

TEM-Hydro Auxiliary Material

The TEM-Hydro is a model of water, carbon, and nitrogen cycling in terrestrial ecosystems. It is grounded within the framework of the previous biogeochemical model TEM 4.3 (Raich et al., 1991, Tian et al., 1999, Felzer et al., 2004). This version of the Terrestrial Ecosystem Model represents carbon and nitrogen in vegetation with multiple pools or “boxes” to refine water-carbon linkages within the model. Below, we describe how vegetation carbon and nitrogen dynamics are simulated in the new version. In Table S1, we give parameter values for the model as calibrated to temperate deciduous and coniferous forests. Carbon and nitrogen dynamics of soil microbes remain the same as in previous versions of the TEM.

The multiple-box vegetation model used in the TEM-Hydro encompasses four plant structural compartments, and one storage compartment; each of these contains a carbon and a nitrogen pool. The four structural compartments consist of leaves, active stem tissue (e.g. sapwood in trees), inactive stem tissue (e.g. heartwood in trees), and fine roots. Functionally, leaves are the photosynthetic organs, active stem tissue is responsible for hydraulic transport and resource storage, inactive stem tissue is non-metabolic and has a purely structural role, and fine roots are responsible for nutrient and water uptake; many of these functional purposes are modeled explicitly within TEM-Hydro. The storage, or labile, compartment can be used either to grow new tissue, or maintain existing tissue. Thus there are ten variables that define the state of the vegetation; we will refer to them in the equations that follow as *labile.c*, *labile.n*, *leaf.c*, *leaf.n*, *stema.c* (active), *stema.n*, *stemi.c* (inactive), *stemi.n*, *root.c*, *root.n*.

Each these variables evolve in time according to a system of coupled differential equations, which is solved using monthly average environmental conditions, but an adaptive Runge-

Kutta integration process (Cheney and Kincaid, 1985) that has time step generally less than one month. In §1 we present the relevant differential equations for the system. Each category of fluxes is then presented in detail in its own section. Photosynthesis (§2) depends on numerous environmental variables, as does nitrogen uptake (§3), and the downregulation of the two fluxes (§4). In §5 we present the details of the respiration model, which is based primarily on tissue nitrogen and temperature. The calculation of the litterfall-related fluxes (§6) are based on lifetime formulations, and the C:N of each compartment. Allocation (§7) is based on algorithms that explicitly consider cost:benefit tradeoffs of adding new tissue, involving knowledge of expected respiration, photosynthesis, and litterfall.

1 Carbon and Nitrogen Fluxes

The governing differential equations for vegetation carbon are as follows:

$$\begin{aligned}
\frac{d}{dt}(labile.c) &= GPP - ALLOCLC - ALLOCSC - ALLOCRC - RMLABILE - RGRWTH \\
\frac{d}{dt}(leaf.c) &= ALLOCLC - RMLEAF - LEAFLTRC \\
\frac{d}{dt}(stema.c) &= ALLOCSC - SENESC - RMSTEM - STEMALTRC \\
\frac{d}{dt}(stemi.c) &= SENESC - STEMILTRC \\
\frac{d}{dt}(root.c) &= ALLOCRC - RMROOT - ROOTLTRC.
\end{aligned} \tag{1}$$

In the above equations, GPP is the photosynthetic rate (gross primary production), and $ALLOCLC$, $ALLOCSC$, and $ALLOCRC$ are carbon allocation rates to leaves, active stem, and fine roots, respectively. Respiration is divided into maintenance ($RMLABILE$, $RMLEAF$, $RMSTEM$, and $RMROOT$ for the labile, leaf, active stem, and root compartments, respectively), as well as growth ($RGRWTH$), which is assumed to occur at the time of allocation. All structural compartments lose carbon also through litterfall/mortality,

represented by *LEAFLTRC* (leaf), *STEMALTRC* (active stem), *STEMILTRC* (inactive stem), and *ROOTLTRC* (fine roots). Finally, inactive stem carbon is assumed to only increase due to senescence from the active stem pool (*SENESC*) – there is no direct allocation to the pool.

