**MEL model description**

The Multiple Element Limitation (MEL) model has been used to study the recovery of northern hardwood forests from harvest (Rastetter et al. 2013) and the recovery of arctic tundra from thermokarst mass wasting (Pearce et al. 2015) and from tundra fire (Jiang et al. 2015). The MEL model couples ecosystem C, N, P, and water cycles and generates output for all stocks and fluxes on a daily time step. The differential equations that describe the mass balance for each of the simulated components of the ecosystem are solved numerically using a 4th-5th order Runge-Kutta integrator with an adaptive time-step size to optimize precision and computation time (Press et al. 1986). The model is coded in Lazarus 2.0.4 (2019) Free Pascal and runs on a PC or Mac computer. The full model source code is available on github.

The stoichiometry of vegetation and soils change in response to changes in the environment and to feedbacks associated with the element and water cycles. The unique approach offered by this model is the continuous adjustment of resource-acquisition potential as the vegetation requirements for resources and their availability in the environment change (Rastetter and Kwiatkowski 2020).

Version VI of the MEL model includes improvements to the plant resource acquisition algorithm described in Rastetter et al. (2013) for version IV. The major modification in version VI is a hierarchical allocation scheme for resource-acquisition effort (Rastetter and Kwiatkowski 2020). We define effort allocated toward a particular resource as the fraction of all vegetation assets (e.g., leaf-root tissue distribution, enzyme production, carbohydrate expenditure) that can be allocated toward the acquisition of resources from the environment. We assume that these assets increase as biomass increases and can be incrementally reallocated among resources. All else being equal, resource acquisition increases monotonically both with biomass and with the effort allocated toward that resource.

This effort is partitioned into primary efforts allocated toward the acquisition of C, N, or P; the sum of these primary efforts is 1. The C effort is further partitioned into sub-efforts allocated toward the acquisition of the interdependent resources CO2, light, and water; the sum of these three sub-efforts is again 1 and the ensuant effort allocated toward each resource is the product of the primary C effort and the sub-effort. The resultant C uptake is the minimum of the CO2-limited, light-limited, or water-limited photosynthesis (Rastetter and Kwiatkowski 2020). Similarly, the N effort is partitioned into sub-efforts allocated toward the acquisition of substitutable N resources ammonium (NH4), nitrate (NO3), dissolved organic N (DON, assumed part of Phase I SOM), or symbiotic N fixation; these four sub-efforts also sum to 1. The resultant N uptake is the sum over these four N sources (Rastetter and Kwiatkowski 2020). Although there are also several sources of P available to the vegetation, an algorithm analogous to the N algorithm for substitutable sources of P has not been developed for the MEL model, nor are the data needed to implement such an algorithm available for most of the sites in our analysis. Therefore, the P effort is all allocated toward the acquisition of phosphate (PO4), which we assume represents the aggregate acquisition from all P sources.

Because assets available for resource acquisition are limited, an incremental increase in the effort allocated toward one resource must be compensated by incremental decreases in the allocation toward other resources. Reallocation of effort between canopy and soil resources results in commensurate changes in leaf and fine root biomass and consequently in leaf-area index (LAI) and fine-root length per unit ground surface. Primary effort is reallocated among C, N, or P based on the ratio of element requirement to element uptake. The requirement is the amount of the element needed to replace losses in respiration and tissue turnover plus make up for prior shortages or surfeits as reflected in the C:N:P ratio of the biomass relative to an allometrically scaled, optimum C:N:P ratio. In the allocation algorithm, both the requirement and uptake are time-averaged to account for seasonal differences between the timing of uptake and loss.

The sub-efforts are allocated based on the incremental increase in uptake per incremental increase in effort allocated (i.e., marginal yield). For the C sub-efforts, the marginal yield is simply the derivative of C uptake with respect to the sub-effort. Thus, the sub-effort is allocated toward the most limiting among CO2, light, and water and results in the highest gain in C per unit effort. For the N sub-efforts, the marginal yield also accounts for the energy cost of the various N sources (e.g., carbohydrate supply to N-fixing symbiont) and the effort needed to acquire the C to pay that cost. Thus, the marginal yield for an N source includes the derivative of N uptake with respect to the allocated sub-effort, the C cost of that N source, and the derivative of C uptake with respect to the primary C effort. All C costs for the N sources are assessed relative to NH4; thus, the NH4 cost is 0 g C g-1 N, the NO3 cost is 2.1 g C g-1N, the DON cost is 3 g C g-1 N, and the symbiotic N fixation cost is 6.4 g C g-1 N (Connor et al. 2011).

We partition vegetation biomass allometrically between woody and active tissues ("active" meaning active in resource acquisition). We further partition the active tissue into leaves and fine roots based on the relative limitation by canopy versus soil resources. The C, N, and P are partitioned among tissues stoichiometrically. Changes in leaf biomass and LAI are based on the degree-day sums in the spring and by day of year in the fall. As indicated above, we assume that photosynthesis is co-limited by CO2, light, and water, that vegetation potentially makes use of NH4, NO3, DON, and symbiotic N fixation, and the only source of P to vegetation is PO4.

Photosynthesis is a unimodal function of daily average air temperature, increasing toward an optimum then declining to zero at a maximum temperature. Respiration for leaves and woody tissues increase exponentially with average daily air temperature (Q10 function). Root respiration, nutrient uptake rates, and symbiotic N fixation increase exponentially with soil temperature. Soil temperature is calculated based on an energy budget like that in Pearce et al. (2015) with a soil heat capacity dependent on soil moisture content. Soil temperature generally follows air temperature, but is cooler in the summer, warmer in the winter, with more damped dynamics, and long periods at 0 oC during periods of freeze and thaw (Fig. 2).

