

*Underestimation of global photosynthesis
in Earth System Models due to
representation of vegetation structure*

Article

Accepted Version

Braghiere, R. K., Quaife, T. ORCID: <https://orcid.org/0000-0001-6896-4613>, Black, E. ORCID: <https://orcid.org/0000-0003-1344-6186>, He, L. and Chen, J. M. (2019)
Underestimation of global photosynthesis in Earth System Models due to representation of vegetation structure. *Global Biogeochemical Cycles*, 33 (11). pp. 1358-1369. ISSN 1944-9224 doi: [10.1029/2018GB006135](https://doi.org/10.1029/2018GB006135) Available at <https://centaur.reading.ac.uk/86393/>

It is advisable to refer to the publisher's version if you intend to cite from the work. See [Guidance on citing](#).

To link to this article DOI: <http://dx.doi.org/10.1029/2018GB006135>

Publisher: American Geophysical Union

All outputs in CentAUR are protected by Intellectual Property Rights law, including copyright law. Copyright and IPR is retained by the creators or other copyright holders. Terms and conditions for use of this material are defined in the [End User Agreement](#).

www.reading.ac.uk/centaur

CentAUR

Central Archive at the University of Reading

Reading's research outputs online

Underestimation of global photosynthesis in Earth System Models due to representation of vegetation structure

R. K. Braghieri^{1,2,3,4}, T. Quaife⁴, E. Black⁵, L. He^{6,7}, and J. Chen⁷

¹ Jet Propulsion Laboratory, California Institute of Technology, 4800 Oak Grove Drive, Pasadena, CA, 91109 USA.

² Joint Institute for Regional Earth System Science and Engineering, University of California at Los Angeles, Los Angeles, CA, 90095 USA.

³ INRA-Supagro, UMR 1222 Eco&Sols, Montpellier, France.

⁴ National Centre for Earth Observation, Department of Meteorology, University of Reading, Reading, United Kingdom.

⁵ National Centre for Atmospheric Science, Department of Meteorology, University of Reading, Reading, United Kingdom.

⁶ Department of Geography and Program in Planning, University of Toronto, Toronto, Canada.

⁷ Laboratory of Environmental Model and Data Optima, Laurel, Maryland, USA.

Corresponding author: Renato K. Braghieri (renato.braghiere@gmail.com)

Key Points:

- Earth System Models (ESMs) may significantly underestimate global photosynthesis because they do not take vegetation structure into account.
- Introducing vegetation clumping into ESMs with multi-layered canopy schemes alleviates light limitation of photosynthesis at lower canopy levels.
- In our study, the addition of vegetation clumping into the land surface scheme of the UKESM resulted in an additional uptake of carbon by photosynthesis of 5.53 PgC yr⁻¹ globally and 4.18 PgC yr⁻¹ between 20°S-20°N latitude.

1 **Abstract**

2 The impact of vegetation structure on the absorption of shortwave radiation in Earth System
3 Models (ESMs) is potentially important for accurate modelling of the carbon cycle and hence
4 climate projections. A proportion of incident shortwave radiation is used by plants to
5 photosynthesize and canopy structure has a direct impact on the fraction of this radiation which
6 is absorbed. This paper evaluates how modelled carbon assimilation of the terrestrial biosphere is
7 impacted when clumping derived from satellite data is incorporated. We evaluated impacts of
8 clumping on photosynthesis using the Joint UK Land Environment Simulator, the land surface
9 scheme of the UK Earth System Model. At the global level, Gross Primary Productivity (GPP)
10 increased by $5.53 \pm 1.02 \text{ PgC yr}^{-1}$ with the strongest absolute increase in the tropics. This is
11 contrary to previous studies that have shown a decrease in photosynthesis when similar clumping
12 data sets have been used to modify light interception in models. In our study additional
13 transmission of light through upper canopy layers leads to enhanced absorption in lower layers in
14 which photosynthesis tends to be light limited. We show that this result is related to the
15 complexity of canopy scheme being used.

16 **Plain Language Summary**

17 Plants need sunlight to photosynthesize; however, the way in which light absorption is typically
18 described by climate models is not very realistic because it does not take into account structural
19 differences in forest canopies. Identifying more realistic ways to represent these processes in
20 forests would allow us to better predict photosynthesis and to have a greater understanding of the
21 impact of future climate change. In our paper we discuss a method to include information about
22 vegetation structure derived from satellites in climate models. Our results indicate that such
23 models underestimate the amount of light reaching plants in the lower layers of dense forests.
24 Consequently, global photosynthesis is likely underestimated in climate models due to a lack of
25 consideration of plant structural variability.

26 **1 Introduction**

27 Understanding the global carbon cycle is critically important for understanding current
28 and future climate change. The terrestrial biosphere sequesters around 25% of anthropogenic
29 carbon emissions (Le Quéré et al., 2018) but there remains uncertainty around exactly what
30 processes drive this (Ciais et al., 2019) and whether or not this sink will be maintained in the
31 future. A reduction in sink strength due to climatic factors could be a significant positive
32 feedback to climate change. To be able to model the future evolution of this uptake of carbon
33 requires the ability to correctly model the underlying processes. This paper focuses specifically
34 on photosynthesis in the terrestrial biosphere and the how we model the light interception in
35 plants which drives this.

36 The uptake of carbon by terrestrial photosynthesis is the largest component flux in the
37 global carbon cycle. Despite this its overall magnitude and global spatial distribution remains
38 poorly understood. Estimates of Gross Primary Productivity (GPP) in the literature range from
39 120 PgC yr^{-1} to 175 PgC yr^{-1} . The estimate of global GPP presented in the first IPCC report was
40 set in the interval $90\text{-}120 \text{ PgC yr}^{-1}$ (Watson et al., 1990) followed by all the other IPCC reports
41 giving a fixed global GPP value equals to 120 PgC yr^{-1} (Melillo et al., 1995; Prentice et al., 2001;
42 Denman et al., 2007). More recently, the last IPCC report (Ciais et al., 2013) updated the value
43 of global GPP to $123 \pm 8 \text{ PgC yr}^{-1}$ based on model tree ensemble (MTE) and Eddy Covariance

44 (EC) flux (Beer et al., 2010); however, the value of GPP strongly depends on the method used
45 and they often disagree in long-term trends and spatial patterns (Jung et al., 2011; Anav et al.,
46 2015; Jiang & Ryu, 2016; Knauer et al., 2017; He, Chen, Liu, et al., 2017; He, Chen, Croft, et al.,
47 2017; MacBean et al., 2018).

48 For the global carbon budget 2007–2016, an imbalance of 0.6 PgC yr^{-1} was estimated,
49 indicating possible underestimated values in carbon sinks, such as global photosynthesis (Le
50 Quéré et al., 2018). Welp et al. (2011) estimated global GPP to be somewhere in between 150-
51 175 PgC yr^{-1} based on $^{18}\text{O}/^{16}\text{O}$, and in a study based on ^{13}C it was found that more GPP should
52 be attributed to the Amazon region (Chen et al., 2017). Koffi et al. (2012) presented a study
53 based on data assimilation with atmospheric CO_2 and ecosystem models with an estimated global
54 GPP of $146 \pm 19 \text{ PgC yr}^{-1}$. More recent studies using Solar Induced Florescence (SIF) predicted
55 global GPP to be 144 PgC yr^{-1} ; closer to most Earth System Models (ESMs) estimates than the
56 MTE or MODIS data sets (Anav et al., 2015).

