Available online at www.sciencedirect.com

SciVerse ScienceDirect

http://www.elsevier.com/locate/biombioe

Net ecosystem production and carbon balance of an SRC poplar plantation during its first rotation☆

M.S. Verlinden [a,*], L.S. Broeckx [a], D. Zona [b], G. Berhongaray [a], T. De Groote [a,c], M. Camino Serrano [a], I.A. Janssens [a], R. Ceulemans [a]

[a] Department of Biology, Research Group of Plant and Vegetation Ecology, University of Antwerp, Universiteitsplein 1, B-2610 Wilrijk, Belgium
[b] Department of Animal and Plant Sciences, The University of Sheffield, Western Bank, Sheffield S10 2TN, UK
[c] Unit Environmental Modelling, VITO, Boeretang 200, B-2400 Mol, Belgium

ARTICLE INFO

Article history:
Received 14 January 2013
Received in revised form
28 May 2013
Accepted 30 May 2013
Available online 22 June 2013

Keywords:
Carbon pools
Carbon fluxes
Net primary production
NEE
Carbon budget
Populus

ABSTRACT

To evaluate the potential of woody bioenergy crops as an alternative energy source, there is need for a more comprehensive understanding of their carbon cycling and their allocation patterns throughout the lifespan. We therefore quantified the net ecosystem production (NEP) of a poplar (*Populus*) short rotation coppice (SRC) culture in Flanders during its second growing season.

Eddy covariance (EC) techniques were applied to obtain the annual net ecosystem exchange (NEE) of the plantation. Further, by applying a component-flux-based approach NEP was calculated as the difference between the modelled gross photosynthesis and the respiratory fluxes from foliage, stem and soil obtained via upscaling from chamber measurements. A combination of biomass sampling, inventories and upscaling techniques was used to determine NEP via a pool-change-based approach.

Across the three approaches, the net carbon balance ranged from 96 to 199 g m^{-2} y^{-1} indicating a significant net carbon uptake by the SRC culture. During the establishment year the SRC culture was a net source of carbon to the atmosphere, but already during the second growing season there was a significant net uptake. Both the component-flux-based and pool-change-based approaches resulted in higher values (47–108%) than the EC-estimation of NEE, though the results were comparable considering the considerable and variable uncertainty levels involved in the different approaches. The efficient biomass production – with the highest part of the total carbon uptake allocated to the aboveground wood – led the poplars to counterbalance the soil carbon losses resulting from land use change in a short period of time.

1. Introduction

At the present day energy from biomass has gained interest as an alternative for fossil fuels and as a possibility to bring down greenhouse gas emissions [1,2]. Land use changes affecting the cycling and storage of carbon (C) in ecosystems [3] are one of the main causes of the increased greenhouse gas levels in the atmosphere [4,5]. However, afforestation of abandoned and marginal farmland can enhance ecosystem C storage and potentially counteract the processes of C loss [6]. Within this

* *Corresponding author*. Tel.: +32 32652827; fax: +32 32652271.
E-mail address: Melanie.Verlinden@ua.ac.be (M.S. Verlinden).

0961-9534/$ – see front matter © 2013 The Authors. Published by Elsevier Ltd. All rights reserved.
http://dx.doi.org/10.1016/j.biombioe.2013.05.033

context the establishment of short rotation coppice (SRC) plantations for bioenergy production has potential for mitigating the rising greenhouse gas levels in the atmosphere [7]. It has been assumed that the net CO_2 emissions from bioenergy cultures are zero [8] or are so-called 'carbon neutral' by taking up as much C during the growth as released upon conversion to energy. However, bioenergy cultures as SRC plantations might act as a CO_2 source, particularly in the short to medium term [9] due to land use changes. During the consequent years they switch to C sinks [8,10–13]. The net C benefit of such plantations is fairly site specific [12]; it is, therefore, important to study and quantify the C cycle of these ecosystems in more detail and to assess their impact on regional C balances [14].

The net C balance of an ecosystem can be assessed by both NEP (net ecosystem production) and NEE (net ecosystem exchange). NEP is the difference between net primary production (NPP) and heterotrophic ecosystem respiration. NPP is the total amount of new organic matter produced during a certain period [15]. It is the difference of the total photosynthetic uptake of CO_2 by the ecosystem – or the gross primary production (GPP) – and the autotrophic ecosystem respiration. NEE is the net CO_2 flux from the ecosystem to the atmosphere [16], which corresponds to the net difference of photosynthetic carbon uptake and the respiration of autotrophs and heterotrophs [17]. NEE equals NEP disregarding sources and sinks for CO_2 not involving conversion to or from organic C [18]. To understand the dynamics of the ecosystem C sinks, it is important to estimate the size of each C pool and to quantify all C fluxes. Studies of the C balance of SRC plantations are rather scarce [19,14,12] and the simultaneous quantification of NEE with eddy covariance techniques, and of NEP with both C flux and C pool assessments were never done before for an SRC culture.

The present study is part of the large-scale POPFULL project [20] which aims to make a full greenhouse gas balance and to investigate the economic and energetic efficiency of an operational SRC culture with poplar. Within this context, the specific objectives of this study were: (i) to quantify the components of the carbon balance of an SRC plantation; (ii) to quantify NEP and determine the sink–source status and (iii) to compare the estimated NEP with NEE measured through eddy covariance techniques. All measurements were performed during the second growth year of the first rotation.

2. Material and methods

2.1. Site and plantation description

The operational POPFULL site is located in Lochristi, province East-Flanders, Belgium (51°06′44″ N, 3°51′02″ E). The region is subjected to an oceanic climate with a long-term average annual temperature and precipitation of 9.5 °C and 726 mm, respectively [21]. According to the Belgian soil classification the area forms part of the sandy region with poor natural drainage [22]. The 18.4 ha site was a former agricultural area consisting of croplands (62%; with corn as the most recent cultivated crop in rotation) and extensively grazed pasture (38%). On 7–10 April 2010 an area of 14.5 ha (excluding the headlands) was planted with 12 selected poplar (*Populus*) and three selected willow (*Salix*) genotypes, representing different species and hybrids of *Populus deltoides*, *Populus maximowiczii*, *Populus nigra*, and *Populus trichocarpa* and *Salix viminalis*, *Salix dasyclados*, *Salix alba* and *Salix schwerinii*. The present study focuses on the poplar genotypes only. Using a modified leek planting machine 25 cm long dormant and unrooted cuttings were planted in a double-row planting scheme with alternating distances of 0.75 m and 1.50 m between the rows and on average 1.10 m between trees within the rows (plant density of 8000 ha^{-1}). The plantation was designed in large monoclonal blocks of eight double rows wide that covered both types of former land use (cropland and grazed pasture). Each genotype has minimum two and maximum four replicated blocks with row lengths varying from 90 m to 340 m. After two years of growth (2010, GY1 (growth year) and 2011, GY2) the plantation was harvested for the first time on 2–3 February 2012 with commercially available SRC harvesters. Trees continue growing as a coppice culture with multiple shoots per stool in the following two-year-rotations. More details on site conditions, on poplar materials and on the plantation lay-out are found in Broeckx et al. [23].

2.2. Meteorological data and soil data

A complete set of environmental variables were recorded continuously from June 2010 till present as described in Zona et al. [24,25]. Soil temperature was monitored from the surface until 1 m depth; air temperature and relative humidity were collected at about 5.4 m above the surface. All sensors for these measurements were placed in the immediate proximity of an eddy covariance (EC) mast (see below). For more details on the instruments used we refer to Zona et al. [24,25].