We partition dead organic matter and associated biota into Phase I and Phase II soil organic matter (SOM; Melillo et al. 1989) and detritus, but do not partition soil into vertical layers. For most of the ecosystems, this detritus is composed of standing dead and coarse woody debris. For prairie ecosystems, detritus includes standing dead leaves and stems. The detritus has a constant stoichiometry and does not decompose directly but instead serves as a time-lag storage that is slowly converted to Phase I SOM where it subsequently decomposes (Hyvönen and Ågren 2001). Phase I SOM represents the young, more active organic matter including aboveground litter and dead roots. It implicitly includes microbial biomass, mineralizes and immobilizes nutrients, and has a flexible C:N:P ratio. Phase II SOM does not immobilize nutrients but continues to mineralize nutrients and has a rate of respiration per unit SOM that is less than that for Phase I SOM. Microbial processing of both Phase I and II SOM increases exponentially with soil temperature (Q10 function) and increases with moisture toward an optimum, then declines as moisture increases above the optimum to account for metabolic inhibition with lower oxygen supply.

Nitrogen and P enter the ecosystem via atmospheric deposition of NH4, NO3¸ PO4, and DON and, in the arctic wet-sedge tundra (ARC-w), via a prescribed rate of hydrologic transport from upland areas. Nitrogen also enters through symbiotic and non-symbiotic N fixation. Phosphorus also enters through weathering of primary and secondary P minerals. We partition the mineral ions into dissolved and adsorbed fractions based on Langmuir isotherms (Weatherley and Miladinovic 2004) and only the dissolved fraction is available for uptake by vegetation and Phase I microbes, for nitrification or denitrification, or to be lost through leaching with soil water. Leaching losses of the ions are proportional to both their concentration in soil water and to losses of water through drainage from the rooting zone. We assume vegetation uptake and leaching of DON are directly from the Phase I SOM and the leaching losses are proportional to Phase I C and N and to water drainage from the rooting zone. For arctic wet-sedge tundra (ARC-w) we simulate run-in from the surrounding watershed of water, NH4, NO3, PO4, dissolved organic C (DOC), and DON based on the simulated losses from the tussock tundra (ARC-t). If the run-in results in soil water exceeding soil porosity, then the excess run-in water and all dissolved material in that run-in simply bypasses the ecosystem.

For all sites, we partition precipitation into intercepted water, snow (if any), and rain. We assume intercepted water evaporates. We add precipitation in excess of the interception maximum for each day either to the snowpack or to the soil water, depending on air temperature (Brubaker et al. 1996). We calculate snowmelt based on net radiation to the snowpack and air temperature (Brubaker et al. 1996). The rate of runoff (soil-water drainage & deep percolation) is proportional to the volume of soil water in excess of field capacity and soil water can take several days to drain to field capacity following heavy rain or snowmelt. We calculate soil water potential based on equations from Clapp and Hornberger (1978). When water is not limiting, water uptake and transpiration depend on leaf area and on canopy CO2 and light limitation (Rastetter and Kwiatkowski 2020). When water is limiting, soil water uptake and transpiration by plants depend on leaf area and is proportional to the soil water potential above the wilting potential and to an index of the daily vapor pressure deficit calculated as the difference between saturation vapor pressure at the daily maximum and minimum temperatures.

Snowpack dynamics were solved with a discrete daily time step as described in Brubaker et al. (1996). Snowmelt and rainfall were added to the soil water on a discrete daily time step. All other differential equations were solved with a 4th/5th order Runge-Kutta numerical integrator with a variable time step to assure accuracy (Press et al. 1986).

**Table S1:** Equations of the MBL MEL VI model. Symbol definitions and units for all variables are listed in Table S2. Equations are grouped into general categories; the same categories are used in Table S2.

