

Implementation of the Perfect Plasticity Approximation with biogeochemical compartments in R

Adam Erickson^{a,*}, Nikolay Strigul^a

^a*Department of Mathematics and Statistics, Washington State University
14204 Salmon Creek Avenue, Vancouver, WA, 98686, USA*

Abstract

Modeling forest ecosystems is a landmark challenge in science, due to the complexity of the processes involved and their importance in predicting future planetary conditions. While there are a number of open-source forest biogeochemistry models, few papers exist detailing the software development approach used to develop these models. This has left many forest biogeochemistry models large, opaque, and/or difficult to use, typically implemented in compiled languages for speed. Here, we present a forest biogeochemistry model from the SORTIE-PPA class of models, PPA-SiBGC. Our model is based on the Perfect Plasticity Approximation with simple biogeochemistry compartments and uses empirical vegetation dynamics rather than detailed prognostic processes to drive the estimation of carbon and nitrogen fluxes. This allows our model to be used with traditional forest inventory data, making it widely applicable and simple to parameterize. We detail the conceptual design of the model as well as the software implementation in the R language for statistical computing. Our aim is to provide a useful tool for the biogeochemistry modeling community that demonstrates the importance of vegetation dynamics in biogeochemical models.

Keywords: Perfect Plasticity Approximation, Forest ecosystem simulation, Forest biogeochemistry models, Individual-based models

*Corresponding author
Email addresses: adam.erickson@wsu.edu (Adam Erickson), nick.strigul@wsu.edu (Nikolay Strigul)

1. Motivation and Significance

The practice of modeling ecological systems began around 1920 with a calculus model of chemical dynamics applied to the trophic interaction of herbivory [1]. The logistic growth model used was inspired by Malthusian carrying capacity [2]. The concept of *Ökologie* (ecology) had been formalized by Haeckel in 1866, with *ecosystems* soon to be coined by Tansley in 1935. Lotka-Volterra equations, a type of periodic Kolmogorov system, were next applied to fish populations [3]. Four decades later, empirical differential equations were developed to model the growth and yield of forest stands [4, 5, 6]. These models extended the principle of growth tables, used in Germany since the 18th century and in China since the 17th century [7].

The simplicity of early forest ecosystem models reflected the computational limits of the era – models were tractable by necessity, solved by mechanical calculators or hand. Digital computers brought a landmark innovation in the ability to explicitly simulate processes of forest succession at an individual-tree level [8]. For the first time, direct analysis of forest dynamics theory [9] was possible. These forest ‘gap’ models exhausted computational resources of the era beyond the stand or landscape scale – a limitation that continues to date. Concurrently, the first one-dimensional physiological or biogeochemical process models and forest fire models were developed. Many components of modern terrestrial biosphere models were built separately and later assembled into comprehensive global modeling systems.

Until recently, the number of transistors in integrated circuits doubled every two years in accordance with Moore’s Law. Despite the growth in compute, gap models remain computationally impractical for regional- or global-scale modeling. While many modeled processes are inherently serial, others are poised to greatly benefit from mass parallelization (e.g., using general-purpose graphics processing units, or GPGPUs). There is surprisingly little research in this area currently, as most modeling groups prefer to add new processes rather than optimize existing ones. Yet, there is a critical need to produce “a relatively

simple mechanistic ecosystem model that is equitable in detail and that will run at large scales” [10]. Such a model is required to improve representation of vegetation dynamics in earth system models in order to produce more robust predictions of the global carbon cycle [11].

35 A lack of detailed field observations made (and still make) models of forest dynamics difficult to parameterize and validate, due to the long timescales and large number of parameters and processes involved [12]. While long-term ecological research (LTER) began formally with NSF funding of six sites in 1980, less than four decades have since passed. There are few research forests with a
40 century of data or more. Even for sites with a long history of data (e.g., Harvard Forest), the sparsity data makes the validation of complex models non-trivial. Meanwhile, forest measurement techniques have radically advanced since the 1980s, first in the 1990s with eddy covariance flux towers and second in the 2000s with geometric point cloud models generated by laser scanning or pho
45 togrammetric computer vision (e.g., structure-from-motion). These new data sources provide detail on forest energy and biogeochemistry fluxes, canopy dynamics, species distributions, demography, and other metrics of vital importance to developing and validating new forest biogeochemistry models.