2.3. Quantification of carbon pools

2.3.1. Foliage pool (F)

Leaf litter was collected during leaf fall from early September to December of GY2 in two plots of 5 × 6 trees for each genotype within each former land use type ($n = 48$). In each plot three perforated litter traps (litter baskets) of 0.57 m × 0.39 m were placed on the ground along a diagonal transect between the rows covering the wide and the narrow inter-row spacings. Every two weeks the litter traps of each plot were emptied and leaf dry biomass was determined after oven drying at 70 °C. Successively collected leaf biomass was cumulated over time to obtain the yearly produced foliage. C mass fractions of the leaves were determined on a mixed subsample of three randomly selected mature leaves of different individual leaf area and from different tree heights per plot in September of GY2, at the time when maximum leaf area index was reached [23]. Leaves of plots with the same genotype × land use type combination were merged, yielding six leaves per mixed sample. Samples were ground and analysed by dry combustion with an NC element analyzer (NC-2100 element analyzer, Carlo Erba Instruments, Italy). These C mass fractions were used to quantify the foliage C production per plot. An average foliage C pool value was then calculated by weighing the averages per genotype × land use type combination with their proportional area in the plantation.

2.3.2. *Aboveground woody biomass pool (Ste + Br)*

Aboveground woody biomass was determined by combining stem diameter inventory data with allometric equations relating woody biomass with stem diameter. Stem diameter at 22 cm above soil level [26,27] was measured in December of GY1 and of GY2 for all trees in one row of each monoclonal block. If a tree had multiple stems, every stem was measured within the tree. Missing trees were recorded as zero to correct for the effective tree density. For each genotype an allometric power relationship was established linking aboveground woody (dry) biomass to stem diameter. Based on the diameter distribution at the end of GY2, ten shoots for each genotype were selected for destructive harvest, covering the widest possible diameter range. Shoot diameter (D) at 22 cm was measured with a digital caliper (model CD-15DC, Mitutoyo Corporation, Japan, 0.01 mm precision). The stem was then harvested at 15 cm above soil level, the average harvesting height of the plantation. After determination of dry biomass (DM) of each stem, values were plotted against diameter and fitted as $DM = a \cdot D^b$ for each of the 12 genotypes (with a and b regression coefficients; cfr. Ref. [27]). All 12 power regressions had an R^2 value of more than 97% with a significance p-level < 0.001. For each genotype a mixed subsample of grated wood material of stem (Ste) and branches (Br) of ten trees was used for the analysis of C mass fraction by dry combustion. From diameter inventories and allometric equations, a weighted average of the change in aboveground woody biomass C pool during the second growing season was calculated as the difference between the standing pool after GY2 and GY1.

2.3.3. *Belowground woody biomass pool (CR) and stump (Stu)*

Coarse root woody biomass was determined by excavation of the root system. Because of the high labour intensity, excavation was restricted to genotypes Koster (*P. deltoides* Marsh × *P. nigra* L.) and Skado (*P. trichocarpa* Hook. × *P. maximowiczii* Henry), selected as most representative for the plantation based on parentage, origin and area coverage in the plantation. For both genotypes five trees of different stem diameters (from 20 mm to 60 mm at 22 cm height) were selected within each of both former land use types. Right after harvest in February 2012, remaining stumps (Stu) and roots were excavated over an area of 1.1 m × 1.125 m (planting distance in the rows × sum of half inter-row distances). All roots within this sampling area were collected, assuming that roots from adjacent trees compensated for roots of the selected tree growing outside the sampled area. Excavation depth was limited to 0.6 m, as very few roots were observed under 0.6 m [28]. Coarse roots (Ø > 2 mm) were sampled, and total dry biomass of these coarse roots (CR) and the remaining 15 cm high stump was determined after oven drying at 70 °C. Since no significant effect was found for genotype or former land use, all data were pooled; belowground woody biomass and stump biomass were plotted against stem diameter at 22 cm. As for aboveground woody biomass (cfr. Section 2.3.2), an allometric power regression was fitted. From the diameter inventory the average belowground woody biomass and stump biomass pool were estimated for both GY1 and GY2. Since no coarse root turnover was observed, the belowground biomass production of the GY2 was calculated as the standing pool after GY2 minus the standing pool after GY1. Dried root wood was grated for CN-analysis. An average of the C mass fraction was used for calculating the belowground woody C pool.

2.3.4. *Fine root pool (FR)*

Sequential soil coring was used to determine fine root production in the same two genotypes as for belowground woody biomass determination, i.e. Koster and Skado. From February to November of GY2 the upper 15 cm soil layer was sampled monthly using an 8 cm diameter × 15 cm deep hand-driven corer (Eijkelkamp Agrisearch equipment, The Netherlands) [29]. At every sampling campaign 20 samples were collected for each genotype of which half in the narrow and half in the wide inter-row spacings, randomly spread over the planting area within the former pasture land use type. Fine roots (Ø < 2 mm) were picked from the sample by hand while (i) separating out weed roots from poplar roots, and (ii) sorting poplar roots in dead and living roots. The sorting of dead and living roots was based on the darker colour and the poorer cohesion between the cortex and the periderm of the dead roots [30]. Following washing, fine poplar roots were oven dried at 70 °C for 1–4 days to determine the dry root biomass per soil surface area. Subsamples of dried roots were grinded and analysed for the C mass fraction (NC-2100 element analyzer, Carlo Erba Instruments, Italy). Fine root production during GY2 (F) was estimated using the decision matrix method for sequential coring based on the changes in pools of living and dead roots between successive samplings [31]. There was a significant difference in fine root biomass between wide and narrow inter-row spacings when compared in a t-test [32]. The cumulative (fine) root biomass production over the year was consequently weighted by the area of inter-row spacings, averaged over both genotypes and converted to carbon using the average fine root C mass fraction.

2.3.5. *Soil carbon pool (S)*

Soil C content (S) was assessed before plantation establishment in GY1 (March 2010). Sampling was performed at 110 spatially distributed locations, of which half in each former land use type [23]. Every 15 cm up to a depth of 90 cm an aggregate sample and a bulk density sample were taken by core sampling (Eijkelkamp Agrisearch equipment, The Netherlands). C mass fractions were determined in three replicates per sample by dry combustion (NC-2100 element analyzer, Carlo Erba Instruments, Italy). From C mass fractions and bulk densities, the carbon pool per 15 cm depth interval was calculated and cumulated over 90 cm. The averages per land use type were weighted by their proportion of plantation area to estimate the initial soil C pool. The input of above- and belowground litter from the poplar trees could lead to a soil C enrichment in the long term, as compared to the arable land where crop residues were removed annually during the former land use. Though even in a shorter term an enriching effect in upper soil layers has been observed in a poplar plantation in Italy [33]. However, soil C pool change generally is a very slow process because compared to the total soil C pool the annual changes are relatively small [34]. We

therefore assumed that the poplar trees had not significantly changed the soil C pool over the two years.

2.4. Quantification of carbon fluxes

2.4.1. Soil CO_2 efflux (R_S)

The CO_2 efflux from the soil (R_S) was monitored by an automated soil CO_2 flux system (LI-8100, LI-COR Biosciences, Lincoln, NE, USA). Sixteen long-term chambers operating as closed systems were connected to an infrared gas analyzer through a multiplexer (LI-8150, LI-COR Biosciences, Lincoln, NE, USA). The 16 chambers were spatially distributed over the plantation covering both former land use types and only two genotypes (Grimminge (*P. deltoides* Marsh. × (*P. trichocarpa* Hook. × *P. deltoides* Marsh.)) and Skado) due to restricted cable lengths. The system was installed at the end of March of GY2 and logged soil CO_2 efflux for each chamber successively every hour until the end of GY2. Soil CO_2 efflux was extrapolated for the period of January–March by a Neural Network analysis based on soil temperature, which was continuously monitored throughout the year (cfr. Section 2.2). Soil CO_2 efflux was independent of the genotype planted, but differed between the two types of former land use [35]. Values of CO_2 efflux were integrated over time and weighted by the proportion of the two former land use types to obtain the plantation average.

