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., 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.

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1 Introduction

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

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

Forest growth models have a different history as they were initially developed to predict successional dynamics and inform forest management (Watt, 1947; Botkin et al., 1972; Vanclay, 1994; Porté and Bartelink, 2002; Liang and Picard, 2013). A key innovation have been gap models that represent recruitment, growth, mortality and competition between individual trees within forest patches. Forest patches are typically the size of a canopy opening created by the fall of a dominant tree (gap, or chablis, Bugmann 2001) and modelled as horizontally homogeneous, with a spatially implicit representation of tree positions. Through the simulation of a large number of patches, gap models can represent spatial heterogeneity due to gap dynamics within stands, and larger-scale applications have been enabled by the increase in computing power and the combination with remote-sensing products (Shugart et al., 2015, 2018, 2020). Overall, these models adopt a finer representation of vegetation structure than classic DGVMs, but biogeochemical processes are generally modeled more coarsely, using ideal yield curves for tree growth rates combined with limiting factors imposed by the patch environment. Since these empirical relationships can only be parameterized on the basis of a large amount of data – readily available in plantations, but difficult to obtain elsewhere –, gap models typically also use plant functional types to simulate diverse forest stands. The number and definition of these groups has been much discussed in the literature, with no clear consensus (Botkin,

1975; Swaine and Whitmore, 1988; Vanclay, 1991; Köhler and Huth, 1998; Köhler et al., 2000; Gourlet-Fleury et al., 2005; Kazmierczak et al., 2014), and these plant functional types are difficult to transfer from one site to another (Picard and Franc, 2003; Picard et al., 2012).

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

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

Therefore, recent developments in DGVMs have sought to better represent plant community structure and diversity. Several cohort-based DGVMs have been developed to refine the representation of vegetation heterogeneity (Moorcroft et al., 2001; Fisher et al., 2015; Longo et al., 2019; Smith et al., 2001; Koven et al., 2020). Continuous representations of functional diversity have also been proposed using the distribution and co-variation of traits at the individual level or trait-climate relationships (Sakschewski et al., 2015; Verheijen et al., 2015; Scheiter et al., 2013; Pavlick et al., 2013; Berzaghi et al., 2020; Van Bodegom et al., 2014). These developments represent major advances in vegetation modelling, but scale mismatches

between field data and model representations limit the ability to assimilate data of various nature and resolution. While inverse modelling approaches can partially alleviate these constraints (Hartig et al., 2012; Dietze et al., 2013; LeBauer et al., 2013; Fer et al., 2018; Lagarrigues et al., 2015), they rely heavily on confidence in the model structure, can therefore raise equifinality issues (Medlyn et al., 2005), and increase rapidly in computational complexity in high-dimensional parameter sets.

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

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

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

existing forest modelling approaches through a better integration of forest structure, diversity and ecosystem functioning in the model representation.

In this contribution, we provide a detailed description of the structure and objectives of the TROLL 4.0 model, discussing how new modeling representations are an outcome of the state of knowledge and the availability of data. Finally, we discuss the limitations of the model and future developments. An evaluation of the model's ability to simulate forest structure, diversity and functioning for two Amazonian forest sites is reported in a companion paper (Schmitt et al., companion paper). The model is written in C++ and wrapped in the R environment through a dedicated package named *rcontroll* (Schmitt et al. 2023).

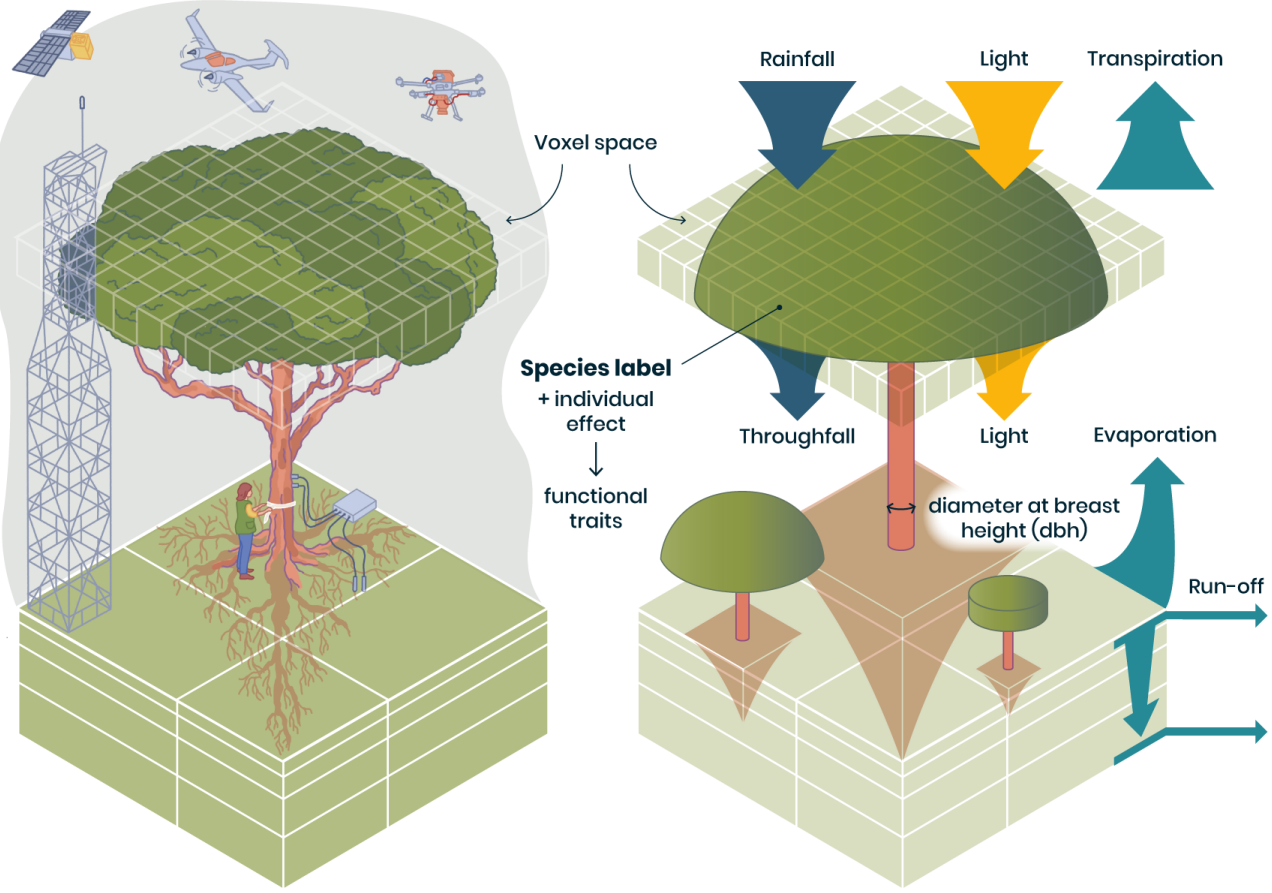

Figure 1: Representation of individual trees in a spatially explicit environment in TROLL 4.0 (right) allowing direct comparison with data of various nature (left). In TROLL 4.0, each tree is composed of a trunk, a crown, whose shape evolves from a cylinder to an umbrella as the tree grows, and root biomass that decreases exponentially with soil depth. Tree dimensions are updated at each timestep, depending on the net assimilated carbon that is allocated to growth, and following allometric relationships depending on tree diameter at breast height (*dbh*). Each tree has a species label associated with plant functional traits, which, together with an individual effect randomly attributed at tree birth, determines the tree's functional traits. These traits are used to parameterize

physiological and demographic processes that govern tree functioning throughout its life cycle. Light diffusion is computed explicitly at each time step and within each voxel from the canopy top to the ground. Water balance is also computed at each timestep, and the resulting water availability across soil voxels influence tree functioning. With this representation of forest structure, composition and functioning, model outputs can be directly compared with a wide range of data, including carbon and water fluxes provided by eddy-flux towers, field inventories, and 3D structure estimates from remote sensing (left). In TROLL 4.0, aboveground voxels typically have a finer horizontal resolution than belowground voxels, but the latter are vertically finer and increasing in thickness with depth (right). This resolution matches the one of fine-scale remote-sensing products or soil water content monitoring (left).

2 Model description

2.1 Environmental conditions

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

2.2 Light availability and aboveground variation in micro-climate

Above ground, the simulated forest stand is represented as a discrete grid of $1m^3$ cubic voxels. Light diffuses vertically through the forest's leaf layers from the top of the canopy to the ground, with one recalculation each day. Variation in the solar zenith angle is thus neglected here, a first assumption made for the model application to tropical regions which could be reconsidered in the future. In a given voxel, light availability is the photosynthetic photon flux density in μmol photons m^{-2} s^{-1} and is computed as a function of the incident light intensity at top canopy ($PPFD_{top}$, see Table A1 for a list of symbols), the cumulated leaf density of voxels above and the (constant) leaf density within the voxel itself. The Beer-Lambert extinction of light within the canopy allows to calculate the incident PPFD (per unit ground area) above any layer at vertical extent v as:

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

where $LAI(v)$ is the cumulated leaf area above height v, and k is the extinction coefficient. We here define $k = k_{geom} \times \text{absorptance}_{\text{leaves}}$, where k_{geom} reflects the geometric arrangement of leaves in the voxel (a value of 0.5 reflecting spherical leaf distribution; Ross, 1981) and $\text{absorptance}_{\text{leaves}}$, the fraction of absorbed light within a single leaf (Long et al., 1993; Poorter et al., 1995). In absence of sufficient relevant species-specific data, both k_{geom} and $\text{absorptance}_{\text{leaves}}$ are here assumed constant across species.

The absorbed light in a layer a of thickness Δa is then

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

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

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

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

Air microenvironmental variation within the canopy is represented as follows. Nighttime temperature (T_{night}) is assumed constant throughout the night and within the canopy, while temperature (T) and vapor pressure deficit (VPD) vary 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 height v above ground, we calculate temperature and VPD as follows:

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

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

where ΔT 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 Δa, temperatures and VPDs are then calculated by averaging both functions from a to $a + \Delta a$:

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

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

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

This empirical representation of variation of T and VPD within the canopy is in qualitative agreement with empirical observations of microclimate gradients within tropical forest canopies (Camargo and Kapos, 1995; Shuttleworth, 1985; Shuttleworth et al., 1989, Tymen et al. 2017), with a consistent buffering effect of forest canopies on understory micro-environment (De Frenne et al., 2019), and a strong control by forest structure (Gril et al., 2023b, a; Tymen et al., 2017; Zellweger et al., 2019). Alternative empirical or process-based representations of micro-environmental variations (e.g. Maclean and Klinges, 2021; Ogée et al., 2003) may be tested in the future, especially for more in-depth explorations of understory biodiversity and functioning under climate change (De Frenne et al., 2021; Haesen et al., 2023).

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

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

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 m), u_* is the friction velocity, κ the von Karman constant (κ=0.40), d the zero-plane displacement height, here assumed to be 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, wind speed decreases as (Inoue 1963):

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

with $\alpha \approx 3$ (Raupach et al., 1996). Wind speed was not computed at the voxel scale, but using the coarser horizontal resolution 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 (8) and (9).

Finally, air CO_2 concentration is assumed constant across the canopy in agreement with observations within a tropical forest site (Buchmann et al., 1997).

