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

Olivier Bouriaud [1,2*], Ernst-Detlef Schulze [3], Konstantin Gregor [4], Issam Boukhris [5,6], Peter Högberg [7], Roland Irslinger [8], Phillip Papastefanou [9], Julia Pongratz [9,10], Anja Rammig [4], Riccardo Valentini [5,6], Christian Körner [11]

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

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

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

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

5. Forest Ecology Lab, Department for Innovation in Biological, Agri-Food and Forest Systems (DIBAF), University of Tuscia, 01100 Viterbo, Italy. (rik@unitus.it; issamboukhris@gmail.com)

6. CMCC Foundation - Euro-Mediterranean Center on Climate Change, 73000 Lecce, Italy.

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

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

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

10. Max Planck Institute for Meteorology (Hamburg, DE)

11. Department of Environmental Sciences Plant Ecology and Evolution, University of Basel, Schönbeintrasse 6. CH-4056 Basel. (ch.koerner@unibas.ch)

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

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Key Points:

- In temperate forests, net CO_2 uptake remains quasi 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.

45 **Abstract**

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

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

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

49 forest carbon sink needs to be examined from a forest stand canopy perspective, where

50 assimilation predominantly occurs in temperate forests. Here we show that a threshold of leaf

51 area exists beyond which additional leaves do not contribute to CO_2 uptake. The associated

52 biomass can be harvested without affecting the forest carbon uptake. Based on eddy

53 covariance measurements we show that CO_2 uptake (GPP) and net ecosystem exchange

54 (NEE) in temperate forests are of similar magnitude in both unmanaged and sustainably

55 managed forests, in the order of 1500-1600 gC m^{-2} y^{-1} for GPP and $542 - 483$ gC m^{-2} y^{-1} for

56 NEE. A threshold located between 3 and 4.5 m^2 m^{-2} LAI (leaf area index) can be used as a

57 threshold of sustainable harvesting with regard to CO_2 uptake. Simulations based on the LPJ-

58 GUESS model reproduce the saturation of GPP and NEP and convergence on the LAI

59 threshold range. Accordingly, in temperate managed forests, trees can be harvested while

60 maintaining a high tree biomass and carbon sink of the remaining stand. In this case,

61 competition between neighbor trees in unmanaged forests is replaced by harvest management

62 and provision of wood products. No difference in the LAI productivity response was

63 observed between managed and unmanaged sites.

64

65

66 **Introduction**

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

87

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

102

103 Here, we introduce the link between photosynthesis and leaf area as a key element in this
104 regulation at stand level. We hypothesize that LAI is not only the link between the
105 atmosphere and the plant, but is also central to the response to management. LAI is indeed
106 largely seen as a driver of both water and carbon fluxes (Reich, 2012; del Campo et al.,
107 2022). Given its high nutrient demand the production of leaves also affect the nutrient cycle
108 (Ollinger et al., 2008) and is a potentially crucial driver of forests response to harvesting.

