

PnET-Succession v1.0.1 Extension User Guide

Eric J. Gustafson
US Forest Service
Northern Research Station

Arjan M.G. de Bruijn
Purdue University

Brian R. Miranda
US Forest Service
Northern Research Station

Last Revised: September 2, 2015

Table of Contents

1	INTRODUCTION.....	5
1.1	Major modifications made to PnET algorithms.....	5
1.2	Advantages and disadvantages of PnET-Succession compared to Biomass Succession.....	5
1.3	Major Releases	7
1.3.1	Version 1.0 (August 2015).....	7
1.4	Minor Releases	7
1.4.1	Version 1.0.1 (Septemeber 2015).....	7
1.5	References	7
1.6	Acknowledgments	7
2	PNET-SUCCESSION	9
2.1	Initializing Biomass.....	9
2.2	LAI Shade Calculation	10
2.3	Cohort Reproduction and Establishment	10
2.4	Cohort Competition	10
2.4.1	Light.....	11
2.4.2	Water.....	12
2.4.3	Other factors.....	16
2.5	Cohort Growth and Ageing	16
2.6	Cohort Senescence and Mortality.....	16
2.7	Dead Biomass Decay.....	16
2.8	References	17
3	INPUT FILE - PNET-SUCCESSION.....	18
3.1	Example PnET-Succession input file	18
3.2	LandisData.....	18
3.3	Timestep.....	18
3.4	StartYear.....	18
3.5	SeedingAlgorithm.....	19
3.6	Latitude.....	19
3.7	MaxDevLyrAv	19
3.8	PNEToutputsites.....	19
3.9	InitialCommunities	19
3.10	InitialCommunitiesMap	19
3.11	PnETGenericParameters	19
3.12	PnETSpeciesParameters	20
3.13	EcoregionParameters	20
4	INPUT FILE – INITIAL COMMUNITY CLASSES.....	21
4.1	Example File.....	21
4.2	LandisData.....	22
4.3	Initial Community Class Definitions	22
4.3.1	MapCode.....	22
4.3.2	Species Present	22
4.3.3	Grouping Species Ages into Cohorts	22

5	INPUT FILE – INITIAL COMMUNITY MAP	23
6	INPUT FILE – CLIMATE	24
6.1.1	<i>Example File #1</i>	<i>24</i>
6.1.2	<i>Example File #2</i>	<i>24</i>
6.2	Header Information.....	25
6.3	Observations.....	25
6.3.1	<i>Year.....</i>	<i>25</i>
6.3.2	<i>Month.....</i>	<i>26</i>
6.3.3	<i>TMax.....</i>	<i>26</i>
6.3.4	<i>TMin.....</i>	<i>26</i>
6.3.5	<i>PAR.....</i>	<i>26</i>
6.3.6	<i>Prec.....</i>	<i>26</i>
6.3.7	<i>CO2.....</i>	<i>26</i>
7	INPUT FILE – GENERIC PNET SPECIES PARAMETERS.....	27
7.1	Example file:	27
7.2	LandisData.....	27
7.3	PnETGenericParameters.....	27
7.4	MaxCanopyLayers.....	27
7.5	IMAX	28
7.6	PreventEstablishment	28
7.7	DVPD1, DVPD2	28
7.8	BFolResp	28
7.9	TORoot/TOWood.....	28
7.10	Q10	28
7.11	FolLignin	28
7.12	KWdLit	29
7.13	InitialNSC.....	29
7.14	MaxSLWFrac	29
7.15	CFracBiomass.....	29
8	INPUT FILE – PNET SPECIES PARAMETERS	30
8.1	Example file:	30
8.2	SpeciesName	30
8.3	FolN.....	30
8.4	SLWmax.....	30
8.5	SLWDel.....	30
8.6	Tofol.....	31
8.7	AmaxA	31
8.8	AmaxB.....	31
8.9	HalfSat.....	31
8.10	H2, H3, H4.....	31
8.11	PsnAgeRed	31
8.12	PsnTMin	32
8.13	PsnTOpt.....	32
8.14	k	32
8.15	WUECnst.....	32
8.16	MaintResp.....	32

8.17	DNSC.....	32
8.18	FracBelowG.....	32
8.19	EstMoist.....	32
8.20	EstRad.....	33
8.21	FracFol.....	33
8.22	FracActWd.....	33
9	INPUT FILE - ECOREGION PARAMETERS	34
9.1	Ecoregion.....	34
9.2	SoilType	34
9.3	RootingDepth	34
9.4	PrecLossFrac	34
9.5	LeakageFrac	34
9.6	ClimateFileName.....	35
10	INPUT FILE – PNETOUTPUTSITES.....	36
10.1	Example file:.....	36
10.2	LandisData	36
10.3	PnEToutputsites	36
11	OUTPUT FILE - SITEDATA TABLE (OPTIONAL PNETOUTPUTSITES OUTPUT)	37
11.1	NrOfCohorts	37
11.2	MaxLayerStdev.....	37
11.3	layers.....	37
11.4	PAR0	37
11.5	Tday(C).....	37
11.6	Precip(mm_mo).....	37
11.7	RunOff(mm_mo).....	37
11.8	Leakage(mm).....	37
11.9	PET(mm)	38
11.10	Evaporation(mm).....	38
11.11	Transpiration(mm).....	38
11.12	Interception(mm).....	38
11.13	Water(mm).....	38
11.14	PressureHead(m).....	38
11.15	SnowPack (mm).....	38
11.16	LAI(m2).....	38
11.17	VPD(kPa).....	38
11.18	GrossPsn(gC/mo).....	38
11.19	NetPsn(gC/mo)	38
11.20	MaintenanceRespiration(gC/mo).....	39
11.21	Wood(gDW)	39
11.22	Root(gDW)	39
11.23	Fol(gDW).....	39
11.24	NSC(gC)	39
11.25	HeteroResp(gC_mo).....	39
11.26	Litter(gDW)	39
11.27	CWD(gDW/m ²).....	39
12	OUTPUT FILE - COHORTDATA TABLE (OPTIONAL PNETOUTPUTSITES OUTPUT).....	40

