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A model using marginal efficiency of investment to analyse carbon and nitrogen interactions in terrestrial ecosystems (ACONITE Version 1)

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Abstract

Carbon (C) and nitrogen (N) cycles are coupled in terrestrial ecosystems through multiple processes including photosynthesis, tissue allocation, respiration, N fixation, N uptake, and decomposition of litter and soil organic matter. Capturing the constraint of N on terrestrial C uptake and storage has been a focus of the Earth System modelling community. However there is little understanding of the trade-offs and sensitivities of allocating C and N to different tissues in order to optimize the productivity of plants. Here we describe a new, simple model of ecosystem C–N cycling and interactions (ACONITE), that builds on theory related to plant economics in order to predict key ecosystem properties (leaf area index, leaf C : N, N fixation, and plant C use efficiency) using emergent constraints provided by marginal returns on investment for C and/or N allocation. We simulated and evaluated steady-state ecosystem stocks and fluxes in three different forest ecosystems types (tropical evergreen, temperate deciduous, and temperate evergreen). Leaf C : N differed among the three ecosystem types (temperate deciduous < tropical evergreen < temperature evergreen), a result that compared well to observations from a global database describing plant traits. Gross primary productivity (GPP) and net primary productivity (NPP) estimates compared well to observed fluxes at the simulation sites. Simulated N fixation at steady-state, calculated based on relative demand for N and the marginal return on C investment to acquire N, was an order of magnitude higher in the tropical forest than in the temperate forest, consistent with observations. A sensitivity analysis revealed that parameterization of the relationship between leaf N and leaf respiration had the largest influence on leaf area index and leaf C : N. Also, a widely used linear leaf N-respiration relationship did not yield a realistic leaf C : N, while a more recently reported non-linear relationship performed better. A parameter governing how photosynthesis scales with day length had the largest influence on total vegetation C, GPP, and NPP. Multiple parameters associated with photosynthesis, respiration, and N uptake influenced the rate of N fixation. Overall, our ability to constrain leaf area index and have spatially and temporally variable leaf C : N

helps address challenges for ecosystem and Earth System models. Furthermore, the simple approach with emergent properties based on coupled C–N dynamics has potential for use in research that uses data-assimilation methods to integrate data on both the C and N cycles to improve C flux forecasts.

1 Introduction

Globally, the biogeochemical cycles of carbon (C) and nitrogen (N) are the most significant in terms of magnitudes, anthropogenic impact and climate feedbacks (IPCC, 2013; Erisman et al., 2013). These cycles are closely coupled, from local to global scales. For instance, rates of C fixation are sensitive to foliar N content (Street et al., 2012; Reich et al., 1994). Thus, high productivity farming is reliant on N inputs (Tilman et al., 2002), and production in many natural ecosystems is N-limited (Shaver and Chapin, 1995; Norby et al., 2010). Rates of autotrophic respiration are linked to plant tissue N content (Reich et al., 2006), so N content is linked to vegetation C use efficiency (Waring et al., 1998). Plant N uptake from soils depends on C investment into root systems and mycorrhizal associations (Drake et al., 2011), which also diverts allocation away from tissues that directly fix C. Plant-microbe associations use C as an energy source to fix atmospheric N into bioavailable forms, at globally significant magnitudes (Rastetter et al., 2001). Decomposition of plant litter and soils is closely determined by its C : N ratio (litter quality) (McClaugherty et al., 1985; Manzoni et al., 2010). Underlying this C/N coupling in the biosphere, we can hypothesise that plants allocate C and N (to foliage, wood, roots, and symbiotes) to optimize returns on investment, i.e. C fixation and N uptake/fixation (Bloom et al., 1985; Hilbert and Reynolds, 1991).

The coupling of C and N in the biosphere interacts with global perturbations to the C and N cycles that have resulted from fossil fuel burning, production of N fertilizers, and land use/land cover change (Le Quere et al., 2009; Gruber and Galloway, 2008). Furthermore, climate, a key factor controlling both the C and N cycles (Schimel et al., 1997), has been altered by changes to the atmospheric composition of C and N (IPCC, 2013; Pinder et al., 2012). Together, these changes to the Earth system have perturbed ecosystem processes, altered C and N cycling, and enhanced terrestrial sinks of C. The adaptation of ecosystem processes and structures to these changes in N and C resource limitations is not well understood, and has led to considerable debate (Magnani et al., 2007; de Vries et al., 2008; Thomas et al., 2010).

We lack basic understanding of biogeochemical sensitivities and trade-offs, particularly in how vegetation adjusts C and N allocation, and thereby structure and function, when relative C and N resource limitations shift. Production (C fixation) is sensitive to leaf traits such as foliar N and to ecosystem properties such as leaf area index (Williams and Rastetter, 1999; Shaver et al., 2007). These parameters show distinct temporal, geographic and successional variation (Wright et al., 2004; Kattge et al., 2011), and are sensitive to global change drivers (Nowak et al., 2004). Plant access to soil N depends on the balance between investment in roots for uptake vs. N fixation, but is also dependent on litter C : N ratio, due to interactions with soil microbes. Land surface models have been developed to include C–N interactions (Thornton et al., 2007; Xu and Prentice, 2008; Zaehle et al., 2010; Sokolov et al., 2008; Gerber et al., 2010; Wang et al., 2010; Wania et al., 2012), but these are typically highly parameterised. For example, empirical parameterisations that describe maximum canopy size (leaf area index; LAI), leaf C : N ratios, and tissue allocation patterns are common at the plant function type (PFT) scale in these models.

Our objective is to describe a new, simple model of ecosystem C–N cycling and interactions, ACONITE (Analysing CarbOn and Nitrogen Interactions in Terrestrial Ecosystems). The need for a new model derives from outstanding uncertainties over key sensitivities of the biosphere to global change, as outlined above. The model builds on theory related to plant economy and optimisation (Bloom et al., 1985). Thus, (i) plants are able to store C and N; (ii) plants produce tissues until the marginal revenue from this increased production is equal to the marginal cost; (iii) allocation is adjusted by plants so resources equally limit growth; (iv) each plant process is limited by the same balance of internal reserves. This approach results in several novel model features.

Title Page
Abstract | Introduction
Conclusions | References
Tables | Figures
◀| |▶
◀ ▶
Back | Close
Full Screen / Esc
Printer-friendly Version
Interactive Discussion

Firstly, the model does not include fixed parameters for maximum LAI, or leaf C : N – instead, these parameters emerge from the calculation of marginal returns calculated separately for C and N investments, and so can vary in response to forcing (climate, fertilization, disturbance). Secondly, the model approach determines the optimal conditions for investment in N fixation over investment in root structure, which can also vary in response to forcing. Thirdly, C use efficiency is an emergent property of the model, linked to relative investment of N into different plant tissues of varying N content.

We use a relatively simple model structure, building on an existing simple C cycle model, DALEC (Williams et al., 2005). Simple, fast-running models with minimal parameters are best suited for inclusions within a data assimilation (DA) framework where large ensemble runs are needed at global scales. DA allows effective evaluation and parameterisation of model structures against broad and independent data sets (Keenan et al., 2011). In this paper we describe the model structure, a sensitivity analysis and an evaluation of model outcomes for temperate and tropical forcing. The model results are also discussed in the context of other C/N interaction modelling approaches, and potential applications in the future.

2 Methods

2.1 Model description

The model operates at a daily resolution, resolving seasonal dynamics in C : N interactions in response to climate forcing. Required climate data are daily maximum and minimum temperature (°C) and total down-welling shortwave radiation ($\mathrm{MJ\,m^{-2}\,d^{-1}}$). In this implementation hydrology is not included, so the evaluations are for selected ecosystems with relatively low water stress. Atmospheric $\mathrm{CO_2}$ concentration is held at 2010 levels for the evaluations. The final forcing term is the rate of N deposition ($\mathrm{g\,N\,m^{-2}\,day^{-1}}$). Transient responses to altered forcing over multiple years are simulated, but our focus here is on evaluating the steady state conditions under consistent forcing, and exploring the role of marginal investment decisions in generating these steady states. The full model code, written in Fortran 90, can be found in the Supplement.

2.1.1 Model structure

The model state variables are stocks of C and N in discrete vegetation and soil pools, linked by specified fluxes (Fig. 1). Plants are represented by respiratory, labile, bud, foliar, fine root and stem pools. The DALEC v1 C model (Fox et al., 2009) has been adjusted here by the redefinition of the labile pool to meet condition (i) above, the addition of a bud pool to connect allocation to previous year's growth, and the addition of a respiratory pool (C_{Ra}) to maintain metabolism during periods of low or no photosynthesis. In the plant, most C pools have a matching N pool, and therefore a C : N (i.e. ratio). The only exception is the C_{Ra} pool, which stores C prior to autotrophic respiration. Dead organic matter pools are partitioned into litter, coarse woody debris (CWD) and soil organic matter (SOM), with matching C and N pools, and hence C : N. The DALEC v1 model has been refined here by the inclusion of a CWD pool. There are also now two inorganic N pools, for NH_4^+ and NO_3^-.

ACONITE describes the plant processes of photosynthesis and root N uptake, into labile C and N stores. It then describes the allocation of labile C to grow plant tissues and to support N fixation. The model simulates allocation of labile N to grow plant tissues and N retranslocation from foliage before senescence. Turnover of plant tissues generates inputs of C and N to specific litter (from foliage and fine roots) or CWD (from stem turnover) pools. CWD pools have a specific temperature controlled residence time, before being transferred to the C or N litter pools. The C litter pool undergoes decomposition into SOM, with a fraction of this turnover respired heterotrophically. The N litter pool decomposes into the SOM N pool. The SOM pools must maintain a fixed C : N, and so adjustments are made to the fluxes of N between the SOM and inorganic pools, and turnover rates of litter. Further details on these processes and their controls are provided below with some equations separated into components to ease understanding. Table 1 and Table 2 describes the mass balance equations and fluxes used in ACONITE.

2.1.2 Photosynthesis

Photosynthesis (gross primary productivity; GPP) is determined using a response surface model, ACM (Aggregated Canopy Model; Williams et al., 1997). ACM is an aggregated model, based on the responses of a detailed ecophysiological model, SPA (Soil–Plant–Atmosphere; Williams et al., 1996), to climate forcing. SPA has been evaluated globally, and for the purposes of this paper has been tested in both temperate forests (Williams et al., 2001) and tropical forests (Fisher et al., 2007). In SPA, photosynthesis is strongly determined by the balance between allocation to leaf area index (LAI, which determines light absorption) and total foliar N (TFN, which is correlated in SPA with the rates of carboxylation and electron transport). Sensitivity analyses of SPA estimates of photosynthesis (Williams and Rastetter, 1999) identified a strong interaction between LAI and TFN, with photosynthesis maximised by a balanced allocation between these two canopy traits.

The inputs to ACM include the climate forcing data (temperature and radiation), atmospheric CO_2 (constant in this study), soil moisture (constant in this study), LAI and total foliar N (both calculated in ACONITE). ACM has been calibrated to reproduce SPA photosynthesis, but using typically measured values of LAI and foliar N (Fox et al., 2009). For the purposes of ACONITE simulations, ACM estimates must also reproduce the declining return on investment linked to imbalanced allocation to LAI or foliar N (Williams and Rastetter, 1999). Therefore the fundamental capacity of the canopy to photosynthesise is adjusted by a saturating function on the ratio LAI : TFN (Eq. 8), introducing a new parameter to ACM. The parameters used in the photosynthesis submodel listed in Table 3.

The maximum photosynthesis is set by ACM (Eq. 4), but the actual photosynthesis is linked to the size of the labile C pool, and the capacity of the plants to store labile C. The size of the store (store_c, Eq. 1) is based on an assumption that storage occurs in, and therefore scales with, fine root (C_{root}) and woody tissues (C_{wood}) according to a parameter ($store\_prop_c$):

$$store_c = (C_{root} + C_{wood})store\_prop_C \tag{1}$$

Photosynthesis is down-regulated (by a factor X_c) according to the saturation status of the labile C store:

$$X_c = \begin{cases} \max\left(0, \left(1 - \frac{C_{labile} - store_c}{store_c}\right)\right), & C_{labile} > store_c \\ 1.0, & C_{labile} \le store_c \end{cases} \tag{2}$$

And photosynthesis only occurs if daily minimum temperature > 0 °C, based on the link between photosynthesis and transpiration, for which liquid water is required:

$$GPP = \begin{cases} GX_c, & T_{min} > 0 \\ 0, & T_{min} \le 0 \end{cases} \tag{3}$$

Photosynthesis is a function of daily irradiance (I, $MJ\,m^{-2}\,d^{-1}$), day-length (ζ, hours), atmospheric [CO_2] (C_a, ppm), an estimated internal [CO_2] (C_i, ppm) and a set of parameters (acm_{1-11}),

$$G = \frac{e_0 I g_c (C_a - C_i)}{e_0 I + g_c (C_a - C_i)}(acm_2 \zeta + acm_5) \tag{4}$$

The light response parameter (e_0) is adjusted by LAI ($L = C_{leaf}/lca$) to reflect self-shading,

$$e_0 = \frac{acm_7 L^2}{L^2 + a_9} \tag{5}$$

And internal [CO_2] is determined by a quadratic solution,

$$C_i = 0.5\left[C_a + q - p + \sqrt{\left((C_a + q - p)^2 - 4\left(C_a q - \mathrm{acm}_3 p\right)\right)}\right] \quad (6)$$

$$q = \mathrm{acm}_3 - \mathrm{acm}_4 \quad (7)$$

Canopy photosynthetic capacity (p) is linked to foliar N, canopy conductance (g_c), but is adjusted by the ratio of LAI : TFN (see above),

$$p = \frac{\mathrm{acm}_1 N_{\mathrm{leaf}}}{g_c} \exp(\mathrm{acm}_8 T_{\max}) \frac{\mathrm{LAI:TFN}}{\mathrm{LAI:TFN} + \mathrm{acm}_{11}} \quad (8)$$

Canopy conductance is a function of the difference between soil water potential and plant wilting point (ψ_d), the hydraulic resistance of the soil–plant continuum (R_{tot}), and the maximum and minimum air temperature ($T_{\max/\min}$, °C),

$$g_c = \frac{|\psi_d|^{\mathrm{acm}_{10}}}{(\mathrm{acm}_6 R_{\mathrm{tot}} + 0.5(T_{\max} - T_{\min}))} \quad (9)$$

2.1.3 Plant N uptake

Plant nutrient uptake is simulated using an extant model of solute uptake at steady state, including active uptake at root surfaces and both diffusion and solution flow of nutrients to the root surface (Nye and Tinker, 1977; Williams and Yanai, 1996). The model is applied individually for uptake of both NH_4^+ or NO_3^- to generate a total N uptake, and parameters used are listed in Table 4.

