

PnET-Succession v3.1 Extension User Guide

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1 Introduction

This document describes the **PnET-Succession** extension for the LANDIS-II model. For information about the model and its core concepts including succession, see the *LANDIS-II Conceptual Model Description*.

The PnET-Succession extension is based on the Biomass Succession extension of Sheller and Mladenoff (2004), embedding elements of the PnET-II ecophysiology model of Aber et al (1995) to simulate growth as a competition for available light and water, replacing the existing competition for “growing space” algorithms. PnET (Photosynthesis and EvapoTranspiration) is a simple, lumped parameter model of carbon and water balances of forests (Aber and Federer 1992), built on two principal relationships: 1) maximum photo-synthetic rate is a function of foliar nitrogen concentration, and 2) stomatal conductance is a function of realized photosynthetic rate.

1.1 Major modifications made to PnET algorithms

Several modifications were made to PnET algorithms to make them tractable at landscape scales, primarily by broadening the scale of integration operations. (1) The timestep was broadened from the daily PnET timestep to monthly. (2) The number of sub-layers within a canopy layer was 50 in PnET, but is here set by the user (IMAX) to increase computational efficiency, where each sub-layer represents an even proportion of the total LAI within the layer. A greater number of subcanopy layers tighten the feedback between photosynthesis and water stress, but significantly increases computation time. (3) The original PnET adds foliage to successively deeper subcanopy layers until there is insufficient light to support photosynthesis. PnET-Succession allocates foliage in proportion to the active wood (xylem) that supports it. (4) Cohort biomass in PnET-Succession is used as a surrogate for tree height to simulate canopy layers, which are added when the variation in biomass among cohorts exceeds a user-defined amount. (5) Photosynthates in PnET-Succession are allocated to four pools (foliage, root, wood and non-structural carbon (reserves, NSC)). Net photosynthesis is initially allocated to the NSC pool, and then foliage allocation occurs, followed by allocation to root and wood pools such that the above- and below-ground biomass ratio is preserved. Maintenance respiration is then deducted from the NSC pool. Details of model structure and modifications can be found in De Bruijn et al (2014).

1.2 Advantages and disadvantages of PnET-Succession compared to Biomass Succession

The goal for PnET-Succession was to make the simulation of growth and competition more mechanistic and more explicitly linked to fundamental drivers that are changing, such as climate and atmospheric composition (e.g., CO₂ and ozone). It is believed that this more mechanistic approach will be more robust for making projections under climate and other global changes (Gustafson 2103).

Advantages of PnET-Succession compared to Biomass Succession

- 1) PnET-Succession replaces the input parameters ANPP_{max} and B_{max} of LANDIS-II Biomass Succession with mechanistic and dynamic calculations of growth and senescence that depend on monthly climatic conditions and competition for resources. Establishment and growth are now emergent properties of the model and are explicitly linked to changing fundamental drivers such as climate and CO₂ concentrations.
- 2) Dynamic calculations of LAI and photosynthesis allow cohorts to die prior to senescence, based on physiological constraints (too few carbon reserves). This can typically occur when carbon reserves production is insufficient to support growth due to shading, water competition, drought, diseases or pests. This allows more realistic simulation of cohort death in the course of stand development (i.e., mortality is highest in the younger cohorts), and a more realistic accounting of biomass accumulation. An added benefit is that the number of cohorts to be simulated is reduced.
- 3) PnET-Succession allows a more explicit simulation of species' survival strategies, by implementing a dynamic competition for light and water. For example, one can parameterize species or species-group combinations of respiration losses and water use efficiency to implement competition advantages or disadvantages for particular species in sites that are dry or shaded due to competing vegetation. PnET-Succession also allows simulation of waterlogging effects on photosynthesis.

Disadvantages of PnET-Succession compared to Biomass Succession

- 1) PnET-Succession requires more parameters, which adds to uncertainty and increases the parameter burden when using the model. However, uncertainty may be no higher than when making *ad hoc* assumptions for other succession extensions about how novel conditions will affect modeled processes.
- 2) Runtimes tend to be somewhat longer, but only slightly longer because many cohorts senesce prior to reaching longevity age, greatly reducing the

number of cohorts that must be simulated. However, in both Biomass Succession and PnET-Succession, simulation of dispersal can be more computationally time consuming than forest growth.

1.3 What's new in Version 3.1

Version 3.1 is compatible with the LANDIS-II core v7.

Added dynamic foliage responses to light (fRad) through dynamic foliar nitrogen (FolN) and foliage fraction (FracFol). See sections 8.25 and 8.26.

1.4 References

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1.6 Release History

1.6.1 Major Releases

1.6.1.1 Version 3.0

Latitude is now an ecoregion parameter, allowing for large study areas with spatially dispersed ecoregions. Latitude is used to compute day length available for photosynthesis.

PnET-Succession v2.0 (and earlier) used equations from early versions of PnET-II to compute the CO₂ enrichment effect (DelAmax). The most recent version of PnET-II uses an equation from Franks et al. (2013), which moderates the CO₂ effect, especially at high CO₂ concentrations. We now use a modified version of the Franks equation that uses internal leaf CO₂ concentrations rather than external leaf CO₂ concentrations (Gustafson et al in prep). The Franks equation lessens the CO₂ enhancement effect, especially at high CO₂ concentrations.

Now PnET-Succession computes a variable (CiModifier) used to modify internal leaf CO₂ concentration (C_i), reflecting reduced conductance as a function of drought stress (fWater), ozone dose, and species ozone tolerance. This is used to reflect stomatal closure caused by water stress, which is modified by stomatal sluggishness (inability to close completely) induced by elevated ozone, modeling its interaction with conductance of CO₂ and water. Absorption of CO₂, O₃, and transpiration of water are all reduced by CiModifier.

Modified the canopy layering algorithm so that all cohort canopy sublayers are assigned to only one main canopy layer (i.e., a cohort cannot span multiple main canopy layers).

Provided a parameter (CO2HalfSatEff) to optionally make HalfSat dynamic as a function of CO₂ concentration. This effect can be turned off by setting to zero.

Provided parameters (FolNInt, FolNSlope) to optionally make FolN dynamic as a function of light (fRad), allowing photosynthetic capability (A_{max}) to vary vertically through the canopy (by canopy sublayer) and in response to cohort release or overtopping. This dynamic effect can be turned off by setting these to 1.0 and 0.0, respectively.

Added optional output variables to the PnETOutputSites file with species-specific amounts of dead wood (WoodySenescence) and foliage (FoliageSenescence) while tracked internally before, were not available as outputs from the respective dead biomass pools. This output is useful for more landscape carbon accounting.

Dropped the WUEConst species parameter. Water use efficiency is now calculated directly from fluxes of water from leaves (J_{H2O}).

Activated the H2 species parameter that allows simulation of waterlogging effects on photosynthesis.

Added the ability to optionally include ozone effects on photosynthesis. These functions are activated only when the climate input file contains a field with monthly cumulative ozone concentrations.

Added the O3GrowthSens parameter to scale the computation of the species-specific ozone effect that reflects the damaging effects of ozone on photosynthetic tissue. This is used to specify species sensitivity to ozone damage of tissues, and is only needed when ozone data are provided in the climate file.

Added the O3StomataSens parameter to reflect species differences in stomatal sluggishness when exposed to ozone. This categorical class impacts how CiModifier is calculated, and is only needed when ozone data are provided in the climate file.

Litter decomposition is now computed once per year, including during initial spin-up.

Added DisturbanceReductions that allow disturbances to impact the existing dead wood and litter pools. Other disturbance impacts on biomass transferring from live to dead pools that used to be included in the AgeOnlyDisturbances file have been moved to the DisturbanceReductions file. Added section to the Users Guide to explain the DisturbanceReductions.

Bug fix to ensure all foliage and NSC are lost when a cohort dies, even though it is not removed until the end of the succession timestep. This step makes the cohorts functionally dead the first year the NSCFrac drops below 0.01.

The Excel worksheet [PnET-Succession function worksheet.xlsx] that is also available from (<http://www.landis-ii.org/extensions/pnet-succession>) is now copied to the 'docs' folder along with the User Guide during installation.

1.6.1.2 Version 2.0 (2016)

New generic parameter: PrecipEvents. Divides incoming monthly precipitation into discrete events within the month ($n = \text{PrecipEvents}$) and applies each portion randomly during the sequence of processing canopy sublayers. This prevents large cohorts from consuming a disproportionate share of the available water in a given month.

New generic parameter: Wythers. Option to apply the foliar respiration modification to increased temperature as described by Wythers et al (2013).

New generic parameter: DTEMP. Option to apply the temperature reduction factor (DTEMP) of PnET-II rather than the original PnET-Succession v1.2 temperature reduction factor. The v1.2 temperature reduction factor does not explicitly penalize photosynthesis at temperatures above PsnTOpt.

New ecoregion parameter: SnowSublimFrac. Snowpack is reduced by this amount prior to snowmelt, representing sublimation and meltwater runoff that does not enter the soil.

New output options for woody senescence and foliage senescence by species.

Bug fixes:

- A bug in the calculation of transpiration was fixed.
- A bug that caused the decomposition of dead pools to not be simulated during spin-up in prior versions was fixed.
- A bug in the calculation of runoff was fixed.
- Biomass values provided to disturbance extensions in prior versions were the sum of above- and below-ground woody biomass, but no foliar biomass. Version 2.0 includes aboveground and foliar biomass to be consistent with other Biomass Succession extensions and is therefore more compatible with biomass disturbance extensions. Specific biomass pools can be now output as maps and total pool sizes using the Output-PnET extension (Section 10).
- Defoliation (by an external disturbance extension) is now applied during June (previously it was January when deciduous species had no foliage).
- A bug in the processing of cohorts killed by disturbance was fixed. The bug prevented disturbances from recording the cohorts being removed.
- A bug in the calculation of snow melt was fixed. The bug caused all snow pack to melt at the same time. The rate of snowmelt was changed to 2.74 mm/°C/day (see 2.4.2.1).
- When snowpack is present, surface PAR is set to 0 which eliminates soil water evaporation under snow (though sublimation of snow occurs instead).

An Excel worksheet [PnET-Succession function worksheet.xlsx] is available from (<http://www.landis-ii.org/extensions/pnet-succession>) that can be used to better understand how selected input parameters affect state variable computations.

1.6.1.3 Version 1.0 (2014)

Original released version

1.6.2 Minor Releases

1.6.2.1 Version 2.1.1 (October 2017)

This release incorporates a change to the Biomass Cohort Library to maintain compatibility with other extensions that use the same library (all extensions that use cohorts with biomass attributes). The edit to the Biomass Cohort Library enabled the proper tracking of dead biomass (additions to the dead pools) when partial cohort removals occurred.

This version also adds compatibility with the Metadata Library that supports output visualization using the VizTool.

1.6.2.2 Version 2.1 (May 2017)

An important bug related to dispersal was fixed in this version. Previously, the age of the **youngest** cohort of a species was used to determine if a mature cohort was present on a site for seeding purposes. The test should use the age of the **oldest** cohort of a species to check for maturity and determine sources of seed for dispersal. This error has been corrected.

Rename [SurfaceRunoff] to [PrecLoss] in the Site Output file to distinguish between water lost due to soil saturation (SurfaceRunOff) and water lost due to other factors (PrecLoss; e.g., slope, impervious surface). Add tracking of PrecLoss variable.

Rename [Layer] to [TopLayer] in the Cohort Output file to denote that the value reported is the highest layer in which the cohort appears. The top canopy layer has the highest layer value.

The allocation of precipitation events to subcanopy layers has been adjusted so that the precip events are randomly assigned to layers, but not constrained to a single event per layer. This can result in multiple precip events occurring (with their associated runoff, interception, leakage, etc.) for a given layer, especially when the number of precipitation events is greater than the number of subcanopy layers on a site. This resolves a discontinuity in the water cycle when the number of cohorts was low relative to the number of precip events.

Bug Fixes:

- Fixed the DiscreteUniformRandom function to be inclusive of the maximum value. Previous implementation may have been slightly biased in the shuffling of subcanopy layers.

2 PnET-Succession

The PnET-Succession Extension generally follows the methods of the Biomass Succession Extension: Age cohorts reproduce, grow (add biomass), age, and die. The PnET-Succession Extension replaces the simple growth and competition algorithms from the Biomass Succession Extension with the photosynthesis and respiration equations from PnET-II to simulate growth of specific cohort biomass components (root, foliage, wood, non-structural carbon) as a competition for water and light.

PnET-Succession simulates the competition of cohorts for water and light as a function of photosynthetic processes. Competition for water is simulated on each site (grid cell) through a dynamic soil water balance that receives precipitation and loses water as runoff, interception, percolation out of the rooting zone and consumption by cohorts through transpiration. Competition for light is modeled by tracking solar radiation through canopy layers (related to cohort age) according to a standard Lambert-Beer formula. PnET-Succession requires average monthly temperature, precipitation, photosynthetically active radiation and atmospheric CO₂ concentration as inputs.

Because monthly climate data are provided as an input to the extension, species establishment probability is also calculated at each time step as a function of the climate conditions during the time step.

The PnET-Succession Extension also changes the calculation of shade. LAI is estimated for multiple canopy layers, and available light is computed for each layer, including the sub-canopy (i.e., ground).