12.1	Age(yr).....	40
12.2	Layer(-).....	40
12.3	LAI(m2).....	40
12.4	GrossPsn(gC/m2/mo).....	40
12.5	FolResp(gC/m2/mo).....	40
12.6	MaintResp(gC/m2/mo).....	40
12.7	NetPsn(gC/m2/mo).....	40
12.8	Transpiration(mm/mo).....	40
12.9	WUE(g/mm).....	41
12.10	Fol(gDW/m ²).....	41
12.11	Root(gDW/m ²).....	41
12.12	Wood(gDW/m ²).....	41
12.13	NSC(gC/m ²).....	41
12.14	NSCfrac(-).....	41
12.15	fWater(-).....	41
12.16	fRad(-).....	41
12.17	fTemp_psn(-).....	41
12.18	fTemp_resp(-).....	41
12.19	fAge(-).....	41
12.20	LeafOn(-).....	42
12.21	FActiveBiomass(gDW_gDW).....	42
13	OUTPUT FILE – ESTABLISHMENT TABLE (OPTIONAL PNETOUTPUTSITES OUTPUT) ..	43
13.1	Year.....	43
13.2	Species.....	43
13.3	Pest.....	43
13.4	fWater.....	43
13.5	fRad.....	43
13.6	Est.....	43
14	APPENDIX. CALIBRATION TIPS.....	44

1 Introduction

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

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

1.1 Major modifications made to PnET algorithms

Several modifications were made to PnET algorithms to make them tractable at landscape scale, primarily by broadening the scale of integration operations. (1) The PnET timestep was broadened from daily to monthly. (2) The number of sub-layers within a canopy layer was 50 in Pnet, but is here dynamically determined with a minimum of 5, where each sub-layer represents an even proportion of the total LAI within the layer. It can increase dynamically when transpiration would otherwise exceed soil water. These smaller subcanopy layers tighten the feedback between photosynthesis and water stress. (3) Cohort biomass 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. (4) Photosynthates are allocated to four pools (foliage, root, wood and non-structural carbon (reserves, NSC)). Net photosynthesis is initially allocated to the NSC pool, and then foliage allocation occurs, followed by allocation to root and wood pools such that the above- and below-ground biomass ratio is preserved. Maintenance respiration is then deducted from the NSC pool. Details of model structure and modifications can be found in De Bruijn et al (2014).

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

The goal for PnET-Succession was to make the simulation of growth and competition more mechanistic and more explicitly linked to fundamental drivers that are changing, such as climate and atmospheric composition (e.g.,

CO₂ and ozone). It is believed that this more mechanistic approach will be more robust for making projections under climate and other global changes (Gustafson 2103).

Advantages of PnET-Succession compared to Biomass Succession

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

Disadvantages of PnET-Succession compared to Biomass Succession

- 1) PnET-Succession requires more parameters, which adds to uncertainty and increases the parameter burden when using the model. However, uncertainty may be no higher than when making *ad hoc* assumptions for other succession extensions about how novel conditions will affect modeled processes.
- 2) Runtimes tend to be somewhat longer, but only slightly longer because many cohorts senesce prior to reaching longevity age, greatly reducing the number of cohorts that must be simulated. In both BiomassSuccession and PnET-Succession, simulation of dispersal is more time consuming than the forest growth part.

1.3 Major Releases

1.3.1 Version 1.0 (August 2015)

First version officially released on LANDIS-II website.

1.4 Minor Releases

1.4.1 Version 1.0.1 (September 2015)

Bug fixed that prevented partial disturbances from removing biomass from cohorts.

1.5 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.
- 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.
- Scheller, R.M. and 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.

1.6 Acknowledgments

Funding for the development of the PnET-Succession extension was provided by a grant from the USDA/NASA NIFA/AFRI program to Purdue University. Valuable scientific contributions to the development of the extension were made by Arjan De Bruijn, Eric J. Gustafson, Brian R. Sturtevant and Mark Kubiske.

Funding for the development of LANDIS-II was provided by the Northern Research Station (Rhinelander, Wisconsin) of the U.S. Forest Service. Valuable contributions to the development of LANDIS-II were made by Robert M. Scheller, Brian R. Sturtevant, Eric J. Gustafson, and David J. Mladenoff.

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 photosynthesis, respiration and transpiration. Competition for light is modeled by tracking solar radiation through canopy layers (related to cohort age) according to a standard Lambert-Beer formula. PnET-Succession requires average monthly temperature, precipitation, photosynthetically active radiation and atmospheric CO₂ concentration as inputs.

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

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

The PnET-Succession Extension tracks biomass in four live pools (foliage, roots, wood and non-structural (C reserves)) and two dead pools (woody and leaf litter).

2.1 Initializing Biomass

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

computationally intensive process that may require significant time for complex initial landscapes. Additionally, climate data are required back to t - oldest cohort age. To facilitate climatic input in years where weather records do not exist, it is possible to supply mean monthly climate data for a range of years (see section 6.2)

This biomass initialization does not account for disturbances that would likely happen prior to initialization and therefore tends to overestimate initial live biomass and underestimate initial dead biomass.

2.2 LAI Shade Calculation

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

2.3 Cohort Reproduction and Establishment

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

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

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

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

2.4 Cohort Competition

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

2.4.1 Light

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

PnET-Succession assumes that LAI and biomass are spatially homogeneous on a site (i.e., cell). PnET-Succession defines canopy layers according to biomass, with high biomass cohorts achieving dominance with regard to access to light. Because senescing trees are more likely to lose biomass due to branches breaking off than due to the top breaking (i.e. they lose biomass without losing height), maximum lifetime biomass of a tree-species cohort is used as a proxy for tree height. Note that changes have been made to the model described paper in Ecological Modeling (De Bruijn et al 2014). We no longer set (arbitrary) age limits on the development of canopy layers. Rather, each cohort is divided into a number IMAX (=5 by default, set in the GenericParameters file) of canopy sublayers of equal biomass (Figure 1, left). The cohort sublayers are overlaid and the model iteratively clusters sublayers into canopy layers until the deviation of the newly formed canopy boundaries (i.e. LyrMax -LyrAv) decreases below a user defined parameter MaxDevLyrAv (Figure 1, right). This process produces boundaries of canopy layers such that the variation of subcanopy boundaries within the canopy layers is minimized and the variance of subcanopy boundary between canopy layers is maximized. MaxDevLyrAv is calibrated by the user to produce the maximum number of canopy layers expected in the system. The maximum number of canopy layers can further be limited with the generic MaxCanopyLayers parameter (section 3.8). Subcanopy layers within a canopy layer have equal access to the light reaching the canopy layer, and the light passing through a canopy layer is a function of the LAI and extinction coefficient of the cohorts making up the canopy layer. Light stress for a cohort is calculated by: $fRad = Radiation / (Radiation + HalfSat)$.

