

PnET-Succession v5.1 Extension User Guide

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NOTICE: Several parameters must be recalibrated from values used with previous versions of PnET-Succession. See Section 1.3 for details.

NOTICE: Seasonality within PnET-Succession is tracked by assuming that January is mid-winter, making its use for southern hemisphere applications problematic. Contact the developers if you are interested in helping to modify the code to resolve these issues.

SUGGESTION: Consult Gustafson *et al.* (2023) [see page 10] for detailed explanations of the parameters and how they are used in PnET-Succession. This user guide gives details on *how* the model is run and the paper provides details on *why* parameters function as they do.

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1 Introduction

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

The PnET-Succession extension (de Bruijn et al. 2014, Gustafson et al. 2023) 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 forest stands (Aber and Federer 1992), built on two principal relationships: 1) maximum photosynthetic 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 foliage within the canopy layer. A greater number of subcanopy layers tightens 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 produce a positive carbon balance. This is computationally time-consuming, so PnET-Succession allocates foliage in proportion to the active wood (xylem) that supports it, and the amount of light (and water) available to each sublayer determines how productive that foliage is. (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. (6) Cohorts die if the NSC pool is depleted at the end of a year. Details of model structure and modifications from PnET-II can be found in de Bruijn et al. (2014) and (for v5.1) Gustafson et al. (2023).

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 2013).

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 light.
- 2) Dynamic calculations of LAI and photosynthesis allow cohorts to die prior to longevity age, 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 during 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 for 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 (starting with v4.0) also allows simulation of waterlogging effects on photosynthesis, including as a function of permafrost dynamics (optional).

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 are longer because there are many more calculations for each cohort. However, the number of cohorts may be less because many cohorts die of stress or senesce prior to reaching longevity age, reducing the number of cohorts that must be simulated.

1.3 What's new in Version 5.1

Versions 5.0 and 5.1 were staged releases that produced a major revision that adds capabilities, increases efficiency, and fixes bugs and discrepancies from PnET-II. It incorporates a new PnET-Succession Cohort library that allows more streamlined

access to PnET-Succession state variables by other extensions, improving efficiency and reducing memory consumption. These versions also include several major bug fixes (described below), several of which fix unintended deviations from PnET equations. **Unfortunately, these fixes require users of earlier versions to recalibrate several parameters.** On the positive side, it is now easier to match empirical growth curves without pushing some parameters beyond their empirical limits, and it more accurately simulates physiological response to input drivers. New and improved (and easier) calibration tips are provided in the Appendix to this user guide.

It is important to note that the model now uses an unmodified light stress equation from PnET-II. Any recalibration exercise should consider the revised life history parameters found in Table 1 of the Appendix.

The ability to execute simulations using multiple threads (parallelization) is now an option. The user must specify the maximum number of threads, recognizing that high numbers may actually slow runtime because of thread locking (see Section 7.31).

1.3.1 Added Features

- New PnET-Succession cohort library streamlines the passing of state variables to and from other extensions
- New algorithm to account for canopy gaps when cohorts are lost, with the space gradually filled by growth of other cohorts (Gustafson et al. 2023)
- Improved estimates of total cell biomass that convert PnET-Succession species biomass density values (g/m^2) to a weighted average cell-level biomass density (Gustafson et al. 2023)
- Parallelization of cohort growth, including during spinup
- Tuning parameter for soil ice computations (adjusts soil thermal conductivity)
- FrostDepth (depth from top of soil profile to the bottom of ice layer in winter) and ActiveLayerDepth (depth from top of soil profile to the top of any permafrost ice layer in summer) are optional outputs
- Optional output maps of albedo (landscape reflectance). The algorithms are valid in boreal ecosystems only
- New option to generate maps of total cell biomass (all cohorts)
- Optional output of maps and summaries of each biomass pool and selected combinations
- Improved evapotranspiration (ET) estimation methods and additional ET component outputs

1.3.2 Bug Fixes

A thorough code audit was completed, and several bugs were uncovered.

- In previous versions, photosynthates (NSC) were properly converted from gC to gDW when allocated to the foliage biomass pool, but allocations to the wood and root biomass pools were not converted but were reported as gDW. This was fixed, resulting in much higher amounts of wood and root biomass for each cohort.
Calibrations conducted with prior versions should be verified and potentially

adjusted. Studies conducted with prior versions typically calibrated species parameters to produce biomass outputs matching empirical values, so the behavior was valid while the magnitudes of the input parameters were not. Recalibration exercises have shown that it is now easier to match empirical growth curves without resorting to parameter values outside empirical limits.

- Evaporation was not properly computed when PAR units were W/m^2 .
- Reduction factors (except ozone) were applied to NetPsn rather than to GrossPsn (as in PnET-II), making it more difficult for cohorts to be killed by stress. This was fixed, and negative values of NetPsn are now possible. It is now easier for cohorts to experience stress and competitive outcomes respond accordingly.
- LAI of the cohorts within a canopy layer was being summed rather than averaged, resulting in excessive light attenuation and sometimes excessive LAI. Please note that it is incumbent on users to calibrate LAI because there are no checks against unrealistic values in the model, and high values produce excessive attenuation of light through the canopy. See Appendix for guidance.
- The equation computing light stress (fRad) produced excessive light stress when light was abundant, so we reverted to the PnET-II equation. However, light stress is now slightly greater when light is very low.
- The layering algorithm was originally designed to accommodate cohorts with cohort foliage potentially spread across major canopy layers. Beginning with version 3.0, cohorts were completely assigned to only one canopy layer. The layering algorithm did not consistently assign cohorts to layers under this system, so we designed a much simpler (and quicker) algorithm to assign cohorts to layers based on the relative difference in woody biomass among cohorts.
- Re-foliation (after defoliating disturbance) was not allowed in June (the presumed second month of the growing season), which prevented foliation allocation when June was the first month of the growing season. The second month of the growing season is now explicitly computed.

1.4 References

- Aber, J.D., Federer C.A. 1992. A generalized, lumped parameter model of photosynthesis, evapotranspiration and net primary production in temperate and boreal forest ecosystems. *Oecologia* 92: 463-474.
- Aber, J.D., Ollinger, S.V., Federer, A., Reich, P.B., Goulden, M.L., Kicklighter D.W., Melillo J.M., Lathrop R.G. 1995. Predicting the effects of climate change on water yield and forest production in the northeastern United States. *Climate Research* 5:207-222.
- de Bruijn AMG., Gustafson E.J, Sturtevant B., Foster J., Miranda B, Lichti N., Jacobs D.F. 2014. Toward more robust projections of forest landscape dynamics under novel environmental conditions: embedding PnET within LANDIS-II. *Ecological Modelling* 287:44–57.
- Franks, P. J., Adams, M. A., Amthor, J. S., Barbour, M. M., Berry, J. A., Ellsworth, D. S., Farquhar, G. D., Ghannoum, O., Lloyd, J., McDowell, N., Norby, R. J., Tissue, D. T. and von Caemmerer, S. 2013. Sensitivity of plants to changing

- atmospheric CO₂ concentration: from the geological past to the next century. *New Phytologist* 197:1077–1094. doi:10.1111/nph.12104.
- Gustafson, E.J. 2013. When relationships estimated in the past cannot be used to predict the future: using mechanistic models to predict landscape ecological dynamics in a changing world. *Landscape Ecology* 28:1429-1437.
- Gustafson, Eric J., Mark E. Kubiske, Brian R. Miranda, Yasutomo Hoshika, Elena Paoletti. 2018. Extrapolating plot-scale CO₂ and ozone enrichment experimental results to novel conditions and scales using mechanistic modeling. *Ecological Processes* 7:31. DOI: 10.1186/s13717-018-0142-8.
- Gustafson Eric J., Brian R. Miranda, Brian R. Sturtevant, Anatoly Z Shvidenko. 2020a. Simulating growth and competition on wet and waterlogged soils in a forest landscape model. *Frontiers in Ecology and Evolution* 8:598775. doi: 10.3389/fevo.2020.598775.
- Gustafson, Eric J., Brian R. Sturtevant, Brian R. Miranda, Zaixing Zhou. 2023. PnET-Succession v 5.1: Comprehensive description of an ecophysiological succession extension within the LANDIS-II forest landscape model. Published on the Internet by the LANDIS-II Foundation. URL: <https://github.com/LANDIS-II-Foundation/Foundation-Publications/blob/main/Description%20of%20PnET-Succession%20v5.1.pdf>.
- Scheller, R.M., Mladenoff, D.J. 2004. A forest growth and biomass module for a landscape simulation model, LANDIS: Design, validation, and application. *Ecological Modelling* 180(1):211-229.

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1.6 Release History

1.6.1 Major Releases

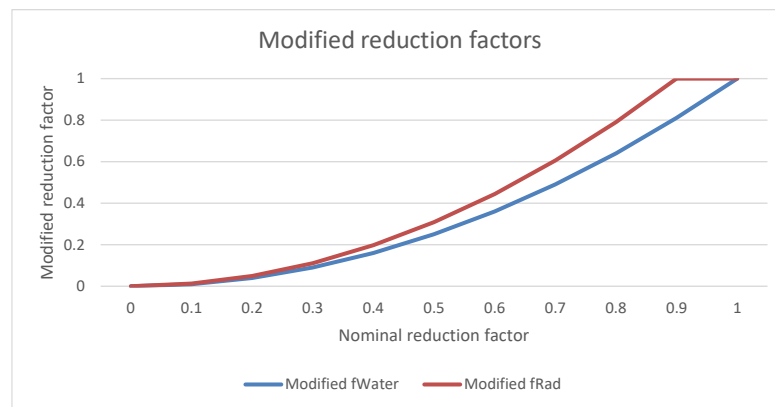
1.6.1.1 Version 4.0 (2020)

Version 4.0 modified the establishment algorithms to improve control of establishment and to reduce the proliferation of cohorts that have little chance of surviving, which can lengthen run times and consume computer memory. The EstMoist and EstRad parameters previously had no effect when a reduction factor equaled (or approached) 1.0, providing limited control over establishment. These parameters are no longer compatible with those of prior versions, but all other inputs from prior versions remain compatible.

Version 4.0 added optional capabilities to simulate hydrologically waterlogged soils, specifically forested wetlands and forests on permafrost (Gustafson et al. 2020a). Forested wetlands are poorly simulated in most forest landscape models, so this was an important advance.

1.6.1.1.1 Added Features

- The EstMod parameters were repurposed to make the light and water effects on establishment to be independently scalable. The figure below represents the impact of the EstMod parameters with value of EstRad = 0.9 and EstWater = 1.0.



- OPTIONAL:** The effect of light on establishment (Pest) can be set to no longer be directly proportional to fRad. Instead, Pest is highest for species with high HalfSat (pioneers) when light is high, and highest for shade-tolerant species when light is low (see figure below). Pest is intermediate for species with mid-range HalfSat in all light environments. The effect of water on Pest remains proportional to fWater. This modification greatly improves the ability of the model to establish species where they are most likely to thrive and to not establish them where they will not be competitive, reducing model runtimes. Note, this capability may be less needed with the bug fixes in v5.1 as described in section 1.3.2 above. Use with caution (i.e., only when all

other attempts to increase establishment of shade-tolerant species or reduce establishment of shade-intolerant species fail).

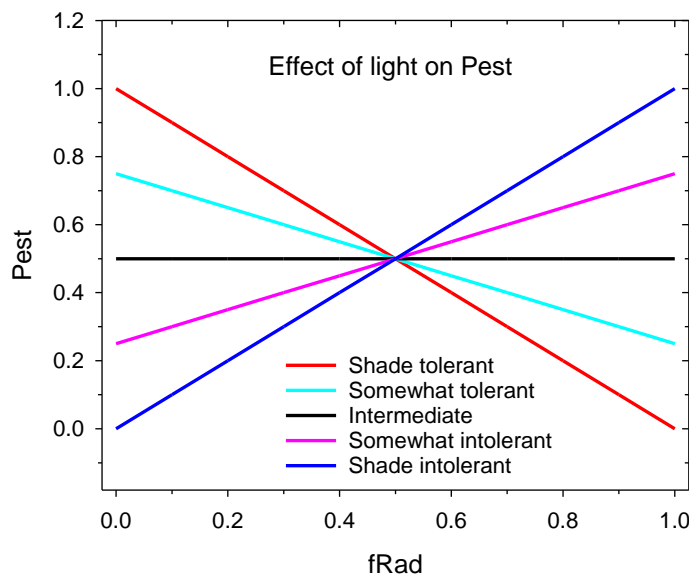


Figure caption. Effect of light (fRad) on Pest when InvertPest=true.

- Parameter MaxPest allows global tuning of absolute establishment probabilities.
- Cohorts are now killed if their biomass drops below initialized biomass (for a new cohort of the species) at the end of a year. Such cohorts are assumed to be inviable, but they may otherwise take many years to die because their maintenance respiration costs are very low.
- To optionally simulate soil ice dynamics (specifically, permafrost), the rooting depth and leakage parameters are now dynamic at a monthly time step, determined by ice depth as driven by the temperature inputs.
- The RunoffCapture parameter optionally allows standing water in an ecoregion, to simulate lowland conditions.

1.6.1.1.2 Bug fixes

- Potential evaporation calculation was modified for consistency in units, using a different formulation (see 2.2.2.2)
- Corrected rounding error that sometimes allowed soil water to be negative under extreme dry conditions.

1.6.1.2 Version 3.0 (2018)

1.6.1.2.1 Added Features

- Latitude can now be used as an ecoregion parameter (or as a global parameter as before), 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. 2018). 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 (Ci), 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 affected 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 (Amax) 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 H1 and H2 species parameters that allow 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.

1.6.1.2.2 Bug Fixes

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

1.6.1.3 Version 2.0 (2016)

1.6.1.3.1 Added Features

- 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 (acclimation) 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 other than by VPD.
- 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.

1.6.1.3.2 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 11).
- 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 2.2.2.1).
- 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.

1.6.1.4 Version 1.0 (2014)

First released version.

1.6.2 Minor Releases

1.6.2.1 Version 3.4 (2019)

Version 3.4 added several new features and corrected some important bugs. Nearly all of the added features are optional, with the intention of maintaining compatibility with inputs that worked in the previous version.

1.6.2.1.1 Added Features

- Optional ability to use the Climate Library to provide climate data.
- New optional PsnTMax species parameter to set the upper temperature limit for photosynthesis. Previously, this was estimated from PsnTMin and PsnTOpt, assuming a symmetrical relationship so that $(PsnTOpt - PsnTMin) = (PsnTMax - PsnTOpt)$.
- New optional CohortBinSize parameter to aggregate cohort age bins to be larger than the extension timestep.
- Optional ability to supply cohort initial biomass in the initial communities file.
- Optional reading of initial litter and dead wood maps.
- New optional RunoffFrac ecoregion parameter to allow prevention of some water runoff.

