature and humidity, wind speed), alongside information on soil water holding capacity and leaf area index to predict temporal variation in soil water content. Daily meteorological data were obtained from the CGMS database of interpolated meteorological data (AGRI4CAST, http://mars.jrc.ec.europa.eu/mars), while soil water holding capacity and leaf area index were assessed in situ. Specifically soil water holding capacity was estimated on the basis of soil depth and type, while leaf area index was quantified using an LAI-2000 analyser (LI-COR).

Using these data, the BILJOU model estimates the daily relative extractable water in the soil (REW, unitless). REW is defined as the ratio between available soil water and maximum extractable water (i.e., water holding capacity) and varies between 1 (field capacity) and 0 (permanent wilting point). When REW > 0.4, soil water conditions are considered non-limiting for transpiration and the rate of stomatal conductance depends primarily on air vapour pressure deficit and irradiance. Instead, when REW < 0.4 soil water shortages induce a drop in stomatal conductance and thus in leaf gas exchange for a large range of tree species (although we acknowledge that the magnitude of these responses is likely species-specific; Granier et al. 1999). From the daily REW estimates we calculated an annual water stress index for each site which cumulates daily REW deficits over the course of the year as: $\frac{1}{0.4} \times \sum_j (0.4 - REW_j)$, where j corresponds to the days when REW < 0.4 (Granier et al. 1999). For each site we then randomly selected a drought year from the three driest years over the 1997–2010 period, and a non-drought year to act as a control among years with a water stress index <6 (set as an arbitrary threshold). Drought and non-drought years selected for each study site are listed in Table 1 (see Grossiord et al. 2014 for further details on the selection of drought and non-drought years).

We note that ideally we would have liked to select multiple drought and non-drought years from each site, in order to better tease apart the abiotic and biotic drivers of isotopic signatures and growth trends. However, logistic constraints meant we could either sample multiple years for a small subset of species and/or sites, or we could

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sample across the entire species pool, but only for two contrasting years at each site. As the main goal of our analysis is to understand whether or not carbon isotope ratios and stem growth show a clear and coordinated response to drought across Europe's forests, we chose to focus on the later of these two options. Further work will be needed to tease apart the ecological, physiological and environmental mechanisms that underpin the general relationships we uncover here.

Carbon isotope analysis

We used wood sampled obtained from dated tree cores to measure the ratio of ^{13}C to ^{12}C – known as $\delta^{13}C$ – in both drought and non-drought years for each target species across the six study regions. A total of 1467 tree cores were collected for this purpose (giving an average of 59 trees per species at each site), the sampling and processing of which is described in detail in Grossiord et al. (2014,b). Cores were collected between March and October of 2012 for a subset of trees in each plot using a 5.15 mm diameter increment borer (Haglöf AB, Sweden). Trees were selected for coring at random, but only dominant and co-dominant trees (defined on the basis of D and CII) were target for isotope analysis to avoid the confounding effect of shading on $\delta^{13}C$ patterns (Ferrio et al. 2003). Samples were oven-dried for 72 h at 60 °C to reach constant weight before being filed with a scalpel for tree-ring dating. Because photosynthates from one growing season can be remobilized and allocated to earlywood formation in the following year (Offermann et al. 2011), thereby potentially confounding isotope – climate signals, we only sampled the latewood of the two target years [see Dietze et al. (2014) for a more in depth discussion on remobilization of non-structural carbohydrates in trees]. Due to difficulties in distinguishing between earlywood and latewood for samples obtained from *Quercus ilex* trees in Spain, this population was excluded from further isotopic analyses. Wood fragments from a given species in a given plot were pooled to obtain enough material for carbon isotope analyses (n = 3–6 trees species^{-1} plot^{-1}). Wood sampled were then ground, yielding between 0.4 and 1.5 mg of wood powder, weighed using a high-precision scale (MX5, Mettler Toldedo, Viroflay, France), placed in tin capsules, and analysed at the Stable Isotope Facility of UC Davis, California, USA with a PDZ Europa 20–20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK). Because the amount of ^{13}C in plants is naturally very low, $\delta^{13}C$ (‰) is typically expressed in relation to a standard as follows:

$$\delta^{13}C = \left(\frac{^{13}C_{plant}/^{12}C_{plant}}{^{13}C_{std}/^{12}C_{std}-1} \right) \times 1000 \qquad (1)$$

where $^{13}C_{plant}/^{12}C_{plant}$ and $^{13}C_{std}/^{12}C_{std}$ are the isotope ratios of the wood samples and of the Vienna Pee Dee Belemnite (VPDB) standard, respectively.

