Modeling ambitions outpace observations of forest carbon allocation

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Key words:

Vegetation model, carbon sink, manipulative experiment, flux tower, climate, ecological scaling

Abstract:

There have been vociferous calls for “tree-centered” vegetation models to refine predictions of forest carbon cycling. Unfortunately, our global survey at flux-tower sites indicates insufficient empirical data support for this much-needed model development. We urge for a new generation of studies across large environmental gradients that strategically pair long-term ecosystem monitoring with manipulative experiments on mature trees. For this, we outline a versatile experimental framework to build cross-scale data archives of carbon uptake and allocation to structural, non-structural, and respiratory sinks. Community-wide efforts and discussions are needed to implement this framework, especially in hitherto underrepresented tropical forests. Global coordination and realistic priorities for data collection will thereby be key to achieve and maintain adequate empirical support for tree-centered vegetation modeling.

Main text:

A changing modeling scope alters data requirements

Are global forests going to continue mitigating anthropogenic CO₂ emissions in a warmer future? Answering this fundamental question requires reliable forecasts of carbon (C), water, and nutrient cycling in forests [1]. Adequate mathematical descriptions of the relevant ecosystem processes are thereby essential. This necessitates the continuous refinement of process-based vegetation models, which in turn requires empirical observations from a broad range of

ecological settings and spatiotemporal scales [2,3]. The required nature of such observations depends on the model structure and incorporated process detail. If these characteristics change – as is currently being argued for [2-5] – forest ecologists are challenged to address emergent needs for data collection and process understanding.

In pursuit of an optimal model structure, vegetation modelers are converging on an intermediate complexity. The target model is broadly applicable across ecosystems, has manageable requirements for input data, and still contains enough physiological detail to simulate the dynamics of all C fluxes and pools. This ideal is being approached from two sides: a top-down approach implemented in dynamic global vegetation models that started with a broad scope and is now adding process detail [2]; and a bottom-up approach in high-resolution ecophysiological models that is now working towards process formulations that depend less on local **parameterization** (see Glossary) [5,6]. The individual tree emerges from this development as the finest scale at which C, water, and nutrient dynamics can be realistically simulated.

In contrast to these ambitions for tree-centered vegetation modeling, the necessary empirical support is presently weak. Several in-depth reviews have recently concluded that i) air- and spaceborne Earth observations have limited capacity to inform whole-tree processes [7], ii) long-term manipulative experiments of mature trees are resource-intensive and thus focus on few sites (e.g. forest free-air CO₂ enrichment experiments, [8]), iii) inference drawn from experiments on seedlings is not necessarily scalable to mature forests [9], and iv) observations of tree-internal C and water dynamics are still too sparse for broadly applicable model parameterization [2-6]. This shortage of observations is compounded by the flexibility of trees to adjust growth, branching patterns, fine-root formation, reproduction, or **non-structural carbohydrate** (NSC) storage under changing climatic and substrate conditions [10-13]. **Carbon allocation** at a given location is also species-specific [14] and modified by disturbance dynamics and legacies of historical land-use [15,16]. We thus argue that the call for ecological *in-situ* studies to understand this allocation complexity ought to be just as loud as the call for improved vegetation models.

Scaling limitations of past and potential for future research on forest C allocation

How come that decades of exciting research on C allocation have not translated into a more robust basis for tree-centered vegetation modeling? The answer likely relates to the limited scalability of existing observations [13,17,18]. This is, in part, because heterogeneous data collection in project-driven research has often prevented cross-scale data archives to inform forest C, water, and nutrient cycling.

Our goal is to propose a suitable experimental framework to harmonize data collection and build cross-scale archives. For this, we consider forested **flux-tower** sites to be a promising starting

point. Their observations range from sub-daily measurements of **C fixation**, respiration, and tree-internal NSC and water transport to seasonal **phenology** and annual biomass increment [19]. Many flux-tower sites also offer high-quality measurements of environmental variables, site ecology, stand and soil characteristics, and the overall C balance. In addition, organized regional networks (e.g. AmeriFlux and others that constitute FLUXNET, the Integrated Carbon Observation System, or the US National Ecological Observatory Network) have long-term plans for monitoring activities [19,20] and open data policies that facilitate data access and use. If fully realized, the flux-tower setup is thus quite unique in providing cross-scale observations to evaluate and develop tree-centered vegetation models [21].

A global survey at flux-tower sites reveals priorities and deficiencies in existing data collections (Figure 1). Most sites have inventoried forest structure and aboveground C stocks. Annual tree growth and foliage turnover have also been measured for the majority of sites, although the continuity, comparability, and time-series length of these measurements is variable. More detailed information on the biomass, structure, and function of individual tree organs are less common, particularly those related to wood density and belowground biomass. Encouragingly, about 50% of sites report precise measurements of water transport and volume increment of tree stems, although the length and temporal resolution of these records varies strongly. By contrast, quantitative information on forest management and tree mortality is still rare, as are terrestrial and airborne **LiDAR** data that could help upscale local observations of forest structure [7,22].

