CONCEPTS, REVIEWS AND SYNTHESES

A tree-ring perspective on the terrestrial carbon cycle

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Abstract Tree-ring records can provide valuable information to advance our understanding of contemporary terrestrial carbon cycling and to reconstruct key metrics in the decades preceding monitoring data. The growing use of tree rings in carbon-cycle research is being facilitated by increasing recognition of reciprocal benefits among research communities. Yet, basic questions persist regarding what tree rings represent at the ecosystem level, how to optimally integrate them with other data streams, and what related challenges need to be overcome. It is also apparent that considerable unexplored potential exists for tree rings to refine assessments of terrestrial carbon cycling across a range of temporal and spatial domains. Here, we summarize recent advances and highlight promising paths of investigation with respect to (1) growth phenology, (2) forest productivity trends and variability, (3) CO_2 fertilization and water-use efficiency, (4) forest disturbances, and (5) comparisons between observational and computational forest productivity estimates. We encourage the integration of tree-ring data: with eddy-covariance measurements to investigate carbon allocation patterns and water-use efficiency; with remotely sensed observations to distinguish the timing of cambial growth and leaf phenology; and with forest inventories to develop continuous, annually-resolved and long-term carbon budgets. In addition, we note the potential of tree-ring records and derivatives thereof to help evaluate the performance of earth system models regarding the simulated magnitude and dynamics of forest carbon uptake, and inform these models about growth responses to (non-)climatic drivers. Such efforts are expected to improve our understanding of forest carbon cycling and place current developments into a long-term perspective.

Keywords Forest · Productivity · Growth · Climate · Ecosystem

Introduction

Forest growth is one of the key processes that need to be assessed at a global scale to understand and quantify the

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short- to long-term impacts of environmental change on the terrestrial carbon cycle. The total terrestrial carbon sink is currently estimated at 2.5 ± 0.8 PgC (Le Quéré et al. 2013), with forests contributing 1.1 ± 0.8 PgC per year (Pan et al. 2011). The considerable uncertainty and the large inter-annual variability associated with the terrestrial carbon sink illustrate that this component of the global carbon cycle is both highly dynamic and remains poorly quantified (Poulter et al. 2014). Investigating the fate of this sink with respect to climate, increasing CO_2, nutrient limitation and deposition, and land-cover change is highly relevant for management and political decision making (Fahey et al. 2009), as well as for the well-being of society. This has accordingly been a major research topic over the past years to decades (Bonan 2008). Despite these efforts, our understanding of carbon dynamics in forest ecosystems is still incomplete at large scales as a consequence of uncertainties in carbon allocation patterns (Brüggemann et al. 2011; Litton et al. 2007), forest management effects (Bellassen et al. 2011), and a paucity of long-term data (Reichstein et al. 2013). These uncertainties are manifested in diverging vegetation model predictions (Friedlingstein et al. 2010; Jones et al. 2013), or misfits between model results and observed trends (Keenan et al. 2012). In addition, uncertainties persist regarding forests' response to climate variability (Babst et al. 2013) and disturbances (Running 2008), as well as long-term effects of nitrogen and CO_2 fertilization (Gedalof and Berg 2010; Law 2013). Together with human land-use, this array of uncertain factors form a very complex set of drivers for large-scale forest growth, which is challenging to resolve and calls for both long-term and large-scale observational records.

Tree rings are a direct measure of stem growth, which represents the principal above-ground carbon accumulation pool and has significant economic and societal value (Fahey et al. 2009). Because tree growth is sensitive to changes in the physical environment, tree rings have often been used to develop intra-annual to centennial records of environmental and anthropogenic drivers including climate (e.g., Frank et al. 2010), disturbances (Esper et al. 2007), light and nutrient availability (Drever and Lertzman 2001), competition (Weber et al. 2008), or management (Brienen and Zuidema 2006). At present, the International Tree Ring Data Bank (ITRDB) is the largest database of tree-ring data providing access to a variety of parameters from more than 3,000 tree-ring sites across the globe. Existing measurements include (1) earlywood, latewood, and total ring-width, (2) wood density (earlywood, latewood, minimum, and maximum density), (3) blue light reflected from the wood surface (Campbell et al. 2007), (4) stable isotope ratios (i.e. carbon, oxygen, hydrogen, nitrogen) in whole wood, holo-, and alpha-cellulose, (5) wood anatomical features (e.g., number, size

and formation of cells, cell lumen, and cell walls), and (6) the abundance of specific chemical compounds (Berger et al. 2004). These data provide extensive information on inter- and intra-annual forest growth dynamics (Babst et al. 2013; Breitenmoser et al. 2014; Briffa et al. 2002; Wettstein et al. 2011) and facilitate a variety of research opportunities to improve understanding of terrestrial carbon cycling.

Here, we review existing literature to identify knowledge gaps where information derived from tree rings can provide insight in the magnitude and variability of the global forest carbon balance and related environmental research. We further encourage the integration of dendroecology with several other disciplines to overcome limitations associated with individual data streams. This may inspire new paths of investigation and broaden the ongoing discussion concerning the terrestrial carbon cycle.

