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Forest fine-root production and nitrogen use under elevated CO_2: contrasting responses in evergreen and deciduous trees explained by a common principle

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Abstract

Despite the importance of nitrogen (N) limitation of forest carbon (C) sequestration at rising atmospheric CO_2 concentration, the mechanisms responsible are not well understood. To elucidate the interactive effects of elevated CO_2 (eCO_2) and soil N availability on forest productivity and C allocation, we hypothesized that (1) trees maximize fitness by allocating N and C to maximize their net growth and (2) that N uptake is controlled by soil N availability and root exploration for soil N. We tested this model using data collected in Free-Air CO_2 Enrichment sites dominated by evergreen (*Pinus taeda*; Duke Forest) and deciduous [*Liquidambar styraciflua*; Oak Ridge National Laboratory (ORNL)] trees. The model explained 80–95% of variation in productivity and N-uptake data among eCO_2, N fertilization and control treatments over 6 years. The model explains why fine-root production increased, and why N uptake increased despite reduced soil N availability under eCO_2 at ORNL and Duke. In agreement with observations at other sites, the model predicts that soil N availability reduced below a critical level diminishes all eCO_2 responses. At Duke, a negative feedback between reduced soil N availability and N uptake prevented progressive reduction in soil N availability at eCO_2. At ORNL, soil N availability progressively decreased because it did not trigger reductions in N uptake; N uptake was maintained at ORNL through a large increase in the production of fast turnover fine roots. This implies that species with fast root turnover could be more prone to progressive N limitation of carbon sequestration in woody biomass than species with slow root turnover, such as evergreens. However, longer term data are necessary for a thorough evaluation of this hypothesis. The success of the model suggests that the principle of maximization of net growth to control growth and allocation could serve as a basis for simplification and generalization of larger scale forest and ecosystem models, for example by removing the need to specify parameters for relative foliage/stem/root allocation.

Keywords: allocation, elevated carbon dioxide, FACE experiments, fine-root longevity, forest growth model, optimization, plant theory, soil N availability, soil N uptake

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Introduction

The long-running forest Free-Air CO_2 Enrichment (FACE) experiments have provided substantial

evidence of ecosystem-level responses to elevated CO_2 (eCO_2), induced by the primary effects of CO_2 on leaf photosynthesis (Gifford, 2004). In the longer term, the response of forests to eCO_2 is a product of direct CO_2 effects and interactions with other resources that influence forest growth and carbon (C) flux. Soil nitrogen (N) availability is of particular importance for longer term responses because it limits forest production and C sequestration (Vitousek & Howarth, 1991), as well as their CO_2 responses (Oren *et al*., 2001; Reich *et al*., 2006a) in many temperate ecosystems. Soil N availability may also be subject to negative feedbacks associated with increased soil and plant N immobilization at eCO_2, leading to progressive N limitation (Comins & McMurtrie, 1993; Luo *et al*., 2004). Soil N availability also modulates the effect of eCO_2 on forest growth through changes in C allocation, (i.e. shifting proportions of C invested in fine root, leaf and wood production). Increased C allocation to wood at eCO_2 could increase the potential carbon sink in forest biomass due to the long mean residence time of wood compared with other tissues, whereas C allocation to root systems may enhance C transfer to soil organic matter pools. Clearly, understanding the interactive effects of eCO_2 and soil N availability is essential for accurate projections of forest responses to rising atmospheric CO_2. Furthermore, to enable such projections, the understanding needs to go beyond qualitative results towards mechanistic formulations that can be used in quantitative models.

In two mature forest FACE experiments located at Duke University and Oak Ridge National Laboratory (ORNL), net primary production (NPP), wood production, fine-root production (*RP*) and N uptake (*Nup*) all increased in response to eCO_2 (Hamilton *et al*., 2002; Norby *et al*., 2004; Norby & Iversen, 2006). The relative increase in NPP at eCO_2 was similar at the two sites. However, *RP* responded more and wood production less at ORNL than at Duke (DeLucia *et al*., 2005). At ORNL, annual *RP* was 91% higher at [CO_2] of 550 $\mu mol\,mol^{-1}$ than at 375 $\mu mol\,mol^{-1}$, whereas at Duke, the mean difference was only 19% (Norby *et al*., 2004; Finzi *et al*., 2006). It has been hypothesized that increased *RP* at eCO_2 is a response to increasing N limitation (Norby *et al*., 2004). However, measured N uptake (*Nup*) increased at eCO_2 at both FACE sites, which is not consistent with the N limitation hypothesis and contrasts to predictions of reduced N uptake at eCO_2 by earlier biogeochemical cycling models (e.g. Rastetter *et al*., 1997; Medlyn *et al*., 2000). This has led to the suggestion that models must be reformulated to allow increased soil N uptake via increased C allocation to fine roots and their means of N acquisition, directly or via microbial activities (Schimel & Bennett, 2004; Finzi *et al*., 2007). However, although N uptake can be increased via root C allocation in different ways at the microscopic level, the ecosystem level mechanisms controlling the total root C allocation and associated N uptake at eCO_2 are not yet well understood.

Here, we analyse the interaction between eCO_2 and soil N availability using a forest C–N model previously described (Franklin, 2007), extended by including N uptake. Whereas, the model by Franklin (2007) included soil effects only indirectly through measured fine-root/leaf ratios; here, the plant is dynamically and directly connected to the soil through fine-root C allocation that responds to soil N availability and plant N demand. This new development of the model is essential for understanding the soil–plant feedback and its consequences for plant growth and soil N availability. In addition to standard modelling of production and respiration, our model uses a controlling principle of plant allocation. Based on evolutionary principles, we assume that maximization of net growth controls tree growth and allocation. This hypothesis successfully predicted responses of NPP and leaf area index (LAI) to eCO_2 at four forest FACE experiments including ORNL and Duke (Franklin, 2007). Here, our objective is to mechanistically explain how the interaction of eCO_2 and soil N availability controls N uptake and C allocation in forests. We test the model by explaining the differences in root allocation and generation of N limitation between the FACE experiments in an evergreen (*Pinus taeda*) forest at Duke and a deciduous forest (*Liquidambar styraciflua*) at ORNL, both with fully developed canopies and occurring in similar climates and latitudes.

Materials and methods

Model

The model described here simulates processes of radiation interception, canopy photosynthesis, autotrophic respiration, C allocation to leaves, fine roots and wood, litterfall and N uptake by roots. In this model, we integrate our previous plant model [i.e. plant production and N demand; Franklin (2007)] with newly developed models of soil N availability, soil N uptake, and the interaction between N uptake and demand. Equations for each process are kept simple so that we can analytically ascertain the plant's integrated response to eCO_2 and soil N availability.