The equations representing nitrogen cycling in vegetation are highly parallel in structure to those governing the carbon cycle (mainly since allocation and litterfall are biomass fluxes that must also include nitrogen):

$$\begin{aligned}
\frac{d}{dt}(\text{labile.n}) &= VNUP - ALLOCLN - ALLOCSN - ALLOCRN + NRESORBL \\
\frac{d}{dt}(\text{leaf.n}) &= ALLOCLN - LEAFLTRN - NRESORBL \\
\frac{d}{dt}(\text{stema.n}) &= ALLOCSN - SENESN - STEMALTRN \\
\frac{d}{dt}(\text{stemi.n}) &= SENESN - STEMILTRN \\
\frac{d}{dt}(\text{root.n}) &= ALLOCRN - ROOTLTRN.
\end{aligned} \tag{2}$$

In the above, *VNUP* is the rate of vegetation nitrogen uptake, and *ALLOCLN*, *ALLOCSN*, and *ALLOCRN* are nitrogen allocation rates to leaves, active stem, and fine roots, respectively. There is no direct analogue for respiration in the nitrogen cycle, but there is an additional resorption flux (*NRESORBL*), whereby dying leaves can transfer some of their nitrogen back to the labile pool. Structural components lose nitrogen mainly via litterfall/mortality: *LEAFLTRN* (leaf), *STEMALTRN* (active stem), *STEMILTRN* (inactive stem), and *ROOTLTRN* (fine roots). Finally, there is a similar senescence flux of nitrogen (*SENESN*) from the active to inactive stem pool.

A primary model assumption in the joint calculation of carbon and nitrogen fluxes is that structural compartments and the litterfall from each possesses a static C:N. These ratios depend on the plant functional type (PFT), and we will refer to them as *cnleaf*

(living leaves), *cnleafltr* (leaf litterfall), *cnstem* (active and inactive stem), and *cnroot* (fine roots); the C:N of the labile compartment is allowed to vary somewhat. These assumptions place useful constraints on the allocation, respiration, litterfall, and resorption fluxes.

2 Photosynthesis

The TEM-Hydro continues to use a semi-empirical equation for canopy photosynthesis (or gross primary production, GPP), based on limiting a maximum rate of carbon assimilation (C_{max}) by factors of light, moisture, temperature, carbon dioxide, ozone, and nutrient availability. This version differs from previous published versions of TEM in that it explicitly uses leaf area index (LAI) in calculating GPP , and in that C_{max} represents a maximum leaf-level, rather than canopy-level, photosynthetic rate. In the case that nitrogen uptake does not limit photosynthesis (see §4 for the general case), potential GPP , or GPP_P , is given as follows:

$$GPP_P = C_{max} \times f_T \times f_{H_2O} \times f_{C_{a,D}} \times f_{O_3} \times \int_0^{LAI} f_{PAR} dL, \quad (3)$$

where f_T , f_{H_2O} , $f_{C_{a,D}}$, f_{O_3} , and f_{PAR} are, respectively, functions of temperature, soil moisture stress, carbon dioxide concentration and vapor pressure deficit, ozone, and photosynthetically active radiation, all of which range from 0 to 1. Photosynthesis is calculated as an average rate during daylight hours during a month. The integral of f_{PAR} is necessary to scale the leaf-level (differential) light response to a canopy-level (integrated) function, and requires knowledge of the light distribution within the canopy. LAI is related to the leaf carbon stock by the specific leaf area (sla) parameter, which varies among PFTs based on Schulze et al. (1994):

$$LAI = sla \times leaf.c. \quad (4)$$

The function f_{PAR} represents the leaf-level response to light, modeled as a rectangular hyperbola with half-saturation constant k_I :

$$f_{PAR} = \frac{k_{ext} \times PAR(L)}{k_I + k_{ext} \times PAR(L)}, \quad (5)$$

where $PAR(L)$ is expressed in units of W m^{-2} , and depends on the radiation at the top of the canopy, PAR_0 , and the overlying leaf area index, L . We assume that photosynthetically active radiation attenuates exponentially (Beer's law) according to L , with an extinction coefficient k_{ext} :

$$PAR(L) = PAR_0 \times e^{-k_{ext}L}. \quad (6)$$

Performing the integral from $L = 0$ to $L = LAI$, we obtain the canopy-scale light response function:

$$\begin{aligned} \int_0^{LAI} f_{PAR} dL &= \int_0^{LAI} \frac{k_{ext} \times PAR(L)}{k_I + k_{ext} \times PAR(L)} dL \\ &= \frac{1}{k_{ext}} \ln\left(\frac{k_I + k_{ext} \times PAR}{k_I + k_{ext} \times PAR \times e^{-k_{ext}LAI}}\right) \end{aligned} \quad (7)$$