Plot-level values were used to calculate the mean $\delta^{13}C$ (±95% confidence intervals) of each species at each site (25 populations in total after having excluded *Quercus ilex* in Spain) for both drought and non-drought years ($\delta^{13}C_{dry}$ and $\delta^{13}C_{wet}$, respectively). Using these data we then calculated the mean change (±95% confidence intervals) in $\delta^{13}C$ between drought and non-drought years ($\Delta\delta^{13}C$, defined as $\delta^{13}C_{dry} - \delta^{13}C_{wet}$) across all study populations.

Tree growth estimation

In addition to using tree cores for isotope analyses, we also used them to assess growth responses to drought. Tree cores collected to measure growth were collected at the same time as those for isotope analysis, but the number of trees samples was larger (2950 in total, for an average of 113 cores per species at each site, of which those cored for isotopes were mostly a subset). While for isotopes we only sampled large dominant trees, for growth we wanted to explicitly account for the dependency of growth on tree size and therefore used a size-stratified random sampling approach to select trees for coring that would ensure all size classes would be represented by the sample [see Jucker et al. (2014) and Jucker et al. (2016) for details].

Once collected, wood cores were stored in polycarbonate sheeting and allowed to air dry before being mounted on wooden boards and sanded with progressively finer grit sizes. A high resolution flatbed scanner (2400 dpi optical resolution) was then used to image the cores. Yearly radial growth increments (mm yr.$^{-1}$) were measured for each cored tree from the scanned images. To minimise measurement errors associated with incorrectly placed ring boundaries, each sample was cross-dated against a species-level reference curve obtained by averaging all ring-width chronologies belonging to a given species from a given site. Both radial growth measurements and cross-dating were performed using the CDendro software suite (Cybis Elektronik & Data, Saltsjöbaden, Sweden). Radial increments were then converted to basal area increments (BAI, in cm^2). To do this we first reconstructed each tree's past diameters by progressively subtracting annual diameter increment (assumed to be twice the radial growth) from its current day diameter which was measured in the field in 2012. We then calculated each years' BAI as: $(\pi \times (D_{t2}/2)^2) - (\pi \times (D_{t1}/2)^2)$, where D_{t2} is the tree's diameter in the most recent time period (e.g., end of 2011) and D_{t1} is its diameter at the previous time step (2010 in this case).

Because the extent to which trees are affected by drought is known to be size-dependent (e.g., Zang et al. 2012; Bennett et al. 2015; Grote et al. 2016), directly

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relating growth and isotope values without accounting for differences in the size distribution of trees used to calculate them could affect results. To address this issue, we developed a statistical model that explicitly accounts for the effect of tree size on growth, and then used the model to estimate the stem growth of a tree of comparable size to that sampled for isotopes for each of the 26 study populations (see below for details). The model was fit separately to data from the drought and non-drought year, as well as to data from one year post-drought in order to test for lagged growth response to drought. Specifically, for each species at each site we modelled BAI as the following function of D and CII:

$$\log (BAI) = \rho_0 + \rho_1 \times \log(D) + \rho_2 \times CII + \varepsilon \qquad (2)$$

where ρ_{0-2} are parameters to be estimated from the data, and ε is the residual error. The model structure follows that of Jucker et al. (2014) and Jucker et al. (2016), where BAI is expressed as a power-law function of D (log-log relationship; Rüger et al. 2012), while competitive inhibition by taller neighbours is assumed to be an exponential function of CII (log-linear scale; Caspersen et al. 2011).

Using eq. (2), for each study population we estimated the BAI (±95% confidence intervals) of a tree with a stem diameter in the 75th percentile and CII = 4 (corresponding to a tree with ≥90% of its vertically projected crown exposed to full overhead light; Clark and Clark 1992) under drought conditions (BAI_{dry}), in the non-drought year (BAI_{wet}), and one year post-drought ($BAI_{dry + 1}$). From these we then computed the percentage change in BAI between drought and non-drought years as: $\Delta BAI = \left(\frac{1-BAI_{dry}}{BAI_{wet}}\right) \times 100$; and between one year post-drought and non-drought conditions as: $\Delta BAI_{lag} = \left(\frac{1-BAI_{dry+1}}{BAI_{wet}}\right) \times 100$. 95% confidence intervals for ΔBAI and ΔBAI_{lag} were estimated using Monte Carlo simulations that account for the uncertainty in BAI_{dry}, BAI_{wet} and $BAI_{dry + 1}$ values. Note that because in Spain the year post-drought coincided with the year that was selected as the non-drought control (see Table 1), we were unable to calculate ΔBAI_{lag} for trees at this site.