Plant production and N demand

Canopy photosynthesis is calculated from the nonrectangular hyperbolic light response of leaf photosynthesis (Cannell & Thornley, 1998). Light-saturated

photosynthetic rate (A_{max}) is linearly related to leaf nitrogen per unit area (N_A), $A_{max} = a(N_A - N_{min})$, where a is the slope of the relationship and N_{min} is its x-intercept. The initial slope of the photosynthetic light response is the quantum efficiency ($\phi = 2.73\,\mu g\,C\,J^{-1}$, Wong *et al*., 1979). Effects of [CO_2] on photosynthesis are introduced as an increase in the leaf photosynthetic capacity per unit N (a) and an increase in ϕ (Cannell & Thornley, 1998). Leaf photosynthesis is integrated over the canopy to evaluate gross primary production (GPP), assuming optimal N_A distribution and optimal LAI (L) as described in Franklin (2007). where I_a is absorbed photosynthetically active radiation (PAR), h is day length, N_c is canopy N content and θ is the curvature of photosynthetic light response. Because GPP is co-limited by N_c (through photosynthetic capacity) and incoming PAR, GPP is a saturating function of N_c at constant PAR (mathematical derivations are given in Appendix).

$$GPP = h\frac{\phi I_a + a(N_c - N_{min}L) - \sqrt{[\phi I_a + a(N_c - N_{min}L)]^2 - 4\phi I_a a(N_c - N_{min}L)\theta}}{2\theta} \quad (1)$$

NPP is calculated from GPP by subtracting maintenance respiration R_m and growth respiration: $NPP = y(GPP - R_m)$, where growth respiration is a fixed fraction ($1/y - 1$) of NPP and $y = 0.72$ (Choudhury, 2001). R_m is expressed as a linear function of N_c and the amount of N in other respiring tissues (Reich *et al*., 2006b). Total maintenance respiration is $R_m = rN_c(1 + f_r q_r + f_s)$, where r is respiration rate per unit N, f_r is the root to leaf N ratio ($f_r = N_r/N_c$), f_s is the sapwood to leaf N ratio ($f_s = N_s/N_c$) and q_r is a factor that accounts for the higher respiration rate per unit N in fine roots relative to foliage (Ryan *et al*., 1996). Litter production (T) of foliage (FP) and fine roots (RP) is determined from mean residence times and N : C ratios of leaves (t_c, n_c) and fine roots (t_r, n_r), and is expressed as a linear function of tissue N contents, $T = FP + RP = N_c[(1/n_c t_c) + f_r/(n_r t_r)]$. As GPP is a saturating function of N_c, whereas both R_m and T are proportional to N_c, net plant growth G, defined as:

$$G = NPP - T = y(GPP - R_m) - T = yGPP - wN_c \quad (2)$$

has a maximum with respect to N_c, where N_c is optimal (N_c^*) [Appendix Eqn (A5)]. G includes woody tissue (stem, branches and coarse roots) increment and reproductive production.

The parameter w in Eqn (2) represents the carbon costs per N_c, and is a function of f_r: $w = yr(1 + f_r q_r + f_s) + [1/(n_c t_c) + f_r/(n_r t_r)]$. An increase in f_r increases w through an increased in fine-root N requirement per N_c, which increases the C costs per N_c and leads to a lower optimal N_c (N_c^*) and lower GPP, as illustrated in Fig. 1a. Whereas, canopy C costs are tied linearly to N_c, root C costs and production (RP), determined by the optimality condition for G, has a maximum with respect to N_c as illustrated in Fig. 1a.

The choice of net plant growth G as optimization target rests on the assumption that maximizing G (size increase and reproduction) is a plausible strategy for maximizing fitness in the face of competition over the lifetime of a tree (Franklin, 2007). It is assumed that canopies that have reached steady state (i.e. peak LAI), such as at Duke and ORNL, thereafter always have optimal N_c. The optimal value of canopy N (N_c^*) can be combined with equations above for GPP [Eqn (1)], R_m and T to determine values of GPP, NPP, G and LAI for optimized canopies (Franklin, 2007). Plant productivity is then controlled by changes in (1) photosynthetic parameters a and ϕ, which affect GPP; (2) allocation parameters (f_r and f_s), leaf and fine-root N : C ratios (n_c and n_r) and residence times (t_c and t_r), which affect R_m and T and (3) environmental parameters such as incident PAR (I_0). Because T is assumed to be in steady state at fixed parameter values, productivity should be evaluated for a time period longer than t_c and t_r and not for shorter term fluctuations.

The N demands (Nd, Fig. 1b and d) associated with the carbon fluxes in Fig. 1a are determined by the N : C ratios and turnover times of the plant parts:

$$Nd = Gn_G + \frac{N_c(1 - q_{rf})}{t_c} + \frac{N_c f_r}{t_r}, \quad (3)$$

where n_G is the mean N : C ratio of tissues other than leaves and fine roots, (i.e. mainly wood), and q_{rf} is the fraction of N resorbed before leaf senescence. N demand of G and foliage [first and second term of Eqn (3)] are monotonically decreasing with f_r (through decreasing N_c^*), whereas root N demand [last term of Eqn (3)] has a maximum, due to the maximum of root C allocation (Fig. 1a).

The N demand curves in Fig. 1b and d represent the rate of N uptake required to support annual growth predicted by the growth model. It includes CO_2 effects on photosynthesis and canopy N, and consequent changes in allocation to foliage, wood and fine roots. However, it does not describe how N uptake (Nup) is related to soil N availability.

