

Saturating response of photosynthesis to increasing leaf area index allows selective harvest of trees without affecting forest productivity

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Authors' response to

RC1: '[Comment on egusphere-2024-3092](#)', Anonymous Referee #1

General comments:

The authors of this study investigated the impact of harvesting on the fluxes of carbon in forests over a large gradient. Based on eddy covariance measurements and on modelling approach, the authors explored the hypothesis that below a certain value of LAI, any forest management action such as harvesting or pruning does not affect Net Ecosystem Productivity. On the basis of a non-linear relationship between gross primary production (GPP) and leaf area index (LAI) characterised by saturation above a threshold of 4-5 m² m⁻², they concluded that above this value, the reduction in leaf area (due to forest management) therefore has little effect on net CO₂ uptake and that it remains constant after partial harvesting.

Overall, the study is well structured and of great interest. However, I would suggest some major revisions, detailed below.

Major comments:

With regard to LAI values, it is difficult to understand whether the threshold value indicated by the authors is relevant whatever the PFT. In fact, the definition of LAI varies between deciduous and coniferous stands, due in particular to a difference in clumping index. As a result, its impact on carbon fluxes can also be expected to be different. This point deserves to be discussed. In addition, the results based on the analysis of carbon fluxes measured by eddy covariance technique should be further discussed in the light of the 'known' uncertainties concerning the estimation of GPP and Reco during the day.

We thank you very much for reviewing our paper, his appraisal, and for providing these insightful comments or critics.

In general, it is difficult to assess the contribution of using the LPJ-GUESS model. This tool was mainly used to confirm the non-linear relationship between GPP and LAI and to confirm the LAI threshold value, but it could have been used to go further in analysing the weak impact of forest management (competition for light, for example).

This is a very valid point. We used the model specifically to look at the LAI-GPP-relationship for different cohorts. This allows us to address one important shortcoming of the observations, namely that we do not know what GPP would have been if LAI were at a different value than observed. It also enables looking at the age cohorts at the same time step (which is what we did in Fig. 4), which allows us to exclude further factors like CO₂ fertilization that influence GPP and LAI over time.

We do acknowledge that the model could be used to investigate other things, but as written in our answer below, the model was not designed to capture detailed site-specific aspects of observation sites. Furthermore, the way we set the simulations up was to understand the GPP of tree cohorts of various LAIs at the same site for the same climatic and atmospheric conditions. From the plots in Figure 4 we can see that additional LAI for an age cohort will not increase GPP after an LAI of around 4. However, the total LAI of the simulated area (which is the weighted average of all the cohorts standing there) did not exceed this threshold by much. In response to your comment, we will now add these total LAI and total GPP numbers to the plot as well and describe it better, since we indeed did not explain this very well. The model will actually prevent high stand LAI through self-thinning in temperate regions, which is why we resolved this by looking at the age cohorts.

We agree that such an analysis regarding the relationships among simulated attributes and fluxes would be very interesting and important. However, this would require a substantial number of additional model simulations, which would likely be enough material for separate publication.

We acknowledge this idea of the reviewer and will add a statement regarding next steps to the discussion, as well as further explanation on the choice of the modeling.

Specific comments:

151-153: For the sites studied, are the age and forest management of the plot described, and how have these characteristics been taken into account in the analysis?

Indeed, the referee makes an important point, namely that several eddy sites neglected the auxiliary data. We had deleted sites, because of missing data.

In as much as they are described we used the available data. the forest management in particular was described. The management type is described in Table S1 , and the harvest operations are being listed up and quantified in terms of biomass decrease in S 3.

162-166: For estimating LAI based on remote sensing, is the spatial resolution of MODIS images sufficient, particularly in relation to the size of the plots (consistent with the comparison with carbon flux measurements), to detect differences in LAI between managed and unmanaged sites?

This is a very interesting point. The footprint of the EC measurements is a lot larger than the MODIS pixels (about 1 km²: see Aubinet, 2012). This is coherent with the fact that the processes analysed in our study are inherently large-scale processes (as opposed to fine-scale, i.e., tree level). This is also the only meaningful scale to consider the effects of harvesting since partial harvesting is creating heterogeneities at fine scale but we only consider the overall stand-level consequences over the EC footprint.

We were more concerned by saturation in LAI prediction from remote-sensed products. In our revision, we will pay attention that this is made clear.

223-227: In general, it is difficult to assess the contribution of using the LPJ-GUESS model in this study because the description is not very detailed: how is competition for light taken into account, in particular as a function of tree density, the age of the tree stand, etc.? how do photosynthesis parameters vary as a function of age, as a function of PFT? how does a reduction in soil water impact photosynthesis and/or production?