- New optional LeafOnMinT species parameter to allow separate control of the beginning and end of the growing season, apart from the control of photosynthesis rate at low temperatures (PsnTMin).
- New optional ColdTol species parameter to identify the minimum temperature for survival of the species cohorts.
- New WinterStd ecoregion parameter to estimate the extreme cold temperature from the monthly average TMin.
- Added EstablishmentTable output option.
- Added MortalityTable output option.
- Additional information in output files.
- Cohorts can re-flush foliage following defoliation caused by a disturbance extension. Refoliation occurs at 70% of ideal foliage, for deciduous (TOfol = 1) cohorts that experience > 60% defoliation in a given year. Refoliation has additional cost to NSC, and cohorts that do not re-leaf still experience additional NSC losses.

1.6.2.1.2 Bug Fixes:

- Correction to the initialization of foliage for initial communities that are replicated in the initial community map. Failure to initialize foliage correctly caused cohorts to die immediately following spin-up, but only on sites that were duplicated in the initial communities map, and were not included as PnETOutputSites.
- Correction to the accumulation of cohort biomass when combining multiple cohorts less than the timestep (or CohortBinSize) age.
- Correction to the calculation of GrossPsn that resulted in cases of transpiration exceeding soil water.
- Correction to the DTemp response calculation that resulted in values <0.

1.6.2.2 Version 3.3 (Internal Release)

Added support for providing initial cohort biomass (no spin-up)

1.6.2.3 Version 3.2 (Internal Release)

Added support for Climate Library.

1.6.2.4 Version 3.1 (September 2018)

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 8.31 and 8.32.

1.6.2.5 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.

1.6.2.6 Version 2.1 (May 2017)

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.

1.6.2.6.1 Bug Fixes:

- 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 now uses the age of the **oldest** cohort of a species to check for maturity and determine sources of seed for dispersal.
- 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 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 and sub-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. Users have the option of providing initial aboveground live biomass values for each cohort or allowing PnET-Succession to estimate the biomass from the age using a “spinup” period to grow the cohorts to their initial age. Optionally, users can provide biomass values but allow spinup to determine the canopy layer of the cohort based on the maximum biomass attained during spinup. This properly initializes cohorts that have less biomass than expected for their age because of disturbance. The required format for initial communities with biomass values is consistent with the text and map formats produced by the Biomass Community Output extension. When initial biomass values are not provided, 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: spin up is a computationally intensive process that

may require significant time for complex initial landscapes with lots of cohort combinations. Additionally, climate data are required back to the 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 6.1.1).

The biomass initialization by spinup 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 (slight priority), older cohorts may have an advantage during spin-up. Furthermore, some cohorts may not survive spin-up.

2.2 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 (DelAmaz) is applied for CO₂ concentrations above 350 ppm, and this acts as a reduction factor when CO₂ is below 350.

2.2.1 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 evenly or randomly distributed across 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) as described by Gustafson et al. (2023). Cohorts no longer can have their foliage distributed across multiple major canopy layers. Cohorts within a major canopy layer have equal access to the light reaching the canopy layer, and the light passing through each cohort's canopy sublayers is a function of the LAI and extinction coefficient of the cohorts. Transmissivity of the light passing through a layer to the layer below it is the weighted average of the transmissivity of the contributing cohorts within the layer, weighted by their areal proportion of the layer. Light stress for a cohort is no longer calculated by $fRad = Radiation / (Radiation + HalfSat)$; the equation from PnET-II is now used: $fRad = 1 - EXP(Radiation * LN(2) / HalfSat)$.

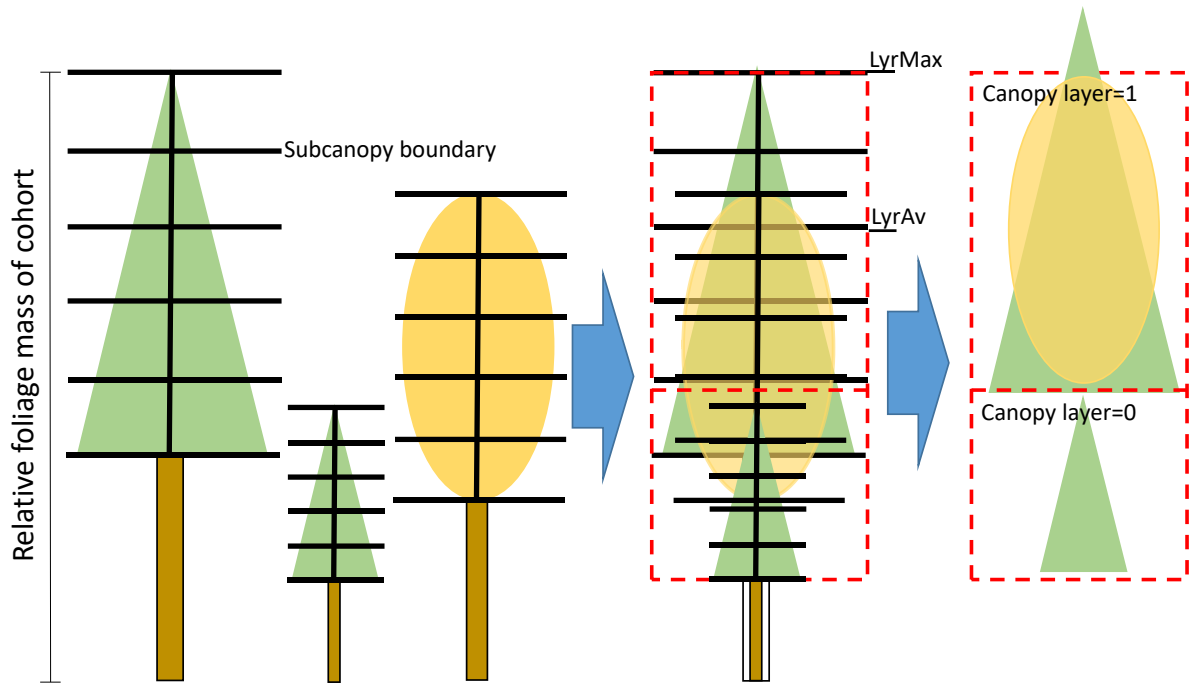


Figure 1. Canopy layer assignment. Each tree represents the foliage of a species-cohort on a site, and the solid horizontal lines are subcanopy boundaries (IMAX=5). Dotted lines are computed major canopy layers based on the difference in biomass (surrogate for height) of the cohorts on the site. All cohort subcanopy layers are assigned to a single canopy layer. Note that the diagram shows canopy shape only to help distinguish cohorts; in the model, subcanopy layers represent cohort foliage across the site, not tree crowns, and all subcanopy layers have equal biomass.

2.2.2 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).

2.2.2.1 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).

$$Interception = P \times (1 - e^{(-PrecipIntConst * LAI)})$$

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 snowpack 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 (in a given month). This random assignment ensures that all layers have equal priority (over time) 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 water actually infiltrating the soil is:

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

where P is precipitation.

2.2.2.2 Water Out

Water that infiltrates the soil is subject to both fast and slow “leakage”. Infiltration is limited by the soil saturation point (θ_s), and any water in excess of saturation is subject to immediate runoff. Typically, all water above saturation would run off the site, but when using the optional RunoffCapture parameter a specified amount of the potential runoff can stay on the site to create a supersaturated condition (i.e., standing water). RunoffCapture values greater than 0 specifies how much depth (in mm) of standing water may accumulate, and a value of 0 will prevent any standing water.

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 upland 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. The rate of evaporation is a function of available water, total site LAI (shading), temperature and daylength to calculate a reference evapotranspiration (RET) based on Hamon (1961). Potential evaporation (PE) is calculated as the RET diminished by shading from the canopy LAI.

Actual evaporation (AE) is limited by the available water (above wilting point) in the portion of the soil from which evaporation can draw (EvapDepth):

$$AE = \text{Min}(PE, (\text{Water} - \text{WiltPt}) * \text{EvapDepth})$$

AET is limited to the water above the wilting point, so that evaporation ceases when the soil water falls to the wilting point. AET is also limited to the soil depth given by the EvapDepth ecoregion parameter. *De facto* evaporation is 0.0 when LAI > 3.0. Also, it is assumed that there is no soil evaporation when snow cover is present.

In reality, when some snow melts prior to soil thaw, it runs off and does not become soil water. The best way to account for this (when not modeling soil freezing) is to add the proportion of the snowpack lost to runoff to the SnowSublimFrac parameter (section 9.12).

$$\text{WaterOut} = \text{Runoff} + \text{Leakage} + \text{Transpiration} + \text{Evaporation}$$

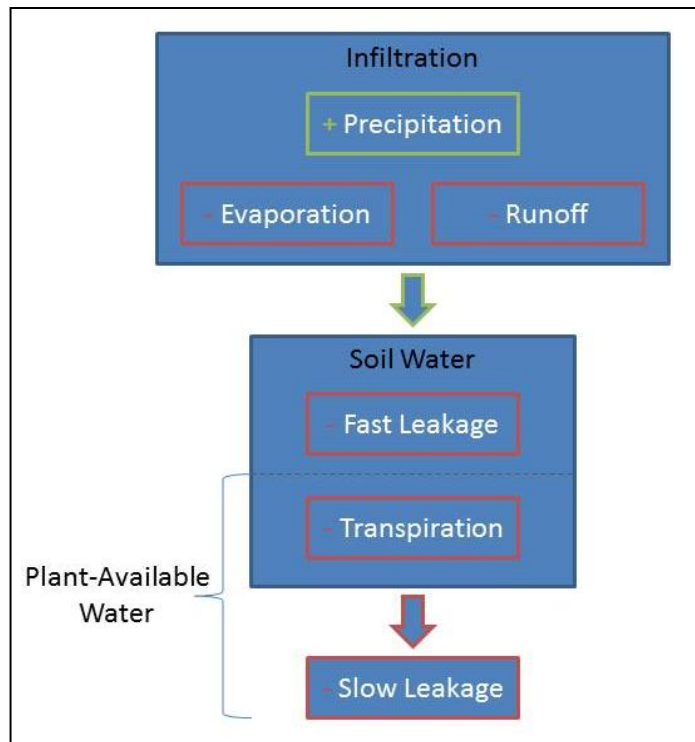


Figure 2. Soil water processes in PnET-Succession

2.2.2.3 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)) can be set to negative values to allow some photosynthesis when the soil is saturated beyond field capacity (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. Soils at field capacity typically have a pressure head=3.6 m, which is used as the default for H2. 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 trees experience no water stress until soil water potential drops below a threshold (H4) and photosynthesis abruptly ceases. Therefore $H3=H4$ is recommended. Many literature sources use a generic H4 (cessation of photosynthesis because of inadequate water) of -153 m pressure head (wilting point), although this does not recognize differences in drought tolerance. One source of estimates for drought, waterlogging (and light) tolerance parameters is the TRY database (Kattge, J. et al. 2020), where the TRY variable ‘Species tolerance to waterlogging’ is relevant to H1/H2, and the TRY variable ‘Species tolerance to drought’ is relevant for H3/H4. Another source is Niinemets and Valladares (2006).

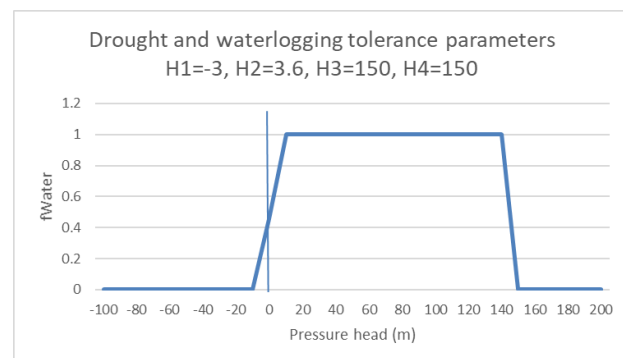
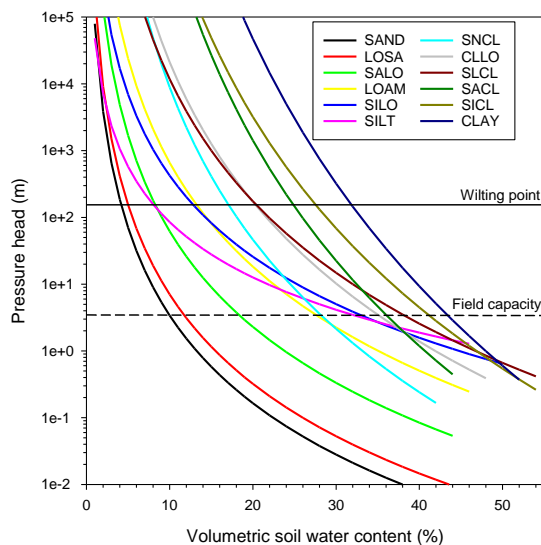


Figure 3. Default pressure head curves (left) and an example of how water stress (fWater, right) is affected by waterlogging and drought tolerance parameters. fWater is calculated by linear interpolation between parameters H1-H4 as shown.

Starting with v3.0, water stress (fWater) is used as a reduction factor for stomata-regulated processes such as 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 sluggishness (due to ozone) and is equal to fWater when ozone is simulated (see 2.2.3.2 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.

2.2.3 Other factors

2.2.3.1 Temperature

Vapor pressure deficit is typically 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 PsnTMin, to 1 at PsnTOpt. Supra-optimal temperatures do not reduce the temperature reduction factor (unless DTEMP=true; see Section 7.22), 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 7.21).

2.2.3.2 Ozone

Ozone can dramatically reduce photosynthesis rates by damaging photosynthetic tissues and inhibiting stomatal function. The model simulates 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 effects will be simulated.

The stomatal sluggishness effects of ozone are simulated by altering (increasing) CiModifier (see 2.2.2.3 for water stress influence on CiModifier) to reflect the inhibited 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 ozone capabilities can be found in Gustafson et al. (2018).

2.3 Cohort Growth and Ageing

The model computes gross photosynthesis, and net photosynthesis is estimated by subtracting foliar respiration from gross 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 allocation ratios specified by the user. 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 length to each existing cohort age.

Cohort wood biomass and foliage can be directly altered by disturbance extensions. Partial disturbances can remove portions of total biomass. Defoliation disturbances can directly remove foliage, without altering the wood biomass. The loss of foliage has subsequent consequences for photosynthetic capacity due to less leaf area. Starting with v3.4, cohorts can re-flush foliage following defoliation if they have sufficient carbon reserves (NSC). Refoliation occurs at 70% of the calculated ideal foliage, for deciduous cohorts ($TO_{fol} = 1$) that experience >60% defoliation in a given year. Refoliation has additional cost to NSC (95% of ideal foliage), and cohorts that do not re-foliate still experience additional NSC losses (10% of ideal foliage).

2.4 Cohort Senescence and Mortality

Senescence is implemented simplistically as a reduction of gross photosynthetic rate with age such that respiration eventually exceeds production, ensuring that cohorts will be dead by their longevity age. 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 (f_{Age}), which reaches zero at the longevity specified in the LANDIS-II species parameter file. Cohorts are also considered inviable and removed when their biomass falls below their initial biomass value.

2.5 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).

2.6 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) is 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 once per timestep, using the average light and water conditions during optimal months, up to three physiologically active months in the year, based on temperature. The first active month each year is not used for establishment calculations, assuming that trees put resources into leaf and stem growth in the first month, and seeds first become available in the second month.

