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# Carbon allocation to biomass production of leaves, fruits and woody organs at seasonal and annual scale in a deciduous- and evergreen temperate forest

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## Abstract

Carbon taken up by the forest canopy is allocated to tree organs for biomass production and respiration. Because tree organs have different life span and decomposition rate, the tree C allocation determines the residence time of C in the ecosystem and its C cycling rate. The study of the carbon-use efficiency, or ratio between net primary production (NPP) and gross primary production (GPP), represents a convenient way to analyse the C allocation at the stand level. Previous studies mostly focused on comparison of the annual NPP-GPP ratio among forests of different functional types, biomes and age. In this study, we extend the current knowledge by assessing (i) the annual NPP-GPP ratio and its interannual variability (for five years) for five tree organs (leaves, fruits, branches, stem and coarse roots), and (ii) the seasonal dynamic of NPP-GPP ratio of leaves and stems, for two stands dominated by European beech and Scots pine.

The average NPP-GPP ratio for the beech stand (38%) was similar to previous estimates for temperate deciduous forests, whereas the NPP-GPP ratio for the pine stand (17%) is the lowest recorded till now in the literature. The proportion of GPP allocated to leaf NPP was similar for both species, whereas beech allocated a remarkable larger proportion of GPP to wood NPP than pine (29% vs. 6%, respectively). The interannual variability of the NPP-GPP ratio for wood was substantially larger than the interannual variability of the NPP-GPP ratio for leaves, fruits and overall stand and it is likely to be controlled by previous year air temperature (both species), previous year drought intensity (beech) and thinning (pine). Seasonal pattern of NPP-GPP ratio greatly differed between beech and pine, with beech presenting the largest ratio in early season, and pine a more uniform ratio along the season. For beech, NPP-GPP ratio of leaves and stems peaked during the same period in the early season, whereas they peaked in opposite periods of the growing season for pine. Seasonal differences in C allocation are likely due to functional differences between deciduous and evergreen species and temporal variability of the sink strength.

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The similar GPP and autotrophic respiration between stands and the remarkable larger C allocation to wood at the beech stand indicate that at the beech ecosystem C has a longer residence time than at the pine ecosystem. Further research on belowground production and particularly on fine roots and ectomycorrhizal fungi likely represents the most important step to progress our knowledge on C allocation dynamics.

## 1 Introduction

Forest ecosystems account for 52% of the total terrestrial carbon (C) sink (Grace, 2004) and are of crucial importance in re-absorbing CO<sub>2</sub> emissions from anthropogenic activities (Bonan, 2008; Ciais et al., 2008). Despite the great research efforts in quantifying the C exchange between forests and the atmosphere, little knowledge is yet available on the fate on the C in the ecosystem once taken up by the leaves i.e. the process of C allocation. In fact, C (assimilates) allocation is ignored in many studies of ecosystem C cycling because of its complexity: C allocation is the outcome of many processes which ultimately involve all the internal, environmental and genetic factors that regulate plant subsistence and development (Cannell and Dewar, 1994). Nevertheless, C allocation among plant processes (e.g. respiration, biomass production) and organs (e.g. leaves, reproductive organs, stem) is a key process in the C cycle because it determines the residence time and location of C in the ecosystem (Campioli et al., 2008). For example, C used for maintenance respiration returns to the atmosphere within few hours-days; C allocated to structural biomass of organs with high turnover and decomposition rate, such as deciduous leaves, returns to the atmosphere within few months-years, whereas C allocated to organs with lower turnover and decomposition rate, such as stem wood, returns to the atmosphere only after decades or centuries (Campioli et al., 2008). In other words, allocation crucially determines the long-term rate of ecosystem respiration, the major C flux released by ecosystems (Trumbore, 2006).

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Carbon allocation in plants can be assessed directly by following the fate of unusual C isotopes ( $C^{13}$  and  $C^{14}$ ) once taken up by the leaves (i.e. isotope labelling). This technique allows a very detailed description of C allocation but it is very complicated to apply to high stature vegetation (e.g. forest stands) and to obtain quantitative estimates at seasonal and annual scale. Alternatively, C allocation can be derived indirectly by integrating ecosystem C fluxes obtained from independent assessments for the same site and period (Granier et al., 2000; Gough et al., 2008; Ohtsuka et al., 2009) e.g. vegetation C uptake (through assessment of gross primary production, GPP), vegetation C release (through assessment of autotrophic respiration) and C allocated to biomass production (through assessment of organ-specific net primary production, NPP).

A way to analyse the ecosystem C fluxes creating the C allocation pattern in forests is through the study of the NPP-GPP ratio, also called the carbon-use efficiency (DeLucia et al., 2007). This ratio has many qualities: (i) it is intuitive, (ii) it is easily comparable among different forest type, (iii) it is applicable to total NPP or to the NPP of the different tree organs separately, (iv) it is applicable to different temporal scales and (v) it is readily usable in models. Modelling C allocation is a great effort because (as mentioned above) C allocation is actually the result of a multitude of processes (maintenance, storage of reserve resources, turnover, reproduction, responses to environmental stresses etc.). Therefore the opportunity to model the allocation pattern by simulating stand photosynthesis and GPP (processes relative well understood and accurately modelled; Farquhar et al., 1980) and the use of the NPP-GPP ratio is appealing (Landsberg and Waring, 1997; Thornely and Cannell, 2000; Mäkelä and Valentine, 2001). The study of the NPP-GPP ratio and its possible uniformity across forest types (Waring et al., 1998) has been revised recently by DeLucia et al. (2007) for about 60 sites. However, in most of the studies reviewed, the analysis of the NPP-GPP ratio had limitations as e.g. (i) it was restricted to annual scale assessment with little information about inter-annual variability or seasonal dynamic, (ii) little attention was given to the difference in NPP-GPP ratio among different tree organs and (iii) there were technical imperfections because values of GPP were often non-independent of NPP (i.e. GPP derived from

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NPP measurements) or modelled.

The main objective of this study was to elucidate the fate of the C taken up through photosynthesis (GPP) by analysing the NPP of two typical temperate forests: a deciduous stand dominated by European beech (*Fagus sylvatica* L.) and an evergreen stand dominated by Scots pine (*Pinus sylvestris* L.). In details, we aimed at investigating the annual NPP-GPP ratio for five major tree organs (leaves, fruits, branches, stems and coarse roots) and their interannual and seasonal variability. Annual tree organ NPP was assessed by biometric methods or litter collection; seasonal production was inferred from repeated measurements of stem characteristics (e.g. diameter and wood density) and leaf canopy (e.g. leaf area index), whereas GPP was derived from continuous micrometeorological measurements through the eddy covariance (EC) methodology.

