Wood phenology, not carbon input, controls the interannual variability of wood growth in a temperate oak forest

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Summary

- Although the analysis of flux data has increased our understanding of the interannual variability of carbon inputs into forest ecosystems, we still know little about the determinants of wood growth. Here, we aimed to identify which drivers control the interannual variability of wood growth in a mesic temperate deciduous forest.
- We analysed a 9-yr time series of carbon fluxes and aboveground wood growth (AWG), reconstructed at a weekly time-scale through the combination of dendrometer and wood density data.
- Carbon inputs and AWG anomalies appeared to be uncorrelated from the seasonal to interannual scales. More than 90% of the interannual variability of AWG was explained by a combination of the growth intensity during a first 'critical period' of the wood growing season, occurring close to the seasonal maximum, and the timing of the first summer growth halt. Both atmospheric and soil water stress exerted a strong control on the interannual variability of AWG at the study site, despite its mesic conditions, whilst not affecting carbon inputs.
- Carbon sink activity, not carbon inputs, determined the interannual variations in wood growth at the study site. Our results provide a functional understanding of the dependence of radial growth on precipitation observed in dendrological studies.

Introduction

Temperate forests cover 6% of the global land area, and contribute to 13% of the annual fixation of carbon (C) in the continental live biomass (Saugier *et al.*, 2001; Pan *et al.*, 2013). Contrasting with a global trend of decrease in the world's forest area driven by deforestation in the tropics, the temperate forest area (FAO, 2011) and C stocks are currently increasing, although early signs of saturation of this C sink are appearing (at least in Europe; Nabuurs *et al.*, 2013). The C sequestration potential of forests lies in their stocking of C as wood (and derived products) and soil organic matter. The C stored in wood originates from photosynthesis, and typically represents 10–25% of the annual gross primary productivity (GPP) in temperate forests (Luyssaert *et al.*, 2007; Wilkinson *et al.*, 2012; Babst *et al.*, 2014).

Although it is clearly established that regional averages of wood production and GPP are closely linked over large climatic gradients (e.g. across biomes in Litton *et al.*, 2007), there is conflicting evidence about the dependence of wood growth on GPP and, more generally, C inputs (e.g. net ecosystem productivity, NEP) at the stand scale. A survey of the literature indicates that a positive correlation of wood growth with C inputs (GPP or NEP) is not systematic at the annual scale (Table 1). Indeed, if wood is by far the most important plant C pool in a mature forest, its annual increment is typically of the same order of magnitude as other C pools (e.g. leaves, roots, fruits), and there is a priori no functional reason to expect a constant allocation of C among these pools.

The growth of a tree organ is a complex process, controlled by an ensemble of environmental and internal drivers that modulate the progress of an ontogenetic pattern of development from the first meristem cell division until organ maturity. C and other atomic constituents of organic matter are required for the formation of new tissues, but C acquisition is not necessarily the limiting factor for growth (Körner, 2015), at least at scales from days to weeks. The C allocated to a growing organ may originate from photosynthates that may have been acquired several days (Dannoura *et al.*, 2011) and up to years (Gaudinski *et al.*, 2009) ago, possibly resulting in a phase difference between organ growth and C acquisition (Richardson *et al.*, 2013). In addition to the availability of C for growth, environmental drivers, such as temperature and water availability, are determinants of organ phenology (Delpierre *et al.*, 2015) and growth rate (Fatichi *et al.*, 2014; Lempereur *et al.*, 2015), as expected from evidence at the cell and tissue scales (Lockhart, 1965; Muller *et al.*, 2011). Interestingly, organ growth seems to be more sensitive than C acquisition to low temperatures and soil water stress (Hsiao *et al.*, 1976; Lempereur *et al.*, 2015), explaining, for instance, the increase in C reserves observed along altitudinal gradients (Fajardo *et al.*, 2012).

Table 1 Literature review; assessment of the correlation of wood growth with carbon inputs

| Species | Latitude (°N) | Altitude (m asl) | Climate | Link aboveground wood growth/C flux | | | | | | Method for estimating wood growth | n (yr) | Reference |
| | | | | Annual | | Seasonal | | Daily | | | | |
				GPP	NEP	GPP	NEP	GPP	NEP			
Picea mariana	55.9	unknown	Boreal	No	+					TRW	10	Rocha *et al.* (2006)
Pinus sylvestris	61.9	180	Boreal		No					TRW + WD	13	Babst *et al.* (2014)
Picea abies	46.8	1640	Mountainous		+	+			−	Auto dendrometer	11	Zweifel *et al.* (2010)
Mixed decid.	36.1	1420	Cool-temp.		+					Annual inventories	6	Ohtsuka *et al.* (2009)
Mixed conif.	45.4	60	Cool-temp.		No					Inventories	10	Richardson *et al.* (2013)
Mixed decid.	39.3	290	Temperate		No					Band dendrometer	13	Brzostek *et al.* (2014)
Fagus sylvatica	55.5	40	Temperate		+					TRW + WD	12	Babst *et al.* (2014)
Fagus sylvatica	51.1	430	Temperate	No						Band dendrometer	6	Mund *et al.* (2010)
Fagus sylvatica	48.5	300	Temperate	+	No					Band dendro + stand inventories	10	Granier *et al.* (2008)
Pinus sylvestris	51.3	15	Temperate		No					TRW + WD	10	Babst *et al.* (2014)
Picea abies	51.0	320	Temperate		+					TRW + WD	13	Babst *et al.* (2014)
Quercus ilex	43.7	270	Mediterranean	+	+	+	No	−	−	Auto dendrometer	8	Lempereur *et al.* (2015)
Pinus pinaster	43.7	0	Mediterranean		No					TRW + WD	9	Babst *et al.* (2014)

We report the sign (+ or −) of significant correlations between wood growth and ecosystem carbon fluxes (GPP, gross primary productivity; NEP, net ecosystem productivity) integrated at different time-scales. Non-significant correlations ($P > 0.05$) are reported as 'no'. On average, the probability level of non-significant correlations was $P = 0.40$ (for studies at the annual scale). Missing values indicate that the correlation was not assessed in the publication. masl, metres above sea level; TRW, tree ring width; WD, wood density.

The limitation of organ growth capacity (*sink limitation*) by environmental conditions is expected to be particularly marked in climatic zones characterized by low temperature or water stresses (e.g. boreal or mountainous climate for temperature limitation, Leuzinger *et al.*, 2013; and Mediterranean climate for water stress limitation, Lempereur *et al.*, 2015). To date, we know little of the relative influence of C availability and sink limitation on the modulation of growth in mesic climatic conditions. Although increasing water stress has been proposed to limit wood production in North American temperate deciduous forests (Brzostek *et al.*, 2014), no direct evidence of an absence of coincident C limitation has been demonstrated.