109

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

123

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

129 consequences of wood harvesting on forests carbon sink strength. Here we intend to show
130 that sustainable management replaces natural competition by regulating leaf area without
131 affecting ecosystem fluxes in temperate forests. Based on observational data, literature and
132 modeling we want to identify mechanistic reasons for this presumption and explore the
133 possibilities of defining levels of sustainable partial cuttings from the perspective of carbon
134 fluxes, key to designing forest managements strategies able to maintain high biomass as well
135 as forest C uptake over multiple cutting cycles. We use the model LPJ-GUESS to illustrate
136 the diminishing returns of GPP with increasing LAI in models as well.
137
138 **Materials and methods**
139
140 ***Observational flux data based on eddy covariance measurements on the FLUXNET sites.***
141 In its 2015 release, FLUXNET represented 212 sites worldwide of eddy covariance. In order
142 to measure the impact of management over the carbon fluxes, we have compiled flux data
143 from the 29 FLUXNET sites (https://fluxnet.org/data/fluxnet2015-dataset/) that comprise 19
144 managed and 10 unmanaged sites (unmanaged is used in the sense of "intact" forests of
145 Roebroek et al., 2023) with long-term measurements (i.e., >10 years, whenever possible) in
146 temperate forests (**Supp. Table S1**). Unfortunately, there is no site that covers unmanaged
147 conifers. For each site we have compiled the forest type, stand type, and the fluxes over their
148 monitoring period. We completed these data with estimations of the LAI during the period
149 2000-2020 and of the standing biomass.
150 Noticeably, selective harvesting took place on 11 of the managed sites during the period of
151 flux monitoring, several interventions being quite intensive (Supp. Table S3): for instance,
152 36% LAI removal in Fontainebleau site (FR), 30% removal in Bily Kriz site (CZ). Other
153 managed sites have experienced interventions prior to the monitoring but not necessarily
154 during the monitoring period, given the long periods of time separating interventions.
155 Furthermore, during the period of flux monitoring, forests experienced repeated events of
156 storm, drought and heat such as that of 2003, affecting ecosystem fluxes independent of
157 management.
158 Further, we have compiled LAI estimations for the analyses, for each of the FLUXNET sites.
159 LAI measurements, however, are not standard across sites, and field measurements are not
160 always available (5 sites had no field measurements). In this situation remote-sensed
161 estimations were used instead based on the MCD15A3H version 6.1 MODIS data level 4 (see
162 **Supplementary Table S1**, with references for each estimation). Field-based measurements
163 were based on hemispherical images with site-specific clumping factors (Gielen et al. 2018).
164
165 The eddy covariance method measures high-frequency atmospheric CO_2, concentrations and
166 wind speed fluctuations which are then used to compute net ecosystem exchange (NEE).
167 These measurements are then used to compute net ecosystem exchange (NEE) with inherent
168 uncertainties due to instrument limitations, atmospheric conditions, and data processing
169 methods. Flux data were filtered based on USTAR threshold levels, following the method
170 described by Pastorello et al. (2020), to exclude measurements taken under low turbulence
171 conditions. Errors have been estimated using bootstrapping 200 times with different friction
172 velocity values.

173   The fluxes of carbon exchanged between the forest ecosystem and the atmosphere are
174   generally divided into components that are physiologically meaningful: the gross primary
175   production (GPP) corresponds to the photosynthesis of plants, and the ecosystem respiration
176   (Reco) releasing CO_2. Reco consists of plant respiration (so-called autotrophic respiration)
177   and respiration by heterotrophic organisms (so-called heterotrophic respiration). The NEE
178   can be estimated by eddy covariance, partitioning into the other elementary fluxes follows
179   data-driven models (Valentini et al., 2002) and is here expressed following the biospheric
180   convention (i.e., negative when CO_2 leaves the atmosphere).
181

182   We compared the mean fluxes during the period of time available of managed and
183   unmanaged sites. For testing the significance of differences in NEE we used the Wilcoxon
184   rank test because data were not distributed normally. GPP and Reco have a distribution that
185   does not differ significantly from a normal distribution. The Mann-Whitney test has been
186   implemented to compare managed versus unmanaged sites which works with unequal sample
187   sizes. For GPP and Reco, their distributions being normal (Lasslop et al. 2018), but their
188   variances unequal, the Welch t-test was used instead. Subsequently, two-way analysis of
189   variance for unbalanced designs was performed on the data to check if the interaction
190   between the management and the number of observations by FLUXNET site has a significant
191   effect on GPP, Reco, and NEE.
192   The relationship between GPP and LAI for the FLUXNET observational site was represented
193   as a nonlinear asymptotical model. The fitting was based on the nonlinear fit function *nls* (nls
194   standing for nonlinear least square) in R. The pseudo-R^2 represents the proportion of variance
195   that was explained by the model, in lieu of the R^2 which assumptions cannot be completely
196   satisfied with nonlinear models (Schabenberger and Pierce 2002). It was computed as
197   *pseudo-R^2* = 1 − (var(y_{fit})/var(y)), where var(y_{fit}) is the variance of the predicted value (GPP
198   here), while var(y) is the variance of the variable (GPP) within the dataset. All statistical
199   analyses were performed in R version 4.3.2 (R Core Team, 2023).
200

