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

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Key Points:

- In temperate forests, net CO_2 uptake remains constant after partial harvesting.
- The relation between Gross primary production (GPP) and leaf area index (LAI) shows saturation above 4.5 m^2 m^{-2}.
- Harvest-related reduction of leaf area thus has little effects on the uptake if LAI remains above the threshold.

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Abstract

Maintaining or increasing forest carbon sinks is considered essential to mitigate the rise of atmospheric CO_2 concentrations. In contrast, harvesting trees is perceived as having negative consequences on both the standing biomass stocks and the carbon sink strength. However, the forest carbon sink needs to be examined from a forest stand canopy perspective since carbon assimilation occurs in the canopy. Here we show that a threshold of leaf area exists beyond which additional leaves do not contribute to CO_2 uptake. The associated biomass can be harvested without affecting the forest carbon uptake. Based on eddy covariance measurements we show that CO_2 uptake (GPP) and net ecosystem exchange (NEE) in temperate forests are of similar magnitude in both unmanaged and sustainably managed forests, in the order of 1500-1600 gC m^{-2} y^{-1} for GPP and 542 – 483 gC m^{-2} y^{-1} for NEE. A threshold located between 3 and 4.5 m^2 m^{-2} LAI (leaf area index) can be used as a threshold of sustainable harvesting with regard to CO_2 uptake. Simulations based on the LPJ-GUESS model reproduce the saturation of GPP and NEP and convergence on the LAI threshold range. Accordingly, in temperate managed forests, trees can be harvested while maintaining a high tree biomass and carbon sink of the remaining stand. In this case, competition between neighbor trees in unmanaged forests is replaced by harvest management and provision of wood products. No difference in the LAI productivity response was observed between managed and unmanaged sites.

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Introduction

At times of increasing global change and a demand for wood to replace fossil fuel products, it becomes of eminent importance to know the role of forest management and wood harvest in mitigating climate change. Following the EU definitions on storage and uptake respectively (EU 2018), two major ways exist by which forests may contribute to the efforts of climate mitigation: the storage of biomass on site within the forest ecosystem and the storage of wood in products or their use for substitution of fossil-fuel or carbon-intensive materials (Gregor et al., 2024). It is generally assumed that storage and C stocks can be sustained or increased only by increasing the area of forests, or by stopping wood procurement from forests (no management). However, halting management will probably have little long-term effects on the forest carbon sink and stocks at landscape level, considering the environmental risks associated with climate change that strongly increase the chances of stand collapse (Roebroek et al., 2023). This is supported by Pretzsch et al. (2023), who observed that self-thinning losses could be equivalent to wood extraction by management. Luyssaert et al. 2011 also show that management keeps forest stands close but below self-thinning, albeit at different stand density and volume. Besides ensuring a sustained carbon sink, harvesting wood products can substitute carbon-intensive materials and the energy use of wood residues and end-of-life wood products can substitute energy from fossil fuels (Cowie et al., 2021; Schulze et al., 2022). Thus, understanding the consequences of selective harvesting on the carbon balance and sink strength of forests is a key element to future projections on the role of forests to climate change mitigation.

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Previous studies showed that forest productivity was not necessarily affected by selective harvesting (including various forms of thinning) across a large range of cutting intensities (Skovsgaard 2009, Amiro et al., 2010; Peters et al., 2013; Bond-Lamberty et al., 2015; Noormets et al., 2015). Forestry studies such Assmann (1970) likewise evidenced the fact controlled thinnings have no long-term negative effects on productivity and could even increase it. The mechanisms involved in explaining the resilience of productivity to management are based on the enhanced productivity of the remaining trees. Reasons for this are, for example, improved light conditions, nutrient and water supply and overall light use (Mund et al., 2010; Saunders et al., 2012; Sohn et al., 2016; del Campo et al., 2022). Compensatory contribution of subcanopy individuals can locally also be observed (Vesala et al., 2015). Several such factors and interaction pathways have been identified (e.g., Noormets et al., 2015, Fig. 1) but canopy density, as quantified by leaf area index (LAI, the cumulated area of leaves per ground square meter, expressed in m^2 m^{-2}) was not taken into consideration despite its key role in CO_2 uptake.

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Here, we introduce the link between photosynthesis and leaf area as a key element in this regulation at stand level. We hypothesize that LAI is not only the link between the atmosphere and the plant, but is also central to the response to management. LAI is indeed largely seen as a driver of both water and carbon fluxes (Reich, 2012; del Campo et al., 2022). Given its high nutrient demand the production of leaves also affect the nutrient cycle (Ollinger et al., 2008) and is a potentially crucial driver of forests response to harvesting.

Harvesting inevitably results in a reduction of the amount of canopy leaves, best quantified by LAI. It can be assumed that a reduction of LAI would lead to a decrease in productivity. However, there are indications of a saturation of several canopy processes resulting in a non-linear relation between leaf area index at stand level (Soimakallio et al., 2021) that make the response of productivity to disturbances complex (Glatthorn et al., 2017; Stuart-Haëntjens et al., 2015). Given the exponential light extinction with canopy depth, as described by Monsi and Saieki 1953 (see Hirose 2005), a rise in LAI must have diminishing returns in terms of light capture and CO_2 assimilation. Concerning canopy conductance, Schulze et al 1994 concluded to a saturation of around 3.5 m^2 m^{-2}. These elements suggest that productivity could also have a non-linear response to reductions of LAI, and hence to management, while examined at stand level. Regardless of the mechanisms, however, the effects appear beyond a yet unknown level of biomass removal. A comparison across temperate forests beyond the site-level analyses is lacking.

