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) based on the outcome of assessments of the marginal change in net C or N uptake associated with a change in allocation of C or N to plant tissues. 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 simulated leaf C:N that compared better to the global trait database than the linear relationship. 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 allow spatially and temporally variable leaf C:N can help address challenges simulating these properties in 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 (Erisman et al., 2013; IPCC, 2013). These cycles are closely coupled, from local to global scales. For instance, rates of C fixation are sensitive to foliar N content (Reich et al., 1994; Street et al., 2012). Thus, high productivity farming is reliant on N inputs (Tilman et al., 2002), and production in many natural ecosystems is N-limited (Norby et al., 2010; Shaver and Chapin, 1995). 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)(Manzoni et al., 2010; McClaugherty et al., 1985). 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 (Gruber and Galloway, 2008; Le Quere et al., 2009). 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 (de Vries et al., 2008; Magnani et al., 2007; 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 (Shaver et al., 2007; Williams and Rastetter, 1999). These parameters show distinct temporal, geographic and successional variation (Kattge et al., 2011; Wright et al., 2004), 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 versus 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 (Gerber et al., 2010; Smith et al., 2014; Sokolov et al., 2008; Thornton et al., 2007; Wang et al., 2010; Wania et al., 2012; Xu and Prentice, 2008; Zaehle et al., 2010), 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. 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 (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 CO_2 concentration is held at 2010 levels for the evaluations. The final forcing term is the rate of N deposition (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 supplemental information.

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 (Figure 1). Plants are represented by respiratory, labile, bud, leaf, fine root and stem pools. These pools are similar to the DALEC v1 C model (Fox et al., 2009) except that the labile pool has been subdivided into a bud pool that stores C before allocation to leaves and 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 addition of a CWD pool and two inorganic N pools (NH_4^+ and NO_3^-) are key differences between the DALEC v1 and ACONITE models.

ACONITE simulates the accumulation of C (photosynthesis) and N (root N uptake, N Fixation, and N retranslocation during leave senescence) into the labile C and N stores. Labile C and N are allocated to tissue growth. Labile C is also used for growth respiration, maintenance respiration, and N fixation. 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 a SOM C pool, 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 describe the mass balance equations and fluxes used in ACONITE.

2.1.2 Photosynthesis

Photosynthesis (gross primary productivity; GPP) is determined using a modified version of 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 leaf area index (LAI, the surface available for light absorption), and total leaf N (*Nleaf*; 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 *Nleaf* , 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), leaf area index (LAI, linked to leaf C) 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). In the ACONITE version of ACM, photosynthetic capacity is reduced when the ratio of LAI to N_{leaf} falls. Thus, a canopy with a given N_{leaf} is more productive with a larger LAI. To achieve this, GPP is adjusted by a monotonically saturating function on the ratio LAI:N_{leaf} (Equation 7), introducing a new parameter to ACM. When LAI:N_{leaf} is large, the adjustment tends to 1: as this ratio declines, the adjustment factor falls slowly at first, but then increasingly fast as N_{leaf} becomes concentrated in a smaller and smaller total leaf area. The parameters used in the photosynthesis sub-model are listed in Table 3.

Maximum photosynthesis is set by ACM (Equation 3), but the actual photosynthesis is a function of the size of the labile C pool, and the capacity of the plants to store labile C (Equation 38) Photosynthesis (G) is down-regulated (by a factor X_c) according to the saturation status of the labile C store :

$$X_c = \begin{cases} \max\left(0, \left(1 - \frac{C_{labile} - store_{maxc}}{store_{maxc}}\right)\right), & C_{labile} > store_{maxc} \\ 1.0, & C_{labile} \leq store_{maxc} \end{cases} \quad \text{Equation 1}$$

Gross primary productivity (GPP) only occurs if daily minimum air temperature (T_{min}) > 0°C:

$$GPP = \begin{cases} X_c GPP^*, & T_{min} > 0 \\ 0, & T_{min} \leq 0 \end{cases} \quad \text{Equation 2}$$

This function is required because photosynthesis relies on a water supply from soil that is restricted when soil moisture is frozen, and also because photosynthetic apparatus is damaged by freezing conditions (Linder and Troeng, 1980). We use an air temperature threshold for simplicity, but acknowledge that soil temperature would provide a more reliable forcing. Photosynthesis (before potential down-regulation by freezing temperatures and labile C saturation; GPP^*) is a function of daily irradiance (I, MJ m^{-2} d^{-1}), day-length (ζ, hours), atmospheric [CO_2](C_a, ppm), estimated internal [CO_2] (C_i, ppm), and a set of parameters ($acm_{1\text{-}11}$),

$$GPP^* = \frac{e_0 I g_c (C_a - C_i)}{e_0 I + g_c (C_a - C_i)} (acm_2 \zeta + acm_5) \quad \text{Equation 3}$$

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

$$e_0 = \frac{acm_7 L^2}{L^2 + acm_9} \quad \text{Equation 4}$$

And C_i is determined by a quadratic solution,

$$C_i = 0.5\left[C_a + q - p + \sqrt{((C_a + q - p)^2 - 4(C_a q - acm_3 p))}\right] \quad \text{Equation 5}$$

where

$$q = acm_3 - acm_4 \quad \text{Equation 6}$$

Canopy photosynthetic capacity (p) is linked to total foliar N (N_{leaf}), canopy conductance (g_c), and maximum daily air temperature (T_{max}) but is adjusted by the ratio of LAI: N_{leaf} (see above),

$$p = \frac{acm_1 N_{leaf}}{g_c} \mathrm{e}^{acm_8 T_{max}} \frac{\text{LAI:}N_{leaf}}{\text{LAI:}N_{leaf} + acm_{11}} \quad \text{Equation 7}$$

Canopy conductance (g_c) 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),

$$g_c = \frac{|\psi_d|^{acm_{10}}}{(acm_6 R_{tot} + 0.5(T_{max} - T_{min}))} \quad \text{Equation 8}$$

2.1.3 Plant N uptake

Plant nutrient uptake is simulated using an existing model of solute uptake at steady state (Nye and Tinker, 1977; Williams and Yanai, 1996). Active uptake of N occurs at root surfaces with diffusion and solution flow supplying N to determine the rooting zone concentration. The model is applied individually for the uptake of both NH_4^+ or NO_3^- to generate a total N uptake. The parameters governing N uptake are found in Table 4.

The rooting zone nutrient concentration (C_{av}, mmol m^{-3}) is calculated as the mineral N (N, which is either NH_4^+ or NO_3^-) pools distributed over a defined rooting depth (r_{depth}), with molar conversions:

$$C_{av} = \frac{N}{r_{depth}}\frac{1000}{14} \qquad \text{Equation 9}$$

Uptake rate of N (U_N) is a function of the root surface area ($r_{surfarea}$), root absorbing power (α ; Eq. 14), the air temperature (T_a) adjusted maximum rate of uptake ($I_{temp;}$ Equation 16), and the degree of down-regulation of uptake (X_N; Equation 20), multiplied by the number of seconds in a day (S = 86400) to provide daily mass values. Specific parameters are used for NH_4^+ or NO_3^-:

$$U_N = r_{surfarea}\alpha\, I_{temp} X_N S \qquad \text{Equation 10}$$

Root surface area is a function of root radius (r_{radius}) and root length (r_{length}),

$$r_{surfarea} = 2\pi r_{radius} r_{length} \qquad \text{Equation 11}$$

Root length depends (r_{length}) on the variable fine root C stock (C_{root}), C concentration of biomass (c_{conc}) and the volumetric mass density of biomass ($r_{density}$)

$$r_{length} = \frac{C_{root}}{c_{conc} r_{density} \pi {r_{radius}}^2} \qquad \text{Equation 12}$$

The mean half distance between roots (r_x) is

$$r_x = \sqrt{\frac{r_{depth}}{\pi r_{length}}} \qquad \text{Equation 13}$$

The root absorbing power (α) 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)

$$\alpha = \frac{c_o}{K_m + c_o}$$ Equation 14

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; Equation 19), a factor (γ; Equation 18) related to diffusion coefficients (D) and buffering (β) specific to the solute type, and a dimension factor (δ; Equation 17) linked to root structure,

$$c_o = \frac{1}{2\delta v_0}\left(-I_{temp} + \delta I_{temp} + c_{av}v_0 - \delta k_m v_0 + \sqrt{4c_{av}\delta k_m {v_0}^2 + \left(-I_{temp} + \delta I_{temp} + c_{av}v_0 - \delta K_m v_0\right)^2}\right)$$ Equation 15

I_{temp} is determined from the maximum rate of uptake at 20ºC, I_{max}, modified by a Q10 function (Q_a) adjusted by average daily air temperature (T_a, ºC),

$$I_{temp} = I_{max} Q_a^{\frac{T_a - 20}{10}}$$ Equation 16

The dimension factor (δ) linked to root structure is:

$$\delta = \frac{2}{2-\gamma}\frac{\left(\left(\frac{r_x}{r_{radius}}\right)^{2-\gamma} - 1\right)}{\left(\left(\frac{r_x}{r_{radius}}\right)^{2} - 1\right)}$$ Equation 17

An additional factor (γ) is related to diffusion coefficients (D) and buffering (β) specific to the solute type:

$$\gamma = \frac{r_{radius} v_0}{\beta_{NH4} D_{NH4}}$$ Equation 18

The parameters in Equation 18 are adjusted according to whether NO_3^- or NH_4^+ uptake is being determined.