2.4.2. Woody tissue CO_2 efflux (R_{Ste+Br})

On both genotypes Grimminge and Skado stem CO_2 efflux was measured during two intensive field campaigns in GY2. The first campaign was carried out during four days from 8 to 12 August of GY2, whereas the second campaign took place from 26 to 30 November of GY2 when trees were in a dormant state. For both genotypes five trees of different diameters (ranging from 29.7 mm to 50.0 mm, and from 29.9 mm to 50.1 mm at 22 cm height for the first and second campaign, respectively) were selected and measured four times during each measuring campaign at different times of the day. The LI-6400XT gas analyzer (LI-COR Biosciences, Lincoln, NE, USA) was used as an open system in combination with a Plexiglas stem cuvette of 17 cm length and with a diameter of 11 cm (cfr. Ref. [36]). The cuvette was assembled on collars, sealed air-tight at approximately 1 m stem height; for each measurement stem diameter at the attachment point was also recorded. The stem cuvette was equipped with an infrared thermocouple to measure stem temperature during each measurement and covered with aluminium foil to avoid possible CO_2-refixation of the bark. Before each measurement, the sample and reference cells of the gas analyzer were matched after the air in the cuvette was allowed to mix and to stabilize for 30 min. Five successive measurements were taken and the average was used for further calculations.

Stem CO_2 efflux data were tested for genotype and diameter effects, but no significant effects were found. Consequently data of August – with a temperature range of 17.8–27.4 °C – and data of November – with a temperature range of 8.2–14.1 °C – were pooled to establish two Q_{10} functions, i.e. one for the growing season and one for the dormant period. The following exponential temperature response was fitted (Eq. (1), originating from Ref. [37]):

$$SE = E_{10} \cdot Q_{10^{((T-10)/10)}} \quad (1)$$

with SE = stem CO_2 efflux, E_{10} = stem CO_2 efflux at a standard temperature of 10 °C, T = temperature and Q_{10} = the change in the rate of stem CO_2 efflux with a 10 °C change in stem temperature. Stem temperature was closely related to air temperature ($p \leq 0.01$), which was logged half-hourly during the year (cfr. Section 2.2). Stem diameter increment was logged (Point Dendrometer ZN11-O_x-WP, Zweifel Consulting, Switzerland) during GY2 from March to December and showed a linear increase in diameter from April to September. The average stem surface area was calculated from the weighted average stem diameter and stem height over the plantation (data published in Ref. [23]). The contribution of branches in the aboveground tree structure (data from Ref. [38]) was also included. Combined with the average tree density an estimate of yearly woody tissue CO_2 efflux was obtained.

2.4.3. Foliar respiration (R_F)

Leaf gas exchange was measured with a portable open-path gas exchange measurement system (LI-6400, LI-COR Biosciences, Lincoln, NE, USA) equipped with a leaf chamber fluorometer (LI-6400-40, LI-COR Biosciences, Lincoln, NE, USA). Four trees of six genotypes (Bakan and Skado (*P. trichocarpa* Hook. × *P. maximowiczii* Henry); Grimminge; Koster and Oudenberg (*P. deltoides* Marsh × *P. nigra* L.); Wolterson (*P. nigra* L.)) were selected for the measurements. The first mature leaf of the current-year shoot in the upper canopy was sampled for gas exchange measurements in monthly campaigns from May to September of GY2. Photosynthetic light response curves were obtained by measurements of the net photosynthetic rate at photosynthetic photon flux densities (PPFD) of 1500, 1000, 800, 600, 400, 200, 100 and 0 μmol m^{-2} s^{-1} (blue-red LED source type LI-6400-02B, 13% blue light). Leaves were allowed to equilibrate at least 2 min at each step before logging the data. The following conditions were maintained in the cuvette: CO_2 concentration of 400 μmol mol^{-1}, block temperature of 25 °C and vapour pressure deficit of 1.07 kPa ± 0.03. The PPFD response curve, representing the net photosynthetic rate as a function of PPFD, was fitted to the data by a rectangular hyperbola according to Marshall and Biscoe [39] and Thornley and Johnson [40]. Dark respiration at leaf scale (R_{dark}) was obtained from the y-axis intercept (i.e. the net photosynthetic rate at 0 μmol m^{-2} s^{-1}).

The evolution of leaf area was monitored for all 12 genotypes by monthly leaf area index (LAI) measurements from April to November of GY2 (cfr. Ref. [38]). In four replicated measurement plots per former land use type and per genotype LAI was measured indirectly using an LAI-2200 Plant Canopy Analyzer (LI-COR Biosciences, Lincoln, NE, USA). Measurements were taken along two diagonal transects in each plot with the sensor parallel to the rows and perpendicular to the rows, by comparison of above- and below-canopy readings with a 45° view cap. An average LAI over all genotypes was calculated at each measurement time.

No significant seasonal trend in R_{dark} was observed, hence R_{dark} was averaged over time and genotypes. As foliar dark respiration generally decreases from the upper to the lower canopy [41–44], this value was multiplied by a factor 0.75 [44].

This factor is the ratio of foliar respiration rates of sunlit leaves in the upper crown to leaves in medium light, representing the main proportion of the canopy for *P. deltoides*. Since a constant block temperature was set, no R_{dark}-temperature relationship was established. To approach the temperature response of foliar (dark) respiration, a Q_{10} value of 2.1 was used, established for *P. deltoides* leaves in a mid-canopy position [44]. The combination of this R_{dark} value with the evolution of LAI during the season resulted in an estimation of the total foliar respiration at ecosystem scale (R_F) for GY2.

2.4.4. *Gross primary production (GPP)*

Gross Primary Production (GPP) was estimated using the terrestrial biosphere model ORCHIDEE (ORganizing Carbon and Hydrology in Dynamic EcosystEms [45]). This process-based model simulating the phenomena of the terrestrial carbon cycle, calculates the C_3 photosynthesis according to Farquhar et al. [46]. The annual GPP was estimated from LAI, from the photosynthetic parameters, i.e. maximum carboxylation rate (V_{cmax}) and maximum electron transport rate (J_{max}), and from a set of meteorological parameters (short and long-wave radiation, precipitation, wind velocity, humidity, temperature and pressure of the air).

Values for the photosynthetic parameters V_{cmax} and J_{max} were obtained through gas exchange measurements. The experimental design was the same and the measuring protocol was similar as the one explained above for the PPFD response curves to determine foliar respiration. The PPFD was fixed at a saturating value of 1500 μmol s^{-1} m^{-2}. Leaves were acclimatized for 10 min at a CO_2 concentration in the leaf cuvette of 400 μmol mol^{-1}, after which the net photosynthetic rate at a sequence of ten different CO_2 concentrations (i.e. 400, 300, 250, 150, 100, 50, 500, 750, 1000 and 1250 μmol mol^{-1}) was measured. Values for V_{cmax} and J_{max} were determined from the A–C_i response curves using the equations of Farquhar et al. [46].

2.4.5. *Net ecosystem exchange (NEE)*

Net Ecosystem Exchange (NEE) was monitored using the eddy covariance (EC) technique. An EC mast was installed in the northeastern part of the plantation in June of GY1 and was continuously operated to the present day. The mast included a sonic anemometer for the measurement of the three-dimensional wind components, wind speed, wind direction, and a closed-path CO_2/H_2O infrared analyzer (LI-7000, LI-COR Biosciences, Lincoln, NE, USA) among others. The CO_2 and sonic wind speed were recorded at 10 Hz using a model CR 5000 data logger (Campbell Scientific, Logan, Utah, USA). Fluxes of CO_2 were calculated using the EdiRe software (R. Clement, University of Edinburgh, UK [47]) and averaged over 30 min. Data were filtered and gap filled after which these data were used to calculate cumulative NEE averaged for GY2. Further details on the EC unit, on the gap filling procedure, and on the flux calculations are described in Zona et al. [25]. Only poplars were included in the footprint of the EC mast.

