It is not just a 'trade-off': indications for sink- and source-limitation to vegetative and regenerative growth in an old-growth beech forest

Martina Mund[1] iD, Mathias Herbst[2], Alexander Knohl[3,4] iD, Bertrand Matthäus[5] iD, Jens Schumacher[6] iD, Peter Schall[1] iD, Lukas Siebicke[3], Rijan Tamrakar[3,7] iD and Christian Ammer[1,4] iD

[1]Silviculture and Forest Ecology of the Temperate Zones, University of Göttingen, Büsgenweg 1, D-37077, Göttingen, Germany; [2]German Meteorological Service, Centre for Agrometeorological Research, Bundesallee 33, D-38116, Braunschweig, Germany; [3]Bioclimatology, University of Göttingen, Büsgenweg 2, D-37077, Göttingen, Germany; [4]Centre of Biodiversity and Sustainable Land Use (CBL), University of Göttingen, Büsgenweg 1, D-37073, Göttingen, Germany; [5]Max Rubner-Institute, Federal Research Institute of Nutrition and Food, Schützenberg 12, D-32756, Detmold, Germany; [6]Institute of Mathematics, University of Jena, Ernst-Abbe-Platz 2, D-07743, Jena, Germany; [7]School of Natural Sciences, Bangor University, Bangor, LL57 2UW, UK

Author for correspondence:
Martina Mund
Tel: +49 551 395974
Email: martina.mund@forst.uni-goettingen.de

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Summary

• Controls on tree growth are key issues in plant physiology. The hypothesis of our study was that the interannual variability of wood and fruit production are primarily controlled directly by weather conditions (sink limitation), while carbon assimilation (source limitation) plays a secondary role.

• We analyzed the interannual variability of weather conditions, gross primary productivity (GPP) and net primary productivity (NPP) of wood and fruits of an old-growth, unmanaged *Fagus sylvatica* forest over 14 yr, including six mast years.

• In a multiple linear regression model, *c.* 71% of the annual variation in wood-NPP could be explained by mean air temperature in May, precipitation from April to May (positive influence) and fruit-NPP (negative influence). GPP of June to July solely explained *c.* 42% of the variation in wood-NPP. Fruit-NPP was positively related to summer precipitation 2 yr before ($R^2 = 0.85$), and negatively to precipitation in May ($R^2 = 0.83$) in the fruit years. GPP had no influence on fruit-NPP.

• Our results suggest a complex system of sink and source limitations to tree growth driven by weather conditions and going beyond a simple carbon-mediated 'trade-off' between regenerative and vegetative growth.

Introduction

Sink or source limitations to tree growth and their underlying mechanisms are key issues in plant physiology. They are fundamental both to the understanding of tree growth and to its modeling under a changing climate. The term 'source limitation' describes the dominant restriction (or control) on individual plant growth or single plant organs by the availability of resources, mainly photo-assimilates. Resources can be limited directly by insufficient supply, insufficient mobilization or translocation of resources to the location of demand, or competition among different sinks. By contrast, 'sink limitation' postulates a control by factors that influence growth processes (e.g. cell division, cell expansion) directly so that the affected plant or organs are not able to use the available resources (Wareing & Patrick, 1975; Wardlaw, 1990; Kozlowski & Pallardy, 1997; White *et al.*, 2016).

The strong impact of weather conditions on annual stem growth is well known (Schweingruber, 1988; Fritts, 2001;

Pretzsch, 2009; Way & Oren, 2010). Similarly, the role of weather conditions in the synchronization and extent of periodically high fruit production (masting) is also generally accepted (Pearse *et al.*, 2016). However, current knowledge of the underlying control mechanisms and their interactions remains ambiguous. In their reviews on environmental controls, Körner (2003, 2013, 2015) and Millard *et al.* (2007) concluded that tree growth is not limited by carbon, at least in most cases and under current climatic conditions. In this context, Sala *et al.* (2011) and Piper & Fajardo (2011) questioned the hypothesis that the often observed size- or age-related decline of tree and stand growth is due to an increasing shortage of carbon. Accordingly, Fatichi *et al.* (2018) suggested a better representation of sink-driven control mechanisms for plant growth in terrestrial biosphere models. Case studies on annual stem growth, weather conditions and net ecosystem carbon fluxes have provided strong evidence that stem growth is limited more directly by water deficits and temperature than by carbon assimilation (Mund *et al.*, 2010; Delpierre *et al.*, 2015; Lempereur *et al.*, 2015). Klein *et al.* (2016) showed that

trees are able to grow and to store carbon simultaneously and that the amount of starch stored in the stem is sufficient, at least theoretically, for stem growth over 7–30 yr. However, if parts of the carbon reserves cannot be remobilized and thus are *de facto* sequestered (Millard *et al.*, 2007; Palacio *et al.*, 2014), a carbon limitation may occur despite high quantities of stored carbon.

The often observed reduction in stem growth in mast years is frequently interpreted as a 'trade-off' (or 'switching') between vegetative and regenerative growth resulting from a preferential allocation of (limited) resources to fruits (Kelly & Sork, 2002; Monks & Kelly, 2006; Han *et al.*, 2011; Pearse *et al.*, 2016). Most recently, Hacket-Pain *et al.* (2015, 2018) interpret fruit production as an important factor determining the interannual variability in stem growth and explaining indirect climate effects on stem growth.

The negative correlation between stem and fruit growth and the high investment of nutrient resources into fruit production, particularly in tree species with large fruits and strong periodicity in fruiting, supports the assumption that masting is controlled by resource availability (Piovesan & Adams, 2001; Kelly & Sork, 2002; Schmidt, 2006; Yasumura *et al.*, 2006; Eichhorn *et al.*, 2008; Drobyshev *et al.*, 2014; Hacket-Pain *et al.*, 2015; Ascoli *et al.*, 2017; Han & Kabeya, 2017; Vacchiano *et al.*, 2017). However, it is not clear which nutrients are most critical for the regenerative cycle (Crone & Rapp, 2014; Pearse *et al.*, 2016; Allen *et al.*, 2017). When interpreting the negative relationship between wood and fruit growth as a 'trade-off', many studies focus on carbon as the most limited resource for which wood and fruits compete (Miyazaki, 2013; Drobyshev *et al.*, 2014; Hacket-Pain *et al.*, 2017; Rosati *et al.*, 2018). Water availability is often neglected as a potential driver for masting or is considered just as a resource needed for carbon assimilation (Vacchiano *et al.*, 2018).

In Fig. 1 the potential control on tree growth by weather conditions is embedded in a schematic framework of carbon allocation. A shortage of carbon would imply a strong competition between fruit and wood growth for carbon and thus a carbon-mediated 'trade-off' between these two sinks. At the tree level, utilization of carbon reserves seems to be the most reasonable and efficient way to minimize this competition. However, the use of carbon reserves does not indicate *per se* a shortage of recent assimilates or a limitation to growth at the tree level, nor does it suggest *per se* a triggering of flower bud initiation by high carbon reserves. Instead, it may represent a kind of 'fine-tuning' (Han *et al.*, 2016) of carbon allocation to balance periods or locations of extraordinarily high or low sink strength.

The objective of this study was to identify the main drivers for the interannual variability in wood and fruit production, and thus to understand the often-observed negative relationship between vegetative and regenerative growth. The hypothesis is that, under current environmental conditions, the interannual variability of wood and fruit production are primarily controlled directly by weather conditions (sink limitation), while variations in carbon assimilation (source limitation) play a secondary role. To test this hypothesis, we analyzed the interannual variability of weather conditions, gross primary productivity (GPP) as an estimate for carbon assimilation, and net primary productivity of

wood (wood-NPP) and fruits (fruit-NPP) in an old-growth, unmanaged European beech (*Fagus sylvatica*) forest in central Germany over 14 yr (2003–2016). The study period included 6 yr of 'common' to 'abundant' masting. A close correlation between weather conditions and wood- or fruit-NPP but not between GPP and wood- or fruit-NPP would indicate a control of growth directly by weather conditions, or by other resources than carbon. Moreover, a different response of wood- and fruit-NPP to weather conditions would suggest different control mechanisms for vegetative and regenerative growth.