Over the past century, models of forest ecosystems grew in complexity from
50 differential equations to detailed models of physiological and spatial processes. This progression entailed seven landmark stages of model development: (*i*) growth-and-yield tables or equations [7]; (*ii*) physical soil-plant-atmosphere continuum models [13]; (*iii*) forest fire models [14]; (*iv*) forest ‘gap’ models [8, 12]; (*v*) ‘big-leaf’ physiological process models including early land surface mod
55 els [15, 16]; (*vi*) hybrid and landscape models [17, 18]; (*vii*) ‘cohort-leaf’ hybrid models including ED/ED2/FATES [19, 20], LM3-PPA [21], and the simple PPA-SiBGC compartment model presented herein. Model stages *i*–*v* entailed increases in complexity with each new process, resulting in the desire for new approximation schemes in stage *vii* models. While stage *vi* models expanded to
60 include modeling spatial processes at the landscape scale, stage *vii* models blend physiological and demographic processes through robust gap model reductions.

Thus, current state-of-the-art (stage *vii*) models follow the modeling approach advocated in the seminal works of [22] and [23]: *prefer realism and generality to precision*.

65 Models of forest ecosystems entail a number of scale- and application-specific assumptions. Historically, this has required the selection of different models for different applications or research questions [24, 25]. Terrestrial biosphere models, for example, were separated into diagnostic and prognostic models [26]. While model structure diverged over the previous four decades into specialized
70 applications, it has converged during the past two with the development of hybrid models. The recent development of 'cohort-leaf' models has made this convergence complete, integrating aspects of each class of model, from individual-based gap models to global-scale terrestrial biosphere models. The distinction between diagnostic and prognostic models has similarly faded.

75 It is beneficial to comprehend that the mathematical approximations developed in stage VII models were made possible by detailed individual-based gap models. In effect, gap models were applied as generative models to produce data for difficult-to-measure dynamics needed in developing approximations. This is conceptually similar to the *sim2real* paradigm currently at the forefront of artificial
80 intelligence and robotics research [27]. Using gap models as data generators was necessary due to a lack of detailed long-term observational data. In other words, the approximations are model emulators, as demonstrated in the seminal publication describing the PPA model [28, 29]. Unlike most statistical emulators (e.g., machine learning models), the PPA model is analytically tractable,
85 thereby surpassing the requirement for an efficient model approximation providing macroscopic equations of forest dynamics [10].

In recent work [30], we demonstrated that the PPA model extended with simple biogeochemistry compartments (PPA-SiBGC) is adequate to produce model realism and precision surpassing LANDIS-II and its latest NECN biogeo-
90 chemistry model, which is an adaptation of the CENTURY model. This work is important because it demonstrates that improving the representation of vegetation dynamics in forest biogeochemistry models may yield model accuracy

surpassing far more complex models lacking explicit canopy dynamics. Moreover, our presented model is computationally efficient, with speeds an order of magnitude faster than LANDIS-II despite being implemented in an interpreted rather than compiled language (R rather than C#).

2. Conceptual Framework

In the following sections we describe the conceptual framework behind the PPA-SiBGC model.

2.1. Perfect Plasticity Approximation

The Perfect Plasticity Approximation (PPA) model [28] was developed based on the SORTIE individual-based model of forest ecosystems, or gap model [31]. The PPA model reduces the dimensionality of the classical SORTIE gap model by approximating the 3-D geometric interactions of individual tree crowns at the cohort level. The PPA model was based on the observation that the inclusion of phototropism (i.e., stem-leaning) and crown plasticity (i.e., space-filling) in the crown-plastic SORTIE model, CP-SORTIE, reduced the variation in canopy join height to a negligible level [28]. Thus, assuming perfect plasticity would yield zero variation in canopy join height, allowing the canopy to simply and effectively be segmented into separate canopy layers. This property is extremely important for application in modern terrestrial biosphere models, which widely adopt one-dimensional big-leaf representation of processes. The PPA model is succinctly described by Equation 1:

$$1 = \int_{z^*}^{\infty} \sum_{j=1}^k N_j(z) A_j(z^*, z) dz \quad (1)$$

where k is the number of species, j is the species index, $N_j(z)$ is the density of species j at height z , $A_j(a^*, z)$ is the projected crown area of species j at height z , and dz is the derivative of tree height. Thus, we compute the height where the integral of tree crown area is equal to the stand ground area. This yields the theoretical z^* height that marks the transition from above to below

one canopy layer [28]. There may be one or many z^* heights. The number of
120 theoretical z^* heights in a stand is a function of the stand's leaf-area index, or
LAI, where $n_{z^*} = \lfloor \text{LAI} \rfloor$. Each additional closed canopy layer, including shrubs
and grasses, follows the form z^{**} , z^{***} , *et cetera*.

This partitioning of canopy layers allows for the use of separate coefficients
or models of growth, mortality, and fecundity to be applied across the strata.
125 The first moment of these canopy layer dynamics accurately approximates the
dynamics of individual-based models [28]. We extend the SORTIE-PPA model
by adding a simple compartment-based representation of biogeochemistry using
allometric and stoichiometric relations, along with simple prognostic (i.e.,
climate-driven) model of soil respiration [32, 33] and a constant representation
130 of organic carbon by soil type [34].

