

TREES Model Introduction

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The Terrestrial Regional Ecosystem Exchange Simulator (TREES) is a dynamic biophysical process-based simulation model. It is designed for simulating land-based systems, it uses leaf area and ground area as scalars, and so the model can be used at plant, stand, or landscape (regional) scales without any modification to the model code. TREES solves vertical, one-dimensional processes from a lower boundary, *e.g.* impermeable bedrock layer, to the atmosphere within the turbulent boundary layer of vegetation (see **Box 1**). This type of model is commonly called a soil-vegetation-atmosphere transfer (SVAT) model, but TREES has a few tricks that distinguish it from many other 1-D vegetation models. First, it couples canopy processes (*e.g.*, stomatal conductance, photosynthesis, and transpiration) to a soil-plant hydraulic system that supports cavitation in the plant xylem. This gives the model the ability to retain a memory of successive drought exposure on plants, and enables it to predict a wide range of emergent physiological responses to stressors using observational data (Mackay *et al.*, 2015; Tai *et al.*, 2017; Johnson *et al.*, 2018; McDowell *et al.*, 2019; Wang *et al.*, 2020). Second, a newer version of the model grows the canopy and roots as functions of resource (*e.g.*, carbon and nitrogen) limitations, hydraulic limitations on water accessibility and transport of water and nutrients from roots to leaves, and non-structural carbon and amino acids from the canopy down to roots (Mackay *et al.*, 2020). Third, a novel canopy growth model allows for linking genetic complexity and dynamic physiological responses to environmental conditions (Wang *et al.*, 2019), which also provides an alternative growth model for annuals to use instead of the climate-driven canopy phenology (Savoy and Mackay, 2015) used for simulating perennials. Fourth, TREES is equipped with both C3 and C4 photosynthesis models. Fifth, nitrogen cycling components connect microbial processes (*e.g.*, immobilization, ammonification, nitrification) to plant-mediated substrates (*e.g.*, organic material turnover and root exudates), affected by soil temperature and hydraulic properties, within rhizospheres tied to root growth dynamics.

TREES is a dynamic model, which means it updates its states (or pools) at each time step based on fluxes of water, carbon, nitrogen, and a memory of the lowest predawn water potential to which the simulated xylem has been exposed. The model keeps track of carbon pools (*e.g.*, leaf, stem, fine and coarse roots, non-structural carbon, amino acids, soil organic material, microbial biomass), nitrogen (*e.g.*, organic, ammonium, nitrate, amino acids), and water in the soil in multiple layers. The model is forced with micrometeorological data (**Table 1**) at 30-minute time steps, and it is parameterized with two additional files (**Tables 2** and **3**). One file contains the parameters shown in **Table 2**, which allow for specification of site properties, physical traits of the plant canopy that influence energy transfers, biological traits for photosynthesis and hydraulics, soil physical properties, root growth traits, microbial traits, and traits associated with leaf growth. The second parameter file shown in **Table 3** provides a way of specifying the hydraulic architecture of the soil-plant system, including axial and lateral lengths, and initial proportional root areas in each layer. This “param_mod” file has a

There are three output files (**Table 4-6**). The primary flux and pool outputs are shown in **Table 4**. Note that the number of columns in this output file depends on how many soil-root layers are defined (see **Table 3**). **Table 5** provides information that can be used to reconstruct the cavitation status of each element of the plant at each time step. Specifically, all the information needed to reconstruct maximum (cavitated) hydraulic conductance and how the vulnerability curves have been modified from their native forms as a result of water stress. **Table 6** reports on the growth of individual leaves when the individual leaf growth model is used.