201   ***Harvesting and carbon fluxes***
202   Harvesting takes many forms in forest management and can have different intensities.
203   Harvesting is defined in a general way as the removal of wood by tree cuttings of any kind,
204   thus including tending, thinning (targeting either dominant or sub-dominant trees) and
205   selective cuttings from either status. While short- and medium-term effects of selective
206   harvesting are being considered, this study will not cover the comparison of forest products
207   with other bioenergy sources (product and energy substitution). In the following, clear-
208   cutting, or final felling of a rotation, are treated separately from selective cuttings as they
209   need an assessment at landscape or management unit-scale. The measurement of carbon
210   fluxes using the EC method is limited to a plot-scale, with a footprint commonly of about 0.1
211   km^2. Throughout this study, harvesting refers to practices of selective harvesting at low to
212   moderate intensity as common in temperate forests. For example, removal of harvest
213   residuals is widely seen as negative because of the nutrient and soil carbon depletion it causes
214   (Achat et al., 2015, Mayer et al., 2020).
215

216

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. S2). 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. 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

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

267

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

296

297 ### *Responses of fluxes to sustainable harvesting: empirical evidence from eddy covariance*
298 The FLUXNET associated site data showed that past and current management has little
299 influence on the aboveground biomass and LAI of the sites (**Fig. 2**). Highest biomass was
300 reached with the old-growth *Eucalyptus regnans* (F. Muell.) site in Australia (Wallaby Creek

301   site, with 36106 g dry matter m^{-2}). Unfortunately, there is no managed site of *E. regnans* for
302   comparison. Otherwise, the range of values is very similar among managed and unmanaged
303   sites.

304

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

319

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

336

337   **Discussion**

338   With the introduction of the eddy covariance method, long time series of carbon fluxes
339   became available over a variety of biomes, with most monitoring sites being under regular
340   forest management (Franz et al., 2018). Based on these time series, our synthesis showed
341   here that GPP and NEE remain largely unaffected by partial harvesting, as also reported by

342   site-level analyses for several forest types and species (Granier et al., 2008; Launianen et al.,
343   2022; Lindroth et al., 2018; Pilegaard et al., 2011; Peichl et al., 2022; Vesala et al., 2005).
344   These results are in agreement with the long-established empirical knowledge that stand
345   productivity remains unaffected by thinnings when their intensity remains below a threshold
346   (expressed in terms of stem density or basal area) (Assmann 1970, Pretzsch and Schütze
347   2009). Similarly, Vesala et al., 2005 observed no visible effects of thinnings on the NEE
348   despite the reduction of LAI from 8 to 6 m^2 m^{-2} in a Scots pine (*Pinus sylvestris* L.) stand.
349   Granier et al. (2008) reported for *Fagus sylvatica* (L.) stands no decrease in either NEE or
350   GPP despite the thinning that decreased LAI from 7.4 to 4.8 m^2 m^{-2}. These results are in
351   agreement with Herbst et al. (2015) and are confirmed by the global database of Luyssaert et
352   al. (2007) which shows that managed forests globally achieved similar, or even larger GPP,
353   than unmanaged forests.