We thank the reviewer for pointing out that we did not adequately explain the LPJ-GUESS processes. As the LPJ-GUESS model is only applied without modifications in this study, we wanted to avoid redundant explanation of its processes. However, we should have made clearer where such information can be found and more explicitly refer to the comprehensive description in Smith et al. (2014). We will consequently add more detailed descriptions in the supplements that are relevant to the simulations we conducted for this manuscript plus some sentences regarding the main processes in the main manuscript.

Competition for light is based on weighting the leaf area (or LAI) of each simulated tree cohort, i.e. a tree cohort that has more leaves within a canopy layer will get more light. A cohort with a higher tree density can have a higher canopy leaf area leading to more light access. With rising age, the cohort mortality probability increases, reducing the tree density and thereby also the canopy leaf area. Photosynthesis parameters do not vary with tree age but are influenced by many other environmental and physiological parameters, for example, the maximum carboxylation rate $V_{c_{max}}$ is a function of leaf nitrogen content.

A reduction in soil water content induces stomatal closure via a PFT-specific parameterization. Stomatal closure will then in turn lead to reduced levels of photosynthesis and subsequently lower growth.

228-230: Does this mean that carbon allocation is only calculated on an annual time step in the model? There are seasonal dynamics that affect the respiration rate associated with organ growth and therefore the NEE. This point needs to be clarified in relation to the conclusions of this study.

Yes, allocation is only calculated at the end of the year. However, photosynthesis and respiration and therefore also NEE are calculated daily and accumulated towards the end of year. By doing so, seasonal dynamics are taken into account, for example NPP can become negative during the dry seasons of the year due to closed stomates but maintenance respiration still occurs. We acknowledge that not having seasonal or daily allocation is still a limitation of the model, but accumulating on an annual basis has been proven a reasonable simplification for many forests.

Furthermore, we here only compare the model to yearly values of observed GPP, therefore we find this appropriate.

230-232: Does the SLA vary with position in the canopy (profile of SLA?) relative to leaf exposure to incoming radiation? This is an important point to take into account when considering light competition and its impact on NEP in relation to tree density.

Unfortunately, the eddy flux measurement observes the canopy as a whole. Thus, the Flux sites do not cover this aspect. Experimental data may be available, but probably only in the form of experiments restricted both in time and space. However, we think that this would not change our analysis which refers to a “stand” treatment.

From the modelling perspective, the model used belongs to the family of the big-leaf models. It hasn't been parametrized to reproduce within-canopy SLA variations. Moreover, SLA seems to be highly influenced by the light conditions themselves, so we could expect that a single parameter is not a viable option. Thus, we cannot include this in our analyses.

In our anticipated revision we have to make this limitation clearer.

237-238: How does clumping index vary between PFTs, stand age and tree density? Is this variation taken into account when analysing the results?

Thank you for bringing this point, which is will be discussed in the anticipated revision. There are two important elements regarding the clumping, which we anticipate to include in the manuscript: i) LAI estimations on the flux sites already take the clumping into account and ii) the spatial scale considered here is not easily connected to clumping.

The LAI on the monitoring sites was estimated based on hemispherical photographs. It also appears that the site managers have long studied the parameters necessary to do the estimations of LAI, and have estimated a clumping factor. So, while we fully agree that leaf clumping is an important factor when estimating LAI, but that it has been accounted for in our measurements.

About the second point, the canopy structure being a highly variable feature within a single stand, it is probably difficult to isolate this as a parameter or a driver. The difference between PFTs is visible in Figure 1 (subfigure showing **GPP = f(LAI)**).

We hope that our anticipated changes to the paper will satisfy the concerns by the referee.

267-268: Is the threshold of $4.5 \text{ m}^2/\text{m}^2$ the same regardless of the clumping effect? Is this value the same for coniferous stands? Generally speaking, there is no discussion of the definition of LAI for a deciduous stand and that for a stand of conifers (see lines 285 & 305-307).

Yes, we believe that $4.5 \text{ m}^2/\text{m}^2$, while not being necessarily a unique and fixed threshold, likely represents an upper bound valid for all temperate forest types, including both, coniferous as well as broad-leaved forests. The main reason for this is that the non-linear relations among processes concerning the light absorption, the photosynthesis and the gas exchange were observed consistently in all forest types.

As shown in Fig. 1., the threshold is common to PFTs, one that integrates to a large extent the clumping effect. The data of coniferous and broad-leaved forest are well mixed. There is no difference detectable.

In the anticipated revision we will address this problem by highlighting the fact that the underlying processes were shown to be independent of the forest types.

