

Rooting vegetation models in realism

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Funding information

Horizon Europe ERC Advanced Grant, Grant/Award Number: 101020824

Process-based terrestrial biosphere models (TBMs), also known as vegetation models, are how we predict large scale biological responses and biogeochemical feedbacks to climate change. Their incorporation into larger climate models underpins future global climate change scenarios published by the Intergovernmental Panel on Climate Change and how vegetation processes are represented contributes to uncertainty in future predictions. Models must be simple to represent vegetation generally and universally, at global scales and in future environments without current analogues. They must also be informed by theory and tested against data to demonstrate their reliability.

Terrestrial biosphere models usually represent canopies as more complex than root systems. This is pragmatic, because both data and theory of canopy structure and function is more abundant than roots. Leaves in plant canopies are responsible for the most important chemical reaction on earth—photosynthesis. Leaves are arranged to optimise net photosynthesis given constraints (e.g. shading, nutrient availability) and capturing this has been a key driver in elaboration of canopies in TBMs. Since the 1990s, this has been enabled by the advanced state of theory on photosynthetic chemistry, development of remote sensed measurements of potential photosynthetic activity, and networks of land surface gas and energy exchange measurements such as eddy covariance towers and manipulative ecosystem experiments. Field measurement sites often have data on other properties of the ecosystem which can be used to fit the model, but this data is usually concentrated above ground.

On the other hand, root systems have received far less attention in TBMs. Despite this, roots account for 1/3 of living plant biomass, critical functions including water and nutrient uptake, interactions with both plant competitors and herbivores, mycorrhizal fungi and

microbes critical for overall plant and ecosystem function, and thus overall integration of all major biogeochemical cycles. Roots are considerably harder to sample than leaves, as they are in a dense, opaque subterranean environment. Consequently, both data and general predictive theory is less advanced. In TBMs, root systems are typically represented simplistically. At best, this is usually fine roots (short lived, analogous to leaves) and coarse roots (semi-permanent, analogous to woody above ground tissue). This mirrors a common and functionally limited interpretation in empirical field studies based on root size, with a typical threshold at 2 mm diameter, omitting mycorrhizal fungi completely. This structure is appealing because size sorting of root samples is comparatively easy compared to other classifications. In models, well known variability of fine roots in three-dimensional space and seasonal time is usually represented by a linear parameter tying roots to leaf activity, by environmental thresholds, or more recently by optimality theory. Optimality is an appealing reduction of complex ecological function to economic principles—that is, minimising 'cost' in one resource of acquiring another or maximising another useful function. However, linking fine root dynamics to optimality typically retains a dependence on leaf activity because leaves are the source of carbon, the 'currency' in the resource trade-off for growing roots. Optimal but asynchronous activity implies either changing 'costs' in the relationship—equally difficult to verify, or reliance on storage pools and mobilization triggers which are equally uncertain and poorly understood from data.

Meanwhile, a wealth of recent studies by root ecologists have elaborated knowledge of root activity. Root phenology has been repeatedly shown to not be synchronous with leaf phenology (Abramoff & Finzi, 2015), a suite of functional root traits and how to measure them has been proposed across multiple studies, and root

This article is a Commentary on Wang et al., <https://doi.org/10.1111/gcb.16659>.

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phenomics—that is, morphological traits—has gained enormous traction in agronomic studies. This raises the question of how to reduce the complexity of belowground interactions in a functional but parsimonious and data-testable way suitable for TBMs to represent this critical part of ecosystems without inherent dependence on leaves.

In this issue of *Global Change Biology*, Wang et al. (2023), propose a modelling structure of root systems, which approximates function through three *functional* pools—TAM, or transport roots (T), absorptive roots (A) and mycorrhizal fungi (M). This both echoes conceptual shifts which have already occurred for both canopies (De Pury & Farquhar, 1997) and microbial pools (e.g. Yu et al., 2020) in models and matches a move from apparent root structure to root function by McCormack et al. (2015). TAM allows divergence in chemical traits and lifespan between roots and fungi. Initiation of root growth is dependent on environmental conditions and independent of leaves. The authors implement this framework into the E3SM land model (ELM), first under an approach which constrains the C:N of the bulk fine root pool and optionally allows vertical distribution changes in the three TAM pools. ELM maintains an overall C allocation to belowground; hence, responses observed are due to functional differences arising from the structural optimisation of the belowground system rather than root: shoot allocation changes. Under this first set of assumptions TAM shows changes in major soil pools and fluxes, especially an increase in simulated fine root biomass and changes in soil carbon storage under all scenarios. Based on this, the authors use a further 'radical' approach that does not maintain the whole system C:N ratio. Such an approach is reasonable given the relatively poor state of *whole ecosystem* stoichiometry data. Under these conditions, forest gross primary productivity is suppressed by around 1/3 because flexible pools and unconstrained stoichiometry induce N limitation. While this model lacks much 'realism' found in more parameterised setups, this agrees with studies suggesting that sink limits to growth are badly described in models. The ELM canopy parameterisation is particularly simple, using a big-leaf paradigm in contrast to modern multi-layered canopies, plus the fixed root: leaf allocation already mentioned. This raises the future question of the effects of a TAM framework in more realistic modelled systems including adjusting allocation and stoichiometry dynamically above and belowground.

