Interactive comment on “Seasonal leaf dynamics for tropical evergreen forests in a process based global ecosystem model” by M. De Weir dt et al.
marjolein.deweirdt@ugent.be

Anonymous Referee 1

Dear referee,

Thank you for your time for reading the paper and providing your positive inputs and comments, which help to improve this paper. We are pleased to send you our responses (C – Referee’s comment, R – Authors’ response)

C: This paper is interesting and well written, and the model improvements do appear to notably increase the fit to observations. My main issue with this method is one that is partly recognized in the conclusions. Namely, the approach appears to assume a constant LAI, as for all biomass allocated to leaves, an exactly equivalent amount is lost at the same time. It is therefore puzzling to me how this model can be spun up in a way that predicts leaf area index? Maybe the idea is that it is driven with observed LAI? It is also unclear how the LAI of 6.0 used in this study was obtained - from the model or from site level observations?

R: Yes, the model does not predict maximum LAI, but during the spin-up the LAI increases up to a maximum LAI, which is inferred from site observations. This is explained in more detail in response to your specific comment (16). Throughout the paper some sentences were adapted to make this more clear for the reader.

C: My other comment is on the assumptions of the optimality approach. The authors assert that LAI is consistent between seasons at these sites but do not provide data to demonstrate this. If we are to assume that forests are light-limited at these two sites, and that light availability varies between seasons, is another potentially optimal strategy to make use of the extra light by growing a thicker canopy during the dry season, thus allowing variation in LAI? Part of the confusion here stems from the fact that the precise goals of the optimal theory used here are never defined, so it is difficult to determine whether the plants are in fact generating a solution which optimal with reference to some hypothesized goal, as the authors assert.

R: The main assumption of our study is that the canopy of these evergreen tropical forests are in an equilibrium state with a constant maximum LAI (i.e. a constant total leaf biomass). Although the total LAI is assumed to be constant, we hypothesize that the canopy is constantly optimizing its photosynthetic capacity by adapting the leaf age distribution. In periods of high productivity a higher photosynthetic capacity is reached by the production of relatively more new leaves and a proportional higher turnover of old leaves. The analysis aims to understand how this changing leaf age distribution drives seasonality in $V_{c,\text{max}}$ and how this impacts the resulting fluxes. We agree that it is possible to study canopy seasonality of these ecosystems with different alternative hypotheses: e.g. seasonal changes in LAI (as suggested in the comment) or seasonal changes of SLA. Nevertheless, we prefer to stick with one hypothesis to keep the analysis focused. We will include in the revised manuscript the suggestions to test the effect of seasonal variations of LAI and SLA in the future. In addition, our assumption of a constant LAI value at Guyaflux and Tapajós km67 is supported by field observations of Bonal et al. (2008) and Malhado et al. (2009).

The hypothesis that seasonal GPP variations are driven by seasonal changes of $V_{c,\text{max}}$ only due to seasonal leaf turnover, without associated changes in LAI, is also supported by findings of Brando et al. (2010), as referred to in the paper, who suggested that seasonal variation in leaf flushing and hence canopy $V_{c,\text{max}}$ are associated with variations in GPP, even when unaccompanied by associated changes in LAI. Several other studies report small or no seasonal changes in LAI differences between wet and dry season for tropical evergreen forest. For example, De Wasseige et al., 2003 reported a
seasonal change in LAI of only 0.34, measured with an LAI-2000 Plant Canopy Analyser in a semi-deciduous forest in Central African Republic. The precise goals of the optimality are explained more in detail in response to your specific comment nr 5.

Specific Comments

(1) P640 L2: representation in global models _is_ highly simplified. “is” was inserted.

(2) P640 L14: patterns are analyzed _in detail_ (not details) changed to “in detail”

(3) P642 L11: It would be easier to assess whether or not evidence is overwhelming in favor of dry season litterfall peaks if the data in these tables were quantitative, or contained an estimate of the magnitude of the effect.
The magnitude of dry/wet season effect on leaf litterfall (%) was added to Table 1.

(4) P643 L20: I think it would be interesting to show these data. It is difficult to determine the strength of the correlations from only the timeseries.

Following lineair relation between leaf litterfall and shortwave downward radiation $SW_{down}$ was tested:

$$\text{LL}_{\text{dec}} = \text{LL min} + (\text{LL max} - \text{LL min}) \left( \frac{SW_{down, \text{avg dec} + 3} - SW_{down, \text{min}}}{SW_{down, \text{max} - SW_{down, \text{min}}}} \right)$$