2.3 Soil water availability

In TROLL 4.0, the belowground part of the ecosystem is explicitly represented, and its discretization is specified by the user, including the number and depth of layers, and horizontal dimensions of the cells. Belowground voxels are typically coarser horizontally (e.g. 25m x 25m, as commonly implemented in gap models Bugmann, 2001), but finer vertically, than aboveground 1-m^3 voxels. Metric-scale lateral water fluxes are difficult to parameterize and evaluate, and neglecting them here limits the computational burden. Soil layers typically increase in thickness with depth, as in most DGVMs or forest physiological models (Prentice et al., 2015) and in standard soil assessments (e.g. Hengl et al., 2017). In this representation, contrasting root depth and access to water can be represented across individual trees together with potential variation in soil properties and hydraulic state. This approach contrasts with some forest dynamics models that use a single-layer belowground representation (e.g. Gutiérrez et al., 2014; Christoffersen et al., 2016; Fyllas et al., 2014).

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

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

where SWC is the soil water content, P the incident rainfall, I the canopy interception, Q the run-off, E the evaporation from the soil, T the transpiration, i.e. the plant water uptake, and L the leakage. This water balance is established for each soil layer, with inputs from upwards and outputs downwards starting from the top layer (l=1): outputs of layer l are inputs for layer $l+1$, with L corresponding to the output of the deepest layer, and P-I-Q to the input of the top layer. The water balance for the top soil layer thus reads:

$$\Delta SWC = SWC(t+1) - SWC(t) = P - I - Q - E - T - L_{1\to 2} \quad (10a)$$

with $L_{1\to 2}$ is the water flow from the first top soil layer to the next one,

and the water balance of the other layers reads:

$$\Delta SWC = SWC(t+1) - SWC(t) = L_{l-1\to l} - L_{l\to l+1} \quad (10b)$$

with $L_{l\to l+1}$ is the water flow from the soil layer l to soil layer l+1, and equals L if layer l is the deepest one. Note that this downward iteration neglects: (i) potential hydraulic lift (upward water redistribution, see e.g. Dawson, 1993; Burgess et al., 1998; Oliveira et al., 2005); and (ii) potential interaction with the water table (Costa et al., 2023; Sousa et al., 2022). Further developments could account for these two mechanisms where they are expected to play a significant role. In particular, flooded

areas could be easily represented, with a shallower soil depth and a prescribed boundary condition, i.e. a shallower water table. We now describe and discuss each term of the water balance and the corresponding modeling choices.

Rainfall. Rainfall (P, in mm) is a model input. It is assumed that the total daily rainfall corresponds to a single event 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., 2014).

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

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

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

Run-off and infiltration. As in most bucket models coupled with a forest dynamics model, the temporal propagation of the wetting front into the soil is not explicitly simulated here, because of the daily timestep and the vertically lumped representation of soil moisture dynamics (e.g., Laio et al., 2001, Guimberteau et al., 2014). When the soil top layer has enough available storage to absorb the totality of the throughfall (*i.e.* when throughfall is smaller than the layer water content at field capacity minus the current soil water content), it is assumed that the increment in soil water content of that top layer is equal to the throughfall. Otherwise, the excess water percolates to the next layer below ($L_{1\to2}$ in Eq. (10a)). In the absence of an explicit wetting front, runoff occurs only when the superficial layer is already saturated, which is similar to Dunne run-off (Dunne and Black, 1970). More complex formulations of run-off exist (d'Orgeval et al., 2008; Guimberteau et al., 2014; Horton, 1933), but because of the high porosity of many tropical forest soils (Hodnett and Tomasella, 2002; Sander 2002) and the lack of explicit topography in this version, our choice is parsimonious.

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

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

where E is in kg m^{-2} s^{-1}, M_w is the molar mass of water vapor (M_w=18 kg mol^{-1}), R is the ideal gas constant (R=8.31 J mol^{-1} K^{-1}), T_s is the temperature at soil surface in K, computed using Eq. (4) at ground level, e_s is the vapor pressure of the soil surface in Pa, e_a is the vapor pressure of air above the soil surface in Pa, r_{soil} is the soil surface resistance in s m^{-1}, and r_{aero} is the aerodynamic resistance to heat transfer in 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, 2013, Eq. (5.14) therein):

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

Where V_w is the partial molal volume of water ($V_w = 18 \times 10^{-6}$ m^3 mol^{-1}), and $e_{sat}(T_s)$ is the saturated vapor pressure at T_s computed following the Buck equation (Jones, 2013, Appendix 4 therein). e_a is by definition equal to $e_{sat}(T_s) - VPD_{ground}$, 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 Merlin et al., 2016, Eq. (12)):

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

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

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

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

Transpiration. Trees transpire soil water from the belowground voxel they are rooted in (see section 2.4.3). For a given tree, the total daily soil water uptake is the sum of the water transpired by leaves across its crown and across day-time 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), section 2.4.3), which depend on root biomass and on the soil hydraulic state in each layer.

For each belowground voxel in layer l, the soil water potential (ψ_l) and the soil hydraulic conductivity (K_l) are computed at each time step from the soil water content in the focal voxel using the van Genuchten-Mualem soil characteristic and hydraulic conductivity curves (Mualem, 1976; van Genuchten, 1980; see Table 1 in Marthews et al., 2014). Parameters of these curves are estimated using regression models (pedotransfer functions) for tropical soils (Hodnett and Tomasella, 2002), except the saturated hydraulic conductivity, which is computed following Cosby et al. (1984; see Table 2 in Marthews et al., 2014). In practice, when only soil texture data is available, TROLL 4.0 contains a default option to apply the texture-based only pedotransfer function provided by Tomasella and Hodnett (1998), coupled to the soil characteristic and hydraulic conductivity curves of Brooks and Corey (1964) (see Tables 1 and 2 in Marthews et al., 2014).

2.4 Representation of trees in the model

2.4.1 Species affiliation and intra-specific trait variability

In TROLL 4.0, each tree (and seed) is attributed a botanical species defined by a taxonomic binomial. It is assumed that the user has sufficiently good knowledge of the tree species growing in the study area so that a list of species-specific mean plant functional trait values can be provided as input. These are the leaf mass per area (LMA, in g m^{-2}), the leaf area (LA, cm^2), the leaf nitrogen content per dry mass (N, in mg g^{-1}), the leaf phosphorous content per dry mass (P, in mg g^{-1}), the wood specific gravity (wsg, in g cm^{-3}), the leaf water potential at turgor loss point (π_{tlp}, in MPa), and three allometric parameters (dbh_{thres}, h_{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 trait values, it is possible to input individual trait values from which a trait variance-covariance matrix is computed

(alternatively the trait variance-covariance matrix can be prescribed). With this option, for each recruited tree, the trait values are drawn from a distribution rather than attributed the species-specific mean value. For each trait i and tree j, the species-specific mean value is multiplied by a factor $e^{\varepsilon_{i,j}}$ where $\varepsilon_{i,j} \sim N(0, \sigma_i)$ where σ_i the trait-specific standard deviation on a logarithmic scale (lognormal variation). The sole exception is wood specific gravity, which we assume to be normally 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 other traits are assumed to be decoupled (Baraloto et al., 2010b). Note that with this implementation, intraspecific variation is not heritable nor structured in space or time, and is thus a surrogate for variability emerging from genetic variation or plasticity (Girard-Tercieux et al., 2023; 2024). A more realistic representation of the latter, especially light-driven trait plasticity along the vertical canopy gradient (Lamour et al., 2023; Lloyd et al., 2010), is left for a future version.

2.4.2 Aboveground structure

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

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

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

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

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 coefficients that are species independent. $\varepsilon_{h,j}$, $\varepsilon_{cr,j}$ and $\varepsilon_{cd,j}$ are tree-level variance terms to simulate intraspecific variation that are randomly drawn at tree birth with $\varepsilon_{h,j} \sim N(0, \sigma_h)$, $\varepsilon_{cr,j} \sim N(0, \sigma_{cr})$, and $\varepsilon_{cd,j} \sim N(0, \sigma_{cd})$. Tree crown architecture is known to depend on species ecological strategies (Bohlman and O'Brien, 2006; Iida et al., 2012; Poorter et al., 2006; Laurans et al., 2024), but given that crown extents are difficult to measure reliably in the dense canopies of tropical forests, we used a single set of parameters for all the species.

In the previous published version (Maréchaux and Chave, 2017), tree crowns were represented as cylinders with homogeneous leaf densities. Since v.3.0, TROLL can also model tree crowns as flexible, umbrella-like shapes with heterogeneous leaf density distributions. Small tree crowns are simulated as cylinders, but consist of up to three separate 1-m layers of leaves (top, intermediate and bottom layer). Each layer can be assigned a percentage of the total leaf area (which results from the processes of carbon allocation to leaf production and leaf shedding, see section 2.6.2) to reflect gradients in leaf densities from the upmost to lower crown layers (e.g., 50%, 30%, 20%; Kitajima et al., 2005), but the default is an equal distribution (33%, 33%, 33%) across all layers. Once a tree surpasses 3 m in crown depth, no new layers are added. In this

case, tree height directly above the tree stem (tree top height) and crown extent are derived using the same allometric equations (16)-(18), but, instead of the flat tops of small trees, it is now possible to prescribe a change in height from the centre of the crown to the crown's edges. Different geometric forms are available to describe this variation, but we here chose a simple linear decrease between the radius at the top of the crown and the radius at the bottom of the crown. The ratio between both radii is controlled through the global parameter *shape_crown*, which varies between 0 (conical shape) and 1 (cylinder), and thus allows for various "conifer-like" and "broadleaf-like" shapes in between. Within the first three metres of the resulting crown shape, leaves are allocated as before and folded around the tree trunk like an umbrella at various stages of opening (see Fig. 1b in Schmitt et al., 2023, and similar tree representations in Strigul et al., 2008). The crown shape only affects the geometry of the crown, not the amount of total leaf area allocated to it (see section 2.6.2).

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

2.4.3 Belowground structure

As in other models (e.g. Xu et al., 2016), TROLL 4.0 makes the assumption that total fine root biomass is equal to leaf biomass. Future developments should endeavor to represent a more explicit belowground allocation scheme (Merganičová et al., 2019; Huaraca Huasco et al., 2021). Direct estimates of individual tree root depth and root distribution are rare in moist tropical forests (Canadell et al., 1996; Jackson et al., 1996, 1999; Nepstad et al., 1994; Cusack et al., 2024; Guerrero-Ramírez et al., 2021). Some studies have quantified the depth of tree water uptake using indirect methods, such as predawn leaf water potential, or isotope labeling (Brum et al., 2019; Stahl et al., 2013), but this does not give access to the actual rooting depth. Tree root depth was here assumed to increase with tree size, and was computed as a function of tree *dbh* as follows (Kenzo et al., 2009, Fig. 4 therein):

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

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 et al. (2009), who reported on data from excavated trees in secondary forests in Malaysia. The first parameter (0.35, root depth at dbh=1cm) was adjusted to avoid unrealistic water depletion of the top soil layer. In the absence of relevant species-specific data, this allometric equation was assumed to hold for all species, even if root depth is known to be highly plastic (e.g. Rowland

et al., 2023). Correlations between rooting depth and leaf phenological habit have been reported, but in drier or more seasonal sites than Amazonian rainforests (Brum et al., 2019; Hasselquist et al., 2010; Smith-Martin et al., 2020), and trait coordination are known to be typically stronger under harsher environmental conditions (Dwyer and Laughlin, 2017; Delhaye et al., 2020).