Materials and Methods

The central methodological approaches of this study are: all measurements are from a single, unmanaged stand growing on a nutrient-rich soil so that effects of recent forest management can be excluded, and limitations by mineral nutrients are probably of minor importance; and we analyzed fruit production as a continuous variable, and used the term 'mast' (defined according to LaMontagne & Boutin, 2009) mainly for comparison with other studies based on fruiting classes. To stress the key role of floral bud initiation for the periodicity of fruit production we used the figurative terms 'off'- or 'on'-years for years below or above a weather signal that may indicate a threshold for fruiting.

Study site

The study site (51°05′N, 10°27′E) is located in the core zone of the Hainich National Park, Germany. The suboceanic–submontane climate of the site in combination with fertile soil conditions (silty-clay Cambisols of 50–70 cm soil depth developed on Triassic limestone, covered with Pleistocene loess deposits) provide nearly optimal growing conditions for beech forests (Mund, 2004). Atmospheric nitrogen (N) depositions at the Hainich region amount to *c.* 20 kg N ha^{-1} yr^{-1} (TLUG, 2017).

European beech (*Fagus sylvatica* L.) dominates the canopy (70% of woody biomass carbon stocks, on average 68% of annual wood growth). European ash (*Fraxinus excelsior* L.) and sycamore maple (*Acer pseudoplatanus* L.) are codominant tree species. Single other deciduous species are admixed. Because of its history and current stand structure, the forest can be characterized as an old-growth, uneven-aged (1–250 yr) mixed beech forest (Mund, 2004). The main biometric stand characteristics are summarized in Table 1.

The study area comprised *c.* 150 ha and was defined by the most probable footprint area of the eddy-covariance (EC) system measuring the CO_2 exchange of the ecosystem (Anthoni *et al.*, 2004) (footprint: upwind area from which the resulting fluxes are detected by the EC system; Schmid, 1994). All tree measurements (see 'Tree measurements, woody biomass and growth estimates' below) were done within the footprint.

GPP derived from EC measurements

GPP as a measure for carbon assimilation of the studied ecosystem was calculated from EC measurements. The EC system consisted
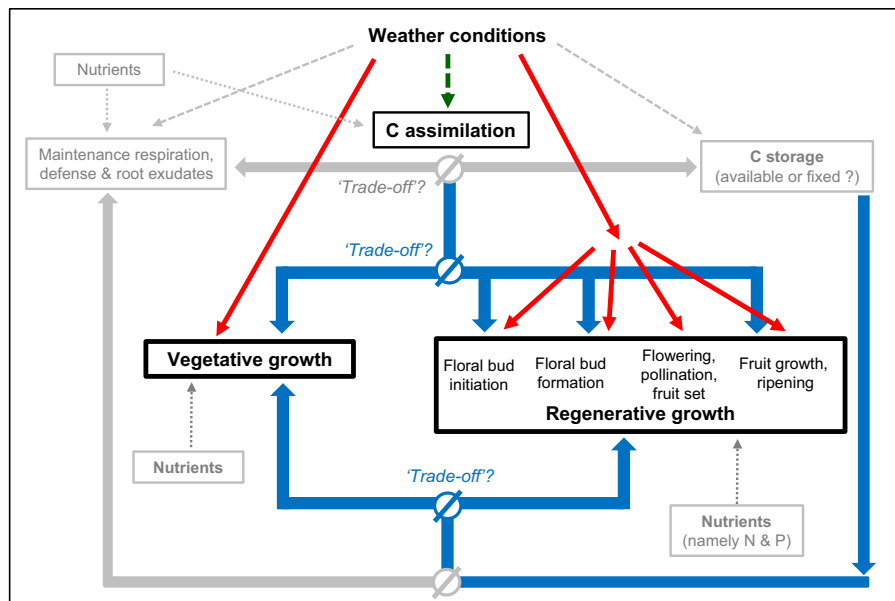
Fig. 1 Schematic framework of a direct control of vegetative and regenerative growth by weather conditions (red continuous arrows) and an indirect control via carbon assimilation (dashed green arrow) and associated carbon allocation schemes. A direct control on growth is equivalent to a 'sink limitation', and an indirect control represents a 'source limitation' (blue arrows, pathways of interest in this study; gray arrows, important pathways and mechanisms not investigated in this study).

Table 1 General stand characteristics of the study site 'Hainich' in 2011.

Species	Fagus sylvatica	Fraxinus excelsior	Acer pseudo-platanus	Others	Total
Stand density (n ha^{-1}) (%)	267 (82)	30 (9)	17 (5)	10 (3)	325 (100)
Arithmetic mean DBH (cm)	29	53	50	46	33
Arithmetic mean tree height (m)	23	34	29	27	25
DBH$_{10}$ (cm)	71	79	71	–	–
Height$_{10}$ (m)	35	37	31	–	–
Basal area (m^2 ha^{-1})	27	7	4	2	39
Timber volume (m^3 ha^{-1})	444	122	55	16	637
Woody biomass C stocks (t C ha^{-1}) (%)	160 (70)	40 (17)	23 (10)	7 (3)	230 (100)

The data include all trees with diameter at breast height ≥ 7 cm. DBH, diameter at breast height, 1.3 m above ground level; DBH$_{10}$ and height$_{10}$, quadratic mean of diameters and its corresponding predicted height of the 10% largest trees; 'Others', species group that includes *Carpinus betulus*, *Acer platanoides*, *Acer campestris* and *Ulmus glabra*. The given C stocks include the above- and below-ground woody biomass of living trees ≥ 7 cm in DBH.

of a sonic anemometer (Solent R3; Gill Instruments, Lymington, UK) mounted at a height of 43.5 m above ground and a closed-path infrared gas analyzer (LI-6262; Li-Cor, Lincoln, NE, USA) located at the base of the tower. For data synchronization, storage and processing the EDDYMEAS software (Meteotools, Jena,

Germany) and EDDYPRO software, v.4.1 (Li-Cor) were used. For more details about the instrumentation we refer to Knohl *et al.* (2003) and Tamrakar *et al.* (2018). The net CO_2 flux (NEE) was finally quality checked, gap filled (Herbst *et al.*, 2015) and partitioned into GPP and total ecosystem respiration (R_{eco}) using the FLUXNET online-tool based on Reichstein *et al.* (2005). The relationships between NEE, GPP, R_{eco} and fruit-NPP or weather conditions of the presented and a neighboring study site were recently analyzed by Tamrakar *et al.* (2018).

In this study, we explicitly restricted our analysis to GPP as an estimate for carbon assimilation at the ecosystem level, which stands at the very beginning of the carbon allocation process (Fig. 1). From a methodological point of view, the NEE measurements are more 'robust' than the derived GPP estimates. However, NEE results from carbon assimilation and the allocation of carbon to respiration or sequestration in different tree compartments and the mineral soil, and thus stands at the end of the allocation process. The absolute values of GPP and R_{eco} are strongly correlated with each other and with NEE because of the flux-partitioning procedure, but the interannual variation of their relative contribution to NEE results mainly from short-term changes in temperature and (indirectly) from soil moisture (Reichstein *et al.*, 2005).

The uncertainty of the GPP estimates is caused by two main imponderables. The first one, which relates to instruments and flux processing and partitioning of NEE into GPP and R_{eco} (Reichstein *et al.*, 2005), typically accounts for c. 5–10% of the flux measurements at 30 min resolution (Foken, 2017). The corresponding uncertainty at the annual time scale is considerably smaller due to time averaging of random uncertainties. We estimated the mean random uncertainty of EC fluxes for the years 2015 and 2016, based on time series analysis of replicated 30 min

flux estimates using the Markov chain Monte Carlo method following Hollinger & Richardson (2005), to be 1.1% of the annual carbon flux budgets. The second and more important source of uncertainty is the representativity of EC measurements under low levels of turbulence, which can lead to advection and storage resulting in a flux, which is undetected by above-canopy EC measurements. The resulting underestimation of R_{eco} is partly addressed by filtering for low friction velocity, $u*$ (Goulden *et al.*, 1996), and by replacing with modeled data from a nocturnal flux-temperature regression (Reichstein *et al.*, 2005). However, advection can lead to additional flux uncertainty despite $u*$-filtering (Kutsch *et al.*, 2008). Kutsch *et al.* (2008) have assessed advection at the current site through measurements and modeling and found that annual NEE estimates from EC were 12% larger than the model. Knohl *et al.* (2003) and Herbst *et al.* (2015) estimated the overall uncertainty of the annual EC-derived NEE, R_{eco} and GPP fluxes at the Hainich site to be *c.* 100 g C m^{-2} yr^{-1}. Nevertheless, we assume the dominant part of the systematic flux errors to persist between years, meaning that the different years will probably be affected by similar systematic errors, which would allow us to quantify valid interannual flux variability by correlation and regression analyses.