Our survey highlights a wealth of existing observations, but also hints at several shortcomings in producing cross-scale information on forest C cycling:

- **Temporal depth:** By 2019, C-flux records exceeded 15 years at 43 sites and 20 years at 23 sites. This timeframe does not allow quantifying the response of C allocation to longer-term processes such as disturbance dynamics [15], management [16], decomposition of soil organic matter [23], or phenotypic and genetic adaptation of trees [24,25]. It allows, however, for increasingly robust statistical integration with seasonal to annual tree growth [26-28], which could link short-term variability in C allocation with longer-term dynamics at the tree and stand levels [29].
- **Monitoring only:** Most flux-tower sites record overall forest responses to environmental variability and changes, but do not attempt to simulate future conditions [8, 30]. Such information would be helpful to parameterize tree-centered vegetation models, especially because of potentially non-linear tree-environment feedbacks [18] that even multi-site syntheses of flux-tower data may not capture [31].
- **Spatial representation:** Sites cluster in temperate regions (Figure 1A,B) and even though new sites are being established in the tropics (e.g. Congoflux) – the current flux-tower network is not representative of boreal and tropical forests that are crucial for terrestrial C cycling [32]. A number of sites are also managed with sometimes poorly documented and heterogeneous

treatments, which may obscure changes in C allocation in response to environmental variability. In addition, such data are often not openly available.

Weighing these strengths and limitations, we conclude that the existing flux-tower network will likely not fully suffice to build the necessary cross-scale data basis to support tree-centered vegetation model development.

Building a cross-scale empirical basis for tree-centered vegetation modeling

We propose a refined experimental framework (Figure 2) for a new generation of *in-situ* studies to improve the consistency, scalability, and predictability of forest C cycle observations:

i. Bridge spatiotemporal scales with an enhanced set of monitoring parameters

Despite laudable efforts to standardize data collection and processing within regional ecological networks [19,20], there is no global consensus as to which ecosystem parameters should be routinely measured at all sites (Figure 1C). And even the most common parameters are prone to scaling uncertainties, as is epitomized by the inconsistent results of comparisons between C fluxes and tree rings [26-28]. This comparison entails a leap in temporal scale from seconds to years and in spatial scale from individual trees to a variable tower footprint, which may simply be too substantial to resolve the dynamic C allocation to wood formation. Intermediate scaling steps are clearly needed to resolve this and many other processes. In the following, we list promising approaches to quantify wood traits and growth, tree hydraulics, belowground allocation and C storage, respiration, and **allometric scaling**.

1) Sub-seasonal tree-specific growth can be measured using **quantitative wood anatomy** [33,34] (Figure 2A). The observed properties and number of cells produced during a growing season provide fundamental measures of intra-annual wood formation [33-37]. To upscale these cell parameters, the timing of cell formation has to be known. This is best achieved through regular (e.g. weekly) collection and wood anatomical analysis of micro-samples to follow the developmental stages of each cell over time [34-35]. This “**xylogenesis**” approach is, however, laborious and restricted to the period of repeated field sampling. We thus recommend initial xylogenesis campaigns for a given ecological setting to calibrate retrospective wood anatomical measurements of increment cores, which can be produced much quicker but are coarser regarding the timing of cell formation [38,39]. By combining the two approaches, precise intra-annual growth records throughout a tree’s life can be developed [40].

2) Linking structural growth more strongly to the water cycle will refine our mechanistic understanding of forest C allocation [6]. We encourage sub-daily measurements of stem water

transport using **sap-flow sensors** [41] and diameter variations using **dendrometers** for a representative set of trees in a given forest stand. Dendrometers are ideally installed at multiple locations along tree stems [42] and on coarse roots [42,43] to capture the full axial variability in diurnal to annual diameter changes. If treated carefully, and especially if supplemented with measurements of NSC dynamics [44] and the chemical composition of the **xylem** sap [45], the resulting information on whole-tree hydraulics and growth can help reconcile the anatomy and function of the xylem in different ecosystems [46,47].

3) Important structural and non-structural (e.g. in rays and **parenchyma cells** [10,11]) C sinks in trees include coarse and fine roots that are challenging to measure empirically and thus often neglected in forest ecological studies. We see great potential to combine temporal information from root dendrometers [42,43] with multi-temporal ground-penetrating radar measurements that are becoming increasingly precise in mapping tree root systems [48]. The resulting quantification of root biomass increment could help disentangle above- and belowground C investments as a function of environmental variability [49]. Fine-root growth also needs to be measured for this purpose, for which a combination of **rhizotrons** and (repeated) soil coring is recommended [50].