The PnET-Succession Extension tracks biomass in four live pools (foliage, roots, wood and non-structural (C reserves)) and two dead pools (woody and leaf litter). For disturbance extensions that request “biomass” from the succession extension, PnET-Succession passes the sum of wood+foliage.

2.1 Initializing Biomass

At the beginning of a scenario, the initial communities begin with appropriate living and dead biomass values estimated for each site. **However, the user does not supply the initial biomass estimates.** Rather, the PnET-Succession extension uses its growth algorithms to iterate the number of time steps equal to the maximum cohort age for each site. Beginning at time (t - oldest cohort age), cohorts are added at each time step corresponding to the time when the existing cohorts were established. Thus, each cohort undergoes growth and mortality for the number of years equal to its current age, and its initial biomass value reflects competition among cohorts. Note: this is a

computationally intensive process that may require significant time for complex initial landscapes. Additionally, climate data are required back to t - oldest cohort age. To facilitate climatic input in years where weather records do not exist, it is possible to supply mean monthly climate data for a range of years (see section 6.1.2)

This biomass initialization does not account for disturbances that would likely happen prior to initialization and therefore tends to overestimate initial live biomass and underestimate initial dead biomass. Because PnET-Succession gives bigger cohorts priority access to light and water, older cohorts may have an advantage during spin-up. Furthermore, some cohorts may not survive spin-up.

2.2 LAI Shade Calculation

Site shade is calculated based on LAI in canopy layers (see section 2.4.1).

2.3 Cohort Reproduction and Establishment

Cohort establishment is the result of two distinct processes: 1) production and dispersal of seeds and 2) seed germination and successful recruitment of a viable new cohort.

Seed is produced by every cohort that is at least the age of sexual maturity. Seed dispersal is modeled as a spatial process according to the dispersal method selected by the user, as in the Biomass Succession extension.

When seeds disperse to a cell, establishment (recruitment) first requires sufficient light (amount dependent on species shade tolerance) and is then stochastic based on a probability of establishment that is calculated as a function of soil moisture and sub-canopy radiation during the time step. Establishment is only attempted during optimal months, computed from the climate file as the first three physiologically active months in the year and one month after the maximum precipitation. Initial biomass is computed for a 1-year old cohort.

Note: this initial cohort will be grouped ('binned') appropriately into a larger cohort (e.g., age 1 – 10) at the next succession time step.

2.4 Cohort Competition

Biomass growth is driven by photosynthesis, which depends on light, soil moisture and foliage biomass. Multiplicative reduction factors are applied to gross photosynthesis to account for water stress, suboptimal radiation, vapor

pressure deficit, and temperature. A similar growth enhancement factor (DelAmax) is applied for CO₂ concentrations above 350 ppm.

2.4.1 Light

The reduction of radiation intensity through the canopy is estimated using an exponential decrease function (i.e., Beer-Lambert law), where incoming radiation drives photosynthetic activity (Aber and Federer, 1992). A laboratory-derived relationship between foliar nitrogen concentration and assimilation rates under optimal growth conditions is used to estimate potential gross photosynthesis.

PnET-Succession assumes that LAI and biomass are spatially homogeneous on a site (i.e., cell). PnET-Succession defines canopy layers according to biomass, with high biomass cohorts achieving dominance with regard to access to light. Because senescing cohorts are more likely to lose biomass due to death of suppressed individuals or branches breaking off rather than due to the top breaking (i.e. they lose biomass without losing height), maximum lifetime biomass of a tree-species cohort is used as a proxy for tree height. Note that changes have been made to the model described paper in Ecological Modeling (De Bruijn et al 2014). We no longer set (arbitrary) age limits on the development of canopy layers. Rather, each cohort is divided into a number IMAX (=5 by default, set in the GenericParameters file) of canopy sublayers of equal biomass (Figure 1, left). The cohort sublayers are overlaid and the model iteratively clusters sublayers into canopy layers until the deviation of the newly formed canopy boundaries (i.e. LyrMax -LyrAv) decreases below a user defined parameter MaxDevLyrAv (Figure 1, right). This process produces boundaries of canopy layers such that the variation of subcanopy boundaries within the canopy layers is minimized and the variance of subcanopy boundary between canopy layers is maximized. MaxDevLyrAv is calibrated by the user to produce the maximum number of canopy layers expected in the system, or to control how long it takes for multiple canopy layers to form. The maximum number of canopy layers can further be limited with the generic MaxCanopyLayers parameter (section 7.4). Subcanopy layers within a canopy layer have equal access to the light reaching the canopy layer, and the light passing through a canopy layer is a function of the LAI and extinction coefficient of the cohorts making up the canopy layer. Light stress for a cohort is calculated by: $fRad = Radiation / (Radiation + HalfSat)$.

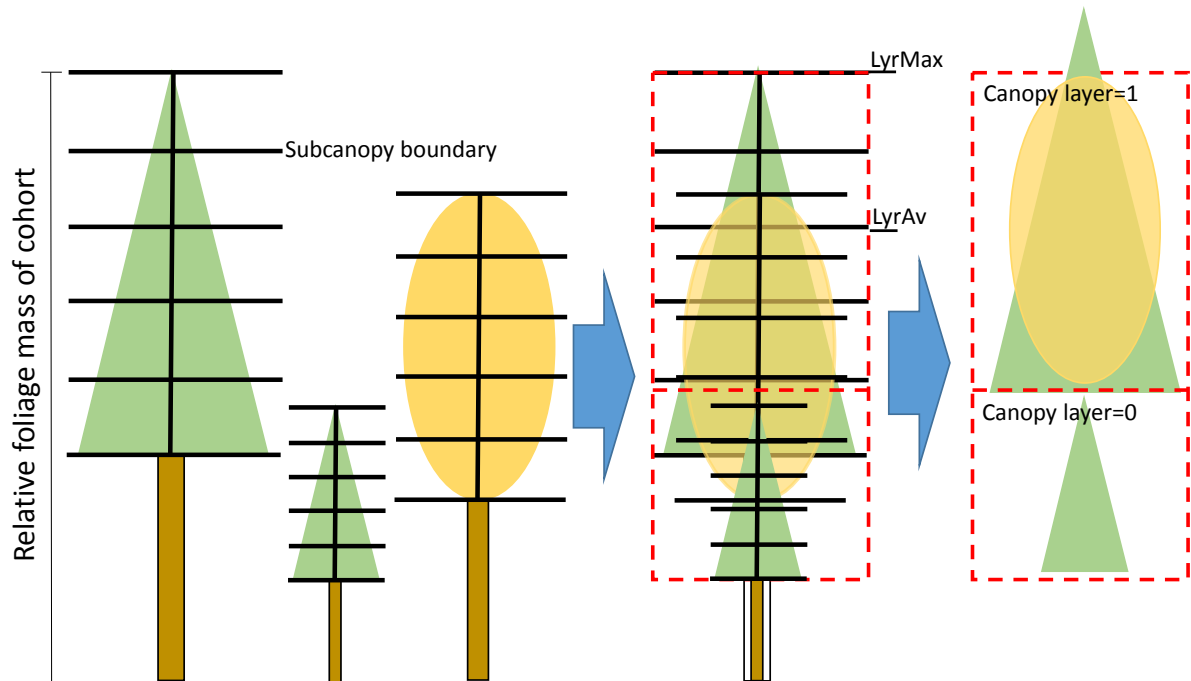


Figure 1. Canopy layer assignment. Each tree represents the foliage of a species-cohort on a site, and the solid horizontal lines are subcanopy boundaries (IMAX=5). Dotted lines are computed canopy layers that minimize the variance of foliage biomass within canopy layers and maximize the variance between canopy layers. All cohort subcanopy layers are assigned to the single canopy layer in which most of the cohort's subcanopy layers occur. Note that the diagram shows canopy shape only to enhance interpretation; in the model, subcanopy layers represent cohort foliage across the site, not tree crowns, and they all have equal biomass.

2.4.2 Water

Soil water is calculated in a bulk-hydrology model that updates soil water depending on precipitation, evaporation, soil drainage and consumption by the trees (Figure 2).

2.4.2.1 Water In

Sources of bulk soil water (*soil_water* in mm) are precipitation (P in mm/month) and melting water (*snow_melt* in mm/mo). Incoming precipitation is intercepted by existing foliage at a rate controlled by a user parameter (PrecipIntConst), which defines the proportion of precipitation intercepted for each unit of leaf area (LAI).

$$Interception = P \times e^{(-PrecipIntConst * LAI)}$$

Intercepted precipitation is assumed to evaporate from the leaf surface and does not enter the soil. Sites with no live cohorts have no precipitation interception. When average temperature is below freezing, precipitation (snow) is not subject to interception and is allocated to *snow_pack* (mm), where it remains until air temperature induces melting. Sublimation of snow is modeled as a direct reduction of snow pack prior to melting at a rate set by the ecoregion parameter *SnowSublimFrac* (default is 0.15 [Hood et al. 1999]). At above-freezing temperatures, snow melts at a rate of 2.74 mm/°C/day (USDA NRCS 2004). Snow melt is not subject to interception by foliage.

The combination of non-intercepted precipitation and snow melt define the potential incoming water. The incoming precipitation is divided into discrete precipitation events, with the number of events within a month set by the *PrecipEvents* ecoregion parameter. Precipitation from individual events is randomly assigned to individual subcanopy layers, with some layers potentially receiving multiple events and others receiving none. This random assignment ensures that all layers have equal priority to the incoming water. The incoming water is subject to surface runoff, which is controlled by a user-defined ecoregion parameter (*PrecipLossFrac*), which is intended to increase with slope or other factors (e.g., rocky soil) that would increase surface runoff even when the soil is not saturated. Incoming precipitation and snowmelt are reduced in proportion to *PrecipLossFrac*, with the runoff not entering the soil. The actual water infiltrating the soil is:

$$WaterIn = (1 - PrecipLossFrac) \times \frac{[snow_melt + P - Interception]}{PrecipEvents}$$

2.4.2.2 Water Out

Water that infiltrates the soil is subject to both fast and slow “leakage”. Infiltration is limited by the soil saturation parameter (θ_s), and any water in excess of saturation is subject to immediate runoff. Fast leakage is correlated to the soil hydraulic conductivity (*Ksat*) and occurs before plants have a chance to utilize water. The ecoregion parameter *LeakageFrac* defines the proportion of water above field capacity (-3.37 m pressure head) that immediately drains through the water profile. A parameter value of 1.0 implies immediate draining to field capacity, which will likely be appropriate for most real applications. Values of less than 1 for *LeakageFrac* could be appropriate to represent soil conditions that prevent leakage through the bottom of the soil profile (e.g., bedrock, clay layer, permafrost). Slow leakage occurs after plant use (transpiration) and evaporation, and keeps the

water level at or below field capacity (-3.37 m pressure head) at the end of each monthly time step.

After fast leakage loss has been subtracted, the soil water is subject to further depletion by transpiration and/or evaporation. Transpiration is calculated as the result of plant growth (see section 2.5). The rate of evaporation is a function of surface radiation (under the canopy), temperature and the soil texture class. Potential evaporation is calculated as a simplified Penman-Monteith calculation according to Priestley and Taylor (1972) as discussed in Brutsaert (1982, p. 217). This method was successfully applied in the PROGRASS model (Calanca et al. 2009).

Actual evaporation is calculated as:

$$\text{AET} = \text{Max}(c \times \text{PET} - \text{Transpiration}, 0),$$

where c is a proportion that decreases linearly from 1.0 when water content is 75% of field capacity, to $c = 0$ when pressure head is 153 m (i.e., the physical wilting point (Fig 3) (Robock et al. 1995)). AET is limited to the water above the wilting point, so that evaporation ceases when the soil water falls to the wilting point. Transpiration is subtracted from evaporation to reflect decreasing evaporation when the vegetation increases. *De facto* evaporation is 0.0 when LAI > 3.0. Also, surface radiation is automatically 0 when snow cover is present, which results in no evaporation under snow pack.

Transpiration is assumed to use water that otherwise would be subject to evaporation. Therefore, when transpiration exceeds evaporation, no additional water is lost to evaporation.

When some snow melts prior to soil thaw, it runs off and should not become soil water. The best way to account for this is to add the proportion of the snowpack lost to runoff to the SnowSublimFrac parameter (section 9.10).