Rooting zone nutrient concentration (C_{av}, $\mathrm{mmol\,m^{-3}}$) is derived from the size of the mineral N (N, which is either NH_4^+ or NO_3^-) pools distributed over a defined rooting depth (r_{depth}), with molar conversions:

$$c_{\mathrm{av}} = \frac{N}{r_{\mathrm{depth}}} \frac{1000}{14} \quad (10)$$

Title Page
Abstract Introduction
Conclusions References
Tables Figures
◀| |▶
◀ ▶
Back Close
Full Screen / Esc
Printer-friendly Version
Interactive Discussion

Uptake rate of N (U_N) is determined by root surface area ($r_{surfarea}$), root absorbing power (α), the temperature adjusted maximum rate of uptake (I_{temp}) and the degree of down-regulation of uptake (X_N), with a scaling adjustment (Z) to provide daily mass values. Specific parameters are used for NH_4^+ or NO_3^-:

$$U_N = r_{surfarea} \alpha I_{temp} X_N Z \tag{11}$$

Root surface area is derived from root radius and root length,

$$r_{surfarea} = 2\pi r_{radius} r_{length} \tag{12}$$

While root radius is a provided parameter, root length is dependent on the variable fine root C stock (C_{root}), and a further parameter describing the C concentration of biomass (c_{conc}) and the volumetric mass density of biomass ($r_{density}$)

$$r_{length} = \frac{C_{root}}{C_{conc} r_{density} \pi r_{radius}^2} \tag{13}$$

A final root dimension required in the model is the mean half distance between roots, r_x

$$r_x = \sqrt{\frac{r_{depth}}{\pi r_{length}}} \tag{14}$$

The degree of down-regulation is dependent on the relative size of the labile N pool and the size of the N store, itself a function of the size of the combined root and wood C pools (reflecting the expected proportionality between biomass and storage capacity of plants),

$$\mathrm{store}_N = (C_{root} + C_{wood})\mathrm{store\_prop}_N \tag{15}$$

Down-regulation occurs based on the proportion of the maximum N store that is filled

$$X_\mathrm{N} = \begin{cases} 1 - (\mathrm{N_{labile}}/\mathrm{store_N}), & \mathrm{N_{labile}} \leq \mathrm{store_N} \\ 0, & \mathrm{N_{labile}} > \mathrm{store_N} \end{cases} \tag{16}$$

The root absorbing power is determined by the concentration of solute at the root surface at steady state (c_o) and the half saturation constant for uptake (k_m)

$$\alpha = \frac{c_\mathrm{o}}{k_\mathrm{m} + c_\mathrm{o}} \tag{17}$$

and the solute concentration is determined as a quadratic solution for the steady state condition, requiring as inputs the temperature modified maximum rate of uptake (I_temp), the inward radial velocity of water at the root surface (v_o), a factor (γ) related to diffusion coefficients (D) and buffering (β) specific to the solute type, and a dimension factor (δ) linked to root structure,

$$\begin{aligned} c_\mathrm{o} = \frac{1}{2\delta v_0}\Big(& -I_\mathrm{temp} + \delta I_\mathrm{temp} + c_\mathrm{av} v_0 - \delta k_\mathrm{m} v_0 \\ & + \sqrt{4 c_\mathrm{av} \delta \mathrm{k}_m v_0^2 + (-I_\mathrm{temp} + \delta I_\mathrm{temp} + c_\mathrm{av} v_0 - \delta k_\mathrm{m} v_0)^2}\Big) \end{aligned} \tag{18}$$

I_temp is determined from the maximum rate of uptake, I_max,

$$I_\mathrm{temp} = I_\mathrm{max} Q_\mathrm{a}^{\frac{T-20}{10}} \tag{19}$$

$$\delta = \frac{2}{2-\gamma} \frac{\left(\left(\frac{r_x}{r_\mathrm{radius}}\right)^{2-\gamma} - 1\right)}{\left(\left(\frac{r_x}{r_\mathrm{radius}}\right)^{2} - 1\right)} \tag{20}$$

$$\gamma = \frac{r_\mathrm{radius} v_0}{\beta_{\mathrm{NH_4}} D_{\mathrm{NH_4}}} \tag{21}$$

We estimate the rate of water influx as a proportion of GPP.

$$v_0 = v\mathrm{GPP} \tag{22}$$

Adding a water cycle is necessary to more mechanistically calculate v, but the current approach captures the dependence of N uptake on transpiration-driven flow of water to the plant.

2.1.4 Plant allocation

Allocation only occurs on days with a defined growth potential (θ), based on phenological relationships (Table 5; Supplement Fig. S1). The start of a temperate growing season is determined by exceeding a growing degree day (GDD) threshold, while the end of the season is linked to a day of year (DOY). The existing code is suitable only for the Northern Hemisphere extra-tropics. (For equatorial regions growth potential is set to θ year-round. Further development is required before the model can be applied in dry tropics where temperature does not control phenology.)

$$\mathrm{growth_{potential}} = \begin{cases} \theta, & \mathrm{GDD} \geq \mathrm{GDD_{start}} \text{ and } \mathrm{DOY} < \mathrm{DOY_{senesc}} \\ 0, & \text{otherwise} \end{cases} \tag{23}$$

At each daily time-step we determine the instantaneous C return on investing further C and N in foliage, maintaining the existing C : N. The GPP and respiration returns are calculated based on the current day environmental conditions. The calculation for deciduous species is based on the net return (photosynthesis “GPPreturn” – maintenance respiration “Ramain”) projected over the remaining growing season, modified by the growth respiration (“Ragrow”; Eq. 50) of the investment.

$$\begin{aligned}\mathrm{Return_{leafCNInstant}} = {} & (\mathrm{GPPreturn_{leafCN}} - \mathrm{RamainReturn_{leafCN}})(\mathrm{DOY_{senesc}} - \mathrm{DOY}) \\ & - \mathrm{RagrowReturn_{leafC}}\end{aligned} \tag{24}$$

For species with leaf lifespans > 12 months (evergreen) an alternative calculation based on leaf turnover time (τ_{leaf}) is used

$$\text{Return}_{\text{leafCNInstant}} = \frac{(\text{GPPreturn}_{\text{leafCN}} - \text{RamainReturn}_{\text{leafCN}})}{\tau_{\text{leaf}}} - \text{RagrowReturn}_{\text{leafC}} \quad (25)$$

Based on these marginal returns, a decision tree is employed to determine allocation patterns from the labile C pool (Supplement Fig. S1). If outside the growth period, any labile C is used to fill the maintenance respiration pool (C_{Ra}) up to its maximum value; this ensures the vegetation has the required reserves to meet metabolic demand during winter. If growth can occur, then the next decision depends on whether Eq. (24) or (25) are positive, and if leaf C is less than its annual maximum. If both are true, then bud C and bud N are converted into foliar C and N, at the target leaf C : N, and the annual requirement for new wood (to support new foliage) is incremented. Labile C and N are then allocated to bud pools, to support future leaf growth, up to the amount required to reach maximum leaf C. Allocation of labile C and N is limited to ensure buds have the target leaf C : N. For C allocation to buds, a requisite amount of C is also allocated to the growth respiration flux.

If the instant returns are not positive, or the maximum leaf C has been attained, then, as above, C and N are allocated to buds. C is allocated to fill the maintenance respiration pool to its maximum size. Then remaining C and N are used to pay down the wood requirement, limited by the size of the labile pools and the need to construct wood at a fixed C : N. Next, labile N and C are allocated at a fixed C : N to grow fine roots up to a maximum root C, described in Sect. 2.1.7. Once the requirements for buds, maintenance respiration, wood and fine roots are met, then the final allocation decision depends on whether the labile C store has reached its maximum (a variable itself; Eq. 42). If the labile C store has not reached capacity, then C is allowed to accumulate. If the store is full, then remaining C is allocated to wood, dependent on N availability. If excess C remains in the labile C store at this point, then it is allocated to excess autotrophic respiration, which leads to N fixation (see Eqs. 37 and 76).

2.1.5 Plant tissue turnover

Turnover of plant tissues is dependent on tissue specific turnover rates (τ) and results in transfer of materials to specific litter pools (Fig. 1; Table 5). For foliage, turnover fluxes (t) involve phenological cues, occurring only after a defined day in the year ($\mathrm{DOY}_{\mathrm{senesc}}$),

$$t_{\mathrm{leafC}} = \begin{cases} \mathrm{C}_{\mathrm{leaf}}\tau_{\mathrm{leaf}}, & \mathrm{DOY} > \mathrm{DOY}_{\mathrm{senesc}} \\ 0, & \text{otherwise} \end{cases} \tag{26}$$

In tropical environments without a distinct growing season, $\mathrm{DOY}_{\mathrm{senesc}}$ is equal to 0 so that turnover occurs throughout the year.

For foliar N, a proportion of foliar turnover is retranslocated, so one fraction is transferred to litter pools:

$$t_{\mathrm{leafN}} = \begin{cases} \mathrm{N}_{\mathrm{leaf}}\tau_{\mathrm{leaf}}(1 - \mathrm{Retrans\_frac}), & \mathrm{DOY} > \mathrm{DOY}_{\mathrm{senesc}} \\ 0, & \text{otherwise} \end{cases} \tag{27}$$

while the remainder is transferred to the labile plant N pool:

$$t_{\mathrm{retransN}} = \begin{cases} \mathrm{N}_{\mathrm{leaf}}\tau_{\mathrm{leaf}}\mathrm{Retrans\_frac}, & \mathrm{DOY} > \mathrm{DOY}_{\mathrm{senesc}} \\ 0, & \text{otherwise} \end{cases} \tag{28}$$

For wood and fine roots, turnover is a continual process without retranslocation:

$$t_{\mathrm{woodC}} = \mathrm{C}_{\mathrm{wood}}\tau_{\mathrm{wood}} \tag{29}$$

$$t_{\mathrm{woodN}} = \mathrm{N}_{\mathrm{wood}}\tau_{\mathrm{wood}} \tag{30}$$

$$t_{\mathrm{rootC}} = \mathrm{C}_{\mathrm{root}}\tau_{\mathrm{root}} \tag{31}$$

$$t_{\mathrm{rootN}} = \mathrm{N}_{\mathrm{wood}}\tau_{\mathrm{root}} \tag{32}$$

Title Page
Abstract Introduction
Conclusions References
Tables Figures
◀I ▶I
◀ ▶
Back Close
Full Screen / Esc
Printer-friendly Version
Interactive Discussion

2.1.6 Plant respiration

Maintenance respiration can be related to the N status of plant tissues, and this observation has formed the basis of models (Cannell and Thornley, 2000). However, the precise relationships are uncertain, so two alternative approaches are explored here.

In the first option, the model builds on the observation from a global plant trait database that respiration is a non-linear function of tissue N concentration (Reich et al., 2008). Tissue N concentration is determined as the ratio N content (mmol) per g of tissue. Tissue mass is determined from tissue C content and a parameter, tissue C concentration, $\mathrm{g\,C\,g^{-1}}$ tissue (c_{conc}). A scalar is applied to convert respiration to daily units. Respiration is only associated with the pools involved in uptake processes (so wood, bud and labile N does not affect the outcome).

Option 1:

$$\begin{aligned}\mathrm{Ra}_{\mathrm{main}} = {} & \left(\left(\exp\left(\mathrm{Ra}_{\mathrm{parm1}} + \mathrm{Ra}_{\mathrm{parm2}} \log\left(\frac{\left(\frac{\mathrm{N}_{\mathrm{leaf}}}{14.0}1000\right)}{\frac{\mathrm{C}_{\mathrm{leaf}}}{\mathrm{C}_{\mathrm{conc}}}}\right)\right)\right)1.2^{-8}\left(\frac{\mathrm{C}_{\mathrm{leaf}}}{\mathrm{C}_{\mathrm{conc}}}\right)86\,400\right) \\ & + \left(\left(\exp\left(\mathrm{Ra}_{\mathrm{parm1}} + \mathrm{Ra}_{\mathrm{parm2}} \log\left(\frac{\left(\frac{\mathrm{N}_{\mathrm{root}}}{14.0}\cdot 1000\right)}{\frac{\mathrm{C}_{\mathrm{root}}}{\mathrm{C}_{\mathrm{conc}}}}\right)\right)\right)1.2^{-8}\left(\frac{\mathrm{C}_{\mathrm{root}}}{\mathrm{C}_{\mathrm{conc}}}\right)86\,400\right) f(T)\end{aligned} \tag{33}$$

In the second option, the approach (Ryan, 1991) is based purely on a linear relationship between the total mass of foliar and fine root N, modified by temperature. Again, respiration is only associated with the leaf and fine root pools.

