

Perspectives for improving carbon and nitrogen allocation in forest models from stand to global scale

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Highlights: We show that using a fixed foliage: fine-root ratio leads to unrealistic modeled responses of forest growth to environmental variability (in particular to soil nitrogen availability). Not only the relative growth of organs (carbon allocation) will be off but also gross primary productivity predictions indirectly suffer from a lack of allocation flexibility. We suggest that applying evolution-based optimization principles to account for allocation plasticity is a key measure to improving future forest models and dynamic global vegetation models (DGVMs).

Keywords: Productivity, tree, uptake, N:C ratio, nitrogen concentration

INTRODUCTION

In times of rising atmospheric carbon dioxide, forest carbon (C) allocation has drawn interest due to its responsiveness and potential effect on the global carbon balance. The differences in lifespan and decomposition rates among tree organs, such as stems and leaves, imply that C allocation in trees strongly influences forest carbon cycling rates. Both productivity and allocation is often controlled by nutrient availability, in particular nitrogen (N) availability, pointing to the fundamental importance of C-N interactions. Whereas the importance of C allocation and its link to N availability is undisputed, there is little consensus on how it should be modeled. Consequently, allocation is the Achilles' heel of most forest models (Landsberg 2003; Le Roux et al. 2001). Although many promising approaches have been developed for the purpose of scientific insight, it is remarkable how rudimentary the representation of C allocation is in comparison to C assimilation (photosynthesis) in most applied forest models. For example, most dynamic global vegetation models (DGVMs) have fixed or only water-dependent C allocation (Ostle et al. 2009). While N limitation has now been included in a number of DGVMs, the underlying assumptions vary and are not always supported by proven mechanisms. For example, some models impose a sudden switch from C to N limitation if N supply does not meet demand set by C productivity. Others models let N limitation control photosynthesis via leaf N:C ratio, while linking N:C of all tissues through proportionality constants. While these assumptions serve to impose N limitation on growth they do not link N limitation to C allocation, although changes in C allocation is an important means for plants to equalize limiting effects of C and N. Another factor that influences allocation is the degree of competition (e.g. for soil N), which has never been considered in large scale models. However, it is not well known how all these potential shortcomings affect DGVM predictions and which aspects should be most urgently addressed.

In contrast to bottom-up and ad-hoc methods of adding N limitation and allocation to existing models, we suggest that plasticity (variability) in growth and allocation can only be properly understood -and therefore efficiently modeled- on the basis of the underlying principles that ultimately control plant behavior as a whole. These evolution-based principles can often be approximated by optimization assumptions (Franklin et al. 2012). Here we present a forest stand model based on well established structural and physiological assumptions assuming that the trees optimize N and C allocation to maximize fitness in response to environmental variables. We evaluated the importance of plasticity in C allocation and N:C ratio as well as the effect of competition for predictions of forest productivity at the stand level and globally.

MODEL

The model is based on a previous model (Franklin et al. 2009) used to explain the forest responses to elevated CO₂ and N availability in free air carbon dioxide experiments (FACE). In this model trees respond to CO₂ and N availability by adjusting C allocation, canopy N content, and leaf area index (LAI).

Photosynthesis is modeled based on leaf N per area and photosynthetically active radiation (PAR). N uptake is a function of fine-root biomass and soil N availability. This model was extended to account for competition among trees for soil N (as done in Franklin et al. 2012), and plasticity in leaf- and wood N:C ratio, which influences N and C demands as well as the relationship between LAI and photosynthetic capacity. Wood N:C ratio was assumed to change in proportion to leaf N:C ratio.

To evaluate the importance of the three factors (i) leaf: root allocation plasticity, (ii) leaf N:C ratio responses, and (iii) root competition, we ran the model with and without each of these effects. The evaluation was done first for the Oak Ridge National Laboratory (ORNL) FACE forest based on data from Franklin et al. (2009) and, second, for potential GPP of a temperate forest stand (parameterized for ORNL FACE site) simulated globally based on gridded data (restricted to non water-limited forest covered grid cells) on PAR, day length, length of growing season, and soil N mineralization.

