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Plant root distributions and nitrogen uptake predicted by a hypothesis of optimal root foraging

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Abstract

CO_2-enrichment experiments consistently show that rooting depth increases when trees are grown at elevated CO_2 (eCO_2), leading in some experiments to increased capture of available soil nitrogen (N) from deeper soil. However, the link between N uptake and root distributions remains poorly represented in forest ecosystem and global land-surface models. Here, this link is modeled and analyzed using a new optimization hypothesis (*MaxNup*) for root foraging in relation to the spatial variability of soil N, according to which a given total root mass is distributed vertically in order to maximize annual N uptake. *MaxNup* leads to analytical predictions for the optimal vertical profile of root biomass, maximum rooting depth, and N-uptake fraction (i.e., the proportion of plant-available soil N taken up annually by roots). We use these predictions to gain new insight into the behavior of the N-uptake fraction in trees growing at the Oak Ridge National Laboratory free-air CO_2-enrichment experiment. We also compare *MaxNup* with empirical equations previously fitted to root-distribution data from all the world's plant biomes, and find that the empirical equations underestimate the capacity of root systems to take up N.

Introduction

Water and nutrients are heterogeneously distributed in soils (Robinson 1996; Hopmans and Bristow 2002; Hodge 2004; Schimel and Bennett 2004). Therefore models of water and nutrient uptake by plants need to consider the spatial distribution of roots. Virtually, all global land-surface and forest ecosystem models do simulate water uptake from multiple soil-depth layers—even models that do not explicitly consider root distributions (Jackson et al. 1996; Woodward and Osborne 2000). Some include equations for water uptake by three-dimensional root distributions (e.g., Somma et al. 1998; Hopmans and Bristow 2002; Simunek and Hopmans 2009), while others have used water-balance modeling to infer optimal root distributions and maximum rooting depths (Kleidon and Heimann 1996; van Wijk and Bouten 2001; Laio et al. 2006; Collins and Bras 2007; Guswa 2008, 2010; Schymanski et al. 2008, 2009).

Modeling of nutrient uptake in global and ecosystem models is rudimentary in comparison to that of water. Most models evaluate nitrogen (N) uptake from simulated bulk soil net N mineralization rate (N_{min}) above a specified soil depth (Parton et al. 1988; Comins and McMurtrie 1993; Jackson et al. 1996, 2000), or from N_{min} multiplied by a take-up fraction represented by an empirical function of total root mass (Mäkelä et al. 2008; Franklin et al. 2009). Few consider how the spatial distribution of roots affects the efficiency of N capture from soil, although the mechanisms of nutrient transport in soils and uptake by roots have been extensively studied (Hopmans and Bristow 2002).

This shortcoming is a concern in modeling of tree responses to elevated CO_2 (eCO_2) because the majority of experiments show that root distributions are altered when trees are grown at eCO_2, involving in particular an increase in rooting depth (Iversen 2010). For example, at the Oak Ridge National Laboratory (ORNL) forest free-air CO_2-enrichment (FACE) experiment, both peak annual root biomass and annual root production approximately doubled at eCO_2 (Iversen et al. 2011), and the greatest increases in root mass occurred at soil depths below 30 cm, leading to enhanced N extraction from deeper in the soil (Iversen 2010; Iversen et al. 2011). At the Duke Forest FACE experiment (Pritchard et al. 2008; Jackson et al. 2009), fine-root biomass increased by 24% in the top 15 cm of soil (Pritchard et al. 2008; Jackson et al. 2009) and there was a shift to deeper rooting (Pritchard et al. 2008; Iversen 2010). Fine root mass also increased at the Rhinelander Forest FACE experiment (Zak et al. 2011).

In all three FACE experiments, increases in annual tree growth at eCO_2 were associated with increased annual uptake of N by tree roots rather than more efficient use of N taken up (Finzi et al. 2007). It remains uncertain, however, whether the increases in annual N uptake at eCO_2 were due to increased N availability or more efficient capture of N available in the soil, due, possibly, to deeper rooting (Iversen et al. 2008; Norby et al. 2010; Drake et al. 2011; Hofmockel et al. 2011; Phillips et al. 2011; Zak et al. 2011). Understanding of how the N-uptake fraction, that is, the proportion of plant-available soil N taken up annually by roots, depends on the amount and vertical distribution of root biomass is a key to predicting tree growth responses to eCO_2 (Iversen et al. 2010), and in turn feedbacks from the terrestrial biosphere to climate (Norby et al. 2010). Moreover, an enhanced understanding of the N-uptake fraction may foster more efficient use of N fertilizers with potential benefits for managed forests, agriculture, and the environment through reduced use of N fertilizers (Tilman et al. 2002).

Current N-uptake models fall well short of providing such an understanding. The above responses of root distributions to eCO_2 and their consequences for N uptake have not yet been incorporated into land-surface models of the terrestrial biosphere, or into ecosystem models. Instead, coupled land-climate models (Friedlingstein and Prentice 2010) are moving apace to incorporate long-term feedbacks associated with immobilization of N in wood and soils at eCO_2 (Comins and McMurtrie 1993; McMurtrie and Comins 1996; Luo et al. 2004), although these feedbacks have yet to be verified in forest FACE experiments (Norby et al. 2010; Hofmockel et al. 2011; Zak et al. 2011).

Our objective in this study was to address these shortcomings through a new model of the N-uptake fraction that takes account of the vertical distribution of plant-available N in the soil. We define N-uptake fraction as the ratio of the annual rate of plant N uptake to the annual rate at which soil N becomes potentially available to plants. (Potential annual plant-available soil N is the annual rate of supply of bioavailable soil N, for which roots and soil microbes compete, sensu Schimel and Bennett 2004). Our model is based on an optimal root-foraging hypothesis (*MaxNup*), according to which "a given total amount of root biomass is distributed vertically in soil in order to maximize annual N supply to aboveground plant organs (i.e., plant N uptake minus the N investment in growing roots)". N uptake by roots at soil depth z is modeled as a saturating function of root-mass density at z. Using this function, *MaxNup* predicts the optimal vertical profile of root-mass density, rooting depth, and annual N uptake as functions of total root mass. We use these predictions to evaluate the N-uptake fraction of trees growing at the ORNL FACE experiment, and compare predicted root distributions with empirical equations previously fitted to root-distribution data from the ORNL FACE experiment (Iversen 2010) and global plant datasets (Gale and Grigal 1987; Jackson et al. 1996; Arora and Boer 2003). Because our model is simpler than previous models of N uptake by spatially distributed root systems (Somma et al. 1998; Hopmans and Bristow 2002; Simunek and Hopmans 2009), we are able to derive new simple analytic expressions for optimal root distributions and maximum N uptake. The power of simple models, in which biological mechanisms can be clearly understood, versus complex or computationally intensive simulation models is expounded by May (2004). To the best of our knowledge, this is the first time a model has been used to evaluate the efficiency of N uptake by a spatially distributed root system.

Methods

The *MaxNup*-optimization hypothesis

According to the *MaxNup* hypothesis, the annual amount of N exported from the root system to support the growth of nonroot tissues (U_{net}, g N m^{-2} land area year^{-1}) is maximized with respect to the vertical distribution of fine-root mass per unit soil volume ($R(z)$, kg DM m^{-3}) and the maximum rooting depth (D_{max}, m), subject to the constraint of a given total amount of root biomass per unit land area (R_{tot}, kg DM m^{-2}). Maximization of U_{net} for a given amount of root biomass is a reasonable modeling objective at an N-limited site, as any nonoptimal root distribution would result in less N export to aboveground pools. The modeled U_{net}–R_{tot} relationship can be viewed as a "return on investment", the return being annual N gain by nonroot tissues for a given carbon (C) investment in roots. (Note: Under conditions where N is nonlimiting but C is limiting, an analogous hypothesis may apply, namely minimization of annual C investment in roots required to achieve a given annual N uptake. This case will not be considered further here.) We implemented *MaxNup* using a simple model of annual N uptake per unit soil volume by roots at depth z ($U_r(z)$, g N m^{-3} year^{-1}) as a saturating function of $R(z)$:

$$U_r(z) = \frac{U_o(z)}{1 + R_o/R(z)}, \quad (1)$$

where $U_o(z)$ (potential annual plant N uptake) is the asymptotic N-uptake rate in the limit $R(z) \to \infty$ and R_o (kg DM m^{-3}), the root-mass density yielding half the potential N-uptake rate, determines the initial slope of the U_r–R relationship. $U_o(z)$ is assumed to be greatest at the soil surface and to decrease exponentially with depth (cf. Jackson et al. 2000; Jobbágy and Jackson 2001):

$$U_o(z) = \frac{U_{max}}{D_o} e^{-z/D_o}, \quad (2)$$

where U_{max} is total potential annual N uptake integrated over all soil depths, and D_o is the length scale for exponential decline of available soil N. The assumption that U_o decreases exponentially with depth is supported by measurements of gross mineralization and extractable inorganic N over depths 0–90 cm at the ORNL experiment (Iversen et al. 2011, 2012). (Note: *MaxNup* may be applied using any given function $U_o(z)$ [eqs. A18 and A19].) Root-mass density R is related to root-length density (L_r, cm root length cm^{-3}): $R = \pi r_o^2 \rho_r L_r$, where r_o (cm) and ρ_r (kg DM m^{-3}) are the radius and tissue density of roots, respectively. Hence, $L_{ro} = R_o/\pi r_o^2 \rho_r$ represents root-length density at half potential N-uptake rate.