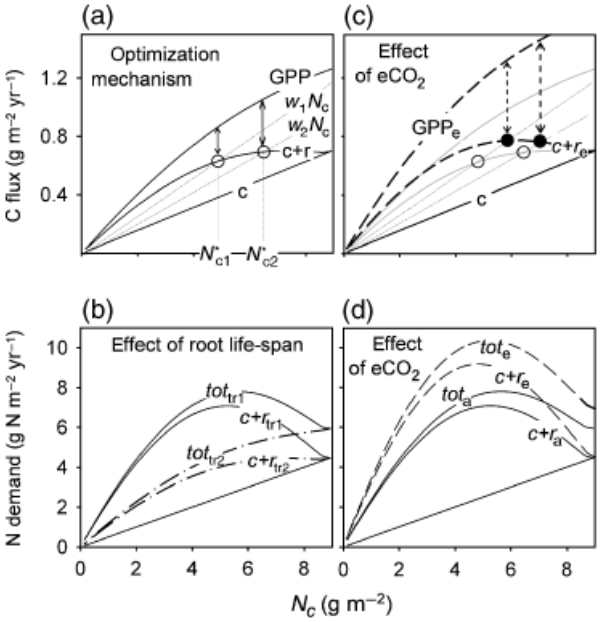

Fig. 1 Mechanisms of canopy optimization and allocation of C and N in response to fine-root : canopy N ratio (f_r). (a) Canopy C gain [gross primary production (GPP)] and canopy C costs (c), i.e. respiration and litter production, are fixed functions of canopy N (N_c). Root C costs are added to c, which gives the total C costs ($c + r$), shown here for two *fixed* values of f_r (w_1N_c, w_2N_c; w = total C costs per N_c). Optimal N_c (N_c^*) occurs where net growth (G, arrows) is maximized, i.e. where wN_c and GPP are parallel (circles). Varying f_r through a range of values shifts the slope of wN_c and, subject to the optimality condition, depicts the total C costs for canopy and roots for the *optimized* canopy ($c + r$). For clarity, effects on tissue N : C ratios (used in the modelling) are not included in this illustration. Values represent Oak Ridge National Laboratory (ORNL). (b) Solid lines show N demands corresponding to the C fluxes in (a) for the canopy (c), root + canopy ($c + r$) and total N demand (tot). The subscripts *tr1* and *tr2* represent fine-root lifespan (t_r) roughly corresponding to ORNL (solid lines) and Duke (dadot lines) values, respectively. t_r for Duke is here three times longer, while root respiration per N is higher than at ORNL, keeping total root C costs per N_c the same for both sites. Other parameters are kept the same as in (a), i.e. representing ORNL. (c) Curves as in (a) for aCO_2 (thin curves, open circles) and curves and symbols for eCO_2 (dashed curves, closed circles). The primary effect of eCO_2 is to raise GPP to GPP_e. According to the mechanism described in (a), for the same values of w_1 and w_2 as in (a), the raised GPP raises both N_c^*(closed circles), G (dotted arrows), and root C costs ($c + r_e$). (d) N demand for aCO_2 (subscript a, solid lines) and for eCO_2 (subscript e, dashed lines) corresponding to the eCO_2 effect on the C fluxes shown in (c).

Soil N uptake

We define soil N availability (*Nav*) as the maximum rate of N uptake per root carbon (C_r) when C_r is small; $Nav = Nup/C_r$ when $C_r \to 0$. Although other, soil-centric perspectives on *Nav* are more commonly used, our plant-centric definition of *Nav* is more relevant for our plant growth modelling. For simplicity, N uptake is represented by an hyperbolic function of C_r, where the mechanism for that relationship is not specified, though it may relate to exploration of the soil volume by roots (McClain *et al*., 2003) including increased rooting depth, solute transport to roots as a function of inter-root distance (Yanai, 1994), increased competitiveness of tree roots for soil N (Schimel & Bennett, 2004) or N uptake via C allocation to mycorrhizal fungi or exudates, all which may scale with C_r (Finzi *et al*., 2007):

$$Nup = Nav\frac{C_r}{(C_r/\lambda) + 1} \quad (4)$$

λ represents C_r required to achieve half-maximum N uptake (cf. McMurtrie, 1985). Saturation of N uptake may be related to limited soil volume, or decreased root-uptake efficiency as the density of roots increases, or spatial variation in N availability, where N rich parts of the soil volume are explored first. *Nup* has a theoretical maximum = $Nav\lambda$ (when $C_r \to \infty$), whose value is of no significance as our model is parameterized and used within a range of much lower *Nup* values.

Balancing N demand and uptake

Rates of N uptake (*Nup*) and N demand (*Nd*) are shown in Fig. 2 as functions of root production (*RP*). The operating point of N use is the intersection *Nup* = *Nd*, which is dynamically stable with respect to changes in soil N availability (*Nav*) or *Nd* (see Appendix).

Elevated CO_2 steepens the relationship between GPP and N_c, which increases the optimal value of N_c for a given f_r, as well as the N demand, as illustrated in Fig. 1c and 1d. The effect is to raise the *Nd* curve illustrated in Fig. 2, and to shift it to the right. This means that for a given *Nav* (which controls the *Nup* curve), *RP*, *Nd* and NPP all increase at eCO_2, although the effect is small at extremely low *Nav* (*Nup*′, Fig. 2). The largest increase in *RP* at eCO_2 occurs at intermediate *Nav*, where N use (intersection of *Nup* and *Nd* curves) is near the peak value of *RP*. With decreasing *Nav*, plant responses to eCO_2 decline dramatically after the value of *RP* passes its peak on the *Nd* curve (Fig. 2). This change in CO_2 response can be explained through the effect of CO_2 on root C allocation shown in Fig. 1c (vertical distance between $c + r$ and c curves). To obtain the same root C allocation for eCO_2 as for aCO_2 at *high* N_c^* (high *Nav*, low f_r) requires little change in f_r, yielding a higher N_c^* at eCO_2 than at aCO_2, which enhances the effect of eCO_2 on production. To obtain the same root C allocation at *low* N_c^*, f_r must be larger for eCO_2 than for aCO_2, yielding a lower N_c^* at eCO_2 than at aCO_2. This lowering

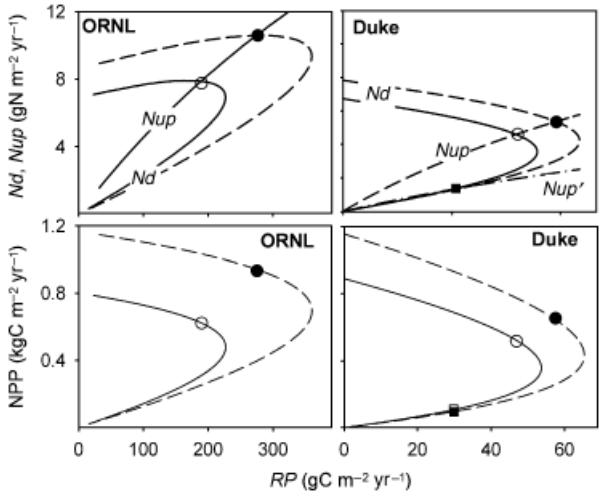

Fig. 2 Balancing N uptake (*Nup*) and demand (*Nd*). Upper panels: *Nup* and *Nd* vs. root production (*RP*) for aCO_2 (solid lines, open symbols) and eCO_2 (dashed lines, closed symbols). The symbols indicate the operating point where *Nup* = *Nd*. The slope of *Nup* is controlled by N availability (*Nav*). For Duke, *Nup*′ (dadot line, squares) represents a hypothetical extremely low *Nav*. Lower panels: net primary production (NPP) corresponding to the *Nd* of the upper panels. Each curve, except *Nup*, depicts an increase in root N/canopy N ratio (f_r) and associated reduction in tissue N:C ratios, starting from $f_r \approx 0$ at the upper left endpoints.