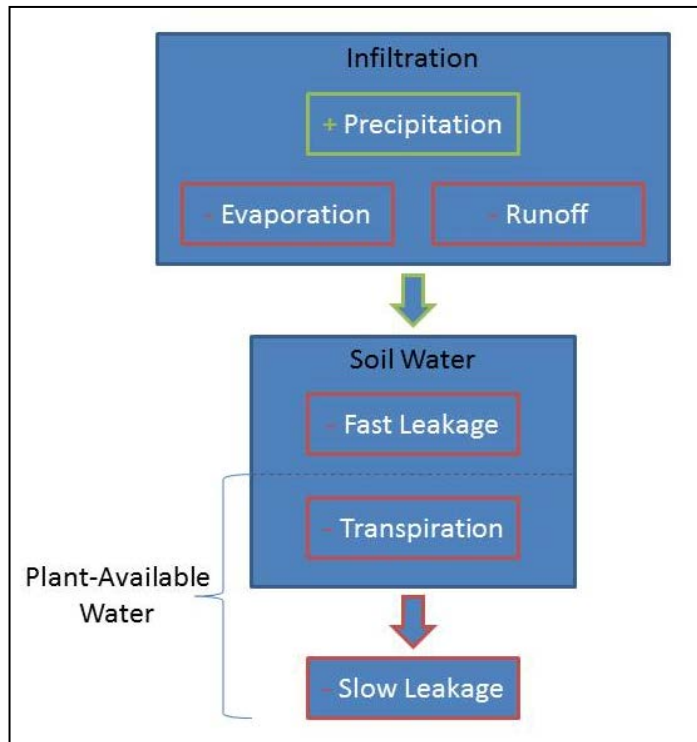


Figure 2. Soil water processes in PnET-Succession

2.4.2.3 Water Stress

Water stress in the model depends on the water pressure in the soil according to Feddes et al. (1978). Water pressure in the soil (water retention curves) depends on soil water content and the soil type according to Saxton and Rawls (2006), who provide equations to estimate water retention curves for soils based on soil texture characteristics (i.e., % sand, % silt, % clay, % organic matter, % gravel, salinity).

Default values for the required parameters (from Saxton and Rawls 2004) are provided with PnET-Succession for 12 different soil types (Figure 3, left panel), but users are able to modify existing soil type parameters or provide custom soil types with parameters. A BEDR (stone) soil type is also included to represent soils with no water holding ability. The user implements a soil type as an ecoregion-specific parameter in the ecoregion parameter table using a corresponding abbreviation for the soil type.

Water stress for a species-cohort is calculated from soil water pressure using four species-specific water pressure thresholds (Figure 3, right panel) labeled

H1-H4 in Feddes et al. (1978). Note that PnET-Succession uses the absolute value of pressure head. Parameter H1 (the pressure head below which photosynthesis cannot occur (waterlogging)) is hardcoded in PnET-Succession (H1 = 0 meter pressure). Often, little is known about H2 (cessation of waterlogging stress), so it is recommended to use the generic value H2=0.0 unless you are explicitly modeling waterlogging effects. H3 (onset of stress caused by too little water) can be set to reflect the drought sensitivity of a species, and should fall somewhere between H2 and H4. Most literature sources use a generic H4 (cessation of photosynthesis because of inadequate water) of -153 m pressure head (wilting point).

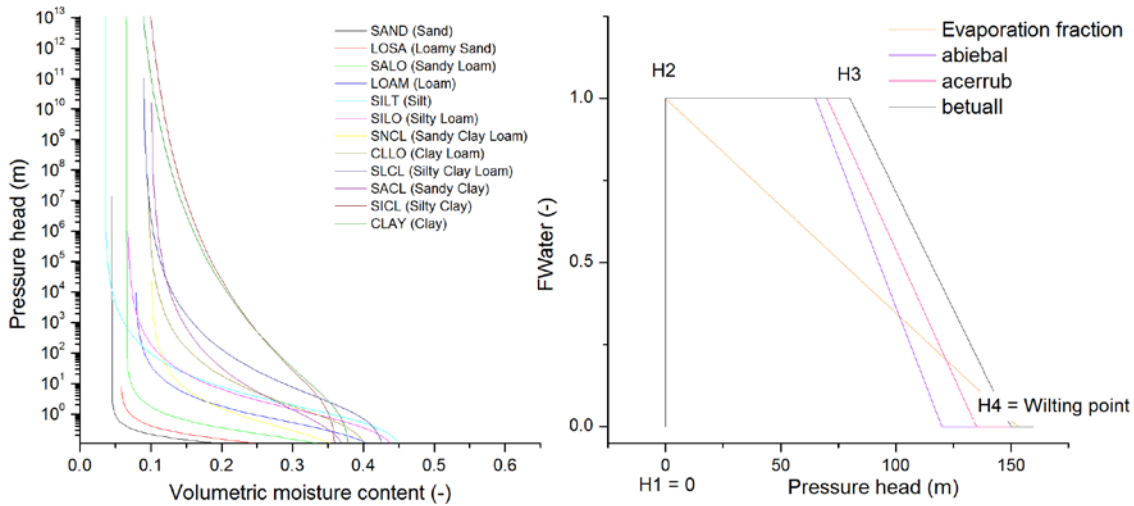


Figure 3. Default pressure head curves (left) and examples of inverse water stress (fWater, right). fWater is calculated by linear interpolation between parameters H1-H4. H1=0 is hardcoded and cannot be changed by the user. In this example all species have H1 and H2 = 0, with varied values for H3 (75 – 100) and H4 (120 – 150).

Starting with v3.0, water stress (fWater) is used as a reduction factor for the absorption of CO₂ and O₃ and the transpiration of water vapor, in addition to its role as a direct growth reduction factor. The internal variable CiModifier is an index of stomatal openness, which is equal to fWater when ozone is not simulated (see 2.4.3.2 for how ozone affects CiModifier). CiModifier acts as a linear reduction factor in the calculation of the conductance of gases between the atmosphere and the leaves.

2.4.3 Other factors

2.4.3.1 Temperature

Vapor pressure deficit is calculated from the temperature fluctuations during the day, and accounts for the effect of elevated atmospheric CO₂. CO₂ affects growth in two ways; 1) it increases water use efficiency and 2) it increases the reference rate of photosynthesis (A_{max}). The temperature reduction factor increases from 0 at P_{snTMin}, to 1 at P_{snTOpt}. Supra-optimal temperatures do not reduce the temperature reduction factor (unless DTEMP=true; see Section 7.19), but net photosynthesis is reduced by VPD effects on conductance and elevated water stress through increased evaporation and transpiration. Foliar respiration is calculated as a user-defined fraction of maximum gross photosynthesis, modified by a temperature reduction factor using a Q-10 relationship. When Wythers=true, foliar respiration is modified to account for acclimation to temperature (see Section 7.18).

2.4.3.2 Ozone

Ozone can dramatically reduce photosynthesis rates by damaging photosynthetic tissues and inhibiting stomatal function. The model will simulate these effects when it is optionally supplied with monthly cumulative growing season ozone dose in the climate file. For applications where ozone is not of interest, simply do not supply ozone inputs and no ozone calculations will be made.

The stomatal sluggishness effects of ozone are simulated by altering (increasing) CiModifier (see 2.4.2.3 for water stress influence on CiModifier) to reflect the limited ability of stomata to completely close. Changes to CiModifier (an index of stomatal openness) ripple through the model, altering the CO₂ fertilization effect (DelA_{max}), water use efficiency and water stress (through transpiration). Species-specific sensitivity to ozone-induced stomatal sluggishness is controlled by the specification of each species as Sensitive, Intermediate or Tolerant (O3StomataSens).

Ozone damage to tissues is simulated using an ozone growth reduction factor (fO₃) that reduces A_{max} to reflect decreased photosynthetic capacity. Species-specific sensitivity to ozone-induced growth reduction is controlled by a scaling parameter (O3GrowthSens) that scales the ozone effect to be higher or lower than the average effect. Technical details of the new ozone capabilities can be found in Gustafson et al (in review). Contact Eric Gustafson (egustafson@fs.fed.us).

2.5 Cohort Growth and Ageing

The model computes net photosynthesis, and gross photosynthesis is estimated by adding foliar respiration to net photosynthesis. Gross photosynthesis is used to compute transpiration. Net photosynthesis production is allocated to maintenance respiration and then to the root, foliage, wood and non-structural biomass pools, according to fixed allocation ratios. A proportion of foliage and wood biomass is also moved to the dead pools to simulate leaf-fall and stem (self-thinning)/branch/root death. Cohort ageing is simply the addition of the time step to each existing cohort age.

2.6 Cohort Senescence and Mortality

Senescence is implemented as a reduction of gross photosynthetic rate with age such that respiration eventually exceeds production and cohorts die. A cohort dies when non-structural carbon decreases to <1% of the combined structural biomass pools. The PsnAgeRed parameter controls the shape of the function used to calculate the age-related reduction factor, which reaches zero at the longevity specified in the LANDIS-II species parameter file.

2.7 Dead Biomass Decay

When a cohort dies and is removed (e.g., harvest or insect mortality), its biomass is added to one or both of the dead biomass pools: woody and leaf. Decomposition rate of woody litter depends on a decay rate that is weighted by additions of woody material and user-supplied species specific decay rates (KWdLit). Decomposition rate of non-woody litter depends on a weighted decay rate according to additions of foliage and their associated decomposition rates that depend on species specific foliage lignin concentrations (FolLignin) and ecosystem determined AET according to Meentemeyer (1978). Disturbances can alter the dead biomass pools. They can add dead biomass (e.g., wind) and/or remove dead biomass (e.g., fire may add some woody dead biomass and remove all leaf dead biomass).

2.8 References

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- Wythers, K.R., P.B. Reich, J.B. Bradford. 2013. Incorporating temperature-sensitive Q₁₀ and foliar respiration acclimation algorithms modifies modeled ecosystem responses to global change. *Journal of Geophysical Research: BioGeosciences* 118:1-14.

3 Input File - PnET-Succession

The input parameters for this extension are specified in two primary input files: the PnET-Succession input file and the PnET Species Parameters input file. The general species parameter input file used by all versions of LANDIS is also required, and is described in Chapter 6 of the *LANDIS-II Model User Guide*. The input files must comply with the general format requirements described in section 3.1 *Text Input Files* in the *LANDIS-II Model User Guide*.

3.1 Example PnET-Succession input file

```
LandisData  "PnET-Succession"

PnET-Succession      Value
>>-----
Timestep  10
StartYear  1961
SeedingAlgorithm  WardSeedDispersal
MaxDevLyrAv  6000

PNEToutputsites  PnETOutput.txt

InitialCommunities      Oconto_initial-communities.txt
InitialCommunitiesMap  Oconto _initial-communities.img

PnETGenericParameters  PnETGenericParameters.txt
PnETSpeciesParameters  PnET_Oconto_species.txt
EcoregionParameters    Oconto _EcoregionParameters.txt
DisturbanceReductions  disturbance_reductions.txt
```

3.2 LandisData

This parameter's value must be "PnET-Succession".

3.3 Timestep

This parameter is the time step of the extension. A value <5 is recommended. Random shuffling of cohort foliage into sub-canopy layers for access to light is done at each time step, so a poor random assignment in a long time step may kill cohorts that would survive with a shorter time step. Longer time steps do not markedly speed up simulations or reduce output because the internal time step of PnET-Succession is monthly, but they do reduce the frequency of outputs. Value: integer >0. Units: years.

3.4 StartYear

This parameter indicates the climate year in which simulation begins. Climate file observations prior to this date are used for spin-up (as necessary)

and observations from this date forward are used for simulations. The climate file may contain more years than will actually be used by the model. Value: integer > 0. Units: years.

3.5 SeedingAlgorithm

This parameter is the seed dispersal algorithm to be used. Valid values are "WardSeedDispersal", "NoDispersal" OR "UniversalDispersal". The algorithms are described in section 4.5.1 *Seeding of the LANDIS-II Conceptual Model Description*.

3.6 PNEToutputsites

Optional: Invoke the output extension PNETOutputsites and specify its input file (see section 10).

3.7 InitialCommunities

This parameter gives the name of the initial communities text file. This file assigns species and cohorts to each value found in the initial communities map (see section 4).

3.8 InitialCommunitiesMap

This parameter gives the file name of the initial communities map. This map contains a unique integer value for each combination of species and cohorts found on the landscape. Each cell value for an active site on the landscape must be one of the map codes listed in the initial communities input file (see section 5).

3.9 PnETGenericParameters

This optional parameter gives the name of a PnET Generic Parameter text file. Any parameter that is not species-specific, or is typically specified in the PnETSpeciesParameter file (Chapter 8), but is identical for all species can be supplied either in the default generic parameter file installed in C:\Program Files\LANDIS-II\v6\bin\extensions\Defaults\GenericPnETSpeciesParameters.txt with the rest of the model, or in a custom generic parameter file specified here. Any parameters not specified in the PnETSpeciesParameter file will be read from the custom generic file, and if not found there, will be read from the default generic file. Thus, values found in the PnETSpeciesParameter file will always take precedence over the default generic file, but cannot be duplicated in the PnETGenericParameters file. The format of the PnET Generic Parameter text file is described in section 7.

3.10 PnET Species Parameters

This parameter gives the name of the PnET Species Parameter text file. The format of this file is described in section 8.

3.11 Ecoregion Parameters

This parameter gives the name of the PnET Ecoregions Parameter text file, which is described in section 9.

3.12 Disturbance Reductions (Optional)

This parameter give the name of the Disturbance Reductions txt file, which is described in section 10. If this parameter is not supplied, all disturbances will cause 100% of cohort biomass to contribute to the dead pools, and dead pools will not be reduced by any disturbances.

4 Input File – Initial community classes

This file contains the definitions of the initial community classes. Each active site on the landscape is assigned to an initial community class. The class specifies the tree species that are present along with the particular age cohorts that are present for each species. Avoiding a proliferation of similar-aged cohorts of the same species on a site will speed run times with little effect on simulation results because those cohorts would be competing with each other.