Option 2:

$$\mathrm{Ra}_{\mathrm{main}} = (\mathrm{N}_{\mathrm{leaf}} + \mathrm{N}_{\mathrm{root}})\,\mathrm{Ra}_{\mathrm{per_{gN}}} f(T) \tag{34}$$

where the temperature response of autotrophic respiration is determined as:

$$f(T) = Q_{\mathrm{a}}^{\frac{T-20}{10}} \tag{35}$$

Autotrophic respiration is also associated with the growth of new tissues, whereby the allocation of C to a pool X (X = bud, fine root or wood) results in an additional fraction that is respired:

$$\mathrm{Ra}_{\mathrm{growth}} = a_{XC}\mathrm{growthresp} \tag{36}$$

Plant maintenance respiration must be maintained each day according to requirements, and hence a buffer pool is required to avoid critical shortages during periods of low or zero growth. This labile respiration pool (C_{Ra}) is topped up from the C_{labile} pool depending on whether a maximum pool size has been attained (see below).

A fraction of labile C can be allocated to excess autotrophic respiration ($\mathrm{Ra}_{\mathrm{excessC}}$) to drive N fixation, if labile C remaining after other allocation (C_{avail}) exceeds the maximum storage capacity ($\mathrm{store}_{\mathrm{c}}$), and growth is occurring

$$\mathrm{Ra}_{\mathrm{excessC}} = (C_{\mathrm{avail}} - \mathrm{store}_{\mathrm{c}})\,\mathrm{growth}_{\mathrm{potential}}\tau_{\mathrm{excessC}} \tag{37}$$

During periods with high maintenance respiration fluxes but little production, plants can draw the storage pools of labile C (both C_{Ra} and C_{labile}) down to zero. To avoid death when this occurs, plants are able to breakdown C allocated to buds for use in emergency maintenance respiration.

$$a_{\mathrm{budC\_2Ramain}} = -\max((C_{\mathrm{Ra}} + C_{\mathrm{labile}} + a_{\mathrm{Ra}_{\mathrm{main}}} - \mathrm{Ra}_{\mathrm{main}}), 0) \tag{38}$$

If $a_{\mathrm{budC\_2Ramain}}$ is positive, N is transferred from the N_{bud} pool to the N_{labile} pool ($a_{\mathrm{budN\_2Ramain}}$) based on the C : N ratio of the bud pools.

2.1.7 Adjustments to maximum plant tissue pool sizes

At the end of each annual cycle, a series of tests are used to determine whether the vegetation should increase, hold, or decrease the maximum leaf C and leaf N. The interaction of these adjustments results in changes to the target leaf C : N and maximum leaf C for the following year. Another set of tests determine adjustments to fine root C. Fine root C : N is not adjusted.

Adjustments to maximum leaf N are based on whether the integrated annual marginal return on leaf N investment is positive for C balance (see Sect. 2.1.9 below), and whether leaf N was deficient in the past year. Leaf N deficit is determined by checking if, on any day with potential growth during the past year, labile N stocks limited the allocation of C to leaf buds (a_{budC}) at the target C : N, by testing the inequality:

$$\frac{a_{\mathrm{budC}}}{\mathrm{target}_{\mathrm{leafCN}}} > \mathrm{N}_{\mathrm{labile}} \cdot \mathrm{growth}_{\mathrm{potential}} \tag{39}$$

The logic behind the tests for changing maximum leaf N is as follows (see Supplement Table S1). If the marginal return on N investment is negative, then maximum leaf N should be decreased next year; the vegetation will improve its C balance by investing less N in foliage in this case. Otherwise, with positive marginal returns on N investment, then if last year's maximum leaf N was not attained, reduce the maximum for the next year; in this case the vegetation is not able to attain the maximum given other allocation pressures and so should be more conservative. If last year's maximum was attained, then if there was no leaf N deficit the maximum leaf N is raised, and otherwise it is held; the deficit here is used to monitor whether N limitation is likely.

Adjustments to maximum leaf C are based on four related tests (see Supplement Table S2). If in the previous year the maximum leaf C was attained, wood and fine root requirements that are based on leaf : stem parameter min_leaf_2_wood and leaf : root relationships were met completely, and the marginal return on C investment is positive, then the maximum leaf C is increased; C is clearly in surplus and can be invested effectively. If in the previous year wood and fine root requirements were unmet, then C demands were not met, and maximum leaf C is decreased. If the marginal return on leaf C investment is negative, then maximum leaf C is decreased to improve the overall C balance. If the maximum leaf C was not attained, then maximum leaf C is reduced if there was no leaf N deficit; in this case the vegetation is C limited, and an adjustment in leaf C : N is required. If there was a leaf N deficit, then maximum leaf C is held.

For fine roots, there are five linked tests used to determine the maximum fine root C (see Supplement Table S3). If the current target fine root C is less than the required root to leaf ratio (parameter min_leaf_to_root), then the maximum root C is increased. If the maximum root C was not attained in the previous year, and that maximum exceeds the required root to leaf ratio, then the maximum is decreased. If the maximum was reached, and the minimum root to leaf ratio is exceeded, then root C is decreased if either the marginal return on CN investment in roots is negative (see Sect. 2.1.9; Eq. 58), or if the N return on C investment into N fixation exceeds the return on investment in roots (see Sect. 2.1.9; Eq. 57). Maximum root C is only increased if the previous maximum was attained, N return on C investment in roots exceeds returns on investment in N fixation, the N return on CN investment in roots is positive, and leaf N was in deficit during the preceding year. These tests show a N requirement by foliage, and that C investment into roots is the most efficient means to relieve this. If there is no leaf N deficit, then the maximum is held. Fine root C : N is held constant in all cases.

After the direction of adjustments to the maximum leaf C, leaf N, and root C are determined by the rules described above, the magnitude of the adjustment ($\text{tissue}_{\text{adjust}}$) is based on a potential proportional rate of change (Max_tissue_adjust) scaled by the magnitude of the marginal return on leaf C : N (see Sect. 2.1.9 for the calculation of marginal returns). Scaling the adjustment by the marginal return allows for larger adjustments when the plant is farther from the optimal tissue allocation. The $\text{tissue}_{\text{adjust}}$ for leaf C, leaf N and root C are based on

$$\text{tissue}_{\text{adjust}} = \min(\text{max\_tissue\_adjust}, (\text{max\_tissue\_adjust}(|\text{Return}_{\text{leafC}} + \text{Return}_{\text{leafN}}|))) \tag{40}$$

2.1.8 Adjustment to plant storage pools

Plants store both C and N in labile pools (C_{labile}, N_{labile}) prior to allocation, and C is also stored in a specific respiratory labile pool (C_{Ra}) to ensure metabolism through periods of low production. Each of these stores has a maximum size ($\text{Store}_{\text{maxC}}$, $\text{Store}_{\text{maxN}}$,

$\text{Store}_{\text{RaC}}$; Table 5), which is dependent on the magnitude of the root and wood tissue pools, which are the assumed locations of these stores, and specific parameters (store_prop_X).

$$\text{Store}_{\text{RaC}} = (C_{\text{wood}} + C_{\text{root}})\text{store\_prop}_{\text{RaC}} \quad (41)$$

$$\text{Store}_{\text{maxC}} = (C_{\text{wood}} + C_{\text{root}})\text{store\_prop}_{\text{C}} \quad (42)$$

$$\text{Store}_{\text{maxN}} = (C_{\text{wood}} + C_{\text{root}})\text{store\_prop}_{\text{N}} \quad (43)$$

2.1.9 Marginal calculations for plants

Marginal returns on investment are calculated each day, to inform daily allocation decisions (see Sect. 2.1.4 above), and also integrated over longer periods of time to adjust maximum structural pools (see Sect. 2.1.7 above) (see Table 5 for parameter values). Calculations are derived by forward finite difference (defined by the parameter add_{c}). The finite differences for N (add_{Nx}) are determined from the fixed difference for C pools, thus:

$$\text{add}_{\text{Nleaf}} = \text{add}_{\text{C}} \cdot \frac{\text{leafN}}{\text{leafC}} \quad (44)$$

$$\text{add}_{\text{Nroot}} = \text{add}_{\text{C}} \cdot \frac{1}{\text{rootCN}} \quad (45)$$

The marginal change to photosynthesis from added leaf C and N, added leaf C and added leaf N respectively are determined using the GPP routine (Eq. 4) with arguments indicated within parentheses thus:

$$\text{GPPreturn}_{\text{leafC}} = \text{GPP}(C_{\text{leaf}} + \text{add}_{\text{C}}, N_{\text{leaf}}) - \text{GPP}(C_{\text{leaf}}, N_{\text{leaf}}) \quad (46)$$

$$\text{GPPreturn}_{\text{leafN}} = \text{GPP}(C_{\text{leaf}}, N_{\text{leaf}} + \text{add}_{\text{Nleaf}}) - \text{GPP}(C_{\text{leaf}}, N_{\text{leaf}}) \quad (47)$$

The marginal change to maintenance respiration is determined similarly – only the equation for simultaneous C and N addition is shown below, with the equations for

C-only and N-only additions following the equations above:

$$\mathrm{RamainReturn}_{\mathrm{leafC}} = \mathrm{Ramain}(\mathrm{C}_{\mathrm{leaf}} + \mathrm{add}_{\mathrm{C}}, \mathrm{N}_{\mathrm{leaf}}) - \mathrm{Ramain}(\mathrm{C}_{\mathrm{leaf}}, \mathrm{N}_{\mathrm{leaf}}) \quad (48)$$

$$\mathrm{RamainReturn}_{\mathrm{leafN}} = \mathrm{Ramain}(\mathrm{C}_{\mathrm{leaf}}+, \mathrm{N}_{\mathrm{leaf}} + \mathrm{add}_{\mathrm{N}}) - \mathrm{Ramain}(\mathrm{C}_{\mathrm{leaf}}, \mathrm{N}_{\mathrm{leaf}}) \quad (49)$$

The marginal change to growth respiration is determined for all cases based on added C,

$$\mathrm{RagrowReturn}_{\mathrm{leafC}} = (1 + \mathrm{growthresp})\mathrm{add}_{\mathrm{C}} \quad (50)$$

To determine the amortised cost of leaf and fine root production, the lifespan of these tissues is incorporated in calculations. The calculations assess whether tissues can repay their costs, using the concept of a time horizon, linked to tissue turnover rate:

$$\mathrm{leaf}_{\mathrm{horizon}} = \begin{cases} 1.0, & t_{\mathrm{leaf}} > \frac{1}{365} \\ 365 t_{\mathrm{leaf}}, & t_{\mathrm{leaf}} \leq \frac{1}{365} \end{cases} \quad (51)$$

$$\mathrm{root}_{\mathrm{horizon}} = 365 t_{\mathrm{root}} \quad (52)$$

Since the returns are integrated over an annual cycle, variation in $\mathrm{leaf}_{\mathrm{horizon}}$ for seasonally deciduous plants is captured in the integrated returns. Therefore the annual return is not scaled by the leaf turnover rate. This $\mathrm{leaf}_{\mathrm{horizon}}$ calculation assumes that all plants with leaf lifespans < 1.0 year ($t_{\mathrm{leaf}} > 1/365$) are seasonally deciduous.

The marginal returns on investments of CN simultaneously (at current ratio), and of C and of N alone on C uptake (net production) can then be determined based on the sensitivity of production and maintenance respiration corrected for leaf lifespan, for growth respiration, and for the initial investment itself:

$$\mathrm{Return}_{\mathrm{leafC}} = \frac{(\mathrm{GPPreturn}_{\mathrm{leafC}} - \mathrm{RamainReturn}_{\mathrm{leafC}})}{\mathrm{leaf}_{\mathrm{horizon}}} - \mathrm{RagrowReturn}_{\mathrm{leafC}} - \mathrm{add}_{\mathrm{C}} \quad (53)$$

$$\mathrm{Return}_{\mathrm{leafN}} = \frac{(\mathrm{GPPreturn}_{\mathrm{leafN}} - \mathrm{RamainReturn}_{\mathrm{leafN}})}{\mathrm{leaf}_{\mathrm{horizon}}} - \mathrm{RagrowReturn}_{\mathrm{leafN}} \quad (54)$$

The marginal returns on N uptake ($\mathrm{UReturn}_X$) are calculated similarly, using the uptake equation (Eq. 11) modified for root parameters thus:

$$\mathrm{Ureturn_{rootC}} = U_{\mathrm{NH_4}}(\mathrm{C_{root}} + \mathrm{add_C}, \mathrm{N_{root}}) + U_{\mathrm{NO_3}}(\mathrm{C_{root}} + \mathrm{add_C}, \mathrm{N_{root}}) - U_{\mathrm{NH_4}}(\mathrm{C_{root}}, \mathrm{N_{root}}) - U_{\mathrm{NO_3}}(\mathrm{C_{root}}, \mathrm{N_{root}}) \quad (55)$$

$$\mathrm{Ureturn_{rootCN}} = U_{\mathrm{NH_4}}(\mathrm{C_{root}} + \mathrm{add_C}, \mathrm{N_{root}} + \mathrm{add_{Nroot}}) + U_{\mathrm{NO_3}}(\mathrm{C_{root}} + \mathrm{add_C}, \mathrm{N_{root}} + \mathrm{add_{Nroot}}) - U_{\mathrm{NH_4}}(\mathrm{C_{root}}, \mathrm{N_{root}}) - U_{\mathrm{NO_3}}(\mathrm{C_{root}}, \mathrm{N_{root}}) \quad (56)$$

The uptake return is then adjusted for root lifespan thus:

$$\mathrm{Return_{rootC}} = \frac{\mathrm{Ureturn_{rootC}}}{\mathrm{root_{horizon}}} \quad (57)$$

For the CN marginal the return must be adjusted for the N invested:

$$\mathrm{Return_{rootCN}} = \frac{\mathrm{Ureturn_{rootCN}}}{\mathrm{root_{horizon}}} - \mathrm{add_{Nroot}} \quad (58)$$

The return on C investment into N fixation is determined from the parameterised N fixation return adjusted by N uptake down-regulation (X_N) and temperature:

$$\mathrm{Return_{Raexcess}} = \mathrm{add_C Nfix_{pergC}} X_\mathrm{N} f(T) \quad (59)$$

Data on the relationship between root N content and N uptake rates (matching the well-established relationship between N concentration and photosynthesis for leaves), is lacking, thus creating a challenge for calculating a return on investment of root N alone ($\mathrm{Ureturn_{rootN}}$). Therefore, the root N return is not used in the current version of ACONITE.