|  |  |  |  |
| --- | --- | --- | --- |
| **Mass balance Equations** | | | |
|  | **Carbon** | | |
| (1) |  | | |
| (2) |  | | |
| (3) |  | (4) |  |
|  | | | |
|  | **Nitrogen** | | |
| (5) |  | | |
| (6) |  | | |
| (7) |  | (9) |  |
| (10) |  | | |
| (11) |  | | |
|  | | | |
|  | **Phosphorus** | | |
| (12) |  | (13) |  |
| (14) |  | (15) |  |
| (16) |  | (17) |  |
| (18) |  |  |  |
| (20) |  | | |
|  | | | |
|  | **Water** | | |
| (21) |  | | |
| (22) |  | | |
|  | | | |
|  | **Other** | | |
| (23) |  | | |
| (24) |  | (25) | *j* = C, N, or P |
| (26) | *j* = C or N  *k* = sub-effort for resource *j* | (27) | *fc* constrained between *fcmin* and 1 |
| (28) | *j* = C, N, or P | (29) | *j* = C, N, or P |
| (30) |  | | |
|  | | | |
|  | **Environment** (equations for ENH4, ENO3, and EPO4 must be inverted to calculate aqueous concentrations) | | |
| (31) |  | | |
| (32) |  | | |
| (33) |  | (34) |  |
| (35) |  | | |
| (36) |  | (37) |  |
| (38) |  | (39) |  |
| (40) |  | (41) |  |
| (42) |  | (43) |  |
| (44) |  | (45) |  |
| (46) |  | (47) |  |
| (48) |  | | |
| (49) |  | (50) |  |
| (51) |  | (52) |  |
| (53) |  | (54) |  |
|  | | | |
|  | **Allometry** (equations for Bt\* and Ba must solved simultaneously) | | |
| (55) |  | (56) |  |
| (57) |  | (58) | for each year |
| (59) |  | (60) |  |
| (61) |  | (62) |  |
| (63) |  | (64) |  |
| (65) |  | (66) |  |
| (67) |  | (68) | for each year |
| (69) |  | (70) |  |
| (71) |  | (72) |  |
|  | | | |
|  | **Canopy Phenology**: | | |
| (73) |  | (74) |  |
| (75) |  | | |
| (76) |  | | |
|  | | | |
|  | **Photosynthesis and Transpiration** | | |
| (77) |  | (78) |  |
| (79) |  | | |
| (80) |  | | |
| (81) |  | | |
| (82) |  | (83) |  |
| (84) |  | (85) |  |
| (86) |  | | |
| (87) |  | | |
|  | | | |
|  | **Plant Respiration and Net Primary Production** | | |
| (88) |  | | |
| (89) |  | | |
| (90) |  | (91) |  |
|  | | | |
|  | **Plant Nutrient Uptake** (paired equations must be solved simultaneously) | | |
| (92) |  | (93) |  |
| (94) |  | (95) | *j*=NH4, and NO3 |
| (96) |  | | |
| (97) |  | | |
| (98) |  | (99) |  |
|  | | | |
|  | **Litter Losses** | | |
| (100) |  | (101) |  |
| (102) |  | (103) |  |
| (104) |  | | |
| (105) |  | | |
| (106) |  | | |
| (107) |  | (108) |  |
| (109) |  | (110) |  |
|  | | | |
|  | **Resource Requirement** | | |
| (111) |  | | |
| (112) |  |  |  |
| (113) |  | (114) |  |
| (115) |  | (116) |  |
|  | | | |
|  | **Plant acclimation** | | |
| (117) | *j* = C, N, or P | (118) | *j* = C, N, & P |
| (119) |  | | |
| (120) |  | (121) |  |
| (122) | *k* = NH4, NO3, doN or Nfix | (123) | *k* = CO2, I, W, NH4, NO3, doN, andNfix  *j* = C when *k*=CO2 I, orW  *j* = N when *k* = NH4, NO3, doN, orNfix |
| (124) | and  *j* = C, N, or P | | |
| (125) | and  *k* = CO2, I, and W for C or NH4, NO3, doN, andNfix for N | | |
|  | | | |
|  | **Hydrology** | | |
| (126) |  | (127) |  |
| (128) |  | | |
| (129) |  | | |
| (130) |  | (131) |  |
| (132) |  | | |
| (133) |  | (134) |  |
| (135) |  | | |
| (136) |  | (137) |  |
| (138) |  | (139) |  |
| (140) |  | (141) |  |
| (142) |  | (143) |  |
| (144) |  | (145) |  |
| (146) |  | (147) |  |
|  | | | |
|  | **Microbial Processes** | | |
| (148) |  | | |
| (149) | *j* = C, N, or P | (150) | *j* = C, N, or P |
| (151) |  | (152) | *j* = N or P |
| (153) |  | (154) |  |
| (155) |  | | |
| (156) |  | | |
| (157) |  | (158) |  |
| (159) |  | (160) | *j* = N or P |
| (161) |  | (162) | *j* = NH4 or NO3 |
| (163) |  | (164) |  |
| (165) |  | (166) | *j* = C, N, or P |
|  | | | |
|  | **Soil Phosphorus Transformations** | | |
| (167) |  | (168) |  |
| (169) |  | (170) |  |
| (171) |  |  |  |
|  | | | |
|  | **Fire**  All fire equations are zero unless the simulation year is a multiple of fire interval (*FI*) and the day of the year is the fire day of the year (*DOYfire*) | | |
| (172) |  | (173) |  |
| (174) |  | (175) |  |
| (176) |  | (177) |  |
| (178) |  | (179) |  |
| (180) |  |  |  |
| (181) |  | (182) |  |
| (183) |  | (184) |  |
|  | | | |
|  | **Summary Variables** | | |
| (185) |  | | |
| (186) |  | | |
| (187) |  | | |
| (188) |  | (189) |  |
| (190) |  | (191) |  |
| (192) |  | (193) |  |
| (194) | + | (195) |  |
| (196) |  | (197) |  |
| (198) |  | (199) |  |

**Table A2:** Variable names and units of the Multiple Element Limitation (MEL) model. The state variables are listed first then the processes and parameters listed by category they are first used in Table A1.