## 2 Materials and methods

### 2.1 Study sites

The study sites are managed experimental stands, intensively investigated in the fields of forest ecology, meteorology, biogeochemistry and tree science. Both stands are part of the European carbon flux monitoring network CarboEurope IP and the Scots pine stand is a level II observation plot of the ICP Forests programme. The annual allocation dynamics was investigated from 1997 till 2001, whereas the seasonal allocation dynamics were analyzed for 1998 at the beech stand and for 2007-2009 at the pine stand (no data on seasonal dynamics were available for the pine stand for the period 1997–2001).

The beech stand (0.6 ha) is located in the central part of the Hesse forest in North-Eastern France (48°40' N, 7°05' E; 305 m a.s.l.; slope less than 5%). The surrounding stands have the same structural characteristics than the experimental plot. The region has a semi-continental climate with long-term means of annual temperature and

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precipitation of 9.2°C and 820 mm, respectively. Annual and growing season temperature and precipitation for the study period are reported in Table 1. The stand is composed for 95% by young European beech (31 years old in 1997), with *Carpinus betulus* L. as second most common species, and only sparse understory vegetation. The stand originated from natural regeneration after clear-cutting a mature beech stand on 1965. A standard management (performed by the French forest service, ONF) for young high forests is applied with a thinning every 5 to 6 years, removing ca. 25% of the basal area. A thinning was performed one year before the study period (end 1995) and in the middle of it (March 1999). Overall, the tree density decreased from 4450 tree ha<sup>-1</sup> in 1997 to 3203 tree ha<sup>-1</sup> in 2001 (Table 1). Between 1997 and 2001, tree height increased from 12.3 to 13.3 m, whereas diameter at breast height (DBH) from 7.0 to 8.4 cm. At the site, the soil is luvisol/stagnic luvisol (FAO classification) with an oligomull humus. Clay contents are about 25-35% within 0–100 cm depth and about 40% below 100 cm. Water content at field capacity reaches 0.4 m<sup>3</sup> m<sup>-3</sup> in the upper layers. For more details see Epron et al. (1999), Granier et al. (2000, 2008).

The Scots pine stand is located at Brasschaat in Northern Belgium (51°18' N, 4°31' E; 16 m a.s.l.; 0.3% slope). The climate is temperate-maritime with long-term means of annual temperature and precipitation of 9.8°C and 767 mm, respectively. Annual and growing season temperature and precipitation for the period 1997–2001 are reported in Table 1. The stand (2.0 ha) belongs to a 300 ha mixed coniferous/broadleaved forest. Only few mature trees other than Scots pine (62 years old in 1997) are present but there is an understory composed of seedlings of various other tree species (e.g. *Betula pendula* Roth, *Sorbus aucuparia* L., *Quercus robur* L., *Quercus rubra* L., *Prunus serotina* Ehrh., *Rhamnus frangula* L.), shrubs (e.g. *Rubus fruticosus* L.), grasses (e.g. *Molinia caerulea* L.) and mosses (e.g. *Hypnum cupressiforme* L. and *Polytrichum commune* L.). The forest was planted in 1934 on former heathland. It has not been used for wood exploitation till the 1980s, when a new management plan was adopted by the Flemish Forest Service (ANB) (Carrara et al., 2003). The original high stocking density (1390 tree ha<sup>-1</sup> in 1980) was decreased by consecutive thinnings

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in 1980s and early 1990s to 538 tree ha<sup>-1</sup> in the winter of 1994–1995 (Čermák et al., 1998). Furthermore, a thinning was carried out in the autumn of 1999, further reducing the tree density to 375 tree ha<sup>-1</sup> (Xiao et al., 2003) (Table 1). Between 1995 and 2001, tree height increased from 20.6 to 21.4 m, whereas DBH from 26.8 to 30.0 cm.

5 The soil is classified as an Albic Hypoluvic Arenosol (World Reference Base for Soil Resources version 2006). The soil is moderately wet because of discontinuous clay lenses (>40% of clay) at a depth of 1.5–2 m, but the soil rarely saturates because of the high hydraulic conductivity in the upper sandy layers. Soil water content typically fluctuates around field capacity (0.16 m<sup>3</sup> m<sup>-3</sup>) (Gielen et al., 2010). For more details

10 see Čermák et al. (1998), Janssens et al. (1999), Curiel Yuste et al. (2005), Nagy et al. (2006), Neiryneck et al. (2008) and Gielen et al. (2010).

## 2.2 Gross primary production

Ecosystem GPP was estimated from vertical CO<sub>2</sub> fluxes above the canopy using the eddy covariance technique (Baldocchi and Meyers, 1998). At both sites, the EC system consisted of a sonic anemometer (Model SOLENT R2, Gill Instruments, Lymington, UK) for wind speed and an infrared gas analyser (IRGA) (Model LI-6262, LI-COR Inc., Lincoln, USA) to measure the CO<sub>2</sub> concentrations. The measurements were conducted at the top of a central tower. At Hesse, the measurement height was 18.5 m (in 1997–1999) and 23 m (in 2000–2001), whereas at Brasschaat the measurement height

15 was 41 m. A detailed description of the experimental setup can be found in Granier et al. (2008) for Hesse, and in Kowalski et al. (2000) and Carrara et al. (2003) for Brasschaat. Half-hourly GPP fluxes were calculated following the recommendations of the Euroflux network (Aubinet et al., 2000; Reichstein et al., 2005; Papale et al., 2006). At Hesse, flux inaccuracies due to temporal differences in the EC footprint and the experimental plot are negligible as the surrounding stands are similar to the experimental plot

20 (see above). At Brasschaat, GPP biased introduced by footprint-inconsistencies were low during the study period (7%) (Nagy et al., 2006).

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## 2.3 Annual production of stems, branches and coarse roots

At Hesse, tree circumferences were available for each of the study years from forest inventories at a representative sub-plot of 0.12 ha (Granier et al., 2008). Annual production of stems, branches and coarse roots (in kg C ha<sup>-1</sup> y<sup>-1</sup>) was calculated from two consecutive estimates of circumference using allometric relationships between circumference and standing biomass (Ottorini and Le Goff, 1998) and C content (Barbaroux et al., 2003) determined at the site for each woody organ. At Brasschaat, tree circumferences from forest inventories (over the total surface of 2.0 ha) were available only before and after the study period (winter 1994–1995 and winter 2001–2002, respectively). The annual production of stems, branches and coarse roots was calculated with a two step procedure. First, we determined the total production between 1995 and 2001 using values of standing biomass derived (as for Hesse) from site specific allometric relationships (Xiao et al., 2003; Curiel Yuste et al., 2005) and C contents (Janssens et al., 1999). Second, we determined the annual production by a weighted division of the total production in seven years. As weighing factors, we used the proportion of annual stem ring width vs. the total stem width increment during the seven years. Ring width series were available for 11 trees representative of the social categories (five dominant/co-dominant, three sub-dominant and three suppressed trees) and DBH classes of the stand (Xiao et al., 2003; Deckmyn et al., 2008).