2.1.10 Soil processes

A simple, 3-pool (CWD, litter, SOM) soil dynamics model is used in this version of ACONITE; other soil decomposition models can be used in future applications. Soil processes are affected by a temperature (T) response function based on a $Q10$ relationship:

$$g(T) = Q_h^{\frac{T-20}{10}} \tag{60}$$

The turnover of coarse woody litter pools is purely a function of temperature and a first order rate constant, consistent with physical breakdown:

$$t_{\mathrm{CWDC}} = \mathrm{C_{cwd}}\tau_{\mathrm{wood}}g(T) \tag{61}$$

$$t_{\mathrm{CWDN}} = \mathrm{N_{cwd}}\tau_{\mathrm{wood}}g(T) \tag{62}$$

The potential turnover of litter C is another temperature dependent first order process, with fluxes to either soil C

$$\mathrm{Pot\_t_{litterC\_soilC}} = \mathrm{C_{litter}}\tau_{\mathrm{litter}}g(T)(1-\mathrm{m\_resp\_frac}) \tag{63}$$

or to the atmosphere, via mineralisation, according to a fractionation parameter

$$\mathrm{Pot\_t_{litterC\_atm}} = \mathrm{C_{litter}}\tau_{\mathrm{litter}}g(T)\mathrm{m\_resp\_frac} \tag{64}$$

Litter N turnover is a similar process:

$$t_{\mathrm{litterN}} = N_{\mathrm{litter}}\tau_{\mathrm{litter}}g(T) \tag{65}$$

Immobilisation is the process whereby mineral N is incorporated into organic, soil N by microbial action. The potential total immobilisation is determined from the potential turnover of litter C, the (fixed) soil C : N ($\mathrm{Soil_{CN}}$) and the turnover of litter:

$$\mathrm{total_{immob}} = (\mathrm{Pot\_t_{litterC\_soilC}}/\mathrm{Soil_{CN}}) - t_{\mathrm{litterN}} \tag{66}$$

If $\mathrm{total}_{\mathrm{immob}} < 0$, then N is mineralised in the form of NH_4. If $\mathrm{total}_{\mathrm{immob}} > 0$, then immobilisation uses NH_4^+ and NO_3^- according to their relative proportions:

$$\mathrm{NH}_{4\mathrm{immob}} = \begin{cases} (\mathrm{Pot\_t}_{\mathrm{litterC\_soilC}}/\mathrm{Soil}_{\mathrm{CN}}) - t_{\mathrm{litterN}}, & \mathrm{total}_{\mathrm{immob}} < 0 \\ \frac{N_{\mathrm{NH}_4}}{N_{\mathrm{NH}_4}+N_{\mathrm{NO}_3}}\mathrm{total}_{\mathrm{immob}}, & \mathrm{total}_{\mathrm{immob}} \geq 0 \end{cases} \tag{67}$$

$$\mathrm{NO}_{3\mathrm{immob}} = \begin{cases} 0, & \mathrm{Pot\_total}_{\mathrm{immob}} < 0 \\ \frac{N_{\mathrm{NO}_3}}{N_{\mathrm{NH}_4}+N_{\mathrm{NO}_3}}\mathrm{total}_{\mathrm{immob}}, & \mathrm{Pot\_total}_{\mathrm{immob}} \geq 0 \end{cases} \tag{68}$$

Both these immobilisations are limited in magnitude by the size of each mineral pool.

The actual turnover of litter C is now determined from the potential values (Eqs. 63 and 64) adjusted by the ratio of actual to potential immobilisation:

$$t_{\mathrm{litterC\_soilC}} = \mathrm{Pot\_t}_{\mathrm{litterC\_soilC}} \frac{\mathrm{NH}_{4\mathrm{immob}} + \mathrm{NH}_{3\mathrm{immob}}}{\mathrm{total}_{\mathrm{immob}}} \tag{69}$$

$$t_{\mathrm{litterC\_atm}} = \mathrm{Pot\_t}_{\mathrm{litterC\_atm}} \frac{\mathrm{NH}_{4\mathrm{immob}} + \mathrm{NH}_{3\mathrm{immob}}}{\mathrm{total}_{\mathrm{immob}}} \tag{70}$$

The turnover of soil C is a temperature dependent first order process:

$$t_{\mathrm{soilC}} = \mathrm{C}_{\mathrm{soil}}\tau_{\mathrm{soil}}g(T) \tag{71}$$

Soil N is lost by two linked processes, with a fractionation into NH_4^+ production

$$t_{\mathrm{soilN}} = \mathrm{N}_{\mathrm{soil}}\tau_{\mathrm{soil}}g(T)(1 - \mathrm{DON\_leach\_prop}) \tag{72}$$

and into dissolved organic N loss, both temperature dependent:

$$L_{\mathrm{DON}} = \mathrm{N}_{\mathrm{soil}}\tau_{\mathrm{soil}}g(T)\mathrm{DON\_leach\_prop} \tag{73}$$

This simple dissolved organic N loss parameterization is broadly designed to represent demand-independent N losses in ACONITE, whereby N is lost through a pathway that cannot be controlled by plant uptake and microbial immobilization (Vitousek et al., 2010). Such a pathway is necessary for simulating N limitation at steady-state when N fixation inputs are included (Menge, 2011).

Nitrification, the production of $\mathrm{NO_3^-}$ from $\mathrm{NH_4^+}$, is another first order temperature dependent process:

$$\mathrm{nitr} = N_{\mathrm{NH_4}}\mathrm{nitr}_{\mathrm{rate}}g(T) \tag{74}$$

Nitrate is leached at a fixed rate:

$$L_{\mathrm{NO_3}} = N_{\mathrm{NO_3}}\mathrm{leach\_rate} \tag{75}$$

The soil parameters are listed in Table 6.

2.1.11 N fixation

N fixation occurs if labile C exceeds its maximum store (i.e. high energy inputs) and the labile N store is less than its maximum (i.e. N demand is not met). In that case, N fixation is calculated as:

$$\mathrm{N_{fix}} = \mathrm{Ra_{excess}}\mathrm{Nfix_{pergC}}X_{\mathrm{N}}f(T) \tag{76}$$

Where N_{fixpergc} is the C cost for fixing N and $\mathrm{Ra_{excess}}$ is from Eq. (37).

2.1.12 Model parameters

Flux rates are determined by a set of parameters controlling photosynthesis (Table 3), nitrogen uptake (Table 4), plant allocation (Table 5), plant turnover (Table 5), calculation of marginal returns (Table 5), and soil dynamics (Table 6). Model parameters were derived from the literature, or estimated in some cases, with sources clearly indicated. A full sensitivity analyses was undertaken.

2.2 Model experiments

We first examined the dynamics of leaf C and N optimization using only the canopy model of ACONITE. The canopy model included the photosynthesis, respiration, and marginal calculations described above. First, we simulated marginal annual C returns for the allocation of leaf C, leaf N, and both leaf C and N together in temperate deciduous and evergreen forests for two specified values of LAI (deciduous: 4.0 and 6.3; evergreen: 4 and 5) to explore how optimal leaf C : N varies with LAI. Second, we simulated marginal returns in temperate deciduous and evergreen forests for two different values of the acm_{11} parameter (0.05 and 0.5), a parameter new to the ACM canopy model. We specifically explored the acm_{11} parameter because prior model analysis indicated that different values are required for deciduous and evergreen forests to ensure proper optimization of leaf C : N ratios. Finally, we simulated marginal returns for the two alternative representations of autotrophic respiration. In Eq. (33), we describe a relationship between mass-based leaf respiration and mass-based leaf N concentration based on the log–log relationships from a plant trait database reported in Reich et al. (2008). The equation and parameters used from Reich et al. (2008) are based on the most comprehensive analysis of leaf respiration to date. However, many ecosystem and Earth System models use a linear relationship between total N and mass-based respiration from Ryan (1991) to parameterize autotrophic respiration (Eq. 34). The Ryan (1991) relationship was based on 16 observations, compared to 2510 observations in Reich et al. (2008). Because the Ryan (1991) equation is widely-used in ecosystem modelling, we explored the sensitivity of leaf C : N optimization to the two alternative parameterization of autotrophic respiration. All simulations using the canopy model were run for one year using Harvard Forest climate data from 2002 to generate annual marginal returns on investment of leaf C, leaf N, and leaf C and N together (g C/g C or N or CN).

Next, using the full ACONITE model, we analysed the qualitative functioning of the model using two different sets of climate forcing, one tropical and one temperate. For

Title Page
Abstract Introduction
Conclusions References
Tables Figures
|◄ ►|
◄ ►
Back Close
Full Screen / Esc
Printer-friendly Version
Interactive Discussion

the temperate forcing, analyses were undertaken for both deciduous forest (leaf lifespan < 1 year) and evergreen forest (leaf life span > 1 year). The temperate climate data were from Harvard Forest (Munger and Wofsy, 1999), at 42.5° N, 72.° W. The tropical climate data were from Manaus (Kruijt et al., 2004) at 2.6° N, 60.2° W.

These tests evaluated the model capacity to resolve seasonality in climate and phenology. Model simulations were run to steady states over 2000 year simulations. Steady state was evaluated by testing the stationarity of C_{soil}, the longest residence time pool. Model assessment involved examination of annual GPP, CUE, foliar C : N, maximum annual LAI against representative ecosystem data. Intra-annual patterns in LAI, GPP, net primary production (NPP), leaf C allocation, wood C allocation, and root C allocation at steady-state for the temperate deciduous and tropical forests are described in the Supplement (Fig. S2).

2.3 Sensitivity analysis

A single factor sensitivity analysis was undertaken for each parameter. We increased each parameter by 10 % and report the sensitivity metric (S: % change in response variable per % increase in parameter value) of maximum annual LAI, annual GPP, annual NPP, CUE, foliar C : N ratio, and annual N fixation at steady state. Positive (negative) values of S indicate a positive (negative) correlation between the parameter and the response variable, where S values greater (less) than one (negative one) are parameters with amplifying sensitivity. The sensitivity analysis was performed for a tropical forest, a deciduous temperate forest, and an evergreen temperate forest at the same sites described above. Parameters with S metrics greater than or equal to 0.1 are listed in Table 8.

3 Results

3.1 Canopy model simulations investigating leaf C : N ratio and LAI dynamics

In the canopy-only experiment for temperate deciduous forest, we found that the calculation of annual marginal yields of leaf C and N allowed for the optimization of leaf C : N based on the leaf parameters (leaf lifespan, specific leaf area), the environmental conditions, and N status of the plant. Initial low leaf C : N (< 19) were linked to positive margins on C investment alone, and so led to the addition of leaf C only (and thus increasing leaf C : N). Initial high leaf C : N (> 35) were linked to positive margins on N investment, and so led to addition of leaf N only (thus decreasing leaf C : N). Intermediate initial leaf C : N (19–35) had positive margins for both C and N investment, and so allow for a flexible leaf C : N based on N status (Fig. 2).

As LAI varied, the range of flexible leaf C : N was altered (Fig. 3). At low LAI, increasing both leaf C and leaf N had positive returns. As LAI increased with a low leaf C : N (Fig. 3a), the marginal return on N investment went negative first; so the plant decreased allocation to N, before decreasing allocation to leaf C, resulting in increased leaf C : N as the plant reaches the maximum LAI yields a positive return on C (hashed shading). However, a large increase in leaf C : N from 20 (a) to 28 (b) reduced the investment return on leaf C and increased the return on leaf N at a given LAI, resulting in a lower maximum LAI and lower leaf C : N. An optimal LAI and leaf N emerged from adjusting allocation so that marginal investment returns were zero for both leaf C and N.

