

Increased forest carbon storage with increased atmospheric CO₂ despite nitrogen limitation: a game-theoretic allocation model for trees in competition for nitrogen and light

RAY DYBZINSKI, CAROLINE E. FARRIOR and STEPHEN W. PACALA

Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ 08544, USA

Abstract

Changes in resource availability often cause competitively driven changes in tree allocation to foliage, wood, and fine roots, either via plastic changes within individuals or through turnover of individuals with differing strategies. Here, we investigate how optimally competitive tree allocation should change in response to elevated atmospheric CO₂ along a gradient of nitrogen and light availability, together with how those changes should affect carbon storage in living biomass. We present a physiologically-based forest model that includes the primary functions of wood and nitrogen. From a tree's perspective, wood is an offensive and defensive weapon used against neighbors in competition for light. From a biogeochemical perspective, wood is the primary living reservoir of stored carbon. Nitrogen constitutes a tree's photosynthetic machinery and the support systems for that machinery, and its limited availability thus reduces a tree's ability to fix carbon. This model has been previously successful in predicting allocation to foliage, wood, and fine roots along natural productivity gradients. Using game theory, we solve the model for competitively optimal foliage, wood, and fine root allocation strategies for trees in competition for nitrogen and light as a function of CO₂ and nitrogen mineralization rate. Instead of down-regulating under nitrogen limitation, carbon storage under elevated CO₂ relative to carbon storage at ambient CO₂ is approximately independent of the nitrogen mineralization rate. This surprising prediction is a consequence of both increased competition for nitrogen driving increased fine root biomass and increased competition for light driving increased allocation to wood under elevated CO₂.

Keywords: carbon storage, competition, elevated CO₂, evolutionarily stable strategy, game theory, nitrogen limitation, tragedy of the commons, wood

Received 10 October 2013; revised version received 26 June 2014 and accepted 22 September 2014

Introduction

The leaf-level effects of elevated CO₂ (eCO₂) on photosynthesis are relatively well understood: Net photosynthetic rates increase as a consequence of increased carboxylation and decreased photorespiration, and water use efficiency improves because plants can take in a greater amount of CO₂ for the same water loss (Drake *et al.*, 1997; Long *et al.*, 2004; Ainsworth & Long, 2005). However, these leaf-level responses do not necessarily translate to ecosystem-level increases in net primary production (NPP) or carbon storage because changes in physiology, photosynthate allocation, or nutrient availability can offset or limit them (Millard *et al.*, 2007; Norby *et al.*, 2010; Norby & Zak, 2011). Nevertheless, we do know that the terrestrial biosphere has taken up and stored a significant fraction of the CO₂ already emitted from fossil fuel burning and

deforestation (Houghton, 2007), partly due to secondary forests that are far from dynamic equilibrium and partly due to intact forests that are approximately in dynamic equilibrium (Bonan, 2008; Lewis *et al.*, 2009; Phillips *et al.*, 2009; Pan *et al.*, 2011; but see Wright, 2013).

Increased carbon storage in secondary forests is relatively well understood. As forests recover from disturbance, wood biomass and carbon storage increase until they reach a dynamic equilibrium in which recruitment and growth are balanced by mortality. In contrast, increased carbon storage in intact forests (or forests where growth and mortality are in dynamic equilibrium) depends on trees' downstream responses to eCO₂, which are poorly understood, against a potentially changing backdrop of other global change factors. Moreover, the baseline carbon accumulation of secondary forests will adjust up or down depending on trees' downstream responses to eCO₂. Thus, articulating the mechanisms by which trees allocate carbon under eCO₂ is critical to understanding how and why such carbon storage occurs and whether it will persist.

Correspondence: Ray Dybzinski, tel. 1-773-760-4092, fax 1-609-258-1712, e-mail: rdybzins@princeton.edu

Carbon stored in living biomass in a forest in dynamic equilibrium can be expressed as the average net primary productivity of carbon (NPP) multiplied by the average residence time of that carbon in living biomass (τ):

$$\text{storage}_{\text{baseline}} = \tau_{\text{baseline}} \text{NPP}_{\text{baseline}}. \quad (1)$$

After a onetime permanent increase in CO_2 , be it gradual or abrupt, the forest comes to a new equilibrium, and the new 'elevated' carbon storage may be expressed as perturbations of these baseline components:

$$\text{storage}_{\text{elevated}} = (1 + \alpha)\tau_{\text{baseline}}(1 + \beta)\text{NPP}_{\text{baseline}}, \quad (2)$$

where α is the additional (or if negative, reduced) carbon residence time under eCO_2 above baseline, and β is the additional (or if negative, reduced) NPP under eCO_2 above baseline.

The change in carbon storage under eCO_2 (i.e. the carbon sink if positive or source if negative) is the difference between these two equations:

$$\text{storage}_{\text{difference}} = (\alpha\beta + \alpha + \beta)\tau_{\text{baseline}}\text{NPP}_{\text{baseline}}. \quad (3)$$

This expression clarifies a potential source of confusion about the meaning of the phrase 'nitrogen limitation of the carbon sink'. Nitrogen limitation will tend to limit the *enhancement* of storage under eCO_2 , [$\text{storage}_{\text{difference}}$, Eqn (3)] because it limits *current* carbon storage [$\tau_{\text{baseline}} \text{NPP}_{\text{baseline}}$, Eqn (1)]. But this effect is not the focus of most of the literature on nitrogen limitation of the carbon sink because measurements of current carbon storage would already allow prediction of $\text{storage}_{\text{difference}}$ if α and β were known with confidence. Instead, the critical unknowns are about the magnitudes and signs of α and β when nitrogen is limiting. A metric that better isolates these issues is:

$$\text{storage}_{\text{ratio}} = \frac{\text{storage}_{\text{elevated}}}{\text{storage}_{\text{baseline}}} = 1 + \alpha\beta + \alpha + \beta. \quad (4)$$

Here, we investigate how α , β , and thus $\text{storage}_{\text{ratio}}$ are predicted to change along a gradient of nitrogen availability under conditions of nitrogen and light limitation.

Although hypotheses regarding eCO_2 's effect on carbon residence time in living biomass (α) under nitrogen limitation appear to be absent from the literature, two hypotheses exist regarding eCO_2 's effect on NPP (β) under nitrogen limitation: Progressive Nitrogen Limitation (PNL) and down-regulation under stoichiometric constraints. PNL states that decreased N : C of plant tissues under eCO_2 will slow decomposition of organic matter and increase the amount of nitrogen sequestered in living and dead organic matter. With more of the

nitrogen in the system sequestered, the nitrogen mineralization rate will decrease. With a lower nitrogen mineralization rate, NPP and thus β will decline (Luo *et al.*, 2004). Despite its logical appeal, empirical support for PNL is limited. Declines in NPP and biomass growth reported in the later years of the Oak Ridge FACE may have been caused by litter feedbacks, but these cannot be attributed to eCO_2 alone because they also occurred in the aCO_2 controls (see Figs 1 and 4b in Norby *et al.*, 2010). Also, there was no evidence of a decline in nitrogen availability or uptake in any other forest FACE experiment (Norby & Iversen, 2006; Zak *et al.*, 2007; Norby & Zak, 2011). In their review of forest FACE experiments, Norby & Zak (2011) write: 'Although the forests were N limited, NPP remained enhanced in eCO_2 , and there was no indication of diminished N availability or uptake (Norby & Iversen, 2006; Zak *et al.*, 2007)'.

Also logically appealing, down-regulation under stoichiometric constraints recognizes that plant growth requires not just carbon, but also nutrients that are functionally paired with carbon. The idea is that if the nutrients available for growth are insufficient to stoichiometrically balance the carbon allocated toward growth, the plant must down-regulate its carbon economy. In an influential paper, Hungate *et al.* (2003) assumed a fixed stoichiometry between carbon and nitrogen for whole trees, wood, and/or soils and calculated the additional nitrogen that would be required to match model predictions of carbon storage that had originally been made without regard to nitrogen. Almost without exception, the additional nitrogen required to balance the stoichiometry far exceeded even the authors' most liberal estimates of increased nitrogen supply, suggesting that the nitrogen-free models exaggerate the terrestrial biosphere's future potential carbon storage. Using similar methodologies, others have reached the same conclusion (Wang & Houlton, 2009; Peñuelas *et al.*, 2013).

However, empirical evidence that trees will cap carbon gain at a given site under eCO_2 to match available N is limited. In their review of forest FACE experiments, Norby & Zak (2011) write: '...conclusions based on a simplistic invocation of Liebig's Law of the Minimum do not hold: Controlled environment experiments demonstrated that N deficiency does not preclude a growth response to eCO_2 '. Any combination of three mechanisms may account for this. First, with more carbon under eCO_2 , trees may be able to take up more nitrogen. Nutrient budget analyses suggest that trees in several forest FACE sites increased nitrogen uptake under eCO_2 (Finzi *et al.*, 2007), and evidence from Duke FACE suggests that eCO_2 caused a small, but potentially critical increase in the nitrogen mineralization rate

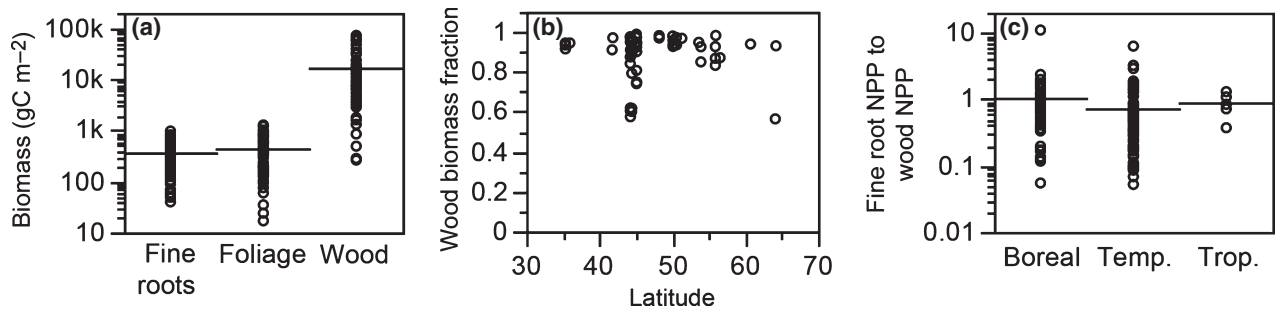


Fig. 1 Biomass and NPP data from forests plots in the FluxNet global network (Luyssaert *et al.*, 2007) demonstrating (a) that wood biomass ($n = 65$) is on average much greater (one-way ANOVA on \log_{10} -transformed data, $P < 0.0001$) than either fine root biomass ($n = 89$) or foliar biomass ($n = 87$); (b) that the fraction of biomass in wood remains high across a latitudinal gradient ($n = 65$); and (c) that the ratio of fine root NPP to wood NPP varies greatly within biomes (boreal $n = 45$, temperate = 88, tropical = 5). Wood here and in the model is taken as the sum of branches, stem, and coarse roots. Lines in (a) and (c) represent means.