In a recent analysis of growth data from the French permanent plot network for the monitoring of forest ecosystems (RENECOFOR), we saw that both C availability (quantified as current and previous year GPP) and sink limitation by water stress determine the spatial and interannual variability of wood growth in temperate French regions (Guillemot *et al.*, 2015). Instead, we noted that most of the variability of wood growth in mountainous and Mediterranean zones was driven by low-temperature and water stress sink limitation.

In this article, we aimed to identify the determinants of the interannual variability of aboveground wood growth (AWG) of a mature *Quercus petraea* forest subject to mesic climatic conditions over a 9-yr period (2006–2014). Specifically, we aimed to establish whether AWG is more dependent on C fuelling from GPP or on constraints imposed by environmental variations at scales ranging from weeks to years. As we observed that AWG did not depend on GPP, we identified which periods of the seasonal pattern of wood growth drove the interannual variations in AWG. We showed that growth during these periods presented clear

responses to environmental variations, and was primarily dependent on water stress.

Materials and Methods

Study site

The Fontainebleau-Barbeau site (FR-Fon, http://www.barbeau. u-psud.fr) is part of a national forest located 70 km southeast of Paris, France (48°28′N, 02°46′E, 100 m above sea level, asl). The stand is composed of sessile oak (*Quercus petraea* (Matt.) Liebl.) as the dominant species (representing 79% of the basal area), with hornbeam (*Carpinus betulus* L.) occupying the understorey (18% of the basal area). The site index (dominant height = 25 m at age 100 yr) indicates that FR-Fon is a fairly productive stand, reaching the average productivity of northern France oak stands (Bergès *et al.*, 2005). Other tree species (e.g. *Pinus sylvestris* L., *Sorbus torminalis* (L.) Crantz, *Corylus avellana* L., *Mespilus germanica* L.) are disseminated throughout the stand, accounting for < 3% of the basal area. Mean annual air temperature and cumulated precipitation are 11.2°C and 677 mm, respectively (1980–2010, Melun weather station, 12 km from the study site), with a homogeneous distribution of precipitation events throughout the year (Supporting Information Fig. S1). The soil is a gleyic luvisol (FAO-ISRIC-ISSS 1998) of c. 90 cm in depth, developed on a millstone bedrock and covered by an oligo-mull humus. Oak roots are able to tap water at least down to 150 cm depth, probably setting the accessible soil water holding capacity at c. 180 mm. The leaf area index (LAI) reached, on average, 6.4 over the 2006–2010 period. A commercial thinning began during the winter of 2010–2011 and was pursued up to the following winter. The
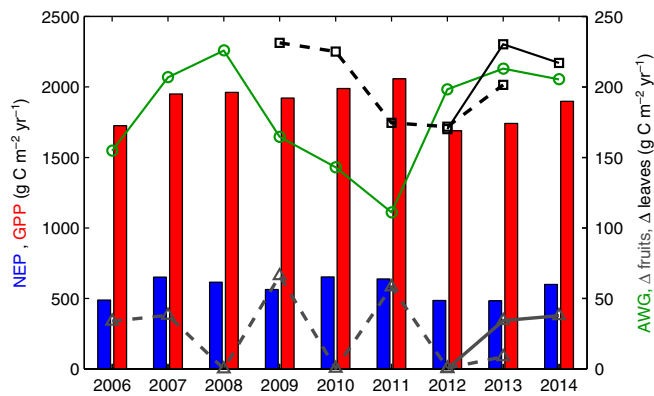
Fig. 1 Annual carbon balance of the Fontainebleau-Barbeau (FR-Fon) oak forest. Carbon (C) inputs appear on the left axis (blue, net ecosystem productivity, NEP; red, gross primary productivity, GPP); biomass increments appear on the right axis (green, oak aboveground wood growth (AWG); grey, fruits; black, leaves). Continuous lines represent direct measurement methods (see the Materials and Methods section for wood; based on litter traps for leaves and fruits). Dashed lines symbolize indirect measurement methods (light interception for leaves; litter traps measured on a nearby stand for fruits).

associated reduction in basal area (−14%) and in LAI (−2.3 points) had no perceptible influence on C inputs (Fig. 1), but reduced annual AWG by 15% over 2011–2014, compared with the calculated yield in the absence of thinning. We notice that LAI had almost fully recovered in 2012 (Fig. 1).

Carbon flux measurements

Energy, water vapour and CO_2 fluxes were measured from March 2005 using an eddy covariance system installed at the top of a 35-m tower. The main flux measurement device was composed of an open-path infrared gas analyser (LI-7500; Li-Cor Inc., Lincoln, NE, USA) and a three-dimensional sonic anemometer (Solent R3; Gill Instruments Ltd, Lymington, Hampshire, UK). Data were processed with EDDYPRO software (v.5.2.1, Li-Cor). Half-hourly CO_2 and H_2O fluxes were corrected for spectral losses (Moncrieff *et al.*, 1997, 2005) and for air density fluctuations (Burba *et al.*, 2008). Data from an additional eddy covariance device (composed of an LI-7200 (Li-Cor) and an HS-50 (Gill Instruments), mounted 2 m apart from the main device from July 2011, were used to gap fill the main time series. Calculated fluxes were quality controlled, gap filled and partitioned into GPP and ecosystem respiration, according to standard procedures (Reichstein *et al.*, 2005; Papale *et al.*, 2006). An annual friction velocity (u^*) threshold value was used to filter out data acquired under stable conditions ($u^*_{threshold} = 0.22 \pm 0.07$ m s^{-1}). Parameter fitting for flux partitioning was performed according to the short-term exponential method (Reichstein *et al.*, 2005).

Dendrometer data and wood phenology indices

In February 2006, 60 dominant and co-dominant oaks were equipped with band dendrometers (DB20; EMS, Brno, Czech

Republic; accuracy = 0.05 mm), after levelling off the bark with a rasp. These trees were in the 90–330-cm interval of circumference at breast height (CBH), spanning the range of growth vigour observed at the site. Dendrometer readings were acquired weekly from early March to the end of October (i.e. including the growing season) and bimonthly during the rest of the year, resulting in 352 readings of CBH increment for each tree over the 2006–2014 period.

We first used the CBH increment data to infer wood phenological stages. (1) The date of spring AWG resumption (AWG$_{start}$) was defined as the latest day of year (DoY) on which the yearly minimum of CBH was observed. (2) The first date of AWG halt (AWG$_{halt}$) was defined as the first DoY following AWG$_{start}$ for which an increment of < 0.05 mm was achieved. At that date (AWG$_{halt}$), $88 \pm 6\%$ of annual wood growth was achieved. (3) The cessation of wood growth (AWG$_{end}$) was defined as the DoY at which 95% of the annual CBH increment was achieved.