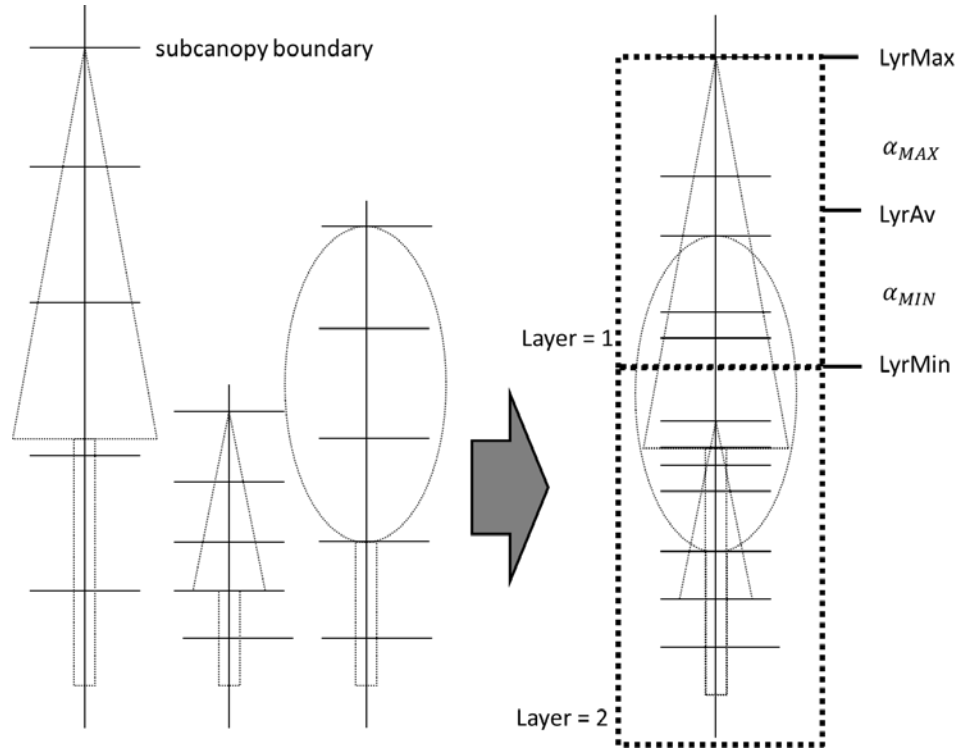


Figure 1. Canopy layer computation. Each tree represents a species-cohort, and the solid horizontal lines are subcanopy boundaries. Dotted lines are computed canopy layer boundaries that determine the assignment of subcanopy layers to canopy layers.

2.4.2 Water

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

2.4.2.1 Water In

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

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

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. At above-freezing temperatures, snow melts at a rate of 0.15 mm/°C/day. 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 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. Incoming precipitation and snowmelt are reduced in proportion to *PrecipLossFrac*, with the runoff not entering the soil. The actual water infiltrating the soil is:

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

2.4.2.2 Water Out

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

After fast leakage loss has been subtracted, the soil water is subject to further depletion by transpiration and/or evaporation. Transpiration is calculated as the result of plant growth (see section 2.4.3). The rate of evaporation is a function of surface radiation (under the canopy), temperature and the soil texture class. Potential evaporation is calculated as a simplified Penmann-Monteith calculation according to Priestley and Taylor (1972) as discussed in Brutsaert (1982, p. 217). This method was successfully applied in the PROGRASS model (Calanca et al. 2009).

Actual evaporation is calculated as:

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

where c is a proportion that decreases linearly from 1.0 when pressurehead is 0.0 m, to $c = 0$ when pressure head is 153 m (i.e., the physical wilting point (Fig 3)). Transpiration is subtracted from evaporation to reflect decreasing evaporation when the vegetation increases. *De facto* evaporation is 0.0 when $\text{LAI} > 1.0$.

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

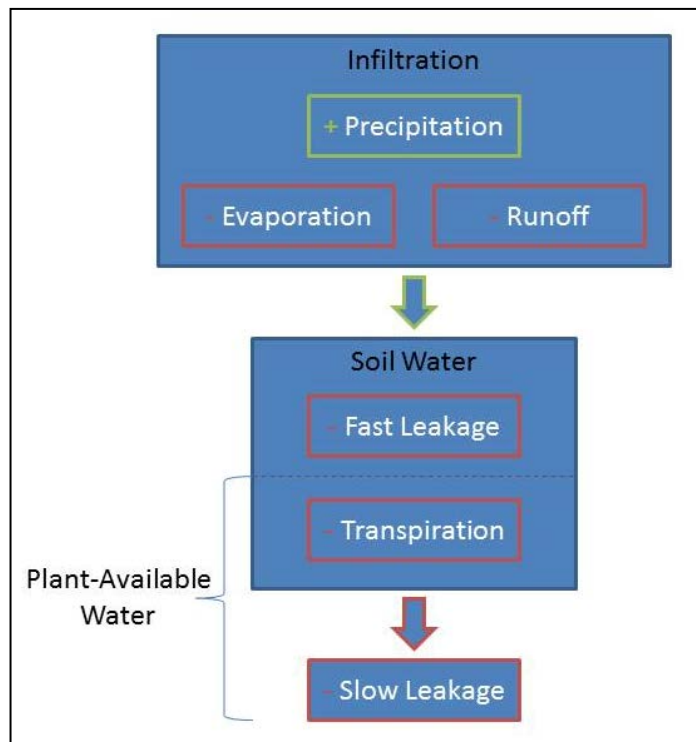


Figure 2. Soil water processes in PnET-Succession

2.4.2.3 Water Stress

Water stress in the model depends on the water pressure in the soil according to Feddes et al. (1978). Water pressure in the soil (water retention curves) depends on soil water content and the soil type according to Saxton and Rawls (2006), who provide equations to estimate water retention curves for

soils based on soil texture characteristics (i.e., % sand, % silt, % clay, % organic matter, % gravel, salinity).

Default values for the required parameters (from Saxton and Rawls 2004) are provided with PnET-Succession for 12 different soil types (Figure 3, left panel), but users are able to modify existing soil type parameters or provide custom soil types with parameters. The user implements a soil type as an ecoregion-specific parameter in the ecoregion parameter table using a corresponding abbreviation for the soil type.