Our representation of plant N uptake per unit soil volume at depth z in terms of one equation for plant-available N at z (eq. 2) and one for the fraction of available N taken up by roots (eq. 1), with root biomass and its depth distribution held constant over time, is a gross simplification of the complex processes, including root–microbe interactions that operate in plant rhizospheres (Schimel and Bennett 2004; Wardle et al. 2004; Frank and Groffman 2009). The advantage of making these simplifications is that they enable us to derive simple analytic expressions (below) for annual N uptake by spatially distributed root systems. However, as discussed in Appendix A1, a mechanistic basis for equation (1) can be derived from the Barber–Cushman (BC) model (Darrah 1993; Yanai 1994) that describes mass flow and diffusion of soil N toward root surfaces down a concentration gradient, and competition between root N uptake and soil microbial N immobilization. In the BC model, nutrient uptake per unit soil volume depends on root surface area per unit soil volume, which is proportional to L_r and nutrient influx I per unit root surface area, which is a function of solute concentration at the root surface (Yanai 1994). The U_r–R relationship derived from the BC model is well approximated by equation (1) (Fig. A1). The value of L_{ro} fitted to the BC model depends on the capacity of roots to absorb solute N and the rate of solute N transport toward root surfaces relative to the rate of N immobilization by microbial decomposers.

Equation (1) is shown in Figure 1a at four soil depths in a system of roots with $R_o = 0.265$ kg DM m^{-3} and $D_o = 0.3$ m. At low root-mass density (R), the bulk of available N is immobilized because the distance between roots is relatively large, which increases the likelihood that solute is immobilized before reaching the root surfaces. As R increases the inter-root distance decreases, so a greater proportion of solute reaches the root surfaces without being immobilized.

The net annual N export to aboveground pools by roots at depth z ($U_n(z)$, g N m^{-3} year^{-1}) is equal to $U_r(z)$ minus the annual N investment in growing roots at depth z:

$$U_n(z) = U_r(z) - N_r R(z)/\tau_r, \quad (3)$$

where N_r (g N kg^{-1} DM) is the N concentration of roots and τ_r (year) is root life span. Equation (3) is derived from equation (1) under assumptions that root mass is maintained at a steady state where annual root production equals annual mortality, and that there is no N retranslocation at root senescence (Gordon and Jackson 2000). In contrast to the U_r–R relationship (Fig. 1a), the U_n–R relationship has a peak that shifts to lower R values with increasing depth z (Fig. 1b).

We applied *MaxNup* to the total annual N exported to aboveground pools (U_{net}, g N m^{-2} year^{-1}) obtained by integrating equation (3) through the rooting zone from $z = 0$ (surface) to $z = D_{max}$ (maximum rooting depth):

$$U_{net} = \int_0^{D_{max}} U_n(z)\, dz. \quad (4)$$

Likewise, annual total N uptake per unit land area (U_{tot}, g N m^{-2} year^{-1}) is the integral of annual uptake per unit soil volume by roots at depth z ($U_r(z)$, g N m^{-3} year^{-1}) from the soil surface to D_{max}:

$$U_{tot} = \int_0^{D_{max}} U_r(z)\, dz, \quad (5)$$

where U_r is a saturating function of $R(z)$ (eq. 1; Fig. 1a). Total root mass per unit land area (R_{tot}, kg DM m^{-2}) is the integral of root-mass density ($R(z)$, kg DM m^{-3}) from the soil surface to D_{max}:

$$R_{tot} = \int_0^{D_{max}} R(z)\, dz. \quad (6)$$

Our optimization hypothesis *MaxNup* is that for a given total root mass R_{tot}, roots are distributed vertically in order to maximize annual N supply to aboveground pools (U_{net}). The optimal solution for $R(z)$ and maximum rooting depth D_{max} is obtained using the Lagrange multiplier method described in Appendix A2. It turns out that if N_r and τ_r are constant throughout the root system, the solution for $R(z)$ that maximizes U_{net} also maximizes U_{tot}.

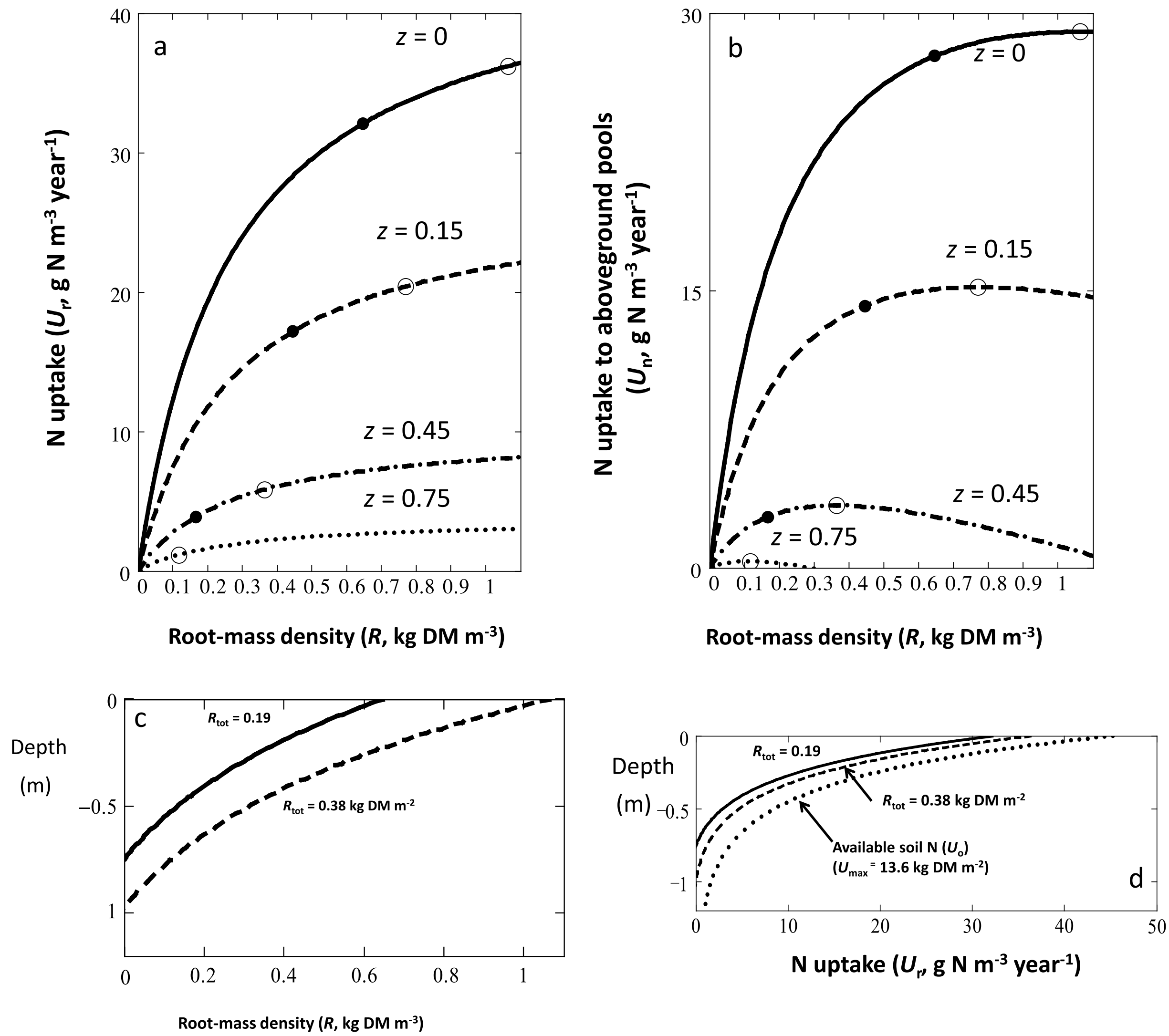

Figure 1. Optimal vertical profiles predicted by *MaxNup*: (a) Total annual N uptake per unit soil volume ($U_r(z)$, g N m^{-3} year^{-1}) and (b) annual N supply to aboveground pools per unit soil volume ($U_n(z)$, g N m^{-3} year^{-1}) versus root-mass density ($R(z)$, kg DM m^{-3}) at the soil surface ($z = 0$) and at depths $z = 0.15$, 0.45, and 0.75 m. The optimal solution is shown for total root mass per unit land area $R_{tot} = 0.19$ (solid circles) and 0.38 (open circles) kg DM m^{-2}. Optimal profiles of (c) $R(z)$ and (d) $U_r(z)$ are shown for $R_{tot} = 0.19$ and 0.38 kg DM m^{-2}, for which $D_{max} = 0.74$ and 0.97 m, $U_{tot} = 6.8$ and 8.7 g N m^{-2} year^{-1}, and $U_{net} = 5.5$ and 6.1 g N m^{-2} year^{-1}, respectively. The vertical profile of potential annual N uptake $U_o(z)$ is shown in (d).

Field site

The model has been parameterized (see Table 1) for plantations of the deciduous tree *Liquidambar styraciflua* (sweetgum) growing over an 11-year period at CO_2 concentrations of 385 (aCO_2) and 550 ppm (eCO_2) at the ORNL FACE experiment. The CO_2 treatment commenced in 1998, 10 years after the plantation was established with two plots operated at eCO_2 and three at aCO_2. The experiment has been described fully elsewhere (see Norby et al. [2010] and references therein). Methods used for root biomass and N-uptake measurements shown in Figure 2 are described in Iversen et al. (2008) and Norby et al. (2008, 2010). Data from the FACE experiment are publicly available through the Carbon Dioxide Information Analysis Center (http://cdiac.ornl.gov), U.S. Department of Energy, Oak Ridge National Laboratory, Oak Ridge, TN.