354

355   The harvest effect on LAI appears to be short-term in temperate forests (del Campo et al.,
356   2022) as also suggested by the available LAI time-series of the sites studied here (**Supp. Fig.
357   S1**). For instance, according to Granier et al. (2008) LAI in *Fagus sylvatica* stands was
358   restored to its pre-thinning level within two years. Disturbances, particularly stand-replacing
359   disturbances such as windthrow, fire or clear-cuts have a different dimension and need to be
360   evaluated at landscape scale. Our study deals with thinning operations where the main
361   canopy is reduced but not removed, keeping LAI beyond or near to its saturation threshold.
362   This also justifies the choice of focusing on temperate forests where the lower species
363   richness and age ranges may slow the recovery of carbon uptake to catastrophic events, in
364   contrast to tropical forests (Brando et al., 2019). For boreal forests, the IBFRA-Report
365   (Högberg et al., 2021) shows that biomass increased significantly over the past decades only
366   in intensively managed landscapes, but not in less intensively managed forest landscapes
367   (i.e., landscapes with a high proportion of unmanaged forests). In the latter, large-scale
368   disturbances such as wildfires caused losses of biomass and prevented a build-up of forest
369   carbon stocks. In comparison, the biomass gain in non-managed temperate forests is very
370   small (Roerbroek et al., 2023). Roerbroek et al. (2023) indeed suggests that betting on
371   increasing the forests stocks is not only risky, given the increases in weather extremes, but
372   loses the societal benefit of wood products as well as the potential to store a portion of the C
373   over longer term.

374

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

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

399 While shade tolerance varies among species (Ameztegui et al., 2016), as reflected by
400 different maximum LAI values (Valladares and Niinemets 2008), the threshold for light
401 compensation is probably very similar across forest types or species despite variations in the
402 canopy structure. Accordingly, in our study, the species traits did not show significant
403 correlations to either LAI or flux values. This suggests that increasing LAI beyond a demand-
404 driven threshold has other functions, for instance a competitive function with neighboring
405 trees (Pretzsch and Schütze 2009, Jucker et al., 2014) not only for light but also for nutrients
406 (e.g., in a pre-emption strategy, Craine and Dybzinski 2013), as a buffer against disturbance
407 (e.g., herbivory) and a pool of nutrient reserves, ready for rapid re-allocation in case of
408 sudden demand (Körner 2009). Anten (2005) shows that canopy photosynthesis models
409 predict LAI values greater than optimal values for photosynthesis and quote theoretical
410 studies that conclude to a LAI always exceeding the physiologically optimal value for
411 competitive purposes. Avoiding a neighbor increases the resources of water and nutrients for
412 the dominant tree. This surplus fraction is temporarily diminished by selective harvesting,
413 explaining the lack of response of the main C fluxes at canopy level across a wide range of
414 LAI. Accordingly, a moderated management can be seen as a substitution of self-thinning
415 when forest stands are kept close but below self-thinning density levels (Luyssaert et al.,
416 2011).

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

429   excess of 5 m^2 m^{-2} (e.g., **Figure 3**) and even over 10 m^2 m^{-2} in shade-tolerant species
430   (Schulze et al., 1994; Asner et al., 2003; Law et al., 2001; Iio and Ito, 2014). Out of the 29
431   sites we studied here (Fig. 1), 16 display LAI values in excess of 4.5 m^2 m^{-2}. Issues related to
432   the leaf clumping, requiring a specific correction factor as specified by the eddy-site protocol
433   (Gielen et al. 2018), add up to the already large uncertainties in the estimated LAI.