as a result of increased microbial activity spurred by increased root exudation (Phillips *et al.*, 2011). Second, trees may change their whole-plant N : C by changing their allocation strategy under $e\text{CO}_2$, as they often do when carbon productivity changes relative to nitrogen availability, e.g. when individuals move from shade to sun or the reverse (Naidu & Delucia, 1997; Ammer, 2003). Relatively small changes in foliage–wood–fine root allocation can dramatically affect the whole-plant N : C of new production because the N : C of wood is an order of magnitude smaller than that of leaves (Zhang *et al.*, 2010). This is consistent with findings that leaf biomass (a nitrogen-rich tissue) remained relatively constant while wood biomass increased in forest FACE experiments (Percy *et al.*, 2002; Norby *et al.*, 2005; Liberloo *et al.*, 2009; McCarthy *et al.*, 2010). Such changes in allocation may also occur via species replacement; within biomes, forests exhibit a large range of relative allocation between fine roots and wood (Fig. 1c). Third, trees may alter the N : C of tissues themselves when provided with more carbon. There exists substantial within- and between-species variation in N : C of foliage, wood, and – especially – fine roots (Kattge *et al.*, 2011). A meta-analysis of CO_2 fertilization experiments, including the FACE sites, found that forest tree species are more flexible in their ability to decrease the N : C of individual tissues in response to $e\text{CO}_2$ than are other ecosystem types (Luo *et al.*, 2006). Meta-analysis also showed that root N : C decreased significantly in FACE studies (Luo *et al.*, 2006; Nie *et al.*, 2013). Again, such changes in tissue N : C may also occur via species replacement.

Franklin *et al.* (2009) modeled the first mechanism, that forests may increase nitrogen uptake under $e\text{CO}_2$. Here, we examine the possibility of avoiding down-regulation under stoichiometric constraints by focusing on the latter two mechanisms: changes in whole-plant N : C via allocational changes and changes in

within-tissue N : C. A defining feature of our approach is that we treat wood not merely as a repository for carbon, but as an active organ that is used in height-structured competition for light (McMurtrie & Dewar, 2013). Height growth evolved in plants as a means to shade neighbors and to avoid being shaded in turn (Givnish, 1982, 1985; Tilman, 1988; Falster & Westoby, 2003; McNickle & Dybzinski, 2013). Trees in closed-canopy forests ceaselessly jockey for light via crown plasticity and height growth that roughly scales as diameter growth over the square root of diameter (Purves *et al.*, 2008). The competitive race for light *appears* to slow once a tree attains the canopy, but it is *never* over. Indeed, a recent global analysis shows that, on average, trees accelerate their carbon accumulation as they increase in size (Stephenson *et al.*, 2014). An individual that fails to at least keep pace with its neighbors will be overtopped (Vandermeer & De La Cerda, 2004) and suffer dramatically reduced survivorship, growth, and fecundity. This dynamic is the basis of the well-established self-thinning law, which may remain in effect even in century-old stands (Pretzsch, 2006). Allocation to wood is also significant from a biogeochemical perspective because the residence time of carbon in wood is between one and three orders of magnitude greater than it is in fine roots, foliage, or seeds (Zhang *et al.*, 2010). Because of this, the overwhelming majority of carbon in living biomass in forests is in wood (Fig. 1).

Here, we ask how increased productivity caused by $e\text{CO}_2$ will alter strategies of the most competitive trees for light and nitrogen in the physiological- and individual-based model originally presented in Dybzinski *et al.* (2011), which predicts allocation to foliage, wood, and fine roots for a stand in dynamic equilibrium (foliage and fine root production balance losses and wood production balances tree mortality). Dybzinski *et al.* (2011) parameterized the model with fine-scale data (i.e. physiological, biogeochemical, and allometric data) and

successfully predicted carbon allocation to foliage, wood, and fine roots along productivity gradients in completely independent global data from FluxNet (Luysaert *et al.*, 2007) and Santantonio (1989). This makes the model a promising candidate for successfully predicting changes in allocation due to eCO₂. The analysis is game-theoretic (Geritz *et al.*, 1998; McGill & Brown, 2007; McNickle & Dybzinski, 2013) because the optimal allocation is determined not by maximizing stand-level growth rates, but by maximizing lifetime reproductive success (i.e. fitness) of a resident relative to all other potential strategies in the environment it creates. A general conclusion from this work is that creating such competitive environments entails substantially greater height growth and root proliferation than would be expected under noncompetitive evolution (Falster & Westoby, 2003; Craine, 2006; McNickle & Dybzinski, 2013). Moreover, such physiologically based game-theoretic analyses, which synthesize the sometimes contrary influences of physiological optimality and competitive optimality, can generate nonintuitive predictions. For example, Farris *et al.* (2013b) presented a game-theoretic model of plant competition for nitrogen and water and found that under some conditions, increasing water availability should, contrary to classic theory, increase fine root allocation to maintain competitive parity. This surprising prediction was confirmed by a grassland resource addition experiment (Farris *et al.*, 2013b). In recognition that similar surprises may lurk elsewhere, we investigate how a physiologically based game-theoretic analysis of an allocation model is influenced by atmospheric CO₂ concentration under conditions of nitrogen limitation.

Materials and methods

Model overview – the Dybzinski et al. (2011) model

In Appendix S1, we describe and analyze a slightly modified version of the model originally presented in Dybzinski *et al.* (2011), which is an extension of the Perfect Plasticity Assumption (PPA) model of forest population dynamics described in its most general form in Strigul *et al.* (2008). The model of Dybzinski *et al.* (2011) includes the carbon and nitrogen budgets of individual trees, where carbon fixed by photosynthesis or nitrogen taken up by fine roots is equal to the sum of organ-level expenditures (see Eqns S3 and S4 in Appendix S1). Individuals' carbon and nitrogen budgets are scaled by their projected crown areas, which are allometrically related to their wood NPP, diameter growth rates, and height growth rates (see Eqns G27–G31, G1, and G2 in Dybzinski *et al.*, 2011). We have shown elsewhere that for a given canopy status, foliage, wood, and fine root allocation per unit crown area are approximately independent of size and that the approximation becomes excellent for canopy-sized trees (Dybzinski *et al.*,

2011; Eqns G27–G30). Thus, although we describe carbon and nitrogen pools on a mass per area-basis and fluxes on a mass per area per time-basis, the model correctly attributes these measures to individuals. Fitness is calculated by integrating reproductive output over the lifetime of a canopy individual, from the time it attains canopy status to its death (see Eqns G34–G37 in Dybzinski *et al.*, 2011). Reproductive output is assumed to be constant per unit projected crown area, but because a tree that grows faster (or slower) than its neighbors will achieve greater (or lesser) projected crown area over its lifetime, it will realize greater (or lesser) lifetime reproductive success (i.e. fitness), all else equal (Eqn G37 in Dybzinski *et al.*, 2011).

Trees compete for nitrogen according to their *relative* ability to capture nitrogen via diffusion or mass flow. Thus, trees with the same fine root biomass per unit crown area and fine root nitrogen concentration (i.e. no relative difference) will capture the same nitrogen per unit crown area regardless of the absolute values of those traits. Only relative differences in those traits will lead to differential nitrogen capture. We assert that this is approximately true for fine root biomass and area that is sufficiently large to prevent leaching of available nitrogen (see Dybzinski *et al.*, 2011 Appendix G), and this assertion is supported by research that shows that the root biomass typical of forests (and thus of our model) is more than sufficient to prevent substantive leaching (Hedin *et al.*, 1995; Perakis *et al.*, 2005; Craine, 2006; Gerber & Brookshire, 2014). Put another way, the dominant fine root biomass should be that which is either physiologically optimal or competitively optimal, whichever is higher, and the evidence suggests that the competitively optimal fine root biomass is higher. However, we note that this does not take into account potential rhizosphere priming effects, which may well increase with absolute measures of root biomass. Finally, trees are light-limited because of self-shading through their crowns.

Although we derive it as an approximation from a full nitrogen cycling model (see Dybzinski *et al.*, 2011, Appendix G), the model's nitrogen mineralization rate is assumed to be independent of the model's state variables at any point along the nitrogen mineralization gradient, a consequence of balanced inputs and outputs for a stand in dynamic equilibrium. However, eCO₂ introduces a perturbation such that the balance of inputs and outputs may change for a given stand as compared to its balance under aCO₂. Specifically, greater storage of nitrogen in wood under eCO₂ may slow the rate of return to the soil organic pool of nitrogen, which in turn should decrease the soil organic pool size and thus decrease the nitrogen mineralization rate, all else equal. Although the model presented in the main text does not permit such progressive nitrogen limitation (i.e. the nitrogen mineralization rate is assumed to be constant and not explicitly affected by changes in nitrogen storage in wood), we present a modified model in Appendix S2 that does account for this dynamic. As shown in Appendix S2, including this feedback on the nitrogen mineralization rate causes a quantitative perturbation on the main text model results but no qualitative change.

Model overview – modifications of the Dybzinski et al. (2011) model presented here

The first modification of Dybzinski *et al.* (2011) is that all tissues are given explicit nitrogen concentrations. To keep the model simple enough to yield analytical results, we assume that foliage and stem wood N : C is fixed but that fine root N : C is variable, either between or within species (Pregitzer *et al.*, 2002; Guo *et al.*, 2004; Jia *et al.*, 2011; Nie *et al.*, 2013). Although foliage N : C commonly decreases under eCO₂, most of this change is due to increased nonstructural carbohydrates, especially in trees (Ainsworth & Long, 2005). The model implicitly includes this as an increase in carbon available for growth and respiration under eCO₂ without specifying its location. The nitrogen in fine roots has explicit functions: structural nitrogen (i.e. the nitrogen in cell walls), which is in fixed proportion to fine root carbon, and metabolic nitrogen (i.e. the nitrogen in proteins that, for example, actively transport nitrate and ammonium into the root or that convert it to organic forms). Strategies are defined by two traits responsible for nitrogen acquisition: the strategy's fine root mass, R (scaled as fine root carbon mass per crown area), and the strategy's ratio of metabolic fine root nitrogen to fine root carbon, ρ . Greater values of ρ lead to greater nitrogen uptake rates, all else equal (Lambers *et al.*, 2008).

