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

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4  **Olivier Bouriaud [1,2*], Ernst-Detlef Schulze [3], Konstantin Gregor [4], Issam Boukhris [5], Peter**
5  **Högberg [6], Roland Irslinger [7], Phillip Papastefanou [3], Julia Pongratz [8,9], Anja Rammig [4],**
6  **Riccardo Valentini [5], Christian Körner [10]**

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8  1. Ștefan cel Mare University of Suceava, Str. Universității 13, 720229 Suceava, Romania.
9  (obouriaud@usm.ro)

10  2. ENSG, IGN, Laboratoire d'Inventaire Forestier, 54000 Nancy, France.

11  3. Max Planck Institute for Biogeochemistry, Jena, Germany. (dschulze@bgc-jena.mpg.de,
12  papa@bgc-jena.mpg.de)

13  4. Land Surface-Atmosphere Interactions, Technical University of Munich.
14  (anja.rammig@tum.de, konstantin.gregor@tum.de)

15  5. University of Tuscia, Dept of Forest Environment and Resources, 01100 Viterbo, Italy.
16  (rik@unitus.it, issamboukhris@gmail.com)

17  6. Department of Forest Ecology and Management, Swedish University of Agricultural
18  Sciences, SE-901 83 Umeå, Sweden. (Peter.Hogberg@slu.se)

19  7. Hochschule für Forstwirtschaft Rottenburg, Schadenweilerhof, Rottenburg a.N., Germany
20  (irslinger@gmx.de)

21  8. Ludwig-Maximilians-Universität München (DE) (julia.pongratz@lmu.de)

22  9. Max Planck Institute for Meteorology (Hamburg, DE)

23  10. University of Basel Department of Environmental Sciences Plant Ecology and
24  Evolution, Schönbeinstrasse 6. CH-4056 Basel. (ch.koerner@unibas.ch)

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26  **Corresponding author:** Olivier Bouriaud, ORCID# 0000-0002-8046-466X,
27  obouriaud@usm.ro

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30  **This file includes:**
31      Main Text (5275 words)
32      Figures 1 to 5
33      Tables 1 to 2
34      Supplementary 1 to 3

35

36  **Key Points:**

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

42

43   **Abstract**

44   Maintaining or increasing forest carbon sinks is considered essential to mitigate the rise of

45   atmospheric $CO_2$ concentrations. In contrast, harvesting trees is perceived as having negative

46   consequences on both the standing biomass stocks and the carbon sink strength. However, the

47   forest carbon sink needs to be examined from a forest stand canopy perspective since carbon

48   assimilation occurs in the canopy. Here we show that a threshold of leaf area exists beyond

49   which additional leaves do not contribute to $CO_2$ uptake. The associated biomass can be

50   harvested without affecting the forest carbon uptake. Based on eddy covariance

51   measurements we show that $CO_2$ uptake (GPP) and net ecosystem exchange (NEE) in

52   temperate forests are of similar magnitude in both unmanaged and sustainably managed

53   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

54   threshold located between 3 and 4.5 $m^2$ $m^{-2}$ LAI (leaf area index) can be used as a threshold

55   of sustainable harvesting with regard to $CO_2$ uptake. Simulations based on the LPJ-GUESS

56   model reproduce the saturation of GPP and NEP and convergence on the LAI threshold

57   range. Accordingly, in temperate managed forests, trees can be harvested while maintaining a

58   high tree biomass and carbon sink of the remaining stand. In this case, competition between

59   neighbor trees in unmanaged forests is replaced by harvest management and provision of

60   wood products. No difference in the LAI productivity response was observed between

61   managed and unmanaged sites.

62

63


64   **Introduction**

65   At times of increasing global change and a demand for wood to replace fossil fuel

66   products, it becomes of eminent importance to know the role of forest management and wood

67   harvest in mitigating climate change. Following the EU definitions on storage and uptake

68   respectively (EU 2018), two major ways exist by which forests may contribute to the efforts

69   of climate mitigation: the storage of biomass on site within the forest ecosystem and the

70   storage of wood in products or their use for substitution of fossil-fuel or carbon-intensive

71   materials (Gregor et al., 2024). It is generally assumed that storage and C stocks can be

72   sustained or increased only by increasing the area of forests, or by stopping wood

73   procurement from forests (no management). However, halting management will probably

74   have little long-term effects on the forest carbon sink and stocks at landscape level,

75   considering the environmental risks associated with climate change that strongly increase the

76   chances of stand collapse (Roebroek et al., 2023). This is supported by Pretzsch et al. (2023),

77   who observed that self-thinning losses could be equivalent to wood extraction by

78   management. Luyssaert et al. 2011 also show that management keeps forest stands close but

79   below self-thinning, albeit at different stand density and volume. Besides ensuring a sustained

80   carbon sink, harvesting wood products can substitute carbon-intensive materials and the

81   energy use of wood residues and end-of-life wood products can substitute energy from fossil

82   fuels (Cowie et al., 2021; Schulze et al., 2022). Thus, understanding the consequences of

83   selective harvesting on the carbon balance and sink strength of forests is a key element to

84   future projections on the role of forests to climate change mitigation.