Establishment probability for a given timestep is generally calculated with the following equations:

$$fRad = \frac{SubcanopyPAR}{SubcanopyPAR + HalfSat}$$

$$fRad = 1 - e^{-PAR_i \frac{\log(2)}{HalfSat}}$$

$$fRadAdj = fRad^2 \times \frac{1}{EstRad^2}$$

$$fRadAdjInt = \frac{HalfSat - MinHalfSat}{HalfSatRange}$$

$$fRadAdjSlope = (fRadAdjInt \times 2) - 1$$

$$fRadFinal = 1 - fRadAdjInt + fRadAdj \times fRadAdjSlope$$

$$fWaterAdj = fWater^2 \times \frac{1}{EstMoist^2}$$

$$p_{Est} = fWaterAdj \times fRadFinal \times MaxPest$$

MinHalfSat is the lowest HalfSat among all modeled species, HalfSatRange is the range of species HalfSat values, and fWater is calculated from available water as described in 2.2.2.3. The establishment modifiers (EstRad and EstMoist) are used to scale the relative impacts of light and water stress on the probability of cohort establishment. EstRad specifies the fRad above which the light environment is optimal for establishment, and EstWater specifies the fWater above which the soil moisture is optimal for establishment.

Initial biomass for a successfully established cohort is computed for a 1-year old cohort. This initial cohort will be grouped ('binned') appropriately into a larger cohort (e.g., age 1 – 10) at the next succession time step.

2.7 References

- Cabrera, M.C.M., J.A.A. Anache, C. Youlton, E. Wendland. 2016. Performance of evaporation estimation methods compared with standard 20 m² tank. *Revista Brasileira de Engenharia Agrícola e Ambiental*, 20, pp. 874-879.
- Court, A. 1951. Temperature frequencies in the United States. *Journal of Meteorology* 8:367–380. [https://doi.org/10.1175/1520-0469\(1951\)008<0367:TFITUS>2.0.CO;2](https://doi.org/10.1175/1520-0469(1951)008<0367:TFITUS>2.0.CO;2)
- de Bruijn A., Gustafson E.J., Sturtevant B.R., Foster J.R., Miranda B.R., Lichti N.I., Jacobs D.F. 2014. Toward more robust projections of forest landscape dynamics under novel environmental conditions: embedding PnET within LANDIS-II. *Ecological Modelling* 287:44–57.
- Feddes, R.A., P.J. Kowalik, and H. Zaradny. 1978. *Simulation of Field Water Use and Crop Yield*. John Wiley & Sons, New York, NY.
- Gustafson, E.J., M.E. Kubiske, B.R. Miranda, Y. Hoshika, E. Paoletti. 2018. Extrapolating plot-scale CO₂ and ozone enrichment experimental results to novel conditions and scales using mechanistic modeling. *Ecological Processes*. 7(1):31-51. <https://doi.org/10.1186/s13717-018-0142-8>.
- Gustafson, Eric J., Brian R. Sturtevant, Brian R. Miranda, Zaixing Zhou. 2023. PnET-Succession v 5.1: Comprehensive description of an ecophysiological succession extension within the LANDIS-II forest landscape model. Published on the Internet by the LANDIS-II Foundation. URL: <https://github.com/LANDIS-II-Foundation/Foundation-Publications/blob/main/Description%20of%20PnET-Succession%20v5.1.pdf>.
- Hood, E., M. Williams, D. Cline. 1999. Sublimation from a seasonal snowpack at a continental, mid-latitude alpine site. *Hydrol. Process*. 13:1781-1797.
- Kattge, J., Bönisch, G., Diaz, S., Lavorel, S., Prentice, I. C., Leadley, P., ... Wirth, C. 2019. TRY plant trait database – enhanced coverage and open access. *Glob Change Biol*. 26:119–188. <https://doi.org/10.1111/gcb.14904>.
- Meentemeyer, V. 1978. Macroclimate and lignin control of litter decomposition rates. *Ecology* 59:465-472.
- Niinemets, Ü., F. Valladares. 2006. Tolerance to shade, drought, and waterlogging of temperate Northern Hemisphere trees and shrubs. *Ecological Monographs* 76:521–547.
- Saxton, K. E. and W. J. Rawls. 2004. Soil water characteristic equations.xls. Online database (<http://hrs1.arsusda.gov/SPAW/SPAWDownload.html>)
- Saxton, K. E., W. J Rawls, J. S. Romberger and R. I. Papendick. 1986. Estimating generalized soil water characteristics from texture. *Soil Sci. Soc. Amer. J.* 50(4):1031-1036.

- Stewart, R. B.; Rouse, W. R. 1976. A simple method for determining the evaporation from shallow lakes and ponds. *Water Resources Research*, v.12, p.623-628.
<http://dx.doi.org/10.1029/WR012i004p00623>
- USDA Natural Resources Conservation Service (NRCS). 2004. National Engineering Handbook Part 630 (Hydrology), Chapter 11 (Snowmelt). Accessed online at:
<http://www.wcc.nrcs.usda.gov/ftpref/wntsc/H&H/NEHhydrology/ch11.pdf>
- 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 the LANDIS-II core 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              5
StartYear             2011
SeedingAlgorithm      WardSeedDispersal

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
ClimateConfigFile      climate-generator.txt
CohortBinSize          10
```

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 ≤ 10 is recommended. Random shuffling of cohort foliage into sub-canopy layers for access to light and water 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 may not markedly speed up simulations because the internal time step of PnET-Succession is monthly, but longer time steps 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 12).

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). Note that all maps must have the same dimensions as the ecoregion map.

3.9 LitterMap (Optional)

This parameter gives the file name of the initial leaf litter map. The values of the map represent the quantity (g/m^2) of leaf litter on each site at the start of the simulation. When providing initial cohort biomass values, it is valuable to also provide initial litter values, which will otherwise start with 0 values. When initial cohort biomass is not provided (estimated by spin-up), then the litter quantity is also estimated during the spin-up phase.

3.10 WoodyDebrisMap (Optional)

This parameter gives the file name of the initial dead woody debris map. The values of the map represent the quantity (g/m^2) of dead wood on each site at the start of the simulation. When providing initial cohort biomass values, it is valuable to also provide initial dead wood values, which will otherwise start with 0 values. When initial cohort biomass is not provided (estimated from spin-up), then the dead wood quantity is also estimated during the spin-up phase.

3.11 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-v7\extensions\Defaults\PnETGenericDefaultParameters.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 PnETGenericParameters 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.

3.12PnETSpeciesParameters

This parameter gives the name of the PnET Species Parameter text file. The format of this file is described in section 7.33.

3.13EcoregionParameters

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

3.14DisturbanceReductions (Optional)

This parameter gives 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.

3.15ClimateConfigFile (Optional)

This optional parameter gives the name of the Climate Library configuration file. Including this optional parameter triggers the model to use the climate library to provide the climate variables used within PnET-Succession. Excluding this parameter will utilize the climate input file(s) referenced in the EcoregionParameters input file, which is described in Section 9.15.

3.16SaxtonAndRawlsParameters (Optional)

This optional parameter gives the name of the soil parameter file should the user wish to use a file other than the default provided and installed with PnET-Succession.

3.17CohortBinSize (Optional)

This optional parameter sets the number of years represented by an age cohort. Typically, the age range of a cohort is determined by the timestep of the succession extension. However, in cases where users want to lump the cohorts into combined age cohorts, while maintaining a more frequent succession timestep, this parameter can be used. The CohortBinSize must be \geq Timestep.

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 directly competing with each other.

Note: The format of the text file produced by the Biomass Community Output extension is compatible as an input initial community file.

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 section 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.

4.3.2.1 Cohort Biomass (optional)

Initial community information can also provide initial biomass values for cohorts. Supplying initial biomass values is optional, and when not provided the extension will use the succession grow functions to grow the cohort to the initial age. Biomass values should represent aboveground live woody biomass density (g/m^2) of the cohort, and should be provided in parentheses following the age.

```
acersacc 10 (2100) 60 (5200) 100 (8500)
```

Biomass values should be greater than 0. A cohort assigned a biomass of 0 will be treated as if no biomass value was provided and will have its biomass estimated through the spin-up process.

Note: There are multiple options to determine how PnET-Succession estimates the appropriate canopy layer of a cohort when given an initial biomass (see section 7.29).

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 or the optional parameter CohortBinSize. This value 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 30 40 190 200
```

5 Input File – Initial community map

This is a raster map 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.

Note: The format of the map file produced by the Biomass Community Output extension is compatible as an input initial community map file.

6 Input File – Climate

This file contains weather (and atmospheric) records of monthly parameter values. The user may optionally access the LANDIS-II climate library instead.

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 <<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 mean daily maximum temperature observed in the month. Value: decimal.
Units: degrees C.

6.3.4 TMin

The mean daily 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. PAR is used as a measure of average instantaneous light intensity during the day, not

a cumulative quantity of light over the day or month. Value: decimal ≥ 0.0 . Units: User choice. Must be $\mu\text{mol}/\text{m}^2/\text{sec}$ or W/m^2 . The units for the half-saturation constant (SpeciesParameter file) must be the same as PAR. Default units is $\mu\text{mol}/\text{m}^2/\text{sec}$; if W/m^2 is used then the PARUnits parameter in the Generic PnET Species Parameters file must be set to W/m^2 .

PAR data is usually called (downwelling) shortwave radiation in data that can be accessed from various sources, such as :

https://cida.usgs.gov/thredds/catalog.html?dataset=cida.usgs.gov/macav2metdata_monthly_historical and outputs from many GCMs. To convert instantaneous global solar radiation (W/m^2) data to PAR ($\mu\text{mol}/\text{m}^2/\text{s}$), multiply by 2.02. If the measurement is daily solar radiation, it likely includes all 24 hours. To convert to daily PAR (PAR_{diel}) and then to daytime average PAR ($\text{PAR}_{\text{daytime}}$), use $\text{PAR}_{\text{daytime}} = \text{PAR}_{\text{diel}} * 24 * 3600 / \text{daylength}$, where day length is the average daylight time in seconds for the month. Monthly $\text{PAR}_{\text{daytime}}$ is simply an average of daily $\text{PAR}_{\text{daytime}}$.

There is some confusion about conversion constants. The following is from <https://www.researchgate.net/post/Can-I-convert-PAR-photo-active-radiation-value-of-micro-mole-M2-S-to-Solar-radiation-in-Watt-m2>. “The approximation $1 \text{ W}/\text{m}^2 \approx 4.6 \mu\text{mole.m}^2/\text{s}$ comes from the Plant Growth Chamber Handbook. Note that the value of 4.57 converts Watts/ m^2 to $\mu\text{mole.m}^2/\text{s}$, assuming that the W/m^2 is for radiation from 400 to 700 nm. However, I don't know that anyone ever measures solar radiation in W/m^2 in the 400 - 700 nm range. Pyranometers measure TOTAL solar radiation. Since only about 45% of the energy of solar radiation is actually in the 400 - 700 nm range. the conversion of TOTAL solar radiation to PAR is ~ 2.1 , rather than 4.57. As mentioned by others, that is an approximation, but a pretty good one.” Another solid and recent source is p. 233 in Mariana Gonçalves dos Reis and Aristides Ribeiro1 (2020, DOI: <http://dx.doi.org/10.31062/agrom.v27i2.26527>), who state that the conversion constant is 2.02. Note that if you choose to use the W/m^2 unit, the conversion to the 400 - 700 nm range ($\text{W}/\text{m}^2 * 0.45$) may still be required.

6.3.6 Prec

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

6.3.7 CO2

Mean monthly atmospheric CO_2 concentration. Value: decimal > 0 . Units: ppm.

6.3.8 O3 (Optional)

Cumulative atmospheric ozone (O_3) dose over 40 ppb (CumD40) for the growing season. Computed by subtracting 40 from each hourly O_3 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. If O_3 is omitted from this file, ozone effects will not be modeled.

7 Input File – Generic PnET Parameters

This file contains PnET parameters that are not species- or ecoregion-specific or are identical for ALL species or ecoregions. Only parameters that are not described in Chapters 8 and 9 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 7.33) and may be species-specific, or in the PnETEcoregionParameter file (Section 9) but none may appear in more than one file.

7.1 Example file:

```
LandisData PnETGenericParameters
```

```
PnETGenericParameters Value
>>-----
MaxCanopyLayers      4
LayerThreshRatio     0.5
IMAX                 5
DVPD1                0.05
DVPD2                2
BFolResp             0.1
MaintResp            0.002
TOroot               0.025
TOwood               0.03
Q10                  2
FolLignin            0.2
KWdLit               0.01
InitialNSC            7
CFracBiomass         0.45
PrecipEvents         11
Wythers              true
DTEMP                true
CO2HalfSatEff        0.0
PreventEstablishment false
SoilIceDepth         true
LeakageFrostDepth    3000 <<mm
MaxPest               0.3 <<Establishment tuning knob
Parallel             8 <<8 appears to be optimal for
PnET-Succession v5.0/5.1
```

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 should not exceed 5 because applying many canopy layers slows the model dramatically. Typical values are 3 to 5. Value: integer >0. Units: count. Default: 3.

7.5 LayerThreshRatio

This optional parameter is used to lump species-age cohorts into canopy layers, and specifies the minimum ratio of cohort-scale woody biomass density between two cohorts that will cause them to be placed into different canopy layers. Cohorts are processed from largest to smallest so that when a maximum number of layers is specified (MaxCanopyLayers), small cohorts that would otherwise be separated are lumped into the lowest layer rather than lumping large, vastly different-sized cohorts into the top layer. For example, a value of 0.67 will cause layering when one cohort's biomass density is two-thirds the size of the other. To turn off canopy layering, use 0.0, or set MaxCanopyLayers=1. Value: decimal ≥ 0.0 . Units: ratio. Default: 0.5.

7.6 PARunits

Boolean variable indicating the units for PAR and HalfSat values. Values: $\mu\text{mol}/\text{m}^2/\text{sec}$ or W/m^2 . Default: $\mu\text{mol}/\text{m}^2/\text{sec}$.

7.7 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, which is acknowledged to be an overly fine resolution. Reducing IMAX saves computation time, with robust results when $\text{IMAX} \geq \sim 5$ (de Bruijn et al. 2014). Default: 5.

7.8 DVPD1, DVPD2

Coefficients for converting vapor pressure deficit (VPD) to fDVPD according to $\text{fDVPD} = 1 - \text{DVPD1} * \text{vpd}^{\text{DVPD2}}$ (fDVPD is a photosynthesis reduction factor caused by vapor pressure). Value: decimal. Units: kPa^{-1} . Default: 2, 0.1.

7.9 BFolResp

Base Foliar Respiration Fraction - Foliar respiration as a fraction of maximum photosynthetic rate. This rate is modified by temperature using a Q10 relationship, and acclimation of foliar respiration rate to elevated temperature (dynamic Q10) is simulated when Wythers=true. Value: $0.0 \leq \text{decimal} \leq 1.0$. Units: proportion. Default: 0.1.