Results

Optimal vertical profiles of root-mass density and N uptake predicted by *MaxNup*

The maximum possible U_{net} would be achieved if root-mass density ($R(z)$) were held at the peak of the U_n–R relationship shown in Figure 1b at all depths z. However, if the total

Table 1. Symbol definitions, source references, units, and parameter values used in the model. Source notations are as follows: (1) Leadley et al. (1997); (2) Jackson et al. (1996); (3) Iversen (2010); (4) Iversen et al. (2012); (5) Arora and Boer (2003); (6) Yanai (1994); (7) Norby et al. (2008); (8) Iversen et al. (2008); (9) Johnson et al. (2004); (10) Norby et al. (2010); (11) Finzi et al. (2007); and (12) Darrah (1993), Somma et al. (1998), Corbeels et al. (2005a, b).

Symbol	Definition and source, (relevant equation)	Value and units
b	Buffer power of soil[1], (A3)	5
$C_s(r)$, C'_s	Solute concentration at radial distance r from the root surface, dimensionless solute concentration, (A3), (A4)	mol N cm^{-3}, -
C_o, C'_o	Solute concentration at the root surface, dimensionless solute concentration at the root surface, (A1), (A8)	mol N cm^{-3}, -
$CRP(z)$	Empirical function for cumulative root proportion to depth z[2,3], (15)	-
D_{max}	Maximum rooting depth, (4)	m
D_o	Length scale for exponential decline of U_o with depth[4], (2)	0.3 m
E	Daily water extraction by roots from unit soil volume, (A3)	cm^3 water cm^{-3} soil volume day^{-1}
$F(z)$	Empirical function for root-depth distribution[5], (14)	m^{-1}
I	Rate of N uptake by root per unit root surface area[6], (A1)	mol N cm^{-2} root surface day^{-1}
$L_r(z)$, L'_r	Root-length density at depth z, dimensionless root-length density, (A1), (A6)	cm root cm^{-3} soil volume, –
L_{ro}	Root-length density at half maximum potential N uptake, (1)	0.77 cm^{-2}
L'_{ro}	Dimensionless root-length density at half-maximum potential N uptake, (A9)	-
N_r	Nitrogen concentration of fine roots[7], (3)	6.8 g N (kg DM)$^{-1}$
r, r'	Radial distance from centre of root, dimensionless radial distance, (A3), (A5)	cm, -
r_o , r'_o	Fine-root radius[8], dimensionless root radius, (A1), (A7)	0.017 cm, -
r_x , r'_x	Inter-root distance[6], dimensionless inter-root distance, (A2), (A7)	cm, -
$R(z)$	Root mass per unit soil volume, or root-mass density at depth z, (1)	kg DM m^{-3}
R_{av}	Average root-mass density over the rooting zone, (A21)	kg DM m^{-3}
R_o	Root-mass density at half maximum potential N uptake, (1)	0.265 kg DM m^{-3}
R_{tot}	Total root biomass per unit land area[7,8], (6)	kg DM m^{-2}
u_{maxi}	Potential N uptake per unit land area on day i, (A31)	g N m^{-2} day^{-1}
$u_{oi}(z)$	Potential N uptake per unit soil volume at depth z on day i, (A29)	g N m^{-3} day^{-1}
$u_{ri}(z)$	N uptake per unit soil volume at depth z on day i, (A29)	g N m^{-3} day^{-1}
U	N uptake per unit soil volume derived from the Barber–Cushman model, (A1)	mol N cm^{-3} day^{-1}
U_o	Potential annual N-uptake rate per unit soil volume[9], (1), (A3)	g N m^{-3} year^{-1}(Main text, Appendices A2 and A3), mol N cm^{-3} day^{-1} (Appendix A1),
$U_o(z)$	Potential annual N uptake per unit soil volume at depth z, (1)	g N m^{-3} year^{-1}
$U_n(z)$	Annual N supply to aboveground pools per unit soil volume, (3)	g N m^{-3} year^{-1}
$U_r(z)$	Annual total N uptake per unit soil volume, (1)	g N m^{-3} year^{-1}
U_{max}	Potential annual N uptake per unit land area integrated over the soil profile $(= \int_0^\infty U_o(z)dz)$[9], (2)	13.6 g N m^{-2} year^{-1}
U_{net}	Annual N supply to aboveground pools per unit land area[7,10], (4)	g N m^{-2} year^{-1}
U_{tot}	Annual total N uptake per unit land area[7,11], (5)	g N m^{-2} year^{-1}
z	Soil depth, (1)	m
Z_o	Length scale for the exponential decline of empirical root distribution with depth[5], (14)	m
α, α'	Root absorbing capacity[1,6], dimensionless root absorbing capacity $(\alpha/\sqrt{\mu\Delta b})$, (A1), (A8)	5.33 cm day^{-1}, -
β	Exponent in the empirical relationship for cumulative root proportion[2,3], (15)	0.914 (tundra), 0.972 (aCO_2), 0.984 (eCO_2)
Δ	Diffusion coefficient of nutrient in soil[1], (A3)	0.052 cm^2 day^{-1}
ϕ_N, ϕ_{net}	Gross N-uptake fraction ($= U_{tot}/U_{max}$) and net N-uptake fraction ($= U_{net}/U_{max}$), (12), (13)	-
ϕ_{N_peak}, ϕ_{net_peak}	Peak values of ϕ_N and ϕ_{net}, (A28), (A27)	-
λ	Lagrange multiplier $\partial U_n/\partial R$, (A10)	g N kg^{-1} DM year^{-1}
μ	Rate of solute loss from the rhizosphere through immobilisation by soil microbes[12], (A3)	day^{-1}
ρ_r	Root-tissue density[8], (1)	380 kg DM m^{-3}
ξ	Expression $\sqrt{R_{tot}N_r/(U_{max}\tau_r) + \phi_{net}}$, (13)	-
τ_r	Root lifespan[8], (3)	1 year
Ψ	Goal function, (A10)	g N m^{-2} year^{-1}
ζ	Expression $R_oD_oN_r/(U_{max}\tau_r)$, (A25)	-

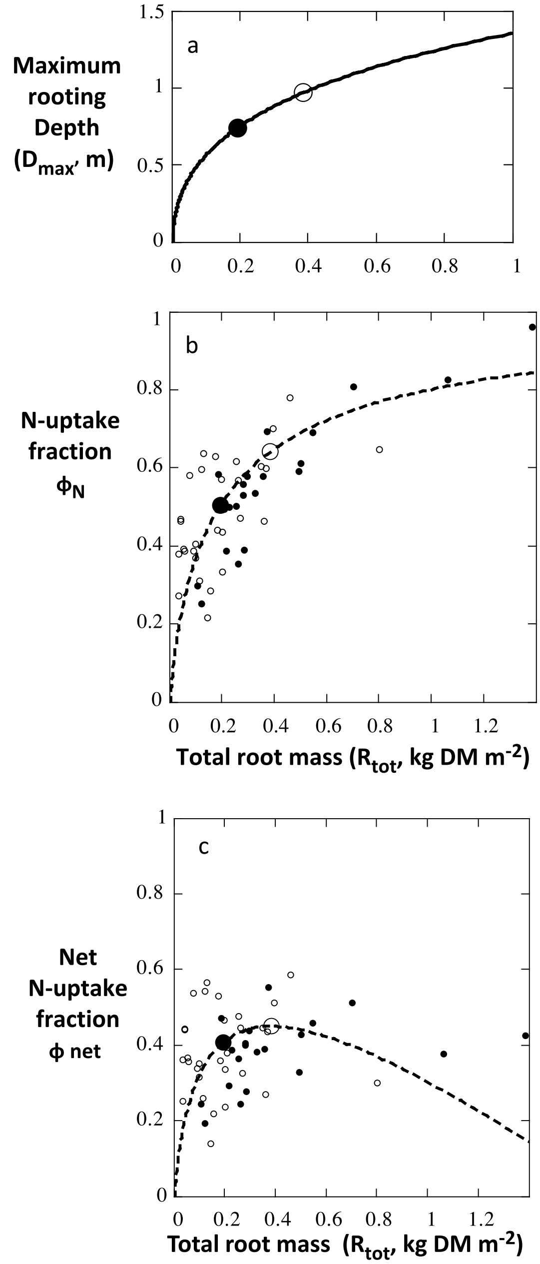

Figure 2. Effects of increasing total root mass predicted by the *MaxNup*-optimization hypothesis: (a) maximum rooting depth (D_{max}, m) versus total root mass per unit land area (R_{tot}, kg DM m^{-2}) (eq. 8); (b) gross N-uptake fraction (ϕ_N) (eq. 12) versus R_{tot}; and (c) net N-uptake fraction (ϕ_{net}) versus R_{tot} (eq. 13). The large closed and open circles represent optimal values of D_{max}, ϕ_N, and ϕ_{net} when $R_{tot} = 0.19$ and 0.38 kg DM m^{-2}, respectively (cf. Fig. 1). The small closed and open circles in (a) represent measured annual N uptake (U_{tot}) divided by U_{max} for elevated (eCO_2) and ambient (aCO_2) CO_2 treatments, respectively, where U_{max} (= 13.6 g N m^{-2} year^{-1}) and R_o (= 0.265 kg DM m^{-3}) were estimated by fitting equation (13) to annual measurements of U_{net} and peak annual root mass (R_{tot}) for all plots at the ORNL FACE experiment. The small closed and open circles in (b) represent measured annual N supply to aboveground pools (U_{net}) divided by U_{max} for eCO_2 and aCO_2 treatments, respectively.