85

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

100

101    Here, we introduce the link between photosynthesis and leaf area as a key element in this
102    regulation at stand level. We hypothesize that LAI is not only the link between the
103    atmosphere and the plant, but is also central to the response to management. LAI is indeed
104    largely seen as a driver of both water and carbon fluxes (Reich, 2012; del Campo et al.,
105    2022). Given its high nutrient demand the production of leaves also affect the nutrient cycle
106    (Ollinger et al., 2008) and is a potentially crucial driver of forests response to harvesting.

107

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

121

122    The impact of harvest on the C cycle is clearly of major importance in the public debate. It is
123    thus necessary to determine the impact of harvesting on the fluxes of carbon in forests based
124    on experimental data over a large gradient, and to discuss the limits in the context of leaf area
125    reduction. In particular, the interactions between management and LAI, and their
126    consequences for the carbon sink strength need to be determined in order to examine the

127 consequences of wood harvesting on forests carbon sink strength. Here we intend to show
128 that sustainable management replaces natural competition by regulating leaf area without
129 affecting ecosystem fluxes in temperate forests. Based on observational data, literature and
130 modeling we want to identify mechanistic reasons for this presumption and explore the
131 possibilities of defining levels of sustainable partial cuttings from the perspective of carbon
132 fluxes, key to designing forest managements strategies able to maintain high biomass as well
133 as forest C uptake over multiple cutting cycles. We use the model LPJ-GUESS to illustrate
134 the diminishing returns of GPP with increasing LAI in models as well.

135
136 **Materials and methods**
137
138 ***Observational flux data based on eddy covariance measurements on the FLUXNET sites.***
139 Overall FLUXNET represents 212 sites worldwide of eddy covariance. In order to measure
140 the impact of management over the carbon fluxes, we have compiled flux data from the 29
141 FLUXNET sites (https://fluxnet.org/data/fluxnet2015-dataset/) that comprise 19 managed and
142 10 unmanaged sites (unmanaged is used in the sense of "intact" forests of Roebroek et al.,
143 2023) with long-term measurements in temperate forests (**Supp. Table S1**). Unfortunately,
144 there is no site that covers unmanaged conifers. For each site we have compiled the forest
145 type, stand type, and the fluxes over their monitoring period. We completed these data with
146 estimations of the LAI during the period 2000-2020 and of the standing biomass.
147 Noticeably, selective harvesting took place on 11 of the managed sites during the period of
148 flux monitoring, several interventions being quite intensive (Supp. Table S3): for instance,
149 36% LAI removal in Fontainebleau site (FR), 30% removal in Bily Kriz site (CZ). Other
150 managed sites have experienced interventions prior to the monitoring but not necessarily
151 during the monitoring period, given the long periods of time separating interventions.
152 Furthermore, during the period of flux monitoring, forests experienced repeated events of
153 storm, drought and heat such as that of 2003, affecting ecosystem fluxes independent of
154 management.

155 Further, we have compiled LAI estimations for the analyses, for each of the FLUXNET sites.
156 LAI measurements, however, are not standard across sites, and field measurements are not
157 always available (5 sites had no field measurements). In this situation remote-sensed
158 estimations were used instead based on the MCD15A3H version 6.1 MODIS data level 4 (see
159 **Supplementary Table S1**, with references for each estimation). Field-based measurements
160 were based on hemispherical images with site-specific clumping factors (Gielen et al. 2018).
161
162 The eddy covariance method does not directly measure $CO_2$ fluxes but instead records high-
163 frequency atmospheric $CO_2$ concentrations and wind speed fluctuations. These measurements
164 are then used to compute net ecosystem exchange (NEE) with inherent uncertainties due to
165 instrument limitations, atmospheric conditions, and data processing methods. Flux data were
166 filtered based on USTAR threshold levels, following the method described by Pastorello et al.
167 (2020), to exclude measurements taken under low turbulence conditions. Errors have been
168 estimated using bootstrapping 200 times with different friction velocity values.
169 The fluxes of carbon exchanged between the forest ecosystem and the atmosphere are
170 generally divided into components that are physiologically meaningful: the gross primary