RESULTS AND DISCUSSION

Previous work has proven the validity of the allocation optimization approach by predicting the observed C allocation shift from wood to fine-roots in response to elevated CO₂, and its reversal after N addition, in FACE experiments (Franklin et al. 2009). It was therefore not surprising that replacing allocation optimization with N:C ratio optimization made the model unable to capture the allocation patterns typically observed in response to changes in soil N availability (Fig. 1). More surprising is that this assumption also led to a much steeper response of GPP to soil N availability than if the trees are allowed to adjust allocation (Fig. 1a). Allowing optimization of leaf N:C ratio in addition to allocation optimization did not change GPP significantly, but it enhanced leaf growth response at low soil N availability (Fig. 1).

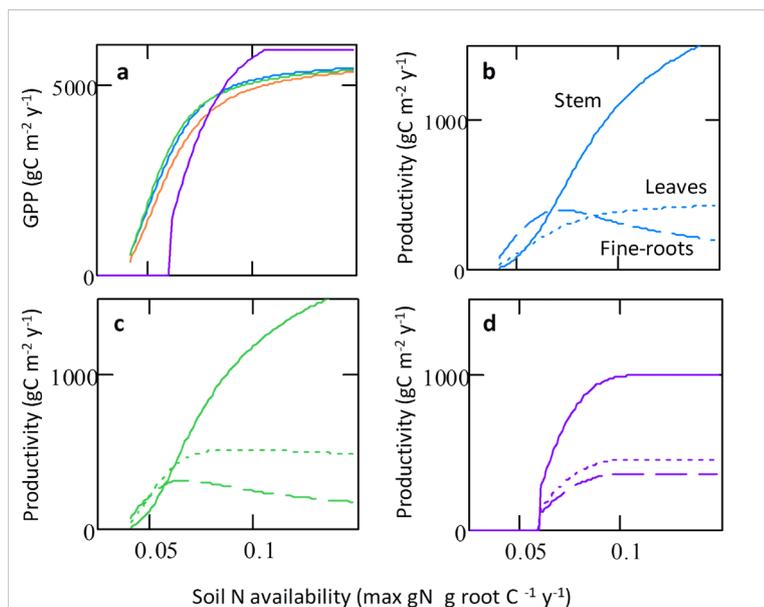


Figure 1. Modeled productivity as a function of soil N availability in the Oak Ridge National Laboratory Free Air Carbon dioxide Experiment (ORNL FACE) site, showing GPP (a) and growth of leaves, stem and fine-roots (b-d). Trees maximize net growth under alternative optimization variables: stem:leaves:root ratio (b-blue lines), stem:leaves:root ratio and leaf N:C ratio with and without root competition, respectively (c-green lines, orange line), and leaf N:C ratio assuming fixed fine-root: foliage ratio (d-purple lines). Observed responses largely agree with model b and c (Franklin et al. 2009).

The global latitudinal analysis showed that assuming that trees acclimate to their environment only via their N:C ratio in foliage (and stem) leads to much stronger, and partly unrealistic, latitudinal variability in gross primary productivity (GPP) than if they are assumed to acclimate C allocation (Fig. 2). Furthermore, in this scenario the model was sometimes not able to find an optimal leaf N:C ratio within the range of realistic values (gaps in the purple line in Fig. 2). If allocation optimization was enabled, simultaneous optimization of leaf N:C had a relatively small additional impact, slightly moderating the latitudinal response. These results suggest that adjustment of C allocation is a much more important response to environmental conditions across a globally latitudinal range than adjustment of leaf (and wood) N:C ratios.