We assumed that vertical tree root distribution follows an exponential profile, as observed empirically at the stand 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 $z_{l+1}(> z_l)$ is computed as:

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

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). The factor 3 was determined so that about 95% of the root biomass is contained between soil surface and RD (note that -log(0.05)≈3) (Arora and Boer, 2003). Tree roots are distributed across vertical layers, but do not spread across belowground voxels horizontally. This assumption was considered as a first parcimonious representation given the size of belowground voxels and the scarcity of data on root horizontal distribution worldwide, and particularly in tropical biomes (see Cusack et al. 2024, where root horizontal distribution is ven not mentioned, but see Schenk and Jackson, 2002 for data on water-limited systems). As a result, trees only deplete the water content of the belowground voxels located below their trunk position and thus compete for water with trees sharing the same belowground voxels only (see section 2.3) but this could be easily revisited in the future.

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

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

where ψ_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 within the layer (minimal root water potential, assumed to be -3 MPa as in Duursma and Medlyn, 2012). G_l, the soil-to-root water conductance in layer l, in mmol H_20 m^{-2} s^{-1} MPa^{-1}, computed as follows (Gardner, 1964):

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

In Eq (22), $L_{a,l}$ is the total root length per unit area in the layer (in m m^{-2}), with the total root length in the layer computed as $RB_l \times SRL$ where SRL is the specific root length, here assumed to be constant (10 m g^{-1}, Bonan et al., 2014; Metcalfe et al., 2008; Weemstra et al., 2016). K_l is the soil hydraulic conductivity of layer l (in mmol H_20 m^{-1} s^{-1} MPa^{-1}, see section 2.3), r_r is the mean fine root radius, here set at 1mm, and r_s is half the mean distance between roots, calculated with the assumption of uniform root spacing in a given layer (Newman, 1969):

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

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

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

2.5 Leaf physiology

The carbon assimilated and the water transpired by a tree within a day are the sum of the leaf-level carbon and water fluxes across day-time half hours. Leaf-level carbon assimilation is computed per crown layer of each tree, using the Farquhar-von Caemmerer-Berry model of C_3 photosynthesis (Farquhar et al., 1980, see section 2.5.1), coupled to the model of stomatal conductance of Medlyn et al. (2011; see section 2.5.2) as in Maréchaux and Chave (2017). In TROLL 4.0 the dependences on leaf temperature (T_l), vapor pressure deficit at the leaf surface (VPD_s), and CO_2 concentration at the leaf surface (c_s) are now determined iteratively at the leaf surface, starting from air temperature (T), air vapor pressure deficit (VPD_a) and air CO_2 concentration (c_a) averaged across the tree crown layer (see sections 2.2 and 2.4.2) and with transpiration computed using the Penman-Monteith equation (see section 2.5.4).

2.5.1 Photosynthesis

In Farquhar et al. (1980), leaf-level net carbon assimilation rate (A_n, µmol CO_2 m^{-2} s^{-1}) is limited by either Rubisco activity (A_v, µmol CO_2 m^{-2} s^{-1}), or RuBP regeneration (A_j, µmol CO_2 m^{-2} s^{-1}):

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

where R_p is the photorespiration rate (µmol C m^{-2} s^{-1}), V_{cmax} is the maximum rate of carboxylation (µmol CO_2 $m^{-2}s^{-1}$), c_i the CO_2 partial pressure at carboxylation sites, Γ^* the CO_2 compensation point in the absence of dark respiration, K_m the apparent kinetic constant of the Rubisco (von Caemmerer, 2000), and J the electron transport rate (µmol e^- m^{-2} s^{-1}), which depends on PPFD through:

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

J_{max} is the maximal electron transport capacity (µmol e^- m^{-2} s^{-1}), θ the curvature factor (unitless), and α the apparent quantum yield to electron transport (mol e^- mol $photons^{-1}$), computed following von Caemmerer (2000) as $\alpha = (1 - LSQ) \times 0.5$, with

LSQ the effective spectral quality of light, fixed at 0.15, and the factor 0.5 accounts for the fact that each photosystem absorbs half of the photons.

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

$$V_{cmax-M}\,(25°C) = min\{-1.56 + 0.43 \times N\ - 0.37 \times LMA\ ;\ -0.80 + 0.45 \times P - 0.25 \times LMA\ \} \quad (26)$$

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

with V_{cmax-M} and J_{max-M} the photosynthetic capacities at 25°C of unstressed mature leaves on a leaf dry mass basis, in μmol CO_2 g^{-1} s^{-1} and μmol e^- g^{-1} s^{-1}, respectively. N and P are leaf nitrogen and phosphorus concentrations in mg g^{-1}, and LMA is the leaf mass per area in g cm^{-2}. V_{cmax-M} and J_{max-M} can be converted into area-based V_{cmax} and J_{max} by multiplying by LMA. We used this leaf trait-based parameterization of $V_{cmax}(25°C)$ and $J_{max}(25°C)$ in the absence of water stress (as in Fyllas et al., 2014; Mercado et al., 2011). The dependence of V_{cmax} and J_{max} with temperature was given by equations in Bernacchi et al. (2003), and the dependence with water availability was modelled by a function of ψ_{pd} (WSF_{ns}, see section 2.5.3, Eq. (40)):

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

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

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

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

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

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

Leaf photorespiration rate R_p (Eq. (24)) was assumed to be a fixed fraction (40%) of leaf dark respiration rate (Eq. (32)-(33); Atkin et al., 2000). We used Atkin et al. (2015) 'broadleaved trees' empirical model to estimate mature leaf dark respiration rates as a function of plant functional traits:

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

with $R_{d\text{-}M}$ the leaf dark respiration rate on a dry mass basis and at reference temperature of 25°C (in nmol CO_2 $g^{-1}s^{-1}$). Multiplying $R_{d\text{-}M}$ by LMA gives the area-based leaf dark respiration R_d (in μmol C m^{-2} s^{-1}). The temperature dependence of mature leaf dark respiration rates was calculated as (Atkin et al., 2015, Eq. (1) therein; see also Heskel et al. 2016):

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

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

2.5.2 Stomatal conductance

Carbon assimilation by photosynthesis is limited by the CO_2 partial pressure at carboxylation sites, which is controlled by stomatal transport as modeled by the diffusion equation:

$$A_n = g_s(c_s - c_i) \quad (34)$$

with g_s the stomatal conductance to CO_2 (mol CO_2 m^{-2} s^{-1}). The representation of stomatal conductance varies greatly across vegetation models (Damour et al., 2010; Bonan et al., 2014; Rogers et al., 2017; see Appendix B, Table B1) and remains an active research topic (Anderegg et al., 2018; Dewar et al., 2018; Lamour et al., 2022; Sperry et al., 2017; Wolf et al., 2016; Sabot et al., 2022). In TROLL 4.0, stomatal conductance to water vapor is simulated as (Medlyn et al., 2011):

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

where g_{sw} is the stomatal conductance to water vapor in mol H_20 m^{-2} s^{-1}, 1.6 is the ratio of the diffusivities of H_2O to CO_2 (Massman,1998), VPD_s is the vapor pressure deficit at the leaf surface in kPa, A_n is the assimilation rate in µmol CO_2 m^{-2} s^{-1} (Eq. (24) above), c_s is the CO_2 concentration at the leaf surface in ppm, g_0 is the minimum conductance for water vapor in mol H_20 m^{-2} s^{-1} (Duursma et al., 2019), and g_1 is a model parameter in $kPa^{1/2}$. Equations 24, 34 and 35 taken together lead to two quadratic equations for c_i, one when Rubisco activity is limiting and one when RuBP regeneration is limiting, and the solution is the highest root.

The parameter g_1 varies with species ecological strategies and carbon cost of water use (Domingues et al., 2014; 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 across plant functional types (e.g. Xu et al., 2016). Here we assumed a dependence of g_1 with wood density (wsg, in g cm^{-3}) as in Lin et al. (2015). We also assumed a dependence with water availability, modelled by a function of ψ_{pd} (WSF_s; see section 2.5.3):

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

This parameterization of g_1 based on wood density is a matter of debate however, and alternatives have been proposed (Wu et al., 2020; Lamour et al., 2023).

The parameter g_0 quantifies water fluxes through the leaf cuticle (cuticular conductance) and from stomatal leaks. Although it is increasingly recognized as a key parameter explaining tree water loss in drought conditions (Cochard, 2021; Martin-StPaul et al., 2017), its values and variation with other functional traits is poorly documented (Duursma et al., 2019; Slot et al., 2021; Nemetschek et al., 2024), and we here assumed a fixed value. Note that some previous studies have defined g_0 as cuticular conductance only, ignoring stomatal leak effects, and thus underestimating g_0.

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

2.5.3 Effect of water availability on leaf-level gas exchange

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

Also, there is no consensus on the relative role of stomatal and non-stomatal limitations on leaf CO_2 assimilation under drying conditions, reflecting contrasted experimental results (Drake et al., 2017; Zhou et al., 2014; Keenan et al., 2010; Appendix B, Table B2). Under stomatal limitation, stomatal closure reduces leaf gas exchanges, and the water stress factor is applied on stomatal conductance, or stomatal conductance model parameters (e.g. g_1). Under non-stomatal limitations, drought (leading to increased leaf temperature and/or decreased leaf water potential) impairs the biochemical photosynthesis apparatus, which results in a reduction of photosynthetic capacities, and/or mesophyll conductance (Flexas et al., 2004, 2012). In this latter case, the water stress factor is applied on V_{cmax} and J_{max} (Drake et al., 2017; Keenan et al., 2010). Some models consider only one limitation, and others both (Appendix B, Table B1).

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

$$\psi_{pd} = \psi_{root} - \rho g h \simeq \psi_{root} - 0.01 \times h \quad (37)$$

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

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

where b is a parameter. To parameterize b, we used the relationship between the leaf water potential at turgor loss point (π_{tlp} in MPa) and the water potential causing 90% of stomatal closure (ψ_{gs90}, in MPa): $\pi_{tlp} = 0.97 \times \psi_{gs90}$ ($P<0.01$, $R^2=0.4$; Fig.

1 in Martin-StPaul et al. 2017), and assumed that $WSF_s \approx 0.1$ at ψ_{gs90} (an approximation given the shape of Eq. (35)), leading to:

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

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

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

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

with a=6 estimated from data reported in Brodribb et al. (2003). In this formula, $WSF_{ns} = ½$ when $\psi_{pd} = \pi_{tlp}$, in agreement with empirical findings (Brodribb et al., 2002; Manzoni, 2014).