The dependence of GPP on temperature (T) is as follows:

$$\begin{aligned} f_T &= \frac{[Q_{ref} \times e^{-\alpha(T-T_{ref})}]^{\frac{T-T_{ref}}{10}} / [1 + e^{0.3(T_{min}-T)} + e^{0.3(T-T_{max})}]}{[Q_{ref} \times e^{-\alpha(T_{opt}-T_{ref})}]^{\frac{T_{opt}-T_{ref}}{10}} / [1 + e^{0.3(T_{min}-T_{opt})} + e^{0.3(T_{opt}-T_{max})}]} : T < T_{opt} \\ &= \frac{(T - T_{min})(T_{max} - T)}{(T - T_{min})(T_{max} - T) + (T - T_{opt})^2} : T \geq T_{opt}, \end{aligned} \quad (8)$$

where T_{min} and T_{max} are PFT-dependent parameters representing lower and upper bounds for photosynthetic activity, and T_{opt} is a 5-year running mean of the warmest monthly temperature. Roughly speaking, this function of temperature decreases exponentially below T_{opt} , and decreases parabolically above T_{opt} , representing enzyme kinetic behavior below

T_{opt} , and general heat stress above T_{opt} . The parameters α and Q_{ref} determine the shape of the roughly exponential segment; we currently use values of $\alpha = 0.01$, $Q_{ref} = 2.07$, and $T_{ref} = 25$ for all PFTs. Other factors equal, one would expect both gross and net photosynthesis to be maximal at T_{opt} . This new formulation has been adopted in conjunction with a modified formula for plant respiration (see §5, Amthor, personal communication), and the two functions share similar structure, though differ in a few parameters.

The soil moisture function is the drying curve from the WBM (Vorosmarty et al., 1998), and depends on the amount of plant extractable water in the soil column ($availw$), divided by the maximum possible amount of extractable water in the given soil profile ($awcap$):

$$f_{H_2O} = \frac{1 - e^{-5 \frac{availw}{awcap}}}{1 - e^{-5}}, \quad (9)$$

This function replaces the previous dependence of photosynthesis on the ratio of estimated to potential evapotranspiration, and a potential evapotranspiration variable is no longer used in the model.

The internal concentration of carbon dioxide (C_i) is based on a function of vapor pressure deficit (f_D), ambient carbon dioxide concentration (C_a), and a stomatal slope parameter (gs_a):

$$C_i = C_a \left(1 - \frac{1.563}{gs_a \times f_D}\right), \quad (10)$$

where 1.563 is the ratio of molecular diffusivity of water vapor to carbon dioxide ($(44/18)^{0.5}$), and we have assumed the “open-stomata” ratio of C_i/C_a consistent with our formulation of stomatal conductance (g_c = canopy conductance; g_s = average stomatal conductance):

$$\begin{aligned} g_c &= gs_{min} \times LAI + gs_a \frac{GPP \times f_D}{C_a} \\ g_s &= g_c / LAI, \end{aligned} \quad (11)$$

where $g_{s_{min}}$ is minimum stomatal aperture ($\text{mmol m}^{-2} \text{s}^{-1}$, taken as 14 for both PFTs we model), and g_{s_a} is the stomatal slope (unitless, taken as 8 for both PFTs). The “open-stomata” limit assumes that the LAI term is negligible compared to the GPP term; together with the diffusion-based formula for GPP:

$$GPP = \frac{g_c}{1.563}(C_a - C_i), \quad (12)$$

the equations can be simultaneously solved for C_i/C_a , arriving at eqn. 10. The function of vapor pressure deficit is based on Federer et al. (1996), and decreases with increasing D , so that C_i/C_a also decreases:

$$f_D = \frac{20}{20 + D}. \quad (13)$$

The dependence of GPP on C_i is modeled as a rectangular hyperbola, with half-saturation constant k_c :

$$f_{C_a,D} = f_{C_i} = \frac{C_i}{k_c + C_i}. \quad (14)$$

The ozone factor, f_{O_3} , represents the detrimental effects of ozone on photosynthesis, as noted by Reich (1987), and modeled by Ollinger et al. (1997). Since ozone damage to leaves is largely cumulative, current conditions determine the time derivative of the ozone factor, rather than the ozone factor itself. This rate of change is equal to healing minus new damages:

$$\begin{aligned} \frac{df_{O_3}}{dt} &= \text{healing rate} - \text{damage rate} \\ \text{healing rate} &= (1 - f_{O_3}) \left[\frac{1}{\tau_{O_3}} + \min\left(\frac{1}{\text{leafc}} \frac{d\text{leafc}}{dt}, 0\right) \right] \\ \text{damage rate} &= \alpha_{O_3} \times g_s \times \text{AOT40}. \end{aligned} \quad (15)$$