amount of root biomass (R_{tot}) is too low, then it is not possible to operate at the peak of the U_n–R relationship at all depths unless maximum rooting depth (D_{max}) is small; a higher value of U_{net} might be achieved by operating to the left of the peak of the U_n–R relationship with deeper roots (larger D_{max}). As shown in Appendix A2, for a given total root mass (R_{tot}), U_{net} is maximized when the increase in N-uptake rate $U_r(z)$ associated with a small local increase in root-mass density $R(z)$ (i.e., the marginal gain in N uptake, $\partial U_r/\partial R$) has the same value throughout the rooting zone, which is given by its value $U_o(D_{max})/R_o$ at the maximum rooting depth (D_{max}), where the optimal $R = 0$ (eq. A17). Provided N_r, τ_r, and R_o (i.e., L_{ro}, r_o, and ρ_r) are independent of z, we obtain the vertical profile of optimal $R(z)$:

$$R(z) = R_o\left(e^{\frac{D_{max}-z}{2D_o}} - 1\right), \quad (7)$$

which is illustrated in Figure 1c. The length scale for the decrease of $R(z)$ in equation (7) ($2D_o$) is twice the length scale for the exponential decrease of available soil N ($U_o(z)$, eq. 2). The optimal profile of $R(z)$ (Fig. 1c) is thus less steep than the profile of $U_o(z)$ (Fig. 1d). (Note: This conclusion might not hold if R_o were a decreasing function of depth.) Total root mass (eq. 6) is

$$R_{tot} = R_o\left(2D_o\left(e^{\frac{D_{max}}{2D_o}} - 1\right) - D_{max}\right). \quad (8)$$

The optimal vertical profile of annual total N uptake $U_r(z)$ is obtained by substituting equation (7) into equation (1):

$$U_r(z) = U_o(z)\left(1 - e^{-\frac{D_{max}-z}{2D_o}}\right). \quad (9)$$

An analogous equation for the optimal profile of N supply to aboveground pools $U_n(z)$ is given by equation (A20). Total annual N uptake U_{tot} and annual N supply to aboveground pools U_{net} are obtained from equations (5) and (4), respectively:

$$U_{tot} = U_{max}\left(1 - e^{-\frac{D_{max}}{2D_o}}\right)^2, \quad (10)$$

where U_{max} is total potential N uptake, and

$$U_{net} = U_{tot} - N_r R_{tot}/\tau_r. \quad (11)$$

The solid circles in Figure 1a and b indicate the optimal values of $U_r(z)$, $U_n(z)$, and $R(z)$ at four soil depths for a total root mass of $R_{tot} = 0.19$ kg DM m^{-2}. Figure 1c and d shows the corresponding complete vertical profiles of optimal $R(z)$ (eq. 7) and $U_r(z)$ (eq. 9) as well as the optimal profiles for a root system with twice the total root mass (R_{tot} = 0.38 kg DM m^{-2}). With this doubling of R_{tot}, the optimal root-mass density $R(z)$ increases throughout the rooting zone, and the maximum rooting depth D_{max} increases from 0.74 to 0.97 m (Figs. 1c and 2a). Total N uptake U_{tot}, evaluated from equation (10), increases from 6.8 to 8.7 g N m^{-2} land area year^{-1}. In contrast, the total potential N uptake over the rooting zone ($U_{max} = \int_0^\infty U_o(z)dz$) is 13.6 g N m^{-2} land area year^{-1}, which greatly exceeds the predicted values of $U_{\rm tot}$, indicating that much available soil N remains untapped by these root systems. In Figure 1d, the optimal profiles of $U_{\rm r}(z)$ are compared with the vertical profile of annual potential N uptake $U_{\rm o}(z)$. The difference between $U_{\rm r}(z)$ and $U_{\rm o}(z)$ is considerable. For these two values of $R_{\rm tot}$, respectively, 50% and 36% of potentially available soil N throughout the rooting zone are not taken up; in fact, as the results below will show, in terms of $U_{\rm net}$, it would be uneconomic to do so due to the additional N cost of growing more root mass.

Relationships between optimal rooting depth, N-uptake fraction, and total root mass predicted by *MaxNup*

The optimization hypothesis *MaxNup* predicts the optimal values of maximum rooting depth ($D_{\rm max}$), total annual N uptake ($U_{\rm tot}$), and annual N export to aboveground pools ($U_{\rm net}$) as functions of total root mass ($R_{\rm tot}$) (eqs. 8, 10, and 11, respectively). $D_{\rm max}$ can be eliminated from equations (8) and (10) to obtain a relationship between the fraction of available N taken up annually ($\phi_{\rm N} = U_{\rm tot}/U_{\rm max}$) and total root mass $R_{\rm tot}$:

$$\left(\frac{\sqrt{\phi_{\rm N}}}{1-\sqrt{\phi_{\rm N}}} + \ln(1-\sqrt{\phi_{\rm N}})\right) = \frac{R_{\rm tot}}{2R_{\rm o}D_{\rm o}}. \qquad (12)$$

An analogous relationship between the fraction of available N distributed to aboveground pools ($\phi_{\rm net} = U_{\rm net}/U_{\rm max}$) and $R_{\rm tot}$ is obtained by combining equations (11) and (12):

$$\left(\frac{\xi}{1-\xi} + \ln(1-\xi)\right) = \frac{R_{\rm tot}}{2R_{\rm o}D_{\rm o}}, \qquad (13)$$

where $\xi = \sqrt{R_{\rm tot}N_r/(U_{\rm max}\tau_{\rm r}) + \phi_{net}}$. Equation (13) was fitted to annual measurements of peak annual root mass to a soil depth of 60 cm ($R_{\rm tot}$) and annual N supply to aboveground pools ($U_{\rm net}$) from the ORNL FACE experiment with $R_{\rm tot}$ as independent variable and $U_{\rm net}$ as dependent variable. Values of $U_{\rm max}$ and the product $R_{\rm o}D_{\rm o}$ were estimated with $\tau_{\rm r} = 1$ year (Iversen et al. 2008) and $N_{\rm r}$ = the average of measured root N concentration over all plots and years (6.8 g N kg^{-1} DM, Norby et al. 2008), yielding $U_{\rm max}$ = 13.6 g N m^{-2} year^{-1} and $R_{\rm o}$ = 0.265 kg DM m^{-3} with $D_{\rm o}$ = 0.3 m. The corresponding value of root-length density at half potential N-uptake rate is $L_{\rm ro}$ = 0.77 cm^{-2}. Modeled relationships between gross N-uptake fraction ($\phi_{\rm N}$) and $R_{\rm tot}$ (eq. 12) and net N-uptake fraction ($\phi_{\rm net}$) and $R_{\rm tot}$ (eq. 13) are shown in Figure 2b and c, respectively, along with data from the ORNL experiment. The modeled relationship between maximum rooting depth ($D_{\rm max}$) and $R_{\rm tot}$ is illustrated in Figure 2a. Initially, both $D_{\rm max}$ and $\phi_{\rm N}$ increase rapidly with $R_{\rm tot}$, but, because N uptake is a saturating function of root-mass density (eq. 1), their rates of increase slow as $R_{\rm tot}$ increases further, with $\phi_{\rm N}$ approaching 1 asymptotically as $R_{\rm tot} \to \infty$. Compared to $\phi_{\rm N}$, the net N-uptake fraction $\phi_{\rm net}$ increases less rapidly with $R_{\rm tot}$ due to the increasing N cost of growing more root mass. $\phi_{\rm net}$ reaches a peak when $R_{\rm tot}$ = 0.38 kg DM m^{-2} (indicated by the open circles in Figs. 1a and b and 2) and then decreases at higher $R_{\rm tot}$ (cf. Franklin et al. 2009). When $\phi_{\rm net}$ is at its peak, $U_{\rm n}(z)$ is maximized with respect to $R(z)$ throughout the rooting zone (i.e., $\partial U_{\rm n}/\partial R) = 0$, open circles Fig. 1b).

The relationships shown in Figure 2b and c indicate that there is a diminishing N return from increased C investment in roots. Under a doubling of $R_{\rm tot}$ from 0.19 to 0.38 kg DM m^{-2} (respectively, large solid and open circles in Fig. 2b and c), $\phi_{\rm N}$ increases by only 28% (0.50–0.64) while $\phi_{\rm net}$ increases by only 11% (0.41–0.45). For both $\phi_{\rm N}$ and $\phi_{\rm net}$, the diminishing returns from increased $R_{\rm tot}$ are associated with competition between N uptake by roots and N immobilization by soil microbes, which led to the saturating $U_{\rm r}$–R relationship in equation (1). For $\phi_{\rm net}$, the more severe negative return from increased $R_{\rm tot}$ beyond the peak reflects the additional N cost of growing more root mass, which may be offset somewhat if the extra roots have lower N concentrations ($N_{\rm r}$), or longer life spans ($\tau_{\rm r}$), or are thicker (higher $r_{\rm o}$) (cf. Iversen et al. 2008) (see Appendices A2 and A3). Thus, if $R_{\rm tot}$ were to exceed its value (0.38 kg DM m^{-2}) for peak $\phi_{\rm net}$, then although total N uptake would increase (cf. Fig. 1d), N supply to aboveground plant organs would decrease, which would seem to be detrimental. However, it may be advantageous to an individual plant for its $R_{\rm tot}$ to increase beyond the peak if it allows that plant to lock up nutrients at the expense of its competitors, and this strategy can be evolutionarily stable (King 1993; Hodge 2009; Dybzinski et al. 2011; Franklin et al. 2012).