Successfully generating these leaf C : N patterns (increase leaf C region, increase leaf N region, and a flexible region) for different parameterised leaf traits (lifespan, leaf mass per area) required a different value for the acm_{11} parameter used in calculating GPP for deciduous and evergreen forests (Fig. 4). Low values of the acm_{11} in deciduous forests led to an unrealistically low leaf C : N and no flexible leaf C : N region (Fig. 4a). In contrast, high values of the acm_{11} parameter applied to evergreen forests (Fig. 4d) did not yield a reasonable maximum leaf C : N. This parameter was introduced to reduce photosynthesis for canopies with LAI : N_{leaf} ratios that diverge from the optimum slope identified in field studies and ecophysiological modelling (Williams and Rastetter, 1999). Further work with ecophysiological modelling is required to generate a more effective representation of this effect in ACM, and to explore the relationship with other leaf traits.

Successfully generating leaf C : N patterns required for leaf C : N optimization also depended on the parameterization of autotrophic respiration (Fig. 5). The widely-used linear relationship between leaf N and respiration from Ryan (1991) generated unreasonably low leaf C : N (< 15) for temperate deciduous forests and for temperature evergreen forests (< 20). The non-linear and steeper relationship from Reich et al. (2008) produced leaf C : N that compared more favourability to plant trait databases (Kattge et al., 2011; see below).

3.2 Steady-state simulations with full ACONITE model across multiple biomes

Steady-state simulations with the full ACONITE model, using the non-linear autotrophic respiration equation (Reich et al., 2008) and the deciduous and evergreen values for the acm_{11} parameter, had patterns in leaf C : N patterns that compared well to patterns from the TRY plant trait database (Kattge et al., 2011). Comparing leaf C : N among temperate deciduous, temperate evergreen, and tropical evergreen trees, both ACONITE and the TRY database found the following order (Table 7): temperate deciduous (ACONITE: 22; TRY: 23) < tropical evergreen trees (ACONITE: 28; TRY 30) < temperate evergreen (ACONITE: 43; TRY 41).

Steady-state values for LAI revealed closed canopies (LAI >> 1) for each ecosystem, with a range of 4.4–6.3, and no clear climate effect (Table 7). Total vegetation C, GPP and NPP all decreased from the tropical simulation to the temperate simulation. CUE was larger in short-lifetime species (temperate deciduous) than longer-lifetime species (temperate evergreen and tropical evergreen). N fixation at steady-state decreased by an order of magnitude from the tropics to temperate forests. Within temperate forests, steady-state values for total vegetation C, GPP, NPP, and N fixation were similar for both deciduous and evergreen forests.

3.3 Parameter sensitivity analysis

Leaf C : N was most sensitive to the parameter (Ra_parm2) describing the slope of the log–log relationship between N concentration and autotrophic respiration (Table 8). A steeper slope of the log–log relationship increased leaf C : N by a proportional amount that exceeded the proportional change in the parameter ($S = 1.1$–1.6). Leaf C : N also increased with leaf-life span, which is governed by the leaf turnover parameter (τ_{leaf}) for the tropical and temperate evergreen forest and the date of leaf drop parameters (SensceStart) for the temperate deciduous forest. Leaf carbon per leaf area (lca) and the Ra_parm2 parameter also influenced the leaf C : N ratio.

Similar to leaf C : N ratio, LAI was most sensitive to the Ra_parm2 parameter, particularly tropical and temperate evergreen forests (Table 8) where the proportional sensitivity was > 1. Other sensitive parameters for LAI were parameters that governed the leaf lifespan (τ_{leaf} and SenceStart), specific leaf area (lca), and the photosynthesis relationship with day length (acm_2). Steeper slopes of the N vs. respiration relationship (Ra_parm2) resulted in larger LAI values, while increasing leaf-lifespan (τ_{leaf} and SenceStart) decreased the LAI. LAI decreased with increased leaf carbon per leaf area (lca).

Total vegetation C stocks, GPP, and NPP were most sensitive to parameters that governed the total photosynthesis relationship with day length (acm_2) and growing season length (SenceStart). Additionally, total vegetation C was most sensitive to the rate of wood turnover (τ_{wood}). Sensitivities were similar across the three forest types, except for the low of sensitivity to growing season length in the tropical forest, consistent with its lack of a seasonal cycle.

N fixation was sensitive to numerous parameters, indicating the strong coupling of C and N dynamics for this process. The strongest sensitivity was to the rate of photosynthesis (acm_2: day length – GPP relationship). N fixation in temperate forests was sensitive to N uptake parameters (r_{radius}, $I_{\max}$, and r_{density}) despite a lack sensitivity of LAI, total vegetation C, GPP, NPP, and leaf C : N to these N uptake parameters.

CUE (the ratio of NPP : GPP) was not strongly sensitive to any parameters ($|S| \leq 0.3$). CUE is a complex outcome of N allocation, which determines both photosynthesis and autotrophic respiration; CUE sensitivity was greatest to photosynthetic parameters (acm_1, acm_2) and to respiration parameters (Qra, Ra_parm1, Ra_parm2, Ra_grow). There was also sensitivity to root CN.

4 Discussion

Here we described and evaluated a simple model of terrestrial C and N dynamics that included prognostic leaf C : N, maximum LAI, N fixation, and plant C use efficiency. Most fundamentally, ACONITE was able to simulate steady-state C and N stocks and fluxes that are qualitatively consistent with biome level observations for a diverse set of environmental conditions, both temperate and tropical, and for deciduous and evergreen forests. ACONITE simulated these patterns in C and N dynamics using a minimal set of parameters based on marginal returns on investment, linked to a hypothesis of plant optimisation.

The simulations presented in this study focused on capturing broad biomes patterns in C and N cycling rather than site-specific dynamics. This is expressed by the use of plant trait parameters from a global database rather than site-level observations and the use of parameters for the canopy photosynthesis calculations from an analysis of deciduous and evergreen eddy-covariance towers in Europe using the DALEC model (Fox et al., 2009). Furthermore, we used a single year of climate data at each site to simulate the steady-state conditions rather than a site-specific climatology.

4.1 Model evaluation

A biome level evaluation suggests that ACONITE captures important patterns in leaf C : N ratios, NPP, and N fixation. ACONITE simulated biome level patterns in leaf C : N that matched observations from a global plant trait database (temperate deciduous < tropical evergreen < temperate evergreen). Capturing these broad biome patterns with ACONITE indicates potential for future research that uses the patterns in leaf mass per area, leaf-life span, and climate to simulate spatial patterns in leaf C : N. However, further exploration is needed into the requirement for two different acm_{11} parameters for different leaf traits. The calibration of the photosynthesis algorithm (ACM) used here was derived based on a fixed exponential decline in N content through the canopy in the SPA model, with no variation linked to leaf traits, and without exploring more extreme ratios of LAI to foliar N. The correction introduced using the acm_{11} parameter requires further work, based on more detailed SPA simulations, to resolve the complex interactions of C and N allocation within plant canopies.

Simulated GPP and NPP generally compared well to observations (Table 7). In the tropics, simulated NPP was within in the estimates for ten Amazonian forests (ACONITE: 1423; observed 930–1700 $\mathrm{g\,C\,m^{-2}\,yr^{-1}}$) (Aragao et al., 2009). For the temperate simulations, modelled NPP also matched estimates for deciduous stands at Harvard Forest, 659 $\mathrm{g\,C\,m^{-2}\,yr^{-1}}$ (Waring et al., 1998). The estimates of GPP in ACONITE are also consistent with independent estimates, for deciduous stands in Harvard Forest, 1246 $\mathrm{g\,C\,m^{-2}\,yr^{-1}}$ (Waring et al., 1998) and for forests in Amazonia, 3094–3138 $\mathrm{g\,C\,m^{-2}\,yr^{-1}}$ (Fisher et al., 2007).

ACONITE simulated observed biome level patterns (Cleveland et al., 1999) in N fixation where N fixation at steady state in the tropics was > 10 times N fixation in the temperate region. N fixation in ACONITE is governed by two temporal scales. The most immediate occurs when the internal capacity to store C is exceeded and the internal capacity to store N is not met. This results in higher N fixation in ecosystems with large energy inputs relative to N available in the soil. At longer time scales, plants increase allocation to roots if there is a larger return of N for C allocated to roots than C allocated to fixation. Increasing root mass increases the uptake of N and increases the internal store of N, thus decreasing N fixation. The dependence of N fixation on both marginal N yield for C allocation and the total availability of C and N in internal storage pools combines recent N fixation modelling approaches that used marginal yields (MEL: Rastetter et al., 2013) and N demand scaled by light (energy) availability (Gerber et al., 2010).

The balance between growth and respiration by plants determines the production of biomass. The fraction of photosynthesis used for growth is known as the C use efficiency (CUE), equivalent to the NPP : GPP ratio. CUE is challenging to determine, but initial estimates suggested it might be a conservative quantity for temperate forests, with a value of ~ 0.5 (Waring et al., 1998). Subsequent studies have suggested that CUE differs by biome, being lower in tropical forests, (Chambers et al., 2004) and lower in older (but not younger) boreal forests (Goulden et al., 2011). The range of CUE for the three ecosystems in this study, 0.44–0.51, is close to the suggested conservative value. Our tropical estimate (0.45), while lower than the temperate estimate, does not match the lower value reported for tropical forests (0.3). Our analysis (Table 8) shows relatively low sensitivity of CUE to several parameters linked to photosynthesis and respiration. A more complete analysis of CUE sensitivity, linked to detailed C and N budgets measurements for tropical ecosystems, would be a valuable next step.

4.2 Critical determinants of emergent properties in ACONITE

One of the most sensitive parameters was the slope of the log–log relationship between leaf N concentration and respiration rates (Table 8). Higher slopes led to increased leaf C : N and LAI. The log–log relationship between mass-based respiration and mass-based N concentration was derived from the analysis of global plant trait database in Reich et al. (2008). This study found that the slope of the relationship was similar among plant organs (leaves, roots, and wood) and plant functional types (gymnosperms, angiosperms, grasses), and that the slope was greater than 1. A slope greater than 1 indicates a higher respiratory cost for N as N concentrations increase (lower leaf C : N), potentially due to a greater proportion of N allocated to metabolically active proteins and faster turnover rate of protein (Reich et al., 2008). This elevated respiratory cost at low leaf C : N is important for defining a lower bound for leaf C : N. This exponentially increasing respiratory cost as the leaf C : N increases led to a higher leaf C : N where the marginal C return for N allocation to leaves is zero. The elevated respiratory costs at low leaf C : N is considerably larger when using the power-law scaling in Reich et al. (2008) than the more widely-used linear scaling from Ryan (1991) (Fig. 5). We suggest that, when using the trade-off between photosynthesis and respiration to calculate N allocation to leaves, ecosystem and Earth System models explore the sensitivity of N allocation to non-linearity in the N-respiration relationship.

Another sensitive parameter (acm_2) describes the slope of relationship between GPP and day-length in the photosynthesis algorithm (ACM). acm_2 functions as a simple linear scalar of GPP, where the scaling magnitude depends on day-length. Therefore GPP increases in proportion to the change in the acm_2 parameter. Because of the large sensitivity of total vegetation C, NPP, and N fixation on photosynthesis, these processes have significant sensitivity to acm_2.

4.3 ACONITE caveats and areas for future development

The ACONITE simulations presented here include key caveats. First, the results presented are for steady-state conditions. Additional evaluation is needed of the timescales over which the C–N feedbacks evolve. These feedbacks influence the rate of change in leaf C : N, LAI and N fixation over time. Accurately modelling the time-scale of C–N feedbacks is a common challenge for all ecosystem and Earth System models with C and N cycles. Second, the version of ACONITE we present here only applies to ecosystems without water limitation of photosynthesis and decomposition. This is a reasonable assumption for the sites used to evaluate models (Eastern temperate US and central Amazon) but including a simple water cycle is required for global application of ACONITE. Third, using the parameterization described above, N limitation is a transient property and was not present at steady state. In ACONITE, over long-time scales without disturbance, the ecosystem is able to entrain enough N from N fixation and N deposition to overcome N limitation. N limitation at steady-state can be parameterized in ACONITE by increasing the loss of N that is not controllable by plant or microbial uptake (Menge, 2011). In ACONITE, this processes is represented by the leaching of DON that is produced through the turnover of soil organic N (parameter: DON_leach_prop). Finally, as a biogeochemical model, ACONITE does not include plant demographic dynamics and, therefore, does not include the dynamics of leaf traits (leaf mass per area and leaf-lifespan) that would change over time through forest succession. Future model development can expand the fundamentals of ACONITE (optimised dynamic LAI, leaf C : N, CUE, and N fixation based on marginal returns on investment) to address these caveats.

4.4 Potential applications for ACONITE

The ability to constrain LAI and have spatially and temporally variable leaf C : N, features of the ACONITE model, are challenges for ecosystem and Earth System models. For example, the O-CN Earth System model includes dynamic leaf C : N but requires parameters for each plant functional type that describe the maximum, minimum, and average leaf C : N (Zaehle et al., 2010). Other ecosystem models, like the PnET-CN model, require the parameterization of maximum and minimum leaf C : N (Aber et al., 1997). Even a recently developed model that shows promise for defining the optimal allocation of leaf N among structural, storage, photosynthetic, and respiration N requires the parameterization of the total leaf functional leaf N (Xu et al., 2012). Here we presented a framework using marginal yields of investment to simulate dynamic leaf C : N without the two or three additional parameters per plant functional type that other models have required. Other ecosystem models include dynamic allocation of C to leaves and roots based on marginal yields (Multiple Element Limitation model: Rastetter et al., 2013) but use fixed C : N of tissues to calculate N allocation. The marginal allocation of both leaf C and N separately based on marginal yields extends the allocation concepts in the MEL model to the allocation of multiple elements. Finally, the dynamic allocation of leaf C (LAI) based on marginal yields can potentially help address issues with higher than observed LAI in Earth System models that results from simply calculating LAI based on the balance of C allocation to leaves and leaf turnover (Lawrence et al., 2011; Oleson, 2013) or without specifying a maximum LAI parameter for each plant function type (Gerber et al., 2010). Overall, the marginal yield framework used to allocate leaf C and N used in ACONITE is designed for application in Earth System models, because it requires minimal parameterization and can be applied to both seasonal and non-seasonal environments and both deciduous and evergreen life history strategies. Application to Earth System models will be associated with additional computational costs for their land surface components, associated with calculating marginal yields for allocation of C and N.

