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# TROLL 4.0: representing water and carbon fluxes, leaf phenology and intraspecific trait variation in a mixed-species individual-based forest dynamics model – Part 1: Model description

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**Short summary:** We describe TROLL 4.0, a simulator of forest dynamics that represents trees in a virtual space at one-meter resolution. Tree birth, growth, death and the underlying physiological processes such as carbon assimilation, water transpiration and leaf phenology depend on plant traits that are measured in the field for many individuals and species. The model is thus capable of jointly simulating forest structure, diversity and ecosystem functioning, a major challenge in modelling vegetation dynamics.

**Abstract.** TROLL 4.0 is an individual-based forest dynamics model that is capable of jointly simulating forest structure, diversity and ecosystem functioning, including the ecosystem water balance and productivity, leaf area dynamics and the tree community functional and taxonomic composition. It represents ecosystem flux processes in a manner similar to dynamic global vegetation models, while adopting a representation of plant community structure and diversity at a resolution consistent with that used by field ecologists. Specifically, trees are modeled as three-dimensional individuals with a metric-scale spatial representation, providing a detailed description of ecological processes such as competition for resources and tree demography. Carbon assimilation and plant water loss are explicitly represented at tree level using coupled photosynthesis and stomatal conductance models, depending on the micro-environmental conditions experienced by trees. Soil water uptake by trees is also modelled. Physiological and demographic processes are parameterized using plant functional traits measured in the field. Here we provide a detailed description and discussion of the implementation of TROLL 4.0. An evaluation of the model at two tropical forest sites is provided in a companion paper (Schmitt et al., submitted companion paper). TROLL 4.0's representation of processes reflects the state of the art, and we discuss possible developments to improve its predictive capability and its capacity to address challenges in forest monitoring, forest dynamics and carbon cycle research.



## 32 **1 Introduction**

33 Modelling vegetation dynamics remains a major challenge (Prentice et al., 2015; Song et al., 2021; Mahnken et al.,  
34 2022), and the wide variety of modelling concepts that coexist depend on models' initial objectives. Early versions of global  
35 vegetation models were developed to provide boundary conditions for energy, carbon and water budgets in global atmospheric  
36 models (Sellers et al., 1986, 1997). With the refinement of modeling concepts and computer power, feedback loops between  
37 the atmosphere and vegetation have gradually been taken into account (Charney, 1975; Cox et al., 2000; Meir et al., 2006),  
38 leading to an improved representation of fluxes of energy, carbon and water across the vegetation layer (Fisher et al., 2015;  
39 Moorcroft, 2003; Pitman, 2003). However, dynamic global vegetation models (DGVMs) typically adopt a simplified  
40 representation of floristic composition and vegetation structure (Fisher et al., 2014; Prentice et al., 2007). In many of these  
41 models, fluxes between vegetation and the atmosphere are still calculated in an average environment per grid cell (e.g.  $1^{\circ} \times 1^{\circ}$ ),  
42 for an average leaf of an individual drawn from a dozen of plant functional types (PFTs). The diversity of plant strategies is  
43 therefore typically represented by a small number of PFTs even in highly diverse tropical forests (Fisher et al., 2014; Poulter  
44 et al., 2011).

45 In parallel, stand-scale process-based models have been developed to better understand the exchanges between  
46 vegetation and the atmosphere through an up-scaling of fine-scale ecophysiological processes, and to account for within-stand  
47 micro-environmental heterogeneity (Wang and Jarvis, 1990; Gu et al., 1999; Williams et al., 1996; Ogée et al., 2003; Duursma  
48 and Medlyn, 2012; Fyllas et al., 2014). These process-based models are conceptually close to DGVMs, but they implement a  
49 more detailed representation of plant structure at the stand scale, and they have nurtured some important advances in DGVM-  
50 development over the past decades (e.g., Chen et al., 2016). Typically used to assimilate eddy-flux data, they do not include  
51 demographic processes however.

52 Forest growth models have a different history as they were initially developed to predict successional dynamics and  
53 inform forest management (Watt, 1947; Botkin et al., 1972; Vanclay, 1994; Porté and Bartelink, 2002; Liang and Picard,  
54 2013). A key innovation have been gap models that represent recruitment, growth, mortality and competition between  
55 individual trees within forest patches. Forest patches are typically the size of a canopy opening created by the fall of a dominant  
56 tree (gap, or chablis, Bugmann 2001) and modelled as horizontally homogeneous, with a spatially implicit representation of  
57 tree positions. Through the simulation of a large number of patches, gap models can represent spatial heterogeneity due to gap  
58 dynamics within stands. Overall, these models adopt a finer representation of vegetation structure than classic DGVMs, but  
59 biogeochemical processes are generally modeled more coarsely, using ideal yield curves for tree growth rates combined with  
60 limiting factors imposed by the patch environment. Since these empirical relationships can only be parameterized on the basis  
61 of a large amount of data – readily available in plantations, but difficult to obtain elsewhere –, gap models typically also use  
62 plant functional types to simulate diverse forest stands. The number and definition of these groups has been much discussed  
63 in the literature, with no clear consensus (Botkin, 1975; Swaine and Whitmore, 1988; Vanclay, 1991; Köhler and Huth, 1998;



64 Köhler et al., 2000; Gourlet-Fleury et al., 2005; Kazmierczak et al., 2014), and these plant functional types are difficult to  
65 transfer from one site to another (Picard and Franc, 2003; Picard et al., 2012).

66 Modelling vegetation from a completely different perspective and building upon flora distribution maps and  
67 biogeographic concepts (Humboldt, 1849; Grisebach, 1872), plant species distribution models have been developed for long  
68 (SDMs; Guisan et al., 2017). Generally, SDMs first estimate the envelope of environmental conditions for a species based on  
69 species occurrence data (Guisan and Thuiller, 2005; Hutchinson, 1957; Soberón, 2007), which is used to infer a probability  
70 distribution in space (Elith and Leathwick, 2009). These models require little knowledge on the processes underlying species  
71 distribution, which explains their widespread use. However, because these models are statistical in nature, their ability to  
72 project future states is unclear, and a great deal of research has been devoted to implementing process-based versions of these  
73 SDMs (Chaine and Beaubien, 2001; Ferrier and Guisan, 2006; Morin and Lechowicz, 2008; Morin and Thuiller, 2009;  
74 Kearney and Porter, 2009; Dormann et al., 2012; Journé et al., 2020).

75 From this brief and non exhaustive overview it emerges that each research community in vegetation modeling  
76 emphasizes one representation of vegetation dimension – functioning, structure or diversity -- to the detriment of the others  
77 (Maréchaux et al., 2021). Data availability and computing power partly explain such tradeoffs, and increasing model  
78 complexity does not necessarily translate into an increase in reliability and robustness (Mahnken et al., 2022; Prentice et al.,  
79 2015). However, a consensus has emerged in the literature that a better integration of plant species diversity, structure and  
80 functioning should improve the predictive power of vegetation models (Purves and Pacala, 2008; Thuiller et al., 2008;  
81 McMahon et al., 2011; Evans, 2012; Dormann et al., 2012; Mokany et al., 2016; Fisher et al., 2018). For example, tree species  
82 diversity influences the productivity and resilience of forest ecosystems (Schnabel et al., 2019), and these biodiversity-  
83 ecosystem functioning relationships result from local interactions where competition for resources is a key process (Fichtner  
84 et al., 2018; Guillemot et al., 2020; Jourdan et al., 2020; Yu et al., 2024; Nemetscheck *et al.* 2024). Similarly, the fine details  
85 of stand structure control the uptake of resources by vegetation (Braghiere et al., 2019, 2021; Brum et al., 2019; Ivanov et al.,  
86 2012; De Deurwaerder et al., 2018), and they also determine the response to environmental stresses and disturbances  
87 (Blanchard et al., 2023; Jucker et al., 2018; Seidl et al., 2014; De Frenne et al., 2019). More generally, the contribution of  
88 vegetation in biogeochemical cycles, albeit typically quantified from stand to global scales (e.g. biomass, productivity),  
89 ultimately depends on individual processes (e.g. mortality, Johnson et al., 2016) controlled by fine-scale heterogeneity and the  
90 various ecological strategies of species (Poorter et al., 2015).

91 Therefore, recent developments in DGVMs have sought to better represent plant community structure and diversity.  
92 Several cohort-based DGVMs have been developed to refine the representation of vegetation heterogeneity (Moorcroft et al.,  
93 2001; Fisher et al., 2015; Longo et al., 2019; Smith et al., 2001). Continuous representations of functional diversity have also  
94 been proposed using the distribution and co-variation of traits at the individual level or trait-climate relationships (Sakschewski  
95 et al., 2015; Verheijen et al., 2015; Scheiter et al., 2013; Pavlick et al., 2013; Berzaghi et al., 2020; Van Bodegom et al., 2014).  
96 These developments represent major advances in vegetation modelling, but scale mismatches between field data and model  
97 representations limit the ability to assimilate data of various nature and resolution. While inverse modelling approaches can



98 partially alleviate these constraints (Hartig et al., 2012; Dietze et al., 2013; LeBauer et al., 2013; Fer et al., 2018; Lagarrigues  
99 et al., 2015), they rely heavily on confidence in the model structure, can therefore raise equifinality issues (Medlyn et al.,  
100 2005), and increase rapidly in computational complexity in high-dimensional parameter sets.

101 Finally, most of these challenges are exacerbated for tropical forests, as they are structurally complex (Doughty et al.,  
102 2023), support a large number of tree species per hectare (up to several hundred, Wilson et al., 2012), and are more difficult  
103 to access for evaluation in the field (Schimel et al., 2015). Given that they provide a range of ecosystem services and play a  
104 major role in regional and global biogeochemical cycles (Beer et al., 2010; Bonan, 2008; Pan et al., 2011; Harper et al., 2013),  
105 tropical forests and their responses to changing environmental factors have been identified as one of the greatest sources of  
106 uncertainty in Earth system models (Koch et al., 2021; Powell et al., 2013; Restrepo-Coupe et al., 2017; Huntingford et al.,  
107 2013). Thus, many advances in vegetation modelling have been, and still are, motivated by the challenge of tropical forests.

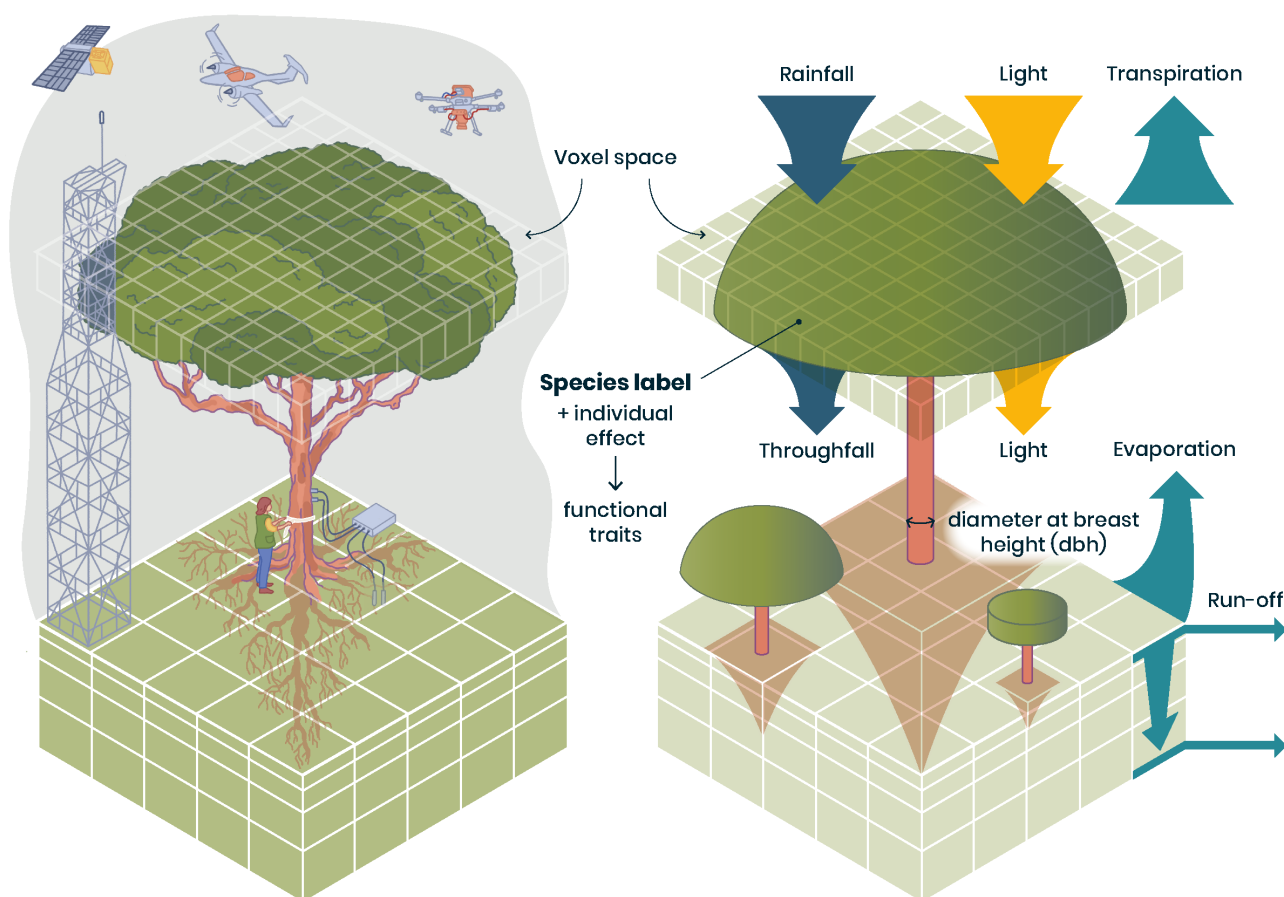
108 Here we describe a major upgrade of the TROLL forest dynamics model (Chave, 1999; Maréchaux and Chave, 2017;  
109 Fischer, 2019), referred to here as TROLL 4.0. TROLL 4.0 brings together various modelling traditions, including elements  
110 of DGVMs, stand-scale process-based models and forest gap models while adopting a species-level representation of plant  
111 diversity, to jointly simulate the functioning, structure and diversity of forest ecosystems, and in particular tropical forests.  
112 TROLL is a spatially explicit forest dynamics model, with an individual- and trait-based representation (Fig. 1). Individual  
113 trees from 1cm diameter at breast height (*dbh*) are explicitly represented in a three-dimensional space discretized at a resolution  
114 of one meter, allowing a fine representation of stand structure and local interactions via explicit competition for resources.  
115 Each tree belongs to a species, with a list of mean traits per species provided as input. These traits control the physiological  
116 and demographic processes of the tree's functioning and life cycle, from recruitment to growth, to seed dispersal and death.  
117 This type of trait-based parameterization is based on recent advances in plant physiology and functional ecology, has been  
118 facilitated by the expansion of large databases of functional traits (Díaz et al., 2016, 2022; Kattge et al., 2011, 2020), in  
119 particular for tropical trees (Baraloto et al., 2010a; Vleminckx et al., 2021).

120 In TROLL 4.0, carbon assimilation and water loss by transpiration are represented explicitly using a photosynthesis  
121 model coupled with a stomatal conductance model. Both take into account variation in micro-environmental conditions  
122 between and within tree crowns, as well as the tree's access to soil water. A water cycle is now simulated, with the state and  
123 dynamics of soil water explicitly represented and coupled with the vegetation dynamics. The influence of water availability  
124 on leaf-level gas exchanges, leaf phenology, tree recruitment and death is parameterized through the leaf water potential at  
125 turgor loss point (Bartlett et al., 2012) and mechanistic-based coordination with other hydraulic traits (Bartlett et al., 2016).  
126 Carbon that is not consumed by the respiration of living tissues is then allocated to leaf production, carbon storage and tree  
127 growth through allometric relationships. Compared to TROLL version 2.3.2 (Maréchaux and Chave, 2017), TROLL 4.0  
128 includes other improvements: plant functional traits can vary among trees of the same species; tree crown shapes can be more  
129 realistic than cylinders; and leaf density can vary within the tree crowns.

130 In this contribution, we provide a detailed description of the structure and objectives of the TROLL 4.0 model,  
131 discussing how new modeling representations are an outcome of the state of knowledge and the availability of data. Finally,



132 we discuss the limitations of the model and future developments. An evaluation of the model's ability to simulate forest  
133 structure, diversity and functioning for two Amazonian forest sites is reported in a companion paper (Schmitt et al., submitted  
134 companion paper). The model is written in C++ and wrapped in the R environment through a dedicated package named  
135 *rcontrol* (Schmitt et al. 2023).  
136



137  
138 **Figure 1: Representation of individual trees in a spatially explicit environment in TROLL 4.0 (right) allowing direct comparison**  
139 **with data of various nature (left). In TROLL 4.0, each tree is composed of a trunk, a crown, whose shape evolves from a cylinder to**  
140 **an umbrella as the tree grows, and root biomass that decreases exponentially with soil depth. Tree dimensions are updated at each**  
141 **timestep, depending on the net assimilated carbon that is allocated to growth, and following allometric relationships depending on**  
142 **tree diameter at breast height (*dbh*). Each tree has a species label associated with plant functional traits, which, together with an**  
143 **individual effect randomly attributed at tree birth, determines the tree's functional traits. These traits are used to parameterize**  
144 **physiological and demographic processes that govern tree functioning throughout its life cycle. Light diffusion is computed explicitly**  
145 **at each time step and within each voxel from the canopy top to the ground. Water balance is also computed at each timestep, and**  
146 **the resulting water availability across soil voxels influence tree functioning. With this representation of forest structure, composition**  
147 **and functioning, model outputs can be directly compared with a wide range of data, including carbon and water fluxes provided by**  
148 **eddy-flux towers, field inventories, and 3D structure estimates from remote sensing (left). In TROLL 4.0, aboveground voxels**  
149 **typically have a finer horizontal resolution than belowground voxels, but the latter are vertically finer and increasing in thickness**  
150 **with depth (right). This resolution matches the one of fine-scale remote-sensing products or soil water content monitoring (left).**



151

## 152 **2 Model description**

### 153 **2.1 Environmental conditions**

154 TROLL 4.0 simulates an idealized forest stand with a typical size of 1 to 100 ha. Parallel computing may be used to simulate  
155 several times the same stand, or to simulate several forest stands with different environmental conditions. Climatic drivers are  
156 similar to those represented in many DGVMs (air temperature, vapor pressure deficit, wind speed, and light intensity above  
157 the canopy, as well as precipitation). The forest ecosystem is divided into an above-ground and below-ground part. Soil is  
158 explicitly represented as a water reservoir, but soil nutrients are not modeled. The topography within a stand is assumed to be  
159 flat.

### 160 **2.2 Light availability and aboveground variation in micro-climate**

161 Above ground, the simulated forest stand is represented as a discrete grid of  $1\text{m}^3$  cubic voxels. Light diffuses through the  
162 forest's leaf layers from the top of the canopy to the ground, with one recalculation each day. In a given voxel, light availability  
163 is the photosynthetic photon flux density in  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$  and is computed as a function of the incident light intensity  
164 at top canopy ( $PPFD_{top}$ , see Table A1 for a list of symbols), the cumulated leaf density of voxels above and the (constant) leaf  
165 density within the voxel itself. The Beer-Lambert extinction of light within the canopy allows to calculate the incident PPFD  
166 (per unit ground area) above any layer at vertical extent  $v$  as:

$$167 \quad PPFD(v) = PPFD_{top} \times \exp[-k \times LAI(v)] \quad (1)$$

168 where  $LAI(v)$  is the cumulated leaf area above height  $v$ , and  $k$  is the extinction coefficient. We here define  $k =$   
169  $k_{geom} \times \text{absorptance}_{leaves}$ , where  $k_{geom}$  reflects the geometric arrangement of leaves in the voxel (a value of 0.5 reflecting  
170 spherical leaf distribution; Ross, 1981) and  $\text{absorptance}_{leaves}$ , the fraction of absorbed light within a single leaf (Long et al.,  
171 1993; Poorter et al., 1995). The absorbed light in a layer  $a$  of thickness  $\Delta a$  is then

$$172 \quad PPFD_{abs}(a) = PPFD_{top} \times \exp[-k \times LAI(a)] - PPFD_{top} \times \exp[-k \times LAI(a + \Delta a)] \quad (2)$$

173 Assuming that leaf area per unit ground area ( $\text{m}^2 \text{m}^{-2}$ ), or  $dens(a)$ , is constant within the layer, this simplifies to:

$$174 \quad PPFD_{abs}(a) = PPFD_{top} \times \exp[-k \times LAI(a)] \times (1 - \exp[-k \times dens(a)]) \quad (3)$$

175 For photosynthesis calculations, absorbed PPFD per unit ground area is converted into absorbed PPFD per unit leaf area by  
176 dividing  $PPFD_{abs}(a)$  by  $dens(a)$ .

177 Air microenvironmental variation within the canopy is represented as follows. Nighttime temperature ( $T_{night}$ ) is  
178 assumed constant throughout the night and within the canopy, while temperature ( $T$ ) and vapor pressure deficit (VPD) vary  
179 across voxels depending on the variable  $\lambda(v) = \frac{LAI(v)}{LAI_{sat}}$  with  $LAI_{sat}$  a threshold LAI and  $LAI(v)$  the LAI above voxel  $v$ . At  
180 height  $v$  above ground, we calculate temperature and VPD as follows:



181  $T(v) = T_{top} - \Delta T \times \lambda(v)$  (4)

182  $VPD(v) = VPD_{top} \times [C_{VPD0} + (1 - C_{VPD0}) \sqrt{(1 - \lambda(v))}]$  (5)

183 where  $\Delta T$  and  $C_{VPD0}$  are set parameters and  $T_{top}$  and  $VPD_{top}$  are values at the top of canopy. For any given layer  $a$  of depth  
184  $\Delta a$ , temperatures and VPDs are then calculated by averaging both functions from  $a$  to  $a + \Delta a$  :

185  $T_{mean}(a) = \frac{1}{\Delta a} \int_a^{a+\Delta a} (T_{top} - \frac{\Delta T}{LAI_{sat}} \times LAI(v)) dv$  (6)

186  $VPD_{mean}(a) = \frac{1}{\Delta a} \int_a^{a+\Delta a} VPD_{top} \times [C_{VPD0} + \frac{(1-C_{VPD0})}{\sqrt{LAI_{sat}}} \sqrt{(LAI_{sat} - LAI(v))}] dv$  (7)

187 Equations 6 and 7 can then be simplified using the assumption of constant leaf density within a layer and redefining  $v$  with  
188 respect to the current layer  $a$ , so that  $LAI(v) = LAI(a) + dens(a) \times v$ .