57 A key process required for modelling photosynthesis is the interception of light, which is
58 typically achieved using a vegetation radiative transfer (RT) model. A commonly used
59 vegetation RT model in many ESMs is the two-stream scheme of Sellers (1985) and a key
60 assumption in the Sellers scheme is that leaves are randomly arranged in a plane parallel
61 medium. This assumption is in common with many other vegetation RT schemes and is almost
62 ubiquitous amongst those used in Climate and Earth System models. In reality, however,
63 vegetation does not arrange itself in such a perfectly random fashion. An important question,
64 therefore, is to ask what extent this assumption affects predictions of the photosynthetic flux of
65 carbon into the land surface.

66 A simplification that results from the plane-parallel turbid medium approximation is a
67 lack of representation of gaps in the canopies. The term ‘gaps’ is used here in the sense of
68 ‘openness’, i.e., canopy openings, which light goes through without being intercepted. For most
69 natural forest stands, savannah, and shrubland, various sizes of gaps exist between and within
70 tree crowns. Neglecting these gaps has been shown to result in errors when estimating shortwave
71 radiation interception.

72 Previous studies have shown that two-stream schemes can exhibit significant biases in
73 comparison to more accurate 3D radiative transfer models and observations (Pinty et al., 2006;
74 Ni-Meister et al., 2010; Kobayashi et al., 2012; Loew et al., 2014; Hogan et al., 2018). Despite
75 this two-stream schemes remain attractive due to their computational efficiency. Highly detailed
76 3D radiative transfer models exist but they cannot be directly used in ESMs due to their
77 computational expense (Yang et al., 2001) and the large number of parameters required (Loew et
78 al., 2014). One approach to account for 3D canopy structure in two-stream schemes is to include
79 simple parameterizations of 3D effects on shortwave radiation partitioning (Pinty et al., 2006). In
80 the present study, we modify JULES, the land surface scheme of the UK Earth System Model
81 (UKESM), to ingest a global dataset of canopy clumping derived from satellite data, in order to
82 determine the impact of vegetation canopy structure on modelled global photosynthesis.

83 Although this modification results less light absorption by vegetation in the model it also drives
84 an additional uptake of carbon by photosynthesis of 5.53 PgC yr^{-1} globally and 4.18 PgC yr^{-1}
85 between 20°S - 20°N latitude. The primary mechanism we attribute this to is the increased amount
86 of light reaching lower layers of the canopy in which photosynthesis tends to be limited by
87 available light. Conversely photosynthesis in the upper canopy layers, which absorb less light
88 once clumping is included, are not typically light limited and so the reduction in absorbed
89 radiation has less impact.

90 2 Models and Methods

91 2.1 Model description

92 The most commonly used method to account for structure in a vegetation RT model is to
 93 introduce a clumping index (Ω) (Nilson, 1971) to scale leaf area index (LAI). This can be easily
 94 implemented into the two-stream scheme; wherever LAI appears in the equations it is scaled by
 95 Ω . Hence the two stream equations become:

$$\begin{aligned}
 96 \quad \bar{\mu} \frac{dI^\uparrow}{dLAI} + [1 - (1 - \beta)\omega]I^\uparrow - \omega\beta I^\downarrow &= \omega\bar{\mu}\beta_0 \exp(-KL \cdot \Omega), \\
 97 \quad \bar{\mu} \frac{dI^\downarrow}{dLAI} + [1 - (1 - \beta)\omega]I^\downarrow - \omega\beta I^\uparrow &= \omega\bar{\mu}(1 - \beta_0) \exp(-KL \cdot \Omega)
 \end{aligned} \tag{1}$$

98 where I^\uparrow and I^\downarrow are the upward and downward diffuse radiative fluxes normalised by the incident
 99 flux at the top of the canopy, μ is the cosine of the Sun zenith angle, or the incident beam, K is
 100 the optical depth of direct beam per unit leaf area and is equal to $G(\mu)/\mu$, where $G(\mu)$ is the
 101 projected area of leaf elements in the direction $\cos^{-1}\mu$ (Ross, 1981), $\bar{\mu}$ is the average inverse
 102 diffuse optical depth per unit leaf area, ω is the scattering coefficient and is given by $\rho_{\text{leaf}} + \tau_{\text{leaf}}$,
 103 the leaf reflectance and transmittance respectively, and L is the cumulative LAI from the top of
 104 the canopy. β and β_0 are upscattering parameters for the diffuse and direct beams, respectively.
 105 In this context Ω corresponds to the structure factor described in Pinty et al. (2006) except that it
 106 is assumed not to vary with zenith angle.

107 The Joint UK Land Environment Simulator (JULES; Best et al., 2011; Clark et al., 2011),
 108 is the land surface scheme of the new UK Earth System Model (UKESM). It uses the Sellers RT
 109 model to calculate light interception and absorption in vegetation. The option to include a
 110 clumping index was added in version 4.6 with a default value of 1.0 (i.e., no clumping), allowing
 111 user to prescribe other values where data is available. The variable was originally implemented
 112 in JULES with a single value per plant functional type (PFT), and it was tested and evaluated
 113 over crops by Williams et al. (2017) who showed that it was necessary to include clumping (i.e.
 114 $\Omega < 1.0$) to correctly model the productivity of maize for a field site in Nebraska, USA. For this
 115 paper we modified JULES to read in a spatially varying map of clumping for each PFT
 116 (described in Section 2.2).

117 We used JULES version 4.6 with the Global Land (GL) 4.0 configuration (Walters et al.,
 118 2014) with the WATCH-Forcing-Data-ERA-Interim data set (Weedon et al., 2014) at 0.5° spatial
 119 resolution and temporal resolution of 3 hours. The Harmonized World Soil Database version 1.0
 120 data set (Nachtergaele et al., 2008) and the model of runoff production (TOPMODEL) were
 121 applied following Clark and Gedney (2008). Leaf area index was determined prognostically by
 122 the JULES phenology module (Cox, 2001) updated every 10 days. Prior to performing the global
 123 scale model simulations, the soil moisture and temperature were brought to equilibrium using a
 124 5-year global spin-up by cycling 1 year of meteorological data. JULES GL4.0 uses 5 PFTs:
 125 broadleaf trees, needle-leaf trees, C3 grasses, C4 grasses, and shrubs.

126 By default, JULES computes light interception and photosynthesis in 10 vertical canopy
 127 layers. Leaf-level photosynthesis in each layer is estimated as the minimum rate of three
 128 assimilation regimes as proposed by Farquhar et al. (1980) and modified by Collatz et al. (1991,
 129 1992): (i) the Rubisco-limited rate or carbon limiting regime; (ii) the light-limited rate, and; (iii)
 130 the carbon compound export limitation for C3 plants or PEP-carboxylase export limitation for
 131 C4 plants, referred to as the electron transport or export limiting regime. The multilayer approach

132 simulates the transition between the Farquhar limiting regimes at each canopy layer, resulting in
133 increased carbon limitation towards the top of the canopy and increased light limitation towards
134 the bottom of the canopy (Clark et al., 2011). The light-limited rate of photosynthesis in each
135 layer is proportional to the fraction of absorbed photosynthetically active radiation (fAPAR) in
136 that layer. Consequently, including clumping in the radiative transfer scheme directly affects the
137 light limited rate of photosynthesis but not the Rubisco or export limited rates.