## 2.4 Seasonal stem production

Estimations of the seasonal stem biomass production were derived from seasonal measurements of stem circumference or stem radius.

At Hesse, the seasonal increase of stem circumference was available from 1996 from manual measurements at breast height done in the same sub-plot investigated for annual increase in stem biomass (Granier et al., 2008). Measurements were available at intervals of 7–15 days during the period of fast growth (May and June) and at intervals of 1–2 months after this period (Granier et al., 2008). The proportional contribution of

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each interval to the annual biomass increment was assumed equal to the proportional contribution of each interval to the annual circumference increment. Such seasonal values of relative biomass production were transformed in absolute values (in  $\text{kg C ha}^{-1} \text{d}^{-1}$ ) for the corresponding interval by multiplication with the annual value of biomass production (see above) and correcting for the seasonal variability in stem wood density. From typical values of ring density available at the site, we approximated the seasonal density evolution as a three step pattern:  $550 \text{ g dm}^{-3}$  from onset of stem growth (late April – early May) till mid June,  $690 \text{ g dm}^{-3}$  from mid June till late July and  $1050 \text{ g dm}^{-3}$  from late July till the end of stem growth (late August – early September) (Bouriaud et al., 2004).

At Brasschaat, the seasonal increase in stem radius was available for 2008 for three trees (at breast height) from electronic point-dendrometers equipped with linear variable displacement transducers (Markasub ag, Olten, Switzerland). The instruments provided half-hourly potentiometer records from which the daily tree radius for the whole year was derived (Bouriaud et al., 2005). Daily values were averaged for the three trees and used to determine the mean stem circumference at seasonal (3 weekly intervals) and annual scale. As for Hesse, the proportional contribution of each 3 weekly interval to the annual stem NPP was derived from the proportional circumference increment for each interval, annual NPP and the seasonal pattern of stemwood density. Annual stem NPP in 2008 was obtained by subtracting the value of standing stem biomass in winter 2007–2008 by the value of standing stem biomass in winter 2008–2009. For winter 2007–2008, stem biomass was calculated by using allometric relationships and values of DBH obtained from forest inventories (see above). Because of the lack of DBH data for the winter 2008–2009, we derived them by using value of DBH in winter 2007–2008 and typical values of annual ring increment (i.e. mean of 6 years 1996–2001). Such assumption does not introduce a major bias as the final objective of this procedure is to study the typical seasonal allocation pattern to stem and not the specific annual values of stem NPP. From measurements at the site, we assumed the stem wood density to be  $365 \text{ g dm}^{-3}$  in the early wood (formed between

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mid April and early June) and  $698 \text{ g dm}^{-3}$  in the late wood (formed between early June and late September) (Vansteenkiste unpublished).

## 2.5 Annual leaf production

Leaf production was derived from oven dried (48 h at  $60\text{--}75^\circ\text{C}$ ) leaf litterfall. At Hesse, fallen leaves were collected from 1997 till 2001 between mid-September and end-November at weekly or biweekly interval in 45 litter-traps of  $0.25 \text{ m}^2$  each (Granier et al., 2008). At Brasschaat, litter fall was collected from 1999 till 2004 during the whole year at about monthly frequency (or biweekly in the autumn) in 10 litter-traps of  $0.28 \text{ m}^2$ . Leaves of deciduous species grow and die in the same growing season and thus, for beech, annual leaf production equals annual leaf litterfall. Needles of coniferous have longer life span and for the Scots pines at Brasschaat the maximal life time is of about 2 years. Previous research at the site showed that 1-year-old needles senesce from September onwards, whereas 2-years-old needles senesce during the whole year until August, when they are practically all shed (Gond et al., 1999; Boccadelli, 2008; Op de Beeck et al., 2010). Therefore, the annual leaf production of year  $x$  was calculated summing leaf litterfall from September of the year  $x+1$  till August of the year  $x+2$ . Leaf production was expressed in  $\text{kg C ha}^{-1} \text{ y}^{-1}$  by using a C content of  $0.47 \text{ g C g}^{-1}$  for beech (Regina et al., 1997) and  $0.48 \text{ g C g}^{-1}$  for pine (Janssens et al., 1999).

## 2.6 Seasonal leaf production

At Hesse, detailed information about seasonal leaf growth (bud burst, development of leaf area index, LAI, and specific leaf area, SLA) was available for 1998 (Barbaroux and Bréda, 2002; Davi et al., 2008). Leaf NPP was calculated weekly for this year from the respective values of LAI and SLA. Because this study focuses on the allocation of current photosynthates to current biomass production, the amount of previous year C reserves used for the construction of current leaf biomass was subtracted to the weekly values of leaf biomass production. Detailed information about this dynamics is reported

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by Dyckmans et al. (2000), who studied the weekly proportion of C reserves and new photosynthates used to produce leaves of young beech for 6 weeks after bud burst. Applying the findings of Dyckmans et al. (2000) to the data of Hesse, we calculated that 80% of the leaf production in the first week after bud burst was sustained by C reserves but that this proportion decreased rapidly (47% and 35% in the second and third week, respectively) and it was negligible from the fourth week onwards.

Seasonal leaf production at Brasschaat was derived from seasonal evolution of the LAI of the current-year needles (Op de Beeck et al., 2010) and their value of SLA (Xiao et al., 2006). The LAI of the current-year needles was calculated as the sum of needle litter fall and the increase of total LAI until its annual maximum (Op de Beeck et al., 2010). Leaf area index was measured indirectly with an optical method (i.e. the digital hemispherical photography) for two years (2007 and 2009) from April to October.

## 2.7 Annual fruit production

At Hesse, onset of fruit production was observed in 2002, when the trees were on average 36 years old (Granier et al., 2008). Thus, reproductive organs were not collected during the study period (1997–2001). At Brasschaat, fruit (cone) production occurs regularly, at least since observations began in 1999. Cones were collected in the litterfall, following the same protocol as reported above for needle production. Like needles, cones start to grow at Brasschaat on the current year ( $x$ ), develop during the next year ( $x + 1$ ) and end their growth 2 years afterwards ( $x + 2$ ) when they fall (mostly) between May and September. Unfortunately, no detailed information is available about the proportion of cone biomass produced during this 2–3 years time period. However, because the size of cones at the end of year  $x$  is small and because not much production is expected in mature cones just before falling in year  $x + 2$ , we assumed entire cone biomass collected in the litter traps during year  $x + 2$  as equivalent to cone NPP for the year  $x + 1$ .