We further used dendrometer records to infer wood biomass increments, as performed in previous studies (Granier *et al.*, 2008; Gough *et al.*, 2009). Dendrometers record stem circumference increments, which respond to two physical processes: wood tissue growth (consisting of the production and differentiation of new wood cells) and variations in tree internal water reservoirs (Betsch *et al.*, 2011). Although tissue growth (the process of interest in our work) contributes to a gain (i.e. positive increment) in circumference, the shrinking and swelling of the water reservoir have reversible impacts on the dendrometer signal. In order to approach as close as possible to the growth process, we smoothed the original dendrometer time series (Hinckley & Lassoie, 1981; Zweifel *et al.*, 2010) before using it to calculate wood biomass increments, by specifying that no apparent shrinkage was allowed (i.e. if CBH$_t$ < CBH$_{t-1}$, then CBH$_t$ is set equal to CBH$_{t-1}$). In order to minimize the influence of diurnal variations in tree internal water reservoirs, dendrometer readings were obtained between 08:00 and 10:00 h (solar time). We further notice that, compared with hourly increments recorded by automatic dendrometers, increments recorded at a weekly time-scale with band dendrometers are larger, and hence less influenced by relative variations in stem water internal reservoirs.

Wood density and ring width determination

In December 2014, 23 dominant and co-dominant oaks were cored for wood density determination and tree ring width (TRW) measurements. Each core was analysed using the X-ray method (Bergès *et al.*, 2008). Each microdensitometric ring profile was divided into 20 intervals of equal width. The seasonal dynamics of wood infradensity were calculated from radial growth dynamics, as inferred from smoothed dendrometer data (Eglin *et al.*, 2010), and averaged across trees before being used for biomass calculations.

Calculation of wood biomass increments

We inferred the seasonal dynamics of AWG for an individual tree (AWGi) from the combined time series of volume growth and wood infradensity profiles:

$$\text{AWGi}_{t,y} = \frac{\mathrm{d}B_{t,y}}{\mathrm{d}t} = \frac{\mathrm{d}V_{t,y}}{\mathrm{d}t} \times \rho_{t,y} \times P_{\text{carb}} \qquad \text{Eqn 1}$$

where B is the aboveground wood biomass of a given tree (g C), V is the tree aboveground wood volume (m^3), ρ is the wood density (kg DM m^{-3}), P_{carb} is the dry matter C content (fixed to 0.50 g C g^{-1} DM), t denotes the date (DoY) of CBH measurement (as reconstructed from dendrometer readings) and y is the year index (2006–2014). Thus, AWGi was calculated at the weekly time-scale, which was the time-scale of dendrometer readings. We notice that the use of increment data acquired along the stem and branches (Latte *et al.*, 2015) would yield more precise estimates of tree volume increment, but would not change the overall temporal signal.

An allometric equation (Eqn 2; Vallet *et al.*, 2006) was used to calculate the aboveground wood volume (including bark and branches) from the tree CBH and height (H):

$$V_{t,y} = f(\text{CBH}_{t,y}, H_{t,y}) \qquad \text{Eqn 2}$$

with:

$$H_{t,y} = g(\text{CBH}_{t,y}) \qquad \text{Eqn 3}$$

We fitted Eqn 3 (Dhôte & Hercé, 1994) on a sample of 61 dominant and co-dominant FR-Fon oaks in 2006.

The scaling-up of biomass increment data from individuals to the tree population scale, yielding the stand AWG (g C m^{-2} per unit time), was based on a stand inventory performed in 2006–2007, updated after the 2010–2011 thinning. We inferred the growth of different diameter classes from empirical relationships between tree diameter class and basal area increment (see Guillemot *et al.*, 2014).

In Eqn 1, we calculated the seasonal dynamics of the wood volume increment ($\frac{\mathrm{d}V_{t,y}}{\mathrm{d}t}$) from an allometric relationship (Eqn 2) designed for the estimation of tree volume at a given date. By doing so, we assumed that primary growth ($= \frac{\mathrm{d}H_{t,y}}{\mathrm{d}t}$) monotonically increases with secondary growth ($= \frac{\mathrm{d}\text{CBH}_{t,y}}{\mathrm{d}t}$). Testing for the introduction of theoretical patterns of seasonal primary growth in the calculation of wood volume (Eqn 2) shows that the inferred seasonal patterns of wood growth are virtually insensitive to the hypothesis of a monotonic increase in primary with secondary growth in our mature forest (in which oak grew by a height of 0.80 m over a 10-yr interval; not shown).

Identification of critical periods in flux time series

We defined, for a given flux (GPP or AWG), 'critical periods' as the short time windows within the year that most significantly affected the magnitude of the annual flux (Le Maire *et al.*, 2010). In this study, we focused our attention on short (14-d) periods of the year which largely explained the magnitude of the annual anomalies in GPP or AWG fluxes. These critical periods were

quantified using correlation between the flux anomalies during a critical period and the annual flux anomalies.

Results

Interannual variability of the C balance (fluxes and biomass production)

The annual AWG represented, on average, $10 \pm 2\%$ (mean $\pm$ SD) of annual GPP and $32 \pm 8\%$ of annual NEP of the study site, analogous to leaf production (Fig. 1). Over the study period, annual AWG was quantitatively higher than fruit production (which was equivalent to 0–52% of annual AWG). Annual AWG was not significantly correlated with either leaf ($r = -0.02$, $P < 0.99$ Spearman rank correlation test) or fruit ($r = -0.40$, $P < 0.33$) production. Ample variations appeared in the annual AWG time series, with maximum values reaching twice the minimum growth.
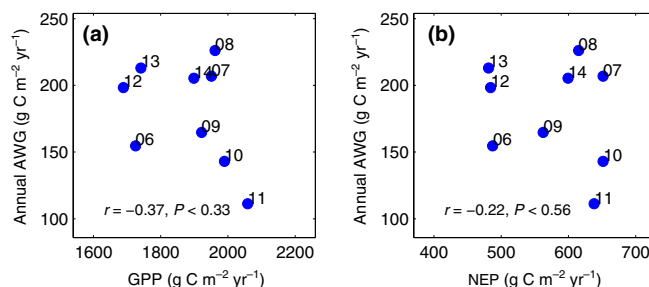
Aboveground wood growth is not correlated with C inputs

The annual input of C, assessed as either GPP or NEP, did not correlate significantly with annual AWG (Fig. 2). An illustrative example was year 2011, for which the highest GPP and lowest AWG over the study period were observed (Fig. 2a). Similarly, no significant correlation was observed between annual AWG and C inputs integrated at a subannual scale (Fig. S2), or between annual AWG and lagged C inputs (not shown).

At seasonal (weekly or monthly) time-scales, AWG appeared to be significantly correlated with C inputs (Table 2). Yet, the correlations vanished when considering annual anomalies of the seasonal patterns, that is, after subtracting the underlying seasonal pattern (Table 2).