138 We performed two runs of JULES for the year 2008 with and without a prescribed value
139 of clumping index. The year was chosen as it is close to the date of production of the clumping
140 map (i.e., 2006) and an ENSO neutral year, unlike 2006-2007, which was a weak El Niño.

141 2.2 Global clumping index map

142 The global clumping map of He et al. (2012) was used to provide clumping index data for
143 JULES. It has a spatial resolution of 500 m and was produced for the year of 2006. We assume
144 that the global clumping index map in 2006 is still reliable for modelling GPP in 2008 since the
145 inter-annual variation of clumping index is general small (He et al., 2016). The data were derived
146 from the NASA-MODIS BRDF/albedo product (MCD43) by considering the difference in
147 forward and backward scattering from the surface, which is primarily controlled by the structure
148 of the vegetation. This follows the methodology of Chen et al. (2005) but with an additional
149 correction to the magnitude of the MODIS hotspot. The method uses a 4-Scale BRDF model
150 (Chen et al. 1997) that considers different scales of canopy clumping: tree groups, tree crowns,
151 branches and shoots. This is equivalent to the assumptions implicit in clumping as implemented
152 in JULES. Pinty et al. (2006) provide a detailed discussion of this type of clumping index as
153 applied to two-stream models.

154 We scaled up the He et al. (2012) data to the resolution of the model run (0.5°) on a per-
155 PFT basis by using the GLC2000 land cover data (Bartholome & Belward, 2005). The GLC2000
156 is also used in the production of the clumping dataset and to prescribe the distribution of the 5
157 PFTs used by JULES. The total clumping index map is shown in Figure 1. Values less than one
158 indicate clumping, with smaller values indicating greater clumping. The most clumped areas are
159 the boreal forests and areas with sparse vegetation, while the least clumped areas are in the
160 presence of grasses, e.g., over savannahs in Africa and crops in the USA and Asia. Tropical
161 forests show intermediate levels of clumping, which does not fit with many below canopy
162 observations of clumping. He et al. (2012) argue that ground based measurements generally
163 underestimate clumping in dense forests (i.e., overestimate the clumping index value) because
164 they are overly affected by lower-level branches. Pisek et al. (2013) further confirmed that in
165 moderate to dense forests with developed bottom layers, *in situ* measurements of clumping near
166 the surface tend to considerably underestimate the overall canopy-level clumping. Olivas et al.
167 (2013) found that the mean LAI above 1 m using litter-fall collection was 5.54 ± 0.3 at an old-
168 growth tropical rainforest, while the effective LAI from hemispherical photographs was only
169 3.45 ± 0.1 , implying a clumping index of 0.62.

170 2.3 Benchmarking data

171 We used the MTE global GPP dataset (Jung et al., 2011) as a reference. It is a monthly
172 global data product at 0.5° resolution which uses a statistical method based on machine learning
173 techniques referred to as model tree ensembles (MTE). The MTE global GPP was trained against
174 flux tower GPP estimates at site level using fAPAR from satellite observations and
175 meteorological data as explanatory variables. Site level GPP estimates from 178 FLUXNET sites

176 were incorporated in the production of the data following quality filtering and partitioning of net
177 ecosystem exchange into GPP and ecosystem respiration based on Lasslop et al. (2010). The
178 MTE product is available since 1982 but it is important to interpret it carefully since flux tower
179 observations started a decade after that with a limited number of sites sparsely distributed and
180 mainly across Europe and North America. Therefore, there is a large uncertainty of the MTE
181 GPP over regions with limited flux tower sites including most parts of Africa and South
182 America, as well as Tropical and Northern Asia (Anav et al., 2015).

183 **3 Results**

184 3.1 The impact of vegetation canopy structure on modelled global fAPAR

185 The first order impact of adding clumping to the vegetation radiative transfer scheme in
186 JULES is to reduce fAPAR. Figure 2 shows a global map of fAPAR differences between JULES
187 with and without clumping included. fAPAR decreases across the entire globe when clumping is
188 added because it acts to decrease the effective leaf area available to intercept light. However, in
189 addition to reducing the overall fAPAR, the relative distribution of absorption vertically through
190 the canopy is also modified. Layers at the bottom canopy have more light directly incident upon
191 them due to greater transmission through the layers above and therefore can potentially also
192 absorb *more* PAR. Because clumping is applied to all layers evenly, each layer absorbs
193 proportionally less of the PAR directly incident upon it, but the *total* amount of incident PAR on
194 layers except for the top one will always be increased relative to the model without clumping.
195 Hence the total absorption of PAR in a layer can increase even though its fAPAR decreases as
196 long as there is sufficient additional radiation reaching it.

197 The average value of fAPAR for the globe in 2008 according to JULES without clumping
198 is 0.607 ± 0.022 (95% confidence interval). Applying the clumping index shifts the average
199 value to 0.576 ± 0.021 , or the equivalent of a total average decrease of 0.032 ± 0.002 (-5.3%).
200 Some locations of the Earth have much larger divergences in fAPAR, for instance Southwest
201 Canada and Northwest USA, Northeast Russia, and high-altitude regions such as the Himalayas
202 and the Andes; these are areas typically associated with needle-leaved trees.

203 3.2 The impact of vegetation canopy structure on global GPP

204 In our model experiment the addition of clumping systematically *increases* carbon
205 assimilation throughout the globe, resulting in an additional 5.53 ± 1.02 PgC yr⁻¹ in GPP. Figure
206 3 shows the difference in GPP between JULES with clumping (JULES-Clump) and the default
207 version of JULES (i.e., without clumping). The strongest difference between the two model
208 setups is found in the tropics (20°S - 20°N) with additional GPP of 4.18 PgC yr⁻¹, or 75% of the
209 total additional carbon, followed by 1.10 PgC yr⁻¹, or approximately 20% of the total extra GPP
210 in the Northern Hemisphere (20°N - 90°N), and 0.25 PgC yr⁻¹ in the Southern Hemisphere (90°S
211 - 20°S), which corresponds to approximately 5% of the total extra GPP.

212 Figure 4a shows the difference in the absolute difference between JULES-Clump and
213 MTE-GPP, and JULES and MTE-GPP. Regions in blue indicate that including clumping moves
214 the JULES prediction toward the MTE estimate, and red areas indicate the opposite, i.e., JULES-
215 Clump presents larger discrepancies than JULES in comparison to the MTE-GPP product.
216 Tropical forests, the temperate forests in North America, and most of the boreal forests generally
217 move closer the MTE data in JULES-Clump. The red areas on Figure 4a, associated with
218 increasing differences between the MTE and modelled GPP prediction when clumping is

219 included are mainly found in the African and Brazilian savannahs, and sparser areas in the
 220 presence of grasses, especially C4 grasses. C4 grasses have previously been shown to be over-
 221 productive in JULES (Harper et al., 2016) and adding clumping makes it more productive in this
 222 study. It is also likely that the MTE data set itself shows an inaccurate representation of GPP for
 223 C4 grasses, since this PFT is not well sampled in the eddy covariance data that the MTE dataset
 224 is based upon.