Tree rings in a carbon cycle context

Tree rings are able to be clearly defined in most extra-tropical and even many tropical areas where the progression of seasons induces distinct annually rhythmic variability in wood cell structures (Cuny et al. 2014). The cambial cell division, enlargement, and lignification of cell walls that result in the final ring characteristics are influenced by numerous physiological processes that are modulated by environmental conditions both prior to and during the growing season (Fritts 1976). Tree rings are thus the final product of manifold mechanisms related to the energy, water, carbon, and nutrient budgets (Fig. 1). The exact characteristics of the division and maturation of cells may be somewhat dependent upon the growth form and physiology of individual species, but ultimately require the immediate or lagged allocation of carbohydrates (Gessler et al. 2009). At the leaf-level, carbon uptake is largely controlled by light, moisture, temperature, atmospheric CO_2, and nutrient availability (Collatz et al. 1991; Farquhar and von Caemmerer 1982). Carbon sequestration further depends on the available leaf area and thus changes seasonally with leaf phenology, particularly for deciduous plants (Chen et al. 1999; Richardson et al. 2009). Natural and anthropogenic forest disturbances additionally influence growth through the competitive balance for limited resources among trees (Veblen et al. 1994). While this complexity makes it challenging to relate tree-ring data to key carbon cycle functions, it represents an opportunity to assess the combined effects of these mechanisms. In the subsequent sections, we will explore ways in which tree-ring parameters can be combined with other data streams (summarized in Table 1) to address pending process-specific but also integrative research questions.
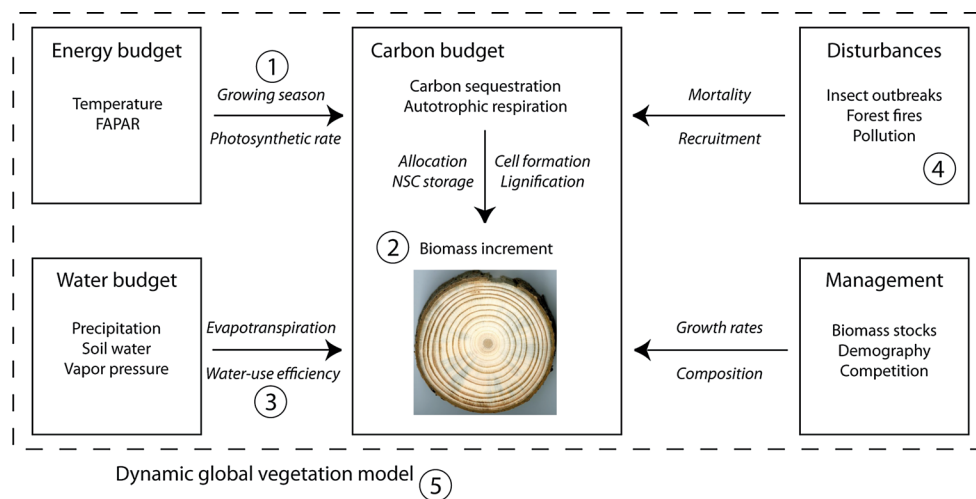
Fig. 1 Schematic view of key drivers and processes (*italics*) leading to the formation of annual growth rings in woody plants. *Numbers* refer to the sections in this paper, where the respective aspects are discussed in detail, as follows: *1* "Cambial phenology and growing season", *2* "Forest productivity and carbon allocation", *3* "CO_2 fertilization and water-use efficiency", *4* "Forest disturbances", *5* "Model evaluation and data assimilation". Regarding the section "Model evaluation and data assimilation", please note that not all dynamic global vegetation models include disturbances and management. The displayed stem disc was sampled from a *Picea abies* individual in Romania (north-eastern Carpathians, 400 m a.s.l.). *FAPAR* fraction of absorbed photosynthetically active radiation, *NSC* non-structural carbohydrates

Cambial phenology and growing season

The distinct growing and dormant seasons represent one of the most fundamental rhythms characteristic of most forest ecosystems. The growing season can be defined as the period when carbon is actively removed from the atmosphere and assimilated during photosynthesis. Growth seasonality in cold and temperate environments is largely driven by a combination of the photoperiod and climate (Polgar and Primack 2011), whereas tree water status has been identified as the primary driver of leaf phenology and cambial growth in seasonally dry tropical forests (Borchert 1999; Trouet et al. 2012). Comparable studies in tropical rainforests are rare (Dié et al. 2012; Pumijumnong and Buajan 2013). Regardless of climatic growth limitations, a temporal offset between cambial growth and other processes such as leaf formation, photosynthesis, or root and shoot elongation may occur. Such offsets are most evident during growth onset and cessation (Polgar and Primack 2011, and references therein).

Cambial activity in broadleaf ring-porous species (e.g., oak) generally starts multiple weeks prior to bud break (Breda and Granier 1996). The early formation and lignification of large vessels facilitates water transport when the tree reaches a high evapotranspiration demand (i.e. at full leaf expansion) but requires a large investment of non-structural carbohydrate (NSC) reserves assimilated during the previous growing season (Dietze et al. 2014). This is expressed in tree-ring data as positive lag-1 autocorrelation and/or significant correlations with previous summer to autumn climate parameters (Babst et al. 2013). The use of NSC for wood formation has also been reported for coniferous or diffuse-porous broadleaf species alike, but with cambial activity starting synchronous with or subsequent to bud break (e.g., in common beech; Cufar et al. 2008). Cambial growth onset typically lags leaf flush in seasonally dry tropical forests, where many tree species are brevi-deciduous and experience a short period of drought-induced deciduousness (Borchert 1999). Cambial activity of these brevi-deciduous species starts much later in the wet season and lasts for only 2–4 months (Trouet et al. 2012). The exact determinism (and definition) of growth onset is still debated, but seems largely controlled by climate (i.e. when temperatures transcend a prescribed threshold; Laube et al. 2014) and hormones (Uggla et al. 1996).
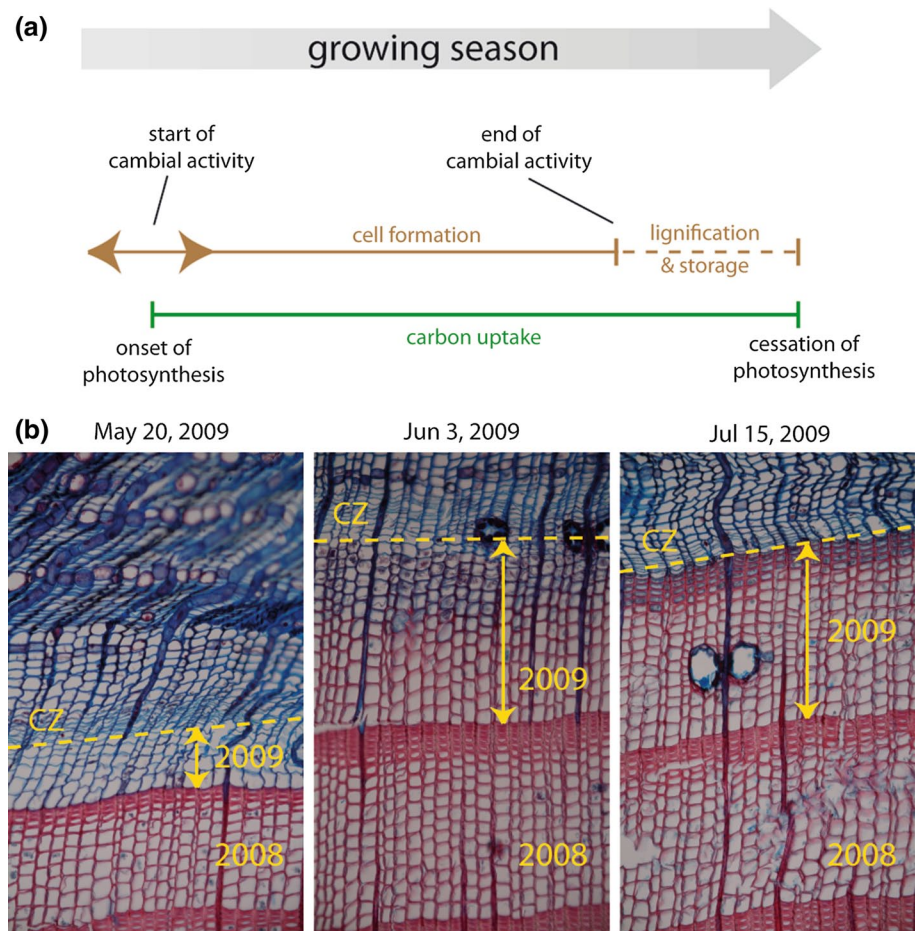
Growth cessation is equally challenging to define and quantify because different mechanisms involved in carbon uptake and wood formation are under different environmental controls (Vaganov et al. 2006) and do not terminate simultaneously (Fig. 2a). Intra-annual tree-ring studies have shown that radial growth typically ceases long before the end of the photosynthetically-active period (King et al. 2013; Moser et al. 2010) and that cell wall-thickening continues after termination of the cambial activity, thereby forming latewood in coniferous species (Fritts 1976). Latewood density in high elevation/latitude conifers is highly temperature sensitive (Esper et al. 2012), integrating influences from meteorological conditions over much of the growing season by the deposition of assimilates in these cell walls. There is also some evidence for late-season