Quantifying the effects of drought on carbon isotope ratios and basal area increments

To test whether drought had a consistent effect on isotope ratios and growth across all study populations, we used one-sample *t*–tests to determine whether mean $\Delta\delta^{13}C$, ΔBAI and ΔBAI_{lag} values differed significantly from zero. Additionally, we also tested whether isotopic and growth responses to drought differed among study sites or between functional groups (conifers vs broadleaves) using a

two-way ANOVA with a Tukey test to correct for multiple comparisons. Lastly, responses of individual study populations to drought were assessed by observing whether the 95% confidence intervals of $\Delta\delta^{13}C$, ΔBAI and ΔBAI_{lag} overlapped with zero or not.

To determine whether increases in $\delta^{13}C$ in response to drought are coupled with declines in BAI (H1) we calculated the Pearson's correlation coefficient (ρ) between $\Delta\delta^{13}C$ and ΔBAI values of all study populations. A negative correlation between $\Delta\delta^{13}C$ and ΔBAI would provide support for H1, and would suggest that $\delta^{13}C$ can be used to quantitatively assess the impacts of drought on tree growth (Fig. 1). Instead, assuming an increase in $\delta^{13}C$ between drought and non-drought years, a lack of correlation between $\Delta\delta^{13}C$ and ΔBAI would suggest that trees are able to maintain growth rates even if stomatal conductance is reduced (H2). Alternatively, a lack of correlation between $\Delta\delta^{13}C$ and ΔBAI could also indicate that growth tends to exhibit a lagged response to drought (H3). To test whether this is the case, we correlated $\Delta\delta^{13}C$ and ΔBAI_{lag} values, with the expectation that a negative correlation between the two would provide support for H3 (Fig. 1). All analyses were conducted using the R statistical software (R Core Development Team 2016).

Results

Changes in carbon isotope ratios and basal area increments in response to drought

The ratio of ^{13}C to ^{12}C increased significantly under drought conditions in 24 of the 25 study populations for which isotopic analysis were conducted ($\Delta\delta^{13}C$ between non-drought and drought year = 0.99‰, $P < 0.001$; Fig. 2a). Across the study sites the magnitude of the increase ranged between 1.29‰ in Finland to 0.76‰ in Spain, but did not differ in a statistically significant way among any of the regions. On average, we found that broadleaves had significantly lower $\delta^{13}C$ values compared to conifers (−27.10‰ compared to −26.18‰ in non-drought conditions, $P = 0.003$, and −26.20‰ compared to −25.03‰ in the drought year, $P < 0.001$). However, the magnitude of the variation in $\delta^{13}C$ between drought and non-drought years was similar in the two functional groups ($\Delta\delta^{13}C = 0.90‰$ and 1.15‰ respectively, $P = 0.22$).