2.2. Allometry and Stoichiometry

The tree allometric model and parameters were adapted from previously
published research [35, 36]. Tree height is modeled as a non-linear function of
stem diameter as follows:

$$h = 1.35 + (h_{max} - 1.35) \times (1 - e^{(-1*b*DBH)}) \quad (2)$$

135 where h is the tree height (m), h_{max} is the maximum potential tree height,
DBH is the depth-at-breast-height (cm), e is Euler's constant, and b is an ex-
ponential decay coefficient. Tree crown radius and depth are also modeled as a
function of DBH, but are instead intercept-free linear models.

$$d_{crown} = cd \times DBH \quad (3)$$

where dp_{crown} is the crown depth (m) and cd is the crown depth regression
140 coefficient. The equation form is similar for crown radius:

$$r_{crown} = cr_1 \times DBH^{cr_2} \quad (4)$$

where r_{crown} is the crown radius (m) and, cr_1 and cr_2 are the crown radius regression coefficients. Basal area is also calculated as a function of DBH, using the forester's constant for DBH in centimeters:

$$ba = DBH^2 \times 0.00007854 \quad (5)$$

National species-specific biomass equations [37] were used to model tree
145 biomass as a function of DBH:

$$\log AGB = \beta_0 + \beta_1 \times \log DBH \quad (6)$$

where AGB is the tree aboveground biomass (kg) and, β_0 and β_1 are regression coefficients. Empirical coefficients are used for the aboveground biomass fractions contained in stem, branch, and leaf compartments, as well as soil. Root biomass is partitioned into coarse and fine root components based on existing
150 equations for the United States [37], following the general form:

$$\log ratio = \beta_0 + \beta_1 \log DBH \quad (7)$$

where *ratio* is the biomass fraction for the root component and, β_0 and β_1 are regression coefficients. The coefficients used for coarse roots were -1.4485 for β_0 and -0.03476 for β_1 . For fine roots, the coefficients were -1.8629 and -0.77534, respectively. The biomass of each root compartment is then calculated
155 by multiplying tree AGB by the corresponding ratio.

Tree belowground biomass is calculated as the sum of root and soil biomass, while total biomass is calculated as the sum of below- and above-ground compartments. Separate empirical biomass carbon fraction and C:N stoichiometric coefficients were used for each compartment. Thus, C and N content are fixed
160 fractions of biomass values, based on empirical point estimates or samples from distributions.

2.3. Soil Respiration

In the PPA-SiBGC model, we use the simple prognostic soil respiration model of Raich *et al.* (2002):

$$R_S = F \times e^{(Q_{10} * T_a)} \times [P / (K + P)] \quad (8)$$

165 where e is Euler's constant, Q_{10} is the respiration temperature sensitivity coefficient per 10 °C increase, b is a temperature sensitivity constant, T_a is mean monthly air temperature (°C), P is mean monthly precipitation (cm), F is the soil respiration rate at 0 °C, K is the half-saturation constant for the hyperbolic relationship between soil respiration and rainfall, and R_S is soil respiration (g
170 C m² day⁻¹). The version of the model used in PPA-SiBGC includes updates parameters based on infrared gas analyzer measurements of soil CO₂ flux [33].

2.4. Soil Organic Carbon

For modeling soil organic carbon (SOC) in PPA-SiBGC, we use the simple approach of Domke *et al.* (2017), which is based on the STATSGO US national
175 soil database. Thus, the model is currently limited to forest soil types present in the US. The model is defined as follows:

$$CS = \left(\sum_{F=1}^j SOC_{SG} \times E \right) \times \left(\sum_{F=1}^j E \right)^{-1} \quad (9)$$

where CS is the county-specific areal SOC by forest type (Mg/ha), SOC_{SG} is the areal SOC for the STATSGO map unit (Mg/ha), E is a vector of weights for the areal coverage of each USFS Forest Inventory and Analysis (FIA) plot,
180 and F is the number of FIA plot records within forest types. We used the best fit model of [34] to model the vertical SOC profile:

$$\log_{10} \text{SOC} = I + \log_{10} D \quad (10)$$

where $\log_{10} \text{SOC}$ is the volumetric soil organic carbon density (Mg C ha⁻¹cm⁻¹), I is the intercept, and D is the profile midpoint depth (cm). We integrated over a range of profile depths to produce total SOC values:

$$\log_{10} \text{SOC}_{100} = \sum_{d=1}^{100} I + \log_{10} d \quad (11)$$

185 where d is the profile midpoint depth (cm). And thus:

$$\text{SOC}_{100} = 10^{\log_{10} \text{SOC}_{100}} \quad (12)$$

Both the original SORTIE-PPA model and the PPA-SiBGC model presented herein have undergone extensive validation with field data. The SORTIE-PPA model validation is described in the original paper [28], while the PPA-SiBGC model was recently validated at two research forests for a range of metrics [30].
190 Despite the simplicity of the representation of biogeochemical dynamics in the PPA-SiBGC model, it outperformed LANDIS-II with NECN (i.e., CENTURY) biogeochemistry across a range of metrics and sites in the model intercomparison exercise [30].