Table 1 Overview of primary data streams used in carbon cycle and climate change research

Data	Temporal resolution	Principal products	Compilations	Primary use	Advantages	Disadvantages
Tree-ring parameters	Seasonal to millennial	Radial growth; wood density; stable isotopes (C, O, H, N); wood anatomical features	Global database (ITRDB); regional-global networks	Paleoclimatology; forest ecology; tree physiology; archaeology	Long time-series; (intra-)annual resolution; reflect changes in the physical environment	Often confined to the stem; fading records towards the present; inconsistent sampling; limited in the tropics
Climate stations	Half-hourly to monthly	Meteorological variables (e.g., T, P, air humidity); plus derivatives (e.g., VPD, drought indices)	Gridded climate data (e.g. CRU, PRISM); Reanalysis data (e.g. NCEP/NCAR, ERA-40)	Climatology; model input; public use	High temporal resolution; standardized/homogenized measurements	Discontinuous records; highly uneven global coverage
Eddy-covariance	Half-hourly	Net carbon balance (NEE) plus derivatives (GPP, TER); meteorological variables	Global network (FLUXNET)	Terrestrial carbon cycle; ecosystem functions	High temporal resolution; integral carbon budgets	Short records; requires gap-filling; variable footprint
Forest inventories/ monitoring plots	Periodic	Radial and height growth; stand dynamics; mortality	Different political organization levels	Terrestrial carbon cycle; forest management; economic demand	Detailed inventories with rich databases; available in most countries	Periodical assessments; discontinuous records; changing management strategies
Remote sensing	~Bi-weekly or periodic	Vegetation indices (e.g., NDVI); forest structure (e.g., LIDAR)	Regional to global data-sets; time-series from individual sensors	Land surface patterns and change	Large-spatial coverage; multispectral information; multitemporal change detection	Needs atmospheric correction; may contain clouds and other artifacts; mainly daytime; cost intensive; indirect estimates of many important parameters
Vegetation models	Variable	Net primary productivity	Multi-model ensembles; model-data fusion	Carbon cycle–climate interactions	Flexible input; different spatial and temporal scales; useful to generalize point observations; consideration and attribution of important physiological processes	Limited to plant functional types; poor representation of lagged effects; biased climate sensitivity; few disturbance parameters
Climate models	Monthly	Predictions of future climate variables	Climate scenario ensembles (e.g., CMIP5)	Climate change	Assess changes in the climatic constraints of carbon cycling	Divergent scenarios; considerable uncertainties in individual parameters

VPD vapor pressure deficit, *NEE* net ecosystem exchange, *GPP* gross primary productivity, *TER* terrestrial ecosystem respiration, *NDVI* normalized difference vegetation index, *LIDAR* light detection and ranging, *ITRDB* international tree-ring data bank, *CRU* Climate Research Unit at the University of East Anglia, *PRISM* Climate Group at Oregon State University, *NCEP/NCAR* reanalysis project at the Earth System Research Laboratory, *ERA-40* reanalysis project at the European Centre for Medium-Range Weather Forecasts

Fig. 2 Timing of cambial and leaf phenology. *The top panel illustrates* the relative timing of photosynthetic activity (*green*) and wood formation (*brown*) throughout the growing season. *The bottom panel demonstrates* on the example of a *Picea abies* individual (Rhone Valley, Central Alps, 800 m a.s.l.), how intra-annual tree-ring studies can inform on timing of wood formation. Thin sections (20 μm; courtesy of Patrick Fonti) were stained to color lignified cells in *red*, non-lignified cells in *dark blue* and cambial cells in *light blue*. The position of the cambial zone (*CZ*) and the width of the evolving tree ring (*yellow arrows*) are indicated (color figure online)

(a) growing season

start of cambial activity — end of cambial activity

cell formation — lignification & storage

onset of photosynthesis — carbon uptake — cessation of photosynthesis

(b) May 20, 2009 Jun 3, 2009 Jul 15, 2009

CZ 2009 2008

climatic influences on cell enlargement and wall-thickening processes in earlier segments of the annual rings (Franceschini et al. 2012). The formation of intra-annual density fluctuations (local increase in wood density typically induced by summer drought in Mediterranean environments; Campelo et al. 2013) is another example of how carbohydrate investment in cell-wall building continues, while radial growth dramatically slows or even temporarily ceases. These processes consume a significant amount of carbon, which may explain the moderate success of some studies comparing inter-annual variability in radial growth (Granier et al. 2008) and in maximum latewood density (Beck et al. 2013; D'Arrigo et al. 2000) with forest productivity. Accounting for variations in wood density improves the agreement between growth variability and integral measurements of forest carbon uptake (Babst et al. 2014b). Yet, the amount and dynamics of photoassimilates stored in above- and below-ground NSC reserves particularly during cambial dormancy remains a challenging research topic (Dietze et al. 2014), as different types of sugars show high variability throughout the growing and dormant seasons depending upon the cambial developmental stage (Simard et al. 2013).

