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Seasonal leaf dynamics for tropical evergreen forests in a process based global ecosystem model

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Abstract

The influence of seasonal phenology in tropical humid forests on canopy photosynthesis remains poorly understood and its representation in global vegetation models highly simplified, typically with no seasonal variability of canopy leaf area properties taken into account. However, recent flux tower and remote sensing studies suggest that seasonal phenology in tropical rainforests exerts a large influence over carbon and water fluxes, with feedbacks that can significantly influence climate dynamics. A more realistic description of the underlying mechanisms that drive seasonal tropical forest photosynthesis and phenology could improve the correspondence of global vegetation model outputs with the wet-dry season biogeochemical patterns measured at flux tower sites. Here, we introduce a leaf Net Primary Production (NPP) based canopy dynamics scheme for evergreen tropical forests in the global terrestrial ecosystem model ORCHIDEE and validated the new scheme against in-situ carbon flux measurements. Modelled Gross Primary Productivity (GPP) patterns are analyzed in details for a flux tower site in French Guiana, in a forest where the dry season is short and where the vegetation is considered to have developed adaptive mechanisms against drought stress. By including leaf litterfall seasonality and a coincident light driven leaf flush and seasonal change in photosynthetic capacity in ORCHIDEE, modelled carbon and water fluxes more accurately represent the observations. The fit to GPP flux data was substantially improved and the results confirmed that by modifying canopy dynamics to benefit from increased light conditions, a better representation of the seasonal carbon flux patterns was made.

1 Introduction

As a major component of the global terrestrial carbon cycle, the tropical forest biome has a significant impact on estimates of the global carbon budget and global climate change feedbacks (Prentice and Lloyd, 1998; Tian et al., 1998; Cox et al., 2000).

Tropical forests are estimated to store 55 % of the global forest carbon stock (Pan et al., 2011) and to account for 34 % of the global terrestrial photosynthesis (Beer et al., 2010). It is still uncertain whether wet tropical forests are a significant global carbon sink (Stephens et al., 2007; Lewis et al., 2004; Phillips et al., 1998; Chambers and Silver, 2004; Luyssaert et al., 2008; Cramer et al., 2004; Pan et al., 2011; Gloor et al., 2009; Lloyd and Farquhar, 2008), but they could turn into a large source of carbon due to dieback (Cox et al., 2004; Malhi et al., 2008, 2009b) or increased disturbances in association with global environmental changes (Golding and Betts, 2008; Phillips et al., 2009; Poulter et al., 2010). It is however certain that the exchange of carbon between the atmosphere and the tropical forest biome forms a major contribution to the seasonal variations seen in the terrestrial carbon cycle (Bousquet et al., 2000; Baker et al., 2008; Poulter et al., 2009).

Global vegetation models have however difficulties in reproducing the seasonal carbon exchange patterns for tropical evergreen forests (Baker et al., 2008; Saleska et al., 2003; Poulter et al., 2009). Using ORCHIDEE (Krinner et al., 2005), a process-based carbon-water-energy model, Verbeeck et al. (2011) showed that the seasonal cycle of net CO_2 exchange and latent heat flux can be significantly improved to match eddy covariance data from two sites in the drought prone forests of the Amazon, by increasing the soil rooting depth parameter in the model from 1.5 m to 10 m, hereby reducing modelled drought stress sensitivity and maintaining high transpiration during the dry season in the model. The study of Verbeeck et al. (2011) also highlighted that the ORCHIDEE modelled phenological processes for tropical evergreen forests were incorrect. In particular, the seasonality inferred for the optimized parameters suggested that the model structure needed improvement, especially a module of leaf renewal before or at the onset of the dry season.

The representation of seasonal variability of canopy properties in global vegetation models is currently highly simplified. Unlike vegetation of temperate or dry regions, tropical evergreen forests show no clear annual pattern of leaf shedding and flushing (Chave et al., 2010) and global vegetation models thus assume no seasonality in phenology for tropical evergreen canopies (Botta et al., 2000; Poulter et al., 2009). It is however important to model leaf turnover correctly, because this process not only affects Gross Primary Productivity (hereinafter GPP) but also drives litterfall, decomposition and biogeochemical cycling of carbon and nutrients.

Tropical trees show a wide range of variation in leaf phenotypic behaviour between and within species, individuals, locations and years Malhado et al., 2009). Nevertheless, high rates of leaf litterfall towards the end of the wet season and onset of dry season and leaf flush are well documented in various rainforests sites (Bradley et al., 2011; Doughty and Goulden, 2008; Goulden et al., 2004; Borchert, 1998; Wright and Cornejo, 1990; Nepstad et al., 2002; Chave et al., 2010). Table 1 reports leaf litterfall measurements from 16 tropical evergreen forests in the world that show distinct seasonal dynamics. Chave et al. (2010) reported a significant positive relationship between rainfall and litterfall seasonality for these and various other sites in Brazil, Peru, Ecuador, Colombia and Panama. In Dimonika, DR Congo (Schwartz and Tondo, 1988), the litter peak times with increased irradiance during the rainy season from November to April while during the dry season, the vegetation receives less radiation due to the presence of a thick rainless fog layer, formed by the influence of the cold Benguela stream. Data from the locations in Table 1 all show increased litterfall with increased radiation, except for Braga-Supay in Peru (Nebel et al., 2001), which shows a litterfall peak in the rainy season during the flooding period. A canopy response to increased light availability over the Amazon is also suggested by satellite vegetation greenness index measurements that suggest a photosynthetic or phenological positive and anticipatory response to elevated light levels during the dry season (Huete et al., 2006; Myneni et al., 2007; Xiao et al., 2005). Yet, the significance of satellite greening during dry periods is subject to intense debate (Myneni et al., 2007; Poulter et al., 2009; Samanta et al., 2010a, b).

This study aims to incorporate the observed seasonality of leaf litterfall in the ORCHIDEE model and more adequately describe the evergreen tropical forest phenology. Replacement of old by young leaves shortly before, at the start, or during the dry season is proposed and tested to see whether it can enhance canopy photosynthetic capacity and optimize the annual forest carbon gain in light limiting conditions. Furthermore it is tested whether the introduced seasonal variability in leaf properties leads to a better representation of GPP in the process-based carbon-water-energy model ORCHIDEE.

The results of these modifications were analysed in detail at a fluxtower site in French Guiana (Bonal et al., 2008) a forest with a short dry season (2–3 months). The effects of the model modifications on leaf age distribution, photosynthetic capacity and Leaf Area Index (hereinafter LAI), were quantified and extensively cross-validated with six years of eddy correlation GPP measurements and leaf litterfall data inventoried at the site. We tested whether by including the changed canopy dynamics a better representation of the seasonal carbon flux patterns was made. An additional validation was performed with litterfall data of the Tapajos site in Brazil.

2 Material and methods

2.1 Modelling strategy

The modelling strategy was chosen after a first exploration of the relation between leaf litterfall data and meteorological data for a site in French Guiana (Guyaflux) and a site in Eastern Amazonia (Tapajós km 67). Good correspondences between measured leaf litterfall and estimates based on specific regressions of climate variables for both locations (data not shown) were found. But introducing such regressions in the global vegetation model would imply introducing site-specific empirical coefficients that do not necessarily hold at a larger scale. Therefore, a seasonal leaf litterfall flux was introduced instead, based on the optimality concept (Hikosaka, 2005) and the assumption of self-thinning of leaves (White, 1981). The optimality concept states that trees and vegetation optimize their use of the available resources to maximize their chances of survival in the strong competition of the crowded forest. Self-thinning is a consequence of the high density of leaves in the canopy of evergreen tropical forest stands and implies that when a new leaf is produced, an older less efficient leaf will shed to prevent self shading and to improve the carbon gain of the canopy. The leaf litterfall in ORCHIDEE was changed and equalized to daily leaf Net Primary Production (NPP_{leaf}) in such a way that that the carbon lost through falling of the oldest leaves equals the carbon amount allocated to the youngest leaves. The canopy leaf biomass is hence modelled to be at steady state with an ever optimal maximum but dual-constrained by light and nutrients. Leaf age and photosynthetic capacity distribution are constantly optimized, responding to seasonal changes in production, according to the available resources and seasonal changes in light availability (Hikosaka, 2005).