Comparison with previous modeling of root-depth distributions

We have compared root-depth distributions predicted by *MaxNup* with the following empirical equations previously fitted to root-distribution data from the ORNL FACE experiment (Iversen 2010) and global plant datasets (Gale and Grigal 1987; Jackson et al. 1996; Arora and Boer 2003):

$$F(z) = e^{-z/Z_{\rm o}}/Z_{\rm o}, \qquad (14)$$

where $F(z)$ represents the fraction of root-mass density at depth z and Z_0 is the length scale of the exponential decline of root-mass density with depth (Arora and Boer 2003), and

$$CRP(z) = 1 - \beta^{100z}, \qquad (15)$$

where $CRP(z)$ represents the cumulative root proportion between the soil surface and depth z (Gale and Grigal 1987; Jackson et al. 1996; Arora and Boer 2003). Equations (14) and (15) are equivalent if $\beta = e^{-1/(100Z_{\rm o})}$. Estimated values of the empirical parameter β for the ambient and elevated CO_2 treatments at the ORNL FACE experiment are 0.972 and 0.984, respectively (Iversen 2010), and range over the world's

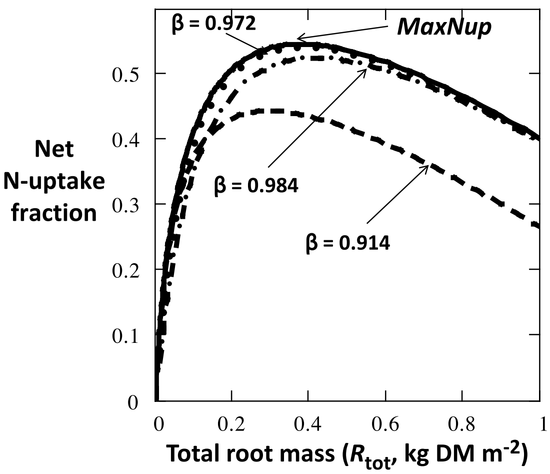

Figure 3. Comparison of net N-uptake fraction (ϕ_{net}) predicted by *MaxNup* versus that obtained from an empirical root-depth distribution. Relationships between ϕ_{net} and R_{tot} obtained for the empirical root distribution (eq. 14) are shown for a shallow-rooted species with $\beta = 0.914$ (dashed line), and for $\beta = 0.972$ (dotted line) and 0.984 (dot–dash line), which are values estimated for aCO_2 and eCO_2 treatments at the ORNL FACE experiment, respectively. Corresponding values of the length-scale Z_o are 0.11, 0.35, and 0.52 m, respectively. For any value of R_{tot}, ϕ_{net} predicted by *MaxNup* exceeds that predicted by the empirical root distributions, though the relationship obtained with $\beta = 0.972$ is similar to that predicted by *MaxNup*.

biomes from 0.914 for tundra vegetation, which tends to be shallow rooted, to 0.976 for temperate coniferous forests (Jackson et al. 1996). A fundamental problem with equation (15) is that it is inconsistent with data on how the *CRP–z* relationship actually changes with increasing total root mass R_{tot}, namely, the maximum rooting depth increases and the entire *CRP–z* relationship shifts downward (Arora and Boer 2003). In contrast, root-depth distributions derived from *MaxNup* (eqs. 7 and A22) are consistent with data in this respect (Fig. 1c), while they are also consistent with equations (14) and (15) near the soil surface. *MaxNup* therefore provides a more robust model of root-depth distribution than do equations (14) and (15).

Figure 3 compares the net N-uptake fraction (ϕ_{net}) predicted by *MaxNup* with that obtained from equation (14) as functions of R_{tot} over a representative range of β values. (The net N-uptake fraction obtained from equation (14) was evaluated from the expression $\int_0^\infty U_n(z)\mathrm{d}z/U_{max}$, where U_n was obtained by substituting eq. 14 into eqs. 1 and 3.) As expected, at any value of R_{tot}, ϕ_{net} predicted by *MaxNup* exceeds the net N-uptake fraction obtained from the empirical distribution (Fig. 3), because U_{net}, and hence ϕ_{net}, is reduced by any departure from the optimal root profile represented by equation (7), or any variation in maximum rooting depth from the optimum. Thus, equation (14) underestimates the capacity of root systems to take up N. The underestimation is especially large for the shallow empirical distribution ($\beta = 0.914$), whereas the empirical distribution with $\beta = 0.972$ only slightly underestimates U_{net}. However, the empirical distribution, which has roots extending to infinite depth, differs qualitatively from that predicted by *MaxNup*, for which maximum rooting depth (D_{max}) varies from 0 to 1.3 m as R_{tot} increases from 0 to 1 kg DM m^{-2} (Fig. 2a).

Discussion

Increased N uptake by forests growing at elevated CO_2

The *MaxNup* hypothesis provides equations predicting how increasing root mass (R_{tot}) affects total annual N uptake (U_{tot}, Fig. 2b) and N supply to aboveground pools (U_{net}, Fig. 2c). These equations are consistent with data from the ORNL FACE experiment (Fig. 2b and c), suggesting that the observed increase in N uptake at eCO_2 in that experiment may be a consequence of the measured increase in root growth at eCO_2. Mechanisms for increased N uptake under eCO_2 at the ORNL experiment were evaluated by Johnson et al. (2004), who used measurements of in situ soil incubations to estimate the size of the mineralizable N pool, which was reasoned to be large enough to have supplied the additional N taken up at eCO_2. It was speculated that plant roots are somehow able to outcompete microbes at eCO_2 (cf. Mosier et al. 2002; Schimel and Bennett 2004). Our modeling supports that view and proposes a mechanism in terms of increased root growth at eCO_2 leading to increased gross N-uptake fraction (ϕ_N). However, the issue of why fine-root biomass increases at eCO_2 at the ORNL FACE and other experiments (e.g., Luo et al. 2006) cannot be resolved by *MaxNup* itself. Resolution of that issue might be achieved by linking *MaxNup* to a compatible model of forest productivity that predicts optimal belowground-C allocation (e.g., Mäkelä et al. 2008; Franklin et al. 2009).

MaxNup offers insight into the puzzling observation from the ORNL FACE experiment that although total annual N uptake increased greatly at eCO_2, the bulk of the increase in N uptake at eCO_2 was used to grow more roots (Iversen et al. 2008; Norby et al. 2010), and there was no difference in annual N supply to aboveground pools between ambient CO_2 (aCO_2) and eCO_2 treatments over 11 years of experimentation. The contrast is illustrated by measured annual values of total N uptake (U_{tot}) and N supply to aboveground pools (U_{net}) shown in Norby et al. (2006, 2010). According to the *MaxNup* hypothesis, ϕ_{net} varies much less than ϕ_N with increasing R_{tot} and even decreases if R_{tot} is large enough (Fig. 2b and c). This prediction may help to explain why measured annual N supply to aboveground pools is insensitive to eCO_2.

Future modeling research on why forest N uptake increases at eCO_2, as reported by Finzi et al. (2007), needs to consider mechanisms other than increased root foraging. These include (1) increased N availability due to accelerated decomposition of soil organic matter associated with enhanced root exudation, the so-called "priming" effect (Finzi et al. 2007; Frank and Groffman 2009; Drake et al. 2011; Phillips et al. 2011; Zak et al. 2011), which was modeled by Schimel and Weintraub (2003) and Blagodatskaya and Kuzyakov (2008); (2) increased asymbiotic N fixation at eCO_2 (Johnson et al. 2004; Hofmockel et al. 2011)); (3) differences in the abundance of N in chemical forms with contrasting mobility in soil (Johnson et al. 2004; Iversen et al. 2011, 2012); and (4) changes in soil N availability over time caused by altered litter C and N inputs to soil (McMurtrie and Comins 1996; McMurtrie et al. 2000; Luo et al. 2004). It would be possible to incorporate mechanisms (1) and (2) into our model in a preliminary way by varying the parameter U_{max}. Mechanism (3) could be incorporated by altering the diffusion coefficient (Δ, eq. A3).

Future model applications

MaxNup makes predictions of the optimal trade-off between average root-mass density over the rooting zone and maximum rooting depth for a given total root mass (eq. A21), which could be tested using root datasets (Jackson et al. 1996; Arora and Boer 2003; Iversen 2010). This proposed work may focus on explaining variation in root-depth distributions between contrasting environments (Jackson et al. 1996) or on analyzing covariation of root traits (cf. Eissenstat et al. 2000).

Validation of equations (7)–(11) derived from *MaxNup* would provide robust predictors of root-depth distributions and N uptake that are suitable for incorporation into forest-ecosystem models and coupled models of land-biogeochemistry and climate. In these larger scale models, daily N uptake could be calculated (see Appendix A4) by multiplying daily soil-N supply derived from an established decomposition model such as CENTURY (Parton et al. 1988) by the gross N-uptake fraction ϕ_N derived from *MaxNup*; only two parameters (R_o and D_o) would be required to calculate ϕ_N (eq. 12). The large-scale models would then be better placed to simulate the effects of global change on rooting depth, root and soil C, plant N uptake, and terrestrial C sequestration. Incorporation of these effects into ecosystem models is crucial so models will have a capacity to simulate the depth distribution of available soil N, and its variation over time, in contrast to our unrealistic assumptions above that the vertical profiles of available soil N (eq. 2) and root biomass are constant over time. According to *MaxNup*, the depth distribution of plant-available soil N determines the depth distribution of roots. However, in natural ecosystems, the depth distribution of available soil N is dependent on the depth distribution of C and N inputs to soil from decomposing roots. Therefore, the depth distribution of roots feeds back on the distribution of available soil N, so that the two distributions may vary in concert during stand development.