Seasonal patterns of wood growth and GPP are partly decoupled

The seasonal patterns of AWG and GPP displayed clear particularities. Spring resumption of GPP was particularly marked from DoY 90 (Fig. 3b), slightly ahead of the stand average date of budburst for hornbeam (DoY 96) and oak (DoY 106). The resumption of oak AWG (AWG$_{\text{start}}$) clearly responded to temperature

Fig. 2 Correlation of annual aboveground wood growth (AWG) with carbon (C) inputs at the Fontainebleau-Barbeau (FR-Fon) oak forest. Particular years appear as numbers (e.g. 2006 = '06'). Annual AWG was correlated with annual (a) gross primary productivity (GPP) or (b) net ecosystem productivity (NEP).

Table 2 Correlation between carbon inputs and aboveground wood growth (AWG) at the Fontainebleau-Barbeau (FR-Fon) oak stand

Time-scale	rGPP	P values (GPP)	rNEP	P values (NEP)	n
Original flux series					
Weekly	0.55	< 0.01	0.53	< 0.01	352
Monthly	0.75	< 0.01	0.74	< 0.01	107
Flux anomalies					
Weekly anomalies	0.04	0.40	−0.02	0.70	352
Monthly anomalies	0.17	0.08	0.09	0.36	107

'Anomalies' were obtained by subtracting the mean annual pattern at the considered scale.
GPP, gross primary productivity; NEP, net ecosystem productivity.

(Notes S1) and occurred, on average, on DoY 92, which was 14 d ahead of oak budburst (Fig. 3a). Late-season cessation of AWG and GPP were clearly out of phase. The first date of growth halt (AWG_{halt}) occurred in early August (average DoY 213, Fig. 3a) before AWG ceased mid-September (AWG_{end}; average DoY 255), whereas GPP decreased to zero > 50 d later (after DoY 310, Fig. 3b).

GPP and growth respond to distinct environmental controls

Within the growing season, fluxes of C input (GPP) and AWG showed strikingly different relationships with environmental variables (Fig. 4). Whereas GPP showed clear positive relationships with incoming radiation (Fig. 4a), temperature (Fig. 4b) and, consequently, VPD (Fig. 4c), AWG showed a marked limitation at low soil water content (SWC, Fig. 4d), which was not observed for GPP. Interestingly, there was an apparent negative response of AWG on VPD (Fig. 4c).
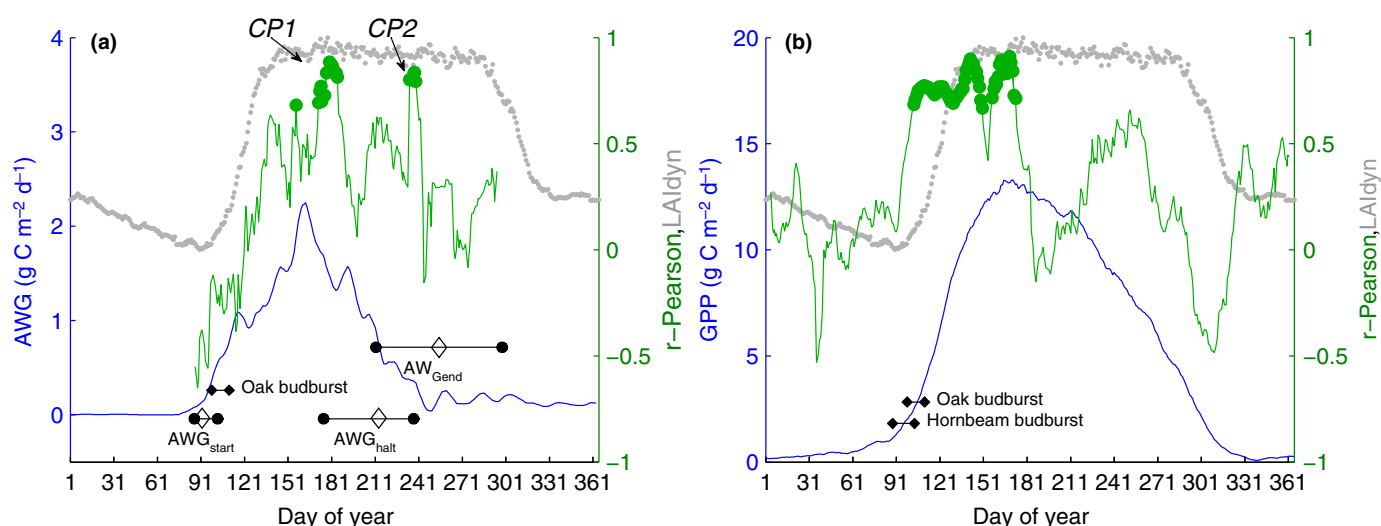
Critical periods determine the interannual variability of wood growth

The critical periods accounting for most of the interannual variability of AWG and GPP also differed. Spring fluxes (DoY 103–173) accounted for most of the interannual variability of GPP (Fig. 3b), whereas two critical periods most strongly influenced the interannual variability of AWG: the first critical period (CP1) centred on DoY 179, occurring just after reaching the maximum growth, and a second critical period (CP2) centred on DoY 236, occurring at the end of the wood growing season (Fig. 3a).

In line with the detection of the two critical periods, both growth during CP1 and the indices of AWG cessation (AWG_{halt} and AWG_{end}) correlated significantly with annual AWG (Fig. 5b–d). By contrast, we observed no significant correlation between annual AWG and the date of spring AWG resumption (AWG_{start}) (Fig. 5a). A stepwise linear combination of these variables reproduced c. 93% of the variance of annual AWG, retaining AWG_{halt} (56.5% of the variance in the linear combination, $P < 0.02$) and growth during CP1 (46.2%, $P < 0.03$) as key phases of the wood formation pattern.

Growth during key phases depends on water stress

The interannual variations in AWG_{halt} were positively correlated with SWC (the higher the soil humidity, the later the occurrence of the first growth halt) and negatively correlated with VPD (the higher the VPD, the earlier the occurrence of growth halt) (Fig. 6). Partial correlation plots showed that the observed correlation with VPD was probably related to the interdependence of VPD and SWC, as the correlation between AWG_{halt} and VPD vanished when SWC was held constant (Fig. S3). In accordance with the positive correlation between AWG_{halt} and SWC, a