The idea behind this rationale is that the canopy aims at maximizing carbon gains with minimum costs and optimizing the use of limiting resources, which most likely are light and nutrients in tropical evergreen forest canopies. The vegetation can optimize light use by investing in new, more efficient leaves which, to prevent self-shading, requires coincident loss of other, older and less efficient ones (Ackerly, 1999; Killingbeck and Whitford, 2001; Malhi et al., 2011). The increased light availability and resulting production in absence of other limitations like on water or nutrients at the beginning of and during the dry season hence drives an increased leaf turnover rate. Simultaneously, the vegetation is expected to optimize nutrient allocation to leaves in time to maximize photosynthesis and minimize respiration. Nutrients are reabsorbed from older leaves and reallocated to younger leaves to enhance the average nitrogen use efficiency and photosynthetic capacity of the canopy (Escudero and Mediavilla, 2003).

Additional to the leaf litterfall structural modification in the model's phenology equations, two standard ORCHIDEE parameter values based on field inventory estimates in Neotropical forests (Malhi et al., 2009a, 2011) were modified for tropical evergreen forests: the fraction of carbon allocated to leaves and the temperature response of fine root maintenance respiration.

2.2 ORCHIDEE model

ORCHIDEE is a global process-based vegetation model (Krinner et al., 2005) that can be run in coupled mode as a part of the IPSL-CM5 Earth-System model and is a valuable tool to understand the interactions between the atmosphere and biosphere and study feedbacks between climate and vegetation cover change.

ORCHIDEE combines a surface-vegetation-atmosphere transfer scheme with explicit parameterizations of ecosystem carbon dynamics. It is composed of two different model components: SECHIBA and STOMATE. The exchange of carbon, energy and water fluxes between the atmosphere and the land surface is calculated with a 30-min time step in the SECHIBA component (Ducoudré et al., 1993). The carbon dynamics of ecosystems are described in the STOMATE component which includes processes like carbon allocation, respiration and the seasonal phenological cycle, of particular interest to this study.

ORCHIDEE distinguishes 13 Plant Functional Types (PFTs, Smith et al., 1997) varying from tropical to temperate or boreal forests, natural or agricultural C3 or C4 grasslands. PFT-specific parameter values (Sitch et al., 2003) and different prognostic phenology schemes can be attributed. The focus in this paper is on the phenology of PFT Tropical Broadleaved Evergreen (TrBE) forest, which in the standard scheme, has no seasonal cycle in leaf litterfall included.

2.2.1 Photosynthesis formulation

Canopy photosynthesis is calculated at the leaf scale following the (Farquhar et al., 1980) model. The formulation of stomatal conductance follows (Ball et al., 1987) where the assimilation rate is linearly related to the CO_2 concentration gradient between atmosphere and the carbon fixation site inside the leaves. The latter is a function of relative air humidity (%), net assimilation rate and atmospheric CO_2 concentration.

The maximum carboxylation capacity of photosynthesis $V_{c,\max}$, further also called photosynthetic capacity, is parameterized as a function of leaf age. It increases from a low initial value during leaf flushing to a prescribed optimum value after full leaf expansion, stays constant at this optimum until 50 % of the critical leaf age is reached, and then decreases to a lower value for the older leaves (Ishida et al., 1999). Figure 1 schematically shows how $V_{c,max}$ changes as a function of leaf age, with 65 µmol CO_2 m^{-2} s^{-1} the optimal maximum light-limited photosynthetic capacity (Krinner et al., 2005).

There are four different leaf age classes inside ORCHIDEE and $V_{c,max}$ age class weighed averages are used to calculate canopy photosynthesis. The relationship in Fig. 1 applies to the top of the canopy but ORCHIDEE includes an exponential decrease of $V_{c,max}$ with canopy depth according to the approach of (Johnson and Thornley, 1984) for the scaling of the different leaf layers to the entire canopy. The relationship shown in Fig. 1 is supported by the findings of (Ackerly and Bazzaz, 1995; Coste et al., 2009; Kitajima et al., 1997, 2002) that showed a decreasing photosynthetic capacity with leaf age for tropical species. Furthermore, Steppe et al. (2011) and Chapin et al. (2002) report on decreasing photosynthetic capacity with leaf age due to modifications in leaf size, thickness, density, foliar nitrogen content and lignin content in species worldwide.

2.2.2 Carbon allocation

Net Primary Production (NPP), calculated as the difference between photosynthesis and autotrophic respiration, is attributed on a daily basis to five different biomass pools: leaves, fine roots, coarse roots, aboveground woody biomass and reproductive tissues (fruits and flowers). The fraction of carbon that is allocated to each carbon pool can be written as (Delbart et al., 2010):

$$f_{\text{alloc,pool}} = \frac{\text{NPP}_{\text{pool}}}{\text{NPP}_{\text{tot}}} \tag{1}$$

with NPP_{pool} the amount of carbon attributed to the biomass pool and NPP_{tot} the total NPP, the latter being calculated in ORCHIDEE as production minus autotrophic respiration, by:

$$\mathrm{NPP_{tot}} = \mathrm{GPP} - \sum_{i=1}^{5} \mathrm{R_{maint,pool_i}} - \sum_{i=1}^{5} \mathrm{R_{growth,pool_i}} \tag{2}$$

with $R_{\mathrm{maint,pool_i}}$ the maintenance respiration and $R_{\mathrm{growth,pool_i}}$ the growth respiration of the biomass pool.

The carbon allocation scheme in ORCHIDEE is base on optimal partitioning theory with the fractions of NPP allocated to the different compartments depending on the availability of light, nitrogen and water (Friedlingstein et al., 1999). Standard ORCHIDEE outputs for the PFT tropical evergreen forest show that the fraction allocated to each pool remains constant throughout the year, the leaf allocation factor ($f_{\mathrm{alloc,leaf}}$) being 0.27. Only when LAI exceeds the maximum value ($\mathrm{LAI_{max}}$), preset to 7 in ORCHIDEE, NPP is no longer attributed to leaves but to woody biomass aboveground instead, implying that $f_{\mathrm{alloc,leaf}}$ drops from 0.27 to 0. In this study, two parameter values are modified for tropical evergreen forest PFT. The first modified parameter is $\mathrm{f_{alloc,leaf}}$ which is increased from 0.27 to 0.30, supported by $\mathrm{NPP_{leaf}}$ estimates reported by Chave et al. (2008) for Nouragues in central French Guiana and by the findings of Malhi et al. (2011) for 35 sites in tropical evergreen forests worldwide. The latter reported a fraction of 0.41 $\mathrm{NPP_{tot}}$ allocated to the entire canopy (leaves, flowers, fruits and fine twigs) that, assuming a leaf carbon content of 73 % (Malhi et al., 2011), results in an $f_{\mathrm{alloc,leaf}}$ value of 0.3. In addition, Malhi et al. (2011) found low variances and small spatial differences in the fraction of $\mathrm{NPP_{tot}}$ allocated to the canopy in 35 tropical forest sites (linear fit with r^2, =0.88, $p < 0.0001$).