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

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

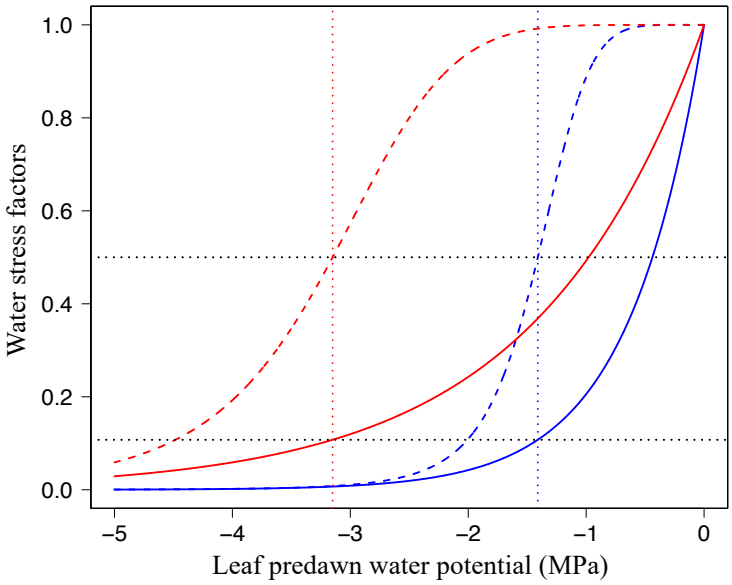

Figure 2: Responses of leaf-level gas exchange to water stress, depending on the leaf drought tolerance. Water stress factors for the stomatal conductance parameter g_1 (stomatal limitation, WSF_s, Eq. (39); solid lines) and for the photosynthetic capacities J_{max} and V_{cmax} (non-stomatal limitation,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

2.5.4 Leaf energy balance

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 through an iterative scheme that solves the leaf energy balance (Medlyn et al., 2007; Wang and Leuning, 1998; Duursma, 2015; Vezy et al., 2018). This is an important step because the leaf boundary layer plays a key role on gas exchanges, and especially so in dense tropical moist forests, given the large size of tropical tree leaves and the low wind speeds within canopies (De Kauwe et al., 2017; Jarvis and McNaughton, 1986; Meinzer et al., 1997). The iterative scheme is as follows. Initially, T_l, 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}) are computed using Eqs (24), (34) and (35); next, the boundary layer conductance and radiation conductance are computed; and finally leaf-level transpiration rate is deduced from the Penman-Monteith equation (Eq. (41) below). After these steps, 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 absolute difference between the T_l of two consecutive iteration is lower than 0.01°C.

Leaf-level transpiration rate E_l (in mol H_20 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 λ is the latent heat of water vapor (in J mol^{-1}), s is the slope of the (locally linearized) relationship between saturated vapor pressure and temperature (in Pa K^{-1}, see Jones, 2013, Eq. (5.15) therein), R_{ni} is the isothermal net radiation (in J m^{-2} s^{-1}), g_H is the total leaf conductance to heat (in mol m^{-2} s^{-1}), C_p is the heat capacity of air (1010 J kg^{-1} K^{-1}), M_a is the molecular mass of air (28.96$\times 10^{-3}$ kg mol^{-1}), γ the psychrometric constant (in Pa K^{-1}), and g_w the total conductance to water vapor (mol H_20 m^{-2} s^{-1}). The latent heat of water vapor λ depends on air temperature as follows:

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

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, σ is the Stefan-Boltzmann constant ($\sigma = 5.67 \times 10^{-8}$ W m^{-2} K^{-4}), ε_l is the emissivity of the canopy leaves, here assumed to be 1, and ε_a the emissivity of the atmosphere. Several models exist for ε_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):

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

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

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

where D_H is the molecular diffusivity to heat ($D_H = 21.5 \times 10^{-6}$ m^2 s^{-1}), P_{ress} the atmospheric pressure (in Pa), R the universal gas constant (R=8.314 J mol^{-1} K^{-1}) 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^{-2} s^{-1}), is given by:

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

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

$$g_r = \frac{4 \times \varepsilon_l \sigma T^3}{C_p M_a} \quad (48)$$

g_w the total conductance to water vapor has two components that represent hydraulic resistances in series: the stomatal conductance (g_{sw}, in mol H_20 m^{-2} s^{-1}, Eq. (35)) and the boundary layer conductance (g_{bw} in mol H_20 m^{-2} s^{-1}) to water vapor:

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

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

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

2.6 Carbon allocation

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

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

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

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

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

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

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 the carbon uptake efficiency ϱ relative to mature leaves is the same in young and old leaves and $\varrho = 0.5$, a value consistent with observations.

TROLL 4.0 partitions autotrophic respiration into maintenance respiration and growth respiration, even if both come from the same biochemical pathways (Amthor, 1984; Thornley and Cannell, 2000). Maintenance respiration ($R_{maintenance}$) has seldom been documented for stem and roots and is inferred empirically (Cavaleri et al., 2008; Meir et al., 2001; Slot et al., 2013; Weerasinghe et al., 2014). Nighttime leaf maintenance respiration is computed using Eqs (32) and (33), using the mean nighttime temperature. As stomatal conductance and dark respiration vary less with leaf age than carbon assimilation rate (Albert et al., 2018; Kitajima et al., 2002; Villar et al., 1995), we assumed that young and old leaves have respiration and

transpiration rate equal to $\varrho' = 0.75$ that of mature leaves, leading to lower water use efficiency than mature leaves. Tree-level nighttime leaf respiration and daytime transpiration are computed as follows at each timestep:

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

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^3 respectively, X being the leaf dark respiration (Eqs. (32) and (33)) or the leaf-level transpiration rate (Eq. (41)) respectively, and C_X is a factor to convert leaf-level rates in μmol C m^{-2} s^{-1} or in mol H_20 m^{-2} s^{-1} in total fluxes per individual per day in gC or m^3, respectively.

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

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

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

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

with λ_1= 0.066 m^2 cm^{-2}, λ_2=0.017 m cm^{-2}, δ_1=-0.018 m^2 cm^{-2}, and δ_2 =1.6 cm^3 g^{-1}, and C_{SA} a conversion factor. In addition to Eq. (55), there are both lower and upper limits on sapwood extent. Sapwood has a minimum thickness of 0.5 cm and any newly grown wood is always considered sapwood, irrespective of leaf area. TROLL 4.0 also imposes an upper limit on sapwood growth based on stem diameter growth, so that increases in living tissue cannot exceed increases in total tissue.

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

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

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

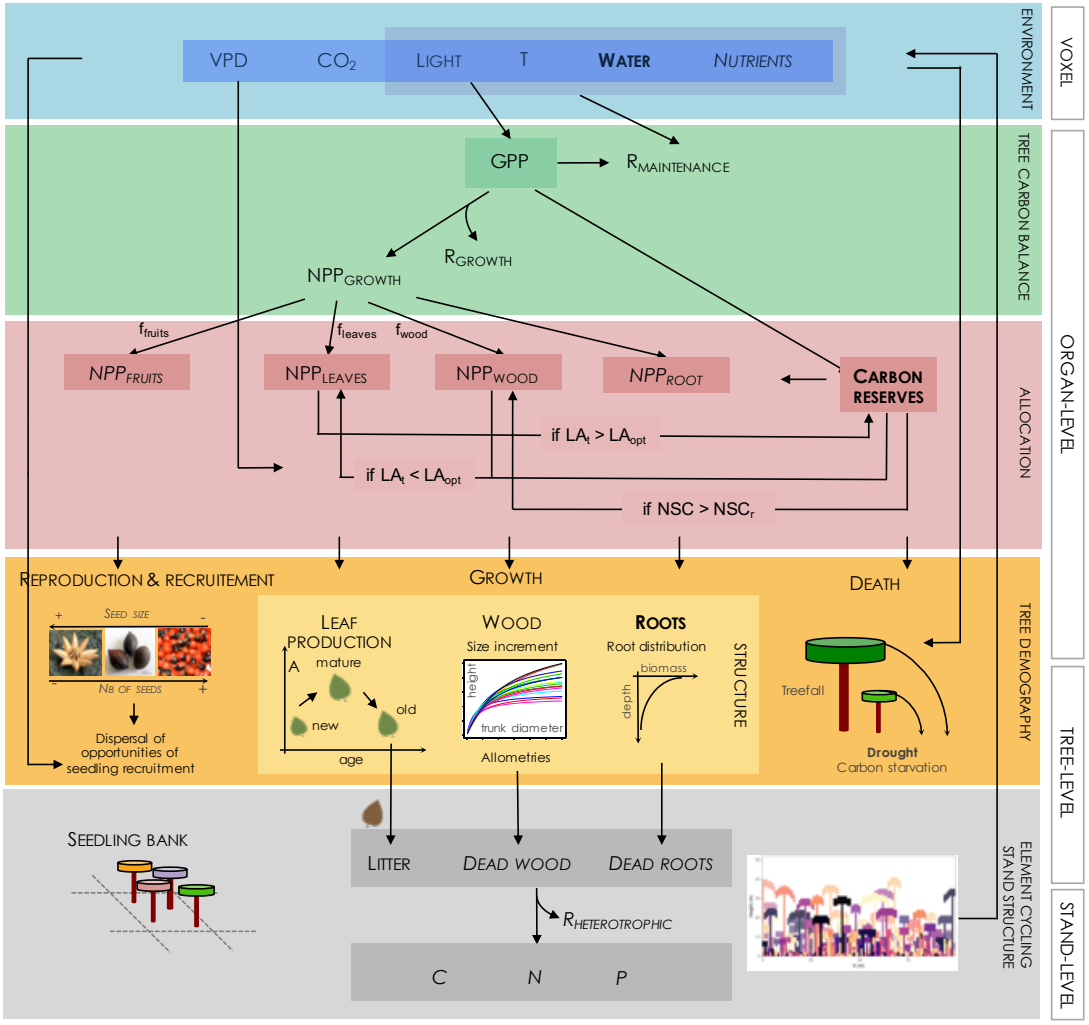

Figure 3: Diagram of structures and processes driving individual and community dynamics, as investigated under the modeling approach adopted in TROLL 4.0. Elements in bold letters refer to novel implementation in comparison to the previous published version, while italic letters refer to elements still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

In a future version, litter decomposition, wood decay and nutrient mineralization, could lead to soil nutrient availability for plant uptake, and take place through the action of soil microorganisms, whose activity, and hence respiration ($R_{HETEROTROPHIC}$), depends particularly on temperature and soil moisture.

2.6.2 Leaf production and leaf shedding

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

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

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

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

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

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

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

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

The loss term LA_{old}/τ_{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 τ_{old}= LL - τ_{young}- τ_{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) and Fig. 4). τ_{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 π_{tlp} with tree height (Maréchaux et al., 2016). The threshold $\psi_{T,o}$ jointly depends on π_{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 π_{tlp}=-1.5 MPa and 58m at π_{tlp}=-3 MPa (when $a_{T,o}$= 0.2 and $b_{T,o} = 0.02$; see Fig. 4). While this scheme is based on process-based observations, parameters $a_{T,o}$, $b_{T,o}$, and δ_o are currently calibrated (see Schmitt et al., companion paper).

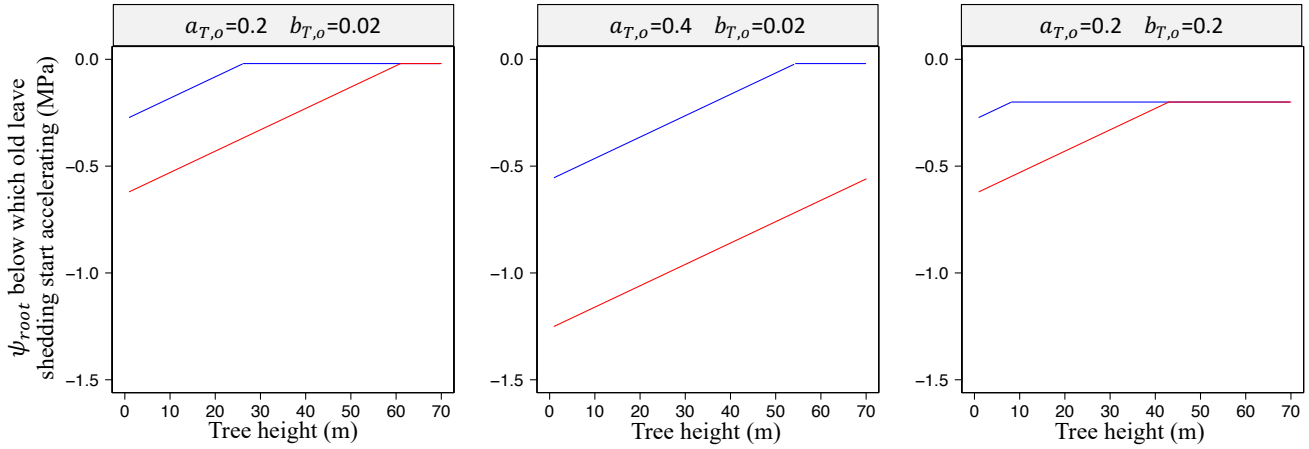

Figure 4: Effect of phenological parameters $a_{T,o}$ and $b_{T,o}$ (Eq. (58)) on the height- and drought tolerance-dependencies of old leaf shedding. Variation of the soil water potential in the root zone (ψ_{root}; Eq. (37)) below which old leaf shedding start accelerating as a function of tree height for different values of $a_{T,o}$ and $b_{T,o}$ and two values of π_{tlp}: π_{tlp}=-1.41 MPa in blue, the least negative value reported in Maréchaux et al., 2015, and π_{tlp}=-3.15 MPa in red, the most negative value reported in Maréchaux et al., 2015, as in Fig. 2.