Fig. 3 Detection of critical periods for the interannual variations in aboveground wood growth (AWG) and gross primary productivity (GPP). Blue, mean annual pattern of (a) AWG and (b) GPP, averaged over the 2006–2014 period. Green lines, Pearson's correlation coefficient computed between the seasonal (14-d moving window) and annual fluxes. Green dots indicate 'critical periods' (CP; see the Materials and Methods section for definition). Grey dots represent the averaged seasonal pattern of leaf area index (LAI) dynamics (normalized 0–1) calculated from photosynthetically active radiation transmittance. Horizontal black lines span the interannual variations in the main phenological events, with the average date marked as a diamond.
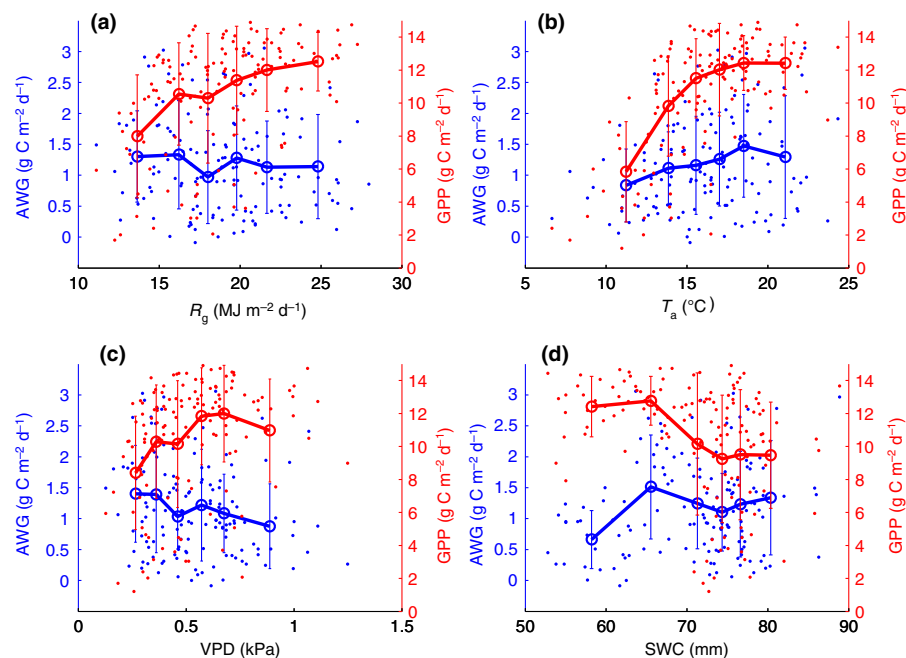
Fig. 4 Environmental dependences of gross primary productivity (GPP) and aboveground wood growth (AWG). The dependences were established on data measured (AWG) or averaged (GPP and environmental variables) at a weekly time-scale (dots). Data used for this graph were sampled each year between the observed date of oak budburst (day of the year (DoY) 106 on average) and the date of first growth halt (DoY 213 on average). For clarity, data have been averaged into bins of equal sample sizes (bold lines). Within-bin SDs appear as vertical lines. Environmental dependences were established with (a) global radiation (R_g, 300–3000 nm), (b) air temperature (T_a), (c) vapour pressure deficit (VPD) and (d) soil water content (SWC, 0–30 cm).
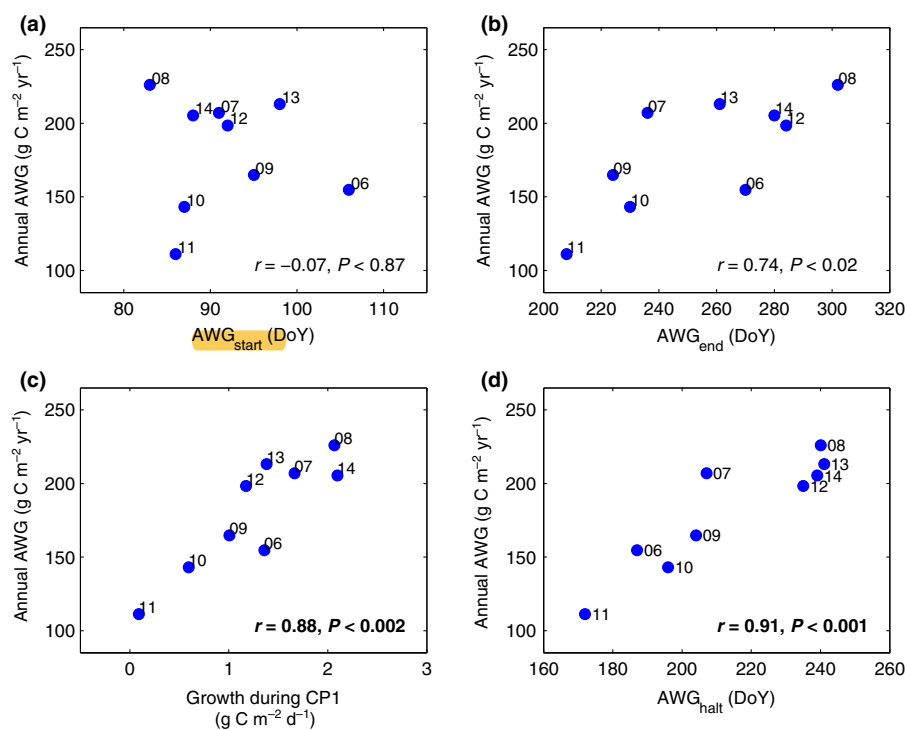
Fig. 5 Dependence of annual wood increment on particular phases of wood formation at the Fontainebleau-Barbeau (FR-Fon) oak forest. Annual aboveground wood growth (AWG) was correlated with wood phenology ((a) start and (b) end of wood growth, (d) date of first growth halt) and (c) the intensity of growth during critical period 1 CP1). See the Materials and Methods section for details. Correlations with variables selected by the stepwise linear model are given in bold type. Particular years appear as numbers (e.g. 2006 = '06').

simple water stress model, defined as the integral of SWC below a threshold, predicted 80% of the interannual variations in AWG$_{halt}$ (Notes S1).

The year-to-year variations in growth during CP1 showed no dependence on GPP (Fig. 7a), whatever the time frame considered, but were partially correlated with early-season NEP (Fig. 7b). The strongest (negative) correlations of growth during CP1 were observed with VPD (Fig. 7c). Similarly, strong positive correlations were observed with SWC (Fig. 7d). Partial correlation plots did not help to disentangle the influences of VPD and

SWC, as correlations of growth during CP1 with VPD (or SWC) vanished when SWC (or VPD) was held constant (Fig. S4).