We estimate the rate of water inflow to the root surface (v_0) as a proportion of GPP

$$v_0 = vGPP \qquad \text{Equation 19}$$

Adding a water cycle is necessary to more mechanistically calculate v_0, but the current approach captures the dependence of N uptake on transpiration-driven flow of water to the plant.

N uptake can be reduced (X_N) when the labile N pool is large relative to the size of the N store (Equation 39).

$$X_N = \begin{cases} 1 - (N_{labile}/store_{maxN}), & N_{labile} \leq store_{maxN} \\ 0, & N_{labile} > store_{maxN} \end{cases} \qquad \text{Equation 20}$$

2.1.4 Plant allocation

Allocation only occurs on days with a positive growth potential ($growth_{potential}$). Growth potential varies over the course of a year based on phenological relationships (Table 5; Supplemental Information Figure S1). Growth potential is > 0 at the start of a temperate growing season, determined as when a growing degree day (GDD_{start}) threshold is exceeded. Growth potential equals 0 at the end of the season, defined by a day of year (DOY_{senesc}). The existing code is suitable only for the northern hemisphere extra-tropics. [For equatorial regions growth potential is set to a positive value (θ) year-round. Further development is required before the model can be applied in dry tropics where temperature does not control phenology.]

$$growth_{potential} = \begin{cases} \theta, & GDD \geq GDD_{start} \text{ and } DOY < DOY_{senesc} \\ 0, & otherwise \end{cases} \qquad \text{Equation 21}$$

At each daily time-step an instantaneous C return ($Return_{leafCNInstant}$) is calculated to determine whether allocation occurs (Equation 54). The instantaneous C return determines whether investing further C and N in foliage, at the current C:N and environmental conditions, will result in a positive net uptake of C after accounting for gross photosynthesis, growth respiration, and maintenance respiration of additional leaf allocation. The marginal calculation is described in Section 2.1.9 Marginal calculations for plants.

Based on the daily marginal returns ($Return_{leafCNInstant}$), a decision tree is employed to determine allocation patterns from the available labile C pool ($C_{avail} = growth_{potential} \cdot C_{labile}$; Supplemental Information Figure S1).

1) If outside the growth period ($growth_{potential} = 0$), C_{labile} is used to fill (via allocation flux $a_{labileRamain}$) the maintenance respiration pool ($C_{labileRa}$) up to its maximum value ($Store_{RaC}$; Equation 37); this ensures the vegetation has the required reserves to meet metabolic demand during winter.

2) If three tests ($growth_{potential} > 0$, $Return_{leafCNInstant} > 0$, and leaf C is less than its annual maximum (*maxleafC*; Section 2.1.7)), then bud C and bud N are converted into foliar C and N, at the target leaf C:N (Section 2.1.7). C_{avail} is then allocated to buds, up to an amount (a proportion of maxleafC; *leafC_2_bud_prop*) that will allow the maximum leaf area to be reached. Allocation of C_{avail} 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 (Equation 32). When foliar C is allocated, an associated allocation of wood must occur during the year to support the new foliage (parameter *min_leaf_2_wood*). A variable (*wood_requirement*) is incremented to track the need for wood – *wood_requirement* increases with foliage allocation and decreases with wood allocation.

3) If $Return_{leafCNInstant} < 0$ or the *maxleafC* has been attained, C and N are allocated to buds for future growth periods, and C is allocated to fill the maintenance respiration pool to its maximum size ($Store_{RaC}$). The remaining C_{avail} and N_{labile} are used to pay down the wood requirement (*wood_requirement*), limited by the size of the labile pools and the need to construct wood at a fixed C:N. After wood allocation the remaining C_{avail} and N_{labile} are allocated at a fixed C:N to grow fine roots up to a maximum root C (*maxrootC*; Section 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. If the C_{labile} has not reached capacity ($Store_{maxC}$), then C_{labile} is allowed to accumulate. If the store is full, then remaining C is allocated to wood, dependent on N availability. If $C_{labile} > Store_{maxC}$ at this point, then the excess is allocated to excess autotrophic respiration ($Ra_{excessC}$), which leads to N fixation (see Equations 33 and 76).

2.1.5 Plant tissue turnover

The turnover of plant tissues (t) is a function of tissue specific turnover rates (τ) and results in transfer of materials to specific litter pools (Figure 1; Table 5). For foliage, turnover fluxes involve phenological cues, occurring only after a defined day in the year (DOY_{senesc}),

$$t_{leafC} = \begin{cases} C_{leaf}\ \tau_{leaf}, & DOY > DOY_{senesc} \\ 0, & otherwise \end{cases} \qquad \text{Equation 22}$$

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

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

$$t_{leafN} = \begin{cases} N_{leaf}\tau_{leaf}(1 - Retrans\_frac), & DOY > DOY_{senesc} \\ 0, & otherwise \end{cases} \qquad \text{Equation 23}$$

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

$$t_{retransN} = \begin{cases} N_{leaf}\tau_{leaf} Retrans\_frac, & DOY > DOY_{senesc} \\ 0, & otherwise \end{cases} \qquad \text{Equation 24}$$

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

$$t_{woodC} = C_{wood}\tau_{wood} \qquad \text{Equation 25}$$

$$t_{woodN} = N_{wood}\ \tau_{wood} \qquad \text{Equation 26}$$

$$t_{rootC} = C_{root}\ \tau_{root} \qquad \text{Equation 27}$$

$$t_{rootN} = N_{root}\tau_{root} \qquad \text{Equation 28}$$

2.16 Plant respiration

Maintenance respiration (Ra_{main}) can be related to the N content 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 (parameters: Ra_{parm1}, Ra_{parm2}) 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, gC g^{-1} tissue (c_{conc}). The respiration is multiplied by a scalar (S = 86400) to convert respiration from per second to per day units. Respiration is only associated with the pools involved in uptake processes (so wood, bud and labile N does not affect the outcome). Because the equation is reported in Reich et al. (2008) as a log-log relationship, option 1 takes the following form:

Option 1:

$$Ra_{main} = \left(\left(exp\left(Ra_{parm1} + Ra_{parm2} log\left(\frac{\left(\frac{N_{leaf}}{14.0}1000\right)}{\frac{C_{leaf}}{c_{conc}}}\right)\right)\right)1.2^{-8}\left(\frac{C_{leaf}}{c_{conc}}\right)S\right) +$$

$$\left(\left(exp\left(Ra_{parm1} + Ra_{parm2} log\left(\frac{\left(\frac{N_{root}}{14.0}1000\right)}{\frac{C_{root}}{c_{conc}}}\right)\right)\right)1.2^{-8}\left(\frac{C_{root}}{c_{conc}}\right)S\right) f(T)$$

Equation 29

In the second option, the approach (Ryan, 1991) is based purely on a linear relationship (parameter: Ra_{pergN}) 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:

$$Ra_{main} = \left(N_{leaf} + N_{root}\right) Ra_{per_{gN}} f(T)$$ Equation 30

In both cases, the sensitivity of autotrophic respiration to average daily air temperature (T_a) is determined as:

$$f(T) = Q_a^{\frac{T_a - 20}{10}} \quad \text{Equation 31}$$

Plant maintenance respiration can occur each day and a buffer pool is required to avoid critical shortages during periods of low or zero photosynthesis. This labile respiration pool ($C_{labile\mathrm{Ra}}$) is topped up from the C_{labile} pool depending on whether a maximum pool size ($Store_{RaC}$) has been attained (Equation 37).