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The impact of harvest on the C cycle is clearly of major importance in the public debate. It is thus necessary to determine the impact of harvesting on the fluxes of carbon in forests based on experimental data over a large gradient, and to discuss the limits in the context of leaf area reduction. 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. Here we intend to show that sustainable management replaces natural competition by regulating leaf area without affecting ecosystem fluxes in temperate forests. Based on observational data, literature and modeling we want to identify mechanistic reasons for this presumption and explore the possibilities of defining levels of sustainable partial cuttings from the perspective of carbon fluxes, key to designing forest managements strategies able to maintain high biomass as well as forest C uptake over multiple cutting cycles. We use the model LPJ-GUESS to illustrate the diminishing returns of GPP with increasing LAI in models as well.

Materials and methods

Observational flux data based on eddy covariance measurements on the FLUXNET sites.

Overall FLUXNET represents 212 sites worldwide of eddy covariance. In order to measure the impact of management over the carbon fluxes, we have compiled flux data from the 29 FLUXNET sites (https://fluxnet.org/data/fluxnet2015-dataset/) that comprise 19 managed and 10 unmanaged sites (unmanaged is used in the sense of “intact” forests of Roebroek et al., 2023) with long-term measurements in temperate forests (**Supp. Table S1**). Unfortunately, there is no site that covers unmanaged conifers. For each site we have compiled the forest type, stand type, and the fluxes over their monitoring period. We completed these data with estimations of the LAI during the period 2000-2020 and of the standing biomass. Noticeably, selective harvesting took place on 11 of the managed sites during the period of flux monitoring, several interventions being quite intensive (Supp. Table S3): for instance, 36% LAI removal in Fontainebleau site (FR), 30% removal in Bily Kriz site (CZ). Other managed sites have experienced interventions prior to the monitoring but not necessarily during the monitoring period, given the long periods of time separating interventions. Furthermore, during the period of flux monitoring, forests experienced repeated events of storm, drought and heat such as that of 2003, affecting ecosystem fluxes independent of management.

Further, we have compiled LAI estimations for the analyses, for each of the FLUXNET sites. LAI measurements, however, are not standard across sites, and field measurements are not always available (5 sites had no field measurements). In this situation remote-sensed estimations were used instead based on the MCD15A3H version 6.1 MODIS data level 4 (see **Supplementary Table S1**, with references for each estimation). Field-based measurements were based on hemispherical images with site-specific clumping factors (Gielen et al. 2018).

The eddy covariance method does not directly measure CO_2 fluxes but instead records high-frequency atmospheric CO_2 concentrations and wind speed fluctuations. These measurements are then used to compute net ecosystem exchange (NEE) with inherent uncertainties due to instrument limitations, atmospheric conditions, and data processing methods. Flux data were filtered based on USTAR threshold levels, following the method described by Pastorello et al. (2020), to exclude measurements taken under low turbulence conditions. Errors have been estimated using bootstrapping 200 times with different friction velocity values. The fluxes of carbon exchanged between the forest ecosystem and the atmosphere are generally divided into components that are physiologically meaningful: the gross primary

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production (GPP) corresponds to the photosynthesis of plants, and the ecosystem respiration (Reco) releasing CO_2. Reco consists of plant respiration (so-called autotrophic respiration) and respiration by heterotrophic organisms (so-called heterotrophic respiration). The NEE can be estimated by eddy covariance, partitioning into the other elementary fluxes follows data-driven models (Valentini et al., 2002).

We compared the mean fluxes during the period of time available of managed and unmanaged sites. For testing the significance of differences in NEE we used the Wilcoxon rank test because data were not distributed normally. GPP and Reco have a distribution that does not differ significantly from a normal distribution. The Mann-Whitney test has been implemented to compare managed versus unmanaged sites which works with unequal sample sizes. For GPP and Reco, their distributions being normal, but their variances unequal, the Welch t-test was used instead. Subsequently, two-way analysis of variance for unbalanced designs was performed on the data to check if the interaction between the management and the number of observations by FLUXNET site has a significant effect on GPP, Reco, and NEE.

The relationship between GPP and LAI for the FLUXNET observational site was represented as a nonlinear asymptotical model. The fitting was based on the nonlinear fit function *nls* (nls standing for nonlinear least square) in R. The pseudo-R^2 represents the proportion of variance that was explained by the model, in lieu of the R^2 which assumptions cannot be completely satisfied with nonlinear models (Schabenberger and Pierce 2002). It was computed as $pseudo\text{-}R^2 = 1 - (\mathrm{var}(y_{fit})/\mathrm{var}(y))$, where $\mathrm{var}(y_{fit})$ is the variance of the predicted value (GPP here), while $\mathrm{var}(y)$ is the variance of the variable (GPP) within the dataset. All statistical analyses were performed in R version 4.3.2 (R Core Team, 2023).

Harvesting and carbon fluxes

Harvesting takes many forms in forest management and can have different intensities. Harvesting is defined in a general way as the removal of wood by tree cuttings of any kind, thus including tending, thinning (targeting either dominant or sub-dominant trees) and selective cuttings from either status. While short- and medium-term effects of selective harvesting are being considered, this study will not cover the comparison of forest products with other bioenergy sources (product and energy substitution). In the following, clear-cutting, or final felling of a rotation, are treated separately from selective cuttings as they need an assessment at landscape or management unit-scale. The measurement of carbon fluxes using the EC method is limited to a plot-scale, with a footprint commonly of about 1 km^2. Throughout this study, harvesting refers to practices of selective harvesting at low to moderate intensity as common in temperate forests. For example, removal of harvest residuals is widely seen as negative because of the nutrient and soil carbon depletion it causes (Achat et al., 2015, Mayer et al., 2020).

