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Seasonal time-course of the above ground biomass production efficiency in beech trees (Fagus sylvatica L.)

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Abstract

· *Key message* In order to record the seasonal changes in aboveground biomass production (trunk and branches) in a forest, changes in wood density must be taken into account. A 60-year-old beech forest displayed a large intra-annual variability in its aboveground woody biomass production efficiency. This variation followed a seasonal trend with a maximum during the summer while gross primary production was rather low.
· *Context* In the current context of land use and climate change, there is a need to precisely quantify the carbon (C) balance of forest ecosystems, and more specifically, of C allocation to tree compartments.
· *Aims* We quantified the seasonal changes in the aboveground biomass production (aBP) of a beech forest growing on two different soils: an alocrisol and a calci-brunisol. In addition, for the alocrisol ecosystem, we assessed the existence and degree of intra-annual variability in the ratio of wood aBP to gross primary production (GPP), i.e., the wood aBP efficiency.

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Contribution of the co-authors
Laura Heid: running field work and data analysis, writing the correct the typo in paperChristophe Calvaruso: providing the biomass production equations and growth dataset, reviewing the manuscript
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Sébastien Conil: manager of the experimental site, supervising the study, reviewing the manuscript
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Bernard Longdoz: initiating the project, designing the experiment, supervising the work, coordinating the research project, reviewing the manuscript

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This article is part of the topical collection on *Estimation of standing forest biomass*

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• **Methods** The study site is a 60-year-old beech forest in northeastern France. An eddy covariance tower records continuously net ecosystem exchange. To investigate the temporal changes in aBP, mini-cores were drilled and diameter at breast height measurements were taken on a monthly basis from 45 trees for both stands studied over 2014.

• **Results** A clear difference in aBP was observed between the two soils with the alocrisol being more productive than the calcibrunisol. For the alocrisol, both woody aBP and GPP changed over the course of the year, reaching peak values during June (6 and 12.5 gC m^{-2} day^{-1}, respectively). Wood applied bias photon-to-current efficiency aboveground Biomass Production Efficiency (aBPE) also showed important intra-annual variations, ranging from 0.09 in September to 0.58 in July. Wood density varied throughout the year, and not taking it into account would have led to an overestimation of aBP by as much as 20% in April and May.

• **Conclusion** Our study highlights the importance of taking wood density into account for intra-annual studies of aBP. Wood aBPE cannot be considered as constant as it fluctuated from 0.09 to 0.58 throughout the year for an annual value of 0.34. The potential error in wood aBPE stemming from not taking these changes into account amounts to 15%.

1 Introduction

As ecosystem management evolves in the context of climate change, understanding and quantifying terrestrial ecosystem carbon (C) sequestration as well as the growth and maintenance of ecosystem services have become major research goals. Climate change is linked to increasing concentrations of greenhouse gases in the atmosphere (IPCC 2013), with carbon dioxide (CO_2) being one of the most important (Cox et al. 2000). CO_2 concentrations have increased by 2.0 ppm per year since the 1980s, and have now reached 399.4 ± 0.1 ppm (Quéré et al. 2016). That is why long-term CO_2 mitigation is such an important issue, inspiring research focused on CO_2 exchange between the atmosphere and the terrestrial environment, and on carbon allocation and its more or less long-term storage in ecosystem (Trumbore 2006).

In the carbon cycle, gross primary production (GPP) is the difference between production by photosynthesis and release by photorespiration. The net ecosystem exchange (NEE) is the sum of the carbon absorbed via photosynthetic processes (GPP) and the carbon released into the atmosphere through plant dark respiration and soil organic matter decomposition (hereafter Reco).The CO_2 budget of an ecosystem is equivalent to the NEE when dissolved CO_2 escaping in the runoff water is negligible. This is typically the case in beech ecosystems of northeastern France (Kindler et al. 2011).

In assessing how the ecosystem uses absorbed C, another important term is "carbon use efficiency" (CUE), which is defined as the net primary production (NPP) to GPP ratio (Gifford 2003; DeLucia et al. 2007). NPP is not easy to record, since it is the sum of aboveground biomass production (which can be obtained from repeated inventories), belowground biomass increment, mycorrhizal fungus productions, root exudates, and the emission of volatile organic compounds. These last three types of C release can account for an NPP between 2 and 50% (Kesselmeier et al. 2002) and are difficult to measure or estimate. Consequently, many studies use biomass production (BP, gC m^{-2}), which is available through

direct measurements in the field, as a proxy for NPP when estimating CUE (Gifford 2003; Drake et al. 2011; Goulden et al. 2011). Then, to avoid misinterpretation, Vicca et al. (2012) introduced a new term, "biomass production efficiency" (BPE), defined as the ratio between BP and GPP for a given ecosystem. Biomass production includes all the biomass produced during the year (aboveground and belowground, including litter), so BPE represents the fraction of the absorbed C dedicated to the elaboration of organic biomass. At the annual scale, BPE depends on different factors. According to Vicca et al. (2012), the availability of nutrients seems to positively impact BPE. The management regime applied to the ecosystem (Campioli et al. 2011, 2015) can also influence BPE through its impact on nutrient availability. BPE can also vary with species, as shown by Ryan et al. (1997); indeed, in their study on plots with two different climate conditions and hosting different species, they highlighted that BPE differed significantly among species, never between sites. In addition, different types of ecosystems have different BPEs; for example, crops usually have a higher BPE (Aubinet et al. 2001) than forests (Malhi et al. 1999; Granier et al. 2000; Vicca et al. 2012; Wu et al. 2013) or grasslands (Ammann et al. 2007; Klumpp et al. 2007). The share of GPP allocated aboveground or belowground varies depending on atmospheric CO_2 concentrations (Matamala et al. 2003, and demonstrated in CO_2 fertilization experiments; Norby and Zak 2011) and on nutrient availability (Sheriff et al. 1986; Giardina et al. 2003).

Annual BPE in forest ecosystems has been investigated, and a model simulating inter-annual growth exists for coniferous forests (Schiestl-Aalto et al. 2015). We still need more knowledge on a larger number of species in order to get a better and larger spatial representativeness. When the intra-annual dynamics of forest BP are investigated, it is important to take into account the time lag between biomass production and radial growth. This lag is due to the increase in wood

density during the growing season (Cuny et al. 2015; Rathgeber et al. 2016), which calls into question calculating BPE with BP values estimated from radial growth only. Furthermore, little is known about the impact of soil type, species, or climate on intra-annual BPE variations (Steppe et al. 2015), and this reflects remaining uncertainties in the models used to predict the spatial variability and the dynamics of C allocation (Campioli et al. 2013).

The aims of this study were, firstly, to obtain a better understanding of intra-annual carbon allocation in a temperate beech forest by quantifying wood aboveground biomass production efficiency (aBPE) from GPP and actual aboveground tree carbon sequestration, which was estimated from volume increment, wood density, and changes in C concentration. In particular, we wanted to examine the seasonal time course in wood aBPE. To date, tree wood production calculated from volume increase (Granier et al. 2008) assumed a fixed density (Delpierre et al. 2016). However, Rathgeber et al. (2016) have assessed different stages in annual ring formation which leads to variations in wood density during the year: the creation of new cells, the enlargement of those cells, deposition of the secondary cell wall, lignification, and lastly, cellular death.

In this paper, we aimed to check whether keeping a constant C allocation throughout the year is an acceptable hypothesis. We also aimed at identifying the factors that contribute to seasonal fluctuations of wood aBP, and particularly at quantifying the contribution of intra-annual variations in wood density. We also wanted to know whether the intra-annual variation in wood density had an impact on the wood aBP seasonal time course in beech trees.

This study also provided us with an opportunity to compare the wood aBP for two beech stands under the same climatic conditions but on two different soils.

In order to answer those questions, we recorded GPP, wood density, and aBP at a monthly time scale in two beech stands from northeastern France. Two forest stands located in northeastern France.