The second modification was made in the parameterisation of fine root maintenance respiration $R_{\mathrm{maint,fineroots}}$, which, by adapting its temperature response, was decreased to be more close to field estimates (Malhi et al., 2009a). $R_{\mathrm{maint,fineroots}}$ is calculated as a function of temperature and biomass, based on the work of Ruimy et al. (1996):

$$R_{\mathrm{maint,fineroots}} = C_{\mathrm{maint},r} B_{\mathrm{fineroots}} \tag{3}$$

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$B_{\text{fineroots}}$ is the fine root biomass and $C_{\text{maint,r}}$ is the maintenance respiration rate, assumed to increase linearly with root-zone temperature, as given by:

$$C_{\text{maint},r} = C_{0,\text{maint},r}(1 + 0.12\,T_{\text{fineroots}}) \tag{4}$$

$C_{0,\text{maint},r}$ is the base maintenance respiration rate defined at 0 °C for fine roots, set to a value of 1.67×10^{-3} g C g C^{-1} day^{-1} for all PFT's in the standard version of ORCHIDEE. The standard ORCHIDEE $R_{\text{maint,fineroots}}$ of 12.43 ± 2.01 Mg C ha^{-1} yr^{-1} is twice as high as field measurements of fine root respiration $R_{\text{fineroots}}$, 5.57 ± 1.85 Mg C ha^{-1} yr^{-1} at Manaus, Tapajós km 67 and Caxiuanã (Malhi et al., 2009a). Hence the value $R_{\text{maint,fineroots}}$ was decreased by adjusting the parameter value $C_{0,\text{maint},r}$ from 1.67×10^{-3} to a value of 0.5×10^{-3} g C g C^{-1} day^{-1} for PFT TrBE. The standard ORCHIDEE $R_{\text{maint,fineroots}}$ value is assumed to be valid for vegetation types worldwide, but Ruimy et al. (1996) however also report on observations that indicate a lower sensitivity to temperature of tropical plants than the temperate or boreal species (Loveys et al., 2003), which supports the adjustment in the parameter value $C_{0,\text{maint},r}$. Note that no structural changes were made in the model formulation for carbon allocation, so that only the parameter values $f_{\text{alloc,leaf}}$ and $C_{0,\text{maint},r}$ for the TrBE PFT have been changed.

2.2.3 Standard ORCHIDEE leaf litterfall

The standard ORCHIDEE version (Krinner et al., 2005) assumes no seasonality in phenology for tropical evergreen forests, and describes leaf age dependent daily leaf litterfall by:

$$\Delta B_{\text{leaf}} = B_{\text{leaf}} \min(0.99, \frac{\Delta t}{A_{\text{crit}}}(\frac{A}{A_{\text{crit}}})^4) \tag{5}$$

with ΔB_{leaf} the daily amount of carbon lost by leaf litterfall, B_{leaf} the leaf biomass, and Δt a daily time step. The leaf litterfall rate depends on leaf age A and on the critical leaf age A_{crit}, which is set to a standard value of 730 days for tropical evergreen forest. The formulation of Eq. (5) implies that young leaves hardly lose any biomass, while older leaves shed rapidly when they approach the critical leaf age A_{crit}.

Equation (5) is applied separately to each of four leaf age classes that each have a different leaf age A, the oldest leaf age class loses the largest amount of biomass and the youngest class loses the smallest amount. A leaf age class bookkeeping model keeps track of the leaf age structure and replaces older leaves by new young ones that are created from $\mathrm{NPP}_{\mathrm{leaf}}$. Carbon is allocated to the youngest leaf age class and leaf mass ages by biomass conversion from age class i to age class i + 1 according to:

$$\Delta B_{i \rightarrow i+1} = B_i \frac{\Delta t}{\tau} \tag{6}$$

with τ being a time constant defined by, $\tau = \frac{A_{\mathrm{crit}}}{n}$, n being the number of leaf age classes ($n = 4$). The total daily leaf litterfall is the weighed average sum of leaf turnover in each of the four leaf age classes.

Leaf age distribution among the four age classes is updated daily, given the fraction of leaf biomass f_i that is aging and enters in leaf age class i calculated by:

$$\tilde{f}_i = \frac{f_i B_{\mathrm{leaf}} + \Delta B_i}{\tilde{B}_{\mathrm{leaf}}} \tag{7}$$

$\tilde{f}_i$ is the new fraction of leaf biomass in age class i and B_{leaf} is the total leaf biomass, sum of biomass over all age classes before aging. $\Delta \mathrm{B}_i$ is the change in biomass due to aging in age class i and $\tilde{B}_{\mathrm{leaf}}$ is the new total leaf biomass summed over all age classes, after aging.

2.2.4 Improved ORCHIDEE leaf litterfall

The standard parameterization of litterfall based on leaf age (Eq. 5) was replaced by a leaf litter dynamics model (scheme shown in Fig. 2) that sets the daily leaf litterfall carbon amount (ΔB_{leaf}) equal to the carbon amount allocated to the leaves ($\mathrm{NPP}_{\mathrm{leaf}}$):

$$\Delta B_{\mathrm{leaf}} = \mathrm{NPP}_{\mathrm{leaf}} \tag{8}$$

This means that every day exactly the same amount of carbon is lost by leaf litterfall as the amount of NPP allocated to the leaves (Sect. 2.3), resulting in a constant overall leaf biomass but with varying leaf age distribution throughout the season. According to Eq. (8) old leaves are immediately replaced by young ones, or the canopy loses, for each amount of carbon of young leaf biomass formed, the same amount of carbon by shedding its oldest leaves. Hence, the leaf age distribution is altered through the mechanism imposed by Eq. (8), and consequently photosynthetic capacity is changed since it is linked to leaf age.

Equation (8) also implies that the modelled pattern of leaf litterfall times with modelled NPP pattern and that the leaf turnover rate increases with increased $\mathrm{NPP}_{\mathrm{leaf}}$. Hence, a seasonal pattern in leaf litterfall is introduced that corresponds with seasonally increased $\mathrm{NPP}_{\mathrm{leaf}}$. As in the standard version of the ORCHIDEE model, the average daily leaf litterfall is calculated as the weighed average sum of leaves fallen in each of the four leaf age classes separately and leaf age fractions are recalculated as in Eq. (7).

Note that this modification is structural and the leaf litterfall TrBE PFT of the standard ORCHIDEE version was replaced, the model version is further referred to as the ORCHIDEE-NLT (ORCHIDEE NPP-based Leaf Turnover) version.

2.3 Site descriptions

The Guyaflux tower site (5°16′54″N, 52°54′44″W) is located in French Guiana, South America, near Sinnamary, in an experimental unit that covers more than 400 ha of pristine, undisturbed wet tropical forest with about 140 tree species per ha (Gourlet-Fleury et al., 2004). Soils in the study area are mainly nutrient-poor acrisols (FAO-ISRIC-ISSS, 1998) with estimates of clay and sand content in the 1 m deep horizon of 43 % and 48 % on top of the hills and 26 % and 65 % on the sandy plateau (Bonal et al., 2008). There are two distinct rainy seasons, a moderate one from December to February and a stronger one from April to July. Of all sites reported in Table 1, Guyaflux has the highest mean annual rainfall (3041 mm). At Guyaflux, of the six years investigated, the lowest amount of rainfall fell in 2004 (2756 mm) and 2007 was the wettest year (3550 mm). Rainfall variability during the long dry season from September to November is high, ranging between 60 mm in 2005 to 306 mm in 2007. Various meteorological variables like down-welling short-wave radiation ($\mathrm{SW_{down}}$ $\mathrm{W\,m^{-2}}$), down-welling long-wave radiation ($\mathrm{LW_{down}}$, $\mathrm{W\,m^{-2}}$), air temperature (T_a, °C) and vapour pressure deficit (VPD, kPa) at Guyaflux show seasonal variations linked to annual rainfall variability, mainly driven by the movement of the Inter-Tropical Convergence Zone (ITCZ). $\mathrm{SW_{down}}$ is about 30 % higher in the dry months compared to the wet months. Figure 3 shows seasonal patterns in SW_{down}, rainfall and the index of Soil Water Content (ISWC), the latter is calculated based on soil water content measurements conducted every two to three weeks in tubes inserted down to 2.6 m depth in the soil and distributed along a 1 km transect (Bonal et al., 2008).