3. Software Description

195 The PPA-SiBGC model is implemented in a standalone R script that is designed to be run from a command-line interface, or CLI. Since the model is implemented in R with no external dependencies, it can be used on any platform that R supports (e.g., Windows, Linux, MacOS). The model implementation begins by loading all input data into memory and parsing the configuration
200 CSV file. If cohort mode is enabled, the *GenerateCohorts* function aggregates the individual trees into cohorts based on a predefined DBH interval (e.g., every 2 cm), recording the number of trees per cohort.

Next, the allometric and stoichiometric C:N equations are applied to the individual trees or cohorts in order to calculate the initial C and N pools. The
205 simulation is then run for each year in the defined temporal range. The overall model process is shown in Algorithm 1.

Algorithm 1 PPA-SiBGC model procedure

```
1: procedure MODEL
2:   Load input files
3:   Generate cohorts
4:   Initialize tree allometry and biogeochemistry
5:   Calculate soil organic matter profile
6:   for year, ...,  $N_{years}$  do
7:     Calculate soil respiration
8:     Calculate  $z^*$  height (PPA algorithm)
9:     for species, ...,  $N_{species}$  do
10:      for type, ...,  $N_{types}$  do
11:        Apply mortality
12:        Apply growth
13:        Calculate allometry
14:      end for
15:      Calculate biomass
16:      Calculate C and N
17:    end for
18:    Append annual outputs to CSV
19:    Calculate year execution time
20:  end for
21:  Calculate total execution time and export to CSV
22: end procedure
```

Vectorization is used where possible to accelerate the model operations. This optimization comes at no cost to the programmer in interpreted languages such as R, as it is built into the language. Distributions such as Microsoft R Open
210 (MRO) ship with the Intel MKL optimized algebra library. An implementation of the PPA algorithm used to find the theoretical z^* height is shown in Algorithm 2:

Algorithm 2 simplified PPA algorithm

Input: $T_1 \dots T_N$ (tree list from forest inventory), A_{field} (field area)

Output: T (height-sorted tree list), z_{star} (calculated z^* height)

```
1: procedure PPA( $T, A_{Field}$ )
2:    $z_{Star} \leftarrow NULL$ 
3:    $T \leftarrow \text{Sort}(T_{Height}, \text{Descending})$     ▷ sort trees by descending height
4:   for  $i = 2, \dots, T_N$  do
5:      $CrownArea_T[i] \leftarrow CrownArea_T[i] + CrownArea_T[i - 1]$ 
6:     if  $CrownArea_T[i] > A_{Field}$  then
7:        $z_{Star} \leftarrow Height_T[i]$ 
8:       return  $T, z_{Star}$                         ▷ return from function
9:     else
10:      continue
11:    end if
12:  end for
13:  return  $T, z_{Star}$                             ▷ return from function
14: end procedure
```

The software implementation provided is an approximation of the PPA algorithm that simplifies its calculation:

```
215 Trees <- Trees[order(Trees$height, decreasing=TRUE),]  
Trees$canopy_area <- cumsum(Trees$crown_a * Trees$n_trees)  
index <- which.min(abs(Trees$canopy_area - field_area))  
220 zstar <- Trees[index,]
```

Our implementation of the soil respiration model [33] is straightforward, as shown below:

```
respiration_soil <- function(Ta, P) {  
225 if (Ta < -13.3) {  
Rs = 0  
} else {  
if (Ta > 33.5) { Ta = 33.5 }  
e = exp(1)  
230 Q10 = 0.05452 ( C -1)  
F = 1.250  
K = 4.259  
Rs = F * e^(Q10 * Ta) * (P / (K + P))  
}  
235 return(Rs)  
}
```