2 Material and methods

2.1 Study site

The study site is located in the state forest of Montiers-sur-Saulx ("Montiers") (48° 32′ 11.85″ N–5° 18′ 48.96″ E, Lorraine, northeastern France), managed by the French National Forest Office (ONF). The stand is even-aged (60 years old) and composed mainly of beech (*Fagus sylvatica* L.; 88% of the stems, with diameter at breast height (DBH) classes and dominance classes similar for the other species). The accompanying tree species are sycamore maple (*Acer pseudoplatanus* L.) and hornbeam (*Carpinus betulus*

L.); understory vegetation is scarce. Average tree height is 25 m, density is about 800 stems/ha, and leaf area index (LAI) is 9. The last thinning occurred in 2010.

The forest is located on a 133-ha topo-sequence, with three main soil types (alocrisol, calci-brunisol, and rendisol, RP 2008 denomination). aBP was estimated for two of these soil types (alocrisol and calci-brunisol), and, because of the eddy covariance footprint (described below), only one (alocrisol) was found to be of interest for our study of aBPE. The characteristics of both stand are described in Table 1 (a). One-hectare study plots were set up on both soils where the regular inventories were performed. The alocrisol stand (S1) included 703 trees (64 dominant, 141 co-dominant, 232 intermediate, and 263 suppressed), and the calci-brunisol stand (S2) included 739 trees (61 dominant, 87 co-dominant, 263 intermediate, and 328 suppressed).

The climate is oceanic temperate with total annual precipitation of 1085 mm and a mean annual temperature (MAT) of 9.6 °C average over the period 1980–2015 (5 °C minimum and 14.1 °C maximum, MAT, Météo, France).

2.2 Eddy covariance and meteorological measurement

2.2.1 Experimental setup

The main piece of equipment at the forest site is a flux tower (45 m height) set up at the end of 2012 bearing an eddy covariance (EC) system consisting of an enclosed infra-red CO_2/H_2O gas analyzer (IRGA, Li-7200, LI-COR, Lincoln, NE, USA) coupled with a 3D sonic anemometer (HS-50, Gill, Hampshire, UK). This system continuously measures CO_2 exchanges at 35 m in height (about 10 m above the forest canopy). The flux tower is also equipped with a system to estimate the amount of CO_2 stored in the air between the soil surface and the EC system. This second system measures CO_2 at different heights along the tower (5, 10, 15, 25, 35 m) making it possible to calculate CO_2 accumulation or absorption (positive or negative values) in and below the forest canopy (storage flux, F_{sc}) as described in Aubinet et al. (2001).

Supporting meteorological instrumentation includes a vertical atmospheric profile system with six probes to measure air temperature and relative humidity (HMP155, Vaisala, Vantaa, Finland) and six 2D sonic anemometers (WindObserver 2, Gill, Hampshire, UK) at 5, 10, 15, 25, 35, and 45 m along the tower; a pyranometer for global radiation (CMP21, Kipp & Zonen, Delft, Netherlands); a direct/diffuse photosynthetically active radiation (PAR) sensor (BF5, Delta-T Devices Ltd., Cambridge, England) and a net radiometer to measure incident and reflected/emitted components of shortwave (SW) and longwave (LW) radiation (CNR4, Kipp & Zonen, Delft, Netherlands). All the radiation sensors are installed at the top

Table 1   Panel a: soil characteristics for the alocrisol and the calci-brunisol. Panel b: annual CO_2 fluxes, annual wood aboveground biomass production (aBP) in gC per square meter per year and annual wood aboveground biomass production efficiency (aBPE) for the alocrisol and the calci-brunisol and values found for similar ecosystems in the literature

	Alocrisol	Calci-brunisol				
Panel a						
pH	< 5	5.2–5.4				
Depth (m)	> 1	< 1				
CEC (cmol kg^{-1})	3.5–6.7	7.6–17.2				
Clay (%)	25–35	58				
Panel b						
Authors	Forest type	NEE (gC m^{-2} year^{-1})	Reco	GPP	Wood aBP	Wood aBPE
This study (alocrisol)	Temperate deciduous	− 549	1089	− 1639	555.0 ± 26.9	0.34
This study Calci-brunisol	Temperate deciduous	/	/	/	416.3 ± 26.3	/
Malhi et al. 1999	Temperate deciduous	− 584	1141	− 1725	189	0.11
Barford et al. 2001	Temperate deciduous and evergreen	− 200	1100	− 1300	140	0.11
Wu et al. 2013	Temperate deciduous	− 277	1624	− 1881	261	0.14
Vicca et al. 2012	Temperate	/	/	− 1320	227	0.43
Vicca et al. 2012	Temperate	/	/	− 1328	361	0.50
Vicca et al. 2012	Temperate	/	/	− 1724	677	0.58

of the tower. A phenological camera (StarDot NetCam SC5) is installed at 35 m in height.

2.2.2 Flux and meteorological data processing

Half-hourly NEE values correspond to the sum of CO_2 flux (F_c, measured by the EC system) and storage flux (F_{sc}, measured by the CO_2 profile system). Divergence from normal CO_2 horizontal advection values (F_a) was excluded since the half hours for which it was significant could not be taken into account because of the u* threshold selection (see below). F_c values are obtained by post-processing the EC system data with the EddyFlux software (EddySoft, Meteotools, MPI, Jena) following the recommendations by Aubinet et al. (1999). The 2D rotation option was selected, as suggested by Finnigan (2004) and Rebmann et al. (2012), and no corrections for high-frequency loss were applied since the air sampling in the LI-7200 is so short (Burba et al. 2012). In addition, LI-7200 does not require any post-treatment for air density variations since high-frequency pressure and temperature are both measured in the analyzer and used online to determine the mixing ratio measurements (Burba et al. 2012).

Data quality control was carried out as follows: (i) aberrant values corresponding to technical problems and inappropriate measurement conditions (liquid water disturbing IRGA or anemometer functioning) were removed; (ii) half hours with a u* below the threshold (0.35 m s^{-1} on our site, determined following the procedure presented in Longdoz et al. (2008)) were not accepted, thus eliminating periods without enough eddies;

and (iii) data corresponding to inappropriate atmospheric conditions for EC (i.e., atmospheric stability or data not fulfilling the integral turbulence characteristic (ITC) test (Beziat 2009)) were rejected. Unaccepted and missing (failure, maintenance) data were then gap-filled with values computed following the procedure in Falge et al. (2001a, 2001b). The resulting NEE was then partitioned between GPP and Reco for the leafy period following Reichstein et al. (2005), as no GPP occurs during the leafless period and was therefore set at 0 during this period. The dates of the beginning and end of the growing period were set by simultaneously following changes in NEE and observing leaf development on the pictures taken three times a day by a camera placed at the top of the tower (phenocam; StarDot NetCam SC 5MP). For 2014, the starting date (budburst) was 10 April, complete development 5 May, and ending date 15 November. GPP and Reco were partitioned by extrapolating Reco which is dependent on temperature, from night fluxes when |NEE$_{measured}$| = |Reco| and applying them to daytime situations (|GPP| = |NEE$_{measured}$| − |Reco$_{estimated}$|). Dependence of Reco on temperature (fitted over a 10-day interval) was preconized by Lloyd and Taylor (1994). We obtained Reco from the following regression equation:

$$Reco = Reco_{10} \times \exp\left(E_0 * \left(\frac{1}{T_{ref} - T_0} - \frac{1}{T - T_0} \right) \right) \quad (1)$$

where Reco$_{10}$ is ecosystem respiration at 10 °C (μmol m^{-2} s^{-1}), T is the soil temperature at 10 cm (°C), E_0 is the activation energy (308.56 kJ mol^{-1}), T_{ref} is the reference value (10 °C),

and T_0 is the activation temperature ($- 46.02$ °C).

Not accounting for soil water content (SWC) in the regression could lead to overestimating GPP; however, in our case, no water stress was observed during the study year (2014). Relative extractable soil water (REW), recorded during 2014, never declined below the 0.4 threshold below which water shortage effects begin (Granier et al. 2007).

2.3 Biomass

2.3.1 Instrumentation and sampling campaigns

Monitoring aboveground tree wood biomass implies quantifying wood volume increment and temporal changes in wood carbon content and wood density. In our study, both instrumentation and sampling were designed to measure all these parameters. At each stand, 45 beech trees distributed across the DBH classes (9 in every DBH class shown in Fig. 1 for each stand) to accurately represent the total population were equipped with manually read dendrometers, to measure diameter at breast height (DBH) once every month during the growing season (6 May, 6 June, 1 July, 29 July, 26 August, 23 September, and 23 November).