Weather conditions and relative plant available water

Air temperature and air humidity (HMP35D sensor; Vaisala, Helsinki, Finland) were recorded at the EC tower above the canopy and were used to calculate the vapor pressure deficit (VPD). Gross precipitation (RainGauge, Young, Traverse City, MI, USA) was collected in a forest clearing 800 m away from the tower. Global radiation (Rg) was measured at the top of the tower (CNR1; Kipp & Zonen BV, Delft, the Netherlands).

The relative plant available water (PAW) was derived from the actual volumetric soil water content (WC_{act}), wilting point (WC_{WP}) and volumetric water content at field capacity (WC_{FC}) (Mund *et al.*, 2010). WC_{act} was measured close to the EC tower by means of four Theta Probes (ML-2x; DeltaT, Cambridge, UK) at a depth of 8 cm, and one Theta Probe at each of the following depths: 16 and 32 cm. WC_{WP} and WC_{FC} were calculated according to Teepe *et al.* (2003) on the basis of soil texture analyses at the study site (Mund, 2004).

Tree measurements, woody biomass and growth estimates

At the beginning of the flux studies (spring 2000), biomass and growth estimates were based on a transect of adjacent inventory plots along the center of the footprint including 14 circular plots, each with a radius of 15 m. In 2005 this set of inventory plots was enlarged by 20 additional plots that were distributed over the entire footprint according to an importance sampling design (Anderson, 1999). Thus, the inventories in 2005 and 2011 included 34 plots that summed to a total area of 2.4 ha.

On the inventory plots, all trees with a diameter at breast height (DBH; 1.3 m above ground level) > 7 cm were measured in 2000, 2005 and 2011. Individual tree height was measured in 2005 (Vertex III, Haglöf, Sweden).

Annual wood-NPP resulted from continuous measurements of diameter increments at breast height (automatic rope dendrometers; Max Planck Institute for Biogeochemistry, Jena, Germany, and manual band dendrometers, D1; UMS GmbH, München, Germany). The dendrometer trees represented all species groups and size classes of the footprint. Because of technical constraints, a natural dieback of single trees that had to be replaced with other trees (in total seven trees), and because of damage to the dendrometers, the total number of valid measurement trees per year varied between 54 and 95. In 2012, the technical necessity to convert all rope dendrometers to band dendrometers reduced the number of valid measurement trees to 33. The tree-based diameter increment was extrapolated to stand level via species-specific linear regression models, which described the relationship between initial basal area and basal area increment of the dendrometer trees, and the tree data of the stand inventories. Above- and below-ground woody biomass per tree were estimated via biomass regression functions with DBH, and for beech, tree height also, as predictor variables (Fehrmann, 2006; Wutzler *et al.*, 2008; Supporting Information Table S1). For the conversion of woody biomass into carbon units, a mean carbon concentration of 50% was assumed.

Annual NPP values of leaves, buds and fruits were derived from litter sampling (2003–2009: 29 traps, 0.5 m^2 per trap, since 2010: 25 traps, 0.25 m^2 per trap). The samples were separated, dried at 70°C and weighed. Mean carbon concentration of leaves was 48% (weighted mean of the different tree species), and that of beech fruits was 54% (weighted mean of seeds and shells; total combustion, elemental analyzer 'VarioEL II', 1998; Elementar Analyse GmbH, Hanau, Germany). Fine root-NPP was estimated via a constant ratio between leaf- and fine root-NPP (Claus & George, 2005; leaf-NPP/fine root-NPP = 1.111). NPP of ground vegetation was assumed to be constant and was taken from a biomass study carried out at the study site in 2000 (67 g C m^{-2} yr^{-1}, G. Gebauer, University Bayreuth, Germany, pers. comm.).

The spatial variation in leaf-, bud- and fruit-NPP is given as the standard deviation of the mean of all litter traps. For wood-NPP, high variation among individual trees as well as errors resulting from the expansion and extrapolation of annual diameter increments of the dendrometer trees to mean wood-NPP at the stand level were considered. The standard error of the estimated annual diameter increment per inventory tree was calculated via bootstrapping with replacement ($n = 200$; R v.3.4.1) of the species-specific linear regression models (see paragraphs above). Total uncertainty of the wood-NPP estimates was then calculated by error propagation and included the error of the diameter increment, the biomass estimates via regression functions (3%) (Mund *et al.*, 2015), the inventories (sampling error, 5.5–8.7%), the tree height measurements (2%) (Kramer & Akça, 1995) and the carbon concentration of wood (1%) (Wirth *et al.*, 2004). As coarse- and fine root-NPP were calculated via constant allometric relationships, their interannual variability may be underestimated. Also, potential interannual variations in wood formation or differences in wood density along the stem or between stem, branches and coarse roots are not reflected in our study.

Correlation and linear regression analyses

We analyzed three major sets of data to identify the influence of single, extraordinary, or mean weather conditions and/or GPP on wood- and fruit-NPP: monthly air temperature and precipitation, relative PAW, onset of the growing season, VPD, Rg and GPP during different periods of the current ($t0$) and the two previous ($t-1$, $t-2$) growing seasons (April–October); daily time series of relative PAW to identify soil drought which may cause the termination of the main phase of stem growth (Mund *et al.*, 2010); and late frost events (daily minimum) in relation to leaf development.

Considering the limited length of our time series, the high number of potentially influencing variables and time periods, and the high multicollinearity among weather variables, we started our analyses based on existing knowledge about the main drivers for stem growth and fruit production of beech. This can be summarized as follows: stem growth is highly sensitive to weather conditions during spring and early summer (Dittmar *et al.*, 2003; Mund *et al.*, 2010); late frost has as negative effect on stem growth (Dittmar *et al.*, 2006); mast years seem to be driven by the combination of a cold, wet summer 2 yr before a mast and a warm, dry summer 1 yr before the mast, and the lack of extreme conditions during flowering; and masting may be supported by high carbon resources assimilated and stored before the mast year (Piovesan & Adams, 2001; Hilton & Packham, 2003; Ichie *et al.*, 2013; Drobyshev *et al.*, 2014).

The relationships between wood-, fruit-, leaf- or total-NPP and weather variables, which describe these potentially growth-relevant weather conditions, were assessed via a correlation matrix (Table S2). All variables that were previously identified as important predictors for individual stem growth of beech and ash at the study site (Mund *et al.*, 2010) as well as variables with $r > 0.4$ were considered in the multiple linear regression analyses. It was assumed that weather variables that influence NPP mainly via their impact on carbon assimilation would have a lower influence on wood-NPP than GPP or might even be replaced by GPP in a multiple linear regression model. Criteria for the exclusion of predictor variables or models were: variance inflation factor (VIF) > 2, the variable with the highest VIF was taken out first (exclusion of multicollinearity); variables with no significant influence ($P > 0.05$); and regression models with lower adjusted R^2 or less significance of the predictor variables. Because of the limited size of the data set, the leave-out-analysis was restricted to single prominent years.

The correlation and linear regression analyses were done using Statistica 13.3 for Windows (StatSoft Inc., Tusla, OK, USA) and Sigmaplot for Windows 12.0.

Strengths and weaknesses of the data set

The most prominent strength of the present study is also its most serious weakness. The study is based on time series of tree growth, weather and GPP in a single, unmanaged stand growing under favorable site conditions. This reduces variations in growth due to management and different site conditions compared to regional studies on masting and stem growth. Substantial changes in the availability of mineral nutrients over the study period cannot be excluded but seem to be of minor importance at this fertile study site. The other side of the coin is that the statistical analyses in this study are limited due to the high number of (often collinear) weather variables compared to only 14 yr of observation. Thus, the results of this study should be interpreted as new insights into the control of vegetative and regenerative growth that go beyond competition for carbon, and that are needed to be confirmed by future studies using comprehensive regional data bases (e.g. the MAST database, Ascoli *et al.*, 2017) and new modeling approaches (Bogdziewicz *et al.*, 2018; Vacchiano *et al.*, 2018).