189 This representation of variation of  $T$  and  $VPD$  within the canopy is in qualitative agreement with empirical  
190 observations of microclimate gradients within tropical forest canopies (Camargo and Kapos, 1995; Shuttleworth, 1985;  
191 Shuttleworth et al., 1989, Tymen et al. 2017), with a consistent buffering effect of forest canopies on understory micro-  
192 environment (De Frenne et al., 2019), and a strong control by forest structure (Gril et al., 2023b, a; Tymen et al., 2017;  
193 Zellweger et al., 2019).

194 Wind speed attenuation inside the canopy is simulated as described in Rau et al. (2022), who explored the effect of  
195 wind speed on forest structure in a forest exposed to cyclones using TROLL. Wind speed is usually measured above the canopy  
196 and decreases as one approaches the canopy top layer, so wind speed at the top of the canopy is (Monteith & Unsworth 2008):

197  $u(z) = \frac{u_*}{\kappa} \ln\left(\frac{z-d}{z_0}\right), \text{ if } z \geq H$  (8)

198 where  $u(z)$  is the horizontal wind speed in  $m s^{-1}$  at a height  $z$  (in m) above ground,  $H$  the height of the top of the canopy (in  
199 m),  $u_*$  is the friction velocity,  $\kappa$  the von Karman constant ( $\kappa=0.40$ ),  $d$  the zero-plane displacement height, here assumed to be  
200 equal to  $0.8H$ , and  $z_0$  the aerodynamic roughness, here assumed to be equal to  $0.06H$  (Rau et al., 2022). Within the canopy,  
201 wind speed decreases as (Inoue 1963):

202  $u(z) = u(H) \exp\left(-\alpha \left(1 - \frac{z}{H}\right)\right), \text{ if } z < H$  (9)

203 with  $\alpha \approx 3$  (Raupach et al., 1996). Wind speed was not computed at the voxel scale, but using the coarser horizontal resolution  
204 of the belowground field (see section 2.3 below, e.g. 25x25 m), and a mean top canopy height  $H$  was computed as input to Eqs  
205 (8) and (9).

### 206 2.3 Soil water availability

207 In TROLL 4.0, the belowground part of the ecosystem is explicitly represented, and its discretization is specified by the user,  
208 including the number and depth of layers, and horizontal dimensions of the cells. Belowground voxels are typically coarser  
209 horizontally (e.g. 25m x 25m, as commonly implemented in gap models Bugmann, 2001), but finer vertically, than  
210 aboveground 1-m<sup>3</sup> voxels. Metric-scale lateral water fluxes are difficult to parameterize and evaluate, and neglecting them





211 here limits the computational burden. Soil layers typically increase in thickness with depth, as in most DGVMs or forest  
212 physiological models (Prentice et al., 2015) and in standard soil assessments (e.g. Hengl et al., 2017). In this representation,  
213 contrasting root depth and access to water can be represented across individual trees together with potential variation in soil  
214 properties and hydraulic state. This approach contrasts with some forest dynamics models that use a single-layer belowground  
215 representation (e.g. Gutiérrez et al., 2014; Christoffersen et al., 2016; Fyllas et al., 2014).

216 The water content in each belowground voxel is simulated using a bucket model, which relies on the vertical water  
217 balance for each voxel. Neglecting horizontal lateral fluxes, the water balance for a given soil column amounts to:

$$218 \Delta SWC = P - I - Q - E - T - L \quad (10)$$

219 where SWC is the soil water content, P the incident rainfall, I the canopy interception, Q the run-off, E the evaporation from  
220 the soil, T the transpiration, i.e. the plant water uptake, and L the leakage. This water balance is established for each soil layer,  
221 with inputs from upwards and outputs downwards starting from the top layer ( $l=1$ ): outputs of layer  $l$  are inputs for layer  $l+1$ ,  
222 with  $L$  corresponding to the output of the deepest layer, and  $P-I-Q$  to the input of the top layer. Note that this downward  
223 iteration neglects: (i) potential hydraulic lift (upward water redistribution, see e.g. Dawson, 1993; Burgess et al., 1998; Oliveira  
224 et al., 2005); and (ii) potential interaction with the water table (Costa et al., 2023; Sousa et al., 2022). Further developments  
225 could account for these two mechanisms where they are expected to play a significant role. In particular, flooded areas could  
226 be easily represented, with a shallower soil depth and a prescribed boundary condition, i.e. a shallower water table. We now  
227 describe and discuss each term of the water balance and the corresponding modeling choices.

228 *Rainfall.* Rainfall ( $P$ , in mm) is a model input. It is assumed that the total daily rainfall corresponds to a single event  
229 of rain per day (one storm, as in, e.g., Rodriguez-Iturbe et al., 1999; Laio et al., 2001; Fischer et al., 2014; Gutiérrez et al.,  
230 2014).

231 *Interception.* Rainfall interception by the canopy is simulated using a model where interception depends on LAI, as  
232 proposed by Liang et al. (1994):

$$233 I = \min(P, K \times LAI) \quad (11)$$

234 where  $K=0.2\text{mm}$  and LAI corresponds to the leaf area index at ground level, averaged across the ground-level aboveground  
235 voxels that contribute to a single belowground voxel (typically  $625=25^2$  aboveground voxels contribute to one belowground  
236 voxel). Similar simple formulations of canopy interception have been used elsewhere (e.g. Liu et al., 2017), and this choice is  
237 justified by the lack of relevant data to properly parameterize more complex formulations at most field sites. More complex  
238 models of rainfall interception also exist however (Rutter and Morton, 1977; Gash, 1979; Gash et al., 1995).

239 *Run-off and infiltration.* As in most bucket models coupled with a forest dynamics model, the temporal propagation  
240 of the wetting front into the soil is not explicitly simulated here, because of the daily timestep and the vertically lumped  
241 representation of soil moisture dynamics (e.g., Laio et al., 2001, Guimberteau et al., 2014). When the soil top layer has enough  
242 available storage to absorb the totality of the throughfall (i.e. when throughfall is smaller than the layer water content at field  
243 capacity minus the current soil water content), it is assumed that the increment in soil water content of that top layer is equal  
244 to the throughfall. Otherwise, the excess water percolates to the next layer below. In the absence of an explicit wetting front,



245 runoff occurs only when the superficial layer is already saturated, which is similar to Dunne run-off (Dunne and Black, 1970).  
246 More complex formulations of run-off exist (d'Orgeval et al., 2008; Guimberteau et al., 2014; Horton, 1933), but because of  
247 the high porosity of many tropical forest soils (Hodnett and Tomasella, 2002; Sander 2002) and the lack of explicit topography  
248 in this version, our choice is parsimonious.

249 *Soil evaporation.* We assumed that water evaporates from the top soil layer only, a reasonable assumption if the top  
250 soil layer is not too thin. We followed Sellers et al. (1992) under which evaporation from the soil is expressed as (see Merlin  
251 et al., 2016 for a review of alternatives):

$$252 \quad E = \frac{M_w}{RT_s} \times \frac{e_s - e_a}{r_{soil} + r_{aero}} \quad (12)$$

253 where  $E$  is in  $\text{kg m}^{-2} \text{s}^{-1}$ ,  $M_w$  is the molar mass of water vapor ( $M_w = 18 \text{ kg mol}^{-1}$ ),  $R$  is the ideal gas constant ( $R = 8.31 \text{ J mol}^{-1}$   
254  $\text{K}^{-1}$ ),  $T_s$  is the temperature at soil surface in K,  $e_s$  is the vapor pressure of the soil surface in Pa,  $e_a$  is the vapor pressure of air  
255 above the soil surface in Pa,  $r_{soil}$  is the soil surface resistance in  $\text{s m}^{-1}$ , and  $r_{aero}$  is the aerodynamic resistance to heat transfer  
256 in  $\text{s m}^{-1}$ . Soil water pressure  $e_s$  is a function of the water potential of the top soil belowground voxel ( $\psi_{soil,top}$ , in MPa; Jones,  
257 2013, Eq. (5.14) therein):

$$258 \quad e_s = e_{sat}(T_s) \times \exp\left(\frac{V_w}{RT_s} \times \psi_{soil,top}\right) = e_{sat}(T_s) \times \exp\left(2.17 \times \frac{\psi_{soil,top}}{T_s}\right) \quad (13)$$

259 Where  $V_w$  is the partial molal volume of water ( $V_w = 18 \times 10^{-6} \text{ m}^3 \text{ mol}^{-1}$ ), and  $e_{sat}(T_s)$  is the saturated vapor pressure at  $T_s$   
260 computed following the Buck equation (Jones, 2013, Appendix 4 therein).  $e_a$  is by definition equal to  $e_{sat}(T_s) - VPD_{ground}$ ,  
261 where the latter is the VPD at ground level in Pa.  $r_{soil}$  is computed following Sellers et al. (1992, Eq. (19) therein, see also  
262 Merlin et al., 2016, Eq. (12)):

$$263 \quad r_{soil} = \exp\left(8.206 - 4.255 \times \frac{\theta_{top}}{\theta_{fc,top}}\right) \quad (14)$$

264 where  $\theta_{top}$  is the water content of the top soil belowground voxel and  $\theta_{fc,top}$  is its water content at field capacity (in  $\text{m}^3$ ).  
265 Aerodynamic resistance  $r_{aero}$  is computed as follows (Merlin et al., 2016, Eq. (B10) therein):

$$266 \quad r_{aero} = \frac{1}{\kappa^2 \times u(Z)} \ln\left(\frac{Z}{Z_m}\right)^2 \quad (15)$$

267 with  $\kappa$  again the von Karman constant ( $\kappa = 0.40$ ),  $u(Z)$  is the wind speed (in  $\text{m s}^{-1}$ ) at reference height  $Z$ , here taken at 1m above  
268 ground, and  $Z_m$  is the momentum soil roughness in m, set to 0.001m.

269 *Transpiration.* Trees transpire soil water from the belowground voxel they are rooted in (see section 2.4.3). For a  
270 given tree, the total daily soil water uptake is the sum of the water transpired by leaves across its crown and across day-time  
271 half hours (see section 2.5.2). Soil layers contribute to water uptake as a function of tree-dependent weights,  $w_l$  (see Eq. (21),  
272 section 2.4.3), which depend on root biomass and on the soil hydraulic state in each layer.

273 For each belowground voxel in layer  $l$ , the soil water potential ( $\psi_l$ ) and the soil hydraulic conductivity ( $K_l$ ) are  
274 computed at each time step from the soil water content in the focal voxel using the van Genuchten-Mualem soil characteristic  
275 and hydraulic conductivity curves (Mualem, 1976; van Genuchten, 1980; see Table 1 in Marthews et al., 2014). Parameters of



276 these curves are estimated using regression models (pedotransfer functions) for tropical soils (Hodnett and Tomasella, 2002),  
277 except the saturated hydraulic conductivity, which is computed following Cosby et al. (1984; see Table 2 in Marthews et al.,  
278 2014). In practice, when only soil texture data is available, TROLL 4.0 contains a default option to apply the texture-based  
279 only pedotransfer function provided by Tomasella and Hodnett (1998), coupled to the soil characteristic and hydraulic  
280 conductivity curves of Brooks and Corey (1964) (see Tables 1 and 2 in Marthews et al., 2014).

## 281 **2.4 Representation of trees in the model**

### 282 **2.4.1 Species affiliation and intra-specific trait variability**

283 In TROLL 4.0, each tree (and seed) is attributed a botanical species defined by a taxonomic binomial. It is assumed that the  
284 user has sufficiently good knowledge of the tree species growing in the study area so that a list of species-specific mean plant  
285 functional trait values can be provided as input. These are the leaf mass per area (LMA, in  $\text{g m}^{-2}$ ), the leaf area (LA,  $\text{cm}^2$ ), the  
286 leaf nitrogen content per dry mass (N, in  $\text{mg g}^{-1}$ ), the leaf phosphorous content per dry mass (P, in  $\text{mg g}^{-1}$ ), the wood specific  
287 gravity (wsg, in  $\text{g cm}^{-3}$ ), the leaf water potential at turgor loss point ( $\pi_{tlp}$ , in MPa), and three allometric parameters ( $\text{dbh}_{\text{thres}}$ ,  
288  $h_{\text{lim}}$ ,  $a_h$ , all in m; see section 2.4.2). The number of species provided in input is not limited. In addition to mean plant functional  
289 trait values, it is possible to input individual trait values from which a trait variance-covariance matrix is computed  
290 (alternatively the trait variance-covariance matrix can be prescribed). With this option, for each recruited tree, the trait values  
291 are drawn from a distribution rather than attributed the species-specific mean value. For each trait  $i$  and tree  $j$ , the species-  
292 specific mean value is multiplied by a factor  $e^{\varepsilon_{i,j}}$  where  $\varepsilon_{i,j} \sim N(0, \sigma_i)$  where  $\sigma_i$  the trait-specific standard deviation on a  
293 logarithmic scale (lognormal variation). The sole exception is wood specific gravity, which we assume to be normally  
294 distributed around the mean with  $\varepsilon_{wsg,j} \sim N(0, \sigma_{wsg})$ . Trait covariance is only considered for leaf N, leaf P and LMA, and  
295 other traits are assumed to be decoupled (Baraloto et al., 2010b). Note that with this implementation, intraspecific variation is  
296 not structured in space or time nor heritable, and is thus a surrogate for variability emerging from genetic variation or plasticity  
297 (Girard-Tercieux et al., 2023; 2024). A more realistic representation of the latter is left for future version.

### 298 **2.4.2 Aboveground structure**

299 Above ground, the tree geometry is represented as a three-dimensional object within the voxelized space and consists of a  
300 trunk and a crown filled with leaves. The trunk is assumed to be a cylinder characterized by its total height and its diameter  
301 ( $\text{dbh}$ , for diameter at breast height, by analogy with forest inventories). The aboveground dimensions of trees are predicted  
302 from their  $\text{dbh}$  via scaling rules. For tree  $j$  with  $\text{dbh}_j$ , we calculate its height  $h_j$ , its crown radius  $cr_j$ , and its crown depth  $cd_j$  as  
303 follows:

$$304 \quad h_j = \frac{h_{\text{lim}} \times \text{dbh}_j}{(a_h + \text{dbh}_j)} \times e^{\varepsilon_{h,j}} \quad (16)$$

$$305 \quad cr_j = e^{a_{cr}} \times \text{dbh}_j^{b_{cr}} \times e^{\varepsilon_{cr,j}} \quad (17)$$



306  $cd_j = \min\left(\frac{h_j}{2}, (a_{cd} + b_{cd} \times h_j) \times e^{\varepsilon_{cd,j}}\right)$  (18)

307 where  $h_{lim}$  and  $a_h$  are species-specific coefficients of the Michaelis-Menten function, and  $a_{cr}$ ,  $b_{cr}$ ,  $a_{cd}$ , and  $b_{cd}$  allometric  
308 coefficients that are species independent.  $\varepsilon_{h,j}$ ,  $\varepsilon_{cr,j}$  and  $\varepsilon_{cd,j}$  are variance terms to simulate intraspecific variation with  
309  $\varepsilon_{h,j} \sim N(0, \sigma_h)$ ,  $\varepsilon_{cr,j} \sim N(0, \sigma_{cr})$ , and  $\varepsilon_{cd,j} \sim N(0, \sigma_{cd})$ . Tree crown architecture is known to depend on species ecological  
310 strategies (Bohlman and O'Brien, 2006; Iida et al., 2012; Poorter et al., 2006; Laurans et al., 2024), but given that crown  
311 extents are difficult to measure reliably in the dense canopies of tropical forests, we used a single set of parameters for all the  
312 species.

313 In the previous published version (Maréchaux and Chave, 2017), tree crowns were represented as cylinders with  
314 homogeneous leaf densities. Since v.3.0, TROLL can also model tree crowns as flexible, umbrella-like shapes with  
315 heterogeneous leaf density distributions. Small tree crowns are simulated as cylinders, but consist of up to three separate 1-m  
316 layers of leaves (top, intermediate and bottom layer). Each layer can be assigned a percentage of the total leaf area (e.g., 50%,  
317 30%, 20%) to reflect gradients in leaf densities from the upmost to lower crown layers (Kitajima et al., 2005), but the default  
318 is an equal distribution (33%, 33%, 33%) across all layers. Once a tree surpasses 3 m in crown depth, no new layers are added.  
319 Instead, the treetop grows quicker in height than the outer crown parts. As a result, the three 1-m layers are folded around the  
320 tree trunk like an umbrella at various stages of opening (see Fig. 1b in Schmitt et al., 2023, and similar tree representations in  
321 Strigul et al., 2008). Different functional forms are available to describe height variation from treetop to crown edge, but here  
322 we chose a simple linear decrease between the radius at the top of the crown to the radius at the bottom of the crown. The ratio  
323 between both radii is controlled through the global parameter *shape\_crown*, which varies between 0 (conical shape) and 1  
324 (cylinder), and thus allows for various “conifer-like” and “broadleaf-like” shapes in between.

325 We also relax the assumption that tree crowns are homogeneously filled across their horizontal extent. In TROLL  
326 4.0, crowns have small 1-m<sup>2</sup> openings (or gaps) in their crowns, parameterized as percentage of total crown area that is not  
327 filled with leaves,  $f_{gap}$ . This allows for the modelling of a spatially heterogeneous light environment in the understory (Tymen  
328 et al., 2017), with a theoretical range from  $f_{gap} = 0\%$  (full crown cover, no openings) to  $f_{gap} = 100\%$  (a hypothetical crown with  
329 no leaf area). When calibrating TROLL for tropical forests with airborne laser scanning (Fischer et al., 2019), we found a value  
330 of  $f_{gap} = 15\%$  to be a good approximation for this within-crown gap fraction. If intraspecific variation in crown extent is  
331 explicitly modelled, the fraction of crown gaps is rescaled so that the absolute crown cover stays constant (i.e., the fraction of  
332 crown gaps is divided by  $e^{2\varepsilon_{cr,j}}$ ). Within species, variation in crown extent is thus assumed as decoupled from variation in leaf  
333 area, i.e., reflecting variation in branch angles and directions, but not branch number or biomass.

### 334 2.4.3 Belowground structure

335 TROLL 4.0 makes the common assumption that total fine root biomass is equal to leaf biomass. Future developments should  
336 endeavor to represent a more explicit belowground allocation scheme (Merganičová et al., 2019; Huaraca Huasco et al., 2021).  
337 Direct estimates of individual tree root depth and root distribution are rare in moist tropical forests (Canadell et al., 1996;



338 Jackson et al., 1996, 1999; Nepstad et al., 1994; Cusack et al., 2024; Guerrero-Ramírez et al., 2021). Some studies have  
339 quantified the depth of tree water uptake using indirect methods, such as predawn leaf water potential, or isotope labeling  
340 (Brum et al., 2019; Stahl et al., 2013), but this does not give access to the actual rooting depth. Tree root depth was here  
341 assumed to increase with tree size, and was computed as a function of tree *dbh* as follows (Kenzo et al., 2009, Fig. 4 therein):

$$342 \quad RD = 0.35 \times dbh^{0.54} \quad (19)$$

343 with root depth, RD, in m, and diameter at breast height, *dbh*, in cm. As in Xu et al. (2016), the exponent was based on Kenzo  
344 et al. (2009), who reported on data from excavated trees in secondary forests in Malaysia. The first parameter (0.35, root depth  
345 at *dbh*=1cm) was adjusted to avoid unrealistic water depletion of the top soil layer. In the absence of relevant species-specific  
346 data, this allometric equation was assumed to hold for all species, even if root depth is known to be highly plastic (e.g. Rowland  
347 et al., 2023). Correlations between rooting depth and leaf phenological habit have been reported, but in drier or more seasonal  
348 sites than Amazonian rainforests (Brum et al., 2019; Hasselquist et al., 2010; Smith-Martin et al., 2020), and trait coordination  
349 are known to be typically stronger under harsher environmental conditions (Dwyer and Laughlin, 2017; Delhaye et al., 2020).

350 We assumed that vertical tree root distribution follows an exponential profile, as observed empirically at the stand  
351 scale (Fisher et al., 2007; Humbel, 1978; Jackson et al., 1996). The fine root biomass in layer *l*, at depths ranging from  $z_l$  to  
352  $z_{l+1}$  ( $> z_l$ ) is computed as:

$$353 \quad RB_l = RB_t \times \left( \exp\left(-3 \frac{z_l}{RD}\right) - \exp\left(-3 \frac{z_{l+1}}{RD}\right) \right) \quad (20)$$

354 where  $RB_t$  is the total tree fine root biomass (in g),  $RB_l$  the fine root biomass in layer *l* (in g), RD the tree rooting depth (in m).  
355 The factor 3 was determined so that about 95% of the tree biomass is contained between soil surface and RD (note that  $-\log(0.05) \approx 3$ )  
356 (Arora and Boer, 2003). Tree roots are distributed across vertical layers, but do not spread across belowground  
357 voxels horizontally. As a result, trees only deplete the water content of the belowground voxels located below their trunk  
358 position (see section 2.3).