To estimate the C content in trunk wood, some samples (980; seven mini-cores per tree and 35 trees for each of the 7 sampling campaigns) were taken from beech trees located outside of the station, using a Trephor® (Rossi et al. 2006), out of 14 tree trunks on the alocrisol and 21 trunks on the calci-brunisol. The sampled trees were representative of the healthy growing population (see Fig. 1 for the DBH distribution) on the two stands. For the alocrisol, this led to the selection of seven trees from the 13-to-28-cm DBH class plus seven trees with a DBH above 28 cm. For the calci-brunisol, in addition seven trees were selected from the 8-to-13-cm DBH class.

In addition to the mini-core sampling, every month from April to November 2014, several micro-cores (1.5–

2.0 cm long and 2 mm in diameter) were taken from 14 dominant (D > 88 cm) trees not used for the mini-cores (seven on each stand), in order to assess wood formation and density dynamics. Cores were taken with a Trephor® all around the stem, 10 cm away from each other (Rossi et al. 2006) (Fig. 2).

2.3.2 Processing samples and biochemical analysis

Each mini-core used for C content was placed in liquid nitrogen immediately after sampling and stored in a specific container. They were then stored at $- 80$ °C before being freeze-dried. The ring under formation was then cut away from each mini-cores and milled into a powder which was passed through an elemental analyzer (ThermoQuest) to determine C and N concentrations.

Monthly wood density was determined through an optical process carried out on the micro-cores following procedures described in Harroué et al. (2011) and Cuny et al. (2012). After sampling, the micro-cores were rapidly returned to the lab, and successively cleaned, dehydrated, and immersed in baths of ethanol, D-limonene, and paraffin (automatic tissue processor STP 121, MM, France). They were then embedded in paraffin blocks (Embedding Station EC 350, MM, France). Finally, thick transverse sections were sliced off (Rotary microtome HM 355S, MM, France), stained with cresyl violet acetate, and permanently mounted on glass slides with Histolaque LMR® for long-term observation. Wood density was then determined on those glass slides.

2.4 Biomass production and determining efficiency

2.4.1 Aboveground wood biomass production

aBP (gC m^{-2} day^{-1}) is the production of aerial wood (aBPw, trunk, and branches). aBPw was calculated as the sum of the individual values for all the sampled trees

Fig. 1 DBH distribution of 60-year-old beech trees on two sites: one on an alocrisol (dark bars) and one on a calci-brunisol (gray bars) located in northeastern France. On each stand 9 trees were selected for each DBH class and were used to get the monthly DBH growth
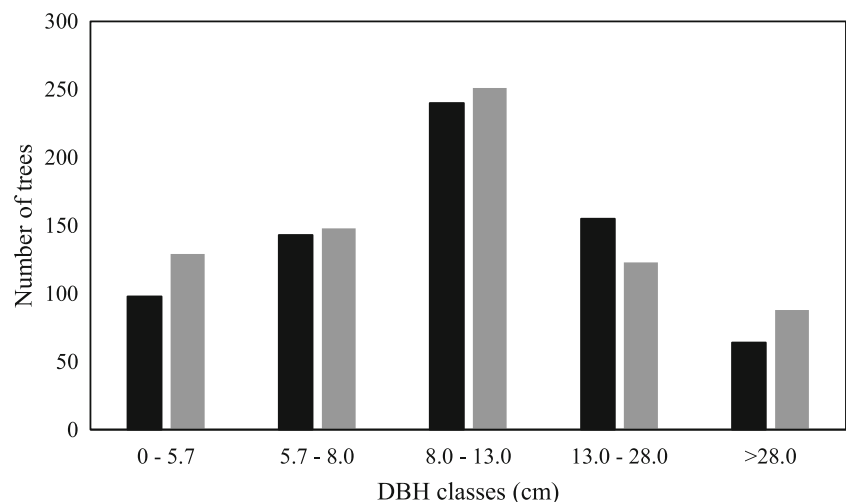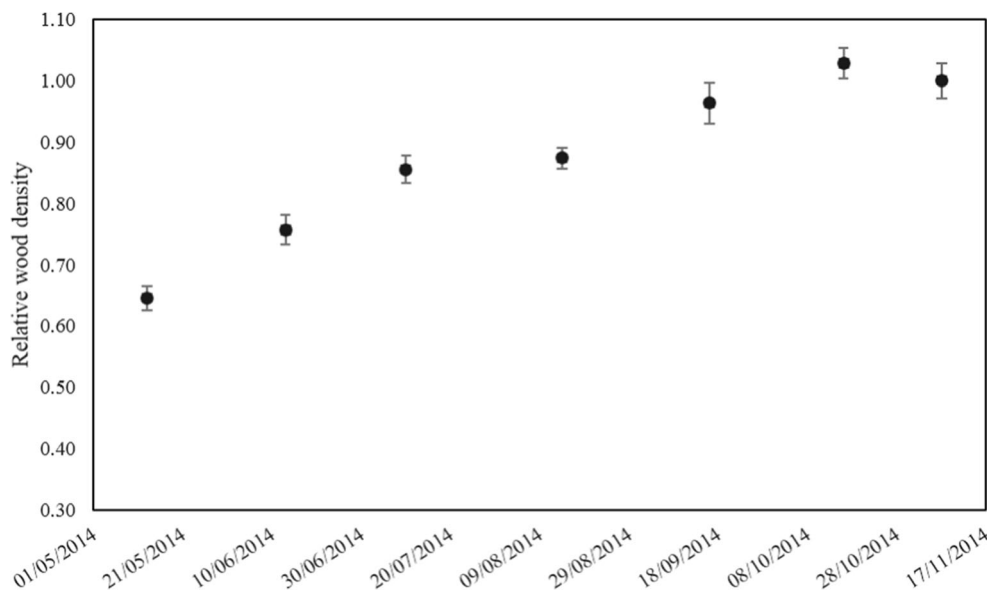
Fig. 2 Intra-annual changes in wood density in relative value to the one at the end of the year (wood density of 1)

at a station (aBPw$_i$) divided by the station surface area (S in m^{-2}):

$$aBP = aBPw = \frac{\sum_i (BPaw_i)}{S} \qquad (2)$$

where aBPw$_i$ is the difference between two successive estimations of aboveground tree woody carbon biomass (aBw in gC) divided by the number of days separating these estimations (every 4 weeks during the growing season). aBw was estimated according to the following equation:

$$aBw = DMaw * Caw \qquad (3)$$

where DMaw is the aerial wood dry matter (gDM) and Caw is the carbon concentration (gC gDM^{-1}).

One Caw value (Eq. 3) was deduced for each month and for each dominance class, by averaging the results of the carbon analysis over the seven samples per class (see above).

DMaw was determined by summing the dry biomass from each tree woody (i.e., excluding leaves) component:

$$DMaw = DMb_{0-4} + DMb_{4-7} + DMb_{7+} + Dmtb$$
$$+ DMw \qquad (4a)$$

with DMb$_{0-4}$, DMb$_{4-7}$, and DMb$_{7+}$ corresponding to branches with diameters of respectively 0–4, 4–7, and > 7 cm; DMtb corresponding to trunk bark; and DMw corresponding to trunk wood.

All dry biomass values were estimated separately by using allometric equations combined with a transformation from volume to dry biomass, and were specifically parameterized for the Montiers forest (Calvaruso et al. 2017).

$$DMb_{0-4} = R\rho_w \times \left(\left(22.3991 + 73.11603 \times e^{(-0.028536 \times age)} \right) \times D^2 H^{0.911918} \right) \qquad (4b)$$

$$DMb_{4-7} = R\rho_w \times \left((20.20171 - 0.089961 \times age) \times D^2 H^{1.534111} \right) \qquad (4c)$$

$$DMb_{7+} = R\rho_w \times \left(5.057486 \times D^2 H^{2.057768} \right) \qquad (4d)$$

$$DMtb = R\rho_w \times (11.641374 + 0.075737 \times age)$$
$$\times D^2 H^{0.877139} \qquad (4e)$$

$$DMw = R\rho_w \times \left(193.387145 - 112.401722 \times e^{(-0.048233 * age)} \right) * D^2 H^{0.97556} \qquad (4f)$$

where D is the diameter at breast height (DBH, m), age is the age of the tree (years), H is the tree height (m), and $R\rho_w$ is the relative wood density corresponding to the ratio of the wood density current value over the final value obtained when wood formation was finished. As in Calvaruso et al. (2017), the equations Eq. 4b–f were elaborated at the end of the growing season when $R\rho_w$ equaled 1.