Results

Interannual variability of NPP

Above- and below-ground wood-NPP varied between $107 \pm 54\ \mathrm{g\,C\,m^{-2}\,yr^{-1}}$ in 2011 and $267 \pm 95\ \mathrm{g\,C\,m^{-2}\,yr^{-1}}$ in 2007 (Fig. 2). Mean wood-NPP of the study period (14 yr) was $201 \pm 80\ \mathrm{g\,C\,m^{-2}\,yr^{-1}}$. Leaf-NPP reached on average $166 \pm 11\ \mathrm{g\,C\,m^{-2}\,yr^{-1}}$, with a minimum in 2011 ($122 \pm 35\ \mathrm{g\,C\,m^{-2}\,yr^{-1}}$) and a maximum in 2008 ($184 \pm 30\ \mathrm{g\,C\,m^{-2}\,yr^{-1}}$). With a coefficient of variation (CV) of 20%, the interannual variability of wood-NPP was almost twice the variability of leaf-NPP (CV 11%).

During the study period, three 'common' masts (2004/2006/2014; $0 < $ standardized deviate ≤ 1, LaMontagne & Boutin, 2009) and three 'abundant' masts (2009/2011/2016; standardized deviate > 1) occurred (Fig. 2). In these years, beech fruits accounted for more than 90% of total fruit-NPP. Total NPP varied between 608 ± 97 and $836 \pm 149\ \mathrm{g\,C\,m^{-2}\,yr^{-1}}$ with an average of $683 \pm 106\ \mathrm{g\,C\,m^{-2}\,yr^{-1}}$ (Table S3).

Extraordinary weather conditions

The study period was characterized by high variability in precipitation (p) and contrasting air temperature (T) in spring (Fig. 3). Most obvious was the low p during the growing seasons in 2003 and 2008 compared to that in 2007, the series of low p in spring 2011 and 2012 followed by high p in spring 2013, and again low p in spring 2015. Temperature in May, identified as the main predictor of individual stem growth of beech at the study site (Mund *et al.*, 2010), was extraordinarily low in 2004, 2010 and 2013.

The time series of relative PAW revealed serious soil drought already at the beginning of May in 2011 and 2016, and very wet conditions in 2009 (Fig. S1).

In 2010 and 2011, late frost with a daily minimum of -0.7 and $-0.5°C$, respectively, occurred during leaf development (Fig. S2). However, these values were above the threshold of $-3°C$ suggested by Dittmar *et al.* (2006) for serious growth reductions. Canopy photographs taken from the top of the eddy-tower showed no leaf damage (data not presented). Therefore, we assumed that at our study site the late frosts were not strong enough to cause substantial damages (in contrast to other regions in 2011; Menzel *et al.*, 2015; Príncipe *et al.*, 2017) and neglected them in the following analyses.
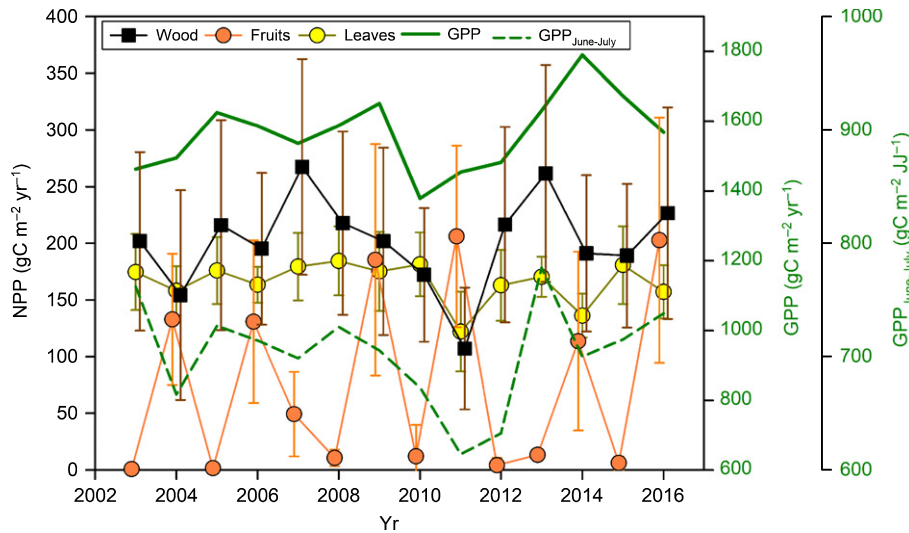
Fig. 2 Annual gross primary productivity (GPP), gross primary productivity in June and July (GPP$_{June–July}$) and net primary productivity (NPP) (mean ± SD) of above- and below-ground wood, leaves and fruits in the beech (*Fagus sylvatica*) forest 'Hainich'.
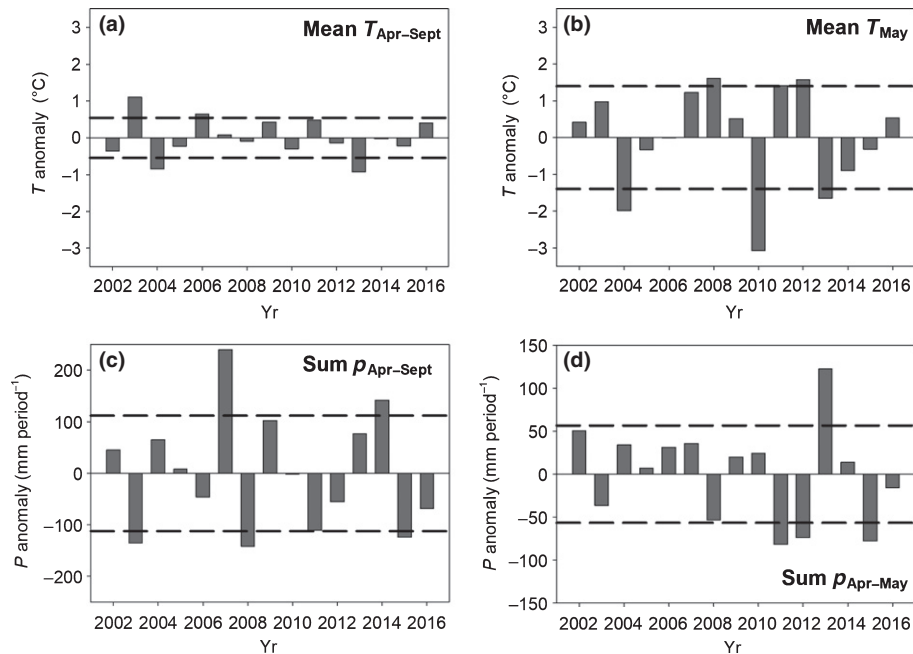

Fig. 3 Anomalies of mean air temperature (*T*) from April to September (a) and in May (b), and precipitation sums (*p*) from April to September (c) and from April to May (d) during the period 2002–2016. The anomalies are defined as the difference between the value of a single year and the mean of the study period. Values above or below the mean ± SD were classified as 'extraordinarily' high or low. The dashed lines mark the ± SD of the means.

Correlations between GPP and wood-NPP

The interannual variability in GPP differed markedly from that of wood-NPP (Fig. 2), and there was no significant (*P* > 0.05) correlation between these two variables (Table S2). However, when considering different time windows within the growing season, significant positive correlations were found between wood-NPP and GPP in summer whereas GPP from June to July (GPP$_{June–July}$) showed the highest correlation coefficient (*r* = 0.65). The correlation between wood-NPP and GPP$_{June–July}$ was strongly affected by the years 2007 and 2012, in which wood-NPP was higher than would be expected from GPP$_{June–July}$

(Fig. 4). If these two years were excluded, the correlation would increase to *r* = 0.94 (considering only wood-NPP of beech: *r* = 0.89). Fruiting clearly had no influence on this relationship. The respective correlation between wood-NPP and NEE was weaker and not significant (Fig. S3).