The Tapajós km 67 tower site (2°51′24″S, 54°57′32″W) is located south of Santarém, Pará, Brazil, near the Tapajós river in an old growth moist Amazonian forest and described in detail by Saleska et al. (2003). Soils in the study area are mainly heavy Belterra clay ferralsols (FAO)/oxisols (USDA) interspersed with sandier patches and low organic matter content (Quesada et al., 2009). The soils in the footprint of the tower contain approximately 68 % clay or clay loam, 32 % sand or sandy loam (Silver et al., 2000). The site is on a gently eastward sloping (<1 %) plateau that extends over 150 km. Tapajós km 67 mean annual rainfall (2120 mm) is close to the mean of all sites reported in Table 1 (2161 mm). There is one distinct dry season (< 100 mm rainfall per month) that extends from July to November. The site shows signs of recovery from past disturbance which caused mortality that resulted in higher wood productivity over a wide area with biomass increments and possibly loss of soil carbon (Rice et al., 2004; Pyle et al., 2008).

2.4 Litterfall data

Litterfall at the Guyaflux site was collected approximately every 20 days from December 2003 to December 2008 in 40 different traps distributed at the corners of 10 inventory plots located in the footprint of the Guyaflux tower, and for eight significantly representative traps (Bonal, pers. comm.) of these 40 from January 2009 to June 2010. Leaf litterfall was sorted from other litter components (twigs, fruits or flowers) during the year 2004 (Hättenschwiler et al., 2008). Average annual total litterfall is 4.7 Mg ha^{-1} yr^{-1}. Both total litterfall and leaf litterfall fraction show a peak at the beginning of the long and the short dry season. Leaf litter was estimated from total litterfall by extrapolating the litterfall fraction of 2004 for every year up to 2009 on the 8 traps dataset. This calculation resulted in an annual leaf litterfall of 2.4 Mg C ha^{-1} yr^{-1} which is 33 % smaller than the average of 3.2 Mg C ha^{-1} yr^{-1} from all sites reported in Table 1.

Litterfall at the Tapajós km 67 tower site was collected and sorted approximately every 14 days from July 2000 through June 2005 by Rice et al. (2004) and the dry matter content of different litter types leaves, fruits and flowers, wood (<2 cm) and miscellaneous were reported. Assuming 50 % carbon content, average annual leaf litterfall was 4.31 Mg C ha^{-1} yr^{-1}. Leaf litterfall for this site shows distinct seasonal dynamics in 2002–2004 with peaks in the middle of the dry season of each consecutive year.

2.5 Eddy covariance measurements

Eddy covariance and meteorological 30 min data (Bonal et al., 2008) are recorded at the Guyaflux site since 2004 with sensors mounted 2 m above a 55 m high tower that was built in an existing, natural 100 m^2 gap. The mean tree height is 35 m, with emergent trees exceeding 40 m and the measurements cover a range of more than 1 km of undisturbed forest in the direction of the prevailing winds.

The eddy fluxdata were processed following the Euroflux methodology described in Aubinet et al. (2000) using standard partitioning methodologies (Papale et al., 2006; Reichstein et al., 2005), where the threshold of friction velocity (u*) below which night-time NEE was correlated with u* was applied. Negative GPP values during daytime were removed (e.g. in 2005, two large negative peaks due to heavy rainfall events that strongly influenced overall GPP profile were removed). For daily means only days with more than 80 % of half hourly data available were retained.

2.6 Model evaluation

The new leaf turnover mechanism (Eq. 8) and the parameter value changes (2.4) were implemented simultaneously in ORCHIDEE-NLT. The ORCHIDEE output, with and without the new phenology mechanism, is evaluated in detail with field measurements of leaf litterfall and eddy flux measurements from the Guyaflux site. Additional validation against leaf litterfall data was performed at the Tapajós km 67 site. Furthermore, modelled $V_{c,\max}$, leaf age and LAI patterns were evaluated.

ORCHIDEE was applied from 2004 until 2009 with half hourly data of down-welling short-wave radiation SW_{down} (W m^{-2}), down-welling long-wave radiation LW_{down} (W m^{-2}), air temperature T_a (K), specific humidity Qa (kg kg^{-1}), wind speed u (m s^{-1}), surface pressure P_s (Pa) and rainfall rate P (mm s^{-1}) (Bonal et al., 2008). A spin-up run with all data was performed for 230 yr until all carbon reservoirs reached steady state equilibrium and NEE levels, soil carbon pools and total CO_2 fluxes were stabilized. Maximum LAI for the standard run was fixed to 7.0 $\text{m}^2\ \text{m}^{-2}$, close to the maximum values reported by Juarez et al. (2007) The soil depth was set at 10 m and the root profile parameter H_{root} at 0.1 according to Verbeeck et al. (2011), corresponding to a root distribution that decreases almost linearly with depth.

Standard and modified GPP model outputs were evaluated against GPP data derived from eddy covariance (EC) measurements to gauge model response to the modifications. Only daytime (8 h–16 h) GPP flux data were analyzed and both the goodness of fit (root mean square error RMSE and Pearson correlation) of the seasonal flux pattern as the GPP response to incoming radiation were analysed based on 10 daily running means.

3 Results and discussion

3.1 Improved leaf litterfall seasonality

The ORCHIDEE-NLT version gives a seasonal pattern in modelled leaf litter that anticipates the peak in light availability seen in the long and short dry seasons and coincides with the timing of leaf litterfall of field inventory for Tapajós km 67 and for Guyaflux (Fig. 4). For both sites, the RMSE decreased compared to the standard version and the correlation with observed litterfall increased, suggesting that a more realistic seasonal pattern was introduced by implementing a productivity (NPP_{leaf}) driven leaf litterfall. The summary statistics for seasonal leaf litterfall pattern evaluated against field inventory data at Guyaflux and Tapajós km 67 site are given in Table 2. The modelled average annual leaf litterfall amount at Tapajós km 67 increases from $1.78 \pm 0.07\,\mathrm{Mg\,C\,ha^{-1}\,yr^{-1}}$ to $2.91 \pm 0.42\,\mathrm{Mg\,C\,ha^{-1}\,yr^{-1}}$ with the new phenology. This value is lower than the field inventory estimate of annual leaf litterfall ($4.31 \pm 1.86\,\mathrm{Mg\,C\,ha^{-1}\,yr^{-1}}$) but close to the annual leaf litterfall of $3.2 \pm 1.03\,\mathrm{Mg\,C\,ha^{-1}\,yr^{-1}}$ averaged over all sites in Table 1.

The modelled average annual leaf litterfall amount at Guyaflux increases from $1.75 \pm 0.04\,\mathrm{Mg\,C\,ha^{-1}\,yr^{-1}}$ to $3.10 \pm 0.75\,\mathrm{Mg\,C\,ha^{-1}\,yr^{-1}}$ with the new phenology. This value is higher than the field inventory estimate of annual leaf litterfall at Guyaflux ($2.40 \pm 1.38\,\mathrm{Mg\,C\,ha^{-1}\,yr^{-1}}$) but close to the annual leaf litterfall of $3.2 \pm 1.03\,\mathrm{Mg\,C\,ha^{-1}\,yr^{-1}}$ averaged over all sites in Table 1. True leaf litter at Guyaflux could also be underestimated by the field measurements due to incorrect estimates, particularly seasonal variations, of the percentage of leaf biomass in the total collected litter, or to difficulties of capturing large leaves, herbivory, in situ decay or decomposition before leaf abscission (Malhi et al., 2011).