For the age factor ("age" in Eq. 4), we used only one value per dominance status and per stand. This value was the mean estimated age for seven trees which were cut during a thinning operation at the end of the 2014 growing season and whose rings were counted on the stump.

The relative wood density $R\rho_w$ (Eq. 4) (one value per month and per station) corresponds to the relative optical density (ratio of current monthly value to final value when wood

formation is completed) measured on the additional trunk micro-cores.

D was measured with manual dendrometers every 4 weeks during the growing season on 45 trees (see Sect. 2) on each stand (90 trees in total). For the other trees (n = about 1600), D was measured with a diameter tape in November 2013 and November 2014, and a percentage of the annual increase was allocated to each month to obtain the monthly D estimate. These percentages were determined by status class (see below) rather than for each tree individually. The trees at each station were classified into three different dominance status classes (dominant/co-dominant, intermediate, and suppressed); the class-percentage values correspond to the average value for all the trees in the same status class as measured with the band dendrometers. The grouping strategy was based on classes having an average annual diameter growth that was significantly different (p value < 0.05).

Height H was assumed to be constant throughout the year and was assessed by measuring 230 trees in November 2013 with a Vertex telemeter. For the remaining trees (n = 1370) inside the measurement area, H was calculated via an allometric relationship (Eq. 5) fitted to the measurement date in November 2013 (Calvaruso et al. 2017).

$$H = 1.3 + (0.91*a + 2.3) \times \left(1 - \exp\left(-b*\frac{D \times \pi}{3.14159}\right)\right)^c \quad (5)$$

where a, b, and c are parameters estimated by regression for each stand and D corresponds to DBH at the start of the 2014 growing season.

2.4.2 Aboveground biomass production efficiency

Wood aboveground biomass production efficiency (wood aBPE) was calculated as the ratio of wood aBP on GPP (with all the variables in gC m^{-2} day^{-1} and integrated over a given period), as defined in Vicca et al. (2012). Wood aBPE was determined monthly with the monthly wood aBP values and the sum of daily GPP over the corresponding period.

In order to obtain the wood aBPE for the two different stands, the temporal changes representative of each soil type must first be estimated. We partitioned the eddy covariance fluxes between the two site areas, thanks to footprint analyses (see Sect. 2.5.2 below). Unfortunately, half-hour data showing a flux of more than 40% in the calci-brunisol ecosystem were relatively rare (less than 5% of the dataset). It was therefore not possible to extract any specific trend in GPP estimation for the calci-brunisol station. As a result, we only used GPP data representative of the alocrisol station and only characterized the alocrisol aBPE.

2.5 Data analysis

2.5.1 Statistical test

A linear regression model was used to determine if Reco depended on different factors (air temperature, soil relative extractable water (REW), global radiation, and GPP). The effects of mean air temperature and GPP were also tested. We used the same tool to test the relationship between GPP and global radiation, and the residuals of this relationship were then tested against vapor pressure deficit (VPD), air temperature, and REW. A statistical test was used to assess whether or not a distinction between the wood aBP at the two stations (on the two different stands) was necessary. As our wood aBP data did not follow a normal distribution, we chose a non-parametrical test (Kruskal-Wallis). The confidence interval were calculated as the standard deviation divided by the square roots of the number of samples.

All the data processing and analysis were carried out with the R 3.0.2 software (R Core Team 2013).

2.5.2 Footprint analysis

The Kljun et al. (2004) footprint model, high-frequency anemometer data, and the soil type map were all employed to determine the percentage of the CO_2 eddy covariance fluxes coming from the areas located on the alocrisol and calci-brunisol stands. This operation was repeated for each half-hour.

Data availability The datasets generated during and/or analyzed during the current study (corrected fluxes, aBP, and aBPE) are available from the corresponding author on request.

3 Results

3.1 Meteorological and flux data

The weather during 2014 was comparable in terms of air temperature and precipitation to the 1934–2015 average recorded at a weather station nearby (less than 40 km; Table 2). Air temperature dropped once (August 17) and peaked three times (9 June, 19 July, 8 September), and daily global radiation followed an usual distribution with three noticeable drops (5 May, 9 July, 12 August) (Fig. 3).

In 2014, the site presented a negative NEE of − 549 gC m^{-2}, which indicates that C was being stored in the ecosystem. Cumulated Reco amounted to 1089 gC m^{-2} and GPP to − 1639 gC m^{-2} (Table 1 (b)).

The leafy season began on 10 April, as assessed with the phenological camera, and ended on 15 November 2014. The curve representing cumulative GPP for the periods we

Table 2   Average mean annual temperature and precipitation for the 1934–2015 period and for the year 2014, measured at two French weather stations (Enerville-aux-Bois (a) and Biencourt-sur-Orge (b), Météo France) close to the Montiers site, in brackets are specified the year of occurrence

Climatic factors	Annual Mean		Absolute minimum		Absolute maximum	
	1934–2015	2014	1934–2015	2014	1934–2015	2014
Temperature (° C) (a)	9.6	10.9	− 24.2 (1956)	− 13.8	39 (2003)	33.4
Precipitation (mm) (b)	1085	1020	797	–	1351	–

included (most of the time for 28 days per period) is presented in Fig. 4b. GPP increases to a peak value of 12.9 gC m^{-2} day^{-1} in June 2014, after which it decreases until November.

3.2 Biomass

3.2.1 Annual biomass production

In 2014, the alocrisol ecosystem produced more biomass (22% in total aBP, 25% in wood BP) than the calci-brunisol ecosystem.

For the complete year 2014, the aboveground BP as determined from our inventory campaigns and allometric

relationships reached 652.27 gC m^{-2} at the alocrisol station (S1) and 514.15 gC m^{-2} at the calci-brunisol station (S2) with a woody BP corresponding respectively to 555 and 416.3 gC m^{-2} (Table 1 (b)).

3.2.2 Intra-annual variation in biomass production

There were large seasonal variations (from 1 in April to 5.7 gC m^{-2} day^{-1} in June for the alocrisol station) in wood aBP (Fig. 5). Though not symmetrical, the general dynamics at both stations were similar, with the highest aBP during June