Discussion

Interannual variability of the C balance (fluxes and biomass production)

Aboveground wood growth accounted for $11 \pm 3\%$ of annual GPP and $37 \pm 10\%$ of annual NEP ($10 \pm 2\%$ and $32 \pm 8\%$,

Fig. 6 Dependence of the first date of growth halt on environmental variables. The annual first date of growth halt (AWG$_{halt}$) was correlated with the environmental variables (a) soil water content (SWC, measured at 0–30 cm) and (b) vapour pressure deficit (VPD) averaged throughout the growing season. The x-axis indicates the start of the averaging interval. The y-axis indicates the length of the averaging interval. For clarity, only the significant ($P < 0.05$) positive (red) or negative (blue) correlations are reported. Green denotes non-significant ($P > 0.05$) correlations. DoY, day of year.
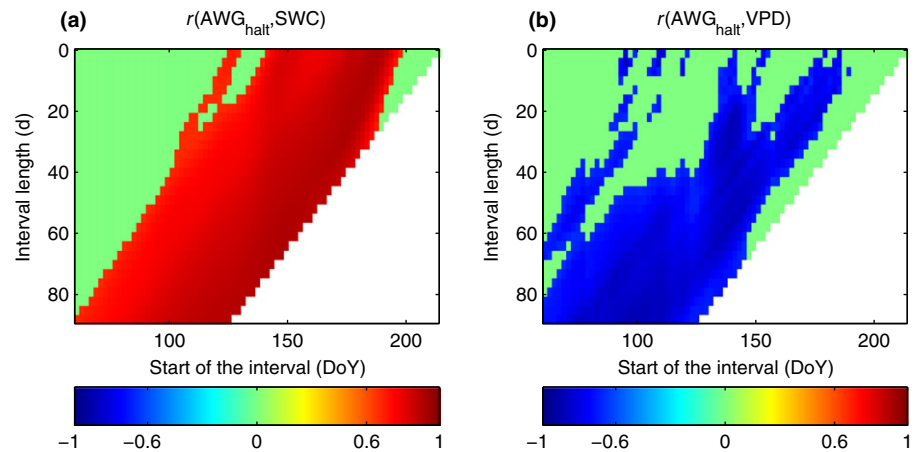
respectively, if considering only the oak component of the forest growth), in line with observations at other forest sites (Babst *et al.*, 2014). A simple C balance analysis (not shown) revealed that the C inputs and growth components were compatible, although the annual values of GPP (1880 ± 130 g C m^{-2} yr^{-1}) appeared in the high range of reported values for temperate deciduous forests (Luyssaert *et al.*, 2007), comparable with those observed in other temperate oak forests (from 1790 to 2110 g C m^{-2} yr^{-1} in Kutsch *et al.*, 2005; Thomas *et al.*, 2011; Wilkinson *et al.*, 2012).

Direct biomass measurements have demonstrated that sound estimates of AWG at the annual scale can be obtained through the combination of TRW and wood density data (Bouriaud *et al.*, 2005). As our aim was to investigate the biomass increment at the seasonal scale, we used dendrometer data as proxies of wood growth. Comparisons made with independent TRW measurements at the same site showed that the annual radius increment calculated from dendrometer and TRW data matched reasonably well ($r = 0.93$, $P < 0.001$). It should be noted that annual TRW and wood density were positively correlated at our site ($r = 0.51$), as already reported in other European deciduous broadleaf forests (Babst *et al.*, 2014). Such positive correlations are common in sessile oak (Zhang *et al.*, 1993), as an increase in growth is associated with a higher proportion of latewood, characterized by having a greater fibre area and whose vessels have reduced lumina compared with earlywood (Tsoumis, 1991; Feuillat *et al.*, 1997). Positive correlations between TRW and wood density tended to amplify AWG fluctuations inferred from dendrometer measurements alone, with the wood density variation responsible for *c.* 30% of the interannual variability of the calculated AWG (whereas the basal area increment explained 60%, not shown).

To our knowledge, this study is the first to evaluate the combined influences of radial growth (through dendrometer measurements) and seasonally resolved wood density on the seasonal variability of wood growth. As a result of the lack of information allowing for separation between volume and mass increments, we assumed that wood was formed immediately in its final state, considering wall thickening to occur instantly (i.e. for a given position in the tree ring, wood density was considered to be

constant over time, Eqn 1). To evaluate this assumption, micro-core data, which are still rare (but see Michelot *et al.*, 2012b), should be used. Indeed, to our knowledge, no study has precisely documented the seasonal or interannual (if any) variability of tissue maturation time in Angiosperms (but see Cuny *et al.*, 2015, for conifers), which could further modify the reconstructed growth patterns. Preliminary analyses revealed that the overall pattern of wood biomass increment showed a lag of *c.* 1 month when using the duration of wood maturation observed for conifers in the calculation of AWG (Fig. S5).

Aboveground wood growth is not correlated with C inputs

The annual AWG was not correlated with C inputs integrated at the annual scale at the study site (Fig. 2). This result is in line with observations in other forest ecosystems (Table 1), and questions the dependence of growth on C inputs. Although wood is the main plant biomass stock in mature forests, its annual increment is of the same order of magnitude as other biomass compartments (which are not perennial: e.g. leaves, fruits; Fig. 1). None of the growth components measured at FR-Fon (namely wood, leaf and fruit compartments) were correlated with the measured C inputs, nor was the sum of all measured growth components (not shown). The decoupling between the interannual variability of total growth and C inputs observed in this study may be attributable to the differential increments of non-measured living C stocks (i.e. roots, reserves, fine-root exudates) and non-living C stocks (soil organic matter).

There is increasing evidence that non-structural C compounds act as a labile C store to which a significant part of the photosynthates is allocated before any inclusion into structural tissues (Gough *et al.*, 2009). The allocation of photosynthates to labile C stores has been shown, for instance, to explain the 1-yr lag correlation between annual C inputs and wood growth in a boreal–northern hardwood transition forest (Richardson *et al.*, 2013). Interestingly, such a lagged correlation was not observed at FR-Fon for any of the considered compartments. It is difficult to draw conclusions in the absence of concurrent measurements of quantitatively
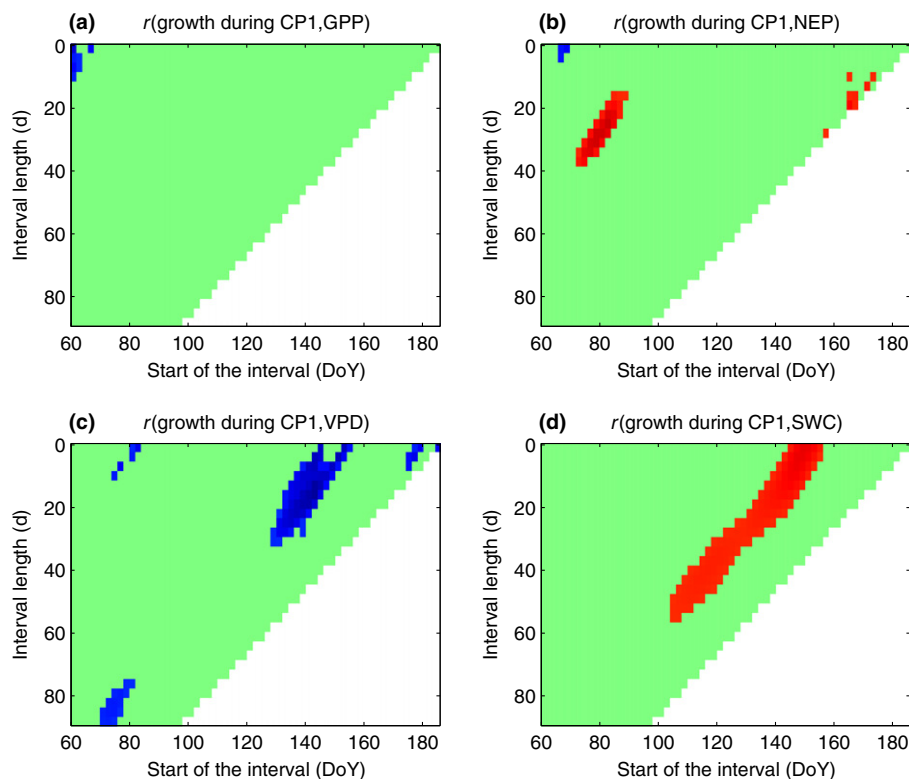
Fig. 7 Dependence of growth during critical period 1 on environmental variables. The intensity of growth during critical period 1 (growth during CP1) was correlated with carbon (C) inputs (a, gross primary productivity, GPP; b, net ecosystem productivity, NEP) and environmental variables (c, vapour pressure deficit, VPD; d, soil water content, SWC, measured at 0–30 cm) averaged throughout the growing season. The x-axis indicates the start of the averaging interval. The y-axis indicates the length of the averaging interval. For clarity, only the significant ($P < 0.05$) positive (red) or negative (blue) correlations are reported. Green denotes non-significant ($P > 0.05$) correlations. DoY, day of year.

