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

This contribution is an important one, in that it provides a functional insight into a long- attested empirical demographic relationship relating plant/tree population density and yield. In spite of its robustness, this fundament of yield science and silviculture (being able to extract trees from a forest without sacrificing total yield, and increase growth of remaining trees in a process that fastens the acquisition of size, thus preserving its long-term sustainability)
remains poorly perceived by ecologists and the general public, causing ill-posed debates in forest sustainability. For this reason, being able to support it by functional process-based grounding is major. This is an originality of the contribution.

Thanks for your general conclusion. This is exactly why we wrote this paper, and we are happy to make any changes that makes this paper stronger. Indeed, the public has bin indoctrinated that harvest is bad. We did not speak this out, but our paper intends to give a functional basis for harvest that has been overlooked in the past: the role of leaf area.

That said, we also wish to share some matter of concern regarding specific aspects of the contribution, in order to give it the broadened perspective it deserves.

1. Constant final yield

One first aspect is the apparent disconnection there is, between this "modern" approach relating C fluxes and NEP from the EC methodology, and the bunch of historical work performed in forestry science to relate yield (ANPP) to stand density, also in agronomy science. The same saturation has been described as "law of final constant yield", "Langsaeter's plateau", the "thinning response hypothesis". Major texts include Yoda et al 1963, Assmann 1970, Pretzsch 2009, but also and more recently the nice synthesis by Weiner and Freckleton 2010 (named "constant final yield").

- ★ Reference to these texts and concepts would allow better connect these findings to a long-established reality.

We thank you for this suggestion. Our manuscript already contains many references, more than 70. But we indeed could make more reference to existing forestry literature. You are totally right, that we are talking about the same "rules" of management, and confirm "old" knowledge with process-based parameters.

If we are allowed to submit a revision, we will extend the text accordingly.

This also raises an issue. The following conclusive statement: This threshold can be used to define sustainable metrics for sustainable harvesting, as those that do not impact the carbon sink strength of the forest stand questions how it can be achieved. When this plateau was established in terms of ANPP = f (stand density), at least direct targets could be formulated

for the prescription of silvicultural regimes. Yet, how may a forest manager easily pilot a LAI target?

- Here, I wonder whether plot density data are available, and to what extent the correlation between LAI and stand density (say BA, or N) would allow capture/confirm the alleged LAI threshold invariant identified, and may pave the way toward these metrics. I would rather incline toward acknowledging the merit of this transposition of initial stand density / yield relationship to LAI / photosynthetic C fixation to ground the previous relationships, and deliver the message that forestry science is justified to do so. Perhaps the aspect may be expanded both in the introduction and discussion.

Thanks for this suggestion. To our knowledge the stand density data are not available as auxiliary data at the moment. Further, the relationship between LAI and stem density is weak or even inexistant:

https://infodoc.agroparistech.fr/index.php?lvl=notice_display&id=95892

For the time being, we only could make the point that future research is needed to translate LAI into a forestry scale. Even though it is not quantitative, forest managers know, if a stand is getting too dense. In this paper it is our aim, to give a functional reason to this empirical knowledge.

2. Tree species diversity and species traits

As written, the paper gives an impression that finding the threshold is so motivating that the issue of variability is a bit discarded. At L277-279, it is even suggested that cross-species variation may be minor, but no reference is suggested for this aspect. By contrast, I would be of the primary opinion that the shade-tolerance of tree species may influence that potential threshold, light-demanding species meeting an earlier LAI threshold than others. This would be consistent with the notion of clear-forest silviculture as envisioned in the 19th century for the management of light-demanding species (e. g. pines, oaks).

- May it be useful to discuss the invariance of this LAI threshold in view of species traits? How far can we go? What may be the implications in terms of experimental designs based on current tower flux facilities? Is it an issue for a near future, or currently out of reach? This discussion would be welcome in the discussion.

We suggest that we extend the text and cite Luyssaert et al (2011) who showed that proper management operates very close to the self-thinning line, independent of tree species. The self-thinning line operates along different stand densities. Thus, this would be a way to translate our “theoretical” paper into forestry operations.

The variability of the threshold, for instance depending on the dominant species and biophysical parameters is largely unknown. We could not go any further with the current data. The uncertainty around the values of that threshold, and its variability, need to be addressed before it can be used as a management tool.