To investigate the effects of eCO₂ in the photosynthesis model, we impose a onetime permanent increase in CO₂ on the trees. To do this, we only change the leaf-level photosynthetic parameters. Following data from Ainsworth & Long (2005), we impose a 47% increase in the light-saturated net photosynthetic rate and a 12% increase in the quantum yield of photosynthesis. We compare the Evolutionarily Stable Strategy (ESS) under aCO₂ with the ESS under eCO₂ as a function of nitrogen availability, and thus predict how nitrogen limitation affects α , β , and the absolute [Eqn (3)] and relative [Eqn (4)] changes in ecosystem carbon storage caused by CO₂ fertilization.

Model solution

We analyze the model for cases in which the nitrogen mineralization rate is great enough to permit canopy closure against a constant background rate of mortality and yet beneath the threshold of nitrogen saturation, such that any increase in nitrogen availability that we analyze would increase NPP, tree growth rates, and equilibrium carbon storage. The competitively optimal allocation strategy is effectively found by introducing 'challengers' with all possible values of traits into monocultures of 'residents' with all possible values of traits. A resident strategy that resists all challengers (i.e. for which resident fitness is greater than any challenger fitness) and that can be arrived at via successive challenges (i.e. is convergence-stable) is deemed an Evolutionarily Stable Strategy (ESS) (Geritz *et al.*, 1998; McGill & Brown, 2007). Convergence stability is proven analytically for approximate solutions (Appendix S1) and checked numerically for exact solutions (Figure S2 in Appendix S1). It is important to emphasize that the model is agnostic about whether the differences between residents and

challengers arise from plasticity, *in situ* evolution, within-species differences, or between-species differences (McNickle & Dybzinski, 2013).

Appendix S1 contains formulae for computing $R^*(\text{CO}_2, \text{N})$, $\rho^*(\text{CO}_2, \text{N})$, $L^*(\text{CO}_2, \text{N})$, and $W^*(\text{CO}_2, \text{N})$, which are competitively optimal (ESS) values, respectively, of fine root mass (gC m^{-2}), the ratio of metabolic fine root nitrogen to total fine root carbon, one-sided leaf area index ($\text{m}^2 \text{m}^{-2}$), and wood NPP ($\text{g m}^{-2} \text{y}^{-1}$), all written as functions of atmospheric CO₂ and the nitrogen mineralization rate, N ($\text{gN m}^{-2} \text{y}^{-1}$). We present a closed-form solution for $\rho^*(\text{CO}_2, \text{N})$ in general (Eqn S18 in Appendix S1) and close approximations to the other ESSs. The approximations rely on the fact that structural fine root nitrogen and stem wood nitrogen represent a small fraction of a tree's annual nitrogen budget (Eqns S36, S38 in Appendix S1). Exact solutions for $R^*(\text{CO}_2, \text{N})$, $L^*(\text{CO}_2, \text{N})$, and $W^*(\text{CO}_2, \text{N})$ are found by solving Eqn (S34) in Appendix S1 numerically and were used to generate all figures. Except where new parameters have been introduced to deal with explicit nitrogen pools or where existing parameter values have been adjusted for the effects of eCO₂ on photosynthesis, all parameter values follow those of Dybzinski *et al.* (2011) and are given again in Appendix S1.

To predict the future behavior of the sink, we convert the annual ESS wood production, $W^*(\text{CO}_2, \text{N})$, into the total density of living wood carbon by dividing $W^*(\text{CO}_2, \text{N})$ by the mean canopy tree mortality rate (assumed to be 0.013 yr^{-1}) or, equivalently, by multiplying $W^*(\text{CO}_2, \text{N})$ by the mean residence time of carbon in living wood (assumed to be 77 year) (Farrior *et al.*, 2013a; Appendix A). We add to this the standing carbon per unit area in foliage and fine roots, $ML^*(\text{CO}_2, \text{N})$, and $R^*(\text{CO}_2, \text{N})$ respectively, where M is leaf mass per area. The sum of these three terms, together with a small, constant NPP associated with fecundity that turns over yearly, gives the total density of living carbon (gC m^{-2}) at equilibrium. This is calculated for the baseline CO₂, giving storage_{baseline} from Eqn (1) and for eCO₂, giving storage_{elevated} from Eqn (2). Carbon residence time is calculated as storage divided by NPP.

Results

Competitive organ-level responses to nitrogen and eCO₂

Consistent with Dybzinski *et al.* (2011), predicted foliage NPP and wood NPP increase (Fig. 2a and c) and predicted fine root NPP decreases (Fig. 2e) with increasing net nitrogen mineralization rate (N), irrespective of CO₂ concentration. Foliage NPP increases with N because construction of the photosynthetic machinery is stoichiometrically constrained by nitrogen availability and because carbon capture is proportional to foliage investment. Up to the point of nitrogen saturation, competitive trees invest as much nitrogen in foliage as they can without compromising physiological function elsewhere. Wood NPP increases with N both

because of the greater carbon revenue (due to the greater foliage NPP) and because relatively more carbon is available from decreased fine root allocation.

The explanation for why fine root NPP decreases with N is more nuanced. The optimal allocation to fine roots for a tree growing in isolation with no evolutionary history of competition (contra-reality) would be the minimum amount necessary to prevent leaching of nitrogen. Assuming no leaching of nitrogen, as we do here for simplicity, such an isolated tree could maximize its wood growth with miniscule fine root investment. At the stand level, such a strategy would be easily outcompeted by one with greater fine root investment, which in turn would be outcompeted by another with even greater fine root investment, and so on. This regress would stop when the resident's fine root NPP is sufficiently high that a challenger with even greater fine root NPP (which would *still* acquire a greater share of nitrogen) would fail to pay for its additional fine root biomass with the extra foliage it was able to build, making it an unsuccessful challenger. This resident would be the competitive dominant (or 'ESS'). Put another way, the competitive dominant's fine root allocation is

such that the marginal cost of additional fine roots is exactly equal to the marginal return of the additional foliage that would be made with the additional N acquired by those additional fine roots. Because the marginal return of additional foliage for a challenger decreases with increasing N due to self-shading, the most competitive fine root NPP also decreases with N .

Under $e\text{CO}_2$, ESS allocation shifts at any given N , though the model makes no statement about how such shifts may be achieved biologically or at what timescale they may occur (we return to this point in the Discussion). Competitively, optimal foliage NPP decreases slightly under $e\text{CO}_2$ (Fig. 2a), balancing the competitive costs and benefits of carbon fixation with the increased nitrogen required for greater wood and fine root NPP under $e\text{CO}_2$ (Fig. 2c and e). These increases represent new competitive optima for light and nitrogen given the increased available photosynthate under $e\text{CO}_2$. The exact same reasoning used above to explain the shift in fine root NPP with N applies here to explain the shift in fine root NPP with $e\text{CO}_2$: the increased carbon allocation to fine roots creates a situation in which a challenger strategy with greater fine root mass, though able

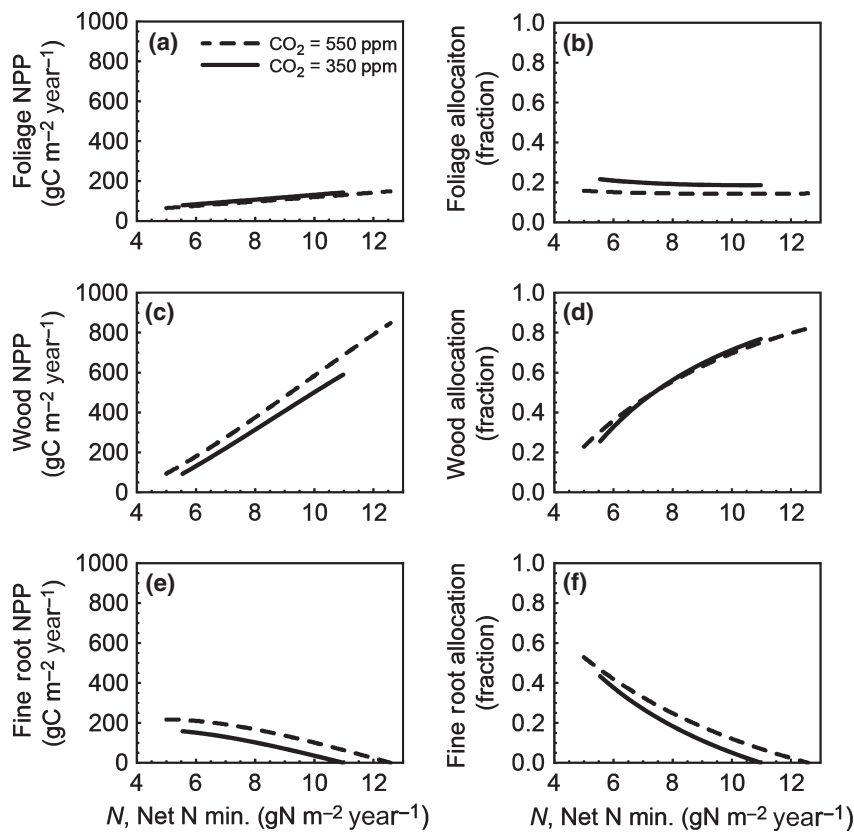


Fig. 2 Predicted competitive organ-level NPP (left-hand panels) and fractional allocation (right-hand panels) at $\text{CO}_2 = 350$ and $\text{CO}_2 = 550$ by net nitrogen mineralization rate. Predictions begin at net nitrogen mineralization rates that permit closed forests composed of ESS individuals and end at net nitrogen mineralization rates that are approximately saturating.

to acquire a greater share of nitrogen, would fail to fix enough carbon with that additional nitrogen to cover the costs of its additional fine roots (Dybzinski *et al.*, 2011). Such a resident can resist invasion by challengers possessing both lesser and greater root mass and is thus the most competitive strategy.

In addition, $e\text{CO}_2$ also extends the range of N over which competitive, nitrogen-limited, closed-canopy forest may persist (Fig. 2). At low N , the transition between open-canopy and closed-canopy forest is determined by the balance between growth rates and mortality rates (Dybzinski *et al.*, 2011). By increasing growth rates against an assumed background of constant mortality, $e\text{CO}_2$ increases the range of closed-canopy forests at low N . Forests transition from nitrogen-limited to nitrogen-saturated when they are able to build enough leaf area that the lowest, most-shaded leaves are just able to pay for themselves (Dybzinski *et al.*, 2011). Thus, by decreasing the light compensation point of photosynthesis and by slightly decreasing foliage NPP at any given N , $e\text{CO}_2$ extends the range over which forests remain nitrogen-limited to higher N .