The healing rate is essentially a sum of two expressions: one of which allows leaves to heal

when LAI is constant or decreasing (both due to cellular repair, and the addition of new leaves to replace those lost as litterfall), with a characteristic healing time τ_{O_3} , and the other of which allows for rapid healing when LAI is increasing (i.e. when the time derivative of leaf carbon is positive). These considerations reflect the practical notion that new leaves come into existence with no ozone damage. The damage rate is quasi flux-based, dependent on the stomatal conductance (g_s), a PFT-dependent damage coefficient (α_{O_3}), and a threshold ozone exposure index (AOT40) (Ollinger et al., 1997). The overall rate of change is restricted so that f_{O_3} always lies between 0 and 1, and f_{O_3} is everywhere set to 1 at the beginning of the simulation.

3 Nitrogen Uptake

Vegetation nitrogen uptake ($VNUP_P$) in the absence of carbon-limitation (see §4 for the general case of $VNUP$) is largely the same as in previous versions of TEM; however, it now depends explicitly on fine root biomass ($root.c$):

$$VNUP_P = N_{\max} \times f_{rmt} \times f_{O_3} \frac{K_{\text{soil}} \times [\text{N}]}{k_{N1} + K_{\text{soil}} \times [\text{N}]} \times \frac{root.c}{k_{rnup} + root.c}. \quad (16)$$

In eqn. 16, N_{\max} is a maximum (pft-dependent) nitrogen uptake rate, K_{soil} is a factor that takes into account the dependence of ion diffusion on soil moisture (related to the cube of volumetric soil moisture), and $[\text{N}]$ is the concentration of available nitrogen in soil water, equal to the amount of available nitrogen in the soil profile divided by the amount of total water in the soil profile (including water below wilting point, non-extractable by plants). Nitrogen uptake is assumed to increase with plant respiration, and thus increases with temperature in the same fashion as respiration (f_{rmt} – see §5); it is also assumed that nitrogen uptake decreases with ozone exposure in the same manner as photosynthesis (f_{O_3}).

The half saturation constants k_{N1} and k_{rnup} are generally chosen so that nitrogen uptake responds strongly to increasing available nitrogen (k_{N1} is substantially greater than typical values of $K_{soil} \times [N]$), but weakly to increasing root biomass (k_{rnup} is substantially less than typical values of $root.c$).

4 Downregulation of Photosynthesis and Nitrogen Uptake

One of the key features of the TEM is its consideration of nitrogen-limitation of plant productivity. Essentially, if too little nitrogen is available for allocation to new growth, photosynthesis is downregulated, and if too little carbon is available for allocation to new growth, nitrogen uptake is downregulated. The degree of downregulation depends on the magnitude of the mismatch in the supply of the two elements relative to demand. A key variable here is the mass ratio of demand of carbon from the labile pool relative to demand of nitrogen from the labile pool:

$$cndemand \equiv \frac{ALLOCLC + ALLOCSC + ALLOCRC + RMLABILE + RGRWTH}{ALLOCLN + ALLOCSN + ALLOCRN}, \quad (17)$$

which is based on eqns. 1 and 2. The potential supply of carbon and nitrogen from the labile pool depends on $(GPP_P + labile.c)$ and $(VNUP_P + labile.n)$:

$$cnsupply \equiv \frac{GPP_P + labile.c}{VNUP_P + labile.n}. \quad (18)$$

If $cnsupply > cndemand$, then growth will be nitrogen-limited; if $cnsupply < cndemand$, growth will be carbon-limited. The actual C:N available for allocation from the labile pool,

is given as:

$$cnavail \equiv \frac{GPP + labile.c}{VNUP + labile.n}, \quad (19)$$

where GPP has been downregulated in the case of nitrogen-limitation (but $VNUP = VNUP_P$), and $VNUP$ has been downregulated in the case of carbon-limitation (but $GPP = GPP_P$). The simplest way to express this downregulation is by relating $cnavail$ to $cnsupply$ and $cmdemand$.