Table 1 Characteristics of the two FACE experiments

Name	Duke	ORNL
Location	Durham, NC, USA	Oak Ridge, TN, USA
Latitude, longitude	35°58′N, 79°05′W	35°54′N, 84°20′W
Annual precipitation (mm)	1140	1390
Annual temperature (°C)	15.5	14.2
Growing season* (days)	200	190
Soil texture	Clay loam	Silty clay loam
Total soil N ($g\,kg^{-1}$)	0.79	1.12
Overstory vegetation	*Pinus taeda* L.	*Liquidambar styraciflua* L.
Peak leaf area index† ($m^2\,m^{-2}$)	3.4	5.5
Day length (h; $s\,day^{-1}$)	50 400‡§	43 200‡¶
Incident PAR (I_0; $J\,s^{-1}\,m^{-2}$)	184‡§	211‡¶

Data taken from Norby *et al*. (2005).
*For deciduous stands, the growing season is the duration that trees have leaves; for the evergreen system, it is the period of active stem growth.
†Values of leaf area index are expressed as projected leaf area per ground area.
‡Growing season average values.
§Norby *et al*. (2003).
¶Delucia *et al*. (2002).
FACE, Free-Air CO_2 Enrichment; ORNL, Oak Ridge National Laboratory; PAR, photosynthetically active radiation.

of N_c^* suppresses the effect of eCO_2 on production and, therefore, on *Nd*. This closes the gap between the *Nd* curves of aCO_2 and eCO_2 at low *Nav* (i.e. for N use on the lower arm of the *Nd* curve in Fig. 2). Hereafter, values of *Nav* that result in an N use on the upper and lower arm of the *Nd* curve relative to that at peak *RP* are referred to as higher and low *Nav*, respectively.

Experiments and measurements

The FACE experiments (Table 1) and datasets are described in detail in Finzi *et al*. (2007). For ORNL FACE, annual data for the years 1998–2003 were used directly, while for Duke, annual data were aggregated to represent averages for the years 1998–1999 and 2002–2004. The time periods selected were based on the availability of fine-root data. The aggregation of annual data at Duke was done because of the relatively long lifespan of roots and leaves in Duke, to better match data with the model assumption that foliage and fine-root biomass are in equilibrium with the optimal state of the plant (see 'Model'). The data include both overstory and understory trees, but only at Duke does the understory contribute significantly to forest production (13% of total aboveground NPP). The ORNL fertilization experiment was performed on a previous FACE plot without CO_2 treatment, where $200\,kg\,ha^{-1}$ of N as urea was added and data collected in 2004 and 2005 (Iversen & Norby, 2008). Measurement of net N mineralization at Duke is described in Finzi *et al*. (2006). Photosynthesis measurements are described for Duke in Crous & Ellsworth (2004) and Crous *et al*. (2008) and for ORNL in Sholtis *et al*. (2004).

Model parameterization and input data

The model was parameterized for six FACE plots at Duke and five FACE plots and two fertilization treatments (six plots pooled per treatment) at ORNL. Constant site mean values were determined for leaf photosynthetic capacity per unit N ($a = 73$, $26\,\mu g\,C\,g^{-1}\,N\,s^{-1}$), respiration rate per N ($r = 0.187$, $0.147\,g\,C\,g^{-1}N\,d^{-1}$), sapwood N/canopy N ($f_s = 1.5$, 0.5), fine-root lifespan ($t_r = 0.53$, 3 years) and fine-root respiration/foliage respiration per N ($q_r = 1$, 3.57), where the values represent ORNL and Duke, respectively. These parameters were estimated by fitting all the modelled and measured values of *RP*, *G*, N_c and *Nd* simultaneously (inverse modelling). This model parameterization approach focuses the subsequent model

evaluation on prediction of the variation among plots and treatments, in particular the CO_2 effects, whereas, biases due to errors in parameter mean values are minimized (Franklin, 2007).

Soil N availability. Soil N availability (*Nav*) was determined for each plot and year using Eqn (4) and measured values of total N uptake and root mass carbon (C_r). In estimating the effects of plot and year on soil N availability (*Nav*), we assumed a constant half-saturation C_r (λ). This assumption is based on the findings that soil volume and root physiology did not vary significantly among CO_2 treatments, plots and years (Norby *et al*., 2004; Pritchard *et al*., 2001), whereas soil N and N mineralization varied. Furthermore, λ was constrained by the assumption that *RP* must never be higher than the *RP* that maximizes net N uptake ($= Nup - $N in root litter production), which sets a lower limit for λ. A further increase in *RP* would reduce net N uptake and therefore be suboptimal. Because a first fit of λ and *Nav* to the complete dataset yielded a λ that was lower than the limit described above, λ equal to the limit (460 and 59.2 g C m^{-2} for ORNL and Duke, respectively) was chosen. λ values higher than this would also be possible but would increase the variation in *Nav* among plots and years. Time and treatment effects on *Nav* were compared using ANCOVA.

Photosynthetic effects of eCO_2. The effects of CO_2 on plant growth were introduced through the observed relative *changes* in the leaf photosynthetic capacity per unit N (effect on $a = a/$site mean of a), and a proportional change in ϕ (effect on $\phi =$ effect on $a/3$). Effects on a for the different rings and years were estimated using measured A_{max} and N_A data using the relationship $A_{max} = a(N_A - N_{min})$, where N_{min} is constant across all treatments. The estimated effects on a for ORNL were 1.29, 1.29, 0.79, 0.79, 1.00, 0.84, 0.84 for the plots 1–7, respectively, where plots 1 and 2 are eCO_2 in the FACE, plots 3–5 are aCO_2 in the FACE experiment, and plots 6 and 7 represent means for six replicate plots each in a fertilization trial (at aCO_2). For Duke, there was no significant difference among plots of the same CO_2 treatment or among years, so only two values for the effect on a were used, 0.85 and 1.15 for aCO_2 and eCO_2, respectively.