|  |  |  |  |
| --- | --- | --- | --- |
| **Description** | **Symbol** | **Units** | **Equation Number or Parameter Value** |
| ***State Variables:*** | | | |
| Biomass carbon | *BC* | g C m-2 | Calculated from initial value and the differential equation (Eq 1-30). The initial values vary by site. |
| Biomass nitrogen | *BN* | g N m-2 |
| Biomass phosphorus | *BP* | g P m-2 |
| Woody debris carbon | *WC* | g C m-2 |
| Woody debris nitrogen | *WN* | g N m-2 |
| Woody debris phosphorus | *WP* | g P m-2 |
| Phase I soil organic carbon | *DC* | g C m-2 |
| Phase I soil organic nitrogen | *DN* | g N m-2 |
| Phase I soil organic phosphorus | *DP* | g P m-2 |
| Phase II soil organic carbon | *SC* | g C m-2 |
| Phase II soil organic nitrogen | *SN* | g N m-2 |
| Phase II soil organic phosphorus | *SP* | g P m-2 |
| Soil NH4 (sorbed + dissolved) | *ENH4* | g N m-2 |
| Soil NO3 (sorbed + dissolved) | *ENO3* | g N m-2 |
| Soil PO4 (sorbed + dissolved) | *EPO4* | g P m-2 |
| Primary mineral phosphorus | *Pa* | g P m-2 |
| Non-occluded phosphorus | *Pno* | g P m-2 |
| Occluded phosphorus | *Poccl* | g P m-2 |
| Soil water | *W* | mm H2O |
| Snowpack | *Wsnow* | mm H2O |
| Soil heat index | *SQ* | arbitrary |
| Carbon effort | *VC* | fraction |
| Nitrogen effort | *VN* | fraction |
| Phosphorus effort | *VP* | fraction |
| CO2 sub effort | *vCO2* | fraction |
| Water sub effort | *vW* | fraction |
| Light sub effort | *vI* | fraction |
| NH4 sub effort | *vNH4* | fraction |
| NO3 sub effort | *vNO3* | fraction |
| doN sub effort | *vdoN* | fraction |
| Nitrogen fixation sub effort | *vNfix* | fraction |
| Canopy fraction | *fc* | unitless |
| Average requirement for *j*, *j*= C, N, P | *Raj* | g *j* m-2 day-1 |
| Average acquisition for *j*, *j*= C, N, P | *Uaj* | g *j* m-2 day-1 |
| Positive degree day | *Ddayp* | °C |
| Negative degree day | *Ddayn* | °C |
| ***Driving Variables:*** | | | |
| Atmospheric CO2 | *Ca* | mol mol-1 | Values vary with site and time. Calibration values are listed in the driver file. |
| Daily total short-wave radiation | *Isw* | MJ m-2 day-1 |
| Daily air temperature minimum | *Tmin* | °C |
| Daily air temperature maximum | *Tmax* | °C |
| Precipitation | *Ppt* | mm H2O day-1 |
| NH4 input | *INH4* | g N m-2 day-1 |
| NO3 input | *INO3* | g N m-2 day-1 |
| PO4 input | *IPO4* | g P m-2 day-1 |
| Dissolved organic carbon input | *IdoC* | g C m-2 day-1 |
| Dissolved organic nitrogen input | *IdoN* | g N m-2 day-1 |
| Apatite input | *IPa* | g P m-2 day-1 |
| Run in | *Rin* | mm H2O day-1 |
| doC in run in | *IRindoC* | g C m-2 day-1 |
| doN in run in | *IRindoN* | g N m-2 day-1 |
| NH4 in run in | *IRinNH4* | g N m-2 day-1 |
| NO3 in run in | *IRinNO3* | g N m-2 day-1 |
| PO4 in run in | *IRinPO4* | g P m-2 day-1 |
| ***Fluxes and Parameters*** | | | |
| ***Environment:*** | | | |
| Simulation time | *t* | day | Varies |
| Day of year | *Doy* | day | Eq. 31 |
| Day of year divisor, use for leap year | *DoyD* | day | 365 |
| Time offset | *Tly* | day | 0 |
| Daylength | *Dl* | hr | Eq 32 |
| Latitude | *lat* | decimal degrees | varies by site |
| Daily average air temperature | *Ta* | °C | Eq. 33 |
| Daily average surface soil temperature | *Ts* | °C | Eq. 44 |
| Daily average snow temperature | *Tsnow* | °C | Eq. 45 |
| Volumetric water content | ** | mm mm-1 soil | Eq. 34 |
| Rooting depth | *z0* | m | varies by site |
| Soil porosity | *js* | volume fraction | varies by site |
| Dryness index | *e* | MPa | Eq 36 |
| Soil volume per unit carbon | *VpC* | m3 g-1 C | Eq. 53 |
| Initial depth of organic layer | *Dop0* | m | varies by site |
| Initial soil organic carbon | *SoC0* | g C m-2 | varies by site |
| Depth of organic layer | *Dop* | m | Eq. 54 |
| Depth of thaw | *Dot* | m | Eq. 35 |
| Initial surface temperature in depth of thaw model | *Tsb* | °C | varies by site |
| Initial surface soil moisture in depth of thaw model | *qb* | m water m-1 pore space | varies by site |
| Depth of thaw fit parameter | *x1* | m pore space m-1 water | -0.37 (Biesinger et al., 2007) |
| Depth of thaw fit parameter | *x2* | °C-1 | 0.62 (Biesinger et al., 2007) |
| Depth of thaw fit parameter | *x3* | m ground °C -1 | 0.01 (Biesinger et al., 2007) |
| Depth of thaw fit parameter | *x4* | m ground | 0.27 (Biesinger et al., 2007) |
| Depth of thaw fit parameter | *x5* | m ground °C -1 | 2.10 (Biesinger et al., 2007) |
| Upward thaw conductivity | *kst* | heat °C-1 | Eq. 39 |
| Unfrozen soil fraction | *fuf* | fraction | Eq. 37 |
| Upward frozen conductivity | *ksf* | heat °C-1 | Eq. 40 |
| Upward conductivity | *ks* | heat °C-1 | Eq. 41 |
| Water heat conductivity | *kW* | heat °C-1 | 0.005 |
| Organic soil heat conductivity | *kso* | heat °C-1 | 0.012 |
| Mineral soil heat conductivity | *ksm* | heat °C-1 | 0.024 |
| Zero low limit | *Ql* | heat | 373.15 |