important pools, such as roots and non-structural C. Yet, the absence of a lagged correlation between C inputs and growth indicates that the determinism of the growth processes is complex at the study site, with different compartments showing annual growth partly independent from other compartments.

Despite the lack of correlation of the annual integrals of GPP and AWG, we observed positive correlations between the seasonal patterns of C inputs (GPP or NEP) and AWG (Table 2). This result is trivial, considering that the processes governing the seasonality of C inputs (canopy development and the maturation of photosynthetic tissues) and wood growth (cambium divisions and xylem maturation) are synchronized overall, being temperature limited in the temperate zone (Delpierre *et al.*, 2015). Interestingly, these C input–wood growth correlations vanished when anomalies to the seasonal pattern were considered (i.e. when the average seasonal pattern was subtracted from the time series), indicating that deviations from the seasonal pattern of C inputs do not yield similar deviations of wood growth. This result indicates that, even at the seasonal scale, the allocation to wood growth in a given year was at least partly independent from the C inputs.

The seasonal patterns of wood growth and GPP are partly decoupled

Detailed attention paid to the seasonal patterns of C inputs and wood growth revealed that, although both seasonal patterns are in phase overall, they display clear particularities. In our data, the timing of oak AWG resumption appeared to be concomitant with the timing of spring GPP resumption (Fig. 3). GPP resumption was not caused by oak leafout (which occurred 10 d later), but by that of hornbeam. Thus, the coincident timing of GPP resumption and AWG is not a cause–effect response, being oak growth dependent on reserves before leafout (Bréda & Granier, 1996; Barbaroux & Bréda, 2002).

Our estimate of seasonal oak AWG peaked on DoY 163, 1 wk earlier than GPP (DoY 171). The peak of GPP was coincident with the summer solstice, characterized by the longest photoperiod and strongest incoming radiation, as observed in other temperate forests (Falge *et al.*, 2002; Wilkinson *et al.*, 2012). Again, to be able to confirm this shift in the timing of AWG, as compared with GPP, there is a need to better characterize the cellular timing of wood formation in oak trees. Most of the existing results concern conifers and document a peak in xylem cell production around the summer solstice (Cuny *et al.*, 2012). Information is scarcer for deciduous trees, but a study conducted in *Quercus petraea* reported a peak in the production of xylem cells (for year 2007, characterized by a particularly advanced timing of spring; Delpierre *et al.*, 2009) in April–May (Gričar, 2010). Wood growth cessation (AWG$_{end}$) occurred, on average, in early September (DoY 255), *c.* 2 months earlier than GPP reached zero, and *c.* 40 d before the forest turned to a C source (DoY 293, not shown). After wood growth ceased, C inputs were probably used for fruit development (data not shown), root growth (Teskey & Hinckley, 1981) and replenishment of C and nitrogen reserves (Bazot *et al.*, 2013; Gilson *et al.*, 2014), as typically observed in temperate forests (Barbaroux & Bréda, 2002).

Water stress determines the interannual variability of wood growth in a mesic temperate forest

Our results demonstrate that the variability of C inputs is not a key determinant of the variability of wood growth at the study temperate oak forest, whatever the time-scale considered. We evidenced that the interannual variations in AWG were strongly conditioned by the timing of first growth halt (AWG$_{halt}$, occurring, on average, on DoY 213, early August) and the intensity of growth during the first 'critical period' of the wood growing season, identified to occur just after the peak of wood growth (CP1, centred on DoY 179, end of June) (Fig. 5). A later occurrence of AWG$_{halt}$ or higher growth during CP1 was associated with a higher annual wood growth. This study thus confirms the key role of the duration of the wood growing period, and particularly the timing of growth cessation, in determining the annual wood growth (Brzostek *et al.*, 2014; Lempereur *et al.*, 2015). At our mesic study site, the intensity of growth during CP1 further explained a large part of AWG, echoing the results of Bréda & Granier (1996), who identified early season (DoY 100–200) growth as a good predictor of annual circumference increment in sessile oak.

The timing of AWG$_{halt}$ was strongly correlated with the seasonal average of SWC (integrated over 0–30 or 0–60 cm). We were not able to identify a unique SWC threshold below which wood growth would stop, contrary to reports for a Mediterranean oak species (*Quercus ilex*; Lempereur *et al.*, 2015) or for European beech (Mund *et al.*, 2010). An earlier study (Bréda *et al.*, 1995) has reported no simple relation between growth cessation and the amount of soil extractable water in *Quercus petraea*. Beyond methodological differences (e.g. relative to Lempereur *et al.*, 2015, who used predawn leaf water potential for the assessment of tree water status), it is likely that the dynamic response of trees to drought differs among species and climatic conditions. Temperate oak forests are, for instance, composed of large trees relative to Mediterranean oak forests, with larger internal water reservoirs which may buffer the impact of soil drying.

Contrasting with the clear dependence of the timing of growth halt on SWC, we found several drivers of the interannual variations in growth during CP1. These included both indicators of the tension in the hydraulic path (i.e. VPD was negatively correlated and SWC was positively correlated, Fig. 7) and early-season C inputs (positive correlation with NEP, Fig. 7). These results echo those of Granier *et al.* (2008), who observed, in a beech stand, a close correspondence of the early-season increment of NEP and wood growth.

It was not possible to identify from dendrometer data which cellular aspects of wood formation were associated with the occurrence of CP1 (centred on DoY 179) and AWG$_{halt}$ (centred on DoY 213), which we identified as the key phases for the determination of the interannual variability of AWG. The transition from earlywood to latewood probably occurs at *c.* DoY 140 at the study site (data not shown). Hence, the key phases most probably modulated the formation of latewood, with cambial cell division typically ending in mid-August (DoY 228) and the

ending of cell maturation occurring by the end of September (DoY 273) in sessile oak (Gričar, 2010).