In addition to applications to Earth system modelling, the ACONITE structure is designed for parameter estimation and uncertainty estimation through assimilation of ecosystem data (Williams et al., 2009). Data-assimilation allows for the formal integration of multiple observations types and pre-existing (prior) parameter estimates, with formal propagation of error statistics. Most applications of data-assimilation for modelling the C cycle have used models with only the C cycle or the C and water cycles represented (Fox et al., 2009). Clearly, adding a N cycle increases the model complexity with additional parameters and equations. However adding a N cycle may also increase the constraints provided by data, because of the tight coupling of the C and N cycles and additional data related to the N cycle that is available for parameter estimation. Carbon only models currently suffer from a lack of constraint on their behaviours (Hill et al., 2012), which may be relieved by the inclusion of N cycle interactions. Whether the constraints provided by the N cycle on C predictions outweigh the cost of the greater model complexity is an important question for advancing C predictions, particularly in N limited regions of the world.

Overall, ACONITE represents a simple approach to modelling both the C and N cycles that simulates emergent properties (leaf C : N, maximum LAI, CUE, and N fixation) without using specific parameters to define properties. These emergent properties increase the flexibility of model applications while reducing total number of parameters required to be estimated through data-assimilation. ACONITE also has a relatively low computational load which allows a rapid and detailed exploration of its parameter space, required for Monte Carlo assimilation approaches. In this study we have shown qualitative similarities in model output with selected biome data. A more comprehensive and ecological challenging study would be to use DA approaches to formally estimate parameter uncertainty that compliments the parameter sensitivity analysis reported here. Such a study would apply ACONITE at many more well studied locations with time series (> decadal) observations of C and N stocks and fluxes, LAI data and local plant trait data on leaf C : N and leaf mass per area. Such a study would provide more robust tests of the theory behind ACONITE and underpin a further activity for global data assimilation, whereby C and N cycles at global scales are analysed, using ACONITE, for consistency with both optimisation theory and observations from global databases and from Earth observation.

Code availability

Code is available in the Supplement or through contacting the authors: R. Q. Thomas (rqthomas@vt.edu) or M. Williams (mat.williams@ed.ac.uk).

Supplementary material related to this article is available online at http://www.geosci-model-dev-discuss.net/7/2525/2014/gmdd-7-2525-2014-supplement.zip.

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Table 1. Mass balance equations used in ACONITE.

Vegetation pool mass balance equations
$\frac{dC_{\mathrm{leaf}}}{dt} = a_{\mathrm{budC\_2leaf}} - t_{\mathrm{leafC}}$
$\frac{dC_{\mathrm{wood}}}{dt} = a_{\mathrm{woodC}} - t_{\mathrm{woodC}}$
$\frac{dC_{\mathrm{root}}}{dt} = a_{\mathrm{rootC}} - t_{\mathrm{rootC}}$
$\frac{dC_{\mathrm{labile}}}{dt} = \mathrm{GPP} - a_{\mathrm{budC}} - a_{\mathrm{woodC}} - a_{\mathrm{rootC}} - a_{\mathrm{LabileRa}_{\mathrm{main}}} - \mathrm{Ra}_{\mathrm{growth}} - \mathrm{Ra}_{\mathrm{excessC}}$
$\frac{dC_{\mathrm{bud}}}{dt} = a_{\mathrm{budC}} - a_{\mathrm{bud}_{\mathrm{C2leaf}}} - a_{\mathrm{budC\_2Ramain}}$
$\frac{dC_{\mathrm{labileRa}}}{dt} = a_{\mathrm{LabileRa}_{\mathrm{main}}} + a_{\mathrm{budC\_2Ramain}} - \mathrm{Ra}_{\mathrm{main}}$
$\frac{dN_{\mathrm{leaf}}}{dt} = a_{\mathrm{budN\_2leaf}} - t_{\mathrm{leafN}} - t_{\mathrm{retransN}}$
$\frac{dN_{\mathrm{wood}}}{dt} = a_{\mathrm{woodN}} - t_{\mathrm{woodN}}$
$\frac{dN_{\mathrm{root}}}{dt} = a_{\mathrm{rootN}} - t_{\mathrm{rootN}}$
$\frac{dN_{\mathrm{labile}}}{dt} = U_{\mathrm{NH_4}} + U_{\mathrm{NO_3}} + U_{\mathrm{Nfix}} + t_{\mathrm{retransN}} + a_{\mathrm{budN\_2Ramain}} - a_{\mathrm{budN}} - a_{\mathrm{woodN}} - a_{\mathrm{rootN}}$
$\frac{dN_{\mathrm{bud}}}{dt} = a_{\mathrm{budN\_2leaf}} - a_{\mathrm{budN\_2Ramain}}$
Litter and organic matter mass balance equations
$\frac{dC_{\mathrm{litter}}}{dt} = t_{\mathrm{leafC}} + t_{\mathrm{rootC}} + t_{\mathrm{CWDC}} - t_{\mathrm{litterC\_soilC}} - t_{\mathrm{litterC\_atm}}$
$\frac{dC_{\mathrm{soil}}}{dt} = t_{\mathrm{litterC\_soilC}} - t_{\mathrm{soilC\_atm}}$
$\frac{dC_{\mathrm{cwd}}}{dt} = t_{\mathrm{woodC}} - t_{\mathrm{CWDC}}$
$\frac{dN_{\mathrm{litter}}}{dt} = t_{\mathrm{leafN}} + t_{\mathrm{rootN}} + t_{\mathrm{CWDN}} - t_{\mathrm{litterN}}$
$\frac{dN_{\mathrm{soil}}}{dt} = t_{\mathrm{litterN}} + U_{\mathrm{NH4\_immob}} + U_{\mathrm{NO3\_immob}} - t_{\mathrm{soilN}} - L_{\mathrm{DON}}$
$\frac{dN_{\mathrm{cwd}}}{dt} = t_{\mathrm{woodN}} - t_{\mathrm{CWDN}}$
Mineral N mass balance
$\frac{dN_{\mathrm{NH4}}}{dt} = \mathrm{Ndep}_{\mathrm{NH_4}} + t_{\mathrm{soilN}} - U_{\mathrm{NH_4}} - U_{\mathrm{NH}_{\mathrm{4immob}}} - \mathrm{nitr}$
$\frac{dN_{\mathrm{NO_3}}}{dt} = \mathrm{Ndep}_{\mathrm{NO_3}} + \mathrm{nitr} - U_{\mathrm{NO_3}} - U_{\mathrm{NO3\_immob}} - L_{\mathrm{NO_3}}$

Table 2. Description of fluxes used in mass balance equations.

Flux	Units	Description
$a_{\mathrm{budC\_2leaf}}$	$\mathrm{g\,C\,m^{-2}\,day^{-1}}$	Allocation from bud C pool to leaf C
t_{leafC}	$\mathrm{g\,C\,m^{-2}\,day^{-1}}$	Turnover of leaf C to litter C; constant over year in humid tropics; seasonal otherwise
a_{woodC}	$\mathrm{g\,C\,m^{-2}\,day^{-1}}$	Allocation from labile C to wood C
t_{woodC}	$\mathrm{g\,C\,m^{-2}\,day^{-1}}$	Turnover of wood C to CWDC pool; occurs throughout year
a_{rootC}	$\mathrm{g\,C\,m^{-2}\,day^{-1}}$	Allocation from labile C to wood C
t_{rootC}	$\mathrm{g\,C\,m^{-2}\,day^{-1}}$	Turnover of root C to litter C pool; occurs throughout year
GPP	$\mathrm{g\,C\,m^{-2}\,day^{-1}}$	Photosynthesis; based on ACM model see text for description
a_{budC}	$\mathrm{g\,C\,m^{-2}\,day^{-1}}$	Allocation of labile C to bud C; a fraction of the potential maximum leaf C
a_{Ramain}	$\mathrm{g\,C\,m^{-2}\,day^{-1}}$	Allocation of labile C to future maintenance respiration; helps prevent carbon starvation during periods of negative NPP
$\mathrm{Ra_{grow}}$	$\mathrm{g\,C\,m^{-2}\,day^{-1}}$	Growth respiration that occurs when tissue is allocated; a constant fraction of carbon allocated to tissue
$\mathrm{Ra_{excess}}$	$\mathrm{g\,C\,m^{-2}\,day^{-1}}$	Respiration that occurs when labile C exceeds a maximum labile C store; used for N fixation
$a_{\mathrm{budC\_2Ramain}}$	$\mathrm{g\,C\,m^{-2}\,day^{-1}}$	Allocation of bud C to maintenance respiration pool when maintain respiration pool reaches zero; represents forgoing future leaf C to prevent carbon starvation
$\mathrm{Ra_{main}}$	$\mathrm{g\,C\,m^{-2}\,day^{-1}}$	Respiration of living tissues; a function of nitrogen content and temperature
$a_{\mathrm{budN\_2leaf}}$	$\mathrm{g\,N\,m^{-2}\,day^{-1}}$	Allocation from bud N pool to leaf C; bud N is set in previous year
t_{leafN}	$\mathrm{g\,N\,m^{-2}\,day^{-1}}$	Turnover of leaf N to litter N; constant over year in humid tropics; seasonal otherwise
t_{retransN}	$\mathrm{g\,N\,m^{-2}\,day^{-1}}$	Reabsorption of N from leaves to labile N
a_{woodN}	$\mathrm{g\,N\,m^{-2}\,day^{-1}}$	Allocation from labile N to wood N
t_{woodN}	$\mathrm{g\,N\,m^{-2}\,day^{-1}}$	Turnover of wood N to CWDN pool; occurs throughout year
a_{rootN}	$\mathrm{g\,N\,m^{-2}\,day^{-1}}$	Allocation from labile N to wood N
t_{rootN}	$\mathrm{g\,N\,m^{-2}\,day^{-1}}$	Turnover of root N to litter N pool; occurs throughout year
$U_{\mathrm{NH_4}}$	$\mathrm{g\,N\,m^{-2}\,day^{-1}}$	Uptake of $\mathrm{NH_4}$ from mineral soil $\mathrm{NH_4}$; based on Williams and Yanai (1996)
$U_{\mathrm{NO_3}}$	$\mathrm{g\,N\,m^{-2}\,day^{-1}}$	Uptake of $\mathrm{NO_3}$ from mineral soil $\mathrm{NO_3}$; based on Williams and Yanai (1996)
U_{Nfix}	$\mathrm{g\,N\,m^{-2}\,day^{-1}}$	Fixation of N from $\mathrm{N_2}$; function of $\mathrm{Ra_{excessC}}$ flux, temperature, N demand, and C cost.
$a_{\mathrm{budN\_2Ramain}}$	$\mathrm{g\,N\,m^{-2}\,day^{-1}}$	When bud C is used for maintenance respiration ($a_{\mathrm{budC\_2Ramain}} > 0$), bud N is returned to the labile N pool
a_{budN}	$\mathrm{g\,N\,m^{-2}\,day^{-1}}$	Allocation of labile N to bud N; occurs in year prior to being displayed as leaf N
t_{CWDC}	$\mathrm{g\,N\,m^{-2}\,day^{-1}}$	Turnover of coarse woody debris C into the litter C pool
$t_{\mathrm{litterC\_soil}}$	$\mathrm{g\,N\,m^{-2}\,day^{-1}}$	Turnover of litter C pool to soil C pool
$t_{\mathrm{litterC\_atm}}$	$\mathrm{g\,N\,m^{-2}\,day^{-1}}$	Turnover of litter C pool released as heterotrophic respiration
$t_{\mathrm{soil\_atm}}$	$\mathrm{g\,N\,m^{-2}\,day^{-1}}$	Turnover of soil C released as heterotrophic respiration
t_{CWDN}	$\mathrm{g\,N\,m^{-2}\,day^{-1}}$	Turnover of coarse woody debris C to litter C pool
t_{litterN}	$\mathrm{g\,N\,m^{-2}\,day^{-1}}$	Turnover of litter N to soil N
U_{NH4immob}	$\mathrm{g\,N\,m^{-2}\,day^{-1}}$	Immobilization of $\mathrm{NH_4}$ to soil N associated with the turnover of litter C and N
U_{NO3immob}	$\mathrm{g\,N\,m^{-2}\,day^{-1}}$	Immobilization of $\mathrm{NO_3}$ to soil N associated with the turnover of litter C and N
t_{soilN}	$\mathrm{g\,N\,m^{-2}\,day^{-1}}$	Mineralization of soil N to $\mathrm{NH_4}$ pool
L_{DON}	$\mathrm{g\,N\,m^{-2}\,day^{-1}}$	Production and leaching of dissolved organic N
$\mathrm{Ndep_{NH_4}}$	$\mathrm{g\,N\,m^{-2}\,day^{-1}}$	Input of N deposition to $\mathrm{NH_4}$ pool
nitr	$\mathrm{g\,N\,m^{-2}\,day^{-1}}$	Nitrification of $\mathrm{NH_4}$ to $\mathrm{NO_3}$
N_{depNO3}	$\mathrm{g\,N\,m^{-2}\,day^{-1}}$	Input of N deposition to $\mathrm{NO_3}$ pool
$L_{\mathrm{NO_3}}$	$\mathrm{g\,N\,m^{-2}\,day^{-1}}$	Leaching of $\mathrm{NO_3}$

Table 3. Photosynthesis parameters (acm_{1-11}) for the aggregated canopy model (ACM), and fixed inputs (final three values in the table), used to determined carbon fixation in ACONITE. * indicates that a parameter is also used in the DALEC-C model.