Predicting wood-NPP

As described in the Materials and Methods section we began our regression analyses for wood-NPP with mean air temperature in May (*T*$_{May}$) as a predictor variable. The weak correlation with this variable was obviously caused by the lowest wood-NPP in
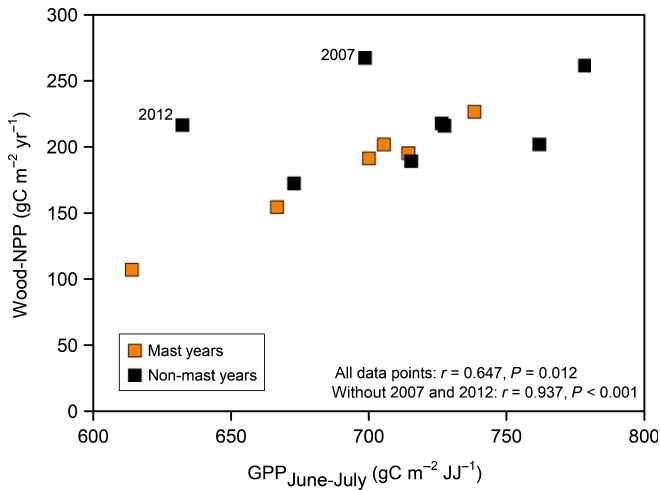
Fig. 4 Relationship between annual net primary productivity of wood (wood-NPP, including above- and below-ground wood) and gross primary productivity in June and July (GPP$_{June-July}$) in the beech (*Fagus sylvatica*) forest 'Hainich'. Mast and nonmast years and the years that strongly affect this relationship (namely, 2007 and 2012) are marked.

2011 and the highest one in 2013 (Fig. S4). In a multiple linear regression analysis, T_{May} together with the precipitation sum of April and May ($p_{April-May}$) (positive influence), and fruit-NPP (negative influence) were identified as significant predictors for wood-NPP (TPF-model, adj. $R^2 = 0.63$; Table 2a), even though none of these variables alone showed a significant correlation with wood-NPP (Fig. S4). According to Pratt's product measure for partitioning total R^2 (Nathans *et al.*, 2012), fruit-NPP explained *c.* 22% of total wood-NPP (Table 2a) and 33% of beech wood-NPP (Table S4). The regression model fitted the measured absolute values and the interannual variability well (Fig. S5). Significant interactive effects of fruit-NPP and weather conditions could not be identified.

All other weather variables considered in this study (Table S2) had no significant effects in the resulting models, were highly correlated with already identified predictor variables, or their combinations resulted in weaker regression models (lower adj. R^2). Leaf-NPP was positively and relatively strongly correlated with wood-NPP ($r = 0.58$, $P < 0.05$) but it did not strengthen the model. GPP$_{June-July}$ improved the prediction of the TPF-model when the negative influence of PAW$_{anoJune-July(t-1)}$ was also considered. The resulting model had a substantially higher adj. R^2 ($= 0.88$) but because of collinearity among the predictor variables (VIF > 2) it was rejected. GPP$_{June-July}$ alone explained 42% of the interannual variation in wood-NPP (Table 2b).

To test the impact of single years we ran the TPF-model without the data of the extraordinary year 2011, only for the nonmast years and the mast years, and the GPP-model without the years 2007 and 2012 (Table 3). In the first case, the predictive power of the TPF-model increased (adj. $R^2 = 0.63$) and the relative influence of the predictor fruit-NPP decreased to only 7% (Table 3a). The resulting model overestimated wood-NPP in 2011 but predicted that of the other years still well (Fig. S5). In nonmast years, T_{May} and $p_{April-May}$ explained almost 91% of the variation in wood-NPP, while fruit-NPP lost its significant influence (Table 3b). In mast years, the predictive power of the TPF-model decreased substantially and none of the predictors was significant (Table 3c). When excluding the years 2007 and 2012, most correlations increased, and GPP$_{June-July}$ increased most, replaced all other variables in the regression models and explained nearly 88% of the variation in wood-NPP (Table 3d).

Correlation between GPP and fruit-NPP

For fruit-NPP, no significant correlations with GPP were found, either in current or in previous years and periods (highest, not significant correlation: GPP$_{June-July(t-1)}$ with $r = 0.41$;

Table 2 Statistics of the linear regression analysis for annual net primary productivity of above- and below-ground wood (wood-NPP) in the beech (*Fagus sylvatica*) forest 'Hainich'.

(a) TPF-model

$R^2 = 0.714$, adj. $R^2 = 0.628$; $P = 0.005$; SE of estimate $= 24.820$

Variable	Coefficient	SE	P	Standardized coefficient	Product measure	VIF
Intercept	−107.132	85.286	0.238			
T_{May}	20.572	6.031	**0.007**	0.730	0.099	1.603
$p_{April-May}$	0.634	0.152	**0.002**	0.885	0.395	1.580
Fruit-NPP	−0.256	0.085	**0.013**	−0.514	0.220	1.023

(b) GPP-model

$R^2 = 0.419$, adj. $R^2 = 0.371$; $P = 0.012$; SE of estimate $= 32.302$

Variable	Coefficient	SE	P
Intercept	−206.053	138.712	0.163
GPP$_{June-July}$	0.579	0.197	**0.012**

T_{May}, mean air temperature in May (°C); $p_{April-May}$, sum of precipitation in April and May (mm); NPP, net primary productivity (g C m^{-2} yr^{-1}); GPP$_{June-July}$, gross primary productivity from June to July (g C m^{-2} JJ^{-1}). Statistically significant values ($P < 0.05$) are indicated in bold type.

(a) TPF-model without the extraordinary mast year 2011

$R^2 = 0.726$, adj. $R^2 = 0.634$; $P = 0.007$; SE of estimate = 19.124

Variable	Coefficient	SE	P	Standardized coefficient	Product measure	VIF
Intercept	−92.367	65.923	0.195			
T_{May}	20.466	4.647	**0.002**	0.932	0.430.	1.472
$p_{April–May}$	0.503	0.126	**0.003**	0.865	0.232	1.546
Fruit-NPP	−0.152	0.076	0.075	−0.364	0.068	1.070

(b) TP-model for nonmast years (2003/2005/2007/2008/2010/2012/2013/2015)

$R^2 = 0.908$, adj. $R^2 = 0.871$; $P = 0.003$; SE of estimate = 11.798

Variable	Coefficient	SE	P	Standardized coefficient	Product measure	VIF
Intercept	−63.237	45.011	0.219			
T_{May}	17.890	3.193	**0.003**	0.919	0.286	1.456
$p_{April–May}$	0.525	0.079	**0.001**	1.087	0.623	1.456

(c) TPF-model for mast-years (2004/2006/2009/2011/2014/2016)

$R^2 = 0.592$, adj. $R^2 = —$; $P = 0.545$; SE of estimate = 42.777

Variable	Coefficient	SE	P	Standardized coefficient	Product measure	VIF
Intercept	−235.140	347.600	0.568			
T_{May}	17.860	28.713	0.597	0.508	−0.051	3.273
$p_{April–May}$	1.135	0.675	0.235	1.174	0.681	2.392
Fruit-NPP	0.323	0.833	0.735	0.311	−0.038	3.142

(d) GPP-model without the years 2007 and 2012

$R^2 = 0.878$; adj. $R^2 = 0.866$; $P < 0.001$; SE of estimate = 14.150

Variable	Coefficient	SE	P
Intercept	−388.875	68.877	**< 0.001**
$GPP_{June–July}$	0.822	0.097	**< 0.001**

T_{May}, mean air temperature in May (°C); $p_{April–May}$, sum of precipitation in April and May (mm); NPP, net primary productivity (g C m^{-2} yr^{-1}); $GPP_{June–July}$, gross primary productivity from June to July (g C m^{-2} JJ^{-1}). Statistically significant values ($P < 0.05$) are indicated in bold type.

Table S2). The correlations of fruit-NPP with leaf-NPP or summer global radiation (Rg) in previous years, variables that might be assumed as proxies for an influence of carbon availability, were higher than those with GPP. Leaf-NPP showed a significant and negative correlation with fruit-NPP ($r = -0.66$), $Rg_{June–July(t-1)}$ a significant and positive and $Rg_{June–July(t-2)}$ a significant and negative one ($r = 0.68$ and $r = -0.66$, respectively; Table S2).