359 The soil water potential in the root zone,  $\psi_{root}$  (in MPa), captures how the plant equilibrates with the soil water state  
360 across its root profile. It is computed as the weighted mean of the belowground voxel water potentials across layers. We used  
361 the weighting scheme proposed by Williams et al. (2001; see also Bonan et al., 2014; Duursma and Medlyn, 2012), which  
362 accounts for the variation of soil water availability and conductance across layers as follows:

$$363 \quad \psi_{root} = \sum_l w_l \times \psi_l \quad \text{with } w_l = \frac{(\psi_l - \psi_{R,min}) \times G_l}{\sum_{ll} (\psi_{ll} - \psi_{R,min}) \times G_{ll}} \quad (21)$$

364 where  $\psi_l$  is the soil water potential in layer *l*, and  $\psi_{R,min}$  is the root water potential below which there is no water uptake  
365 within the layer (minimal root water potential, assumed to be -3 MPa as in Duursma and Medlyn, 2012).  $G_l$ , the soil-to-root  
366 water conductance in layer *l*, in  $\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1} \text{ MPa}^{-1}$ , computed as follows (Gardner, 1964):

$$367 \quad G_l = \frac{2\pi L_{a,l} K_l}{\log\left(\frac{r_s}{r_r}\right)} \quad (22)$$

368 In Eq (22),  $L_{a,l}$  is the total root length per unit area in the layer (in  $\text{m m}^{-2}$ ), with the total root length in the layer computed as  
369  $RB_l \times SRL$  where SRL is the specific root length, here assumed to be constant ( $10 \text{ m g}^{-1}$ , Bonan et al., 2014; Metcalfe et al.,



370 2008; Weemstra et al., 2016).  $K_l$  is the soil hydraulic conductivity of layer  $l$  (in  $\text{mmol H}_2\text{O m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$ , see section 2.3),  $r_r$  is  
371 the mean fine root radius, here set at 1mm, and  $r_s$  is half the mean distance between roots, calculated with the assumption of  
372 uniform root spacing in a given layer (Newman, 1969):

$$373 \quad r_s = \frac{1}{\sqrt{\pi L_{v,l}}} \quad (23)$$

374 where  $L_{v,l}$  is the total root length per unit soil volume in the layer (in  $\text{m m}^{-3}$ ), computed in the same way as  $L_{a,l}$ , but also divided  
375 by layer depth.

376 A range of other models have been used to infer  $\psi_{root}$  using the relative tree root biomass in each layer directly as  
377 weights (De Kauwe et al., 2015; Naudts et al., 2015; Powell et al., 2013; Schaphoff et al., 2018; Sakschewski et al., 2021;  
378 Verbeeck et al., 2011). However, trees do not uptake water simply as a proportion of root density, but can equilibrate with the  
379 wettest soil layers (Schmidhalter, 1997; Duursma and Medlyn, 2012): the contrasting temporal variations in water availability  
380 across layers result in seasonal changes in the depth of active water withdrawal (Bruno et al., 2006; Joetzier et al., 2022). For  
381 instance, cavitation in the driest part of the soil disconnects roots from the soil (Sperry et al., 2002; see also Fisher et al., 2006).  
382 This is likely why deeper roots, although often very rare, disproportionately contribute to sustain forest productivity during  
383 dry seasons.

## 384 2.5 Leaf physiology

385 The carbon assimilated and the water transpired by a tree within a day are the sum of the leaf-level carbon and water fluxes  
386 across day-time half hours. Leaf-level carbon assimilation is computed per crown layer of each tree, using the Farquhar-von  
387 Caemmerer-Berry model of  $C_3$  photosynthesis (Farquhar et al., 1980, see section 2.5.1), coupled to the model of stomatal  
388 conductance of Medlyn et al. (2011; see section 2.5.2) as in Maréchaux and Chave (2017). In TROLL 4.0 the dependences on  
389 leaf temperature ( $T_l$ ), vapor pressure deficit at the leaf surface ( $VPD_s$ ), and  $\text{CO}_2$  concentration at the leaf surface ( $c_s$ ) are now  
390 determined iteratively at the leaf surface, starting from air temperature ( $T$ ), air vapor pressure deficit ( $VPD_a$ ) and air  $\text{CO}_2$   
391 concentration ( $c_a$ ) averaged across the tree crown layer (see sections 2.2 and 2.4.2) and with transpiration computed using the  
392 Penman-Monteith equation (see section 2.5.4).

### 393 2.5.1 Photosynthesis

394 In Farquhar et al. (1980), leaf-level net carbon assimilation rate ( $A_n$ ,  $\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$ ) is limited by either Rubisco activity  
395 ( $A_v$ ,  $\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$ ), or RuBP regeneration ( $A_j$ ,  $\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$ ):

$$396 \quad A_n = \min\{A_v, A_j\} - R_p(T_l) \quad ; \quad A_v = V_{cmax}(T_l, \psi_{pd}) \times \frac{c_i - \Gamma^*}{c_i + K_m(T_l)} \quad ; \quad A_j = \frac{1}{4} \frac{c_i - \Gamma^*(T_l)}{c_i + 2\Gamma^*(T_l)} \quad (24)$$

397 where  $R_p$  is the photorespiration rate ( $\mu\text{mol C m}^{-2} \text{s}^{-1}$ ),  $V_{cmax}$  is the maximum rate of carboxylation ( $\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$ ),  $c_i$  the  
398  $\text{CO}_2$  partial pressure at carboxylation sites,  $\Gamma^*$  the  $\text{CO}_2$  compensation point in the absence of dark respiration,  $K_m$  the apparent



399 kinetic constant of the Rubisco (von Caemmerer, 2000), and  $J$  the electron transport rate ( $\mu\text{mol } e^- \text{ m}^{-2} \text{ s}^{-1}$ ), which depends on  
400 PPFD through:

$$401 \quad J = \frac{1}{2\theta} \left[ \alpha \times \text{PPFD} + J_{\max}(T_l, \psi_{pd}) - \sqrt{\left( \alpha \times \text{PPFD} + J_{\max}(T_l, \psi_{pd}) \right)^2 - 4\theta \times \alpha \times \text{PPFD} \times J_{\max}(T_l, \psi_{pd})} \right] \quad (25)$$

402  $J_{\max}$  is the maximal electron transport capacity ( $\mu\text{mol } e^- \text{ m}^{-2} \text{ s}^{-1}$ ),  $\theta$  the curvature factor (unitless), and  $\alpha$  the apparent quantum  
403 yield to electron transport ( $\text{mol } e^- \text{ mol photons}^{-1}$ ), computed following von Caemmerer (2000) as  $\alpha = (1 - \text{LSQ}) \times 0.5$ , with  
404 LSQ the effective spectral quality of light, fixed at 0.15, and the factor 0.5 accounts for the fact that each photosystem absorbs  
405 half of the photons.

406 The  $V_{c\max}$  and  $J_{\max}$  parameters depend on leaf properties, leaf temperature ( $T_l$ ) and water state (through the leaf  
407 predawn water potential,  $\psi_{pd}$ , see Eq. (37)) and represent a large source of uncertainty in vegetation models (Zaehle et al.,  
408 2005; Mercado et al., 2009; Rogers et al., 2017). In tropical forest environments, Domingues et al. (2010) suggested that  $V_{c\max}$   
409 and  $J_{\max}$  are co-limited by the leaf concentration of nitrogen and phosphorus as follows (see also Walker et al., 2014):

$$410 \quad V_{c\max-M}(25^\circ\text{C}) = \min\{-1.56 + 0.43 \times N - 0.37 \times \text{LMA} ; -0.80 + 0.45 \times P - 0.25 \times \text{LMA} \} \quad (26)$$

$$411 \quad J_{\max-M}(25^\circ\text{C}) = \min\{-1.50 + 0.41 \times N - 0.45 \times \text{LMA} ; -0.74 + 0.44 \times P - 0.32 \times \text{LMA} \} \quad (27)$$

412 with  $V_{c\max-M}$  and  $J_{\max-M}$  the photosynthetic capacities at  $25^\circ\text{C}$  of unstressed mature leaves on a leaf dry mass basis, in  $\mu\text{mol}$   
413  $\text{CO}_2 \text{ g}^{-1} \text{ s}^{-1}$  and  $\mu\text{mol } e^- \text{ g}^{-1} \text{ s}^{-1}$ , respectively.  $N$  and  $P$  are leaf nitrogen and phosphorus concentrations in  $\text{mg g}^{-1}$ , and  $\text{LMA}$  is the  
414 leaf mass per area in  $\text{g cm}^{-2}$ .  $V_{c\max-M}$  and  $J_{\max-M}$  can be converted into area-based  $V_{c\max}$  and  $J_{\max}$  by multiplying by  $\text{LMA}$ .  
415 We used this leaf trait-based parameterization of  $V_{c\max}(25^\circ\text{C})$  and  $J_{\max}(25^\circ\text{C})$  in the absence of water stress (as in Fyllas et  
416 al., 2014; Mercado et al., 2011). The dependence of  $V_{c\max}$  and  $J_{\max}$  with temperature was given by equations in Bernacchi et  
417 al. (2003), and the dependence with water availability was modelled by a function of  $\psi_{pd}$  ( $WSF_{ns}$ , see section 2.5.3, Eq. (40)):

$$418 \quad V_{c\max}(T_l, \psi_{pd}) = V_{c\max}(25^\circ\text{C}) \times e^{\left(26.35 - \frac{65.33}{R \times (T_l + 273.15)}\right)} \times WSF_{ns}(\psi_{pd}) \quad (28)$$

$$419 \quad J_{\max}(T_l, \psi_{pd}) = J_{\max}(25^\circ\text{C}) \times e^{\left(17.57 - \frac{43.54}{R \times (T_l + 273.15)}\right)} \times WSF_{ns}(\psi_{pd}) \quad (29)$$

420 where  $R$  is the molar gas constant ( $0.008314 \text{ kJ K}^{-1} \text{ mol}^{-1}$ ), and  $T_l$  is the internal leaf temperature in Celsius degrees. The  
421 temperature dependence of  $\Gamma^*$  and  $K_m$  followed von Caemmerer (2000):

$$422 \quad \Gamma^*(T_l) = 37 \times e^{\frac{23.4 \times (T_l - 25)}{298 \times R \times (273 + T_l)}} \quad (30)$$

$$423 \quad K_m(T_l) = 404 \times e^{\frac{59.36 \times (T_l - 25)}{298 \times R \times (273 + T_l)}} \times \left( 1 + \frac{210}{248 \times e^{\frac{35.94 \times (T_l - 25)}{298 \times R \times (273 + T_l)}}} \right) \quad (31)$$

424 Temperature dependencies in Eqs (28)-(31) are consistent with Domingues et al. (2010), following recommendations from  
425 Rogers et al. (2017).

426 Leaf photorespiration rate  $R_p$  was assumed to be a fixed fraction (40%) of leaf dark respiration rate (Atkin et al.,  
427 2000). We used Atkin et al. (2015) ‘broadleaved trees’ empirical model to estimate mature leaf dark respiration rates as a  
428 function of plant functional traits:



429  $R_{d-M}(25^{\circ}\text{C}) = 8.5341 - 0.1306 \times N - 0.5670 \times P - 0.0137 \times LMA + 11.1 \times V_{cmax-M} + 0.1876 \times N \times P$  (32)

430 with  $R_{d-M}$  the leaf dark respiration rate on a dry mass basis and at reference temperature of  $25^{\circ}\text{C}$  (in  $\text{nmol CO}_2 \text{ g}^{-1}\text{s}^{-1}$ ).

431 Multiplying  $R_{d-M}$  by LMA gives the area-based leaf dark respiration  $R_d$  (in  $\mu\text{mol C m}^{-2} \text{ s}^{-1}$ ). The temperature dependence of

432 mature leaf dark respiration rates was calculated as (Atkin et al., 2015, Eq. (1) therein; see also Heskell et al. 2016):

433  $R_d(T_l) = R_d(25^{\circ}\text{C}) \times \left[ 3.09 - 0.043 \times \frac{(T_l+25)}{2} \right]^{\frac{(T_l-25)}{10}}$  (33)

434 Long-term acclimation to temperature is not considered in TROLL 4.0 (Kattge and Knorr, 2007; Smith and Dukes, 2013).

### 435 2.5.2 Stomatal conductance

436 Carbon assimilation by photosynthesis is limited by the  $\text{CO}_2$  partial pressure at carboxylation sites, which is controlled by

437 stomatal transport as modeled by the diffusion equation:

438  $A_n = g_s(c_s - c_i)$  (34)

439 with  $g_s$  the stomatal conductance to  $\text{CO}_2$  ( $\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ). The representation of stomatal conductance varies greatly across

440 vegetation models (Damour et al., 2010; Bonan et al., 2014; Rogers et al., 2017; see Appendix B, Table B1) and remains an

441 active research topic (Anderegg et al., 2018; Dewar et al., 2018; Lamour et al., 2022; Sperry et al., 2017; Wolf et al., 2016;

442 Sabot et al., 2022). In TROLL 4.0, stomatal conductance to water vapor is simulated as (Medlyn et al., 2011):

443  $g_{sw} = g_0 + 1.6 \times \left( 1 + \frac{g_1}{\sqrt{VPD_s}} \right) \times \frac{A_n}{c_s}$  (35)

444 where  $g_{sw}$  is the stomatal conductance to water vapor in  $\text{mol H}_2\text{O m}^{-2} \text{ s}^{-1}$ , 1.6 is the factor needed to convert one mole of  $\text{CO}_2$

445 into one mole of  $\text{H}_2\text{O}$ ,  $VPD_s$  is the vapor pressure deficit at the leaf surface in kPa,  $A_n$  is the assimilation rate in  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$

446 (Eq. (24) above),  $c_s$  is the  $\text{CO}_2$  concentration at the leaf surface in ppm,  $g_0$  is the minimum conductance for water vapor

447 in  $\text{mol H}_2\text{O m}^{-2} \text{ s}^{-1}$  (Duursma et al., 2019), and  $g_1$  is a model parameter in  $\text{kPa}^{1/2}$ . Equations 24, 34 and 35 taken together lead

448 to two quadratic equations for  $c_i$ , one when Rubisco activity is limiting and one when RuBP regeneration is limiting, and the

449 solution is the highest root.

450 The parameter  $g_1$  varies with species ecological strategies and carbon cost of water use (Domingues et al., 2014;

451 Franks et al., 2018; Héroult et al., 2013; Lin et al., 2015; Wolz et al., 2017). Consequently, it is expected that  $g_1$  should differ

452 across plant functional types (e.g. Xu et al., 2016). Here we assumed a dependence of  $g_1$  with wood density ( $wsg$ , in  $\text{g cm}^{-3}$ )

453 as in Lin et al. (2015). We also assumed a dependence with water availability, modelled by a function of  $\psi_{pd}$  ( $WSF_s$ ; see

454 section 2.5.3):

455  $g_1 = (-3.97 \times wsg + 6.53) \times WSF_s(\psi_{pd})$  (36)

456 This parameterization of  $g_1$  based on wood density is a matter of debate however, and alternatives have been proposed (Wu

457 et al., 2020; Lamour et al., 2023).

458 The parameter  $g_0$  quantifies water fluxes through the leaf cuticle (cuticular conductance) and from stomatal leaks.

459 Although it is increasingly recognized as a key parameter explaining tree water loss in drought conditions (Cochard, 2021;





460 Martin-StPaul et al., 2017), its values and variation with other functional traits is poorly documented (Duursma et al., 2019;  
461 Slot et al., 2021; Nemetschek et al., 2024), and we here assumed a fixed value. Note that some previous studies have defined  
462  $g_0$  as cuticular conductance only, ignoring stomatal leak effects, and thus underestimating  $g_0$ .

463 Both  $g_0$  and  $g_1$  were assumed not to depend on temperature in the absence of clear empirical evidence for tropical  
464 forest trees (Duursma et al., 2019; Slot et al., 2021; Rogers et al., 2017), but this may be further explored in the future through  
465 measurement and experiment (Cochard, 2021).

### 466 2.5.3 Effect of water availability on leaf-level gas exchange

467 Under water stress, leaf-level gas exchanges and photosynthesis are impaired, but how this is represented varies greatly across  
468 models (Appendix B, Table B1; Powell et al., 2013; Trugman et al., 2018; Verhoef and Egea, 2014). A common approach is  
469 to define a single integrative water stress factor cumulating all effects along the soil-plant-atmosphere pathway, some of which  
470 being difficult to evaluate empirically (e.g. Fischer et al., 2014; Gutiérrez et al., 2014; Krinner et al., 2005; Clark et al., 2011).  
471 This factor is then used to modify the parameters of the stomatal conductance and/or photosynthesis models (Egea et al., 2011;  
472 Verhoef and Egea, 2014). Depending on models, water stress factors have been assumed to depend on soil water content or on  
473 soil water potential in the root zone (De Kauwe et al., 2015; Drake et al., 2017; Joetzjer et al., 2014; Powell et al., 2013;  
474 Trugman et al., 2018). Alternatively, some models have implemented a water stress factor as a function of leaf water potential  
475 ( $\psi_{leaf}$ ; Christoffersen et al., 2016; Duursma and Medlyn, 2012; Kennedy et al., 2019; Xu et al., 2016; see also the pioneer  
476 work of Tuzet et al., 2003) or used optimization approaches (Williams et al., 1996; Anderegg et al., 2018; Sabot et al., 2020;  
477 Sperry et al., 2017; Wolf et al., 2016), to account for the cost of water uptake and transportation in the plant water column.  
478 The shape of such functions remains contentious however (Table B1), resulting in substantial differences in model predictions.

479 Also, there is no consensus on the relative role of stomatal and non-stomatal limitations on leaf  $\text{CO}_2$  assimilation  
480 under drying conditions, reflecting contrasted experimental results (Drake et al., 2017; Zhou et al., 2014; Keenan et al., 2010;  
481 Appendix B, Table B2). Under stomatal limitation, stomatal closure reduces leaf gas exchanges, and the water stress factor is  
482 applied on stomatal conductance, or stomatal conductance model parameters (e.g.  $g_1$ ). Under non-stomatal limitations, drought  
483 (leading to increased leaf temperature and/or decreased leaf water potential) impairs the biochemical photosynthesis apparatus,  
484 which results in a reduction of photosynthetic capacities, and/or mesophyll conductance (Flexas et al., 2004, 2012). In this  
485 latter case, the water stress factor is applied on  $V_{\text{cmax}}$  and  $J_{\text{max}}$  (Drake et al., 2017; Keenan et al., 2010). Some models consider  
486 only one limitation, and others both (Appendix B, Table B1).

487 In TROLL 4.0, two water stress factors are used, one for stomatal limitation, modifying the  $g_1$  parameter ( $WSF_s$ ; Eq.  
488 (36)), and one for non-stomatal limitations, modifying the  $V_{\text{cmax}}$  and  $J_{\text{max}}$  parameters of the photosynthesis model ( $WSF_{ns}$ ; Eq.  
489 (28) and (29)). Both water stress factors are assumed to depend on the leaf predawn water potential ( $\psi_{pd}$ ; De Kauwe et al.,  
490 2015; Verhoef and Egea, 2014), which is a function of the soil water potential in the root zone ( $\psi_{root}$ , Eq. (21)) (Stahl et al.,  
491 2013, but see Bucci et al., 2004; Donovan et al., 2003) as follows (Jones, 2013; Eq. (4.9) therein):



492  $\psi_{pd} = \psi_{root} - \rho gh \approx \psi_{root} - 0.01 \times h$  (37)

493 where  $\rho$  is the density of water,  $g$  the gravitational force ( $g=9.81 \text{ m s}^{-2}$ ), and  $h$  total tree height in m. Here,  $WSF_s$  was computed  
494 as (Zhou et al., 2013; De Kauwe et al., 2015):

495  $WSF_s = \exp(b \times \psi_{pd})$  (38)

496 where  $b$  is a parameter. To parameterize  $b$ , we used the relationship between the leaf water potential at turgor loss point ( $\pi_{tlp}$   
497 in MPa) and the water potential causing 90% of stomatal closure ( $\psi_{gs90}$ , in MPa):  $\pi_{tlp} = 0.97 \times \psi_{gs90}$  ( $P < 0.01$ ,  $R^2 = 0.4$ ; Fig.  
498 1 in Martin-StPaul et al. 2017), and assumed that  $WSF_s \approx 0.1$  at  $\psi_{gs90}$  (an approximation given the shape of Eq. (35)), leading  
499 to:

500  $WSF_s = \exp\left(-2.23 \times \frac{\psi_{pd}}{\pi_{tlp}}\right)$  (39)

501 The link between the leaf water potential at stomatal closure and the leaf water potential at turgor loss point is supported by  
502 several studies (Bartlett et al., 2016b; Brodribb et al., 2003; Farrell et al., 2017; Martin-StPaul et al., 2017; Meinzer et al.,  
503 2016; Rodriguez-Dominguez et al., 2016; Trueba et al., 2019). The formulation of  $WSF_s$  in Eq (39) was preferred over  
504 alternatives, such as a linear relationship between  $WSF_s$  and  $\psi_{pd}$  (Oleson et al., 2008; Powell et al., 2013; Verhoef and Egea,  
505 2014). The latter is less supported by data and leads to threshold responses as soil water content declines and similar responses  
506 across species, in contrast with empirical evidence (Kursar et al., 2009; Zhou et al., 2013).

507 The water stress factor for non-stomatal limitation ( $WSF_{ns}$ ) was computed following Xu et al. (2016):

508  $WSF_{ns} = \left(1 + \left(\frac{\psi_{pd}}{\pi_{tlp}}\right)^a\right)^{-1}$  (40)

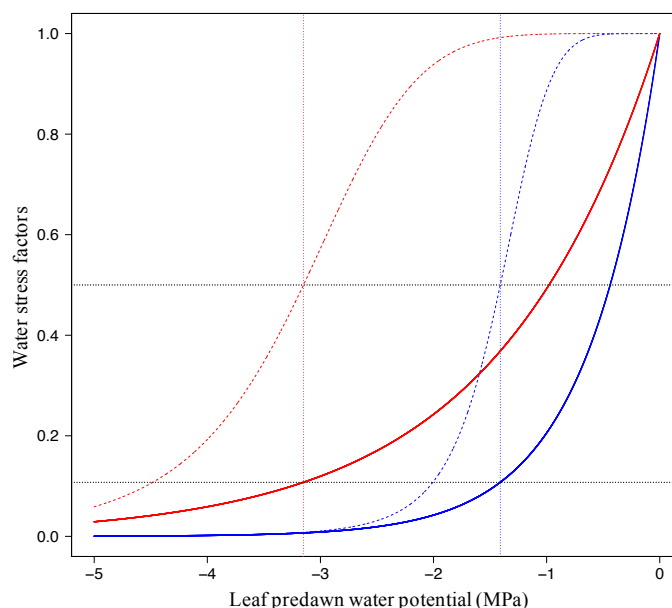
509 with  $a=6$  estimated from data reported in Brodribb et al. (2003). In this formula,  $WSF_{ns} = 1/2$  when  $\psi_{pd} = \pi_{tlp}$ , in agreement  
510 with empirical findings (Brodribb et al., 2002; Manzoni, 2014).