Disentangling wood formation from canopy phenology is a prerequisite to refine remotely-sensed [e.g., light detection and ranging (LIDAR), vegetation indices, phenology cameras] estimates of forest productivity, as changes in photosynthetic activity do not necessarily reflect changes in cambial growth (Fig. 2a). Intra-annual tree-ring studies involving repeated sampling and wood-anatomical analysis of microcores (known as "punching"; Fig. 2b) are a labor-intensive but promising way to assess the exact timing of these species and biome-specific processes, as well as their impacts on carbon accumulation and use. For instance, Rossi et al. (2014) found an exponential increase in cell production in response to an earlier growth onset in Canadian boreal forests. This is particularly relevant in view of the expected prolongation of the growing season under a warming climate (Richardson et al. 2013). Comparable studies in different climate zones and biomes are needed to accurately test the impacts of rising temperatures on forest productivity.

Forest productivity and carbon allocation

Forests worldwide currently mitigate approximately 30 % of all CO_2 emissions from fossil fuel burning and land-use

changes (Canadell and Raupach 2008; Friedlingstein et al. 2010), thereby dampening the magnitude of global warming. This carbon sink, however, varies considerably in space, time, and magnitude requiring extensive and long-term observational records to assess its dynamics. Forest net primary productivity (NPP) is primarily composed of an above- and a belowground component, the latter of which is particularly difficult to measure accurately. Attempts to do so are very time and labor intensive (Clark et al. 2001), and have thus only been performed in very local studies. Aboveground productivity can more readily be quantified via repeated measurements on permanent plots and remote sensing techniques to determine its contribution to NPP (Clark et al. 2001; Litton et al. 2007). The majority of NPP in forest ecosystems is attributed to tree growth and consecutive inventories of tree biometrics (e.g., changes in diameter, height, and canopy status over a 5- to 10-year period) are commonly used to estimate growth and productivity in countries that have established a systematic inventory. Such monitoring initiatives can be complemented with point and band dendrometers to assess the (intra-)annual variation in tree growth in intensive monitoring plots over multiple years (Etzold et al. 2013; Moore et al. 2006). Yet, growth assessments over more than a few decades are rare (but see Zingg 1996), and also the contributions from temporary changes in water status to changes in tree size can be significant (King et al. 2013; Stephenson et al. 2014).

Tree-ring data contribute to resolving temporal limitations of forest inventories and add a long-term perspective on tree growth prior to the initiation of monitoring activities. Radial growth at breast height has been shown to be representative for the entire stem (Bouriaud et al. 2005), but the strength of inferred climate limitations may decrease toward the crown (van der Maaten-Theunissen and Bouriaud 2012) as carbohydrate allocation to proximal sinks appears favored during stress conditions (Woodruff and Meinzer 2011). In combination with appropriate allometric equations (e.g., Zianis et al. 2005), it is possible to reconstruct tree volume and annual aboveground biomass increment from radial tree growth. Carbon accumulation at the tree-level can be inferred from tree biomass if the wood carbon content is precisely known or reasonably approximated to be 50 % of the wood mass (Joosten et al. 2004). In addition, combining tree-ring-based biomass quantification and wood density data with eddy-covariance (EC) measurements provides information about the partitioning of gross primary productivity (GPP) into soil and tree carbon allocation (i.e. volume increment, cell-wall thickening, storage; Babst et al. 2014b). This approach, however, does not account for the depletion and replenishment of NSC reserves that may partly decouple tree growth from net ecosystem productivity. Current theory suggests that carbon allocation to NSC may be active (i.e. at the expense of growth) or passive (if redundant photoassimilates are available), depending on environmental constraints (Dietze et al. 2014). Empirical quantification of storage mechanisms or dynamics in mature trees (e.g., isotopic tracer experiments; Kuptz et al. 2011) or for entire forest stands is rare.