Parameter	Units (for inputs)	Description	Value	Reference
* acm_1		Nitrogen-use efficiency (NUE) parameter	12.0	Fox et al. (2009)
* acm_2		Day length coefficient	1.526	Fox et al. (2009)
* acm_3		Canopy CO_2 compensation point	4.22	Fox et al. (2009)
* acm_4		Canopy CO_2 half-saturation point	208.9	Fox et al. (2009)
* acm_5		Day length scalar intercept	0.0453	Fox et al. (2009)
* acm_6		Hydraulic coefficient	0.378	Fox et al. (2009)
* acm_7		Maximum canopy quantum yield	7.19	Fox et al. (2009)
* acm_8		Temperature coefficient	0.011	Fox et al. (2009)
* acm_9		LAI-canopy quantum yield coefficient	2.10	Fox et al. (2009)
* acm_{10}		Water potential constant	0.79	Fox et al. (2009)
acm_{11}		Half-saturation of LAI-N_{leaf} relationship	T: 0.05 E: 0.05 D: 0.5	
$^*\psi$	MPa	Maximum soil–leaf water potential difference	Input (−2)	Fox et al. (2009)
$^*R_{tot}$	$MPa\,m^2\,s\,mmol^{-1}$	Total plant–soil hydraulic resistance	Input (0.1)	Fox et al. (2009)
*lca	$g\,C\,m^{-2}$	Leaf C per area	T: 53 E: 100 D: 32	Kattge et al. (2011)

T, tropical; E, temperate evergreen, D, temperate deciduous

Title Page
Abstract | Introduction
Conclusions | References
Tables | Figures
◀| |▶
◀ ▶
Back | Close
Full Screen / Esc
Printer-friendly Version
Interactive Discussion

Table 4. Nitrogen uptake parameters, including units, nominal values and their sources. * indicates that a parameter is also used in the DALEC-C model.

Parameter	Units	Description	Value	Reference
r_{radius}	m	Radius of fine root	5×10^{-4}	Fahey et al. (2005) definition of fine root
r_{depth}	m	Depth of soil explored by roots	varies by site	
r_{density}	$\mathrm{g\,m^{-3}}$	Density of root mass	175 000	Comas and Eissenstat (2004)
$^*c_{\mathrm{conc}}$	$\mathrm{g\,C\,g^{-1}}$	C : dry weight ratio	0.5	Widely used
I_{max}	$\mathrm{mmol\,m^{-2}\,s^{-1}}$	Maximal nutrient influx rate	4×10^{-5}	Williams and Yanai (1996)
V	$\mathrm{m\,s^{-1}\,g\,C\,m^{-2}\,day^{-1}}$	Inward radial velocity of water at the root surface	1×10^{-9}	Value in Williams and Yanai (1996); multiplied by daily GPP
$B_{\mathrm{NH_4}}$	Unitless	Soil buffer power (NH_4)	10.0	Williams and Yanai (1996)
$D_{\mathrm{NH_4}}$	$\mathrm{m^{-2}\,s^{-1}}$	Effective diffusion coefficient of the solute through the soil	1×10^{-11}	Williams and Yanai (1996)
$B_{\mathrm{NO_3}}$	Unitless	Soil buffer power (NO_3)	2×10^{-10}	Williams and Yanai (1996)
$D_{\mathrm{NO_3}}$	$\mathrm{m^{-2}\,s^{-1}}$	Effective diffusion coefficient of the solute through the soil	0.5	Williams and Yanai (1996)
K_{m}	$\mathrm{mmol\,m^{-2}\,s^{-1}}$	Half saturation constant for uptake	15.0	Williams and Yanai (1996)
$\mathrm{Nfix}_{\mathrm{pergC}}$	$\mathrm{g\,N\,(g\,C)^{-1}}$	Cost of N fixation	0.11	Gutschick (1981)

Table 5. Plant allocation and turnover parameters, including units, nominal values and their sources. * indicates that a parameter is also used in the DALEC-C model.

Parameter	Units	Description	Value	Reference
*GDDStart	Day	Growing degree day growth begins	100	Aber et al. (1997)
*DOYsenesc	Day	Day of year that growth ends and leaf fall begins	Varies by location	
$^*\tau_{\mathrm{leaf}}$	day^{-1}	Turnover of leaf C and N	T: 0.0019 E: 0.00082 D: > 0.0027	Kattge et al. (2011)
Retrans_frac	proportion	Proportion of leaf N retranslocated to labile N pool	0.5	Widely used
$^*\tau_{\mathrm{wood}}$	day^{-1}	Turnover of wood C and N	T: 9×10^{-6} E: 5×10^{-5} D: 5×10^{-5}	Approximates a 2 % annual mortality rate in temperate forest and 3.3 % annual mortality rate in tropical forest
$^*\tau_{\mathrm{root}}$	day^{-1}	Turnover of root C and N	0.002	Based on Luke McCormack et al. (2013)
τ_{excessC}	day^{-1}	Turnover of labile C when pool exceeds the maximum size of the labile C pool	0.05	
Ra_parm1	nmol g^{-1} s^{-1}	Intercept coefficient for dark respiration vs. nitrogen concentration	0.833	Reich et al. (2008); all plant groups and organs combined
Ra_parm2	Unitless	Exponential coefficient for dark respiration vs. nitrogen concentration	1.268	Reich et al. (2008)
Q_a	Unitless	$Q10$ for maintenance respiration	1.40	Mahecha et al. (2010)
growthresp	proportion	proportion of C allocation to tissue used for respiration	0.28	Waring and Schlesinger. (1985) (TBL 2.3)
store_prop$_{\mathrm{RaC}}$	proportion	Proportion of Wood and Root C that can be used for storage of maintenance respiration	T: 0.01 E: 0.05 D: 0.01	
store_ prop$_{\mathrm{N}}$	proportion	Proportion of Wood and Root C that can be used for storage of labile N	0.001	
store_ prop$_{\mathrm{C}}$	proportion	Proportion of Wood and Root C that can be used for storage of labile C	0.01	
woodCN	g C (g N)$^{-1}$	Wood C : N ratio	500	White et al. (2000)
rootCN	g C (g N)$^{-1}$	Root C : N ratio	50	White et al. (2000)
Min_leaf_2_wood	g wood C g leaf C	Minimum ratio of leaf C production to allocated wood C production	1.5	White et al. (2000)
Min_leaf_2_root	g wood C g^{-1} leaf C	Minimum ratio of leaf C to root C	0.75	
leafC_2_bud_prop	g bud g^{-1} max leaf C	Proportion of maximum leaf C set as buds for next year	T: 0.5 E: 0.1 D: 0.5	
θ	proportion	Proportion of labile C available to use for growth	0.07	
Max_tissue_adjust	proportion day^{-1}	Maximum potential annual proportional change in maximum leaf C and root C	0.1	

T, tropical; E, temperate evergreen, D, temperate deciduous

Table 6. Soil Parameters, including units, nominal values and their sources. * indicates that a parameter is also used in the DALEC-C model.

Parameter	Units	Description	Value	Reference
$^*Q_h$	unitless	Soil respiration Q10	1.4	Mahecha et al. (2010)
SoilCN	g C (g N)^{-1}	Soil C : N ratio	12.0	Thornton and Rosenbloom (2005)
m_resp_frac	Proportion	Proportion of litter C turnover respired	0.5	Typical value from Parton et al. (1993)
$^*\tau_{\text{litter}}$	day^{-1}	Litter turnover rate	0.029	Typical value from Parton et al. (1993)
$^*\tau_{\text{cwd}}$	day^{-1}	Coarse woody debris turnover rate	0.001	Thornton and Rosenbloom (2005)
$^*\tau_{\text{soil}}$	day^{-1}	Soil turnover rate	1×10^{-4}	Assumed 20 year residence time
DON_leach_prop	proportion	Proportion of soil N turnover lost through DON leaching	0.0015	
nitr_rate	day^{-1}	Nitrification rate	0.0001	
leach_rate	day^{-1}	NO_3 leaching rate	0.00001	

Table 7. Steady state values of key ecosystem parameters for the three test systems evaluated with ACONITE.

Plant functional type	LAI	Total Vegetation C $g\,C\,m^{-2}$	GPP $g\,C\,m^{-2}\,yr^{-1}$	NPP $g\,C\,m^{-2}\,yr^{-1}$	Carbon use efficiency	Leaf C : N	N fixation $g\,N\,m^{-2}\,yr^{-1}$
Tropical	5.9	31 300	3130	1423	0.45	28	0.6
Temperate deciduous	6.3	18 900	1320	674	0.51	22	0.01
Temperate evergreen	4.4	20 800	1649	737	0.44	43	0.02

Table 8. Sensitivity metric (S) of key state variables to parameters in ACONITE for three ecosystem types (T, E, D). Only parameters with $|S| \geq 0.1$ are listed.

	LAI			Total Vegetation C			GPP			NPP			CUE			Leaf C : N			N fixation		
Parameter	T	E	D	T	E	D	T	E	D	T	E	D	T	E	D	T	E	D	T	E	D
acm_1	−0.1	−0.2	−0.2	**0.8**	**0.8**	**1.1**	0.3	0.2	0.3	0.6	0.4	0.5	0.3	−0.1	0.3	0.1	0.3	–	**0.6**	**2.3**	**8.4**
acm_2	0.5	0.4	0.6	**1.5**	**1.5**	**1.6**	**1.0**	**0.8**	**1.0**	**1.2**	**1.1**	**1.2**	0.2	−0.1	0.2	−0.1	−0.1	–	**1.2**	**3.5**	**8.1**
acm_4	–	–	−0.1	−0.4	−0.5	−0.5	−0.2	−0.1	−0.3	−0.3	−0.3	−0.3	−0.1	−0.1	−0.1	–	−0.1	–	**−0.3**	**−1.3**	**−3.9**
acm_5	0.1	0.1	0.1	0.4	0.3	0.3	0.2	0.2	0.2	0.3	0.2	0.2	0.1	–	0.1	–	–	–	**0.3**	**0.8**	**1.9**
acm_7	0.4	0.2	0.4	0.9	0.7	0.6	0.7	0.5	0.5	0.7	0.5	0.5	–	–	0.1	−0.2	−0.2	–	**0.7**	**1.6**	**1.7**
acm_8	–	–	–	0.3	0.2	0.3	0.1	0.1	0.1	0.2	0.1	0.1	0.1	0.1	0.1	0.1	–	–	**0.2**	**0.6**	**2.4**
acm_9	0.2	0.2	0.1	–	−0.1	–	–	0.1		–	–	–	–	–	–	0.2	0.2	–	–	−0.7	−0.5
acm_{10}	0.2	0.3	0.4	0.2	0.4	0.3	0.2	0.4	0.3	0.2	0.3	0.3	–	–	–	–	−0.1	–	0.2	0.5	0.2
acm_{11}	0.1	0.1	0.3	−0.1	−0.1	−0.3	–	0.1	−0.2	–	–	−0.1	–	–	–	0.1	0.1	0.3	–	−0.4	−5.2
lca	−0.6	−0.5	−0.7	−0.2	−0.3	−0.3	–	0.1	−0.1	–	0.1	–	–	–	0.1	0.4	0.4	0.4	**–**	**−1.9**	**−6.3**
GDDStart	–	–	–	–	–	−0.1	–	–	–	–	–	–	–	−0.1	–	–	–	–	–	0.2	−0.1
DOYsenensc	–	0.2	0.6	**–**	**1.3**	**1.4**	–	0.7	1.1	**–**	**0.9**	**1.1**	–	0.1	–	–	−0.1	0.5	**–**	**2.4**	**5.4**
t_{leaf}	−0.6	−0.6	–	–	0.1	–	−0.1	–	–	–	–	–	–	–	0.1	−0.5	−0.5	–	–	–	−0.2
Retrans_ frac	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	−0.1
t_{wood}	−0.1	−0.1	–	**−1.6**	**−1.3**	**−1.1**	−0.3	−0.1	−0.1	−0.4	−0.2	–	−0.1	–	–	–	–	–	−0.4	−0.5	–
t_{root}	–	–	–	−0.1	−0.3	−0.1	–	0.1	–	–	0.1	0.1	–	–	0.1	–	–	–	–	–	−0.5
t_{excessC}	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	**−0.1**	**1.0**	**0.9**
Ra_parm1	–	–	−0.1	−0.6	−0.7	−0.4	−0.1	–	−0.2	−0.5	−0.4	−0.3	−0.3	0.2	−0.3	0.5	0.4	0.4	**−0.5**	**−1.9**	**−3.4**
Ra_parm2	**1.0**	**0.9**	**0.4**	−0.2	–	−0.1	–	0.2	−0.1	0.2	0.4	0.1	0.2	= −0.2	0.3	**1.6**	**1.1**	**1.2**	**0.1**	**−1.6**	**−4.5**
Q_a	–	–	–	−0.4	0.6	0.3	−0.1	0.1	–	−0.3	0.3	0.2	−0.2	0.1	0.3	0.4	−0.5	−0.2	**−0.4**	**1.4**	**2.5**
growthresp	−0.1	−0.1	−0.1	−0.4	−0.4	−0.3	−0.1	–	–	−0.4	−0.3	−0.2	−0.2	0.2	−0.2	–	−0.1	–	**−0.4**	**−0.5**	**−1.4**
$store\_prop_C$	0.2	0.1	−0.1	0.5	0.2	0.1	0.3	0.2	0.1	0.4	0.2	–	0.1	−0.1	0.1	–			0.4	0.3	0.8
$store\_prop_N$	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–			–	0.2	0.8
r_{radius}	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	**–**	**1.1**	**1.6**
woodCN	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	−0.2	−0.3
rootCN	–	–	−0.1	0.3	0.4	0.2	–	−0.1	−0.1	0.2	0.2	0.1	0.2	0.1	0.3	–	–	–	**0.2**	**0.5**	**1.6**
Min_leaf_2_wood	0.1	0.1	0.1	0.2	0.3	0.4	0.1	0.2	0.2	0.2	0.2	0.3	0.1	–	0.1	–	–	–	**0.2**	**−0.7**	**−4.2**
Min_leaf_2_root	–	0.1	0.1	−0.3	−0.7	−0.2	–	0.2	0.1	−0.1	–	–	−0.1	−0.1	−0.1	–	–	–	**−0.1**	**−2.4**	**−4.4**
θ	0.1	0.1	–	0.4	0.2	0.1	0.3	0.1	–	0.3	0.1	–	0.1	–	0.1	–	–	–	0.4	0.5	–
r_{density}	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–			**–**	**1.1**	**1.6**
$Root_{\mathrm{depth}}$	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.1
c_{conc}	–	–	–	−0.2	−0.2	−0.2	−0.1	–	−0.1	−0.2	−0.1	−0.1	−0.1	0.1	−0.1	0.2	0.1	0.1	−0.2	0.6	0.7
I_{max}	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	**–**	**−1.3**	**2.1**
K_m	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.1
$Nfix_{\mathrm{pergC}}$	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	**–**	**1.0**	**1.0**
soilCN	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	**−1.1**	**–**	**−0.2**
m_resp_frac	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	**1.0**	**–**	**0.1**
t_{soil}	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–					−0.5
DON_leach_prop	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	**1.0**	**–**	**0.1**
leach_rate	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–		–	−0.1