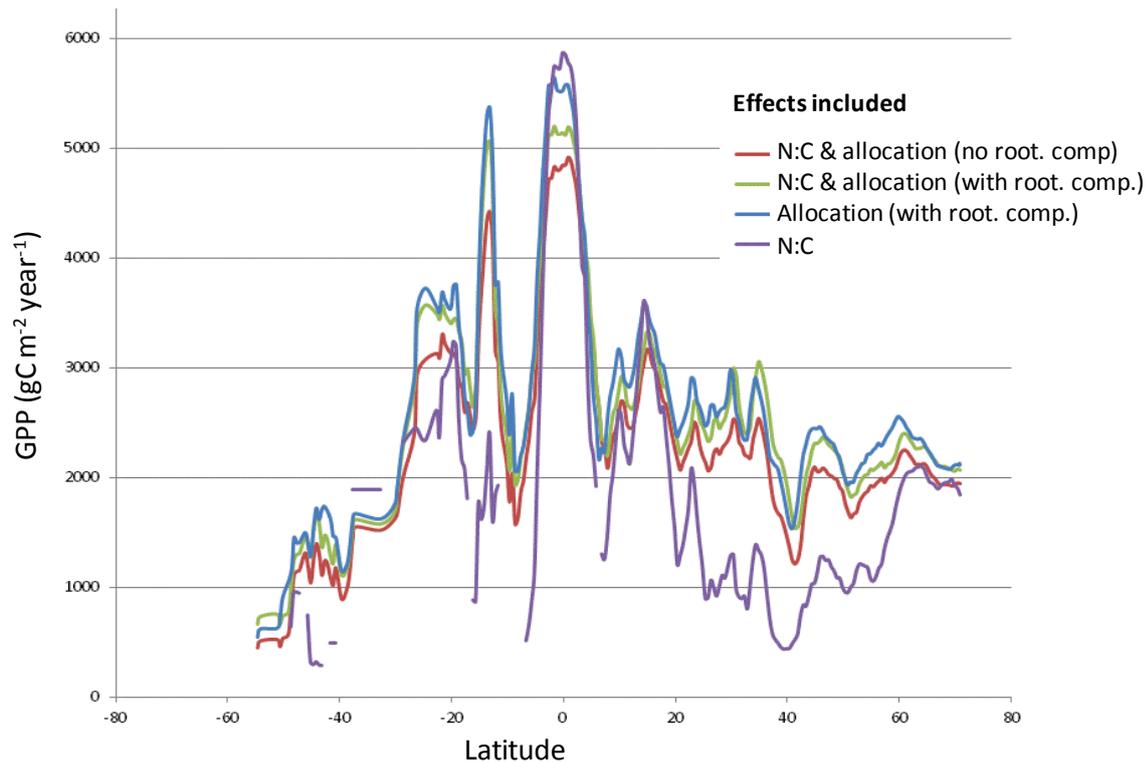


Figure 2. Potential gross primary productivity (GPP) of temperate broadleaf forest (parameterized for the Oak Ridge National Laboratory Free Air Carbon dioxide Experiment- ORNL FACE site) modeled for all grid cells (0.5 x 0.5 degrees) dominated by forest that are not significantly water-limited. The trees adjust to the environment (PAR, length of growing season, day-length, and soil N mineralization) by maximizing net growth (wood growth + reproductive production) by optimizing: leaf N:C ratio (purple line), C allocation (blue line), or leaf N:C and allocation including the effect of root competition (green line) or not (red line).

The inability of the model with fixed root:foliage ratio to match observed allocation patterns at the stand level point to the importance of flexible allocation in forest modeling, not only for growth of different organs but also for GPP (Fig. 1). The global level analysis suggest that this conclusion is relevant also for global modeling of GPP by showing a large effect of allocation optimization on the GPP response to a global latitudinal environmental gradient (Fig. 2). We suggest that applying evolution-based optimization principles to account for allocation plasticity should be a priority measure to improve future forest models and DGVMs, whereas plasticity in N:C ratios and root competition are of secondary importance.

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