511 The parameterization of  $WSF_s$  and  $WSF_{ns}$  based on  $\pi_{tlp}$  is supported by the fact that leaf cells need to maintain turgor  
512 to sustain functioning (Hsiao, 1973). These functions do not depend on  $\pi_{tlp}$  when  $\psi_{pd} = \pi_{tlp}$ , so there is a simple link between  
513 the leaf drought tolerance, as informed by  $\pi_{tlp}$ , and the response of leaf-level gas exchange to water availability. Also, these  
514 equations predict that the decline of stomatal conductance as water availability decreases precedes that of photochemistry,  
515 consistent with observations (Fig. 2; Fatichi et al., 2016; Trueba et al., 2019).

516 Note that, since mesophyll conductance is not explicitly represented here, the effect of water stress on photosynthetic  
517 capacities ( $WSF_{ns}$ ) includes both direct effects on the photosynthetic machinery and indirect effects from the reduction of  
518 mesophyll conductance (Drake et al., 2017; Keenan et al., 2010). Alternative shapes of water stress factors could be explored  
519 in the future, and a more explicit representation of the water flow through the plant water column could be implemented  
520 (Paschalis et al., 2024). In the absence of a clear consensus on the effect of water stress on respiration, TROLL 4.0 does not  
521 assume that respiration depends on water availability (Flexas et al., 2006, 2005; Rowland et al., 2018, 2015; Santos et al.,  
522 2018; Stahl et al., 2013b).



523



524

525 **Figure 2: Responses of leaf-level gas exchange to water stress, depending on the leaf drought tolerance. Water stress factors for the**  
526 **stomatal conductance parameter  $g_1$  (stomatal limitation,  $WSF_s$ , Eq. (39); solid lines) and for the photosynthetic capacities  $J_{max}$  and**  
527  **$V_{cmax}$  (non-stomatal limitation,  $WSF_{ns}$ , Eq. (40); dashed lines) as a function of leaf predawn water potential ( $\Psi_{pd}$ , in MPa).  $WSF_s$**   
528 **are shown for a drought vulnerable species ( $\pi_{tlp}=-1.41$  MPa, the least negative value reported in Maréchaux et al., 2015; blue**  
529 **lines), and for a drought tolerant species ( $\pi_{tlp}=-3.15$  MPa, the most negative value reported in Maréchaux et al., 2015). Vertical**  
530 **dotted lines:  $\pi_{tlp}$ , horizontal dotted black lines:  $WSF_s$  and  $WSF_{ns}$  at  $\pi_{tlp}$ .**

#### 531 2.5.4 Leaf energy balance

532 In TROLL 4.0, leaf temperature ( $T_l$ ), vapor pressure deficit ( $VPD_s$ ) and  $CO_2$  concentration ( $c_s$ ) at the leaf surface are computed  
533 through an iterative scheme that solves the leaf energy balance (Medlyn et al., 2007; Wang and Leuning, 1998; Duursma,  
534 2015; Vezy et al., 2018). This is an important step because the leaf boundary layer plays a key role on gas exchanges, and  
535 especially so in dense tropical moist forests, given the large size of tropical tree leaves and the low wind speeds within canopies  
536 (De Kauwe et al., 2017; Jarvis and McNaughton, 1986; Meinzer et al., 1997). The iterative scheme is as follows. Initially,  $T_l$ ,  
537  $VPD_s$  and  $c_s$  are set equal to surrounding air values ( $T$ ,  $VPD$  and  $c_a$ ). Leaf photosynthesis ( $A_n$ ) and stomatal conductance ( $g_{sw}$ )  
538 are computed using Eqs (24), (34) and (35); next, the boundary layer conductance and radiation conductance are computed;  
539 and finally leaf-level transpiration rate is deduced from the Penman-Monteith equation (Eq. (41) below). After these steps,  
540 new values for  $T_l$ ,  $VPD_s$  and  $c_s$  are computed, and the above steps are repeated until leaf temperature converges, i.e., when the  
541 absolute difference between the  $T_l$  of two consecutive iteration is lower than  $0.01^\circ C$ .

542 Leaf-level transpiration rate  $E_l$  (in  $mol\ H_2O\ m^{-2}\ s^{-1}$ ) is calculated as:



$$E_l = \frac{1}{\lambda} \times \frac{sR_{ni} + VPD_a g_H C_p M_a}{s + \gamma \frac{g_H}{g_w}} \quad (41)$$

where  $\lambda$  is the latent heat of water vapor (in J mol<sup>-1</sup>),  $s$  is the slope of the (locally linearized) relationship between saturated vapor pressure and temperature (in Pa K<sup>-1</sup>, see Jones, 2013, Eq. (5.15) therein),  $R_{ni}$  is the isothermal net radiation (in J m<sup>-2</sup> s<sup>-1</sup>),  $g_H$  is the total leaf conductance to heat (in mol m<sup>-2</sup> s<sup>-1</sup>),  $C_p$  is the heat capacity of air (1010 J kg<sup>-1</sup> K<sup>-1</sup>),  $M_a$  is the molecular mass of air (28.96 × 10<sup>-3</sup> kg mol<sup>-1</sup>),  $\gamma$  the psychrometric constant (in Pa K<sup>-1</sup>), and  $g_w$  the total conductance to water vapor (mol H<sub>2</sub>O m<sup>-2</sup> s<sup>-1</sup>). The latent heat of water vapor  $\lambda$  depends on air temperature as follows:

$$\lambda = (2.501 \times 10^3 - 2.365 \times T) \times 18 \quad (42)$$

The isothermal net radiation  $R_{ni}$  has two components, the absorbed solar radiation ( $S_{abs}$ ), including both PAR and NIR wavebands, and the net longwave radiation (Leuning et al., 1995; Appendix D therein):

$$R_{ni} = S_{abs} - B_{n,0} \times k_d \exp(-k_d LAI) \quad (43)$$

where  $B_{n,0}$  is the net longwave radiation at the top of the canopy, and  $k_d \exp(-k_d LAI)$  accounts for its extinction within the canopy, with  $k_d$  set equal to 0.8. To account for the absorbed NIR radiation at a given height within the canopy in  $S_{abs}$ , we used the relationship reported by Kume et al. (2011; Fig. 4 therein) that links the transmitted NIR to the transmitted and incident PAR, and assumed a leaf absorptance in the NIR equal to 0.1.  $B_{n,0}$  is then computed as the absorbed minus the emitted longwave radiation:

$$B_{n,0} = \varepsilon_l (1 - \varepsilon_a) \sigma T_{top}^4 \quad (44)$$

where  $T_{top}$  is the top canopy air temperature in K,  $\sigma$  is the Stefan-Boltzmann constant ( $\sigma = 5.67 \times 10^{-8}$  W m<sup>-2</sup> K<sup>-4</sup>),  $\varepsilon_l$  is the emissivity of the canopy leaves, here assumed to be 1, and  $\varepsilon_a$  the emissivity of the atmosphere. Several models exist for  $\varepsilon_a$ , with varying performance depending on the sky conditions (Marthews et al., 2012). We here used Dilley and O'Brien (1998), which compromises between parsimony and performance across sky conditions (Marthews et al., 2012; Tables 2 and 5 therein).

$g_H$ , the total leaf conductance to heat, has three components, the boundary layer conductance for free convection  $g_{bHf}$ , the boundary layer for forced convection  $g_{bHu}$ , and the radiation conductance  $g_r$  (Leuning et al., 1995; Jones, 2013):

$$g_H = 2 \times (g_{bHf} + g_{bHu} + g_r) \quad (45)$$

where the factor 2 accounts for the two sides of the leaves.  $g_{bHf}$ , the boundary layer conductance for free convection, is given by:

$$g_{bHf} = 0.5 \times D_H \times \left( \frac{1.6 \times 10^8 \times |T_l - T|}{w_l} \right)^{0.25} \times \frac{P_{ress}}{RT} \quad (46)$$

where  $D_H$  is the molecular diffusivity to heat ( $D_H = 21.5 \times 10^{-6}$  m<sup>2</sup> s<sup>-1</sup>),  $P_{ress}$  the atmospheric pressure (in Pa),  $R$  the universal gas constant ( $R = 8.314$  J mol<sup>-1</sup> K<sup>-1</sup>) and  $T$  the temperature of surrounding air in K. Leaf width  $w_l$  (in m) is estimated as the square root of leaf area ( $w_l = \sqrt{LA}$ ).  $g_{bHu}$ , the boundary layer for forced convection (in mol m<sup>-2</sup> s<sup>-1</sup>), is given by:

$$g_{bHu} = 0.003 \times \sqrt{\frac{u}{w_l}} \times \frac{P_{ress}}{RT} \quad (47)$$



573 where  $u$  is the wind speed in  $\text{m s}^{-1}$  (see Eq. (9)).  $g_r$ , the radiation conductance in  $\text{mol m}^{-2} \text{s}^{-1}$  varies with  $T_a$  as follows (Jones,  
574 2013, p.101 therein):

$$575 \quad g_r = \frac{4 \times \epsilon_l \sigma T^3}{c_p M_a} \quad (48)$$

576  $g_w$  the total conductance to water vapor has two components that represent hydraulic resistances in series: the stomatal  
577 conductance ( $g_{sw}$ , in  $\text{mol H}_2\text{O m}^{-2} \text{s}^{-1}$ , Eq. (35)) and the boundary layer conductance ( $g_{bw}$  in  $\text{mol H}_2\text{O m}^{-2} \text{s}^{-1}$ ) to water vapor:

$$578 \quad g_w = \frac{g_{bw} \times g_{sw}}{g_{bw} + g_{sw}} \quad (49)$$

$$579 \quad \text{with } g_{bw} = 1.075 \times (g_{bHf} + g_{bHu}) \quad (50)$$

580 where 1.075 accounts for the relative diffusivities of heat and water vapor in air. Equations (49) and (50) assume that all leaves  
581 are hypostomatous (stomates on the ground-facing side of the leaves only), a reasonable assumption in tropical forests (Drake  
582 et al., 2019; Muir, 2015).

## 583 2.6 Carbon allocation

### 584 2.6.1. Net carbon uptake: whole-tree integration and respiration

585 At each daily timestep, the individual tree net primary productivity of carbon,  $NPP_{ind}$  (in  $\text{gC}$ ), is obtained by the following  
586 balance equation (Fig. 3):

$$587 \quad NPP_{ind} = GPP_{ind} - R_{maintenance} - R_{growth} \quad (51)$$

588  $GPP_{ind}$  (in  $\text{gC}$ ) is computed each half hour as the carbon assimilation rate  $A_n$  (Eq. (19)), multiplied by the leaf area in each  
589 tree crown layer ( $LA_l$ , in  $\text{m}^2$ ), then summed over tree crown layers and cumulated across the day.

590 Young leaves and old leaves have been reported to have lower photosynthetic capacities and activities than mature  
591 leaves (Doughty and Goulden, 2008; Kitajima et al., 2002, 1997b; Wu et al., 2016; Albert et al., 2018; Menezes et al., 2021).  
592 For each tree, total leaf area ( $LA_t$ ) is partitioned into three leaf age pools: young, mature and old leaves, so that  $LA_t = LA_{young}$   
593  $+ LA_{mature} + LA_{old}$  (all in  $\text{m}^2$ ). These three leaf age pools are assumed to be uniformly distributed within the tree crown. In  
594 young and old leaves, net assimilation rate is a fraction  $\rho < 1$  of that of mature leaves, so that:

$$595 \quad GPP_{ind} = C_{GPP} \times \frac{(\rho \times LA_{young} + LA_{mature} + \rho \times LA_{old})}{LA_t} \sum_l \sum_t A_n(t, l) \times LA_l \quad (52)$$

596 where the factor  $C_{GPP}$  is a conversion factor,  $t$  depicts the daytime half-hours and  $l$  the tree crown layers. Here we assume that  
597 the carbon uptake efficiency  $\rho$  relative to mature leaves is the same in young and old leaves and  $\rho = 0.5$ , a value consistent  
598 with observations.

599 TROLL 4.0 partitions autotrophic respiration into maintenance respiration and growth respiration, even if both come  
600 from the same biochemical pathways (Amthor, 1984; Thornley and Cannell, 2000). Maintenance respiration ( $R_{maintenance}$ ) has  
601 seldom been documented for stem and roots and is inferred empirically (Cavaleri et al., 2008; Meir et al., 2001; Slot et al.,  
602 2013; Weerasinghe et al., 2014). Nighttime leaf maintenance respiration is computed using Eqs (32) and (33), using the mean



603 nighttime temperature. As stomatal conductance and dark respiration vary less with leaf age than carbon assimilation rate  
 604 (Albert et al., 2018; Kitajima et al., 2002; Villar et al., 1995), we assumed that young and old leaves have respiration and  
 605 transpiration rate equal to  $q' = 0.75$  that of mature leaves, leading to lower water use efficiency than mature leaves. Tree-level  
 606 nighttime leaf respiration and daytime transpiration are computed as follows at each timestep:

$$607 \quad X_{ind} = C_X \times \frac{(q' \times LA_{young} + LA_{mature} + q' \times LA_{old})}{LA_t} \sum_l (\sum_i X(i, l)) \times LA_l \quad (53)$$

608 where  $X_{ind}$  is either the carbon respired by leaves during the night or the total water transpired by the tree, in gC or m<sup>3</sup>  
 609 respectively,  $X$  being the leaf dark respiration (Eqs. (32) and (33)) or the leaf-level transpiration rate (Eq. (41)) respectively,  
 610 and  $C_X$  is a conversion factor.

611 Stem maintenance respiration ( $R_{stem}$ , in  $\mu\text{mol C s}^{-1}$ ) was modeled assuming a constant respiration rate per volume of  
 612 sapwood ( $39.6 \mu\text{mol m}^{-3} \text{ s}^{-1}$ , Ryan et al., 1994), so that:

$$613 \quad R_{stem} = C_{sresp} \times 39.6 \times SA \times (h - cd) \quad (54)$$

614 where  $SA$  is the tree sapwood area (in m<sup>2</sup>) and  $C_{sresp}$  is a conversion factor. Stem respiration response to temperature was  
 615 modeled using a  $Q_{10}$  value of 2.0 (Meir and Grace, 2002; Ryan et al., 1994), and using mean daytime and nighttime  
 616 temperatures. Stahl et al. (2011) reported that  $R_{stem}$  varies among individual trees, even when controlling for sapwood volume.  
 617 However, in absence of a clear understanding of the drivers, Eq. (54) is a parsimonious choice. In TROLL 4.0, sapwood area  
 618 is computed dynamically. We used an inversion of the pipe model to derive sapwood area from the tree's leaf area ( $LA_t$ , in  
 619 m<sup>2</sup>), height ( $h$ , in m) and wood density following Fyllas et al. (2014; Eqs (7) and (8) therein):

$$620 \quad SA = C_{SA} \frac{2 \times LA_t}{\lambda_1 + \lambda_2 \times h + \delta_1 + \delta_2 \times wsg} \quad (55)$$

621 with  $\lambda_1 = 0.066 \text{ m}^2 \text{ cm}^{-2}$ ,  $\lambda_2 = 0.017 \text{ m cm}^{-2}$ ,  $\delta_1 = -0.018 \text{ m}^2 \text{ cm}^{-2}$ , and  $\delta_2 = 1.6 \text{ cm}^3 \text{ g}^{-1}$ , and  $C_{SA}$  a conversion factor. In addition  
 622 to Eq. (55), there are both lower and upper limits on sapwood extent. Sapwood has a minimum thickness of 0.5 cm and any  
 623 newly grown wood is always considered sapwood, irrespective of leaf area. TROLL 4.0 also imposes an upper limit on  
 624 sapwood growth based on stem diameter growth, so that increases in living tissue cannot exceed increases in total tissue.

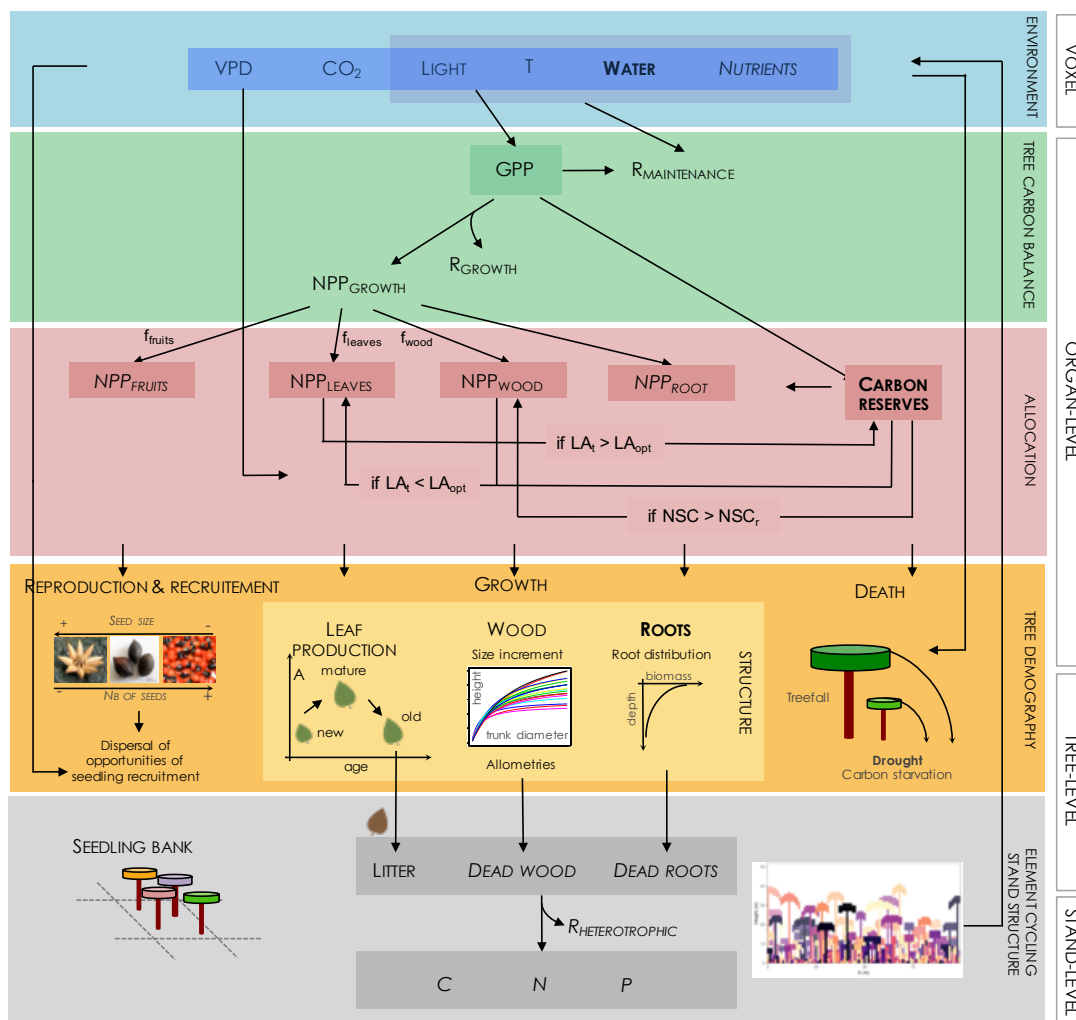
625 Other contributions of maintenance respiration were prescribed as proportions of leaf and stem maintenance  
 626 respiration. Fine root maintenance respiration was assumed to be half of leaf maintenance respiration (Malhi, 2012), and coarse  
 627 root and branch maintenance respirations were assumed to account for half of stem respiration (Asao et al., 2015; Cavaleri et  
 628 al., 2006; Meir and Grace, 2002).

629 Growth respiration ( $R_{growth}$ ) was assumed to account for 30% of the carbon uptake by photosynthesis (gross primary  
 630 productivity) minus the maintenance respiration (Cannell and Thornley, 2000). These assumptions are commonly made in the  
 631 literature, but remain a major source of uncertainty in the carbon flux modeling (Atkin et al., 2014; Huntingford et al., 2013).

632 Contrary to the last published version of TROLL, in which the allocation of  $NPP_{ind}$  to plant organs was fully prescribed  
 633 by fixed factors ( $f_{canopy} = f_{leaves} + f_{fruit} + f_{twigs}$  and  $f_{wood}$ , Maréchaux and Chave, 2017), the allocation scheme implemented in  
 634 TROLL 4.0 can now be additionally modulated depending on the current tree state and it includes an explicit carbon storage  
 635 compartment (sections 2.6.2 and 2.6.3; Fig. 3).