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

$$Ra_{growth} = a_{XC}\ growthresp \quad \text{Equation 32}$$

As described in section 2.1.4, a fraction of labile C can be allocated (at a rate determined by parameter τ_{excessC}) to excess autotrophic respiration (Ra_{excess}) to drive N fixation, if labile C remaining after other allocation (C_{avail}) exceeds the maximum storage capacity ($store_{maxC}$), and growth is occurring

$$Ra_{excess} = (C_{avail} - store_{maxC})\ growth_{potential}\ \tau_{\mathrm{excessC}} \quad \text{Equation 33}$$

During periods with high maintenance respiration fluxes but little production, plants can draw the storage pools of labile C (both $C_{labile\mathrm{Ra}}$ 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 ($a_{budc\_2Ramain}$).

$$a_{budC\_2Ramain} = -\max\left(\left(C_{labileRa} + C_{labile} + a_{Ra_{main}} - Ra_{main}\right), 0\right) \quad \text{Equation 34}$$

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

2.1.7 Annual 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 (*maxleafC*) and leaf N (*maxleafN*). The interaction of these adjustments results in changes to the target leaf C:N ($target_{leafCN}$) and maximum leaf C for the following year. Another set of tests determine adjustments to fine root C (*maxrootC*). Fine root C:N (*rootCN*) is not adjusted.

Adjustments to *maxleafN* are based on: 1) whether the integrated annual marginal return on leaf N investment is positive for C balance (see 2.1.9 Marginal Calculations, below), and 2) 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:

$$\frac{a_{budC}}{target_{leafCN}} > N_{labile}\ growth_{potential} \qquad \text{Equation 35}$$

The logic behind the three tests for changing *maxleafN*, with four outcomes, is as follows:

1) If the marginal return on N investment is negative, *maxleafN* should be decreased next year; the vegetation will improve its C balance by investing less N in foliage in this case.
2) If the marginal return on N investment is positive but last year's *maxleafN* was not attained, decrease *maxleafN* for the next year; in this case the vegetation was not able to attain the maximum given other allocation pressures and so should be more conservative.
3) If the marginal return on N investment is positive, last year's *maxleafN* was also attained, and no leaf N deficit occurred, then *maxleafN* is increased. The tests indicate that N is available for investment and this will result in positive C returns.
4) If the marginal return on N investment is positive, last year's *maxleafN* was attained, and a leaf N deficit occurred, *maxleafN* is held at the previous year *maxleafN*; the deficit signifies that N limitation is likely, even though C returns would be positive.

Adjustments to *maxleafC* are based on four related tests with five possible outcomes:

1) If in the previous year the *maxleafC* was attained, the wood allocation requirement (*wood_requirement*) was met, and the marginal return on C investment is positive, the *maxleafC* is increased; C is clearly in surplus and can be invested effectively.
2) If in the previous year the *maxleafC* was attained and the marginal return on C investment was positive but either the *maxrootC* was not attained or the wood allocation requirement (*wood_requirement*) was not met, *maxleafC* is decreased; in this case the supporting infrastructure for foliage was not attained and so the current *maxleafC* cannot be maintained.
3) If the marginal return on leaf C investment is negative, then *maxleafC* is decreased to improve the overall C balance.
4) If the *maxleafC* was not attained and no leaf N deficit occurred, *maxleafC* is reduced; in this case the vegetation is C limited.
5) If the *maxleafC* was not attained but leaf N deficit occurred, *maxleafC* is held at the previous year *maxleafC*. In this case, *maxleafC* was not attained due to N limitation rather than C limitation. Based on the associated reduction to *maxleafN* described above, the $target_{leafCN}$ will increase.

For fine roots, there are five linked tests with five outcomes used to determine the *maxrootC,* (fine root C:N (*rootCN*) is held constant in all cases).

1) If the current *maxrootC* is less than the required root-to-leaf ratio (parameter *min_leaf_to_root*), the *maxrootC* is increased.
2) If the *maxrootC* was not attained in the previous year and that *maxrootC* exceeds *min_leaf_to_root*, then *maxrootC* is decreased.
3) If *maxrootC* was reached and *min_leaf_to_root* is exceeded and either the marginal return on CN investment in roots is negative (see Section 2.1.9 Marginal calculations for plants; equation 58) or the N return on C investment into N fixation exceeds the return on investment in roots (see Section 2.1.9 Marginal calculations for plants; equation 57), *maxrootC* is decreased. This test shows that resources can be better allocated away from roots, to other tissues or to support N fixation.
4) If *maxrootC* was reached, 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, *maxrootC* is increased These tests show that C investment into roots is the most efficient means to relieve an N deficit by the foliage.

5) If *maxrootC* was reached, N return on C investment in roots exceeds returns on investment in N fixation and the N return on CN investment in roots is positive, but leaf N was not in deficit during the preceding year, the *maxrootC* is held at the previous year value. These tests indicate the current root C is close to optimal.

After the direction of adjustments to the *maxleafC*, *maxleafN*, and *maxrootC* are determined by the rules described above, the magnitude of the adjustment ($tissue_{adjust}$) 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 2.1.9 Marginal calculations 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 $tissue_{adjust}$ for *maxleafC*, *maxleafN*, and *maxrootC* are based on

$$tissue_{adjust} = \min\left(max\_tissue\_adjust\,, (max\_tissue\_adjust(\left|Return_{leafC} + Return_{leafN}\right|)\right)$$

Equation 36

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 ($C_{labile\mathrm{Ra}}$) to ensure metabolism through periods of low production. Each of these stores has a maximum size ($Store_{\mathrm{maxC}}$,$Store_{\mathrm{maxN}}$, $Store_{\mathrm{RaC}}$; 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 ($store\_prop_{\mathrm{X}}$).

$$Store_{RaC} = (C_{wood} + C_{root})\ store\_prop_{RaC} \qquad \text{Equation 37}$$

$$Store_{maxC} = (C_{wood} + C_{root})\ store\_prop_{C} \qquad \text{Equation 38}$$

$$Store_{maxN} = (C_{wood} + C_{root})\ store\_prop_{N} \qquad \text{Equation 39}$$

2.1.9 Marginal calculations for plants

Marginal returns on investment are calculated each day, to inform daily allocation decisions (see 2.1.4), and also integrated over longer periods of time to adjust maximum structural pools (see 2.1.7)(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_{Nleaf} and add_{Nroot}) are determined from the fixed difference for C pools, thus:

$$add_{Nleaf} = add_C . \frac{N_{leaf}}{C_{leaf}} \quad \text{Equation 40}$$

$$add_{Nroot} = add_C . \frac{1}{rootCN} \quad \text{Equation 41}$$

The marginal change to photosynthesis from added leaf C ($GPPreturn_{leafC}$), added leaf N ($GPPreturn_{leafN}$), added leaf C and N together ($GPPreturn_{leafCN}$), are determined using the GPP routine (Equation 2) with arguments relating to tissue pools indicated within parentheses thus:

$$GPPreturn_{leafC} = GPP(C_{leaf} + add_C, N_{leaf}) - GPP(C_{leaf}, N_{leaf}) \quad \text{Equation 42}$$

$$GPPreturn_{leafN} = GPP(C_{leaf}, N_{leaf} + add_{Nleaf}) - GPP(C_{leaf}, N_{leaf}) \quad \text{Equation 43}$$

$$GPPreturn_{leafCN} = GPP(C_{leaf} + add_C, N_{leaf} + add_{Nleaf}) - GPP(C_{leaf}, N_{leaf}) \quad \text{Equation 44}$$

The marginal change to maintenance respiration ($RamainReturn_{leafC,N,CN}$) is determined similarly according to C, N, or C and N changes:

$$RamainReturn_{leafC} = Ramain(C_{leaf} + add_C, N_{leaf}) - Ramain(C_{leaf}, N_{leaf}) \quad \text{Equation 45}$$

$$RamainReturn_{leafN} = Ramain(C_{leaf}, N_{leaf} + add_{Nleaf}) - Ramain(C_{leaf}, N_{leaf}) \quad \text{Equation 46}$$

$$RamainReturn_{leafCN} = Ramain(C_{leaf} + add_C, N_{leaf} + add_{Nleaf}) - Ramain(C_{leaf}, N_{leaf})$$

