

# The influence of climate and fructification on the inter-annual variability of stem growth and net primary productivity in an old-growth, mixed beech forest

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**Summary** The periodic production of large seed crops by trees (masting) and its interaction with stem growth has long been the objective of tree physiology research. However, very little is known about the effects of masting on stem growth and total net primary productivity (NPP) at the stand scale. This study was conducted in an old-growth, mixed deciduous forest dominated by *Fagus sylvatica* (L.) and covers the period from 2003 to 2007, which comprised wet, dry and regular years as well as two masts of *Fagus* and one mast of the co-dominant tree species *Fraxinus excelsior* (L.) and *Acer pseudoplatanus* (L.). We combined analyses of weather conditions and stem growth at the tree level (inter- and intra-annual) with fruit, stem and leaf production, and estimates of total NPP at the stand level. Finally, we compared the annual demand of carbon for biomass production with net canopy assimilation (NCA), derived from eddy covariance flux measurements, chamber measurements and modelling. Annual stem growth of *Fagus* was most favoured by warm periods in spring and that of *Fraxinus* by high precipitation in June. For stem growth of *Acer* and for fruit production, no significant relationships with mean weather conditions were found. Intra-annual stem growth of all species was strongly reduced when the relative plant-available water in soil dropped below a threshold of about 60% between May and July. The inter-annual variations of NCA, total NPP and leaf NPP at the stand level were low (mean values 1313, 662 and 168 g C m<sup>-2</sup> year<sup>-1</sup>, respectively), while wood and fruit production varied more and contrarily (wood: 169–241 g C m<sup>-2</sup> year<sup>-1</sup>; fruits: 21–142 g C m<sup>-2</sup> year<sup>-1</sup>). In all years, an annual surplus of newly assimilated carbon was calculated (on average 100 g C m<sup>-2</sup> year<sup>-1</sup>). The results suggest that stem growth is generally not limited by insufficient

carbon resources; only in mast years a short-term carbon shortage may occur in spring. In contrast to common assumption, stem growth alone is not a sufficient proxy for total biomass production or the control of carbon sequestration by weather extremes.

**Keywords:** *Acer pseudoplatanus*, carbon allocation, carbon balance, drought, *Fagus sylvatica*, *Fraxinus excelsior*, masting, resource limitation, stem growth, unmanaged forest.

## Introduction

The periodic synchronous production of large seed crops by trees is called masting or mast. The advantages and disadvantages of masting behaviour both for parent trees and offspring as well as evolutionary reasons and consequences for forest dynamics have long been the objective of forest and tree physiology research (e.g., Kelly and Sork 2002, Piovesan and Adams 2005, Thomas and Packham 2007, Génard et al. 2008). The interval between consecutive masts and the degree of periodicity is species specific and varies depending on endogenous control, weather conditions and resource availability (Kozłowski and Pallardy 1997b, Selås et al. 2002, Hilton and Packham 2003, Thomas and Packham 2007, Han et al. 2008).

The hypothesis that masting is influenced or even limited by resource availability (resource priming) goes back to the observation that large fruits, like those of *Fagus sylvatica* (L.) (European beech), have a high sink strength for assimilates and nutrients (Kozłowski and Pallardy 1997a). A stimulating effect of high resource availability on fruit production was suggested based on positive relationships between fruit pro-

duction and site index (Schmidt-Vogt 1991a, Övergaard et al. 2007), fertilization (Le Tacon and Oswald 1977, Schmidt-Vogt 1991b) or release cutting (Karlsson and Orlander 2002). However, statistical time series analyses often show a negative correlation between fruit production and radial increment (e.g., *F. sylvatica*: Dittmar et al. 2003, Jochheim et al. 2007; *Picea abies* (L.) Karst.: Selås et al. 2002, Chalupka 2007) indicating a 'switching' of resource use from vegetative growth to reproduction in mast years. Resource switching does not necessarily reflect resource limitation or a trade-off between vegetative and reproductive growth. It rather shows that fructification responds to external or internal conditions in a different way than stem growth, such that weather conditions that enhance reproductive growth are unfavourable for vegetative growth (e.g., Selås et al. 2002, Knops et al. 2007, Hirayama et al. 2008).

Studies of non-structural carbon dynamics in single trees showed that fructification is not limited by carbon availability. Gäumann (1935) already demonstrated a surplus of available carbon in beech trees. For mast years, he calculated that as much as 37% of total available carbon is left over for the next year. Reviews by Körner (2003) and Millard et al. (2007) on carbon physiology generally question a carbon limitation of tree growth under current and future environmental conditions. However, because changes in non-structural carbon during the year can only be measured destructively, these studies are limited to single years and young trees. A retrospective analysis of the past is not possible.

Very little is known about the effects of masting on stem growth and total net primary productivity (NPP) at the stand scale. So far, research activities focusing on the physiology of masting and those focusing on stem growth and its climate sensitivity have remained separate. Growth studies often considered fruiting only as an additional or disturbing factor.

Another major constraint of most time series is that they are only semi-quantitative. They are based on indices and classes of flower or seed production instead of total amounts of produced fruits (seeds plus pericarp), and on tree-ring width instead of total biomass production. Thus, they do

not allow the quantification of the balance of resource use and resource availability.

Despite large efforts in forest dynamics and tree physiology research, there remained two major questions:

- (1) Is reduced stem growth in mast years an effect of resource shifting to high fruit production and thus an indicator of competition between vegetative and reproductive growth for carbon resources, or is it primarily a direct effect of co-occurring weather conditions?
- (2) How far does periodic fructification modify total NPP of forests?

Here we address these questions by combining an analysis of weather conditions and stem growth at the tree level with fruit, stem and leaf production as well as estimates of total NPP at the stand level. This study was conducted in an old-growth, mixed deciduous forest. It covers five consecutive years (2003–07) and comprised wet, dry and regular years, as well as two masts of *F. sylvatica* (L.) and one mast of the co-dominant tree species *Fraxinus excelsior* (L.) (European ash) and *Acer pseudoplatanus* (L.) (sycamore maple). Finally, we compare the annual demand of carbon for biomass production with net carbon availability, which was derived from eddy covariance flux measurements, chamber measurements and modelling. This approach allowed us to identify years of carbon limitation or surplus.

## Materials and methods

### Study site, climate and soil

The study site 'Hainich' (Flux-net acronym: DE-Hai; 51°04'45"N, 10°27'07"E, elevation 430 m a.s.l.) is a CarboEurope-IP verification site and is located in the most protected area (600 ha) of Nationalpark Hainich (7600 ha), central Thuringia, Germany. The study site was established in 1999 with the installation of an eddy covariance tower (Knobl et al. 2003). The forest can be characterized as an old-growth, uneven-aged (1–250 years) mixed beech forest, and it represents a

Table 1. Main stand characteristics.

Species	<i>Fagus</i>	<i>Fraxinus</i>	<i>Acer</i>	Others	Total
Stand density (N ha <sup>-1</sup> )	272.8	41.4	17.2	4.0	335.5
Mean diameter (cm)	27.6	50.7	43.9	36.5	31.4
Mean tree height (m)	22.4	32.3	26.7	24.5	23.9
Basal area (m <sup>2</sup> ha <sup>-1</sup> )	23.3	9.1	2.8	0.4	35.6
Diameter <sub>10</sub> <sup>a</sup> (cm)	67.3	76.3	55.5		63.0
Height <sub>10</sub> <sup>a</sup> (m)	33.3	34.7	29.8		32.6
Timber volume (m <sup>3</sup> ha <sup>-1</sup> )	364.6	159.0	39.7	5.3	568.6
Tree C stocks <sup>b</sup> (t C ha <sup>-1</sup> ) (%)	142.2 (64.2)	60.9 (27.5)	16.2 (7.3)	2.3 (1.0)	221.6 (100)
Leaf biomass (t C ha <sup>-1</sup> ) (%)	1.03 (60.8)	0.50 (29.6)	0.16 (9.3)	0.01 (0.2)	1.70 (100)

<sup>a</sup>Mean of the 10% largest trees.