Meanwhile, our implementation of the soil organic carbon (SOC) profile model [34] is based on a lookup table containing soil classes and corresponding
240 regression model intercepts and slopes. The parameters are extracted and the linear model is applied to calculate SOC along the defined profile interval. By default, the profile interval is set to [1 .. 100].

```
245 soc_depth <- function(order, depth_cm=100) {  
  soc_table = data.frame(  
    order = c("All", "Alfisols", "Andisols",  
              "Aridisols", "Entisols", "Histosols", "Inceptisols",  
              "Mollisols", "Spodosols", "Ultisols", "Vertisols"),  
    intercept = c(1.1795, 1.1122, 1.3837, 0.2065, 0.9300,  
250 1.6227, 1.1631, 1.0163, 1.4262, 1.1576, 0.5145),  
    slope = c(-0.8228, -0.8330, -0.8425, -0.1300,  
              -0.7207, -1.0109, -0.7331, -0.6214, -0.9801, -0.8867,  
              -0.2427)  
  )  
255 rowval = soc_table[soc_table$order==order, ]  
  coeffs = as.numeric(rowval[, c("intercept", "slope")])  
  soc = sapply(seq(1, depth_cm, 1), function(x) {  
    10^(coeffs[1] + coeffs[2] * log10(x))  
  })  
260 return(sum(soc))  
}
```

4. Illustrative Example

For model parameterization, validation, and comparison with the LANDIS-
265 II model at Harvard Forest EMS flux tower in Massachusetts, USA and Jones
Ecological Research Center RD flux tower in Georgia, USA, readers may refer
to our recent model intercomparison paper [30]. An example of running the
PPA-SiBGC program (ppa_v50.r) from the CLI is shown below:

```
270 Rscript --vanilla ppa_v50.r --wd /home/model --verbose
```

Here, the *Rscript* executable is used with the *-vanilla* option to run the
program within a new R session. Additional options include the *-wd* flag to

specify a working or target directory containing parameter files in a pre-defined
275 directory structure and the `-verbose` flag to run the model in verbose mode for
monitoring progress or debugging. The predefined directory structure expected
for model input files containing parameters and drivers (i.e., climate data) is as
follows:

```
lut
├── allometry.csv
├── biomass.csv
├── carbon.csv
├── growth.csv
├── mortality.csv
├── regeneration.csv
├── stoichiometry.csv
├── climate.csv
├── configuration.csv
└── trees.csv
```

Figure 1: Directory structure of PPA-SiBGC inputs

When the simulation run is completed, the following CSV files are produced
280 in an `outputs` directory within the target directory:

```
outputs
├── fluxes.csv
├── loop_times.csv
├── mortality.csv
├── regeneration.csv
├── som.csv
├── trees_[year].csv
└── zstar.csv
```

Figure 2: Directory structure of PPA-SiBGC outputs

These outputs contain the ecosystem biogeochemistry fluxes, time to complete each model iteration, cohort mortality with allometry and biogeochemistry, species regeneration, soil organic matter (SOM) pools, cohort list by simulation year with allometry and biogeochemistry, and the theoretical z^* height by year.

285 **5. Anticipated Impact**

We anticipate that the PPA-SiBGC model will showcase the importance of realistically approximating vegetation dynamics in order to develop forest biogeochemistry models with improved generality and precision. This is because the inclusion of even simple allometric and stoichiometric biogeochemistry re-
290 lations with the PPA model showed accurate estimation of ecosystem fluxes [30]. The robustness of allometric scaling theory, rooted in the self-similarity of tree species and shaped by physical constraints, is well supported in theoretical research using highly detailed models [38]. Thus, species-specific allometric models remain a useful modeling abstraction in global-scale modeling.

295 We believe that our work also demonstrates the the classical modeling trade-off of Levins (1966) between generality, precision, and realism is unduly imposed; in our work, model generality and precision were possible only through enhanced model realism. Thus, no trade-off was apparent in our case. We therefore reiterate his suggestion that modelers focus on improving realism over generality
300 and precision, which may result in improvements of all three criteria.

From a practical standpoint, we hope that our work will help to advance the field by making forest biogeochemistry models more approachable, cross-platform, and easier to use. All input and output files use a CSV file structure in order to facilitate simplified key-value parsing of all data in user-developed
305 programs. This is in contrast to models such as LANDIS-II that use unstructured TXT files that are laborious and inefficient to parse. In future work, we will soon release model wrapper libraries in R and Python for simplifying the operation, parameterization, optimization, and validation of forest ecosystem models.

310 **6. Conclusions**

In conclusion, we provide a new forest biogeochemistry model, PPA-SiBGC, based on the Perfect Plasticity Approximation (PPA) algorithm in the R language of statistical computing. The program is cross-platform and is designed

to be simple to deploy and apply. The program is designed to run from a
315 command-line interface, while all model inputs and outputs are in CSV for-
mat to facilitate simplified data pre- and post-processing. The structure of the
program is simple and effective, using vectorization where possible to speed op-
erations without the programmer and computational overhead of multi-thread
or multi-core parallelization. Our model uses only base R libraries, facilitating
320 ease of deployment across a variety of systems. We demonstrate that effective
forest biogeochemistry models need not be comprised of hundreds of thousands
of lines of code in difficult-to-use compiled languages. In future work, we will
release forest biogeochemistry model wrapper libraries in R and Python to ease
the operation and extend the use of this and other forest biogeochemistry mod-
325 els. All model code is made available at our GitHub repository under an Apache
2.0 license:

```
https://github.com/adam-erickson/ecosystem-model-comparison/blob/  
master/models/ppa\_bgc/hf\_ems/ppa\_v50.r
```