With $\text{LL}_{\text{max}}$, the maximal leaf litterfall, $\text{LL}_{\text{min}}$, the minimum measured leaf litterfall. The comparison in the graph below for Guyaflux shows that this empirical relation results in a good correspondence between measured (light green) and modeled (dark green) leaf litterfall for 2004-2006. However, such a relationship needs site specific parameters $\text{LL}_{\text{max}}$ and $\text{LL}_{\text{min}}$ that are easily applied at sites for which data on leaf litterfall are available, but difficult to apply elsewhere. Therefore such an approach is less useful for a generic model like ORCHIDEE.
In this study we consider optimality as the constant optimization of the ecosystem’s photosynthetic capacity by a higher investment in new leaves and a higher turnover of old leaves during periods of high productivity. We assume that the most limiting resource with seasonally changing availability in these forest types is light. The seasonal leaf turnover scheme that we introduce is thus optimizing the canopies capacity to use light. Of course nutrient limitations also play an important role in these forests, but studying the influence of seasonal variations in nutrient limitation is out of the scope of this study. In the dry season there is more light available and species that can benefit from this increased radiation by increasing its photosynthetic capacity, have a competitive benefit (in terms of increased photosynthesis) compared to species that don’t increase their $V_{c,\text{max}}$ with increased light availability. This strategy aims to maximize net photosynthesis which is one of the possible strategies that increases a tree’s chances of survival in the crowded forest. 

Therefore, a seasonal leaf litterfall flux was introduced instead, assuming optimality in leaf turnover (Hikosaka, 2005) and self-thinning of leaves (White, 1981). The optimality assumption in this context is seen as a mechanism for trees to optimize their use of the light availability by adapting photosynthetic capacity as a mechanism to increase their chances of survival in the strong competition of the crowded forest.

In ORCHIDEE the vertical distribution of young/old leaves is not explicitly modeled, but in reality there is probably a significant relation between leaf life span and height in the canopy. The bottom of the canopy holds shade leaves, these leaves are larger and thinner, inclined 90° and have a higher chlorophyll content. At the top of the canopy, the leaves are smaller, thicker, more inclined (to protect from sun) and have a lower chlorophyll content. As far as we can see there is no literature that reports on measurements of leaf litterfall distribution or leaf age with canopy depth. Perhaps the leaves at the top of the canopy have a shorter turnover cycle and have a lower average leaf age because they are more exposed to extreme temperatures, high light levels, high wind speed or these leaves suffer from water stress first. Leaves inside the canopy or at the bottom of the canopy are more protected from these extremes or they have a lower water stress level. Also Hikosaka et al., 2005 models and refers to reports in literature on longer leaf lifespan at lower irradiance levels, and as light interception decrease with canopy depth (see also comment 11), this suggests that leaves at the bottom of the canopy are older.

Here, with ‘constantly optimized’, it is meant that with every time step (one day) of the simulation, the biomass allocated to new leaves, the leaf biomass lost through turnover and leaf age are updated and this results in an optimized seasonal pattern in photosynthetic capacity. To be more clear, two sentences on this matter (p644, r6-10) were rewritten as in the next remark.
(8) P644 L8: As far as I know, there is no nutrient cycle in the ORCHIDEE model. How is the nutrient availability determined?

There is indeed no nutrient cycle in the ORCHIDEE model, this sentence is about the model changes and referring to nutrients or resources in this sentence is misleading. Two sentences (p644, r6-10) on this matter were modified as follows:
The canopy leaf biomass is hence modelled to be at steady state with an ever optimal maximum. Canopy leaf age is updated day by day, responding to the seasonal changes in production, according to the seasonal changes in light availability resulting in an optimized photosynthetic capacity seasonality (Hikosaka, 2005).

(9) P644 L27: It would be good to have separate simulations that demonstrate the different impacts of the altered litter model and the adjusted allocation and respiration parameters.

Yes, this is indeed interesting. We did a separate simulation where the standard version was adjusted only for allocation and respiration (named ORCHIDEE-AllocResp). It shows that the effect on GPP is entirely due to seasonal changes in V_{\text{cmax}}. Changing the respiration and allocation has no significant impact on GPP. ORCHIDEE-TrBE leaf biomass (390 gC/m²) is lower than ORCHIDEE-AllocResp leaf biomass (454 gC/m²), but it is the increased V_{\text{cmax}} that results in higher GPP. Decreased respiration results in doubling of the fine root biomass (220 to 480 gC/m²).

(10) P646 L5: Krinner et al is the original ORCHIDEE paper. From what data they establish 65 as an appropriate Vcmax for tropical trees? Also, it’s not clear that it is necessarily optimal here - maybe ’maximum’ would be more appropriate?

The V_{\text{cmax}} for tropical trees in Krinner et al. is established after comparison of ORCHIDEE NEE and Q_{\text{LE}} output with eddy covariance flux data from Manaus for 1996 from FluxNet (Baldocchi et al., 2001). Later on, Verbeeck et al., 2011 assimilated eddy flux data for Tapajós km67, optimizing the V_{\text{cmax}} value within the range of 24-130, resulting in an optimized parameter value of 63 ± 20. The V_{\text{cmax}} value of 65 also falls within the range of values currently used in global vegetation models for tropical forests (43–82 mmol m^{-2} s^{-1}) and derived from gas exchange measurements at the Tapajós km 67 site (10–106 mmol m^{-2} s^{-1}) as reported by Domingues et al., 2005. Optimal here refers to the optimal value of 65. With increasing leaf age, V_{\text{cmax}} increases from 25, remains constant at its optimal value of 65 and then decreases again to 20.