Because our model does not permit increased nitrogen uptake under $e\text{CO}_2$, all gains in productivity are possible via shifts in whole-plant stoichiometry as a result of changes in allocation (Fig. 2b,d,f) and changes in fine root metabolic nitrogen concentration (Eqn S18 in Appendix S1). Thus, aboveground and belowground C : N (inverse of N : C) increases under $e\text{CO}_2$ (Fig. 3) as trees become relatively more carbon-rich. The predicted relative shifts in C : N are within the range of values reported for within-species shifts in the meta-analysis of the empirical literature in Luo *et al.* (2006). Note that if $e\text{CO}_2$ causes species replacement, the range of possible shifts in C : N is likely to be much larger. The predicted response ratio of aboveground C : N is approximately constant across the N gradient (Fig. 3a), with a slight increase at low N due to the relatively larger fractional increase in wood allocation at low N (Fig. 2d). The predicted response ratio of belowground C : N increases with N (Fig. 3b) primarily as a result of decreasing allocation to fine roots (Fig. 2f) and occurs despite a decrease in fine root C : N with decreasing fine root biomass (Eqn S18 in Appendix S1).

Ecosystem-level responses to $e\text{CO}_2$

Recall that changes in carbon storage under $e\text{CO}_2$ (Eqns 3 and 4) are a function of changes in NPP under $e\text{CO}_2$ (the results of which are summarized above) and of changes in carbon residence time under $e\text{CO}_2$, which depend on fractional allocation to organs with different carbon residence times. Fractional allocation to foliage is largely unaffected by N (Fig. 2b), whereas fractional

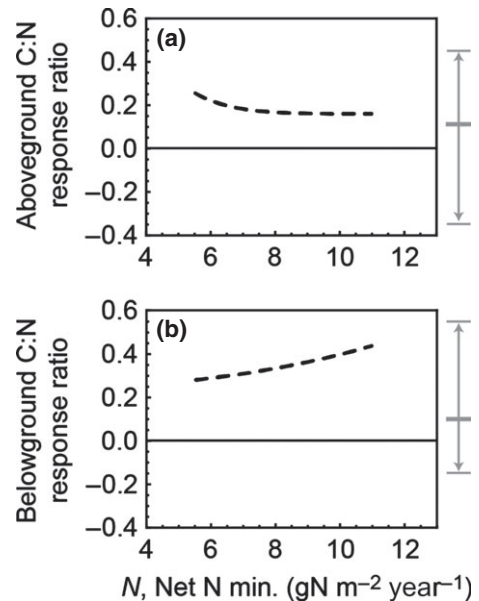


Fig. 3 Predicted changes in aboveground (a) and belowground (b) C : N stoichiometry of new production both due to shifts in allocation among tissues of differing stoichiometries and due to shifts in the metabolic nitrogen concentration of fine roots. Gray bars outside the panels indicate the means (thick lines) and ranges (thin lines) of empirical values for within-species shifts reported in the meta-analysis of Luo *et al.* (2006) (see their Fig. 3). The predicted aboveground C : N at $\text{CO}_2 = 350$ and $\text{CO}_2 = 550$ was calculated as the inverse of the NPP-weighted average of foliage N : C and wood N : C, assuming 75% of wood production is aboveground. The predicted belowground C : N at $\text{CO}_2 = 350$ and $\text{CO}_2 = 550$ was calculated as the inverse of the NPP-weighted average of fine root N : C and wood N : C, assuming 25% of wood production is belowground. The response ratio (vertical axis) was calculated as the difference of the natural log of these predicted values, as in Luo *et al.* (2006).

allocation to wood increases (Fig. 2d) and fractional allocation to fine roots decreases (Fig. 2f) with increasing N . Because $e\text{CO}_2$ increases overall production without appreciably changing foliage NPP, fractional allocation to foliage decreases with $e\text{CO}_2$ (Fig. 2b). In contrast, fractional allocation to fine roots increases under $e\text{CO}_2$ (Fig. 2f). Fractional allocation to wood increases slightly at low N , but decreases slightly at high N under $e\text{CO}_2$ (Fig. 2d).

Under $e\text{CO}_2$, total NPP increases (Fig. 4a), carbon residence time in biomass increases slightly at low nitrogen mineralization rates, but decreases slightly at high nitrogen mineralization rates (Fig. 4c), and carbon storage in biomass increases (Fig. 4e). The increase in total NPP (Fig. 4a) is driven by the leaf-level effects of $e\text{CO}_2$. The shift in carbon residence time in biomass (Fig. 4c) is driven by small shifts in allocation to wood (Fig. 2d), which retains carbon much longer than

foliage or fine roots. As a consequence of these large increases in NPP and the much smaller shifts in carbon residence time, absolute carbon storage in biomass, i.e. $\text{storage}_{\text{difference}}$ [Eqn (3)], increases under $e\text{CO}_2$ and with increasing nitrogen mineralization rate (Fig. 4e).

As expected, baseline NPP (Fig. 4a) increases with increasing nitrogen mineralization rate. However, because the fraction of total LAI made up by light-saturated leaves decreases with increasing LAI and because light-saturated leaves show a larger proportional increase in carbon fixation under $e\text{CO}_2$ compared to light-limited leaves (Ainsworth & Long, 2005), the fraction of enhanced GPP from light-saturated leaves decreases with increasing LAI. Thus, β [Eqn (3)] decreases with increasing nitrogen mineralization rate (Fig. 4b) because LAI increases with increasing nitrogen mineralization rate (Fig. 2a, where LAI is proportional to foliage NPP, Eqn S35 in Appendix S1). Also as expected, baseline carbon residence time (Fig. 4c) increases with increasing nitrogen mineralization rate. However, because the shift in fractional allocation to wood under $e\text{CO}_2$ is greater at low nitrogen mineralization rate as compared to high nitrogen

mineralization rate (Fig. 2d), there is a greater relative increase in carbon residence time under $e\text{CO}_2$ at low nitrogen mineralization rate as compared to high nitrogen mineralization rate [α , Eqn (3)]. Thus, α monotonically declines with increasing nitrogen mineralization rate.

Together, the effects of increased CO_2 on baseline NPP and carbon residence time *increase* with increasing nitrogen mineralization rate (Fig. 4a and c), whereas the α - and β -effects *decrease* with increasing nitrogen mineralization rate (Fig. 4b and d), such that the $\text{storage}_{\text{difference}}$ [Eqn (3)] is less steep across the gradient of nitrogen mineralization rate (Fig. 4f) than it would be otherwise. Consequently, $\text{storage}_{\text{ratio}}$ [Eqn (4)], expressed as the ratio of carbon storage at $\text{CO}_2 = 550$ to carbon storage at $\text{CO}_2 = 350$, actually decreases and plateaus with increasing nitrogen mineralization rate (Fig. 5). Although nitrogen-saturated forests may not retain excess nitrogen (Perakis *et al.*, 2005; Menge *et al.*, 2009), it is worth noting that if they do, $\text{Storage}_{\text{ratio}}$ will increase with increasing nitrogen mineralization rate in the region beyond which forests are currently nitrogen-saturated (e.g. beyond $N = 11 \text{ gN m}^{-2} \text{ yr}^{-1}$ in Fig. 5).

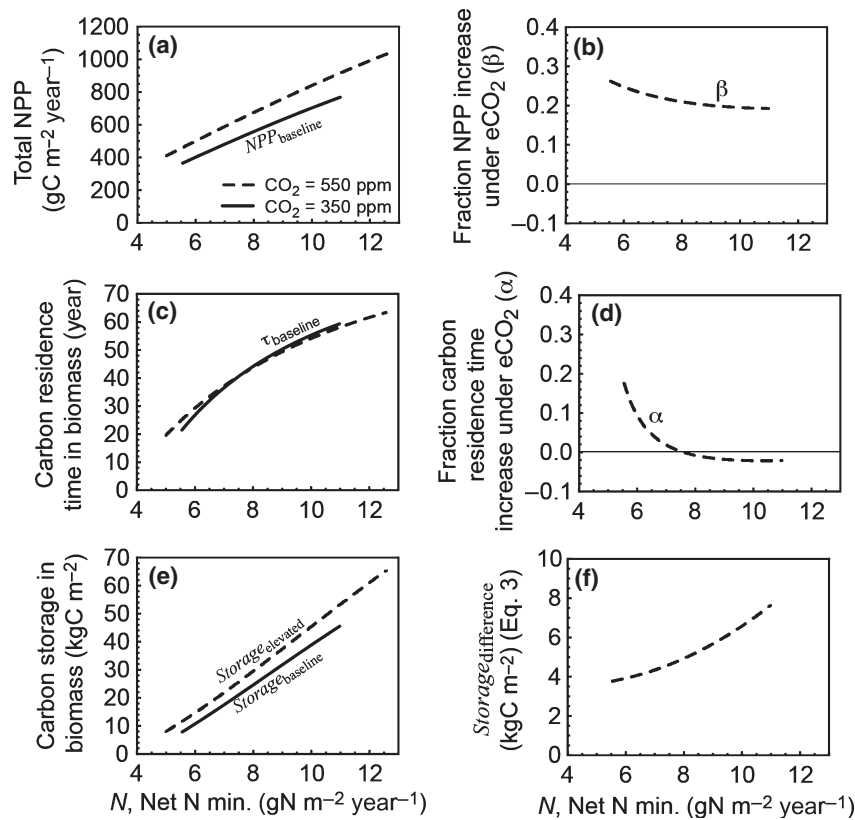


Fig. 4 Predicted summary biogeochemical responses of NPP (a), β (b), carbon residence time (c), α (d), storage (e), and storage difference (f) at $\text{CO}_2 = 350$ and $\text{CO}_2 = 550$ as a function of the nitrogen mineralization rate. The definitions of $\text{NPP}_{\text{baseline}}$, τ_{baseline} , $\text{storage}_{\text{baseline}}$, $\text{storage}_{\text{elevated}}$, α , β , and $\text{storage}_{\text{difference}}$ can be found in Eqns (1)–(3) and the surrounding text. See Appendix S1 for model details.