A series of challenges need to be considered when inferring above-ground forest biomass increment from radial tree growth. First, common dendrochronological sampling designs are often inappropriate for forest productivity estimation, because they rarely reflect the stand structure and density accurately, often lack the necessary biometric and metadata to upscale tree biomass estimates to the site level, and are thus prone to result in biased quantification of growth trends and carbon accumulation (Nehrbass-Ahles et al. 2014). The systematic application of appropriate schemes like the fixed-plot (Babst et al. 2014a; Davis et al. 2009) or random sampling designs at large scales are encouraged to obtain reliable and consistent estimates of above-ground biomass increment and carbon allocation. Second, larger networks are often biased toward areas with strong climatic limitations, facilitating the traditional use of radial growth as a palaeoclimate proxy (Jones et al. 2009). Intensified data collection in temperate regions is thus expected to yield more representative estimates of large-scale forest productivity. Tropical regions are also under-represented, mainly due to the lower proportion of species where ring formation has been demonstrated to be annual. Third, allometric models used to infer above-ground tree biomass from tree dimensions have intrinsic uncertainties that need to be accounted for (Nickless et al. 2011). This issue is not specific to tree-ring studies but equally concerns other biometric approaches based on repeated diameter measurements. Published equations are usually species-specific and almost never developed under the exact same site conditions where they are later applied. Finding appropriate biomass functions for specific sites can thus be challenging, but new local parameterization methods making use of the Bayesian approach seem to open perspectives in this respect (Zell et al. 2014). Fourth, tree-ring data reflect the forest structure in the sampling year, whereas temporal changes in forest demography and composition cannot reliably be reconstructed. Uncertainties associated with tree mortality, disturbances, or management increase considerably back in time and are characterized as the "fading record problem". Hence, the site history needs to be considered in stand-level biomass reconstructions and can further be supported by the collection of relict material (Daniels et al. 1997), by responses of surviving trees to formerly present individuals (e.g., growth releases; Rubino and McCarthyz 2004), or by medium-term trends in modeled NPP (Fig. 3). And fifth, upscaling plot level data to larger areas is challenging, especially under variable forest structure and composition. A combination of tree-ring and remotely sensed
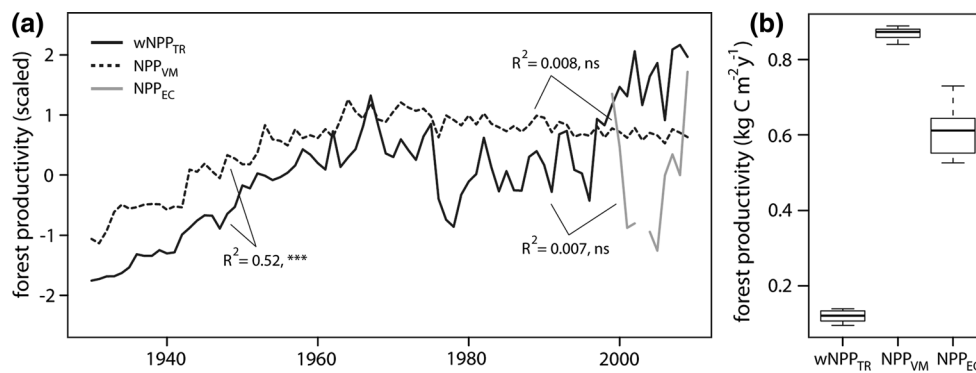
Fig. 3 Example for multiple estimates of forest productivity at the flux-tower site in Braschaat (Belgium). **a** The inter-annual to decadal variability in woody NPP from tree-rings ($wNPP_{TR}$, *Pinus sylvestris*, source: Babst et al. 2014a), NPP estimates from the ORCHIDEE-FM dynamic global vegetation model (NPP_{VM}, see Babst et al. 2013, supplementary material for description), and NPP estimates from eddy-covariance data (NPP_{EC}, 50 % of annual GPP as obtained from the European Fluxes database, www.europe-fluxdata.eu) is presented. **b** Magnitude of the three data streams over the 1999–2009 period. The following significance codes are used for linear regression models: ***$p < 0.001$, **$p < 0.01$, *$p \leq 0.05$, ns $p > 0.05$

data appears promising to evaluate the extent to which limited-scale records of forest growth reflect landscape or regional vegetation performance. Recently developed remote sensing technologies include airborne or terrestrial LIDAR for high-resolution forest survey (Andersen et al. 2005; Magney et al. 2014) and the use of hyperspectral estimates of physiological parameters for improved modeling of aboveground productivity (Houborg et al. 2013; Smith et al. 2002).

All the above-mentioned approaches have their own advantages, but we find that no single method is able to draw an accurate picture of terrestrial carbon accumulation in woody biomass. The combination of these methods (e.g., as illustrated in Fig. 3) should be aimed at in any study related to forest growth. Some notable examples are Berner et al. (2011), Beck et al. (2013), Poulter et al. (2013), and Bunn et al. (2013), who compared canopy reflectance as expressed by the normalized difference vegetation index (NDVI) and cambial productivity (radial growth and maximum latewood density), or Girardin et al. (2014) who combined inventory, tree-ring, and satellite data to relate recent forest growth to aboveground biomass increment over the past centuries.

CO_2 fertilization and water-use efficiency

One of the major uncertainties that will co-determine the fate of the terrestrial carbon cycle in the Anthropocene is the magnitude or even existence of enhanced plant growth at higher CO_2 concentrations. Trees regulate the gas exchange at the leaf-level via their stomata in response to environmental conditions and the atmospheric CO_2 concentration (c_a). This physiological adaptation serves to optimize the ratio between carbon assimilation and evaporative water loss [water-use efficiency (WUE)] and represents a primary link between plant functioning and anthropogenic perturbations of the carbon cycle (Franks et al. 2013). The rising c_a over the industrial period has continuously increased the amount of carbon available for plant photosynthesis (Drake et al. 1997). This has led to a widely debated CO_2 fertilization hypothesis, suggesting that an increase in c_a should exert a positive effect on NPP (Ainsworth and Long 2005). Numerous studies have found a positive relationship between c_a and WUE (e.g., Battipaglia et al. 2013; Medlyn et al. 1999), but a related fertilizing effect on tree growth remains highly uncertain. Some studies reported increased growth rates that were hypothesized to be at least partly attributable to CO_2 fertilization (Huang et al. 2007; Koutavas 2013; McMahon et al. 2010), whereas other investigations found no such effects (Levesque et al. 2014; Gedalof and Berg 2010; Peñuelas et al. 2011). The absence of a measurable fertilization effect on growth from tree-ring records could be explained, e.g., by secondary limitations that prevent increased C assimilation from being fully realized (Andreu-Hayles et al. 2011). Furthermore, possible methodological constraints may hinder the clear detection of CO_2 fertilization effects in tree rings (Girardin et al. 2011). For instance, the differentiation of CO_2-enhanced growth from tree age/size trends in tree-ring width measurements (Frank et al. 2009), classically applied sampling procedures that focus on a selection of dominant individuals (Nehrbass-Ahles et al. 2014), and significant variation in tree-ring data driven by climatic fluctuations may obscure the growth response to CO_2. It has also been reported that trees may only benefit from higher c_a in their early growth phase (Hättenschwiler et al. 1997) or if other resources are not limiting (Norby et al. 2010). In addition, a ^{13}C tracer experiment in mature temperate trees revealed

that strongly elevated c_a led to a higher carbon transfer belowground, whereas photosynthetic capacity and stem growth remained largely unaffected (Körner et al. 2005). The latter finding, while somewhat species-specific, indicates that more carbon is passing through but not remaining in trees under higher c_a.