Further, may the design structure of EC sites allow to explore, at least a bit, the issue, e. g. by ranging sites according to some community weighted mean of the shade-tolerance trait (TRY) and see whether it correlates to some parameter related to the fit of the non-linear responses to LAI? I have this impression that a prescriptive unique threshold value should be avoided.

- Is it possible, or prohibitive, to explore a quick statistical relationship between the position of the threshold and a community weighted-mean of shade tolerance?

Thank you for this comment. We tried to use the TRY-database, but did not come to a useful result. The problem is, that, with stand growth, we operate at different stand densities. The "beauty" of using eddy-fluxes is, that it integrates over the whole canopy.

We suggest, that if we are allowed to submit a revision, we will make this point clearer.

3. The role of excess LAI

In the discussion, the adaptive significance of "excess LAI" is discussed, which suggests that excess LAI may serve the purpose of better tree resilience to abiotic or biotic disturbances. If so, while saturation is good news for the C storage, it is not necessarily the same for other functions related to resilience, in the present environment. Since it is indicated that some monitoring plots experience heat/drought or other disturbances over the period, may this be tested, or is it out of reach?

- I am uncertain about whether this test may be easy. At least, a better balance of the corresponding paragraph, and the trade-off it may induce in a silvicultural approach, is welcome.

Thank for this comment. We only discuss the role of excess LAI. To our experience it has a role only in competition. It has a cost of putting these leaves into position and to maintain them with water and nutrients. Thus, we do not think that they contribute to resilience. Management basically replaces natural competition. Unwanted competitors are taken out, favoring the target species/individual.

4. Methodological aspects

In general, it is quite hard to grasp the monitoring period under study, precisely. And also to compare it to management events, in order to perhaps question the ranking of managed/unmanaged plots. It may seem worrisome that only 11/19 plots classified as "managed" did not show any management event over the monitoring period in view of the rapidity of LAI reconstitution in general.

- May this have contributed to dampen the difference between managed / non-managed forests? Shouldn't this be discussed a bit (and if possible, tested? And if untested, what would be the perspectives ?)

To our feeling there is some bias, because it is cumbersome to harvest next to the tower. Timo Vesala, Finland, can tell stories about hand-carried timber. Thus, in managed forests there is the tendency by managers not to come next to this monitoring tower.

Thus, we are not surprised that the majority of tower sites remained untouched, even though the forest remains a managed structure. Maybe flux net has to move towers periodically, as we suggested in our paper published in Annals of Forest Science (Schulze et al, 2022: https://infodoc.agroparistech.fr/index.php?lvl=notice_display&id=95892). If we are allowed to submit a revision, we will clarify this point.

It was also very difficult to me to understand whether GPP/NEP data come from field plot measurement, or from LPJ-guess, and also what specific role does the model indeed play.

- I have this impression that the modelling objective may be specified more clearly in

the dedicated section, and early in the introduction. E. g., is it because it is feared that the integration scale difference between plot and EC towers may have a role?

All our data come from field measurements. We used the model only to show that the field observations can be reproduced by modelling and to compensate the imbalance in managed/unmanaged or forest types (conifer/broadleaved/mixed). This is important to show that we did understand the main processes.

Your concern is well taken. We must make clear that the datapoints are measured data.

5. Local detailed comments

Line 78-79: Bontemps 2021 (Plos) does not suggest any saturation of the carbon stock in European forests.

At stand level there exists a limit, the increase in stock is not indefinite. Trees must make a new tree-ring in order to survive. But the risk of failure increases with volume and canopy height. This is why even protected stands eventually level off (Nagel et al 2023). If we are allowed to submit a revision, we will clarify this point.

Line 95-98: the saturation of forest productivity with stand density has been a cornerstone of silviculture since the elaboration of the scientific principles of forest management. It is a bit frustrating it is not mentioned a bit more in-depth, a law known as the thinning response hypothesis, Langsaetter's law, and more generally in agricultural yield science, as the law of final constant yield.

We agree that our paper should make a better link to earlier observations, where the law of final constant yield is a key observation, and our observations and modelling results are very well in line with this law. If we are allowed to submit a revision, we will clarify this point.