4.1 Example File

```
LandisData "Initial Communities"

>>Old jackpine oak
MapCode 7
  acerrubr 30
  pinubank 90
  pinuresi 110 140
  querelli 40 240

>> young jackpine oak
MapCode 0
  pinubank 50
  querelli 10 70

>> young aspen
MapCode 2
  poputrem 10

>> old maple hardwoods
MapCode 55
  abiebals 10 60 120
  acerrubr 90 120
  acersacc 20 50 150 200
  betualle 40 140 200
  fraxamer 10 100 180
  piceglau 180
  querrubr 100 160 180
  thujocci 200 260
  tiliamer 20 80 150
  tsugcana 30 80 120 220 320 340

>> old pine - spruce - fir
MapCode 6
  abiebals 10 50 80
  piceglau 100 180 220
  pinuresi 140 180
  pinustro 200 280 350
```

4.2 LandisData

This parameter's value must be "Initial Communities".

4.3 Initial Community Class Definitions

Each class has an associated map code and a list of species present at sites in the class.

4.3.1 MapCode

This parameter is the code used for the class in the input map (see chapter 5). Value: $0 \leq \text{integer} \leq 65,535$. Each class map code must be unique. Map codes can appear in any order, and need not be consecutive.

4.3.2 Species Present

A list of species present at the class' sites comes after the map code. Each species is listed on a separate data line.

```
species age age age ...
```

The species name comes first, followed by one or more ages. The name and ages are separated by whitespace. An age is an integer and must be between 1 and the species' Longevity parameter. The ages can appear in any order.

```
acersacc 10 5 21 60 100
```

The list may be empty, which will result in the sites in the class being initialized with no species cohorts.

4.3.3 Grouping Species Ages into Cohorts

The list of ages for each species is grouped into cohorts based on the succession extension's timestep. This timestep determines the size of each cohort. For example, if the timestep is 20, then the cohorts are ages 1 to 20, 21 to 40, 41 to 60, etc.

Suppose an initial community class has this species in its list:

```
acersacc 10 25 30 40 183 200
```

If the succession timestep is 10, then the cohorts for this species initially at each site in this class will be:

```
acersacc 10 20 30 40 190 200
```

5 Input File – Initial community map

This is a GIS file of the initial community classes. Each active site on the landscape is assigned to a MapCode that links to the initial community class defined in the Initial Community Class Definitions. The file can be in any valid LANDIS-II map format.

6 Input File – Climate

This file contains weather records of monthly parameter values.

6.1.1 Example File #1

Year	Month	Tmax	Tmin	Prec	PAR	CO2
1700-1979	1	1.57	-7.86	96.59	493.10	335
1700-1979	2	3.46	-6.94	87.36	671.21	335
1700-1979	3	8.54	-3.16	110.79	852.52	335
1700-1979	4	15.50	2.34	110.38	925.71	335
1700-1979	5	20.37	7.69	133.10	873.77	335
1700-1979	6	24.39	12.38	123.72	872.04	335
1700-1979	7	26.28	14.81	135.81	847.05	335
1700-1979	8	25.64	14.00	109.89	842.81	335
1700-1979	9	22.07	10.13	100.57	760.33	335
1700-1979	10	16.06	4.03	89.03	624.86	335
1700-1979	11	9.83	-0.88	101.25	463.20	335
1700-1979	12	3.77	-5.33	100.48	411.67	335
1980	1	1.57	-7.21	53.32	496.07	338
1980	2	-0.37	-9.99	47.78	697.67	338
1980	3	6.85	-4.81	133.22	857.97	338
1980	4	14.52	2.06	139.30	907.75	338
1980	5	21.07	7.89	122.41	927.89	338
1980	6	23.51	9.96	137.54	925.58	338
1980	7	26.88	15.04	154.32	818.81	338
1980	8	26.42	15.58	169.70	799.45	338
1980	9	23.97	11.23	65.91	797.72	338
1980	10	14.23	2.19	76.10	634.71	338
1980	11	7.82	-2.33	93.34	445.37	338
1980	12	3.12	-6.90	47.77	468.97	338

6.1.2 Example File #2

Year	Month	Tmax	Tmin	PAR	Prec	CO2	O3
1995	1	-4.22	-13.70	262.4	9.9	367	0.0
1995	2	-4.21	-14.7	487.9	13	367	0.0
1995	3	5.08	-6.67	1012.02	35.9	367	0.0
1995	4	7.58	-3.68	741.21	49.3	367	0.0
1995	5	18.37	5.12	1021.65	103.4	367.7	2769
1995	6	27.26	12.67	1292.2	21.5	362.8	3279
1995	7	26.37	14.15	1287.3	137.2	367.9	3589
1995	8	25.87	15.41	1118.77	145.8	372.5	5686
1995	9	19.55	6.24	770.17	65.6	364.9	7723
1995	10	12.10	2.72	531.73	138	368	8167
1995	11	-1.58	-10.74	299.5	51.6	368	0.0
1995	12	-5.45	-15.41	233.53	34.5	368	0.0

6.2 Header Information

The first line of the file must contain the following text:

```
Year Month TMax TMin PAR Prec CO2 O3 <optional>
```

6.3 Observations

Subsequent lines of the file contain monthly values for each variable. Observations must appear in chronological order.

6.3.1 Year

The year of the weather observation. Alternatively, a range of years may appear, delineated by a hyphen (see example 6.1.2). Value: 4-digit integer >0.

6.3.2 Month

The month of the weather observation. Value: $1 \leq \text{integer} \leq 12$.

6.3.3 TMax

The maximum temperature observed in the month. Value: decimal. Units: degrees C.

6.3.4 TMin

The minimum temperature observed in the month. Value: decimal. Units: degrees C.

6.3.5 PAR

Mean monthly value of Photosynthetically Active Radiation during daylight hours. Value: decimal ≥ 0.0 . Units: User choice. Typically $\mu\text{mol}/\text{m}^2/\text{sec}$ or W/m^2 . The units for the half-saturation constant (SpeciesParameter file) must be the same as PAR. **THE MODEL WILL NOT CHECK TO ENSURE THAT THE UNITS ARE THE SAME.** This is a user responsibility.

6.3.6 Prec

The sum of precipitation observed in the month. Value: decimal ≥ 0 . Units: mm.

6.3.7 CO2

Mean monthly atmospheric CO₂ concentration. Value: decimal > 0 . Units: ppm.

6.3.8 O3 (Optional)

Cumulative atmospheric ozone (O₃) dose over 40 ppb (CumD40) for the growing season. Computed by subtracting 40 from each hourly O₃ value and summing non-negative values for all hours between 0800 and 1900 hours in the month. Each monthly total is added to the previous monthly total to give the cumulative growing season hourly dose through the current month. Value: decimal ≥ 0 . Units: ppb-h.

7 Input File – Generic PnET Species Parameters

This file contains PnET parameters that are not species-specific or are identical for all species. Only parameters that are not described in Chapter 8 are described here. Parameters may appear in any order. **NOTE:** Any of these parameters may instead be set in the PnETGenericDefaultParameters.txt file in the Defaults folder found where PnET-Succession is installed (usually in C:\Program Files\...\extensions\). Parameters set here will over-ride settings in the PnETGenericDefaultParameters file. Also, most (but not all) of these parameters may instead appear in the PnETSpeciesParameter file (Section 8), but may not appear in both files.

7.1 Example file:

```
LandisData PnETGenericParameters

PnETGenericParameters Value
>>-----
MaxCanopyLayers      2
MaxDevLyrAv          6000
IMAX                  10
PreventEstablishment true
DVPD1                 0.05
DVPD2                 2
BFolResp              0.1
MaintResp             0.002
TOroot                0.02
TOwood                0.01
Q10                   2
FolLignin             0.2
KWdLit                0.01
InitialNSC            7
CFracBiomass          0.45
PrecipEvents          11
Wythers               true
DTEMP                 true
```

7.2 LandisData

This parameter's value must be "PnETGenericParameters".

7.3 PnETGenericParameters

This keyword must be followed by "Value".

7.4 MaxCanopyLayers

Optional parameter that caps the number of canopy layers that can be implemented. Typically, forest canopy layers will not exceed 5 and applying many canopy layers slows the model dramatically. The number of canopy layers should primarily be regulated through MaxDevLyrAv, but when MaxDevLyrAv is given low values, the result would otherwise be an extreme number of canopy layers. MaxCanopyLayers has a default value of 5.

7.5 MaxDevLyrAv

This optional parameter is used to lump species-age cohorts into canopy layers, and specifies the maximum variation of cohort biomass that can occur within a canopy layer. It is given a default value of a maximum float, which results in a single canopy layer regardless of biomass distribution amongst subcanopy layers (see section 2.4.1).

7.6 IMAX

Optional: Each cohort is subdivided into a number of layers (IMAX) for integration. In PnET (Aber and Federer, 1992), the number of subcanopy layers was fixed at 50. Reducing IMAX saves computation time, with robust results when $IMAX \geq \sim 5$ (De Bruijn et al. 2014). When omitted, the model uses the default $IMAX=10$.

7.7 DVPD1, DVPD2

Coefficients for converting vapor pressure deficit (VPD) to DVPD according to $DVPD = 1 - DVPD1 * vpd^{DVPD2}$ (photosynthesis reduction factor due to vapor pressure). Value: decimal. Units: kPa⁻¹.

7.8 BFolResp

Base Foliar Respiration Fraction - Foliar respiration as a fraction of maximum photosynthetic rate. Value: $0.0 \leq \text{decimal} \leq 1.0$. Units: proportion.

7.9 MaintResp

Loss of NSC due to maintenance respiration. This rate is modified by temperature using a Q10 relationship, and is applied to the biomass pool monthly. Value: $0.0 \leq \text{decimal} \leq 1.0$. Units: proportion of NSC lost per month.

7.10TORoot/TOWood

Turnover of Root/Wood - Fraction of root/wood biomass lost per year to damage, breakage or death. Value: $0.0 \leq \text{decimal} \leq 1.0$. Units: proportion per year.

7.11Q10

Respiration Q_{10} value for foliar respiration, a measure of the rate of change of respiration when temperature is increased by 10 °C. Value: $0.0 \leq \text{decimal} \leq 10.0$. Units: none.

7.12FolLignin

Mass fraction of lignin in foliage tissue. Value: $0.0 \leq \text{decimal} \leq 0.8$. Units: gr/gr.

7.13KWdLit

Annual decomposition rate (decay constant, k) of woody litter. Value: $0.0 \leq \text{decimal} \leq 0.4$. Units: proportion per year.

7.14InitialNSC

Amount of NSC assigned to newly established cohorts. Value: integer > 0. Units: g.

7.15CFracBiomass

Carbon fraction of biomass by weight. Value: $0.0 \leq \text{decimal} \leq 1.0$. Units: proportion.

7.16PrecipEvents

Monthly total precipitation is evenly divided among this number of events to allow cohorts more opportunities to compete stochastically for incoming water. Lower values tend to reduce the competitiveness of species with lower H3/H4 values. Default=11. Value: decimal ≥ 1.0 . Units: count.

7.17PreventEstablishment

Boolean variable turning establishment on or off. Value= “true” or “false”.

7.18 Wythers

Boolean variable turning the Wythers correction on or off. The Wythers algorithm accounts for acclimation of foliar respiration to elevated temperatures (Wythers et al 2013). Value: true/false.

7.19 DTEMP

Boolean variable turning the PnET-II DTEMP temperature reduction factor (Aber and Federer 1992) on or off. A value of “true” uses the DTEMP function, which reduces NetPsn symmetrically from 1.0 at PsnTOpt to 0.0 at both PsnTMin and PsnTMax. PsnTMax is computed as $PsnTOpt + (PsnTOpt - PsnTMin)$. A value of “false” will use the original PnET-Succession (v1.0) function that behaves the same as DTEMP at temperatures below PsnTOpt, but does not reduce NetPsn at temperatures above PsnTOpt, relying solely on VPD-driven reductions to drop NetPsn to zero at about 40 °C. DTEMP produces somewhat more of a NetPsn penalty above PsnTOpt for species with PsnTOpt <~24 °C. The difference between the functions is small for species with PsnTOpt >24 °C. Value: true/false.

8 Input File – PnET Species Parameters

These parameter values typically vary by species. If they do not, they may more conveniently be placed in the PnETGenericParameters file (Section 7).

All parameters for a species appear on a single line. Parameters may appear in any order.

8.1 Example file:

LandisData PnETSpeciesParameters

```

PnETSpeciesParameters  FolN  SLWmax      SLWDel      TOfol  AmaxA  AmaxB
      HalfSat    H3    H4    PsnAgeRed  PsnTMin    PsnTOpt    k
      DNSC  FracBelowG  EstMoist  EstRad      FracFol    FrActWd
CO2HalfSatEff  O3StomataSens  O3GrowthSens      FolNInt    FolNSlope

abiebal    1.5    160    0    0.25  5.3    21.5  150    150    275    5    2
      19    0.5    0.05  0.25  10    3    0.053  0.00002  0.5  Sensitive
      2.0    0.8    0.4

acerrub    2.5    65    0.2    1    -46    71.9  200    150    500    5    4
      26    0.58  0.05  0.33  5    5    0.028  0.00004  0.0  Sensitive
      2.0    0.5    1.0

acersac    2.4    50    0.2    1    -46    71.9  100    150    275    5    2
      23    0.58  0.05  0.33  10    1    0.02  0.00002  0.0  Tolerant
      0.0    0.8    0.4
    
```

8.2 LandisData

This parameter's value must be "PnETSpeciesParameters".