| Zero high limit | *Qh* | heat | 400 |
| Thaw heat capacity | *aQh* | heat °C -1 | Eq. 43 |
| Frozen heat capacity | *aQl* | heat °C -1 | Eq. 42 |
| Heat capacity of water | *cW* | heat °C -1 | 4.2 |
| Heat capacity of organic soil | *cso* | heat °C -1 | 0.58 |
| Heat capacity of mineral soil | *csm* | heat °C -1 | 3.28 |
| Air entry water content | *i* | mm mm-1 soil | Eq. 46 |
| Water content at field capacity for plants | *fp* | mm mm-1 soil | varies by site |
| Wilting point water content | *w* | mm mm-1 soil | varies by site |
| Soil water potential | *s* | MPa | Eq. 48 |
| Water potential at field capacity | *f* | MPa | -0.01 |
| Water potential at wilting | *w* | MPa | -1.5 |
| Water potential at air entry | *i* | MPa | Eq. 46 |
| Bulk density | *s* | Mg soil m-3 | varies by site |
| Dissolved NH4 | *NNH4aq* | mol N L-1 | Eq. 49 |
| Dissolved NO3 | *NNO3aq* | mol N L-1 | Eq. 50 |
| Dissolved PO4 | *PPO4aq* | mol P L-1 | Eq. 51 |
| Soil NH4 sorption capacity | *SNH4* | g N Mg-1 soil | 402 |
| Soil NH4 affinity constant | *NH4* | mol N L-1 | 786 |
| Soil NO3 sorption capacity | *SNO3* | g N Mg-1 soil | 10 |
| Soil NO3 affinity constant | *NO3* | mol N L-1 | 300 |
| Soil PO4 sorption capacity | *SPO4* | g P Mg-1 soil | 62 |
| Soil PO4 affinity constant | *PO4* | mol P L-1 | 150 |
| Internal temporary variables used to simplify the code | *b, C* |  | Eq. 38 & 47 |
| Plant available doC | *PadoC* | mol C L-1 | Eq. 52 |
| Dissolved organic C fraction | *bdoC* | g C m-2 | ?? |
| C:N of plant available dom | *qdom* | g C g-1 N | 3.7 |
| ***Allometry:*** | | | |
| Total biomass | *Bt* | g DW m-2 | Eq. 57 |
| Total biomass with full canopy | *Bt\** | g DW m-2 | Eq. 60 |
| Active biomass | *Ba* | g DW m-2 | Eq. 59 |
| Leaf biomass | *BL* | g DW m-2 | Eq. 61 |
| Wood biomass | *BW* | g DW m-2 | Eq. 63 |
| Root biomass | *BR* | g DW m-2 | Eq. 65 |
| Leaf effort | *VL* | fraction | Eq. 55 |
| Root effort | *VR* | fraction | Eq. 56 |
| Plant C:DW ratio | *sC* | g C g-1 DW | 0.475 |
| Maximum active biomass | *Bamax* | g DW m-2 | varies by site |
| Ba:Bt slope | *B* | unitless | 0.92 |
| Allometric parameter | *B* | unitless | 0.95 |
| Leaf area index | *L* | m2 m-2 | Eq. 62 |
| Leaf area index at current active biomass assuming a full canopy | *Lmax* | m2 m-2 | Eq. 66 |
| LAI at peak season | *Lpeak* | m2 m-2 | Eq. 68 |
| Shading index of standing dead | *SW* | m2 m-2 | varies by site |
| Specific leaf area | *asla* | m2 g-1 DW | varies by site |
| Root length | *Rl* | m m-2 soil | Eq. 67 |
| Specific root length | *asRl* | m g-1 DW | varies by site |
| Optimum plant N concentration | *sN* | g N g-1 DW | Eq. 70 |
| Optimum plant P concentration | *sP* | g P g-1 DW | Eq. 72 |
| Actual plant N concentration | *sNa* | g N g-1 DW | Eq. 69 |
| Actual plant P concentration | *sPa* | g P g-1 DW | Eq. 71 |
| Leaf N:DW | *sNL* | g N g-1 DW | varies by site |
| Wood N:DW | *sNW* | g N g-1 DW | varies by site |
| Root N:DW | *sNR* | g N g-1 DW | varies by site |
| Leaf P:DW | *sPL* | g P g-1 DW | varies by site |
| Wood P:DW | *sPW* | g P g-1 DW | varies by site |
| Root P:DW | *sPR* | g P g-1 DW | varies by site |
| ***Canopy Phenology:*** | | | |
| Evergreen canopy fraction | *fcmin* | unitless | varies by site |
| Canopy growth | *Gfc* | fraction day-1 | Eq. 75 |
| Canopy litter | *Lfc* | fraction day-1 | Eq. 76 |
| Canopy growth water response | *GcT* | unitless | Eq. 73 |
| Canopy growth water sensitivity | *Gfc* | unitless | 0.5a |
| Canopy litter water response | *LcW* | unitless | Eq. 74 |
| Canopy growth rate | *Gfc* | °C-1 day-1 | varies by site |
| canopy feedback exp | *fc* | unitless | 0.01a |
| Wilting amplitude | *w* | unitless | 1.3a |
| Degree day bud break | *Ddbud* | °C day | varies by site |
| Day fall starts | *Dfs* | day | varies by site |
| Canopy litter temperature rate | *cT* | day-1 | varies by site |
| Canopy litter moisture rate | *cW* | day-1 | varies by site |
| ***Photosynthesis/Transpiration:*** | | | |
| Photosynthesis | *UC* | g C m-2 day -1 | Eq. 85 |
| C limited photosynthesis | *PsC* | g C m-2 day-1 | Eq. 82 |
| Light limited photosynthesis | *PsIrr* | g C m-2 day-1 | Eq. 83 |
| Water limited photosynthesis | *PsW* | g C m-2 day-1 | Eq. 84 |
| Carboxylation maximum | *PCx* | g C m-2 hr-1 | Eq. 77 |
| Photosynthesis CO2 rate constant | *gC* | g C m-2 leaf hr-1 | varies by site |
| CO2 compensation point | ** | mol mol-1 | Eq. 78  McMurtrie et al, 1992. |
| CO2 half saturation constant | *kC* | mol mol-1 | Eq. 79  McMurtrie et al, 1992. |
| Soil limited canopy conductance | *ccs* | mm H2O MPa-1 hr-1 | Eq. 86 |
| Plant water uptake | *UW* | mm H2O day-1 | Eq. 87 |
| PET-root sensitivity | *kE* | Mg soil hr-1 MPa-1 m-1 root | varies by site |
| Photosynthesis light maximum | *PIx* | g C m-2 hr-1 | Eq. 81 |