<sup>b</sup>Tree C stocks include stem wood, branches, twigs, coarse and fine roots, and leaves. Reference dates: stem data = winter 2004/2005; leaf biomass = 1999. The species group 'Others' include four *C. betulus*, four *A. platanoides*, one *A. campestre* and one *U. glabra*.

forest type that would dominate naturally on nutrient-rich soils in central Europe (Ellenberg 1996, Bolte et al. 2007). *Fagus sylvatica* dominates the canopy, and *Fraxinus excelsior* and *Acer pseudoplatanus* are co-dominant tree species (Table 1). Single trees of *Carpinus betulus* (L.) (European hornbeam), *Acer platanoides* (L.) (Norway maple), *Acer campestre* (L.) (hedge maple), *Ulmus glabra* (Huds.) (wych elm) and other deciduous species are admixed as remnants of a former management regime. The main stand characteristics are summarized in Table 1.

The suboceanic–submontane climate in combination with fertile soil conditions (silty-clay Cambisol of 50–70-cm soil depth; Mund 2004) provides nearly optimal growing conditions for mixed deciduous forests. In addition to the naturally high nutrient availability, the site receives annual bulk nitrogen depositions of about  $12.8 \pm 3.3$  kg N ha<sup>-1</sup> (Mund 2004).

The study site has continuously been forested with broad-leaved tree species since the early 1500s (Mund 2004). Since 1997, when the Nationalpark was established, the forest has been totally unused. In the previous 40 years, only single trees of high commercial value were removed. Therefore, management effects on current growth and fruiting can be excluded.

The study area or stand was defined by the most probable footprint area of the eddy covariance system (Göckede et al. 2004, Rebmann et al. 2005). The ‘main footprint’ includes the area from which the resulting fluxes are detected by the eddy covariance tower with a probability of >65%. It corresponds with the main wind direction (south-west) and was about 450 m long and on average 200 m wide (~9 ha).

#### Stem increment at tree level

In March 2002, 58 rope dendrometers were installed at breast height of visually healthy and vital trees, distributed randomly within the main footprint, over all tree sizes ( $d > 10$  cm) and four species groups (for details, see Figure S1 available as Supplementary Data at *Tree Physiology* Online). In March 2005, this tree collective was enlarged by an additional 30 tape dendrometers installed at *Fagus*, *Fraxinus* and *A. pseudoplatanus* trees with  $d \geq 30$  cm to improve the growth estimates for those size classes and tree species that account for the largest proportion of total wood production as shown for selection forests nearby (Erteld et al. 2005). The data of the first year after dendrometer installation were not used in this study because the ropes and tapes need some time before they are adjusted tightly to the stem surface (see Keeland and Sharitz 1993). The record of each tree was manually examined and single, non-plausible values (e.g., unrealistic high changes caused by swelling of the bark after rainfall) were excluded. Details of the dendrometers and the data examination are available as Supplementary Data at *Tree Physiology* Online.

Basal area increment increased with increasing tree size, but there was no allometric function that could properly describe the entire population. In particular, stem growth of the suppressed trees was not proportionally reduced compared with tree size, indicating strong asymmetric competition.

Therefore, we normalized the individual stem increment in two different ways. The normalization to the mean individual stem increment over the last 5 years (relative growth anomaly) reduced the variability between single trees and implied dependency between repeated measurements of the same individual. Normalization to the individual tree diameter (relative diameter increment, RDI) in combination with a classification into trees <25 cm and trees  $\geq 25$  cm in diameter resulted in a tree-size-independent growth parameter that allows for a linear statistical analysis of annual means equivalent to absolute values of diameter increment, and for a plain analysis of the time series.

Historical tree-ring data of *Fagus* from two dendrochronological studies (Skomarkova et al. 2006, Kahl 2008) carried out at the same site were analysed to interpret current stem growth in the context of long-term growing conditions at the study site. Long-term time series for the other tree species at the Hainich–Dün region are still in progress.

#### Stand inventories and NPP at stand level

In early spring 2000 and 2005, we recorded a row of 14 tree inventory plots (radius = 15 m, in total 9896 m<sup>2</sup>) within the main footprint area. Stem diameter at 1.3 m above ground level ( $d$ ) was measured in 2000 and 2005, and tree height in 2005. Living timber volume (stems and branches  $\geq 7$  cm in diameter) was estimated using a standard regression of forestry practice (Mette and Korell 1986; Equation S1 available as Supplementary Data at *Tree Physiology* Online). Woody biomass including stem, branches and coarse roots of living trees with  $d \geq 7$  cm were calculated by biomass regressions and coefficients taken from a recent meta-analysis of published tree sampling data of in total 443 harvested *F. sylvatica* trees (Wutzler et al. 2008; Equations S2–S4, available as Supplementary Data at *Tree Physiology* Online). To our knowledge, there are no adequate biomass functions, including branch and root biomass, available for the other tree species of the study site.

Volume and woody biomass of all trees within the inventory plots were summed up and normalized to 1 ha or 1 m<sup>2</sup>, respectively. Woody biomass was converted to carbon units assuming a carbon concentration of 50%<sub>dw</sub> (Wutzler et al. 2008).

Changes in woody biomass stocks and their uncertainties were calculated using Markov chain Monte Carlo (MCMC) integration. Since tree height was measured only in 2005, we based the calculation of changes in woody biomass on a simplified allometric equation of the type:

$$w_j = \beta_{0,j} d^{\beta_{1,j}} \quad (1)$$

where  $w_j$  = mass of the  $j$ th compartment (kg<sub>dw</sub>) and  $\beta_{0,j}$  and  $\beta_{1,j}$  = compartment-specific allometric coefficients (dimensionless).

The allometric equations were fitted simultaneously in a Bayesian framework with the MCMC algorithm implemented in WinBUGS 1.4. At each iteration of the algorithm,

the sampled allometric coefficients were used to calculate the biomass increment of each inventoried tree, which were then summed at the plot level. (Further details can be found in the Supplementary Data available at *Tree Physiology Online*.) For an extrapolation of individual tree growth to the stand level, we multiplied the diameter of each tree of the 14 inventory plots with the mean RDI per species group and year, starting from the inventory in 2005 backwards to 2002 and forwards to 2007. Tree diameter was then extrapolated to woody biomass as described above for the stand inventories. The differences between the years resulted in total wood NPP.

The annual production of leaves, buds and fruits was derived from litter sampling in 29 traps (each 0.5 m<sup>2</sup>) distributed over the main footprint. The litter was sampled every 2 weeks from October to November and every 2 months over the rest of the year. The samples were dried at 70 °C for 3 days and weighed. Mean carbon concentration of leaves was 48.2%, and that of fruits 50% (nuts and pericarp) (total combustion, elemental analyser 'VarioEL II', 1998, Elementar Analyse GmbH, Hanau, Germany). Fine root (<2 mm) NPP in 2002 were taken from a repeated sampling at the Hainich site by Claus and George (2003). For the other years, a fine root/leaf ratio of 0.9 was used based on repeated fine root and leaf litter sampling at eight beech forests in Central and Western Europe (Claus and George 2003). For the ground vegetation, a constant above- and belowground NPP of 67 g C m<sup>-2</sup> year<sup>-1</sup> was used, which resulted from a repeated biomass sampling at the Hainich site in 2002 by Graef and Gebauer (2003).

#### Relative plant-available water

According to Lebourgeois et al. (2005), we related the intra-annual records of stem growth to soil moisture expressed as the relative plant-available water (rel. PAW). The rel. PAW was derived from the actual volumetric water content (WC<sub>akt</sub>; %<sub>Volume</sub>) by Eq. (2):

$$rel.PAW = \frac{(WC_{akt} - WC_{WP})}{(WC_{FC} - WC_{WP})} \cdot 100 \quad (2)$$

where WC<sub>FC</sub> = volumetric water content at field capacity, WC<sub>WP</sub> = wilting point. WC<sub>akt</sub> was measured by means of four Theta Probes (ML-2x; DeltaT, Cambridge, UK) in 8-cm soil depth, one in 16 and one in 32-cm soil depth. This distribution reflects the distribution of the main root biomass by depth.

#### Eddy covariance measurements and estimates of available carbon

Ecosystem net carbon and water vapour fluxes were measured continuously since 1999 with an eddy covariance system consisting of a sonic anemometer (Solent R3, Gill Instruments, Lymington, UK) mounted at 43.5 m and a LI 6262 infrared gas analyser (LiCor, Lincoln, NE, USA) located at the base of the tower. For details about instrumentation

and data processing, we refer to Knohl et al. (2003), Anthoni et al. (2004) and Kutsch et al. (2008).