S, (% change in state variable/% change in parameter);
T, tropical; E, temperate evergreen, D, temperate deciduous;
bold, Sensitivity to parameter is proportional or larger than the percentage change in parameter;
(–), Sensitivity < |0.1|.

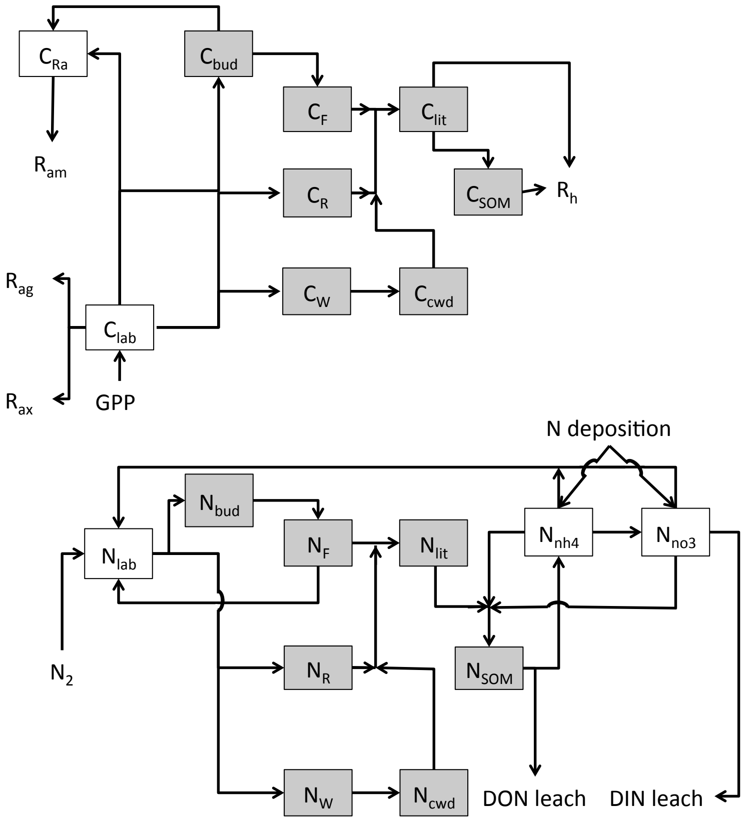

Fig. 1. Structure of ACONITE, showing pools (boxes) and fluxes (arrows). The gray boxes are pool with C : N ratios. The top panel shows the C cycle, and the bottom panel shows the N cycle. F = foliage, R = fine roots, W = wood, lab = labile, Ra = autotrophic respiration, Rag = growth respiration, Ram = maintenance respiration, lit = litter, SOM = soil organic matter, cwd = coarse woody debris, bud = bud.

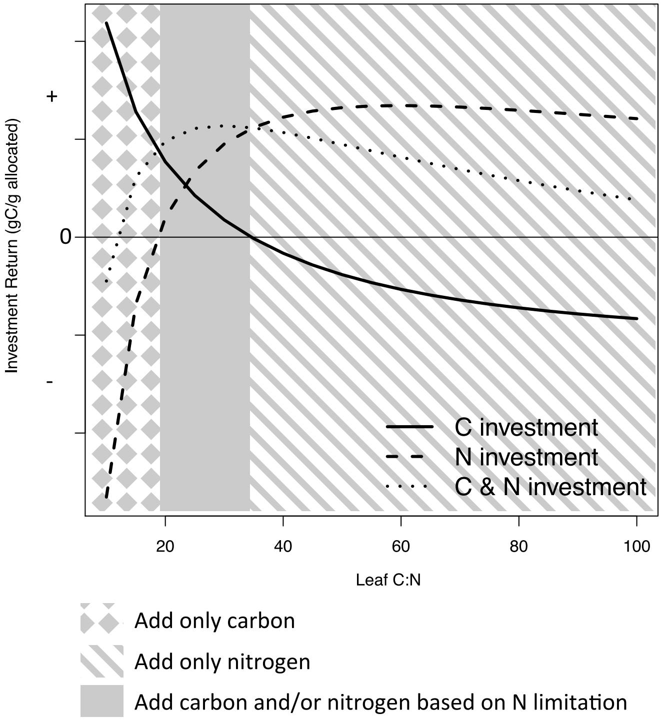

Fig. 2. A schematic illustrating the adjustment of leaf C : N for a given leaf area index using the marginal C returns on investment of leaf C and leaf N. At low leaf C : N, leaf N has a negative return and leaf C has a positive return on investment that results in allocation to increase the leaf C : N (diamond shading). At high leaf C : N, leaf N has a positive return and leaf C has a negative return that results in allocation to decrease the leaf C : N (hashed shading). At intermediate leaf C : N, allocation of both leaf C and N are positive and allocation adjustments reflects where tissue growth is limited by N availability.

Title Page
Abstract
Introduction
Conclusions
References
Tables
Figures
◀◀
▶▶
◀
▶
Back
Close
Full Screen / Esc
Printer-friendly Version
Interactive Discussion

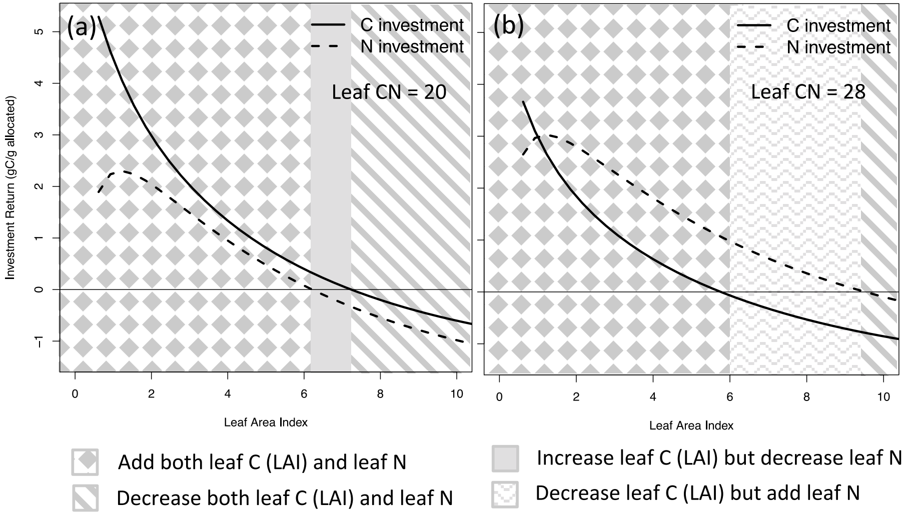

Fig. 3. A schematic illustrating the simultaneous adjustment of leaf area index (LAI) and leaf C : N (see legend above) based on the C return on marginal investment of leaf C (solid line) and leaf N (dashed line). **(a)** shows the situation with a leaf C : N of 20 and **(b)** shows the situation with a leaf C : N of 28, as examples. An optimal LAI and leaf N emerges from adjusting allocation so that marginal investment returns are zero for both leaf C and N.

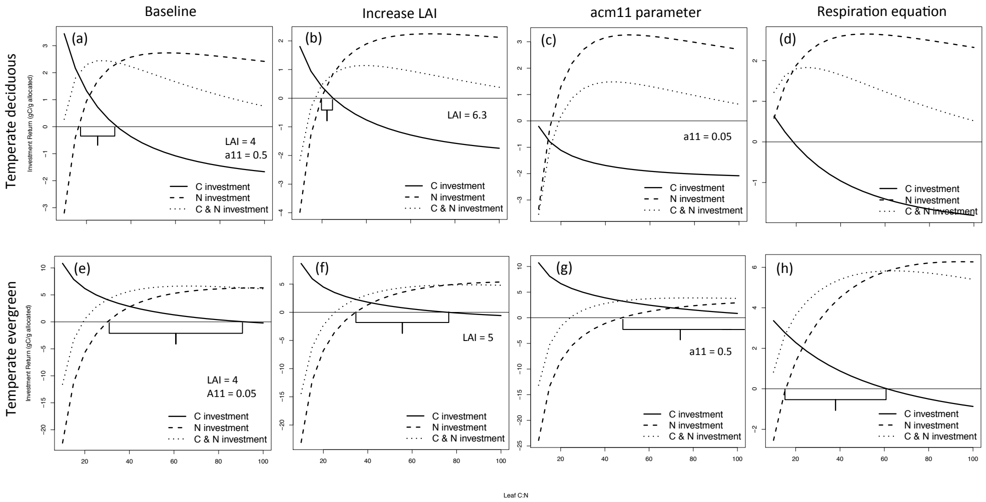

Fig. 4. Sensitivity of the range of leaf C : N with positive C returns on marginal investment of leaf C and leaf N for a temperate deciduous **(a–d)** and an evergreen **(e–h)** forest. The range of leaf C : N with positive returns increases with leaf area index (**a** vs. **b**; **e** vs. **f**) and depends on the acm_{11} parameter (**a** vs. **c**; **e** vs. **g**), and the non-linearity of the leaf respiration parameterization (**a** vs. **d**; **e** vs. **h**). (**a** and **e**) use the log–log relationship between N concentration and leaf respiration from Reich et al. (2008) and (**d** and **h**) use the linear relationship from Ryan (1991). Brackets indicate range of leaf C : N where leaf C : N can vary based on N status of the plant.

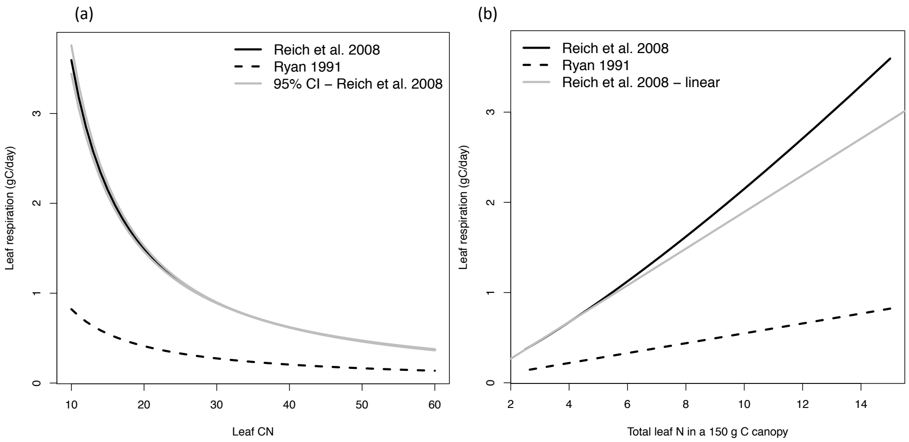

Fig. 5. Leaf respiration increases non-linearly with leaf N using the Reich et al. (2008) parameterization and linearly with leaf N using the Ryan (1991) parameterization. Total canopy leaf respiration for a plant with 150 g C m^{-2} canopy is shown as a function of leaf N, expressed on a leaf C : N basis **(a)** and a total canopy leaf N basis **(b)**. The 95 % uncertainty from Reich et al. is shown as gray lines in **(a)**. The non-linearity of the Reich et al. (2008) equation is illustrated by extrapolating the initial slope (gray line) in **(b)**.