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

176

177   We compared the mean fluxes during the period of time available of managed and
178   unmanaged sites. For testing the significance of differences in NEE we used the Wilcoxon
179   rank test because data were not distributed normally. GPP and Reco have a distribution that
180   does not differ significantly from a normal distribution. The Mann-Whitney test has been
181   implemented to compare managed versus unmanaged sites which works with unequal sample
182   sizes. For GPP and Reco, their distributions being normal, but their variances unequal, the
183   Welch t-test was used instead. Subsequently, two-way analysis of variance for unbalanced
184   designs was performed on the data to check if the interaction between the management and
185   the number of observations by FLUXNET site has a significant effect on GPP, Reco, and
186   NEE.
187   The relationship between GPP and LAI for the FLUXNET observational site was represented
188   as a nonlinear asymptotical model. The fitting was based on the nonlinear fit function *nls* (nls
189   standing for nonlinear least square) in R. The pseudo-$R^2$ represents the proportion of variance
190   that was explained by the model, in lieu of the $R^2$ which assumptions cannot be completely
191   satisfied with nonlinear models (Schabenberger and Pierce 2002). It was computed as
192   *pseudo-$R^2$* $= 1 - (\text{var}(y_{fit})/\text{var}(y))$, where $\text{var}(y_{fit})$ is the variance of the predicted value (GPP
193   here), while $\text{var}(y)$ is the variance of the variable (GPP) within the dataset. All statistical
194   analyses were performed in R version 4.3.2 (R Core Team, 2023).

195

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

210

211

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

214 To investigate the impact of LAI on GPP, we used the dynamic global vegetation model LPJ-
215 GUESS v4.1.1 (Smith et al., 2014, Nord, 2021) to simulate the main carbon fluxes (GPP,
216 Reco and NEP) on all the eddy-covariance sites used in the study. The ability of LPJ-GUESS
217 to estimate LAI and GPP values worldwide has been proven in numerous studies (e.g., Vella
218 et al. 2023 and Ito et al. 2017, see also Fig. SF2). Therefore, the model is well suited for the
219 analyses. LPJ-GUESS simulates detailed vegetation structure (including cohorts of various
220 ages) based on mechanistic modeling of ecosystem processes including photosynthesis,
221 establishment, growth, allocation, competition, water and nutrient limitation, and mortality of
222 plant functional types (PFTs). The latter are represented by parameters defining plant
223 characteristics such as bioclimatic limits, growth form, or shade-tolerance.
224 In the model, at the end of each year, cumulative net primary productivity is distributed
225 among the leaf, root, sapwood and heartwood compartments of a plant, based on allometric
226 equations and allocation routines per year (Smith et al., 2014). The model belongs to the big
227 leaf family, representing the canopy as a single layer. This modelling is compatible with the
228 spatial of the study: the footprint of eddy covariance being typically in order of 100 ha. LAI
229 is calculated as the product of the carbon mass of the leaves times the specific leaf area, the
230 specific leaf area being a PFT parameter. LAI is computed proportionally to the phenology
231 fraction of the PFTs, that is, the fraction of potential leaf cover. The phenology of a PFT can
232 be raingreen, summergreen or evergreen. LAI is also influenced by the phenology: depending
233 on the environmental conditions, the phenology fraction can depend on growing degree days
234 and drought stress related model states. The amount of light taken up by the canopy, and thus
235 contributing to carbon allocation, is governed by LAI, based on the Lambert-beer law
236 (Prentice et al, 1993) assuming a site-specific surface leaf mass ratio not varying within the
237 canopy. The model outputs stand level LAI, taking into account the number of trees per area
238 and the crown areas of the various cohorts. The photosynthesis model used in LPJ-GUESS is
239 based on Collatz et al. (1991) which is a simplification of the Farquhar et al. (1980) model
240 and the carbon allocation model based on Smith et al. (2001). Photosynthesis and respiration
241 are calculated daily and accumulated towards the end of a year, allowing to represent
242 seasonal dynamics.
243
244 For the LAI analysis, we ran LPJ-GUESS until 2015 using daily climate data from the
245 FLUXNET2015 sites, i.e., precipitation, temperature, and shortwave radiation. For each site,
246 we prescribed the forest type as described in Table S2. We used 1000 years for the spinup
247 period (to bring soil pools close to equilibrium) by detrending and recycling the first 10 years
248 of each site's climate data. $CO_2$ concentrations were taken from (Büchner and Reyer, 2022).
249 We used the default global parametrization of LPJ-GUESS with global PFTs, without any
250 form of management.
251 Stochastic disturbance intervals were kept at default values while fire was not simulated.
252