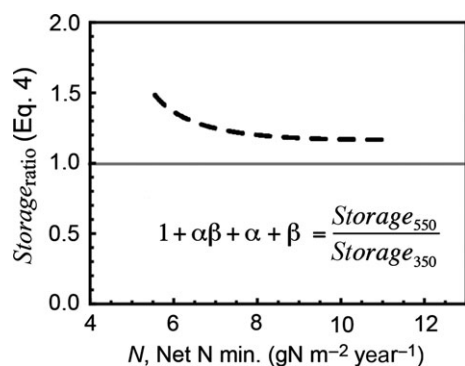


Fig. 5 The relative increase in carbon storage, i.e. $\text{storage}_{\text{ratio}}$ [Eqn (4)], as a function of the nitrogen mineralization rate. Figures of α and β are included in Fig. 4.

This is because $e\text{CO}_2$ raises the threshold for nitrogen saturation and thus ecosystem responsiveness to increasing nitrogen availability (compare the limits of nitrogen saturation under $a\text{CO}_2$ and $e\text{CO}_2$ in Fig. 2).

Down-regulation under stoichiometric constraints

Appendix S1 contains an analysis in which we show that down-regulation of carbon fixation is never a competitive optimum in our model. Trees at an ESS use all the carbon and nitrogen they harvest. The analysis introduces a down-regulation parameter that allows a tree to decrease its gross carbon gain by decreasing its foliage investment. With less carbon than its neighbors, a tree is forced to reduce either its wood production or its fine root production. Reduced wood production decreases its ability to overtop neighbors and puts it at risk of being overtopped itself, and reduced fine root production decreases its nitrogen uptake relative to that of its neighbors. Thus, we show that the competitively optimal solution is no down-regulation at all. The same result holds if down-regulation simply decreases carbon gain without decreasing foliage investment. In our model, trees use the extra carbon under $e\text{CO}_2$ without additional nitrogen by shifting allocation among tissues (which vary in their stoichiometries, Eqn S34 in Appendix S1) and by adjusting fine root metabolic nitrogen concentration (Eqn S18 in Appendix S1), which together serve to decrease whole-plant N : C (or, equivalently, increase whole-plant C : N, Fig. 3). Note that the analysis does not admit the possibility of allocating carbon to nonstructural or nonrespiratory processes, such as rhizosphere exudates.

Discussion

Understanding the consequences of elevated atmospheric CO_2 on the world's carbon-storing forests in the

face of pervasive nutrient limitation is a critical research goal (Norby & Zak, 2011). Here, we model tree allocation from a competitive perspective, whereby wood serves first and foremost as an offensive and defensive weapon in height competition but whose carbon allocation must trade-off with equally critical allocation to fine roots for nitrogen competition and foliage for carbon fixation. Such game-theoretic models can have surprising, nonintuitive predictions, and many of these have been supported empirically (Gersani *et al.*, 2001; Craine, 2006; Farris *et al.*, 2013b). As may have been expected, the absolute increase in carbon storage under $e\text{CO}_2$, $\text{storage}_{\text{difference}}$ [Eqn (3)], is predicted to increase as nitrogen becomes less limiting (Fig. 4f) simply because baseline NPP and carbon residence time increase as nitrogen becomes less limiting (Fig. 4a and c). However, the more interesting and surprising result is that the relative increase in stand-level carbon storage under $e\text{CO}_2$, $\text{storage}_{\text{ratio}}$ [Eqn (4)], is predicted to be approximately independent of nitrogen limitation (Fig. 5). Given our parameterization, $\text{storage}_{\text{ratio}}$ is predicted to actually increase as nitrogen becomes more limiting. Our results also show that trees that down-regulate their carbon fixation are not favored. As in other 'goal oriented' models, our modeled trees can avoid such down-regulation by shifting allocation among tissues of differing stoichiometry and/or by adjusting tissue-level stoichiometry. However, the reason for avoiding down-regulation is biologically motivated by a competition-based or game-theoretic analysis: any strategy in a closed-canopy, nitrogen-limited forest that forgoes carbon or nitrogen will always be outcompeted by a strategy that uses all of the nitrogen and carbon that it can acquire. This occurs despite simultaneous nitrogen- and light limitation in all the cases we consider. We note that our model does not consider rhizosphere priming (Cheng *et al.*, 2014), which has the potential to increase a tree's nitrogen uptake rate at the expense of carbon for organ allocation. Thus, rhizosphere priming may manifest as organ-level down-regulation that is still competitively optimal.

Model predictions and empirical data

The model predicts competitive strategies that are consistent with many of the results from forest FACE experiments (Norby & Zak, 2011). With the exception of the later years at ORNL FACE (Norby *et al.*, 2010), forest FACE sites with both open and closed canopies showed comparable increases in NPP under $e\text{CO}_2$ (~23%), which is approximately the level expected from a simple, unlimited extrapolation of the biochemistry of photosynthesis (Norby *et al.*, 2005). Our model predicts

a comparable 20–26% increase across the entire range of nitrogen limitation (Fig. 4b). Leaf area index (LAI) generally increased in stands with open and expanding canopies (Norby *et al.*, 2005). Sites with closed canopies had higher LAI than those with open canopies, but LAI in closed sites was generally unaffected by eCO₂. Similarly, our model of closed-canopy forests predicts that LAI should remain approximately constant under eCO₂ (Fig. 2a, where $LAI \propto NPP$ in the model, Eqn S35 in Appendix S1). Wood increment increased in all forest FACE experiments under eCO₂ (Percy *et al.*, 2002; Norby *et al.*, 2005; Liberloo *et al.*, 2009; McCarthy *et al.*, 2010), and fine root production and/or standing fine root biomass increased under eCO₂ in most forest FACE sites (Lukac *et al.*, 2003; Pregitzer *et al.*, 2008; Jackson *et al.*, 2009; Iversen *et al.*, 2012; Nie *et al.*, 2013; Smith *et al.*, 2013a). Similarly, our model predicts increases in both wood and fine root production (Fig. 2c and e), and the model's predicted decrease in fine root biomass (where biomass is proportional to production in the model, Eqn S35 in Appendix S1) with increasing nitrogen availability is consistent with forest FACE responses to nitrogen addition (Jackson *et al.*, 2009 see their Fig. 5).

Nevertheless, such qualitative agreement of the model predictions with results from forest FACE experiments must be viewed with caution for at least three reasons. First, there are several relevant processes that are not included in the model, including rhizosphere priming (Phillips *et al.*, 2011), herbivory (Knepp *et al.*, 2005), and nonstructural carbohydrate pools (Handa *et al.*, 2005), and numerous processes that are included are held constant under eCO₂, such as reproductive allocation (Ladeau & Clark, 2006), foliage and wood stoichiometry, tissue turnover times, and others. In addition, our analysis takes no account of the quantitative diversity of photosynthetic responses to eCO₂, instead using only the mean response of trees (Ainsworth & Long, 2005). Second, the number of forest FACE sites is small relative to the variability in allocation patterns evidenced by forests around the world (Fig. 1). If, as seems likely, allocational responses to eCO₂ are variable (or are functions of allocation), then the small number of forest FACE sites are unlikely to capture the mean response of the world's forests. Third, only one forest FACE site used old growth forest (Swiss Canopy Crane FACE, e.g. Bader *et al.*, 2013) and that site had no stand-level replication. Other sites used established closed-canopy plantations (Duke FACE and Oak Ridge FACE), while the remaining sites used planted saplings (Rhineland FACE, Bangor FACE) or coppiced saplings (Pop-Euro FACE) (Norby & Zak, 2011; Smith *et al.*, 2013b). Thus, not all model assumptions will have been met by the stands comprising the

forest FACE sites. However, for closed-canopy forests at least, there is evidence to suggest that allocational patterns to foliage, wood, and fine roots are similar in stands of all ages at a given site (Fig. 6g–o), despite large differences in mean tree size (Fig. 6a–c) and stand density (Fig. 6d–f). Thus, our model's allocation predictions, which assume dynamic equilibrium of a stand, may be good approximations for younger closed-canopy stands for which foliage and fine root masses are in dynamic equilibrium, but for which population structure is still far from dynamic equilibrium.

On the other hand, the model results do not explain other experimental eCO₂ work on individual plants. For example, short-term experiments with seedlings and saplings using factorial manipulation of nutrients and CO₂ have found a significant positive effect of nutrient availability on relative (eCO₂/aCO₂) biomass (Curtis & Wang, 1998). In contrast, our model predicts a slightly negative effect of nutrient availability on relative storage (Fig. 5). This may indicate a problem with the model, or it may highlight the difference between the optimal physiological response of a plant growing in isolation vs. the optimal competitive response of a plant growing among competitors (Gersani *et al.*, 2001; Craine, 2006). Other experimental work suggests that severe nitrogen limitation might prevent additional carbon sequestration entirely. Whole-tree chamber experiments in boreal forest showed no effect of eCO₂ on growth without nitrogen amendments (Sigurdsson *et al.*, 2013), and NPP in eCO₂ plots at the ORNL FACE fell back to match controls in the final years of the experiment, presumably due to decreasing nitrogen availability associated with stand development and exacerbated by eCO₂ (Norby *et al.*, 2010).