7.10MaintResp

Loss of NSC due to maintenance respiration, specified as a proportion of active wood biomass. This rate is modified by temperature using a Q10 relationship (Q10 is dynamic when Wythers=true), and is applied to the NSC pool monthly. Value: $0.0 \leq \text{decimal} \leq 1.0$. Units: proportion of active wood biomass (amount to be removed from NSC pool as maintenance respiration) per month. Default: 0.002.

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. Q10 is dynamic around the specified value when Wythers=true. Value: $0.0 \leq \text{decimal} \leq 10.0$. Units: none. Default: 2

7.12FolLignin

Mass fraction of lignin in foliage tissue. Value: $0.0 \leq \text{decimal} \leq 0.8$. Units: gr/gr. Default: 0.2

7.13KWdLit

Annual decomposition rate (decay constant, k) of woody litter. Value: $0.0 \leq \text{decimal} \leq 0.4$. Units: proportion per year. Default: 0.1.

7.14InitialNSC

Amount of NSC assigned to newly established cohorts. Value: integer > 0. Units: g. Default: 7.

7.15CFracBiomass

Carbon fraction of biomass by weight. This parameter may be specified with species-specific values in the PnETSpeciesParameters input file. Value: $0.0 \leq \text{decimal} \leq 1.0$. Units: proportion. Default: 0.45.

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. Value: decimal ≥ 1.0 . Units: count. Default=11.

7.17PrecipEventsWithReplacement

Monthly precipitation amounts are divided into discrete precipitation events, which are randomly assigned to cohort sub-layers. When events are distributed to sub-layers, the sub-layers can be randomly selected with or without replacement. With replacement (true), some sub-layers can have multiple events while others have none. Without replacement (false) the events will be distributed to all of the sub-

layers before any gets multiple events assigned. Value: “true” or “false”. Default: true.

7.18ETExtCoeff

ETExtCoeff is a generic canopy extinction coefficient used to reduce soil water evaporation as LAI increases. Value: $0.0 \leq \text{decimal} \leq 1.0$. Units: none. Default=0.65.

7.19RETCropCoeff

The crop coefficient scalar for the reference evapotranspiration (RET). The overall calculated RET is scaled proportionally according to this coefficient. This parameter serves as a direct adjustment to all levels of evaporation. Value: decimal > 0. Units: None. Default: 0.30.

7.20PreventEstablishment

Boolean variable turning establishment on or off. Value= “true” or “false”. Default: false. Preventing establishment is commonly used only during species calibration simulations.

7.21Wythers

Boolean variable turning the Wythers correction on or off. The Wythers algorithm accounts for acclimation of respiration (foliar and maintenance) to elevated temperatures by modifying Q10 according to temperature (Wythers et al. 2013). When Wythers is true, the base foliar respiration rate is calculated solely from temperature instead of using the BFolResp parameter. Value: true/false. Default: true.

7.22DTEMP

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 computes PsnTMax using PsnTMin and PsnTOpt. 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. Default: true.

7.23MaxPest

Tuning parameter used to raise or lower the establishment probability (Pest) of species by the same proportion. It is typically used as a generic parameter, but it can be used as a species parameter. EstMoist and EstRad can be used to equalize the effect of water and light, linking these effects to the tolerance of the species to each factor, and MaxPest is used to control overall cohort proliferation. Note that this parameter gives the maximum Pest for the time step; for different values of Timestep, the calibration of MaxPest should be verified. . It is also affected by CohortBinSize, so MaxPest should

be calibrated for a specific combination of Timestep and CohortBinSize. Value: $0.0 \leq$ decimal. Units: proportion. Default: 1.0 (Pest not modified).

7.24AmaxFrac

The fraction of the early morning instantaneous photosynthetic rate that represents mean daily photosynthetic rate. Units: fraction. Default: 0.75.

7.25InvertPest (Optional)

Boolean variable activating the optional inversion of the effect of fRad on Pest as a function of HalfSat (see description and diagram in section 1.6.1.1.1). Values: true or false. Default: false.

7.26SoilIceDepth (Optional)

Boolean variable activating the optional simulation of soil ice depth and its effects on leakage. Not recommended unless soil ice information is needed for your study because it slows run time. Values: true or false. Default: false.

7.27LeakageFrostDepth (Optional)

Soil ice depth at which frozen soil no longer impedes soil drainage. LeakageFrac gradually increases from 0.0 when ice depth is \leq RootingDepth to 1.0 at LeakageFrostDepth. Can be omitted when SoilIceDepth=false. Value: integer >0 . Units: mm. Default: 0.0.

7.28FrostFactor (Optional)

Tuning parameter for adjusting soil ice depth. This parameter is applied as a multiplier to soil thermal conductivity (combined effect of soil texture and water content). Conductivity refers to the transmissibility of heat or cold through a substance. Increasing thermal conductivity increases the amplitude of soil temperature variation through the year, keeping monthly temperatures closer to the 12-month mean. Values < 1 will reduce the thermal conductivity of the soil (as computed from published equations), and values > 1 will increase the thermal conductivity of the soil. Values: decimal ≥ 0 . Default: 1.0.

7.29InitialCommunitiesSpinup (Optional)

Specify how initial communities will be generated. “Spinup” option causes any biomass values given in the IC communities file to be ignored and the model generates initial biomass by simulating cohort from age=1; “NoSpinup” uses IC communities file biomass values and does not execute spinup, using that biomass to determine canopy layer; “SpinupLayers” also uses IC communities file biomass values but also executes spinup for the sole purpose of determining the canopy layer of the cohort based on the maximum biomass achieved during spinup. Values: “Spinup”, “NoSpinup”, “SpinupLayers”. Default: “Spinup” when no biomass values are provided, “SpinupLayers” when biomass values are provided.

7.30 SpinupWaterStress (Optional)

Boolean variable activating waterlogging stress during spin up. For species with H1 or H2 values >0, cohorts may die from waterlogging stress when they are initialized by spinup on empty sites because transpiration is initially very low. This parameter is used to prevent that; it can be set to “true” when the landscape is very wet. Values: true or false. Default: false (waterlogging stress is ignored during spin up.).

7.31 Parallel (Optional)

Specify the maximum number of threads for parallel execution. For version 5 of PnET-Succession, set this parameter to 8 threads or fewer; any higher results in excessive wait-times (slower processing) due to thread-locking. We hope to improve performance further in future releases.

The use of parallel processing results in loss of absolute repeatability because random deviates are accessed indeterminately. To mitigate this, it is advisable to maintain the same maximum number of threads in factorial experiments and replicates. Values: integer ≥ 1 , or ‘true’. ‘true’ will let the operating system decide, and this will invariably result in very long runtimes because of thread-locking. Default: 1 (no parallel processing).

7.32 CohortStacking (Optional)

Specify the canopy cohort processing method (Gustafson et al. 2023). To use the method found in versions prior to PnET-Succession v.5 (stacked), set this parameter to ‘true.’ Default: ‘false’ (canopy proportion weighted-average method).

7.33 CanopySumScale (Optional)

Scales the degree to which the constraint that cumulative canopy proportions cannot exceed 1 is enforced. CanopySumScale scales the relative rate at which excess canopy proportion (>1) is removed. The parameter is ignored when CohortStacking=true. Value: $0.0 \leq \text{decimal} \leq 1.0$. Units: proportion. Default: 0.206.

8 Input File – PnET Species Parameters

The parameters in this file typically vary by species. If they are the same for all species, they may more conveniently be placed in the PnETGenericParameters file (Section 7). All parameters for a species appear on a single line. Parameters and species 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	FracBelowG	EstMoist	EstRad	FracFol	FrActWd	CO2HalfSatEff				
abiebal 1.0 115 0 0.2 5.3 21.5 134 100 140 5 0.8 16.8 0.5 0.35										
1 .098 0.07 0.00005 0.5										
acerrub 2.0 60 0.2 1 -46 71.9 181 105 145 5 1.75 25.5 0.58 0.35										
1 0.92 0.024 0.00004 0.0										
acersac 1.9 62 0.2 1 -46 71.9 149 104 143 5 1.8 25.5 0.58 0.37										
1 0.98 0.024 0.000036 0.0										

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 FoIN

Foliar nitrogen content (% by weight). Value: $0 < \text{decimal} < 10$. Units: %.

8.5 SLWmax

Specific leaf weight at the top of canopy. Values < 40 may result in extremely high LAI in lower canopy sublayers when $\text{SLWDel} > 0$. Value: $0 < \text{decimal} < 1000$. Units: g/m^2 .

8.6 SLWDel

Rate of change per sublayer in specific leaf weight from the top of a cohort's canopy to the bottom. SLW increases when $\text{SLWdel} > 1$. Set to zero to make SLW constant throughout a canopy layer. Value: $0.0 \leq \text{decimal} \leq 2$. Units: proportion of SLWmax.

8.7 MaxLAI (Optional)

Maximum LAI (leaf area index) that the species can achieve in its lifetime, and it is typically computed by the model using other parameters (Gustafson et al. 2023). However, it can be specified here to control the early part of the species growth curve because values less than the (default) calculated value will allow cohorts to fill the canopy space faster. However, MaxFracFol is the recommended choice to control the early part of the species growth curve. Value: $0.0 \leq \text{decimal}$. Units: $\text{m}^2 \text{ leaves/m}^2 \text{ ground}$. Default: computed from other parameters.

8.8 TOFol

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

8.9 TORoot/TOWood

Turnover of Root and Wood biomass. This is the fraction of root/wood biomass lost per year to damage, breakage or death of individual stems (self-thinning). Value: $0.0 \leq \text{decimal} \leq 1.0$. Units: fraction per year. Default: 0.02, 0.01.

8.10 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: $-500 < \text{decimal} < +500$

8.11AmaxB

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

8.12HalfSat

Half saturation light level for photosynthesis. Lower values reflect more shade tolerance. Value: integer >0. Units: User choice between $\mu\text{mol/m}^2/\text{sec}$ or W/m^2 . The units of PAR in the climate input file must be the same as those of HalfSat. **THE MODEL CANNOT VERIFY THAT THE UNITS ARE THE SAME.** This is a user responsibility. If units of W/m^2 are used, set the PAR_W_m2 equal to 'true' (section 7.28) to ensure that evaporation is computed correctly. 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.

8.13H1, H2, H3, H4

Water stress parameters according to Feddes et al. (1978). See Section 2.2.2.3 for a discussion about estimating these parameters. H1 may take a negative value to produce $f_{\text{Water}} > 0.0$ when pressure head=0 (waterlogging tolerance). H1, H2, H3 and H4 should be successively larger positive values. Note that this is the absolute value of actual pressure head values. Value: $0.0 < \text{decimal}$. Units: m pressure head. Defaults: 0, 3.64, 150, 150.

8.14PsnAgeRed

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: $y = \left(\frac{\text{age}}{\text{longevity}} \right)^{\text{PsnAgeRed}}$. Cohorts die when NSC is $< 1\%$ of the value of the other biomass pools combined at the end of a calendar year. Value: $0.0 < \text{decimal}$. Units: proportion per year. Default: 5.

8.15LeafOnMinT

Minimum temperature for active growing season. Compared to Tmin (from climate input file) to determine start and end month of each growing season. Foliage is allocated during the first growing season month and some or all is dropped (depending on TOFol) after the last month. Reduce LeafOnMinT to lengthen the growing season. Value: decimal. Units: °C. Default: none provided.

8.16PsnTMin

Minimum average **daytime** temperature (Tday) for photosynthesis. The temperature reduction factor will equal 0 in months when Tday is below this value. Value: decimal. Units: °C.

8.17PsnTOpt

Optimal average **daytime** temperature (Tday) for photosynthesis. The temperature reduction factor will equal 1.0 in months when Tday is equal to this value. Value: decimal \geq PsnTMin. Units: °C.

8.18PsnTMax (Optional)

Maximum average **daytime** temperature (Tday) for photosynthesis. The temperature reduction factor will equal 0 in months when Tday is above this value. Typically not greater than ~37°C. Value: decimal \geq PsnTOpt. Units: °C.

If PsnTMax is not provided, an estimated value of PsnTMax is calculated as (PsnTOpt + PsnTOpt – PsnTMin), which is consistent with earlier versions of the model. However, values >40 may occur.

8.19ColdTol (Optional)

Cold tolerance. Coldest temperature that the species can survive. Note: cohorts may resprout after being cold-killed if their resprout probability >0. Value: decimal. Units: °C. Default: -9999 (not specified).

8.20k

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

8.21DNSC

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. Default: 0.05.

8.22FracBelowG

Fraction of non-foliar biomass that is allocated belowground (root pool). Allocations vary each year to maintain this fraction. Value: $0.0 \leq \text{decimal} \leq 1.0$. Units: proportion. Default: 0.33

8.23EstMoist

Scaling parameter that causes the maximum expected value of fWater to equal 1.0 when computing Pest. Because fWater usually equals 1.0 at some time in a season or simulation, this parameter is typically set equal to 1.0. Typically used to make light and water have an equal effect on establishment. Value: $0.0 \leq \text{decimal} \leq 1.0$. Units: proportion. Default: 1.0.

8.24EstRad

Scaling parameter that causes the maximum expected value of fRad to equal 1.0 when computing Pest. Because fRad almost never equals 1.0 during a simulation, this parameter is typically set equal to the maximum fRad value observed in the first year when a single cohort of a species is grown on an open site. Typically used to make light and water have an equal effect on establishment. Value: $0.0 \leq \text{decimal} \leq 1.0$.

Units: proportion. Default: 1.0.

8.25FracFol

Fraction of the amount of active woody biomass (above and belowground) that determines the amount of foliage maintained each year. The active fraction of woody biomass is calculated by the model using FrActWd (section 8.26). Value: $0.0 \leq \text{decimal} \leq 1.0$. Units: proportion per year. Default: 0.033.

8.26FrActWd

Shape parameter of a 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. Default: 0.00004.

8.27CO2HalfSatEff (Optional)

Slope coefficient used to reduce HalfSat (increase shade tolerance) as CO₂ concentration increases. Value: $\text{decimal} \leq 0.0$. Units: unitless. Set to zero to turn off this effect. See PnET-Succession function worksheet.xlsx to see how the parameter affects HalfSat. Default: 0.0 (no effect).

8.28CO2AMaxBEff (Optional)

The proportional change in AmaxB at 550ppm CO₂ relative to 350ppm CO₂. Value: $\text{decimal} \geq 0.0$. Units: proportion. Omit parameter or set to 1.0 to turn off this effect. Default: 1.0 (no effect).

8.29O3StomataSens (Optional)

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

8.30O3GrowthSens (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 (no effect).

8.31 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. Defaults: -9999, 0.0.

8.32 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=-9999, 0.0. Omit these parameters, or set MaxFracFol equal to FracFol, to turn off effect. See PnET-Succession function worksheet.xlsx to see how the parameters affect FracFol.

8.33 LifeForm (Optional)

Specify the life form (stature) of the species to determine if there are limits to the species' major canopy layer. In PnET-Succession, biomass is a proxy for height. Canopy layering is determined by cohort biomass, and “trees” can exist in any canopy layer. Species that can exist only in the lowest canopy layer can be identified as “ground” lifeforms. In v5.1, the life form of a species is “tree” by default, and any string value for this parameter that contains “ground” will be limited to only being in the lowest canopy layer.