636



637

638 **Figure 3: Diagram of structures and processes driving individual and community dynamics, as investigated under the modeling**  
 639 **approach adopted in TROLL 4.0. Elements in bold letters refer to novel implementation in comparison to the previous published**  
 640 **version, while italic letters refer to elements still not included in this present version. Abiotic environment is modeled at the voxel**  
 641 **scale and drive C assimilation in the leaves (gross primary productivity, GPP) and maintenance respiration rates of the different**  
 642 **plant organs ( $R_{\text{MAINTENANCE}}$ ). The C amount resulting from the balance between GPP and  $R_{\text{MAINTENANCE}}$  can be used for tissue**  
 643 **production ( $NPP_{\text{FRUITS}}$ ,  $NPP_{\text{LEAVES}}$ ,  $NPP_{\text{WOOD}}$  and  $NPP_{\text{ROOTS}}$ ) or stored (**CARBON RESERVES**) in the different tree organs. Both**  
 644 **allocations induce metabolic costs ( $R_{\text{GROWTH}}$  and  $R_{\text{STORAGE}}$ ; but the latter is not represented nor included). **CARBON RESERVES****  
 645 **represents non-structural carbohydrates (NSC), mainly stored as sugar or starch, and its maximal storage capacity is given by  $NSC_r$ .**  
 646 **Allocation to these different compartments follows a hierarchical scheme initialized by default proportions ( $f_{\text{fruits}}$ ,  $f_{\text{leaves}}$ ,  $f_{\text{wood}}$ ). If the**  
 647 **tree leaf area ( $LA_t$ ) exceeds the optimal leaf area ( $LA_{\text{opt}}$ , a function of both tree properties and its micro-environment), then the**  
 648 **surplus of  $NPP_{\text{LEAVES}}$  is allocated to carbon reserves. If the tree leaf area is lower than optimal, then  $NPP_{\text{WOOD}}$ , and if further needed,**  
 649 **carbon reserves, are mobilized for leaf production. If carbon reserves surpass storage capacity ( $NSC_r$ ), then stored carbohydrates**  
 650 **are used for woody growth. C allocated to tissue production leads to an increment of trunk diameter and height following allometric**  
 651 **relationships, and the production of new young leaves and roots. Simultaneously with tissue turnover, this leads to the update of leaf**  
 652 **density and root biomass distribution, influencing both abiotic environment (eg. light diffusion and water interception) and light**  
 653 **and element acquisition, and thus carbon assimilation and metabolism. C allocated to reproduction leads to the production of seeds,**  
 654 **which are dispersed randomly. This generates a spatially-explicit seedling bank, from which winners are locally recruited depending**



655 on both light and water availability. Tree death may be triggered by environmental or mechanical constraints, or carbon starvation.  
656 In a future version, litter decomposition, wood decay and nutrient mineralization, could lead to soil nutrient availability for plant  
657 uptake, and take place through the action of soil microorganisms, which activity, and hence respiration ( $R_{\text{HETEROTROPHIC}}$ ), depends  
658 particularly on temperature and soil moisture.  
659

## 660 2.6.2 Leaf production and leaf shedding

661 Leaf phenology is a key driver of the variation of tropical forest productivity (Manoli et al., 2018; Restrepo-Coupe et al., 2013;  
662 Wu et al., 2017). However, its underlying drivers remain poorly understood, and its representation in vegetation models  
663 remains challenging (Chen et al., 2020; Restrepo-Coupe et al., 2017). In ORCHIDEE, Chen et al. (2020, 2021) proposed a leaf  
664 phenological scheme in which the production of young leaves is partly controlled by incident shortwave radiation, while the  
665 shedding of old leaves is controlled by vapor pressure deficit. This scheme reproduces the simultaneous increase in leaf  
666 production and litterfall observed in many Amazonian rainforest sites where productivity increases during the dry season  
667 (Chave et al., 2010; Wagner et al., 2016; Yang et al., 2021), but not the observed seasonality in productivity at some sites (e.g.  
668 GUYAFLUX eddy-flux site in French Guiana, Chen et al., 2020). Additionally, this scheme overlooks the contrasted leaf  
669 phenological patterns observed across canopy individuals within and across species within communities (Nicolini et al., 2012;  
670 Loubry, 1994). In ED2, Xu et al. (2016) implemented a leaf phenological scheme driven by water availability in the root zone  
671 in a seasonally dry tropical forest. Since leaf shedding is often triggered by drought-induced loss of leaf turgor in these systems  
672 (Sobrado, 1986), leaf shedding and production are assumed to depend on the difference between leaf predawn water potential  
673 and leaf water potential at turgor loss point. However, such a scheme cannot simulate the simultaneous leaf production and  
674 shedding observed in moist tropical forests.

675 In TROLL 4.0, we propose an alternative approach. At each timestep, the optimal tree total leaf area ( $LA_{\text{opt}}$ ) is  
676 estimated as the leaf area beyond which producing more leaves leads to a net carbon loss due to self-shading and respiration  
677 costs.  $LA_{\text{opt}}$  depends on tree crown size and leaf area density (section 2.4.2), leaf photosynthetic capacities and respiration rate  
678 (section 2.5.1), and local light environment. At each timestep, the amount of carbon allocated to the production of new young  
679 leaves,  $NPP_{\text{leaves}}$ , and to woody growth,  $NPP_{\text{wood}}$ , are determined by default as:  $NPP_{\text{leaves}} = f_{\text{leaves}} \times NPP_{\text{ind}}$ , with  
680  $f_{\text{leaves}} = 0.68 \times f_{\text{canopy}}$  (Chave et al., 2008, 2010; Maréchaux and Chave, 2017), and  $NPP_{\text{wood}} = 0.6 \times f_{\text{wood}} \times NPP_{\text{ind}}$ ,  
681 where the factor 0.6 accounts for the fact that about 40% of woody NPP is actually used for branch fall repair (Malhi et al.,  
682 2011). When leaf area  $LA_t$  exceeds  $LA_{\text{opt}}$ ,  $NPP_{\text{leaves}}$  is reduced so that  $LA_t = LA_{\text{opt}}$ . Second, if the carbon allocated to leaf  
683 production is not sufficient to compensate leaf loss, then the carbon attributed by default to tree woody growth is mobilized  
684 for leaf production until leaf loss is compensated. If not sufficient, the tree carbon storage (see section 2.6.3) is then also  
685 mobilized. Hence this scheme prioritizes the maintenance of the assimilating tissues over woody growth (Schipper et al.,  
686 2015). The variation of leaf area for each leaf age pool is then computed as follows:

$$687 \Delta LA_{\text{young}} = \frac{2 \times NPP_{\text{leaves}}}{LMA} - \frac{LA_{\text{young}}}{\tau_{\text{young}}}$$





$$\Delta LA_{mature} = \frac{LA_{young}}{\tau_{young}} - \frac{LA_{mature}}{\tau_{mature}}$$

$$\Delta LA_{old} = \frac{LA_{mature}}{\tau_{mature}} - \frac{LA_{old}}{\tau_{old}} \quad (56)$$

where  $\tau_{young}$ ,  $\tau_{mature}$ ,  $\tau_{old}$  are the residence times in each class (in yr), so that  $LL = \tau_{young} + \tau_{mature} + \tau_{old}$  with LL the maximal tree leaf lifespan (in yr). LL is inferred from the tree LMA, using the following empirical relationships (Schmitt, 2017):

$$LL = \frac{1}{12} \max(3, 12.755 \times \exp(0.007 \times LMA - 0.565 \times N)) \quad (57)$$

$\tau_{young}$  was fixed to  $\min(LL/3, 1/12)$  yr (Doughty and Goulden, 2008; Wu et al., 2016), and  $\tau_{mature}$  as a third of total leaf lifespan.

The loss term  $LA_{old}/\tau_{old}$  corresponds to the rate of leaf litterfall at each timestep. In the previous TROLL version, litterfall resulted from the dynamics of leaf biomass with  $\tau_{old} = LL - \tau_{young} - \tau_{mature}$ . This leaf shedding scheme is passive and does not simulate the observed seasonality in leaf litterfall. Here we propose a new approach to simulate leaf shedding. We first observed that within species and sites, canopy trees can shed their leaves at different times, suggesting that causal environmental drivers should display fine-scale heterogeneity in space (unlike atmospheric shortwave radiation and vapor pressure deficit). In addition, old leaves display nutrient resorption before abscission (Albert et al., 2018; Kitajima et al., 1997a; Urbina et al., 2021); similarly, solute translocation from older to younger leaves can lower osmotic potential and leaf water potential at turgor loss point, thus increasing the drought tolerance of younger leaves to the detriment of older leaves (Pantin et al., 2012). We therefore used predawn leaf water potential as a trigger of leaf shedding as in Xu et al., (2016), but with different thresholds for leaves of different ages, older leaves being more susceptible to a small decrease in tree water availability, while younger leaves can maintain turgor and grow at the same time. More specifically, we defined the following threshold:

$$\psi_{T,o} = \min(a_{T,o} \times \pi_{tlp} - 0.01 \times h - b_{T,o}) \quad (58)$$

The first term in  $\psi_{T,o}$  with  $a_{T,o} < 1$  represents old leaves' lower ability to maintain turgor as soil dries. The second term modulates this susceptibility to drought depending on tree height (Bennett et al., 2015): it induces a susceptibility to a (small) decrease  $b_{T,o} > 0$  in soil water availability for large trees, while preventing them from constantly shedding their old leaves at fast pace (see Eq. (37)).  $\tau_{old}$  is then updated using a multiplying factor  $f_o$  ( $0.001 \leq f_o \leq 1$ ). Initially,  $\tau'_{old} = f_o \tau_{old}$  with  $f_o = 1$ , which is updated daily as follows:  $f'_o = f_o - \delta_o$  when  $\psi_{pd} < \psi_{T,o}$  and  $f'_o = f_o + \delta_o$  when  $\psi_{pd} > \psi_{T,o}$ , always assuming that  $f_o$  has 0.001 as a lower bound, and 1 as an upper bound.

We assumed no variation of  $\pi_{tlp}$  with tree height (Maréchaux et al., 2016). The threshold  $\psi_{T,o}$  jointly depends on  $\pi_{tlp}$  and tree height  $h$  to account for drought tolerance and tree height on leaf-level water stress. Practically, the tree height above which old leaves becomes susceptible to a small decrease in soil water availability is  $H_{T,o} = -100 \times (a_{T,o} \pi_{tlp} + b_{T,o})$  in m: 28 m at  $\pi_{tlp} = -1.5$  MPa and 58m at  $\pi_{tlp} = -3$  MPa (when  $a_{T,o} = 0.2$  and  $b_{T,o} = 0.02$ ). While this scheme is based on process-based observations, parameters  $a_{T,o}$ ,  $b_{T,o}$ , and  $\delta_o$  are currently calibrated (see Schmitt et al., submitted companion paper).



### 719 2.6.3 Carbon storage

720 In TROLL 4.0, trees can store carbon explicitly in non-structural carbohydrates. The maximal amount of carbon a tree can  
721 store and remobilize is determined as follows:

$$722 \quad NSC_r = 1000 \times 0.5 \times 0.05 \times 1.25 \times AGB \quad (59)$$

723 where  $NSC_r$  stands for non-structural carbohydrates (in gC),  $AGB$  is the tree aboveground biomass (in kg), and  $1000 \times 0.5$   
724 converts biomass in kg into C in g (Elias and Potvin, 2003). It is assumed that NSC can account for 10% of the tree biomass,  
725 half of which is mobilizable (Martínez-Vilalta et al., 2016), hence the factor 0.05. The other half of NSC supports critical  
726 metabolic functions or is no longer accessible. The factor 1.25 accounts for an additional 25% biomass storage in coarse roots,  
727 so  $1.25 \times AGB$  is total tree biomass (Ledo et al., 2018).  $AGB$  is computed following (Chave et al., 2014; Eq. (5) therein):

$$728 \quad AGB = 0.0559 \times wsg \times dbh^2 \times h \quad (60)$$

729 where  $dbh$  is in cm,  $h$  in m and  $wsg$  in  $g\ cm^{-3}$ . The NSC storage compartment is filled by the potential carbon surplus resulting  
730 from the allocation to leaf production, i.e.  $f_{leaves} \times NPP_{ind} - NPP_{leaves}$ , if positive. If the storage compartment has reached  
731 its maximal capacity  $NSC_r$ , then the surplus is allocated to woody growth.

### 732 2.6.4 Growth

733 The net primary production allocated to woody growth,  $NPP_{wood}$ , depends on the outcome of allocation to leaf  
734 production and carbon reserves (see sections 2.6.2 and 2.6.3; Fig. 3). In TROLL 4.0, hydraulic control on carbon assimilation  
735 and leaf phenology both influence carbon allocation to trunk growth (e.g. Doughty et al., 2014; Farrior et al., 2013;  
736 Friedlingstein et al., 1999), but turgor-mediated processes are not explicitly modeled (Coussement et al., 2018; Peters et al.,  
737 2023; Muller et al., 2011; Körner, 2015).  $NPP_{wood}$  is converted into an increment of stem volume,  $\Delta V$  in  $m^3$ , as follows:

$$738 \quad \Delta V = 10^{-6} \times \frac{NPP_{wood}}{0.5 \times wsg} \times Senesc(dbh) \quad (61)$$

739 where the factor 0.5 converts dry biomass units into carbon units (Elias and Potvin, 2003). The function  $Senesc(dbh)$  is  
740 designed so that the largest trees cannot allocate carbon as efficiently into growth, reflecting empirical evidence of a size-  
741 related relative growth decline in trees (Yoda et al., 1965; Ryan et al., 1997; Mencuccini et al., 2005; Woodruff and Meinzer,  
742 2011; Stephenson et al., 2014). We assumed that trees cannot exceed a trunk diameter of  $dbh_{max} = \frac{3}{2} dbh_{thresh}$ , where  
743  $dbh_{thresh}$  depends on species-specific information provided by the user (see section 2.4.1), so that:

$$744 \quad Senesc(dbh) = \begin{cases} 1 & \text{when } dbh \leq dbh_{thresh} \\ \max\left(0; 3 - 2 \frac{dbh}{dbh_{thresh}}\right) & \text{when } dbh > dbh_{thresh} \end{cases} \quad (62)$$

745 Trunk diameter growth increment  $\Delta dbh$  (in m), is computed from  $\Delta V$  as follows.  $V = C \pi \left(\frac{dbh}{2}\right)^2 h$ , where  $C$  is a form  
746 factor (Chave et al. 2014, Eq. (5) therein). The term  $h$  (in m) is total tree height inferred from the  $dbh$  following Eq. (16), this  
747 leads to an expression of  $V$  as a function of  $dbh$  only. This function can be inverted to estimate  $\Delta dbh$  as a function of  $\Delta V$ ,  
748 which is known from Eq. (61). Tree height and crown dimensions are then updated using Eqs (16), (17) and (18).



## 749 2.7 Tree demography

### 750 2.7.1 Seed production, dispersal and recruitment

751 The starting point for a tree life cycle, as represented in TROLL 4.0 is an event of seed dispersal into the seed bank. On each  
752 1x1 m ground site and for each species  $s$ , a ‘seed’ bank stores all the seeds dispersed from the mature trees as well as from an  
753 external seed rain. The seed bank is updated once a year. Here, our conceptual ‘seeds’ represent opportunities of seedling  
754 recruitment rather than as true seeds, since not all seed dispersal events are modeled explicitly, and the seed-to-seedling  
755 transition is implicit.

756 In TROLL 4.0 trees are assumed to become fertile above a diameter threshold  $dbh_{mature}$  that depends on the tree  
757 maximal size (Visser et al., 2016) as follows:

$$758 \quad dbh_{mature} = 0.5 \times dbh_{thresh} \quad (63)$$

759 This relationship is drawn from direct observations of reproductive status of tree species in the tropical forest of Barro Colorado  
760 Island, Panama, with maximal tree  $dbh$  spanning a range of 0.05 to 2 m (see Fig. S9 in Visser et al., 2016;  $R^2=0.81$ ,  $n=60$   
761 species). The number of reproduction opportunities per mature tree,  $n_s$ , is assumed fixed and equal for all individuals, and its  
762 value is user-defined. This assumption of a fixed reproductive opportunity per tree is predicated on the fact that there is a trade-  
763 off between seed number and seed size, itself related to seed and seedling survival. Thus, the probability of germination does  
764 not depend strongly on seed size or on the number of produced seeds and can be assumed a zero-sum game (Coomes and  
765 Grubb, 2003; Moles et al., 2004; Moles and Westoby, 2006). Each of the  $n_s$  events is scattered away from the tree in a random  
766 direction and at a distance randomly drawn from a Rayleigh distribution, thus allowing for potential long-dispersal events.  
767 Although seed dispersal distance is known to vary depending on dispersal syndrome and plant traits (Tamme et al., 2014;  
768 Seidler and Plotkin, 2006; Muller-Landau et al., 2008), the scale parameter  $\sigma_{disp}$  of the distribution is here fixed across species  
769 and individuals.

770 The intensity of the external seed rain is quantified by  $N_{tot}$  (in number of incoming seeds per hectare) and its species  
771 composition is defined by the relative abundances of species  $f_{reg,s}$ , both being user-defined. Hence, for each species  $s$ ,  $n_{ext,s}$   
772 events of dispersal due to seeds immigrating from the outside occurred, with:

$$773 \quad n_{ext,s} = N_{tot} \times f_{reg,s} \times n_{ha} \quad (64)$$

774 with  $n_{ha}$  the number of hectares of the simulated plot. These reproduction opportunities are uniformly distributed within the  
775 simulated area.

776 If several species are competing for recruitment in a local seed bank, one of the species is picked at random as the  
777 winner out of all the seeds present, as in a lottery model (Chesson and Warner, 1981). The recruitment event occurs only if  
778 ground-level light availability is sufficiently high. To test if this condition is met, the seedling is first attributed individual trait  
779 values depending on the species-specific averages (see section 2.4.1). These traits values are then used to determine the  
780 maximum LAI ( $LAI_{max}$ ) the seedling would support under average environmental conditions, with  $LAI_{max}$  defined as the



781 threshold beyond which the seedling leaf assimilation would be less than respiration (see section 2.6.2). The seedling can be  
782 recruited if the site LAI at ground level is lower than  $LAI_{max}$ .

783 Water availability is also key to seedling performance (Engelbrecht et al., 2006; Johnson et al., 2017; Kupers et al.,  
784 2019), hence TROLL 4.0 now implements an additional water-dependent dependence on seedling establishment (Craine et al.,  
785 2012; Paine et al., 2018). Seedling recruitment is possible only if top-layer soil water potential is less negative than half the  
786 turgor loss point ( $\pi_{tlp}/2$ ). Such parameterization is motivated by the fact that, at turgor loss point, the seedlings would not  
787 germinate, and a certain level of turgor is needed for germination and growth (Bradford, 1990; Daws et al., 2008; Coussement  
788 et al., 2018; Hsiao, 1973; Fatichi et al., 2016).

789 If both conditions on light and water availability are met, the newly recruited tree is initialized with a  $dbh=0.01m$ , a  
790 total leaf area  $LA_t = 0.25 \times LA_{opt}$  distributed across the three leaf age pools in proportion to their relative span ( $\tau_{young}/LL$ ,  
791  $\tau_{mature}/LL$ ,  $\tau_{old}/LL$ ; see section 2.6.2), and a carbon storage compartment filled at half its maximum  $NSC_r$  (see section 2.6.3).

792 The assumptions here made on tree reproduction largely reflect limited knowledge on these processes, which remains  
793 major sources of uncertainty in current models (König et al., 2022; Hanbury-Brown et al., 2022; Díaz-Yáñez et al., 2024).

## 794 2.7.2 Mortality

795 Mortality processes also play a key role in forest structure and carbon balance (Sevanto et al., 2014; Friend et al., 2014; Johnson  
796 et al., 2016; Esquivel-Muelbert et al., 2020; McDowell et al., 2022). TROLL 4.0 explicitly represents several important  
797 mechanisms of tree mortality. At each timestep, individual tree death rate (in events  $yr^{-1}$ ; Sheil et al. 1995) is:

$$798 d = d_b + d_{starv} + d_{treefall} + d_{drought} \quad (65)$$

799 where  $d_b$  is a background death rate,  $d_{starv}$  represents death due to carbohydrate shortage (carbon starvation),  $d_{treefall}$   
800 represents death due to treefall (including trees indirectly killed by neighboring fallen trees), and  $d_{drought}$  the drought-induced  
801 tree mortality.

802 Background mortality  $d_b$  encapsulates death events that are not attributed to any specific mechanism in the model.  
803 Mortality rate is known to vary greatly among species, and we here assume that it is negatively correlated with tree wood  
804 density, as observed pan-tropically (King et al., 2006; Kraft et al., 2010; Poorter et al., 2008; Wright et al., 2010). This  
805 dependence illustrates a trade-off between investment into construction costs and risk of mortality (Chave et al., 2009). We  
806 assumed the following relationship:

$$807 d_b = m \times \left(1 - \frac{wsg}{wsg_{lim}}\right) \quad (66)$$

808 where  $m$  (in events  $yr^{-1}$ ) is the reference background mortality rate for a species with low wood density and is user-specified.  
809  $wsg_{lim}$  is a value large enough so that  $d_b$  always remains positive (here set at  $1 \text{ g cm}^{-3}$ ).



810 A tree can also die because of carbohydrate shortage in case of prolonged stress ( $d_{starv}$  in Eq. (65)). In TROLL 4.0  
811 that includes an explicit carbohydrate storage compartment, the tree dies of carbon starvation when this compartment is empty  
812 and  $NPP_{ind} \leq 0$  (Eq. (51)).

813 Tree death may be caused by treefalls (term  $d_{treefall}$  in Eq. (65)). To simulate this process, we first define a stochastic  
814 threshold  $\theta$ , depending on the tree maximal height, and prescribed at tree birth. Then, the tree can fall with a probability equal  
815 to  $1 - \frac{\theta}{h}$  (Chave, 1999) each month. As TROLL 4.0 uses a daily timestep, this probability is uniformly distributed across the  
816 days of one month. The parameter  $\theta$  is computed for each tree, as follows:

$$817 \theta = h_{max} \times (1 - v_T \times |\zeta|) \quad (67)$$

818 where  $h_{max}$  is maximal tree height (i.e. the tree height computed using Eq. (16) at  $dbh_{max}$ ),  $v_T$  is a variance term,  $|\zeta|$  is the  
819 absolute value of a random Gaussian variable with zero mean and unit standard deviation.  $v_T$  is modified at tree level so that  
820 high risks of treefall ( $> 99.5^{th}$  percentile of the Gaussian variable) occur at the same height for all individuals of the same  
821 species. This implicitly introduces a growth-mortality trade-off, as more slender trees (larger ratio of height to trunk diameter)  
822 should reach this height threshold quicker. The orientation of tree falls is random. Trees on the trajectory of the falling tree can  
823 be damaged, especially if they are smaller than the fallen tree (van der Meer and Bongers, 1996). To model this effect, an  
824 individual variable  $hurt$  is defined. If a tree is within the trajectory of the fallen stem or of the fallen crown, its variable  $hurt$  is  
825 updated to  $h$  and  $\frac{h-CR}{2}$ , respectively, if it was lower, where  $h$  and  $CR$  are the tree height and crown radius of the fallen tree,  
826 respectively. The probability to die due to another treefall is then  $1 - \frac{1}{2} \frac{h}{hurt \times e^{\varepsilon_{h,j}}}$ , where  $h$  is the height of the focal tree and  
827  $e^{\varepsilon_{h,j}}$  (see Eq. (16)) accounts for the fact that slender individuals (higher tree height deviation) would be more vulnerable to  
828 treefall. Such tree can either fall and itself damage other trees or dies standing, depending on the user choice. The  $hurt$  variable  
829 is reset to zero at each timestep.