Due to the modification, mean modelled LAI value decreased from 6.9 (standard version) to $6.0\,\mathrm{m^2\,m^{-2}}$ (ORCHIDEE-NLT) and instead of showing small seasonal changes, LAI now remains constant due to balanced leaf allocation and litterfall (Fig. 5). Various authors report different LAI field estimates for tropical evergreen forests but an

LAI value of 6.0 $m^2\,m^{-2}$ is close to the estimated mean LAI of 5.7 $m^2\,m^{-2}$ reported by Malhado et al. (2009) measured across 50 experimental plots around the Tapajós km 67 site. Juarez et al. (2008) report an average LAI of 5.5 to 6.0 $m^2\,m^{-2}$ at the experimental site in Tapajós km 83. At Guyaflux, the mean Plant Area index (PAI, $m^2\,m^{-2}$) of the inventory plots around the Guyaflux tower measured with a LAI2000 (LI-COR Inc., Lincoln, NE, USA) is estimated at 7.0 $m^2\,m^{-2}$ (Bonal et al., 2008) but PAI is higher than LAI because it includes the trunks and branches of the trees around the measurement point. Bonal et al. (2008) report that PAI did not differ between the wet and long dry period of 2005 and Malhado et al. (2009) could not detect significant seasonal variation in LAI measurements. The standard version of the ORCHIDEE model would allocate carbon to woody aboveground biomass when a maximum LAI of 7.0 $m^2\,m^{-2}$ is reached. Due to the modification, the leaf carbon is balanced and the spillover mechanism to woody biomass carbon pool is no longer needed. The resulting aboveground wood production is $3.65 \pm 1.25\,\mathrm{Mg\,C\,ha^{-1}\,yr^{-1}}$, which is realistic when compared with field inventory estimates that range from $2.02 \pm 0.20\,\mathrm{Mg\,C\,ha^{-1}\,yr^{-1}}$ in Caxiuanã (Almeida, unpublished data) to $3.81 \pm 0.22\,\mathrm{Mg\,C\,ha^{-1}\,yr^{-1}}$ in Tapajós km 67 (Rice et al., 2004).

3.2 Improved $V_{\mathrm{c,max}}$ seasonality

ORCHIDEE's leaf age class scheme keeps track of leaf age structure and replaces the old senescent leaves by new young ones, created from primary production assimilates. By including seasonal leaf litterfall dynamics as in Eq. (8), the proportions of young and old leaves within a vegetation canopy changes over seasons. Increasing leaf litterfall in the dry season causes a more pronounced seasonal change in leaf age (32 days younger in dry season than in wet season, compared to 19 days for the standard ORCHIDEE). Consequently, the mean leaf age decreases from 535 ± 7 to 324 ± 16 days. Leaf ages of 300 to 789 days for thirteen species in French Guiana were reported by Coste et al. (2011) for 2 to 4-yr-old seedlings in a greenhouse, while Reich et al. (2004) report leaf ages between 76 to 1693 days for adult Amazonian trees.

Younger leaves are modelled to have a higher photosynthetic capacity than older leaves in ORCHIDEE (Fig. 1) and the leaf age dependent decrease of $V_{c,max}$ causes that the seasonally changed age structure of leaves indirectly induces a seasonal canopy $V_{c,max}$ pattern (Fig. 6). The leaf age decrease results in a $V_{c,max}$ increase at the top of canopy from 44 to 59 µmol m^{-2} s^{-1} and at the lower end of the canopy from 14 to 20 µmol m^{-2} s^{-1} that results in an overall increase in GPP (see Sect. 3.4). A resulting GPP response is supported by the findings of Brando et al. (2010) that suggested that seasonal variation in leaf flushing and hence canopy $V_{c,max}$, are associated with variations in GPP, even when unaccompanied by associated changes in LAI.

The canopy integrated value $V_{c,max}$ values (Johnson and Thornley, 1984) are 23 µmol m^{-2} s^{-1} for the standard ORCHIDEE and 32 µmol m^{-2} s^{-1} for ORCHIDEE-NLT. However, the exponential canopy profile of Johnson and Thornley (1984) was described for crops and the observed vertical leaf profiles of nitrogen through the canopy from a site in Amazonia (Mercado et al., 2007) indicates a linear decrease of $V_{c,max}$, less steep than that predicted by the exponential decrease implemented in ORCHIDEE. Modelled canopy integrated photosynthetic capacity would be higher if a linear decrease was implemented. We therefore suggest to test the impact of a linear decrease in the vertical $V_{c,max}$ profile within the canopy in future studies.

Both standard and ORCHIDEE-NLT modelled $V_{c,max}$ fall within the wide range of values measured at the Tapajós km 67 site from 10 (bottom canopy) to 106 (top canopy) μmol m^{-2} s^{-1} and fall within the range of values currently used in global vegetation models for tropical forests (43–82 µmol m^{-2} s^{-1}, Domingues et al., 2005). The canopy integrated modelled $V_{c,max}$ value (23 to 32 µmol m^{-2} s^{-1}) is close to the value of 29 µmol m^{-2} s^{-1} reported by Kattge et al. (2009) for oxisols, a tropical soil type that is very poor in nutrients. The annual pattern in Fig. 6 shows a more pronounced wet and dry season $V_{c,max}$. Nevertheless, the introduced seasonality is modest, which corresponds to the $V_{c,max}$ seasonality retrieved by data assimilation in ORCHIDEE by Verbeeck et al. (2011).

3.3 Impact on NPP

The decreased (fine root) maintenance respiration in the modified model results in NPP model outputs that are more realistic and more close to field inventory estimates made at various Neotropical evergreen rainforest sites. Indeed, NPP_{tot} increased from $7.7 \pm 4.6\,\text{Mg C ha}^{-1}\,\text{yr}^{-1}$ in the standard ORCHIDEE version to $10.5 \pm 7.0\,\text{Mg C ha}^{-1}\,\text{yr}^{-1}$ in ORCHIDEE-NLT, which is close to values reported by Malhi et al., 2009a (10.1 ± 1.4, 10.1 ± 1.4 and $10.1 \pm 1.4\,\text{Mg C ha}^{-1}\,\text{yr}^{-1}$ for Manaus, Tapajós and Caxiuanã, respectively). Aragao et al. (2009) report an average NPP_{tot} of $12.8 \pm 1.3\,\text{Mg C ha}^{-1}\,\text{yr}^{-1}$ for 10 sites in Brazil, Peru and Colombia and Malhi et al., 2011 report an estimate of $12.4 \pm 4.4\,\text{Mg C ha}^{-1}\,\text{yr}^{-1}$ for 35 tropical sites worldwide. The modifications result in an ORCHIDEE NPP_{leaf} that increased from $2.0 \pm 0.2\,\text{Mg C ha}^{-1}\,\text{yr}^{-1}$ to $3.3 \pm 0.4\,\text{Mg C ha}^{-1}\,\text{yr}^{-1}$. At Guyaflux the field inventory estimate of leaf litterfall (2004–2009) is $2.4\,\text{Mg C ha}^{-1}\,\text{yr}^{-1}$. Values of $2–8\,\text{Mg C ha}^{-1}\,\text{yr}^{-1}$ were reported by Rice et al. (2004), Brando et al. (2008) and Chave et al. (2010).

Nevertheless, we should keep in mind that making field inventory estimates of NPP_{tot} is challenging and the component most well studied and quantified is aboveground wood productivity while below ground components are less well known (Aragao et al., 2009).

3.4 Impact on GPP

The increased $V_{\text{c,max}}$ parameter value (Sect. 4.2) results in a GPP increase ($38\,\text{Mg ha}^{-1}\,\text{yr}^{-1}$ versus $34\,\text{Mg ha}^{-1}\,\text{yr}^{-1}$) compared to the standard ORCHIDEE version, which is close to the annual mean of flux derived GPP ($37\,\text{Mg ha}^{-1}\,\text{yr}^{-1}$).

At Guyaflux, all six years of eddy covariance measurements showed a higher GPP (mean of $3.03\,\text{g C m}^{-2}\,\text{s}^{-1}$) in the dry season (June through December) than in the wet season (mean of $2.70\,\text{g C m}^{-2}\,\text{s}^{-1}$). The ORCHIDEE-NLT model better captures these dry and wet season variations (mean of $3.05\,\text{g C m}^{-2}\,\text{s}^{-1}$ for dry season and $2.80\,\text{g C m}^{-2}\,\text{s}^{-1}$ for wet season) than the standard version (mean of $2.58\,\text{g C m}^{-2}\,\text{s}^{-1}$

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for dry season and 2.43 $\mathrm{g\,C\,m^{-2}\,s^{-1}}$ for wet season). Both GPP model outputs showed an annual seasonal cycle with dry season increases and wet season lower productions that follow the seasonal pattern in $\mathrm{SW_{down}}$ (Fig. 7). However, the more pronounced wet and dry season $V_{\mathrm{c,max}}$ variation (Fig. 6) results in a more pronounced relative dry season GPP increase in ORCHIDEE-NLT, being 23 % in the standard and 27 % in the modified version, which is close to the relative wet and dry season GPP difference in fluxdata of 29 %. So, not only the average mean GPP value has improved through this by a higher $V_{\mathrm{c,max}}$ value, but also the seasonality in GPP has changed – although not drastically- with dry and wet season variations better captured due to more pronounced $V_{\mathrm{c,max}}$ variations.