A modular set of models that was applied successfully to different types of ecosystems before (Kutsch et al. 2001a) was adapted to the Hainich site to obtain daily values of net carbon dioxide uptake of the canopy as described in Kutsch et al. (2008). For the present study, the model system was additionally fine-calibrated in a top-down approach by optimizing the modelling results against highest quality eddy covariance data.

The 'net canopy assimilation' (NCA) is defined as the carbon that is gained by the canopy and that is available for the rest of the tree. It is derived by subtracting foliage night-time respiration from daytime net carbon uptake of the canopy and reflects the amount of new available assimilates better than gross primary production derived from standard flux partitioning of eddy covariance data.

Net primary production (NPP<sub>modelled</sub>) was then calculated on an annual basis by subtracting total plant respiration from NCA (Eq. 3).

$$NPP = NCA - R_{WOOD} - R_{Saut} \quad (3)$$

where NPP = modelled net primary productivity (g m<sup>-2</sup> year<sup>-1</sup>), R<sub>WOOD</sub> = modelled respiration of aboveground wood biomass (g m<sup>-2</sup> year<sup>-1</sup>), R<sub>Saut</sub> = modelled autotrophic belowground respiration (g m<sup>-2</sup> year<sup>-1</sup>).

#### Software

For data management and simple mathematical operations, Microsoft Excel 2007 was used. Graphical presentations and non-linear regression analysis were carried out with SigmaPlot for Windows 2004 (version 9.01). The analysis of variance (ANOVA) and linear regression analysis were done with the 'Visual GLM module' of the software STATISTICA for Windows (StatSoft Inc., 2000). For the MCMC technique, WinBUGS 1.4 was used. The eddy flux data were calculated for 30-min intervals by means of the post-processing program 'eddyflux' (Kolle and Rebmann 2007).

## Results

#### Weather conditions during the study period

Monthly temperature and precipitation anomalies (Figure 1) indicate a dry period during the months of June, July and August in 2003 and during June and July in 2006. The precipitation deficit in June 2006 was more prominent than in June 2003 and comparable to that of the extraordinary dry year 1976 (pointer year), but the dry period from June to July was followed by a wet and cold August. On the contrary, in 2003 the dry period continued throughout the whole month of August, resulting in the warmest and driest growing season of the studied period (Figure 1) with strong physiological impact (A. Knohl, W.L. Kutsch, M. Mund, C. Rebmann, H.E. Arends, O.

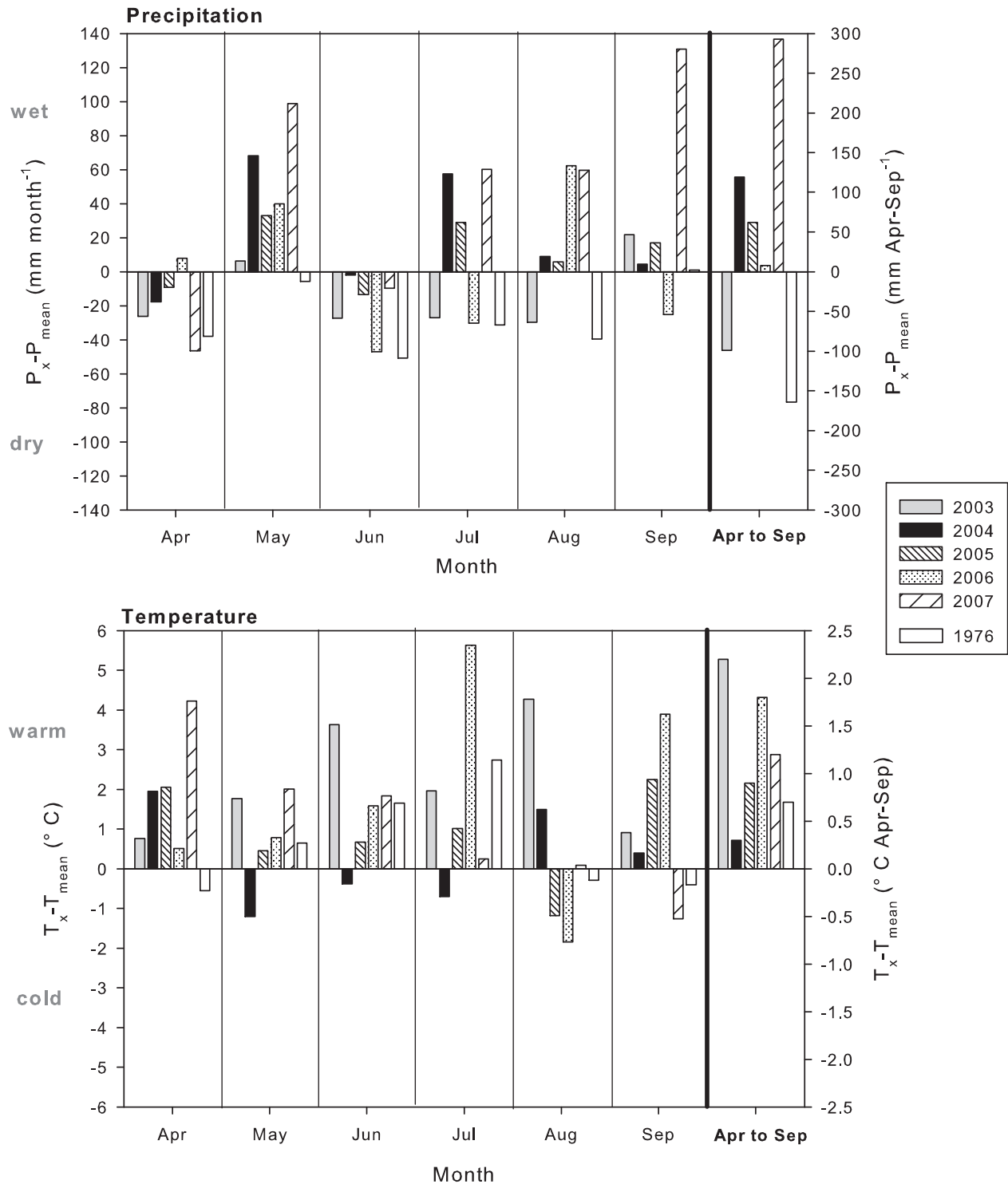


Figure 1. Precipitation and temperature anomalies from April to September of the study period and the pointer year 1976. The anomaly is defined as the difference between the means of a single year ( $P_x$ ) and the long-term mean (1961–90,  $P_{\text{mean}}$ ). Data sources: study period 2003–07: meteorological station of the study site (Olaf Kolle, personal communication). Long-term means and data from 1976: weather station 'Leinefelde', about 30 km to the north of the study site, 356 m a.s.l., 51°23'N, 10°18'E (DWD (Deutscher Wetterdienst) 2004).

Kolle and E.-D. Schulze, in preparation). However, compared with the drought in western and southern Europe, the Hainich site was only moderately affected (Ciais et al. 2005).

Weather conditions in 2004 were characterized by low air temperatures and high precipitation from May to July, followed by a moderate autumn. The year 2005 can be classified

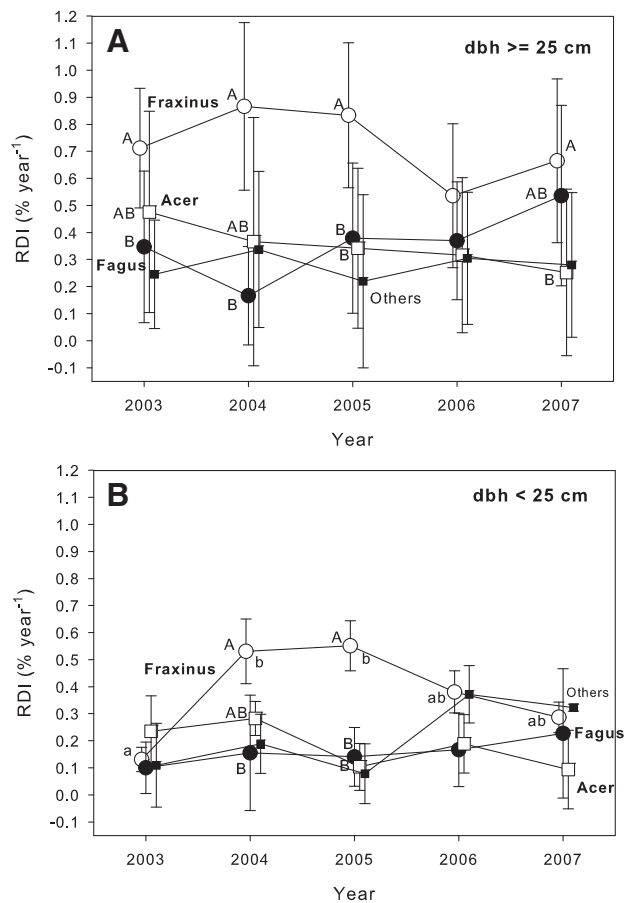


Figure 2. Relative diameter increment (RDI) of the years 2003–07. (A) Trees with a  $d \geq 25$  cm. (B) Trees with a  $d < 25$  cm. Lowercase letters indicate significant differences among years of the same species, capitals significant differences among species in the same year (factorial ANOVA, excluding the species group ‘Others’, type VI (effective hypothesis) sums of squares,  $P < 0.05$ , Newman–Keuls test). Years or species with no significant differences are not ended with letters.

as a normal year. The growing season of the year 2007 was unusually wet and moderately warm.