Modelling analysis of the impact of an increasing LAI gradient on CO_2 fluxes exchanged, using the process-based model.

To investigate the impact of LAI on GPP, we used the dynamic global vegetation model LPJ-GUESS v4.1.1 (Smith et al., 2014, Nord, 2021) to simulate the main carbon fluxes (GPP, Reco and NEP) on all the eddy-covariance sites used in the study. The ability of LPJ-GUESS to estimate LAI and GPP values worldwide has been proven in numerous studies (e.g., Vella et al. 2023 and Ito et al. 2017, see also Fig. SF2). Therefore, the model is well suited for the analyses. LPJ-GUESS simulates detailed vegetation structure (including cohorts of various ages) based on mechanistic modeling of ecosystem processes including photosynthesis, establishment, growth, allocation, competition, water and nutrient limitation, and mortality of plant functional types (PFTs). The latter are represented by parameters defining plant characteristics such as bioclimatic limits, growth form, or shade-tolerance.

In the model, at the end of each year, cumulative net primary productivity is distributed among the leaf, root, sapwood and heartwood compartments of a plant, based on allometric equations and allocation routines per year (Smith et al., 2014). The model belongs to the big leaf family, representing the canopy as a single layer. This modelling is compatible with the spatial of the study: the footprint of eddy covariance being typically in order of 100 ha. LAI is calculated as the product of the carbon mass of the leaves times the specific leaf area, the specific leaf area being a PFT parameter. LAI is computed proportionally to the phenology fraction of the PFTs, that is, the fraction of potential leaf cover. The phenology of a PFT can be raingreen, summergreen or evergreen. LAI is also influenced by the phenology: depending on the environmental conditions, the phenology fraction can depend on growing degree days and drought stress related model states. The amount of light taken up by the canopy, and thus contributing to carbon allocation, is governed by LAI, based on the Lambert-beer law (Prentice et al, 1993) assuming a site-specific surface leaf mass ratio not varying within the canopy. The model outputs stand level LAI, taking into account the number of trees per area and the crown areas of the various cohorts. 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). Photosynthesis and respiration are calculated daily and accumulated towards the end of a year, allowing to represent seasonal dynamics.

For the LAI analysis, we ran LPJ-GUESS until 2015 using daily climate data from the FLUXNET2015 sites, i.e., precipitation, temperature, and shortwave radiation. For each site, we prescribed the forest type as described in Table S2. We used 1000 years for the spinup period (to bring soil pools close to equilibrium) by detrending and recycling the first 10 years of each site's climate data. CO_2 concentrations were taken from (Büchner and Reyer, 2022). We used the default global parametrization of LPJ-GUESS with global PFTs, without any form of management.

Stochastic disturbance intervals were kept at default values while fire was not simulated.

Results

Saturated response of fluxes to LAI

Regular management actions were performed in most of the managed sites during the monitoring period with removals as high as 30% of the stems for some sites during the monitoring period (**Sup. Table 3**). Managed sites are mostly age-selection (forests stands composed of trees of similar age, obtained from harvesting trees at a prescribed age), natural regeneration and plantations. In the whole flux network, there is only one pair of managed and unmanaged sites: DE-Hai (Hainich, unmanaged) and DE-Lnf (Leinefelde, managed) representing *Fagus sylvatica* (L.) stands with similar stand densities or basal area.

The data from the FLUXNET sites show a response of GPP to LAI only for LAI values less than ~4 m^2 m^{-2} (**Fig. 1**) but the GPP does not increase at higher LAI. It is interesting to note that most managed forests operate above the range of saturating LAI with a mean of 4.74 ± 1.33 m^2 m^{-2}, despite harvesting. Likewise, the data shows a saturation of GPP even in managed sites, with values reaching a plateau in the order of 1770 gC m^{-2} year^{-1} at LAI values as low as 2 m^2 m^{-2}. Based on the GPP-LAI regression, 95% of GPP (1680 gC m^{-2} year^{-1}) is reached at LAI of 2.7 to 4.0 m^2 m^{-2} depending on the forest type. The exact location of the LAI saturation point can only be approximated given the uncertainty in both LAI and C flux data, which is larger in LAI than in fluxes (**Fig. 1** and **Sup Table 1**). The site at Parco Ticino Forest (Italy) has been fertilized. It indicates the importance of nutrition in forest ecosystems as a GPP value above 1800 gC m^2 y^{-1} was reached at low LAI (< 2 m^2 m^{-2}). However, even with fertilization, the fluxes and LAI values remain in the range of other sites. Reco had a smaller overall variability than GPP (1082 ± 151 gC m^2 y^{-1}) and showed no response to LAI. Likewise, there was no response to forest types. The net ecosystem exchange (the balance between photosynthesis and respiration, GPP – Reco = NEP) did not show any significant response to LAI, with values largely scattered around the mean (343 ± 151 gC m^{-2} year^{-1}).

The data represent a mixture of remotely-sensed and field-based LAI for different forest types. Given the large variability among sites, differences in fluxes for managed and unmanaged forests in **Figure 1** are not significant (**Table 1**).