2.6.3 Carbon storage

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

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

where NSC_r stands for non-structural carbohydrates (in gC), AGB is the tree aboveground biomass (in kg), and 1000×0.5 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, half of which is mobilizable (Martínez-Vilalta et al., 2016), hence the factor 0.05. The other half of NSC supports critical metabolic functions or is no longer accessible. The factor 1.25 accounts for an additional 25% biomass storage in coarse roots, so $1.25 \times AGB$ is total tree biomass (Ledo et al., 2018). AGB is computed following (Chave et al., 2014; Eq. (5) therein):

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

where dbh is in cm, h in m and wsg in g cm^{-3}. Note that Eqs. (59) and (60), together with Eq. (61) below, induce a growth-storage trade-off mediated by wood density variation across individual and species, in agreement with observations (Signori-Müller et al., 2022). The NSC storage compartment is filled by the potential carbon surplus resulting from the allocation to leaf production, i.e. $f_{leaves} \times NPP_{ind} - NPP_{leaves}$, if positive. If the storage compartment has reached its maximal capacity NSC_r, then the surplus is allocated to woody growth.

2.6.4 Growth

The net primary production allocated to woody growth, NPP_{wood}, depends on the outcome of allocation to leaf production and carbon reserves (see sections 2.6.2 and 2.6.3; Fig. 3). In TROLL 4.0, hydraulic control on carbon assimilation

and leaf phenology both influence carbon allocation to trunk growth (e.g. Doughty et al., 2014; Farrior et al., 2013; Friedlingstein et al., 1999), but turgor-mediated processes are not explicitly modeled (Coussement et al., 2018; Peters et al., 2023; Muller et al., 2011; Körner, 2015). NPP_{wood} is converted into an increment of stem volume, ΔV in m^3, as follows:

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

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

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

Trunk diameter growth increment Δdbh (in m), is computed from ΔV as follows. $V = C\ \pi(\frac{dbh}{2})^2 h$, where C is a form 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 leads to an expression of V as a function of dbh only. This function can be inverted to estimate Δdbh as a function of ΔV, which is known from Eq. (61). Tree height and crown dimensions are then updated using Eqs (16), (17) and (18).

2.7 Tree demography

2.7.1 Seed production, dispersal and recruitment

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 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 external seed rain. The seed bank is updated once a year. Here, our conceptual 'seeds' represent opportunities of seedling recruitment at 1 cm dbh (henceforth denoted "reproduction opportunities") rather than as true seeds, since not all seed dispersal events are modeled explicitly, and the seed-to-seedling transition is implicit.

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

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

This relationship is drawn from direct observations of reproductive status of tree species in the tropical forest of Barro Colorado 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 species). The number of reproduction opportunities per mature tree, n_s, is assumed fixed and equal for all individuals, and its value is user-defined. This assumption of a fixed reproductive opportunity per tree is predicated on the fact that there is a trade-off between seed number and seed size, itself related to seed and seedling survival. Thus, the probability of germination does

not depend strongly on seed size or on the number of produced seeds and can be assumed a zero-sum game (Coomes and 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 direction and at a distance randomly drawn from a Rayleigh distribution, thus allowing for potential long-dispersal events. Although seed dispersal distance is known to vary depending on dispersal syndrome and plant traits (Tamme et al., 2014; Seidler and Plotkin, 2006; Muller-Landau et al., 2008), the scale parameter σ_{disp} of the distribution is here fixed across species and individuals.

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

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

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

If several species are competing for recruitment in a local seed bank, one of the species is picked at random as the winner out of all the seeds present, as in a lottery model (Chesson and Warner, 1981). The recruitment event occurs only if ground-level light availability is sufficiently high. To test if this condition is met, the seedling is first attributed individual trait values depending on the species-specific averages (see section 2.4.1). These trait values are then used to determine the maximum LAI (LAI_{max}) the seedling would support under average environmental conditions, with LAI_{max} defined as the threshold beyond which the seedling leaf assimilation would be less than respiration (see section 2.6.2). The seedling can be recruited if the site LAI at ground level is lower than LAI_{max}.

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

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

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

2.7.2 Mortality

Mortality processes also play a key role in forest structure and carbon balance (Sevanto et al., 2014; Friend et al., 2014; Johnson

et al., 2016; Esquivel-Muelbert et al., 2020; McDowell et al., 2022). TROLL 4.0 explicitly represents several important mechanisms of tree mortality. At each timestep, individual tree death rate (in events yr^{-1}; Sheil et al. 1995) is:

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

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

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

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

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

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

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

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

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 absolute value of a random Gaussian variable with zero mean and unit standard deviation. v_T is modified at tree level so that high risks of treefall (> 99.5th percentile of the Gaussian variable) occur at the same height for all individuals of the same species. This implicitly introduces a growth-mortality trade-off, as more slender trees (larger ratio of height to trunk diameter) should reach this height threshold quicker. The orientation of tree falls is random. Trees on the trajectory of the falling tree can be damaged, especially if they are smaller than the fallen tree (van der Meer and Bongers, 1996). To model this effect, an 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 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, 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 $e^{\varepsilon_{h,j}}$ (see Eq. (16)) accounts for the fact that slender individuals (higher tree height deviation) would be more vulnerable to

868 treefall. Such tree can either fall and itself damage other trees or dies standing, depending on the user choice. The *hurt* variable
869 is reset to zero at each timestep.
870 Finally, prolonged drought is also a source of mortality. Drought-induced mortality is triggered when the leaf predawn
871 water potential ψ_{pd} is below a lethal level (ψ_{lethal}), and ψ_{lethal} is computed from the leaf water potential at turgor loss point,
872 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
873 dry and moist biomes), as follows:
874 $$\psi_{lethal} = -0.9842 + 3.1795 \times \pi_{tlp} \quad (68)$$

875 **3 Modelling protocol**

876 **3.1 Model inputs**

877 TROLL 4.0 requires five input files to run a simulation: (i) global parameters, (ii) species parameters, (iii) soil characteristics,
878 and finally, meteorological drivers varying at (iv) half-hour and (v) daily step.
879 The global input file contains parameters that define the simulation set-up (e.g. the number of timesteps, size of the
880 simulated plot and of the belowground voxels), and values for biophysical parameters that remain constant throughout the
881 simulation and are not species- or tree-specific. These include the light attenuation coefficient, allocation parameters, minimal
882 death rate, and more (see Table A1). Parameter values can be varied across simulations, to test model sensitivity, transfer
883 across sites, or any other reason. The species input file contains mean functional traits for at least one species and with no
884 upper bound (see Table A1). Functional trait values can be prescribed from local field measurements, or retrieved from global
885 trait databases (e.g. Kattge et al., 2020; Díaz et al., 2022).
886 The soil input file contains the soil variables needed for the pedotransfer functions, i.e. soil texture (proportion of silt,
887 clay and sand), soil organic matter content, dry bulk density, soil pH, and cation exchange capacity, for each soil layer, with
888 thickness of each layer. The number of soil layers is at least one, and is not theoretically limited. Lacking local soil data, model
889 users may retrieve soil parameters from online databases (e.g. Poggio et al., 2021), bearing in mind the uncertainties of such
890 products, especially in tropical areas (Khan et al., 2024).
891 Meteorological drivers are provided in two files, depending on their temporal resolution in the model. Daytime
892 temperature, vapor pressure deficit, incident irradiance and wind speed at a reference height above the canopy are provided
893 for every half-hour, while average nighttime temperature and cumulative rainfall are provided at a daily timestep. Such data
894 can typically be retrieved from meteorological stations embedded in eddy-flux towers, or from global products (Muñoz-Sabater
895 et al., 2021), as in Schmitt et al. (2023).

3.2 Initial conditions

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

3.3 Standard outputs

TROLL 4.0 provides a range of outputs related to forest structure, forest composition and diversity, and ecosystem functioning (e.g., carbon and water fluxes; Fig. 5). It simulates forest structure and composition and provides outputs comparable to those measured in the field: tree size distribution, tree spatial distribution, biomass accumulation curve, functional trait distribution, canopy height and leaf area index maps (Maréchaux and Chave, 2017), and more generally all information that can be retrieved from a detailed field inventory or a meter-scale airborne laser scanning survey (Fischer et al., 2019). In TROLL 4.0, other outputs are also available: litterfall fluxes, carbon and water fluxes comparable to the ones provided by eddy-flux towers, soil water state (content and water potential). An evaluation of these outputs for two Amazonian forest sites is provided in a companion paper (Schmitt et al., companion paper).