Fig. 3 Time course of daily mean air temperatures (in °C) and daily cumulated global radiation (in mm) during the year 2014 obtained at the EC tower
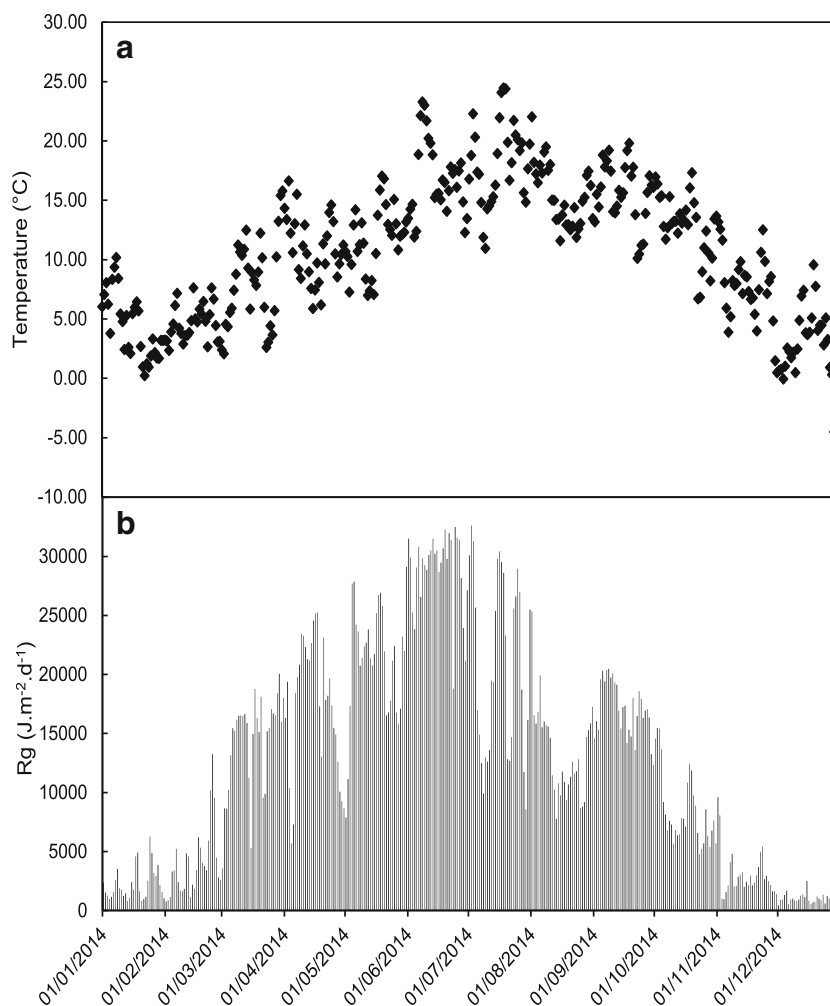
Fig. 4 Daily changes in NEE, Reco, and GPP fluxes during 2014 (**a**) and in cumulated GPP for the periods corresponding to BP estimates (**b**)
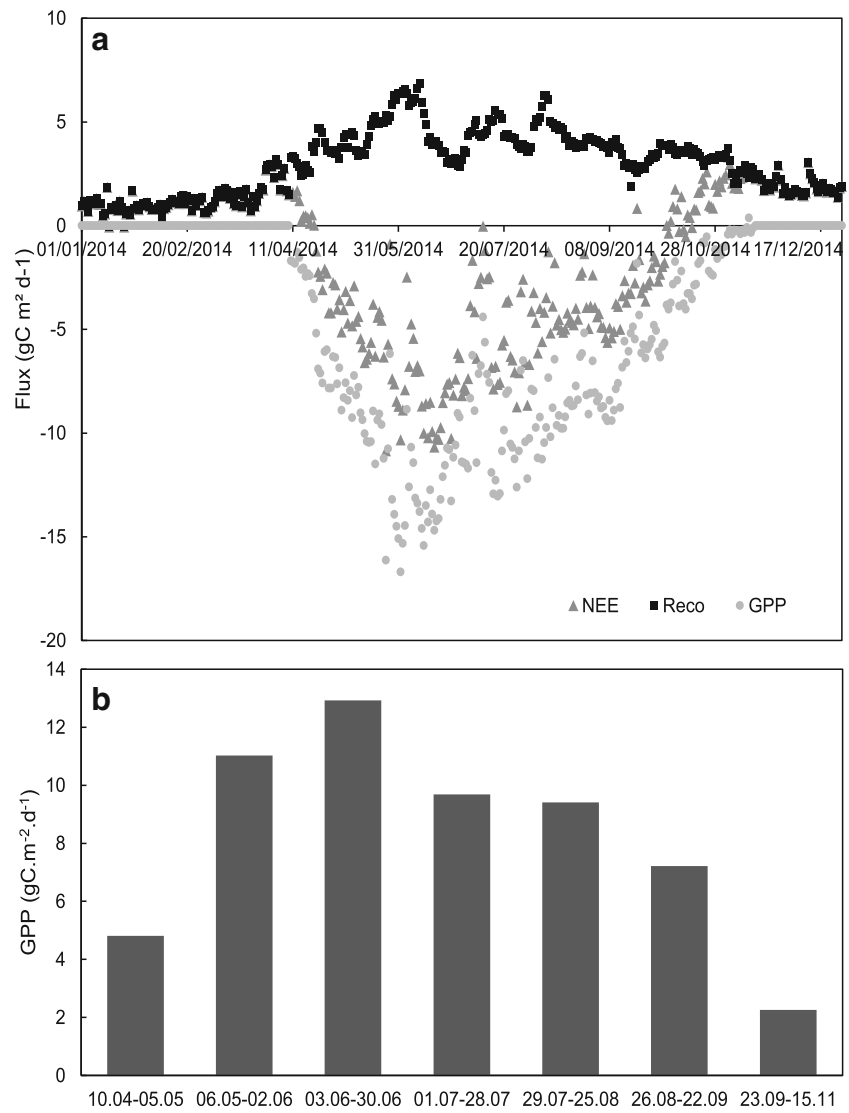

Fig. 5 Intra-annual changes in woody aboveground biomass production in the year 2014 for the alocrisol station under the hypothesis of a constant density (of 1) or of a variable and recorded density (black and black striped bars) and for the calci-brunisol station under the same hypothesis as previously cited (gray and gray striped bars). Error bars represent confidence interval
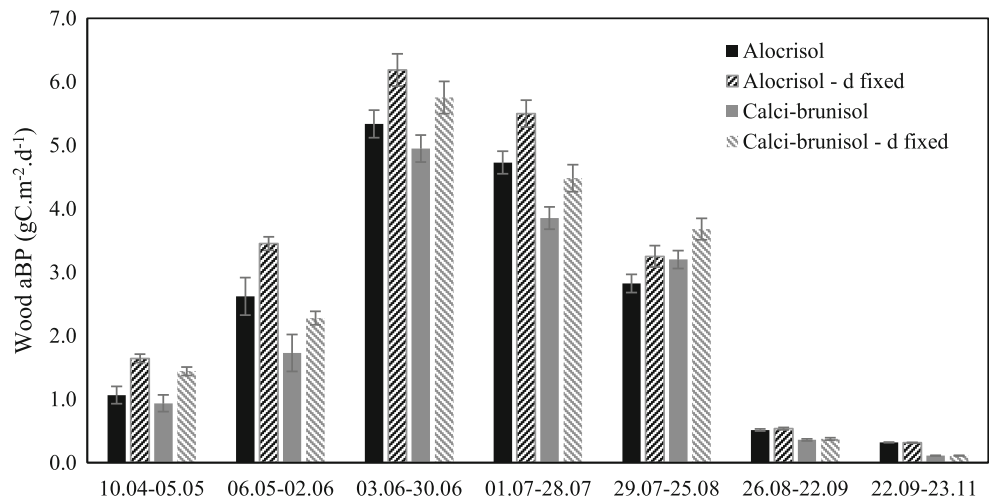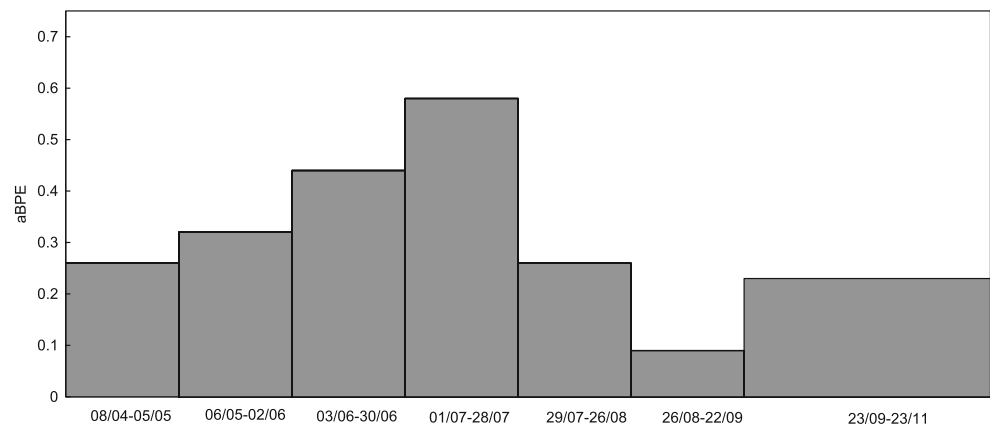
Fig. 6 Intra-annual changes in woody aboveground biomass production efficiency (aBPE) for the alocrisol (S1) stand, corresponding to the ratio of the cumulated wood aBP obtained in a month to the cumulated monthly GPP calculated

(5.7 and 4.9 gC m^{-2} day^{-1} for the alocrisol and calci-brunisol, respectively) then a decrease at the end of the growing season.