#### Stem increment at tree level

Stem increment of individual trees did not reveal any tree-specific trends (depicted as anomalies of mean increment of each tree; Figure S1, available as Supplementary Data at *Tree Physiology Online*). Also, tree size had no significant influence on the growth anomalies (linear regression analysis,  $P > 0.05$ ).

The inter-annual variability of the mean RDI of the same species was low compared with the high variability among tree individuals (see error bars in Figure 2). Thus, within the same species, the differences between years were not statistically significant, except for small *Fraxinus* trees ( $d < 25$  cm) showing in 2003 a significantly lower RDI than in 2004 and 2005 (Figure 2, Table 2). Large *Fraxinus* trees ( $d \geq 25$  cm) had in

Table 2. Statistics of the comparison of annual and species-specific relative diameter increment (RDI; factorial ANOVA, type VI (effective hypothesis) sum of squares), excluding the species group ‘Others’.

Factors	SS	DF	MS	F	P
Trees with $d \geq 25$ cm					
Intercept	42.828	1	42.828	498.634	<0.000
Species	5.877	2	2.939	34.212	<0.000
Year	0.367	4	0.092	1.067	0.374
Species $\times$ year	2.001	8	0.250	2.912	0.004
Trees with $d < 25$ cm					
Intercept	2.784	1	2.784	134.900	0.000
Species	0.371	2	0.186	8.989	0.001
Year	0.158	4	0.039	1.912	0.125
Species $\times$ year	0.330	8	0.041	1.997	0.069

most years, and small *Fraxinus* trees in 2004 and 2005, a significantly higher RDI than *Fagus* or *Acer* (Figure 2A). It is notable that, in 2004, large *Fraxinus* trees had the highest RDI of the studied period and large *Fagus* trees the lowest one.

The beginning of stem growth, measurable as an increase in stem diameter, is generally expected when the 7-day running mean of air temperature reaches 10 °C for at least 5 days (Menzel et al. 2003). This relationship was valid for *Fraxinus*, while stem growth of *Fagus*, *Acer* and the Others showed a delay of stem growth for nearly one and a half months in 2004 and 2005 (Figure 3). Air temperatures below  $-3$  °C at the days of leaf unfolding that were reported to have a strong and sustained negative effect on stem growth of *Fagus* (Dittmar et al. 2006) did not occur during the entire study period. Also, a delay in leaf unfolding could not explain the delay in stem growth in 2004 and 2005 as shown by a phenology study using daily canopy photos of the study site (Ahrends et al. 2009). In 2004, *Acer* and the Others balanced the delayed start of stem growth due to relatively high growth rates in June and July, while stem growth of *Fagus* was low over the entire growing season, resulting in the lowest RDI of the studied period. In 2005, *Fagus* could partly compensate for the delay of stem growth later on in the growing season.

The cumulative RDI from April to November (Figure 3) revealed the dominant role of the period between May and mid-July for annual stem growth. During this period, the highest stem growth rates were observed, and until the end of July 70–90% of total annual increment was already produced in all years and by all species. This corresponds with previous studies on *Fagus* that identified May–July as the period of highest sensitivity of annual ring width to current weather conditions (Dittmar et al. 2003, Piovesan et al. 2003). However, the strict temporal frame of high growth rates in all years, irrespective of weather conditions, indicates inherent growth patterns that might be controlled by other factors such as photoperiodism. The main growth period seemed to be terminated when relative plant-available water (rel. PAW) in soil dropped below about 60% as clearly indicated in mid-June in 2003 by all studied species (Figure 3).

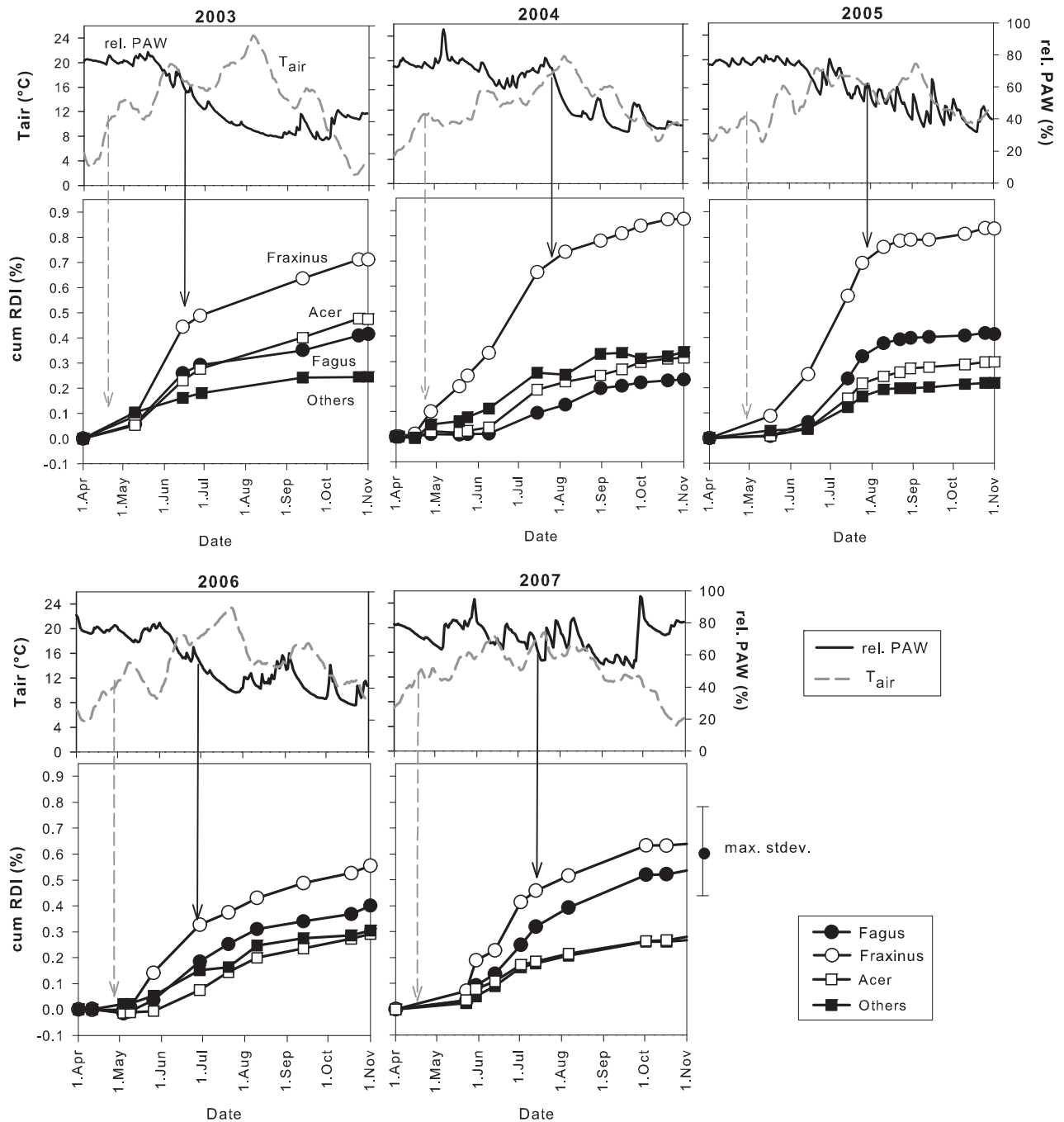


Figure 3. Cumulative relative diameter increment (RDI;  $d \geq 25$  cm) through the growing season in comparison with relative plant-available water (PAW) in soil and air temperature (7-day running mean). The arrows mark thresholds of weather conditions that may directly control for stem increment. Grey arrow: 7-day running mean of air temperature has exceeded 10 °C for at least 5 days. Black arrow: rel. PAW dropped <60% for the first time during the growing season.