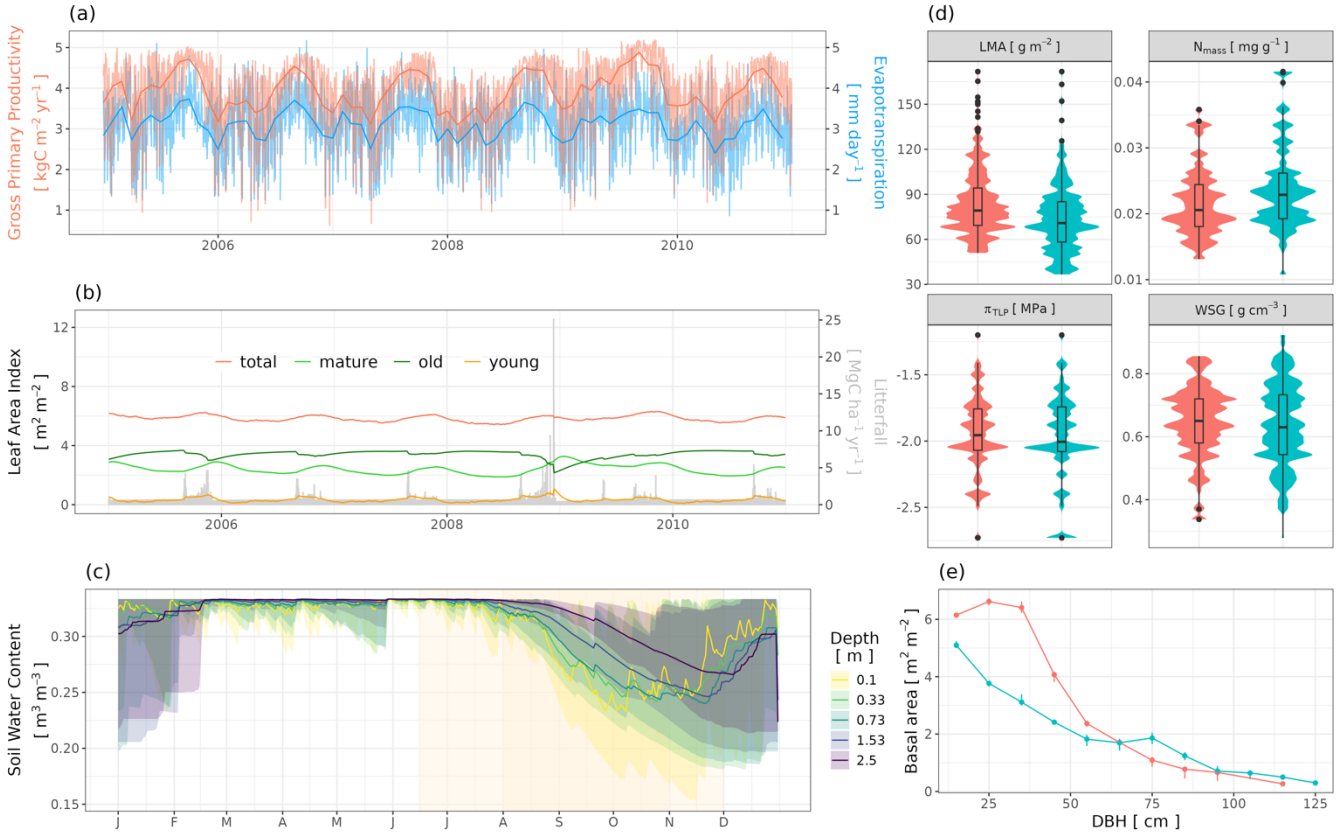

Figure 5: Examples of outputs provided by TROLL 4.0 and related to ecosystem functioning, diversity and structure. (a) Temporal variations of gross primary productivity (red) and evapotranspiration (blue) within and across years. (b) Variation in total leaf area index (red line) and leaf area index per leaf age cohort (young, mature, old; yellow, light green and dark green lines, respectively), together with litterfall (grey bars), within and across years. (c) Mean seasonal variations of water content in soil layers of different depths, with the vertical yellow band in the background depicting the dry season. (d) Distribution of functional traits. (e) Distributions of basal area per diameter class. Panels (a), (b) and (c) show outputs for an Amazonian forest site (Paracou), panels (d) and (e) show outputs for two Amazonian sites (Paracou, red; Tapajos, blue), see Schmitt et al., companion paper for details on similation set-ups.

4 Discussion

TROLL 4.0 is part of a novel generation of forest growth models designed to bridge the gap between traditional forest growth models and process-based models informed by ecophysiology. It includes an integration of processes underlying ecosystem fluxes closer to a modern DGVM than most other forest growth simulators. It also includes representation of plant community structure and diversity at a resolution similar to that used by ecologists in the field. This enables a direct comparison with a range of field data, including forest inventories, trait distribution, fine- and large-scale remote-sensing products, or

eddy-covariance data. Overall, these different features allow it to address a range of questions, from fundamental ones in community and theoretical ecology such as the mechanisms of species coexistence or the link between biodiversity and ecosystem functioning, to more applied ones such as the design of forest management guidelines to sustain forest resilience under climate change. Here we discuss the assumptions of the water cycle newly included in the model, as well as transferability and limitations of the current model version.

4.1 Simulating water fluxes and forest responses to water availability

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

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

These developments have striven to follow the parsimonious principle: more complex representations do not systematically result in increased model reliability and robustness, especially if the additional parameters are poorly constrained (Mahnken et al., 2022; Prentice et al., 2015). The soil hydraulic state is simulated using a bucket model (Budyko, 1961; Manabe1969; Vargas Godoy et al., 2021). In the future, more complex representations of soil water dynamics could be implemented at finer temporal and spatial resolutions, such as the implementation of Richards' equation (Richards, 1931), and integration of lateral flows, but this would be at a serious computational cost. These could be compared with the current simpler representation to assess the relevance of increasing complexity in various contexts and soil data availability (Van Nes and Scheffer, 2005). However, two aspects were considered to be needed in the current version, based on biological considerations. First, we implemented a multi-layer soil model, a more detailed representation compared with other models using a bucket model approach (e.g. Fischer et al., 2014; Laio et al., 2001). This was motivated by the need to account for contrasting rooting strategies and access to water among coexisting plants, which is an under-explored, but likely key, aspect of community dynamics in forests (Brum et al., 2019; De Deurwaerder et al., 2018; Ivanov et al., 2012). Second, we assumed that the depth of tree water uptake is not only controlled by the distribution of root biomass (as in Naudts et al., 2015; Sakschewski et al.,

2021; Paschalis et al., 2024), but also by soil water state and its vertical variation (as in Williams et al., 1996; Duursma and Medlyn, 2012). These improvements are relevant to the temporal variation of water retrieval depth (Bruno et al., 2006) and the sustained dry-season productivity in rainforest ecosystems (Restrepo-Coupe et al., 2017).

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

The effects of water availability on plant function and tree demography were implemented through trait-based parameterization, which allows a range of responses between trees and species. This was made possible through the use of leaf water potential at turgor loss point (π_{tlp}), a leaf-level trait that is mechanistically linked to plant responses to water availability (Bartlett et al., 2016b) and that is measurable at the community scale in diverse systems through a well-validated method (Maréchaux et al., 2016; Griffin-Nolan et al., 2019; Sun et al., 2020; Bartlett et al., 2012a). Leaf water potential at turgor loss point varies greatly across species within Amazonian forest communities (Maréchaux et al., 2015; Ziegler et al., 2019), and this diversity explains contrasting responses to water availability at the leaf and plant levels (Martin-StPaul et al., 2017; Maréchaux et al., 2018; Powell et al., 2017), and species distribution at local, regional and global scales (Bartlett et al., 2016a; Baltzer et al., 2008; Lenz et al., 2006; Bartlett et al., 2012b). The relationships implemented here involving π_{tlp} have a mechanistic basis, as discussed above. However, the relationships controlling the effect of water availability on (1) leaf shedding, (2) seed germination and seedling recruitment, and (3) drought-induced mortality would deserve in-depth

exploration. More generally, these three processes remain key aspects of community dynamics and ecosystem functioning in high need of sustained empirical investigation (Albert et al., 2019; Díaz-Yáñez et al., 2024; McDowell et al., 2022).

4.2 Model-data integration, transferability and limitations

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

The knowledge derived from field data can be directly assimilated in TROLL 4.0. As opposed to most DGVMs whose representation of vegetation does not allow this type of assimilation, this offers new perspectives for inference or calibration (Dietze et al., 2013; Fer et al., 2018; Hartig et al., 2012; LeBauer et al., 2013), which could help inform the development of DGVMs. For example, TROLL 4.0 may act as an integrator of data of different types, such as field inventories and remote-sensing, to constrain allometries that would be biased or poorly grounded if relying on a unique data source (Fischer et al., 2019). Also, as many uncertainties in current DGVMs have been related to their aggregated representation of vegetation structure and biodiversity, TROLL 4.0 can be used to directly test the sensitivity of a range of processes shared with DGVMs to such representation, for example by performing simulations with different numbers and identity of species or spatial resolutions, to then inform DGVMs on the corresponding needed developments. TROLL 4.0 is also easy to use and test by field ecologists as it simulates trees, not cohorts, PFTs, or gap patches: it can reproduce classical experiments in community or ecosystem ecology (e.g. Crawford et al., 2021; Schmitt et al., 2020) while overcoming known empirical challenges such as low repeatability (Schnitzer and Carson, 2016) or limited spatial footprint (Estes et al., 2018). TROLL 4.0 can be compared with data under the control of different biophysical processes supporting a more robust evaluation, and limiting equifinality issues (Franks et al., 1997; Medlyn et al., 2005). Finally, the model is parameterized based on traits directly measured in the field, improving model transferability (Rau et al., 2022a).

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

computational costs, especially by leveraging large scale remote sensing products (Rödig et al., 2017; Sato et al., 2007; Shugart et al., 2015).

4.3 Current and future developments

TROLL 4.0 aims at reflecting the state of the art in plant physiology and ecology, and, as a result, reflects the corresponding knowledge gaps, which can lead to an unbalanced representation across processes. TROLL is being continuously developed, as knowledge and data availability progress, specific questions to address with the model emerge, or important limitations are identified. In a companion paper (Schmitt et al., companion paper), we use data from forest inventories, litter traps, eddy-flux towers and remote sensing products to evaluate and discuss the performance and limitations of TROLL 4.0 at two forest sites. We here mention several on-going or future developments.

Empirical findings suggest that the contribution of undisturbed tropical forests to the global carbon sink is declining (Hubau et al., 2020; Qie et al., 2017), pointing to the need of integrated modelling to understand and predict such trends (Yao et al., 2023, 2024; Koch et al., 2021). Among the possible steps forward with TROLL 4.0 are an improved representation of stomatal conductance and its coupling with photosynthesis (Lamour et al., 2022, 2023; Dewar et al., 2018), as well as respiration response and acclimation to climatic drivers (Smith and Dukes, 2013; Collalti et al., 2020; Slot et al., 2013; Rowland et al., 2015). This notably includes the integration of light-driven plasticity in leaf traits, which has been recently highlighted as an important model development to robustly up-scale leaf-level gas exchange into ecosystem-level water and carbon balance (Fisher and Koven, 2020; Lamour et al., 2023; Xu et al., 2021; Xu and Trugman, 2021). Improvements on the carbon budget would also be important, with more explicit carbon allocation to respiration, reproductive organs and belowground structures, under the control of environmental drivers (Fig. 3). However, such developments would rely on limited empirical or experimental knowledge belowground (Cusack et al., 2024) and scarce information on tree reproductive strategies (Igarashi et al., 2024; Vacchiano et al., 2018; Norden et al., 2007). An improved representation and evaluation of drought-induced tree mortality would be another important step forward as it might play a key role in the observed changing dynamics and functional and floristic turnover (Esquivel-Muelbert et al., 2019; Feeley et al., 2011; Hubau et al., 2020; Qie et al., 2017). Information provided by long-term through fall exclusion experiments would offer interesting opportunities for model development and evaluation (Powell et al., 2013; Yao et al., 2022).

Tropical forest disturbance by land use change, fire regimes, and other degradations are an important source of carbon emissions (Lapola et al., 2023), and they must be represented in models. For instance, it is important to understand how edge effects affect the forest microclimate, and consequently forest dynamics, functioning and composition (Camargo and Kapos, 1995; Nunes et al., 2022). To this end, micro-climate models could be coupled to or embedded within TROLL (Gril et al., 2023a; Maclean and Klinges, 2021). Fragmentation also impacts seed dispersal, and thus seed rain and seed bank intensity and composition (Warneke et al., 2022; Cubiña and Aide, 2001). Improving TROLL's representation of seed dispersal ability and germination as a function of plant trait and dispersal mode is key to capture the effect of forest loss and fragmentation on forest functioning and biodiversity (Seidler and Plotkin, 2006; Muller-Landau et al., 2008; Tamme et al., 2014; Chase et al., 2020;

Riva and Fahrig, 2023). More generally, one overarching objective is to improve the model's representation of processes involved in forest regeneration, to simulate secondary forest dynamics and resilience to disturbances (Hanbury-Brown et al., 2022; Díaz-Yáñez et al., 2024; Poorter et al., 2023; Albrich et al., 2020).