Acknowledgements

330 Funding: This work was supported by the U.S. Army Corps of Engineers
[contract number W912HQ-18-C-0007].

References

- [1] A. J. Lotka, Analytical Note on Certain Rhythmic Relations in Organic
Systems, Proceedings of the National Academy of Sciences of the United
335 States of America 6 (7) (1920) 410–415. doi:[https://doi.org/10.1073/
pnas.6.7.410](https://doi.org/10.1073/pnas.6.7.410).
URL <http://www.pnas.org/content/6/7/410>
- [2] T. R. Malthus, An essay on the principle of population, as it affects the
future improvement of society. With remarks on the speculations of Mr.

- 340 Godwin, M. Condorcet, and other writers., J. Johnson, London, 1798.
URL <https://archive.org/details/essayonprincip100malt>
- [3] V. Volterra, *Variazioni e fluttuazioni del numero d'individui in specie animali conviventi*, 2nd Edition, Memoria della Reale Accademia Nazionale dei Lincei, Citta di Castello, 1926.
- 345 [4] R. E. Buckman, Technical Bulletin 1272: Growth and yield of red pine in Minnesota, Tech. rep., US Department of Agriculture, Forest Service (1962).
- [5] J. L. Clutter, Compatible Growth and Yield Models for Loblolly Pine, *Forest Science* 9 (3) (1963) 354–371. doi:10.1093/forestscience/9.3.354.
350 354.
URL <http://dx.doi.org/10.1093/forestscience/9.3.354>
- [6] J. W. Moser, O. F. Hall, Deriving Growth and Yield Functions for Uneven-Aged Forest Stands, *Forest Science* 15 (2) (1969) 183–188. doi:10.1093/forestscience/15.2.183.
355 183.
URL <http://dx.doi.org/10.1093/forestscience/15.2.183>
- [7] J. K. Vanclay, *Modelling forest growth and yield: applications to mixed tropical forests*, CABI Publishing Series, CAB International, Wallingford, UK, 1994.
URL <https://books.google.com/books?id=JnhFAQAAIAAJ>
- 360 [8] D. B. Botkin, J. F. Janak, J. R. Wallis, Some ecological consequences of a computer model of forest growth, *Journal of Ecology* 60 (3) (1972) 849–872.
- [9] H. H. Shugart, *A Theory of Forest Dynamics: The Ecological Implications of Forest Succession Models*, Springer-Verlag, New York, 1984.
- 365 [10] G. C. Hurtt, P. R. Moorcroft, S. W. P. And, S. A. Levin, Terrestrial models and global change: challenges for the future, *Global Change Biology* 4 (5) (1998) 581–590. doi:10.1046/j.1365-2486.1998.t01-1-00203.x.

URL <https://onlinelibrary.wiley.com/doi/abs/10.1046/j.1365-2486.1998.t01-1-00203.x>

- [11] R. A. Fisher, C. D. Koven, W. R. L. Anderegg, B. O. Christoffersen, M. C. Dietze, C. E. Farrior, J. A. Holm, G. C. Hurtt, R. G. Knox, P. J. Lawrence, J. W. Lichstein, M. Longo, A. M. Matheny, D. Medvigy, H. C. Muller-Landau, T. L. Powell, S. P. Serbin, H. Sato, J. K. Shuman, B. Smith, A. T. Trugman, T. Viskari, H. Verbeeck, E. Weng, C. Xu, X. Xu, T. Zhang, P. R. Moorcroft, Vegetation demographics in Earth System Models: A review of progress and priorities, *Global Change Biology* 24 (1) (2018) 35–54. doi:10.1111/gcb.13910.

URL <https://onlinelibrary.wiley.com/doi/abs/10.1111/gcb.13910>

- [12] H. Bugmann, A review of forest gap models, *Climatic Change* 51 (2001) 259–305.

- [13] S. Manabe, Climate and the Ocean Circulation, *Monthly Weather Review* 97 (11) (1969) 739–774. doi:10.1175/1520-0493(1969)097<0739:CATOC>2.3.CO;2.

URL [https://doi.org/10.1175/1520-0493\(1969\)097%7B%7D3C0739:CATOC%7D3E2.3.COhttp://0.0.0.2](https://doi.org/10.1175/1520-0493(1969)097%7B%7D3C0739:CATOC%7D3E2.3.COhttp://0.0.0.2)

- [14] R. C. Rothermal, A Mathematical Model for Predicting Fire Spread in Wildland Fuels, Tech. rep., US Forest Service (1972).