Interestingly, we observed no influence of the date of AWG$_{start}$ on the interannual variations in AWG. The influence of mid- and late-season growth on the interannual variations in AWG contrasted with the observations for GPP, for which spring was the period determining most of the interannual variations (Fig. 3b; see also Delpierre *et al.*, 2009). This result contrasts with observations in other European forests, for which summer fluxes have been identified to drive most of the interannual variability of GPP (Le Maire *et al.*, 2010). It is likely that part of the difference stems from the periods studied, including (Le Maire *et al.*, 2010) or not (this work) the record-breaking 2003 summer heatwave and drought (see Delpierre *et al.*, 2012).

GPP and growth respond to distinct environmental controls during the growing season

Weekly estimates of wood growth and GPP showed distinct environmental controls within the growing season (Fig. 4). GPP displayed clear dependences on temperature and radiation, but was fairly insensitive to variations in the atmospheric (VPD) or edaphic (SWC) water constraints. Wood growth, however, was partially dependent on temperature (as observed, for example, in *Quercus ilex*, Lempereur *et al.*, 2015), and seemed to be especially sensitive to tensions on the hydraulic path. In particular, we found a notable dependence on SWC, characterized by a strong reduction in growth observed under a 65-mm water threshold (over 30 cm soil), equivalent to *c.* 50% of the relative extractable water for this soil depth, and a negative dependence on increasing VPD. The results presented here were obtained with smoothed band dendrometer data, corrected, at least partially, for the influence of shrinkage (Hinckley & Lassoie, 1981; Zweifel *et al.*, 2005). Hence, we are confident that the observed response to VPD illustrates a dependence of growth processes (possibly cell elongation, which is more sensitive than cell division to a decrease in turgor potential, Hsiao *et al.*, 1976) on the gradual increase in the water column tension caused by a combination of increasing VPD and lower SWC.

Generic nature of the observed response of sessile oak growth to water stress

Sessile oak usually shows a positive dependence of its ring width on precipitation, even in mesic climatic conditions (Barbaroux, 2002; Mérian *et al.*, 2011; Michelot *et al.*, 2012a). Interestingly, we observed such a positive dependence of TRW on precipitation, which is mostly conserved over time, notably for spring (March–May) precipitation events (Fig. 8). The key phases of wood growth explaining annual AWG at the study site are centred on late June (CP1, DoY 179) and early August (AWG$_{halt}$, DoY 213, Fig. 5), but clearly respond to variations in spring and summer water balance (Figs 6, 7), which are partly driven by spring precipitation events. It is therefore possible that the dependence of oak growth on key phases evidenced over the 2006–2014 period is a general feature, having driven growth over the
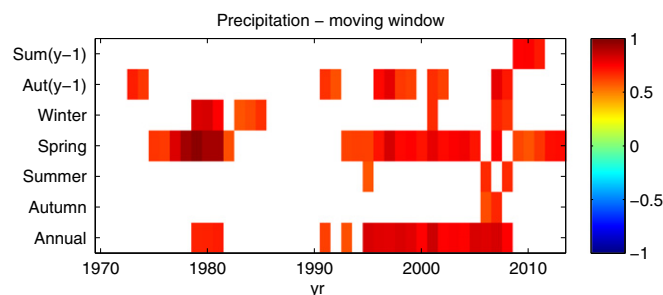
Fig. 8 Dendroclimatic analysis of the Fontainebleau-Barbeau (FR-Fon) oak stand. Correlations were established between seasonal precipitation (*y*-axis; winter, December–February; spring, March–May; summer (sum), June–August; autumn (aut), September–November) and the average tree ring width (TRW) of 10 dominant and co-dominant trees, over 10-yr moving windows, for the 1961–2013 period. The end year of the analysed interval appears on the *x*-axis. Colour, significant (*P* < 0.10) Pearson's correlation coefficient. White, non-significant correlations.

past decades at the study site (Fig. 8), and worth investigating at other temperate forests.

Conclusions and perspectives

This article demonstrates that wood growth and ecosystem C inputs display distinct seasonal patterns under mesic climatic conditions, where multiple environmental drivers may sequentially limit C acquisition and allocation. It reinforces the view that wood growth does not necessarily depend on C inputs at an annual scale, and that an anomaly of the seasonal pattern of C input does not systematically translate into an anomaly of wood growth.

In addition to regional studies aimed at the investigation of the broad determinants of continental-scale gradients of growth (Litton *et al.*, 2007; Vicca *et al.*, 2012), there is clearly a need for a better characterization of the seasonal patterns of allocation to organ growth in forest ecosystems, and for a more systematic comparison of seasonal tree growth patterns with C flux data. Although there is increasing evidence that C inputs and allocation are at least partially decoupled in forest ecosystems, we still have a limited understanding of the determinants of organ growth phenology (Delpierre *et al.*, 2015) and of the seasonal dynamics of C allocation (Lempereur *et al.*, 2015; this work).

Our work is a first attempt to identify and understand the environmental and C-related determinants of key periods in the process of wood growth. The next step is to describe more precisely the seasonality of processes (cambium division, xylem enlargement and maturation) underlying the observed dynamics of wood growth, and to quantify the associated C investments. More than measuring a circumference increment or, at best, a number of cells at different states of differentiation (Rossi *et al.*, 2009; Michelot *et al.*, 2012b), we require an assessment of both the radial increment and the seasonal evolution of the density of new tissues (Cuny *et al.*, 2015). A continuous monitoring of wood tissue formation (e.g. image analysis of microcore samples) over several contrasted growing seasons is key to advancing our understanding of both the dynamics and determinants of wood formation.

Such information is crucial for the implementation of more realistic representations of growth and C allocation in process-based models of forest functioning (Guillemot *et al.*, 2015; Schiestl-Aalto *et al.*, 2015), and to be able to represent the proper dynamics of C acquisition and C allocation in forests under global change.

Author contributions

N.D. and E.D. designed the research and analysed the data. D.B., N.D. and E.D. collected and prepared the data. N.D. and E.G. wrote the manuscript, with inputs from D.B. and E.D.

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Supporting Information

Additional supporting information may be found in the online version of this article.

Fig. S1 Monthly means of temperature and precipitation at the Fontainebleau-Barbeau (FR-Fon) temperate oak forest.

Fig. S2 The interannual variability of wood growth does not depend on seasonal carbon (C) inputs.

Fig. S3 Partial correlation plot for the dependence of the date of growth halt (AWG_{halt}) on environmental variables.

Fig. S4 Partial correlation plot for the dependence of growth during critical period 1 (CP1) on environmental variables.

Fig. S5 Influence of wood maturation time on the seasonal pattern of wood growth.

Notes S1 Modelling wood phenology.

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