Predicting fruit-NPP

The strongest predictor for fruit-NPP was precipitation (p) from June to August 2 yr before, here expressed as the precipitation anomaly of this period ($p_{anoJune–Aug(t-2)}$ = difference between the sum of precipitation from June to August in ($t-2$) and the respective long-term mean 2000–2016). The positive response to this weather signal explained 85% (linear function) to 94% (sigmoid function) of the variation in fruit-NPP (Table 4a, b; Fig. 5a). Furthermore, it seems to indicate a threshold for the occurrence of fruit years ('on'-years), and thus for flower bud initiation.

$p_{anoJune–Aug}$ in ($t-1$) could also work as a significant predictor, but its negative relationship with fruit-NPP was weaker and it did not indicate a clear threshold for the onset of fruiting (Fig. 5a). The same held for summer Rg in ($t-1$) and ($t-2$), which showed a significant negative correlation with respective summer p ($r = -0.73$ and -0.69, respectively). Here, it is also important to note that there was a significant negative correlation of p or Rg between consecutive years (p: $r = 0.73$, Rg: $r = 0.60$), indicating an alternating climatic pattern of wet and dry summers.

In 'on'-years, p_{May} solely explained almost 83% of the variation in fruit-NPP (Table 4c; Fig. 5b). When considering all years, p_{May} had no predictive power for fruit-NPP. GPP of any studied window in the previous or current year did not contribute significantly to the prediction of fruit-NPP.

Discussion

In the present study, we analyzed fruit and wood growth as integrative and equivalent components of plant growth and considered their relationships with GPP and weather conditions as well as their interrelationship. The GPP estimates as a measure for recent carbon assimilates represent a key, up to now rarely

Table 4 Statistics of the linear and sigmoid regression analysis for annual net primary productivity of fruits (fruit-NPP) in the beech (*Fagus sylvatica*) forest 'Hainich'.

(a) Linear regression

$R^2 = 0.846$, adj. $R^2 = 0.833$; $P < 0.001$; SE of estimate $= 33.365$

Variable	Coefficient	SE	P
Intercept	74.587	8.920	**<0.001**
$p_{\text{anoJune–Aug}(t-2)}$	1.132	0.139	**<0.001**

(b) Sigmoid regression with $f(x) = a/(1 + \exp(-(x-b)/c))$ and $x = p_{\text{anoJune–Aug}(t-2)}$

$R^2 = 0.943$, adj. $R^2 = 0.932$; $P < 0.001$; SE of estimate $= 21.275$

Variable	Coefficient	SE	P
a	197.448	17.203	**<0.001**
b	24.158	6.771	**0.004**
c	19.439	4.762	**0.002**

(c) Linear regression for the 'on'-years ($p_{\text{anoJune–Aug}(t-2)} > 0$ mm) only

$R^2 = 0.827$; adj. $R^2 = 0.793$; $P = 0.004$; SE of estimate $= 25.720$

Variable	Coefficient	SE	P
Intercept	260.282	25.319	**<0.001**
p_{May} (mm)	−1.165	0.238	**0.004**

$p_{\text{anoJune–Aug}(t-2)}$, precipitation anomaly June to August 2 yr before (mm); p_{May}, precipitation in May (mm); NPP, net primary productivity (g C m^{-2} yr^{-1}). Statistically significant values are indicated in bold type.

Fig. 5 Mean annual net primary productivity of fruits (fruit-NPP) ± SD in the beech (*Fagus sylvatica*) forest 'Hainich' as a function of precipitation anomalies from June to August ($p_{\text{anoJune–Aug}}$) 2 yr ($t-2$) and 1 yr ($t-1$) before (a), and of precipitation in May (p_{May}) of the fruit years ('on'-years) (b). Precipitation anomalies denote deviations of precipitation over a given period of time from the respective long-term mean (here 2000–2016). Dashed blue line: threshold $p_{\text{anoJune–Aug}(t-2)} = 0$. Solid lines, linear regression lines; dashed black line, sigmoid regression line.

considered, predictor variable in the context of tree growth and the controversy about a sink or source limitation to tree growth.

The main results of our study are as follows. The interannual variation in wood-NPP could be explained significantly by additive effects of T_{May} and $p_{\text{April–May}}$ in spring (positive relationship) and annual fruit-NPP (negative relationship). While annual GPP was unrelated to wood-NPP, GPP$_{\text{June–July}}$ influenced wood-NPP significantly. Fruit-NPP was positively controlled by $P_{\text{anoJune–Aug}(t-2)}$ and in fruit years ('on'-years), negatively by p_{May}. Neither annual nor seasonal GPP of the current or the previous 2 yr had a significant influence on fruit-NPP. Thus, wood- and fruit-NPP responded differently to GPP and differently to weather conditions, as illustrated in Fig. 6.

Control of wood growth by weather conditions and fruit production

The additive, direct (i.e. without an influence of GPP) effects of temperature and precipitation already in spring suggested by the TPF-model (Table 2a) could be related to the first processes of wood formation. The positive influence of spring temperature may reflect the need for adequate heat to stimulate the onset of cambial activity (Deslauriers *et al.*, 2008; Begum *et al.*, 2018). The positive influence of precipitation could result from the high need for water to promote the division and expansion of cambium cells (Lebourgeois *et al.*, 2005; Palacio *et al.*, 2014).