253 **Results**

254

255 *Saturated response of fluxes to LAI*

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

263

264    The data from the FLUXNET sites show a response of GPP to LAI only for LAI values less
265    than ~4 $m^2$ $m^{-2}$ (**Fig. 1**) but the GPP does not increase at higher LAI.  It is interesting to note
266    that most managed forests operate above the range of saturating LAI with a mean of 4.74 ±
267    1.33 $m^2$ $m^{-2}$, despite harvesting. Likewise, the data shows a saturation of GPP even in
268    managed sites, with values reaching a plateau in the order of 1770 gC $m^{-2}$ $year^{-1}$ at LAI
269    values as low as 2 $m^2$ $m^{-2}$. Based on the GPP-LAI regression, 95% of GPP (1680 gC $m^{-2}$
270    $year^{-1}$) is reached at LAI of 2.7 to 4.0 $m^2$ $m^{-2}$ depending on the forest type. The exact location
271    of the LAI saturation point can only be approximated given the uncertainty in both LAI and
272    C flux data, which is larger in LAI than in fluxes (**Fig. 1** and **Sup Table 1**). The site at Parco
273    Ticino Forest (Italy) has been fertilized. It indicates the importance of nutrition in forest
274    ecosystems as a GPP value above 1800 gC $m^2$ $y^{-1}$ was reached at low LAI ($< 2$ $m^2$ $m^{-2}$).
275    However, even with fertilization, the fluxes and LAI values remain in the range of other sites.
276    Reco had a smaller overall variability than GPP (1082 ± 151 gC $m^2$ $y^{-1}$) and showed no
277    response to LAI. Likewise, there was no response to forest types. The net ecosystem
278    exchange (the balance between photosynthesis and respiration, GPP – Reco = NEP) did not
279    show any significant response to LAI, with values largely scattered around the mean (343 ±
280    151 gC $m^{-2}$ $year^{-1}$).
281    The data represent a mixture of remotely-sensed and field-based LAI for different forest
282    types. Given the large variability among sites, differences in fluxes for managed and
283    unmanaged forests in **Figure 1** are not significant (**Table 1**).
284    It is notable that under management LAI was similar to that of unmanaged stands (4.74 ±
285    1.33 for managed sites versus 4.40 ± 0.82 $m^2$ $m^{-2}$ for unmanaged sites, n.s.), despite the
286    removal of parts of the canopy due to management in the past (**Fig. 2**). LAI was indeed
287    strongly reduced during the monitoring period by thinnings ranging from 26 to 36% in four
288    of the managed sites (**Sup Table 3**). For instance, the low (3.6 $m^2$ $m^{-2}$) LAI value at site CS-
289    BK1 (*Picea abies* L.) reflects the 26% removal that occurred at the end of the monitoring
290    period. The dynamic of LAI on the sites show that the reduction of the LAI by harvesting is
291    limited to a few years following the harvesting (**Sup Fig. 1**).

292

293    ***Responses of fluxes to sustainable harvesting: empirical evidence from eddy covariance***
294    The FLUXNET associated site data showed that past and current management has little
295    influence on the aboveground biomass and LAI of the sites (**Fig. 2**).  Highest biomass was
296    reached with the old-growth *Eucalyptus regnans* (F. Muell.) site in Australia (Wallaby Creek
297    site, with 36,106 g dry matter $m^{-2}$). Unfortunately, there is no managed site of *E. regnans* for

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

300

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

315

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

332

333   **Discussion**

334   With the introduction of the eddy covariance method, long time series of carbon fluxes
335   became available over a variety of biomes, with most monitoring sites being under regular
336   forest management (Franz et al., 2018). Based on these time series, our synthesis showed
337   here that GPP and NEE remain largely unaffected by partial harvesting, as also reported by
338   site-level analyses for several forest types and species (Granier et al., 2008; Launianen et al.,