Water stress for a species-cohort is calculated from soil water pressure using four species-specific water pressure thresholds (Figure 3, right panel) labeled H1-H4 in Feddes et al. (1978). Note that PnET-Succession uses the absolute value of pressure head. Parameter H1 (the pressure head below which photosynthesis cannot occur (waterlogging)) is hardcoded in PnET-Succession ($H1 = 0$ meter pressure). Often, little is known about H2 (cessation of waterlogging stress), so it is recommended to use the generic value $H2=0.0$. H3 (onset of stress caused by too little water) can be set to reflect the drought sensitivity of a species, and should fall somewhere between H2 and H4. Most literature sources use a generic H4 (cessation of photosynthesis because of inadequate water) of -153 m pressure head (wilting point).

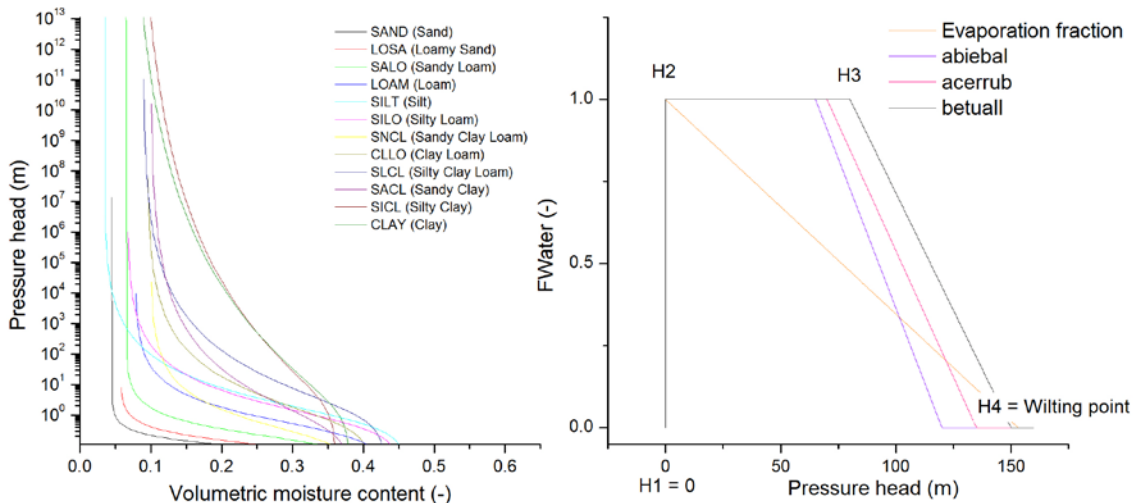


Figure 3. Default pressure head curves (left) and examples of inverse water stress (fWater, right). fWater is calculated by linear interpolation between parameters H1-H4. $H1=0$ is hardcoded and cannot be changed by the user. In this example all species have H1 and H2 = 0, with varied values for H3 (75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

2.4.3 Other factors

Vapor pressure deficit is calculated from the temperature fluctuations during the day, and accounts for the effect of elevated atmospheric CO₂. CO₂ affects growth in two ways; 1) it increases water use efficiency and 2) it increases the reference rate of photosynthesis (A_{max}). The temperature reduction factor increases linearly from 0 at P_{snTMin}, to 1 at P_{snTOpt}. Supra-optimal temperatures do not reduce the temperature reduction factor, but net photosynthesis is reduced through increased respiration costs 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.

2.5 Cohort Growth and Ageing

Net photosynthesis is estimated by subtracting respiration from gross photosynthesis. Resulting net photosynthesis is then allocated to maintenance respiration and then to the root, foliage, wood and non-structural biomass pools, according to fixed allocation ratios. A proportion of foliage and wood biomass is also moved to the dead pools to simulate leaf-fall and branch/root death. Cohort ageing is simply the addition of the time step to each existing cohort age.

2.6 Cohort Senescence and Mortality

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

2.7 Dead Biomass Decay

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

and/or remove dead biomass (e.g., fire may add some woody dead biomass and remove all leaf dead biomass).

2.8 References

- Brutsaert, W. 1982. *Evaporation into the Atmosphere: Theory, History and Applications*. Springer, NY.
- P. Lazzarotto, P. Calanca, J. Fuhrer. 2009. Dynamics of grass–clover mixtures—An analysis of the response to management with the PROductive GRASSland Simulator (PROGRASS). *Ecological Modelling* 220:703–724.
- 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.
- Meentemeyer, V. 1978. Macroclimate and lignin control of litter decomposition rates. *Ecology* 59:465-472.
- Priestley C.H.B. and R.J. Taylor. 1972. On the assessment of surface heat flux and evaporation using large-scale parameters. *Monthly Weather Review* 100(2):81-92
- Saxton, K. E. and W. J. Rawls. 2004. Soil water characteristic equations.xls. Online database (<http://hrsl.arsusda.gov/SPAW/SPAWDownload.html>)
- Saxton, K. E., W. J Rawls, J. S. Romberger and R. I. Papendick. Estimating generalized soil water characteristics from texture. *Soil Sci. Soc. Amer. J.* 50(4):1031-1036. 1986.

3 Input File - PnET-Succession

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

3.1 Example PnET-Succession input file

```
LandisData "PnET-Succession"

PnET-Succession      Value
>>-----
Timestep    10
StartYear   1961
SeedingAlgorithm WardSeedDispersal
Latitude    45
MaxDevLyrAv 8000

PNEToutputsites  PNETOutput.txt

InitialCommunities Mid-succ-One_cell_initial-communities.txt
InitialCommunitiesMap One_cell_initial-communities.img

PNETGenericParameters PNETGenericParameters.txt
PNETSpeciesParameters PNET_Oconto_species.txt
EcoregionParameters AssembX_4cell_EcoregionParameters.txt
```

3.2 LandisData

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

3.3 Timestep

This parameter is the time step of the extension. 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 Latitude

This parameter is the approximate latitude of the study area. Value: -90 < integer < 90. Units: degrees of latitude.

3.7 MaxDevLyrAv

This optional parameter is used to lump species-age cohorts into canopy layers, and specifies the maximum variation of cohort biomass that can occur within a canopy layer. It is given a default value of a maximum float, which results in a single canopy layer regardless of biomass distribution amongst subcanopy layers (see section 2.4).

3.8 PNEToutputsites

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

3.9 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 chapter 4).

3.10 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 chapter 5).