Equation 47

The marginal change to growth respiration (*$RagrowReturn_{leafC}$*) is determined for all cases based on added C,

$$RagrowReturn_{leafC} = (1 + growthresp)add_C \qquad \text{Equation 48}$$

To determine the time-integrated cost of leaf and fine root production, the lifespan of these tissues is used to assess whether tissues can repay their costs over the period that the plant will retain the tissue. The period, or time horizon, differs whether it is used to inform daily allocation decisions (see 2.1.4) or for annual adjustments to the maximum structural pools (see 2.1.7). In daily allocation for leaves, the time horizon is inversely proportional to the remaining days in the growing season (DOY_{senesc} – DOY) for deciduous species and to the leaf turnover time (τ_{leaf}) for species with leaf lifespans >12 months (evergreen).

$$leaf_{horizonD} = \begin{cases} 1/(DOY_{senesc} - DOY),\ t_{leaf} > \frac{1}{365} \\ t_{leaf},\ \ t_{leaf} \leq \frac{1}{365} \end{cases} \qquad \text{Equation 49}$$

The leaf horizon used for the annual adjustment to the maximum size of the leaf pool is

$$leaf_{horizonA} = \begin{cases} 1.0,\ t_{leaf} > \frac{1}{365} \\ 365\, t_{leaf},\ \ t_{leaf} \leq \frac{1}{365} \end{cases} \qquad \text{Equation 50}$$

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

The annual adjustment of the maximum size of the fine root pool uses

$$root_{horizon} = 365\, t_{root} \qquad \text{Equation 51}$$

The marginal returns on investments of C ($Return_{leafC}$) and of N ($Return_{leafN}$) 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:

$$Return_{leafC} = \frac{(GPPreturn_{leafC} - RamainReturn_{leafC})}{leaf_{horizon}} - RagrowReturn_{leafC} - add_C$$

Equation 52

$$Return_{leafN} = \frac{(GPPreturn_{leafN} - RamainReturn_{leafN})}{leaf_{horizon}}$$

Equation 53

The marginal return for daily allocation ($Return_{leafCNInstant}$) is based on the C return on allocation of both leaf C and leaf N:

$$Return_{leafCNInstant} = \frac{(GPPreturn_{leafCN} - RamainReturn_{leafCN})}{leaf_{horizon}} - RagrowReturn_{leafC} - add_C$$

Equation 54

The marginal returns on N uptake ($UReturn_X$) are calculated similarly, using the uptake equation (equation 10) modified for root parameters thus (arguments are shown in parentheses):

$$Ureturn_{rootC} = U_{NH4}(C_{root} + add_C, N_{root}) + U_{NO3}(C_{root} + add_C, N_{root}) - U_{NH4}(C_{root}, N_{root}) - U_{NO3}(C_{root}, N_{root})$$

Equation 55

$$Ureturn_{rootCN} = U_{NH4}(C_{root} + add_C, N_{root} + add_{Nroot}) + U_{NO3}(C_{root} + add_C, N_{root} + add_{Nroot}) - U_{NH4}(C_{root}, N_{root}) - U_{NO3}(C_{root}, N_{root})$$

Equation 56

The uptake return ($Return_{rootC}$) is then adjusted for root lifespan thus:

$$Return_{rootC} = \frac{Ureturn_{rootC}}{root_{horizon}}$$

Equation 57

For the CN marginal ($Return_{rootCN}$) the return must be adjusted for the N invested:

$$Return_{rootCN} = \frac{Ureturn_{rootCN}}{root_{horizon}} - add_{Nroot} \quad \text{Equation 58}$$

The return on C investment into N fixation ($Return_{Raexcess}$) is determined from the parameterised N fixation return ($N_{fixpergC}$) adjusted by N uptake down-regulation (X_N, Equation 20) and temperature (Equation 31):

$$Return_{Raexcess} = add_C \, Nfix_{pergC} \, X_N \, f(T) \quad \text{Equation 59}$$

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 ($Ureturn_{rootN}$). Therefore, the root N return is not used in ACONITE version 1.0.

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 the average daily air temperature (T_a) based on a Q10 relationship:

$$g(T) = Q_h^{\frac{T_a - 20}{10}} \quad \text{Equation 60}$$

The turnover of coarse woody litter pools (t_{CWDC} and t_{CWDN}) is purely a function of temperature and a first order rate constant, consistent with physical breakdown:

$$t_{CWDC} = C_{cwd} \tau_{cwd} g(T) \quad \text{Equation 61}$$

$$t_{CWDN} = N_{cwd} \tau_{cwd} g(T) \quad \text{Equation 62}$$

The potential turnover of litter C ($Pot\_t_{litterC\_soilC}$) is another temperature dependent first order process, with fluxes to either soil C

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

or to the atmosphere ($Pot\_t_{litterC\_atm}$), via mineralisation, according to a fractionation parameter (m_resp_frac)

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

Litter N turnover ($t_{litterN}$) is a similar process:

$$t_{litterN} = N_{litter}\tau_{litter}g(T) \quad \text{Equation 65}$$

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

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

If $total_{immob}$ <0, then N is mineralised in the form of NH_4^+. If $total_{immob}$ > 0, then immobilisation uses NH_4^+ ($NH4_{immob}$) and NO_3^- ($NO3_{immob}$) according to their relative proportions:

$$NH4_{immob} = \begin{cases} (Pot\_t_{litterC\_soilC}/Soil_{CN}) - t_{litterN}, & total_{immob} < 0 \\ \frac{N_{NH4}}{N_{NH4} + N_{NO3}} total_{immob}, & total_{immob} \geq 0 \end{cases} \quad \text{Equation 67}$$

$$NO3_{immob} = \begin{cases} 0, & Pot\_total_{immob} < 0 \\ \frac{N_{NO3}}{N_{NH4} + N_{NO3}} total_{immob}, & Pot\_total_{immob} \geq 0 \end{cases} \quad \text{Equation 68}$$

Both these immobilisations are limited in magnitude by the size of each mineral pool. The actual turnover of litter C ($t_{litterC\_soil}$ and $t_{litterC\_atm}$) is now determined from the potential values ($Pot\_t_{litterC\_soilC}$) adjusted by the ratio of actual to potential immobilisation:

$$t_{litterC\_soilC} = Pot\_t_{litterC\_soilC} \frac{NH4_{immob} + NH3_{immob}}{total_{immob}} \quad \text{Equation 69}$$

$$t_{litterC\_atm} = Pot\_t_{litterC\_atm} \frac{NH4_{immob} + NH3_{immob}}{total_{immob}}$$ Equation 70

The turnover of soil C (t_{soilC}) is a temperature dependent first order process:

$$t_{soilC} = C_{soil}\, \tau_{soil}\, g(T)$$ Equation 71

Soil N is lost to N mineralization (t_{soilN}; NH_4^+ production)

$$t_{soilN} = N_{soil}\, \tau_{soil} g\,(T)\,(1 - DON\_leach\_prop)$$ Equation 72

and a fraction (DON_leach_prop) is dissolved organic N loss (L_{DON}):

$$L_{DON} = N_{soil}\, \tau_{soil}\, g(T)\, DON\_leach\_prop$$ Equation 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 (*nitr*), the production of NO_3^- from NH_4^+, is another first order temperature dependent process that uses a turnover parameter ($nitr_{rate}$):

$$nitr = N_{NH4}\, nitr_{rate}\, g(T)$$ Equation 74

Nitrate is leached (L_{NO3}) at a fixed rate (*leach_rate*):

$$L_{NO3} = N_{NO3}\, leach\_rate$$ Equation 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 N_{labile} is less than $Store_{maxN}$ (i.e. N demand is not met). N fixation (N_{fix}) is calculated as :

$$N_{fix} = Ra_{excess}\, Nfix_{pergC}\, X_N\, f(T) \quad \text{Equation 76}$$

Where $N_{fixpergc}$ is the C cost for fixing N and Ra_{excess} is from Equation 33.

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 Equation 39, 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 (Equation 30). 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 performed three numerical experiments to analyse the qualitative functioning of the model using two different sets of climate forcing, one tropical and one temperate. For the temperate forcing, two separate simulations were performed using a deciduous forest (leaf lifespan <1 year) and evergreen forest (leaf life span > 1 year). The model was run to steady state using a 2000 year simulation that cycled through climate data from Harvard Forest (Munger and Wofsy, 1999), at 42.5°N, 72.0°W. Steady state was evaluated by testing the stationarity of C_{soil}, the longest residence time pool. The tropical simulation paralleled the temperate simulation with tropical tree parameters and climate data from Manaus (Kruijt et al., 2004) at 2.6°N, 60.2 °W.