- [15] R. E. Dickinson, A. Henderson-Sellers, P. J. Kennedy, M. F. Wilson, NCAR Technical Note NCAR/TN-275-+STR: Biosphere-atmosphere Transfer Scheme (BATS) for the NCAR Community Climate Model, Tech. rep., National Center for Atmospheric Research, Boulder, CO, USA (1986). doi:10.5065/D6668B58.

- [16] P. J. Sellers, Y. Mintz, Y. C. Sud, A. Dalcher, A Simple Biosphere Model (SIB) for Use within General Circulation Models, *Journal of the Atmospheric Sciences* 43 (6) (1986) 505–531.

395 doi:10.1175/1520-0469(1986)043<0505:ASBMFU>2.0.CO;2.

URL [http://dx.doi.org/10.1175/1520-0469\(1986\)043%7B%7D3C0505:ASBMFU%7D3E2.0.CO2](http://dx.doi.org/10.1175/1520-0469(1986)043%7B%7D3C0505:ASBMFU%7D3E2.0.CO2)

[17] A. Mäkelä, J. Landsberg, A. R. Ek, T. E. Burk, M. Ter-Mikaelian, G. I. Ågren, C. D. Oliver, P. Puttonen, Process-based models for forest ecosystem management: current state of the art and challenges for practical implementation, *Tree Physiology* 20 (5-6) (2000) 289–298.
400 doi:10.1093/treephys/20.5-6.289.

URL <http://treephys.oxfordjournals.org/content/20/5-6/289.abstract>

[18] H. Kimmins, J. A. Blanco, B. Seely, C. Welham, K. Scoullar, *Forecasting Forest Futures: A Hybrid Modelling Approach to the Assessment of Sustainability of Forest Ecosystems and Their Values*, Taylor & Francis Group, 2010.

410 URL <https://www.crcpress.com/Forecasting-Forest-Futures-A-Hybrid-Modelling-Approach-to-Kimmins-Blanco-Seely-Welham-Scoullar/p/book/9781844079223>

[19] P. R. Moorcroft, G. C. Hurtt, S. W. Pacala, A method for scaling vegetation dynamics: The ecosystem demography model (ED), *Ecological Monographs* 71 (4) (2001) 557–586. doi:10.1890/0012-9615(2001)071[0557:AMFSVD]2.0.CO;2.

415 URL [http://dx.doi.org/10.1890/0012-9615\(2001\)071\[0557:AMFSVD\]2.0.CO;2](http://dx.doi.org/10.1890/0012-9615(2001)071[0557:AMFSVD]2.0.CO;2)

[20] D. Medvigy, S. C. Wofsy, J. W. Munger, D. Y. Hollinger, P. R. Moorcroft, Mechanistic scaling of ecosystem function and dynamics in space and time: Ecosystem Demography model version 2, *Journal of Geophysical Research: Biogeosciences* 114 (G1). doi:10.1029/2008JG000812.

420 URL <http://dx.doi.org/10.1029/2008JG000812>

[21] E. S. Weng, S. Malyshev, J. W. Lichstein, C. E. Farrior, R. Dybzinski, T. Zhang, E. Shevliakova, S. W. Pacala, Scaling from individual trees to

- forests in an Earth system modeling framework using a mathematically
tractable model of height-structured competition, *Biogeosciences* 12 (9)
425 (2015) 2655–2694. doi:10.5194/bg-12-2655-2015.
URL <https://www.biogeosciences.net/12/2655/2015/>
- [22] R. Levins, *The Strategy of Model Building in Population Biology*, *American Scientist* 54 (4) (1966) 421–431.
- 430 [23] R. MacArthur, R. Levins, Competition, habitat selection, and character displacement in a patchy environment, *Proceedings of the National Academy of Sciences* 51 (6) (1964) 1207–1210. doi:10.1073/pnas.51.6.1207.
URL <http://www.pnas.org/content/51/6/1207>
- 435 [24] H. Kimmins, J. A. Blanco, B. Seely, C. Welham, K. Scoullar, J. P. (Hamish) Kimmins, J. A. Blanco, B. Seely, C. Welham, K. Scoullar, Complexity in modelling forest ecosystems: How much is enough?, *Forest Ecology and Management* 256 (10) (2008) 1646–1658. doi:<https://doi.org/10.1016/j.foreco.2008.03.011>.
440 URL <http://www.sciencedirect.com/science/article/pii/S0378112708002478><http://linkinghub.elsevier.com/retrieve/pii/S0378112708002478>
- [25] W. Jin, H. S. He, F. R. T. III, Are more complex physiological models of forest ecosystems better choices for plot and regional
445 predictions?, *Environmental Modelling & Software* 75 (2016) 1–14. doi:<https://doi.org/10.1016/j.envsoft.2015.10.004>.
URL <http://www.sciencedirect.com/science/article/pii/S1364815215300621>
- [26] M. Heimann, G. Esser, A. Haxeltine, J. Kaduk, D. W. Kicklighter,
450 W. Knorr, G. H. Kohlmaier, A. D. McGuire, J. Melillo, B. Moore, R. D. Otto, I. C. Prentice, W. Sauf, A. Schloss, S. Sitch, U. Wittenberg,