Another potential application of *MaxNup* is to quantify the effect of N fertilization on the efficiency of N capture by roots. Experiments in forests (Miller et al. 1976), peatland (Iversen et al. 2011) and agricultural systems (Tilman et al. 2002; Chen et al. 2011) have shown that N-uptake efficiency decreases with N addition. However, there is a dearth of models that relate the fraction of fertilizer taken up to the spatial distributions of available soil N and roots. If an improved understanding of N-uptake fraction based on *MaxNup* leads to more efficient utilization of N fertilizers, then it may be possible to optimize yield with reduced N fertilizer inputs, with benefits to food security and the environment (Tilman et al. 2002; Parry and Hawkesford 2010). Fertilizer practices conducive to improved N-uptake efficiency may include optimal spatial placement of fertilizer, timing of fertilizer applications, use of organic rather than inorganic N fertilizers (which would have different diffusion rates in soil and hence different R_o, as well as different root absorbing capacities), and mixed cropping (Tilman et al. 2002; Chen et al. 2011; Good and Beatty 2011).

Finally, we note three generalizations of the model presented here. First, *MaxNup* predicts that the marginal gain in nutrient uptake $\partial U_n / \partial R$ is constant throughout the rooting zone. This prediction was applied here to an idealized soil in which N availability decays exponentially with soil depth (eq. 2), but should hold more generally (see eqs. A12 and A19), including to three-dimensional and patchy distributions of available soil N (Robinson 1996; Hopmans and Bristow 2002; Hodge 2004; Schimel and Bennett 2004). Furthermore, it should be possible to apply *MaxNup* to soil nutrients other than N, whose availability decreases with soil depth (Jackson et al. 2000; Jobbágy and Jackson 2001); it is advantageous that the Barber–Cushman model has been parameterized for a wide range of nutrients (e.g., Darrah 1993; Yanai 1994). Second, root distributions are presumably optimized relative to the supply of water as well as nutrients (Kleidon and Heimann 1996; van Wijk and Bouten 2001; Laio et al. 2006; Collins and Bras 2007; Guswa 2008, 2010; Schymanski et al. 2008, 2009). Analogous to *MaxNup* would be the prediction of root distributions that maximize water uptake for a given total root mass (*MaxWup*). However, important differences between *MaxWup* and *MaxNup* would be that in dry conditions available soil water may increase with soil depth, in contrast to our assumption (eq. 2) that N availability decreases with depth, and that plants may sometimes need to be conservative in their water use, or may need to maintain some deep tap roots in order to survive drought periods. Third, extension of the *MaxNup* hypothesis, as presented above, to systems limited by two (or more) resources (water or different chemical forms of N or different nutrients) could be accomplished by modifying the optimization hypothesis to consider maximization of multiple objective functions (annual uptake of each resource) under the constraint of fixed annual C investment in roots. That hypothesis would lead to an equation, relating annual C investment in roots to uptake fractions of each resource; C investment in roots could include C costs of N acquisition (Fisher et al. 2010) and root-respiratory costs integrated over the root life span (cf. the leaf-life span integrals in McMurtrie and Dewar (2011)).

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Conflict of Interest

The authors declare no conflict of interest.

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Appendix A1. Relationship between N uptake U_r and root-length density L_r

In our root-optimization model, annual N uptake per unit soil volume at depth z ($U_r(z)$, g N m^{-3} year^{-1}) is a rectangular hyperbolic function of root-mass density ($R(z)$, kg DM m^{-3}) (eq. 1), where $U_o(z)$ is the upper limit to N-uptake rate by roots at depth z (potential annual N uptake) and R_o is the root-mass density at half potential N uptake. Equation (1) can also be expressed as a rectangular hyperbolic function of root-length density $L_r(z) = R(z)/(\pi r_o^2 \rho_r)$ (cm^{-2}), in which the root-length density at half potential N uptake is $L_{ro} = R_o/(\pi r_o^2 \rho_r)$.

The purpose of this section is to clarify the mechanistic basis of the U_r–L_r relationship by deriving it from the Barber–Cushman (BC) model (Darrah 1993; Yanai 1994), an established mechanistic model of solute transport in soil and uptake by roots. In particular, we show how the parameter $L_{ro} = R_o/\pi r_o^2 \rho_r$ is related to root and soil properties, and justify the assumption implicit in equation (1) that N uptake U_r is linearly related to potential N-uptake rate U_o.

In the BC model, nutrient uptake rate per unit soil volume (U, mol cm^{-3} day^{-1}) is proportional to root surface area per unit soil volume:

$$U = 2\pi r_o L_r I, \quad \text{(A1)}$$

where r_o (cm) is root radius, I is the rate of active nutrient uptake per unit root surface area (mol cm^{-2} day^{-1}), which is often expressed as a Michaelis–Menten function of solute concentration at the root surface (C_o, mol cm^{-3}). Following Yanai (1994), we consider the case $I = \alpha\ C_o$, where α (cm day^{-1}) is root absorbing capacity, which is assumed to be constant. Solute moves to the root surface by mass flow and diffusion down a concentration gradient generated by uptake at the root surface; the concentration gradient may be reversed at high rates of mass flow. In order to calculate C_o, we need to determine the concentration of solute in solution ($C_s(r)$, mol cm^{-3}) at radial distances r extending from the root surface r_o to a distance r_x, the half-distance to nearest neighboring root (assuming radial symmetry). For a regular array of parallel roots, the value of r_x is inversely related to root-length density L_r:

$$L_r = \frac{1}{\pi(r_x^2 - r_o^2)}. \quad \text{(A2)}$$

Let U_o (mol cm^{-3} day^{-1}) and μ (day^{-1}) represent, respectively, rates of supply of plant-available N per unit soil volume and solute loss, for example, through immobilization by microbial decomposers, which compete with plant roots for available solute (Darrah 1993; Mosier et al. 2002; Schimel and Bennett 2004; Frank and Groffman 2009) and are assumed here to be uniformly distributed, or through abiotic or chemical immobilization (e.g., associated with decomposition of lignified litter; Corbeels et al. 2005a, b). We assume that the inter-root distance is much smaller than the length scale for vertical variation of U_o ($r_x \ll D_o$), so that the depth-dependence of U_o can be neglected in solving for $C_s(r)$ at a particular soil depth. The BC model, as formulated by Yanai (1994), determines $C_s(r)$ by considering the steady-state balance between nutrient inputs to and outputs from a unit-length cylinder of radius r surrounding the root surface with $r_o \le r \le r_x$. Nutrient inputs (mol N cm^{-1} root length day^{-1}) to the cylinder occur through the supply rate U_o (which is spatially uniform within the cylinder), and mass flow and diffusion toward the root surface:

$$\text{N input} = \pi(r^2 - r_o^2)U_o + \pi(r_x^2 - r^2)EC_s(r) + 2\pi r \Delta b \frac{dC_s}{dr},$$

where E (cm^3 water cm^{-3} soil volume day^{-1}) is the rate of extraction of water by roots from unit soil volume, Δ (cm^2 day^{-1}) is the effective diffusion coefficient of nutrient in soil, and b is soil buffering power (cf. Darrah 1993; Yanai 1994). We assume that the rate of water extraction E by roots is determined by plant evaporative demand, and that water is supplied at the same rate E uniformly distributed within unit soil volume. Nutrient outputs from the cylinder are through uptake at the root surface (at $r = r_o$), and immobilization within the cylinder, which is proportional to the local solute concentration (Corbeels et al. 2005a, b):

$$\text{N output} = 2\pi r_o I + \mu 2\pi \int_{r_o}^{r} rC_s(r)dr.$$

Differentiating the N-balance equation (N input = N output) with respect to r leads to the second-order differential equation:

$$U_o + \frac{E}{2r}(r_x^2 - r^2)\frac{dC_s}{dr} + \frac{\Delta b}{r}\frac{d}{dr}\left(r\frac{dC_s}{dr}\right) = (\mu + E)C_s \quad \text{for } r_o \le r \le r_x. \quad \text{(A3)}$$

The two boundary conditions are that solute flux is (1) zero at $r = r_x$, and (2) equal to uptake per unit root surface area at $r = r_o : I = \frac{1}{2r_o}(r_x^2 - r_o^2)EC_o + \Delta b \frac{dC_s}{dr}|_{r_o}$.