The LifeForm parameter is also used in the calculation of the optional albedo output variable by the optional PnET-Succession output extension (see Section 11.6 for details and acceptable parameter values). Values: string containing ‘tree’ or ‘ground’ (not case sensitive). Default: ‘tree’.

8.34 MossScalar (Optional)

This is a unit converter (multiplier) to convert the biomass value of a pseudo species (typically representing moss) to a depth. Purpose is to estimate the insulation value of the pseudo species when computing the soil temperature profile. This parameter is not needed when SoilIce=false. Depth (in meters) = species.biomass*MossScalar. Set MossScalar to zero for species that are not a soil-insulating groundcover species. See PnET-Succession function worksheet.xlsx to see how the parameter affects moss depth. Value: $0.0 \leq \text{decimal}$. Units: meters. Default: 0.

9 Input file - Ecoregion parameters

9.1 Example file:

```
LandisData  EcoregionParameters

EcoregionParameters SoilType Latitude RootingDepth PrecLossFrac
LeakageFrac PrecIntConst SnowSublimFrac ClimateFileName

ecol  SALO  45.2  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 in section 2.2.2.3). 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\v6\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 and USDA soil types. Value: 4-letter string, case sensitive.

9.5 Latitude

This parameter is the approximate latitude of the ecoregion, used to compute daylength. NOTE: the PnET-Succession extension is not currently configured to work properly in the southern hemisphere. Value: $0 < \text{decimal} < 90$. 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 soil water "bucket." Value: integer ≥ 0 . Units: mm.

9.7 PrecLossFrac

Precipitation Loss Fraction. Proportion of precipitation that does not enter the soil (e.g., runoff induced by topographic slope). In lieu of specific empirical estimates, this can be set equal to the decimal equivalent of the mean slope (%) found in the topography of the ecoregion. Value: $0.0 \leq \text{decimal} \leq 1.0$. Units: proportion.

9.8 EvapDepth

Soil depth below which water cannot be evaporated. Value: $0 \leq \text{integer} < \text{RootingDepth}$. Units: mm. Default: 005.

9.9 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. Default: 1.0.

9.10 RunoffCapture (Optional)

Height above soil surface that water can reach before any runoff occurs, representing height of basin outlet. This parameter is used to allow soil water to accumulate above saturation (i.e., flooded). RunoffCapture only applies to water that exceeds the soil porosity (saturation) and would cause it to all run off when RunoffCapture = 0 (the previous model behavior). Any excess water (above saturation) is retained in the soil “bucket” until evaporation, interception, transpiration and leakage (if any) collectively exceeded cumulative precipitation inputs (i.e., consumed all excess water). Value: $\text{decimal} \geq 0.0$. Units: mm. Default: 0.0.

9.11 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 2.2.2.1. Value: $\text{decimal} \geq 0.0$. Units: unitless. Default: 0.1.

9.12 SnowSublimFrac

Fraction of the annual 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.

9.13 MossDepth (Optional)

The ecoregion has moss (or a generic insulating layer) of this depth on every cell. The only function of this parameter is to increase the insulation of soil and affect the soil temperature profile. This parameter has no effect on establishment of cohorts (i.e., no shade is cast) and is not dynamic (does not change in response to disturbance or succession). Dynamic moss can be simulated using pseudo species (non-trees) and the parameter MossScalar (section 0). Value: $0.0 \leq \text{decimal}$. Units: meters. Default: 0.

9.14 WinterSTD (Optional)

Standard deviation of hourly winter temperatures. Used in conjunction with ColdTol to determine if cohorts survive the estimated extreme coldest temperature each month. Cohort is killed when:

$$[Tave - 3 \times WinterSTD] < ColdTol$$

sensu Court 1951. Value: decimal ≥ 0.0 . Units: °C. Default: 0.0.

9.15 ClimateFileName

This parameter gives the name of the climate file for the ecoregion. The user may specify the same file for multiple ecoregions. This parameter can be omitted if the climate library is used, and any value(s) for this parameter will be ignored if the climate library is specified in a ClimateConfigFile (section 3.15).

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. For Wood-, Fol- and RootReduction, the parameter determines what proportion of the dead material (wood, foliage or root portion) is removed from the site instead of being added to the local dead pools. For DeadWood- and LitterReduction, the parameter determines the proportion of the dead pool that is eliminated when a disturbance of a certain type happens on the site.

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 active in the model run. 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 the removed 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, effectively the proportion that gets removed from the site instead of entering the local dead 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). These parameters do not impact that amount of biomass removed by the disturbance, only the accounting of what happened to the biomass that went from live to dead.

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
WoodBiomass          output/biomass/{species}/WoodBiomass_{timestep}.img
>>FoliageSenescence  output/Senescence/{species}/FolSenescence_{timestep}.img
>>WoodySenescence    output/Senescence/{species}/WoodSenescence_{timestep}.img
AnnualPsn            output/AnnualPsn/{species}/Psn_{timestep}.img
RootBiomass output/RootBiomass/RootBM-{timestep}.img
WoodyDebris          output/WoodyDebris/WoodyDebris-{timestep}.img
Litter               output/NonWoodyDebris/Litter-{timestep}.img
CohortBalance        output/TotalCohorts.csv
EstablishmentTable   output/EstablishTable.csv
MortalityTable       output/MortalityTable.csv
Water                output/SoilWater/water_{timestep}.img
```

Albedo output/Albedo/MonthlyAlbedo_{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, determining how often requested outputs will be generated. 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 Output File Name Templates

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 to 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, although some multiply by 100 to convert proportions to integer percentages as described below.

Here are the valid variable names and the required naming variables and file type of the output files: All variables are optional and can appear in any order. **Note: if {species} is given as an option in the paths listed below but {species} is omitted, only the AllSpecies outputs will be generated. Use this to reduce unwanted species-level outputs.**

Many mapped outputs also include a CSV file with the average value (active cells only) of each map.

WoodBiomass, path/{species}/filename-{timestep}.mapextension

Map. Values: value at the end of the last succession timestep. Units: gDW /m2. WoodBiomass is aboveground wood, but not foliage biomass.

FoliageBiomass, path/{species}//filename-{timestep}.mapextension

Map. Values: : maximum values (all cohorts combined) from the last 12 months of the succession timestep. Units: gDW /m2. FoliageBiomass includes foliage only.

- RootBiomass, path/{species}/filename-{timestep}.mapextension
Map. Values: value at the end of the last succession timestep. Units: gDW /m2.
RootBiomass represents both coarse and fine roots.
- NSC, path/{species}/filename-{timestep}.mapextension
Map. Values: value at the end of the last succession timestep. Units: gC/m2.
NSC includes Non-Structural Carbon (reserves) only.
- Wood-RootBiomass, path/{species}/filename-{timestep}.mapextension
Map. Values: value at the end of the last succession timestep. Units: gDW/m2.
Biomass is the sum of wood and roots, but not foliage biomass. Outputs of biomass for all species combined (AllSpecies) is also output.
- Wood-FoliageBiomass, path/{species}/filename-{timestep}.mapextension
Map. Values: value at the end of the last succession timestep. Units: gDW/m2.
Biomass is the sum of wood and foliage biomass, but not roots.
- WoodySenescence, path/{species}/filename-{timestep}.mapextension
Map. Values: value at the end of the last succession timestep. Units: g/m2.
Outputs woody biomass of the species added to woody dead pool.
- FoliageSenescence, path/{species}/filename-{timestep}.mapextension
Map. Values: value at the end of the last succession timestep. Units: g/m2.
Outputs foliage biomass of the species added to litter dead pool.
- AETAvg, path/{species}/filename-{timestep}.mapextension
Map. Values: AETAvg is average monthly actual evapotranspiration across the last 12 months of the timestep. Units: mm.
- PET, path/{species}/filename-{timestep}.mapextension
Map. Values: PET is total potential evapotranspiration across the last 12 months of the timestep. Units: mm.
- AgeDistribution, path/filename-{timestep}.mapextension
Map. Values: count at the end of the last succession timestep. Units: # unique age cohorts. A .csv file is also generated at each timestep with an age-class histogram for each species at the end of the timestep.
- AnnualPsn, path/{species}/filename-{timestep}.mapextension
Map. Values: the sum of MonthlyNetPsn values across the last 12 months of the timestep. Units: g/m2.
- CohortsPerSpecies, path/{species}/filename-{timestep}.mapextension
Map. Values: value at the last succession timestep. Units: # cohorts of the species.
- Establishment, path/{species}/filename-{timestep}.mapextension
Map. Values: 0 = No Presence, 1 = Continued Presence. 2 = Discontinued Presence, 3 = New Presence.
- EstablishmentProbability, path/{species}/filename-{timestep}.mapextension
Map. Values: average values (multiplied by 100) of the months in the last year of the succession timestep. Units: probability (as %).

- LeafAreaIndex, path/{species}/filename-{timestep}.mapextension
Map. Values: maximum values (all cohorts combined) from the last 12 months of the succession timestep. Units: m² leaf/m² ground. Summary file gives mean LAI of vegetated cells (LAI>0).
- MonthlyFolResp, path//filename-{timestep}.mapextension
Map. Values: average values for each month of the last year of the succession timestep. Units: g/m². *
- MonthlyGrossPsn, path/filename-{timestep}.mapextension
Map. Values: average values for each month of the last year of the succession timestep. Units: g/m².
- MonthlyNetPsn, path/filename-{timestep}.mapextension
Map. Values: average values for each month of the last year of the succession timestep. Units: g/m².
- MonthlyMaintResp, path/filename-{timestep}.mapextension
Map. Values: average values for each month of the last year of the succession timestep. Units: g/m².
- Albedo, path/filename-{timestep}.mapextension
Map. Values: average values for each month of the years of the last succession timestep. Units: DHR (directional hemispherical reflectance (black sky (shortwave) albedo), which is a ratio of reflected solar radiation to incoming solar radiation. DHR is multiplied by 100 to produce integer (% reflectance) output.
- MonthlyAvgSnowPack, path/filename-{timestep}.mapextension
Map. Values: average values for each (of 12) month of the succession timestep. Units: mm water equivalent.
- MonthlyActiveLayerDepth, path/filename-{timestep}.mapextension
Map. Values: depth to the top of the permafrost ice layer in the given summer month of the last year of the succession timestep. Units: cm. Output only for the months May-August. Values will equal Rooting Depth+LeakageFrostDepth when the ice layer >= that value. SoilIceDepth must be set to true.
- MonthlyFrostDepth, path/filename-{timestep}.mapextension
Map. Values: depth to unfrozen soil in the given winter month of the last year of the succession timestep. Units: cm. Output only for the months December-March. Values will equal Rooting Depth+LeakageFrostDepth when ice extends to a depth >= that value. SoilIceDepth must be set to true.
- SiteMossDepth, path/filename-{timestep}.mapextension
Map. Values: depth of moss or other species that insulate the soil. Units: cm.
Can only be generated when the optional MossDepth and MossScalar parameters have at least one non-zero value.
- WoodyDebris, path/filename-{timestep}.mapextension
Map. Values: value at the end of the last succession timestep. Units: g/m².

Litter, path/filename-{timestep}, mapextension

Map. Values: value at the end of the last succession timestep. Units: g/m².

SubCanopyPAR, path/filename-{timestep}.mapextension

Map. Values: maximum growing season values from the last succession timestep. Units: W/m² or mmol/m², depending on input units.

Water, path/filename-{timestep}.mapextension

Map. Values: average monthly value for the last succession timestep. Units: cm/m.

CohortBalance, path/filename.textextension

Tab-delimited text file containing landscape total or average values of the following variables for each time step. Variables are defined as indicated above.

of cohorts (landscape total)

Average Age of all cohorts on the landscape (years)

Average Wood-root (biomass) / site (g/m²)

Average LAI / site (m²)

Average Water / site (mm)

July SubCanopy PAR / site (W/m² or μ mol/m², depending on input units)

Litter / site (gDW/m²)

WoodyDebris / site (gDW/m²)

AverageWoodFoliage / site (g/m²)

AverageRoot / site (g/m²)

AverageWood / site (g/m²)

AverageFoliage / site (g/m²)

NSC / site (gC/m²)

AverageAET / site (mm/yr)

EstablishmentTable, path/filename.textextension

Tab-delimited text file containing landscape total number of cohorts established (by species and cause) for each time step.

MortalityTable, path/filename.textextension

Tab-delimited text file containing landscape total number of cohorts killed (by species and cause) for each time step.

11.6 Notes on albedo computations

Purpose: produce maps of albedo (earth surface reflectance) based on the vegetation on each cell.

Background: Land cover produces an important feedback between the earth system and atmosphere system by determining how solar radiation is reflected or absorbed. Albedo is the common measure of this reflectance, with higher values representing greater reflectance. In forested landscapes where forest covers large territories, changes in albedo can influence climate by altering how much solar radiation is re-radiated as heat. Albedo varies by forest type (deciduous, conifer, mixed), leaf area and canopy structure, forest floor characteristics (snow cover, plant ground cover), and phenology (leaf-on and -off date), so dynamic forest composition, age and climate can result in dynamic albedo.

Algorithm: Uses empirical data of Lukeš et al. 2013, which measured albedo in pure stands as a function of leaf area. Lower LAI means more of albedo is driven by the forest floor. Thus, the approach here is to compute albedo using the LAI of each canopy type on a cell to control for the effect of forest floor. Maps are produced for each month of the last year of each output time step. Note: this extension should be used with caution in biomes other than boreal because the equations were derived from boreal forests, which have unique leaf and forest floor characteristics.

Equations used: y is albedo, x is LAI of the canopy type.

Dark (less reflective) conifer: $y = -0.067\ln(x) + 0.2095$ (Lukeš et al. 2013). Snow (>100mm), add 80% (Betts and Ball 1997). Snow effect increases linearly as snow depth increases from 0 to 100 mm. Constrain x to be no less than 0.7 for computations.

Light (more reflective) conifer: $y = -0.054\ln(x) + 0.2082$ (Lukeš et al. 2013). Snow, add 75% (Betts and Ball 1997). Constrain x to be no less than 0.7 for computations.

Deciduous: $y = -0.0073x + 0.231$ (Lukeš et al. 2013). Snow, add 35% (Betts and Ball 1997)

Grass or moss or open: $y = 0.24$ (Betts and Ball 1997). Snow, add 312.5% ($y = 0.75$) (Betts and Ball 1997)

Cell albedo (y) is computed as a weighted average in the topmost layer with LAI>1, weighting by proportion of leaf area of each canopy type. Note that y is multiplied by 100 to produce integer (% reflectance) output. Albedo is not estimated for non-active cells.