Other treatment effects. Changes in tissue N : C ratios (n) for estimates in Figs 3–6 were taken from measurements. For the illustration of theoretical response curves (Fig. 2), changes in n in response to *Nav* were modelled using an empirically determined relation between f_r and n that passes through the observed values. $n_x = n_{x-obs}(1 - (f_r/p_1)^{p_2})/(1 - (f_{r-obs}/p_1)^{p_2})$, where x stands for leaf, fine roots or wood and *obs* are observed values. p_1, p_2 are parameters, with values 7, 0.35 and 7, 0.7 for ORNL and Duke, respectively. For ORNL, n was related to f_r for all the tissues (i.e. leaves, fine roots and wood). For Duke, n varied only for foliage, while n of fine roots and wood were constant. For the fertilized stands at ORNL, $f_s =$ sapwood N/canopy N was estimated to have decreased by 40% compared with control stands due to increased LAI and lagging increase in sapwood area, due to the short duration of the fertilization exposure. For longer time responses, sapwood area/LAI is not changed by fertilization (Hubbard *et al*., 2004; Samuelson & Stokes, 2006).

Results

Model validity

The model was evaluated using input data on soil N availability (*Nav*) derived for each plot and year, tissue N : C ratios (n) taken from measurements, and photosynthetic effects of eCO_2 on a and ϕ derived from independent measurements – see 'Materials and methods'. Of these parameters, the model was most sensitive to a and *Nav*, and was relatively insensitive to tissue N : C ratios.

We did not use direct measures of soil N availability for *Nav* because of the paucity of data and because, our definition of *Nav* is not equivalent to any available soil measure. *Nav* does not correspond to common views of N availability as a pool or flux of free N in the soil, or as N taken up by the plants. Instead, *Nav* represents the maximum potential N flux that can be extracted from the soil per root mass by a single root in the soil [Eqn (4)], which presents a rhizo-centric view of plant-N uptake feedback (Phillips, 2007). The exact mechanisms, which may include absorption of mineralized N, stimulation of N mineralization via C exudation and competition with microbes for N (Schimel & Bennett, 2004), are of subordinate importance for this ecosystem level analysis (see also 'Discussion'). However, modelled trends in *Nav* (Fig. 3) correlate with observed N mineralization over time at Duke (Fig. 4), relative plot differences in extractable NO_3^- at ORNL (Fig. 4) and a reduction in gross N mineralization at eCO_2 observed for 2 years at ORNL (Zak *et al*., 2003). These relationships indicate that *Nav* is not only a useful representation of a virtually un-measurable entity but also is linked to independently measured soil properties. *Nav* declined over time and was significantly ($P = 0.0114$) lower at eCO_2 than at aCO_2 and at ORNL but not at Duke (Fig. 3). *Nav* declined faster at eCO_2 than at aCO_2 at ORNL, although the difference was not significant

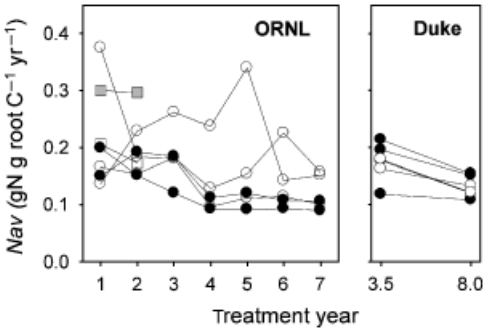

Fig. 3 Estimated soil nitrogen availability (*Nav*). Symbols: Open – aCO_2, closed – eCO_2, grey – fertilized, circles – Free-air CO_2 enrichment (FACE) plots, squares – fertilization experiment at Oak Ridge National Laboratory (ORNL). For ORNL, points show annual values for the period 1998–2004 and 2004–2005 for the FACE and fertilization plots, respectively. For Duke, the points represent mean values for the periods 1998–1999 and 2002–2004. Values calculated from measured N uptake and fine-root C using Eqn (4).

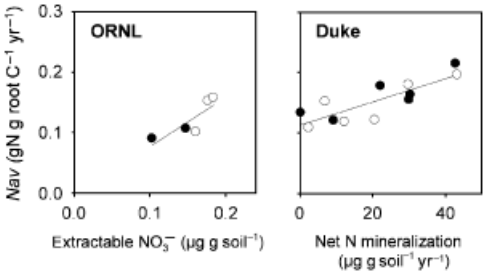

Fig. 4 Modelled soil N availability (*Nav*) vs. measured extractable NO_3^- in Oak Ridge National Laboratory (ORNL) and Net N mineralization in Duke. Symbols as in Fig. 3.

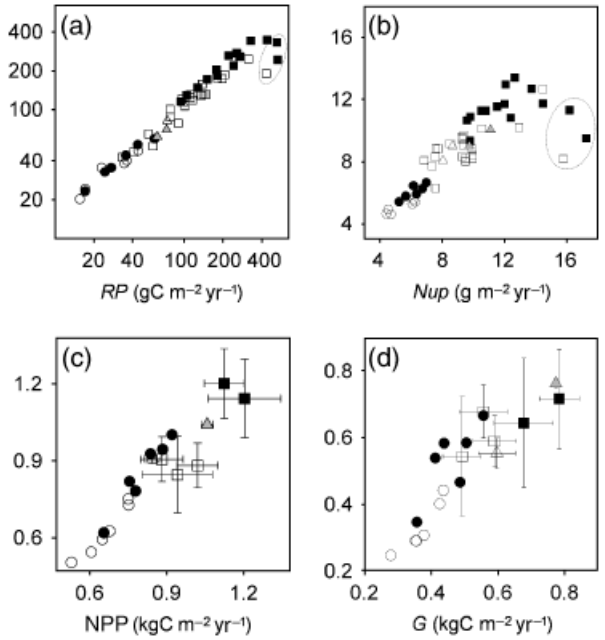

Fig. 5 Modelled (*y* axis) vs. measured (*x* axis) data. Symbols: circles – Duke Free-air CO_2 enrichment (FACE), Squares – Oak Ridge National Laboratory (ORNL) FACE, triangles – ORNL fertilization trial, Open symbols – aCO_2, black – eCO_2, grey – N fertilized. Encircled points are outliers. (a) Annual fine-root production (*RP*) (logarithmic scale), $r^2 = 0.95$. (b) Nitrogen uptake (*Nup*), $r^2 = 0.85$. (c) net primary production (NPP). Results for three FACE aCO_2 and two eCO_2 plots, and two fertilized and two unfertilized treatments at ORNL are represented by means and bars. Bars represent standard deviation among years, $r^2 = 0.92$. (d) Net growth (*G*). Symbols and bars as in (c), $r^2 = 0.80$. Each point represents, for Duke – one plot and one period (mean over 2–3-year period), for ORNL FACE *RP* and *Nup* – 1 year and one plot, for ORNL FACE NPP and *G* – mean values over 7 years, and for ORNL fertilization 1 year and a 6 plot average.