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## 2.8 Calculation and statistic

Results of annual and seasonal dynamics of C allocation are expressed as ratio between NPP and GPP. For conciseness, the proportion of GPP allocated to leaf NPP, fruit NPP, stem NPP, total wood NPP and total stand NPP will be indicated in the text, as  $NPP_L$ -GPP,  $NPP_F$ -GPP,  $NPP_S$ -GPP,  $NPP_W$ -GPP and  $NPP_T$ -GPP, respectively. We have not estimated confidence intervals to the NPP-GPP ratios as they are derived from many datasets (e.g. DBH inventories, allometric relationships, litter fall, tissue C concentration, CO<sub>2</sub> fluxes) carrying dissimilar sets of errors. A preliminary analysis to relate  $NPP_L$ -GPP,  $NPP_F$ -GPP and  $NPP_W$ -GPP to environmental and stand variables was done by calculating the Pearson's Correlation coefficient (SPSS 16.0, SPSS Inc., an IBM Company, Chicago, USA) between each NPP-GPP ratio and current growing season meteorological conditions (i.e. May-August means of air temperature and precipitation), current growing season drought intensity index (DII; Bréda et al., 2006), previous year meteorological conditions (annual means of air temperature and precipitation), previous year DII, and tree density, separately.

## 3 Results

### 3.1 Annual production and standing tree biomass

The average amount of C taken up annually by the beech stand in the period 1997–2001 was 14.4 Mg C ha<sup>-1</sup> y<sup>-1</sup> of which 1.3 and 4.0 Mg C ha<sup>-1</sup> y<sup>-1</sup> were invested in leaf and wood NPP, respectively (Fig. 1a). The interannual variability is low-moderate for GPP and leaf NPP (CV= 0.12 – 0.19) and large for wood NPP (CV = 0.29) (Fig. 1a). Partitioning of wood NPP into stems, branches and coarse roots was 54–57%, 14–16% and 28–31%, respectively (Fig. 2a). Over the 5 year period, thinning does not affect the trends in annual wood NPP (Fig. 2a), neither the tree standing biomass which regularly increases from 1997 till 2001 (Fig. 2b).

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For pine, average GPP amounted to  $12.7 \text{ Mg C ha}^{-1} \text{ y}^{-1}$ , whereas leaf NPP, fruit NPP and wood NPP were restricted to about  $0.6\text{--}0.8 \text{ Mg C ha}^{-1} \text{ y}^{-1}$  each (Fig. 1c). The interannual variability was low for GPP and leaf NPP ( $\text{CV} = 0.09$ ), moderate for fruit NPP ( $\text{CV} = 0.22$ ) and large for wood NPP ( $\text{CV} = 0.33$ ) (Fig. 1c). Branches and coarse roots accounted each for about 15% of wood NPP, whereas the large majority of wood production was represented by stem NPP (about 70% of wood NPP) (Fig. 2c). The thinning of autumn 1999 reduced wood NPP of about 50% (Fig. 2c) and increased standing biomass per tree of about 45% (Fig. 2d).

### 3.2 Annual allocation pattern

The  $\text{NPP}_T\text{-GPP}$  was on average 38% for beech and 17% for pine, with annual ranges of 28–49% and 15–19%, respectively (Figs. 1b and d). For both stands, the largest  $\text{NPP}_T\text{-GPP}$  was in 1997.  $\text{NPP}_L\text{-GPP}$  was comparable for both stands (6–9%), whereas  $\text{NPP}_W\text{-GPP}$  of beech (29%) was about six times the corresponding ratio for pine (5%) (Figs. 1b and d). The interannual variability of  $\text{NPP}_T\text{-GPP}$  was substantially larger for beech ( $\text{CV} = 0.26$ ) than for pine ( $\text{CV} = 0.09$ ). As for the absolute values of NPPs reported above, the variability of  $\text{NPP}_L\text{-GPP}$  ( $\text{CV} = 0.06\text{--}0.17$ ) and  $\text{NPP}_F\text{-GPP}$  ( $\text{CV} = 0.22$ ) was lower than the variability of  $\text{NPP}_W\text{-GPP}$  ( $\text{CV} = 0.35\text{--}0.36$ ), particularly for pine (Fig. 1d).

The correlation analysis between the proportion of GPP allocated to biomass production of leaves, fruits and wood revealed (i) a significant positive relationship ( $p < 0.0001$ ;  $R^2 = 0.99$ ) between  $\text{NPP}_W\text{-GPP}$  and the drought stress intensity of the previous year for beech, (ii) a significant negative relationship ( $p = 0.02\text{--}0.03$ ;  $R^2 = 0.82\text{--}0.87$ ) between  $\text{NPP}_W\text{-GPP}$  and the annual temperature of the previous year for both the beech and the pine stand, (iii) a significant positive relationship ( $p = 0.03$ ;  $R^2 = 0.84$ ) between  $\text{NPP}_W\text{-GPP}$  and tree density at the pine stand, and that (iv)  $\text{NPP}_F\text{-GPP}$  at the pine stand tended to be positively correlated ( $p = 0.09$ ;  $R^2 = 0.67$ ) to the growing season precipitation and negatively correlated to the growing season drought stress intensity ( $p = 0.10$ ;  $R^2 = 0.65$ ).

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### 3.3 Seasonal production

The seasonal pattern (5-year average, 1997–2001) of beech GPP presented a sharp but regular increase in late April – late May, an 8 weeks period of high GPP rates (100–110 kg C ha<sup>-1</sup> d<sup>-1</sup>) and afterwards a gradual decrease that became more sharp in October (Fig. 3a). Overall, beech GPP was significantly different from zero between late April and early November. The seasonal pattern of pine GPP was very symmetric, with a fairly exponential increase from January till May, a 10 weeks period of high GPP rates (65–75 kg C ha<sup>-1</sup> d<sup>-1</sup>) and a fairly exponential decrease afterwards (mid August–December) (Fig. 3b).

For beech, leaf production occurred in 6 weeks between early May and mid June, with a sharp increase in production in mid May and a steady decline afterwards (Fig. 4a). For pine, leaf production lasted 24 weeks, from early April till mid September, with production peaking in mid June, decreasing remarkable in mid July and presenting a second (but lower) peak in mid August (Fig. 4b).