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Box 1. High-level view of processes in TREES. Functions in blue involve soil or xylem hydraulics, and those in red involve nitrogen cycling.

trees_main.cpp

- Read in parameter files
- Open output files and write out headers
- Call simulator()

simulator.cpp

- Compute soil hydraulic properties
- Initialize state variables
- Initialize bgc()
- Initialize hydraulicModel()
- Call hydraulic model setup()
- Time loop {
 - Read in one line from the driver file
 - Recall hydraulic model setup() to account for plant growth
 - Call simulation_functions()
 - Write results to output files }

simulation_functions.cpp

- Compute canopy phenology or leaf area growth, one of:
 - compute_GSI_LAI() in process_functions.cpp, or
 - bgc.updateLeafCarbonNitrogenPools(), or
 - bgc.updateLeaf()
- Call infiltration() sub-model in process_functions.cpp
- Call aerodynamic conductance with stability corrections in process_functions.cpp
- Compute canopy absorb_rad() in process_functions.cpp
- Compute root weighted soil water potential
- Compute water stress function used to scale initial Gs
- Call compute_canopy_evaporation() in process_functions.cpp
- Loop until hydraulics converges {
 - First iteration, calc_gvc(4 parameters) initial guess in process_functions.cpp
 - Subsequently, call DoHydraulicModel() and calc_gvc(10 parameters)
 - Compute sun and shade leaf temperatures
 - Compute sun and shade photosynthesis, calling one of:
 - bgc.photosynthesis() or bgc.coupledA3_gc() or bgc.coupledA4_gc()
 - Compute revised sun and shade stomatal conductances
 - Call do_pm() in process_functions.cpp to compute transpiration for sun and shade
 - Compute sun and shade leaf surface vapor pressure deficits
 - Re-call aerodynamic conductance in process_functions.cpp }
- Compute rhizosphere fluxes
- Compute ground surface evaporation
- Compute transpiration removal from each rhizosphere
- Call capillary_rise() in process_functions.cpp
- Call bgc.storeGlycineAndSerine()
- Compute maintenance respiration and update NSC
- Compute cost of loading NSC into the phloem
- Compute growth potential
- Call bgc.computeLeafAllocation()
- Call bgc.updateStemCarbonNitrogenPools()
- Call bgc.updateRootCarbonNitrogenPools()
- Compute NSC needed for defense
- Compute the circadian control of chloroplast starch and sugar
- Call bgc.computeRootExudates()
- Call bgc.computeRootNitrogenUptake()
- Call bgc.computeLeaching()
- Call bgc.updateRhizospherePools()
- Compute total respiration, NPP, and NEE
- Compute snowmelt
- Call infiltration() in process_functions.cpp

Table 1. Information on the TREES driver (time-series of micrometeorological data) used as forcing for the model. Note that TREES must have data in 30-minute time steps (= 48 time steps per day).

Input Column	Units	Description	Notes
Date	YEARDAY	Using year as well as day the code will expect leap-years to have 366 days	For example, 2020300 is YEAR 2020 DAY 300
Time	Half-hours	Starting at 0 (midnight), incrementing by 0.5, ending with 23.5 (11:30 pm) for each day	The model expects 48 time steps per day
u_ref	m s ⁻¹	Wind velocity at the reference height (assumed to be above the canopy)	This cannot have zeroes; model will force value > 0.0
t_ref	deg C	Temperature at the reference height	This is a critical value to have
d_ref	kPa	Vapor pressure deficit of the atmosphere at the reference height	This is a critical value to have
precip	mm	Precipitation above the canopy or irrigation made directly to the soil surface	This is a critical value to have
q_par	umol m ⁻² s ⁻¹	Incoming photosynthetically active radiation	This is a critical value to have
t_canopy	deg C	Temperature within the canopy; use the same value as t_ref if you don't have this observation	
d_canopy	kPa	Vapor pressure deficit within the canopy; use d_ref if you don't have this observation	
p_atm	kPa	Atmospheric pressure observed at your location; can be computed from elevation	This is a critical value to have
CO2_atm	ppm	Concentration of carbon dioxide in the atmosphere	This is a critical value to have
T0	deg C	Temperature at the ground surface	
Tsurf	deg C	Temperature of the top soil layer	
Troot	deg C	Average temperature of the root zone	
Zw	m	Depth of the water table; can be used to provide a water source from below	This can be enabled or disabled in simulation_functions.c
xylem scalar	unitless	Has been used for multiple purposes; currently, a 1.0 does nothing, 0.99 forces xylem refilling	
Carbon flux	umol m ⁻² s ⁻¹	Legacy column for use with the Bayesian MCMC algorithm	Use -999 if you have no data
Water flux	mm 30min ⁻¹	Legacy column for use with the Bayesian MCMC algorithm	Use -999 if you have no data
		Note: There can be no missing entries on a line	
		Also: Missing time steps will yield unexpected results, as the model uses location (.p file), date, and time to compute clear-sky radiation and day length	