830 Finally, prolonged drought is also a source of mortality. Drought-induced mortality is triggered when the leaf predawn  
831 water potential  $\psi_{pd}$  is below a lethal level ( $\psi_{lethal}$ ), and  $\psi_{lethal}$  is computed from the leaf water potential at turgor loss point,  
832 using the relationship provided by the global meta-analysis of Bartlett et al. (2016;  $P=0.03$ ,  $R^2=0.31$ ,  $n=15$  species from tropical  
833 dry and moist biomes), as follows:

$$834 \psi_{lethal} = -0.9842 + 3.1795 \times \pi_{ttp} \quad (68)$$

### 835 3 Modelling protocol

#### 836 3.1 Model inputs

837 TROLL 4.0 requires five input files to run a simulation: (i) global parameters, (ii) species parameters, (iii) soil characteristics,  
838 and finally, meteorological drivers varying at (iv) half-hour and (v) daily step.



839 The global input file contains parameters that define the simulation set-up (e.g. the number of timesteps, size of the  
840 simulated plot and of the belowground voxels), and values for biophysical parameters that remain constant throughout the  
841 simulation and are not species- or tree-specific. These include the light attenuation coefficient, allocation parameters, minimal  
842 death rate, and more (see Table A1). Parameter values can be varied across simulations, to test model sensitivity, transfer  
843 across sites, or any other reason. The species input file contains mean functional traits for at least one species and with no  
844 upper bound (see Table A1). Functional trait values can be prescribed from local field measurements, or retrieved from global  
845 trait databases (e.g. Kattge et al., 2020; Díaz et al., 2022).

846 The soil input file contains the soil variables needed for the pedotransfer functions, i.e. soil texture (proportion of silt,  
847 clay and sand), soil organic matter content, dry bulk density, soil pH, and cation exchange capacity, for each soil layer, with  
848 thickness of each layer. The number of soil layers is at least one, and is not theoretically limited. Lacking local soil data, model  
849 users may retrieve soil parameters from online databases (e.g. Poggio et al., 2021), bearing in mind the uncertainties of such  
850 products, especially in tropical areas (Khan et al., 2024).

851 Meteorological drivers are provided in two files, depending on their temporal resolution in the model. Daytime  
852 temperature, vapor pressure deficit, incident irradiance and wind speed at a reference height above the canopy are provided  
853 for every half-hour, while average nighttime temperature and cumulative rainfall are provided at a daily timestep. Such data  
854 can typically be retrieved from meteorological stations embedded in eddy-flux towers, or from global products (Muñoz-Sabater  
855 et al., 2021), as in Schmitt et al. (2023).

### 856 **3.2 Initial conditions**

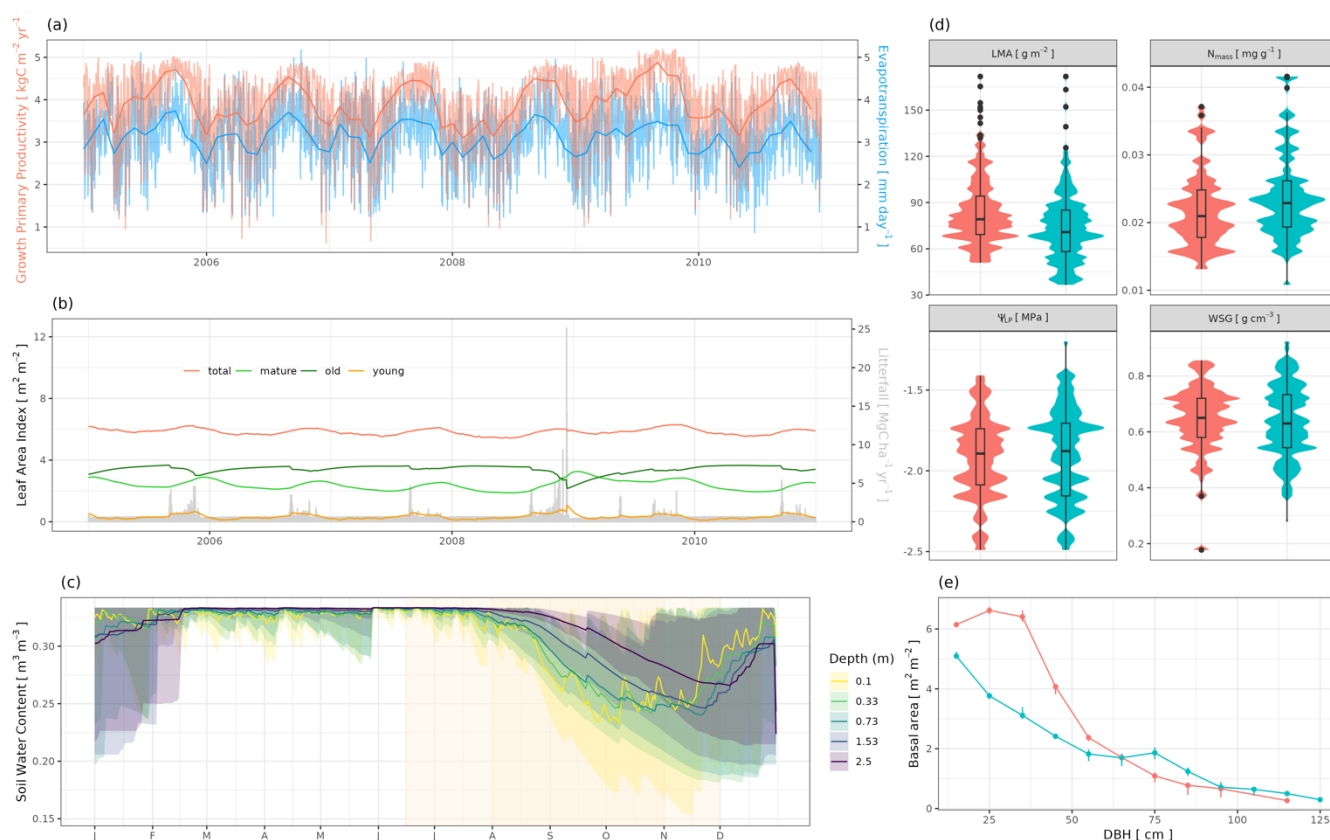
857 Two types of initial conditions are useful in most practical settings, and are implemented in TROLL 4.0. First, the user can  
858 simulate forest regeneration from bare ground. In this case, forest succession is initiated by the external seed rain, the  
859 composition and intensity of which are user-defined (see above). The steady-state forest composition and structure are thus  
860 emergent properties of the community assembly mechanisms embedded in the model, and the user-specified seed rain. The  
861 second option is to prescribe an initial forest state. This requires that an initial forest state be provided as an additional input  
862 file. The code is designed to adapt to the level of information provided by the inventory file, from a minimal requirement of  
863 tree *dbh* to the full list of individual variables for each tree. For individual variables missing in the input file, these are either  
864 computed from the model relationships or drawn at random. This second initial condition matches a real site forest state given  
865 the available data, but will require careful calibration to maintain the forest state over a longer time period (e.g. Fischer et al.,  
866 2019). A more common use case is to restart new simulations from an output of a previous simulation, e.g., to perform virtual  
867 experiments controlling the initial state.

### 868 **3.3 Standard outputs**

869 TROLL 4.0 provides a range of outputs related to forest structure, forest composition and diversity, and ecosystem functioning  
870 (e.g., carbon and water fluxes; Fig. 4). It simulates forest structure and composition and provides outputs comparable to those



871 measured in the field: tree size distribution, tree spatial distribution, biomass accumulation curve, functional trait distribution,  
 872 canopy height and leaf area index maps (Maréchaux and Chave, 2017), and more generally all information that can be retrieved  
 873 from a detailed field inventory or a meter-scale airborne laser scanning survey (Fischer et al., 2019). In TROLL 4.0, other  
 874 outputs are also available: litterfall fluxes, carbon and water fluxes comparable to the one provided by eddy-flux towers, soil  
 875 water state (content and water potential). An evaluation of these outputs for two Amazonian forest sites is provided in a  
 876 companion paper (Schmitt et al., submitted companion paper).  
 877



878 **Figure 4: Examples of outputs provided by TROLL 4.0 and related to ecosystem functioning, diversity and structure. (a) Temporal**  
 879 **variations of gross primary productivity (red) and evapotranspiration (blue) within and across years. (b) Variation in total leaf area**  
 880 **index (red line) and leaf area index per leaf age cohort (young, mature, old; yellow, light green and dark green lines, respectively),**  
 881 **together with litterfall (grey bars), within and across years. (c) Mean seasonal variations of water content in soil layers of different**  
 882 **depths, with the vertical yellow band in the background depicting the dry season. (d) Distribution of functional traits. (e)**  
 883 **Distributions of basal area per diameter class. Panels (a), (b) and (c) show outputs for an Amazonian forest site (Paracou), panels**  
 884 **(d) and (e) show outputs for two Amazonian sites (Paracou, red; Tapajos, blue), see Schmitt et al., submitted companion paper. for**  
 885 **details on simulation set-ups.**  
 886



## 887 **4 Discussion**

888 TROLL 4.0 is a novel generation of forest growth models designed to bridge the gap between traditional forest growth  
889 models and process-based models informed by ecophysiology. It includes an integration of processes underlying ecosystem  
890 fluxes closer to a modern DGVM than most other forest growth simulators. It also includes representation of plant community  
891 structure and diversity at a resolution similar to that used by ecologists in the field. This enables a direct comparison with a  
892 range of field data, including forest inventories, trait distribution, fine- and large-scale remote-sensing products, or eddy-  
893 covariance data. Here we discuss the assumptions of the water cycle newly included in the model, as well as transferability  
894 and limitations of the current model version.

### 895 **4.1 Simulating water fluxes and forest responses to water availability**

896 Previous versions of TROLL assume that water availability does not limit ecosystem fluxes and dynamics, a strong but  
897 reasonable assumption in a light-limited forest like in Eastern Amazonia (Guan et al., 2015; Wagner et al., 2016; Maréchaux  
898 and Chave, 2017). However, such a simplification does not allow to account for drought-induced inter-annual variability in  
899 forest dynamics (Bonal et al., 2008; Aguilos et al., 2018; Leitold et al., 2018) or to transfer the model to sites where water  
900 availability is limiting. As droughts will be important drivers for tropical ecosystems in the future (Duffy et al., 2015), such a  
901 simplification does not allow to project future states of forest under climate change.

902 In TROLL 4.0, we implemented a full water cycle. We introduced a belowground field with a hydraulic state coupled  
903 to the vegetation, and a representation of the response of leaf gas exchanges to local atmospheric conditions and their control  
904 by the leaf boundary layer. This detailed representation is commonplace DGVMs (Prentice et al., 2007) but to our knowledge,  
905 it is new for an individual-based spatially explicit forest dynamic simulator. This paves the way for explorations and projections  
906 of the independent effects of soil water availability and atmospheric demand on ecosystem functioning (Novick et al., 2016;  
907 Santos et al., 2018), community composition and structure (Esquivel-Muelbert et al., 2019; Fauset et al., 2012; Slik, 2004;  
908 Feeley et al., 2011).

909 These developments have striven to follow the parsimonious principle: more complex representations do not  
910 systematically result in increased model reliability and robustness, especially if the additional parameters are poorly  
911 constrained (Mahnken et al., 2022; Prentice et al., 2015). The soil hydraulic state is simulated using a bucket model (Budyko,  
912 1961; Manabe 1969; Vargas Godoy et al., 2021). In the future, more complex representations of soil water dynamics could be  
913 implemented at finer temporal and spatial resolutions, such as the implementation of Richards' equation (Richards, 1931), and  
914 integration of lateral flows, but this would be at a serious computational cost. These could be compared with the current simpler  
915 representation to assess the relevance of increasing complexity in various contexts and soil data availability (Van Nes and  
916 Scheffer, 2005). However, two aspects were considered to be needed in the current version, based on biological considerations.  
917 First, we implemented a multi-layer soil model, a more detailed representation compared with other models using a bucket  
918 model approach (e.g. Fischer et al., 2014; Laio et al., 2001). This was motivated by the need to account for contrasting rooting





919 strategies and access to water among coexisting plants, which is an under-explored, but likely key, aspect of community  
920 dynamics in forests (Brum et al., 2019; De Deurwaerder et al., 2018; Ivanov et al., 2012). Second, we assumed that the depth  
921 of tree water uptake is not only controlled by the distribution of root biomass (as in Naudts et al., 2015; Sakschewski et al.,  
922 2021; Paschalis et al., 2024), but also by soil water state and its vertical variation (as in Williams et al., 1996; Duursma and  
923 Medlyn, 2012). These improvements are relevant to the temporal variation of water retrieval depth (Bruno et al., 2006) and  
924 the sustained dry-season productivity in rainforest ecosystems (Restrepo-Coupe et al., 2017).

925 The control of leaf gas exchange by water availability has been implemented by means of multiplicative soil water  
926 stress factors. Although the use of such factors has been debated (Powell et al., 2013; Joetzjer et al., 2014), it has been preferred  
927 over a more explicit representation of the water flow through the plant column (e.g. Yao et al., 2022; Christoffersen et al.,  
928 2016; Cochard et al., 2021; De Cáceres et al., 2023). Although the stem hydraulic traits that would be needed for parameterizing  
929 an explicit plant water flow module have been increasingly measured over the past decades, data availability for tropical tree  
930 species remains low in regards to the actual number of species coexisting in these communities. Alternatively, correlative  
931 relationships have been used to infer these traits from more easily measured traits (Christoffersen et al., 2016; Xu et al., 2016).  
932 However, these are context dependent (Brodrribb, 2017; Rosas et al., 2019) and have at best low statistical support in rainforest  
933 communities that are loosely constrained by water availability (Dwyer and Laughlin, 2017; Delhayé et al., 2020; Maréchaux  
934 et al., 2020). Innovative methods alleviate the difficulties of robustly measuring the vulnerability of tropical trees to embolism  
935 (Cochard et al., 2016; Sergent et al., 2020; Garcia et al., 2023), and this could provide a key motivation for a more explicit  
936 module of plant water flow in TROLL (Kennedy et al., 2019; Paschalis et al., 2024). Such developments could be necessary  
937 to correctly represent the legacy of drought in forest ecosystems (Paschalis et al., 2024; Anderegg et al., 2015). However, two  
938 important aspects were taken into account in the implementation of the multiplicative water stress factors in TROLL 4.0. These  
939 factors were parameterized based on soil water potential as independent variable, and not soil water content, the former directly  
940 controlling water availability for plants, while the effect of soil water content is strongly mediated by soil properties (Novick  
941 et al., 2022). Also, different water stress factors were used for stomatal and non-stomatal limitations, in order to capture the  
942 sequence of effects of decreasing water availability on plant function (Trueba et al., 2019; Fatichi et al., 2016; Hsiao, 1973).

943 The effects of water availability on plant function and tree demography were implemented through trait-based  
944 parameterization, which allows a range of responses between trees and species. This was made possible through the use of leaf  
945 water potential at turgor loss point ( $\pi_{t_{lp}}$ ), a leaf-level trait that is mechanistically linked to plant responses to water availability  
946 (Bartlett et al., 2016b) and that is measurable at the community scale in diverse systems through a well-validated method  
947 (Maréchaux et al., 2016; Griffin-Nolan et al., 2019; Sun et al., 2020; Bartlett et al., 2012a). Leaf water potential at turgor loss  
948 point varies greatly across species within Amazonian forest communities (Maréchaux et al., 2015; Ziegler et al., 2019), and  
949 this diversity explains contrasting responses to water availability at the leaf and plant levels (Martin-StPaul et al., 2017;  
950 Maréchaux et al., 2018; Powell et al., 2017), and species distribution at local, regional and global scales (Bartlett et al., 2016a;  
951 Baltzer et al., 2008; Lenz et al., 2006; Bartlett et al., 2012b). The relationships implemented here involving  $\pi_{t_{lp}}$  have a  
952 mechanistic basis, as discussed above. However, the relationships controlling the effect of water availability on (1) leaf



953 shedding, (2) seed germination and seedling recruitment, and (3) drought-induced mortality would deserve in-depth  
954 exploration. More generally, these three processes remain key aspects of community dynamics and ecosystem functioning in  
955 high need of sustained empirical investigation (Albert et al., 2019; Díaz-Yáñez et al., 2024; McDowell et al., 2022).

## 956 **4.2 Model-data integration, transferability and limitations**

957 TROLL 4.0 simulates forest structure and diversity, while expanding the types of data with which its results can be compared  
958 (Schmitt et al., submitted companion paper). The individual-based species-specific representation of forest yields virtual forest  
959 inventories, including the location of each individual, their botanical identity, and their dimensions, and virtual airborne laser  
960 scanning point clouds (Fischer et al., 2019; Schmitt et al., 2023). TROLL 4.0 additionally provides water, carbon and litter  
961 flux dynamics that are directly comparable to eddy-flux tower data and litter trap monitoring at fine temporal resolutions, and  
962 this specificity has numerous advantages.

963 Data-driven knowledge can be directly assimilated in TROLL 4.0, offering new perspectives for inference or  
964 calibration (Dietze et al., 2013; Fer et al., 2018; Hartig et al., 2012; LeBauer et al., 2013; Fischer et al., 2019). TROLL 4.0 can  
965 help inform the development of DGVMs, in which the representation of vegetation does not allow this type of assimilation  
966 (Fischer et al., 2019). TROLL 4.0 is also easy to use and test by field ecologists as it simulates trees, not cohorts, PFTs, or gap  
967 patches: it can reproduce classical experiments in community or ecosystem ecology (e.g. Crawford et al., 2021; Schmitt et al.,  
968 2020) while overcoming known empirical challenges such as low repeatability (Schnitzer and Carson, 2016) or limited spatial  
969 footprint (Estes et al., 2018). TROLL 4.0 can be compared with data under the control of different biophysical processes  
970 supporting a more robust evaluation, and limiting equifinality issues (Franks et al., 1997; Medlyn et al., 2005). Finally, the  
971 model is parameterized based on traits directly measured in the field improving model transferability (Rau et al., 2022a).

972 The individual-scale and spatially-explicit representation of TROLL 4.0 comes with a computational burden. For a  
973 reference 4-ha area starting from bare ground, and 600 years of simulation, the computational cost of TROLL 4.0 is about  
974 1820 min, compared with version TROLL2.3 (Maréchaux and Chave 2017) about 12 min. While the shift from a monthly to  
975 a daily timestep explains the multiplication by a factor of 30 between the two versions, the addition of a belowground field  
976 and of an iterative scheme to simulate leaf gas exchanges explains for a great part the remaining factor of five. Several  
977 developments should reduce this computational cost: tree demographic processes do not need to be simulated at the daily  
978 timestep and could be represented at a monthly resolution; vegetation models already implement such nested time scales  
979 (Moorcroft, 2006). We are also confident that further computer time reduction will be brought about by code optimization.  
980 Finally, several strategies can be implemented to up-scale the outputs of individual-based models at reduced computational  
981 costs, especially by leveraging large scale remote sensing products (Rödig et al., 2017; Sato et al., 2007; Shugart et al., 2015).

## 982 **4.3 Current and future developments**

983 TROLL 4.0 is a reflection on the state of the art and knowledge gaps in plant physiology and ecology, resulting in an  
984 unbalanced representation across processes. TROLL is being continuously developed, as knowledge and data availability



985 progress, specific questions to address with the model emerge, or important limitations are identified. In a companion paper  
986 (Schmitt et al., submitted companion paper), we use data from forest inventories, litter traps, eddy-flux towers and remote  
987 sensing products to evaluate and discuss the performance and limitations of TROLL 4.0 at two forest sites. We here mention  
988 several on-going or future developments.

989 Empirical findings suggest that the contribution of undisturbed tropical forests to the global carbon sink is declining  
990 (Hubau et al., 2020; Qie et al., 2017), pointing to the need of integrated modelling to understand and predict such trends (Yao  
991 et al., 2023, 2024; Koch et al., 2021). Among the possible steps forward with TROLL 4.0 are an improved representation of  
992 stomatal conductance and its coupling with photosynthesis (Lamour et al., 2022, 2023; Dewar et al., 2018), as well as  
993 respiration response and acclimation to climatic drivers (Smith and Dukes, 2013; Collalti et al., 2020; Slot et al., 2013; Rowland  
994 et al., 2015). Improvements on the carbon budget would also be important, with more explicit carbon allocation to reproductive  
995 organs and belowground structures, under the control of environmental drivers (Fig. 3). However, such developments would  
996 rely on limited empirical or experimental knowledge belowground (Cusack et al., 2024) and scarce information on tree  
997 reproductive strategies (Igarashi et al., 2024; Vacchiano et al., 2018; Norden et al., 2007). An improved representation and  
998 evaluation of drought-induced tree mortality would be another important step forward as it might play a key role in the observed  
999 changing dynamics and functional and floristic turnover (Esquivel-Muelbert et al., 2019; Feeley et al., 2011; Hubau et al.,  
1000 2020; Qie et al., 2017). Information provided by long-term through fall exclusion experiments would offer interesting  
1001 opportunities for model development and evaluation (Powell et al., 2013; Yao et al., 2022).

1002 Tropical forest disturbance by land use change, fire regimes, and other degradations are an important source of C  
1003 emissions (Lapola et al., 2023), and they must be represented in models. For instance, it is important to understand how edge  
1004 effects affect the forest microclimate, and consequently forest dynamics, functioning and composition (Camargo and Kapos,  
1005 1995; Nunes et al., 2022). To this end, micro-climate models could be coupled to or embedded within TROLL (Gril et al.,  
1006 2023a; Maclean and Klinges, 2021). Fragmentation also impacts seed dispersal, and thus seed rain and seed bank intensity and  
1007 composition (Warneke et al., 2022; Cubiña and Aide, 2001). Improving TROLL's representation of seed dispersal ability and  
1008 germination as a function of plant trait and dispersal mode is key to capture the effect of forest loss and fragmentation on forest  
1009 functioning and biodiversity (Seidler and Plotkin, 2006; Muller-Landau et al., 2008; Tamme et al., 2014; Chase et al., 2020;  
1010 Riva and Fahrig, 2023). More generally, one overarching objective is to improve model's representation of processes involved  
1011 in forest regeneration, to simulate secondary forest dynamics and resilience to disturbances (Hanbury-Brown et al., 2022; Díaz-  
1012 Yáñez et al., 2024; Poorter et al., 2023; Albrich et al., 2020).