In contrast, while BAI was 11.9% lower on average during the drought year, this decline in BAI in response to drought was not significant when analysed across species ($P = 0.15$). Only seven of the 26 populations showed a significant decline in BAI under drought conditions (Fig. 2b). Four of these were from a single site (Romania, where BAI declined by 39.8% under drought conditions, significantly more than at any other site), while three constitute separate populations of a single species (*Picea*
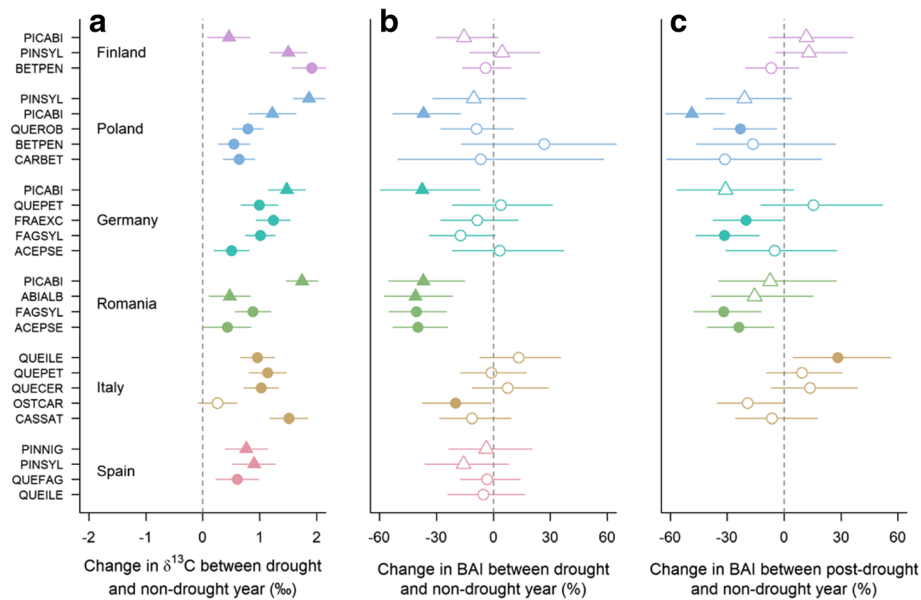
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Fig. 2 Change in species (**a**) $\delta^{13}C$, (**b**) basal area increments (BAI) between drought and non-drought years, and (**c**) difference in BAI one year post drought and non-drought conditions. Species names are abbreviated using the first three letters of the genus and species name (see Table 1 for full species names). Circles are broadleaved species, while triangles represent conifers. Filled symbols indicate differences that are significantly different from zero, with error bars corresponding to 95% confidence intervals. Note that in panel (**a**) *Quercus ilex* was not targeted for isotope analysis in Spain due to difficulties in distinguishing between earlywood and latewood. In panel (**c**) species from Spain are not shown because for this site the year post-drought coincided with the year that was selected as the non-drought control (see Table 1 for details)

abies) which were sampled at multiple sites along the latitudinal gradient. When comparing the response of conifers and broadleaves, we found that the broadleaves were only marginally less susceptible to drought (ΔBAI = −21.5% and −6.9% respectively, P = 0.07).

H1 versus H2: are increases in $\delta^{13}C$ in response to drought coupled with declines in BAI?

When we compared changes in $\delta^{13}C$ and BAI between drought and non-drought years, we found no evidence that the magnitude of changes in carbon isotope ratios were coupled with those in stem growth [Fig. 3; Pearson's correlation coefficient (ρ) between $\Delta\delta^{13}C$ and ΔBAI between drought and non-drought years = −0.03, P = 0.87]. Across all study species, only *Picea abies* – which was sampled at four
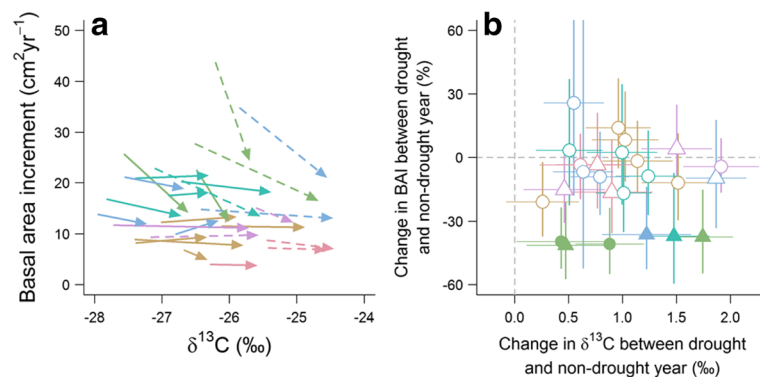

Fig. 3 Relationship between changes in $\delta^{13}C$ and those in basal area increments (BAI) between drought and non-drought years across all study populations. In panel (**a**) the start of the arrow corresponds to the non-drought year, while the tip indicates $\delta^{13}C$ and BAI values under drought conditions. Arrows that point to the right indicate an increase in $\delta^{13}C$ between non-drought and drought years, while arrows that point down correspond to a decline in BAI in response to drought. Continuous arrows denote broadleaved species, while conifers are shown as dashed lines. Panel (**b**) relates changes in BAI between drought and non-drought years (i.e., values reported in Fig. 2b) to ones in $\delta^{13}C$ (shown in Fig. 2a). Circles are broadleaved species, while triangles represent conifers. Filled symbols indicate species for which changes in $\delta^{13}C$ and BAI were both significantly different from zero, with error bars correspond to 95% confidence intervals. The colour scheme of the arrows and points follows that of Fig. 2

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sites along the latitudinal gradient – showed a clear association between increased δ^{13}C and decreased growth under drought conditions (ΔBAI = –31.7% on average; Fig. 2). This is in contrast to species such as *Pinus sylvestris* (sampled at three sites), which showed a strong drought signal in carbon isotope ratios, but only a marginal and non-significant decline in growth (ΔBAI = –7.2% on average, Fig. 2).