The three simulations evaluated the model capacity to resolve differences in seasonality of climate forcing and phenology. We examined the annual GPP, annual carbon use efficiency (CUE; ratio of NPP to GPP), foliar C:N, maximum annual LAI and compared to 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 supplemental material (Figure 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 (Figure 2).

As LAI varied, the range of flexible leaf C:N was altered (Figure 3). At low LAI, increasing both leaf C and leaf N had positive returns. As LAI increased with a low leaf C:N (Figure 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 with 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 (Figure 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 (Figure 4a). In contrast, high values of the acm_{11} parameter applied to evergreen forests (Figure 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 (Figure 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 *Ra_parm2* 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 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 was not strongly sensitive to any parameters (|S| ≤ 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 (Q_a, *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 biome 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 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 gC 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 gC m^{-2} yr^{-1} (Waring et al., 1998) and for forests in Amazonia, 3094-3138 gC 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) (Figure 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 U.S. 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 and Friend, 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 the current version of ACONITE, the respiration of excess labile C is used for N fixation when N is limiting. Future model extensions can more mechanistically allocate this respired C to different forms of N, based on the uptake cost of each form. For example, the Fixation and Uptake of Nitrogen (FUN) model provides an example of how to allocate C respiration to N uptake, based on the comparison of C costs of N fixation, active N uptake from inorganic forms in the soil, and retranslocation (Fisher et al., 2010). The FUN model could be further expanded to include marginal returns of N on C allocation to soil microbes (soil priming) or mycorrhizal allocation. Combining elements of ACONITE and FUN would allow for more mechanistic predictions of both LAI and leaf C:N from ACONITE and the allocation of respiration to N uptake from FUN.

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 an 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 complements 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.

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Code availability

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

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Table 1. Mass balance equations used in ACONITE.

Vegetation pool mass balance equations

$$\frac{dC_{leaf}}{dt} = a_{budC\_2leaf} - t_{leafC}$$
$$\frac{dC_{wood}}{dt} = a_{woodC} - t_{woodC}$$
$$\frac{dC_{root}}{dt} = a_{rootC} - t_{rootC}$$
$$\frac{dC_{labile}}{dt} = GPP - a_{budC} - a_{woodC} - a_{rootC} - a_{LabileRa_{main}} - Ra_{growth} - Ra_{excess}$$
$$\frac{dC_{bud}}{dt} = a_{budC} - a_{bud_{C2leaf}} - a_{budC\_2Ramain}$$
$$\frac{dC_{labileRa}}{dt} = a_{LabileRa_{main}} + a_{budC\_2Ramain} - Ra_{main}$$
$$\frac{dN_{leaf}}{dt} = a_{budN\_2leaf} - t_{leafN} - t_{retransN}$$
$$\frac{dN_{wood}}{dt} = a_{woodN} - t_{woodN}$$
$$\frac{dN_{root}}{dt} = a_{rootN} - t_{rootN}$$
$$\frac{dN_{labile}}{dt} = U_{NH4} + U_{NO3} + U_{Nfix} + t_{retransN} + a_{budN\_2Ramain} - a_{budN} - a_{woodN} - a_{rootN}$$
$$\frac{dN_{bud}}{dt} = a_{budN\_2leaf} - a_{budN\_2Ramain}$$

Litter and organic matter mass balance equations

$$\frac{dC_{litter}}{dt} = t_{leafC} + t_{rootC} + t_{CWDC} - t_{litterC\_soilC} - t_{litterC\_atm}$$
$$\frac{dC_{soil}}{dt} = t_{litterC\_soilC} - t_{soilC\_atm}$$
$$\frac{dC_{cwd}}{dt} = t_{woodC} - t_{CWDC}$$
$$\frac{dN_{litter}}{dt} = t_{leafN} + t_{rootN} + t_{CWDN} - t_{litterN}$$
$$\frac{dN_{soil}}{dt} = t_{litterN} + U_{NH4\_immob} + U_{NO3\_immob} - t_{soilN} - L_{DON}$$
$$\frac{dN_{cwd}}{dt} = t_{woodN} - t_{CWDN}$$

Mineral N mass balance

$$\frac{dN_{NH4}}{dt} = Ndep_{NH4} + t_{soilN} - U_{NH4} - U_{NH4_{immob}} - nitr$$
$$\frac{dN_{NO3}}{dt} = Ndep_{NO3} + nitr - U_{NO3} - U_{NO3\_immob} - L_{NO3}$$

Table 2. Description of fluxes used in mass balance equations

Flux	Units	Description
a_{budC_2leaf}	gC m^{-2} day^{-1}	Allocation from bud C pool to leaf C
a_{woodC}	gC m^{-2} day^{-1}	Allocation from labile C to wood C
a_{rootC}	gC m^{-2} day^{-1}	Allocation from labile C to wood C
$a_{budC\_2Ramain}$	gC 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
a_{budC}	gC m^{-2} day^{-1}	Allocation of labile C to bud C; a fraction of the potential maximum leaf C
a_{Ramain}	gC m^{-2} day^{-1}	Allocation of labile C to future maintenance respiration; helps prevent carbon starvation during periods of negative NPP
a_{budN_2leaf}	gN m^{-2} day^{-1}	Allocation from bud N pool to leaf C; bud N is set in previous year
$a_{budN\_2Ramain}$	gN m^{-2} day^{-1}	When bud C is used for maintenance respiration ($a_{budC\_2Ramain} > 0$), bud N is returned to the labile N pool
a_{budN}	gN m^{-2} day^{-1}	Allocation of labile N to bud N; occurs in year prior to being displayed as leaf N
GPP	gC m^{-2} day^{-1}	Photosynthesis; based on ACM model see text for description
L_{DON}	gN m^{-2} day^{-1}	Production and leaching of dissolved organic N
L_{NO3}	gN m^{-2} day^{-1}	Leaching of NO3
$Ndep_{NH4}$	gN m^{-2} day^{-1}	Input of N deposition to NH4 pool
$nitr$	gN m^{-2} day^{-1}	Nitrification of NH4 to NO3
N_{depNO3}	gN m^{-2} day^{-1}	Input of N deposition to NO3 pool
Ra_{grow}	gC m^{-2} day^{-1}	Growth respiration that occurs when tissue is allocated; a constant fraction of carbon allocated to tissue
Ra_{excess}	gC m^{-2} day^{-1}	Respiration that occurs when labile C exceeds a maximum labile C store; used for N fixation
Ra_{main}	gC m^{-2} day^{-1}	Respiration of living tissues; a function of nitrogen content and temperature
t_{CWDC}	gN m^{-2} day^{-1}	Turnover of coarse woody debris C into the litter C pool
t_{leafC}	gC m^{-2} day^{-1}	Turnover of leaf C to litter C; constant over year in humid tropics; seasonal otherwise
$t_{litterC\_soil}$	gN m^{-2} day^{-1}	Turnover of litter C pool to soil C pool
$t_{litterC\_atm}$	gN m^{-2} day^{-1}	Turnover of litter C pool released as heterotrophic respiration
t_{rootC}	gC m^{-2} day^{-1}	Turnover of root C to litter C pool; occurs throughout year
t_{soil_atm}	gN m^{-2} day^{-1}	Turnover of soil C released as heterotrophic respiration
t_{woodC}	gC m^{-2} day^{-1}	Turnover of wood C to CWDC pool; occurs throughout year
t_{CWDN}	gN m^{-2} day^{-1}	Turnover of coarse woody debris C to litter C pool
$t_{litterN}$	gN m^{-2} day^{-1}	Turnover of litter N to soil N
t_{leafN}	gN m^{-2} day^{-1}	Turnover of leaf N to litter N; constant over year in humid tropics; seasonal otherwise
$t_{retransN}$	gN m^{-2} day^{-1}	Reabsorption of N from leaves to labile N
a_{woodN}	gN m^{-2} day^{-1}	Allocation from labile N to wood N
t_{woodN}	gN m^{-2} day^{-1}	Turnover of wood N to CWDN pool; occurs throughout year
a_{rootN}	gN m^{-2} day^{-1}	Allocation from labile N to wood N
t_{rootN}	gN m^{-2} day^{-1}	Turnover of root N to litter N pool; occurs throughout year
t_{soilN}	gN m^{-2} day^{-1}	Mineralization of soil N to NH4 pool
U_{NH4}	gN m^{-2} day^{-1}	Uptake of NH_4 from mineral soil NH_4; based on Williams and Yanai 1996
U_{NO3}	gN m^{-2} day^{-1}	Uptake of NO_3 from mineral soil NO_3; based on Williams and Yanai 1996
U_{Nfix}	gN m^{-2} day^{-1}	Fixation of N from N_2; function of Ra_{excess} flux, temperature, N demand, and C cost.