339  2022; Lindroth et al., 2018; Pilegaard et al., 2011; Peichl et al., 2022; Vesala et al., 2005).
340  These results are in agreement with the long-established empirical knowledge that stand
341  productivity remains unaffected by thinnings when their intensity remains below a threshold
342  (expressed in terms of stem density or basal area) (Assmann 1970, Pretzsch and Schütze
343  2009). Similarly, Vesala et al., 2005 observed no visible effects of thinnings on the NEE
344  despite the reduction of LAI from 8 to 6 $m^2$ $m^{-2}$ in a Scots pine (*Pinus sylvestris* L.) stand.
345  Granier et al. (2008) reported for *Fagus sylvatica* (L.) stands no decrease in either NEE or
346  GPP despite the thinning that decreased LAI from 7.4 to 4.8 $m^2$ $m^{-2}$. These results are in
347  agreement with Herbst et al. (2015) and are confirmed by the global database of Luyssaert et
348  al. (2007) which shows that managed forests globally achieved similar, or even larger GPP,
349  than unmanaged forests.
350
351  The harvest effect on LAI appears to be short-term in temperate forests (del Campo et al.,
352  2022) as also suggested by the available LAI time-series of the sites studied here (**Supp. Fig.
353  SF1**). For instance, according to Granier et al. (2008) LAI in *Fagus sylvatica* stands was
354  restored to its pre-thinning level within two years. Disturbances, particularly stand-replacing
355  disturbances such as windthrow, fire or clear-cuts have a different dimension and need to be
356  evaluated at landscape scale. Our study deals with thinning operations where the main
357  canopy is reduced but not removed, keeping LAI beyond or near to its saturation threshold.
358  This also justifies the choice of focusing on temperate forests where the lower species
359  richness and age ranges may slow the recovery of carbon uptake to catastrophic events, in
360  contrast to tropical forests (Brando et al., 2019). For boreal forests, the IBFRA-Report
361  (Högberg et al., 2021) shows that biomass increased significantly over the past decades only
362  in intensively managed landscapes, but not in less intensively managed forest landscapes
363  (i.e., landscapes with a high proportion of unmanaged forests). In the latter, large-scale
364  disturbances such as wildfires caused losses of biomass and prevented a build-up of forest
365  carbon stocks. In comparison, the biomass gain in non-managed temperate forests is very
366  small (Roerbroek et al., 2023). Roerbroek et al. (2023) indeed suggests that betting on
367  increasing the forests stocks is not only risky, given the increases in weather extremes, but
368  loses the societal benefit of wood products as well as the potential to store a portion of the C
369  over longer term.
370
371  We propose that most of the decoupling between selective harvesting and $CO_2$ fluxes is
372  mediated by the intrinsically nonlinear response of the dominant processes to LAI with a
373  saturation point reached at 3-4.5 $m^2$ $m^{-2}$ but with uncertainties around this value. The
374  threshold itself may show some variability, for instance related to plant functional types. The
375  eddy covariance fluxes suggested a slightly higher relation between GPP and LAI than
376  broadleaved (Fig. 1a). The model simulations likewise suggested varying level of saturations
377  depending on the sites. Further studies could help locate this threshold more precisely, by
378  increasing the number of observations and addressing the uncertainties, particularly those
379  related to LAI estimates.
380  This nonlinear response, particularly the existence of a saturation point, is related to the
381  existence of a fraction of the canopy leaf area not necessary for productivity but serving other
382  functions such as competition, or redundancy in case of competition. In forest management it

383     is known that about a third of the green foliaged tree crown can be pruned to improve stem
384     quality without affecting growth (Burschel and Huss 2003). Diffuse light can penetrate
385     deeper into the canopy and reach lower levels of leaves, but the gain in photosynthesis may
386     not counterbalance the cost of producing and maintaining saturated canopies. The carbon
387     balance of a living branch may be close to the light compensation point of photosynthesis and
388     respiration (Schulze 1970), with a photosynthesis activity just at the level needed to keep a
389     shaded branch alive. Similarly, in the simulations of the model LPJ-GUESS, small trees with
390     low LAI operate at a higher level of light extinction due to shadowing by bigger trees, which
391     leads to very low GPP as no direct sunlight can reach any leaves (Fig. 4). Shadowing also
392     leads to a reduction in Reco, however a minimum maintenance respiration of the leaves is
393     always needed to sustain functioning of the leaves.
394

395     While shade tolerance varies among species (Ameztegui et al., 2016), as reflected by
396     different maximum LAI values (Valladares and Niinemets 2008), the threshold for light
397     compensation is probably very similar across forest types or species despite variations in the
398     canopy structure. Accordingly, in our study, the species traits did not show significant
399     correlations to either LAI or flux values. This suggests that increasing LAI beyond a demand-
400     driven threshold has other functions, for instance a competitive function with neighboring
401     trees (Pretzsch and Schütze 2009, Jucker et al., 2014) not only for light but also for nutrients
402     (e.g., in a pre-emption strategy, Craine and Dybzinski 2013), as a buffer against disturbance
403     (e.g., herbivory) and a pool of nutrient reserves, ready for rapid re-allocation in case of
404     sudden demand (Körner 2009). Anten (2005) shows that canopy photosynthesis models
405     predict LAI values greater than optimal values for photosynthesis and quote theoretical
406     studies that conclude to a LAI always exceeding the physiologically optimal value for
407     competitive purposes. Avoiding a neighbor increases the resources of water and nutrients for
408     the dominant tree. This surplus fraction is temporarily diminished by selective harvesting,
409     explaining the lack of response of the main C fluxes at canopy level across a wide range of
410     LAI. Accordingly, a moderated management can be seen as a substitution of self-thinning
411     when forest stands are kept close but below self-thinning density levels (Luyssaert et al.,
412     2011).
413

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

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

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

449

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

466

467  **Conclusions**

468    • Based on observational and modeling evidence, it appears that LAI regularly exceeds
469      levels required to sustain carbon assimilation in naturally growing forest ecosystems.