| Photosynthesis light rate constant | *gI* | g C m-2 leaf hr-1 | varies by site |
| Light extinction | *kI* | m2 gnd m-2 | 0.5 |
| Light half saturation constant | *HSI* | MJ m-2 hr-1 | 5 |
| Photosynthesis temperature response function | *fPT* | unitless | Eq. 80 |
| Ps temperature response lower limit | *TaPs* | °C | 70 |
| Ps temperature response upper limit | *TbPs* | °C | 40 |
| Ps Tmin response shape parameter | *aPs, bPs* | °C-1 | 0.04 and 0.2 |
| Temperature Ps is acclimated to | *Tave0* | °C | varies by site |
| Current average growing season temperature | *Tave* | °C | varies by site |
| UW:UC scaler | *scg* | g C MPa mol air m-2 mm-1 H2O mol-1 CO2 | varies by site |
| ***Plant respiration and Net Primary Production*** | | | |
| Plant respiration | *RCPt* | g C m-2 day -1 | Eq. 91 |
| Maintenance respiration | *RCPTm* | g C m-2 day-1 | Eq. 89 |
| Metabolic plant respiration | *RCPm* | g C m-2 day-1 | Eq. 88 |
| Active biomass respiration rate | *rma* | g C g-1 N day-1 | varies by site |
| Woody biomass respiration rate | *rmW* | g C g-1 N day-1 | varies by site |
| Sapwood:heartwood partitioning exponent | *krmw* | m2 g-1 DW | 0a |
| Plant respiration temperature response | *Q10R* | unitless | 2a |
| Growth respiration rate | *rg* | fraction | 0.28a |
| Net primary production | *NPP* | g C m-2 day-1 | 2a |
| ***Plant nutrient uptake:*** | | | |
| Plant doC uptake | *UdoC* | g C m-2 day -1 | Eq. 97 |
| Plant NH4 uptake | *UNH4* | g N m-2 yr -1 | Eq. 95 |
| Plant NO3 uptake | *UNO3* | g N m-2 yr -1 | Eq. 95 |
| Plant doN uptake | *UdoN* | g N m-2 yr -1 | Eq. 98 |
| Symbiotic N fixation | *UNfix* | g N m-2 yr -1 | Eq. 94 |
| Plant PO4 uptake | *UPO4* | g P m-2 yr -1 | Eq. 96 |
| Root radius | *Rr* | m | 0.0005a |
| Average between root distance | *Rd* | m | Eq. 93 |
| Maximum between root half distance | *Rdmax* | m | 0.008a |
| Near root depletion factor | *NRD* | unitless | Eq. 92 |
| NH4 uptake C cost | *NNH4Ccost* | g C g-1 N | 0a |
| NO3 uptake C cost | *NNO3Ccost* | g C g-1 N | 2.1 |
| doN uptake C cost | *NdoNCcost* | g C g-1 N | 3 |
| Nfix uptake C cost | *NfixCcost* | g C g-1 N | 6.4 |
| *Uj* temperature response, *j*=Nfix, NH4, NO3, doC, PO4 | *Q10j* | unitless | 2a |
| *Uj* uptake rate, *j*=Nfix, NH4, NO3 | *gj* | g N m-1 root day-1 | varies by site |
| *UdoC* uptake rate | *gdoC* | g C m-1 root day-1 | varies by site |
| *UPO4* uptake rate | *gPO4* | g P m-1 root day-1 | varies by site |
| Near root *j* concentration, *j*=NH4, NO3 | *NjaqR* | mol L-1 | Eq. 95 |
| Near root PO4 concentration | *PO4aqR* | mol L-1 | Eq. 96 |
| Near root doC concentration | *doCaqR* | mol L-1 | Eq. 97 |
| Diffusion constant for *j*, *j*=NH4, NO3, PO4, and doC | *Dj* | m2 day-1 | NH4: 0.0000864  NO3: 0.0000403  PO4: 0.0000239  doC: 0.0000239 |
| Half saturation constant for *j*, *j*=NH4, NO3, PO4, and doC | *kj* | mol L-1 | NH4: 100  NO3: 100  PO4: 30  doC: 850 |
| N fixation LAI cutoff | *Lcrit* | m2 m-2 | 3\* |
| N fixation LAI sensitivity | *Nfix* | m2 m-2 | 7a |
| ***Plant litter fall:*** | | | |
| Fine litter carbon | *LitC* | g C m-2 day -1 | Eq 101 |
| Fine litter nitrogen | *LitN* | g N m-2 day -1 | Eq. 105 |
| Fine litter phosphorus | *LitP* | g P m-2 day -1 | Eq. 106 |
| Coarse woody litter carbon | *LcWC* | g C m-2 day -1 | Eq. 108 |
| Coarse woody litter nitrogen | *LcWN* | g N m-2 day -1 | Eq. 109 |
| Coarse woody litter phosphorus | *LcWP* | g P m-2 day -1 | Eq. 110 |
| Fine litter 🡪 standing dead C | *LitCDebris* | g C m-2 day-1 | Eq. 101 |
| Fine litter 🡪 standing dead N | *LitNDebris* | g N m-2 day-1 | Eq. 102 |
| Fine litter 🡪 standing dead P | *LitPDebris* | g P m-2 day-1 | Eq. 103 |
| Leaf litter N:DW | *sNLl* | g N g-1 DW | varies by site |
| Wood litter N:DW | *sNWl* | g N g-1 DW | varies by site |
| Root litter N:DW | *sNRl* | g N g-1 DW | varies by site |
| Leaf litter P:DW | *sPLl* | g P g-1 DW | varies by site |
| Wood litter P:DW | *sPWl* | g P g-1 DW | varies by site |
| Root litter P:DW | *sPRl* | g P g-1 DW | varies by site |
| Leaf litter | *LL* | g DW m-2 day-1 | Eq. 100 |
| Evergreen leaf turnover rate | *maL* | day-1 | varies by site |
| Wood turnover rate | *mW* | day-1 | varies by site |
| Fine root turnover rate | *maR* | day-1 | varies by site |
| Coarse wood turnover rate | *mcW* | day-1 | varies by site |
| Coarse wood turnover exponent | *mcWex* | unitless | 0.5a |
| Coarse wood litter fall | *LcWD* | g DW m-2 day-1 | Eq. 107 |
| fraction fine litter to standing dead | *fDebris* | g C g-1 DW | varies by site |
| C:N of fine standing dead litter | *qNLDebris* | g C g-1 N | varies by site |
| C:P of fine standing dead litter | *qPLDebris* | g C g-1 P | varies by site |
| N to dry weight of coarse woody litter | *sNWwl* | g N g-1 DW | varies by site |