8.3 PnETSpeciesParameters (species name)

The species name as it appears in the species parameter input file (see Chapter 6 of the *LANDIS-II Model User Guide*).

8.4 FolN

Foliar nitrogen content (%). Value: 0<decimal <10. Units: %.

8.5 SLWmax

Maximum specific leaf weight at the top of canopy. Value: 0<decimal <1000. Units: g/m².

8.6 SLWDel

Rate of change in specific leaf weight from the top of a canopy layer to the bottom. Set to zero to make SLW constant throughout a canopy layer. Value: $0.0 \leq \text{decimal} \leq 2$. Units: g^{-1}fol .

8.7 Tofol

Turnover of foliage - Fraction of foliage biomass lost per year. Typically the reciprocal of leaf longevity. Value: $0.0 \leq \text{decimal} \leq 1.0$. Units: proportion per year.

8.8 AmaxA

Intercept of relationship between foliar N and maximum net photosynthetic rate. Units: $\text{nmol CO}_2 \text{ g}^{-1} \text{ leaf s}^{-1}$. Value: $-500 < \text{decimal} < +500$

8.9 AmaxB

Slope of relationship between foliar N and maximum net photosynthetic rate, such that $A_{\text{max}} (\text{nmol CO}_2 \text{ g}^{-1} \text{ leaf s}^{-1}) = A_{\text{maxA}} + A_{\text{maxB}} * \text{FoliarN}$. Units $\text{nmol CO}_2 \text{ g}^{-1} \text{ leaf s}^{-1}$. Value: decimal > 0 .

8.10HalfSat

Half saturation light level for photosynthesis. Lower values reflect more shade tolerance. Value: integer > 0 . Units: User choice. Typically $\mu\text{mol}/\text{m}^2/\text{sec}$ or W/m^2 . The units of PAR in the climate input file must be the same as HalfSat. **THE MODEL WILL NOT CHECK TO ENSURE THAT THE UNITS ARE THE SAME.** This is a user responsibility. Note: HalfSat is the only parameter that determines shade tolerance in PnET-Succession; the ShadeTolerance parameter required in the LANDIS-II species file is ignored by PnET-Succession.

8.11H2, H3, H4

Water stress parameters according to Feddes et al. (1978). See Section 2.4.2.3. H1 is hardcoded at 0 meter pressure head. H2, H3 and H4 should be successively larger positive values. Note that this is the absolute value of values usually reported in the literature. Units: m pressure head.

8.12PsnAgeRed

Reduction factor reducing leaf photosynthesis rate as cohorts age, with $f_{\text{Age}}=1.0$ at age 1 and $f_{\text{Age}}=0.0$ at the longevity specified in the LANDIS-II species parameter file. Longevity should be specified as longevity under

optimal conditions because the various reduction factors will combine to almost always result in cohort death prior to the specified longevity age. A value <1.0 results in a rapid initial decline in max photosynthesis with age, a value of 1.0 results in a linear decline and a value >1.0 results in slow initial decline, according to $y=(age/longevity)^{PsnAgeDecline}$. Cohorts die when NSC is $<1\%$ of the value of the other biomass pools combined at the end of a calendar year. Value: $0.0 < \text{decimal} < \text{infinity}$. Units: proportion per year.

8.13 PsnTMin

Minimum temperature for photosynthesis. Value: decimal ≥ 0.0 . Units: °C.

8.14 PsnTOpt

Optimal temperature for photosynthesis. Value: decimal ≥ 0.0 . Units: °C.

8.15 k

Canopy light attenuation constant (light extinction coefficient). Value: $0.0 \leq \text{decimal} \leq 1.0$. Units: none.

8.16 DNSC

Proportion of NSC relative to total active biomass that will be maintained as long as net photosynthesis exceeds maintenance respiration. Value: $0.0 \leq \text{decimal} \leq 1.0$. Units: proportion of active biomass.

8.17 FracBelowG

Fraction of non-foliar biomass that is belowground (root pool). Allocations vary at each time step to maintain this fraction. Value: $0.0 \leq \text{decimal} \leq 1.0$. Units: proportion.

8.18 EstMoist

Tuning parameter to control the sensitivity of establishment (Pest) to soil moisture. Calculated using $fWater^{EstMoist}$ where $fWater$ = the growth response to sub, or supra optimal water content according to Section 2.4.2.3 and Figure 3 (right pane). High values make establishment more sensitive to moisture stress. A value of 1.0 results in a linear relationship between moisture stress and Pest, and little additional effect occurs with values over 50 . Value: $0.0 \leq \text{decimal}$. Units: unitless.

8.19EstRad

Tuning parameter to control the sensitivity of establishment (Pest) to light level (radiation). Calculated using $(\text{sub-canopy radiation}/(2*\text{HalfSat}))^{\text{EstRad}}$. High values make establishment more sensitive to radiation stress. A value of 1.0 results in a linear relationship between light availability and Pest, and little additional effect occurs with values over 50. Value: $0.0 \leq \text{decimal}$. Units: unitless.

8.20FracFol

Fraction of the amount of active woody biomass (above and belowground) that is allocated to foliage per year. The active fraction of wood is calculated by the model using FracActWd. Value: $0.0 \leq \text{decimal} \leq 1.0$. Units: proportion per year.

8.21FrActWd

Shape parameter of negative exponential function that calculates the amount of woody biomass that has active xylem capable of supporting foliage. All wood is active when the parameter =0.0, and increasing values decrease the fraction of active wood as biomass increases according to: $\text{active_wood} = e^{-\text{FrActWd} * \text{biomass}}$. Value: $0.0 \leq \text{decimal} \leq 0.4$. Units: unitless.

8.22CO2HalfSatEff (Optional)

Slope coefficient used to reduce HalfSat (increase shade tolerance) as CO₂ concentration increases. Value: $\text{decimal} \leq 0.0$. Units: unitless. Default=0.0. Set to zero to turn off this effect. See PnET-Succession function worksheet.xlsx to see how the parameter affects HalfSat.

8.23O3StomataSens (Optional)

Categorical parameter indicating the species' susceptibility of the stomata to ozone-induced sluggishness. Values: one of – Sensitive, Intermediate, Tolerant.

8.24O3GrowthSens (Optional)

Scaling parameter controlling the species' susceptibility to ozone-induced tissue damage. Zero indicates no sensitivity to ozone, 2.0 indicates twice as much sensitivity as 1.0, 3.0 indicates three times as much sensitivity as 1.0. Value: $0.0 \leq \text{decimal}$. Units: unitless. Default=0.0. Set to zero to turn off effect.

8.25 MaxFolN, FolNShape (Optional)

Parameters controlling the dynamic response of foliar nitrogen (FolN) to light according to:

$$\text{AdjFolN} = \text{FolN} + ((\text{MaxFolN} - \text{FolN}) * (\text{fRad} ^ \text{FolNShape}))$$

FolN is used as the minimum bound for AdjFolN. Values: $0.0 \leq \text{decimal}$.
Units: %N by weight. Omit these parameters to turn off effect. See PnET-Succession function worksheet.xlsx to see how the parameters affect FolN.

8.26 MaxFracFol FracFolShape (Optional)

Parameters controlling the dynamic response of fraction of foliage (FracFol) to light according to:

$$\text{AdjFracFol} = \text{FracFol} + ((\text{MaxFracFol} - \text{FracFol}) * (\text{fRad} ^ \text{FracFolShape}))$$

FracFol is used as the minimum bound for AdjFracFol. Values: decimal ≥ 0.0 . Units: proportion, unitless. Defaults=1.0, 0.0. Omit these parameters to turn off effect. See PnET-Succession function worksheet.xlsx to see how the parameters affect FracFol.

9 Input file - Ecoregion parameters

9.1 Example file:

```
LandisData EcoregionParameters
EcoregionParameters SoilType Latitude RootingDepth
PrecLossFrac LeakageFrac PrecIntConst SnowSublimFrac
ClimateFileName
ecol SALO 46 1000 0.0 1.0 0.11 0.15 Climate-input.txt
```

9.2 LandisData

This parameter's value must be "EcoregionParameters".

9.3 EcoregionParameters (ecoregion name)

The ecoregion name given must be defined in the ecoregion input file (see chapter 7 in the *LANDIS-II Model User Guide*). Ecoregions may appear in any order.

9.4 SoilType

Abbreviation for the predominant soil type in the ecoregion. Soil type is used in the model to determine the water retention curve of the soil (see Figure 3 and section 2.4.2.3). Soil type names can be any character string that also appears in the corresponding soil parameters file (SaxtonAndRawlsParameters). A default version of this parameter file installs with the extension (C:\Program Files\LANDIS-II\6\bin\extensions\Defaults), and supports the following soil types: SAND (sand), LOSA (loamy sand), SALO (sandy loam), LOAM (loam), SILO (silt loam), SILT (silt), SNCL (sandy clay loam), CLLO (clay loam), SLCL (silty clay loam), SACL (sandy clay), SICL (silty clay), CLAY (clay), BEDR (stone). These categories correspond with FAO soil types. Value: 4-letter string, case sensitive.

9.5 Latitude

This parameter is the approximate latitude of the ecoregion, used to compute daylength. Value: -90 < integer < 90. Units: degrees of latitude.

9.6 RootingDepth

This represents the rooting zone, the soil depth to which roots typically penetrate. Using the bucket-model analogy, this determines the depth of the “bucket.” Value: integer ≥ 0 . Units: mm.

9.7 PrecLossFrac

Precipitation Loss Fraction. Proportion of precipitation that does not enter the soil (e.g., runoff not due to soil saturation). Value: $0.0 \leq \text{decimal} \leq 1.0$. Units: proportion.

9.8 LeakageFrac

Leakage Fraction. Proportion of soil water above field capacity that is subject to “fast leakage” (see Figure 2). Fast leakage is the drainage of infiltrated water that leaks out of the rooting zone soil more quickly than plants can access the water. Therefore, water lost to fast leakage is not available for transpiration. A value of 1.0 for LeakageFrac will cap plant available water at field capacity. Value: $0.0 \leq \text{decimal} \leq 1.0$. Units: proportion.

9.9 PrecIntConst

This represents the rate of precipitation interception for each unit of leaf area index, which is lost to evaporation, and therefore does not enter the soil. See the interception equation in section 2.4.2.1. Value: decimal ≥ 0.0 . Units: unitless.

9.10 SnowSublimFrac

Fraction of the snowpack that sublimates. This fraction is removed just prior to snowmelt. Recommended default is 0.15 (Hood et al 1999). Value: $0.0 \leq \text{decimal} \leq 1.0$. Units: proportion. Default = 0.15.

9.11 ClimateFileName

This parameter gives the name of the climate file for the ecoregion. The user may specify the same file for multiple ecoregions.

10 Input File – DisturbanceReductions

This file contains parameters that define how different disturbances impact the wood, roots and foliage being added to or removed from the dead pools.

10.1 Example file:

```
LandisData  DisturbanceReductions
>>-----
DisturbanceReductions  fire  wind  harvest  bda
WoodReduction          0.33  0    0.70    0
FolReduction           1    0    0       0
RootReduction          0    0    0       0
DeadWoodReduction      0.7  0    0       0
LitterReduction        0.9  0    0.1    0
```

10.2 LandisData

This parameter's value must be "DisturbanceReductions".

10.3 DisturbanceReductions Table

This table contains the proportional reductions that should be applied to wood, root and foliage biomass as well as dead wood and litter when different disturbance types are applied. The first value in the table should be 'DisturbanceReductions'.

The columns of the table represent the different disturbance types. These can be any disturbance types that are in use in the model. Including disturbance types in this table that are not used in a given simulation scenario is acceptable and has no impact.

The rows of the table represent the different impacts on biomass or dead pools that disturbances might have. The five rows should be labeled: 'WoodReduction', 'FolReduction', 'RootReduction', 'DeadWoodReduction' and 'LitterReduction'. The values for WoodReduction, RootReduction and FolReduction represent the proportion of biomass (wood, root or foliage) that gets reduced prior to the transfer of biomass into the dead wood (wood and root) or litter (foliage) pools. These values represent how much of the cohorts are consumed by the disturbance (e.g., fire), or removed from the site as part of the disturbance (e.g., harvest).

The values for DeadWoodReduction and LitterReduction represent the proportion of the dead pool mass that is consumed or reduced due to the disturbance. The reductions of the dead pools are applied to the existing pool masses prior to additions caused by a new disturbance.

11 Input File - Output-PnET

This file contains parameters for the optional PnET-Succession output extension.

11.1 Example file:

```
LandisData "Output-PnET"  
Timestep 10  
Species All  
Biomass output/biomass/{species}/Biomass_{timestep}.img  
FoliageSenescence  
output/Senescence/{species}/FolSenescence_{timestep}.img  
WoodySenescence  
output/Senescence/{species}/WoodSenescence_{timestep}.img  
AnnualPsn output/AnnualPsn/{species}/Psn_{timestep}.img  
BelowgroundBiomass output/BGB/BGB-{timestep}.img  
WoodyDebris output/WoodyDebris/WoodyDebris-{timestep}.img  
Litter output/NonWoodyDebris/Litter-{timestep}.img  
CohortBalance output/TotalCohorts.txt  
Water output/SoilWater/water_{timestep}.img
```

11.2 LandisData

This parameter's value must be "Output-PnET".