H3: do trees show a lagged growth response to drought?

Similarly, while on average BAI one year post-drought remained 11% lower than in the non-drought year (Fig. 2c), across species this trend did not emerge as statistically significant ($P = 0.65$). Six of 22 sampled populations showed significantly lower growth one year-post drought (three of which had also exhibited depressed BAI in the drought year itself; Fig. 2b–c). Again, we found no relationship between the magnitude of a species' increase in δ^{13}C during drought and its decline in growth one year post-drought (Fig. 4; $\rho = 0.05$, $P = 0.82$). Of the species that exhibited drought legacy effects, *Fagus sylvatica* showed significantly lower growth at both sampled sites in the post-drought year (ΔBAI$_{lag}$ = –31.6% on average, Fig. 2c). In contrast *Picea abies* – which exhibited the strongest declines in growth under drought conditions (Fig. 2b) – showed signs of recovery in the post-drought year at three of the four sampled sites (Fig. 2c). More generally, when comparing the growth response of conifers and broadleaves one year post-drought we found no significant differences among the two groups (ΔBAI$_{lag}$ = –14.0% and –9.9% respectively, $P = 0.99$).

Discussion

Across a wide range of environmental conditions, forest types and tree species we found carbon isotope ratios of wood to be a strong and reliable indicator of past drought occurrence (Fig. 2a). However, despite this clear physiological signal of drought on δ^{13}C, we only found a weak and context-dependent effect of these same drought events on tree growth (Fig. 2b). Previous studies have suggested that the relationship between carbon isotopes and growth might not be a simple one (Ferrio et al. 2003; Peñuelas et al. 2008; Jansen et al. 2013; Hentschel et al. 2016; Shestakova et al. 2017), but to our knowledge none had explored the relationship across a broad enough range of species and environmental conditions to draw this conclusion robustly. The relatively small declines in growth we observed in response to drought suggest that most European tree species are – on average – able to maintain growth under conditions of low soil water availability.

This is not to say that water availability is not a key factor in determining tree growth across Europe's forests (Boisvenue and Running 2006; Babst et al. 2013). In fact, previous analyses of stand-level climatic determinants of productivity across the FunDivEUROPE plot network revealed that with the exception of Finland, where growth was primarily temperature-limited, water availability was the primary driver of inter-annual variation in wood production (Jucker et al. 2014; Jucker et al. 2016). However, what these analyses also clearly showed was that the intensity and timing of drought events was just as important in determining annual growth patterns. Taking the sites in Spain and Italy as an example, year-to-year variation in productivity in these drought-prone Mediterranean forests was only weakly correlated with cumulative water shortages across the year, and instead depended strongly on water availability during the early stages of the growing season (Jucker et al. 2016). Consequently, while δ^{13}C is a useful indicator of past drought events, changes in these isotopic signatures may not necessarily translate directly to changes in annual growth (Fig. 3). In this respect, understanding the climatic triggers of tree growth – and how these vary among forest types, tree species and locally adapted populations – is critical to forecasting carbon dynamics in the face of climate change (Frank et al. 2015). Only by doing this will
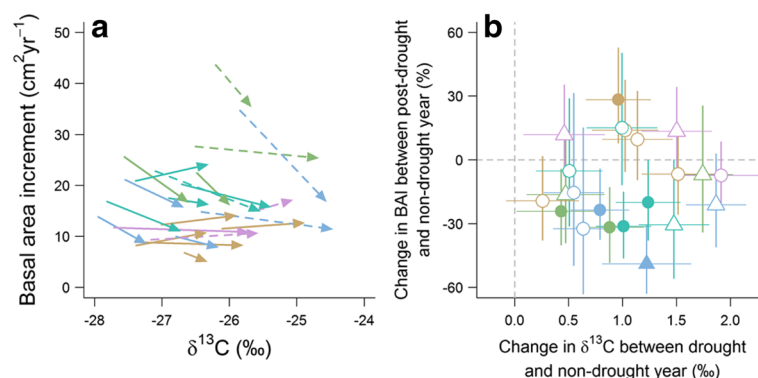