1013 Finally, TROLL 4.0 includes major developments that should facilitate its transferability across sites. The explicit  
1014 integration of the ecosystem water balance and vegetation responses to soil water availability now allows to consider spatio-  
1015 temporal extrapolation along water stress gradients. The integration of soil topography and heterogeneity would also be an  
1016 important advance for improved genericity. As nutrient availability is being altered by human activities (Peñuelas et al., 2013),  
1017 the explicit integration of a nutrient cycle with nitrogen and phosphorous colimitation will be a useful advance in the future



1018 (Fernández-Martínez et al., 2014; Turner et al., 2018). Similarly, the extension of tree functioning responses to a broader range  
1019 of temperatures, should support the transferability of TROLL to temperate and boreal forests.

## 1020 **5. Conclusion**

1021 TROLL 4.0 represents an advance over previous versions as it bridges across forest model types, while maintaining a  
1022 representation consistent with field ecology and ecosystem science. TROLL 4.0 simulates the responses of tropical forests to  
1023 water availability through the explicit representation of water dynamics belowground and its coupling with leaf-level gas  
1024 exchanges and demographic processes. This comes at a computational cost, and a future task is to conduct code optimization  
1025 and parallelization, and up-scaling in combination with remote-sensing products. The representation of processes in TROLL  
1026 4.0 mirrors an unbalanced state of the art, but its ability to dialogue with a range of data of various nature, makes it a valuable  
1027 tool to take up the fundamental and applied research challenges on tropical forests. TROLL 4.0 has benefited from observations  
1028 and field experiments that feed the development of models (Medlyn et al., 2015; Paschalis et al., 2020), while modeling  
1029 exercises inform and guide empirical approaches (Medlyn et al., 2016; Norby et al., 2016; Pacala and Rees, 1998). This is  
1030 possible because of the fine scale representation of forest structure and diversity and the trait-based parameterization of  
1031 processes in the model.

1032

1033

1034 *Code and data availability.* The code of TROLL 4.0 is available at <https://github.com/TROLL-code/TROLL>, a DOI will be  
1035 linked to this repository upon publication. Additionally, TROLL 4.0 can be set-up and run, and its outputs can be analyzed  
1036 with an updated version of the R package rcontroll: <https://github.com/sylvainschmitt/rcontroll/tree/TROLLV4>, also available  
1037 in R through the command `devtools::install_github("sylvainschmitt/rcontroll", ref = "TROLLV4")`.

1038

1039 *Supplement.* The supplement related to this article will be available online upon publication acceptance.

1040

1041 *Author contributions.* IM led TROLL 4.0, and designed the implementation of the water cycle and its coupling to vegetation.  
1042 FJF co-led TROLL 4.0 and designed the new implementation of intra-specific variability and crown shapes. SS and JC  
1043 contributed ideas and discussions. IM wrote the paper with contributions from all authors.

1044

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1046

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2419 **Appendix A**

2420 **Table A1. List of symbols and variables.**

Symbols	Definition	Units	Nature	Equations
<b>Physical constants</b>				
$M_w$	Molar mass of water vapor	kg mol <sup>-1</sup>	Constant	12
R	ideal gas constant	J mol <sup>-1</sup> K <sup>-1</sup>	Constant	12-13, 28-31, 46-47
$V_w$	Partial molal volume of water	m <sup>3</sup> mol <sup>-1</sup>	Constant	13
$\kappa$	von Karman constant	unitless	Constant	8, 15
g	Gravity constant	m s <sup>-2</sup>	Constant	37
$\rho$	Density of water	kg m <sup>-3</sup>	Constant	37
$M_a$	Molecular mass of air	kg mol <sup>-1</sup>	Constant	41, 48
$C_p$	Heat capacity of air	J kg <sup>-1</sup> K <sup>-1</sup>	Constant	41, 48
$\gamma$	Psychrometric constant	Pa K <sup>-1</sup>	Constant	41
$D_H$	Molecular diffusivity to heat	m <sup>2</sup> s <sup>-1</sup>	Constant	46
$\sigma$	Stefan-Boltzmann constant	W m <sup>-2</sup> K <sup>-4</sup>	Constant	44, 48
<b>Aboveground environment</b>				
PPFD <sub>top</sub>	Photosynthetic photon flux density at canopy top	$\mu\text{mol photons m}^{-2} \text{ s}^{-1}$	Updated at half hourly step, given as input	1
$T_{top}$	Temperature at canopy top	°C	Updated at half hourly step, given as input	4, 6, 44
VPD <sub>top</sub>	Vapour pressure deficit at canopy top	kPa	Updated at half hourly step, given as input	5, 7
$u_{top}$	Wind speed at a reference height above the canopy	m s <sup>-1</sup>	Updated at half hourly step, given as input	Sections 2.1 and 2.2
$T_{night}$	Nighttime temperature	°C	Updated daily, given as input	Section 2.2
PPFD	Incident photosynthetic photon flux density	$\mu\text{mol photons m}^{-2} \text{ s}^{-1}$	Computed every half hour	1, 25
T	Temperature	°C	Computed every half hour	4, 42, 46-48
VPD	Vapour pressure deficit	kPa	Computed every half hour	5
u	Wind speed	m s <sup>-1</sup>	Computed every half hour	8, 9, 15, 47
$c_a$	CO <sub>2</sub> concentration	$\mu\text{mol mol}^{-1}$ (ppm)	Constant	Section 2.5
$P_{ress}$	Atmospheric pressure	Pa	Constant	46-47
PPFD <sub>abs</sub>	Absorbed photosynthetic photon flux density	$\mu\text{mol photons m}^{-2} \text{ s}^{-1}$	Computed every half hour	2
$T_{mean}$	Temperature, averaged per crown layer	°C	Computed every half hour	6
VPD <sub>mean</sub>	Vapour pressure deficit, averaged per crown layer	kPa	Computed every half hour	7
LAI	Cumulated leaf area per ground area	m <sup>2</sup> m <sup>-2</sup>	Computed daily for each voxel	1-3, 11, 43
dens	Averaged leaf area density per unit ground area	m <sup>2</sup> m <sup>-2</sup>	Computed daily, averaged per layer	3, 6-7



$k$	Effective light extinction coefficient	unitless	Fixed, computed from $k_{geom}$ and $absorptance_{leaves}$	1
$k_{geom}$	Light extinction coefficient reflecting the geometric arrangement of leaves	unitless	Constant, given as input	1
$absorptan_{ce_{leaves}}$	Fraction of absorbed light within a single leaf	unitless	Constant, given as input	1
$LAI_{sat}$	LAI threshold for computing microenvironmental variation within the canopy	$m^2 m^{-2}$	Constant	4-7
$\Delta T$	Parameter of the within-canopy variation in temperature	$^{\circ}C$	Constant	4, 6
$C_{VPD0}$	Parameter of the within-canopy variation in vapour pressure deficit	unitless	Constant	5, 7
$u^*$	friction velocity	$m s^{-1}$	Constant	
$d$	zero-plane displacement height	m	Computed from the locally averaged canopy height (H)	8
$z_0$	aerodynamic roughness	m	Computed from the locally averaged canopy height (H)	8
$H$	Top canopy height	m	Computed daily	8-9
$\alpha$	Parameter of wind speed decrease within the canopy	unitless	Constant	9
<hr/>				
Water balance				
$P$	Precipitation	mm	Updated daily, given as input	10
$I$	Interception	mm	Computed daily	10, 11
$Q$	Run-off	$m^3$	Computed daily	10
$E$	Evaporation from the soil	$kg m^{-2} s^{-1}$	Computed daily	10, 12
$T$	Tree transpiration	$m^3$	Computed daily	10
$L$	Leakage	$m^3$	Computed daily	10
$K$	Parameter for rainfall interception	mm	Constant	11
$T_s$	Temperature at soil surface	K	Computed daily	12, 13
$e_s$	Vapor pressure of the soil surface	Pa	Computed daily	12
$e_a$	Vapor pressure of air above the soil surface	Pa	Computed daily	12
$e_{sat}$	saturated vapor pressure	Pa	Computed daily	13
$r_{soil}$	Soil surface resistance	$s m^{-1}$	Computed daily	12, 14
$r_{aero}$	Aerodynamic resistance to heat transfer	$s m^{-1}$	Computed daily	12, 15
$Z$	Reference height for $r_{aero}$ computation	m	Constant	15
$Z_m$	Momentum soil roughness	m	Constant	15
$\psi_l$	Soil water potential of layer l	MPa	Computed daily	21
$K_l$	Soil hydraulic conductivity of layer l	$kg m^{-2} s^{-1}$	Computed daily	22





$\psi_{soil,top}$	Water potential of the top soil belowground voxel	MPa	Computed daily	13
$\theta_{top}$	Water content of the top soil belowground voxel	m <sup>3</sup>	Computed daily	14
$\theta_{fc,top}$	water content at field capacity of the top soil belowground voxel	m <sup>3</sup>	Computed daily	14
<hr/>				
Species and tree characteristics				
LMA	Leaf mass per area	g m <sup>-2</sup>	Species-specific means: constant, provided as input; tree-specific values: randomly attributed at tree birth	26, 27, 32, 56
LA	Leaf area	cm <sup>2</sup>	Species-specific means: constant, provided as input; tree-specific values: randomly attributed at tree birth	46-47
N	Leaf nitrogen content per dry mass	mg g <sup>-1</sup>	Species-specific means: constant, provided as input; tree-specific values: randomly attributed at tree birth	26, 27, 32
P	Leaf phosphorous content per dry mass	mg g <sup>-1</sup>	Species-specific means: constant, provided as input; tree-specific values: randomly attributed at tree birth	26, 27, 32
wsg	Wood specific gravity	g cm <sup>-3</sup>	Species-specific means: constant, provided as input; tree-specific values: randomly attributed at tree birth	36, 55, 60-61, 66
$\pi_{tlp}$	Leaf water potential at turgor loss point	MPa	Species-specific means: constant, provided as input; tree-specific values: randomly attributed at tree birth	39-40, 58, 68, section 2.7.1
dbh <sub>thres</sub>	Threshold diameter at breast height, beyond which growth senescence starts	m	Species-specific means: constant, provided as input; tree-specific values: randomly attributed at tree birth	62, 63



$dbh_{max}$	Maximal tree diameter at breast height	m	Computed once per tree	Section 2.6.4
$h_{lim}$	Asymptotic height (parameter of Michaelis-Menten function)	m	Species-specific means: constant, provided as input	16
$h_{max}$	Maximal tree height	m	Species-specific means: constant, provided as input	67
$a_h$	Parameter of Michaelis-Menten function	m	Species-specific means: constant, provided as input	16
$f_{reg,s}$	Relative abundance of species $s$ in the external seed rain	unitless	Species-specific, provide as input	64
$w_l$	Leaf width	m	Computed for each tree	46-47
LL	Leaf lifespan	yr	Computed for each tree	57
$\varepsilon_{i,j}$	Individual effects for trait or variable $i$ and tree $j$	See traits	Randomly attributed at tree birth	Sections 2.4.1 and 2.4.2
$\sigma_i$	standard deviation for intraspecific variability in trait or variable $i$	See traits	Constant, provided as input	Sections 2.4.1 and 2.4.2
dbh	Tree diameter at breast height	m	Tree variable, updated at each timestep	16, 17, 19, 60-62
h	Tree height	m	Tree variable, updated at each timestep	16, 37, 54-55, 58, 60
cr	Tree crown radius	m	Tree variable, updated at each timestep	17
cd	Tree crown depth	m	Tree variable, updated at each timestep	18, 54
$a_{cr}$	Coefficients of crown radius allometry	unitless	Species-independent constant, provided as input	17
$b_{cr}$	Coefficients of crown radius allometry	unitless	Species-independent constant, provided as input	17
$a_{cd}$	Coefficients of crown depth allometry	m	Species-independent constant, provided as input	18
$b_{cd}$	Coefficients of crown depth allometry	unitless	Species-independent constant, provided as input	18
$shape_{crown}$	Ratio between the radius of the crown at the top of the tree to the radius at the bottom of the crown being a global parameter	unitless	Global parameter, provided as input	Section 2.4.2
$f_{gap}$	Fraction of gaps (openings) in tree crowns	unitless	Constant, provided as input	Section 2.4.2
RD	Tree root depth	m	Tree variable, updated at each timestep	19
RB <sub><i>t</i></sub>	Total tree fine root biomass	g	Tree variable, updated at each timestep	20



$RB_l$	Tree fine root biomass in layer l	g	Tree variable, updated at each timestep	20
$\psi_{root}$	Soil water potential in the tree root zone	MPa	Tree variable, updated at each timestep	21, 37
$\psi_{R,min}$	Root water potential below which there is no soil water uptake	MPa	Constant	21
$G_l$	soil-to-root water conductance in layer l	$\text{mmol H}_2\text{O m}^{-2} \text{s}^{-1} \text{MPa}^{-1}$	Variable, computed for each tree and layer at each timestep	21, 22
$L_{a,l}$	Tree total root length per unit area in layer l	$\text{m m}^{-2}$	Variable, computed for each tree and layer at each timestep	22
$L_{v,l}$	Tree total root length per unit soil volume in layer l	$\text{m m}^{-3}$	Variable, computed for each tree and layer at each timestep	23
$SRL$	Specific root length	$\text{m g}^{-1}$	Constant	22
$r_s$	Mean fine root radius	m	Constant	22
$r_s$	half of the mean distance between roots	m	Variable, computed for each tree and layer at each timestep	22, 23
<b>Leaf physiology</b>				
$T_l$	Leaf temperature	°C	Computed half-hourly for each crown layer	24, 25, 28-31, 33, 46
$VPD_s$	Vapor pressure deficit at the leaf surface	kPa	Computed half-hourly for each crown layer	35
$c_s$	CO <sub>2</sub> concentration at the leaf surface	$\mu\text{mol mol}^{-1}$ (ppm or $\mu\text{bar}$ )	Computed half-hourly for each crown layer	34
$c_i$	CO <sub>2</sub> concentration at carboxylation sites	$\mu\text{mol mol}^{-1}$ (ppm or $\mu\text{bar}$ )	Computed half-hourly for each crown layer	24, 34
$A_n$	Leaf-level net carbon assimilation rate	$\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$	Computed half-hourly for each crown layer	24, 52
$A_v$	Leaf-level net carbon assimilation rate limited by Rubisco activity	$\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$	Computed half-hourly for each crown layer	24
$A_j$	Leaf-level net carbon assimilation rate limited by RuBP regeneration	$\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$	Computed half-hourly for each crown layer	24
$R_p$	Photorespiration rate	$\mu\text{mol C m}^{-2} \text{s}^{-1}$	Computed half-hourly for each crown layer	24
$R_d$	Leaf dark respiration rate	$\mu\text{mol C m}^{-2} \text{s}^{-1}$	Computed half-hourly for each crown layer	33
$R_{d-M}$	Leaf dark respiration rate on a leaf dry mass basis	$\text{nmol CO}_2 \text{g}^{-1} \text{s}^{-1}$	Computed half-hourly for each crown layer	32
$V_{cmax}$	Maximum rate of carboxylation	$\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$	Computed half-hourly for each crown layer	24, 26, 28
$V_{cmax-M}$	Maximum rate of carboxylation on a leaf dry mass basis	$\mu\text{mol CO}_2 \text{g}^{-1} \text{s}^{-1}$	Computed half-hourly for each crown layer	26
$J$	Electron transport rate	$\mu\text{mol } e^- \text{m}^{-2} \text{s}^{-1}$	Computed half-hourly for each crown layer	24, 25
$J_{max}$	maximal electron transport capacity	$\mu\text{mol } e^- \text{m}^{-2} \text{s}^{-1}$	Computed half-hourly for each crown layer	25, 29



$J_{max-M}$	maximal electron transport capacity on a leaf dry mass basis	$\mu\text{mol } e^- \text{ g}^{-1} \text{ s}^{-1}$	Computed half-hourly for each crown layer	27
$\Gamma^*$	CO <sub>2</sub> compensation point in the absence of dark respiration	$\mu\text{bar}$	Computed half-hourly for each crown layer	24, 30
$K_m$	Apparent kinetic constant of the Rubisco	$\mu\text{bar}$	Computed half-hourly for each crown layer	24, 31
$\theta$	Curvature factor	unitless	Constant	25
$\alpha$	Apparent quantum yield to electron transport	$\text{mol } e^- \text{ mol photons}^{-1}$	Constant	25
LSQ	Effective spectral quality of light	unitless	Constant	25
$g_s$	stomatal conductance to CO <sub>2</sub>	$\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$	Computed half-hourly for each crown layer	34
$g_{sw}$	stomatal conductance to water vapor	$\text{mol H}_2\text{O m}^{-2} \text{ s}^{-1}$	Computed half-hourly for each crown layer	35
$g_0$	minimum leaf conductance for water vapor	$\text{mol H}_2\text{O m}^{-2} \text{ s}^{-1}$	Constant, provided by the user	35
$g_1$	Parameter of the stomatal conductance model	$\text{kPa}^{0.5}$	Computed daily for each tree	35, 36
$\psi_{pd}$	Leaf predawn water potential	MPa	Tree variable, computed daily	24, 25, 28, 29, 36-40
$WSF_{ns}$	Water stress factor for non-stomatal limitation	unitless	Tree variable, computed daily	28, 29, 40
$WSF_s$	Water stress factor for stomatal limitation	unitless	Tree variable, computed daily	36, 38-39
a	Parameter of $WSF_{ns}$	unitless	Constant	40
b	Parameter of $WSF_s$	unitless	Computed from tree-specific $\psi_{ttp}$	39, 39
$E_l$	Leaf-level transpiration rate	$\text{mol H}_2\text{O m}^{-2} \text{ s}^{-1}$	Computed half-hourly for each crown layer	41
$\lambda$	Latent heat of water vapor	$\text{J mol}^{-1}$	Computed half-hourly for each crown layer	41, 42
s	slope of the (locally linearized) relationship between saturated vapor pressure and temperature	$\text{Pa K}^{-1}$	Computed half-hourly for each crown layer	41
$R_{ni}$	isothermal net radiation	$\text{J m}^{-2} \text{ s}^{-1}$	Computed half-hourly for each crown layer	41, 43
$g_H$	total leaf conductance to heat	$\text{mol m}^{-2} \text{ s}^{-1}$	Computed half-hourly for each crown layer	41, 45
$g_{bHf}$	boundary layer conductance for free convection	$\text{mol m}^{-2} \text{ s}^{-1}$	Computed half-hourly for each crown layer	45, 46, 50
$g_{bHu}$	boundary layer for forced convection	$\text{mol m}^{-2} \text{ s}^{-1}$	Computed half-hourly for each crown layer	45, 47, 50
$g_r$	radiation conductance	$\text{mol m}^{-2} \text{ s}^{-1}$	Computed half-hourly for each crown layer	45, 48
$g_w$	total leaf conductance to water vapor	$\text{mol H}_2\text{O m}^{-2} \text{ s}^{-1}$	Computed half-hourly for each crown layer	41, 49
$g_{bw}$	boundary layer conductance to water vapor	$\text{mol H}_2\text{O m}^{-2} \text{ s}^{-1}$	Computed half-hourly for each crown layer	49, 50
$S_{abs}$	Absorbed solar radiation (PAR and NIR)	$\text{J m}^{-2} \text{ s}^{-1}$	Computed half-hourly for each crown layer	43



$B_{n,0}$	Net longwave radiation at the top of the canopy	$\text{J m}^{-2} \text{s}^{-1}$	Computed every half hour	43, 44
$k_d$	Coefficient of extinction of longwave radiation	Unitless	Constant	43
$\varepsilon_l$	Emissivity of the canopy leaves	Unitless	Constant	44, 48
$\varepsilon_a$	Emissivity of the atmosphere	Unitless	Computed every half hour	44
<b>Tree carbon allocation and demography</b>				
$GPP_{ind}$	Tree-level gross primary productivity	gC	Computed daily	51
$NPP_{ind}$	Tree-level net primary productivity	gC	Computed daily	51
$NPP_{leaves}$	Tree-level net primary productivity allocated to leaf production	gC	Computed daily	56
$NPP_{wood}$	Tree-level net primary productivity allocated to woody growth	gC	Computed daily	61
AGB	Tree aboveground biomass	kg	Computed daily	59-60
$R_{maintenan}$	Tree-level maintenance respiration	gC	Computed daily	51
$R_{stem}$	Stem maintenance respiration	$\mu\text{mol C s}^{-1}$	Computed daily	54
$R_{growth}$	Tree-level growth respiration	gC	Computed daily	51
$LA_t$	Tree-level total leaf area	$\text{m}^2$	Updated daily	55
$LA_{opt}$	Optimal tree leaf area	$\text{m}^2$	Updated daily	Section 2.6.2
$LA_l$	Leaf area in tree crown layer 1	$\text{m}^2$	Updated daily	51, 52-53
$LA_{young}$	Tree-level young leaf area	$\text{m}^2$	Updated daily	52-53, 56
$LA_{mature}$	Tree-level mature leaf area	$\text{m}^2$	Updated daily	52-53, 56
$LA_{old}$	Tree-level old leaf area	$\text{m}^2$	Updated daily	52-53, 56
$q$	Ratio of young or old leaf assimilation rate over mature leaf assimilation rate	unitless	Constant	52
$q'$	Ratio of young or old leaf respiration rate over mature leaf respiration rate	unitless	Constant	53
$\tau_{young}$	Leaf residence time in the young age pool	yr	Computed for each tree	56
$\tau_{mature}$	Leaf residence time in the young age pool	yr	Computed for each tree	56
$\tau_{old}$	Leaf residence time in the young age pool	yr	Computed for each tree	56
SA	Tree sapwood area	$\text{m}^2$	Updated daily	54, 55
$\lambda_1$	Parameter for sapwood area computation	$\text{m}^2 \text{cm}^{-2}$	Constant	55
$\lambda_2$	Parameter for sapwood area computation	$\text{m cm}^{-2}$	Constant	55
$\delta_1$	Parameter for sapwood area computation	$\text{m}^2 \text{cm}^{-2}$	Constant	55
$\delta_2$	Parameter for sapwood area computation	$\text{cm}^3 \text{g}^{-1}$	Constant	55