(11) P646 L10: Why do Johnson and Thornley use this approach? Is it based on photosynthetic capacity acclimating perfectly to light attenuation?

Yes indeed, Johnson and Thornley parameterize photosynthetic capacity as an exponentially decreasing function of canopy depth, with light interception decrease with canopy depth, based on the Monsi-Saeki theory for the light-intercepting characteristics of the canopy.

(12) P647 L14: What are the implications here of fixing the leaf allocation and turning off the Friedlingstein 1999 allocation model? Surely this will affect the capacity of the model to simulate resource limited systems and make it less applicable elsewhere? On this note, it would be good to indicate whether the changes in this model are recommended changes to the whole ORCHIDEE model that will work in other ecosystems, or whether they help in understanding this system but are no generally applicable. My feeling is that the latter is
more true, and in that case, it is difficult to see how this can be moved back into a more general land surface scheme. Are there any alterations to the methods that would make the model generalisable?

Simulations for different evergreen forest sites in the Amazon with the standard ORCHIDEE model (including the Friedlingstein scheme) showed that resources were never modeled to be limiting, resulting in constant allocation factors. There is thus no impact of moisture, temperature or nitrogen availability on the allocation factors for these rainforest sites in the model. Model outputs are very sensitive to the allocation factors and hence they should be treated very carefully. For now, according to the knowledge from field measurements, no clear rule or relationship could be found that determines the allocation in tropical evergreen forests. In addition, the Friedlingstein allocation scheme has never been tested/validated specifically for tropical forests. Therefore, for now, it was decided to keep the allocation factors fixed based on the reports in Malhi et al., 2009. The leaf turnover mechanism that we propose in the paper is indeed meant as a PFT specific phenology scheme for evergreen tropical forest. Nevertheless, it would be interesting to test a similar approach for other evergreen PFTs.

(13) P650 L18: The name ORCHIDEE-NLT really does seem like it is concerned with needle leaf trees. I would consider an alternative naming scheme.

The name ORCHIDEE-TrBE (ORCHIDEE-Tropical Broadleaf Evergreen) was used throughout the revised manuscript.

(14) P653 L8: The word ’evaluated’ here seems to imply that they were tested against data, to me. Maybe ’examined’ might be more appropriate?

It was changed to ‘examined’.

(15) P654 L24: The justification for the overestimation of litterfall at Guyaflux might well also apply at Tapajos, which would make matters worse?

Yes, at Tapajós measured leaf turnover is higher than modeled leaf turnover, the justification was removed.

(16) P654 L26: Apologies if I’ve missed this, but I really don’t understand how this model predicts LAI, given the litterfall calculations. This needs to be explained before this paper can be finalized, in my opinion.

Apologies for this misunderstanding, the model does not predict maximum LAI. In the new model version the LAI stays constant at the level that is reached during the spin up of the model. The maximum LAI reached in the spin-up is determined by a pre-defined threshold. In this study we have used a value of 6 based on field observations. A sentence was added (p. 654, r27):

During the model spin up LAI increases up to a pre-defined threshold. For the two sites studied here LAI is set constant at 6 m² m⁻², lower than the mean LAI of 6.9 m² m⁻² in the standard version but more close to the field estimates, ranging between 5.5 and 6 reported for the respective sites (Juaréz et al., 2008, Malhado et al., 2009). Instead of showing small seasonal changes, modeled LAI now remains constant due to balanced leaf allocation and litterfall (Fig. 5). In future regional model runs for the Amazon, we plan to include spatial variation in the maximum LAI inferred from remote sensing data.
(17) P657 L25: It’s nice to see that this model actually predicts the right-way round response to the dry season, given how very difficult this appears to be in land surface models in general...

Yes it is.

(18) Figure 3: Leaf litterfall data is not presented in this figure, in contradiction to the legend.

Legend was adapted.

(19) Figure 5: Are there no data on LAI against which this can be assessed?

Measured PAI at Guyaflux (with LAI 2000) was added to the graph of Figure 5.

(20) Figure 8: The GPP at low irradiance for the original model (green) look very high. Is this the right output you have plotted?

Thank you for this remark. I indeed made a mistake in the plot and the high GPP values at low irradiance were incorrect. We made the correct plot now and a sentence on Figure 8 (p658, r24-26) was rewritten: The higher $V_{c,max}$ value in ORCHIDEE-TrBE version (Fig. 6) results in a higher GPP$_{max}$ plateau in the response curve compared to the plateau of the standard ORCHIDEE version.