470    • Above its saturation value of 3-4.5 $m^2\ m^{-2}$, additional increases in LAI are not linked
471      to increased productivity, but may contribute to other functions selected in evolution,
472      such as competition with adjacent trees, resource storage and buffering against
473      herbivory.

474    • We can explain the lack of impact of harvesting on the $CO_2$ uptake by the existence of
475      non-linear processes governed that saturate around LAI values of 4.5 $m^2\ m^{-2}$.

476    • Selective harvesting does not reduce the forest carbon sink strength when LAI is
477      maintained beyond its threshold.

478    • This threshold can be used to define sustainable metrics for sustainable harvesting, as
479      those that do not impact the carbon sink strength of the forest stand.

480    • Harmonized and periodic measurements of the forest carbon stock and LAI, and of
481      harvesting impacts on these, should be promoted at flux sites.

482
483
484
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487    writing, and reviewed the manuscript.
488
489    **Competing Interest Statement:** At least one of the (co-)authors is a member of the editorial board of
490    Biogeosciences.
491

502    **Open research**

503    The data presented and analyzed in this study are available directly from the supplementary
504    information files, in tables S1 to S3. These tables also contain references to data sources.
505    Figures were made with R version 4.3.2 (R Core Team, 2023) (https://www.R-project.org/).
506

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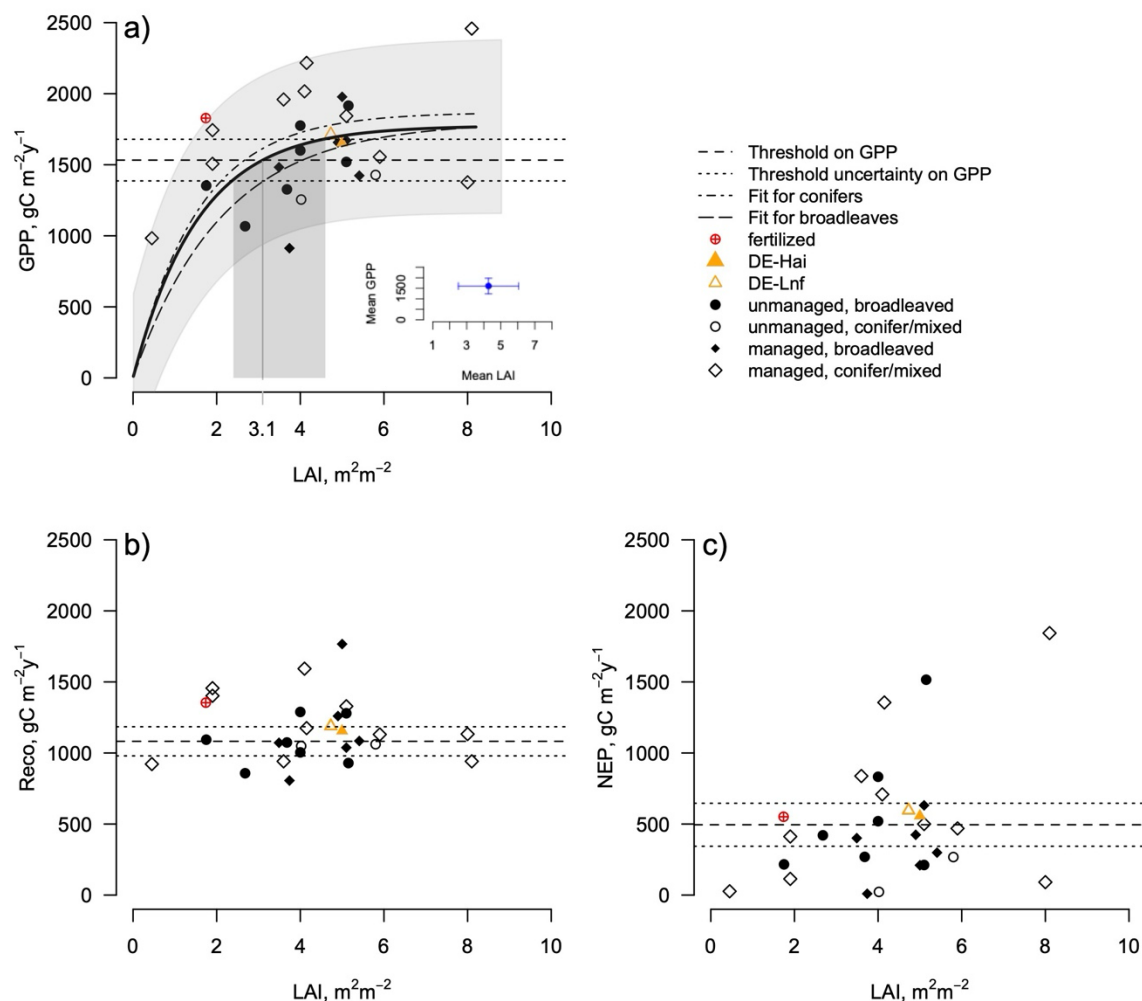728    methods and sensors. Sensors, 9 (4), 2719–2745, 2009.