The negative influence of fruit-NPP on wood-NPP in the TPF-model (Table 2a) could result from insufficient
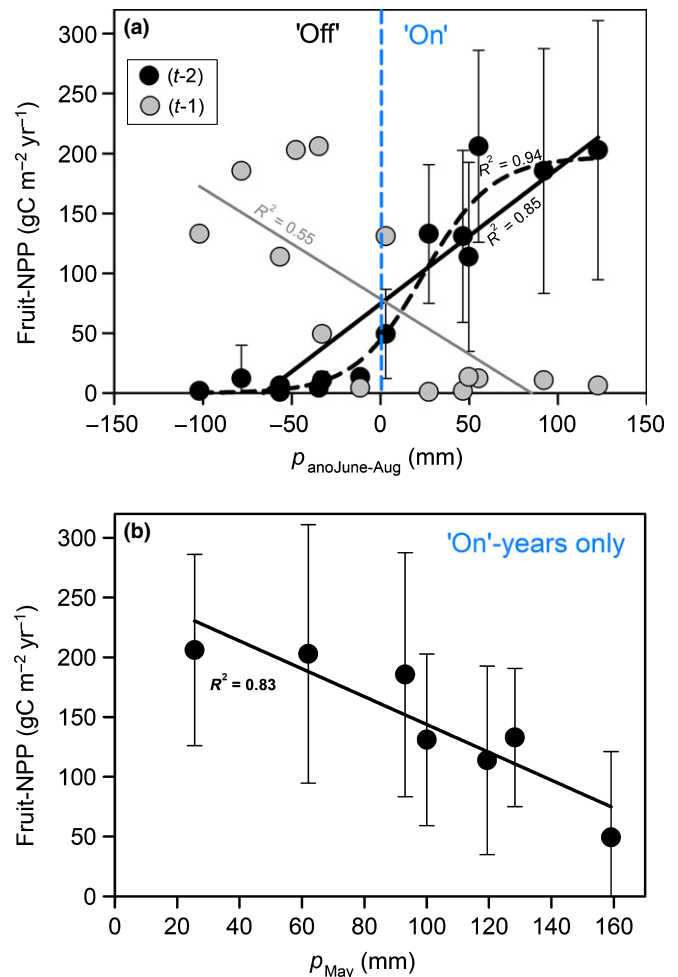
mobilization and allocation of carbon reserves at the beginning of the growing season (Mund *et al.*, 2010) when the carbon demand for leaf (Dyckmans *et al.*, 2000; Barbaroux *et al.*, 2003), fruit (Han *et al.*, 2016) and stem growth (Kozlowski & Pallardy, 1997; Skomarkova *et al.*, 2006) is high and new assimilates are not yet available. After full leaf development (mid- to end of May, Fig. S2) current assimilation may reduce or counteract this imbalance. Such a temporal carbon limitation would represent the upper limit of 'fine-tuning' by carbon reserves (Han *et al.*, 2016) and would mark a transition from sink-limitation to source-limitation. The strength of a negative impact of fruiting on wood growth may depend not only on the amount of fruits, and thus weather conditions in previous years (see the section 'Triggering of fruit production' below), but also on co-occurring stress (namely drought) that reduces GPP or the transport of recent assimilates (Hacket-Pain *et al.*, 2017; Salmon *et al.*, 2019).
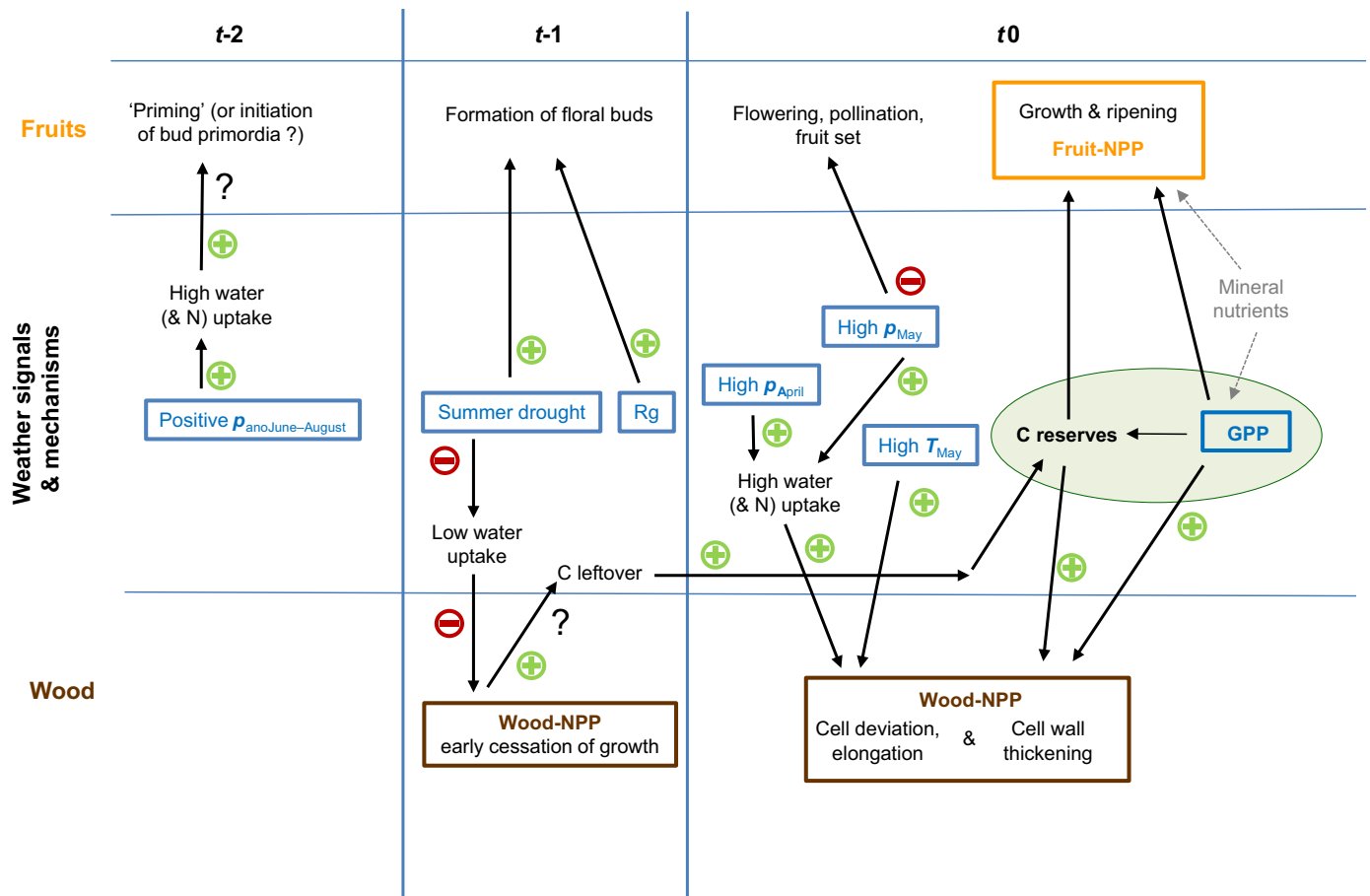
Fig. 6 Schematic overview of the variables and mechanisms that may control annual net primary productivity of above- and below-ground wood (wood-NPP) and fruits (fruit-NPP) of beech forests directly or indirectly over 3 yr. The positive and negative signs mark potential growth controls discussed in this study. (t0), fruit year; (t–1), 1 yr before the fruit year; (t–2), 2 yr before the fruit year; $p_{anoJune–Aug}$, precipitation anomaly from June to August; Rg, global radiation; T_{May}, mean air temperature in May; $p_{April–May}$, sum of precipitation in April and May; p_{May}, precipitation in May; C, carbon; N, nitrogen; GPP, gross primary productivity. A potential influence of mineral nutrients on GPP and fruit growth in the fruit year (gray) was not investigated in this study.

Another carbon-mediated linkage between wood- and fruit-NPP may work over 2 yr. Serious summer drought can lead to an early cessation of the main phase of stem growth despite recovery of carbon assimilation after drought (Mund et al., 2010; Delpierre et al., 2015). Even when drought also reduces GPP, more carbon might be left and stored than in years with high growth rates. With successful pollination, the 'carbon-leftover' might promote fruit-NPP in the following spring.

The positive correlation of leaf-NPP with wood-NPP but negative correlation with fruit-NPP may refer to the weak but significant correlation between GPP_{July} and leaf-NPP ($r = 0.546$; Table S2). The negative correlation between leaf- and fruit-NPP probably results from a replacement of leaf buds with fruit buds during development of the regenerative shoot system of beech (Innes, 1994; Gruber, 2003; Seidling, 2007). The reduction of leaves could be associated with a reduction in GPP, which in turn may reduce wood-NPP. However, the reduction in the number of leaves was at least partly compensated for by higher assimilation rates per leaf biomass (Table S5). Even in 2011, when leaf-NPP decreased by 26% compared to its mean, GPP_{July} decreased only by 15%.

A fourth linkage between wood- and fruit-NPP might be associated with the contradictory effect of p_{May} on wood- and fruit-NPP (Tables 2a, 4c). While high p in May supports wood formation, it reduces fruit production probably due to its negative impact on pollen coupling (Satake & Iwasa, 2000; Röhrig et al., 2006; Koenig et al., 2015; Abe et al., 2016). Thus, p_{May} might be a weather signal that leads to a 'trade-off' between fruit- and wood-NPP that is not mediated by carbon (or other nutrients).

The relative impact of fruiting or masting on wood growth may vary substantially among tree species (fruit size, degree of masting, type of pollination) and site conditions (e.g. nutrient and water supply). Fruit trees growing in plantations, for example, show a much higher negative correlation between fruit- and wood-NPP (Kozlowski & Pallardy, 1997; Rosati et al., 2018) than forest trees (Hacket-Pain et al., 2017; this study Tables 2a, 3a), which may be related to a higher crop yield and thus a higher allocation of GPP to fruits in fruit trees. For example, in an apple orchard, c. 39% of GPP was allocated to fruit-NPP (Zanotelli et al., 2015), while at our study site it was < 17%, including a rough estimate for a higher use of carbon for lipid synthesis (Kozlowski & Pallardy, 1997).

Control of wood growth by carbon assimilation

A weak or no influence of GPP on wood-NPP would question a strong limitation to wood growth by carbon availability (Rocha *et al.*, 2006; Delpierre *et al.*, 2015). Instead it suggests direct control mechanisms such as those described above. However, the strong influence of $GPP_{June–July}$ on wood-NPP, observed for most of the years in this study (GPP-Model, Tables 2b, 3d; Fig. 4), indicates that usually recent assimilates were used during the main phase of stem growth (Mund *et al.*, 2010). In summer of some years (2007 and 2012) also carbon reserves might have been mobilized and used in addition to recent assimilates. In the latter case, additional direct control mechanisms would be needed that dominate over the control by $GPP_{June–July}$. We have not yet been able to identify any weather signal that may have worked as such a driver for wood growth in 2007 and 2012.