2.5. *Carbon balance*

The value of NEE measured through EC was compared with the NEP determined via two different approaches, i.e. the pool-change-based approach and the component-flux-based approach. The sum of the changes in carbon pools of the different plant components represents the bulk of the net primary production (NPP), which is the result of GPP and the autotrophic respiration [16,48]. In this study, the total autotrophic respiration (R_{aut}) was calculated as the sum of foliar respiration, stem CO_2 efflux and 40% of the soil CO_2 efflux ($R_{S\ aut}$) representing root respiration [35,49]. NEP results from NPP and the heterotrophic respiration (R_{het}), which was taken as the remaining 60% of the total soil CO_2 efflux thereby ignoring respiration from aboveground animals and microbes. NEP was calculated via the pool-change-based approach as:

$$NEP = NPP - R_{het} = F + (Ste + Br) + Stu + CR + FR - 0.6 \cdot R_S \quad (2)$$

where all values are expressed in g m^{-2} y^{-1} of carbon. A few minor components of possible C losses were not taken into account for the NEP calculation, i.e. non-CO_2 losses as CO, CH_4, volatile organic compounds (VOCs) to the atmosphere, dissolved organic carbon (DOCs) to deeper soil layers, mycorrhizae, understory weed growth and herbivory. By applying the component-flux-based approach, NEP was calculated as the incoming GPP flux minus the total ecosystem respiration:

$$NEP = GPP - R_{eco} = GPP - (R_S + R_{Ste+Br} + R_F) \quad (3)$$

where R_{eco} represents the total ecosystem respiration calculated as the sum of R_S, R_{Ste+Br} and R_F, also expressed in g m^{-2} y^{-1} of carbon.

NEE, which is mostly defined as the measured flux from the ecosystem to the atmosphere has an opposite sign to NEP; a negative NEE means an uptake by the ecosystem. For reasons of consistency with NEP, the positive value of NEE in this study means a net uptake of carbon.

The contribution of NPP within GPP is often termed carbon use efficiency (CUE), being the ratio of the net production to the sum of the net production and the respiratory cost (NPP/[NPP + Respiration]).

3. Results

As for nearly all terrestrial biomes [50], the largest C pool in the ecosystem was situated in the soil till 90 cm depth (S; Fig. 1a). Among the persisting C pools of the plant system (woody biomass), the highest amount of carbon was stored in the aboveground woody biomass (Fig. 1). The area weighted average over all genotypes of the root:shoot ratio was 0.46 after GY2. The results of the pool-change-based and component-flux-based measurements are graphically presented in Figs. 1b and 2. The NEE for GY2 determined via EC was valued at 96 g m^{-2} y^{-1} carbon uptake, whereas NEP was estimated to be 140 and 199 g m^{-2} y^{-1} through the pool-change-based and component-flux-based approach, respectively. The NEP values estimated through both the component-flux-based and the pool-change-based approaches were 108% and 47% higher, respectively, than the NEE value of the EC. However, considering the magnitude of the components of the NEP calculation (Fig. 2) and the considerable uncertainty levels in the three techniques, results were comparable (asterisks in Fig. 2). The positive value of NEP showed that the ecosystem was already a net sink for CO_2 in GY2. Whereas the

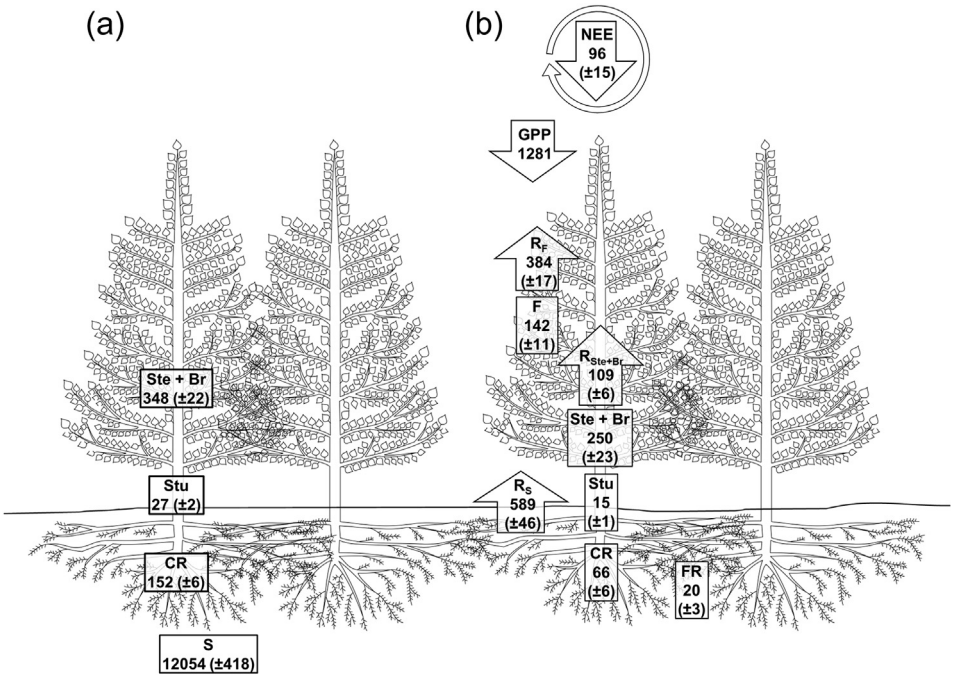

Fig. 1 – Components and processes of the carbon balance of a high-density poplar plantation during its second year of growth. (a) Bold outlined boxes on the left-hand side represent the standing C pools after two growth years (values in g m^{-2}). (b) Boxes on the right-hand side trees represent annual pool changes, and arrows represent annual integrated C fluxes for the second growing season (values in g m^{-2} y^{-1}). Averaged values are given with standard errors (GPP was a modelled parameter, not including an error range). (Ste + Br) = aboveground woody biomass pool, Stu = aboveground woody stump (15 cm stem) pool remaining after coppicing, CR = coarse root (Ø > 2 mm) pool, S = soil pool till 90 cm depth (determined before plantation establishment), F = foliage pool, FR = fine root (Ø < 2 mm) pool, R_S = total soil CO_2 efflux, R_{Ste+Br} = CO_2 efflux from aboveground woody biomass and R_F = foliar respiration. NEE = net ecosystem exchange measured through the eddy covariance technique (indicated by the circular arrow), which in this case results in a net carbon uptake.

plantation was still a net C source during the first year GY1 [25], the C assimilation of trees (GPP of 1281 g m^{-2} y^{-1}) in the following year exceeded the absolute value of total R_e. By summing all C pools, NPP was estimated at 493 ± 27 g m^{-2} y^{-1} (average ± standard error) and the total autotrophic respiration (R_{aut}) was estimated at 729 ± 26 g m^{-2} y^{-1}. Furthermore, the sum of R_{aut} and NPP resulted in 1222 ± 37 g m^{-2} y^{-1}, in which they contribute 60% and 40% (CUE), respectively (Table 1). This sum – defined as GPP – was very close (only 4.6% lower) to the simulated GPP from the ORCHIDEE-model using leaf gas exchange measurements.

Soil CO_2 efflux, stem + branch CO_2 efflux and foliar respiration accounted for 54%, 10% and 35% of the total ecosystem respiration, respectively (Table 1). When these three respiratory fluxes were related to GPP, they respectively consumed 46%, 9% and 30% of the total carbon uptake. The remaining 15% of GPP formed NEP. Whereas the aboveground biomass pool showed the highest changes over GY2 it produced the lowest integrated CO_2 efflux. The aboveground biomass pool had the highest share of NPP (51%) followed by the foliage (29%). Both fine (4% of NPP) and coarse roots (13% of NPP) showed the lowest biomass production among all biomass pools – excluding the stump biomass which was considered part of the aboveground woody biomass.

4. Discussion

Our SRC plantation already represented a significant C sink after two years while other SRC plantations established on agricultural land took two [12] or more than four years [9] before becoming an annual net C sink. During the first years after plantation establishment, crop growth is generally not sufficiently high to compensate for the C losses due to land use change. Several studies showed an initial decrease in the soil C pool during the first years after SRC planting on agricultural soils and grasslands due to intensive mineralization after cultivation [8,10–13,51]. An integrative study looking at patterns in C cycling across biomes showed that the general trend of negative NEP rates of young (0–10 years) temperate forests was caused by the high heterotrophic respiration rates resulting from disturbance [52]. Likewise, soil C content declined in our plantation during the first two years of growth [35]. However, our present results showed that the growth performance of the poplar canopy counterbalanced this loss already in the second year of growth. Without taking into account other greenhouse gases, this suggests a promising role for SRC with poplar on former agricultural lands with high available nitrogen levels.