In particular, Saturating response of photosynthesis to increasing leaf area index allows selective harvest of trees without affecting forest productivity may be rephrased as Saturating response of forest ANPP to increasing stand density allows selective harvest of trees without affecting forest productivity.

Line 122: why it would have impact on CO_2 assimilation is less clear.

We cited Monsi and Saeki. We will try to edit this part to make it more clear

Line 128: and certainly also, across tree species, given that their sensibility to light (shade-tolerance) may have a contrasted effect on a unique LAI threshold.

We guess, there is a limitation to deal with shade tolerance in our paper, because the eddy-flux measurement derives a bulk flux of the whole canopy.

We will refer to Luyssaert et al. (2011) where the main observation was that proper management is close to the self-thinning line

Line 133-135: In particular, the interactions between management and LAI, and their consequences for the carbon sink strength need to be determined in order to examine the consequences of wood harvesting on forests carbon sink strength.

This is exactly the focus of our paper, and we believe that the importance of LAI in the relation between management and carbon sink strength needed to be brought back into discussions.

+ line 138-140: explore the possibilities of defining levels of sustainable partial cuttings from the perspective of carbon 140 fluxes, key to designing forest managements strategies

But how in practice, can we transfer a target N trees / ha under management into a LAI reduction / ha, especially since selective thinning can be deployed for different strategies (thinning from above / below)?

Thinning from above and from below have the same target, namely to regulate biomass/ha, i.e. stem density. Which thinning method gets used is related to the anticipated wood use. In spruce, thinning from above provides a large stem volume based on the assumption that thin stems can resume growth.

In beech, the early thinning is also from above, taking away stems with multiple branches (low quality wood) and later we support the dominant stem for higher growth.

In both cases Luyssaert et al (2011) showed that proper management operates close to self-thinning. Here we show that the distance to self-thinning may be the extra leaf area that can be taken out without harm.

Nevertheless, as stated at an earlier comment, there may not be any relation between stem density and LAI.

Line 154-155: what is the monitoring period exactly? Is it 2000-2020 as suggested by LAI measurements? If so, one may wonder about the significance of being classified as managed forests for those 8 study sites out of 19 that were matter of no harvesting over the period.

In our Annals-Paper (Schulze et al., 2022 op. cit.) we show how management "jumps" across the property. Thus, it is possible, especially in older stands, that no harvest takes place in a given 20 yr period, e.g. in oak, and if there is a measuring tower (see above).

Line 164-166: were these MODIS-based estimates compared against measurements for those sites where site measurements for LAI do exist?

Yes, the values are presented in the supplementary table 1. As a regrettable limitation to this comparison, the LAI values do not correspond to the same year or period in time. This is one of the reasons why we advocate for more consistent and frequent measurements throughout the network.

Line 168-173: in addition, may it be possible to specify a bit across which spatial range do the flux measurements integrate and to what extent there are representative of fluxes within the perimeter of the study sites?

The actual footprint of eddy covariance towers remains difficult to determine, but are in the order of 1 km^2 (see Aubinet, 2012). We are not aware of any publication that would present in a standard way the current estimation of the footprints.

Line 183-185: then if GPP and Reco are gaussian, why the difference = NEE would not be so? Are their discrepancies to be expected in this budget?

> GPP and Reco are not calculated from eddy covariance recordings the same way. They both involve several steps which are only partially independent. Both compensation and amplification may occur.

L 203: but also suppressed trees, with varying LAI

> Your point is well taken, but we are afraid we cannot deal with all aspects of the "real world" of forest management. For example, in broadleaved stands we leave suppressed trees, because they do not harm, and shade the trunk of the dominant target tree, and it would cost work-time to cut them down without any use.
>
> Obviously, a technical paper is needed to relate the findings of this study to forest management

Line 209-210: then how can it be that measured fluxes are representative of forest plot dynamic?

> Indeed, the flux network replaces time by space. In the study of Luyssaert et al (2021) about old-growth forests it was made visible how fluxes explain stand dynamics. We will refer to this study.

Line 218: on monitoring plots, wasn't it possible to more directly measure tree-driven GPP, or at least compare?

> Some stations measure GPP with chambers as well, but these data were not continuous and not available for all sites. The amount of work involved is probably discouraging, given that multiple trees would need to be monitored in order to obtain reliable per-area figures.