$U_{NH4immob}$	gN m^{-2} day^{-1}	Immobilization of NH4 to soil N associated with the turnover of litter C and N
$U_{NO3immob}$	gN m^{-2} day^{-1}	Immobilization of NO3 to soil N associated with the turnover of litter C and N

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	
*lca	g C m^{-2}	Leaf C per area	T: 53 E: 100 D: 32	Kattge et al. 2011
*R_{tot}	MPa m^2 s $mmol^{-1}$	Total plant–soil hydraulic resistance	Input (0.1)	Fox et al. 2009
*ψ	MPa	Maximum soil–leaf water potential difference	Input (-2)	Fox et al. 2009

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

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
*c_{conc}	g C g^{-1}	C:dry weight ratio	0.5	Widely used
D_{NH4}	m-2 s^{-1}	Effective diffusion coefficient of the solute through the soil	1 x 10^{-11}	(Williams and Yanai, 1996)
D_{NO3}	m^{-2} s^{-1}	Effective diffusion coefficient of the solute through the soil	0.5	(Williams and Yanai, 1996)
I_{max}	mmol m^{-2} s^{-1}	Maximal nutrient influx rate	4 x 10^{-5}	(Williams and Yanai, 1996)
K_m	mmol m^{-2} s^{-1}	Half saturation constant for uptake	15.0	(Williams and Yanai, 1996)
$Nfix_{pergC}$	gN/gC	Cost of N fixation	0.11	(Gutschick, 1981)
r_{radius}	m	Radius of fine root	5 x 10^{-4}	(Fahey et al., 2005) definition of fine root
r_{depth}	m	Depth of soil explored by roots	varies by site	
$r_{density}$	g m^{-3}	Density of root mass	175000	(Comas and Eissenstat, 2004)
v	m s^{-1} (gC m^{-2} $day^{-1})^{-1}$	Inward radial velocity of water at the root surface per unit of daily photosynthesis	1 x 10^{-9}	Value in Williams and Yanai (1996); scaled by daily GPP
β_{NH4}	Unitless	Soil buffer power (NH_4)	10.0	(Williams and Yanai, 1996)
β_{NO3}	Unitless	Soil buffer power (NO_3)	2 x 10^{-10}	(Williams and Yanai, 1996)

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
**DOYsenesc*	Day	Day of year that growth ends and leaf fall begins	Varies by location	
**GDDStart*	Day	Growing degree day growth begins	100	(Aber et al., 1997)
growthresp	proportion	proportion of C allocation to tissue used for respiration	0.28	(Waring and Schlesinger., 1985) (TBL 2.3)
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	
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	
Max_tissue_adjust	proportion day^{-1}	Maximum potential annual proportional change in maximum leaf C and root C	0.1	
Q_a	Unitless	Q10 for maintenance respiration	1.40	(Mahecha et al., 2010)
Retrans_frac	proportion	Proportion of leaf N retranslocated to labile N pool	0.5	Widely used
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)
rootCN	gC/gN	Root C:N ratio	50	(White et al., 2000)
$store\_prop_{RaC}$	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	
$store\_prop_{N}$	proportion	Proportion of Wood and Root C that can be used for storage of labile N	0.001	
$store\_prop_{C}$	proportion	Proportion of Wood and Root C that can be used for storage of labile C	0.01	
woodCN	gC/gN	Wood C:N ratio	500	(White et al., 2000)
θ	proportion	Proportion of labile C available to use for growth	0.07	Approximates a 2-week turnover time for labile pools; a balance between buffering the labile pools and allowing for responsive growth at realistic time

				scales
$*\tau_{leaf}$	day^{-1}	Turnover of leaf C and N	T: 0.0019 E: 0.00082 D: > 0.0027	(Kattge et al., 2011)
$*\tau_{wood}$	day^{-1}	Turnover of wood C and N	T: 9x10-6 E: 5x10-5 D: 5x10-5	Approximates a 2% annual mortality rate in temperate forest and 3.3% annual mortality rate in tropical forest
$*\tau_{root}$	day^{-1}	Turnover of root C and N	0.002	Based on (McCormack et al., 2013)
$\tau_{excessC}$	day^{-1}	Turnover of labile C when pool exceeds the maximum size of the labile C pool	0.05	

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

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	31300	3130	1423	0.45	28	0.6
Temperate deciduous	6.3	18900	1320	674	0.51	22	0.01
Temperate evergreen	4.4	20800	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| ≥ 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
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
DON_leach_prop	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.0	-	0.1
DOY_{Sensce}	-	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
GDDStart	-	-	-	-	-	-0.1	-	-	-	-	-	-	-	-0.1	-	-	-	-	-	0.2	-0.1
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
I_{max}	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-1.3	2.1
K_m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.1
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
leach_rate	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-0.1
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
m_resp_frac	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.0	-	0.1
$Nfix_{pergC}$	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.0	1.0
Qa	-	-	-	-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
Retrans_frac	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-0.1

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
r_{radius}	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.1	1.6
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
$r_{density}$	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-			-	1.1	1.6
r_{depth}	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.1
$store\_prop_C$	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
soilCN	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-1.1	-	-0.2
woodCN	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-0.2	-0.3
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	-
τ_{leaf}	-0.6	-0.6	-	-	0.1	-	-0.1	-	-	-	-	-	-	-	0.1	-0.5	-0.5	-	-	-	-0.2
τ_{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	-
τ_{root}	-	-	-	-0.1	-0.3	-0.1	-	0.1	-	-	0.1	0.1	-	-	0.1	-	-	-	-	-	-0.5
τ_{soil}	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-					-0.5
$\tau_{excessC}$	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-0.1	1.0	0.9

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

Figure Captions

Figure 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. All pools and flux correspond Tables 1 and 2. R_h includes both litter ($t_{litterC\_atm)}$ and soil C (t_{soil_atm}) respiration fluxes. CWD = coarse wood debris