4) Besides tree-internal C dynamics, respiration processes need to be better constrained. The temperature-dependent ecosystem respiration from flux towers integrates all **autotrophic and heterotrophic respiration** components, which may obscure their individual responses to environmental variability. Efforts to partition ecosystem respiration should be intensified to develop long-term records of stem [51], root [52], soil [23], or leaf respiration [53]. Novel and low-cost systems are becoming available that facilitate such measurements and allow capturing substantial between-tree variability in respiration [51]. If conducted systematically, such data will help refine the representation of respiration processes in tree-centered vegetation models.

5) Finally, terrestrial LiDAR could greatly facilitate the upscaling of individual tree allometries [7,22]. Exceptionally precise information on tree volume can be extracted from LiDAR point clouds that, combined with radial growth and wood density measurements, allows reconstructing tree and stand biomass in units that are comparable to C-fluxes. This should circumvent uncertainties from common allometric biomass equations and minimize spatial sampling biases when quantifying forest productivity [17]. LiDAR further represents an intermediate scaling step between tree-level measurements and air- or space-borne monitoring of forest biomass [7].

ii. Pair long-term monitoring sites with manipulative experiments

Ecosystems worldwide will likely face future environmental conditions and variability that have no analogue in the recent past and are thus not yet represented by monitoring. Manipulative experiments to simulate such conditions and observe the responses of C allocation and other ecosystem functions are thus indispensable (Figure 2B). Yet, manipulations under field

conditions are often incompatible with long-term monitoring setups. They can also be very resource-intensive [8,54] and have thus focused on key ecosystems and sites [30]. We see some drawbacks in this focus, because i) results may be challenging to scale across the landscape, ii) many field manipulations have remained short-term, making it difficult to distinguish transient from lasting changes, and iii) we believe that the broad environmental research community should engage in building cross-scale data archives.

We advocate for the strategic pairing of long-term monitoring sites (with or without flux towers) with spatially separated manipulative experiments conducted under similar ecological conditions (climate, soil, vegetation) and using comparable instrumentation (Figure 2B). Successful examples of such pairing exist [55], where long-term monitoring constitutes an important benchmark for anomalies in ecosystem functioning caused by a given manipulation. Yet, few flux-tower or other long-term monitoring sites currently have designated experimental partner sites. Possible low-cost manipulations include: tree defoliation or shading to identify priorities for C storage, growth, or reproduction under resource limitation [56]; **phloem** removal (“girdling”) to provoke changes in wood structure [57] and track the remobilization of stored NSC [58]; or litter manipulations and soil fertilization to assess changes in soil organic matter, microbial communities, and soil respiration [23,59]. More demanding experiments warm or cool tree organs [60] or soil to assess changes and acclimation of root and soil respiration, decomposition of organic matter, coarse- or fine-root biomass, and C stocks under climate change [23,52]. As water limitation on forests is increasing worldwide, manipulations of water input can provide important insight, e.g., in the response of tree biophysical processes, growth, and soil biogeochemistry to irrigation-stop [61], air humidity [62], or rainfall exclusion experiments [42,63]. Existing designs range from affordable “umbrella-type” rain shelters to expensive mobile roofs over the canopy [63] or whole-tree chambers [54]. Very advanced infrastructure also allows elevating [8,64] or lowering [65] the atmospheric CO₂ concentration and isotopic composition (i.e. **tracer experiments** [66]). Finally, experimental planting and **common-garden experiments** [67,68] are promising to evaluate the impacts of different tree populations and soil types on C cycling in trees.

Balancing the costs and benefits of field measurements

Paired monitoring-manipulation sites would ideally represent the full range of environmental conditions that trees experience worldwide. This ideal is challenged by the oftentimes substantial time and resource demands of continuous field and laboratory measurements, and by logistical hurdles in remote areas. Also, not all types of measurements are suited for all ecosystems, e.g., as many tropical tree species lack a clear annual rhythm of vegetative and dormant seasons [69]. Hence, we have to prioritize between core measurements at all sites and such that are ecosystem-specific or optional if the available resources suffice. In Figure 3, we propose an admittedly

subjective ranking of parameters regarding this cost-utility trade-off. Utility thereby targets tree-centered vegetation model development (i.e. “model-data integration by design” [2,8,30]), but also reflects other important uses such as ecological monitoring, fundamental process understanding, new methodological developments, or forest inventories. With this, we hope to stimulate a community-wide discussion (see Box 1 for key questions) on how to best achieve and maintain cross-scale data archives globally. Importantly, this discussion needs to involve large existing research infrastructures to get recognition and long-term support for such archives, and to ensure open data access and sharing according to the FAIR principles [70].