For nearly every monthly period, the difference between the two stands was significant (p value < 0.05; Fig. 5), with the alocrisol consistently producing more biomass than the calci-brunisol except for the period from 29 July to 25 August.

3.2.3 Effects of correcting for density

Equation 4a–f includes both allometric relationships (transforming DBH and height to volume) and transforms volume to dry biomass. The latter calculation requires accounting for the final wood density value at the end of the 2014 growing season (Eq. 4a–f was established at the end of the season). This means that using Eq. 4a–f for monthly wood aBP estimates throughout the year 2014 (when wood density was lower than the final value) would lead to an overestimation of woody aBP. Therefore, we used the density measured monthly to calculate corrections for wood aBP. The trend for relative wood density (ρ_w in Eq. 4) is presented in Fig. 2. Density increases from 0.7 to 1 with an especially clear rise at the beginning and end of the growing season. The degree of overestimation for woody aBP when temporal variations in density are not taken into account can be estimated by comparing the results with and without this correction. Differences between corrected and uncorrected values of aBP range from 4 to 54% (Figs. 2 and 5), the larger percentage corresponding to the first period, when wood density is smallest. If the final wood density was used throughout the year for the different periods, the overestimation for total annual aBP would be 20%.

3.2.4 Biomass production efficiency

The wood aBP of the beech trees represented 34% of the annual GPP (Table 1 (b)). There was a clear, very large intra-annual variation in woody aBPE which climbed from

April to a peak value of 0.6 in July (Fig. 6), then fell by 50% to 0.25 between July and August, then continued to decrease regularly, reaching 0.11 in September. Finally, a single, final rise to 0.24 occurred in November.

4 Discussion

4.1 Meteorological and flux data

Our site was an important C sink during the study year, and this is normal for beech forests in northeastern France (Granier et al. 2008). When no water limitation is recorded, Reco is limited only by C supply and enzymatic activity (T), and GPP is limited by global variation.

NEE (− 549 gC m^{-2}) was in the higher range of what is found in the literature for temperate deciduous forest ecosystems (from − 257 to − 585 gC m^{-2}, mean value − 339 ± 368 gC m^{-2}, Table 1 (b)). This NEE value was especially due to a higher-than-usual GPP (− 1639 gC m^{-2} for our alocrisol station compared with 1016 to 1880 gC m^{-2} and a mean value of 1820 ± 805 gC m^{-2} in the literature (Valentini et al. 1996; Malhi et al. 1999; Granier et al. 2000, 2008) combined with a relatively standard Reco value (1089 gC m^{-2} for our alocrisol station compared with 544 to 1425 gC m^{-2} and a mean value of 1136 ± 373 gC m^{-2} in the literature).

4.2 Biomass production

In the literature, annual aBP values range from as low as 140 gC m^{-2} in a temperate mixed forest (Wu et al. 2013) to 677 gC m^{-2} for a very fertile temperate forest (Vicca et al. 2012), the mean value being 366 ± 233 gC m^{-2} (Valentini et al. 1996; Knohl et al. 2003; Curtis et al. 2005; Granier et al. 2008; Vicca et al. 2012; Wu et al. 2013). This places

our results in the higher range (652 and 514 gC m^{-2} for the alocrisol and the calci-brunisol stations, respectively).

Our aBP values were significantly different on the two stands. The alocrisol ecosystem produced more biomass than the calci-brunisol system, as found in Calvaruso et al. (2017). This difference can be linked to the type of soil, its depth, and also the stand management history. In our study, this difference in aBP stemmed from very high C production by the dominant and co-dominant trees at the alocrisol station (data not shown). Taken individually, the dominant and co-dominant trees at this station had higher aBP when compared to the trees at the calci-brunisol station, where stem density was greater. Stem density did not compensate for lower C production since, per surface unit, aBP was nearly three times higher for dominant and co-dominant trees at the alocrisol station. Consequently, the difference in stand aBP is probably due to the higher aboveground biomass of the dominant and co-dominant trees at the alocrisol station at the beginning of the study year. The origin of this situation is not known, but soil nitrogen concentrations N (gN m^{-3}) could provide an explanation. Nitrogen levels in the soil solutions from the first 10 cm were clearly higher throughout the study year for the alocrisol stand (0.8–2.0 mg N L^{-1} versus 0.6 to 1.6 mg N L^{-1} in calci-brunisol stand; Kirchen, personal communication). This could explain the strong early growth observed on the alocrisol soil (Lawrence 2001; Finzi et al. 2007). The alocrisol also has deeper organic soil than the calci-brunisol; previous droughts could therefore have had more impact on development in the calci-brunisol ecosystem, thus hindering biomass acquisition and growth in 2014.

The computed error for the calculation of monthly aBP from DMaw (in gDM) amounted to 15% when adding the errors that could stem from the different corrections applied (wood growth, wood C concentration, and wood density).

At both stands, we found quite a large variation in wood density during wood formation throughout the year. This phenomenon had already been observed (Rathgeber et al. 2016) and corresponds to the thickening of the cell walls. Our results reinforce the importance of including this variation in density when working on intra-annual biomass production, as Delpierre et al. (2016) have already highlighted. Indeed, not taking changing wood density into account and instead using the final value for all intermediate estimations would have led, in our study, to overestimating aBP by as much as nearly 50% for some periods, and by about 20% when these intermediate values were cumulated on an annual basis for 2014. This confirms that dendrometer measurements alone are not sufficient when attempting to understand the monthly dynamics of the C balance in forest ecosystems (Cuny et al. 2015).

4.3 Efficiency

Throughout 2014, aBP was consistently lower than GPP for each period. GPP may not be the sole C source for aBP, as the C stored from the previous year could also provide C fuel. However, with our dataset, we were unable to trace the origins of C in the biomass produced as this would have required using other techniques such as isotopic tracing (Carbone et al. 2013). The proportion of C in GPP not allocated to aBP could be expelled during Reco, stored in root BP (up to 24% of total GPP; Arneth et al. 1998) or devoted to the production of reproductive organs, but could also be given off in VOCs and exudates. The partitioning of the C between these different fluxes is not known.

Wood aBPE (0.34) is in the upper range of what can be found in the literature, with values from 0.11 for *Quercus alba* L./*Quercus prinus* L. (Malhi et al. 1999) to 0.38 for a *Fagus sylvatica* L. (Wu et al. 2013) with a mean overall value of 0.22 ± 0.12 for temperate forests (Ryan et al. 1995; Valentini et al. 1996; Granier et al. 2000; Barford et al. 2001; Curtis et al. 2005; Vicca et al. 2012; Wu et al. 2013). Woody aBPE in our study presented a large seasonal fluctuation with a relatively symmetric trend. This shape was different from our aBP curve, thus revealing the occurrence of a discrepancy between the behavior of raw C flux (for biomass production) and the coefficient of allocation (for efficiency). The woody aBPE bell-shaped curve resembled the photoperiod curve; this may indicate synchronization without giving any causality, which should not be overlooked when allocation schemes are established in certain ecosystem models.

June and July are the months when the percentage of assimilated C allocated to aerial wood is the highest. This maximum-efficiency period is when high GPP most enhances wood production.

In addition to variation in annual BP-to-GPP ratio among forests (DeLucia et al. 2007; Vicca et al. 2012) that was already studied, we showed that there was also an important variation within a forest throughout the year. This variation is important to take into account in intra-annual studies as using a fixed value in forest models could result to an overestimation or underestimation of C allocated to biomass depending on the season.

5 Conclusion

This study demonstrates the importance of taking wood density into account when conducting seasonal monitoring of an aboveground wood carbon budget, since not doing so could result in an overestimation of woody aBP during some periods of the year of about 20%. Temporal variability in woody aBPE is important: maximum values occur during summer, reflecting trends for several other environmental variables

and showing the importance of taking into account the variable allocation coefficient over time in a functioning forest model (Guillemot et al. 2017).

Compliance with ethical standards

Conflict of interest   The authors declare that they have no conflict of interest.