$f_{\text{canopy}}$	Fraction of $NPP_{\text{ind}}$ allocated to tree canopy (including leaves, fruits and twigs)	unitless	Constant, given as input	Sections 2.6.1 and 2.6.2
$f_{\text{leaves}}$	Fraction of $NPP_{\text{ind}}$ allocated to leaves	unitless	Constant	Section 2.6.2, 56
$f_{\text{fruit}}$	Fraction of $NPP_{\text{ind}}$ allocated to fruits	unitless	Constant	Section 2.6.1
$f_{\text{twigs}}$	Fraction of $NPP_{\text{ind}}$ allocated to twigs	unitless	Constant	Section 2.6.1
$f_{\text{wood}}$	Fraction of $NPP_{\text{ind}}$ allocated to wood	unitless	Constant, given as input	Section 2.6.2
$\psi_{T,o}$	Water potential threshold for accelerating old leaf shedding	MPa	Computed daily for each tree	58
$a_{T,o}$	Parameter to compute $\psi_{T,o}$ (modulates old leaf drought tolerance)	unitless	Constant, given as input	58
$b_{T,o}$	Parameter to compute $\psi_{T,o}$ (modulates the height dependence of leaf susceptibility to drought)	MPa	Constant, given as input	58
$f_o$	Factor of the acceleration of old leaf shedding	unitless	Updated daily for each tree	Section 2.6.2
$\delta_o$	Parameter controlling the pace of old leaf shedding acceleration ( $\Delta f_o$ )	unitless	Constant, given as input	
$NSC_r$	Maximal amount of stored non-structural carbohydrates	gC	Updated daily for each tree	59
$\Delta V$	Increment of stem volume	m <sup>3</sup>	Computed daily for each tree	61
$Senesc$	Growth senescence factor	unitless	Computed daily for each tree	61-62
$\Delta dbh$	Trunk diameter growth	m	Computed daily for each tree	Section 2.6.4
$dbh_{\text{mature}}$	Diameter threshold beyond which the tree is fertile	m	Computed once for each tree	63
$\sigma_{\text{disp}}$	Scale parameter of the Rayleigh distribution for seed dispersal	m	Constant	Section 2.7.1
$n_s$	Number of reproduction opportunities per mature tree	number of seeds	Constant	Section 2.7.1
$N_{\text{tot}}$	Intensity of the external seed rain	number of seeds per hectare	Constant, given as input	64
$n_{\text{ext},s}$	Species-specific number of dispersal events due to the external seed rain	number of seeds	Computed once for each species	64
$n_{\text{ha}}$	Area of the simulated plot	ha	Constant, computed from dimensions given as input	64
$LAI_{\text{max}}$	LAI threshold beyond which the seedling leaf carbon balance is negative	m <sup>2</sup> m <sup>-2</sup>	Computed once for each tree	Section 2.7.1



$d$	Tree death rate	events yr <sup>-1</sup>	Updated daily at tree level	65-66
$d_b$	Background death rate	events yr <sup>-1</sup>	Computed once per tree	65
$m$	reference background mortality rate	events yr <sup>-1</sup>	Constant, provided as input	66
$ws_{g_{lim}}$	Parameter of $d_b$	g cm <sup>-3</sup>	Constant	66
$d_{starv}$	Death rate due to carbon starvation	events yr <sup>-1</sup>	Updated daily at tree level	65
$d_{treefall}$	Death rate due to treefall	events yr <sup>-1</sup>	Updated daily at tree level	65
$\theta$	Parameter of treefall probability	m	Computed once per tree	67
$d_{drought}$	Death rate due to drought	events yr <sup>-1</sup>	Updated daily at tree level	65
$v_T$	Variance for treefall probability	unitless	Computed once per tree	67
hurt	Parameter of secondary treefall probability	m	Updated daily for each tree	Section 2.7.2
$\psi_{lethal}$	Water potential threshold for drought-induced mortality	MPa	Computed once per tree	68

2421

Appendix B

**Table B1. Representation of stomatal conductance, water stress effect on leaf gas exchange and tree transpiration in several vegetation**

**models.**  $g_0$ , cuticular or minimal stomatal conductance, i.e.  $g_s$  when  $A \rightarrow 0$ ;  $A$ ,  $\text{CO}_2$  assimilation rate;  $c_s$ ,  $\text{CO}_2$  concentration at the leaf surface;  $D_s$ , vapour pressure deficit at the leaf surface;  $h_s$ , fractional relative humidity at the leaf surface;  $\Gamma$ ,  $\text{CO}_2$  compensation point;  $V_{\text{cmax}}$  and  $J_{\text{max}}$  are the maximum carboxylation rate and electron transport rate. All 0 subscript denotes the values without water stress (except for  $g_0$  by convention). Note stomatal conductance to  $\text{H}_2\text{O}$  is 1.6 times higher than stomatal conductance to  $\text{CO}_2$ , we here only represent stomatal conductance to  $\text{H}_2\text{O}$ .

Vegetation model	Stomatal conductance		Water stress effect on leaf gas exchange		Tree transpiration	
	Name	Reference	Type	Model		Reference/type
ED2	(Longo et al., 2018; Medvigy et al., 2009)	Cohort-based vegetation model	$g_s = g_0 + \frac{a_1 \times A}{(c_s - \Gamma)(1 + \frac{D_s}{D_0})}$	(Leuning, 1995)/ empirical model	<p>The plant net <math>\text{CO}_2</math> assimilation and evapotranspiration rates (<math>x_{\text{net}}</math>) are computed as a linear combination of their rates under open (<math>x_0</math>) and close (<math>x_c</math>) stomata:</p> $x_{\text{net}} = f x_0 + (1 - f) x_c$ <p>with <math>f = \frac{1}{1 + \frac{\text{Demand}}{\text{Supply}}} = \frac{1}{1 + \frac{E_0 \times LA}{K \times W_{\text{avail,tot}} \times B_{\text{root}}}}</math></p> <p>where <math>E_0</math> is the evapotranspiration rate under conditions of open stomata times and LA the total plant leaf surface area, and <math>W_{\text{avail,tot}}</math> is the amount of water accessible by the vegetation layer, <math>B_{\text{root}}</math> the plant root biomass, and <math>K</math> an optimized constant.</p>	<p>Computed with:  <math>E_0 = \varphi_0 \times SLA \times B_{\text{leaf}}</math>                  with <math>B_{\text{leaf}}</math> the tree leaf biomass and <math>\varphi_0</math> its evapotranspiration rate, obtained by solving a set of 6 equations of 6 unknowns (after determining the leaf temperature using a surface energy balance submodel), among which:  <math>\varphi_0 = g_{\text{bw}} \times (e_s - e_a)</math>  <math>\varphi_0 = g_s \times (e_l - e_s)</math></p>
ED2-hydro	(Powell et al., 2018; Xu et al., 2016)	ED2 with a new module of plant hydraulics	<p>Solution of:</p> $\frac{\partial}{\partial g_w} (A_{\text{net}} - \lambda g_w D_a) = 0$ <p>with <math>g_w = \frac{g_s g_b}{g_s + g_b}</math></p> <p>and <math>\lambda</math> is the Lagrangian multiplier of the optimization problem, representing the marginal water use efficiency (marginal increase in <math>A_{\text{net}}</math> per unit change of water loss)</p>	(Vico et al., 2013)/ optimization model, under $\text{CO}_2$ (Rubisco) and light (RuBP regeneration/electr on transport) co-limitations	$V_{\text{cmax}} = V_{\text{cmax},0} \times \left[ 1 + \left( \frac{\psi_{\text{leaf}}}{\pi_{\text{tip}}} \right)^a \right]^{-1}$ $J_{\text{max}} = J_{\text{max},0} \times \left[ 1 + \left( \frac{\psi_{\text{leaf}}}{\pi_{\text{tip}}} \right)^a \right]^{-1}$ <p>where <math>V_{\text{cmax},0}</math> and <math>J_{\text{max},0}</math> denotes the photosynthetic capacities without water stress, and <math>a</math> is a shape factor estimated from Brodribb et al. (2003).</p>	<p>Similarly to Medvigy et al. 2009,  <math>E_0 = \frac{g_s g_b}{g_s + g_b} \times D_a \times LA</math></p>
TFS	(Fyllas et al., 2014)		$g_s = g_0 + 1.6 \times \left( 1 + \frac{g_1}{\sqrt{D_s}} \right) \times \frac{A}{c_s}$ <p><math>g_1</math> is an empirical coefficient*, associated to the water use efficiency (to the Lagrangian).</p>	(Medlyn et al., 2011)/ optimization, for ele tron-transport limited photosynthesis (light limitation)	$g_s = g_{s,0} \times \frac{\theta_l - \theta_{\text{wp}}}{\theta_{fc} - \theta_{\text{wp}}}$ <p>where <math>\theta_{\text{wp}}</math>, <math>\theta_{fc}</math>, <math>\theta_{\text{wp}}</math> are the actual soil water available for tree i, and the soil water content at field capacity and wilting point respectively.</p>	<p>Following MAESTRA (Medlyn et al., 2007), an iterative procedure is used to solve the energy balance of the canopy of each tree, under which the Penman-Monteith equation is used to estimate canopy transpiration.</p>





TFS-Hydro	(Christoffersen et al., 2016)	TFS with a new module of plant hydraulics	$g_s = g_{s,0} \times \left[ \frac{\psi_{leaf}}{1 + \psi_{g_s,50}} \right]^{a_{g_s}-1}$ <p>where <math>\psi_{g_s,50}</math> is the leaf water potential at 50% stomatal closure (assumed a 1:1 relationship between <math>\psi_{g_s,50}</math> and the water potential at 20% loss of xylem hydraulic conductivity (<math>P_{20,x}</math>), following results from (Brodrribb et al., 2003)), and <math>a_{g_s}</math> is the slope of the curve at <math>\psi_{leaf} = \psi_{g_s,50}</math>, computed from <math>\psi_{g_s,50}</math> using the same relationship that relates <math>\alpha_x</math> and <math>P_{50,x}</math>.</p>	$g_s = g_{s,0} \times \sum_j \tau_j \frac{\psi_j - \psi_c}{\psi_o - \psi_c}$ <p>where <math>\psi_j</math> is the soil water potential of soil layer j, and <math>\psi_o</math> and <math>\psi_c</math> are the soil water potential at which the stomata are fully open and fully closed respectively, and <math>\tau_j</math> is the relative root fraction of soil layer j.</p>	$V_{c,max} = V_{c,max,0} \times \sum_j \tau_j \frac{\psi_j - \psi_c}{\psi_o - \psi_c}$	<p>Iterative procedure</p> <p>An iterative procedure is used to solve the energy balance (determine the leaf temperature and internal CO<sub>2</sub>)</p>
Multi-layer CLM4.5	(Bonan et al., 2014)	DGM	$g_s = g_0 + g_1 \times A \times \frac{h_s}{C_s}$ <p><math>g_s</math> is iteratively computed such that (1) further opening does not yield a sufficient carbon gain per unit water loss (defined by a stomatal efficiency parameter) or (2) further opening causes leaf water potential to decrease below the minimum sustainable leaf water potential that prevents xylem cavitation</p>	<p>(Ball et al., 1987; Collatz et al., 1991) empirical</p> <p>Inspired from the SPA model (Williams et al., 1996) optimization within limitations imposed by water use efficiency, plant water storage, and soil-to-leaf water transport</p> <p>(Medlyn et al., 2011) optimization, under light</p>	<p>The optimization includes a dependence to <math>\psi_{leaf}</math>, where <math>\psi_{leaf}</math> is computed at each timestep (30-60 min) with Darcy's law (soil-to-leaf pathway, including capacitance).</p>	<p>CML4.5 default:</p> $V_{c,max} = V_{c,max,0} \times \sum_j \tau_j \frac{\psi_j - \psi_c}{\psi_o - \psi_c}$
CLM5	(Kennedy et al., 2019)	Stand-based	$g_s = g_0 + 1.6 \times \left(1 + \frac{g_1}{\sqrt{D_s}}\right) \times \frac{A}{C_s}$			



MAESPA	(Duursma et al., 2012)	Individual- and stand-based model	<p><math>g_s</math> is an empirical coefficient*, associated to the water use efficiency (to the Lagrangian).</p> $g_s = g_0 + 1.6 \times \frac{A}{C_s} \times \frac{1 + e^{s_f \psi_f}}{1 + e^{s_f(\psi_f - \psi_{leaf})}}$ <p>where <math>\psi_{leaf}</math> is computed at each time step using Darcy's law (<math>E_L = k_L \times (\psi_{soil} - \psi_{leaf})</math>)</p>	limitation (RuBP regeneration)	(Tuzet et al., 2003)/ empirical	<p>Already implemented in <math>g_s</math> computation.</p> <p>Standard version of CABLE (De Kauwe et al., 2015a) :</p> $g_1 = g_{1,0} \times \sum_j \frac{\theta_i - \theta_{wp}}{\theta_{fc} - \theta_{wp}}$ <p>with <math>\theta_i</math> the volumetric soil water content and <math>\theta_{fc}</math> the fraction of root mass in soil layer <math>j</math>, and <math>\theta_{wp}</math> the soil wilting point and <math>\theta_{fc}</math> its field capacity.</p> <p>New expression for drought sensitivity of gas exchange:</p> $V_{c,max} = V_{c,max,0} \times \frac{1 + e^{s_f \psi_f}}{1 + e^{s_f(\psi_f - \psi_{pd})}}$ <p>where <math>b</math> is a fitted (species-specific) parameter representing the sensitivity of <math>g_1</math> to leaf predawn water potential <math>\psi_{pd}</math> and taken from (Zhou et al., 2013, 2014), while <math>g_{1,0}</math> values are drawn from (Lin et al., 2015).</p>	<p><math>V_{c,max}</math></p> $= V_{c,max,0} \times 2^{-\frac{(\psi_{leaf})^{a_{gs}}}{(\psi_{gs,50})^{a_{gs}}}}$ <p>where <math>\psi_{gs,50}</math> is the leaf water potential at 50% loss of stomatal conductance and <math>a_{gs}</math> is a shape-fitting parameter. The solution for vegetation water potential is the set of values that matches supply with demand, maintaining water balance across each of the vegetation water potential nodes (<math>\psi_{root}</math>, <math>\psi_{stem}</math>, <math>\psi_{shoot-leaf}</math>, <math>\psi_{shade-leaf}</math>) based on Darcy's law (without capacitance).</p>	<p>concentration), under which transpiration is computed as</p> $E_0 = \frac{g_s g_b}{g_s + g_b} \times D_a \times LA$
CABLE	(De Kauwe et al., 2015a, b)	two-leaf canopy model separated into sunlit and shaded	<p>(Medlyn et al., 2011)/ optimization, under light limitation (RuBP regeneration)</p> <p>(was the model of (Leuning, 1995) in previous versions of CABLE (Wang et al., 2011))</p> $g_s = g_0 + 1.6 \times (1 + \frac{g_1}{\sqrt{D_s}}) \times \frac{A}{C_s}$	limitation (RuBP regeneration)	(Medlyn et al., 2011)/ optimization, under light limitation (RuBP regeneration)	<p>Following MAESTRA (Medlyn et al., 2007), an iterative procedure is used to solve the energy balance of the canopy of each tree, under which the Penman-Monteith equation is used to estimate canopy transpiration.</p> <p>transpiration from the vegetation to the atmosphere is controlled by several resistances operating in series, both above (aerodynamic) and within the canopy (stomatal and leaf boundary layer), and longwave radiative balance through radiative conductance on net available energy. These resistances in serial, result in a relatively weak coupling between the canopy surface and the atmosphere.</p>	<p>concentration), under which transpiration is computed as</p> $E_0 = \frac{g_s g_b}{g_s + g_b} \times D_a \times LA$	
ORCHID EE	(Krinner et al., 2005; Naudts et al., 2015)	DGVM (vegetation is represented using a single layer,	$g_s = mA \frac{h_r}{c_a} + b$	limitation (RuBP regeneration)	(Ball et al., 1987)	<p>In the version of (Krinner et al., 2005):</p> <p>The photosynthetic capacities, <math>V_{c,max}</math> and <math>J_{max}</math>, are multiplied by a water stress factor that is:</p>	<p>concentration), under which transpiration is computed as</p> $E_0 = \frac{g_s g_b}{g_s + g_b} \times D_a \times LA$	



<p>with m and b derived from laboratory measurements.</p>	<p>The model calculates plant water supply according to the implementation of hydraulic architecture by (Hickler et al., 2006), i.e. using Darcy's law and accounting for the hydraulic resistances of fine roots, sapwood and leaves. If the transpiration calculated by the energy budget exceeds the amount of water a plant can transport from the soil to its stomata, transpiration is limited to the plant water supply, and stomatal conductance is then recalculated such that the transpiration equals the amount of water a plant can transport. The energy budget and photosynthesis are then recalculated. This may require up to 10 iterations to converge.</p>	<p>1 if <math>f_w &gt; f_o</math></p> $1 - \frac{f_w - f_c}{f_o - f_c} \text{ if } f_c < f_w < f_o$ <p>0 if <math>f_w &lt; f_c</math></p> <p>with <math>f_w</math> the water fraction available for the plant in the root zone, and <math>f_c</math> and <math>f_o</math> the soil water fractions inducing, respectively, closure and maximum opening of stomata.</p>	<p>In the CAN version of (Naudts et al., 2015):</p>
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LPI	(Sitch et al., 2003)	<p>The model uses the Farquhar model of photosynthesis as generalized for global modelling purposes by (Collatz et al., 1991). In absence of water stress, canopy conductance is derived from the daytime carbon assimilation rate:</p> $g_c = g_{min} + \frac{1.6 A}{c_a(1 - \lambda)}$	(Collatz et al., 1991)	<p>Under water stress i.e. when <math>\min [1, \frac{E_{supply}}{E_{demand}}] &lt; 1</math>,</p> <p>The equations of evapotranspiration rate, assimilation rate and the one related assimilation rate and canopy conductance are solved simultaneously to yield values of canopy conductance consistent with the transpiration rate.</p>	<p>&lt; 1 Daily evapotranspiration is calculated for each PFT as the minimum of a plant- and soil-limited supply function (<math>E_{supply}</math>) and the atmospheric demand (<math>E_{demand}</math>). <math>E_{supply}</math> is the product of a plant root-weighted soil moisture availability and a maximum transpiration rate; <math>E_{demand}</math> is calculated following Monteith's empirical relation between evaporation efficiency and surface conductance, that uses <math>g_{pot}</math>, the nonwater-stressed potential canopy conductance calculated by the photosynthesis routine</p>
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30 \*although fitted empirically to leaf exchange experimental data (Lin et al., 2015), attempts have been made to relate  $g_l$  to functional traits and/or  
 31 climatological variables (wood density, Lin et al., 2015; leaf  $\delta^{13}C$ , Franks et al., 2018), based on the premise that water use efficiency should be  
 32 associated to functional strategies. See also values reported in Domingues et al. (2014).



2434 **Table B2. Examples of observational or experimental studies that explored the relative roles of stomatal and non-**  
 2435 **stomatal limitations of photosynthesis under drought conditions.**

Key message for vegetation models	Reference	Studied system	Main results
Stomatal-limitation only	Santos et al., 2018	57 canopy and understory trees within a central Amazonian forest	Photosynthesis decreased during the extreme dry season, and this was only related to stomatal closure (decline in stomatal conductance) and not to leaf biochemical changes (sustained chlorophyll concentration and fluorescence, and nutrient concentration).
	Rowland et al., 2015	Trees in the Throughfall Exclusion and control plots in Caixuana, Amazonia.	No differences in $V_{cmax}$ and $J_{max}$ between the throughfall exclusion plot and the control plot.
	Trueba et al., 2019	Mature individuals of 10 angiosperms species located on the campus of UCLA and a park in LA	The stomatal and leaf hydraulic systems (50% loss of $g_s$ , $K_{leaf}$ ) show early functional declines before cell integrity is lost. Substantial damage to the photochemical apparatus (maximum quantum yield of the photosystem) occurs at extreme dehydration, after turgor loss and complete stomatal closure, and seems to be irreversible.
Both stomatal and non-stomatal limitations	Zhou et al., 2013	Meta-analysis of 22 experimental datasets where photosynthesis, stomatal conductance and predawn leaf water potential were measured at increasing water stress, spanning a range of plant functional types	Photosynthesis was found almost universally to decrease more than could be explained by the reduction in $g_1$ (parameter of the Medlyn model), implying a decline in apparent carboxylation capacity ( $V_{cmax}$ ).
	Zhou et al., 2014	Two experiments, one in Australia on Eucalyptus, one in Spain on Quercus, on plants grown in glasshouses under control conditions. The non-stomatal response was partitioned into effects on mesophyll conductance ( $g_m$ ), the maximum Rubisco activity ( $V_{cmax}$ ) and the maximum electron transport rate ( $J_{max}$ ).	They found consistency among the drought responses of $g_1$ , $g_m$ , $V_{cmax}$ and $J_{max}$ , suggesting that drought imposes limitations on Rubisco activity and RuBP regeneration capacity concurrently with declines in stomatal and mesophyll conductance. Within each experiment, the more xeric species showed relatively high $g_1$ under moist conditions, low drought sensitivity of $g_1$ , $g_m$ , $V_{cmax}$ and $J_{max}$ , and more negative values of the critical pre-dawn water potential at which $V_{cmax}$ declines most steeply, compared with the more mesic species. Results showed that the decline in $V_{cmax}$ is not explained just by the decline in $g_m$ , but by the decline in both $g_m$ and $V_{cmax}$ .
	Egea et al., 2011	Outputs from a coupled A-gs model that uses a soil water content-dependent water stress factor were compared to leaf-level values obtained from the literature.	The sensitivity analyses emphasized the necessity to combine both stomatal and non-stomatal limitations of A in coupled A-gs models to accurately capture the observed functional relationships A vs. $g_s$ and A/ $g_s$ vs. $g_s$ in response to drought. Accounting for water stress in coupled A-gs models by imposing either stomatal or biochemical limitations of A, as commonly practiced in most ecosystem models, failed to reproduce the observed functional relationship between key leaf gas exchange attributes.
	Drake et al., 2017	Plants in pots of four tree species originating from contrasting	as soil water content ( $\theta$ ) was reduced under increasing drought, all species responded by reducing $g_s$ , resulting in reduced $C_i$ and $A_{sat}$ . However, $A_{sat}$ was reduced to



		hydrological environment, placed in the field under rainout shelters. Comparison with coupled stomatal conductance-photosynthesis model.	a larger degree than would be predicted only by stomatal reduction of $C_i$ , indicating a coincident reduction in photosynthetic capacity with declining $\theta$ . The best model include both stomatal and non-stomatal limitations.
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## References of Appendix B

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