It is notable that under management LAI was similar to that of unmanaged stands (4.74 ± 1.33 for managed sites versus 4.40 ± 0.82 m^2 m^{-2} for unmanaged sites, n.s.), despite the removal of parts of the canopy due to management in the past (**Fig. 2**). LAI was indeed strongly reduced during the monitoring period by thinnings ranging from 26 to 36% in four of the managed sites (**Sup Table 3**). For instance, the low (3.6 m^2 m^{-2}) LAI value at site CS-BK1 (*Picea abies* L.) reflects the 26% removal that occurred at the end of the monitoring period. The dynamic of LAI on the sites show that the reduction of the LAI by harvesting is limited to a few years following the harvesting (**Sup Fig. 1**).

Responses of fluxes to sustainable harvesting: empirical evidence from eddy covariance

The FLUXNET associated site data showed that past and current management has little influence on the aboveground biomass and LAI of the sites (**Fig. 2**). Highest biomass was reached with the old-growth *Eucalyptus regnans* (F. Muell.) site in Australia (Wallaby Creek site, with 36,106 g dry matter m^{-2}). Unfortunately, there is no managed site of *E. regnans* for

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comparison. Otherwise, the range of values is very similar among managed and unmanaged sites.

The comparison of the fluxes reveals that the net ecosystem exchange (the balance between photosynthesis and respiration) was not significantly different in managed and unmanaged sites (-542 ± 219 gC m^{-2} $year^{-1}$ for managed sites against -483 ± 306 gC m^{-2} $year^{-1}$, mean ± sd for unmanaged sites) over an observation period of more than a decade (**Table 2**). Management was not a significant effect for GPP or NEP. As shown in **Fig. 3**, Reco and GPP tended to be higher in managed sites (Reco: 1213 ± 121 gC m^{-2} $year^{-1}$ in managed sites versus 1079 ± 98 in unmanaged sites; GPP: 1715 ± 192 gC m^{-2} $year^{-1}$ in managed sites versus 1489 ± 183 gC m^{-2} $year^{-1}$). The paired DE-Hai and DE-Lnf unmanaged sites had very similar values of both GPP (1709 gC m^{-2} $year^{-1}$ in the managed site DE-Lnf vs. 1653 gC m^{-2} $year^{-1}$) and NEP (1189 vs 1155 gC m^{-2} $year^{-1}$). We investigated whether the forest type had any influence on the LAI or the fluxes, since conifers tend to have higher LAI values with few exceptions. A linear model was fitted to the data and showed no significant influence of management or forest type (**Table 2**). Interactions between forest type and management were not significant either.

Process based model simulations: sensitivity to LAI

We applied the LPJ-GUESS process-based dynamic vegetation-terrestrial ecosystem model to further investigate the relationship between LAI and GPP, Reco and NEP, on each of the FLUXNET sites. According to the simulations, within a given site, GPP increased with LAI, near linearly for LAI < 3 m^2 m^{-2}, showing a clear inflection around this value (**Fig. 4**) but with some variability among sites. The simulations illustrated the diminishing returns of large LAI (LAI > 4), whereby large cohorts with high LAI contributed most to the total GPP, due to the light extinction also represented in the model. Noticeably, the modelled LAI was always lower than the observed LAI, suggesting that the stands actually operate at LAI values in excess of the C-balance-optimal LAI. Reco followed a very similar pattern than GPP, albeit starting at higher values for very low LAI level and having a smaller increase with LAI than GPP. GPP and Reco curves cross each other at different LAI values (between 1 and 3 m^2 m^{-2}) depending on the sites, at which point NEP becomes positive but shows a strong saturation after with no response at all to LAI. Thus, across all sites and regardless of the forest types, NEP becomes positive (forest acts as a sink) for LAI in excess of 3 m^2 m^{-2} but, beyond 4.5 m^2 m^{-2}, increases in LAI do not result in increases in NEP.

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Discussion

With the introduction of the eddy covariance method, long time series of carbon fluxes became available over a variety of biomes, with most monitoring sites being under regular forest management (Franz et al., 2018). Based on these time series, our synthesis showed here that GPP and NEE remain largely unaffected by partial harvesting, as also reported by site-level analyses for several forest types and species (Granier et al., 2008; Launianen et al., 2022; Lindroth et al., 2018; Pilegaard et al., 2011; Peichl et al., 2022; Vesala et al., 2005). These results are in agreement with the long-established empirical knowledge that stand productivity remains unaffected by thinnings when their intensity remains below a threshold (expressed in terms of stem density or basal area) (Assmann 1970, Pretzsch and Schütze 2009). Similarly, Vesala et al., 2005 observed no visible effects of thinnings on the NEE despite the reduction of LAI from 8 to 6 m^2 m^{-2} in a Scots pine (*Pinus sylvestris* L.) stand. Granier et al. (2008) reported for *Fagus sylvatica* (L.) stands no decrease in either NEE or GPP despite the thinning that decreased LAI from 7.4 to 4.8 m^2 m^{-2}. These results are in agreement with Herbst et al. (2015) and are confirmed by the global database of Luyssaert et al. (2007) which shows that managed forests globally achieved similar, or even larger GPP, than unmanaged forests.