As explained in detail in Appendix S2, the fact that predicted wood NPP increases under eCO₂ (Fig. 2c) causes a predicted increase in nitrogen storage in trees (Figure S3 in Appendix S2). This is nitrogen that, under aCO₂, would have been allocated to foliage or fine roots and thus returned to the soil relatively quickly. Their predicted storage under eCO₂ raises a question: will shifting this stored nitrogen away from the soil pool decrease the net nitrogen mineralization rate, and, if so, will the decreased NPP associated with the lower net nitrogen mineralization rate reduce, negate, or even reverse the carbon storage prediction of the model via progressive nitrogen limitation? To answer this question, we present a modified model in Appendix S2 that includes a soil organic nitrogen pool and a decline in the net nitrogen mineralization rate as the soil organic nitrogen pool decreases (which occurs as trees store more nitrogen in wood under eCO₂). The results indicate that increased nitrogen storage by trees will reduce, but not negate or reverse, the carbon storage

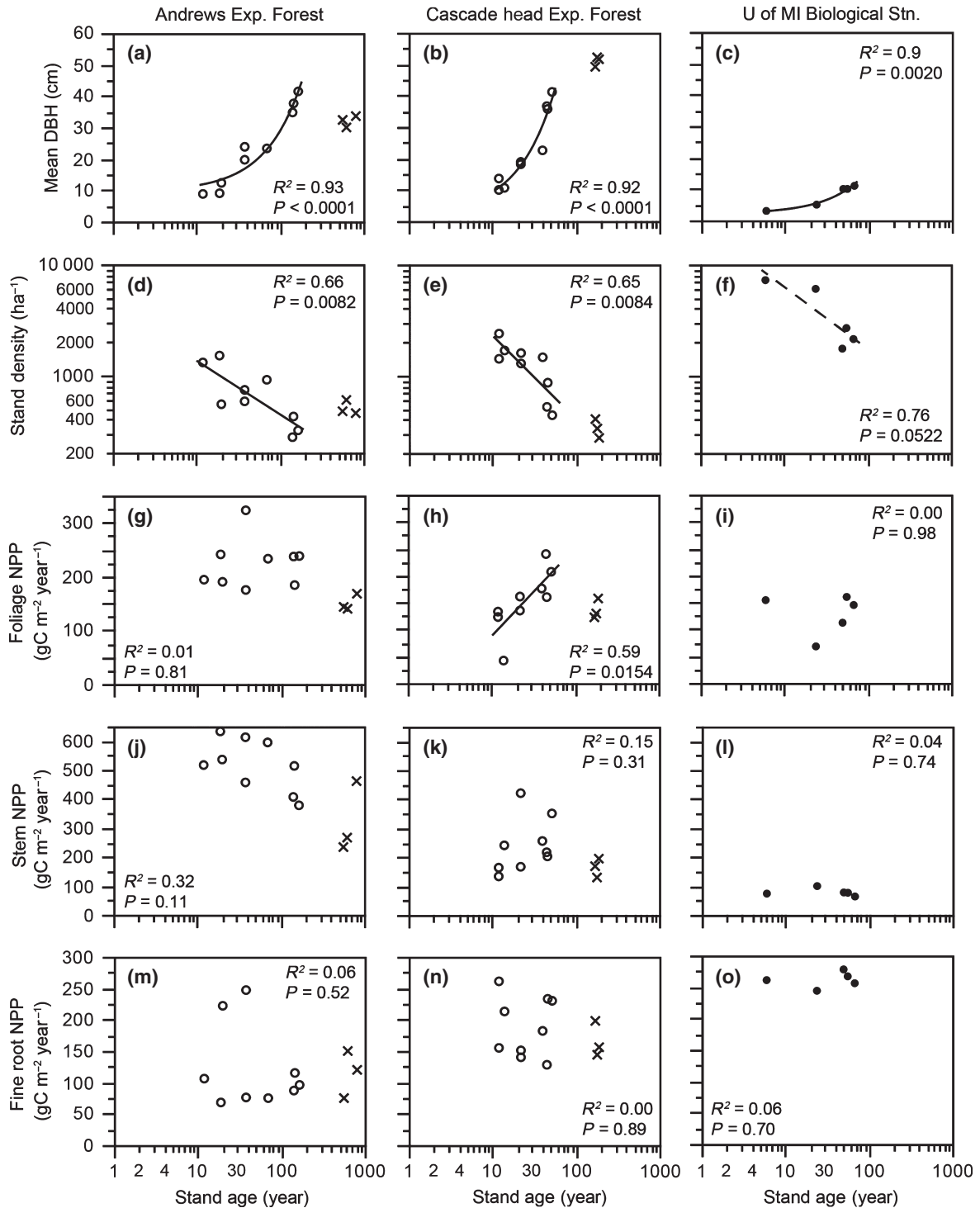


Fig. 6 Mean tree DBH (first row), stand density (second row), and organ NPP (remaining rows) along successional chronosequences at Andrews Experimental Forest (first column), Cascade Head Experimental Forest (second column), and the University of Michigan Biological Station (third column) show that large changes in individual tree size and stand density are accompanied by small or no differences in per-ground-area measures of organ NPP. Data are from the FluxNet global network (Luyssaert *et al.*, 2007). Open circles represent gymnosperm-dominated stands; closed circles represent angiosperm-dominated stands; and crosses represent gymnosperm-dominated old growth stands, which are not included in fits. Including old growth stands in fits changes the significance in two panels: (h) becomes nonsignificant ($R^2 = 0.06$, $P = 0.43$); and (j) becomes significant ($R^2 = 0.54$, $P = 0.0064$). Fits in the first two rows are log-log, and fits to NPP data are log-linear.

predictions of our main text model. The reduction becomes less severe as the fraction of total system nitrogen in trees becomes smaller, and data suggest that this fraction is small (~7%) in extant forests (Figure S4 in Appendix S2).

A competitive mechanism for allocational shifts under eCO₂

There are several hypotheses that have been put forward to explain the observed shifts in allocation of trees exposed to eCO₂ (see below). We add the hypothesis that evolution has favored strategies that not only optimize physiological function in response to eCO₂, but that also maintain competitive dominance in response to eCO₂ by influencing the resource environment and the costs/benefits of different allocation strategies for competitors (Franklin *et al.*, 2012; McNickle & Dybzinski, 2013). Specifically, because the roots of individual trees are comingled (Gilman, 1988; Stone & Kalisz, 1991; Casper *et al.*, 2003; Gottlicher *et al.*, 2008; Jones *et al.*, 2011), trees may 'over-invest' in fine roots relative to physiological necessity such that any unilateral increase in fine roots, which results in a net nutrient and/or water gain, comes at a net carbon cost (Gersani *et al.*, 2001; Craine, 2006; O'Brien *et al.*, 2007; Dybzinski *et al.*, 2011; Farrior *et al.*, 2013a; McNickle & Dybzinski, 2013). In the model, the increased quantum yield of photosynthesis under eCO₂ requires a *greater* 'over-investment' in fine roots to prevent individuals with even greater fine root allocation from benefitting. Note that this mechanism may explain the pervasive increase in fine root biomass observed in FACE experiments without requiring any detectable net benefit, i.e. trees may increase fine root biomass under eCO₂ just to maintain competitive parity.

Similarly, because the race for light is – even for canopy trees – never over (see Introduction), we expect evolution to favor strategies that maximize height and branch growth within the constraints of other tree functions (Givnish, 1982; Falster & Westoby, 2003; McMurtrie & Dewar, 2013; McNickle & Dybzinski, 2013). Wood has much lower nutrient concentrations than other tree organs (Whittaker *et al.*, 1979; Kattge *et al.*, 2011), and although the absolute amount of nutrients in wood may be large, the annual investment of nutrients in wood is relatively small (Whittaker *et al.*, 1979). Even though wood is relatively inexpensive in terms of nutrients, it is critical to an individual's survival and reproduction. Indeed, a unilateral shift in allocation away from wood in an ESS stand in favor of fine roots or foliage may boost an individual's carbon capture in the short term, but because it would be eventually overtopped as a result, it will result in a large net

loss in the long term. Again, the ESS balances the conflicting competitive and physiological demands for carbon and nitrogen allocation to foliage, wood, and fine roots such that any unilateral shift in allocation away from the ESS, be it foliage, wood, or fine roots, will result in lowered fitness.

Existing hypotheses and competitive allocation responses are not mutually exclusive

Other possible explanations for the observed shifts in allocation of trees exposed to eCO₂ focus on the ways in which those shifts may garner more nitrogen at the stand level. Franklin *et al.* (2009) parameterize a whole-stand model of photosynthesis and allocation under nitrogen limitation using data from the Duke and ORNL FACE sites and successfully predict NPP, root production, and growth of multiple plots across multiple years. The key to that success is an assumed phenomenological relationship between increasing fine root production and increasing nitrogen uptake that they fit to the data without actually measuring nitrogen uptake. McMurtrie & Dewar (2013) make a similar assumption in their maximized wood allocation model.

Including a relationship between increasing fine root production or biomass and increasing nitrogen uptake, as these models do, will produce results that are qualitatively similar to those of our model. Specifically, whenever the ratio of nitrogen uptake relative to carbon fixation declines, either due to a decreasing nitrogen mineralization rate or increased carbon fixation (e.g. from eCO₂), the optimal solution will be to increase fine root biomass. This is also true of our own model if we remove competition and allow nitrogen uptake to be a function of absolute root biomass. Franklin *et al.*'s (2009) assumption is supported by the nitrogen and carbon budget analysis of three forest FACE sites (Finzi *et al.*, 2007). Empirical studies have found support for possible mechanistic links between increased fine root production (or biomass) and increased stand-level nitrogen uptake under eCO₂, including increased uptake at depth (Iversen, 2010), increased competitiveness against microbes (Hu *et al.*, 2001), and priming of microbes to induce greater rhizosphere nitrogen mineralization rates (Phillips *et al.*, 2011).

Such explanations complement the explanation put forth here, an explanation that suggests that competition motivates the shifts in allocation of trees exposed to eCO₂ with no net benefit at the stand level. Not only are these two classes of mechanism not mutually exclusive but they also may reinforce one another to the benefit of increased carbon sinks in response to eCO₂. In other words, if trees can increase nitrogen

uptake and make good competitive use of additional carbon at constant nitrogen uptake, then there are two routes to sustaining carbon sinks, both of which avoid down-regulation of carbon fixation. Indeed, the truth may reside at the intersection of these mechanisms, i.e. some degree of changed allocation under eCO₂ may alter resource capture at the stand level and some degree may be strictly competitive with no net benefit at the stand level. Note that models fit to data using only one of these mechanisms would explain the variance due to both mechanisms without giving any indication that there were actually two mechanisms at work. But as in all situations where multiple mechanisms operate in concert, the fit of a single-mechanism model would be unlikely to extrapolate well to other sites and conditions. Moreover, the point of intersection between these two mechanisms may vary with the huge range of factors that characterize and impact forests around the world, and it may change over time if trees exhaust their ability to increase nitrogen uptake rates with greater carbon revenue. Given the range of possibilities, future research that combines the different physiological mechanisms described above within a game-theoretic framework such as the one we present here will likely be fruitful.

Mechanisms by which trees may respond to eCO₂

How might trees 'know' how to respond in a competitively optimal way to eCO₂, as our hypothesis suggests they should? Although there is circumstantial evidence for their existence, there are no identified mechanisms by which plants can directly sense CO₂ concentrations (Sage, 2002), and CO₂ concentrations have been between ~180 ppm and ~280 ppm for at least the last 800 000 years preceding the Industrial Revolution (Tripathi *et al.*, 2009). It therefore seems unreasonable to suspect that the proximate mechanism behind a plastic response of trees to eCO₂ – be it physiologically optimizing, competitively optimizing, or both – is CO₂ concentration itself. Rather, the more likely proximate mechanisms are assessments of physiological performance relative to light availability and the revenues and costs of carbon, water, and soil resources. It may seem foreign to consider these sorts of signals beyond their role in helping a plant maintain physiological optimality, but the ubiquity of seedling responses to crowding (Smith, 1982) and sapling responses to forest gaps (Naidu & Delucia, 1997; Ammer, 2003) provide examples of plastic plant responses that are clearly competitive in nature, and there is evidence that plants may plastically respond in a similar manner below-

ground (McNickle & Dybzinski, 2013). On the other hand, if trees do not harbor sufficient plasticity to remain the competitive dominant under eCO₂ given the environmental conditions in which they are currently established, then we should expect substantial species turnover and/or evolution in the decades and centuries to come as the more competitive strategies colonize and/or leave behind more relatively successful offspring.