Required input parameters: LifeForm (canopy type) of each species. Currently valid types are dark conifer, light conifer, deciduous, ground cover (typically moss or grass). Because the LifeForm parameter is used for other purposes (e.g., layering), the albedo computations search LifeForm values for these mutually exclusive (not case-sensitive) strings to determine canopy type: 'dark', 'light', 'decid', 'open', or 'grass'. If none of these strings are found, the default is 'decid'. Examples of valid LifeForm values include 'dark_conif_tree', 'light_tree', 'grass_ground'. Note that the layering algorithm assumes that any LifeForm value with the string 'ground' can only be in the lowest canopy layer, so include the string 'tree' in all species that should not be constrained in layering. See section 8.33 for more details on LifeForm.

Literature Cited

Betts and Ball. 1997. Albedo over the boreal forest. J. GEOPHYSICAL RESEARCH 102(D24):28901-28909.

Lukeš Petr, Pauline Stenberg, Miina Rautiainen. 2013. Relationship between forest density and albedo in the boreal zone. Ecological Modelling 261–262:74-79.
<https://doi.org/10.1016/j.ecolmodel.2013.04.009>.

12 Input File – PNETOutputsites

This file contains parameters for the site data output extension. This extension outputs state variables each month for individual grid cells (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          10
Site2 178        294
Site3 81         12
```

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 (or start of simulation if NoSpinup is used) 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.

13.1Time

Simulation year and month (as decimal).

13.2Year

Simulation year.

13.3Month

Simulation month.

13.4Ecoregion

Ecoregion for the cell.

13.5SoilType

Soil type assigned to the cell's ecoregion.

13.6NrOfCohorts

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

13.7MaxLayerRatio

Maximum ratio of biomass values between all combinations of cohorts present on the cell. These ratios are used to assign cohorts to canopy layers (section 2.2.1).

13.8Layers

Number of canopy layers on the cell.

13.9SumCanopyProp

Sum of the canopy proportions of all cohorts on the site, scaled to not exceed 1.0 for each major layer, as modified by CanopySumScale parameter. Values less than 1.0 indicate canopy gaps.

13.10 PAR0

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

13.11 Tmin(C)

Tmin from the climate file.

13.12 Tave(C)

Mean air temperature (°C), computed as the average of TMin and TMax from the climate file.

13.13 Tday(C)

Mean air temperature (°C) in the daytime, derived as the average of Tave and TMax.

13.14 Tmax(C)

Tmax from the climate file.

13.15 Precip(mm_mo)

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

13.16 CO2(ppm)

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

13.17 O3(cum_ppb_h)

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

13.18 RunOff(mm_mo)

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

13.19 Leakage(mm)

Water lost out of the bottom of the rooting zone.

13.20 Potential Evaporation(mm)

Potential EvapoTranspiration. Potential evaporation is calculated according to Hamon (1961).

13.21 Evaporation(mm)

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

13.22 PotentialTranspiration(mm) (mm)

Potential transpiration of all cohorts.

13.23 Transpiration(mm)

Actual transpiration of all cohorts.

13.24 Interception(mm)

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

13.25 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).

13.26 Water(mm/m)

Proportional amount of soil water (mm water per m of soil profile) as calculated by the bulk hydrology model. 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.

13.27 PressureHead(m)

Absolute value of pressure head (at the end of the month) as calculated by the bulk hydrology submodel (m).

13.28 Available water (mm)

Amount of available soil water, above the soil frost line (if any). Available water is $\text{Water} * \text{RootingDepth}$, multiplied by the proportion of the soil that is above the frost line.

13.29 SnowPack(mm)

Water equivalent contained in the snowpack (mm).

13.30 LAI(m²)

Leaf Area Index (all species combined)

13.31 VPD(kPa)

Mean vapor pressure deficit for the month (kPa).

13.32 GrossPsn(gC/mo)

Gross photosynthesis of all species combined ($\text{gC} / \text{m}^2 / \text{mo}$).

13.33 NetPsn(gC/mo)

Net photosynthesis of all species combined ($\text{gC} / \text{m}^2 / \text{mo}$).

13.34 MaintenanceRespiration(gC/mo)

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

13.35 Wood(gDW)

Sum of (canopy-weighted) aboveground woody biomass of all species (gDW).

13.36 Root(gDW)

Sum of (canopy-weighted) root biomass of all species (gDW)

13.37 Fol(gDW)

Sum of (canopy-weighted) foliage biomass of all species (gDW).

13.38 NSC(gC)

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

13.39 HeteroResp(gC_mo)

Heterotrophic respiration (decay of dead pools).

13.40 Litter(gDW/m²)

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

13.41 CWD(gDW/m²)

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

13.42 WoodySenescence (gDW/m²)

Total woody biomass added to the dead pool each month.

13.43 FoliageSenescence (gDW/m²)

Total litter biomass added to the dead pool each month.

13.44 SubcanopyPAR

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

13.45 SoilDiffusivity(mm²_s)

Thermal diffusivity of the soil given the texture and water content.

13.46 ActiveLayerDepth(mm)

Depth to the top of soil ice layer in summer. Will be RootingDepth+LeakageFrostDepth when permafrost is not present.

13.47 LeakageFrac(-)

Computed LeakageFrac (dependent on active layer depth).

13.48 AverageAlbedo(ratio_W_m2)

Average albedo of the vegetation on the site.

13.49 FrostDepth(mm)

Depth to unfrozen soil in the winter. Will be RootingDepth+LeakageFrostDepth when permafrost is present. Will be 0 when soil is not frozen to a depth of at least 25 cm.

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 (as decimal).

14.2 Year

Simulation year.

14.3 Month

Simulation month.

14.4 Age(yr)

Current age of the cohort (calendar years).

14.5 TopLayer(-)

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

14.6 CanopyLayerProp

Proportional weight within the layer based on relative cohort LAI (LAI/MaxLAI); this is the weighting attribute used to compute cohort's contribution to total site biomass.

14.7 CanopyGrowingSpace

Proportional space a cohort is allowed to occupy. This is a permanent constraint on CanopyLayerProp; a value of 1 means it has not yet been part of a layer with a closed canopy (CanopyLayerProp ≥ 1.0).

14.8 LAI(m2)

Leaf area index of the cohort's canopy.

14.9 Site LAI(m2)

Leaf area index of the site that is contributed by the cohort.

14.10 GrossPsn(gC/m2/mo)

Cohort gross photosynthesis (gC/m2/mo).

14.11 FolResp(gC/m2/mo)

Cohort foliar respiration (gC/m2/mo).

14.12 MaintResp(gC/m2/mo)

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

14.13 NetPsn(gC/m2/mo)

Cohort net photosynthesis (gC/m2/mo).

14.14 Transpiration(mm/mo)

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

14.15 WUE(g/mm)

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

14.16 Fol(gDW/m²)

Cohort-level biomass density of the cohort foliage pool (gDW/m²).

14.17 Root(gDW/m²)

Cohort-level biomass density of the cohort root pool (gDW/m²).

14.18 Wood(gDW/m²)

Cohort-level biomass density of the cohort wood pool (gDW/m²).

14.19 Site Fol(gDW)

Foliar biomass accounting for the cohort's proportional weighting (gDW/m²).

14.20 Site Root(gDW)

Root biomass accounting for the cohort's proportional weighting (gDW/m²).

14.21 Site Wood(gDW)

Aboveground woody biomass accounting for the cohort's proportional weighting (gDW/m²).

14.22 NSC(gC/m²)

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

14.23 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.

14.24 fWater(-)

Reduction factor related to water availability.

14.25 Water(mm/m)

Average volumetric soil water value (mm water per 1000 mm (1 m) of soil profile) used to compute pressure head (soil water potential).

14.26 PressureHead(m)

Pressure head value (soil water potential) used to compute fWater across all cohort sublayers.

14.27 fRad(-)

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

14.28 fOzone(-)

Reduction factor related to ozone effects.

14.29 DelAmax(-)

Enhancement factor related to CO₂ effects on photosynthesis.

14.30 fTemp_psn(-)

Reduction factor related to sub-optimal temperature for photosynthesis.

14.31 fTemp_resp(-)

Reduction factor related to temperature effects on maintenance respiration.

14.32 fAge(-)

Reduction factor for age-related declines in photosynthesis efficiency.

14.33 LeafOn(-)

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

14.34 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.

14.35 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.

14.36 AdjFracFol(-)

Adjusted FracFol. When using the optional MaxFracFol and FracFolShape parameters, the adjusted FracFol can be different from the species FracFol value, depending on canopy position and the resulting PAR. Averaged across the cohort's subcanopy layers.

14.37 CiModifier(-)

Modification factor for gas conductance due to stomatal sluggishness caused by ozone. Value of 1.0 indicates no modification in conductance. Averaged across the cohort's subcanopy layers.

14.38 AdjHalfSat(-)

Adjusted HalfSat. When using the optional CO2HalfSatEff, the adjusted HalfSat can be different from the nominal species HalfSat value, depending on CO₂ concentration. 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.

14.39 Limiting Factor

Indicates the most limiting factor on photosynthesis, including death by extreme cold (and the temperature that killed the cohort).

15 Output file – Establishment Table (Optional PNEToutputsites output)

This comma-delimited table reports site-level establishment information for each species. The reported values reflect mean state variable values in the model during one PnET-Succession time step.

15.1 Year

Simulation year (timestep).

15.2 Species

Species.

15.3 Pest

The cumulative probability of establishment for the species during the given time step as a function of the monthly values of water and PAR. Each timestep probability is:

$$P_{est} = fRad \times fWater \times MaxPest$$

Where fRad and fWater are the average reduction factor values for the 2nd through 4th growing season months across all timestep years.

15.4 FWater_Avg

The average water availability reduction factor (fWater) value across the 2nd-4th growing season months each year in the time step.

15.5 FRad_Avg

The average light availability reduction factor (fRad) value across the 2nd-4th growing season months each year in the time step.

15.6 ActiveMonths

The number of growing season months used for calculating establishment (2nd-4th growing season months) within the timestep for the given species.

15.7 Est

Indicates if an establishment of the species by seeding would occur on the site in the time step IF seeds were able to reach the site and the site did not have planting,

serotiny or resprouting occur. Actual establishment additionally requires a source tree within seeding distance.

16 Output file – Mortality Table (Optional PNEToutputsites output)

For each time step the model outputs the number of cohorts of each species killed by the major sources of mortality (Succession (competitive exclusion), Cold, Harvest, Fire, Wind and Other (all of the other disturbance extensions invoked for the run)).

17 Output file – Establish Table (Optional PNEToutputsites output)

For each time step the model outputs the number of cohorts of each species established by the four sources of cohort establishment (Planting, Serotiny, Resprouting and Seeding).

18 Appendix. Calibration tips.

Calibration tips

August 8, 2023

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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 because it is completely based on empirically observed inputs (parameters) and relationships (see Aber et al. 1995). However, because foliar nitrogen (FolN) takes a single value that is used by the model as the sole determinant of photosynthetic capacity, it should be calibrated because FolN can vary widely within a species in nature. In PnET-Succession, some changes have been made to foliage computations to make them tractable at landscape scales, and these modifications use non-empirical parameters. Therefore, because the model is designed to use empirically known parameters to mechanistically simulate growth and competition based on first principles of physiology, the primary purpose of calibration of PnET-Succession is to get photosynthetic capacity (via Foliar Nitrogen) and amount of foliage correct. A secondary purpose is to calibrate parameters (species and ecoregion) that determine hydrology and response to water and temperature. This means that of the dozens of parameters used by PnET-Succession, very few need calibration, and most applications can use empirically derived (or default) values for most parameters. Because the amount of foliage of a cohort through time is rarely known empirically, calibration involves setting the

empirically known parameters and then modifying foliar nitrogen and foliage parameters to get simulated biomass growth to match empirical growth curves that were measured and simulated under ideal growing conditions.

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, or those generated by the forest stand model FVS. Use the PNEToutputSites option to produce the cohort growth output files needed for calibration. There are several calibration approaches used by others to achieve the goal of calibrating model outputs to empirical data of analogous measures of actual tree behavior. Such calibration approaches may require modifications to the strategy described here.

To produce predictable competitive interactions that can be controlled by intuitive modification of a small number of parameters for individual species, it is helpful to use common parameter values across all species whenever 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 life history 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, AmaxA, AmaxB, k, and FracBelowG.

Because PnET-Succession is designed to apply reduction (stress) factors to an optimal photosynthesis rate (Amax), the goal of calibration is to produce an accurate estimate of Amax and foliage amount under optimal site and climate conditions, with the accuracy being assessed by comparing simulated biomass growth (or an analogous measure) to empirical growth. Thus, you will calibrate to empirical growth rates on the best sites, recognizing that those growth rates may have been achieved with sometimes less optimal climate conditions than those used for calibration. Calibration is best done by modifying only FolN (to control relative productivity), and FracFol, FrActWd and SLWmax (to control gross foliage amount and LAI, which determines the ability to access light).

I set up a landscape with a single active cell and initialize that cell with a single species at a time. I calibrate species under good to ideal growing conditions, recognizing that their growth will be less under poorer conditions and when competing with other cohorts because stress factors will be greater. However, if you know the conditions under which your growth curves were generated, use those conditions. I calibrate on a soil with above average (but not the greatest) water holding capacity (e.g., SILO) and a weather stream with average or better precipitation for the regions where the species are typically found and calibrate to the higher range of the growth curves available. Because biomass accumulation is ultimately limited by water, your precipitation inputs should not be much greater than is typical for your study area. Some people set up a landscape with 2-4 active cells, each with a different soil (ecoregion) to simultaneously generate a range of growth curves across a gradient of site

quality). *HINT: you can create a small map with a unique value for each cell and use the same map for initial conditions and ecoregions by associating appropriate conditions to the map values in each case. Map values that are unassigned are ignored, so you can easily select the cell(s) to use for simulations.*

The key is to calibrate under nearly ideal conditions, or conditions that reflect those that produced the growth curves to which you are calibrating. I use a constant climate for calibrating, to avoid confounding the calibration by extreme events. I am content if my calibrated curve produces growth somewhat better than the average of my empirical growth data or near the highest growth curve, because calibration represents near ideal conditions. If your empirical data do not include all biomass (such as branches and tops) you should calibrate to somewhat exceed empirical values. 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 or R. 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. Others have written R scripts to automate the generation of plots comparing model outputs to empirical data. Calibration is an iterative, highly repetitive process, so automation is extremely valuable. The goal is to find the set of species parameter values that produces a growth curve that best matches the empirical growth curve(s). Recognize that you are not trying to match the empirical curve exactly, but using empirical curves to provide approximate targets. The model equations may produce a curve shape that is somewhat different than your empirical curves (likely generated under specific conditions) and forcing the model to exactly match empirical curves may reduce its validity in landscape simulations. In particular, you should try to match the biomass accumulation where growth begins to plateau and produce relative rates of initial growth that reflect each species' growth strategy (i.e., continuum of pioneer v. shade-tolerant).