Furthermore, we found that GPP model outputs were more close to the eddy correlation based estimates of GPP, as RMSE has decreased from $1.75 \times 10^{-5}\,\mathrm{g\,C\,m^{-2}\,s^{-1}}$ to $1.04 \times 10^{-5}\,\mathrm{g\,C\,m^{-2}\,s^{-1}}$ and the correlation has increased from 0.55 to 0.66. Wet season correlation (0.62) for ORCHIDEE-NLT GPP is higher than the dry season correlation (0.39), suggesting that the implementation in ORCHIDEE of some processes that typically occur in the dry season, possibly drought stress, still need improvement.

3.5 Impact on GPP response to light

The wet and dry season response curves of GPP to $\mathrm{SW_{down}}$ for flux data and model outputs (Fig. 8) show a nearly linear increase with increasing light availability after which the curve flattens and GPP does not increase any further with increasing light availability and a plateau $\mathrm{GPP_{max}}$ is attained. At these high light levels ($\mathrm{SW_{down}} > 300\,\mathrm{W\,m^{-2}}$), photosynthesis is limited by Rubisco activity and $V_{\mathrm{c,max}}$ determines the level of maximum photosynthesis that can be attained since there is a modelled linear relation between $V_{\mathrm{c,max}}$ and light saturated . The higher dry season $V_{\mathrm{c,max}}$ value in ORCHIDEE-NLT version (Fig. 6) results in a higher $\mathrm{GPP_{max}}$ plateau in the response curve compared to the plateau of the wet season.

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4 Conclusions

The productivity driven mechanism of seasonal leaf litter that was introduced in ORCHIDEE, corresponds well with field inventory data for tropical forests and times with its seasonality. By including tropical forest leaf litterfall and a coincident leaf flush in ORCHIDEE, modelled carbon fluxes more accurately represent observations, suggesting that seasonal leaf litterfall is strongly coupled to seasonal changes in productivity. In general, the fit to GPP flux data was improved and the results confirm that at the Guyaflux site, by modifying canopy dynamics to benefit from increased production due to favourable light conditions, a better representation of the seasonal carbon flux patterns was made.

In this new version, carbon allocation to the leaves was increased and more closely fit to field inventory estimates for the Neotropics by lowering the maintenance respiration of fine roots and increasing the fraction of carbon allocated to leaves. The ‘overflow’ mechanism of carbon to aboveground woody biomass when a maximum LAI is reached is no longer needed and the modification balances the leaf carbon cycle. Future work can test the effect of the modification on aboveground woody biomass, possibly for the whole Amazon basin. Modelled LAI now remains at a constant level, i.e. $6.0\,\mathrm{m^2\,m^{-2}}$ for the Guyaflux site, the canopy carbon content hence is at steady state with an ever optimal maximum leaf biomass amount in the canopy, but leaf age and $V_{\mathrm{c,max}}$ dynamics are constantly optimized, responding to seasonal changes in production, according to the available resources and light availability.

We are aware that the self thinning approach that we applied here to old-growth forests might be less applicable to secondary or disturbed forests that have not yet grown the maximum leaf biomass or LAI that can be attained inside the canopy under the given circumstances at the site (light and nutrient availability). Future work should therefore test our productivity driven approach of modelling leaf litterfall for other tropical forest types, like secondary forests or perhaps flooded tropical forests. Additionally, the impact of spatial variation in soil fertility and nutrient contents of soils on $V_{\mathrm{c,max}}$ and spatial variability in GPP could be tested.

The analysis revealed a stronger dry season response of GPP to light compared to the wet season and a higher sensitivity of GPP to changes in $V_{\mathrm{c,max}}$ in the dry season compared to the wet season. The modified $V_{\mathrm{c,max}}$ value results in an annual cycle of GPP that matches the increased uptake of carbon during the dry season and the pronounced seasonal changes between dry and wet seasons. In future work we could also represent the true tropical evergreen canopy properties in more detail by including a more realistic gradient in $V_{\mathrm{c,max}}$, possibly based on leaf nitrogen content measurements, and see how it affects the carbon simulations.

We successfully represented the annual GPP cycle at a single location in the Neotropics during six years of simulation (2004–2009). The more adequate representation of seasonal canopy dynamics and a correct representation of GPP brings more confidence in simulated carbon fluxes and feedbacks with climate change scenarios of the global vegetation model. Future analysis should be extended to other locations and different tropical forest types, not necessarily light limited, to see if we can reproduce the seasonal and also interannual variability in carbon uptake across the entire Amazon basin or the Central African forests by including productivity driven leaf turnover.

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Table 1. Overview of litterfall time series in literature for tropical evergreen forests. Most datasets are reported in graphs and tables of the references, Tapajós km 67 and Guyaflux data are indicated (*). For each site the country code CC, site name, geographical coordinates (latitude, longitude degrees), mean annual rainfall P_{ann} (mm), altitude (m a.s.l.), period of measurements and reference are reported. Annual average leaf litterfall is given in Mg DM ha^{-1} y^{-1}. LM indicates whether leaves were separately measured (Y/N), forest type and remarks are also given. All forests are undisturbed unless other mentioned. Country code abbreviations: BR: Brazil, CI: Ivory Coast, DRC: Democratic Republic of the Congo, FG: French-Guiana, PE: Peru, VZ: Venezuela.

CC	Site name	Lat.	Long.	Altitude	P_{ann}	Forest type	Litter peak period	leaf litterfall	LM	Remarks	Period	Reference
BR	Colônia do Apiaú Roraima	02°34′N	61°18′W	100–180	2000	terra firme	transition from wet to dry season (Sept–Nov) secondary peak end of dry season (March–April)	5.57	Y	–	23/12/1988–23/12/1989	(Barbosa & Fearnside, 1996)
BR	Jari landholding Para	00°27′S	51°40′W	5–20	2293	riparian primary forest	dry season (Aug–Nov)	7.84	Y	–	01/09/2004–01/10/2005	(Barlow et al., 2007)
BR	Embrapa Amazônia Ocidental	03°08′S	59°52′W	50	2400	primary forest	dry season (Aug–Oct)	6.66	Y	extensive timber extraction	01/08/997–01/02/999	(Martius et al., 2003)
BR	Mata de Piedade Pernambuco	07°49′S	35°00′W	113	1520	atlantic rainforest	dry season (Aug–Jan)	8.55	Y	–	01/08/2003–01/09/2005	(Schessl et al., 2007)
BR	Maraca Island Roraima	03°20′N	61°20′W	95	1800	boundary rainforest savannah	dry season (Oct–March)	6.30	Y	nutrient-poor soils	17/04/1987–15/04/1988	(Scott et al., 1992)
BR	Santarém Tapajós km 67*	02°51′S	54°57′W	88	2120	terra firme	end of wet season +dry season (Aug–Oct)	8.40	Y	flat high plateau (150 km)	14/07/2000–11/06/2005	(Rice et al., 2008)

Table 1. Continued.