11.3 Timestep

This parameter is the time step of the extension. Value: integer > 0. Units: years.

11.4 Species

This keyword lists the species for which data are to be output. Value: space-delimited list of species names or the generic term All.

11.5 Map Name Template

Subsequent input lines list the variables to be output along with the output file naming rules. List one variable per line. Each line begins with the variable to be output, followed by a description of where the output files are placed and

their naming convention. The first portion lists the directory where the files should be placed, relative the location of the scenario text file (e.g., `output/agemaps/`). The second portion includes one or two variables (depending on the variable) for creating file names. `{species}` will be replaced with the species name. `{timestep}` will be replaced with the output time step. Other characters can be inserted as desired. An appropriate file extension (e.g., `.img`, `.txt`) should also be included for the type of output. For example:

```
Water output/SoilWater/water-{timestep}.img
```

Note: Most output maps are not compatible with the .gis map output type because the values are not integers.

Here are the valid variable names and the required naming variables and file type of the output files: All variables are optional.

Biomass, `{species}`, `{timestep}`. Map. Units: g/m². Biomass is the sum of wood and roots, but not foliage biomass.

AbovegroundBiomass, `{timestep}`. Map. Units: g/m².

AbovegroundBiomass includes aboveground wood and foliage.

BelowgroundBiomass, `{timestep}`. Map. Units: g/m².

BelowgroundBiomass includes roots only.

WoodySenescence, `{species}`, `{timestep}`. Map. Units: g/m². Outputs woody biomass of the species added to woody dead pool.

FoliageSenescence, `{species}`, `{timestep}`. Map. Units: g/m². Outputs foliage biomass of the species added to litter dead pool.

LeafAreaIndex, `{species}`, `{timestep}`. Map. Units: m².

Establishment, `{species}`, `{timestep}`. Map. Units: # cohorts

EstablishmentProbability, `{species}`, `{timestep}`. Map. Units: probability.

MonthlyNetPsn, `{species}`, `{timestep}`. Map. Units: g/m².

MonthlyFolResp, `{species}`, `{timestep}`. Map. Units: g/m².

MonthlyGrossPsn, `{species}`, `{timestep}`. Map. Units: g/m².

MonthlyMaintResp, `{species}`, `{timestep}`. Map. Units: g/m².

Water, `{timestep}`. Map. Units: mm.

SubCanopyPAR, `{timestep}`. Map. Units: W/m² or mmol/m², depending on input units.

CohortsPerSpecies, `{timestep}`. Map. Units: count.

AnnualPsn, {timestep}. Map. Units: g/m².

WoodyDebris, {timestep}. Map. Units: g/m².

Litter, {timestep}. Map. Units: g/m².

AgeDistribution, {timestep}. Map. Units: # cohorts

WoodSenescence, {species}, {timestep}. Map. Units: g/m².

FoliageSenescence {species}, {timestep}. Map. Units: g/m².

CohortBalance, {filename}. Tab-delimited text file containing landscape total or average values of the following variables for each time step.

of cohorts (landscape total)

Average Age of all cohorts on the landscape (years)

Average Biomass / site (g/m²)

Average LAI / site (m²)

Average Water / site (mm)

SubCanopy PAR / site (W/m² or $\mu\text{mol}/\text{m}^2$, depending on input units)

Litter / site (gDW/m²)

WoodyDebris / site (gDW/m²)

AverageBelowGround / site (g/m²)

AverageFoliage / site (g/m²)

AverageNSC / site (gC/m²)

AverageAET / site (mm/yr)

NOTE: for variables denoted Monthlyxxx, the first output maps (year zero) represent an average of all of spin-up, and after the first time step values are the average of all the years between time steps.

12 Input File – PNEToutputsites

This file contains parameters for the site data output extension. This extension outputs state variables each month for individual sites. This extension is used primarily for calibrating input parameters because it slows model execution.

12.1 Example file:

```
LandisData PNEToutputsites

>>PNEToutputsites MapCoordinatesX MapCoordinatesY
      MapCoordinatesMaxX      MapCoordinatesMaxY
>>-----
>>Site1      715,187.037 4,413,258.694      734284.375 4413934

PNEToutputsites Row Column
>>-----
Site1 1      1
Site2 1      2
```

12.2 LandisData

This parameter's value must be "PnEToutputsites".

12.3 PnEToutputsites

This keyword is followed by either map coordinate keywords or grid coordinate keywords (row/column). Each site (cell) to be output is listed on subsequent lines with a Site number and the appropriate coordinates (map coordinates must be compatible with the input maps). See example above for syntax.

13 Output file - SiteData Table (Optional PNEToutputsites output)

This comma-delimited table contains site-level PnET state variable values at the end of each month from the start of the spin-up period to the end of the simulation. The sites reported are specified in the input file. Values are for the entire cell and include the presence of all species and cohorts on the cell. Units for each variable are given in the header. This output is turned on in the PnET-Succession Input File by specifying the cell(s) to be output.

13.1 Time

Simulation year.

13.2 Ecoregion

Ecoregion for the cell.

13.3 SoilType

Soil type assigned to the cell's ecoregion.

13.4 NrOfCohorts

Number of cohorts (all species) occurring on the cell.

13.5 MaxLayerStdev

Maximum standard deviation of biomass of all cohorts present on the cell. Used to calculate the number of canopy layers (section 2.4).

13.6 Layers

Number of canopy layers on the cell.

13.7 PAR0

Photosynthetically Active Radiation (light) above the upper canopy layer. Same units as PAR in the input climate file.

13.8 Tday(C)

Mean air temperature (°C) in the daytime, derived from TMin and TMax from the climate file.

13.9 Precip(mm_mo)

The monthly precipitation (as read from the climate file, mm/mo).

13.10 CO2(ppm)

Monthly CO₂ concentration (as read from the climate file, parts per million)

13.11 O3(cum_ppb_h)

Monthly ozone dosage (as read from the climate file). Units should be ppb-h (see 6.3.8).

13.12 RunOff(mm_mo)

Monthly runoff that occurs from precipitation when the soil is saturated (mm/mo).

13.13 Leakage(mm)

Water lost out of the bottom of the rooting zone.

13.14 PET(mm)

Potential EvapoTranspiration. Potential evapotranspiration is computed as the value under minimum advection according to Priestley and Taylor (1972) as discussed in Brutsaert (1982, p. 217). Code from the PROGRASS model (Lazzarotto et al. 2009).

13.15 Evaporation(mm)

Precipitation lost to evaporation from the soil surface as a function of the LAI on the site.

13.16 Transpiration(mm)

Transpiration of all cohorts.

13.17 Interception(mm)

Precipitation intercepted by foliage and stems and not entering the soil.

13.18 PrecLoss(mm/mo)

Monthly precipitation runoff that occurs due to surface conditions (e.g., slope, impervious surface) when the soil is not fully saturated (mm/mo).

13.19 Water(mm)

Amount of soil water as calculated by the bulk hydrology model (mm). Note that this gives the amount of water at the end of the month. To compute the amount of water at the beginning of the month, sum water, evaporation and transpiration.

13.20 PressureHead(m)

Pressure head (at the end of the month) as calculated by the bulk hydrology model (m).

13.21 SnowPack (mm)

Water equivalent contained in the snowpack (mm).

13.22 LAI(m²)

Leaf Area Index (all species combined)

13.23 VPD(kPa)

Mean vapor pressure deficit for the month (kPa).

13.24 GrossPsn(gC/mo)

Gross photosynthesis of all species combined (gC/ m²/mo).

13.25 NetPsn(gC/mo)

Net photosynthesis of all species combined (gC/m²/mo).

13.26 MaintenanceRespiration(gC/mo)

Maintenance respiration of all species combined (gC/mo).

13.27 Wood(gDW)

Sum of aboveground woody biomass of all species (gDW).

13.28 Root(gDW)

Sum of root biomass of all species (gDW)

13.29 Fol(gDW)

Sum of foliage biomass of all species (gDW).

13.30 NSC(gC)

Sum of NSC (Non-structural carbon) of all species (gC).

13.31 HeteroResp(gC_mo)

Heterotrophic respiration (decay of dead pools).

13.32 Litter(gDW/m²)

Biomass (all species) in the litter dead biomass pool (gDW/m²).

13.33 CWD(gDW/m²)

Biomass (all species) in the coarse woody debris dead biomass pool (gDW/m²).

13.34 WoodySenescence (gDW/m²)

Total woody biomass added to the dead pool each month.

13.35 FoliageSenescence (gDW/m²)

Total litter biomass added to the dead pool each month.

13.36 SubcanopyPAR

Photosynthetically Active Radiation (light) below all canopy layers (i.e., at ground level). Same units as PAR in the input climate file.

14 Output file - CohortData Table (Optional PNEToutputsites output)

This table contains monthly PnET cohort-level state variable values for the sites specified in the input file. A file is created when a cohort is established, and the records give month-end state variable values for the cohort from establishment to death (or the end of the simulation). Files are also produced for cohorts established during the spin-up period. Units for each variable are given in the header. This output is turned on in the PNEToutputsites input file by specifying the cell(s) to be output.

14.1 Time(yr)

Simulation year.

14.2 Age(yr)

Current age of the cohort (calendar years).

14.3 TopLayer(-)

The highest layer number to which the cohort is assigned, with 0 being the lowest layer.

14.4 LAI(m²)

Leaf area index of the cohort.

14.5 GrossPsn(gC/m²/mo)

Cohort gross photosynthesis (gC/m²/mo).

14.6 FolResp(gC/m²/mo)

Cohort foliar respiration (gC/m²/mo).

14.7 MaintResp(gC/m²/mo)

Cohort maintenance respiration, including tissue repair and nutrient transport (gC/m²/mo). This amount comes out of the NSC pool.

14.8 NetPsn(gC/m²/mo)

Cohort net photosynthesis (gC/m²/mo).

14.9 Transpiration(mm/mo)

Cohort water actually lost to transpiration (mm/mo).

14.10 WUE(g/mm)

Cohort mean water use efficiency (gC/mm H₂O).

14.11 Fol(gDW/m²)

Biomass of the cohort foliage pool (gDW/m²).

14.12 Root(gDW/m²)

Biomass of the cohort root pool (gDW/m²).

14.13 Wood(gDW/m²)

Biomass of the cohort wood pool (gDW/m²).

14.14 NSC(gC/m²)

Amount of carbon in the cohort non-structural carbon pool (gC/m²).

14.15 NSCfrac(-)

Fraction of carbon in the cohort non-structural carbon pool relative to active biomass (NSC / (FActiveBiom * (wood + root+ foliage)). Cohorts die when NSCfrac is <0.01 at the end of a calendar year.

14.16 fWater(-)

Reduction factor related to water availability.

14.17 fRad(-)

Reduction factor related to light availability at the top of the canopy layer occupied by a cohort.

14.18 fOzone(-)

Reduction factor related to ozone effects.

14.19 DelAmax(-)

Enhancement factor related to CO₂ effects on photosynthesis.

14.20 fTemp_psn(-)

Reduction factor related to sub-optimal temperature for photosynthesis.

14.21 fTemp_resp(-)

Reduction factor related to temperature effects on maintenance respiration.

14.22 fAge(-)

Reduction factor for age-related declines in photosynthesis efficiency.

14.23 LeafOn(-)

Indicates growing season status. When TRUE, new foliage can be added and old foliage has not yet been dropped.

14.24 FActiveBiomass(gDW_gDW)

Fraction of active biomass. Indicates the computed fraction of wood biomass that is considered active and able to transport water to support foliage.

14.25 AdjFolN(gN_gC)

Adjusted foliar nitrogen (gN/gC). When using the optional FolNInt and FolNSlope parameters, the adjusted FolN can be different from the species FolN value, depending on canopy position and the resulting PAR. Averaged across the cohort's subcanopy layers.

14.26 CiModifier(-)

Reduction factor for gas conductance due to stomatal closure caused by water stress and modified by ozone. Value of 1.0 indicates no reduction in conductance. Averaged across the cohort's subcanopy layers.

14.27 AdjHalfSat(-)

Adjusted HalfSat. When using the optional CO2HalfSatEff, the adjusted HalfSat can be different from the species HalfSat value, depending on concentration of CO₂. Averaged across the cohort's subcanopy layers. Units are typically $\mu\text{mol}/\text{m}^2/\text{sec}$ or W/m^2 and will be the same as the input units of PAR in the climate input file and the species HalfSat value.

15 Output file – Establishment Table (Optional PNEToutputsites output)

This comma-delimited table reports site-level establishment information for each species. The reported values reflect state variables in the model at intervals of one PnET-Succession time step.

15.1 Year

Simulation year (timestep).

15.2 Species

Species.

15.3 Pest

Probability of establishment for the species during the given time step as a function of the values of water and PAR. $Pest = fRad^{EstRadSensitivity} * fWater^{EstMoistSensitivity}$.

15.4 fWater

Water availability reduction factor.

15.5 fRad

Light availability reduction factor.

15.6 Est

Indicates if an establishment of the species can occur in the time step. Actual establishment additionally requires a source tree within seeding distance.