The threshold of 60% rel. PAW is comparable to that previously reported for stem growth (e.g., Bogeat-Triboulot et al. 2007), but it is higher than the threshold of 45–50% for a reduction in stomatal conductance or net carbon assimilation rates (Gollan et al. 1985, Bogeat-Triboulot et al. 2007, A. Knohl, W.L. Kutsch, M. Mund, C. Rebmann, H.E. Arends, O. Kolle and E.-D. Schulze, in preparation). In contrast to stem

growth, stomatal conductance and carbon assimilation rates recovered when the rel. PAW exceeded again the threshold.

Despite the drastic effect of soil water stress on current stem growth, the impact on the annual sum in 2003 was low due to the early onset of stem growth and due to high growth rates (associated with unusually warm weather conditions) at the beginning of the growing season before the

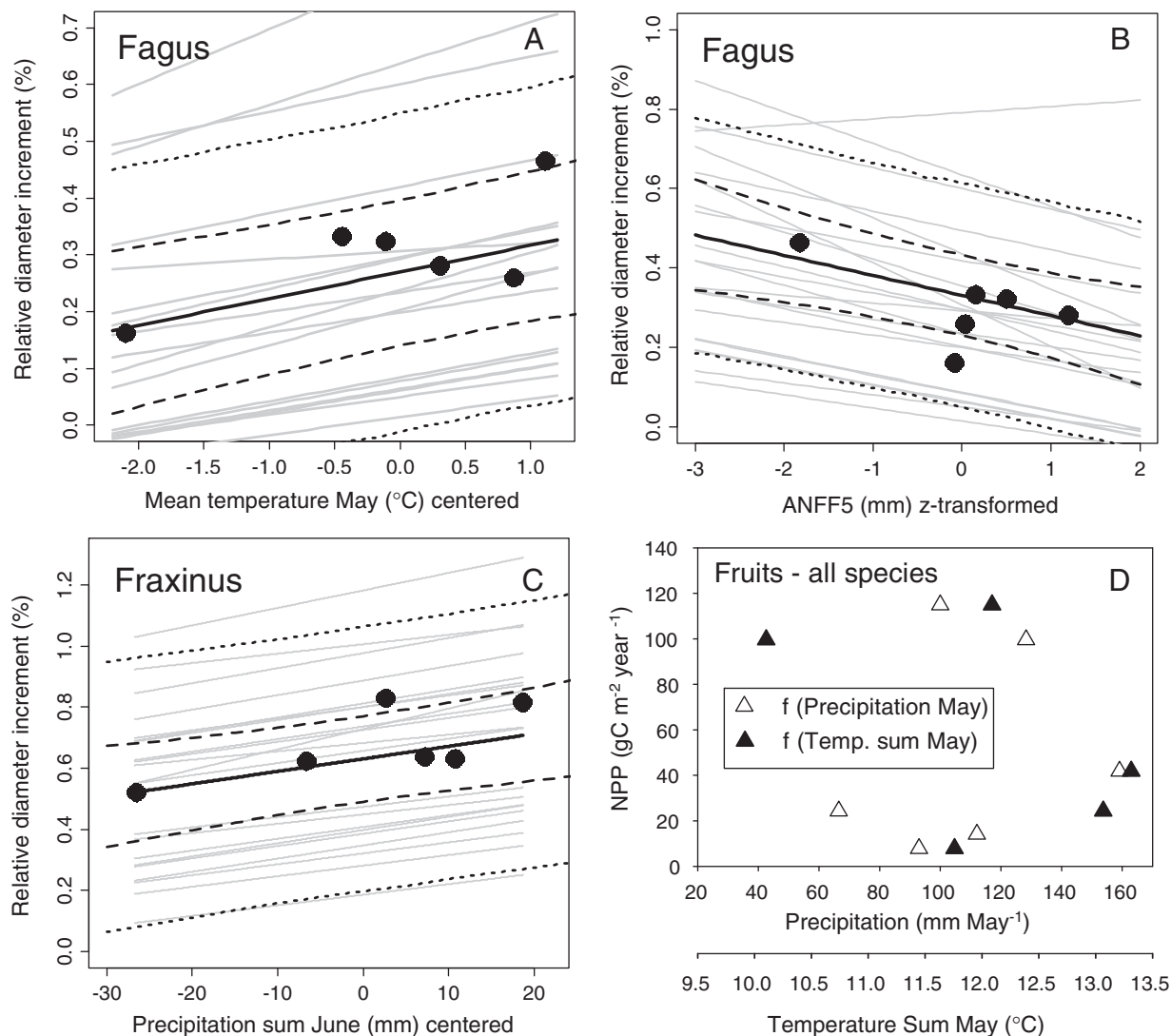


Figure 4. Relationship between stem growth (A–C) or fruit production (D) and current weather conditions. Figures A–C show the relationships of the individual sampling trees (grey lines), the fixed effects relationship (black line), the mean values for RDI across the sample trees (black dots), the 95% credible interval arising from the parameter uncertainty only (long dashed line) and the 95% credible interval considering also the residual error (short dashed line) (mixed-effects model analysis, see also Table 3). ANFF5 = first consecutive 5 days with mean air temperature >10 °C. Mean May temperature = 12.2 °C. Mean precipitation sum of June = 57.2 mm. Mean ANFF5 = 122.7 (SD 8.6). Fruit production does not show any relationship with current weather conditions, as exemplified here for May temperature and precipitation.

drought started. The length of the period with rel. PAW <60%, or a second dry period in late summer or autumn as in 2004 and 2006, seemed to have only a marginal effect on annual stem growth (Figure 3).

A regression analysis specified the impact of weather conditions during the main growth phase on final annual RDI (mixed-effects model, Figure 4, Table 3). *Fagus* showed a strong trend towards a positive relationship between annual

Table 3. Statistical parameters of the best model for the tree species *F. sylvatica* and *F. excelsior* (mixed-effects model analysis). Criteria for the selection of the models were: (i) low deviation information criterion (DIC); (ii) difference between the models <2: models are more or less equivalent, differences of 5–10 indicate that one model is clearly better, differences >10: more positive model does not need to be considered; (iii) high regression coefficient ( $R^2$ ) and adjusted regression coefficient (adj  $R^2$ ); (iv) ecologically plausible direction of the relationship; (v) the 95% credible interval of the slope of the fixed effect does not include zero. This criterion was not fulfilled for mean air temperature in May (\*).

Species	Predictor	Slope	DIC	$R^2$	Adj $R^2$
<i>Fagus</i>	Mean air temperature in May	(*)	-98.516	0.7281	0.6489
<i>Fagus</i>	First day of the year at which mean air temperature was >10 °C for five consecutive days	-0.05056	-117.815	0.7788	0.6910
<i>Fraxinus</i>	Precipitation sum of June	0.06497	-10.208	0.6623	0.5677



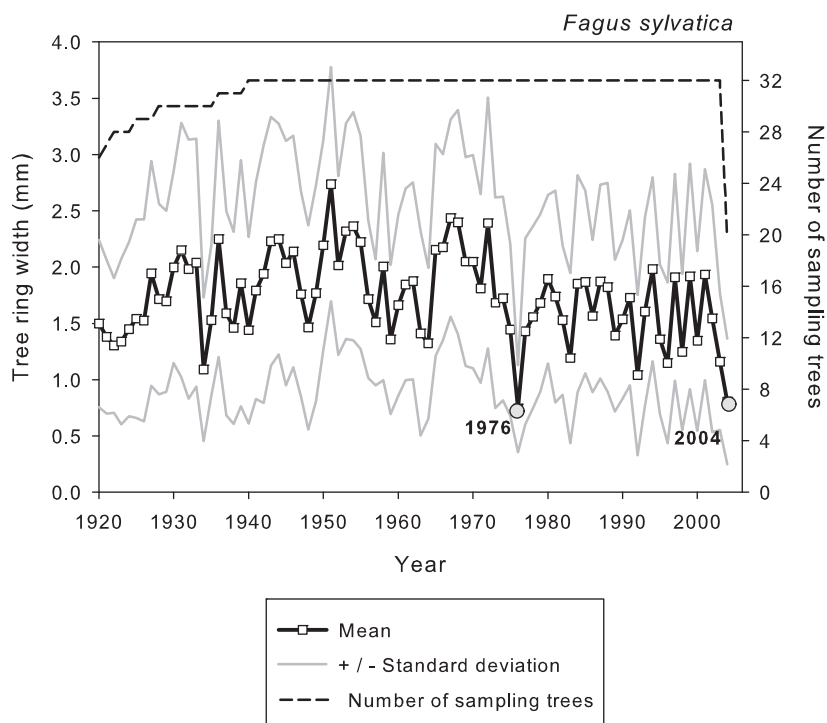


Figure 5. Chronology of tree-ring width of dominant *Fagus* trees from 1920 to 2004. The time series includes no de-trending procedures or any kind of normalization because the tree-ring data did not show an age trend over the last 50 years. The number of sampling trees per year differed depending on the length of the cores and the sampling dates. Data sources: Skomarkova et al. (2006) (12 trees); Kahl (2008) (20 trees).