Tree-ring stable isotope measurements (informing carbon uptake at the leaf level) are a well-established tool that can be used to improve our understanding of CO_2-fertilization effects and disentangle ecophysiological processes related to plant water and carbon cycling (Gessler et al. 2009). According to the theory of Farquhar et al. (1982), the ratio between the intercellular CO_2 concentration (c_i) and c_a is a proxy for kinetic isotope effects and drives the $^{13}CO_2$ discrimination at the leaf-level. The resulting $\delta^{13}C$ of photosynthate (with some downstream compound specific fractionation; see below) is imprinted in wood cellulose and thus allows inferring physiological connections to stomatal conductance, WUE, and climatic constraints (Gessler et al. 2009). The quality of these links appears to be stable across scales, as most (but not all; Battipaglia et al. 2013) empirical evidence suggests that plants undergo physiological adaptation to changes in c_a to keep the relative gradient for CO_2 diffusion into the leaf ($1 - c_i/c_a$) close to constant (Franks et al. 2013). Leaf-level effects can, however, be obscured by post-carboxylation fractionation that may occur between CO_2 assimilation and allocation of carbohydrates to tree-ring cellulose (Brüggemann et al. 2011; Gessler et al. 2014). As a consequence, $\delta^{13}C$ may change (1) as photosynthate is moved to and from starch storage pools, (2) prior to and during transport from a leaf to cambial tissue, or (3) during respiration of some fraction of the photosynthate prior to cellulose synthesis (Helle and Schleser 2004; Gessler et al. 2014). Numerous studies, however, have found a strong relationship between tree-ring $\delta^{13}C$ and climate variables (e.g., Masson-Delmotte et al. 2005), suggesting work is also required to differentiate environmental imprints from CO_2 effects.

Separating the impacts of carbon assimilation (demand for CO_2) and stomatal conductance (supply of CO_2) based on tree-ring $\delta^{13}C$ variation alone is challenging. The "dual isotope" concept proposed by Scheidegger et al. (2000) facilitates the interpretation of $\delta^{13}C$ variation by measuring $\delta^{18}O$ from the same material. Oxygen isotope variation is viewed as a measure of evaporative flux as it depends on stomatal conductance, but less directly on photosynthetic rates. This dual approach has successfully been used to interpret $\delta^{13}C$ variation in tree rings (Brooks and Mitchell 2011), but caution must be exercised regarding a number of model assumptions (Roden and Siegwolf 2012). $\delta^{18}O$ variation in tree-ring cellulose is a function of source water $\delta^{18}O$, atmospheric humidity (or VPD), atmospheric vapor $\delta^{18}O$, kinetic and equilibrium fractionation associated

with water flux into the leaf, biochemical fractionation during sucrose synthesis, and the proportion of O that is exchanged with stem water at the site of cellulose synthesis (Roden et al. 2000; Treydte et al. 2014).

The above framework is useful in deriving comparable estimates of both WUE and wood increment and in comparing their inter-annual to decadal variability. Yet, there is evidence that the relationship between WUE and cellulose $\delta^{13}C$ may be more detectable during periods and/or in regions with relatively frequent and pronounced droughts (Sarris et al. 2013). At the same time, drought conditions lead to stomatal closure, increased NSC utilization (McDowell et al. 2011), and a reduction in carbon uptake and growth, at least partly explaining the absence of a growth increase in response to higher WUE in some earlier studies. Thorough testing of these mechanisms will require large networks of tree-ring stable isotope records that can provide new insight into observed global NPP trends over recent decades (Zhao and Running 2010). Our understanding of how shifts in WUE translate into productivity changes may further be enhanced by combining carbon and oxygen isotope measurements from wood cellulose with EC quantifications of the carbon, water, and energy budgets across ecosystems (Belmecheri et al. 2014).

Forest disturbances

Natural and anthropogenic forest disturbances and combinations thereof are the primary avenues through which forest ecosystems may be converted from carbon sinks into sources (Veblen et al. 1994), thereby releasing large amounts of carbon into the atmosphere over short time periods. Disturbances resulting from human activities include land-use changes such as deforestation and forest harvesting (Masek et al. 2011), as well as land management practices. The major natural disturbances acting on landscape scales are wildfires (Page et al. 2002), insect defoliation (Hicke et al. 2012), and short-term weather events such as wind and snow storms (Chambers et al. 2007). The carbon cycle responses to forest disturbances are complex and can show non-linear, threshold-like behavior (Breshears and Allen 2002). These responses also involve different time scales, from a carbon source immediately after disturbance to a legacy sink in case of forest regrowth for decades after disturbance. Assessment of disturbance impacts is further complicated by interactions among different types of disturbances (McCullough et al. 1998) and their feedbacks with ongoing and projected climate change (Flannigan et al. 2009; Scholze et al. 2006; Yue et al. 2013). Advanced understanding and quantification of specific disturbance regimes across a range of spatiotemporal scales will serve to improve reconstructions and projections of carbon cycling (Kasischke et al. 2013).

Land management records (Masek et al. 2011) or remotely sensed data of the affected area (Frolking et al. 2009) have been used to derive spatially extensive estimates for disturbance history. These datasets combined roughly cover the past century (Kasischke et al. 2013) and can be used to quantify disturbance type, frequency (Zeng et al. 2009), seasonal timing (Turetsky et al. 2011), event length (Hogg et al. 2005), spatial extent (Kasischke et al. 2002), intensity (Proulx and Greene 2001), and severity (Turetsky et al. 2011). Disturbance history inferred from tree rings complements land management and satellite records and importantly provides a historical (pre-satellite era or even pre-twentieth century) context for recent disturbance events (Pederson et al. 2014). This is particularly relevant for natural forest disturbances (i.e. wildfire, insect outbreaks, and storms) for which only limited observational data are available at the landscape scale and whose characteristics have changed over time (i.e. pre- vs. post-human settlement) and are expected to continue to change with projected climate trends.