Finally, TROLL 4.0 includes major developments that should facilitate its transferability across sites. The explicit integration of the ecosystem water balance and vegetation responses to soil water availability now allows it to consider spatio-temporal extrapolation along water stress gradients. The integration of soil topography and heterogeneity would also be an important advance for improved genericity. As nutrient availability is being altered by human activities (Peñuelas et al., 2013), the explicit integration of a nutrient cycle with nitrogen and phosphorous colimitation will be a useful advance in the future (Fernández-Martínez et al., 2014; Turner et al., 2018). Similarly, the extension of tree functioning responses to a broader range of temperatures, should support the transferability of TROLL to temperate and boreal forests.

5. Conclusion

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

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

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

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

Competing interests. The authors declare that they have no conflict of interest.

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Appendix A

Table A1. List of symbols and variables.

Symbols	Definition	Units	Nature	Equations
Physical constants				
M_w	Molar mass of water vapor	kg mol^{-1}	Constant	12
R	ideal gas constant	J mol^{-1} K^{-1}	Constant	12-13, 28-31, 46-47
V_w	Partial molal volume of water	m^3 mol^{-1}	Constant	13
κ	von Karman constant	unitless	Constant	8, 15
g	Gravity constant	m s^{-2}	Constant	37
ρ	Density of water	kg m^{-3}	Constant	37
M_a	Molecular mass of air	kg mol^{-1}	Constant	41, 48
C_p	Heat capacity of air	J kg^{-1} K^{-1}	Constant	41, 48
γ	Psychrometric constant	Pa K^{-1}	Constant	41
D_H	Molecular diffusivity to heat	m^2 s^{-1}	Constant	46
σ	Stefan-Boltzmann constant	W m^{-2} K^{-4}	Constant	44, 48
Aboveground environment				
$PPFD_{top}$	Photosynthetic photon flux density at canopy top	μmol photons m^{-2} 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_{top}	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^{-1}	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	μmol photons m^{-2} 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^{-1}	Computed every half hour	8, 9, 15, 47
c_a	CO_2 concentration	μmol mol^{-1} (ppm)	Constant	Section 2.5
P_{ress}	Atmospheric pressure	Pa	Constant	46-47
$PPFD_{abs}$	Absorbed photosynthetic photon flux density	μmol photons m^{-2} s^{-1}	Computed every half hour	2
T_{mean}	Temperature, averaged per crown layer	°C	Computed every half hour	6
VPD_{mean}	Vapour pressure deficit, averaged per crown layer	kPa	Computed every half hour	7
LAI	Cumulated leaf area per ground area	m^2 m^{-2}	Computed daily for each voxel	1-3, 11, 43
dens	Averaged leaf area density per unit ground area	m^2 m^{-2}	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
$absorptance_{leaves}$	Fraction of absorbed light within a single leaf	unitless	Constant, given as input	1
LAI_{sat}	LAI threshold for computing microenvironemntal variation within the canopy	$m^2\ m^{-2}$	Constant	4-7
ΔT	Parameter of the within-canopy variation in temperature	°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
α	Parameter of wind speed decrease within the canopy	unitless	Constant	9
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
ψ_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
θ_{top}	Water content of the top soil belowground voxel	m^3	Computed daily	14
$\theta_{fc,top}$	water content at field capacity of the top soil belowground voxel	m^3	Computed daily	14
Species and tree characteristics				
LMA	Leaf mass per area	g m^{-2}	Species-specific means: constant, provided as input; tree-specific values: randomly attributed at tree birth	26, 27, 32, 56
LA	Leaf area	cm^2	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^{-1}	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^{-1}	Species-specific means: constant, provided as input; tree-specific values: randomly attributed at tree birth	26, 27, 32
wsg	Wood specific gravity	g cm^{-3}	Species-specific means: constant, provided as input; tree-specific values: randomly attributed at tree birth	36, 55, 60-61, 66
π_{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_{thres}	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
σ_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_t	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
ψ_{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	mmol H_20 m^{-2} s^{-1} 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	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	m m^{-3}	Variable, computed for each tree and layer at each timestep	23
SRL	Specific root length	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
Leaf physiology				
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_2 concentration at the leaf surface	μmol mol^{-1} (ppm or μbar)	Computed half-hourly for each crown layer	34
c_i	CO_2 concentration at carboxylation sites	μmol mol^{-1} (ppm or μbar)	Computed half-hourly for each crown layer	24, 34
A_n	Leaf-level net carbon assimilation rate	µmol CO_2 m^{-2} s^{-1}	Computed half-hourly for each crown layer	24, 52
A_v	Leaf-level net carbon assimilation rate limited by Rubisco activity	µmol CO_2 m^{-2} s^{-1}	Computed half-hourly for each crown layer	24
A_j	Leaf-level net carbon assimilation rate limited by RuBP regeneration	µmol CO_2 m^{-2} s^{-1}	Computed half-hourly for each crown layer	24
R_p	Photorespiration rate	µmol C m^{-2} s^{-1}	Computed half-hourly for each crown layer	24
R_d	Leaf dark respiration rate	µmol C m^{-2} s^{-1}	Computed half-hourly for each crown layer	33
R_{d-M}	Leaf dark respiration rate on a leaf dry mass basis	nmol CO_2 $g^{-1}s^{-1}$	Computed half-hourly for each crown layer	32
V_{cmax}	Maximum rate of carboxylation	µmol CO_2 $m^{-2}s^{-1}$	Computed half-hourly for each crown layer	24, 26, 28
V_{cmax-M}	Maximum rate of carboxylation on a leaf dry mass basis	µmol CO_2 g^{-1} s^{-1}	Computed half-hourly for each crown layer	26
J	Electron transport rate	µmol e^- m^{-2} s^{-1}	Computed half-hourly for each crown layer	24, 25
J_{max}	maximal electron transport capacity	µmol e^- m^{-2} s^{-1}	Computed half-hourly for each crown layer	25, 29

J_{max-M}	maximal electron transport capacity on a leaf dry mass basis	µmol e^- g^{-1} s^{-1}	Computed half-hourly for each crown layer	27
Γ^*	CO_2 compensation point in the absence of dark respiration	μbar	Computed half-hourly for each crown layer	24, 30
K_m	Apparent kinetic constant of the Rubisco	μbar	Computed half-hourly for each crown layer	24, 31
θ	Curvature factor	unitless	Constant	25
α	Apparent quantum yield to electron transport	mol e^- mol $photons^{-1}$	Constant	25
LSQ	Effective spectral quality of light	unitless	Constant	25
g_s	stomatal conductance to CO_2	mol CO_2 m^{-2} s^{-1}	Computed half-hourly for each crown layer	34
g_{sw}	stomatal conductance to water vapor	mol H_20 m^{-2} s^{-1}	Computed half-hourly for each crown layer	35
g_0	minimum leaf conductance for water vapor	mol H_20 m^{-2} s^{-1}	Constant, provided by the user	35
g_1	Parameter of the stomatal conductance model	$kPa^{0.5}$	Computed daily for each tree	35, 36
ψ_{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 ψ_{tlp}	39, 39
E_l	Leaf-level transpiration rate	mol H_20 m^{-2} s^{-1}	Computed half-hourly for each crown layer	41
λ	Latent heat of water vapor	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	Pa K^{-1}	Computed half-hourly for each crown layer	41
R_{ni}	isothermal net radiation	J m^{-2} s^{-1}	Computed half-hourly for each crown layer	41, 43
g_H	total leaf conductance to heat	mol m^{-2} s^{-1}	Computed half-hourly for each crown layer	41, 45
g_{bHf}	boundary layer conductance for free convection	mol m^{-2} s^{-1}	Computed half-hourly for each crown layer	45, 46, 50
g_{bHu}	boundary layer for forced convection	mol m^{-2} s^{-1}	Computed half-hourly for each crown layer	45, 47, 50
g_r	radiation conductance	mol m^{-2} s^{-1}	Computed half-hourly for each crown layer	45, 48
g_w	total leaf conductance to water vapor	mol H_20 m^{-2} s^{-1}	Computed half-hourly for each crown layer	41, 49
g_{bw}	boundary layer conductance to water vapor	mol H_20 m^{-2} s^{-1}	Computed half-hourly for each crown layer	49, 50
S_{abs}	Absorbed solar radiation (PAR and NIR)	J m^{-2} s^{-1}	Computed half-hourly for each crown layer	43

$B_{n,0}$	Net longwave radiation at the top of the canopy	J m^{-2} s^{-1}	Computed every half hour	43, 44
k_d	Coefficient of extinction of longwave radiation	Unitless	Constant	43
ε_l	Emissivity of the canopy leaves	Unitless	Constant	44, 48
ε_a	Emissivity of the atmosphere	Unitless	Computed every half hour	44
Tree carbon allocation and demography				
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	μmol C s^{-1}	Computed daily	54
R_{growth}	Tree-level growth respiration	gC	Computed daily	51
LA_t	Tree-level total leaf area	m^2	Updated daily	55
LA_{opt}	Optimal tree leaf area	m^2	Updated daily	Section 2.6.2
LA_l	Leaf area in tree crown layer l	m^2	Updated daily	51, 52-53
LA_{young}	Tree-level young leaf area	m^2	Updated daily	52-53, 56
LA_{mature}	Tree-level mature leaf area	m^2	Updated daily	52-53, 56
LA_{old}	Tree-level old leaf area	m^2	Updated daily	52-53, 56
ϱ	Ratio of young or old leaf assimilation rate over mature leaf assimilation rate	unitless	Constant	52
ϱ'	Ratio of young or old leaf respiration rate over mature leaf respiration rate	unitless	Constant	53
τ_{young}	Leaf residence time in the young age pool	yr	Computed for each tree	56
τ_{mature}	Leaf residence time in the young age pool	yr	Computed for each tree	56
τ_{old}	Leaf residence time in the young age pool	yr	Computed for each tree	56
SA	Tree sapwood area	m^2	Updated daily	54, 55
λ_1	Parameter for sapwood area computation	m^2 cm^{-2}	Constant	55
λ_2	Parameter for sapwood area computation	m cm^{-2}	Constant	55
δ_1	Parameter for sapwood area computation	m^2 cm^{-2}	Constant	55
δ_2	Parameter for sapwood area computation	cm^3 g^{-1}	Constant	55

f_{canopy}	Fraction of NPP_{ind} allocated to tree canopy (including leaves, fruits and twigs)	unitless	Constant, given as input	Sections 2.6.1 and 2.6.2
f_{leaves}	Fraction of NPP_{ind} allocated to leaves	unitless	Constant	Section 2.6.2, 56
f_{fruit}	Fraction of NPP_{ind} allocated to fruits	unitless	Constant	Section 2.6.1
f_{twigs}	Fraction of NPP_{ind} allocated to twigs	unitless	Constant	Section 2.6.1
f_{wood}	Fraction of NPP_{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
δ_o	Parameter controlling the pace of old leaf shedding acceleration (Δf_0)	unitless	Constant, given as input	
NSC_r	Maximal amount of stored non-structural carbohydrates	gC	Updated daily for each tree	59
ΔV	Increment of stem volume	m^3	Computed daily for each tree	61
$Senesc$	Growth senescence factor	unitless	Computed daily for each tree	61-62
Δdbh	Trunk diameter growth	m	Computed daily for each tree	Section 2.6.4
dbh_{mature}	Diameter threshold beyond which the tree is fertile	m	Computed once for each tree	63
σ_{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_{tot}	Intensity of the external seed rain	number of seeds per hectare	Constant, given as input	64
$n_{ext,s}$	Species-specific number of dispersal events due to the external seed rain	number of seeds	Computed once for each species	64
n_{ha}	Area of the simulated plot	ha	Constant, computed from dimensions given as input	64
LAI_{max}	LAI threshold beyond which the seedling leaf carbon balance is negative	$m^2\ m^{-2}$	Computed once for each tree	Section 2.7.1

d	Tree death rate	events yr^{-1}	Updated daily at tree level	65-66
d_b	Background death rate	events yr^{-1}	Computed once per tree	65
m	reference background mortality rate	events yr^{-1}	Constant, provided as input	66
wsg_{lim}	Parameter of d_b	g cm^{-3}	Constant	66
d_{starv}	Death rate due to carbon starvation	events yr^{-1}	Updated daily at tree level	65
$d_{treefall}$	Death rate due to treefall	events yr^{-1}	Updated daily at tree level	65
Θ	Parameter of treefall probability	m	Computed once per tree	67
$d_{drought}$	Death rate due to drought	events yr^{-1}	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
ψ_{lethal}	Water potential threshold for drought-induced mortality	MPa	Computed once per tree	68

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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 -> 0; A, CO_2 assimilation rate; c_s, 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; Γ, CO_2 compensation point; V_{cmax} and J_{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 H_20 is 1.6 times higher than stomatal conductance to CO_2, we here only represent stomatal conductance to H_20.