The harvest effect on LAI appears to be short-term in temperate forests (del Campo et al., 2022) as also suggested by the available LAI time-series of the sites studied here (**Supp. Fig. SF1**). For instance, according to Granier et al. (2008) LAI in *Fagus sylvatica* stands was restored to its pre-thinning level within two years. Disturbances, particularly stand-replacing disturbances such as windthrow, fire or clear-cuts have a different dimension and need to be evaluated at landscape scale. Our study deals with thinning operations where the main canopy is reduced but not removed, keeping LAI beyond or near to its saturation threshold. This also justifies the choice of focusing on temperate forests where the lower species richness and age ranges may slow the recovery of carbon uptake to catastrophic events, in contrast to tropical forests (Brando et al., 2019). For boreal forests, the IBFRA-Report (Högberg et al., 2021) shows that biomass increased significantly over the past decades only in intensively managed landscapes, but not in less intensively managed forest landscapes (i.e., landscapes with a high proportion of unmanaged forests). In the latter, large-scale disturbances such as wildfires caused losses of biomass and prevented a build-up of forest carbon stocks. In comparison, the biomass gain in non-managed temperate forests is very small (Roerbroek et al., 2023). Roerbroek et al. (2023) indeed suggests that betting on increasing the forests stocks is not only risky, given the increases in weather extremes, but loses the societal benefit of wood products as well as the potential to store a portion of the C over longer term.

We propose that most of the decoupling between selective harvesting and CO_2 fluxes is mediated by the intrinsically nonlinear response of the dominant processes to LAI with a saturation point reached at 3-4.5 m^2 m^{-2} but with uncertainties around this value. The threshold itself may show some variability, for instance related to plant functional types. The eddy covariance fluxes suggested a slightly higher relation between GPP and LAI than broadleaved (Fig. 1a). The model simulations likewise suggested varying level of saturations depending on the sites. Further studies could help locate this threshold more precisely, by increasing the number of observations and addressing the uncertainties, particularly those related to LAI estimates.
This nonlinear response, particularly the existence of a saturation point, is related to the existence of a fraction of the canopy leaf area not necessary for productivity but serving other functions such as competition, or redundancy in case of competition. In forest management it

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is known that about a third of the green foliaged tree crown can be pruned to improve stem quality without affecting growth (Burschel and Huss 2003). Diffuse light can penetrate deeper into the canopy and reach lower levels of leaves, but the gain in photosynthesis may not counterbalance the cost of producing and maintaining saturated canopies. The carbon balance of a living branch may be close to the light compensation point of photosynthesis and respiration (Schulze 1970), with a photosynthesis activity just at the level needed to keep a shaded branch alive. Similarly, in the simulations of the model LPJ-GUESS, small trees with low LAI operate at a higher level of light extinction due to shadowing by bigger trees, which leads to very low GPP as no direct sunlight can reach any leaves (Fig. 4). Shadowing also leads to a reduction in Reco, however a minimum maintenance respiration of the leaves is always needed to sustain functioning of the leaves.

While shade tolerance varies among species (Ameztegui et al., 2016), as reflected by different maximum LAI values (Valladares and Niinemets 2008), the threshold for light compensation is probably very similar across forest types or species despite variations in the canopy structure. Accordingly, in our study, the species traits did not show significant correlations to either LAI or flux values. This suggests that increasing LAI beyond a demand-driven threshold has other functions, for instance a competitive function with neighboring trees (Pretzsch and Schütze 2009, Jucker et al., 2014) not only for light but also for nutrients (e.g., in a pre-emption strategy, Craine and Dybzinski 2013), as a buffer against disturbance (e.g., herbivory) and a pool of nutrient reserves, ready for rapid re-allocation in case of sudden demand (Körner 2009). Anten (2005) shows that canopy photosynthesis models predict LAI values greater than optimal values for photosynthesis and quote theoretical studies that conclude to a LAI always exceeding the physiologically optimal value for competitive purposes. Avoiding a neighbor increases the resources of water and nutrients for the dominant tree. This surplus fraction is temporarily diminished by selective harvesting, explaining the lack of response of the main C fluxes at canopy level across a wide range of LAI. Accordingly, a moderated management can be seen as a substitution of self-thinning when forest stands are kept close but below self-thinning density levels (Luyssaert et al., 2011).

These non-linear relations of a variety of processes with LAI caused by a saturation of GPP and NEE at values around 3-4.5 $m^2\ m^{-2}$ (see ex. Asner et al., 2003; Hirose 2005) have long been known, although not previously related to the resilience to selective harvesting. This includes ecosystem respiration: according to Zhao et al. (2021), at high LAI, respiration - particularly heterotrophic respiration- increases faster than GPP, which results in a reduction of NPP for values larger than 5.6 $m^2\ m^{-2}$. In our analysis, the model did not go so far as to project a negative impact of LAI on NEP, but the high cost of producing and maintaining leaves and particularly shade leaves (Niinemets 2010), largely suggests this. A similar result was obtained using the model CASTANEA which reproduced the nonlinear responses of fluxes to LAI (Davi et al., 2006). In contrast, field measurements based on leaf collection, hemispherical photographs or light transmission through plants, frequently report values in excess of 5 $m^2\ m^{-2}$ (e.g., **Figure 3**) and even over 10 $m^2\ m^{-2}$ in shade-tolerant species

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(Schulze et al., 1994; Asner et al., 2003; Law et al., 2001; Iio and Ito, 2014). Out of the 29 sites we studied here (Fig. 1), 16 display LAI values in excess of 4.5 m^2 m^{-2}. Issues related to the leaf clumping, requiring a specific correction factor as specified by the eddy-site protocol (Gielen et al. 2018), add up to the already large uncertainties in the estimated LAI.