273-275 & 394-396: This result is relatively expected because if the LAI value increases, we expect an increase in biomass (linked to an increase in canopy photosynthesis) which leads to an increase in growth respiration, one of the two components of autotrophic respiration. Why not use the model to deeply analyse the differences in partitioning of the two components of autotrophic respiration (respiration due to the energy cost of tissue maintenance and respiration due to the cost of tissue construction during the growth phase) between sites and forest management to confirm the hypotheses proposed by the authors? Can the model support the hypotheses mentioned, particularly with regard to the non-linear relationships found with GPP, the distribution of NEE between GPP and Reco, and even the distribution of Reco between growth respiration and maintenance respiration?

The photosynthesis model used in LPJ-GUESS is based on Collatz et al. 1991 which is a simplification of the Farquhar et al. 1980 model and the carbon allocation model based on

Smith et al. 2001. It would indeed be interesting to disentangle the types of respiration through modeling, but in LPJ-GUESS, growth and maintenance respiration follow are expressed via a simple relationship, therefore this is not possible.

$$\text{Growth respiration} = 0.25 (\text{GPP} - \text{maintenance respiration})$$

Regarding the other aspects, we will add further insights on the modeled vs observed fluxes, see also our answer below.

417-418: Yes, a discussion on the uncertainty of the GPP estimate could be added, as well as for Reco values during the day (see also lines 304-305). The impact of the age of the stands selected for this study on the growth respiration rate in terms of the amount of living tissue (not total above-ground biomass) should be discussed. An increase in growth respiration could also be expected if there is a stand management practice such as pruning.

We acknowledge that these are interesting points that would allow to go deeper into the processes and feedbacks that stand beyond the responses that we observe in the experimental data. The partitioning into R_a and R_h bears additional uncertainties, which we cannot resolve with the existing data. This is future research, maybe not possible on all sites, depending the on the availability of parameters.

420-421: Why didn't the authors try to validate the model's predictions of NEE, GPP and Reco on these two sites? Once this had been done, the model could have been used to validate the hypothesis of an equilibrium LAI and to confirm the threshold value of $4.5 \text{ m}^2/\text{m}^2$, and to test the impact of a change in the clumping index due to forest management.

This is a reasonable point. However, the problem is that LPJ-GUESS is not designed to perfectly capture highly site-specific properties. We aligned the simulations in this study with the observations to get model results also for the various climates, soils, and species types. Capturing the exact details of a site, including exact age distributions, and management impacts, would require detailed data for the sites that are not available and even then probably not capture the exact properties of the sites. We used the model here to show the non-linear response of GPP to LAI.

In fact, the default management scheme in LPJ-GUESS is based on executing thinning when LAI gets above a threshold, therefore this cannot be used for this experiment.

Nevertheless, we will add further validation of the model (see also our answer below) and try again whether we can include more model results to back the claim for management as well.

Fig 1: The GPP/LAI relationship is difficult to interpret due to the high variability of GPP values (e.g. for managed conifer/mixed). No point corresponds to the case of managed broadleaves (mentioned in the legend). For the Reco/LAI relationship, it would be interesting to indicate the uncertainties on the graph in the same way as for the GPP/LAI relationship.

The managed broadleaved sites are present in the figure (filled diamonds). There are 5 such sites in our analyses. We will improve the readability of the figures for the revision.

The imbalance in the sites (managed/unmanaged, conifer/broadleaved) is an important current issue. The modelling intends to bridge the gap. It largely confirms that the relationship observed would hold in many other situations. Uncertainties are indeed quite large in fluxes.

Also, proper management operates near the self-thinning line (Luyssaert et al., 2011, see above). Therefore, the mixture of sites strengthens our argument, that a fraction of growth can be harvested without significantly impacting the fluxes.

In the anticipated revision we will carefully check that this point is made clear.

Fig 3: as for figure 1, it would be interesting to identify coniferous sites from broadleaves sites.

Certainly, this is a good point and one that is totally feasible.

Fig 4: Why not show the measured NEE in addition to the simulated NEE?

Thank you for this suggestion! The reason was that we plotted the LAI and Fluxes of all age cohorts that were simulated by the model, leading to one dot per age cohort. For this, no measurement data is available, only for the entire site. Our plot shows the LAI-GPP relationship of cohorts of various ages and thus LAI, while all other factors (e.g., climate and CO₂) are equal, since they are simulated at the same site for the same year (we will make this more specific in the figure caption).

However, we can compare the total fluxes with the modeled total fluxes and add these to the plots. Below is a simple example showing two additional plotted points for observed and modeled total LAI and GPP (we will then come up with a more detailed plot regarding uncertainties and so on, this is just as an indication).