## 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.
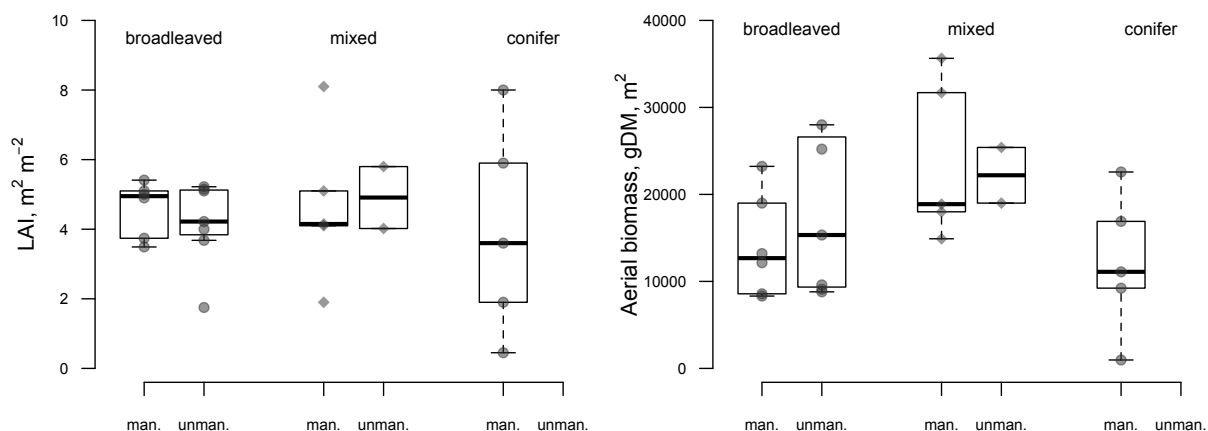1), ±10% confidence intervals are displayed in gray.

740
741 **Figure 2**. Comparison of the LAI and aboveground biomass values for the managed and
742 unmanaged sites, depending on the forest type. The site AU-Wac (Australia, natural
743 *Eucalyptus regnans* F. Muell.) is an extreme value due to low decomposition (Supp. Fig. 2)
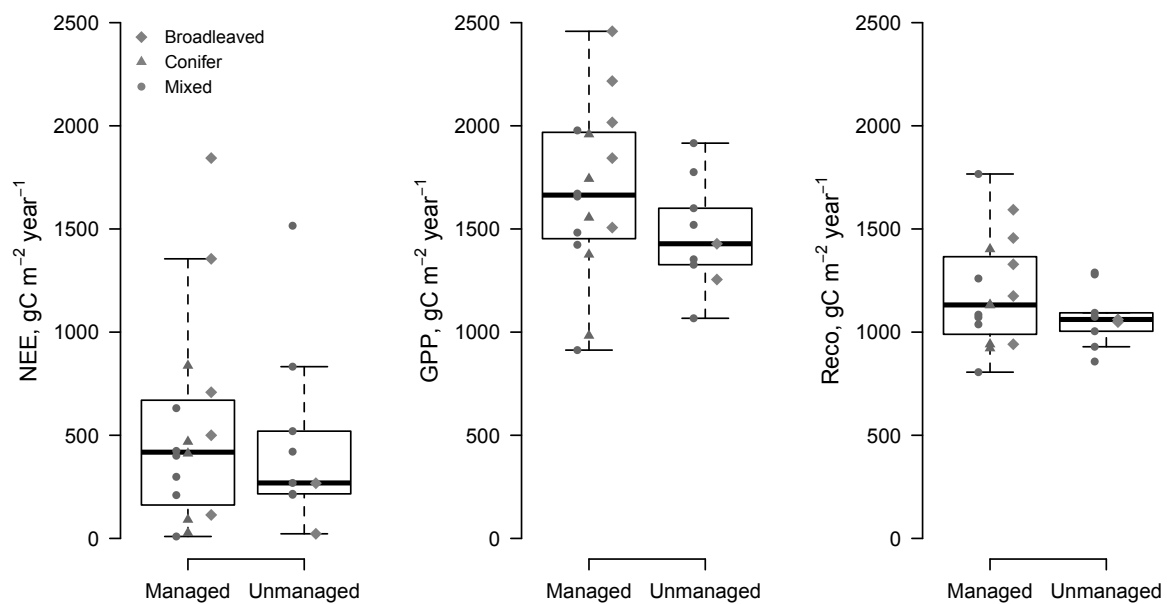744 and was not included in the biomass comparison.
745