3.11 PnETGenericParameters

This optional parameter gives the name of a PnET Generic Parameter text file. Any parameter that 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:\Programs\...\Extensions\GenericPnETSpeciesParameters.txt with the rest

of the model, or in a custom generic parameter file specified here. Any parameters not specified in the PnETSpeciesParameter file will be read from the custom generic file, and if not found there, will be read from the default generic file. Thus, values found in the PnETSpeciesParameter file will always take precedence over generic files. The format of the PnET Generic Parameter text file is described in chapter 7.

3.12 PnETSpeciesParameters

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

3.13 EcoregionParameters

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

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.

4.1 Example File

```
LandisData "Initial Communities"

>>Old jackpine oak
MapCode 7
  acerrubr 30
  pinubank 80 90
  pinuresi 110 140
  querelli 40 120 240

>> young jackpine oak
MapCode 0
  pinubank 30 50
  querelli 10 40 70

>> young aspen
MapCode 2
  poputrem 10 20

>> old maple hardwoods
MapCode 55
  abiebals 10 60 120
  acerrubr 90 120
  acersacc 20 50 150 200
  betualle 40 140 200
  fraxamer 10 100 130 180
  piceglau 180
  querrubr 100 160 180
  thujocci 200 240 260
  tiliamer 20 80 110 150
  tsugcana 30 80 120 220 320 340

>> old pine - spruce - fir
MapCode 6
  abiebals 10 50 80
  piceglau 100 140 180 200 220
  pinuresi 140 160 180
  pinustro 200 280 350
```

4.2 LandisData

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

4.3 Initial Community Class Definitions

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

4.3.1 MapCode

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

4.3.2 Species Present

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

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

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

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

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

4.3.3 Grouping Species Ages into Cohorts

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

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

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

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

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

5 Input File – Initial community map

This is a GIS file of the initial community classes. Each active site on the landscape is assigned to a MapCode that links to the initial community class defined in the Initial Community Class Definitions.

6 Input File – Climate

This file contains weather records of monthly parameter values.

6.1.1 Example File #1

Year	Month	TMax	TMin	PAR	Prec	CO2
2007	1	11.86	-13.39	564.2	1.651	383
2007	2	17.93	-8.45	698.7	1.7272	383
2007	3	24.73	-10.18	872.0	2.921	383
2007	4	25.05	-2.853	930.5	4.0132	383
2007	5	27.72	3.424	890.4	4.1449	383
2007	6	35.24	8.7	1069.0	0.928	383
2007	7	36.35	12.75	891.1	3.7338	383
2007	8	34.15	13.64	927.9	5.0806	383
2007	9	30.44	6.647	875.3	5.7138	383
2007	10	26.67	-3.804	836.2	0.4064	383
2007	11	21.84	-9.4	660.5	0.2794	383
2007	12	17.03	-10.49	579.8	3.5304	383
2008	1	11.81	-14.41	622.1	1.2192	385
2008	2	19.35	-8.78	792.4	1.9558	385
2008	3	21.74	-9.21	930.0	1.0922	385
2008	4	25.86	-5.333	1045.2	0.4826	385
2008	5	31.97	0.023	1014.7	1.1176	385
2008	6	34.43	8.84	1042.4	0	385
2008	7	33.24	11.32	836.7	10.368	385
2008	8	32.81	11.46	918.0	7.8738	385
2008	9	29.71	5.53	900.8	1.1176	385
2008	10	26.3	-2.018	775.7	6.0198	385
2008	11	21.96	-7.66	671.0	0.4064	385
2008	12	20.11	-10.58	532.7	1.4224	385

6.1.2 Example File #2

Year	Month	TMax	TMin	PAR	Prec	CO2
1900-2007	1	11.86	-13.39	564.2	1.651	383
1900-2007	2	17.93	-8.45	698.7	1.7272	383

1900-2007	3	24.73	-10.18	872.0	2.921	383
1900-2007	4	25.05	-2.853	930.5	4.0132	383
1900-2007	5	27.72	3.424	890.4	4.1449	383
1900-2007	6	35.24	8.7	1069.0	0.928	383
1900-2007	7	36.35	12.75	891.1	3.7338	383
1900-2007	8	34.15	13.64	927.9	5.0806	383
1900-2007	9	30.44	6.647	875.3	5.7138	383
1900-2007	10	26.67	-3.804	836.2	0.4064	383
1900-2007	11	21.84	-9.4	660.5	0.2794	383
1900-2007	12	17.03	-10.49	579.8	3.5304	383
2008	1	11.81	-14.41	622.1	1.2192	385
2008	2	19.35	-8.78	792.4	1.9558	385
2008	3	21.74	-9.21	930.0	1.0922	385
2008	4	25.86	-5.333	1045.2	0.4826	385
2008	5	31.97	0.023	1014.7	1.1176	385
2008	6	34.43	8.84	1042.4	0	385
2008	7	33.24	11.32	836.7	10.368	385
2008	8	32.81	11.46	918.0	7.8738	385
2008	9	29.71	5.53	900.8	1.1176	385
2008	10	26.3	-2.018	775.7	6.0198	385
2008	11	21.96	-7.66	671.0	0.4064	385
2008	12	20.11	-10.58	532.8	14.224	387

6.2 Header Information

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

```
Year      Month  TMax    TMin    PAR      Prec     CO2
```

6.3 Observations

Subsequent lines of the file contain monthly values for the 7 variables. Observations must appear in chronological order.

6.3.1 Year

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

6.3.2 Month

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

6.3.3 TMax

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

6.3.4 TMin

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

6.3.5 PAR

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

6.3.6 Prec

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

6.3.7 CO2

Atmospheric CO₂ concentration. Value: decimal > 0 . Units: ppm.

7 Input File – Generic PnET Species Parameters

This file contains PnET parameters that are identical for all species. Only parameters that are not described in Chapter 8 are described here.

Parameters may appear in any order. **NOTE:** Any of these parameters may instead be set in the PnETGenericDefaultParameters.txt file in the Defaults folder found where PnET-Succession is installed (usually in C:\Programs\...\Extensions\). Parameters set here will over-ride settings in the PnETGenericDefaultParameters file.