16 Appendix. Calibration tips.

Calibration tips

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General

One of the compelling features of PnET-Succession is that its parameters are mostly empirically estimable values, and it autonomously produces very realistic growth responses under a wide variety of abiotic conditions when its parameters are set correctly. The developers of the PnET model claim (perhaps too optimistically) that PnET does not need calibration, but there are some changes that have been made to PnET-Succession to make it tractable at landscape scales that cause the model to require modest calibration. However, of the dozens of parameters used by PnET-Succession, only a few typically need calibration, and most applications can use default values for most parameters.

I calibrate each species separately, using a single cohort initialized on a single cell and grown for about 150 years. I compare simulated biomass (wood) growth through time with empirical biomass growth curves. Use the PNEToutputsites option to produce the cohort growth output files needed for calibration.

To produce predictable competitive interactions that can be controlled by intuitive modification of a small number of parameters for individual species, it is best to use common parameter values across all species as much as possible. These can be conveniently maintained (and modified as necessary) in the GenericPnETSpeciesParameters file. Other parameters vary by life history trait or growth form, and each species having a particular trait should have the same (or similar) parameter value to represent that trait. Examples of such traits include shade tolerance (HalfSat), drought tolerance (H3 & H4), extinction coefficient (k), relationship between foliar N and photosynthetic capacity (AmaxA and AmaxB), leaf weight change by canopy position (SLWdel) and fraction of foliar biomass relative to active wood biomass (FracFol). Parameters that the model is highly sensitive to (for which common values should be used as much as possible) include: MaintResp, TOrroot, TOwood, BFolResp, FracBelowG, FracFol and FrActWd.

Calibration is ideally done by modifying only FolN (to control relative productivity), FracFol (to control gross LAI and the initial growth part of the growth curve), SLWmax (to fine-tune mature LAI and the ability to compete for light), and FrActWd (which controls the amount of foliage in mature cohorts and the maximum height of the growth curve). FracFol and FrActWd can have a profound effect on the competitive ability of cohorts, so to achieve reasonable competitive interactions it is best to find a common value to use for both of these

parameters for all species having a common growth form (deciduous v. conifer), modifying them only for species that have exceptionally unusual growth curves. *FracFol* must generally be much higher for conifers because their *AmaxA* and *AmaxB* terms produce much less growth per unit of foliage. Find a value that generally works for all species of a growth form and be hesitant to modify it for individual species unless there is a compelling biological or empirical reason.

I set up a landscape with a single active cell, and initialize it with a single species at a time. I calibrate species under good to ideal growing conditions, recognizing that their growth will and should be less under poorer conditions and when competing. I calibrate on a soil with relatively high water holding capacity (e.g., SALO) and a weather stream with average or better precipitation for the regions where the species are typically found. I calibrate with *PsnTOpt* of all species set to approximate the average growing season temperature (mean of *Tmax* and *Tmin*) found in the weather stream, avoiding the hassle of creating a different weather stream for each species. The key is to calibrate under nearly ideal conditions (i.e., growing season temperatures approximating *PsnTOpt*). Thus, regardless of what the actual species *PsnTOpt* is, it will have been calibrated to grow its best when the actual temperature it experiences is near its *PsnTOpt*. I use a constant climate for calibrating, to avoid confounding the calibration by extreme events. Again, nearly ideal conditions are the goal. Consequently, I am content if my calibrated curve produces growth somewhat better than the average of my empirical growth data. Use CO₂ (and O₃ if applicable) values typical of those experienced by the trees measured for your empirical biomass growth curves.

The calibration process is expedited by plotting simulated wood biomass against empirical growth data in a spreadsheet. I create a separate spreadsheet tab for each species and also plot foliage biomass and LAI. Other variables for which empirical data are available can also be plotted against each other. Using a macro, I can quickly copy and paste data from the cohort output file of PnET-Succession to iteratively achieve the desired behavior through multiple model runs.

MaintResp is a critical parameter for PnET-Succession because it is the primary determinant of cohort growth limitations and death, and growth is highly sensitive to variation in this parameter. Unfortunately, this parameter is rarely known empirically, so it must be calibrated. If *MaintResp* is too low, cohorts will never die from stress and growth will be virtually unconstrained. If *MaintResp* is too high, growth will quickly level off because of high maintenance costs and cohorts will be highly susceptible to stress. For most studies, competitive outcomes should be a function of competition for light and water, not from a difference in maintenance costs. Therefore, it is recommended to find a value for *MaintResp* that works across life history traits and growth forms. This is fairly easily done. Choose some representative species having generic growth parameters (including great longevity) and simulate their growth curves, searching for a value of *MaintResp* that flattens (levels off)

the growth curve after a few decades. Then gradually reduce MaintResp until the growth curve takes the shape of that typically seen in the growth curves of your long-lived species. Select a value of MaintResp that produces acceptable behavior for all life forms, etc., and use it for all species. In summary, you are searching for a value that is as high as it can be without creating a flattened growth curve.

Useful empirical data needed for calibration.

1. The range of FolN for each species across sites, age, canopy position. This is a great starting point and helps put bounds on acceptable values, but it is important to recognize that productivity is closely related to FolN in PnET, so it is more important that FolN reflect relative productivity among species rather than matching empirical values closely. That said, it is usually possible to select a value of FolN that is within the range of empirically measured values. If you have empirical values of Amax, use your values of AmaxA and AmaxB (or see Fig. 2 in Aber et al 1996) to estimate the FolN that produces that Amax value. NOTE: if you plan to implement dynamic FolN (FolNInt and FolNSlope set to values other than default), then be sure to set FolNInt and FolNSlope to values you will use in your simulations.
2. Species SLWmax helps determine LAI. Thicker leaves (higher SLW) reduce LAI. LAI determines the ability of a cohort to compete for light, so it is important to calibrate so that LAI approximates empirical values. Again, it is more important to get LAI approximately right than to keep SLWmax within the empirical range.
3. Growth curves by species. Growth and yield tables are useful for this purpose and volume measures can be converted to biomass using specific gravity values for the species (Miles and Smith 2009). Ensure that units are the same as output by PnET-Succession. Most growth and yield tables account for only the merchantable part of trees, so consider them to be near the lower boundary of the woody biomass output of PnET-Succession. The primary feature of the growth curve that you should calibrate to is the maximum height of the curve. The rate of initial increase can be matched quite readily using FracFol, but if you have different values of FracFol across species, the lower valued species will compete poorly. So, avoid the temptation to match the initial rate of increase and focus instead on the height of the curve. Make modest exceptions for species that tend to outgrow their competitors when establishing on open sites (e.g. pioneer species) and for species that have unusually slow growth compared to competitors with similar life history traits (e.g., white cedar, hemlock). The shape of the senescence decline can be controlled by PsnAgeRed, but again resist the temptation to calibrate this individually for each species unless the species has well-known anomalous senescence characteristics.

Calibration procedure

1. First, set parameter values that are known from the literature (e.g., TOFol, FolN, SLW, HalfSat, PsnTMin, PsnTOpt, k, etc.). When there is considerable range in empirical values, begin with an intermediate value. HalfSat should be varied to reflect shade tolerance, because the LANDIS-II shade tolerance parameter has no effect in PnET-Succession. Some PnET parameters (e.g., SLWDel, AmaxA, AmaxB, Q10, DVPD1, DVPD2) are hard to estimate and most studies use generic values (e.g., Aber et al 1995, Ollinger and Smith 2005). Decide whether you will use the Wythers=TRUE option; I recommend using it. NOTE: if you use dynamic FolN, you should start with FolN values near the bottom of their empirical range.
2. Use the GenericPnETSpeciesParameters file for all parameters that are never varied among species. Set parameters that will be held constant for your particular experiment or study (e.g., TOroot/wood, BaseFolResp, InitialNSC, etc.) Again, it is advisable to hold as many parameters constant across species as possible to allow you less confounded control of competitive interactions with the remaining parameters.
3. PsnTMin controls the length of the growing season. You should verify that the appropriate months are active (LeafOn=TRUE). PsnTMin should vary coarsely according to leaf-on and leaf senescence dates, and typically ranges from 0-3 °C for temperate species. PsnTMin will also control how productive the species is at the beginning and end of the growing season, and will produce a growth response to shifts in temperature even when the number of growing season months is unchanged. Similarly, in some years you may get some modeled photosynthesis activity in a month when the species is not typically active, but this is not a problem as long as NetPsn is quite low in those months.
4. In lieu of empirical values, PsnTOpt can be estimated using the average mid-summer temperature at the center of the species' range. Note that temperatures above PsnTOpt will limit photosynthesis only through VPD effects. Use the DTEMP=true option to impose a greater heat-related penalty on species with PsnTOpt <24 °C. Use the PnET-Succession function worksheet to explore how the DTEMP option affects photosynthesis.
5. Calibration tuning is best done by matching simulated wood biomass increase to empirical biomass values for a species through time. If your empirical values represent something less than whole tree aboveground biomass, your tuned values should be higher than the empirical values. Your goal is not to match the empirical curve exactly, but to approximate it. Simulate a monoculture and plot Wood and Root+Wood (whole tree) biomass through time. There are some published estimates of whole tree biomass through time by species groups to provide some indication of belowground biomass (e.g., Smith et al 2006). Comparison of empirical aboveground and whole tree biomass can help you estimate the FracBelowG parameter. The calibration simulations should run for at least as many years as your empirical data, and it may be informative to see how the model extrapolates growth beyond your empirical data. When you find it difficult to match an empirical growth curve without setting a parameter outside its empirical range or to a very different value than similar species, modifying FracBelowG (or TOWood or

TORoot) can produce a marked effect on the growth curve with a small change in value. An increase in one pool will reduce the other pool. It would be beneficial to have some justification for your selected value from empirical evidence.

6. Choose a single soil type for calibration of all species, preferably a soil type that is both common and productive. Ultimately, growth is limited by water, so you want to calibrate under somewhat ideal conditions to reflect realistic competition for water. I typically do not choose the soil type with the greatest water holding capacity, but one that is above average. Soil water is determined by inputs (precipitation) and outputs (PrecLossFrac, percolation out of the rooting zone (controlled by SoilType) and transpiration). Tuning of soil water is done primarily with PrecLossFrac, LeakageFrac and SoilType, which assumes that transpiration is correct if the photosynthesis and growth behavior is correct. PrecLossFrac typically represents water lost where slope is sufficient for water to run off before it can enter the soil. You should calibrate for a slope condition that is flatter than average in your study area.
7. Calibrate all species under optimal temperature and precipitation conditions, which will result in growth reductions under other conditions. If you don't uniformly calibrate species under optimal conditions, then their competition will be unrealistic and unpredictable during simulations. This is most easily done by using a fixed annual weather stream (long-term monthly averages), calculating the mean growing season temperature (mean of TMin and TMax though the growing season months), and setting PsnTOpt of ALL species to the July value of TMax (for calibration ONLY). To ensure comparability of tuned parameters, use a common PsnTMin also. Use typical monthly precipitation values. When you finish calibration, remember to set PsnTOpt (and PsnTMin) of each species back to its real value. During your simulation applications, whenever a species receives a monthly temperature that is equal to its real PsnTOpt, it will then perform as calibrated and growth will decline as temperatures depart from its optimal temperature.
8. You will need starting parameter values. Here are some generic ones for temperate forest species that are widely used in PnET-Succession simulations:
 - a. SLWDel: 0.0 for evergreen, 0.2 for deciduous
 - b. AmaxA: 5.3 for evergreen, -46 for deciduous
 - c. AmaxB: 21.5 for evergreen, 71.9 for deciduous
 - d. BFolResp: 0.1
 - e. k: 0.5 for evergreen, 0.58 for deciduous
 - f. DNSC: 0.05
 - g. Q10: 2
 - h. DVPD1: 0.05
 - i. DVPD2: 2
 - j. IMAX: 5-10 (there is a significant performance cost with values higher than these)
 - k. TOWood: 0.01
 - l. TORoot: 0.02

Here are some other values I have used, but which you may need to modify for your purposes:

- a. HalfSat: 300 ($\mu\text{mol/s}$) for shade-intolerant, 100 for shade-tolerant; I use a gradient across 5 classes.
 - b. H3/H4: 100/140 for drought intolerant, 118/153 for drought tolerant; I use a gradient across 4 classes.
 - c. MaintResp: 0.002
 - d. PsnAgeRed: 5
 - e. FracBelowG: 0.33
 - f. FracFol: 0.10 for evergreen, 0.02 for deciduous
 - g. FracActWd: 0.00004
 - h. PrecipEvents: 9-11
 - i. EstMoist, EstRad: 2.8
9. Relative growth rate among species should be controlled with FolN. Conifers and deciduous species must have FolN scaled separately because they use different values of AmaxA and AmaxB. Unless specific, high quality estimates of AmaxA and AmaxB are known, it is recommended to use the values commonly used in PnET publications (see above). Published values of FolN are commonly available, but use these only as a starting point. **In PnET-Succession, FolN is the primary parameter that controls relative growth rate (Amax) among species.** Set FolN of your suite of species based on what is known about relative growth rates among your species. Be aware that differences in shade tolerance and drought tolerance will prevent FolN from scaling perfectly with growth rate among all species. I have found that FolN should be increased ~ 0.1 for each decrease in shade tolerance class (of 5 classes) to produce approximately the same growth rate. However, you should be able to use a FolN value for each species that is within the range of empirical values. If you find you must use a FolN value that is out of range, modify other parameters to bring it within range, starting with FracFol, FracActWd or FracBelowG. Don't forget that you will have a different range of FolN values for species with different AmaxA and AmaxB values. If you are using dynamic FolN, check the AdjFolN values to see if they vary within empirical limits.
10. Foliage biomass is controlled by FracFol and FrActWd, and you will find that FracFol also tightly controls the lag time of significant biomass increase (early years). Because this lag time has a strong effect on competitive ability in PnET-Succession, it is recommended that you attempt to use common (or very similar) values of FracFol and FrActWd. It may be preferable to have similar lag times than to match empirical lag times closely; this will produce better competitive interactions in the model. Super slow-growing species (e.g., white cedar, black spruce) may be an exception. Often empirical growth curves are measured in mixed forests, and shade-tolerant species (e.g., eastern hemlock) will tend to have longer lag times than when grown in the open as in the calibration simulations. You should monitor the shape of the foliage curve along with

the biomass curve. If FrActWd is too high, foliage biomass will decline markedly with age, which is not likely realistic. If it is too low, foliage biomass will increase indefinitely, which is also not realistic. Experience shows that a value of 0.00004 will produce a level or slightly declining foliar biomass after about 50 years.