The lack of scaling between forest biomass and plant respiration (Piao et al., 2010) reflects the fact that the mass of live tissues -that is, of respiring tissues- is much smaller than that of total biomass, basically scaling to the parenchyma fraction in sapwood volume and small branches only (Thurner et al., 2019). The disturbance-related increase in soil respiration, for instance promoted by a short-term increase in root mortality (Raich and Nadelhoffer 1989), could be comparable in magnitude to the reduction in plant respiration due to the amount of sapwood harvested and the reduced influx of fresh litter (Davidson et al., 2002), and explain the invariance of Reco. Surveying or modelling respiration has proved to be particularly difficult (Phillips et al., 2017, Ciais et al., 2021) and results in uncertainties, which also impact confidence in GPP estimates that could hide some effects. The lack of response of Reco to LAI needs further investigations. Similarly, the in-depth analysis of the processes by which the C fluxes remain constant over a large range of LAI and the reason for the saturation based on the LPJ-GUESS model remains to be done. Simulating management could help bring explanations to these behaviors. The model LPJ-GUESS may not be the best suited model for such study though, because thinning induces many changes to the canopy structure and light condition, difficult to represent in a big-leaf model. Its carbon allocation is not daily but seasonal, which could also be a limitation to fine-scale analyses. Despite these limitations, the model reproduced the saturation and confirmed that the stands generally function at LAI values beyond exceeding this saturation point.

Unfortunately, the Hainich/Leinefelde *Fagus sylvatica* (L.) sites are the only paired sites of managed versus unmanaged sites within the flux network. The global eddy-flux network was indeed strongly focused on climate as a main driver of fluxes, rather than management. The management gradient represented by these sites is thus not complete, for instance the intensity and types of management actions are not controlled. Although the unmanaged conifer sites are currently not monitored, the NEP values for unmanaged conifer stands reported in synthesis studies (Luyssaert et al., 2007) do not suggest that unmanaged conifer stands would behave differently and have higher a NEP than managed ones. We nevertheless highlight the potential of such paired studies and hope that research on management will be more integrated in the future to improve our understanding of its short, medium and long-term impact on the carbon balance of forests. This imbalance and low replication contributed to the difficulties in locating the saturation threshold. We therefore also underline the lack of common and frequent reporting on the aboveground biomass and annual LAI on the FLUXNET sites, on harvested volumes whenever management interventions occur. Annual measurements of LAI and repeated study after disturbance should be considered. These critical data would strongly help measure the impact of management on the carbon cycle.

Conclusions

- Based on observational and modeling evidence, it appears that LAI regularly exceeds levels required to sustain carbon assimilation in naturally growing forest ecosystems.
- Above its saturation value of 3-4.5 m^2 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.
- We can explain the lack of impact of harvesting on the CO_2 uptake by the existence of non-linear processes governed that saturate around LAI values of 4.5 m^2 m^{-2}.
- Selective harvesting does not reduce the forest carbon sink strength when LAI is maintained beyond its threshold.
- 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.
- Harmonized and periodic measurements of the forest carbon stock and LAI, and of harvesting impacts on these, should be promoted at flux sites.

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Author Contributions: Conceptualization, O.B., E.D.S. and C.K.; methodology, O.B. and E.D.S.; writing original draft preparation O.B. and E.D.S. All authors contributed to the writing, and reviewed the manuscript.

Competing Interest Statement: At least one of the (co-)authors is a member of the editorial board of Biogeosciences.

Acknowledgements

This work was supported by a grant of the Ministry of Research, Innovation and Digitization, CNCS- UEFISCDI, project number PN-III-P4-PCE-2021-1677, within PNCDI III. KG acknowledges funding by the Bavarian State Ministry of Science and the Arts in the context of the Bavarian Climate Research Network (bayklif) through its BLIZ project (Grant No. 7831-26625- 2017, \url{www.bayklif-bliz.de}). RV and IB are supported by AGRITECH — PNRR (Italian National Plan of Recovery and Resilience), identification code CN00000022 WP 4.3.3. Authors are very grateful to Susan Trumbore for her comments and suggestions on the manuscript.

Open research

The data presented and analyzed in this study are available directly from the supplementary information files, in tables S1 to S3. These tables also contain references to data sources. Figures were made with R version 4.3.2 (R Core Team, 2023) (https://www.R-project.org/).