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 in the units used by the model, 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. Values that work well for many temperate ecosystems are between 0.0015 and 0.002.

CAUTION: turn off establishment for calibration runs to avoid confounding growth curves with randomly established competing cohorts.

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 than matching empirical values. That said, it is usually (but not always) 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 the values you will use in your final simulations while calibrating.
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 produces realistic response to light. Again, it is more important to get LAI approximately right than to keep SLWmax within the empirical range. Out-of-range SLWmax values often indicate that FracFol values are incorrect. Note that higher LAI increases within-canopy competition for light and will modestly depress growth even of a single cohort. I have found that LAI values exceeding those given in Table 1 may greatly reduce the amount of light penetrating canopy layers, thus impacting growth, competition and establishment.
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. I have recently begun calibrating to growth curves generated by the FVS model for various soil types. One advantage is that the curves for all species are directly comparable, and your parameters will produce realistic competition among species. The primary feature of the growth curve that you should calibrate to is the maximum height of the PnET-Succession curve, realizing that FVS does not simulate senescence and age limitations as PnET-Succession does. The rate of initial increase can be matched quite readily using MaxFracFol (see below), and it is important that the initial growth part of your curves reflect the ability of species to gain a height advantage in the competition for light. 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 (i.e., they always have a long decline or always die abruptly). Note that others have successfully calibrated to NEE data from flux towers, so do not feel constrained to use only growth and yield data. Other data sources can serve as a validation of your calibrations.

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 set 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, especially for climate change research. NOTE: if you use dynamic FolN, you should start with FolN values near the low end of their empirical range.
2. Use the GenericPnETSpeciesParameters file for all parameters that are not varied among species. Set parameters that will be held constant for your particular experiment or study (e.g., MaintResp, InitialNSC, etc.) Again, it is advisable to hold as many parameters constant (or similar) across species as possible to allow you less confounded control of competitive interactions with the remaining parameters. Recognize that parameters held constant only within life forms or shade-tolerance classes cannot be maintained in the GenericPnETSpeciesParameters file because those values are applied to ALL species. Verify that you are content with the generic settings, including those in the Defaults folder where PnET-Succession is installed. If you do not like the system defaults (in the User Guide), be sure to set them in your GenericPnETSpeciesParameters file. Note that you must be sure to use the same generic values you use for calibration when running your production simulations.
3. Set shade, drought and waterlogging tolerance by class. Set parameters that are related to shade tolerance (e.g., Table 1). Please realize that most published HalfSat values are instantaneous measurements in full sunlight. PnET PAR inputs are monthly averages of daily light levels (including night). The most appropriate setting of HalfSat values for PnET-Succession is approximately one-half of the light saturation point (LSP). Use published HalfSat or LSP values to understand relative shade-tolerance among species and refer to Table 1 below for appropriate starting absolute values.
4. Temperature parameters provide an important link between climate and species growth, and they should be calibrated carefully when conducting climate-related studies. LeafOnMinT controls the length of the growing season by comparing LeafOnMinT to monthly Tmin. Calibration also involves verifying that the appropriate months are active (LeafOn=TRUE) given the climate inputs. LeafOnMinT should vary approximately with leaf-on and leaf senescence dates, and typically ranges between 2-4 °C for temperate species, and between 0.5 and 2.5 for boreal species.
5. Set photosynthesis temperature parameters (usually based on range maps), remembering that temperature parameters are based on Tday (average daytime temperature). You can find CONUS Tday and Tmin maps (.img format) on a GitHub link found on the PnET-Succession LANDIS-II web page. Values used successfully for prior model versions are not affected by the recent bug fixes. PsnTMin controls how productive the species is at the beginning and end of the growing season and will produce a modest 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 for the entire month, but this is not a problem if

- NetPsn is quite low in those months. Note that PsnTMin, PsnTOpt and PsnTMax values are compared to Tday (average daytime temperature), not Tmax (daytime high temperature), and should be set accordingly. I typically vary PsnTMin among species relative to the April average daytime temperature isotherms at their northern range boundaries ($\text{PsnTMin} = \text{April Tday}/4$).
6. In lieu of empirical values, PsnTOpt can be estimated using the average mid-summer Tday (3 warmest months) at the center of the species' range. This can be approximated by subtracting a degree or two from the July Tday value.
 7. For the most realistic high temperature response, use the DTEMP=true option. Empirical values for maximum temperature limits to photosynthesis are typically instantaneous photosynthesis rates, while PnET-Succession interprets PsnTMax as the average **daytime** temperature above which there is no photosynthesis. Thus, PsnTMax should be lower than the typical bio-chemical limit of 39-40 °C. I use PsnTMax to make more northerly species less competitive than southerly species as climate warms. PsnTMax is typically closer to PsnTOpt than is PsnTMin. I usually vary PsnTMax among species relative to the July Tday isotherms at their southern range boundaries unless those boundaries are clearly related to a factor other than temperature. I have found that Tday is usually lower at this isotherm than is a reasonable value for PsnTMax, so I typically add 4 degrees to each. See example input file at the end of this Appendix for values I have used. I have found that PsnTMax does not tightly limit growth under warmer conditions because warmer conditions also lengthen the growing season, and the species will do very well early and late in the growing season even though it may be completely shut down in mid-summer.
 8. Calibration tuning can be 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 (optionally) 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 if you wish. 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 (after many different attempts) 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 (above- or below-ground biomass) will reduce the other pool. It would be beneficial to have some justification for your selected value from empirical evidence.
 9. Choose a single soil type for calibration of all species, preferably a soil type that is both common and highly productive. This enables you to estimate comparable life history trait parameters, ensuring that competition is realistic. Remember that you are not calibrating growth *per se*, but the FolN and foliage settings that will produce realistic growth under any set of abiotic conditions. Ultimately, monoculture 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 well 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. If you have species that are found only in wetlands, you should calibrate those on a wetland ecoregion, having RunoffCapture and LeakageFrac parameter settings that produce appropriate soil saturation. RunoffCapture represents the maximum depth of standing water across the ecoregion, and LeakageFrac can be used to reflect any impermeable soil layer that reduces drainage. In lieu of empirical data to help set these parameters, tune them such that the species typically found there can survive and the hydrology mimics reality. Species that are found on both upland and lowland sites should be calibrated on both types of sites, focusing on H1 and H2 on lowland sites and H3 and H4 on upland sites.

10. 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), using typical monthly precipitation values. You should use growing season temperatures approximating PsnTOpt. This is most easily done by temporarily setting PsnTxxx values to match those of the climate inputs during the three warmest months of the growing season. Note that the model compares PsnTxxx values to Tday (output in the Site.csv file), not Tmax. Don't forget to set PsnTxxx values back to actual values when finished calibrating.
11. Adjust parameters to be calibrated to values that make sense relative to other species; you want to ensure that calibrated parameters will allow realistic simulated competition. Pioneers tend to have the highest FracFol, FolN, and lowest FracBelowG; Shade-tolerants tend to be the opposite. See Table 1 for potential starting-point values, recognizing that for some species you may need to tune some of them considerably.
12. Because FracFol has a large impact on the competitiveness of species that establish together, I suggest that you initially set nominal FracFol as indicated in Table 1. Species with higher FracFol will tend to get a better access to light as they develop, and these cohorts will tend to shade cohorts with lower FracFol, so shaded cohorts need to be more shade-tolerant to survive. FracFol determines foliage under full-canopy conditions (i.e., mature cohorts, where self-shading is high). However, I have found that I must tune FracFol considerably for some species to achieve realistic LAI values; do not feel constrained to keep FracFol at the values suggested in Table 1.
13. I use MaxFracFol to control foliage for young cohorts in open-grown conditions. You will tune MaxFracFol (and shape) to get the initial growth to be approximately the same for most species (except slow-growing species); see notes below for more information on this point. I usually tune the initial part of each growth curve after I have tuned the peak of the growth curve for all species. I have found that some re-visiting of calibrated parameters for a species may be iteratively required to keep parameter settings consistent

among species. Calibrating MaxFracFol last does not affect the peak of the growth curve and prevents having to re-calibrate MaxFracFol multiple times. If you find that you cannot get adequate early growth with even very high values of MaxFracFol (usually only happens for evergreen species with TOfol=0.5), you may need to lower TOfol slightly (e.g., TOfol=0.4). This happens when there is not enough NSC available to produce the additional foliage every year.

14. **IMPORTANT NOTE.** If you have a curve that abnormally flattens after about year 50 after modifying some parameter other than MaintResp, it is likely because of lack of water, often caused by excess foliage that consumes water. Try reducing foliage (with FracFol and/or FracActWd) and increasing FolN to get a curve with a more gradually tapering shape. You'll need to ensure that LAI stays within bounds for the species.

Table 1. General starting values for calibration (in the absence of definitive empirical values). These are a starting point only; substantial departures from these may be required for some species.

Shade Tol Category	Tolerant	Somewhat-tol	Intermediate	Somewht-intol	Intolerant
HalfSat (mmol)	150	181	212.5	244	275
FolN (decid/conif)	2.2/1.1	2.4/1.3	2.6/1.5	2.8/1.7	2.9/1.9
SLWmax (approx.)	70/150	75/175	80/200	85/225	90/250
FracFol (decid/conif)	0.014/0.05	0.014/0.055-	0.015/0.06	0.017-0.065	0.018/0.07
Maximum LAI	<5.0	<4.5	<3.5	<2.8	<2.5
FracBelowG	0.37	0.35	0.33	0.31	0.29
MaxFracFol	Start by	setting this	equal to	FracFol	raise as needed
Wood at age 14 (g/m ²)	235	360	440	560	670
EstRad	0.976	0.954	0.928	0.900	0.870
BFoliarResp	0.090	0.095	0.100	0.105	0.110
CFracBiomass	0.5??	more study	0.45	needed	0.4??

15. Set FolN and SLWmax to their empirical mean values to start. It is more important to set FolN to represent photosynthetic capacity relative to other species than to match empirical observations (because the model uses FolN as a proxy for photosynthetic capacity). Use Table 1 as a starting place.
16. The model now assumes that you have calibrated each species so that its LAI is appropriate because there are no limits on LAI imposed by the model. Excessively high LAI will reduce light such that all the cohorts in the cell may be excessively light stressed. See Table 1 for suggested LAI limits.
17. Because of the new canopy-weighting scheme in v. 5.1, **it is important** that LAI remain (approximately) stable after it reaches its peak. Otherwise, cohort growth (and biomass) declines even when it is thriving or is the sole cohort on the site. This

- requires that you monitor LAI during calibration. Note: an LAI decline when senescence begins (fAge declines below ~0.6) need not (and cannot) be prevented.
18. This requires setting FracActWd to a much lower value than in prior model versions, typically between 0.00002 and 0.000025. Use the highest value that produces steady LAI after peak.
 19. Formerly, I limited biomass accumulation by raising FracActWd, which achieved its goal by reducing foliage (productivity) as the cohort increased in size. Now, I raise TOWood and ToRoot (biomass loss) instead, achieving the goal of limiting biomass accumulation by subtracting more biomass every year. Start with wood and root turnover parameters set to 0.03 and adjust as needed to achieve the desired peak of the growth curve. Once calibration is achieved, values for TOWood and TORoot can be traded without affecting calibration. If the amount of dead wood produced is too much, TOWood can be reduced with a concomitant increase in TORoot. Note that the biomass lost from wood becomes woody debris but biomass lost from roots just vaporizes (i.e., it is not tracked).
 20. Attaining LAI near empirical targets is primarily controlled by FracFol, and I have found that it needs to be a lot lower than before, and FracFol does not necessarily vary consistently with HalfSat (as suggested in Table 1). SLWmax is also used, but I have found that one cannot always sufficiently control LAI with an SLWmax value that is within empirical limits.
 21. Here's what each parameter controls in terms of the growth curve (through simulated time):
 - FracFol controls amount of foliage when light is limited (when canopy is closed), that is, as cohort matures. This has an important effect on the amount of biomass growth and how fast that growth occurs. (Note that FracFol will have markedly different values between deciduous (lower) and evergreen (higher) species, because their AmaxA and AmaxB values differ and therefore the photosynthetic output of a unit of foliage differs.)
 - FracActWd (fraction of woody biomass that is active xylem, supporting foliage) is a shape parameter that controls amount of foliage (and LAI) as the cohort matures (near the peak of the growth curve), and therefore has an important effect on biomass at the peak of the growth curve. Lower values produce more foliage (higher LAI) as cohort matures, and more foliage generally produces more biomass growth, although increased LAI will depress growth through internal shading. As noted above, I no longer use FracActWd to inhibit the growth curve for low biomass tree or shrub species. Instead, use FracFol, FolN and TOWood and TORoot. FracBelowG may also be used for short-statured pseudo species.
 - MaxFracFol controls amount of foliage when light is not limited (in open sun), that is, when the cohort is newly established. This partly determines how quickly a cohort puts on biomass early in life (the beginning of the growth curve). Note that MaxFracFol (as a parameter value) will always be higher than the realized MaxFracFol (during simulations) because fRad almost never actually reaches 1.0