It is useful to express equation (A3) in terms of dimensionless variables. If $I = \alpha C_o$ (Yanai 1994) and transport by mass-flow is ignored ($E = 0$), which is a reasonable approximation under many circumstances (Nye 1977; Robinson 1986), the dimensionless variables are

$$C_s' = C_s \Big/ \frac{U_o}{\mu}, \quad \text{(A4)}$$

$$r' = r \Big/ \sqrt{\frac{\Delta b}{\mu}}, \quad \text{(A5)}$$

$$L_r' = L_r \Big/ \frac{\mu}{\Delta b}, \quad \text{(A6)}$$

and eqn (A3) becomes

$$1 + \frac{1}{r'}\frac{d}{dr'}\left(r'\frac{dC_s'}{dr'}\right) = C_s' \quad \text{for } r_o' \le r' \le r_x', \quad \text{(A7)}$$

subject to the boundary conditions $dC_s'/dr' = 0$ at $r' = r_x'$ and $dC_s'/dr' = \alpha' C_s'$ at $r' = r_o'$, where $\alpha' = \alpha/\sqrt{\mu \Delta b}$. Uptake as a proportion of nutrient supply is (from eq. A1)

$$U/U_o = 2\pi r_o' L_r' \alpha' C_o'. \quad \text{(A8)}$$

Numerical solution is obtained by writing equation (A7) as a pair of first-order differential equations for rates of change of C_s' and dC_s'/dr', and then finding a solution that satisfies boundary conditions at both $r' = r_o'$ and $r' = r_x'$. The solution shows that solute concentration is depleted adjacent to the root (cf. Yanai 1994). The modeled relationship between U/U_o and L_r' derived from equation (A8) is shown in Figure A1. U/U_o increases with L_r and is asymptotic to 1 in the limit of high L_r, which is consistent with equation (1). The qualitative explanation for this pattern is that at low L_r (i.e., high r_x), available soil N (U_o) is mostly immobilized by soil microbes before reaching the root surface. As L_r increases, r_x decreases so that more solute reaches the root surface instead of being immobilized. N uptake by the root U approaches U_o asymptotically in the limit $L_r \to \infty$ (i.e., $r_x \to r_o$). The rectangular-hyperbolic function

$$\frac{U}{U_o} = \frac{1}{1 + L_{ro}'/L_r'}, \quad \text{(A9)}$$

is a good approximation to the U–L_r relationship derived from the numerical solution of equation (A7) (Fig. A1). Values of L_{ro}' that best fit the relationship between U/U_o and L_r' shown in Figure A1 are $L_{ro}' = 0.64$, 1.02, and 5.05 when $\alpha' = 1000$, 100, and 10, respectively. As an aside, the dependence of L_{ro} on $\mu/(\Delta b)$ (eq. A6) implies that the root-length density required for uptake of 50% of available N is inversely related to ion mobility (Δ) (cf. Raven et al. 1992; Cambui et al. 2011).

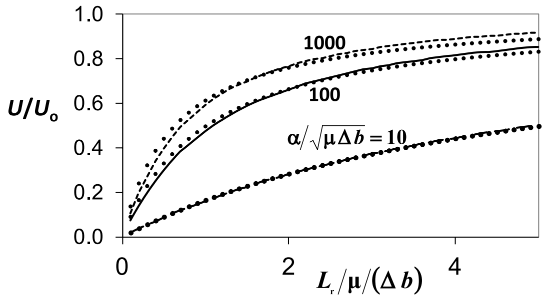

Figure A1. Relationship between the ratio U/U_o and dimensionless root-length density ($L_r/(\mu/\Delta b)$) derived by solving the Barber–Cushman model (eq. A3), where U = uptake per unit soil volume (mol N cm^{-3} day^{-1}) and U_o = rate of supply (mol cm^{-3} day^{-1}). Relationships are shown for a dimensionless root radius $r_o/\sqrt{(\Delta b / \mu)} = 0.0035$ and three values of the dimensionless parameter combination $\alpha/\sqrt{(\mu\ \Delta b)} = 10$ (long dashed line), 100 (solid line), and 1000 (short dashed line). Solutions assume zero mass flow ($E = 0$). Least-squares fits of the rectangular hyperbolic function are represented by dotted lines adjacent to each curve. Estimated values of $L_{ro}/(\mu\ /\ \Delta b)$ are 5.05, 1.02, and 0.64, respectively.

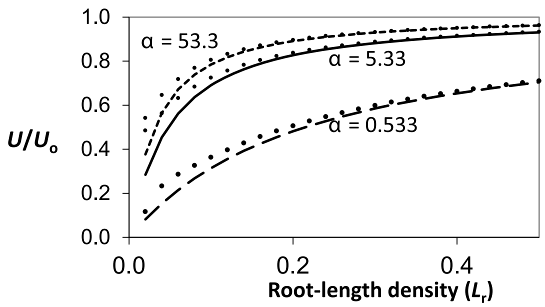

Figure A2. Relationship between simulated N uptake represented by the ratio U/U_o and root-length density (L_r) derived by solving the Barber–Cushman model (eq. A3), with and without mass flow. Simulations without mass flow (water extraction rate $E = 0$) are shown for three values of root absorbing capacity ($\alpha = 0.533$ [long dashed line], 5.33 [solid line], and 53.3 [short dashed line] cm day^{-1}). Simulations with mass flow ($E = 0.01$ cm^3 water cm^{-3} soil volume day^{-1}) are represented by dotted lines adjacent to each curve.

Simulations including mass flow are shown in Figure A2. We assume water extraction rate $E = 0.01$ cm^3 water cm^{-3} soil volume day^{-1}, which is a credible value, noting that the volumetric water content of most soils is in the range 0.1 –0.4 cm^3 water cm^{-3} soil volume at field capacity. Simulated daily N uptake U is enhanced when mass flow is included (Fig. A2), and the mass-flow effect can be large at low root-length densities. Further research is required to determine how the shape of the U–L_r relationship changes when E is large or when uptake kinetics of roots and microbes are modeled as Michaelis–Menten functions of C_o, and to determine using *MaxNup* how the relationship between total N uptake and total root mass is affected. Note that the numerical solution for the U–L_r relationship derived from equation (A3) could be substituted directly into equation (A14) (below) to obtain the optimum solution for $U_n(z)$ throughout the root zone, thus obviating the need for an empirical approximation to the U_r–R relationship such as equation (1).

There is a discrepancy in timescales between the BC model, which simulates short-term solute transport processes, and equation (1), which evaluates annual N uptake. However, uptake is proportional to U_o in both equations, so that comparison across timescales is reasonable provided L_r and L_{ro} are constant over an annual timescale. The issue of extrapolating from daily to annual timescales is discussed further in Appendix A4 below.

Appendix A2. Maximizing net supply to aboveground pools: solution by the Lagrange multiplier method

Our hypothesis of optimal root function is that annual net N supply to aboveground pools per unit land area (U_{net}, g N m^{-2} year^{-1}, eq. 4) is maximized with respect to the vertical profile of root mass per unit soil volume ($R(z)$) and maximum rooting depth (D_{max}, m) under the constraint that total root biomass per unit land area (R_{tot}, kg DM m^{-2}, eq. 6) is fixed. This constrained optimization problem may be solved by the Lagrange multiplier method. We introduce a Lagrange multiplier λ for the constraint of fixed R_{tot} and maximize the goal function:

$$\Psi = \int_0^{D_{max}} U_n(R(z), z)\mathrm{d}z - \lambda \int_0^{D_{max}} R(z)\mathrm{d}z, \tag{A10}$$

independently with respect to $R(z)$ and D_{max}, where the function $U_n(R(z),z)$ is given by equation (3). The explicit z-dependence of U_n indicated here arises because potential N uptake (U_o, g N m^{-3} year^{-1}), and N concentration (N_r, g N kg^{-1} DM) and longevity (τ_r, year) of roots are functions of z (cf. Pregitzer et al. 1998; Iversen et al. 2008, 2011; Iversen 2010). The modeled relationship between U_n and R, obtained when U_o decreases exponentially with z (eq. 2) and N_r and τ_r do not vary with z, is shown in Figure 1b.

Under small variations $\delta R(z)$ and δD_{max}, the change in Ψ is

$$\begin{aligned}\delta\Psi &= \int_0^{D_{max}} \left(\frac{\partial U_n}{\partial R} - \lambda\right)\delta R(z)\,\mathrm{d}z \\ &\quad + \int_{D_{max}}^{D_{max}+\delta D_{max}} (U_n(R(z), z) - \lambda R(z))\,\mathrm{d}z \\ &= \int_0^{D_{max}} \left(\frac{\partial U_n}{\partial R} - \lambda\right)\delta R(z)\mathrm{d}z + (U_n(R(D_{max}), D_{max}) \\ &\quad - \lambda R(D_{max}))\delta D_{max}.\end{aligned} \tag{A11}$$

Setting this change to zero gives

$$\frac{\partial U_n}{\partial R} = \lambda \quad \text{for } 0 \le z \le D_{max}, \tag{A12}$$

and

$$U_n(R(D_{max}), D_{max}) = \lambda R(D_{max}). \quad (A13)$$

Combining equations (A12) and (A13) gives

$$\frac{\partial U_n}{\partial R} = \frac{U_n(R(D_{max}), D_{max})}{R(D_{max})} \quad \text{for } 0 \leq z \leq D_{max}. \quad (A14)$$

Since equation (A14) holds at $z = D_{max}$, it follows that

$$\frac{\partial}{\partial R}(U_n/R) = 0 \quad \text{at} z = D_{max}, \quad (A15)$$

so that root-scale N-uptake efficiency, defined as N supply to aboveground pools either per unit root mass (U_n/R), or per unit root N ($U_n/(R N_r)$), is maximized at the base of the rooting zone. Furthermore it follows from equation (1) that $\frac{\partial}{\partial R}(U_n/R) < 0$ if $R > 0$, and hence that root-scale N-uptake efficiency is not maximized elsewhere in the root system. It also follows from equations (1) and (A15) that $R(D_{max}) = 0$ and $\frac{U_r(D_{max})}{R(D_{max})} = \frac{U_o(D_{max})}{R_o(D_{max})}$. Equation (A14) then becomes

$$\frac{\partial U_n}{\partial R} = \frac{U_o(D_{max})}{R_o(D_{max})} - \frac{N_r(D_{max})}{\tau_r(D_{max})} \quad \text{for } 0 \leq z \leq D_{max}. \quad (A16)$$

If the N concentration and life span of roots do not vary with depth, then U_{tot} is maximized when U_{net} is maximized, and at the optimum we have

$$\frac{\partial U_r}{\partial R} = \frac{U_o(D_{max})}{R_o(D_{max})} \quad \text{for } 0 \leq z \leq D_{max}. \quad (A17)$$

The optimal solutions for $U_r(z)$ versus $R(z)$ and $U_n(z)$ versus $R(z)$ are shown in Figure 1a and b, respectively, for total root mass $R_{tot} = 0.19$ kg DM m^{-2} (closed circles, $\partial U_r/\partial R = 14.5$ and $\partial U_n/\partial R = 7.7$ g N kg^{-1} DM year^{-1}) and $R_{tot} = 0.38$ kg DM m^{-2} (open circles, $\partial U_r/\partial R = 6.8$ g N kg^{-1} DM year^{-1} and $\partial U_n/\partial R = 0$). Thus, for $R_{tot} = 0.38$ kg DM m^{-2}, $U_n(z)$ is maximized with respect to $R(z)$ throughout the rooting zone.