References

Ammann C, Flechard CR, Leifeld J, Neftel A, Fuhrer J (2007) The carbon budget of newly established temperate grassland depends on management intensity. Agric Ecosyst Environ 121:5–20. https://doi.org/10.1016/j.agee.2006.12.002

Aubinet M, Chermanne B, Vandenhaute M, Longdoz B, Yernaux M, Laitat E (2001) Long term carbon dioxide exchange above a mixed forest in the Belgian Ardennes. Agric For Meteorol 108:293–315. https://doi.org/10.1016/S0168-1923(01)00244-1

Aubinet M, Grelle A, Ibrom A et al (1999) Advances in ecological research. Academic press. In: Fitter AH, Raffaelli DG (eds) Estimates of the annual net carbon and water exchange of forests: the EUROFLUX methodology, pp 113–175

Barford CC, Wofsy SC, Goulden ML, et al (2001) Factors controlling long- and short-term sequestration of atmospheris CO_2 in a midlatitude forest. science 294:1688-1691. https://doi.org/10.1126/science.1062962

Beziat P (2009) Effet des conditions environnementales et des pratiques culturales sur les flux de carbone, d'énergie et l'efficience de l'utilisation de l'eau dans les agrosystèmes : mesures et modélisations de la parcelle au paysage. Université Toulouse III Paul Sabatier, Thèse de doctorat

Burba G, Schmidt A, Scott RL, Nakai T, Kathilankal J, Fratini G, Hanson C, Law B, McDermitt DK, Eckles R, Furtaw M, Velgersdyk M (2012) Calculating CO_2 and H_2O eddy covariance fluxes from an enclosed gas analyzer using an instantaneous mixing ratio. Glob Change Biol 18:385–399. https://doi.org/10.1111/j.1365-2486.2011.02536.x

Calvaruso C, Kirchen G, Saint-André L, Redon PO, Turpault MP (2017) Relationship between soil nutritive resources and the growth and mineral nutrition of a beech (*Fagus sylvatica*) stand along a soil sequence. Catena 155:156–169. https://doi.org/10.1016/j.catena.2017.03.013

Campioli M, Gielen B, Göckede M, Papale D, Bouriaud O, Granier A (2011) Temporal variability of the NPP-GPP ratio at seasonal and interannual time scales in a temperate beech forest. Biogeosciences 8:2481–2492. https://doi.org/10.5194/bg-8-2481-2011

Campioli M, Verbeeck H, Van den Bossche J et al (2013) Can decision rules simulate carbon allocation for years with contrasting and extreme weather conditions? A case study for three temperate beech forests. Ecol Model 263:42–55. https://doi.org/10.1016/j.ecolmodel.2013.04.012

Campioli M, Vicca S, Luyssaert S, Bilcke J, Ceschia E, Chapin FS III, Ciais P, Fernández-Martínez M, Malhi Y, Obersteiner M, Olefeldt D, Papale D, Piao SL, Peñuelas J, Sullivan PF, Wang X, Zenone T, Janssens IA (2015) Biomass production efficiency controlled by management in temperate and boreal ecosystems. Nat Geosci 8: 843–846. https://doi.org/10.1038/ngeo2553

Carbone MS, Czimczik CI, Keenan TF, Murakami PF, Pederson N, Schaberg PG, Xu X, Richardson AD (2013) Age, allocation and availability of nonstructural carbon in mature red maple trees. New Phytol 200:1145–1155. https://doi.org/10.1111/nph.12448

Cox PM, Betts RA, Jones CD, Spall SA, Totterdell IJ (2000) Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model. Nature 408:184–187. https://doi.org/10.1038/35041539

Cuny HE, Rathgeber CBK, Frank D, Fonti P, Mäkinen H, Prislan P, Rossi S, del Castillo EM, Campelo F, Vavrčík H, Camarero JJ, Bryukhanova MV, Jyske T, Gričar J, Gryc V, de Luis M, Vieira J, Čufar K, Kirdyanov AV, Oberhuber W, Treml V, Huang JG, Li X, Swidrak I, Deslauriers A, Liang E, Nöjd P, Gruber A, Nabais C, Morin H, Krause C, King G, Fournier M (2015) Woody biomass production lags stem-girth increase by over one month in coniferous forests. Nat Plants 1:15160. https://doi.org/10.1038/nplants.2015.160

Cuny HE, Rathgeber CBK, Lebourgeois F, Fortin M, Fournier M (2012) Life strategies in intra-annual dynamics of wood formation: example of three conifer species in a temperate forest in north-east France. Tree Physiol 32:612–625. https://doi.org/10.1093/treephys/tps039

Curtis PS, Vogel CS, Gough CM, Schmid HP, Su HB, Bovard BD (2005) Respiratory carbon losses and the carbon-use efficiency of a northern hardwood forest, 1999–2003. New Phytol 167:437–456. https://doi.org/10.1111/j.1469-8137.2005.01438.x

Delpierre N, Berveiller D, Granda E, Dufrêne E (2016) Wood phenology, not carbon input, controls the interannual variability of wood growth in a temperate oak forest. New Phytol 210:459–470. https://doi.org/10.1111/nph.13771

DeLucia EH, Drake JE, Thomas RB, Gonzalez-Meler M (2007) Forest carbon use efficiency: is respiration a constant fraction of gross primary production? Glob Change Biol 13:1157–1167. https://doi.org/10.1111/j.1365-2486.2007.01365.x

Drake JE, Davis SC, Raetz LM, DeLUCIA EH (2011) Mechanisms of age-related changes in forest production: the influence of physiological and successional changes. Glob Change Biol 17:1522–1535. https://doi.org/10.1111/j.1365-2486.2010.02342.x

Falge E, Baldocchi D, Olson R, Anthoni P, Aubinet M, Bernhofer C, Burba G, Ceulemans R, Clement R, Dolman H, Granier A, Gross P, Grünwald T, Hollinger D, Jensen NO, Katul G, Keronen P, Kowalski A, Ta Lai C, Law BE, Meyers T, Moncrieff J, Moors E, William Munger J, Pilegaard K, Rannik Ü, Rebmann C, Suyker A, Tenhunen J, Tu K, Verma S, Vesala T, Wilson K, Wofsy S (2001a) Gap filling strategies for long term energy flux data sets. Agric For Meteorol 107:71–77. https://doi.org/10.1016/S0168-1923(00)00235-5

Falge E, Baldocchi D, Olson R, Anthoni P, Aubinet M, Bernhofer C, Burba G, Ceulemans R, Clement R, Dolman H, Granier A, Gross P, Grünwald T, Hollinger D, Jensen NO, Katul G, Keronen P, Kowalski A, Lai CT, Law BE, Meyers T, Moncrieff J, Moors E, Munger JW, Pilegaard K, Rannik Ü, Rebmann C, Suyker A, Tenhunen J, Tu K, Verma S, Vesala T, Wilson K, Wofsy S (2001b) Gap filling strategies for defensible annual sums of net ecosystem exchange. Agric For Meteorol 107:43–69. https://doi.org/10.1016/S0168-1923(00)00225-2

Finnigan JJ (2004) A re-evaluation of long-term flux measurement techniques part II: coordinate systems. Bound-Layer Meteorol 113:1–41. https://doi.org/10.1023/B:BOUN.0000037348.64252.45

Finzi AC, Norby RJ, Calfapietra C, Gallet-Budynek A, Gielen B, Holmes WE, Hoosbeek MR, Iversen CM, Jackson RB, Kubiske ME, Ledford J, Liberloo M, Oren R, Polle A, Pritchard S, Zak DR, Schlesinger WH, Ceulemans R (2007) Increases in nitrogen uptake rather than nitrogen-use efficiency support higher rates of temperate forest productivity under elevated CO_2. Proc Natl Acad Sci 104: 14014–14019. https://doi.org/10.1073/pnas.0706518104

Giardina CP, Ryan MG, Binkley D, Fownes JH (2003) Primary production and carbon allocation in relation to nutrient supply in a tropical experimental forest. Glob Change Biol 9:1438–1450. https://doi.org/10.1046/j.1365-2486.2003.00558.x

Gifford RM (2003) Plant respiration in productivity models: conceptualisation, representation and issues for global terrestrial carbon-cycle research. Funct Plant Biol 30:171–186

Goulden ML, Mcmillan AMS, Winston GC et al (2011) Patterns of NPP, GPP, respiration, and NEP during boreal forest succession. Glob Change Biol 17:855–871. https://doi.org/10.1111/j.1365-2486.2010.02274.x