While this is interesting the authors highlight the considerable challenges of data parameterisation for both pools and partitioning coefficients belowground. Root ecology is perhaps the most urgent area for simplification of complex functional and community ecology into simple rules applicable at scale because it is unlikely that an alternate 'big data' remote sensing driven approach—otherwise providing valuable solutions in global change ecology—could replace this knowledge in the opaque soil system. One of the most exiting implications of the TAM framework is that this is a *relatively* straightforward to conceptually approach and could drive a model-led testing through targeted quantification of three defined pools; transport roots (T), absorption roots (A) and mycorrhizal fungi (M). Nonetheless as the authors acknowledge, this is difficult to optimise because of the multidimensional partitioning problem inherent to such a framework, which increases uncertainty because as well as

depth and time (phenology) differences, there are three pools to consider.

So the question remains as how to test this function. Size is the most common differentiation between roots in most field studies because morphological characteristics are simpler to measure in an already challenging measurement environment. This distinction led to the classical—and still common—size threshold of fine roots. The functional definition of transport and absorptive roots is also reflected in branching order, colour and lifespan; absorptive roots are more distal, less lignified and shorter lived than transport roots (McCormack et al., 2015). This lifespan difference is because absorption consumes locally available resources. Continuous root observational measurements able to distinguish between living and dead roots and/or separate roots by appearance could thus provide a piece in this functional challenge. Vitality is also important because roots decompose in situ. The biogeochemical function of roots differs when they are living or when they are litter. While there is no way at present to make such measurements at the sort of long-term field experiments critical for parameterising TBMs, concurrently, root phenotyping approaches are developing in agronomy. A key challenge in closing this data-model gap, is how to transfer practical phenomic measurements belowground. While not yet established, technological advances such as non-visible imaging (Picon-Cochard et al., 2009) or AI-assisted tools (Han et al., 2021) potentially allowing quantification of growth peaks in fine roots (Nair et al., 2022) could not only increase throughput but fundamentally change the data available for frameworks such as TAM.

If root data for TBM parameterisation is limited, data on mycorrhizal fungi are even more so. Mycorrhizal incorporation into TBM is appealing from a process-driven point of view (Treseder, 2016) but also very difficult. Currently with the exception of the FUN (Fixation and Uptake of Nitrogen) framework (Fisher et al., 2010)—where mycorrhizal type sets the cost of an optimal C:N exchange rate of different ways to acquire N but not an actual mycorrhizal pool—mycorrhizal dynamics are not included in TBMs. Incorporation of the explicit M pool in the TAM framework is thus a testable hypothesis, if models are fit to sites where mycorrhizal biomass can be quantified.

Terrestrial biosphere models must be simple to prevent overfitting but complex enough to be trusted as our main predictive tool for an uncertain future. While root system representation up to now have been simple, this has not arisen out of model parsimony but rather a data bias towards aboveground processes. Wang et al., 2023, propose a functional structure to the root system with potential for reducing uncertainty in belowground function under global change, potentially testable with development of modern observational approaches. This opens the way for potential model-led collaborations in the future.

ACKNOWLEDGMENTS

The author acknowledges ERC ADG 'TERRAFORM' (Grant ID: 101020824), awarded to Jennifer McElwain for supporting this article. Open access funding provided by IReL.

CONFLICT OF INTEREST STATEMENT

The author declares no conflict of interest.

DATA AVAILABILITY STATEMENT

No data are associated with this article.

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How to cite this article: Nair, R. (2023). Rooting vegetation models in realism. *Global Change Biology*, 00, 1–3. <https://doi.org/10.1111/gcb.16699>