At first glance, the TPF-model and the GPP-model seem to represent competing models for wood growth. However, when considering the temporal windows of the predictor variables and the temporal separation of water- and carbon-consuming processes in wood formation (Babst *et al.*, 2014; Cuny *et al.*, 2015) a sequential coupling of the models seems to be feasible. Cell expansion due to water inflow represents the phase of volume increment, but it is not the main phase of carbon sequestration in wood. Cell-wall thickening, the process during which most carbon is sequestered, lasts only for a few weeks after cell expansion (Babst *et al.*, 2014), and reaches its maximum at tree level up to 4 wk later than cell expansion or diameter increment (Cuny *et al.*, 2015). Thus, in spring wood growth may depend mainly on temperature and water availability as suggested by the TPF-model, and in summer mainly on carbon assimilation in agreement with the GPP-model.

Triggering of fruit production

The strongest driver for fruit-NPP we found was $p_{anoJune–Aug(t−2)}$. This variable defined a threshold for fruiting ('on/off'-years), and it influenced the final amount of fruit mass produced in the fruit year (Fig. 5a). When considering the multiple collinearity among weather signals (namely p, T and Rg) and the negative correlation between wet, cold and dry, hot conditions in consecutive summers (see also Ascoli *et al.*, 2017) this driver may not contradict but complete the often-observed weather cues for periodically high fruit production such as high temperature or drought in the previous summer or differences in summer temperature between the preceding 2 yr (Piovesan & Adams, 2001; Kelly & Sork, 2002; Gruber, 2003; Kelly *et al.*, 2013; Drobyshev *et al.*, 2014; Hacket-Pain *et al.*, 2015; Kon & Saito, 2015; Ascoli *et al.*, 2017; Vacchiano *et al.*, 2017). However, the lack of any significant correlation between fruit-NPP and GPP during any period of the current or the previous 2 yr questioned the assumption that the weather signals would trigger fruit production via carbon assimilation (Gruber, 2003; Müller-Haubold *et al.*, 2015).

A triggering of fruiting by high precipitation in ($t−2$) could be explained by higher decomposition rates and a higher water uptake associated with an higher uptake of nutrients in wet compared to dry years, leading to higher levels of mineral nutrients in ($t−1$) that may promote bud formation ('resource priming', Ascoli *et al.*, 2017). A priming via high carbon assimilation in ($t−2$) seems to be unlikely as no significant correlation between $p_{June–August}$ and GPP was found (see also Tamrakar *et al.*, 2018). Floral gene expression and bud formation in ($t−1$) might additionally be stimulated by high radiation and/or soil water deficits associated with a multihormonal control of fruit set (Bernier & Périlleux, 2005; Ruan *et al.*, 2012).

Another potential explanation for a strong triggering of fruit-NPP already in ($t−2$) could be that the initiation of bud primordia either for the vegetative or for the regenerative shoot system of beech occurred already 2 yr before the fruit year, as suggested by morphogenetic studies of Gruber (2003). For this early initiation of bud primordia, however, we could not find further confirmation in the literature.

Conclusions

Our results suggest a complex system of sink and source limitations to tree growth of beech forests driven by weather conditions over 3 yr. The results for fruit-NPP support the hypothesis of a direct control, or of a control by resources other than carbon, while the results for wood-NPP indicate a variable system of direct and indirect controls depending on weather conditions, fruiting and carbon availability. Thus, the negative relationship between fruit- and wood-NPP should not be interpreted just as a carbon-mediated 'trade-off' between regenerative and vegetative growth.

Even though the results of this study need to be confirmed by regional, long-term studies, they already reinforce the warning by Knops *et al.* (2007) that the negative correlation between stem and fruit growth 'does not necessarily imply a causal mechanism and should not be used as the only evidence supporting a trade-off'. Furthermore, they suggest coupling the system of 'climate-driven resource dynamics' for masting in (forest) tree species (Allen *et al.*, 2017), with corresponding dynamics for wood growth (Hacket-Pain *et al.*, 2018) and direct control mechanisms (e.g. multiple hormonal control and gene expression, Vacchiano *et al.*, 2018). From a carbon-centric view, the most important remaining question is, how much of the stored carbon reserves in mature trees can be remobilized (Millard *et al.*, 2007; Sala *et al.*, 2012; Richardson *et al.*, 2013; Rocha, 2013; Hartmann & Trumbore, 2016) and used either for regenerative or for vegetative growth, defense and root exudates (Fig. 1). For the future it seems worthwhile to set up experimental studies that allow us to track the production and allocation of carbon and hormones after manipulating carbon sources and sinks (e.g. by defoliation or fruit thinning) in whole, mature and masting forest trees.

Author contributions

MM initiated and designed the study, collected data and conducted analyses, and wrote the manuscript. CA contributed to the study design, its conduction and the preparation of the manuscript. MH, AK, LS and RT provided datasets and contributed to manuscript preparation. BM conducted analyses and provided information. JS and PS contributed to the statistical design and calculations. All authors contributed to the interpretation of the results and to manuscript revision and editing.

Data availability statement

The weather data and the EC data of this study are available at the fluxnet database (https://fluxnet.fluxdata.org/). The data for 2000–2012 are published under the reference: Alexander Knohl, Frank Tiedemann, Olaf Kolle, Ernst-Detlef Schulze, Werner Kutsch, Mathias Herbst, Lukas Siebicke (2000–2012) FLUXNET2015 DE-Hai Hainich, https://doi.org/10.18140/FLX/1440148. The inventory, litter fall and stem increment data used in this study are published at the iDiv Data Repository (http://idata.idiv.de/ddm/Data/ShowData/1815) under the reference: Martina Mund, Christian Ammer, Ernst-Detlef Schulze (2019) Stand inventories, litter fall and basal area increment at an unmanaged, old-growth mixed beech forest at the 'Hainich National Park' (DE-Hai), https://doi.org/10.25829/idiv.1815-13-2790.

ORCID

Christian Ammer (iD) https://orcid.org/0000-0002-4235-0135
Alexander Knohl (iD) https://orcid.org/0000-0002-7615-8870
Bertrand Matthäus (iD) https://orcid.org/0000-0002-0537-0903
Martina Mund (iD) https://orcid.org/0000-0001-7181-1626
Peter Schall (iD) https://orcid.org/0000-0003-4808-818X
Jens Schumacher (iD) https://orcid.org/0000-0002-8419-4820
Rijan Tamrakar (iD) https://orcid.org/0000-0002-1967-5599

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Fig. S1 Relative plant available water (rel. PAW) in the soil of the beech (*Fagus sylvatica*) forest 'Hainich' from 1 April to 1 September during the study period.

Fig. S2 Minimum daily air temperature in spring 2010 and 2011 compared to leaf development and the 0°C isoline in the beech (*Fagus sylvatica*) forest 'Hainich'.

Fig. S3 Relationship between annual net primary productivity of above- and below-ground wood (wood-NPP) and net ecosystem exchange in June and July ($NEE_{June–July}$) in the beech (*Fagus sylvatica*) forest 'Hainich'.

Fig. S4 Relationships between annual net primary productivity of above- and below-ground wood (wood-NPP) and mean temperature in May (T_{May}), sum of precipitation from April to May

($p_{\text{April–May}}$) and fruit-NPP in the beech (*Fagus sylvatica*) forest 'Hainich'.

Fig. S5 Measured and predicted annual net primary productivity of above- and below-ground wood (wood-NPP) in the beech (*Fagus sylvatica*) forest 'Hainich'.

Table S1 Biomass regression functions used in this study.

Table S2 Pearson correlation coefficients of variables considered in this study.

Table S3 Main ecosystem carbon fluxes in the beech (*Fagus sylvatica*) forest 'Hainich'.

Table S4 Statistics of the multiple linear regression analysis for annual net primary productivity of above- and below-ground wood (wood-NPP) of European beech (*Fagus sylvatica*) at the study site 'Hainich'.

Table S5 Ratio between gross primary productivity (GPP) and net primary productivity of leaves (leaf-NPP) in the beech (*Fagus sylvatica*) forest 'Hainich'.

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