The majority of tree ring-based fire history studies use heat-caused lesions in the boles of surviving trees to date historical low intensity surface fires (Swetnam and Baisan 1996). Tree-ring cross-dating can also be used to date synchronized recruitment events that result from severe crown fires in closed-canopy forests (e.g., Brown and Wu 2005). These techniques are useful for stand level (Taylor and Skinner 1998) to regional scale (Trouet et al. 2010) assessments, and have advanced our understanding of fire regimes regarding frequency, extent, and seasonality. The long (typically 200+ years) fire histories allow characterization of fire climatology on inter-annual to multidecadal time-scales (e.g., Swetnam 1993) and assessment of the modulating role of temperature and atmospheric circulation patterns on summer drought (Trouet et al. 2010), spring snowpack duration, and fire season length (Westerling et al. 2006), which regulate fire occurrence and severity. These historical interannual to centennial fire regime dynamics include fire return intervals and fire–climate–vegetation interactions, facets that can be integrated with predictive models to refine projections of ecosystem change under future warming (Kelly et al. 2013).

In a similar way, tree-ring-based reconstructions of insect outbreak occurrences can help elucidate their impact on forest ecosystem dynamics. Forest insect defoliation events often result in decreased tree biomass increment and in wood anatomical changes, and can thus be analyzed using dendrochronological methods (Schweingruber et al. 1979). By compiling tree- and site-level defoliation data, forest insect population dynamics can be studied across spatial and temporal scales (Babst et al. 2010; Speer et al. 2001). Particularly relevant to the study of carbon cycle dynamics are (1) the oscillatory behavior of many forest insect populations and how it is influenced by climate change (Bale et al. 2002) and (2) the interaction between insect outbreaks and other disturbances (e.g., wildfire). Insect population cycles are the result of trophic interactions or maternal effects (Berryman 1996), and tree-ring studies have demonstrated the century-long regularity of these cycles for various insect species (e.g., Boulanger and Arseneault 2004; Esper et al. 2007). In the case of the European larch budmoth, evidence suggests that the absence of peak outbreak events in recent decades may be attributable to anthropogenic warming (Johnson et al. 2010).

A third forest disturbance agent that can be studied using dendrochronological methods is forest blowdown caused by windstorms. Such events can be detected in tree-ring series by identifying growth suppressions resulting from traumatic canopy loss and growth releases in surviving trees that benefit from canopy opening (Hadley and Knapp 2011). Windthrow-related tree growth anomalies compiled at the site and regional level provide evidence for the timing, frequency, and intensity of wind storms and their role on regional forest ecology (Seidl and Blennow 2012). Windstorms modulate forest structure and demography (Harcombe et al. 2004), and have the potential to convert forests from carbon sinks to sources, and then sinks again during recovery (Lindroth et al. 2009). Global climate model projections suggest an increase in extreme wind events and disturbances under future climate scenarios (Blennow and Olofsson 2008). This affects other disturbance agents and can further exacerbate future disturbance regimes. Windstorms interact with wildfire disturbance through the creation of large fuel loads (Weisberg and Swanson 2003) and with insect colonization success through reduced tree growth and vigor related to root and crown damage (Komonen et al. 2011). Such disturbance interactions, as well as decadal- to centennial-scale forest disturbance dynamics, form an important limitation in our understanding of the future role of disturbances in the regional to global forest carbon balance. Tree-ring records from surviving trees can provide a long-term perspective on disturbance dynamics, but provide limited direct information on large-scale mortality and changes in stand density (except death dates and recruitment timing; Pederson et al. 2014).

Model evaluation and data assimilation

Dynamic vegetation models are an essential instrument used to investigate the magnitude and spatiotemporal dynamics of the global terrestrial carbon cycle, upscale in situ observations of ecosystem productivity, and infer and project relevant ecosystem processes (Sitch et al. 2008). Despite the improvements achieved by comparing

multi-model ensembles (Friedlingstein et al. 2006), persistent challenges continue to hamper reducing the uncertainty in predictions of the forest carbon sink and its response to changes in environmental forcing. Uncertainties may derive from fluctuations in land cover and use (Kaplan et al. 2012), from climatic input data (Poulter et al. 2011), or from model parameters and structure that do not fully capture the spatiotemporal variability in ecosystem processes (Keenan et al. 2012). The latter problem is expressed, e.g., through discrepancies between the observed and simulated climate responses of forests (Babst et al. 2013; Piao et al. 2013), the limited consideration of carry-over effects from the previous growing season typically found in observational growth records (Wettstein et al. 2011), or an unrealistic timing of growth onset and cessation (Kucharik et al. 2006; Richardson et al. 2013).

Constraining vegetation model simulations with in situ observations is a promising method to reduce the above caveats if the uncertainty in both model and observational data is accurately considered (Keenan et al. 2011). Eddy-covariance quantification of ecosystem carbon uptake and release have been employed most frequently for this purpose (Beer et al. 2010), but may not be sufficient to constrain medium- to long-term trends in forest carbon accumulation. This is due to (1) the influence of processes and disturbances which are not considered in the models (Keenan et al. 2012), (2) the generally short time series offered by EC measurements and the focus of the EC method on informing fast processes, (3) the unequal abundance of flux towers among different forest types, and (4) the inability to derive carbon allocation patterns from CO_2 fluxes measured above the canopy. Tree-ring parameters have rarely been assimilated into carbon-cycle models, but constraining a process model using biometric estimates of growth led to reductions in parameter uncertainty and improved statistical confidence in model predictions (Richardson et al. 2010). Using tree-ring records to extend estimates of growth over longer periods in model-data fusion exercises should thus be encouraged.

Tree-ring archives are now reaching reasonable global coverage (St. George and Ault 2014; Breitenmoser et al. 2014) and offer valuable opportunities to inform vegetation models about annually resolved and long-term forest growth variability and to some extent disturbances. Large-scale growth reductions after disturbances and subsequent recovery need to be considered when past changes in the forest carbon sink are assessed (Bellassen et al. 2011). Hence, potential exists for the use of tree rings to benchmark forest productivity simulations, either through direct comparison of simulated NPP increment with radial growth trends (Malmström et al. 1997) or through comparison of

observed versus simulated sensitivities of forests to environmental drivers (Babst et al. 2013). Another interesting path is the possibility to incorporate a process-based model [Vaganov-Shashkin-Lite (VS-lite); Tolwinski-Ward et al. (2011)] to simulate radial tree growth within a fully fledged climate model. The VS-lite model requires only climatic and geographic input data, and this forward modeling approach has been shown to simulate tree-ring chronologies across the globe reasonably well (Breitenmoser et al. 2014). Efforts in modeling radial stem growth from vegetation models will facilitate comparisons between real and simulated tree-ring data (Li et al. 2014). This is crucial, as it will eliminate the need to transform tree-ring data into derived variables such as NPP—a process that introduces new uncertainties—for comparison with or assimilation into modeling frameworks.