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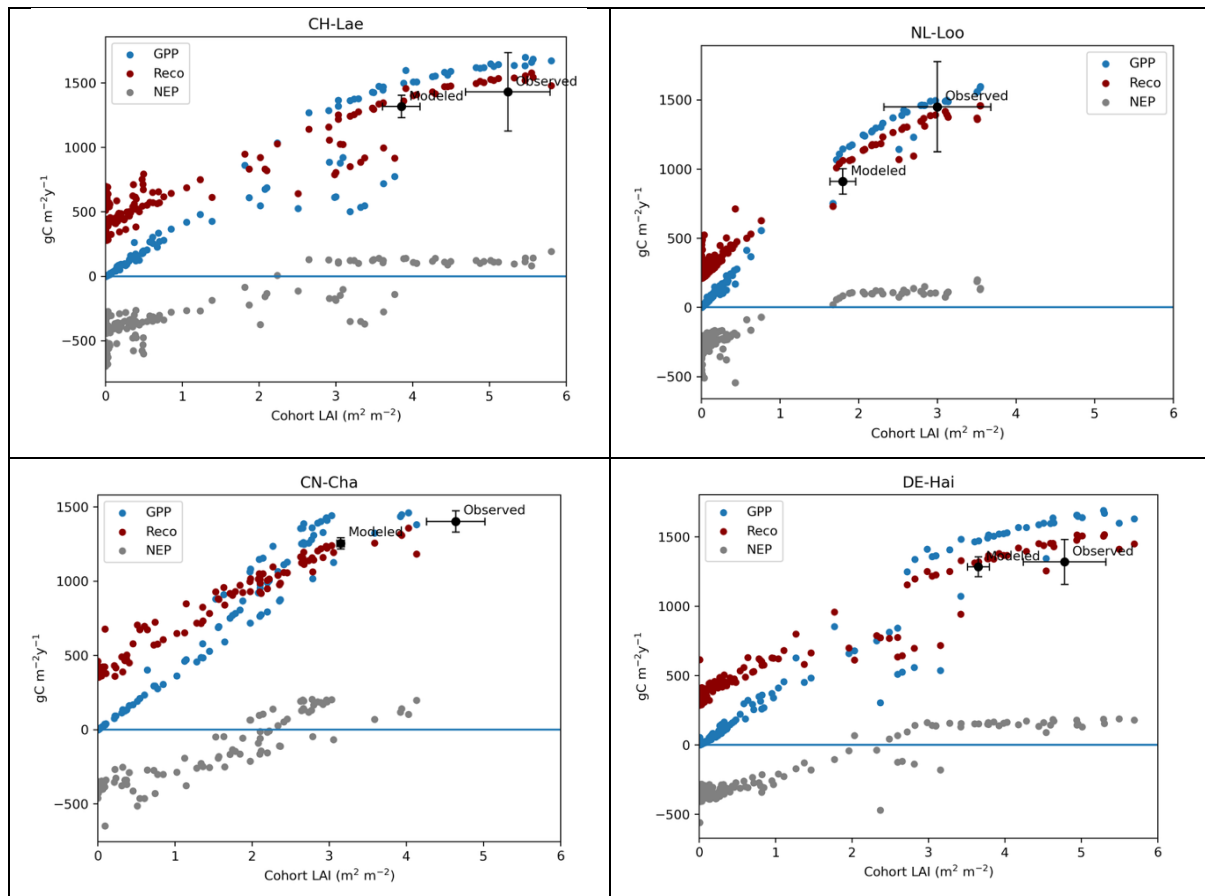Dots represent the site-level mean values over the monitoring period.

**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.

760 **Table 1**. Effect of management type over the fluxes monitored on eddy correlation sites of
761 temperate northern-hemisphere (N = 29 FLUXNET sites, of which 18 managed and 10
762 unmanaged, after the exclusion of the Parco Ticino site (IT) of fertilized Populus), and fit
763 statistics of the nonlinear asymptotical models. Management is tested as a two-levels fixed
764 factor (managed/unmanaged) taken as Wilcoxon rank test for NEE, Welch t-test for GPP,
765 Reco and LAI. Pseudo-$R^2$ values were estimated from modeled and observed values (see
766 Methods section).
767

| *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 |

768
769

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

|  | Estimate | std. error | t value | Pr(>\|t\|) |
|---|---|---|---|---|
| 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 |

773