CC	Site name	Lat.	Long.	Altitude	P_{ann}	Forest type	Litter peak period	leaf litterfall	LM	Remarks	Period	Reference
BR	Juruena, Mato Grosso	10°25′S	58°46′W	280	2379	terra firme mixed hardwood/palm in riparian zone	dry season (May–Sept)	5.90	Y	plateaus and riparian hillslopes	01/09/2003–01/08/2004	(Selva et al., 2007)
BR	Dimona, 80 km North of Manaus Amazonas	2°30′S	60°00′W	130	2200	evergreen, non-inundated lowland	dry season (June–Sept)	7.21	N	strong micro- relief	11/06/1990–05/01/1994	(Sizer et al., 2000)
BR	Curuá-Una Forest Reserve, Para	02°00′S	54°00′W	180	1900	terra firme planalto	end of wet season + dry season (July–Nov)	6.87	Y	–	01/10/1994–01/10/1995	(Smith et al., 1998)
CI	Yapo, 40 km North of Abidjan	05°43′N	04°03′W	110	1800	evergreen rainforest	end of wet season + part of dry season (Nov–Jan)	6.69	Y	–	01/07/1967–01/10/1969	(Bernhard, 1971)
CI	Banco, Abidjan	05°23′N	04°03′W	55	2100	evergreen rainforest	dry season (Jan–March)	8.12	Y	–	01/04/1966–01/09/1968	(Bernhard, 1971)
DRC	Dimonika, Mayombe	04°11′S	12°23′E	360	1495	evergreen rainforest	before and during peak radiation period (Nov–March)	4.80	Y	lower radiation in dry season due to fog	24/02/1987–16/02/1988	(Schwartz and Tondo, 1988)
FG	Guyaflux*	05°17′N	52°54′W	10–40	3041	lowland tropical wet	end of wet season–dry season (June–Sept) secondary peak short dry season (Febr–March)	4.70	N	succession of small, elliptical hills	19/12/2003–03/06/2010	(This study)
PA	Barro Colorado Island	09°09′N	79°51′W	60	2612	tropical semideciduous forest –	dry season (Dec–Apr)	8.50	Y	mixture deciduous-evergreen	25/11/1985–29/11/2010	(Wieder and Wright, 1995)
PE	Braga-Supay and Lobillo Jenaro herrera	04°55′S	73°44′W	110	2715	floodplain forest	peak rainfall and flooding period (Feb–May)	4.17	N	–	01/12/1997–01/12/1998	(Nebel et al., 2001)
VZ	La Sabanita San Ignacio de Yuruaní	05°00′N	61°01′W	1200	2200	submontane moist forest	second half wet season -start dry season (Sept–Nov) secondary peak second half dry season (Feb–March)	4.76	N	extremely nutrient-poor and stony soil	28/07/1990–25/07/1991	(Priess et al., 1999)

Table 2. Goodness of fit evaluation statistics for standard and modified ORCHIDEE modelled leaf litterfall evaluated against field inventory leaf litterfall at Guyaflux (2.40 Mg C ha^{-1} yr^{-1}) and Tapajós km 67 (4.32 Mg C ha^{-1} yr^{-1}).

	Guyaflux		Tapajós km 67	
	standard	NLT	standard	NLT
mean modeled leaf litterfall	1.75	3.10	1.78	2.91
RMSE	1.23	1.07	3.02	1.99
pearson correlation	−0.20	0.73	−0.27	0.61

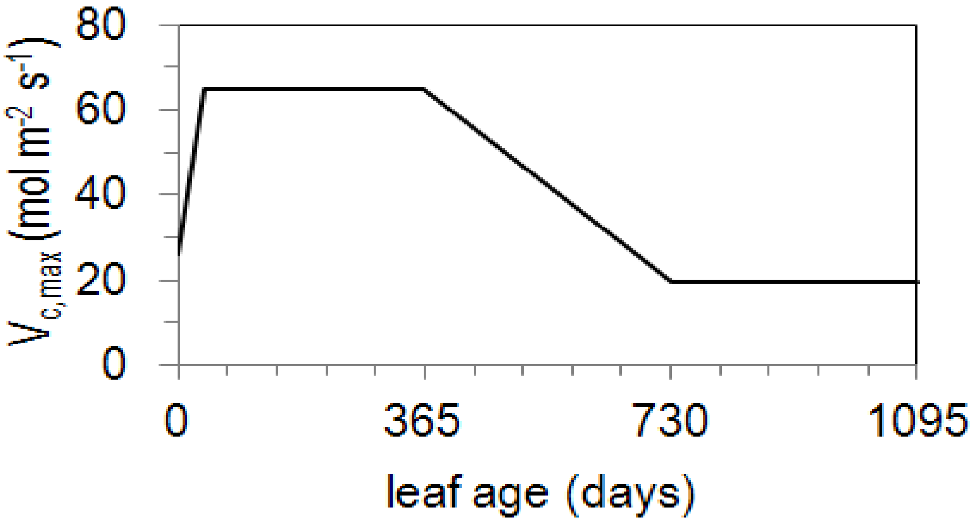

Fig. 1. In ORCHIDEE, leaf photosynthetic capacity ($V_{c,max}$) is determined as a function of leaf age. The slope of the curve is determined by a critical leaf age parameter, which is 730 days for tropical evergreen forests.

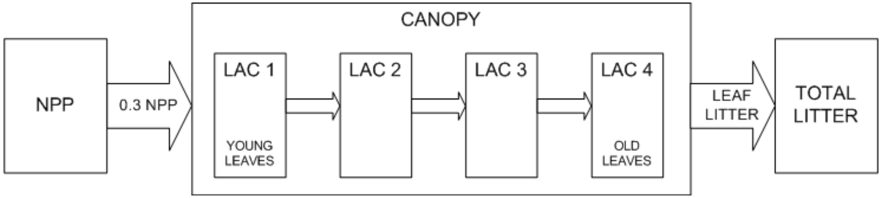

Fig. 2. Schematic representation of the new leaf turnover scheme implemented in ORCHIDEE-NLT. The amount of carbon allocated to youngest leaves equals the amount of carbon lost by litterfall of oldest leaves. The canopy leaf biomass consists of four different leaf age classes (LAC) and biomass is passed from younger LAC to older LAC.

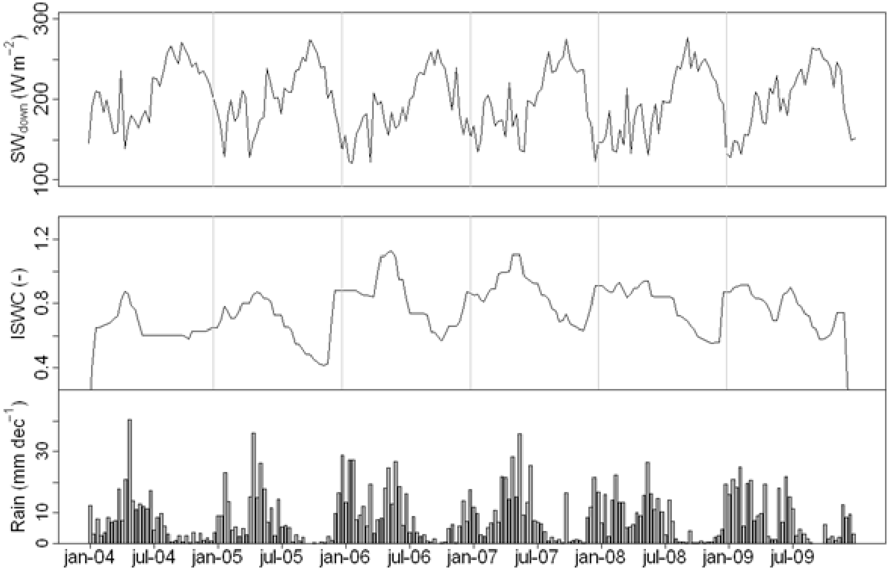

Fig. 3. Seasonal patterns in leaf litterfall, SW$_{down}$, index of Soil water content (ISWC) and rainfall at Guyaflux over 2004–2009 (data from Bonal et al., 2008 and from this study).