In the case of nitrogen-limitation, GPP is lowered so that:

$$cnavail = cmdemand \left(2 - \frac{cmdemand}{cnsupply} \right), \quad (20)$$

and since $cmdemand < cnsupply$, it follows that $cmdemand < cnavail < 2 \times cmdemand$. This formula implies that more extreme nitrogen limitation ($cnsupply$ much larger than $cmdemand$) causes larger downregulation of GPP . The only exception for equation 20 is if it would require GPP to be less than zero, in which case GPP is set to zero. Thus, writing the expression for GPP in the case of n-limitation, based on eqns. 19 and 20,

$$GPP = \max\left(0, cmdemand(VNUP + labile.n) \left(2 - \frac{cmdemand}{cnsupply} \right) - labile.c\right). \quad (21)$$

In the case of carbon-limitation, $VNUP$ is lowered so that:

$$cnavail = cmdemand \frac{1}{2 - \frac{cnsupply}{cmdemand}}, \quad (22)$$

from which it follows similarly that $cmdemand/2 < cnavail < cmdemand$. More extreme carbon limitation ($cmdemand$ much greater than $cnsupply$) results in more extreme downregulation of $VNUP$. Again, an exception is made if this downregulation implies $VNUP$ less than zero, in which case $VNUP$ is set to zero. Thus, using eqns. 19 and 22, $VNUP$ in

the case of c-limitation is given as:

$$VNUP = \max\left(0, \frac{GPP + \text{labile.c}}{cndemand} \left(2 - \frac{cnsupply}{cndemand}\right) - \text{labile.n}\right). \quad (23)$$

This method of downregulation, of both GPP and $VNUP$, is similar to that used in past versions of the TEM for downregulating $VNUP$, but differs significantly due to the inclusion of a labile carbon pool in the TEM-Hydro. We have attempted to maintain parallelism between the element cycles by downregulating uptake of carbon and nitrogen in a similar fashion.

5 Respiration

Respiration is divided among growth and maintenance rates. Growth respiration is assumed to equal 25% of the total carbon allocated to new tissue (see §7), and maintenance rates are based on temperature and tissue nitrogen:

$$\begin{aligned} RMLEAF &= K_r \times f_{rmt} \times \text{leaf.c}/c\text{nleaf} \\ RMSTEM &= K_r \times f_{rmt} \times f_{\text{live}} \times \text{stema.c}/c\text{nstem} \\ RMROOT &= K_r \times f_{rmt} \times \text{root.c}/c\text{nroot} \\ RMLABILE &= K_r \times f_{rmt} \times \text{labile.c}/c\text{nalloc}, \end{aligned} \quad (24)$$

where K_r is a calibrated, PFT-dependent coefficient, f_{live} is the fraction of active stem tissue that is living, $c\text{nalloc}$ is the allocation-weighted average C:N of structural tissue. The temperature-dependence of respiration is given by f_{rmt} :

$$f_{rmt} = \frac{[Q_{ref} \times e^{-\alpha(T-T_{ref})}]^{\frac{T-T_{ref}}{10}} / [1 + e^{(\beta-T)} + e^{(T-\gamma)}]}{[Q_{ref} \times e^{-\alpha(T_{opt}-T_{ref})}]^{\frac{T_{opt}-T_{ref}}{10}} / [1 + e^{(\beta-T_{opt})} + e^{(T_{opt}-\gamma)}]}, \quad (25)$$

where β (-5 °C) and γ (55 °C) are lower and upper temperatures for respiration (rates drop rapidly for $T < \beta$ or $T > \gamma$). The parameters Q_{ref} , α , T_{ref} , and T_{opt} are identical to those used in the temperature dependence of photosynthesis (eqn. 8). This function is based on the respiration formula from LaRS (Amthor, personal communication), and normalized to a value of unity at T_{opt} .

6 Litterfall

Litterfall and senescence rates for carbon are generally simple to calculate, as they are based on lifetime formulations:

$$\begin{aligned}
 LEAFLTRC &= leaf.c/\tau_{leaf} \\
 STEMALTRC &= stema.c/\tau_{stem} \\
 SENESC &= stema.c/\tau_{senes} \\
 STEMILTRC &= stemi.c/\tau_{stem} \\
 ROOTLTRC &= root.c/\tau_{root},
 \end{aligned} \tag{26}$$

where τ_{leaf} , τ_{stem} , and τ_{root} are, respectively, the leaf, whole-stem, and fine-root turnover times, and τ_{senes} is the characteristic time for the conversion of active stem tissue to inactive stem tissue. The case of cold-deciduous leaves is slightly more complicated, the value of τ_{leaf} takes different values during the summer and winter (12 months and 1/3 month, respectively – only the former value is listed in Table S1). The associated nitrogen fluxes are tied to the carbon fluxes via C:N ratios:

$$\begin{aligned}
 LEAFLTRN &= LEAFLTRC/cnleafltr \\
 NRESORBL &= LEAFLTRC/cnleaf - LEAFLTRN
 \end{aligned}$$

$$\begin{aligned}
STEMALTRN &= STEMALTRC/cnstem \\
STEMILTRN &= STEMILTRC/cnstem \\
SENESN &= SENESC/cnstem \\
ROOTLTRN &= ROOTLTRC/cnroot.
\end{aligned}
\tag{27}$$