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

453

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

470

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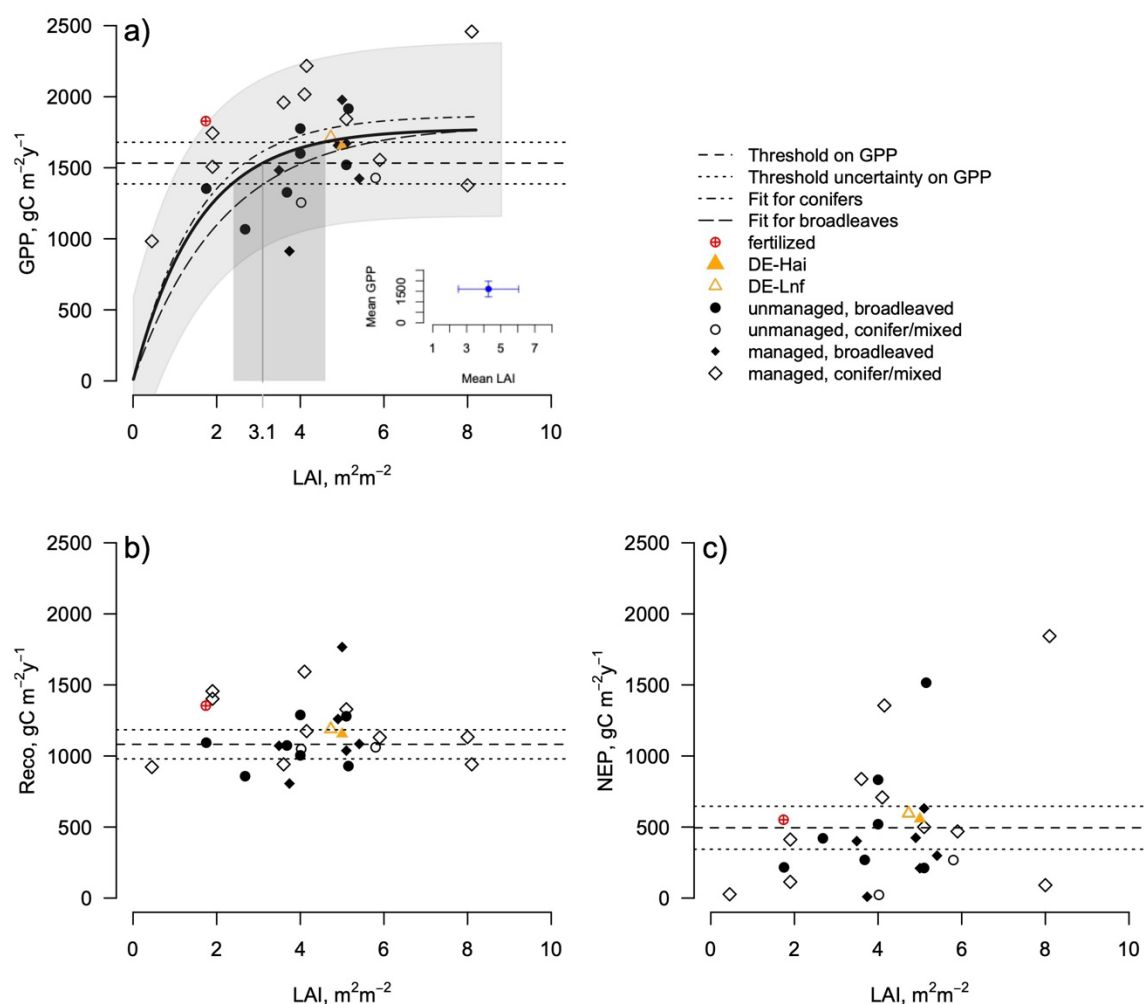
Figure 1. Relation between the GPP (a), the Reco (b), the NEP (= -NEE, c) and the LAI on the eddy covariance sites (FLUXNET sites, see Supp. Table S1,2) of both managed and unmanaged temperate forests per stand types.