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Seasonal leaf dynamics for tropical evergreen forests in a process

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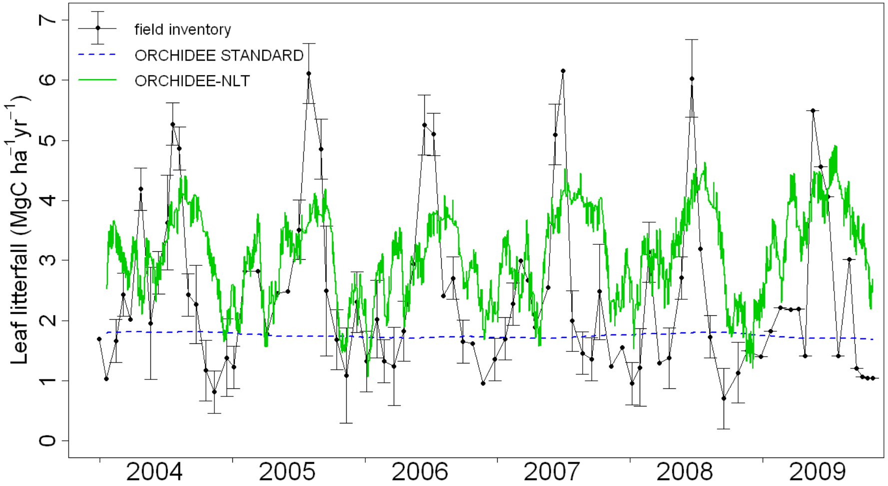

Fig. 4. Modelled and measured seasonal patterns of leaf litterfall (MgC ha^{-1} yr^{-1}). Field inventory measurements are compared with the standard model and the modified ORCHIDEE-NLT leaf litterfall at Guyaflux from 2004 to 2009.

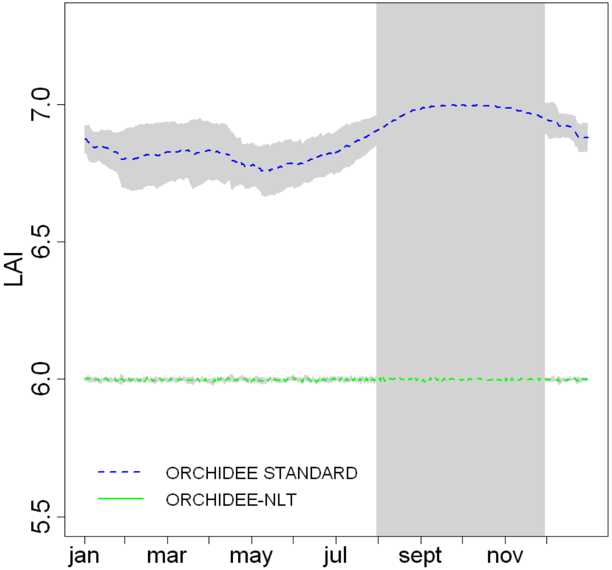

Fig. 5. LAI mean annual time profile plotted along with standard deviation (grey) of 2004–2009 period for **(a)** standard ORCHIDEE and **(b)** ORCHIDEE-NLT. The dry period (<100 mm month−1) is shaded.

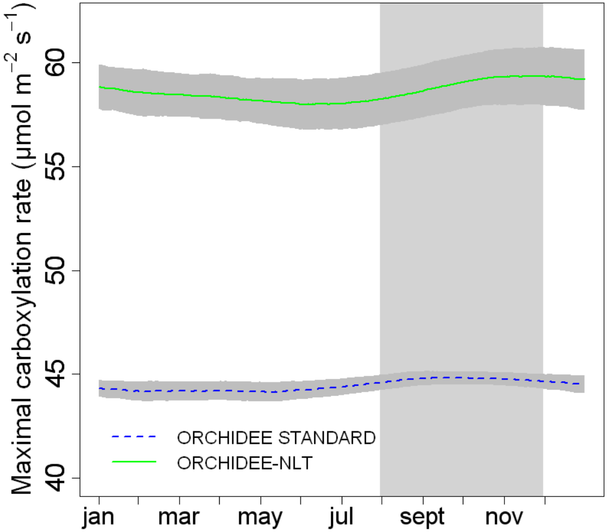

Fig. 6. $V_{c,max}$ (μmol CO$_2$ m^{-2} s^{-1}) mean annual time profile plotted along with standard deviation (grey) of 2004–2009 period for **(a)** standard ORCHIDEE and **(b)** ORCHIDEE-NLT. The dry period (<100 mm month^{-1}) is shaded.

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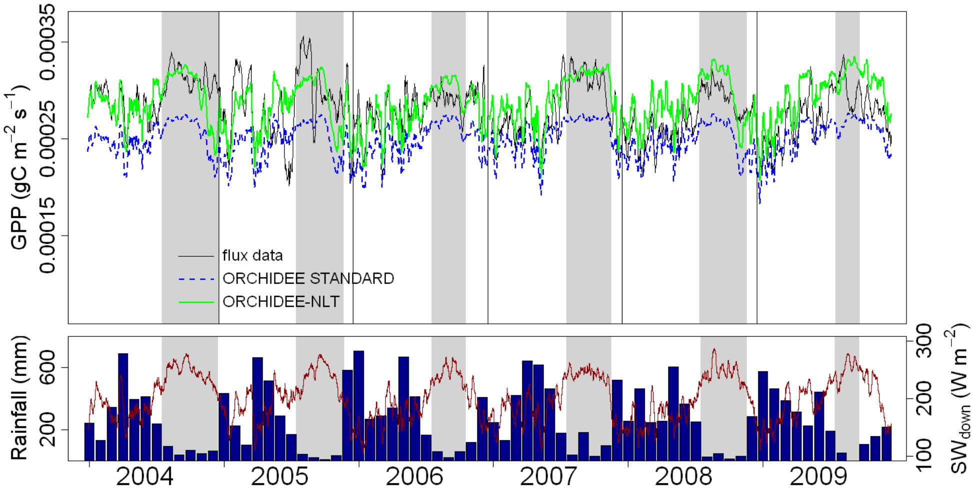

Fig. 7. Run-sequence moving averages at Guyaflux for a time window of 10 days including only daytime data (8 h–16 h) of **(a)** measured and modeled GPP fluxdata, standard ORCHIDEE and modified ORCHIDEE-NLT **(b)** 30 daily running mean down-welling shortwave radiation SWdown and monthly rainfall. Dry periods are shaded in gray (<100 mm month^{-1}).

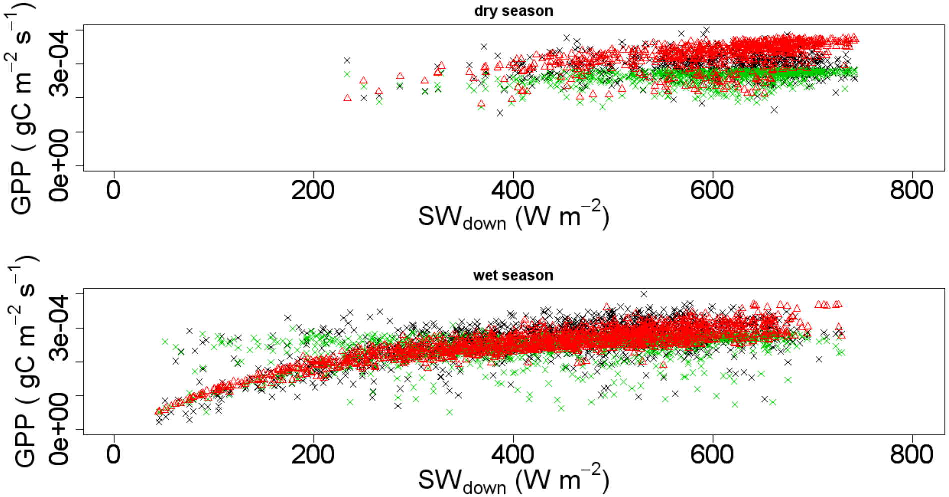

Fig. 8. The relationship between GPP (g C m^{-2} s^{-1}) fluxtower data (black), ORCHIDEE model outputs from the standard version (green) and the modified ORCHIDEE-NLT version (red) and SW$_{down}$ (Wm^{-2}) from 2004 until 2009. Models are plotted for wet season **(a)** and dry season **(b)** (threshold monthly rainfall > 100 mm); daily means calculated from daytime (8 h–16 h) data.