7.1 Example file:

```
LandisData PnETGenericParameters

PnETGenericParameters Value
>>-----
MaxCanopyLayers      2
IMAX                 10
PreventEstablishment true
DVPD1                0.05
DVPD2                2
BFolResp             0.1
TOroot               0.02
TOwood               0.01
Q10                  2
FolLignin            0.2
KWdLit               0.01
InitialNSC           7
MaxSlwFrac           0.5
CFracBiomass         0.45
FolAddResp           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 will not exceed 5 and applying many canopy layers delays the model dramatically. The number of canopy layers should primarily be regulated through MaxDevLyrAv, but when MaxDevLyrAv is given low values, the result would otherwise be an

extreme number of canopy layers. MaxCanopyLayers has a default value of 5.

7.5 IMAX

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

7.6 PreventEstablishment

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

7.7 DVPD1, DVPD2

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

7.8 BFolResp

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

7.9 TORoot/TOWood

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

7.10Q10

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

7.11FolLignin

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

7.12 KWdLit

Annual decomposition rate of woody litter. Value: $0.0 \leq \text{decimal} \leq 0.4$.
Units: percent per year.

7.13 InitialNSC

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

7.14 MaxSLWFrac

DEF??. Value: integer > 0. Units: g.

7.15 CFracBiomass

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

8 Input File – PnET Species Parameters

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

8.1 Example file:

```
PnETSpeciesParameters
SpeciesName FolN SLWmax SLWDel TOfol AmaxA AmaxB
HalfSat H3 H4 PsnAgeRed PsnTMin
PsnTOpt k WUEcnst MaintResp DNSC
FracBelowG EstMoist EstRad FracFol
FrActWd
abiebal 1.5 160 0 0.25 5.3 21.5 150 150
275 5 2 19 0.5 7 0.0025 0.05
0.25 10 3 0.053 0.00002
acerrub 2.5 65 0.2 1 -46 71.9 200 150
500 5 4 26 0.58 8 0.0025 0.05
0.33 5 5 0.028 0.00004
acersac 2.4 50 0.2 1 -46 71.9 100 150
275 5 2 23 0.58 6 0.0025 0.05
0.33 10 1 0.02 0.00002
```

8.2 SpeciesName

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

8.3 FolN

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

8.4 SLWmax

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

8.5 SLWDel

Rate of change in specific leaf weight from the top of the canopy to the bottom. Set to zero to make SLW constant throughout canopy. Value: 0.0≤ decimal ≤2. Units: g⁻¹fol.

8.6 Tofol

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

8.7 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: $-500 < \text{decimal} < +500$

8.8 AmaxB

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

8.9 HalfSat

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

8.10H2, H3, H4

Water stress parameters according to Feddes et al. (1978). See chapter 2.8. H1 is hardcoded at 0 meter pressure head. H2, H3 and H4 should be successively larger positive values. Note that this is the absolute value of values usually reported in the literature.

8.11PsnAgeRed

Reduction factor reducing leaf photosynthesis rate as cohorts age, with $f_{\text{Rad}}=1.0$ at age 1 and $f_{\text{Rad}}=0.0$ 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 $y = (\text{age}/\text{longevity})^{\text{PsnAgeDecline}}$. Cohorts die when NSC is $< 1\%$ of the value of the other biomass pools combined at the end of a calendar year. Value: $0.0 < \text{decimal} < \text{infinity}$. Units: proportion per year.

8.12PsnTMin

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

8.13PsnTOpt

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

8.14k

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

8.15WUECnst

Constant in equation for computing water use efficiency (WUE) as a function of VPD. $WUE = WUECnst / VPD$. Higher values result in higher WUE. Value: decimal > 0.0 . Units: none.

8.16MaintResp

Loss of NSC due to maintenance respiration, depends on biomass according to $Loss = MaintResp * Biomass$. Value: $0.0 \leq$ decimal ≤ 1.0 . Units: proportion of NSC lost per month.

8.17DNSC

Fraction of NSC relative to total non-foliar biomass that will be maintained as long as net photosynthesis exceeds maintenance respiration. Value: $0.0 \leq$ decimal ≤ 1.0 . Units: proportion of NSC.

8.18FracBelowG

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

8.19EstMoist

Tuning parameter to control the sensitivity of establishment (P_{est}) to soil moisture. Calculated using $f_{Water}^{EstMoist}$ where f_{Water} = the growth response to sub, or supra optimal water content according to 2.4.2 and figure 3 (right pane). High values make establishment more sensitive to moisture stress. A value of 1.0 results in a linear relationship between moisture stress and P_{est} , and little additional effect occurs with values over 50. Value: $0.0 \leq$ decimal. Units: unitless.

8.20EstRad

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

8.21FracFol

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

8.22FracActWd

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

9 Input file - Ecoregion parameters

9.1 Ecoregion

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.

9.2 SoilType

Abbreviation for the predominant soil type in the ecoregion. Soil type is used in the model to determine the water retention curve of the soil (see Figure 3 and section 2.4.2.3). Soil type names can be any character string that also appears in the corresponding soil parameters file (SaxtonAndRawlsParameters). A default version of this parameter file installs with the extension (C:\Program Files\LANDIS-II\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). These categories correspond with FAO soil types. Value: 4-letter string.

9.3 RootingDepth

Rooting depth, rooting depth in PnET-Succession is particularly important because it affects water storage capacity of the soil.

9.4 PrecLossFrac

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

9.5 LeakageFrac

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

9.6 ClimateFileName

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

10 Input File – PNEToutputsites

This file contains parameters for the site data output extension.

10.1 Example file:

```
LandisData PNEToutputsites

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

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

10.2 LandisData

This parameter's value must be "PnEToutputsites".

10.3 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.

11 Output file - SiteData Table (Optional PNEToutputsites output)

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

11.1 NrOfCohorts

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

11.2 MaxLayerStdev

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

11.3 layers

Number of canopy layers on the cell.

11.4 PAR0

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

11.5 Tday(C)

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

11.6 Precip(mm_mo)

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

11.7 RunOff(mm_mo)

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

11.8 Leakage(mm)

Water lost out of the bottom of the rooting zone.

11.9PET(mm)

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

11.10 Evaporation(mm)

Precipitation lost to evaporation from the soil surface as a function of the LAI on the site. Evaporation decreases linearly to reach 0.0 when LAI>1.

11.11 Transpiration(mm)

Transpiration of all cohorts.

11.12 Interception(mm)

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

11.13 Water(mm)

Amount of soil water as calculated by the bulk hydrology model (mm).

11.14 PressureHead(m)

Pressure head as calculated by the bulk hydrology model (m).

11.15 SnowPack (mm)

Water equivalent contained in the snowpack (mm).