225 Figure 4c shows the total GPP in PgC yr⁻¹ for each box in Figure 4b for the MTE-GPP
 226 product, JULES and JULES-Clump, respectively. The error bars on the MTE product were
 227 calculated as the weighted sum of the averaged standard deviation of the ensemble mean of the
 228 25 best model trees associated with the MTE-GPP product for the year 2008. JULES-Clump
 229 consistently shows a higher GPP than the default JULES for all the evaluated areas with a larger
 230 absolute impact over the boxes in the tropics, i.e., Central and South America, $\Delta\text{GPP} = 2.03 \text{ PgC}$
 231 yr^{-1} , or 36.7% of the total additional GPP generated by the addition of clumping, followed by
 232 Africa, $\Delta\text{GPP} = 1.10 \text{ PgC yr}^{-1}$, or 19.9% of the total additional GPP, and South and Southeast
 233 Asia, $\Delta\text{GPP} = 1.05 \text{ PgC yr}^{-1}$, or 19.0% of the total additional GPP. Alone, the tropics are
 234 responsible for an extra 4.18 PgC per year (75.6% of the global ΔGPP).

235 Globally, the 5.53 PgC yr⁻¹ caused by the inclusion of vegetation clumping is equivalent
 236 to an additional 4.8% of GPP for the year of 2008. Although for the majority of regions in Figure
 237 4b JULES GPP are within the error bars of the MTE product, JULES-Clump is closer to the
 238 estimates of the MTE, except for Africa, where JULES is lower than the MTE GPP and JULES-
 239 Clump is higher than it. The most significant change is observed over Central and South America
 240 where the prediction of GPP without clumping is low compared to the MTE GPP.

241 The additional GPP resulting from including clumping is not evenly distributed vertically
 242 though the canopy. The difference in zonal mean GPP in each canopy layer between JULES with
 243 and without clumping is shown in Figure 5. In particular there is a strong enhancement of GPP in
 244 the lower canopy layers for the tropics, whereas the top 3 or 4 layers exhibit reduced
 245 photosynthesis. This is caused by the increase in PAR absorption in the lower layers described in
 246 Section 3.1. Because these layers tend to be light limited this results in a significant boost to the
 247 overall canopy photosynthesis compared to the upper layers which are generally not light limited
 248 (Jogireddy et al., 2006; Mercado et al., 2007; Alton et al., 2007; Huntingford et al., 2008). For
 249 the bottom two layers of the canopy GPP increased more than 50% throughout all latitudes. This
 250 adds further weight to the arguments of He et al. (2018) who highlight the importance of shade
 251 leaves in global photosynthesis.

252 3.3 Is the impact of vegetation canopy structure on global GPP impacted by diffuse
 253 radiation?

254 Throughout all simulations performed in this study the percentage of diffuse incident
 255 shortwave radiation was held constant and equal to 40% as a proxy average value for the whole
 256 globe (Harper et al., 2016). However, the consideration of gaps through the addition of clumping
 257 into the radiative transfer scheme in JULES can enhance the amount of shortwave radiation
 258 reaching bottom layers of the vegetation canopy, as previously discussed. This is true for both
 259 natures of incident light, i.e., either direct, collimated beams, or diffuse, isotropic shortwave
 260 radiation. However, is the impact of canopy clumping on GPP affected by the amount of diffuse
 261 radiation?

262 In order to verify the effect of diffuse light on the impact of clumping on GPP, a test was
 263 performed for 12 FLUXNET sites for the year of 2008 with JULES and JULES-Clump for four

264 different ratios of incident diffuse shortwave radiation to global incident shortwave radiation:
265 20%, 40% (used in all the other runs), 60%, and 80% (Figure 6). Results indicate that across all
266 the evaluated sites, differences in monthly mean GPP fluxes between JULES and JULES-Clump
267 are independent of the amount of diffuse shortwave radiation reaching the surface.

268 One observable pattern in Figure 6 is the diffuse fertilisation effect (Mercado et al., 2009)
269 clearly noticed in sites with high LAI values, e.g., the tropics (BR-Ma2, BR-Sa1) throughout the
270 year, temperate forests (JP-Tak, US-MMS, US-Ha1) and boreal/needle-leaved forests (FI-Hyy,
271 FI-Kaa, DE-Tha) in Summer time, while places with smaller or no noticeable differences
272 between JULES and JULES-Clump are noticed in sites that are not limited by light, because of
273 small LAI values, often associated with drier/grassland sites (ES-Es1, ES-LMa, US-FPe).

274 **4 Discussion**

275 The only other study of which we are aware that tackles this question on a global scale is
276 that of Chen et al. (2012). In that study the authors used a related dataset to prescribe clumping in
277 the Boreal Productivity Simulator (BEPS; Liu et al., 1997) but found that global GPP was
278 *reduced* by 12.1 PgCyr^{-1} . The critical difference between our study and that of Chen et al. (2012)
279 is in the treatment of canopy radiative transfer: our model uses multiple canopy layers each with
280 different proportions of sunlit and shaded leaves, whereas Chen et al. (2012) use a single layer
281 split into sunlit and shaded leaves (a so-called ‘two-leaf’ model). As discussed in the previous
282 sections our result is caused by the greater penetration of light into lower layers boosting
283 photosynthesis in layers that are light-limited. The phenomena we illustrate is to some degree
284 analogous to the so-called “diffuse light fertilisation effect” which has been shown previously to
285 enhance global GPP after the eruption of Mount Pinatubo in 1991 (Mercado et al., 2009). Diffuse
286 light is able to penetrate further down into the canopy than direct beam irradiance.

287 Single layer models cannot redistribute absorbed radiation vertically in the manner we
288 have shown using a layered canopy model. Consequently, there is no preferential alleviation of
289 light-limited photosynthesis at lower levels and no boost to overall canopy photosynthesis.
290 Other examples of models with multi-layered canopy schemes include EALCO (Wang et al.,
291 2001), EDv2.1 (Medvigy et al., 2009), LPJ-GUESS (Smith et al., 2001; Smith et al., 2014),
292 SDGVM (Woodward et al., 1995), and TECO (Wang et al., 2009), and so, similar results would
293 be expected from these models assuming the model structure allows for the inclusion of
294 clumping in the canopy radiation scheme.

295 There is some empirical evidence from field based studies that supports our finding that
296 structure increases GPP (Ahl et al., 2004; Duursma & Makela, 2007; Hardiman et al., 2011;
297 Bohn & Huth, 2017). Hardiman et al. (2011) showed departures from randomness in forest
298 canopies boosted productivity in a transition zone between boreal forests and Northern mixed
299 hardwood. The authors suggested that changes in canopy structure can contribute to resilience
300 of the functioning of ecosystems trees. Atkins et al. (2018) affirms that the inclusion of canopy
301 structural complexity metrics in canopy light absorption models could increase confidence in
302 predictions of biogeochemical cycles and energy balance. Their study including sites from the
303 National Ecological Observation Network and university field stations found that canopy
304 structure was strongly coupled with fAPAR under high light environments, while under low light
305 conditions, when diffuse light predominates, light scattering weakened the dependency of
306 fAPAR on structure. Also, the authors found that a multivariate model including parameters of
307 canopy structure and leaf area index explained around 89% of the inter-site variance in fAPAR.
308 Another observational study by Fahey et al. (2016) found an important contribution of bottom

309 layers of a North American site to canopy productivity as whole. The authors found a connection
310 between sub-canopy tree growth and fAPAR, and indicated a relationship between sub-canopy
311 light availability and canopy structure. Although, they found that sub-canopy growth response
312 was not mediated by fAPAR alone.