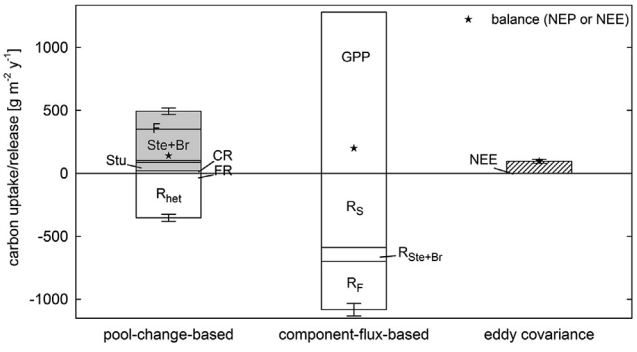

Fig. 2 – Components of the carbon balance (in g m^{-2} y^{-1}), using three different approaches where uptake and storage are displayed as positive, and release or loss are displayed as negative. The left bar stands for the pool-change-based approach (pool change bars filled in grey); the middle bar stands for the component-flux-based approach (non-filled bars represent integrated fluxes); the right-hand bar represents the eddy covariance measurements (hatched bar). Error bars indicate standard errors (GPP was a modelled parameter, not including an error range). Asterisks show the net result (carbon balance) representing the NEP or NEE for the eddy covariance measurements. For exact values, we refer to the text and to Fig. 1. (Ste + Br) = aboveground woody biomass pool, Stu = aboveground stump (15 cm stem) pool remaining after coppicing, CR = coarse root (Ø > 2 mm) pool, F = foliage pool, FR = fine root (Ø < 2 mm) pool, R_S = total soil CO_2 efflux, R_{het} = heterotrophic soil respiration (60% of R_S), R_{Ste+Br} = CO_2 efflux from aboveground woody biomass and R_F = foliar respiration. NEE = net ecosystem exchange measured through the eddy covariance technique, which in this case results in an uptake.

Table 1 – Relative contribution of carbon pool changes to the net primary production (NPP) and the gross primary production (GPP) and relative contribution of fluxes within the total ecosystem respiration (R_{eco}) and GPP. Values are given in percentage of NPP, R_{eco} and GPP. F = foliage pool, (Ste + Br) = aboveground woody biomass pool (stem + branches), Stu = aboveground woody stump (15 cm stem) pool remaining after coppicing, CR = coarse root (Ø > 2 mm) pool, FR = fine root (Ø < 2 mm) pool, R_{Ste+Br} = CO_2 efflux from aboveground woody biomass, R_F = foliar respiration and R_S = the total annual soil CO_2 efflux which is divided in 40% $R_{S\ aut}$ attributed to autotrophic soil (root) respiration and 60% $R_{S\ het}$ as heterotrophic soil respiration.

	NPP	R_{eco}	GPP
NPP	**100**		**40.4**
F	28.8		11.6
Ste + Br	50.6		20.4
Stu	3.1		1.3
CR	13.3		5.4
FR	4.1		1.7
R_{aut}		**67.4**	**59.6**
R_{Ste+Br}		10.1	9.0
R_F		35.5	31.4
$R_{S\ aut}$		21.8	19.3
$R_{het} \approx R_{S\ het}$		**32.6**	

Only few studies have assessed the NEP and NPP for a poplar SRC plantation during the first rotation. In a Free Air CO_2 Enrichment (FACE) experiment, Gielen et al. [19] studied net carbon storage in a poplar (*P. nigra* and *Populus euramericana*) SRC ecosystem in central Italy. In the second year after establishment a very high NPP of 1284 g m^{-2} y^{-1} of carbon and an average NEP of 1066 g m^{-2} y^{-1} were reached in the control treatment. Very contrasting results were found for an SRC plantation in Flanders with *P. trichocarpa* × *P. deltoides*, *Salix viminalis*, *Betula pendula* and *Acer pseudoplatanus*, reporting values after the second growth year of 310 g m^{-2} y^{-1} and −360 g m^{-2} y^{-1} for NPP and NEP, respectively [9]. In this last mentioned study no weed control, fertilization or irrigation were applied. Combined with the high heterotrophic soil respiration rate (670 g m^{-2} y^{-1}), this lack of management resulted in a net C source after the second year [9]. In contrast the SRC plantation in the aforementioned FACE experiment was growing in a warmer Mediterranean climate, was irrigated, weeds were removed and herbivores were treated [19]. Moreover, carbon input to the soil was higher than the soil C loss in that study.

Our EC estimate of NEE fell within the range of 70–740 g m^{-2} y^{-1} reported for temperate forests [53]. The differences between the EC result and the NEP estimations, however, are higher than most studies implementing both EC and ecological inventory techniques for estimating NEE and NEP in forest ecosystems. On average, estimates of the net C balance differed between these techniques by 20–30%, although ranging from 7% to 148% [54–59]. Moreover, differences between NEP and NEE estimates in the aforementioned studies were not systematic across sites; at some sites NEP seemed to overestimate NEE, while the opposite was true in others.

The quantification of NEE from EC measurements is prone to several uncertainties. The main sources of error of EC measurements are associated with (i) the spatial representativeness of the measured fluxes (footprint issue), (ii) the summation procedure, (iii) the data gap filling and (iv) corrections to night-time data [47]. The precision of the annual integrated EC flux measurements was previously reported as ±5% [60,61]; for ideal sites, i.e. extensive canopies on flat terrain, this error bond was set at ±50 g m^{-2} y^{-1} [62]. The uncertainty of the annual NEE flux in our plantation was estimated at 15 g m^{-2} y^{-1} [25], which is, however, much smaller than the differences with NEP estimations. We hypothesize that the component-flux-based approach to determine NEP was the least accurate due to the large uncertainties introduced during upscaling both in space and time. Despite the high precision of foliar CO_2 efflux measurements at leaf scale, crude assumptions were made concerning daily and seasonal evolution which were largely based on growth and temperature, possibly introducing uncertainties in the annual estimates. Spatial uniformity was assumed when scaling up from the leaf to the tree and the stand levels. Similar arguments hold for the woody tissue respiration. A major difficulty involved in measurements of soil, stem and foliar respiration is the respired CO_2 which dissolves in the xylem sap. This

portion of respired CO_2 is transported away from the location of production – roots or stem – via the sap flow to upward locations – up to stem, branches and foliage – where it is released to the atmosphere [63–66] or possibly fixed by photosynthesis [65]. Consequently, CO_2 efflux measured at a specific location within the tree cannot be considered as the respiration of the measured tissue. Root (and stem) respiration could therefore have been underestimated, whereas stem and foliar respiration could be overestimated. The largest uncertainty involved in the soil CO_2 efflux estimation was the upscaling from a limited number of chambers to the total plantation area (spatial heterogeneity). However, high temporal accuracy was achieved since soil CO_2 efflux was monitored continuously. The relatively simple measures of aboveground C pools (i.e. Ste + Br and F) had a high precision and small aggregation errors since detailed inventories over the whole plantation and among all genotypes were made. Errors in pool change calculations were also limited since the changes are in the same order of magnitude as the pools themselves. Belowground woody biomass had a lower accuracy due to the smaller sample size and the limited number of genotypes that could be sampled. Fine root production is associated with larger uncertainties, which applies in general, regardless the method used [67,68]. The largest uncertainty in the pool-change-based approach was, however, the inclusion of the $R_{S\ het}$ which resulted from the partitioning of the total R_S in an autotrophic and a heterotrophic part [35].

A few missing C pools and fluxes, although of minor importance, also hampered closing the carbon balance. Non-CO_2 losses as CO, CH_4 as well as VOCs to the atmosphere, DOCs to deeper soil layers, mycorrhizae, understory weed growth and herbivory were not counted in the NEP calculation. All these carbon balance related processes are usually negligible, but they remain difficult to quantify or to measure [15,69,70]. Small release fluxes of CH_4 were measured at our SRC site [25]. From preliminary results of average DOC concentration and water balance data, the losses of DOCs during GY2 were estimated at 4.7 g m^{-2} y^{-1}, which could be considered as irrelevant with regard to the magnitude of GPP and even NEE. Foliage C losses due to herbivory on the *Populus* trees were estimated at maximal 1% (personal observations), in contrast to the *Salix* species in our plantation, on which we observed substantial infestations of willow beetles (*Phratora vulgatissima*). Emissions of VOCs represented an estimated C loss of 1–2% of GPP of which more than 90% is represented by isoprene (personal communication based on preliminary analysis of PTR–TOF–MS-based flux data; F. Brilli). This C loss corresponded to 13–25 g m^{-2} y^{-1} which was comparable with previous findings for forests [15,71,72]. The understory of herbs dominated by thistles (*Cirsium arvense*) was sparse, and was not quantified in the present study.