Table 2. TREES parameters. Colors are used to distinguish parameters associated with each photosynthesis model, an older C3 Farquhar model, an experimental C3 model that includes novel nitrogen assimilation, and a C4 model.

[illegible]

Table 3. This ‘param_mod’ file describes the plant hydraulic segments, including lateral and axial shoot module (one) and six lateral and axial root modules with soil-root layer thicknesses of 5, 10, 15, 10, 5, and 55 cm. The sixth layer contains no roots.

Name in param mod file	Value	Description
#_of_shoot_modules	1	TREES is currently set up to use one lateral shoot in the hydraulic model
leaf_area_fraction	1	By default with one shoot module this should be set to 1
length_lateral	0.1	This is a scalar that is multiplied by length_axial to get lateral stem length
length_axial	20	Length of the axial stem in meters
#_of_root_modules	6	This can be from 1 to 21; typical numbers are 4 to 7
leaf_area_fraction	0.213	This sets the initial fraction of leaf (and root) area supported by this layer
length_lateral	2	This is a scalar that is multiplied by the sum of axial lengths to get lateral root length in this layer
length_axial	0.05	This layer has a thickness of 5 cm
leaf_area_fraction	0.213	
length_lateral	2	
length_axial	0.1	This layer has a thickness of 10 cm
leaf_area_fraction	0.32	
length_lateral	1.5	This layer has a lateral root extent that is 75% of that of the surface layer
length_axial	0.15	
leaf_area_fraction	0.213	
length_lateral	1	
length_axial	0.1	
leaf_area_fraction	0.041	
length_lateral	0.1	
length_axial	0.05	
leaf_area_fraction	0.0000001	Setting this to a very small number sets the fine root area for this layer to near zero
length_lateral	0.0000001	Setting this to a very small number (<0.00001) means this layer will never grow fine roots
length_axial	0.55	

Table 4. TREES main outputs (.sim). Each column is output at each 30-minute time step. This can produce a big file of about 20 MB per year of simulation.