For both species, stems started to growth at about the same time as leaves (Fig. 4c and d). For beech, stem growth presented a pattern similar to the growth pattern of leaves i.e. highest production in early season and a decline afterwards, but the maximal production rate was 22 kg C ha<sup>-1</sup> d<sup>-1</sup> (50% lower than the leaf maximal production rate) and stem growth lasted till late August (whereas leaf growth till early June) but with a ca. 2 weeks stop in mid-late July (Fig. 4c). On the other hand, like the needles, pine stems presented two growth peaks (in early- and late growing season) and a growth decline (in the middle of the growing season). However, seasonality of pine leaves and stems differed, with stem having the highest growth rates and productive period in the late season (Fig. 4d), whereas leaves in the early season. For pine, maximal stem production rate was about 40% larger than maximal leaf production rate.

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### 3.4 Seasonal allocation pattern

Overall, for the period between early May and early June, the proportion of GPP allocated to leaf- and stem NPP (i.e.  $NPP_L$ -GPP plus  $NPP_S$ -GPP) at the beech stand was above 30%, with values of about 60–70% in mid May. After this period, GPP was allocated only to stem production (leaf growth stopped in early June) and  $NPP_S$ -GPP was low (less than about 20%) and decreased along the season (Fig. 4e). For beech, maximal  $NPP_L$ -GPP was 59% (in early-mid May), whereas maximal  $NPP_S$ -GPP was 22% (mid-late May).

Despite similar trends for ca. the first 8 weeks of the growing period,  $NPP_L$ -GPP and  $NPP_S$ -GPP had opposite developments at the pine stand, with e.g. larger allocation to leaves in early-mid June vs. larger allocation to stem in mid-late July, a peak allocation to stem in mid August vs. a peak allocation to leaves in late August and a substantial amount of GPP allocated to stem in September while a minimal amount of GPP was allocated to leaves in the same period (Fig. 4f). Thus, overall, the proportion of GPP allocated to leaf- and stem NPP ( $NPP_L$ -GPP plus  $NPP_S$ -GPP) was rather constant during the season with slightly lower values in July (14–18%) and slightly larger values in early-mid May (23%) and mid-late August (24–26%) (Fig. 4f).  $NPP_L$ -GPP was maximal in early season (16%), whereas  $NPP_S$ -GPP was maximal in the late season (19%).

## 4 Discussion

### 4.1 Annual allocation pattern

Averages over 5 years showed that a young beech stand has a  $NPP_T$ -GPP of about 38%, whereas for a mature Scots pine stand the same ratio is much lower, about 17%. These values are important because (i) estimates of  $NPP_T$ -GPP are scarce for stands at a non-juvenile phase of development (i.e. >20 years old), and because (ii) minimum  $NPP_T$ -GPP was previously thought to be 22% (DeLucia et al., 2007). Despite

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the similar proportion of C invested in leaf production, a remarkable difference was observed in the amount of C invested in wood production between the two stands. Whereas for beech, on average 29% of the annual GPP was invested in wood NPP, for pine this was only 5% (about 6% before thinning and about 3% after thinning). Reviewing data from 29 contrasting forests, Litton et al. (2007) found that the proportion of GPP allocated to aboveground wood NPP varies from 8 to 31%. Whereas the results obtained for the beech stand are in the upper part of this range, the proportion of C invested in wood NPP at the pine stand fall out of the range. The low  $NPP_w$ -GPP found at the pine stand might partially be due to ageing (Mäkela and Valentine, 2001). For instance, the  $NPP_w$ -GPP was on average 24% for a 35–45 years old Scots pine stand in southern Finland (Ilvesniemi et al., 2009). On the other hand, the large cone production (on average 6% of GPP) might have diverted C resources otherwise available for wood production. This hypothesis is somewhat corroborated by the fact that the interannual variability of  $NPP_F$ -GPP and  $NPP_w$ -GPP (CV of 0.22 and 0.35, respectively) are larger than the interannual variability of the proportion of GPP allocated to wood and fruits together (CV = 0.14) (data not shown).

The difference in C allocation to biomass production between the stands is substantial, with beeches allocating a proportion of their GPP to aboveground NPP plus coarse root NPP more than double than the corresponding proportion for pines. Therefore, it is likely that, compared to beeches, pines invest a larger amount of GPP in processes other than biomass production (respiration) or in the production of fine roots, the only tree organ not considered in this study. Estimates available for both stands in 2000–2001, show that the proportion of GPP allocated to autotrophic respiration is very similar between stands: 46% and 44% for beech and pine, respectively (Nagy et al., 2006; Granier et al., 2008). By exclusion, the difference in beech and pine allocation pattern seems therefore due to the production of fine roots. Data available substantiate this hypothesis, as at the nutrient-poor pine stand a larger proportion of GPP is allocated to fine root NPP than at the nutrient-rich beech stand (13% vs. 5% in 1997, respectively) (Granier et al., 2000; Janssens et al., 2002). This agrees with basic allocation

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theories (e.g. the root-shoot functional balance of Davidson 1969) and recent review on C allocation dynamics in forests (Litton et al., 2007), which report a larger investment belowground in case of limited nutrients. On the other hand, the low  $NPP_w$ -GPP for pine might be due partly to an overestimation of the actual pine GPP. The method we used to determine GPP, i.e. the eddy covariance methodology, is accurate and provides continuous measurements but it does not discriminate between under- and overstory C fluxes. This drawback is negligible for the beech stand, where no understory is present, but it might introduce approximations for the pine stand, where understory vegetation is present (grasses, seedlings and shrubs). In any case, we can summarize that at the beech stand a substantial amount of GPP is allocated to the production of slow decomposable C pools (woody tree biomass) whereas at the pine stand a substantial amount of GPP is allocated to the production of fast decomposable C pools (non-woody tree biomass, understory vegetation). In other words, even in case the two ecosystems have for the same period a similar gross C uptake (GPP), C release (TER, total ecosystem respiration) and thus net ecosystem exchange (NEE), the C sequestration capacity of the pine stand is in the long-term lower than the C sequestration capacity of the beech stand.

Assuming for the sites an annual allocation of 17–38% of GPP for the production of leaves, fruits and wood (this study), 5–13% of GPP to the production of fine roots (Granier et al., 2000; Janssens et al., 2002) and 44–46% of GPP consumed for autotrophic respiration (Nagy et al., 2006; Granier et al., 2008), a relevant portion of GPP remains “unexploited”, i.e. 11–26%. Beside production of structural biomass and respiration, part of the gross C uptake of trees is used also for the production of non-structural biomass as C compounds for ectomycorrhizal fungi, root exudates, carbohydrates reserves and volatile organic compounds (VOCs). These components are very difficult to assess and data on the production of non-structural biomass are scattered or lacking at the sites. Whereas root exudates are estimated to account for 2–4% of NPP in plants (Jones et al., 2004), annual net increase of carbohydrate reserves for about 0.5–1.5% of GPP at our beech site (Barbaroux et al., 2003) and VOCs for max 1% of

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GPP in temperate forests (Guenther et al., 1995), C transfers to symbiotic fungi might be much more important and represent a significant C allocation sink. For instance, in a recent review, Hobbie (2006) reported that the contribution of ectomycorrhizal fungi may be up to 21% of NPP in plants. Therefore, more information about the plant-root fungi C transfer, fungi biomass production and fungi growth dynamics are necessary to elucidate the GPP allocation pattern in temperate forests and current state-of-art studies (and modeling) need to take into account this uncertainty.

