

# 1 TEM-Hydro Appendix

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3 The TEM-Hydro is a model of water, carbon, and nitrogen cycling in terrestrial ecosys-  
4 tems. It is grounded within the framework of the previous biogeochemical model TEM  
5 4.3 (Raich et al., 1991, Tian et al., 1999, Felzer et al., 2004). This version of the Terres-  
6 trial Ecosystem Model represents carbon and nitrogen in vegetation with multiple pools or  
7 “boxes” to refine water-carbon linkages within the model. Below, we describe how vegeta-  
8 tion carbon and nitrogen dynamics are simulated in the new version. In Table A1, we give  
9 parameter values for the model as calibrated to temperate deciduous and coniferous forests.  
10 Carbon and nitrogen dynamics of soil microbes remain the same as in previous versions of  
11 the TEM.

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

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

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

## 35 1 Carbon and Nitrogen Fluxes

36 The governing differential equations for vegetation carbon are as follows:

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

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

43 represented by *LEAFLTRC* (leaf), *STEMALTRC* (active stem), *STEMILTRC* (inactive  
 44 stem), and *ROOTLTRC* (fine roots). Finally, inactive stem carbon is assumed to only in-  
 45 crease due to senescence from the active stem pool (*SENEC*) – there is no direct allocation  
 46 to the pool.

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

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

50 In the above, *VNUP* is the rate of vegetation nitrogen uptake, and *ALLOCLN*, *ALLOCSN*,  
 51 and *ALLOCRN* are nitrogen allocation rates to leaves, active stem, and fine roots, respec-  
 52 tively. There is no direct analogue for respiration in the nitrogen cycle, but there is an  
 53 additional resorption flux (*NRESORBL*), whereby dying leaves can transfer some of their  
 54 nitrogen back to the labile pool. Structural components lose nitrogen mainly via litter-  
 55 fall/mortality: *LEAFLTRN* (leaf), *STEMALTRN* (active stem), *STEMILTRN* (inac-  
 56 tive stem), and *ROOTLTRN* (fine roots). Finally, there is a similar senescence flux of  
 57 nitrogen (*SENEC*) from the active to inactive stem pool.

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

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

## 64 2 Photosynthesis

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

$$g_c = gs_{min} \times LAI + gs_a \frac{GPP \times f_D}{C_a}$$

$$g_s = g_c / LAI, \quad (11)$$

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

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

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

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

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

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

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

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

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

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

### 136 3 Nitrogen Uptake

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

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

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



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

## 152 4 Downregulation of Photosynthesis and 153 Nitrogen Uptake

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

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

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

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

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

165 is given as:

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

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

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

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

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

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

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

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

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

181 the case of c-limitation is given as:

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

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

## 187 5 Respiration

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

$$\begin{aligned} RMLEAF &= K_r \times f_{rmt} \times leaf.c/cnleaf \\ RMSTEM &= K_r \times f_{rmt} \times f_{live} \times stema.c/cnstem \\ RMROOT &= K_r \times f_{rmt} \times root.c/cnroot \\ RMLABILE &= K_r \times f_{rmt} \times labile.c/cnalloc, \end{aligned} \quad (24)$$

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

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

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

## 199 **6 Litterfall**

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

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

202 where  $\tau_{leaf}$ ,  $\tau_{stem}$ , and  $\tau_{root}$  are, respectively, the leaf, whole-stem, and fine-root turnover  
 203 times, and  $\tau_{senes}$  is the characteristic time for the conversion of active stem tissue to inactive  
 204 stem tissue. The case of cold-deciduous leaves is slightly more complicated, the value of  $\tau_{leaf}$   
 205 takes different values during the summer and winter (12 months and 1/3 month, respectively  
 206 – only the former value is listed in Table A1). The associated nitrogen fluxes are tied to the  
 207 carbon fluxes via C:N ratios:

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

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

## 208 7 Allocation

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

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

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

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

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

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

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

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

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

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

243 nitrogen present in leaves:

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

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

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

245 with the lifetime-weighted nitrogen contents defined as above.

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

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

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

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

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

256 tissue can be simplified to:

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

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

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

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



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

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

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

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

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

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

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

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

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

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

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

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

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

306

## Table A1: TEM-Hydro Vegetation Parameters

307

Parameter	Deciduous Forest	Coniferous Forest	Units	Source
$C_{max}$	22.53	14.67	$\mu\text{mol m}^{-2} \text{s}^{-1}$	calibrated
$sla$	0.0242	0.00863	$\text{m}^2 \text{gC}^{-1}$	Schulze et al., 1994
$T_{min}$	0	-1	$^{\circ}\text{C}$	Tian et al., 1999
$T_{max}$	34	34	$^{\circ}\text{C}$	Tian et al., 1999
$k_c$	200	200	ppmv $\text{CO}_2$	Sokolov et al., 2008
$k_I$	36.3	36.3	$\text{W m}^{-2}$	Raich et al., 1991
$\tau_{O_3}$	12	12	months	estimated
$\alpha_{O_3}$	$2.6 \times 10^{-6}$	$0.7 \times 10^{-6}$	damage per exposure	Felzer et al., 2004
$N_{max}$	356.0	231.0	$\text{gN m}^{-2} \text{month}^{-1}$	calibrated
$k_{N1}$	0.0042	0.0042	$\text{gN kgH}_2\text{O}^{-1}$	Tian et al., 1999
$k_{rnup}$	128.3	97.4	$\text{g rootC m}^{-2}$	calculated from avg. root C
$K_r$	0.127	0.136	$\text{gC gN}^{-1}$ at $T_{opt}$	calibrated
$cnleaf$	23.8	47.5	$\text{gC gN}^{-1}$	Magill et al., 1997
$cnstem$	300	500	$\text{gC gN}^{-1}$	estimated
$cnroot$	44.6	57.7	$\text{gC gN}^{-1}$	McClaugherty et al., 1982
$cnleafltr$	57.3	48.8	$\text{gC gN}^{-1}$	calibrated
$flive$	0.17	0.07	fraction	Friend et al., 1997
$\tau_{leaf}$	12	24	months	Kucharik et al., 2000
$\tau_{root}$	12	12	months	Kucharik et al., 2000
$\tau_{stem}$	66.76	64.3	years	calibrated
$\tau_{senesc}$	10	10	years	estimated
$p_{leafc}$	0.59	0.42	fraction	calibrated
$r_{stemc:rootc}$	0.934	0.779	ratio	McClaugherty et al., 1982

308

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