313 On a global scale it will be necessary to provide observation of canopy structure from
314 remote sensing instruments. The method of He et al. (2012) can, potentially, be repeated for
315 every year of the MODIS archive and is applicable to other missions with similar characteristics
316 such as Sentinel-3. Arguably, however, this problem also needs addressing using observations
317 that are more directly related to forest structure such as space borne LiDAR from missions such
318 as NASA GEDI (Hancock et al., 2019), or long wavelength RADAR from JAXA's ALOS
319 PALSAR the upcoming ESA Biomass mission. Terrestrial and airborne observations will also
320 be critically important (Longo et al., 2016; Ferraz et al., 2018; Rödiger et al., 2018) and the
321 increased interest in terrestrial scanning LiDAR may help to answer some of these questions
322 (Disney et al., 2010; Mulatu et al., 2019).

323 Our result that tropical photosynthesis is being underestimated in JULES likely applies to
324 the terrestrial biosphere components of all ESMs. Multilayered models will respond in the same
325 way when clumping is introduced, i.e. with greater penetration of light to lower levels. We also
326 argue that single layer models do not represent the impact of clumping of photosynthesis
327 correctly. It is clear, however, that much more investigation is required to understand the correct
328 way to represent structure in these models. The technique used in JULES to include clumping is
329 relatively simple albeit based on well-established theoretical considerations (e.g., Nilson 1971).
330 We note that there are more sophisticated approaches available (Kucharik et al., 1999; Pinty et
331 al., 2006; Ni-Meisters et al., 2010) but these rely on additional parameters which must either be
332 calculated by the underlying land surface model, or input as ancillary data.

333 **5 Conclusion**

334 Our work suggests that ESMs may significantly underestimate photosynthesis in tropical
335 forests because they do not take vegetation structure into account. The dominant effect that
336 introducing clumping has in our study is to alleviate light limitation at lower canopy levels. This
337 tends to have the greatest impact where leaf area index is high and where photosynthesis is not
338 limited by light in higher canopy layers. In our study this effect accounted for an additional
339 uptake of carbon by photosynthesis globally of 5.53 PgCyr⁻¹ and 4.18 PgCyr⁻¹ between 20°S-
340 20°N latitude.

341 **Acknowledgements and Data**

342 The authors declare no conflicts of interest. This research was supported by the 'Science without
343 Borders' program (grant number 9549-13-7) financed by CAPES – Brazilian Federal Agency for
344 Support and Evaluation of Graduate Education within the Ministry of Education of Brazil, and
345 the European Union's Horizon 2020 Research and Innovation programme under grant agreement
346 N. 727217. Tristan Quaipe's contribution was funded by the NERC National Centre for Earth
347 Observation (grant number NE/R016518/1). The global clumping index map by He et al.
348 (2012) is available for download through the following
349 link: https://daac.ornl.gov/VEGETATION/guides/Global_Clumping_Index.html. The global
350 clumping index map per PFT used in this study and a UNIX patch file for JULES version 4.6 is
351 available from <https://github.com/braghiere/JULES-Clump>. The JULES code is available from
352 the UK Met Office code repository: <https://code.metoffice.gov.uk/>. Model simulation results are

353 available from <https://doi.org/10.6084/m9.figshare.9727865.v1>. We also thank M. Reichstein and
 354 M. Jung for providing MTE-GPP data through the site: [https://www.bgc-](https://www.bgc-jena.mpg.de/bgi/index.php/Services/Overview)
 355 [jena.mpg.de/bgi/index.php/Services/Overview](https://www.bgc-jena.mpg.de/bgi/index.php/Services/Overview). The authors thank Pier Luigi Vidale, Sue
 356 Grimmond, Peter North, and the two anonymous reviewers, whose comments improved the
 357 manuscript.

358 References

- 359 Ahl, D. E., Gower, S. T., Mackay, D. S., Burrows, S. N., Norman, J. M., & Diak, G. R. (2004).
 360 Heterogeneity of light use efficiency in a northern Wisconsin forest: implications for
 361 modeling net primary production with remote sensing. *Remote Sensing of Environment*,
 362 93(1–2), 168–178. <https://doi.org/10.1016/j.rse.2004.07.003>
- 363 Alton, P., Mercado, L., & North, P. (2007). A sensitivity analysis of the land-surface scheme
 364 JULES conducted for three forest biomes: Biophysical parameters, model processes, and
 365 meteorological driving data. *Global Biogeochemical Cycles*, 21(1).
- 366 Anav, A., Friedlingstein, P., Beer, C., Ciais, P., Harper, A., Jones, C., et al. (2015).
 367 Spatiotemporal patterns of terrestrial gross primary production: A review. *Reviews of*
 368 *Geophysics*, 53(3), 785–818. <https://doi.org/10.1002/2015RG000483>
- 369 Atkins, J. W., Fahey, R. T., Hardiman, B. H., & Gough, C. M. (2018). Forest Canopy Structural
 370 Complexity and Light Absorption Relationships at the Subcontinental Scale. *Journal of*
 371 *Geophysical Research: Biogeosciences*, 123(4), 1387–1405.
 372 <https://doi.org/10.1002/2017JG004256>
- 373 Bartholomé, E., & Belward, A. S. (2005). GLC2000: a new approach to global land cover
 374 mapping from Earth observation data. *International Journal of Remote Sensing*.
 375 <https://doi.org/10.1080/01431160412331291297>
- 376 Best, M. J., Pryor, M., Clark, D. B., Rooney, G. G., Essery, R. L. H., Menard, C. B., et al.
 377 (2011). The Joint UK Land Environment Simulator (JULES), model description. Part 1:
 378 Energy and water fluxes. *Geoscientific Model Development*, 4, 677–699. Retrieved from
 379 <http://nora.nerc.ac.uk/15031/>
- 380 Bohn, F. J., & Huth, A. (2017). The importance of forest structure to biodiversity–productivity
 381 relationships. *Royal Society Open Science*, 4(1), 160521.
 382 <https://doi.org/10.1098/rsos.160521>
- 383 Chen, J. M., & Leblanc, S. G. (1997). A four-scale bidirectional reflectance model based on
 384 canopy architecture. *IEEE Transactions on Geoscience and Remote Sensing*, 35, 1316 –
 385 1337. <https://doi.org/10.1109/36.628798>
- 386 Chen, J. M., C. H. Menges, & S. G. Leblanc. (2005). Global derivation of the vegetation
 387 clumping index from multi-angular satellite data. *Remote Sensing of Environment*, 97: 447-
 388 457. <https://doi.org/10.1016/j.rse.2005.05.003>