Fig. 4 Relationship between changes in δ^{13}C in response to drought and changes in basal area increments (BAI) between drought and one year post-drought years. The interpretation of the figure is analogous to that of Fig. 3. Species from Spain are not shown because for this site the year post-drought coincided with the year that was selected as the non-drought control (see Table 1 for details)

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we be able to develop models that accurately capture the response of forests to extreme events such as severe droughts (Babst et al. 2013; Rammig et al. 2015).

While recent work has shown that stomatal regulation and function can vary considerably among temperate trees (Wolz et al. 2017), carbon isotope changes in response to drought were remarkably consistent across a diverse group of species and a range of environmental conditions (Fig. 2a). For example, even though we found that on average broadleaf species had carbon isotope compositions that were around 1‰ lower than those of conifers, the magnitude of the $\delta^{13}C$ change in response to drought was statistically indistinguishable between the two groups. Similarly, we found no systematic differences in the degree to which $\delta^{13}C$ increased in response to drought across the six study sites, despite the fact these represent strongly contrasting forest types and environmental conditions. By contrast, growth responses to drought varied considerably among species and study sites (Fig. 2b). Consistently with what has been previously reported in the literature, Norway spruce (Picea abies) emerged as particularly susceptible to drought (e.g., Zang et al. 2014), while species such as Scots pine (Pinus sylvestris) showed greater resistance to drought across a range of provenances. With the exception of trees sampled at the site in Romania and Norway spruce trees from Poland and Germany, the only other species to show significant declines in growth in response to drought was Ostrya carpinifolia. This matches previous reports showing that, relative to other species it typically coexists with, O. carpinifolia can be considered drought-intolerant (Nardini et al. 2016). What is perhaps more interesting is that O. carpinifolia was also the only species we sampled to not exhibit a significant increase in $\delta^{13}C$ following drought. So not only are growth and isotopic responses not coordinated in this species, they are actually contrasting. Further work is needed to shed light on the physiological mechanisms that underpin this result.

Isotopic responses to drought were remarkably conserved even when looking across multiple populations of the same species sampled at different sites along the latitudinal gradient. For instance, Norway spruce trees growing in Germany, Romania and Poland showed almost identical increases in $\delta^{13}C$ during drought years (matching the strong declines in growth observed at these sites for this species). In Finland, spruce trees did show a less pronounced increase in $\delta^{13}C$ in response to drought compared to the other three sites. However, this was also associated with a much weaker (and non-significant) decline in growth at this site, likely reflecting the lower intensity of the drought event in Finland relative to the other sites (Table 1), as well as the fact that in high-latitude forests photosynthetic activity and growth are primarily limited by temperature rather than by water availability (Babst et al. 2013; Jucker et al. 2016). The same pattern, whereby species sampled at multiple sites exhibited increases in $\delta^{13}C$ during drought years that were comparable in magnitude, was also found for sycamore (Acer pseudoplatanus), European beech (Fagus sylvatica), sessile oak (Quercus petraea) and Scots pine. The only exception we found to this pattern was birch (Betula pendula), which exhibited a much more pronounced increase in $\delta^{13}C$ at the site in Finland compared to that in Poland (despite the fact that the drought at the second of these two sites was more intense and lasted longer; Table 1).

In terms of site-specific responses, a clear pattern to emerge from our analysis is that all four species from the site in the Carpathian Mountains of Romania showed very strong declines in growth in response to the drought of 2003 (Fig. 2b). In fact this one site accounted for more than half of the statistically significant growth declines in response to drought we observed across the 26 populations studies here. One possible explanation for this is that while the 2003 drought at the Romanian site reached a lower peak intensity compared to the sites in Italy and Germany (Table 1), drought conditions at the Romanian site began earlier in the year and extended right through to the following growing seasons (see Supporting Information of Grossiord et al. 2014). This would again suggest that critical to understanding the effects of drought on growth is factoring in not just the occurrence, but also the timing, duration and intensity of drought events, as well as the local adaptation or preconditioning of trees to drought. In addition to this, another factor that could have contributed to the strong drought response in Romania is the high basal area of the stands at this site (Table 1), which previous work has shown can modulate the impact of drought on forest growth by exacerbating belowground competition for water (Bottero et al. 2017).