11.16 LAI(m2)

Leaf Area Index (all species combined)

11.17 VPD(kPa)

Mean vapor pressure deficit for the month (kPa).

11.18 GrossPsn(gC/mo)

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

11.19 NetPsn(gC/mo)

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

11.20 MaintenanceRespiration(gC/mo)

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

11.21 Wood(gDW)

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

11.22 Root(gDW)

Sum of root biomass of all species (gDW)

11.23 Fol(gDW)

Sum of foliage biomass of all species (gDW).

11.24 NSC(gC)

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

11.25 HeteroResp(gC_mo)

Heterotrophic respiration (decay of dead pools).

11.26 Litter(gDW)

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

11.27 CWD(gDW/m²)

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

12 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.

12.1 Age(yr)

Current age of the cohort (calendar years).

12.2 Layer(-)

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

12.3 LAI(m²)

Leaf area index of the cohort.

12.4 GrossPsn(gC/m²/mo)

Cohort gross photosynthesis (gC/m²/mo).

12.5 FolResp(gC/m²/mo)

Cohort foliar respiration (gC/m²/mo).

12.6 MaintResp(gC/m²/mo)

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

12.7 NetPsn(gC/m²/mo)

Cohort net photosynthesis (gC/m²/mo).

12.8 Transpiration(mm/mo)

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

12.9 WUE(g/mm)

Cohort mean water use efficiency (g/mm).

12.10 Fol(gDW/m²)

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

12.11 Root(gDW/m²)

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

12.12 Wood(gDW/m²)

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

12.13 NSC(gC/m²)

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

12.14 NSCfrac(-)

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

12.15 fWater(-)

Reduction factor related to water availability.

12.16 fRad(-)

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

12.17 fTemp_psn(-)

Reduction factor related to sub-optimal temperature for photosynthesis.

12.18 fTemp_resp(-)

Reduction factor related to temperature effects on maintenance respiration.

12.19 fAge(-)

Reduction factor for age-related declines in photosynthesis efficiency.

12.20 LeafOn(-)

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

12.21 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.

13 Output file – Establishment Table (Optional PNEToutputsites output)

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

13.1 Year

Simulation year (timestep).

13.2 Species

Species.

13.3 Pest

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

13.4 fWater

Water availability reduction factor.

13.5 fRad

Light availability reduction factor.

13.6 Est

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

14 Appendix. Calibration tips.

1. First, set parameter values that are known from the literature (e.g., TOFol, FoIN, SLW, HalfSat, PsnTMin, PsnTOpt, k, etc.). When there is considerable range in values, begin with an intermediate value. HalfSat should be varied to reflect shade tolerance, because the LANDIS-II shade tolerance parameter has no effect in PnET-Succession. Some Pnet parameters (e.g., SLWDel, AmaxA, AmaxB, Q10, DVPD1, DVPD2) are hard to estimate and most studies use generic values (e.g., Aber et al 1995, Ollinger and Smith 2005).
2. Set parameters that will be held constant for your particular experiment or study (e.g., TOrroot/wood, BaseFolResp, InitialNSC, MaxSlwFrac, etc.) It is best to include these in the PnETGenericParameters file.
3. PsnTMin controls the length of the growing season. You should verify that the appropriate months are active (LeafOn=TRUE). PsnTMin should vary coarsely according to leaf-on and leaf senescence dates, and typically ranges from 0-4 °C for temperate species. PsnTMin will also control how productive the species is at the beginning and end of the growing season, and will produce a growth response to shifts in temperature even when the number of growing season months is unchanged. Similarly, in some years you may get some photosynthesis activity in a month when the species is not typically active, but this is not a problem as long as NetPsn is quite low in those months.
4. In lieu of empirical values, PsnTOpt can be estimated using the average mid-summer temperature at the center of the species' range. Note that temperatures above PsnTOpt will not reduce photosynthesis, but they will increase respiration costs, thus lowering NetPsn.
5. Calibration tuning is best done by matching simulated biomass increase to empirical biomass values for a species through time. 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. Simulate a monoculture and plot Wood and Root+Wood (whole tree) biomass through time. There are some published estimates of whole tree biomass through time by species groups to provide some indication of belowground biomass (e.g., Smith et al 2006). 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.
6. Choose a single soil type for calibration of all species, preferably a soil type that will produce some water stress midway through the simulation for all or most species. This is important because most empirical data is from fully stocked stands where there is competition for water, and this will help ensure that your calibrated species will have comparable parameter values and will therefore compete realistically under

realistic conditions. 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.

7. Calibrate all species under optimal temperature and precipitation conditions, which will result in growth reductions under other conditions. If you don't uniformly calibrate species under optimal conditions, then their competition will be unrealistic and unpredictable during simulations. This is most easily done by using a fixed annual weather stream (long-term monthly averages), calculating the mean growing season temperature (mean of TMin and TMax though the growing season months), and setting PsnTOpt of ALL species to that value (for calibration ONLY). To ensure comparability of tuned parameters, use a common PsnTMin also. Use average monthly precipitation. When you finish calibration, remember to set PsnTOpt (and PsnTMin) of each species back to its real value. During your simulation applications, whenever a species receives a monthly temperature that is equal to real PsnTOpt, it will then perform as calibrated and growth will decline as temperatures depart from its optimal temperature.
8. You will need starting parameter values. Here are some generic ones for temperate forest species:
 - 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. HalfSat: 600 ($\mu\text{mol/s}$) for shade-intolerant, 250 for shade-tolerant; use a gradient
 - e. H3/H4: 100/150 for drought intolerant, 150/400 for drought tolerant; use gradient
 - f. PsnAgeRed: 5
 - g. WUEc: 6 or 7. Start with the lower value for species that are known to be less water efficient.
 - h. MaintResp: 0.0025
 - i. k: 0.5 for evergreen, 0.58 for deciduous
 - j. DNSC: 0.05
 - k. FracBelowG: 0.33
 - l. FracFol: 0.13 for evergreen, 0.035 for deciduous
 - m. FracActWd: 0.00005
9. Verify MaintResp by looking for a plateau effect (cap) on wood and root biomass growth. If MaintResp is too high the curve will abruptly plateau rather than gradually taper. If MaintResp is too low, cohorts will fail to die when they are stressed or as they approach longevity. It is recommended to use a common MaintResp rather than tune biomass growth curves using MaintResp unless relative MaintResp values are

empirically well-known. MaintResp is a primary driver of cohort mortality and species competitive interactions may not be reliable with different MaintResp values. Therefore, find a MaintResp value that works for all species. Find a value that is just below that which creates a plateau effect in your species.