- 389 Chen, J. M., Mo, G., Pisek, J., Liu, J., Deng, F., Ishizawa, M., & Chan, D. (2012). Effects of
390 foliage clumping on the estimation of global terrestrial gross primary productivity. *Global*
391 *Biogeochemical Cycles*, 26(1).
- 392 Chen, J. M., Mo, G., & Deng, F. (2017). A joint global carbon inversion system using both CO₂
393 and ¹³CO₂ atmospheric concentration data. *Geoscientific Model Development*, 10(3), 1131–
394 1156. <https://doi.org/10.5194/gmd-10-1131-2017>
- 395 Ciais, P., Sabine, C., Bala, G., Bopp, L., Brovkin, V., Canadell, J., et al. (2013). Carbon and
396 Other Biogeochemical Cycles. In T. F. Stocker, D. Qin, G.-K. Plattner, M. Tignor, S. K.
397 Allen, J. Boschung, et al. (Eds.), *Climate Change 2013 - The Physical Science Basis* (pp.
398 465–570). Cambridge, United Kingdom and New York, NY, USA: Cambridge University
399 Press.
- 400 Ciais, P., Tan, J., Wang, X., Roedenbeck, C., Chevallier, F., Piao, S.-L., et al. (2019). Five
401 decades of northern land carbon uptake revealed by the interhemispheric CO₂ gradient.
402 *Nature*, 568(7751), 221–225. <https://doi.org/10.1038/s41586-019-1078-6>
- 403 Clark, D. B., & Gedney, N. (2008). Representing the effects of subgrid variability of soil
404 moisture on runoff generation in a Land surface model. *Journal of Geophysical Research*
405 *Atmospheres*. <https://doi.org/10.1029/2007JD008940>
- 406 Clark, D. B., Mercado, L. M., Sitch, S., Jones, C. D., Gedney, N., Best, M. J., et al. (2011). The
407 Joint UK Land Environment Simulator (JULES), model description. Part 2: Carbon fluxes
408 and vegetation dynamics. *Geoscientific Model Development*, 4, 701–722.
409 <https://doi.org/10.5194/gmd-4-701-2011>
- 410 Collatz, G. J., Ball, J. T., Grivet, C., & Berry, J. a. (1991). Physiological and environmental
411 regulation of stomatal conductance, photosynthesis and transpiration: a model that includes
412 a laminar boundary layer. *Agricultural and Forest Meteorology*, 54(2–4), 107–136.
413 [https://doi.org/10.1016/0168-1923\(91\)90002-8](https://doi.org/10.1016/0168-1923(91)90002-8)
- 414 Cox, P. M. (2001). Description of the " TRIFFID " Dynamic Global Vegetation Model. *Hadley*
415 *Centre Technical Note*, 24, 1–17.
- 416 Denman, K. L., Brasseur, G., Chidthaisong, A., Ciais, P., Cox, P. M., R.E. Dickinson, D.
417 Hauglustaine, C. Heinze, E. Holland, D. Jacob, U. Lohmann, S Ramachandran, P. L., et al.
418 (2007). Couplings Between Changes in the Climate System and Biogeochemistry. In S.
419 Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K. B. Averyt, et al. (Eds.), *Climate*
420 *Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth*
421 *Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge, United
422 Kingdom and New York, NY, USA: Cambridge University Press.
- 423 Disney, M. I., Kalogirou, V., Lewis, P., Prieto-Blanco, A., Hancock, S., & Pfeifer, M. (2010).
424 Simulating the impact of discrete-return lidar system and survey characteristics over young

- 425 conifer and broadleaf forests. *Remote Sensing of Environment*.
426 <https://doi.org/10.1016/j.rse.2010.02.009>
- 427 Duursma, R. A., & Makela, A. (2007). Summary models for light interception and light-use
428 efficiency of non-homogeneous canopies. *Tree Physiology*, 27(6), 859–870.
429 <https://doi.org/10.1093/treephys/27.6.859>
- 430 Fahey, R. T., Stuart-Haëntjens, E. J., Gough, C. M., De La Cruz, A., Stockton, E., Vogel, C. S.,
431 & Curtis, P. S. (2016). Evaluating forest subcanopy response to moderate severity
432 disturbance and contribution to ecosystem-level productivity and resilience. *Forest Ecology
433 and Management*, 376, 135–147. <https://doi.org/10.1016/j.foreco.2016.06.001>
- 434 Farquhar, G. D., Caemmerer, S., & Berry, J. A. (1980). A biochemical model of photosynthetic
435 CO₂ assimilation in leaves of C₃ species. *Planta*, 149(1), 78–90.
436 <https://doi.org/10.1007/BF00386231>
- 437 Ferraz, A., Saatchi, S., Xu, L., Hagen, S., Chave, J., Yu, Y., et al. (2018). Carbon storage
438 potential in degraded forests of Kalimantan, Indonesia. *Environmental Research Letters*,
439 13(9), 095001. <https://doi.org/10.1088/1748-9326/aad782>
- 440 Hancock, S., Armston, J., Hofton, M., Sun, X., Tang, H., Duncanson, L. I., et al. (2019). The
441 GEDI simulator: A large-footprint waveform lidar simulator for calibration and validation
442 of spaceborne missions. *Earth and Space Science*, 2018EA000506.
443 <https://doi.org/10.1029/2018EA000506>
- 444 Hardiman, B. S., Bohrer, G., Gough, C. M., Vogel, C. S., & Curtis, P. S. (2011). The role of
445 canopy structural complexity in wood net primary production of a maturing northern
446 deciduous forest. *Ecology*. <https://doi.org/10.1890/10-2192.1>
- 447 Harper, A. B., Cox, P. M., Friedlingstein, P., Wiltshire, A. J., Jones, C. D., Sitch, S., et al.
448 (2016). Improved representation of plant functional types and physiology in the Joint UK
449 Land Environment Simulator (JULES v4.2) using plant trait information. *Geoscientific
450 Model Development*, 9(7), 2415–2440.
- 451 He, L., Chen, J. M., Pisek, J., Schaaf, C. B., & Strahler, A. H. (2012). Global clumping index
452 map derived from the MODIS BRDF product. *Remote Sensing of Environment*, 119, 118–
453 130.
- 454 He, L., Liu, J., Chen, J. M., Croft, H., Wang, R., Sprintsin, M., et al. (2016). Inter- and intra-
455 annual variations of clumping index derived from the MODIS BRDF product. *International
456 Journal of Applied Earth Observation and Geoinformation*.
457 <https://doi.org/10.1016/j.jag.2015.07.007>
- 458 He, L., Chen, J. M., Croft, H., Gonsamo, A., Luo, X., Liu, J., et al. (2017). Nitrogen Availability
459 Dampens the Positive Impacts of CO₂ Fertilization on Terrestrial Ecosystem Carbon and
460 Water Cycles. *Geophysical Research Letters*. <https://doi.org/10.1002/2017GL075981>

- 461 He, L., Chen, J. M., Liu, J., Bélair, S., & Luo, X. (2017). Assessment of SMAP soil moisture for
462 global simulation of gross primary production. *Journal of Geophysical Research:*
463 *Biogeosciences*. <https://doi.org/10.1002/2016JG003603>
- 464 He, L., Chen, J. M., Gonsamo, A., Luo, X., Wang, R., Liu, Y., & Liu, R. (2018). Changes in the
465 Shadow: The Shifting Role of Shaded Leaves in Global Carbon and Water Cycles Under
466 Climate Change. *Geophysical Research Letters*. <https://doi.org/10.1029/2018GL077560>
- 467 Hogan, R. J., Quaife, T., & Braghieri, R. (2018). Fast matrix treatment of 3-D radiative transfer
468 in vegetation canopies: SPARTACUS-Vegetation 1.1. *Geoscientific Model Development*,
469 *11*(1), 339–350. <https://doi.org/10.5194/gmd-11-339-2018>
- 470 Huntingford, C., Fisher, R. A., Mercado, L., Booth, B. B. B., Sitch, S., Harris, P. P., et al. (2008).
471 Towards quantifying uncertainty in predictions of Amazon “dieback”. *Philosophical*
472 *Transactions of the Royal Society of London. Series B, Biological Sciences*, *363*(1498),
473 1857–64. <https://doi.org/10.1098/rstb.2007.0028>
- 474 Le Quéré, C., Andrew, R. M., Friedlingstein, P., Sitch, S., Pongratz, J., Manning, A. C., et al.
475 (2018). Global Carbon Budget 2017. *Earth System Science Data*, *10*(1), 405–448.
476 <https://doi.org/10.5194/essd-10-405-2018>
- 477 Longo, M., Keller, M., Dos-Santos, M. N., Leitold, V., Pinagé, E. R., Baccini, A., et al. (2016).
478 Aboveground biomass variability across intact and degraded forests in the Brazilian
479 Amazon. *Global Biogeochemical Cycles*, *30*(11), 1639–1660.
480 <https://doi.org/10.1002/2016GB005465>
- 481 Jiang, C., & Ryu, Y. (2016). Multi-scale evaluation of global gross primary productivity and
482 evapotranspiration products derived from Breathing Earth System Simulator (BESS).
483 *Remote Sensing of Environment*. <https://doi.org/10.1016/j.rse.2016.08.030>
- 484 Jogireddy, V., Cox, P. M., Huntingford, C., Harding, R. J., & Mercado, L. M. (2006). *An*
485 *improved description of canopy light interception for use in a GCM land-surface scheme:*
486 *calibration and testing against carbon fluxes at a coniferous forest*. Exeter, UK.
- 487 Jung, M., Reichstein, M., Margolis, H. A., Cescatti, A., Richardson, A. D., Arain, M. A., et al.
488 (2011). Global patterns of land-atmosphere fluxes of carbon dioxide, latent heat, and
489 sensible heat derived from eddy covariance, satellite, and meteorological observations.
490 *Journal of Geophysical Research: Biogeosciences*. <https://doi.org/10.1029/2010JG001566>
- 491 Knauer, J., Zaehle, S., Reichstein, M., Medlyn, B. E., Forkel, M., Hagemann, S., & Werner, C.
492 (2017). The response of ecosystem water-use efficiency to rising atmospheric
493 CO₂ concentrations: sensitivity and large-scale biogeochemical implications. *New*
494 *Phytologist*. <https://doi.org/10.1111/nph.14288>