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Figures and Tables

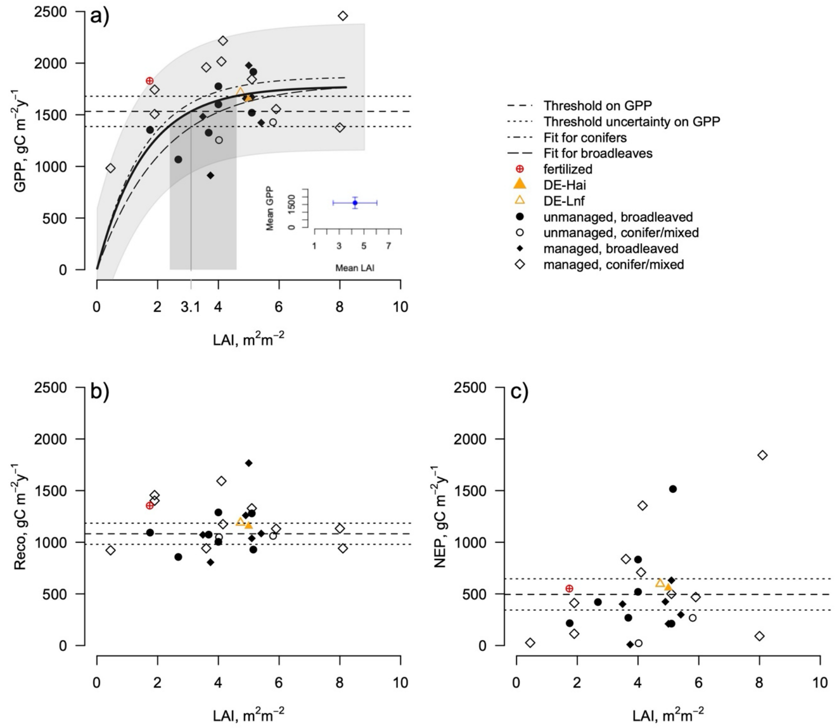

Figure 1. Relation between the GPP (a), the Reco (b), the NEP (= -NEE, c) and the LAI on the eddy covariance sites (FLUXNET sites, see Supp. Table S1,2) of both managed and unmanaged temperate forests per stand types.

The dashed lines represent mean and confidence interval of the GPP and NEP across all sites. The gray band represents the confidence interval of the regression on all sites and all forest types. The fertilized site is identified (Parco Ticino), along with the couple DE-Hai (unmanaged) and DE-Lnf (managed). The exponential models illustrate the tendencies (Tab. 1), ±10% confidence intervals are displayed in gray.

Deleted: Curves show the fits for broadleaves (green), conifers and mixed forests (red), and all sites together (black).

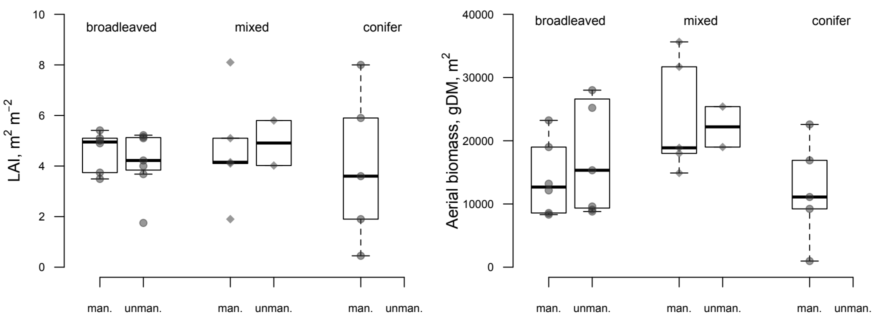

Figure 2. Comparison of the LAI and aboveground biomass values for the managed and unmanaged sites, depending on the forest type. The site AU-Wac (Australia, natural *Eucalyptus regnans* F. Muell.) is an extreme value due to low decomposition (Supp. Fig. 2) and was not included in the biomass comparison.

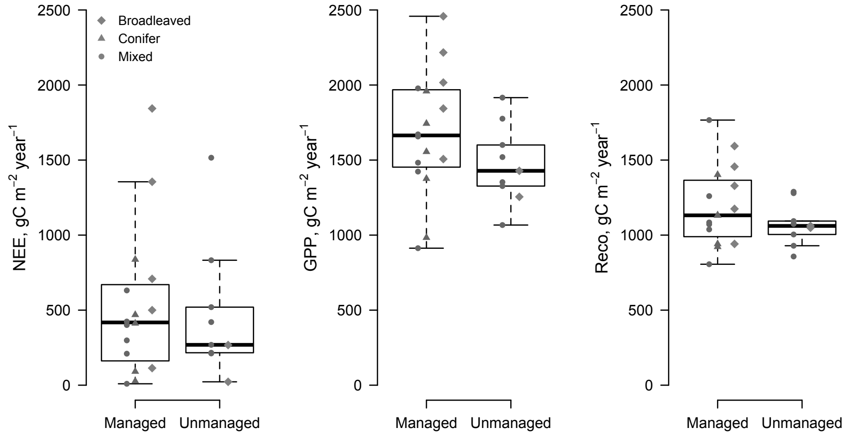

Figure 3. Comparison of the flux data from managed and unmanaged FLUXNET sites. Dots represent the site-level mean values over the monitoring period.

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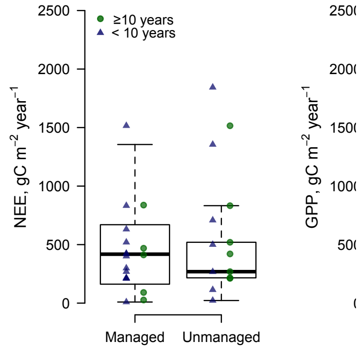