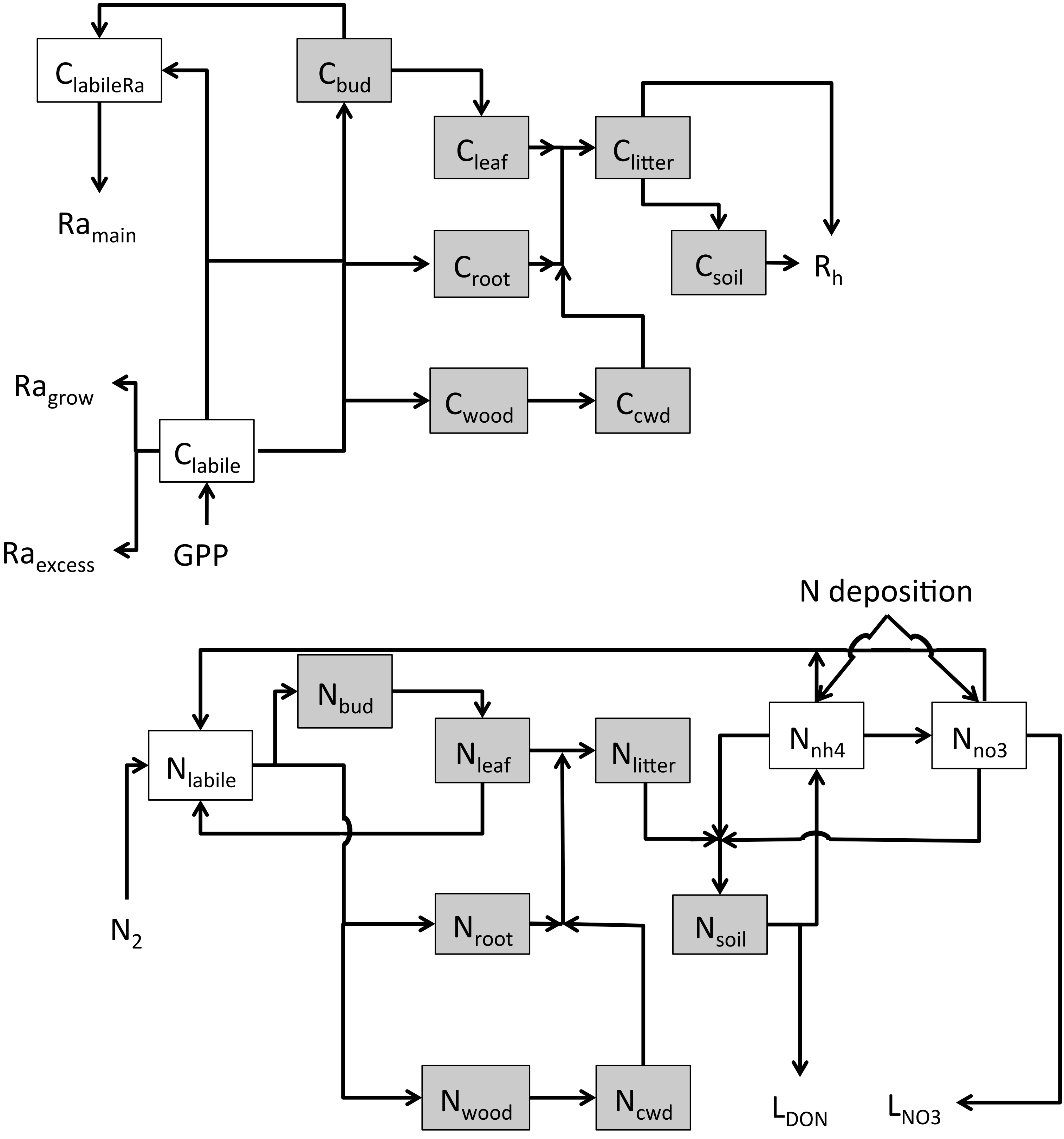
Figure 2. A schematic illustrating the adjustment of leaf C : N for a given leaf area index using the marginal C returns on investment of leaf C and leaf N. At low leaf C : N, leaf N has a negative return and leaf C has a positive return on investment that results in allocation to increase the leaf C:N (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.

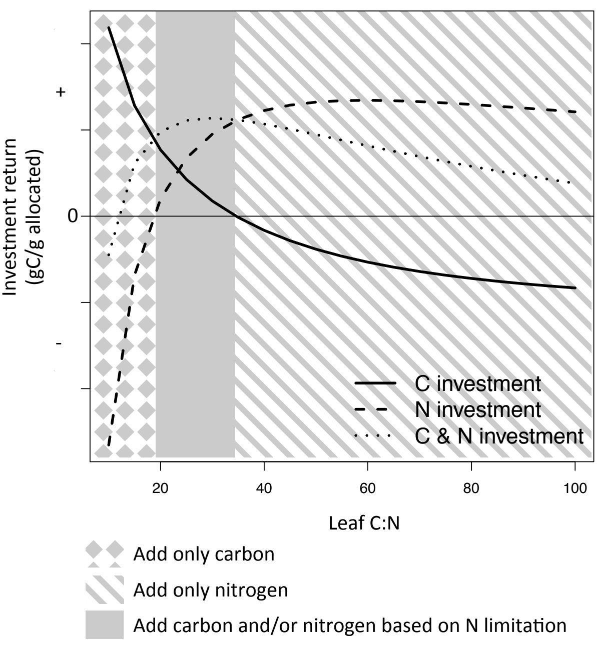
Figure 3. A schematic illustrating the simultaneous adjustment of leaf area index (LAI) and leaf C:N (see legend above) based on the C return on marginal investment of leaf C (solid line) and leaf N (dashed line). Panel (a) shows the situation with a leaf C:N of 20 and (b) shows the situation with a 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.

Figure 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

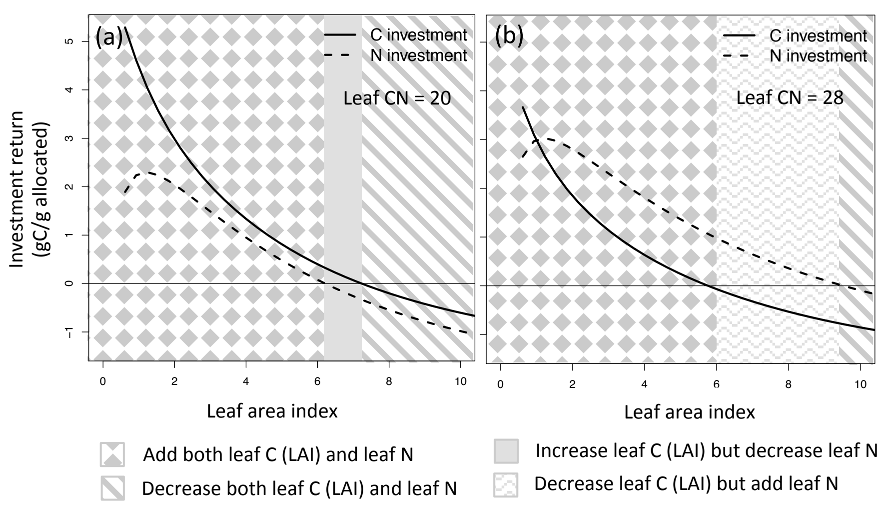
leaf C : N with positive returns increases with leaf area index (a vs. b; e vs. f) and depends on the acm11 parameter (a vs. c; e vs. g), and the non-linearity of the leaf respiration parameterization (a vs. d; e vs. h). (a and e) use the log–log relationship between N concentration and leaf respiration from Reich et al. (2008) and (d and h) use the linear relationship from Ryan (1991). Figure'X."(a,b)'Temperate'Deciduous'(a11'='0.5),'(c,d)' Brackets indicate range of leaf C : N where leaf C : N can vary based on N status of the plant.

Figure 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).