7 Allocation

Allocation of labile carbon and nitrogen resources is strongly based on a cost:benefit analysis performed at each timestep: it is desirable from a carbon standpoint for the plant to add leaves if the expected marginal benefit (MB) exceeds the expected marginal cost (MC), where the plant’s “currency” is carbon. In other words, the model seeks to determine whether an investment of carbon in producing new leaves will return more carbon to the labile pool than it consumes. Allocation which occurs based on such a favorable cost:benefit analysis will be termed “investment-allocation.” Since investment-allocation successfully returns more than it consumes, there is also a need for another type of allocation, which occurs when the size of the labile carbon pool exceeds the allowed storage space in structural tissues. We refer to this brand of allocation as “windfall-allocation,” since it is the result of profits on the plant’s past investments, which cannot be accrued physically beyond a certain point.

First we will discuss the cost:benefit framework pertinent to investment-allocation. The benefits of leaf area are clear: larger leaf area means greater gross primary production (GPP), and thus greater total carbon gains. Thus, given a formula for GPP that depends on LAI , we consider the marginal benefit (MB) of added LAI to be equivalent to the partial derivative of GPP with respect to LAI :

$$MB = \frac{\partial GPP}{\partial LAI}
\tag{28}$$

Differentiating the expression for GPP is straightforward; we can simply eliminate the integral over LAI in equation 3, and evaluate the integrand f_{PAR} at the bottom of the canopy ($L = LAI$):

$$\frac{\partial GPP}{\partial LAI} = C_{max} \times f_T \times f_{H_2O} \times f_{C_a,D} \times f_{O_3} \times (f_{PAR(L)}|_{L=LAI}). \quad (29)$$

The costs of additional leaf area comprise both maintenance and construction. These costs are incurred both directly, due to the leaf tissue itself, and indirectly, due to any other plant tissue that is required to support the new leaves. The marginal maintenance and construction costs are termed MC_m and MC_c , respectively, and the direct and indirect components of each are distinguished by the further subscript d or i. The direct marginal cost of leaf maintenance is simply the derivative of $RMLEAF$ with respect to LAI , or using equations 4 and 24,

$$MC_{m,d} = \frac{K_r \times f_{rmt}}{sla \times cnleaf}. \quad (30)$$

Determining indirect costs of both maintenance and construction requires knowledge of how much root and stem allocation is associated with allocation to leaves. This amount of “associated” allocation is determined by the PFT-specific “allocation fractions”: p_{leafc} , p_{rootc} , and p_{stemc} . Due to the criterion that the allocation fractions must together sum to unity, determining the three fractions only requires two parameters: the leaf allocation fraction (p_{leafc}), and the ratio of stem to root allocation ($r_{stemc:rootc}$):

$$\begin{aligned} p_{rootc} &= (1 - p_{leafc}) \frac{1}{1 + r_{stemc:rootc}} \\ p_{stemc} &= (1 - p_{leafc}) \frac{r_{stemc:rootc}}{1 + r_{stemc:rootc}}. \end{aligned} \quad (31)$$

The indirect maintenance cost is then equal to the direct maintenance cost, multiplied by a lifetime-weighted ratio of nitrogen present in supporting tissue (active stem and roots) to

nitrogen present in leaves:

$$\begin{aligned}
MC_{m,i} &= MC_{m,d} \frac{NT_{stem} + NT_{root}}{NT_{leaf}} \\
NT_{stem} &= f_{live} \times p_{stemc} \times \tau_{stem} / cn_{stem} \\
NT_{root} &= p_{rootc} \times \tau_{root} / cn_{root} \\
NT_{leaf} &= p_{leafc} \times \tau_{leaf} / cn_{leaf}
\end{aligned} \tag{32}$$

The total marginal maintenance cost of added leaf area is thus:

$$MC_m = MC_{m,d} \left(1 + \frac{NT_{stem} + NT_{root}}{NT_{leaf}} \right) \tag{33}$$

with the lifetime-weighted nitrogen contents defined as above.