Line 145-246: at this point, the issue of variability across tree species turns an issue. What are the species covered in the 30 monitoring plots? How do they match the PFT of LPJ-guess? To what extent there is a risk to remove this variability?

> The list of the dominant species can be found in the site description, and is described in the supplementary table. It is probably not so much the variability of species that creates issues in detecting management effects on carbon fluxes, than the fact that the replication is very low, and that the current data are not balanced in regard to the PFTs. We acknowledge this in the manuscript and advocate for a more balanced sampling of the PFTs and a better representation of management.

L253-254: can it be specified whether the management operations described on the monitoring plots were introduced into LPJ-guess? Or else?

> Management operations did not occur on all plots. The objective of the modelling was not to reproduce these operations, which would require a lot of parametrization work. This could be the object of a further study.

L262-263: I would say this (should) has(ve) been the main concern of silviculture since its foundation!

Indeed, but on a volume/ha basis, and not explained by fluxes. We will make this link if we are allowed to submit a revision.

L299: finally, what is the monitoring period for the study? 10 years? 20 years? Else?

Please refer to the Supp table 1.

Fig1a: full red squares not specified. Further, only clear footprint of a saturation given by open red squares.

Sorry that our figure caption was not complete. In a revised paper we will take care of this.

L324: A bit puzzling that the 1st paragraph seeks to establish this result and ground it in the recent literature, with no reference at all to the classical forestry literature. Could this be a little bit better balanced, for the sake of enlarging the audience?

We like to thank for this comment. See above, we will make this link in a revision

L335-339: how may this be evaluated properly? Are there any data possibilities available to support the issue?

Yes, it could happen in future, if harvest was recognized by the micro-met people. We addressed this in Forest Ecosystems (Schulze et al., 2021)

L377-379: yet what allows to justify this statement? It may be conversely expected that the saturation point is reached at lower LAI for light-demanding tree species, in line with the clear forest management strategy. Not?

We agree, the link to species traits and overall behavior needs to be established. At the moment we believe that the data available is insufficient for such objective. We are left to hypotheses, but this one seems quite reasonable.

L399-401: and also, this has been observed in empirical studies of forest yield, whereby an optimum, instead of a plateau, has also been detected.

The empirical studies of yield suggest an optimum in relation to the stem density or the standing biomass. It is unclear if this would necessarily translate into an optimum in relation to LAI because LAI is not related to either stem density or standing biomass. It could be hypothesized however that, in some particular situations, a response to LAI would display an optimum instead of a plateau.

I am a bit puzzled with two conclusions:

Above its saturation value of ~ 4 m2 m-2, additional increases in LAI are not linked to increased productivity, but may contribute to other functions selected in evolution, such as competition with adjacent trees, resource storage and buffering against herbivory

Then, should this additional LAI have adaptive functions, some of these being adaptations to biotic or abiotic pressure of the environment, should we understand that – while decreasing LAI may be of minor impact on the strength of the C sink – it may impact stand/tree resilience to abiotic/biotic disturbances. Isn't it important as well? Shouldn't it be discussed?

We suggested that a fraction of the leaf area is not contributing to increasing the productivity and that it may serve other functions. We agree that the resistance to pathogens (i.e., having spare leaves) could be one such function.

This threshold can be used to define sustainable metrics for sustainable harvesting, as 448 those that do not impact the carbon sink strength of the forest stand. And how? When this plateau was established in terms of ANPP = f (stand density), at least direct targets could be formulated for the prescription of silvicultural regimes. Yet, how may a forest manager easily pilot a LAI target?

Probably, this is future research. These days a forest manager can get satellite LAI from public data, but this was never been suggested that foresters observe LAI.

In a more technical oriented paper, we could address all the suggested concerns of "real" forest management

Jean-Daniel Bontemps, Laboratory of forest inventory, Nancy, France, 23rd January 2025

Statement of conflicts of interest

The author declares to maintain a recurrent professional relationship with the first author of this paper. Due to its interest in forest dynamics (demographic, not functional), he first volunteered a few remarks about the paper, which the first author considered worth of interest to be posted publicly in the discussion of this paper.

Scientific discussions are always welcome and often lead to valuable insights. We truly appreciated the constructive exchange of ideas, which helped refine certain aspects of this work by highlighting key findings as well as remaining questions and caveats. We hope these discussions and debates will be useful for future research.