(Figs 3 and 4). To test the model's validity, modelled results were compared with measured data. Modelled and measured root production (*RP*), N uptake, NPP and net growth (*G*) are shown in Fig. 5. Results are shown for each year at ORNL and for periods of 2–3 years at Duke.

There was strong agreement between model and measurement data at both sites. Between 80% and 95% of variation in measurements is described by the model (Fig. 5), indicating that the model was well suited to describe linkages between photosynthetic processes and soil N availability, which were parameterized from independent datasets (see 'Methods'). The agreement for *RP* may seem predetermined as root C was used in the estimation of *Nav*. However, the fitting of *Nav* constrains only one of the curves determining *RP*, [i.e. N uptake (*Nup*) but not the demand (*Nd*, Fig. 2)], which depends on the other independent parameters of which *a* is the most influential. For ORNL, there are three outliers (Fig. 5a and b) for which *RP* and *Nup* are underestimated because measured *RP* values are much higher than the maximum possible model *RP* (cf. Fig. 2). The outliers correspond to observations of unusually deep roots and may be influenced by rapid dynamic changes in root mass, not compatible with the equilibrium assumption in the model. However, given the small number of outliers and the difficulty of measuring *RP*, measurement error can be a contributing factor, which may also have contributed to the slight divergence between modelled and measured NPP at low NPP (Fig. 5c), where *RP* is a large fraction of NPP. In order to focus on the interaction of eCO_2 effects and soil N availability, the model does not include effects of annual climate variation on productivity, especially the effects of droughts on NPP and its allocation (McCarthy

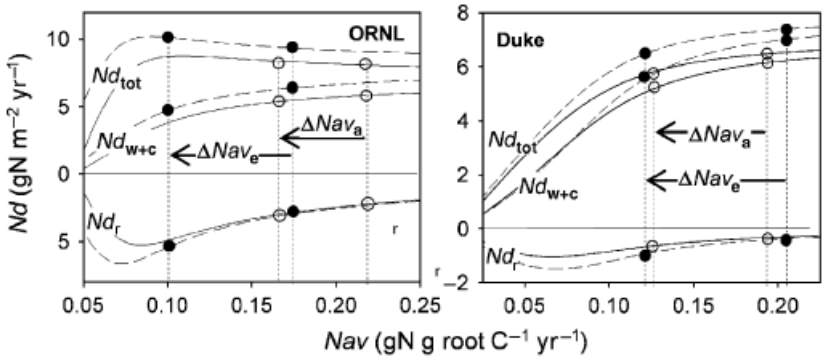

Fig. 6 Changes in N use (*Nd*) and soil N availability (*Nav*) over time modelled for an aCO_2 (open circles, solid lines) plot and an eCO_2 plot (black symbols, dashed lines) at each site. Δ*Nav* (arrows) show the reduction in *Nav* between treatment years 3.5–8 and 1–5 for Duke and Oak Ridge National Laboratory (ORNL), respectively (cf. 1 Fig. 3). Nd_{tot}, Nd_{w+c} and Nd_r are total, wood + foliage and fine-root N use, respectively.

et al., 2006). It is, therefore, not surprising that the model does not capture the inter-annual variation in NPP and *G* at ORNL, and that modelled and measured *G* diverge for some periods under eCO_2 at Duke (Fig. 5d). In summary, despite the highly aggregated and simplified representation of processes in the model, it appears to provide a working mechanistic explanation of the interaction of forest production and N uptake in the studied forests.

Discussion

Potential uncertainties

The simplicity of the model makes it clear that the qualitative conclusions are sensitive to only a few key model assumptions. These assumptions are (1) photosynthesis and maintenance respiration are linked to tissue N, (2) C and N allocation is regulated to maximize *G* (or some property closely related to *G*) and (3) *Nup* increases with root C and soil N availability (*Nav*). The first assumption, although not valid for all leaves (Maier *et al*., 2008), has strong support (e.g. Reich & Ellsworth, 1998; Reich *et al*., 2006b; Crous *et al*., 2008). The second assumption has been evaluated in Franklin (2007) and the last assumption corresponds to the observations used here and reported previously (Norby *et al*., 2004).

The N uptake model based on root C and *Nav* is by necessity a simplified aggregation of many processes, such as allocation to mycorrhiza and exudates that are involved in plant N uptake. For example, from the relationship between *Nav* and N mineralization at Duke (Fig. 4), it is clear that N mineralization alone does not explain total soil N availability to the plant (*Nav*). Although separating the processes involved in N uptake would be desirable, such a model would not be testable based on currently available data. This means that we are implicitly assuming that the total effect of all processes on N uptake is proportional to fine-root C. Globally, this assumption is supported by observations that arbuscular mycorrhiza is correlated to fine-root biomass rather than soil organic matter (Treseder & Cross, 2006). Our model is consistent with observations that mycorrhizal root colonization (Parrent & Vilgalys, 2007; Garcia *et al*., 2008) and soil microbial activity (Sinsabaugh *et al*., 2003) are not strongly affected by the CO_2 treatments in our sites, in contrast to increases observed in fine roots and N uptake. Another indication that fine roots exert strong influence on soil activity, which may be linked to N uptake, is that the spatial distribution of soil respiration reflected the fine root distribution at Duke (Andrews *et al*., 1999).

In a C budget perspective, enhanced allocation to mycorrhiza and root exudation per fine-root C at eCO_2 (Norby *et al*., 1987) would constitute a part of NPP not accounted for in the observations (Schäfer *et al*., 2003). In this model, an underestimation of measured below ground C export would primarily result in a model parameterization overestimating the root respiration per N (q_r, see 'Model'), whereas other parameters are more constrained by aboveground data. This potential error may have consequences for the soil C budget, but it has no impact on plant growth and N uptake within our model framework.