At our SRC site fine roots constituted only 4% (Table 1) of the annual NPP whereas for forests it typically ranges from 8% to 76% [73]. The poor rooting reflected the mesic conditions and the high nitrogen (N) availability of the soil in our plantation, resulting in a lower investment (C allocation) in roots as compared to aboveground biomass [74]. This benefited wood production at an even young plantation age, taking the highest of the total NPP among the different C pools. Foliage had the second largest contribution in NPP. *Populus* trees show an indeterminate growth habit [75,76], characterized by continuous shoot growth and leaf production over the growing season. Young developing leaves are net importers of assimilates. When fully expanded they export both acropetally to developing leaves and basipetally to stem and roots until matured; afterwards translocation is mostly to the lower stem and roots [75,76]. Mature leaves generally use 20–30% of the C fixed for respiration and maintenance, the remaining 70–80% is exported to developing leaves and stem and roots [77]. Our findings of R_F partitioning for 31% in GPP confirm these general observations. R_F corresponded to half of the autotrophic respiration and was comparable to previous findings in broadleaved forests [78]. This high respiratory cost of foliage could be attributed to the high cellular activity in developing leaves [79]. R_F contributed the second highest within the R_{eco}; R_S took the highest share of R_{eco} of 54% which is slightly lower than the European average of 63% [80]. In forest ecosystems soil carbon efflux is the largest respiratory C flux and following GPP the second most important C flux [81–85].

The 40% overall CUE value is within the average range of 39–59% previously reported for temperate deciduous forests [86–89]. However, it is much lower than the 60–69% reported for a *Populus* SRC plantation in the second year of growth [19] and lower than the reported average of 58 ± 3% (±st. dev.) for forests with high-nutrient availability [90] which generally invest a larger fraction of GPP to wood compared to forests with low-nutrient availability [86]. In comparison with the low measured R_{Ste+Br} the high share of NPP represented in the aboveground wood production of our SRC plantation (Table 1), suggested an efficient production of wood. This could further justify a high interest in SRC cultures since the wood is the harvestable, and thus economically interesting part.

In conclusion, we were able to quantify all carbon pools and fluxes determining the C balance of this fast-growing SRC culture. The ecosystem was a net carbon sink in the second year of the first rotation, although the results of the different assessment techniques differed in the exact values. The highest respiratory flux was represented by the soil CO_2 efflux whereas the aboveground woody biomass showed the largest carbon pool change.

Acknowledgements

This research has received funding from the European Research Council under the European Commission's Seventh Framework Programme (FP7/2007–2013) as ERC grant agreement n°. 233366 (POPFULL), as well as from the Flemish Hercules Foundation as Infrastructure contract ZW09-06. Further funding was provided by the Flemish Methusalem Programme and by the Research Council of the University of Antwerp. G. Berhongaray is a grantee of the Erasmus-Mundus External Cooperation under the EADIC lot 16 Programme; D. Zona was supported by a Marie Curie Reintegration grant (PIRG07-GA-2010-268257) of the European Commission's Seventh Framework Programme; T. De Groote is a PhD fellow of the Research Foundation – Flanders (FWO) and the Flemish Institute for Technological Research (VITO). We gratefully acknowledge

the excellent technical support of Joris Cools, the logistic support of Kristof Mouton at the field site, as well as Gerrit Switsers and Nadine Calluy for carbon and nitrogen analyses.

REFERENCES

[1] Buyx A, Tait J. Ethical framework for biofuels. Science 2011;332:540–1.

[2] Sadrul Islam AKM, Ahiduzzaman M. Biomass energy: sustainable solution for greenhouse gas emission. AIP Conf Proc 2012;1440:23–32.

[3] Houghton RA. The annual net flux of carbon to the atmosphere from changes in land use 1850–1990. Tellus 1999;51B(2):298–313.

[4] Kalnay E, Cai M. Impact of urbanization and land-use change on climate. Nature 2003;423(6939):528–31.

[5] Lal R. Soil carbon sequestration to mitigate climate change. Geoderma 2004;123(1–2):1–22.

[6] Ross DJ, Tate KR, Scott NA, Wilde RH, Rodda NJ, Townsend JA. Afforestation of pastures with *Pinus radiata* influences soil carbon and nitrogen pools and mineralisation and microbial properties. Aust J Soil Res 2002;40(8):1303–18.

[7] House JI, Prentice IC, Le Quere C. Maximum impacts of future reforestation or deforestation on atmospheric CO_2. Glob Change Biol 2002;8(11):1047–52.

[8] Hansen EA. Soil carbon sequestration beneath hybrid poplar plantations in the north central United States. Biomass Bioenergy 1993;5(6):431–6.

[9] Vande Walle I. Carbon sequestration in short-rotation forestry plantations and in Belgian forest ecosystems. PhD thesis, Universiteit Gent, Ghent; 2007.

[10] Grigal DF, Berguson WE. Soil carbon changes associated with short-rotation systems. Biomass Bioenergy 1998;14(4):371–7.

[11] Hellebrand HJ, Straehle M, Scholz V, Kern J. Soil carbon, soil nitrate, and soil emissions of nitrous oxide during cultivation of energy crops. Nutr Cycl Agroecosyst 2010;87(2):175–86.

[12] Arevalo CBM, Bhatti JS, Chang SX, Sidders D. Land use change effects on ecosystem carbon balance: from agricultural to hybrid poplar plantation. Agr Ecosyst Environ 2011;141(3–4):342–9.

[13] Zenone T, Chen J, Deal MW, Wilske B, Jasrotia P, Xu J, et al. CO_2 fluxes of transitional bioenergy crops: effect of land conversion during the first year of cultivation. Glob Change Biol Bioenergy 2011;3(5):401–12.

[14] Vande Walle I, Samson R, Looman B, Verheyen K, Lemeur R. Temporal variation and high-resolution spatial heterogeneity in soil CO_2 efflux in a short-rotation tree plantation. Tree Physiol 2007;27(6):837–48.

[15] Clark DA, Brown S, Kicklighter DW, Chambers JQ, Thomlinson JR, Ni J. Measuring net primary production in forests: concepts and field methods. Ecol Appl 2001;11(2):356–70.

[16] Chapin III FS, Woodwell GM, Randerson JT, Rastetter EB, Lovett GM, Baldocchi DD, et al. Reconciling carbon-cycle concepts, terminology, and methods. Ecosystems 2006;9(7):1041–50.

[17] Reichstein M, Stoy PC, Desai AR, Lasslop G, Richardson AD. Partitioning of net fluxes. In: Aubinet M, Vesala T, Papale D, editors. Eddy covariance: a practical guide to measurement and data analysis. Dordrecht: Springer; 2012. p. 263–89.

[18] Lovett GM, Cole JJ, Pace M. Is net ecosystem production equal to carbon accumulation? Ecosystems 2006;9(1):1–4.

[19] Gielen B, Calfapietra C, Lukac M, Wittig VE, De Angelis P, Janssens IA, et al. Net carbon storage in a poplar plantation (POPFACE) after three years of free-air CO_2 enrichment. Tree Physiol 2005;25(11):1399–408.

[20] POPFULL system analysis of a bio-energy plantation: full greenhouse gas balance and energy accounting [Project Description on the Internet]. Antwerp: University of Antwerp. Available from:, http://webh01.ua.ac.be/popfull/docs/folder_POPFULL_ENG_comp.pdf; 2010 [accessed 21.05.13].