Leaves also have a construction cost – carbon used in leaf tissue is lost and cannot be used at another time by the plant, and allocation to leaves also requires additional allocation to support tissue. The direct construction cost of additional leaf area is equal to the carbon content of the additional leaves, plus the construction respiration cost (an extra 25 %). However, this is a one-time investment, and in order to compare it to the monthly benefits and costs above, the construction cost must be levelled by the expected leaf lifetime, in order to get a cost per month:

$$MC_{c,d} = \frac{1}{\tau_{leaf}} \frac{1.25}{sla}. \tag{34}$$

The construction costs of associated root and stem allocation are equal to the direct cost of leaf construction, multiplied by the ratios of root and stem carbon to leaf carbon:

$$MC_{c,i} = MC_{c,d} \frac{p_{rootc} + p_{stemc}}{p_{leafc}}. \tag{35}$$

Furthermore, since $p_{leafc} + p_{rootc} + p_{stemc} = 1$, the total marginal construction cost of leaf

tissue can be simplified to:

$$MC_c = MC_{c,d} \left(1 + \frac{p_{rootc} + p_{stemc}}{p_{leafc}} \right) = MC_{c,d} \frac{1}{p_{leafc}} \quad (36)$$

Nitrogen allocation does not occur in the same proportions as carbon allocation (eqn. 31) due to the fact that the C:N of the different structural compartments are not identical. Separate calculation of the nitrogen allocation fractions is required to compare the emptying rate of the labile carbon and nitrogen pools and ensure that neither is depleted below zero. Based on the carbon allocation fractions, and the C:N of different structural plant material, we can calculate nitrogen allocation fractions that sum to unity:

$$\begin{aligned} p_{leafn} &= \frac{p_{leafc}}{cn_{leaf}} \left(\frac{p_{leafc}}{cn_{leaf}} + \frac{p_{stemc}}{cn_{stem}} + \frac{p_{rootc}}{cn_{root}} \right)^{-1} \\ p_{stemn} &= \frac{p_{stemc}}{cn_{stem}} \left(\frac{p_{leafc}}{cn_{leaf}} + \frac{p_{stemc}}{cn_{stem}} + \frac{p_{rootc}}{cn_{root}} \right)^{-1} \\ p_{rootn} &= \frac{p_{rootc}}{cn_{root}} \left(\frac{p_{leafc}}{cn_{leaf}} + \frac{p_{stemc}}{cn_{stem}} + \frac{p_{rootc}}{cn_{root}} \right)^{-1}. \end{aligned} \quad (37)$$

Plant phenological class is allowed to fall into one of two categories, and has a strong influence on investment-allocation. Evergreen PFTs allow investment-allocation (though it does not necessarily occur) in all seasons, while cold-deciduous PFTs allow investment-allocation only in the warm season (defined as $T > T_{crit}$, where $T_{crit} = 8$ °C for temperate deciduous forests), and have stronger allocation to leaves early in the season. We indicate below the effect of phenology on allocation by using the binary variable ϕ , equal to 0 when investment-allocation is not allowed, and 1 when investment-allocation is allowed. Additionally, for the purposes of construction costs, the meaning of τ_{leaf} varies between phenological classes. For evergreen vegetation, τ_{leaf} is always equal to a nominal PFT-dependent value; for cold-deciduous vegetation, τ_{leaf} depends upon the expected time remaining in the growing season, based on a moving average of temperature patterns in previous growing seasons.

Investment-allocation is allowed only when both $MB > MC$ (where $MC = MC_m + MC_c$) and the PFT-dependent environmental rules are met. The fractional monthly rates of investment-allocation (indicated by the subscript I) from the labile carbon and nitrogen pools are set based on the net benefit:cost ratio, $(MB/MC - 1)$, phenology, and the allocation fractions for carbon and nitrogen (eqns. 31 and 37):

$$\begin{aligned}
ALLOCLC_I &= \phi \times p_{\text{leafc}} \times (MB/MC - 1) \times \text{labile.c} \\
ALLOCS_C_I &= \phi \times p_{\text{stemc}} \times (MB/MC - 1) \times \text{labile.c} \\
ALLOCR_C_I &= \phi \times p_{\text{rootc}} \times (MB/MC - 1) \times \text{labile.c} \\
ALLOCLN_I &= \phi \times p_{\text{leafn}} \times (MB/MC - 1) \times \text{labile.n} \\
ALLOCSN_I &= \phi \times p_{\text{stemn}} \times (MB/MC - 1) \times \text{labile.n} \\
ALLOCRN_I &= \phi \times p_{\text{rootn}} \times (MB/MC - 1) \times \text{labile.n}.
\end{aligned} \tag{38}$$