A potentially more important uncertainty for this study pertains to the hypothesis that fine-root mean residence time (t_r) decreases with soil N availability (Nadelhoffer, 2000). Although shifts in t_r with eCO_2 have not been found in the experiments evaluated here (Pritchard *et al*., 2001; Norby *et al*., 2004), the consequence would be slight shifts of the N demand (*Nd*) curves due to increased *RP* at high *Nd* and decreased *RP* at low *Nd* (Fig. 2). Because of the relative flatness of

the upper arm of the *Nd* curves, the effect would be largest at low *Nd*. But more importantly, even a doubling of t_r at very low *Nd* would not qualitatively change the conclusions for the effects of CO_2 and *Nav*.

Soil N availability effects on the responses to eCO_2

The model implies that increased fine-root production *(RP)* at eCO_2 is an unavoidable consequence of the combination of increased N demand (*Nd*) and constant N uptake (*Nup*) as functions of *RP* (Fig. 2). The increase in *RP* at eCO_2 is greatest at a value of *Nav* (Nav_0) that, in Fig. 2, makes *Nup* cross *Nd* near the maximum *RP*. If *Nav* exceeds Nav_0, then *RP* is a decreasing function of *Nav*, whereas if *Nav* is less than Nav_0 (lower than any observation at Duke or ORNL), *RP* is an increasing function of *Nav*. Although none of our data falls on the lower arm of the *Nd* curve ($Nav < Nav_0$), the general shape of the curve is plausible, because if *Nd* approaches zero, so must *RP* and NPP. The different responses at higher vs. low *Nav* may be a reason for the variable, both positive and negative, root production responses to soil N availability observed (Nadelhoffer, 2000). In the case of progressive reduction in *Nav*, our model predicts that aboveground eCO_2 responses will decrease, whereas *RP* will increase until *Nav* drops below Nav_0, where all CO_2 responses will decline dramatically. This decline is caused by reduced allocation of N to canopy photosynthesis (reduced N_c^*), which reduces the impact of the leaf photosynthetic stimulation at eCO_2 (see 'Model'). This type of declining CO_2 response has been observed in a nutrient-poor woodland (Day *et al*., 2006; Hungate *et al*., 2006) and provides an explanation for the observations that CO_2 responses of both roots and aboveground parts are declining at low N availability at some sites (Pregitzer *et al*., 2000; de Graaff *et al*., 2006).

The model implies that, unless *Nav* is very low, N use efficiency (NUE = NPP/N use) increases with CO_2 due to increased production per canopy N (Fig. 1c) and with *Nav* due to increased relative allocation to *G* (mainly wood), because wood has a lower N : C ratio than litter (Fig. 2). In accordance with this, the strongest NUE increase at eCO_2 among forest FACE sites was observed at the site where N was least limiting (PopFACE; Calfapietra *et al*., 2007; Finzi *et al*., 2007), whereas the absence of an increase in NUE at eCO_2 at ORNL is explained by the concurrent decrease in *Nav* (Fig. 4). Our prediction of increasing NUE at higher soil N availability is in line with recent findings regarding resource use efficiency (Binkley *et al*., 2004; Stape *et al*., 2004; Franklin, 2007). However, our results contrast to the earlier methods of NUE estimation based on aboveground litter production only (Pastor & Bridgham, 1999), which, therefore, do not capture the allocation shifts between fine roots and wood that strongly contribute to the relationships predicted here. Generalizing our model implies that increased resource use efficiency follows when increased availability of a limiting resource (here N), given sufficient time for plant acclimation, reduces the acquisition and maintenance C costs (here root C allocation, cf. Fig. 1) per unit resource.

Differences in the CO_2 response between an evergreen forest (Duke) and a deciduous forest (ORNL)

On average, the CO_2 response of fine-root production (*RP*) is smaller and the response of wood production is larger at Duke compared with ORNL (DeLucia *et al*., 2005). This allocation difference is of significance as wood production results in longer term biomass carbon sequestration than fine-root production. In our framework, the allocation difference between the sites is mainly related to two factors: the different effects of CO_2 on *Nav* in the two sites and the difference in fine-root lifespan (t_r).

The model predicts that reduced *Nav* at eCO_2 contributed to increased *RP* at ORNL, while for Duke, there is no consistent effect of eCO_2 on *Nav*. At both sites and under both aCO_2 and eCO_2, *Nav* as well as observed N mineralization in Duke and extractable NO_3^- in ORNL declined over time (Figs 3 and 4). However, a reduction in *Nav* gives rise to different feedbacks on N use *(Nd)* in the two sites, caused by the strongly differing t_r between the species [0.53 year at ORNL and 3 years at Duke, roughly matching measured values (Norby *et al*., 2004; Strand *et al*., 2008)]. The large difference in t_r, which also has been confirmed using an isotope tracer (Matamala & Schlesinger, 2000), means that most of the fine-root C (75%) at ORNL is allocated to litter production with associated N use, whereas at Duke, most of the fine-root C allocation (82%) is ultimately respired with no associated N use (Fig. 1b). As illustrated in Fig. 6a (and explained by the shape of the upper arm of *Nd* in Fig. 2a), despite decreasing *Nav*, the short t_r and associated high production and N use of fine roots maintain a high total *Nd* at ORNL. This high *Nd* at declining *Nav* should contribute to continuing reduction in *Nav*, unless root litter N is efficiently remineralized. However, observations of increased total soil N at eCO_2 (Johnson *et al*., 2004), despite increased N uptake and unchanged leaf litterfall, indicate that additional inputs of root litter N to the soil are not quickly recycled. In accordance with predicted consequences of reduced *Nav*, extractable NO_3^- and observed wood/root production ratio (*G*/*RP*) declined over time at ORNL, where the decline was stronger at eCO_2 than at aCO_2. At Duke, due to low root N use, reductions in *Nav*

generate reductions in *Nd* (Figs 6b and 2b), providing a negative feedback on further reduction in *Nav*. This feedback may have prevented or delayed a similar decline in the relative allocation to wood at eCO_2 as at ORNL. Generalizing this result implies that species with slow root turnover and low fine-root N use, such as evergreens, are less likely to cause progressive reduction in *Nav*. These species may, therefore, be less prone to progressive N limitation of wood production and associated biomass carbon sequestration at eCO_2 than species with fast root turnover, such as many deciduous trees (Withington *et al*., 2006). However, for a thorough evaluation of this hypothesis, longer term studies are recommended, as well as studies that quantify parallel below ground C inputs and their effect on N uptake.