RDI and mean air temperature in May. A significant negative correlation was found with the first day of the year at which mean air temperature was  $>10^{\circ}\text{C}$  for five consecutive days. Thus, the earlier the first warm period begins, the higher the annual stem growth. This temperature threshold was reached 4–10 days earlier than that supposed for the beginning of tree growth (Figure 3; Menzel et al. 2003), underlining the importance of the early stem growth phase for total annual stem increment. Other thresholds or periods of mean temperature or precipitation conditions resulted in much weaker or non-plausible regression models. Mean annual RDI of *Fraxinus* showed a significant positive correlation with the sum of precipitation in June (Table 3). For stem growth of *Acer* and the other species, no significant relationships were found.

The master chronology of *Fagus* clearly identified the year 1976 as the most severe pointer year of the last 80 years (Figure 5). In 1976, precipitation from April to September was only 195 mm, which is equivalent to about 54% of the long-term mean (Figure 1). In June, precipitation was about 70% lower in 1976 than in 2003. The master chronology also revealed that in the moderately wet and cold year, 2004, the second lowest stem growth of the last 80 years was achieved. This raised the question if low air temperature in May alone could have caused the strong reduction and delay in stem growth in 2004 or if changes in carbon availability and allocation due to masting that will be analysed in the following paragraph are an additional factor.

#### Total NPP and the carbon balance at stand level

Annual leaf biomass production estimated by annual leaf litter fall ranged between  $159\text{ g C m}^{-2}\text{ year}^{-1}$  in 2004 and  $176\text{ g C m}^{-2}\text{ year}^{-1}$  in 2005, which is equivalent to an amplitude of only 10% to the mean. Maximum variation of wood production at stand level was 37% to the mean. The lowest wood production was observed in 2004 with  $169\text{ g C m}^{-2}\text{ year}^{-1}$ , and the highest in 2007 with  $241\text{ g C m}^{-2}\text{ year}^{-1}$  (Figure 6A, Table 4). The strongest inter-annual variation was observed for fruit production. In 2003, 2005 and 2007, only 45, 21 and  $68\text{ g C m}^{-2}\text{ year}^{-1}$ , respectively, were produced (including buds, seeds, fruit shells or other appendages). In 2004 and 2006, fruit production almost tripled to 133 and  $142\text{ g C m}^{-2}\text{ year}^{-1}$ , respectively. These amounts are similar to leaf production and accounted for 20% of total biomass production. In 2006, *Fagus*, *Fraxinus* and *Acer*, showed high fruit production. Fruit biomass of *Fagus* only was lower than in 2004 ( $\sim 100\text{ g C m}^{-2}\text{ year}^{-1}$ ), but it was still comparable to mean values of high beech masts in Germany (Burschel 1966, Burschel and Huss 1987). Contrary to stem growth, fruit production did not show any correlation with current weather conditions (Figure 4).

Over the entire studied period, total NPP varied only between  $618\text{ g C m}^{-2}\text{ year}^{-1}$  in 2003 and  $702\text{ g C m}^{-2}\text{ year}^{-1}$  in 2007 (equivalent to a maximum difference of 13% to the mean) (Figure 6A, Table 4). In 2004, reduced wood production of *Fagus* was partly buffered by a small increase in

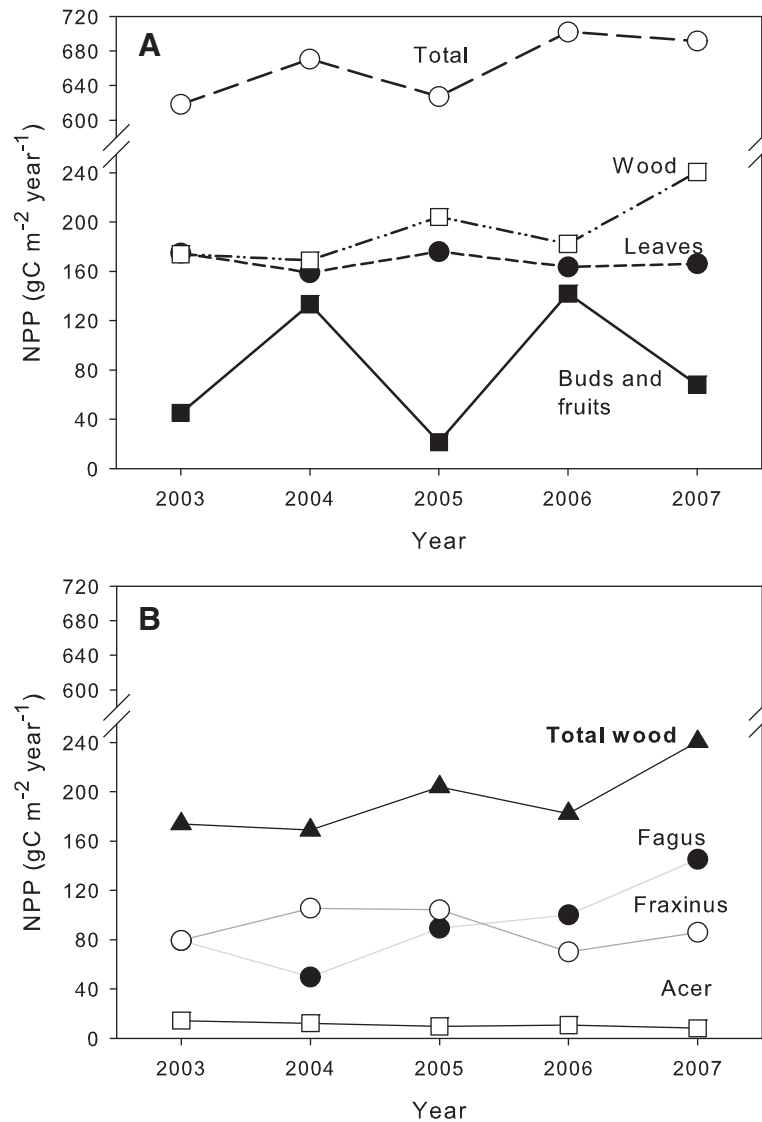


Figure 6. (A) Net primary production (NPP) of leaves, buds and fruits and woody biomass (above and below ground) from 2003 to 2007, and (B) wood NPP separated for the main tree species. Except for fruit biomass, the inter-annual differences are not significant.

wood production of *Fraxinus*, and vice versa in 2006 (Figure 6B; see also Figure 2A). The remaining differences in wood production in 2004 and 2006 were overcompensated for by the high fruit production in these years (Figure 6A). This indicates that fruit production competes with wood production and that additional carbon resources have to be used in the mast years compared with regular years.

Balancing the amount of carbon that was used for tree growth and that was available due to current net canopy assimilation (NCA) as derived from the eddy covariance and the flux model, an annual surplus of new carbon was identified for all years (Table 4). This surplus ranged between  $28 \text{ g C m}^{-2} \text{ year}^{-1}$  in 2003 and  $186 \text{ g C m}^{-2} \text{ year}^{-1}$  in 2005. There was no significant relationship between annual wood production and NCA (Figure 7) nor between wood produc-

tion and NCA during the main growth phase from May to July ( $R^2 = 0.25$ ,  $P = 0.39$ , data not shown). Instead, the annually remaining new carbon was strongly positively correlated with annual NCA (Figure 7). This means that the more new carbon remained unused, the higher the annual carbon gain was. In 2005, almost 13% of NCA was not used for current tree growth (Table 4). It could be assumed that the surplus was transferred to the carbon reserves, and that this process occurred mainly in August and September when stem increment is already strongly reduced, while the net canopy carbon uptake lasted until the onset of leaf fall at the beginning of October (data not shown; see also Skomarkova et al. 2006). However, the calculated surplus may also indicate that there is a substantial transfer of carbon to fine roots or to mycorrhiza and soil microorganisms, eventually leading to carbon accumulation in the soil (see discussion below).