Future directions

We have described and analyzed a game-theoretic model of tree competition for nitrogen and light and compared predictions of the most competitive allocation strategies under ambient and elevated atmospheric CO₂. Across a range of nitrogen availability, the most competitive strategies use the greater carbon budget under eCO₂ to increase NPP to wood and fine roots, while reducing fine root nitrogen concentration, to maintain competitive parity belowground for nitrogen and aboveground for light. The net result of these strategic shifts is a predicted increase in carbon storage in trees. It remains to be seen how this prediction will interact with other factors, such as rhizosphere priming (Phillips *et al.*, 2011), optimal leaf stoichiometry and physiology (Dybzinski *et al.*, 2013), and temperature and moisture effects on mineralization (Sokolov *et al.*, 2008; Thornton *et al.*, 2009; Esser *et al.*, 2011). Such processes will affect the magnitude of carbon sequestration in different (and changing) environments because trees competitively allocate carbon and nutrients differently under differing constraints of water, nutrients, light, and CO₂ availability (Franklin *et al.*, 2009; Dybzinski *et al.*, 2011, 2013; Farrior *et al.*, 2013a; McMurtrie & Dewar, 2013). Thus, we suggest that discovering and quantifying multiple resource constraints in a competitive context and the ways that climate change will alter them will yield robust, mechanistically-based predictions of future carbon sequestration.

Acknowledgements

We thank S. Keel, D. Menge, S. Rabin, E. Shefer, E. Shevliakova, Z. Subin, A. Wolf, and our reviewers for greatly improving this paper. We thank all site investigators, their funding agencies, the various regional flux networks [Afriflux, AmeriFlux, AsiaFlux, CarboAfrica, CarboEurope-IP (integrated project), ChinaFlux, Fluxnet-Canada, KoFlux, LBA (Large-Scale Biosphere-Atmosphere Experiment in Amazonia), NECC (Nordic Centre for Studies of Ecosystem Carbon Exchange), OzFlux, TCOS (Terrestrial Carbon Observation System)-Siberia, USCCC (United States-China Carbon Consortium)], and the Fluxnet project for making their data available. We gratefully acknowledge the support of the Princeton Carbon Mitigation Initiative (CMI) and the USDA Forest Service.

References

- Ainsworth EA, Long SP (2005) What have we learned from 15 years of free-air CO₂ enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy. *New Phytologist*, **165**, 351–371.
- Ammer C (2003) Growth and biomass partitioning of *Fagus sylvatica* L. and *Quercus robur* L. seedlings in response to shading and small changes in the R/FR-ratio of radiation. *Annals of Forest Science*, **60**, 163–171.
- Bader MKF, Leuzinger S, Keel SG, Siegwolf RTW, Hagedorn F, Schleppi P, Korner C (2013) Central European hardwood trees in a high-CO₂ future: synthesis of an 8-year forest canopy CO₂ enrichment project. *Journal of Ecology*, **101**, 1509–1519.
- Bonan GB (2008) Forests and climate change: forcings, feedbacks, and the climate benefits of forests. *Science*, **320**, 1444–1449.
- Casper BB, Schenk HJ, Jackson RB (2003) Defining a plant's belowground zone of influence. *Ecology*, **84**, 2313–2321.
- Cheng WX, Parton WJ, Gonzalez-Meler MA *et al.* (2014) Synthesis and modeling perspectives of rhizosphere priming. *New Phytologist*, **201**, 31–44.
- Craine JM (2006) Competition for nutrients and optimal root allocation. *Plant and Soil*, **285**, 171–185.
- Curtis PS, Wang XZ (1998) A meta-analysis of elevated CO₂ effects on woody plant mass, form, and physiology. *Oecologia*, **113**, 299–313.
- Drake BG, Gonzalez-meler MA, Long SP (1997) More efficient plants: a consequence of rising atmospheric CO₂? *Annual Review of Plant Physiology and Plant Molecular Biology*, **48**, 609–639.
- Dybzinski R, Farrior C, Wolf A, Reich PB, Pacala SW (2011) Evolutionarily stable strategy carbon allocation to foliage, wood, and fine roots in trees competing for light and nitrogen: an analytically tractable, individual-based model and quantitative comparisons to data. *American Naturalist*, **177**, 153–166.
- Dybzinski R, Farrior CE, Ollinger S, Pacala SW (2013) Interspecific vs. intraspecific patterns in leaf nitrogen of forest trees across nitrogen availability gradients. *New Phytologist*, **200**, 112–121.
- Esser G, Kattge J, Sakalli A (2011) Feedback of carbon and nitrogen cycles enhances carbon sequestration in the terrestrial biosphere. *Global Change Biology*, **17**, 819–842.
- Falster DS, Westoby M (2003) Plant height and evolutionary games. *Trends in Ecology & Evolution*, **18**, 337–343.
- Farrior CE, Dybzinski R, Levin SA, Pacala SW (2013a) Competition for water and light in closed-canopy forests: a tractable model of carbon allocation with implications for carbon sinks. *American Naturalist*, **181**, 314–330.
- Farrior CE, Tilman D, Dybzinski R, Reich PB, Levin SA, Pacala SW (2013b) Resource limitation in a competitive context determines complex plant responses to experimental resource additions. *Ecology*, **94**, 2505–2517.
- Finzi AC, Norby RJ, Calfapietra C *et al.* (2007) Increases in nitrogen uptake rather than nitrogen-use efficiency support higher rates of temperate forest productivity under elevated CO₂. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 14014–14019.
- Franklin O, McMurtrie RE, Iversen CM *et al.* (2009) Forest fine-root production and nitrogen use under elevated CO₂: contrasting responses in evergreen and deciduous trees explained by a common principle. *Global Change Biology*, **15**, 132–144.
- Franklin O, Johansson J, Dewar RC, Dieckmann U, McMurtrie RE, Brannstrom A, Dybzinski R (2012) Modeling carbon allocation in trees: a search for principles. *Tree Physiology*, **32**, 648–666.
- Gerber S, Brookshire ENJ (2014) Scaling of physical constraints at the root-soil interface to macroscopic patterns of nutrient retention in ecosystems. *American Naturalist*, **183**, 418–430.
- Geritz SAH, Kisdi E, Meszina G, Metz JAJ (1998) Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree. *Evolutionary Ecology*, **12**, 35–57.
- Gersani M, Brown JS, O'Brien EE, Maina GM, Abramsky Z (2001) Tragedy of the commons as a result of root competition. *Journal of Ecology*, **89**, 660–669.
- Gilman EF (1988) Tree root spread in relation to branch dripline and harvestable root ball. *HortScience*, **23**, 351–353.
- Givnish TJ (1982) On the adaptive significance of leaf height in forest herbs. *American Naturalist*, **120**, 353–381.
- Givnish TJ (1985) Plant stems: biomechanical adaptation for energy capture and influence on species distributions. In: *Plant Stems: Physiology and Functional Morphology* (ed Gartner BL), pp. 3–49. Chapman and Hall, New York.
- Gottlicher SG, Taylor AFS, Grip H, Betson NR, Valinger E, Hogberg MN, Hogberg P (2008) The lateral spread of tree root systems in boreal forests: estimates based on N-15 uptake and distribution of sporocarps of ectomycorrhizal fungi. *Forest Ecology and Management*, **255**, 75–81.
- Guo DL, Mitchell RJ, Hendricks JJ (2004) Fine root branch orders respond differentially to carbon source-sink manipulations in a longleaf pine forest. *Oecologia*, **140**, 450–457.
- Handa IT, Korner C, Hattenschwiler S (2005) A test of the tree-line carbon limitation hypothesis by *in situ* CO₂ enrichment and defoliation. *Ecology*, **86**, 1288–1300.
- Hedin LO, Armesto JJ, Johanson AH (1995) Patterns of nutrient loss from unpoluted, old-growth temperate forests: evaluation of biogeochemical theory. *Ecology*, **76**, 493–509.
- Houghton RA (2007) Balancing the global carbon budget. *Annual Review of Earth and Planetary Sciences*, **35**, 313–347.
- Hu S, Chapin FS, Firestone MK, Field CB, Chiariello NR (2001) Nitrogen limitation of microbial decomposition in a grassland under elevated CO₂. *Nature*, **409**, 188–191.
- Hungate BA, Dukes JS, Shaw MR, Luo YQ, Field CB (2003) Nitrogen and climate change. *Science*, **302**, 1512–1513.
- Iversen CM (2010) Digging deeper: fine-root responses to rising atmospheric CO₂ concentration in forested ecosystems. *New Phytologist*, **186**, 346–357.
- Iversen CM, Keller JK, Garten CT, Norby RJ (2012) Soil carbon and nitrogen cycling and storage throughout the soil profile in a sweetgum plantation after 11 years of CO₂-enrichment. *Global Change Biology*, **18**, 1684–1697.
- Jackson RB, Cook CW, Phippen JS, Palmer SM (2009) Increased belowground biomass and soil CO₂ fluxes after a decade of carbon dioxide enrichment in a warm-temperate forest. *Ecology*, **90**, 3352–3366.
- Jia SX, Wang ZQ, Li XP, Zhang XP, McLaughlin NB (2011) Effect of nitrogen fertilizer, root branch order and temperature on respiration and tissue N concentration of fine roots in *Larix gmelinii* and *Fraxinus mandshurica*. *Tree Physiology*, **31**, 718–726.
- Jones FA, Erickson DL, Bernal MA *et al.* (2011) The roots of diversity: below ground species richness and rooting distributions in a tropical forest revealed by DNA barcodes and inverse modeling. *PLoS ONE*, **6**, e24506.
- Kattge J, Diaz S, Lavorel S *et al.* (2011) TRY - a global database of plant traits. *Global Change Biology*, **17**, 2905–2935.
- Knepp RG, Hamilton JG, Mohan JE, Zangerl AR, Berenbaum MR, Delucia EH (2005) Elevated CO₂ reduces leaf damage by insect herbivores in a forest community. *New Phytologist*, **167**, 207–218.
- Ladeau SL, Clark JS (2006) Elevated CO₂ and tree fecundity: the role of tree size, interannual variability, and population heterogeneity. *Global Change Biology*, **12**, 822–833.
- Lambers H, Chapin FS, Pons TL (2008) *Plant Physiological Ecology*. Springer-Verlag, New York.
- Lewis SL, Lopez-Gonzalez G, Sonke B *et al.* (2009) Increasing carbon storage in intact African tropical forests. *Nature*, **457**, U1003–U1003.
- Liberloo M, Lukac M, Calfapietra C *et al.* (2009) Coppicing shifts CO₂ stimulation of poplar productivity to above-ground pools: a synthesis of leaf to stand level results from the POP/EUROFACE experiment. *New Phytologist*, **182**, 331–346.
- Long SP, Ainsworth EA, Rogers A, Ort DR (2004) Rising atmospheric carbon dioxide: plants face the future. *Annual Review of Plant Biology*, **55**, 591–628.
- Lukac M, Calfapietra C, Godbold DL (2003) Production, turnover and mycorrhizal colonization of root systems of three populus species grown under elevated CO₂ (POPFACE). *Global Change Biology*, **9**, 838–848.
- Luo Y, Su B, Currie WS *et al.* (2004) Progressive nitrogen limitation of ecosystem responses to rising atmospheric carbon dioxide. *BioScience*, **54**, 731–739.
- Luo YQ, Hui DF, Zhang DQ (2006) Elevated CO₂ stimulates net accumulations of carbon and nitrogen in land ecosystems: a meta-analysis. *Ecology*, **87**, 53–63.
- Luyssaert S, Inglima I, Jung M *et al.* (2007) CO₂ balance of boreal, temperate, and tropical forests derived from a global database. *Global Change Biology*, **13**, 2509–2537.
- McCarthy HR, Oren R, Johnsen KH *et al.* (2010) Re-assessment of plant carbon dynamics at the Duke free-air CO₂ enrichment site: interactions of atmospheric [CO₂] with nitrogen and water availability over stand development. *New Phytologist*, **185**, 514–528.
- McGill BJ, Brown JS (2007) Evolutionary game theory and adaptive dynamics of continuous traits. *Annual Review of Ecology and Systematics*, **38**, 403–435.
- McMurtrie RE, Dewar RC (2013) New insights into carbon allocation by trees from the hypothesis that annual wood production is maximized. *New Phytologist*, **199**, 981–990.
- McNickle GG, Dybzinski R (2013) Game theory and plant ecology. *Ecology Letters*, **16**, 545–555.
- Menge DNL, Pacala SW, Hedin LO (2009) Emergence and maintenance of nutrient limitation over multiple timescales in terrestrial ecosystems. *American Naturalist*, **173**, 164–175.