The low interannual variability of the fraction of GPP allocated to leaf NPP indicates that leaf NPP is mainly controlled by current photosynthetic uptake. On the other hand, the large interannual variability of the fraction of GPP allocated to the other tree organs indicates that important factors other than current GPP are affecting the allocation of C to pine wood, pine cones and beech wood. Because of the limited number of replicate years ( $n = 5$ ), we could not perform comprehensive statistical analysis to evaluate accurately the influence of environmental drivers on the interannual variability of NPP-GPP ratios. However, preliminary correlation analysis with basic environmental variables, meteorological conditions and tree density revealed significant relationships and possible trends. As a main result, we obtained that  $NPP_w$ -GPP is related to the meteorological and environmental conditions of the previous year rather than the ones of the current growing season. This “memory-effect” of trees is of particular interest and likely linked to the status of the carbohydrates reserves of trees. The negative relationship between  $NPP_w$ -GPP and the previous year temperature can be due to the fact that C reserve accumulation might be larger in a less warm year due to larger C assimilation (less heat stress to leaves) and, in particular, less autotrophic respiration. Therefore, trees with larger C reserves might have an enhanced growth the next growing season, resulting in larger  $NPP_w$ -GPP (note that GPP varies little among years). For beech, we obtained also a strong positive correlation between  $NPP_w$ -GPP and the previous year drought intensity. This counter-intuitive relationship might be explained by the fact that the drought stress intensities observed during the study period 1997–2001 were low. In such conditions, tree fit is not significantly damaged and, while their biomass

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5 growth is reduced because of the water limitation, their photosynthetic uptake continues, enhancing the C reserve accumulation (Cannell and Dewar, 1994; Barbaroux and Bréda, 2002). Therefore, the effect of previous year low drought stress and low annual temperature might be similar. However, for pine the effect of previous year temperature  
10 on  $NPP_w$ -GPP might be confused by the effect of the thinning occurred at the site in autumn 1999 (see below). On the contrary, our results indicate that current year water status might have an impact on the fruit NPP, with lower  $NPP_f$ -GPP in case of lower precipitation and more intense drought stress. These preliminary results on a limited sample size suggest that further research on the effect of environmental variables on  
15 the C allocation pattern at stand level and organ NPP-GPP ratio can be promising. Relevant datasets might become available in the future if annual production data would be reconstructed at sites with long-term (e.g. 15 years) GPP records from EC towers.

The study of the effect of thinning on stand production and C allocation was not one of our main goals. However, it is noteworthy to report the overall impact that  
20 thinning had at the two stands. Whereas at the beech stand thinning seems to have not affected wood NPP and tree standing biomass, at the pine stand thinning seems to have reduced remarkably wood NPP and increased remarkably the standing biomass per tree (Fig. 2). This was due to the different thinning intensity (the trees removed were 24% at Hesse and 30% at Brasschaat), the different thinning strategy (at Hesse, most  
25 of the trees removed were dominant, whereas at Brasschaat most of the trees removed were suppressed) and, particularly, to the different age and growth responsiveness of the trees at the two sites. In fact, it is likely that the studied young beeches react fast to the released competition and that their biomass production per tree increased after the thinning. For instance, the stand LAI (decreased by 35% after thinning) fully recovered in only one year (Granier et al., 2008). On the other hand, the studied mature pines might react very slowly (or not at whole) to the released competition because of their dominant status or their limited growth capacity (Curiel Yuste et al., 2005).

Finally, we observed that the interannual variability of  $NPP_T$ -GPP is lower than the interannual variability of  $NPP_w$ -GPP and  $NPP_f$ -GPP, indicating that some trades off

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in C allocation might exist. This dynamics, pointing to a conservative amount of GPP allocated to aboveground and to woody organs is highly interesting and deserve further research also.

## 4.2 Seasonal allocation pattern

5 The seasonal pattern observed for leaf- and stem NPP at the beech stand is typical for single leaf-flush deciduous species. The stop in stem growth in mid-late July and the low values of stem NPP which characterized the subsequent weeks (0–6 kg C ha<sup>-1</sup> d<sup>-1</sup>) corresponded to a drought period (Barbaroux and Bréda, 2002). In years without drought, stem NPP rates in mid July – late August are substantially larger  
10 (8–16 kg C ha<sup>-1</sup> d<sup>-1</sup>) and stem growth ceases in late August – early September (data not shown). Beech trees allocated to stem NPP and, particularly, to leaf NPP a very large proportion of GPP in the earliest part of the growing season and only very limited GPP portions during the remaining part of the year. Deciduous trees are forced to such large GPP investment in the early season to build up the leaf canopy and best exploit  
15 the favourable conditions for C assimilation during this period (e.g. high insolation, mild temperature, high soil water content) and, secondary, to produce the woody vessels needed to provide water and mechanical support to the newly formed leaves. Because of this extremely large GPP investment in leaves and wood, it is expected that C allocation to other tree organs is minimized in this period. For instance, fine root growth  
20 was reported to start at the site only at the end of May (Barbaroux et al., 2003), when the proportion of GPP allocated to leaves and wood is already declining.

The seasonal patterns of leaf- and stem NPP in pine are completely different than the ones observed for beech. Evergreens do not need to produce a fully new canopy in the early season, as the 1-year old leaves have a relatively high photosynthetic capacity  
25 (Op de Beeck et al., 2010) and the hydraulic system remains operational throughout the winter. Therefore, it is more cost-effective for pine to opt for a gradual growth pattern, as this requires overall less energy and fewer reserves of resources. Indeed, we detected leaf- and stem NPP throughout the growing season and the total proportion of GPP

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allocated to leaves and stems ( $NPP_L-GPP$  plus  $NPP_S-GPP$ ) is generally rather similar and low. However, leaves and stems did not present the same seasonal growth pattern, rather the opposite, with increments in leaf NPP corresponding to declines in wood NPP (particularly in the early season) and vice versa (particularly in the late season).