Total allocation is calculated based on these equations for investment, as well as windfall-allocation. In our model framework, stem and root tissues are considered to be storage spaces for labile carbon – if the mass of the labile carbon pool exceeds two thirds of the mass of the live stem and root pools, the windfall, W_c , is required to be immediately allocated:

$$W_c = \text{labile.c} - (2/3) \times (f_{\text{live}} \times \text{stema.c} + \text{root.c}) \tag{39}$$

Windfall-allocation C and N fractions for evergreen PFTs are identical to those for investment-allocation. For cold-deciduous PFTs, though, no windfall is allocated to leaves, since a surplus of labile carbon tends to occur near the end of the growing period, when senescence is imminent and allocation to new leaves is not observed. We define the windfall-allocation fractions ($p_{\text{leafc,W}}, p_{\text{stemc,W}}, p_{\text{rootc,W}}, p_{\text{leafn,W}}, p_{\text{stemn,W}}, p_{\text{rootn,W}}$) as identical to the allocation fractions from eqns. 31 and 37 for evergreen PFTs, and calculated from those equations using

$p_{\text{leafc}} = 0$ for cold-deciduous PFTs. Then, windfall-allocation (indicated by subscript W) is given as:

$$\begin{aligned}
ALLOCLC_W &= p_{\text{leafc},W} \times W_c \\
ALLOCSW &= p_{\text{stemc},W} \times W_c \\
ALLOCRW &= p_{\text{rootc},W} \times W_c \\
ALLOCLN_W &= p_{\text{leafn},W} \times W_c \times (\text{labile.n}/\text{labile.c}) \\
ALLOCSN_W &= p_{\text{stemn},W} \times W_c \times (\text{labile.n}/\text{labile.c}) \\
ALLOCRN_W &= p_{\text{rootn},W} \times W_c \times (\text{labile.n}/\text{labile.c}).
\end{aligned} \tag{40}$$

While we do not explicitly model an upper limit for nitrogen-storage in the labile pool, the term $W_c \times (\text{labile.n}/\text{labile.c})$ ensures that the “extra” nitrogen available for windfall-allocation represents the same fraction of the labile nitrogen pool as windfall carbon represents of the labile carbon pool.

Total allocation is based on the sum of investment-allocation (eqn. 38), windfall-allocation (eqn. 40), and maintenance respiration (eqn. 24):

$$\begin{aligned}
ALLOCLC &= \min(ALLOCLC_{I+W}, ALLOCLN_{I+W} \times \text{cnleaf}) + RMLEAF \\
ALLOCSW &= \min(ALLOCSW_{I+W}, ALLOCSN_{I+W} \times \text{cnstem}) + RMSTEM \\
ALLOCRW &= \min(ALLOCRW_{I+W}, ALLOCRN_{I+W} \times \text{cnroot}) + RMROOT \\
ALLOCLN &= \min(ALLOCLN_{I+W}, ALLOCLC_{I+W}/\text{cnleaf}) \\
ALLOCSN &= \min(ALLOCSN_{I+W}, ALLOCSW_{I+W}/\text{cnstem}) \\
ALLOCRN &= \min(ALLOCRN_{I+W}, ALLOCRW_{I+W}/\text{cnroot}).
\end{aligned} \tag{41}$$

Here, due to space considerations, terms with summed subscripts denote the sum of the terms

indicated by each individual subscript (e.g. $ALLOCLC_{I+W} = ALLOCLC_I + ALLOCLC_W$). The *min* functions are used to ensure that allocation is regulated by the size of both the labile carbon and nitrogen pools, and to ensure that allocation occurs in the required C:N for each structural compartment. Allocation also is used to shift labile carbon into the structural pools to pay for maintenance respiration costs. So the terms $RMLEAF$, $RMSTEM$, and $RMROOT$ do not affect the size of the leaf, stem, or root pools, since an identical carbon flux is being concurrently removed from the structural pools as maintenance respiration. Growth respiration is assumed equal to 1/4 of the carbon allocated to new tissue:

$$RGRWTH = 0.25 \times (ALLOCLC + ALLOCSC + ALLOCRS - RMLEAF - RMSTEM - RMROOT). \quad (42)$$

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