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.
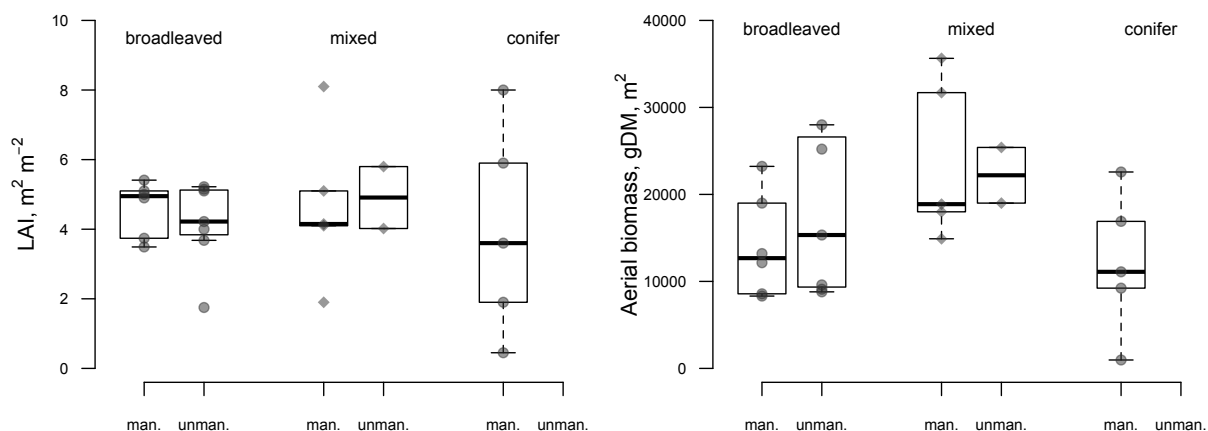
Figure 2. Comparison of the LAI and aboveground biomass values for the managed and unmanaged sites, depending on the forest type. The site AU-Wac (Australia, natural *Eucalyptus regnans* F. Muell.) is an extreme value due to low decomposition (Supp. Fig. 2) and was not included in the biomass comparison.
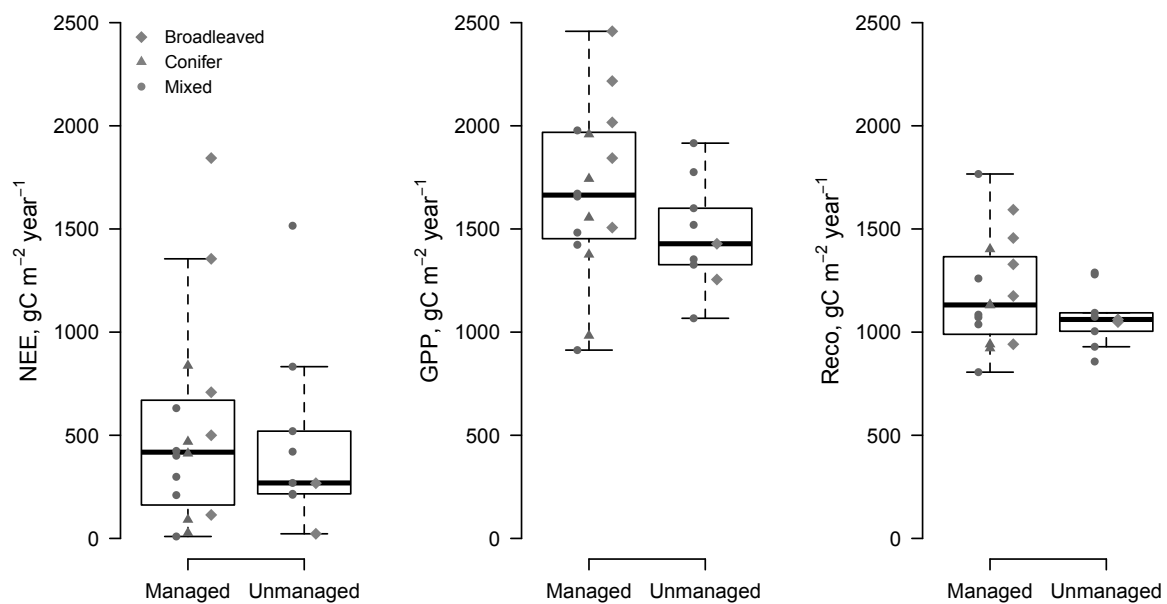
752
753 **Figure 3**. Comparison of the flux data from managed and unmanaged FLUXNET sites.
754 Dots represent the site-level mean values over the monitoring period.
755
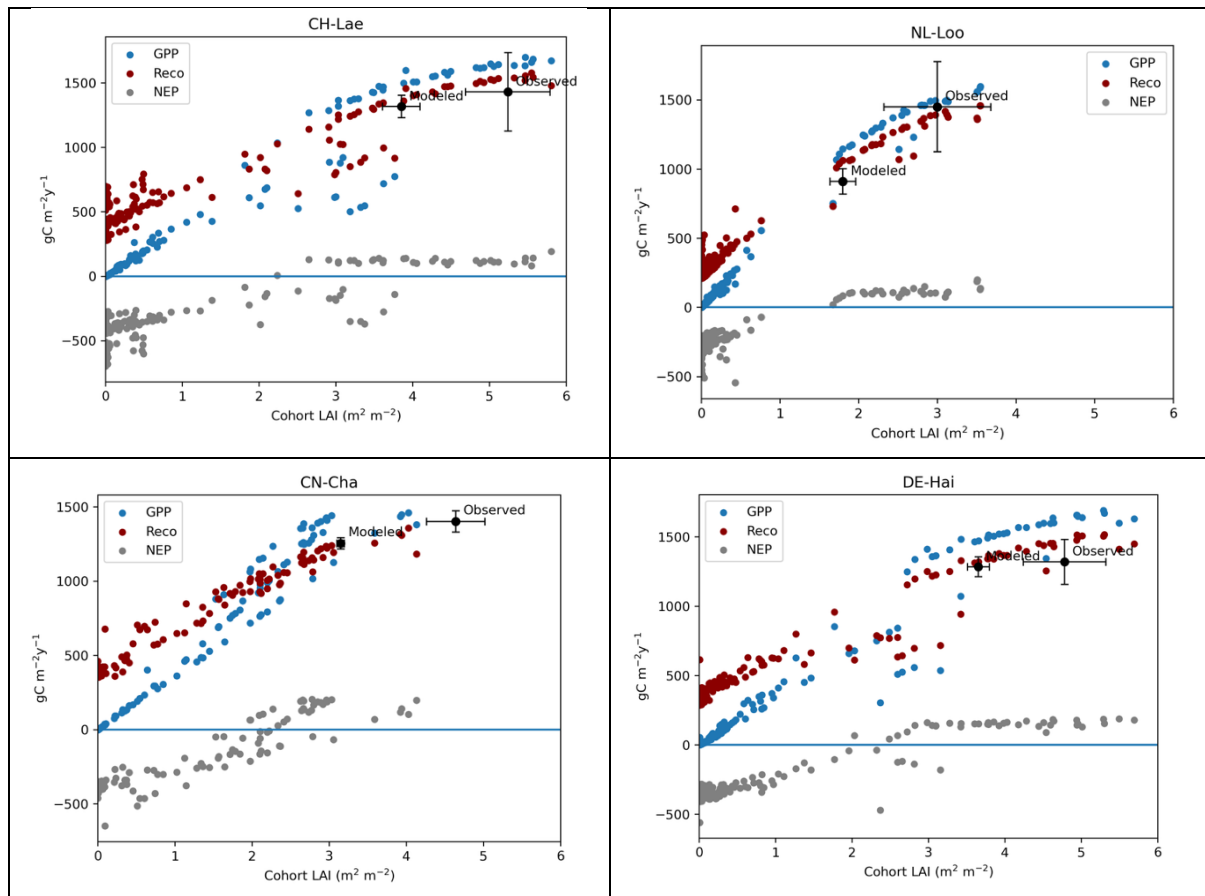
Figure 4. Variations of GPP, NEP and Reco along a gradient of LAI as modelled using LPJ-GUESS shown for 4 sites with contrasted maximum LAI and forest types: CH-Lae for mixed forest type with high LAI, NL-Loo for conifers with low LAI, DE-Hai broadleaved with high LAI and CN-Cha with low LAI broadleaved. 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.

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

773

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

774

775

776   **Table 2**. Estimation of the effect of management and forest type on the LAI or on the fluxes.
777   Interactions (management x type) were tested and not found significant, and are therefore not
778   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

779