| P to dry weight of coarse woody litter | *sPWwl* | g P g-1 DW | varies by site |
| ***Requirement and Plant acclimation:*** | | | |
| Growth C requirement | *RCg* | g C m-2 day-1 | Eq. 111 |
| Growth N requirement | *RNg* | g N m-2 day-1 | Eq. 113 |
| Growth P requirement | *RPg* | g P m-2 day-1 | Eq. 114 |
| Stoichiometric feedback | *kq* | unitless | 0.5a |
| Total *j* requirement, *j*= C, N, P | *Rjt* | g *j* m-2 day-1 | Eq. 112, 114, & 116 |
| Marginal C yield *j*, *j*= CO2, W, I | *yj* | g C m-2 day-1 | Eq. 119-121 |
| Marginal N yield *j*, *j*= NH4, NO3, Nfix, doN | *yj* | g N m-2 day-1 | Eq. 122 |
| Weighted mean of yield | *yja* | g j m-2 day-1 | Eq 123 |
| kick starter for primary effort  *j*= NH4, NO3, doN, Nfix | *j* | day-1 | Eq. 124 |
| small increment used in various equations | *0* | varies | 0.001a |
| kick starter for sub-effort *k*  k= NH4, NO3, Nfix, doN, CO2, W, I | *k* | fraction of effort day-1 | Eq. 125 |
| switches used in the kick starter equations | *Vj, vk*,  *hVj, mvk* | fraction of effort day-1  day-1 | Eq 124 & 125 |
| Requirement ratio for *j*, *j*= C, N, P | *j* | unitless | Eq. 117 |
| Time averaged uptake of *k* | *Uka* | g *k* m-2 day-1 | Eq 28 |
| Time averaged requirement of *k* | *Rka* | g *k* m-2 day-1 | Eq 29 |
| Maximum requirement to uptake ratio | ** | unitless | 10a |
| Mean requirement:uptake ratio |  | unitless | Eq. 118 |
| ***Hydrology and material losses:*** | | | |
| Rainfall | *Rfl* | mm H2O day-1 | Eq. 126 |
| Snowfall | *Sfl* | mm H2O day-1 | Eq. 127 |
| Interception | *Intr* | mm H2O day-1 | Eq. 128 |
| Snowmelt | *Sm* | mm H2O day-1 | Eq. 129 |
| Deep percolation and subsurface lateral flow | *Ro* | mm H2O day-1 | Eq. 135 |
| Surface runoff | *ROvf* | mm H2O day-1 | Eq. 142 |
| Snowmelt infiltration | *InfS* | mm H2O day-1 | Eq. 130 |
| Rainfall infiltration | *InfR* | mm H2O day-1 | Eq. 132 |
| Throughfall | *Thf* | mm H2O day-1 | Eq. 131 |
| Infiltration excess overland flow | *OvfI* | mm H2O day-1 | Eq. 133 |
| Snowmelt overland flow | *OvfS* | mm H2O day-1 | Eq. 134 |
| Total Overland flow | *Ovf* | mm H2O day-1 | ??? |
| Subsurface doC leaching | *LdoC* | g C m-2 day-1 | Eq. 139 |
| Subsurface doN leaching | *LdoN* | g N m-2 day -1 | Eq. 138 |
| Subsurface NH4 leaching | *LNH4* | g N m-2 day -1 | Eq. 136 |
| Subsurface NO3 leaching | *LNO3* | g N m-2 day -1 | Eq. 137 |
| Subsurface PO4 leaching | *LPO4* | g P m-2 day -1 | Eq. 140 |
| Surface doC leaching | *ROvfdoC* | g C m-2 day -1 | Eq. 146 |
| Surface doN leaching | *ROvfdoN* | g N m-2 day -1 | Eq. 147 |
| Surface NH4 leaching | *ROvfNH4* | g N m-2 day -1 | Eq. 143 |
| Surface NO3 leaching | *ROvfNO3* | g N m-2 day -1 | Eq. 144 |
| Surface PO4 leaching | *ROvfPO4* | g P m-2 day -1 | Eq. 145 |
| Interception volume | *IntV* | mm H2O m-2 leaf day-1 | varies by site |
| Non-leaf surface area | *NLsfc* | m2 m-2 | 0a |
| Mid wood biomass | *MBW* | g DW m-2 | 100a |
| Interception branch exponent | *NLe* | unitless | 0.4a |
| Snow critical temperature | *Tcrit* | °C | 0.75 |
| Shortwave melt coefficient | *SWC* | unitless | 0.1 |
| Latent heat of fusion | *LHF* | MJ mm-1 m-2 | 0.334 |
| Longwave melt coefficient | *sB* | unitless | 2.1 |
| Convective coefficient | *Cc* | mm °C -1 day-1 | 2 |
| Soil drainage rate | *drain* | day-1 | varies by site |
| field capacity for runoff. | *fro* | mm mm-1 soil | typically *fro*=*fp*, sites with standing water should set *fro*>*fp* |
| DON leaching coefficient | *aLdoN* | m2 g-1 C mm-1 | varies by site |
| DOM leaching C:N | *sLdoM* | g C g-1 N | 15.32a |
| Total N leaching | *LNtot* | g N m-2 day-1 | Eq 141 |
| ***Microbial processes:*** | | | |
| Woody litter *j* activation  *j*= C, N, or P | *LcWja* | g *j* m-2 day -1 | Eq. 149 |
| Phase I to Phase II soil transition  *j*= C, N, or P | *Tiij* | g *j* m-2 day -1 | Eq. 151-152 |
| Phase II soil respiration | *MiiC* | g C m-2 day -1 | Eq. 157 |
| Phase II nitrogen mineralization | *MiiN* | g N m-2 day-1 | Eq. 159 |
| Phase II phosphorus mineralization | *MiiP* | g P m-2 day-1 | Eq. 158 |
| Microbial NH4 uptake | *UNH4m* | g N m-2 day-1 | Eq. 162 |
| Microbial NO3 uptake | *UNO3m* | g N m-2 day-1 | Eq. 162 |
| Microbial PO4 uptake | *UPO4m* | g P m-2 day-1 | Eq. 164 |
| Non-symbiotic fixation | *NNsfix* | g N m-2 day-1 | Eq. 156 |
| Nitrification | *Nitr* | g N m-2 day-1 | Eq. 154 |
| Denitrification | *DNtr* | g N m-2 day-1 | Eq. 153 |
| Phase I soil respiration | *RCm* | g C m-2 day-1 | Eq. 166 |
| Phase I nitrogen mineralization | *RNm* | g N m-2 day-1 | Eq. 166 |
| Phase I phosphorus mineralization | *RPm* | g P m-2 day-1 | Eq. 166 |
| Microbial temperature and moisture factor | *dW* | unitless | Eq. 148 |
| Optimum fraction water filled pore space | *Wopt* | fraction | varies by site |
| Minimum fraction water filled pore space | *Wmin* | fraction | 0.01a |