Conclusions

We modelled effects of eCO_2 and soil N availability based on essentially only two independent input variables, mean photosynthetic capacity per leaf N (*a*) and soil N availability (*Nav*). Despite this simplicity, model predictions were consistent with measurements of N uptake, production and allocation at ambient and eCO_2 in two FACE experiments and a fertilization experiment. In addition, the model provides an explanation for declining CO_2 responses observed at other more strongly nutrient limited sites. We attribute the models' ability to integrate responses to eCO_2 and soil N availability over a range of conditions to the applied optimization perspective. In addition to commonly used statistical analysis of *what* happened and process modelling of *how* things happen, here we hypothesized *why* trees behave as they do. The hypothesis, that trees maximize their net growth and reproduction (*G*), integrates all individual plant processes and responses to eCO_2 and ensures that their joint behaviour is optimal. In this integrated framework, empirical results may be placed into a bigger picture, not limited by the range of experimental growing conditions. For example, the negative effect of aboveground productivity on root C allocation in the FACE sites under current conditions (Palmroth *et al*., 2006) is predicted to switch to a positive effect at lower soil N availabilities (*Nav*) (Fig. 2). Furthermore, our model suggests that dominance of LAI effects on aboveground eCO_2 responses (McCarthy *et al*., 2006) is mainly limited to expanding canopies, low *Nav* and low LAI [see also Franklin (2007)], while for higher *Nav*, nitrogen use efficiency responses are larger.

The model suggests that the sensitivity of biomass C sequestration to soil N availability (*Nav*) differs among species differing in root lifespan (t_r). Because a short t_r leads to high N uptake despite declining *Nav*, the model suggests that species with short t_r (e.g. at ORNL) are more prone to progressive reduction in *Nav* and therefore N limitation of carbon sequestration in woody biomass, than long t_r species, such as evergreen trees (e.g. at Duke). In order to evaluate the importance of this result for long-term forest C balance, the principles for integrating responses to different factors presented here could be incorporated into forests ecosystem models that include explicit modelling of the soil. Ultimately, our model could provide a basis for the improvement of large-scale forest and vegetation dynamics models by replacing fixed but uncertain parameters (such as fine root/leaf production) with dynamic optimization.

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Appendix

Derivation of canopy photosynthesis, GPP

Canopy photosynthesis (GPP) is calculated by integration of leaf photosynthesis (GPP_{leaf}) over canopy depth (z). A_{max} is a function of N per leaf area (N_A), $A_{max} = a(N_A - N_{min})$, where N_A is derived as a function of z assuming an optimal nitrogen distribution [Eqn (A2)] as described in (Franklin & Ågren, 2002). PAR absorbed by a leaf is related to canopy depth according to $I(z) = I_0 k e^{-kz}$, where k is the light extinction coefficient and I_0 is incident PAR above the canopy. The integral in Eqn (A1) is easily calculated by first separating out the z dependence through the factor ke^{-kz}, which occurs in all terms of the integrand.

$$\mathrm{GPP} = \int_0^L \mathrm{GPP}_{\mathrm{leaf}}\mathrm{d}z = \int_0^L \frac{\phi I(z) + A_{\max}(z) - \sqrt{[\phi I(z) + A_{\max}(z)]^2 - 4\phi I(z) A_{\max}(z)\theta}}{2\theta}\mathrm{d}z \quad \text{(A1)}$$

$$N_A(z) = \frac{(N_c - N_{\min}L)k\mathrm{e}^{-kz}}{1 - \mathrm{e}^{-kL}} + N_{\min}. \quad \text{(A2)}$$

Derivation of optimal N_c

Optimal N_c is derived through maximization of G with respect to N_c. To simplify calculations, the substitution $N_P = N_c - N_{min}L$ is made, so that optimal N_c is given by

$$\frac{\mathrm{d}G}{\mathrm{d}N_c} = \frac{\mathrm{d}G}{\mathrm{d}N_P}\frac{\mathrm{d}N_P}{\mathrm{d}N_c} = \frac{\mathrm{d}G}{\mathrm{d}N_P} = 0. \quad \text{(A3)}$$

Using the last expression in Eqn (A3) and $G = y\mathrm{GPP} - w\,N_c$

$$\frac{\mathrm{d}}{\mathrm{d}N_P}G = y\frac{\mathrm{d}}{\mathrm{d}N_P}\mathrm{GPP} - w = \frac{hya}{2\theta}\left(1 - \frac{\phi I_a + aN_P - 2\phi I_a\theta}{\sqrt{(\phi I_a + aN_P)^2 - 4\phi I_a a N_P \theta}}\right) - w. \quad \text{(A4)}$$

Solving Eqn (A4) = 0 for N_P gives two solutions where one is negative and the other is

$$N_P = \frac{I_a}{a}\phi\left[\sqrt{\frac{1-\theta}{\frac{ahy}{w} - \theta}}\left(\frac{ahy}{w} - 2\theta\right) + 2\theta - 1\right]. \quad \text{(A5)}$$

Substituting again $N_p = N_c - N_{min}L$ gives optimal N_c (N_c^*)

$$N_c^* = \frac{I_a}{a}\phi\left[\sqrt{\frac{1-\theta}{\frac{ahy}{w}-\theta}}\left(\frac{ahy}{w}-2\theta\right)+2\theta-1\right] + N_{min}L = \frac{I_a\varepsilon_{max}}{a}+N_{min}L \quad \text{where}$$

$$\varepsilon_{max} = \phi\left[\sqrt{\frac{1-\theta}{\frac{ahy}{w}-\theta}}\left(\frac{ahy}{w}-2\theta\right)+2\theta-1\right]$$

Stability of N uptake and demand

In Fig. 2, there is a single value of *RP* where *Nd* is equal to *Nup*. For other values of *RP*, *Nd* is either less than or greater than *Nup*. If *Nup* is less than *Nd*, the plant will experience an N deficit, in response to which the plant will increase the ratio of root N/canopy N (f_r) leading to a decline in N_c^*. As f_r increases, the value of *Nd* will move along the N-demand curve in Fig. 2 towards the intersection where *Nd* = *Nup*. Conversely, if *Nup* exceeds *Nd*, then f_r will decline over time and the value of *Nd* will move in the opposite direction along the N-demand curve towards the intersection shown in Fig. 2. Thus, in both cases, C allocation will change over time so that N demand approaches N uptake. In that sense, the intersections in Fig. 2, where *Nd* = *Nup*, represent stable operating points in terms of root production and N use.