[21] Klimaat in de wereld klimatogram Gent-Melle. Brussels: Royal Meteorological Institute of Belgium. Available from: http://www.meteo.be/gfx/climatograms/nl6434.png [in Dutch, accessed 21.05.13].

[22] Van Ranst E, Sys C. Eenduidige legende voor de digitale bodemkaart van Vlaanderen (Schaal 1:20 000). Gent: Laboratorium voor Bodemkunde; 2000 [in Dutch].

[23] Broeckx LS, Verlinden MS, Ceulemans R. Establishment and two-year growth of a bio-energy plantation with fast-growing *Populus* trees in Flanders (Belgium): effects of genotype and former land use. Biomass Bioenergy 2012;42:151–63.

[24] Zona D, Janssens IA, Gioli B, Jungkunst HF, Camino Serrano M, Ceulemans R. N_2O fluxes of a bio-energy poplar plantation during a two years rotation period. Glob Change Biol Bioenergy, 2012, http://dx.doi.org/10.1111/gcbb.12019.

[25] Zona D, Janssens IA, Aubinet M, Gioli B, Vicca S, Fichot R, et al. Fluxes of the greenhouse gases (CO_2, CH_4 and N_2O) above a short-rotation poplar plantation after conversion from agricultural land. Agr Forest Meteorol 2013;169:100–10.

[26] Ceulemans R, Pontailler JY, Mau F, Guittet J. Leaf allometry in young poplar stands: reliability of leaf area index estimation, site and clone effects. Biomass Bioenergy 1993;4(5):315–21.

[27] Pontailler JY, Ceulemans R, Guittet J, Mau F. Linear and non-linear functions of volume index to estimate woody biomass in high density young poplar stands. Ann For Sci 1997;54(4):335–45.

[28] Berhongaray G, King JS, Janssens IA, Ceulemans R. An optimized fine root sampling methodology balancing accuracy and time investment. Plant Soil 2013;366(1–2):351–61.

[29] Oliveira MRG, Van Noordwijk M, Gaze SR, Brouwer G, Bona S, Mosca G, et al. Auger sampling, ingrowth cores and pinboard methods. In: Smit AL, Bengough AG, Engels C, Van Noordwijk M, Pellerin S, Van de Geijn SC, editors. Root methods: a handbook. Berlin: Springer-Verlag; 2000. p. 175–210.

[30] Janssens IA, Sampson DA, Cermak J, Meiresonne L, Riguzzi F, Overloop S, et al. Above- and belowground phytomass and carbon storage in a Belgian Scots pine stand. Ann For Sci 1999;56(2):81–90.

[31] Fairley RI, Alexander IJ. Methods of calculating fine root production in forests. In: Fitter AH, Atkinson D, Read DJ, editors. Ecological interactions in soil: plants, microbes and animals. Oxford: Blackwell Scientific Publications; 1985. p. 37–42.

[32] Berhongaray G, King JS, Janssens IA, Ceulemans R. Fine root biomass and turnover of two fast-growing poplar genotypes in a short-rotation coppice culture. Plant Soil, 2013, http://dx.doi.org/10.1007/s11104-013-1778-x.

[33] Hoosbeek MR, Lukac M, van Dam D, Godbold DL, Velthorst EJ, Biondi FA, et al. More new carbon in the mineral soil of a poplar plantation under Free Air Carbon Enrichment (POPFACE): cause of increased priming effect? Global Biochem Cycles 2004;18(1):GB1040.

[34] Rodeghiero M, Heinemeyer A, Schrumpf M, Bellamy P. Determination of soil carbon stocks and changes. In: Kutsch WL, Bahn M, Heinemeyer A, editors. Soil carbon dynamics: an integrated methodology. Cambridge: Cambridge University Press; 2009. p. 49–75.

[35] Verlinden MS, Broeckx LS, Wei H, Ceulemans R. Soil CO_2 efflux in a bioenergy plantation with fast-growing *Populus* trees – influence of former land use, inter-row spacing and genotype. Plant Soil, 2013, http://dx.doi.org/10.1007/s11104-013-1604-5.

[36] Liberloo M, De Angelis P, Ceulemans R. Stem CO_2 efflux of a *Populus nigra* stand: effects of elevated CO_2, fertilization, and shoot size. Biol Plant 2008;52(2):299–306.
[37] van't Hoff JH. Lectures on theoretical and physical chemistry. Part I. London: Edward Arnold; 1898.
[38] Broeckx LS, Verlinden MS, Vangronsveld J, Ceulemans R. Importance of crown architecture for leaf area index of different *Populus* genotypes in a high-density plantation. Tree Physiol 2012;32(10):1214–26.
[39] Marshall B, Biscoe P. A model for C_3 leaves describing the dependence of net photosynthesis on irradiance. J Exp Bot 1980;31(120):29–39.
[40] Thornley JHM, Johnson IR. Plant and crop modelling: a mathematical approach to plant and crop physiology. Oxford: Clarendon Press; 1990.
[41] Brooks JR, Hinckley TM, Ford ED, Sprugel DG. Foliage dark respiration in *Abies amabilis* (Dougl.) Forbes: variation within the canopy. Tree Physiol 1991;9(3):325–38.
[42] Ellsworth DS, Reich PB. Canopy structure and vertical patterns of photosynthesis and related leaf traits in a deciduous forest. Oecologia 1993;96(2):169–78.
[43] Mitchell KA, Bolstad PV, Vose JM. Interspecific and environmentally induced variation in foliar dark respiration among eighteen southeastern deciduous tree species. Tree Physiol 1999;19(13):861–70.
[44] Griffin KL, Turnbull M, Murthy R. Canopy position affects the temperature response of leaf respiration in *Populus deltoides*. New Phytol 2002;154(3):609–19.
[45] Krinner G, Viovy N, de Noblet-Ducoudré N, Ogée J, Polcher J, Friedlingstein P, et al. A dynamic global vegetation model for studies of the coupled atmosphere–biosphere system. Glob Biogeochem Cycles 2005;19(1):GB1015.
[46] Farquhar GD, von Caemmerer S, Berry JA. A biochemical model of photosynthetic CO_2 assimilation in leaves of C_3 species. Planta 1980;149(1):78–90.
[47] Aubinet M, Grelle A, Ibrom A, Rannik Ü, Moncrieff J, Foken T, et al. Estimates of the annual net carbon and water exchange of forests: the EUROFLUX methodology. Adv Ecol Res 2000;30:113–75.
[48] Luyssaert S, Reichstein M, Schulze ED, Janssens IA, Law BE, Papale D, et al. Toward a consistency cross-check of eddy covariance flux-based and biometric estimates of ecosystem carbon balance. Glob Biogeochem Cycles 2009;23(3):GB3009.
[49] Hanson PJ, Edwards NT, Garten CT, Andrews JA. Separating root and soil microbial contributions to soil respiration: a review of methods and observations. Biogeochemistry 2000;48(1):115–46.
[50] Bolin B, Sukumar R, Ciais P, Cramer W, Jarvis P, Kheshgi H, et al. Global perspective. In: Watson R, Noble I, Bolin B, Ravindranath NH, Verardo DJ, Dokken DJ, editors. Land use, land-use change, and forestry – a special report of the IPCC. Cambridge: Cambridge University Press; 2000. p. 23–52.
[51] Nikièma P, Rothstein DE, Miller RO. Initial greenhouse gas emissions and nitrogen leaching losses associated with converting pastureland to short-rotation woody bioenergy crops in northern Michigan, USA. Biomass Bioenergy 2012;39:413–26.
[52] Pregitzer KS, Euskirchen ES. Carbon cycling and storage in world forests: biome patterns related to forest age. Glob Change Biol 2004;10(12):2052–77.
[53] Baldocchi D, Falge E, Gu L, Olson R, Hollinger D, Running S, et al. FLUXNET: a new tool to study the temporal and spatial variability of ecosystem-scale carbon dioxide, water vapor and energy flux densities. Bull Am Meteorol Soc 2001;82(11):2415–34.
[54] Curtis PS, Hanson PJ, Bolstad P, Barford C, Randolph JC, Schmid HP, et al. Biometric and eddy-covariance based estimates of annual carbon storage in five eastern North American deciduous forests. Agr Forest Meteorol 2002;113(1–4):3–19.
[55] Ehman JL, Schmid HP, Grimmond CSB, Randolph JC, Hanson PJ, Wayson CA, et al. An initial intercomparison of micrometeorological and ecological inventory estimates of carbon exchange in a mid-latitude deciduous forest. Glob Change Biol 2002;8(6):575–89.
[56] Black K, Bolger T, Davis P, Nieuwenhuis M, Reidy B, Saiz G, et al. Inventory and eddy covariance-based estimates of annual carbon sequestration in a Sitka spruce (*Picea sitchensis* (Bong.) Carr.) forest ecosystem. Eur J For Res 2007;126(2):167–78.
[57] Ohtsuka T, Mo W, Satomura T, Inatomi M, Koizumi H. Biometric based carbon flux measurements and net ecosystem production (NEP) in a temperate deciduous broad-leaved forest beneath a flux tower. Ecosystems 2007;10(2):324–34.
[58] Gough CM, Vogel CS, Schmid HP, Su H-B, Curtis PS. Multi-year convergence of biometric and meteorological estimates of forest carbon storage. Agr Forest Meteorol 2008;148(2):158–70.
[59] Wang M, Guan D-X, Han S-J, Wu J-L. Comparison of eddy covariance and chamber-based methods for measuring CO_2 flux in a temperate mixed forest. Tree Physiol 2010;30(1):149–63.
[60] Goulden ML, Munger JW, Fan SM, Daube BC, Wofsy SC. Measurements of carbon sequestration by long-term eddy covariance: methods and a critical evaluation of accuracy. Glob Change Biol 1996;2(3):169–82.
[61] Moncrieff JB, Malhi Y, Leuning R. The propagation of errors in long-term measurements of land–atmosphere fluxes of carbon and water. Glob Change Biol 1996;2(3):231–40.
[62] Baldocchi DD. Assessing the eddy covariance technique for evaluating carbon dioxide exchange rates of ecosystems: past, present and future. Glob Change Biol 2003;9(4):479–92.
[63] Teskey RO, McGuire MA. Carbon dioxide transport in xylem causes errors in estimation of rates of respiration in stems and branches of trees. Plant Cell Environ 2002;25(11):1571–7.
[64] Saveyn A, Steppe K, McGuire MA, Lemeur R, Teskey RO. Stem respiration and carbon dioxide efflux of young *Populus deltoides* trees in relation to temperature and xylem carbon dioxide concentration. Oecologia 2008;154(4):637–49.
[65] Teskey RO, Saveyn A, Steppe K, McGuire MA. Origin, fate and significance of CO_2 in tree stems. New Phytol 2008;177(1):17–32.
[66] Aubrey DP, Teskey RO. Root-derived CO_2 efflux via xylem stream rivals soil CO_2 efflux. New Phytol 2009;184(1):35–40.
[67] Vogt KA, Vogt DJ, Bloomfield J. Analysis of some direct and indirect methods for estimating root biomass and production of forests at an ecosystem level. Plant Soil 1998;200(1):71–89.
[68] Janssens IA, Sampson DA, Curiel-Yuste J, Carrara A, Ceulemans R. The carbon cost of fine root turnover in a Scots pine forest. Forest Ecol Manag 2002;168(1–3):231–40.
[69] Ciais P, Wattenbach M, Vuichard N, Smith P, Piao SL, Don A, et al. The European carbon balance. Part 2: Croplands. Glob Change Biol 2010;16(5):1409–28.
[70] Smith P, Lanigan G, Kutsch W, Buchmann N, Eugster W, Aubinet M, et al. Measurements necessary for assessing the net ecosystem carbon budget of croplands. Agr Ecosyst Environ 2010;139(3):302–15.
[71] Hamilton JG, DeLucia EH, George K, Naidu SL, Finzi AC, Schlesinger WH. Forest carbon balance under elevated CO_2. Oecologia 2002;131(2):250–60.
[72] Ciccioli P, Brancaleoni E, Frattoni M, Marta S, Brachetti A, Vitullo M, et al. Relaxed eddy accumulation, a new technique