5 Therefore, within an overall stable allocation scheme along the season (i.e. constant sum of  $NPP_L-GPP$  plus  $NPP_S-GPP$ ) some hierarchical rules are present (e.g.  $NPP_L-GPP > NPP_S-GPP$  or vice versa) which are driven by seasonality (Lacointe, 2000). Peaks in allocation to leaves in mid June suggest that even for evergreen species a substantial leaf growth in the early season might be advantageous. On the other  
10 hand, peak allocation to stems in late August might indicate that (i) stem is a sink less important than leaves and it receives C only when the leaf C needs are satisfied or (ii) stem growth is more important than leaf growth (i.e. stem has higher position than leaves in the sink hierarchy) in late season because stem growth is positively correlated to the process of reserves storage (Lacointe, 2000) particularly important in  
15 the late season (Barbaroux and Bréda, 2002).

## 5 Conclusions

The annual analysis of the C allocation for a young beech stand and a mature Scots pine stand revealed that the proportion of GPP allocated to NPP was more than double for the former than the latter, despite the similar GPP. The proportion of GPP allocated  
20 to leaf biomass is similar for both species, whereas the proportion of GPP allocated to wood biomass is about six times larger for beech than for pine. These results, combined with previous knowledge on similar autotrophic respiration at the stands, indicate that C has a longer residence time at the beech ecosystem than at the pine ecosystem or, in other words, that the C sequestration capacity of the beech stand  
25 is larger than the C sequestration capacity of the pine stand. The multi-annual analysis revealed a large variability in the proportion of GPP allocated to wood biomass (larger than the variability of the proportion of GPP allocated to leaves, fruits and to

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the overall aboveground NPP plus coarse roots NPP) that could be controlled by previous year meteorological conditions, drought stress and thinning. Seasonal pattern of C allocation greatly differed between beech and pine (NPP-GPP ratio largest in early season for beech and more uniform for pine) and between pine leaves and pine stems (NPP-GPP ratios peaking in opposite periods). Such differences are explained by functional differences between species (e.g. deciduousness vs. evergreenness) and by temporal-dependent sink strength of pine leaves and pine stems related to growth and C reserves dynamics. Our analysis, combined with previous research conducted at the two studied stands, evidenced that the most needed improvements to deepen our knowledge on C allocation dynamics and NPP-GPP ratios concern the belowground stand compartment, as fine roots and particularly mycorrhizal fungi, which contribution to NPP and C allocation pattern might be substantial but totally disregarded for the majority of forest ecosystems.

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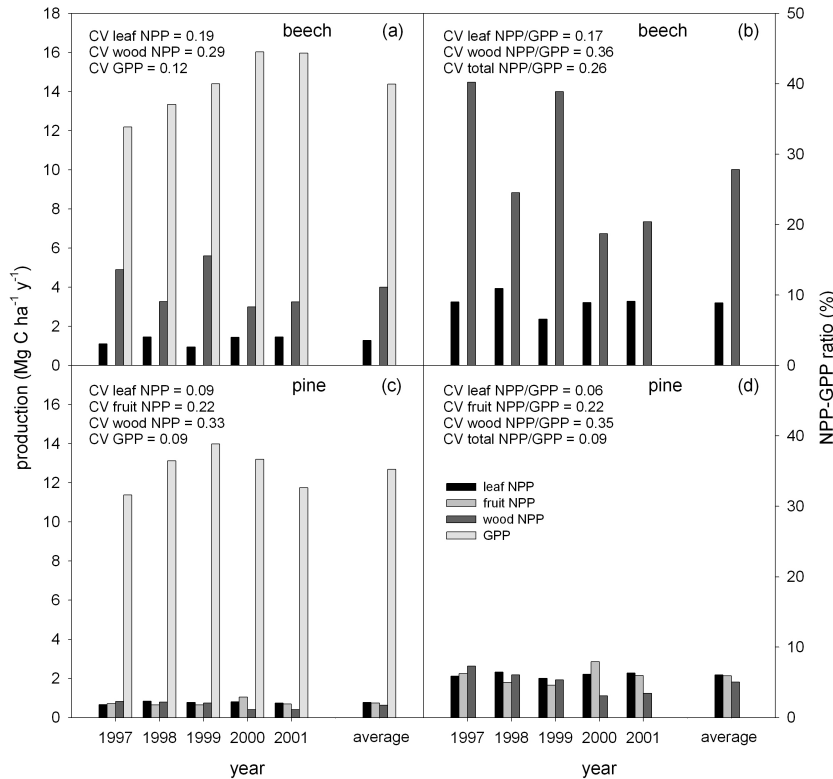
**Table 1.** Annual- and growing season meteorological conditions (air temperature and precipitation), drought stress intensity and tree density at the experimental stands during the study period.

| variable                                   | period     | Hesse ( <i>Fagus sylvatica</i> ) |       |      |      |       | Brasschaat ( <i>Pinus sylvestris</i> ) |      |      |      |      |
|--|------------|----------------------------------|-------|------|------|-------|--|------|------|------|------|
|  |            | 1997                             | 1998  | 1999 | 2000 | 2001  | 1997                                   | 1998 | 1999 | 2000 | 2001 |
| temperature (°C)                           | annual     | 11.4                             | 10.8  | 11.6 | 12.7 | 11.3  | 10.5                                   | 10.7 | 11.5 | 10.9 | 10.6 |
|  | May–August | 16.4                             | 16.4  | 16.6 | 16.5 | 17.1  | 16.7                                   | 16.3 | 18.2 | 16.0 | 16.7 |
| precipitation (mm)                         | annual     | 871                              | 974   | 1091 | 1017 | 1151  | 672                                    | 1042 | 809  | 895  | 960  |
|  | May–August | 362                              | 252   | 354  | 398  | 285   | 317                                    | 209  | 275  | 350  | 277  |
| drought intensity index (-) <sup>(a)</sup> | annual     | 3.85                             | 10.68 | 0    | 0    | 11.05 | 0.04                                   | 2.15 | 4.49 | 0    | 0.45 |
| tree density (tree ha <sup>-1</sup> )      | annual     | 4450                             | 4450  | 3364 | 3297 | 3203  | 538                                    | 538  | 538  | 375  | 375  |

<sup>(a)</sup> values vary from 0 (no drought) to 90–100 (most severe drought) (Bréda et al., 2006).

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**Fig. 1.** Gross primary production (GPP) of tree canopy and net primary production (NPP) of tree organs (leaves, fruits and stem, branches and coarse roots, considered together as woody organs) at the beech stand of Hesse (France) and at the Scots pine stand of Brasschaat (Belgium) for the period 1997–2001. Data are reported as annual values and 5-year averages (with coefficient of variation, CV) for **(a)** GPP and NPP at Hesse, **(b)** NPP-GPP ratio at Hesse, **(c)** GPP and NPP at Brasschaat, and **(d)** NPP-GPP ratio at Brasschaat.