| Moisture response shape parameter | *Jmoist* | unitless | varies by site |
| Microbial temperature response | *Q10m* | unitless | 2a |
| Coarse woody debris turnover rate | ** | day-1 | varies by site |
| Phase I to Phase II transition rate | *aTii* | m4 g-1 N g-1 P day-1 | varies by site |
| Phase II soil C:N | *qNSii* | g C g-1 N | varies by site |
| Phase II soil C:P | *qPSii* | g C g-1 P | varies by site |
| Phase II mineralization rate | *aMii* | day-1 | varies by site |
| Maximum C efficiency | *eC* | unitless | 0.6a |
| Microbial return C:N | *N* | g C g-1 N | varies by site |
| Microbial return C:P | *P* | g C g-1 P | varies by site |
| Microbial use C:N | *N* | g C g-1 N | Eq. 160 |
| Microbial use C:P | *P* | g C g-1 P | Eq. 160 |
| Total microbial *j* use, *j*= C, N, P | *Mj* | g *j* m-2 day-1 | Eq. 157-159 |
| Actual microbial *j* efficiency, *j*= C, N, P | *j* | unitless | Eq. 161, 163, & 165 |
| Soil turnover rates, *j*= C, N, P | *j* | day-1 | varies by site |
| Wood nonsymbiotic N fixation | *NnsfixW* | g N m-2 day-1 | Eq. 155 |
| Woody N fixation rate constant | *Nnsfix* | day-1 | 0a |
| Soil N fixation rate constant | *Nnsfix* | g2 N g-2 C day-1 | varies by site |
| Soil N fixation cutoff | *qNnsfix* | g C g-1 N | varies by site |
| Microbial *j* uptake rate, *j*= NH4, NO3, PO4 | *j* | g N or P g-1 C day-1 | varies by site |
| Microbial *j* half saturation constant, *j*= NH4, NO3, PO4 | *kj* | mol L-1 | NH4: 50a  NO3: 50a  PO4: 20a |
| Nitrification rate | *rrNitr* | g N m-2 day-1 | varies by site |
| Nitrification half saturation constant | *kNitr* | mol N L-1 | 70a |
| Denitrification rate | *aDNtr* | g N m-2 day-1 | varies by site |
| Denitrification half saturation constant | *kDNtr* | mol N L-1 | 70a |
| Denitrification minimum soil moisture | *D* | fraction | 0.3a |
| ***Soil P transformations:*** | | | |
| Primary mineral weathering | *Paw* | g P m-2 yr -1 | Eq. 167 |
| PO4 precipitation | *PO4p* | g P m-2 yr -1 | Eq. 169 |
| Non-occluded P weathering | *Pnow* | g P m-2 yr -1 | Eq. 168 |
| Non-occluded P stabilization | *Pnos* | g P m-2 yr -1 | Eq. 171 |
| Occluded P weathering | *Pocclw* | g P m-2 yr -1 | Eq. 170 |
| Primary mineral weathering rate | *rPaw* | day-1 | varies by site |
| Nonoccluded formation rate | *rPO4p* | g P L mmol-1 m-2 day-1 | varies by site |
| Nonoccluded weathering rate | *rPnow* | day-1 | varies by site |
| Occluded formation rate | *rPnos* | day-1 | 0, grouped all P minerals under primary minerals |
| Occluded weathering rate | *rPocclw* | day-1 |
| ***Prairie fire:*** | | | |
| Biomass C loss by fire | *FBC* | g C m-2 day -1 | Eq. 172 |
| Biomass N loss by fire | *FBN* | g N m-2 day -1 | Eq. 173 |
| Biomass P loss by fire | *FBP* | g P m-2 day -1 | Eq. 174 |
| leaf fraction burned | *ffLL* | fraction day -1 | varies by site |
| wood fraction burned | *ffWL* | fraction day -1 | varies by site |
| Woody debris C loss by fire | *FWC* | g C m-2 day -1 | Eq. 175 |
| Woody debris N loss by fire | *FWN* | g N m-2 day -1 | Eq. 176 |
| Woody debris P loss by fire | *FWP* | g P m-2 day -1 | Eq. 177 |
| Phase I soil C loss by fire | *FDC* | g C m-2 day -1 | Eq. 178 |
| Phase I soil N loss by fire | *FDN* | g N m-2 day -1 | Eq. 179 |
| Phase I soil P loss by fire | *FDP* | g P m-2 day -1 | Eq. 180 |
| woody debris fraction burned | *ffWDL* | fraction day -1 | varies by site |
| soil fraction burned | *ffDL* | fraction day -1 | 0a |
| N volatilized by fire | *FNvol* | g N m-2 day -1 | Eq. 181 |
| NO3 residue from fire | *FNO3* | g N m-2 day -1 | Eq. 182 |
| P volatilized by fire | *FPvol* | g N m-2 day -1 | Eq. 183 |
| PO4 residue from fire | *FPO4* | g N m-2 day -1 | Eq. 184 |
| biomass N fraction volatilized | *fBNv* | fraction | varies by site |
| woody debris N fraction volatilized | *fWNv* | fraction | varies by site |
| soil N fraction volatilized | *fDNv* | fraction | varies by site |
| biomass P fraction volatilized | *fBPv* | fraction | varies by site |
| woody debris P fraction volatilized | *fWPv* | fraction | varies by site |
| soil P fraction volatilized | *fDPv* | fraction | varies by site |
| ***Summary variables:*** | | | |
| Total N deposition | *Ndept* | g N m-2 day-1 | Eq. 189 |
| Total plant N uptake | *UNt* | g N m-2 day-1 | Eq. 192 |
| Net ecosystem *j* balance, *j*= C, N, P, and W | *Nejb* | g *j* m-2 day-1 or  mm H2O day-1 | Eq. 185-187 |
| Net *j* mineralization, *j*= N, P | *Netjmin* | g *j* m-2 day-1 | Eq. 190 & 191 |
| Nitrogen use efficiency | *NUE* | g C g-1 N | Eq. 195 |
| Phosphorus use efficiency | *PUE* | g C g-1 P | Eq. 196 |
| Water use efficiency | *WUE* | g C mm-1 H2O | Eq. 194 |
| Net ecosystem production | *NEP* | g C m-2 day-1 | Eq. 193 |
| Total soil *j* | *SOjt* | g *j* m-2 day-1 | Eq. 197-199 |

aAssumed values

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