Vegetation model			Stomatal conductance		Water stress effect on leaf gas exchange		Tree transpiration
Name	**Reference**	**Type**	**Model**	**Reference/type**	**Stomatal limitations**	**Non-stomatal limitations**	
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	The plant net CO_2 assimilation and evapotranspiration rates (x_{net}) are computed as a linear combination of their rates under open (x_o) and close (x_c) stomata: $x_{net} = f x_o + (1-f) x_c$ with $f = \frac{1}{1+\frac{Demand}{Supply}} = \frac{1}{1+\frac{E_0 \times LA}{K \times W_{avail,tot} \times B_{root}}}$ where E_0 is the evapotranspiration rate under conditions of open stomata times and LA the total plant leaf surface area, and $W_{avail,tot}$ is the amount of water accessible by the vegetation layer, B_{root} the plant root biomass, and K an optimized constant.		Computed with: $E_0 = \varphi_0 \times SLA \times B_{leaf}$ with B_{leaf} the tree leaf biomass and φ_0 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: $\varphi_0 = g_{bw} \times (e_s - e_a)$ $\varphi_0 = g_s \times (e_l - e_s)$
ED2-hydro	(Powell et al., 2018; Xu et al., 2016)	ED2 with a new module of plant hydraulics	Solution of : $\frac{\partial}{\partial g_w}(A_{net} - \lambda g_w D_a) = 0$ with $g_w = \frac{g_s g_b}{g_s + g_b}$ and λ is the Lagrangian multiplier of the optimization problem, representing the marginal water use efficiency (marginal increase in A_{net} per unit change of water loss)	(Vico et al., 2013)/ optimization model, under CO_2 (Rubisco) and light (RuBP regeneration/electron transport) co-limitations	$\lambda = \lambda_0 \times \exp(\beta \times \psi_{pd})$ with λ_0 the value of λ when there is no water stress and β an empirical factor taken from Manzoni *et al.* (2011)	$V_{cmax} = V_{cmax,O} \times \left[1 + \left(\frac{\psi_{leaf}}{\pi_{tlp}}\right)^a\right]^{-1}$ $J_{max} = J_{max,O} \times \left[1 + \left(\frac{\psi_{leaf}}{\pi_{tlp}}\right)^a\right]^{-1}$ where $V_{cmax,O}$ and $J_{max,O}$ denotes the photosynthetic capacities without water stress, and a is a shape factor estimated from Brodribb *et al.* (2003).	Similarly to Medvigy et al. 2009, $E_0 = \frac{g_s g_b}{g_s + g_b} \times D_a \times LA$
TFS	(Fyllas et al., 2014)		$g_s = g_0 + 1.6 \times (1 + \frac{g_1}{\sqrt{D_s}}) \times \frac{A}{c_s}$ g_1 is an empirical coefficient*, associated to the water use efficiency (to the Lagrangian).	(Medlyn et al., 2011)/ optimization, for electron-transport limitated photosynthesis (light limitation)	$g_s = g_{s,0} \times \frac{\theta_i - \theta_{wp}}{\theta_{fc} - \theta_{wp}}$ where θ_{wp}, θ_{fc}, θ_{wp} are the actual soil water available for tree i, and the soil water content at field capacity and wilting point respectively.	-	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.

TFS-Hydro	(Christoffersen et al., 2016)	TFS with a new module of plant hydraulics	"	"	$g_s = g_{s,0} \times \left[1 + \left(\frac{\psi_{leaf}}{\psi_{g_s,50}}\right)^{a_{g_s}}\right]^{-1}$ where $\psi_{g_s,50}$ is the leaf water potential at 50% stomatal closure (assumed a 1:1 relationship between $\psi_{g_s,50}$ and the water potential at 20% loss of xylem hydraulic conductivity ($P_{20,x}$), following results from (Brodribb et al., 2003)), and a_{g_s} is the slope of the curve at $\psi_{leaf} = \psi_{g_s,50}$, computed from $\psi_{g_s,50}$ using the same relationship that relates a_x and $P_{50,x}$.	-	"
Multi-layer CLM4.5	(Bonan et al., 2014)	DGVM	$g_s = g_0 + g_1 \times A \times \frac{h_s}{c_s}$	(Ball et al., 1987; Collatz et al., 1991)/ empirical	$g_0 = g_{0,0} \times \sum_j r_j \frac{\psi_j - \psi_c}{\psi_o - \psi_c}$ where ψ_j is the soil water potential of soil layer j, and ψ_o and ψ_c are the soil water potential at which the stomata are fully open and fully closed respectively, and r_j is the relative root fraction of soil layer j.	$V_{c,max} = V_{c,max,0} \times \sum_j r_j \frac{\psi_j - \psi_c}{\psi_o - \psi_c}$	Iterative procedure
			g_s 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	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	The optimization includes a dependence to ψ_{leaf}, where ψ_{leaf} is computed at each timestep (30-60 min) with Darcy's law (soil-to-leaf pathway, including capacitance).	-	
CLM5	(Kennedy et al., 2019)	Stand-based	$g_s = g_0 + 1.6 \times (1 + \frac{g_1}{\sqrt{D_s}}) \times \frac{A}{c_s}$	(Medlyn et al., 2011)/ optimization, under light	-	CML4.5 default: $V_{c,max} = V_{c,max,0} \times \sum_j r_j \frac{\psi_j - \psi_c}{\psi_o - \psi_c}$	An iterative procedure is used to solve the energy balance (determine the leaf temperature and internal CO_2

			g_1, is an empirical coefficient*, associated to the water use efficiency (to the Lagrangian).	limitation (RuBP regeneration)	-	$V_{c,max} = V_{c,max,0} \times 2^{-\left(\frac{\psi_{leaf}}{\psi_{gs,50}}\right)^{a_{gs}}}$ where $\psi_{g_s,50}$ is the leaf water potential at 50% loss of stomatal conductance and a_{g_s} 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 (ψ_{root}, ψ_{stem}, $\psi_{sunlit-leaf}$, $\psi_{shade-leaf}$) based on Darcy's law (without capacitance).	concentration), under which transpiration is computed as $E_0 = \frac{g_s g_b}{g_s + g_b} \times D_a \times LA$.
MAESPA	(Duursma et al., 2012)	Individual- and stand-based model	$g_s = g_0 + 1.6 \times \frac{A}{c_s} \times \frac{1 + e^{s_f \psi_f}}{1 + e^{s_f(\psi_f - \psi_{leaf})}}$ where ψ_{leaf} is computed at each time step using Darcy's law ($E_L = k_L \times (\psi_{soil} - \psi_{leaf})$)	(Tuzet et al., 2003)/ empirical	Already implemented in g_s computation.	-	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.
CABLE	(De Kauwe et al., 2015a, b)	DGVM (vegetation is represented using a single layer, two-leaf canopy model separated into sunlit and shaded [illegible])	$g_s = g_0 + 1.6 \times (1 + \frac{g_1}{\sqrt{D_s}}) \times \frac{A}{c_s}$	(Medlyn et al., 2011)/ optimization, under light limitation (RuBP regeneration) (was the model of (Leuning, 1995) in previous versions of CABLE (Wang et al., 2011)	Standard version of CABLE (De Kauwe et al., 2015a) : $g_1 = g_{1,0} \times \sum_i r_i \frac{\theta_i - \theta_{wp}}{\theta_{fc} - \theta_{wp}}$ with $\theta_i$the volumetric soil water content and $r_i$the fraction of root mass in soil layer j, and θ_{wp} the soil wilting point and θ_{fc} its field capacity.	-	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 a 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.
					New expression for drought sensitivity of gas exchange: $g_1 = g_{1,0} \times \exp(b \times \psi_{pd})$, where b is a fitted (species-specific) parameter representing the sensitivity of g_1 to leaf predawn water potential ψ_{pd} and taken from (Zhou et al., 2013, 2014), while $g_{1,0}$ values are drawn from (Lin et al., 2015).	$V_{c,max} = V_{c,max,0} \times \frac{1 + e^{s_f \psi_f}}{1 + e^{s_f(\psi_f - \psi_{pd})}}$ where $s_f$and $\psi_f$are fitted (species-specific) parameters drawn from (Zhou et al., 2013, 2014).	
ORCHIDEE	(Krinner et al., 2005; Naudts et al., 2015)	DGVM	$g_s = mA\frac{h_r}{c_a} + b$	(Ball et al., 1987)	In the version of (Krinner et al., 2005): -	The photosynthetic capacities, Vcmax and Jmax, are multiplied by a water stress factor that is:	

			with m and b derived from laboratory measurements.			$1\ if\ f_w > f_o$ $1 - \frac{f_w - f_c}{f_o - f_c}\ if\ f_c < f_w < f_o$ $0\ if\ f_w < f_c$ with f_w the water fraction available for the plant in the root zone, and f_c and f_o the soil water fractions inducing, respectively, closure and maximum opening of stomata.	
					In the CAN version of (Naudts et al., 2015): 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.	-	

LPJ	(Sitch et al., 2003)	DGVM	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: $g_c = g_{min} + \frac{1.6\,A}{c_a(1-\lambda)}$	(Collatz et al., 1991)	Under water stress i.e. when $\min\left[1; \frac{E_{supply}}{E_{dema,d}}\right] < 1$, 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.	< 1Daily evapotranspiration is calculated for each PFT as the minimum of a plant- and soil-limited supply function (E_{supply}) and the atmospheric demand (E_{demand}). E_{supply} is the product of a plant root-weighted soil moisture availability and a maximum transpiration rate; E_{demand} is calculated following Monteith's empirical relation between evaporation efficiency and surface conductance, that uses gpot, the nonwater-stressed potential canopy conductance calculated by the photosynthesis routine

*although fitted empirically to leaf exchange experimental data (Lin et al., 2015), attempts have been made to relate g1 to functional traits and/or 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 associated to functional strategies. See also values reported in Domingues *et al.* (2014).

2532 **Table B2. Examples of observational or experimental studies that explored the relative roles of stomatal and non-**
2533 **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 fluoresecnce, 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% lost of gs, 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. gs and A/gs vs. gs 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 constrating	as soil water content (θ) was reduced under increasing drought, all species responded by reducing gs, resulting in reduced Ci and Asat. However, Asat 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 Ci, indicating a coincident reduction in photosynthetic capacity with declining θ. The best model include both stomatal and non-stomatal limitations.

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