Output Column	Units	Description	Notes
ti		year-date-hour	
simET	mm s-1	evapotranspiration	This can be compared to eddy covariance tower ET data
WPlant_K	mmol m-2 s-1 MPa-1	whole plant hydraulic conductance	This is the full rhizosphere-plant hydraulic conductance
Soil_Psi	MPa	soil water potential	This is a root profile weighted average
Leaf_Psi	MPa	leaf water potential	
Psi_Crit	MPa	critical leaf water potential	
Ecrit	mmol m-2 s-1	critical transpiration	Maximum transpiration without causing hydraulic failure
Ec	mmol m-2 s-1	transpiration	
RhizFluxX	mmol m-2 s-1	rhizosphere flux - one column per soil-root layer	X = 0, 1, 2...N soil-root layers
Gs	mol m-2 s-1	stomatal conductance	This is a canopy average stomatal conductance
LAI	m2 -m-2	actual leaf area index	
SLA	m2 kgC-1	Specific leaf area	
liveLAI	m2 -m-2	forecast live leaf area index	This variable is used internally to compute LAI potential for next year in perennials
Rmaint	kgC ha-1	maintenance respiration	Whole plant
Rgrowth	kgC ha-1	growth respiration	Whole plant
leafNSC	kgC ha-1	non-structural carbon	
stemNSC	kgC ha-1	non-structural carbon	
rootNSC	kgC ha-1	non-structural carbon	
chloroSarch	kgC ha-1	non-structural carbon	Follows a diel cycle; drives allocation of carbon for growth
chloroSugar	kgC ha-1	non-structural carbon	Follows a diel cycle; drives allocation of carbon for growth
waterStress	unitless	stress = Ecrit / Esat, plant is water stressed when this value is less than 1.0	Used for initial guess at stomatal conductance; used to reduce quantum yield
litterH2O	m3 m-3	litter layer water content	
thetaX	m3 m-3	layer soil water content - one column per soil-root layer	X = 0, 1, 2...N soil-root layers
thetaRoot	m3 m-3	root average soil water content	
Can_Evap	mm s-1	free evaporation from wet canopy	
Snowpack	m	snow water equivalent	
SnowEdef	deg C-1	snow energy deficit	
Vcmax25	umol m-2 s-1	maximum carboxylation at 25 C	Currently writes out zeros for photosynthesis models 2 and 3
Vcmax_sun	umol m-2 s-1	leaf level Vcmax	Currently writes out zeros for photosynthesis models 2 and 4
Vcmax_shd	umol m-2 s-1		Currently writes out zeros for photosynthesis models 2 and 5
Jmax25	umol m-2 s-1	maximum J at 25 C	Currently writes out zeros for photosynthesis models 2 and 6
J_sun	umol m-2 s-1	leaf level J	Currently writes out zeros for photosynthesis models 2 and 7
J_shd	umol m-2 s-1		Currently writes out zeros for photosynthesis models 2 and 8
Asun	umol m-2 s-1	leaf level photosynthesis	
Ashd	umol m-2 s-1		
Lsun	m2 m-2	leaf level area	
Lshd	m2 -m-2		
Tsun	deg C	leaf level temperature	
Tshd	deg C		
Dsun	kPa	leaf level vapor pressure deficit	
Dshd	kPa		
CI_sun	ppm	leaf level intercellular CO2	
CI_shd	ppm		
PARsun	umol m-2 s-1	leaf level absorbed PAR	
PARshd	umol m-2 s-1		
gs_sun	mol m-2 s-1	leaf level stomatal conductance	
gs_shd	mol m-2 s-1		
NEE	umol m-2 s-1	net ecosystem exchange	This can be compared to eddy covariance tower ET data
NPP	umol m-2 s-1	net primary production	
R_total	umol m-2 s-1	total respiration	
R_ag	umol m-2 s-1	aboveground respiration	
R_bg	umol m-2 s-1	belowground respiration	
Rd_sun	umol m-2 s-1	dark respiration	
Rd_shd	umol m-2 s-1		
Csapwood	kgC ha-1	stem carbon	
FibRootCX	kgC ha-1	root order 1 carbon content, one column per soil-root layer	X = 0, 1, 2...N soil-root layers
FineRootCX	kgC ha-1	root order 2 carbon content, one column per soil-root layer	X = 0, 1, 2...N soil-root layers
TotRootCX	kgC ha-1	total root carbon content, one column per soil-root layer	X = 0, 1, 2...N soil-root layers
FineRootCNX	kgC kgN-1	root orders 1&2 carbon to nitrogen ratio, one column per soil-root layer	X = 0, 1, 2...N soil-root layers
LeafCN	kgC kgN-1	leaf C:N	
humusCX	kgC ha-1	humus carbon content, one column per soil-root layer	X = 0, 1, 2...N soil-root layers
RhizCX	kgC ha-1	labile organic carbon, one column per soil-root layer	X = 0, 1, 2...N soil-root layers
RhizNIX	kgN ha-1	labile organic nitrogen, one column per soil-root layer	X = 0, 1, 2...N soil-root layers
AAexudateCX	kgC ha-1	amino acid content, one column per soil-root layer	X = 0, 1, 2...N soil-root layers
SugarExudateCX	kgC ha-1	sugar exudate content, one column per soil-root layer	X = 0, 1, 2...N soil-root layers
MicrobCX	kgC ha-1	live microbial carbon, one column per soil-root layer	X = 0, 1, 2...N soil-root layers
MicrobNX	kgN ha-1	live microbial nitrogen, one column per soil-root layer	X = 0, 1, 2...N soil-root layers
RhizN-	kgN ha-1	rhizosphere nitrate content	
RhizN+	kgN ha-1	rhizosphere ammonium content	
PlantN	kgN ha-1	total plant nitrogen	
PlantNstat	unitless	Combined index of N available to the plant relative to N needed for incremental growth	
RLA	m2 root m-2 leaf	root-to-leaf area ratio	
arX	m2 root layer m-2 total root	fraction of root area in layer, one column per soil-root layer	X = 0, 1, 2...N soil-root layers