- 495 Kobayashi, H., Baldocchi, D. D., Ryu, Y., Chen, Q., Ma, S., Osuna, J. L., & Ustin, S. L. (2012).
496 Modeling energy and carbon fluxes in a heterogeneous oak woodland: A three-dimensional
497 approach. *Agricultural and Forest Meteorology*, 152(1), 83–100.
- 498 Koffi, E. N., Rayner, P. J., Scholze, M., & Beer, C. (2012). Atmospheric constraints on gross
499 primary productivity and net ecosystem productivity: Results from a carbon-cycle data
500 assimilation system. *Global Biogeochemical Cycles*.
501 <https://doi.org/10.1029/2010GB003900>
- 502 Kucharik, C. J., Norman, J. M., & Gower, S. T. (1999). Characterization of radiation regimes in
503 nonrandom forest canopies: theory, measurements, and a simplified modeling approach.
504 *Tree Physiology*, 19(11), 695–706.
- 505 Lasslop, G., Reichstein, M., Papale, D., Richardson, A., Arneeth, A., Barr, A., et al. (2010).
506 Separation of net ecosystem exchange into assimilation and respiration using a light
507 response curve approach: Critical issues and global evaluation. *Global Change Biology*.
508 <https://doi.org/10.1111/j.1365-2486.2009.02041.x>
- 509 Le Quéré, C., Andrew, R. M., Friedlingstein, P., Sitch, S., Hauck, J., Pongratz, J., et al. (2018).
510 Global Carbon Budget 2018. *Earth System Science Data*, 10(4), 2141–2194.
511 <https://doi.org/10.5194/essd-10-2141-2018>
- 512 Liu, J., Chen, J. M., Cihlar, J., & Park, W. M. (1997). A process-based boreal ecosystem
513 productivity simulator using remote sensing inputs. *Remote Sensing of Environment*.
514 [https://doi.org/10.1016/S0034-4257\(97\)00089-8](https://doi.org/10.1016/S0034-4257(97)00089-8)
- 515 Loew, A., Van Bodegom, P. M., Widlowski, J. L., Otto, J., Quaife, T., Pinty, B., & Raddatz, T.
516 (2014). Do we (need to) care about canopy radiation schemes in DGVMs? Caveats and
517 potential impacts. *Biogeosciences*, 11(7), 1873–1897.
- 518 MacBean, N., Maignan, F., Bacour, C., Lewis, P., Peylin, P., Guanter, L., et al. (2018). Strong
519 constraint on modelled global carbon uptake using solar-induced chlorophyll fluorescence
520 data. *Scientific Reports*, 8(1), 1973. <https://doi.org/10.1038/s41598-018-20024-w>
- 521 Medvigy, D., Wofsy, S. C., Munger, J. W., Hollinger, D. Y., & Moorcroft, P. R. (2009).
522 Mechanistic scaling of ecosystem function and dynamics in space and time: Ecosystem
523 Demography model version 2. *Journal of Geophysical Research: Biogeosciences*, 114(1).
- 524 Melillo, J., Prentice, I., Farquhar, G., & Leemans, R. (1995). Terrestrial biotic responses to
525 environmental change and feedbacks to climate. In J. Houghton, L. Meira Filho, & B.
526 Callander (Eds.), *Climate change 1995: the science of climate change* (pp. 447–81).
527 Cambridge, England: Cambridge University Press.
- 528 Mercado, L. M., Huntingford, C., Gash, J. H. C., Cox, P. M., & Jogireddy, V. (2007). Improving
529 the representation of radiation interception and photosynthesis for climate model

- 530 applications. *Tellus, Series B: Chemical and Physical Meteorology*, 59(3), 553–565.
531 <https://doi.org/10.1111/j.1600-0889.2007.00256.x>
- 532 Mercado, L. M., Bellouin, N., Sitch, S., Boucher, O., Huntingford, C., Wild, M., & Cox, P. M.
533 (2009). Impact of changes in diffuse radiation on the global land carbon sink. *Nature*,
534 458(7241), 1014–7. <https://doi.org/10.1038/nature07949>
- 535 Mulatu, K., Decuyper, M., Brede, B., Kooistra, L., Reiche, J., Mora, B., & Herold, M. (2019).
536 Linking Terrestrial LiDAR Scanner and Conventional Forest Structure Measurements with
537 Multi-Modal Satellite Data. *Forests*, 10(3), 291. <https://doi.org/10.3390/f10030291>
- 538 Nachtergaele, F., van Velthuisen, H., Verelst, L., Batjes, N., Dijkshoorn, K., van Engelen, V., et
539 al. (2008). Harmonized World Soil Database (version 1.0). Rome, Italy and IIASA,
540 Laxenburg, Austria: FAO.
- 541 Nilson, T. (1971). A theoretical analysis of the frequency of gaps in plant stands. *Agricultural*
542 *Meteorology*, 8, 25–38. [https://doi.org/10.1016/0002-1571\(71\)90092-6](https://doi.org/10.1016/0002-1571(71)90092-6)
- 543 Olivas, P. C., Oberbauer, S. F., Clark, D. B., Clark, D. A., Ryan, M. G., O'Brien, J. J., &
544 Ordoñez, H. (2013). Comparison of direct and indirect methods for assessing leaf area index
545 across a tropical rain forest landscape. *Agricultural and Forest Meteorology*, 177, 110–116.
546 <https://doi.org/10.1016/j.agrformet.2013.04.010>
- 547 Pinty, B., Lavergne, T., Dickinson, R. E., Widlowski, J. L., Gobron, N., & Verstraete, M. M.
548 (2006). Simplifying the interaction of land surfaces with radiation for relating remote
549 sensing products to climate models. *Journal of Geophysical Research: Atmospheres*,
550 111(2).
- 551 Pisek, J., & Oliphant, A. J. (2013). A note on the height variation of foliage clumping:
552 comparison with remote sensing retrievals. *Remote Sensing Letters*, 4(4), 400–408.
553 <https://doi.org/10.1080/2150704X.2012.742212>
- 554 Prentice, I. C., Farquhar, G. D., Fasham, M. J. R., Goulden, M. L., Heimann, M., Jaramillo, J. V.,
555 et al. (2001). The carbon cycle and atmospheric carbon dioxide. In *Climate change 2001:
556 the scientific basis: contribution of working group I to the Third Assessment Report of the
557 Intergovernmental Panel on Climate Change*. <https://doi.org/10.1256/004316502320517344>
- 558 Rödiger, E., Cuntz, M., Rammig, A., Fischer, R., Taubert, F., & Huth, A. (2018). The importance
559 of forest structure for carbon fluxes of the Amazon rainforest. *Environmental Research*
560 *Letters*, 13(5), 054013. <https://doi.org/10.1088/1748-9326/aabc61>
- 561 Ross, J. (1981). *The radiation regime and architecture of plant stands*. Boston: Junk.
562 <https://doi.org/10.1007/978-94-009-8647-3>
- 563 Smith, B., Prentice, I. C., & Sykes, M. T. (2001). Representation of vegetation dynamics in the
564 modelling of terrestrial ecosystems: Comparing two contrasting approaches within