Table 4. Estimates of annually remaining carbon, excluding the use of carbon reserves.

Year	2003	2004	2005	2006	2007	Mean 2000/2005
			g C m <sup>-2</sup> year <sup>-1</sup>			
Leaf NPP	175	159	176	163	166	
Bud + fruit NPP	45	133	21	142	68	
				(beech only: 102)		
Wood NPP <sub>dendrometer</sub> <sup>a</sup>	174	169	204	182	241	
Fine root NPP <sup>b</sup>	157	142	158	147	150	
Ground vegetation NPP <sup>b</sup>	67	67	67	67	67	
Total NPP <sub>dendrometer</sub>	618	671	627	702	692	
Annual NCA	1113	1290	1447	1341	1376	
Annual R <sub>stem/roots</sub>	466	531	634	550	583	
Annual C available for growth <sup>c</sup>	647	759	813	791	793	
Annually remaining C <sub>dendrometer</sub> <sup>d</sup>	28	88	186	89	101	
NCA May–July	788	781	845	726	812	
R <sub>stem/roots</sub> May–July	229	226	282	242	254	
C available for growth May–July <sup>c</sup>	559	555	563	484	558	
Total NPP <sub>inventories 2000/2005</sub>						726
Annually remaining C <sub>inventories 2000/2005</sub> <sup>d</sup>						99

NPP, net primary production; NCA, net canopy assimilation; R, respiration.

<sup>a</sup>Extrapolated dendrometer data, Equations S4–S6 (available as Supplementary Data at *Tree Physiology* Online).

<sup>b</sup>Repeated sampling, fine roots: Claus and George (2003); ground vegetation: Graef and Gebauer (2003).

<sup>c</sup>C available = NCA – R<sub>stem/roots</sub>.

<sup>d</sup>Remaining carbon = NCA – R<sub>stem/roots</sub> – total NPP.

According to the repeated stand inventory, on average 257 g C m<sup>-2</sup> year<sup>-1</sup> (95% credibility interval: 12–467 g C m<sup>-2</sup> year<sup>-1</sup>) were sequestered in woody tree biomass. This estimate is about 30% higher than the mean of the dendrometer-based estimate for wood NPP and resulted in a total NPP estimate of 726 g C m<sup>-2</sup> year<sup>-1</sup>. The independent flux modelling resulted with 762 g C m<sup>-2</sup> year<sup>-1</sup> in a slightly higher total NPP than the repeated stand inventory completed by leaf and fruit production. All these approaches to calculate total NPP as well as the NCA rates are associated with high uncertainties. The

main reason for the discrepancy between dendrometer-based and repeated inventory-based estimates could be the high proportion of dendrometer trees with zero increment at breast height in 2003 and 2004 (5 and 9%, respectively) or with a continuous decrease in stem diameter over the entire study period despite their visually estimated fitness at the time when the dendrometers were installed (8%). A precursory termination of stem increment was already described by Pastur et al. (2007), but it might not be representative of the entire tree population of the study site. The most critical point of both wood

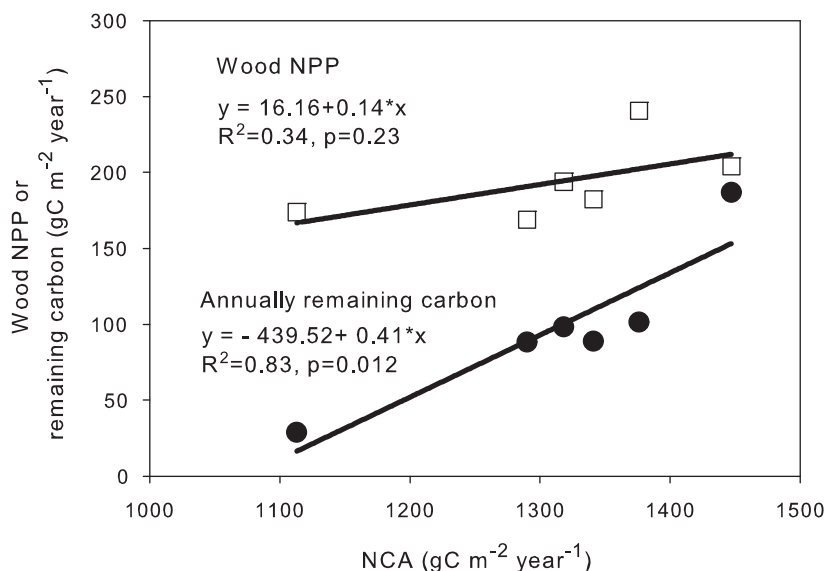


Figure 7. Relationship between NCA (net canopy assimilation) and net primary production of wood (wood NPP) and between NCA and annually remaining new carbon (see Table 4).

NPP estimates is that they are based on changes in diameter increment at breast height only. The ratio between stem growth at breast height and total stem growth depends on weather conditions, the crown position and local light conditions. Stem increment at breast height most likely overestimates total stem increment in wet years and underestimates it in dry years (Bouriaud et al. 2005). In suppressed trees, there may be very little production of xylem in the lower stem (Kozłowski and Pallardy 1997b). In homogeneous managed beech forests, the error of biomass expansion and its extrapolation to stand level summed up to  $\geq 40\%$  (Wutzler et al. 2008).

The error of the flux model-derived data may be in the same order of magnitude. Here, the main sources of uncertainty are the upscaling of the chamber flux measurements that are based mainly on leaf area index and light attenuation in the canopy, and the occurrence of advection at the study site that interferes with the eddy flux measurements (Kutsch et al. 2008). Nevertheless, even when the mean inventory-based NPP was taken that was about 30% higher than the dendrometer-based one, on average almost  $100 \text{ g C m}^{-2}$  of new assimilates were left over every year (Table 4).

## Discussion

Our analysis showed that the inter-annual variations in NCA, total NPP and leaf NPP were small in an old-growth mixed deciduous forest, while wood and fruit production varied more and contrarily.

### Resource shifting

At first glance, the decreasing contribution of wood production to NPP during masting in our results supports the hypothesis of a resource shift from wood to fruit production in mast years. However, there are two major observations indicating that there is no simple relationship between carbon availability and stem growth at the Hainich forest:

- (1) The decrease in wood production in 2004 and 2006 was less than the increase in fruit production (Figure 6). Thus, additional carbon resources have to be used in the mast years compared with regular years.
- (2) Stem growth was correlated with current weather conditions but fruit production was not.
- (3) An apparent annual surplus of new carbon was calculated for all years (Table 4), and the higher was the annual carbon gain, the more carbon was not used for biomass production (Figure 7).

Consequently, the question arises, why do trees not use all or at least more available carbon for stem growth? We assume that the answer to this question lies at the demand site of stem growth. We hypothesize that current and previous weather conditions control for the total pool of available carbon (recent assimilates and reserves) that could be used for

tree growth (resource priming), but stem growth is mainly controlled directly by current weather conditions or endogenous control mechanisms. Thus, a surplus of new assimilates has no or only a minor effect on annual stem growth.

This hypothesis is in accordance with Höll (1997) who supposed that in diffuse-porous species such as *F. sylvatica*, wood construction could be entirely supplied by new assimilates, and with a historical study (Gäumann 1935) and recent reviews (Körner 2003, Millard et al. 2007) that generally questioned a carbon limitation of tree growth. There should be carbon reserves at a magnitude of several hundred grams of carbon per square metre per year. Hoch et al. (2003), for example, calculated that in deciduous trees non-structural carbon (NSC) reserves would equal four times the demand for the whole leaf canopy, and that deciduous trees have a large capacity to store NSC in woody biomass. Even large changes in NSC would be hard to detect by measurements of total carbon concentrations of wood as they were used in this study to convert woody biomass into carbon units. Thus, the calculated surplus of new carbon may accumulate in woody biomass.