Table 5. Hydraulic outputs used to reconstruct vulnerability to cavitation curves and identify hydraulic conductance changes in different xylem elements.

Output Column	Units	Description	Notes
ti		year-date-hour	
latStemK	mmol m-2 s-1 MPa-1	Lateral stem hydraulic conductance	Ignore this variable
latRootKX	mmol m-2 s-1 MPa-1	Lateral root hydraulic conductance, one column for each soil-root layer	X = 0, 1, 2, ..., N; ignore this variable
StemAxialYm	MPa	Axial stem minimum water potential reached	
StemLatYm	MPa	Lateral stem minimum water potential reached	
RootAxialYmX	MPa	Axial root minimum water potential reached, one column for each soil-root layer	X = 0, 1, 2, ..., N
RootLatYmX	MPa	Lateral stem minimum water potential reached, one column for each soil-root layer	X = 0, 1, 2, ..., N
StemAxialKm	mmol m-2 s-1 MPa-1	Axial stem maximum hydraulic conductance	
StemLatKm	mmol m-2 s-1 MPa-1	Lateral stem maximum hydraulic conductance	
RootAxialKmX	mmol m-2 s-1 MPa-1	Axial root maximum hydraulic conductance, one column for each soil-root layer	X = 0, 1, 2, ..., N
RootLatKmX	mmol m-2 s-1 MPa-1	Lateral root maximum hydraulic conductance, one column for each soil-root layer	X = 0, 1, 2, ..., N
StemAxial_b	-Mpa	Axial stem Weibull b parameter	
StemLat_b	-Mpa	Lateral stem Weibull b parameter	
RootAxial_bN	-Mpa	Axial root Weibull b parameter, one column for each soil-root layer	X = 0, 1, 2, ..., N
RootLat_bN	-Mpa	Lateral root Weibull b parameter, one column for each soil-root layer	X = 0, 1, 2, ..., N
StemAxial_c	unitless	Axial stem Weibull c parameter	
StemLat_c	unitless	Lateral stem Weibull c parameter	
RootAxial_cN	unitless	Axial root Weibull c parameter, one column for each soil-root layer	X = 0, 1, 2, ..., N
RootLat_cN	unitless	Lateral root Weibull c parameter, one column for each soil-root layer	X = 0, 1, 2, ..., N
Notes: These outputs are used to reconstruct vulnerability curves and hydraulic conductance of each plant segment at any point in time			
Reference: Mackay et al 2015 Water Resources Research			

Table 6. Individual leaf model output of time series of each leaf area.

Output Column	Units	Description	Notes
ti		year-date-hour	
Area_Leaf_X	cm2	Area of individual leaf, one column per leaf	X = 0, 1, 2, ..., N
Reference: Wang et al 2019 Journal of Experimental Botany			