- 565 European climate space. *Global Ecology and Biogeography*. <https://doi.org/10.1046/j.1466-822X.2001.00256.x>
- 567 Smith, B., Wärlind, D., Arneth, A., Hickler, T., Leadley, P., Siltberg, J., & Zaehle, S. (2014).
568 Implications of incorporating N cycling and N limitations on primary production in an
569 individual-based dynamic vegetation model. *Biogeosciences*. <https://doi.org/10.5194/bg-11-2027-2014>
- 571 von Caemmerer, S., & Farquhar, G. D. (1981). Some relationships between the biochemistry of
572 photosynthesis and the gas exchange of leaves. *Planta*. <https://doi.org/10.1007/BF00384257>
- 573 von Caemmerer, S. (2000). Biochemical models of leaf photosynthesis. *Techniques in Plant
574 Sciences*. <https://doi.org/10.1017/CBO9781107415324.004>
- 575 Walters, D. N., Williams, K. D., Boutle, I. A., Bushell, A. C., Edwards, J. M., Field, P. R., et al.
576 (2014). The Met Office Unified Model Global Atmosphere 4.0 and JULES Global Land 4.0
577 configurations. *Geoscientific Model Development*, 7(1), 361–386.
- 578 Wang, S., Grant, R. F., Verseghy, D. L., & Black, T. A. (2001). Modelling plant carbon and
579 nitrogen dynamics of a boreal aspen forest in CLASS - The Canadian Land Surface
580 Scheme. *Ecological Modelling*. [https://doi.org/10.1016/S0304-3800\(01\)00284-8](https://doi.org/10.1016/S0304-3800(01)00284-8)
- 581 Wang, Y. P., & Houlton, B. Z. (2009). Nitrogen constraints on terrestrial carbon uptake:
582 Implications for the global carbon-climate feedback. *Geophysical Research Letters*.
583 <https://doi.org/10.1029/2009GL041009>
- 584 Watson, R. T., Rohde, H., Oeschger, H., & Siegenthaler, U. (1990). Greenhouse gases and
585 aerosols. In J. T. Houghton, B. A. Callandar, & S. K. Varney (Eds.), *Climate change: the
586 IPCC scientific assessment* (pp. 7–40). Cambridge, England: Cambridge University Press.
- 587 Weedon, G. P., Balsamo, G., Bellouin, N., Gomes, S., Best, M. J., & Viterbo, P. (2014). The
588 WFDEI meteorological forcing data set: WATCH Forcing data methodology applied to
589 ERA-Interim reanalysis data. *Water Resources Research*, 50(9), 7505–7514.
- 590 Welp, L. R., Keeling, R. F., Meijer, H. A. J., Bollenbacher, A. F., Piper, S. C., Yoshimura, K., et
591 al. (2011). Interannual variability in the oxygen isotopes of atmospheric CO₂ driven by El
592 Niño. *Nature*. <https://doi.org/10.1038/nature10421>
- 593 Williams, K., Gornall, J., Harper, A., Wiltshire, A., Hemming, D., Quaife, T., et al. (2017).
594 Evaluation of JULES-crop performance against site observations of irrigated maize from
595 Mead, Nebraska. *Geoscientific Model Development*, 10(3), 1291–1320.
596 <https://doi.org/10.5194/gmd-10-1291-2017>
- 597 Woodward, F. I., Smith, T. M., & Emanuel, W. R. (1995). A global land primary productivity
598 and phytogeography model. *Global Biogeochemical Cycles*.
599 <https://doi.org/10.1029/95GB02432>

600 Yang, R., Friedl, M. A., & Ni, W. (2001). Parameterization of shortwave radiation fluxes for
 601 nonuniform vegetation canopies in land surface models. *Journal of Geophysical Research*,
 602 *106*(D13), 14275. <https://doi.org/10.1029/2001JD900180>

603 Yang, W., Ni-Meister, W., Kiang, N. Y., Moorcroft, P. R., Strahler, A. H., & Oliphant, A.
 604 (2010). A clumped-foliage canopy radiative transfer model for a Global Dynamic
 605 Terrestrial Ecosystem Model II: Comparison to measurements. *Agricultural and Forest*
 606 *Meteorology*, *150*(7–8), 895–907. <https://doi.org/10.1016/j.agrformet.2010.02.008>

607 **Figure captions**

608 **Figure 1.** Global map of the MODIS derived clumping index at 0.5° resolution for the year 2006
 609 scaled up from the 500m He et al. (2012) clumping dataset.

610 **Figure 2.** Spatial distribution of total fAPAR difference (JULES with clumping – JULES
 611 without clumping) for the year of 2008.

612 **Figure 3.** Difference in GPP between JULES with clumping and JULES without clumping.
 613 Global average values are indicated at the bottom of the figures in PgC yr⁻¹ with the 95%
 614 confidence interval. Grey areas represent regions with no data.

615
 616 **Figure 4. a.** The difference in the absolute GPP between JULES without clumping and the MTE
 617 data, and JULES with clumping and the MTE data. Regions in blue indicate model improvement
 618 by addition of vegetation clumping; **b.** map showing the regions used in the analysis; **c.** Total
 619 (area weighted sum over box area) JULES (green), JULES-Clump (green) and observation based
 620 (MTE; black dots and error bars) GPP fluxes for the year of 2008 at regional scales. Error bars
 621 indicate the weighted sum of the averaged standard deviation of the ensemble mean of the 25
 622 best model trees associated with the MTE-GPP product.

623
 624 **Figure 5.** Zonal mean vertical profile of **a.** absolute and difference in GPP between JULES-
 625 Clump and JULES without clumping.; **b.** Total GPP zonal mean of MTE, JULES-Clump (red),
 626 and JULES (blue). 1 standard deviation ($\pm 1\sigma$) of the spatial mean for each product is represented
 627 by the filled areas.

628
 629 **Figure 6.** Monthly mean fluxes of GPP for 12 FLUXNET sites from JULES (continuous line)
 630 and JULES-Clump (dashed line) for four different percentages of incident diffuse shortwave
 631 radiation: 20% (red), 40% (blue), 60% (green), and 80% (yellow).