Guillemot J, Francois C, Hmimina G, et al (2017) Environmental control of carbon allocation matters for modelling forest growth. New Phytol 214:180–193. https://doi.org/10.1111/nph.14320

Granier A, Bréda N, Longdoz B, Gross P, Ngao J (2008) Ten years of fluxes and stand growth in a young beech forest at Hesse, Northeastern France. Ann For Sci 65:704–704. https://doi.org/10.1051/forest:2008052

Granier A, Ceschia E, Damesin C, Dufrene E, Epron D, Gross P, Lebaube S, le Dantec V, le Goff N, Lemoine D, Lucot E, Ottorini JM, Pontailler JY, Saugier B (2000) The carbon balance of a young beech forest. Funct Ecol 14:312–325. https://doi.org/10.1046/j.1365-2435.2000.00434.x

Harroué M, Cornu E, Rathgeber CKB (2011) Méthodes de prélèvement et de préparation des échantillons pour l'étude de l'activité cambiale et de la formation du bois. Cah Tech INRA 73:45–62

IPCC (2013) Climate change 2013: the physical science basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergover mental Panel on Climate Change. Cambridge, United Kingdom and New York, NY, USA

Kesselmeier J, Ciccioli P, Kuhn U, Stefani P, Biesenthal T, Rottenberger S, Wolf A, Vitullo M, Valentini R, Nobre A, Kabat P, Andreae MO (2002) Volatile organic compound emissions in relation to plant carbon fixation and the terrestrial carbon budget. Glob Biogeochem Cycles 16:1126. doi: 10.1029/2001GB001813, 73-1, 73-9

Kindler R, Siemens J, Kaiser K et al (2011) Dissolved carbon leaching from soil is a crucial component of the net ecosystem carbon balance. Glob Change Biol 17:1167–1185. https://doi.org/10.1111/j.1365-2486.2010.02282.x

Kljun N, Calanca P, Rotach MW, Schmid HP (2004) A simple parameterisation for flux footprint predictions. Bound-Layer Meteorol 112:503–523. https://doi.org/10.1023/B:BOUN.0000030653.71031.96

Klumpp K, Soussana J-F, Falcimagne R (2007) Effects of past and current disturbance on carbon cycling in grassland mesocosms. Agric Ecosyst Environ 121:59–73. https://doi.org/10.1016/j.agee.2006.12.005

Knohl A, Schulze E-D, Kolle O, Buchmann N (2003) Large carbon uptake by an unmanaged 250-year-old deciduous forest in Central Germany. Agric For Meteorol 118:151–167. https://doi.org/10.1016/S0168-1923(03)00115-1

Lawrence D (2001) Nitrogen and phosphorus enhance growth and luxury consumption of four secondary forest tree species in Borneo. J Trop Ecol 17:859–869. https://doi.org/10.1017/S0266467401001638

Lloyd J, Taylor JA (1994) On the temperature dependence of soil respiration. Funct Ecol 8:315. https://doi.org/10.2307/2389824

Longdoz B, Gross P, Granier A (2008) Multiple quality tests for analysing CO_2 fluxes in a beech temperate forest. Biogeosciences 5:719–729. https://doi.org/10.5194/bg-5-719-2008

Malhi Y, Baldocchi DD, Jarvis PG (1999) The carbon balance of tropical, temperate and boreal forests. Plant Cell Environ 22:715–740. https://doi.org/10.1046/j.1365-3040.1999.00453.x

Matamala R, Gonzàlez-Meler MA, Jastrow JD, Norby RJ, Schlesinger WH (2003) Impacts of fine root turnover on forest NPP and soil C sequestration potential. Science 302:1385–1387. https://doi.org/10.1126/science.1089543

Norby RJ, Zak DR (2011) Ecological lessons from free-air CO_2 enrichment (face) experiments. Annu Rev Ecol Evol Syst 42:181–203. https://doi.org/10.1146/annurev-ecolsys-102209-144647

Quéré CL, Andrew RM, Canadell JG, et al (2016) Global carbon budget 2016. Earth Syst Sci Data 8:605–649. https://doi.org/10.5194/essd-8-605-2016

R Core Team (2013) R: a language and environment for statistical computing. R foundation for Statistical Computing, Vienna

Rathgeber CBK, Cuny HE, Fonti P (2016) Biological basis of tree-ring formation: a crash course. Front Plant Sci 7:. https://doi.org/10.3389/fpls.2016.00734

Rebmann C, Kolle O, Heinesch B, Queck R, Ibrom A, Aubinet M (2012) Data acquisition and flux calculations. In: Aubinet M, Vesala T, Papale D (eds) Eddy covariance. Springer Netherlands, pp 59–83

Reichstein M, Falge E, Baldocchi D, Papale D, Aubinet M, Berbigier P, Bernhofer C, Buchmann N, Gilmanov T, Granier A, Grunwald T, Havrankova K, Ilvesniemi H, Janous D, Knohl A, Laurila T, Lohila A, Loustau D, Matteucci G, Meyers T, Miglietta F, Ourcival JM, Pumpanen J, Rambal S, Rotenberg E, Sanz M, Tenhunen J, Seufert G, Vaccari F, Vesala T, Yakir D, Valentini R (2005) On the separation of net ecosystem exchange into assimilation and ecosystem respiration: review and improved algorithm. Glob Change Biol 11: 1424–1439. https://doi.org/10.1111/j.1365-2486.2005.001002.x

Rossi S, Menardi R, Anfodillo T (2006) Trephor: a new tool for sampling microcores from tree stems. IAWA J 27:89–97. https://doi.org/10.1163/22941932-90000139

RP (2008) Référentiel pédologique 2008, Association française pour l'étude du sol (Afes), Quae

Ryan MG, Lavigne MB, Gower ST (1997) Annual carbon cost of autotrophic respiration in boreal forest ecosystems in relation to species and climate. J Geophys Res Atmospheres 102:28871–28883. https://doi.org/10.1029/97JD01236

Ryan MG, Gower ST, Hubbard RM, et al (1995) Woody tissue maintenance respiration of four conifers in contrasting climates. Oecologia 101:133–140. https://doi.org/10.1007/BF00317276

Schiestl-Aalto P, Kulmala L, Mäkinen H, Nikinmaa E, Mäkelä A (2015) CASSIA—a dynamic model for predicting intra-annual sink demand and interannual growth variation in Scots pine. New Phytol 206:647–659. https://doi.org/10.1111/nph.13275

Sheriff DW, Nambiar EKS, Fife DN (1986) Relationships between nutrient status, carbon assimilation and water use efficiency in *Pinus radiata* (D. Don) needles. Tree Physiol 2:73–88. https://doi.org/10.1093/treephys/2.1-2-3.73

Steppe K, Sterck F, Deslauriers A (2015) Diel growth dynamics in tree stems: linking anatomy and ecophysiology. Trends Plant Sci 20: 335–343. https://doi.org/10.1016/j.tplants.2015.03.015

Trumbore S (2006) Carbon respired by terrestrial ecosystems—recent progress and challenges. Glob Change Biol 12:141–153. https://doi.org/10.1111/j.1365-2486.2006.01067.x

Valentini R, De ANGELIS P, Matteucci G et al (1996) Seasonal net carbon dioxide exchange of a beech forest with the atmosphere. Glob Change Biol 2:199–207. https://doi.org/10.1111/j.1365-2486.1996.tb00072.x

Vicca S, Luyssaert S, Peñuelas J, Campioli M, Chapin FS III, Ciais P, Heinemeyer A, Högberg P, Kutsch WL, Law BE, Malhi Y, Papale D, Piao SL, Reichstein M, Schulze ED, Janssens IA (2012) Fertile

forests produce biomass more efficiently. Ecol Lett 15:520–526. https://doi.org/10.1111/j.1461-0248.2012.01775.x

Wu J, Larsen KS, van der Linden L, Beier C, Pilegaard K, Ibrom A (2013) Synthesis on the carbon budget and cycling in a Danish, temperate deciduous forest. Agric For Meteorol 181:94–107. https://doi.org/10.1016/j.agrformet.2013.07.012

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