- Millard P, Sommerkorn M, Grelet GA (2007) Environmental change and carbon limitation in trees: a biochemical, ecophysiological and ecosystem appraisal. *New Phytologist*, **175**, 11–28.
- Naidu SL, Delucia EH (1997) Growth, allocation and water relations of shade-grown *Quercus rubra* L saplings exposed to a late-season canopy gap. *Annals of Botany*, **80**, 335–344.
- Nie M, Lu M, Bell J, Raut S, Pendall E (2013) Altered root traits due to elevated CO₂: a meta-analysis. *Global Ecology and Biogeography*, **22**, 1095–1105.
- Norby RJ, Iversen CM (2006) Nitrogen uptake, distribution, turnover, and efficiency of use in a CO₂-enriched sweetgum forest. *Ecology*, **87**, 5–14.
- Norby RJ, Zak DR (2011) Ecological lessons from free-air CO₂ enrichment (FACE) experiments. *Annual Review of Ecology, Evolution, and Systematics*, **42**, 181–203.
- Norby RJ, Delucia EH, Gielen B *et al.* (2005) Forest response to elevated CO₂ is conserved across a broad range of productivity. *Proceedings of the National Academy of Sciences of the United States of America*, **102**, 18052–18056.
- Norby RJ, Warren JM, Iversen CM, Medlyn BE, McMurtrie RE (2010) CO₂ enhancement of forest productivity constrained by limited nitrogen availability. *Proceedings of the National Academy of Sciences of the United States of America*, **107**, 19368–19373.
- O'Brien EE, Brown JS, Moll JD (2007) Roots in space: a spatially explicit model for below-ground competition in plants. *Proceedings of the Royal Society B-Biological Sciences*, **274**, 929–934.
- Pan YD, Birdsey RA, Fang JY *et al.* (2011) A large and persistent carbon sink in the world's forests. *Science*, **333**, 988–993.
- Peñuelas J, Poulter B, Sardans J *et al.* (2013) Human-induced nitrogen–phosphorus imbalances alter natural and managed ecosystems across the globe. *Nature Communications*, **4**, 2934.
- Perakis SS, Compton JE, Hedin LO (2005) Nitrogen retention across a gradient of N-15 additions to an unpolluted temperate forest soil in Chile. *Ecology*, **86**, 96–105.
- Percy KE, Awmack CS, Lindroth RL *et al.* (2002) Altered performance of forest pests under atmospheres enriched by CO₂ and O-3. *Nature*, **420**, 403–407.
- Phillips OL, Aragao LEOC, Lewis SL *et al.* (2009) Drought sensitivity of the Amazon rainforest. *Science*, **323**, 1344–1347.
- Phillips RP, Finzi AC, Bernhardt ES (2011) Enhanced root exudation induces microbial feedbacks to N cycling in a pine forest under long-term CO₂ fumigation. *Ecology Letters*, **14**, 187–194.
- Pregitzer KS, DeForest JL, Burton AJ, Allen MF, Ruess RW, Hendrick RL (2002) Fine root architecture of nine North American trees. *Ecological Monographs*, **72**, 293–309.
- Pregitzer KS, Burton AJ, King JS, Zak DR (2008) Soil respiration, root biomass, and root turnover following long-term exposure of northern forests to elevated atmospheric CO₂ and tropospheric O-3. *New Phytologist*, **180**, 153–161.
- Pretzsch H (2006) Species-specific allometric scaling under self-thinning: evidence from long-term plots in forest stands. *Oecologia*, **146**, 572–583.
- Purves DW, Lichstein JW, Strigul N, Pacala SW (2008) Predicting and understanding forest dynamics using a simple tractable model. *Proceedings of the National Academy of Sciences*, **105**, 17018–17022.
- Sage RF (2002) How terrestrial organisms sense, signal, and respond to carbon dioxide. *Integrative and Comparative Biology*, **42**, 469–480.
- Santantonio D (1989) Dry-matter partitioning and fine-root production in forests — new approaches to a difficult problem. In: *Biomass Production by Fast-Growing Trees* (eds Periera JS, Landsberg JJ), pp. 57–72. Netherlands, Kluwer Academic Publishers, Dordrecht.
- Sigurdsson BD, Medhurst JL, Wallin G, Eggertsson O, Linder S (2013) Growth of mature boreal Norway spruce was not affected by elevated [CO₂] and/or air temperature unless nutrient availability was improved. *Tree Physiology*, **33**, 1192–1205.
- Smith H (1982) Light quality, photoperception, and plant strategy. *Annual Review of Plant Physiology and Plant Molecular Biology*, **33**, 481–518.
- Smith AR, Lukac M, Bambrick M, Miglietta F, Godbold DL (2013a) Tree species diversity interacts with elevated CO₂ to induce a greater root system response. *Global Change Biology*, **19**, 217–228.
- Smith AR, Lukac M, Hood R, Healey JR, Miglietta F, Godbold DL (2013b) Elevated CO₂ enrichment induces a differential biomass response in a mixed species temperate forest plantation. *New Phytologist*, **198**, 156–168.
- Sokolov AP, Kicklighter DW, Melillo JM, Felzer BS, Schlosser CA, Cronin TW (2008) Consequences of considering carbon-nitrogen interactions on the feedbacks between climate and the terrestrial carbon cycle. *Journal of Climate*, **21**, 3776–3796.
- Stephenson NL, Das AJ, Condit R *et al.* (2014) Rate of tree carbon accumulation increases continuously with tree size. *Nature*, **507**, 90–93.
- Stone EL, Kalisz PJ (1991) On the maximum extent of tree roots. *Forest Ecology and Management*, **46**, 59–102.
- Strigul N, Pristinski D, Purves D, Dushoff J, Pacala S (2008) Scaling from trees to forests: tractable macroscopic equations for forest dynamics. *Ecological Monographs*, **78**, 523–545.
- Thornton PE, Doney SC, Lindsay K *et al.* (2009) Carbon-nitrogen interactions regulate climate-carbon cycle feedbacks: results from an atmosphere-ocean general circulation model. *Biogeosciences*, **6**, 2099–2120.
- Tilman D (1988) *Plant Strategies and the Dynamics and Structure of Plant Communities*. Princeton University Press, Princeton.
- Tripathi AK, Roberts CD, Eagle RA (2009) Coupling of CO₂ and ice sheet stability over major climate transitions of the last 20 million years. *Science*, **326**, 1394–1397.
- Vandermeer J, De La Cerda IG (2004) Height dynamics of the thinning canopy of a tropical rain forest: 14 years of succession in a post-hurricane forest in Nicaragua. *Forest Ecology and Management*, **199**, 125–135.
- Wang YP, Houlton BZ (2009) Nitrogen constraints on terrestrial carbon uptake: implications for the global carbon-climate feedback. *Geophysical Research Letters*, **36**, L24403.
- Whittaker RH, Likens GE, Bormann FH, Easton JS, Siccama TG (1979) The Hubbard Brook ecosystem study: forest nutrient cycling and element behavior. *Ecology*, **60**, 203–220.
- Wright SJ (2013) The carbon sink in intact tropical forests. *Global Change Biology*, **19**, 337–339.
- Zak DR, Holmes WE, Pregitzer KS (2007) Atmospheric CO₂ and O-3 alter the flow of N-15 in developing forest ecosystems. *Ecology*, **88**, 2630–2639.
- Zhang L, Luo YQ, Yu GR, Zhang LM (2010) Estimated carbon residence times in three forest ecosystems of eastern China: applications of probabilistic inversion. *Journal of Geophysical Research: Biogeosciences*, **115**, G01010.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

- Appendix S1.** Detailed model description and analysis.
- Appendix S2.** Nitrogen cycling model modification: accounting for effects of nitrogen storage in wood on the net nitrogen mineralization rate, allocation, and carbon storage.