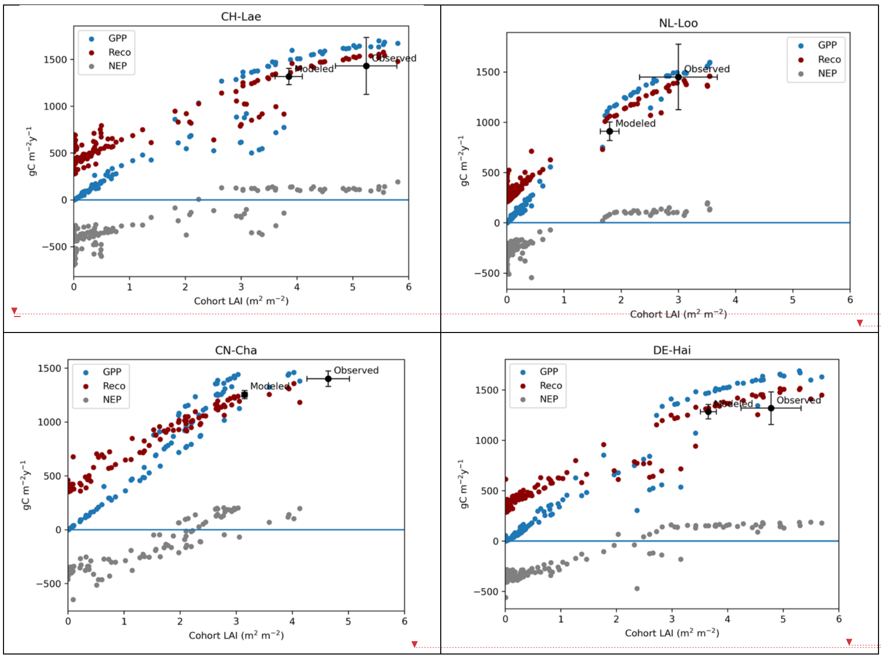

Figure 4. Variations of GPP, NEP and Reco along a gradient of LAI as modelled using LPJ-GUESS shown for 4 sites with contrasted maximum LAI and forest types: CH-Lae for mixed forest type with high LAI, NL-Loo for conifers with low LAI, DE-Hai broadleaved with high LAI and CN-Cha with low LAI broadleaved. Each dot represents the fluxes of a particular tree cohort simulated at a given site.

The model runs reveal that LAI in excess of 4 m^2 m^{-2} does not promote GPP or NEP. NEP becomes positive (forest acts as a sink) for LAI in excess of 3 m^2 m^{-2} but, beyond 4 m^2 m^{-2}, increases in LAI do not result in increases in NEP.

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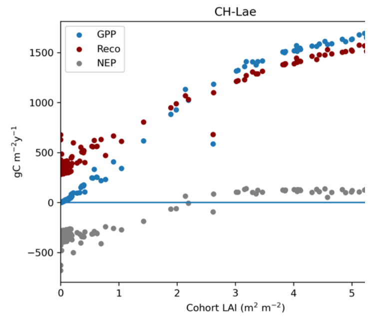

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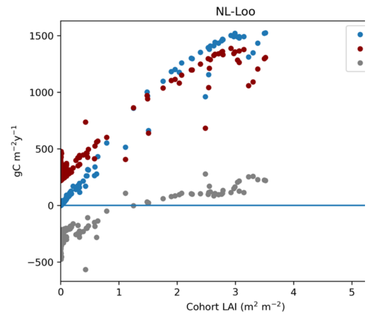

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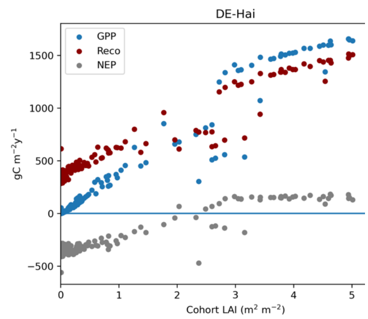

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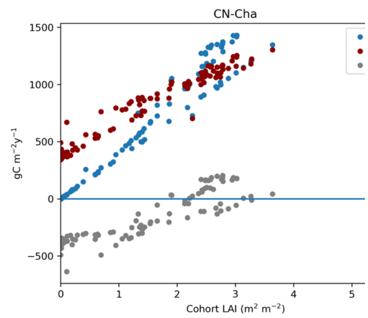

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Table 1. Effect of management type over the fluxes monitored on eddy correlation sites of temperate northern-hemisphere (N = 29 FLUXNET sites, of which 18 managed and 10 unmanaged, after the exclusion of the Parco Ticino site (IT) of fertilized Populus), and fit statistics of the nonlinear asymptotical models. Management is tested as a two-levels fixed factor (managed/unmanaged) taken as Wilcoxon rank test for NEE, Welch t-test for GPP, Reco and LAI. Pseudo-R^2 values were estimated from modeled and observed values (see Methods section).

Flux	Welch / t-test	*p-value*
NEE	W = 83	0.7595
GPP	t = 1.745	0.0929
Reco	t = 1. 711	0.0991
GPP ~ a(1 - exp(c*LAI)), pseudo-R^2 = 0.517*		
Estimate (std error)	*t value*	*Pr(>|t|)*
a = 996.798 (116.443)	15.242	5.99e-16
c = -0.184 (0.161)	-4.011	0.000354
NEE ~ a(b -exp(c*LAI)), pseudo-R^2 = 0.935*		
Estimate (std error)	*t value*	*Pr(>|t|)*
a = 648.998 (15180.454)	0.043	0.966
b = 1.199 (4.684)	0.043	0.966
c = -1.091 (51.191)	-0.79	0.938

Table 2. Estimation of the effect of management and forest type on the LAI or on the fluxes. Interactions (management x type) were tested and not found significant, and are therefore not presented here.

	Estimate	std. error	t value	$Pr(>\vert t\vert)$
LAI_mix ~ Management + type, $F(3, 25) = 0.3592$, $p = 0.7829$				
Intercept	4.233	0.789	5.358	1.48e-05***
Management	0.064	1.029	0.062	0.951
Conifer	1.209	1.258	0.961	0.346
Mixed	0.488	1.109	0.440	0.664