Although we did find some evidence that low soil moisture availability in one year could affect growth trends in the next (Fig. 2c), across our study sites these legacy effects of drought were not as pervasive as reported elsewhere (Anderegg et al. 2015). Instead, legacy effects of drought varied considerably among species, and with few exceptions seemed to reflect slow, progressive recovery from drought rather than a lagged response sensu stricto (which would manifest as little or no change in growth during the drought year, followed by a more pronounced decline in the following year). Overall, this recovery appears to have been faster for conifers than angiosperms, which is consistent with the results of a recent large scale study on forest resilience to drought across the Northern hemisphere (Gazol et al. 2017). Norway spruce for instance showed signs of recovery at three of the four sites where it was sampled.

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By contrast, European beech showed a clear lag phase in its growth response, with both populations studied here exhibiting significantly suppressed growth one year post-drought (Fig. 2c). That being said, accounting for lagged growth responses to drought did not reveal a coordinated response between carbon isotopes ratios and growth under conditions of low soil moisture availability (Fig. 4).

While we attribute the lack of correlation between changes in $\delta^{13}C$ and ones in BAI to the ability of trees to sustain growth under conditions of low water availability, a number of caveats related to the approach we used to look for associations between $\delta^{13}C$ and BAI measurements should be kept in mind when interpreting our results. The most important of these is that we were only able to compare a single drought and non-drought year at each site. As mentioned previously, in defining our sampling strategy we chose to maximise the geographic and taxonomic coverage of our dataset in an attempt to provide a first comprehensive test of whether or not carbon isotope ratios and stem growth rates show coordinated responses to drought across Europe's forests. However, this came at the expense of being able to replicate our analysis across multiple drought/non-drought events within each site. In this respect, a fully resolved chronology of both $\delta^{13}C$ and BAI would have allowed us to more effectively account for legacy effects of climate on growth and isotope ratios. It also would have provided an opportunity to explore how other factors such as vapour pressure deficit, nitrogen availability, insect and pathogen outbreaks, or masting events might affect both $\delta^{13}C$ and BAI (e.g., Hacket-Pain et al. 2015). Our results clearly suggest that shifts in carbon isotope ratios associated with stomatal regulation during drought do not directly translate into declines in stem growth. Uncovering the physiological processes that underpin these complex patterns is an important next step.

An additional issue with relating $\delta^{13}C$ and BAI using our approach which is worth considering is that while BAI integrates growth across the entire year, $\delta^{13}C$ is calculated exclusively for latewood samples to avoid issues with the remobilization of photosynthates at the beginning of the growing season. As a result, $\delta^{13}C$ primarily reflects climatic conditions in the later part of the growing season, leading to a potential mismatch with the processes that shape annual trends in BAI. That being said, teasing apart the seasonal dynamics of the drought years we selected suggests this is unlikely to be a major issue in our case. This is because across all study sites we found that the water stress index used to identify drought years had very similar values whether it was calculated across the entire calendar year or whether we restricted it exclusively to the growing season (Table 1). Regardless of this, a more detailed analysis of within-year variation in $\delta^{13}C$ and BAI that explicitly accounts for carbon remobilization between storage pools would certainly help clarify the physiological mechanisms that underpin both isotopic discrimination and growth (e.g., Helle and Schleser 2004). Lastly, because we had to aggregate samples for isotopic analyses, all of our comparisons between $\delta^{13}C$ and BAI are made at the population level and potentially ignore important variation among individual trees. In this respect, an advantage of working at the individual tree level would have been the ability to tease apart the effects of tree size on both growth and $\delta^{13}C$ (e.g., Koch et al. 2004) under varying conditions of soil water availability.

Conclusions

Across a diverse group of tree species and a range of environmental conditions carbon isotope ratios were strongly influenced by drought, with all but one of the populations sampled in this study exhibiting a significant increase in $\delta^{13}C$ under drought conditions. However, this strong isotopic signature did not translate into an equally clear growth response to drought, as most tree species were able to maintain growth even under conditions of low soil water availability. As a result, while $\delta^{13}C$ provides a powerful indicator of past drought occurrence, by themselves carbon isotope ratios tell us little about how carbon sequestration and allocation to wood are affected by conditions of low water availability across Europe's forests.

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