11. Before adjusting the height of the biomass curve, verify that LAI is not way out of bounds for the species. LAI is controlled by FracFol, FrActWd, SLWmax (and SLWdel). FracFol directly controls the amount of foliar biomass, and LAI is calculated by dividing foliage biomass by SLWmax. Note that FolN and SLWMax are generally inversely correlated in the literature. SLWdel controls the reduction of SLW from top to bottom in the canopy, and can have a large effect on LAI when there is a lot of foliage biomass. To estimate whether SLW at the bottom of the canopy may be reasonable, use $SLW_{min} = SLW_{max} - SLW_{del} * \text{foliage biomass}$. FrActWd controls the amount of foliage biomass later in life, and has an important effect on maximum LAI achieved; use this to control LAI if SLWmax values are well established empirically. In lieu of empirical values, LAI should generally range between 2-4 for shade intolerant species and 4-6 for shade tolerant species, with values over 7 not unreasonable for highly shade tolerant species. LAI is fairly insensitive to changes in FolN, so fine tuning FolN will not spoil your tuning of LAI.
12. The height of the biomass growth curve is primarily controlled by FolN, FracFol, FrActWd, but is ultimately determined by water limitation. Remember that FracBelowG, TORoot, TOWood also have an effect. H3/H4 has a slight effect by modifying water stress and HalfSat can modify light stress. Also remember that MaintResp can cause the curve to plateau regardless of other parameter settings. It is recommended to make major adjustments to the height of the biomass curve with FracFol, FrActWd and then fine-tune it using FolN and SLWmax (within empirical limits). Note that raising LAI using SLWmax generally reduces the height of the growth curve slightly, presumably because less light penetrates deeper into the canopy. When calibrating conifers, note that higher values of TOfol depress the growth curve because more of the NetPsn is needed to build leaves. Thus, higher FolN may be needed for species with shorter leaf longevity compared to similar species with longer leaf longevity.
13. The timing of the peak of the biomass growth curve is primarily determined by species longevity. To modify the timing of the onset of senescence, adjust PsnAgeRed. A value of 5 seems to work well for most species.
14. You should be able to control most aspects of the shape of the biomass growth curve. The initial increase is controlled with FracFol, the height by FolN and FrActWd, and the decline by longevity and PsnAgeRed. Fine-tuning is done with FolN and SLW. FolN has a predictable effect on the growth curve, but you may find SLW a bit more erratic because it interacts with foliage biomass and leaf area to affect light competition within the canopy. FolN tends to shift all parts of the growth curve up or down without changing its shape. For species that accumulate markedly less biomass than most species, reduce FracFol modestly and/or increase FrActWd to 0.00005 or 0.00006.

15. NetPsn is primarily controlled by FracF and FracActWd, given FolN, SLW and BaseFolResp. Transpiration is highly correlated with GrossPsn, scaled by WUE (which is modified by CO₂ and O₃ through their effect on Ci. Recall that GrossPsn is calculated by PnET-Succession using NetPsn and BaseFolResp, which is not intuitive.
16. DNSC is the target proportion of carbon reserves that is maintained, and it has little effect on cohort competition unless it is set so low that the cohort has minimal reserves to survive stress, or so high that the species can rarely be stressed enough to die. Set this in the middle of the range of empirical measures of total % sugars and starch in active tissues. In lieu of empirical values, use 0.05.
17. InitialNSC similarly has little effect on cohort competition unless values among species vary by more than an order of magnitude.
18. Establishment probability is reduced in direct proportion to light and water photosynthesis reduction factors for the species at the time of establishment when EstMoistSens and EstRadSens = 1.0. On sites with no light or water stress, probability of establishment would equal 1.0, which is unreasonably high, so it is calibrated to an appropriate magnitude using EstMoistSens and EstRadSens. This cannot be done on a single cell, and must be done on a landscape before you conduct landscape-scale experiments. In lieu of concrete evidence that one factor is more important than the other, keep the values the same. I tune such that the number of cohorts on the landscape quickly finds an equilibrium under a scenario that mimics historical conditions. I used a value of 2.8 of most species in western Maryland. Modify these values to weight the influence of the light and water reduction factors on establishment if the conditions for optimal establishment vary markedly from the conditions for optimal growth.

General notes. 1) Again, to ensure realistic competition, it is advisable to use common parameter values across species, unless you have empirical data that are comparable and reliable across species. If you are planning to experimentally vary some parameters, holding the others constant will improve the signal from your experiment. Minimizing species differences in parameters such as SLWDel, PsnAgeRed, k, MaintResp, DNSC, WUEc, FracBelowG, FracFol and FracActWd will make competitive interactions more predictable. Hold these as close to each other as possible, varying other parameters to calibrate as much as possible within empirical limits. However, when you cannot calibrate adequately using the common parameter values, do not hesitate to vary the one or two other parameters that will produce good performance. It is very likely that such modifications reflect biological reality. 2) Use the PnET-Succession function worksheet to help you understand how the parameters determine the behavior of cohort state variables as a function of the abiotic inputs, both intermediate variables and the ones that ultimately reflect competition and growth (e.g., NetPsn, foliar and wood biomass, NSCfrac). It is available from the PnET-Succession page of the LANDIS-II website (www.landis-ii.org/extension/pnet-succession) and in the 'docs' folder where this User Guide was installed. 3) It is highly recommended that you verify your calibrations by simulating several

similar species together to ensure that they in fact compete as expected. If not, often a slight tweak of one parameter can bring them in line with expectation. The likely parameters to tweak are FolN (general growth rate), H3/H4 (competition for water) and HalfSat (competition for light), or FracFol (amount of foliage).

Here are some commonly used generic values, for your reference.

LandisData PnETGenericParameters

PnETGenericParameters	Value
BFolResp	0.1
TOroot	0.02
TOwood	0.01
MaxDevLyrAv	6000
MaxCanopyLayers	2
IMAX	5
DNsc	0.05 <<target NSCfraction
MaintResp	0.002
FracBelowG	0.33
KWLit	0.1 <<0.075 for hardwoods and 0.125 for softwoods (Mattson 1987)
FolLignin	0.2 <<Range in Aber and Melillo (1982) = 0-0.25
Wythers	true
PrecipEvents	11
EstMoist	2.8
EstRad	2.8
DTEMP	true

Here are some species parameters that have been calibrated in various ecosystems in the Midwestern and northeastern U.S., mostly using a SALO soil. These can be used as a starting point, but they should be calibrated for your study area. FolN was NOT dynamic. Note that AmaxA and AmaxB are not shown, and vary between deciduous and evergreen as described above.

LandisData PnETSpeciesParameters

>>calibrated for Wythers=true

Species	FolN	SLW max	TO Fol	Half Sat	H3	H4	Psn TMin	Psn TOpt	Frac Fol	FrAct Wd	KWd Lit	Fol Lignin
>>Upper Midwest												
abiebals	0.9	225	0.25	150	105	143	2	19	0.1	0.00004	0.023	0.2
acerrubr	2.2	60	1	150	111	147	3	26	0.02	0.00004	0.081	0.11
acersacc	2.1	47	1	100	105	143	3	23	0.02	0.00004	0.075	0.11
betualle	2.2	50	1	150	105	143	3	21	0.02	0.00004	0.045	0.2
betupapy	2.4	75	1	250	100	140	3	21	0.022	0.00004	0.045	0.2

carycord	2.5	70	1	250	105	143	3	25	0.02	0.00004	0.05	0.2
fagugran	2.0	47	1	100	111	147	3	23	0.02	0.00004	0.047	0.2
fraxamer	2.5	60	1	200	111	147	3	25	0.02	0.00004	0.075	0.12
fraxnigr	2.6	65	1	250	100	140	3	23	0.02	0.00004	0.045	0.2
fraxpenn	2.5	60	1	200	111	147	4	25	0.02	0.00004	0.05	0.2
larilari	2.7	60	1	300	105	143	1	20	0.022	0.00004	0.028	0.2
piceglau	1.1	225	0.25	200	111	147	2	21	0.1	0.00004	0.025	0.2
picemari	1.0	200	0.25	200	111	147	2	20	0.08	0.00006	0.025	0.2
pinubank	1.3	245	0.333	300	118	153	2	20	0.1	0.00004	0.025	0.2
pinuresi	1.5	230	0.333	250	118	153	3	21	0.1	0.00004	0.023	0.2
pinustro	1.8	220	0.5	200	111	147	3	21	0.1	0.00004	0.125	0.25
popubals	2.4	85	1	300	100	140	1	19	0.025	0.00004	0.046	0.2
popugran	2.5	85	1	300	100	140	2	22	0.025	0.00004	0.046	0.2
poputrem	2.5	85	1	300	100	140	2	21	0.025	0.00004	0.043	0.2
prunsero	2.5	70	1	250	111	147	3	25	0.022	0.00004	0.075	0.18
queralba	2.7	70	1	250	118	153	2	26	0.02	0.00004	0.063	0.17
querelli	2.6	65	1	250	118	153	2	21	0.02	0.00004	0.05	0.2
quermacr	2.7	60	1	200	118	153	3	23	0.02	0.00004	0.05	0.2
querrubr	2.6	60	1	200	111	147	2	24	0.02	0.00004	0.075	0.17
quervelu	2.3	55	1	200	114	148	2	24	0.02	0.00004	0.075	0.2
thujocci	1.0	130	0.5	200	105	143	3	20	0.08	0.00006	0.026	0.2
tiliamer	2.5	50	1	150	111	147	3	23	0.02	0.00004	0.075	0.12
tsugcana	1.4	105	0.333	90	105	143	3	21	0.07	0.00004	0.028	0.2
>>Mid-Atlantic												
castdent	2.6	50	1	150	114	148	2	24	0.02	0.00004	0.043	0.09
caryglab	2.1	60	1	200	111	147	3	27	0.02	0.00004	0.166	0.17
lirituli	2.8	85	1	300	100	140	3	25	0.025	0.00004	0.107	0.16
magnacum	2.4	55	1	200	100	140	2	24	0.025	0.00005	0.075	0.11
nyssylv	2.1	50	1	100	105	143	3	27	0.02	0.00004	0.126	0.12
pinuechi	1.5	235	0.333	300	118	153	3	25	0.1	0.00004	0.125	0.25
pinupung	1.2	200	0.333	300	118	153	3	21	0.08	0.00004	0.125	0.25
pinurigi	1.4	235	0.333	300	118	153	3	21	0.1	0.00004	0.063	0.25
pinuvirg	2.0	240	0.5	300	118	153	3	21	0.1	0.00004	0.125	0.25
quercocc	2.8	75	1	300	114	148	2	24	0.022	0.00004	0.05	0.17
querprin	2.6	65	1	250	118	153	2	24	0.02	0.00004	0.17	0.26
robipseu	2.4	85	1	300	105	143	3	25	0.025	0.00004	0.015	0.26
sassalbi	2.5	65	1	300	105	143	2	26	0.02	0.00004	0.075	0.12
ulmuamer	2.5	55	1	200	105	143	3	27	0.02	0.00004	0.075	0.12
juglnigr	2.8	70	1	250	105	143	3	27	0.02	0.00004	0.075	0.12
betulent	2.4	75	1	250	105	143	3	23	0.022	0.00004	0.18	0.15
caryovat	2.2	60	1	150	111	147	3	25	0.02	0.00004	0.166	0.17
ostrvirg	1.9	50	1	100	111	147	3	26	0.02	0.00004	0.075	0.17
platocci	2.6	55	1	200	105	143	3	27	0.02	0.00004	0.075	0.11
>>Northeast												
acerpens	1.9	45	1	100	111	147	2	20	0.02	0.00004	0.075	0.25
piceabie	1.2	220	0.25	200	111	147	2	20	0.1	0.00004	0.125	0.25
picerube	0.9	200	0.25	150	111	147	2	20	0.1	0.00004	0.125	0.25
prunpens	2.6	85	1	250	111	147	2	20	0.03	0.00004	0.075	0.186

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