Appendix A3. Solving equation (A16) for the optimal vertical profiles of root-mass density and N uptake as functions of maximum rooting depth D_{max}

From eqn 1 we obtain

$$\frac{\partial U_r}{\partial R} = \frac{U_o(z) R_o(z)}{(R_o(z) + R(z))^2}. \quad (A18)$$

Substituting equation (A18) into equation (A16) and using equation (3) gives

$$\frac{U_o(z) R_o(z)}{(R_o(z) + R(z))^2} - \frac{N_r(z)}{\tau_r(z)} = \frac{U_o(D_{max})}{R_o(D_{max})} - \frac{N_r(D_{max})}{\tau_r(D_{max})}. \quad (A19)$$

For given functions $U_o(z)$, $R_o(z)$, $N_r(z)$, and $\tau_r(z)$, equation (A19) can be solved to determine the optimal vertical root distribution $R(z)$. Assuming that N_r, τ_r, and R_o (i.e., L_{ro}, r_o, and ρ_r) are independent of z and that available soil N declines exponentially with soil depth (eq. 2), we obtain solutions for the optimal vertical profiles of root-mass density ($R(z)$, eq. 7) and annual total N uptake ($U_r(z)$, eq. 9), total root mass (R_{tot}, eq. 8), total annual N uptake (U_{tot}, eq. 10), annual N supply to aboveground pools (U_{net}, eq. 11), gross N-uptake fraction ($\phi_N = U_{tot}/U_{max}$, eq. 12), and net N-uptake fraction ($\phi_{net} = U_{net}/U_{max}$, eq. 13). The optimal vertical profile of annual N supply to aboveground pools $U_n(z)$ is obtained by substituting equations (7) and (9) into equation (3):

$$U_n(z) = U_o(z)\left(1 - e^{-\frac{D_{max}-z}{2D_o}}\right) - \frac{N_r R_o}{\tau_r}\left(e^{\frac{D_{max}-z}{2D_o}} - 1\right). \quad (A20)$$

Average root-mass density over the rooting zone is $R_{av} = R_{tot}/D_{max}$. Root systems with a given total root mass (R_{tot}) can range from shallow rooted (small D_{max}) with large average root-mass density (large R_{av}) to deep rooted (large D_{max}) with small R_{av}. From equation (8), the optimal value of R_{av} satisfies the equation:

$$1 + \frac{R_{av}}{R_o} = \frac{e^{R_{tot}/(2D_o R_{av})} - 1}{R_{tot}/(2D_o R_{av})}. \quad (A21)$$

It follows from equation (A21) that for a given R_{tot}, optimal R_{av} is an increasing function of R_o and a decreasing function of D_o. Hence, for a given total root mass, the optimal root system will tend to be shallow with high R_{av} if R_o is large and D_o is small, and deep with low R_{av} if R_o is small and D_o is large.

The cumulative root proportion (*CRP*) between the soil surface and depth z can be obtained from equation (7):

$$CRP(z) = \int_0^z R(z)\mathrm{d}z/R_{tot} = 1 - \frac{e^{-\frac{z}{2D_o}} - \left(1 + \frac{D_{max}-z}{2D_o}\right)e^{-\frac{D_{max}}{2D_o}}}{1 - \left(1 + \frac{D_{max}}{2D_o}\right)e^{-\frac{D_{max}}{2D_o}}}. \quad (A22)$$

Equations (8), (10), and (11) can be expressed in terms of dimensionless variables $D'_{max} = D_{max}/D_o$, $R'_{tot} = R_{tot}/(R_o D_o)$, $\phi_N = U_{tot}/U_{max}$ (gross N-uptake fraction), and $\phi_{net} = U_{net}/U_{max}$ (net N-uptake fraction) to obtain

$$R'_{tot} = (2(e^{D'_{max}/2} - 1) - D'_{max}), \quad (A23)$$

$$\phi_N = \left(1 - e^{-D'_{max}/2}\right)^2, \quad (A24)$$

$$\phi_{\mathrm{net}} = \phi_{\mathrm{N}} - R'_{\mathrm{tot}}\zeta, \quad \text{(A25)}$$

where the dimensionless quantity $\zeta = R_{\mathrm{o}} D_{\mathrm{o}} N_r/(U_{\max}\tau_{\mathrm{r}})$. The peak value of net N-uptake fraction ϕ_{net}, shown in Figure 2c, occurs when $D_{\max} = -D_{\mathrm{o}} \ln(\zeta)$, and

$$R_{\mathrm{tot}} = R_{\mathrm{o}} D_{\mathrm{o}}(2(1/\sqrt{\zeta} - 1) + \ln(\zeta)). \quad \text{(A26)}$$

The peak value of φ_{net} is

$$\phi_{\mathrm{net\_peak}} = 1 - 4\sqrt{\zeta} + 3\zeta - \zeta \ln(\zeta). \quad \text{(A27)}$$

The value of φ_{N} when φ_{net} is maximized is

$$\phi_{\mathrm{N\_peak}} = (1 - \sqrt{\zeta})^2. \quad \text{(A28)}$$

Using parameter values for sweetgum at the ORNL FACE site (Table 1), we obtain $\zeta = 0.0398$, so that at the peak $D_{\max} = 0.97$ m, $R_{\mathrm{tot}} = 0.38$ kg DM m^{-2}, $\varphi_{\mathrm{N\_peak}} = 0.64$ and $\varphi_{\mathrm{N\_peak}} = 0.45$.

Appendix A4. Extension of root-optimization model to accommodate variation of N availability over time

According to equation (1), the upper limit to N uptake by roots at depth z ($U_{\mathrm{o}}(z)$) is an annual rate. However, many soil N-cycling models allow N supply to vary on a daily time-step, for example, as a function of daily soil moisture and temperature (Parton et al. 1988; Comins and McMurtrie 1993; Corbeels et al. 2005a, b). This variation can be accommodated within the *MaxNup*-optimization hypothesis by defining $u_{\mathrm{oi}}(z)$ (g N m^{-3} day^{-1}) as potential daily N uptake per unit soil volume at depth z on day i. Then N uptake per unit soil volume at depth z on day i is

$$u_{\mathrm{ri}}(z) = \frac{u_{\mathrm{oi}}(z)}{1 + R_{\mathrm{o}}/R(z)}. \quad \text{(A29)}$$

If root-mass density at z $R(z)$ and root-N concentration $N_{\mathrm{r}}(z)$ are constant over the year, then annual N supply to aboveground pools is

$$U_{\mathrm{net}} = \sum_{i=1}^{365} \int_0^{D_{\max}} \frac{u_{\mathrm{oi}}(z)}{1 + R_{\mathrm{o}}/R(z)} \mathrm{d}z - \int_0^{D_{\max}} \frac{N_{\mathrm{r}}(z)}{\tau_{\mathrm{r}}(z)} R(z) \mathrm{d}z. \quad \text{(A30)}$$

Assuming that the length scale for the exponential decrease of available soil N with depth (D_{o}) is constant over the year, we have

$$u_{\mathrm{oi}}(z) = \frac{u_{\mathrm{maxi}}}{D_{\mathrm{o}}} e^{-z/D_{\mathrm{o}}}, \quad \text{(A31)}$$

where u_{maxi} is potential N uptake per unit land area on day i integrated over all soil depths. Note that potential N uptake varies from day to day, but its distribution with depth does not. Equation (A30) can be written as

$$U_{\mathrm{net}} = \left(\frac{\sum_{i=1}^{365} u_{\mathrm{maxi}}}{D_{\mathrm{o}}} \right) \int_0^{D_{\max}} \frac{e^{-z/D_{\mathrm{o}}}}{1 + R_{\mathrm{o}}/R(z)} \mathrm{d}z - \int_0^{D_{\max}} \frac{N_{\mathrm{r}}(z)}{\tau_{\mathrm{r}}(z)} R(z) \mathrm{d}z. \quad \text{(A32)}$$

Equations in Appendices A2 and A3 above are retrieved if $U_{\max}$ in equation (2) is replaced by $\sum_{i=1}^{365} u_{\mathrm{maxi}}$. This extension indicates how the predictions of *MaxNup* could be incorporated into daily time-step ecosystem and land-surface models.