Concluding remarks

We are concerned that the much-needed advances in tree-centered vegetation modeling may be slowed down because the necessary cross-scale empirical observations are not being developed at the same pace and are often not openly available. To stimulate a new generation of field studies that can reduce this imbalance and help fill existing knowledge gaps (see Outstanding Questions), we propose a versatile experimental framework that strategically pairs long-term ecosystem monitoring with manipulative experiments. This way, our understanding of C, water, and nutrient dynamics in trees can be refined and scaling biases minimized. Implementing this experimental framework across ecosystems and biomes will require a community-wide dialogue on priorities and standards for data collection, the “yield-on-cost” of various types of observations, and the necessary funding, infrastructure, and coordination.

Acknowledgements:

We are grateful to all principal investigators of flux-tower sites that participated in our survey. We thank David J.P. Moore, Bert Gielen, Miro Demol, Christian Ginzler, and Alicja Babst-Kostecka for fruitful discussions. F.B. acknowledges funding from the project “Inside out” (#POIR.04.04.00-00-5F85/18-00) funded by the HOMING programme of the Foundation for Polish Science co-financed by the European Union under the European Regional Development Fund. R.L.P. acknowledges support from the Swiss National Science Foundation (P2BSP3-184475). DP acknowledges support from the ENVRIFAIR H2020 European project (GA 824068)

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Figure legends:

Figure 1. Overview of *in-situ* observations collected at currently or historically active flux-tower sites. (A) The sites included in our survey (n = 90, vegetation type = forest, time-series length > 5 consecutive years as of 2019) have a broad distribution across geographic and climatic space, but (B) the tropical and boreal domains are underrepresented compared to the global forest area (forest = above 60% tree cover in the MODIS land-cover product, <https://lpdaac.usgs.gov>; climate data from Worldclim version 2; www.worldclim.com/version2). (C) The reported parameters in our survey have been grouped according to their scope in the context of the forest C balance. Colors refer to categories of parameters that are relevant to tree-centered vegetation modeling. For 67 sites, the principal investigators participated in our survey; for 23 additional sites, we obtained the relevant information from online resources or publications.

Figure 2. Experimental framework to strategically pair monitoring of C allocation processes in forests with manipulative experiments. (A) Existing and newly establishing monitoring sites should aim at consistent observations of C allocation to autotrophic and heterotrophic respiration, above- and belowground structural biomass, and non-structural carbohydrate pools. A suggested (but not exhaustive) set of measurements are displayed in grey, with numbers referring to the corresponding sections in the main text. Parameters are shown in black and processes in black *italic*. (B) Each monitoring site is ideally paired with other, ecologically comparable sites, where manipulative experiments are conducted on mature trees. We propose six main types of manipulations, each with one or multiple possible approaches displayed in grey.

Figure 3. Ranking of observations regarding a trade-off between the costs and utility of measurements to improve tree-centered vegetation modeling. Categories correspond to different forest ecosystem processes, characteristics, and drivers (colors as in Figure 1C). This ranking is admittedly subjective and will need to be adjusted as new methodologies and technologies to measure ecosystem parameters are being developed.

Figure 1

474
475 Figure 2

Figure 3

Text boxes:

Box 1. Key questions for a community-wide discussion on how to build and maintain cross-scale data archives on C allocation in trees and forests

Priority questions:

- What are the criteria for site selection to achieve the best possible representation of global forests? How to best integrate existing flux-tower and other long-term ecological monitoring networks with newly establishing monitoring-manipulation sites?
- Considering the trade-off between the costs and utility of various types of measurements (Figure 3), which are the core parameters that should be measured at all paired monitoring-manipulation sites?
- What is the optimal temporal resolution and quality of each type of measurement to support tree-centered vegetation modelling?
- How can we best standardize data collection, processing, uncertainty quantification, archiving, and sharing according to the FAIR principles [70]?
- How to ensure the continuation of data collection beyond the duration of individual research projects? What are available funding mechanisms? How could a global initiative be coordinated and led?

Additional questions:

- Should manipulative experiments be specifically planned to support “model-data integration by design” [2,8,30] or should they rather be diverse to explore various mechanisms and leave room for the unexpected?
- How should human management be considered in monitoring and manipulative experiments?
- How can the paired monitoring-manipulation sites be integrated with other long-term ecological networks (e.g. national forest inventories) that exceed the temporal depth of flux-tower sites? What are our options for retrospective analyses of management impacts and disturbance dynamics to assess ecosystem processes over longer time scales in the pre-monitoring period?
- What is the best format to prepare *in-situ* observations from paired monitoring-manipulation sites for the ground-truthing and calibration of air- and space-borne remote sensing data?
- Should there be designated cyber infrastructure (e.g. data centers), where monitoring, experimental, and modeling data come together? How could they be best established and supported? How can we achieve open access for all data streams?