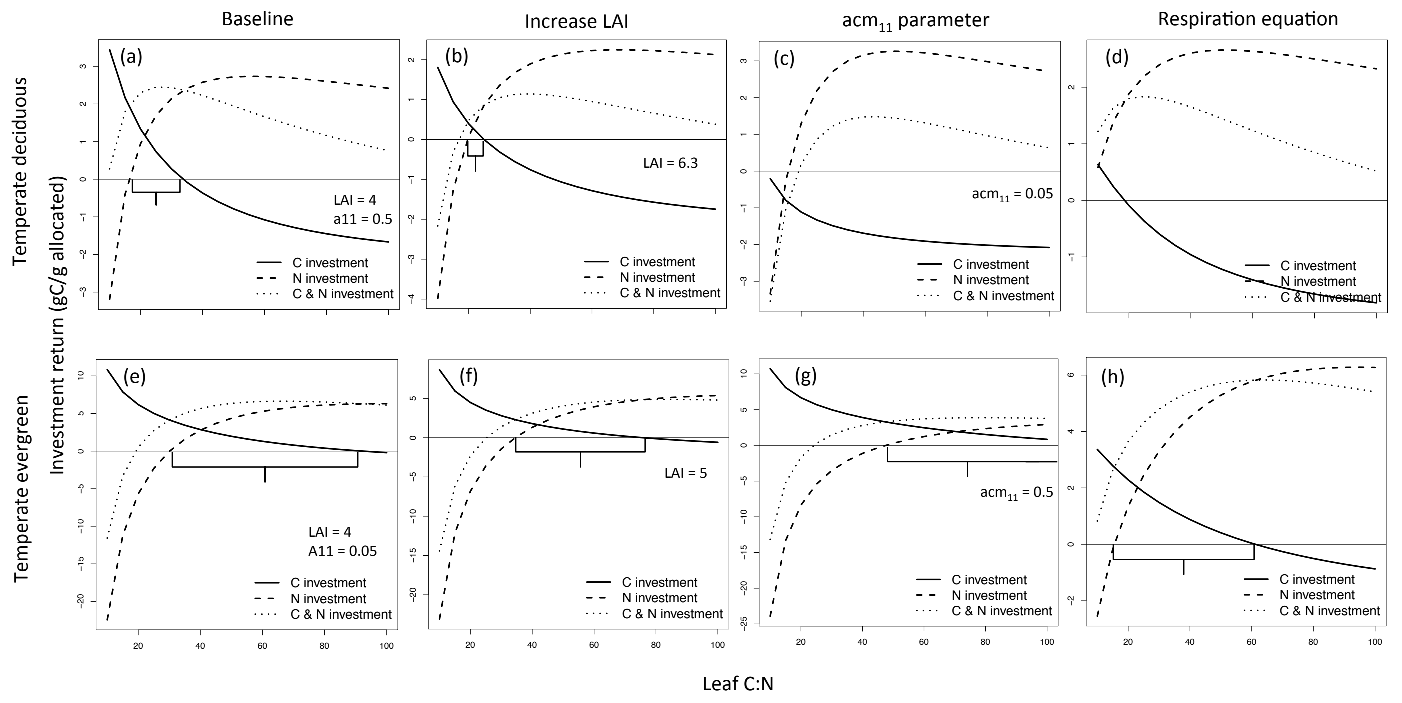

C_labileRa
C_bud
C_leaf
C_litter
Ra_main
C_root
C_soil
R_h
Ra_grow
C_wood
C_cwd
C_labile
Ra_excess
GPP
N deposition
N_bud
N_labile
N_leaf
N_litter
N_nh4
N_no3
N_2
N_root
N_soil
N_wood
N_cwd
L_DON
L_NO3



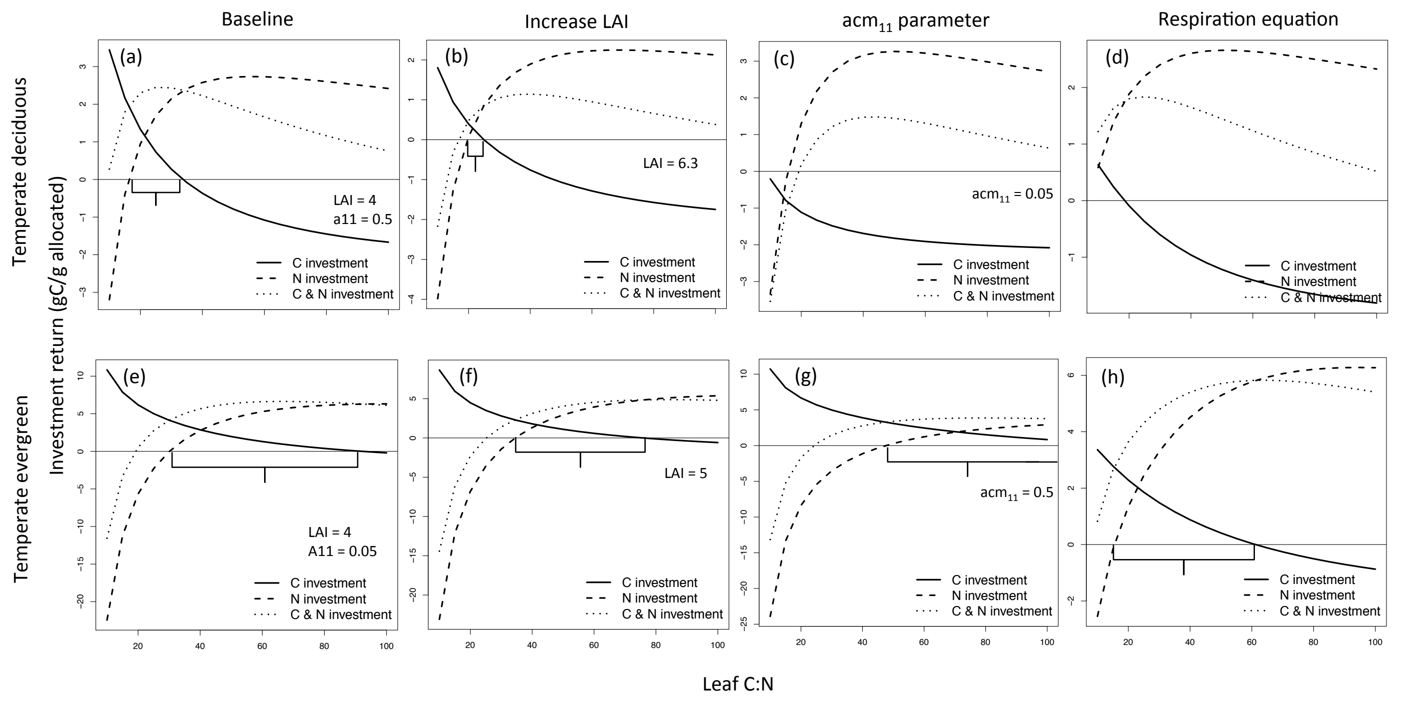
Investment return
(gC/g allocated)
+
0
-
20
40
60
80
100
Leaf C:N
C investment
N investment
C & N investment
Add only carbon
Add only nitrogen
Add carbon and/or nitrogen based on N limitation



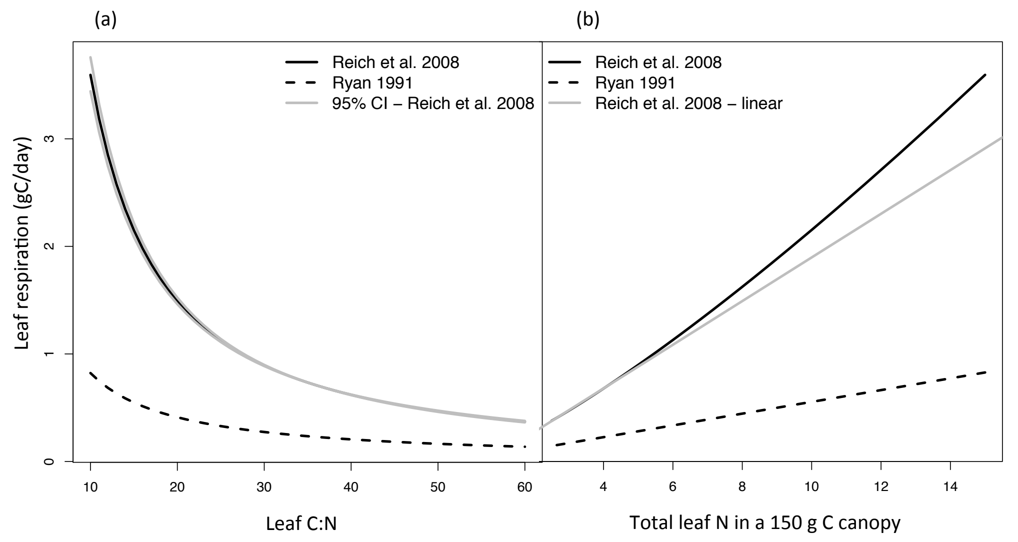
(a)
C investment
N investment
Leaf CN = 20
(b)
C investment
N investment
Leaf CN = 28
Investment return
(gC/g allocated)
5
4
3
2
1
0
−1
0
2
4
6
8
10
Leaf area index
Add both leaf C (LAI) and leaf N
Decrease both leaf C (LAI) and leaf N
Increase leaf C (LAI) but decrease leaf N
Decrease leaf C (LAI) but add leaf N



Baseline
Increase LAI
acm_{11} parameter
Respiration equation
Temperate deciduous
Temperate evergreen
Investment return (gC/g allocated)
(a)
LAI = 4
a11 = 0.5
(b)
LAI = 6.3
(c)
acm_{11} = 0.05
(d)
(e)
LAI = 4
A11 = 0.05
(f)
LAI = 5
(g)
acm_{11} = 0.5
(h)
C investment
N investment
C & N investment
Leaf C:N



Baseline
Increase LAI
acm_{11} parameter
Respiration equation
Temperate deciduous
Temperate evergreen
Investment return (gC/g allocated)
(a)
LAI = 4
a11 = 0.5
(b)
LAI = 6.3
(c)
acm_{11} = 0.05
(d)
(e)
LAI = 4
A11 = 0.05
(f)
LAI = 5
(g)
acm_{11} = 0.5
(h)
C investment
N investment
C & N investment
Leaf C:N



(a)
(b)
Reich et al. 2008
Ryan 1991
95% CI – Reich et al. 2008
Reich et al. 2008
Ryan 1991
Reich et al. 2008 – linear
Leaf respiration (gC/day)
0
1
2
3
10
20
30
40
50
60
4
6
8
10
12
14
Leaf C:N
Total leaf N in a 150 g C canopy