10. The separation between plots of above ground biomass and total biomass (roots and wood) is controlled by FracBelowG. An increase in one pool will reduce the other pool.
11. Relative growth rate among species should be controlled with FolN and SLWmax. Conifers and deciduous species must be scaled separately when they use different values of AmaxA and AmaxB. Unless specific, high quality estimates of AmaxA and AmaxB are known, it is recommended to use the values commonly used in PnET publications (5.3, 21.5 for conifers and -46, 71.9 for deciduous, respectively). Note that FolN and SLWMax are typically inversely correlated. Published values of FolN are commonly available, but use these only as a starting point. **In PnET-Succession, FolN is the primary parameter that controls relative growth rate (Amax) among species.** Set FolN of your suite of species based on what is known about relative growth rates among your species. However, you should be able to use a FolN value that is within the range of empirical values. If you find you must use a FolN value that is out of range, modify other parameters, starting with WUEc and FracFol. Don't forget that you will have a different range of FolN values for species with different AmaxA and AmaxB values.
12. Foliage biomass is controlled by FracFol and FrActWd, and you will find that it also tightly controls the lag time of significant biomass increase (early years). Because this lag time has a strong effect on competitive ability in PnET-Succession, it is recommended that you attempt to use common values of FracFol and FrActWd. It may be preferable to have similar lag times than to match empirical lag times closely; this may produce better competitive interactions in the model. I have found it quite useful to tune this is to control the number of years it takes to reach an arbitrary amount of biomass (e.g., 5000 g/m²), with the fastest growing species reaching that threshold about 5-6 years sooner than the slowest (e.g., 27 v. 33 years). Super slow-growing species (e.g., white cedar, black spruce) may be an exception. One approach that has worked is to use the same (or very similar) FracFol and FrActWd values for all species with a similar niche, defined by shade-tolerance (HalfSat) or drought tolerance (H4). Often empirical growth curves are measured in mixed forests, and shade-tolerant species will tend to have longer lag times than when grown in the open (e.g., eastern hemlock). You should monitor the shape of the foliage curve along with the biomass curve. If FrActWd is too high, foliage biomass will decline with age, which is not likely realistic. If it is too low, foliage biomass will increase indefinitely, which is also not realistic. Experience shows that values between 0.0003 and 0.0005 will produce a level or slightly declining foliar biomass after about 50 years.

13. Before adjusting the height of the biomass curve, verify that LAI is not unrealistically high or low for the species. LAI is controlled by SLW, SLWdel and FrActWd. LAI is a derived variable that basically divides foliage biomass by SLW. SLW has a major effect on LAI and a modest effect on the biomass growth curve. SLWdel controls the reduction of SLW from top to bottom in the canopy, and can have a large effect on LAI when there is a lot of foliage biomass. To estimate whether SLW at the bottom of the canopy may be reasonable, use $SLW_{min} = SLW_{max} - SLW_{del} * \text{foliage biomass}$. FrActWd controls the amount of foliage biomass later in life, and has an important effect on maximum LAI achieved; use this to control LAI if SLW values are well established empirically. It is recommended that you wait to fine-tune LAI to within the empirical range after the growth curve is close to the desired shape. In lieu of empirical values, LAI should generally range between 2-4 for shade intolerant species and 4-6 for shade tolerant species.
14. The height of the biomass growth curve is primarily controlled by WUEc, FolN, SLW, TORoot, TOWood. Remember that MaintResp can cause the curve to plateau regardless of other parameter settings. It is recommended to keep TORoot/wood constant among species. It is recommended to make major adjustments to the height of the biomass curve with WUEc and then fine-tune it using FolN and SLWmax. Note that WUEc does not correlate with WUE across species because several parameters determine actual WUE. Additional adjustments can then be made by adjusting FolN and SLW within empirical limits. It also seems advisable to try to use a common WUEc value for species in a similar niche (e.g., shade-tolerance, drought-tolerance) to allow them to compete properly.
15. The timing of the peak of the biomass growth curve is primarily determined by species longevity and secondarily by PsnAgeRed. If the species tends to not die at longevity, adjust PsnAgeRed. A value of 5 seems to work well for most species.
16. You should be able to control most aspects of the shape of the biomass growth curve. The initial increase is controlled with FracFol, the height by WUEc and the decline by longevity and PsnAgeRed. Fine-tuning is done with FolN and SLW. FolN has a predictable effect on the growth curve, but you may find SLW a bit more erratic because it interacts with foliage biomass and leaf area to affect light competition within the canopy.
17. NetPsn is primarily controlled by FracF and FracActWd, given FolN, SLW and BaseFolResp. Transpiration is highly correlated with Net Psn, scaled by WUE. Recall that GrossPsn is calculated by PnET-Succession using NetPsn and BaseFolResp, which is not intuitive.
18. dNSC 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.

19. InitialNSC similarly has little effect on cohort competition unless values among species vary by more than an order of magnitude.
20. EstMoistSens and EstRadSens. Establishment probability is reduced in proportion to light and water photosynthesis reduction factors for the species at the time of establishment when EstMoistSens and EstRadSens = 1.0. Modify these values to weight the influence of the light and water reduction factors on establishment if the conditions for optimal establishment vary markedly from the conditions for optimal growth.
21. **General notes.** 1) To ensure realistic competition, it is advisable to use common parameter values across species whenever possible. If you are planning to experimentally vary some parameters, holding the others constant will improve the signal from your experiment. Minimizing species differences in parameters such as SLWDel, PsnAgeRed, k, MaintResp, DNSC, WUEc, FracBelowG, FracFol and FracActWd will make competitive interactions more predictable. Hold these as close to each other as possible, varying other parameters to calibrate as much as possible within empirical limits. However, when you cannot calibrate adequately using the common parameter values, do not hesitate to vary the one or two other parameters that will produce good performance. It is very likely that such modifications reflect biological reality. 2) It is highly recommended that you verify your calibrations by simulating several similar species together to ensure that they in fact compete as expected.

References

- Aber, JD, Ollinger SV, Federe 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.
- 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.
- Miles P, Smith WB. 2009. Research Note-NRS-38. Specific gravity and other properties of wood and bark for 156 tree species found in North America. Res. 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.