- in a simulation (because PAR inputs reflect average light during day and across all the days of the month (i.e., daylength varies and some days are cloudy).
- MaxFracFol (and FracFolShape) allow more foliage to be produced in response to higher light conditions, controlling the early part of the growth curve. See PnET-Succession worksheet for visualization of the effect of these parameters. Use this to meet your biomass-at-age-14 targets (see #24 below).
 - SLWmax controls LAI for a given amount of foliage, with greater values reducing LAI. SLWmax affects LAI throughout the growth curve. LAI is determined by two factors: the amount of foliage and the thickness of leaves (SLWmax). Thus, simultaneous tuning of foliage (FracFol, FracActWd) and leaf thickness (SLWmax) is required. Reducing LAI will modestly raise the height of the growth curve (less internal shading) and vice versa, so SLWmax can often be used for fine-tuning of the growth curve.
22. First calibrate the peak part of the growth curve by keeping FracFol and MaxFracFol at the same value. This will often result in inadequate growth early in the growth curve, but this will be resolved in a subsequent step.
 23. Getting correct settings for the peak of the growth curve requires simultaneous and iterative tuning of FracFol, FolN, TOWood/TORoot and SLWmax. It is important to get both LAI and biomass growth tuned correctly, and these three parameters interact to achieve that goal.
 - a. If you need a large adjustment of the height of the growth curve (up or down), use TOWood/TORoot to get it close.
 - b. LAI is tuned primarily with FracFol and TOWood/TORoot (to control the wood biomass accumulation that determines foliage (through FracFol)), with SLWmax used for more fine tuning. This may require some tradeoffs, because you will want to keep SLWmax within empirical limits. LAI impacts the growth curve, but once you have calibrated FracFol, TOWood/TORoot and SLWmax, LAI generally will not vary with other parameter changes. In lieu of empirical values, use LAI targets given in Table 1. I recommend avoiding LAI values much above 5.0 for any species because light attenuation becomes excessive.
 - c. At any time in the tuning process you can modestly adjust the height of the entire growth curve with FolN, staying within empirical limits (unless empirical limits do not reflect relative productivity of the species (relative to similar species), a situation that is not entirely uncommon).
 - d. Refrain from doing much fine tuning until you complete Step 23b, because LAI changes will modify your curve.
 24. Adjust the initial part of the growth curve (especially if the species has rapid initial growth) using MaxFracFol and FracFolShape (6 is a good starting value). This allows you to add foliage when the cohort is newly established (has lots of light), while retaining nominal FracFol under normal light conditions. The shape parameter is used to control the range of light levels over which the increase in foliage is produced. Increasing the shape parameter limits the response to increasingly high light conditions, while lowering it spreads the response over a greater range of light conditions. This may require some creative experimentation. Use the PnET-Succession worksheet to find parameter values that will produce desired FracFol

values given the fRad (light stress) values seen in the growing season of the first year and a late year (when biomass is near peak). The fRad values through time can be found in the CohortOutput file used to assess biomass growth. A very useful metric to judge how well species will compete on newly disturbed sites is to calibrate the Wood biomass value at age 14 (see Table 1 for possible target values). Exceptionally slow-growing species should not be forced to meet the targets in Table 1. Note that setting $\text{MaxFracFol} < \text{FracFol}$ is acceptable if a reduction in early growth is needed to meet targets for Wood biomass value at age 14.

25. In short-lived species (usually species with high growth rates), you can use PnsAgeRed (limits Psn as a function of age) to depress mid-age growth (if you are unable to do it using means already described). See the PnET-Succession worksheet to see how this parameter affects growth. Short-lived species also tend to grow fast and have higher maintenance respiration rates, so raising MaintResp is another option to depress the curve. However, this may make them more prone to competition mortality. In longer-lived species that tend to get heart rot, large dead branches (e.g. red maple), or lots of self-thinning mortality, you could raise TOwood to depress the height of growth curve.
26. Finally, EstRad can be set equal to the highest fRad value seen in the first couple of growing seasons (Age=1-2). Thus, the effect of light on establishment is scaled to the best-case light conditions possible. Values in Table 1 are based on my experience, but you should confirm them by checking a few species against your own outputs. Please share with me anything you may learn about setting EstRad. Note: EstMoist is almost always set to 1.0 because fWater regularly equals 1.0 during simulations (see PnET-Succession User Guide for details).
27. Note that species with dramatically different initial growth curve shapes may not compete as expected. When one cohort accrues a significantly bigger biomass, it may overtop the other, which puts the lower cohort at a significant disadvantage. Keep this in mind as you calibrate growth curves; for each species you may want to favor a shape that is somewhat consistent with other species that have the same growth strategy (e.g., pioneers v. shade-tolerants). Calibrating growth to strictly match empirical growth curves may cause competition behavior in the model that is unrealistic.
28. It is prudent to test the competitive behavior of pairs of species to ensure that the behavior is appropriate. I recommend that you conduct some tests of two and/or three species combinations using your calibration setup to ensure that species compete as you would expect. Extremely poor competitive ability usually results only when a cohort is inappropriately overtopped by another and becomes light-starved. Some users conduct tests (or even calibrate concurrently) on different soil types, which is especially useful for checking growth under waterlogged and drought conditions. Small tweaks to the H parameters can often greatly improve performance on those soils while having little effect on performance on the mesic soil. Anomalies can be corrected with modest tweaks of one or two parameters to ensure that the cohorts grow sufficiently similar to remain in the same canopy layer. You can also adjust the LayerThreshRatio parameters if needed to achieve desired canopy layering behavior. The currently recommended value is 0.5, but you may find that another value is better (e.g., 0.67).

29. You will need starting parameter values. Here are some generic ones for temperate forest species that are good starting points:

- 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. This can be varied slightly by shade-tolerance (HalfSat) if desired.
- 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; I have always used 5.)
- k. TOWood: 0.03
- l. TORoot: 0.03

Here are some other PnET-Succession parameter values I have used that you may need to modify for your species:

- a. H1/H2: 0/4 for most species. Use -3.1/2 for species that are moderately waterlogging tolerant and -5/0.5 for species that are very waterlogging tolerant. This allows some photosynthesis even on saturated soils. To produce a gradient of waterlogging tolerance among species, use the PnET-Succession function worksheet to find values that produce the desired gradient in the reduction in photosynthesis on saturated soil (pressure head between 0 and 3.6).
- b. H3/H4: Because most trees can fully access water until water potential drops below a threshold (H4), I now recommend that H3=H4. Set H3 and H4 to 140 for drought intolerant and 153 for drought tolerant; I typically use a gradient across four drought-tolerance classes.
- c. PsnAgeRed: 5
- d. KWLit 0.1 <<0.075 for hardwoods and 0.125 for softwoods (Mattson 1987)
- e. FolLignin 0.2 <<Range in Melillo et al (1982) = 0-0.25

Here are some generic parameter values that I have used.

- f. Wythers true
- g. PrecipEvents 11
- h. DTEMP true
- i. MaxCanopyLayers 5 <<Very little light can penetrate more than 5 layers unless LAI is quite low in each layer.
- j. LayerThreshRatio 0.5
- k. MaintResp 0.002
- l. EvapDepth 25 <<Default=25.

Here are some generic ecoregion parameter values that I have used.

- m. RootingDepth 1000 << upland ecoregions; I use 500 (mm) for lowlands
- n. RunoffCapture 0 << upland ecoregions; I use 300 (mm) for lowlands
- o. LeakageFrac 1.0 <<upland ecoregions; I use 0.02 for lowlands
- p. PrecIntConst 0.1 <<upland ecoregions; may be 0.05 for sparsely populated lowlands

- q. LeakageFrostDepth 3000 <<(mm) only applies with permafrost turned on
 - r. WinterSTD 6.67 <<ranges between 6.67 (52 deg. N) and 9.2 (70N) in Siberia. See map in Court (1951) for USA estimates.
 - s. MaxPest 1.0 << Time step dependent. MaxPest=TS length/10
30. 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. If you find that a species growth does not respond to increases in FracFol or MaxFracFol it may be that it may have insufficient carbon reserves to construct the requested foliage; in such cases, try raising DNSC.
31. InitialNSC similarly has little effect on cohort competition unless values among species vary by more than an order of magnitude.
32. Establishment probability (Pest) is a function of the light and water photosynthesis reduction factors for the species at the time of establishment. The two reduction factors are rarely scaled the same in that fWater commonly takes values of 1.0, while fRad may never exceed values considerably lower than that. To give both reduction factors the same weight, set each establishment modifier equal to the highest expected reduction factor value. This can be estimated by using the maximum value for each factor seen in the calibration files for each species. Typically, EstMoist will equal 1.0, and EstRad may range from 0.85-0.98. Furthermore, establishment rates are sometimes too high or too low using Pest as calculated directly from the two main reduction factors. Consider the parameter MaxPest to be a tuning knob to dial all establishment rates up or down. This cannot be done on a single cell and must be done on a landscape before you conduct landscape-scale experiments. I don't have enough experience to provide concrete guidance. I suggest starting with a MaxPest value of 1.0 (no alteration of Pest) and tune up or down from there if cohort numbers indefinitely increase or decrease, or if mean # of cohorts per cell consistently exceeds about 12. Values of 0.15 or less are not unusual. MaxPest is dependent on the PnET-Succession time step, meaning that you must reset its value when you change the time step. We think it may be as simple as reducing the value in proportion to the change in time step length. For example, if the length of the time step is reduced by half, also reduce the value of MaxPest by half. We are working on a way to modify the code to make MaxPest time-step invariant, but have not yet found a robust method. If establishment seems unresponsive to MaxPest, it may be that you have too many canopy layers, and very little light is reaching the forest floor on most cells.
33. WinterSTD. See map in Court (1951) for values in the US. Otherwise, estimate from weather data using methods in Court (1951).
34. After several years of using PnET-Succession, I am still learning things about model behavior, and revising my calibration protocol. If you should learn something that would improve this calibration guide, please share it with me at eric.gustafson@usda.gov.

General notes. 1) Again, to ensure realistic competition, it is advisable to use common parameter values across species as much as possible, 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 and FracBelowG, 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). 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 expectations.

Generating PAR values. See section 6.3.5 of the User Guide.

Here are some species parameters that have been calibrated in various ecosystems in northern Wisconsin (U.S.A), mostly using a SILO soil. These can be used as a starting point, but they should at a minimum be tested 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. TORoot was generally the same as TOWood.

LandisData PnETSpeciesParameters

>>calibrated for Wythers=true

>>Generated August 2022 by Eric Gustafson. Attribution appreciated.

Species	FoIN	SLWmax	TOfol	TOWood	HalfSat	H1	H2	H3	H4	LeafOnMinT	PsnTMin	PsnTOpt	PsnTMax	FracFol	FracWood
abiesals	1	145	0.2	0.03	134	-1.5	3	14	14	1.9	0.8	16.8	27	0.07	0.00003
acerrubr	2.35	73	1	0.037	181	-2	2	14	14	2.4	1.75	25.5	32.2	0.014	0.000022
acersacc	2.3	70	1	0.03	149	0	4	14	14	2.5	1.8	25.5	31	0.016	0.000023
betualle	2.3	67	1	0.032	181	-0.75	3	15	15	2.5	1.8	21.7	30.5	0.013	0.000022
betupapy	2.8	90	1	0.033	244	0	4	14	14	1.75	0.5	16.5	28.5	0.018	0.00003
carycord	2.7	95	1	0.037	244	-0.75	3	16	16	3	1.25	26.7	34	0.013	0.000022

fagug ran	2. 2	75	1	0.03	148	0	4	1 4 0	1 4 0	2.2	1.7	26.7	34.2	0.01 5	0.00 002
fraxa mer	2. 5	72	1	0.03	212 .5	- 0. 75	3	1 4 5	1 4 5	2.3	1.2	26.5	34.1	0.01	0.00 0022
fraxn igr	2. 4	85	1	0.03 5	244	- 4. 5	1 . 5	1 3 6	1 3 6	2.1	1	21	29.5	0.01 3	0.00 0026
fraxp enn	2. 4	85	1	0.03 5	244	- 3. 3	2	1 5 2	1 5 2	2.5	1.8	25.5	34.2	0.01 3	0.00 0026
larila ri	2. 4	81	1	0.03 3	275	- 3. 5	1 . 5	1 4 5	1 4 5	1.5	0.17 5	18.5	29.9	0.01 1	0.00 0023
piceg lau	1. 3	225	0.2	0.03 5	197	0	4	1 5 2	1 5 2	1.5	0.17 5	15.1	26.6	0.05	0.00 0022
pice mari	1	225	0.1 8	0.03	197	- 4. 5	1 . 5	1 3 8	1 3 8	1.5	0.17 5	15.1	26.6	0.04	0.00 0022
pinub ank	1. 9	260	0.2 5	0.03	250	0	5	1 6 0	1 6 0	1.75	0.5	16	28.1	0.06	0.00 0036
pinur esi	1. 7	240	0.3	0.02 9	228	0	4	1 5 2	1 5 2	2.25	1.3	18.6	28.2	0.04 5	0.00 0021
pinus tro	1. 5	200	0.3 3	0.03 5	197	- 0. 75	3	1 5 2	1 5 2	2.3	1.4	21.5	30	0.04	0.00 002
popu bals	2. 9	86	1	0.04	275	- 0. 5	4	1 4 5	1 4 5	1.6	0.3	15.1	29	0.01 8	0.00 004
popu gran	2. 9	86	1	0.04	275	- 0. 5	4	1 5 2	1 5 2	2.3	1.4	23.5	31	0.01 8	0.00 004
poput rem	2. 9	86	1	0.04	275	0	4	1 4 5	1 4 5	1.6	0.3	18.5	29.8	0.01 8	0.00 004
pruns ero	3	90	1	0.03 5	244	0	4	1 5 2	1 5 2	2.8	2.2	26	34.5	0.01 5	0.00 0028
quera lba	2. 8	95	1	0.03 4	244	0	4	1 6 0	1 6 0	3	1.25	26.7	34	0.01 2	0.00 002
quere lli	2. 8	80	1	0.03	244	0	4	1 6 0	1 6 0	2.5	1.8	25	33	0.01 3	0.00 0027
quer macr	2. 5	80	1	0.03 2	212 .5	- 0. 75	3	1 6 0	1 6 0	2.5	1.25	24.7	34	0.01 3	0.00 0022
querr ubr	2. 7	86	1	0.03	212 .5	0	4	1 5 2	1 5 2	2.5	1.25	25.6	34.1	0.01 3	0.00 0019

querv elu	2. 7	80	1	0.03	212 .5	0	4	1 5 2	1 5 2	3.15	2.62 5	27	34.4	0.01 4	0.00 0023
thujo cci	0. 9	240	0.3 3	0.03 1	197	- 4. 5	1 . 5	1 5 2	1 5 2	2.2	1.25	21.3	29.9	0.06	0.00 0024
tilia mer	2. 6	67	1	0.03	181	0	4	1 5 2	1 5 2	2.4	1.7	24	32.2	0.01 3	0.00 0022
tsugc ana	1. 4	170	0.3	0.03	133	0	4	1 4 0	1 4 0	2.5	1.8	21	29.5	0.05	0.00 0018
ulmu amer	2. 5	73	1	0.03	212 .5	- 3. 5	1 . 5	1 4 5	1 4 5	2.25	1.3	26.3	35	0.01	0.00 0022

References

- Melillo, JM, Aber JD, Muratore JF. 1982. Nitrogen and Lignin Control of Hardwood Leaf Litter Decomposition Dynamics. *Ecology* 63:621-626.
- Aber, JD, Ollinger SV, Federer A, Reich PB, Goulden ML, Kicklighter DW, Melillo JM, Lathrop RG Jr. 1995. Predicting the effects of climate change on water yield and forest production in the northeastern United States. *Climate Research* 5:207-222.
- Aber, JD, Reich, PB, Goulden, ML. 1996. Extrapolating leaf CO₂ exchange to the canopy: a generalized model of forest photosynthesis compared with measurements by eddy correlation. *Oecologia* 106:257-265.
- Court, A. 1951. Temperature frequencies in the United States. *Journal of Meteorology* 8:367–380. [https://doi.org/10.1175/1520-0469\(1951\)008<0367:TFITUS>2.0.CO;2](https://doi.org/10.1175/1520-0469(1951)008<0367:TFITUS>2.0.CO;2)
- Gustafson, EJ, Kern, CC, Miranda, BR, Sturtevant, BR, Bronson, DR, Kabrick, JM. 2020b. Climate adaptive silviculture: how much will it take to produce resilient forest landscapes? *Forest Ecology and Management Volumes* 470–471, 118208. DOI:10.1016/j.foreco.2020.118208
- Ollinger SV, Smith M-L. 2005. Net primary production and canopy nitrogen in a temperate forest landscape: an analysis using imaging spectroscopy, modeling and field data. *Ecosystems* 8:760-778.
- Mattson KG, Swank WT, Waide JB. 1987. Decomposition of woody debris in a regenerating, clear-cut forest in the Southern Appalachians. *Canadian Journal of Forest Research* 17:712-721.
- Miles P, Smith WB. 2009. Specific gravity and other properties of wood and bark for 156 tree species found in North America. Research Note NRS-38. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northern Research Station. 35 p.
- Smith, J.E., Heath, L.S., Skog, K.E., Birdsey, R.A. 2006. Methods for calculating forest ecosystem and harvested carbon with standard estimates for forest types of the United States. USDA Forest Service General Technical Report NE-343. Northeastern Research Station, Newtown Square, PA, USA. 216 p.