Perspectives

We recognize that no individual discipline or method is capable of conclusively resolving forest carbon cycling at large spatial scales and high temporal resolution. Instead, recent efforts have highlighted the benefits of combining multiple data streams to constrain the spatiotemporal dynamics of forest growth and productivity. Continued efforts to synthesize data products and thereby accumulate the strengths of individual approaches are desirable to improve empirical estimates, model structures, and calibrations and projections of ecosystem functions in a warming world. In this respect, tree rings provide valuable input on multiple temporal scales (Fig. 4), as they continue to be measured worldwide, from arctic environments, where growth is largely happening below ground (Buchwal et al. 2013), to the tropics, where a research focus remains on identifying species and regions where annual rings are formed (Trouet et al. 2012).

Based on our literature review, the following applications of tree-ring archives appear most promising for improving our understanding of terrestrial carbon cycling:

1. Tree-ring quantification of the annual biomass increment can (1) contribute to refining forest carbon budgets, (2) be combined with EC measurements to inform carbon allocation patterns, (3) be used in combination with airborne estimates of forest growth and structure, or (4) improve the temporal resolution of periodical forest inventories. Thereby, consistent sampling schemes are required to produce comparable results across various climate zones and forest types (Babst et al. 2014a; Nehrbass-Ahles et al. 2014).

2. Estimates of WUE based on tree-ring stable isotopes provide information on the response of forest carbon

Fig. 4 Overview of temporal scales where tree-ring data can provide information on ecosystem processes. The increment core was sampled from a *Picea abies* individual in Romania (north-eastern Carpathians, 400 m a.s.l.)
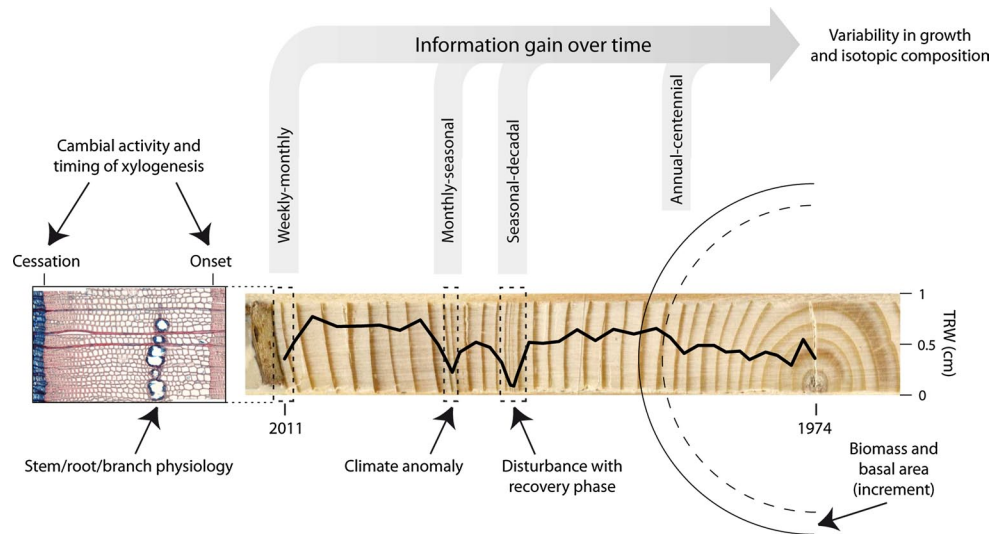
uptake to environmental constraints, such as drought. Such data are promising in order to refine the simulated response of NPP to climatic limitations in current-generation earth system models, which are known to be overly drought sensitive compared to tree-ring observations (Babst et al. 2013). They also provide long-term records of the WUE and its recent fluctuations in response to the combined effects of CO_2 and climate forcing.

3. The repeated sampling and wood anatomical analysis of micro-cores allows for cambial phenology and wood formation to be disentangled from leaf phenology observed during monitoring programs or using digital image analysis (Richardson et al. 2013). This may provide new insights into carbon allocation dynamics at and between growth onset and cessation, which is particularly relevant for the depletion and replenishment of non-structural carbohydrate reserves (Dietze et al. 2014). In this context, wood density or wood anatomical measurements can provide additional information on the fate of assimilates after the termination of radial growth and before the end of the photosynthetically active period.

4. The magnitude and seasonality of forests' response to environmental drivers largely determines the productivity changes if a growth limitation shift occurs. These can be short-term events such as climate extremes or disturbances, which are difficult to predict (Seneviratne 2012), or longer-term changes in the base climate. Tree rings are an instrument to assess (non-)climatic forest growth limitations and can be used, e.g., to benchmark the climate sensitivity of large-scale NPP estimates (Babst et al. 2013).

5. Tree rings provide an opportunity to place current environmental changes into a centennial to millennial context. Besides reconstructing climate fluctuations (Büntgen et al. 2011; Trouet et al. 2009) or the temperature sensitivity of the atmospheric CO_2 concentration (Frank et al. 2010), the long-term perspective offered by tree-ring archives allows the observation of trends in the occurrence of extreme events (Battipaglia et al. 2010). Extreme events can have disproportionally large effects on ecosystems and society, and, as they are rare by definition, require analyses that transcend the timescales captured by instrumental records.

Communication among research communities needs to be further stimulated as a step towards fully harnessing the scientific potential highlighted herein. Carbon-cycle research transcends traditional applications of tree-ring proxies and is only slowly entering the scope of dendrochronology. In turn, the value of tree rings in a carbon context has yet to be fully recognized. Bridging existing gaps is thus inevitable for successful implementation of novel paths of investigation. Furthermore, multidisciplinary collaborations are considerably facilitated by publicly available data from growing international platforms such as FLUXNET or the ITRDB. Contributions to these and other archives can thus only be encouraged as they continuously extend the scales of possible studies and are crucial for maintaining an active dialogue between researchers and with funding agencies.

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