for measuring emission and deposition fluxes of volatile organic compounds by capillary gas chromatography and mass spectrometry. J Chromatogr 2003;985(1–2):283–96.
[73] Ostonen I, Lõhmus K, Pajuste K. Fine root biomass, production and its proportion of NPP in a fertile middle-aged Norway spruce forest: comparison of soil core and ingrowth core methods. For Ecol Manage 2005;212(1–3):264–77.
[74] Ågren GI, Franklin O. Root:shoot ratios, optimization and nitrogen productivity. Ann Bot-Lond 2003;92(6):795–800.
[75] Dickson RE. Assimilate distribution and storage. In: Raghavendra AS, editor. Physiology of trees. New York: John Wiley and Sons Inc.; 1991. p. 51–85.
[76] Friend AL, Coleman MD, Isebrands JG. Carbon allocation to root and shoot systems of woody plants. In: Davis TD, Haissig BE, editors. Biology of adventitious root formation. New York: Plenum Press; 1994. p. 245–73.
[77] Geiger DR. Understanding interactions of source and sink regions of plants. Plant Physiol Biochem 1987;25(5):659–66.
[78] Hagihara A, Hozumi K. Respiration. In: Raghavendra AS, editor. Physiology of trees. New York: John Wiley & Sons Inc.; 1991. p. 87–110.
[79] Tichá I, Čatský J, Hodáňová D, Pospíšilová J, Kaše M, Šesták Z. Gas exchange and dry matter accumulation during leaf development. In: Šesták Z, editor. Photosynthesis during leaf development. Prague: Academia; 1985. p. 157–216.
[80] Janssens IA, Lankreijer H, Matteucci G, Kowalski AS, Buchmann N, Epron D, et al. Productivity overshadows temperature in determining soil and ecosystem respiration across European forests. Glob Change Biol 2001;7(3):269–78.
[81] Lavigne MB, Ryan MG, Anderson DE, Baldocchi DD, Crill PM, Fitzjarrald DR, et al. Comparing nocturnal eddy covariance measurements to estimates of ecosystem respiration made by scaling chamber measurements at six coniferous boreal sites. J Geophys Res 1997;102(D24):28977–85.
[82] Law BE, Ryan MG, Anthoni PM. Seasonal and annual respiration of a ponderosa pine ecosystem. Glob Change Biol 1999;5(2):169–82.
[83] Longdoz B, Yernaux M, Aubinet M. Soil CO_2 efflux measurements in a mixed forest: impact of chamber disturbances, spatial variability and seasonal evolution. Glob Change Biol 2000;6(8):907–17.
[84] Pilegaard K, Hummelshoj P, Jensen NO, Chen Z. Two years of continuous CO_2 eddy-flux measurements over a Danish beech forest. Agr Forest Meteorol 2001;107(1):29–41.
[85] Curiel Yuste J, Nagy M, Janssens IA, Carrara A, Ceulemans R. Soil respiration in a mixed temperate forest and its contribution to total ecosystem respiration. Tree Physiol 2005;25(5):609–19.
[86] Waring RH, Landsberg JJ, Williams M. Net primary production of forests: a constant fraction of gross primary production? Tree Physiol 1998;18(2):129–34.
[87] DeLucia EH, Drake JE, Thomas RB, Gonzales-Meler M. Forest carbon use efficiency: is respiration a constant fraction of gross primary production? Glob Change Biol 2007;13(6):1157–67.
[88] Litton CM, Raich JW, Ryan MG. Carbon allocation in forest ecosystems. Glob Change Biol 2007;13(10):2089–109.
[89] Campioli M, Gielen B, Göckede M, Papale D, Bouriaud O, Granier A. Temporal variability of the NPP–GPP ratio at seasonal and interannual time scales in a temperate beech forest. Biogeosciences 2011;8(9):2481–92.
[90] Vicca S, Luyssaert S, Penuelas J, Campioli M, III Chapin FS, Ciais P, et al. Fertile forests produce biomass more efficiently. Ecol Lett 2012;15(6):520–6.