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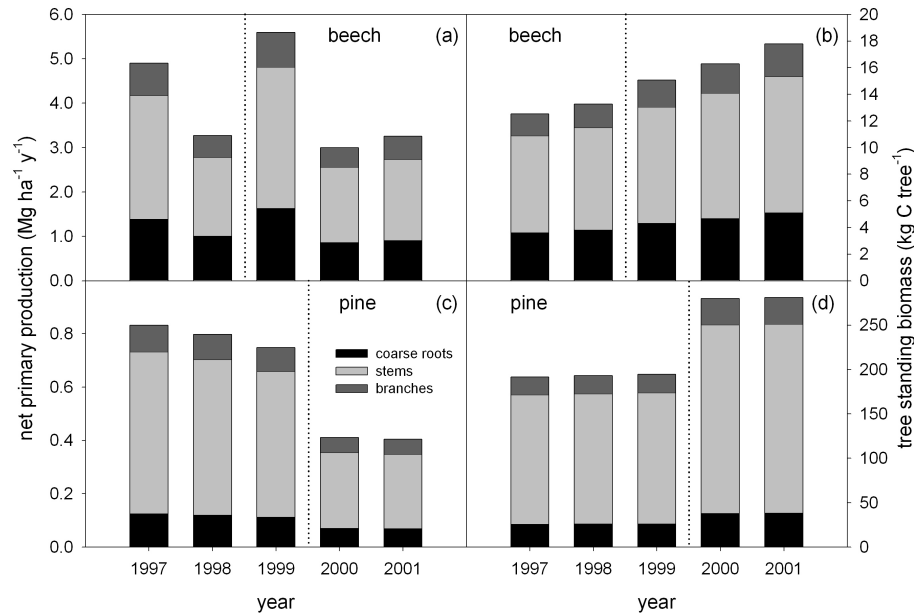
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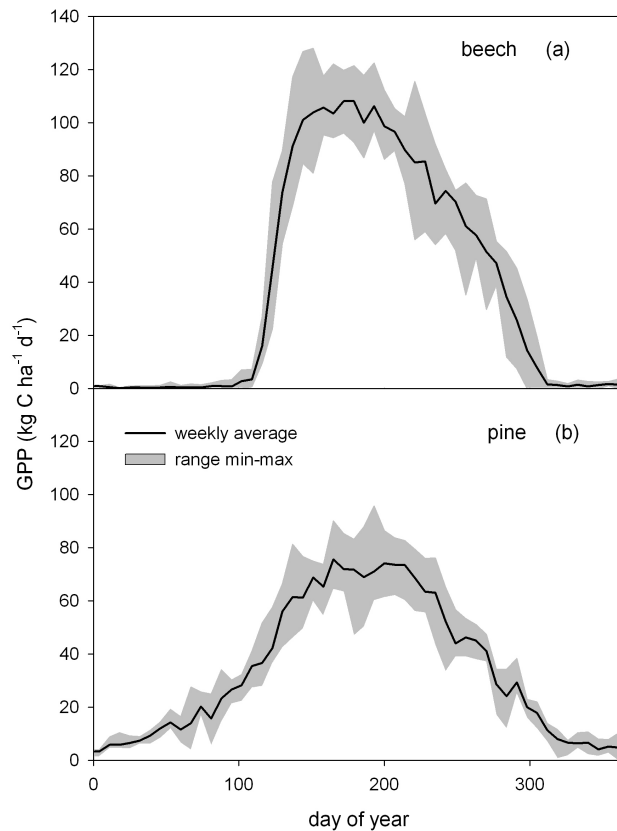


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**Fig. 2.** Annual net primary production (NPP) per unit of surface (in  $\text{Mg C ha}^{-1} \text{y}^{-1}$ ) and standing biomass per tree ( $\text{kg C tree}^{-1}$ ) at the beech stand of Hesse (France) and at the Scots pine stand of Brasschaat (Belgium) for the period 1997–2001: **(a)** NPP at Hesse, **(b)** tree standing biomass at Hesse, **(c)** NPP at Brasschaat, and **(d)** tree standing biomass at Brasschaat. The dotted line corresponds to a thinning (24% beeches removed at Hesse and 30% pines removed at Brasschaat).



**Fig. 3.** Weekly values of gross primary production (GPP) (average and minimal-maximal range) averaged over a 5 years period (1997–2001) at **(a)** the beech stand of Hesse (France) and **(b)** the Scots pine stand of Brasschaat (Belgium).

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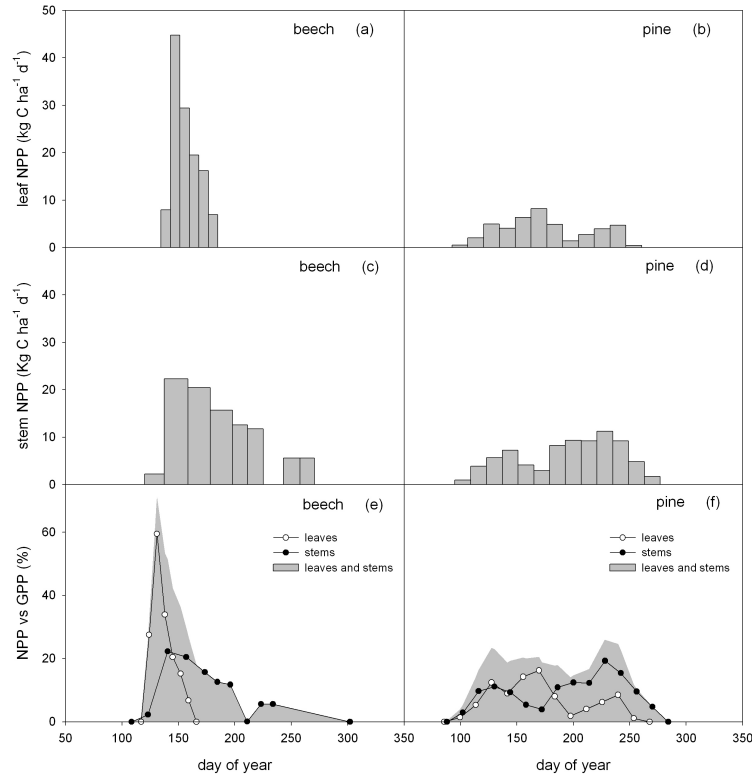
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**Fig. 4.** Seasonal pattern (a–d) of net primary production (NPP) and (e–f) of the ratio NPP vs GPP (gross primary production), for leaves and stems at the beech stand of Hesse (France) in 1998 and at the Scots pine stand of Brasschaat (Belgium) in 2007–2009.