It could be argued against the hypothesis of a demand-driven tree growth that large sinks for assimilated carbon were neglected, in particular: (i) fine roots that can have very high turnover rates, mostly in dry years (Meier and Leuschner 2008), and (ii) the transport of NSC to mycorrhiza and soil microorganisms (e.g., Högberg et al. 2008, Dannenmann et al. 2009). In our approach, these carbon sinks should be indirectly included because the carbon release associated with the decomposition and activity of fine roots, mycorrhiza and soil microorganisms is part of the ecosystem carbon fluxes measured by the eddy covariance method. Only an increase in soil organic matter due to these processes (carbon transfer  $>$  respiration losses) would be an undetected carbon sink. Assuming a carbon accumulation rate in the soil of about  $50 \text{ g C m}^{-2} \text{ year}^{-1}$ , which equals recent findings at the study site (M. Schrupf, personal communication), only about  $50 \text{ g m}^{-2} \text{ year}^{-1}$  of the new carbon assimilates would remain unused. This amount is low compared with the uncertainties of our calculations (see above), but considering also the existence of carbon reserves, a carbon limitation of tree growth seems to be unlikely.

Our second hypothesis is that in mast years a different situation can occur: fruit production is such a strong additional carbon sink that a temporal shortage of carbon supply can occur for other tree compartments at the beginning of the growing season when current assimilation rates are low and fruit and wood production both need carbon reserves (Röhrig et al. 1978, Atkinson and Denne 1988, Lebourgeois et al. 2005, Keel et al. 2006). Until mid-May, even leaf production depends on carbon reserves (Dyckmans et al. 2000, Barbaroux et al. 2003). Periodically, high fruit production is, in evolutionary terms, highly important for tree regeneration (synchronization to reduce losses by predators; Thomas and Packham 2007), and it is reasonable that after the initiation of fruit buds 2 years before fruit ripening, the tree ensures successful fruiting by maximum carbon supply independent

of inter-annual changes in weather conditions. This can be realized most steadily when fruits are predominantly supplied with carbon, and under unfavourable weather conditions and in spring also with carbon reserves (see also Kozłowski and Pallardy 1997b).

Even though the physiological mechanism of the supposed carbon allocation pattern remains unclear, we assume that fruit production has a higher sink strength than stem growth, and this could be a key factor in explaining the extraordinarily low stem growth in spring 2004: the cold May in 2004, associated with low current assimilation rates, forced the use of carbon reserves that should have been sufficient as indicated by the calculated surplus of new carbon at the end of 2003 (Table 4), but their mobilization and allocation might have been too slow compared with the additional high demand for fruit production. In this context, it is important to note that the low stem growth at the Hainich site in spring 2004 was most likely not a 'carryover effect' or 'time-lag effect', reflecting delayed damage effects of the drought in 2003 as hypothesized for other sites (Bréda et al. 2006, Granier et al. 2008), but the effect of a rapid change in carbon allocation patterns within the trees due to masting. Substantial damage by the drought in 2003 are questionable at our study site. First, serious damage would be expected to cause a reduction in total tree productivity in the following year, and not only a delay of stem growth for nearly one and a half months (Figure 3). Second, there was no 'carryover effect' on tree-ring width of *Fagus* in the year after the very severe drought in 1976 (Figure 5); why should it occur after the moderate drought in 2003, above all when the physiological most critical water stress (rel. PAW <45–50%; Gollan et al. 1985, Bogeat-Triboulot et al. 2007) was reached when most growth processes have already been finished (Figure 3)?

The hypothesized temporal carbon shortage in spring of mast years does not conflict with findings on the role of green infructescence tissue for assimilate supply of fruits (Hoch and Keel 2006) or with findings of girdling experiments that indicate complete carbon autonomy of fruit-bearing branches (Hoch 2005). Those findings show the high productivity of single fruit-bearing branches, and from an evolutionary point of view the need for a safe and steady high carbon supply of fruits, but they do not reflect carbon control and allocation patterns at tree level when the fruit-bearing branches are linked to and confronted with high carbon demand for wood growth.

#### *Periodic fructification and total NPP*

Inter-annual variation in NCA and total NPP was small at the Hainich forest despite high variation in climatic conditions, particularly in precipitation during the growing season, and stem growth. In 2004 and 2006, low NCA was associated with slightly lower leaf biomass, which in turn could be related to relatively low air temperatures in spring and a high proportion of fruit-bearing shoots. The fluorescences of trees compete as shoot equivalents with leaf-bearing shoots, so that in mast years the florescence or fruits can displace leaves (In-

nes 1994, Seidling 2007). The drought in 2003 could have also affected bud formation resulting in a reduced number of leaves and leaf surface area (Bréda et al. 2006). The effect of a calamity of *Phyllaphis fagi* in 2004 (data base on forest protection of Thuringian State Forestry, Gotha, Germany) on leaf biomass and vitality of trees over the sapling stage is assumed to be very small.

The relatively low variability of total NPP over the studied period implies that the mixed beech forest at Hainich has a relatively high resilience to dry years. This is in agreement with the impacts of drought on ecophysiological response functions at stand level of the same study site (A. Knohl, W.L. Kutsch, M. Mund, C. Rebmann, H.E. Arends, O. Kolle and E.-D. Schulze, in preparation) and with a number of other publications focusing on the role of water stress for beech forests (e.g., Kutsch et al. 2001b, Dittmar et al. 2003, Leuzinger et al. 2005, Schipka et al. 2005, Bolte et al. 2007). The low inter-annual variability of total NPP that resulted from the uncorrelated growth of different tree compartments corresponds surprisingly well with findings from a fire-prone Scots pine forest in Siberia (Wirth et al. 2002). At this very different ecosystem, the low inter-annual variability of total NPP was related to high needle production in years of low wood production, and vice versa.

Consequently, as long as current weather conditions are not too extreme, stem growth of the study site would not be substantially affected by the high carbon demand of fruit production (see above). This assumption corresponds with a recent study on individual spruce trees (*P. abies*) where, over a period of 3 years, no trade-off effects between vegetative and reproductive tree growth were found (Seifert and Müller-Starck 2009). It seems unlikely that the observed increase in masting in beech forests from every 5–10 years to every 2–4 years over the last three decades (Paar et al. 2000, Schmidt 2006) would substantially reduce timber production and tree vitality as previously supposed (Övergaard et al. 2007, Seidling 2007). On the contrary, the shortening of the masting cycle may reflect the high carbon supply of trees over the last decades, which is probably caused by increased air temperatures and N depositions.

Our time series on weather, fruit production and available carbon also questions the mechanism supposed for mast initiation of *Fagus*. For *Fagus*, Piovesan and Adams (2001) suggested that a moist cool summer 2 years before beech masting supports the refill of carbohydrate reserves and 'primes' the tree to respond to a drought in the following year by initiating flower buds. This mechanism of mast initiation perfectly fits the situation in 2004 at Hainich: moist, cool year in 2002, drought in 2003 and high mast in 2004. In contrast, the mast in 2006 could not be related to the proposed pattern. The growing season in 2004 was wet and cool with only moderate NCA rates, while the weather conditions in 2005 were normal (Figure 1). Thus, we assume that an extraordinary dry year before the mast is of minor importance, and high carbon availability is a necessary precondition but not a sufficient one for a beech mast.

For species with relative small fruits such as *Fraxinus* or *Acer*, carbon resources are of minor importance. Individual vital trees of *Fraxinus*, for example, can fructificate over several consecutive years (Tapper 1996). For *Fraxinus*, a mast is more a consequence of the number of fruiting trees than of fruit production per tree, and the main function of climate appears to be the synchronization of fructification (Tapper 1996).

## Conclusions

The most important implications for the ongoing research of forest growth, climate change and carbon sequestration in forest ecosystems are:

- In contrast to common assumption, stem growth alone is not a sufficient proxy for total biomass production or the control of carbon sequestration by weather extremes.
- Total biomass production of the old-growth, mixed beech forest at Hainich has a relatively high resilience to dry years.
- Stem growth at the forest Hainich is generally not limited by insufficient carbon resources, and this raises the question if increasing atmospheric CO<sub>2</sub> concentrations can increase tree growth at temperate forests.
- Carbon accumulation and allocation in trees and its interaction with fruit production may explain the sometimes weak correlation between net annual carbon fluxes of a forest stand measured by the eddy covariance method and those derived from inventory or tree-ring studies (Rocha et al. 2006, Gough et al. 2008, Ohtsuka et al. 2009).

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## Supplementary Data

Supplementary data for this article are available at *Tree Physiology* Online.

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