- G. Würth, Evaluation of terrestrial carbon cycle models through simulations of the seasonal cycle of atmospheric CO₂: First results of a model intercomparison study, *Global Biogeochemical Cycles* 12 (1) (1998) 1–24.
455 doi:10.1029/97GB01936.
URL <https://agupubs.onlinelibrary.wiley.com/doi/abs/10.1029/97GB01936>
- [27] E. Tzeng, C. Devin, J. Hoffman, C. Finn, P. Abbeel, S. Levine, K. Saenko, T. Darrell, Adapting Deep Visuomotor Representations with Weak Pair-
460 wise Constraints, ArXiv e-prints arXiv:1511.07111.
- [28] N. Strigul, D. Pristinski, D. Purves, J. Dushoff, S. Pacala, Scaling from trees to forests: tractable macroscopic equations for forest dynamics, *Ecological Monographs* 78 (4) (2008) 523–545. doi:10.1890/08-0082.1.
URL <http://dx.doi.org/10.1890/08-0082.1>
- 465 [29] N. Strigul, Individual-Based Models and Scaling Methods for Ecological Forestry: Implications of Tree Phenotypic Plasticity, in: J. M. Garcia, J. J. D. Casero (Eds.), *Sustainable Forest Management*, IntechOpen, Rijeka, 2012, Ch. 20, pp. 359–384. doi:10.5772/29590.
URL <https://doi.org/10.5772/29590>
- 470 [30] A. Erickson, N. Strigul, A forest biogeochemistry model intercomparison on the East Coast of the United States, bioRxiv doi:10.1101/464578.
URL <https://www.biorxiv.org/content/early/2018/11/07/464578>
- [31] S. W. Pacala, C. D. Canham, J. Saponara, J. A. Silander, R. K. Kobe, E. Ribbens, Forest models defined by field measurements: estimation, error
475 analysis and dynamics, *Ecological Monographs* 66 (1) (1996) 1–43. doi:10.2307/2963479.
URL <http://dx.doi.org/10.2307/2963479>
- [32] J. W. Raich, C. S. Potter, Global patterns of carbon dioxide emissions from soils, *Global Biogeochemical Cycles* 9 (1) (1995) 23–36. doi:10.

- 480 1029/94GB02723.
URL <https://agupubs.onlinelibrary.wiley.com/doi/abs/10.1029/94GB02723>
- [33] J. W. Raich, C. S. Potter, D. Bhagawati, Interannual variability in global soil respiration, 198094, *Global Change Biology* 8 (8) (2002) 800–
485 812. arXiv:<https://onlinelibrary.wiley.com/doi/pdf/10.1046/j.1365-2486.2002.00511.x>, doi:10.1046/j.1365-2486.2002.00511.x.
URL <https://onlinelibrary.wiley.com/doi/abs/10.1046/j.1365-2486.2002.00511.x>
- [34] G. M. Domke, C. H. Perry, B. F. Walters, L. E. Nave, C. W. Woodall,
490 C. W. Swanston, Toward inventory-based estimates of soil organic carbon in forests of the united states, *Ecological Applications* 27 (4) (2017) 1223–1235. arXiv:<https://esajournals.onlinelibrary.wiley.com/doi/pdf/10.1002/eap.1516>, doi:10.1002/eap.1516.
URL <https://esajournals.onlinelibrary.wiley.com/doi/abs/10.1002/eap.1516>
495 1002/eap.1516
- [35] C. D. Canham, K. D. Coates, P. Bartemucci, S. Quaglia, Measurement and modeling of spatially explicit variation in light transmission through interior cedar-hemlock forests of British Columbia, *Canadian Journal of Forest Research* 29 (11) (1999) 1775–1783. doi:10.1139/x99-151.
500 URL <http://www.nrcresearchpress.com/doi/abs/10.1139/x99-151>
- [36] B. S. Case, H. L. Buckley, A. A. Barker-Plotkin, D. A. Orwig, A. M. Ellison, When a foundation crumbles: forecasting forest dynamics following the decline of the foundation species *Tsuga canadensis*, *Ecosphere* 8 (7) (2017) e01893. doi:10.1002/ecs2.1893.
505 URL <https://esajournals.onlinelibrary.wiley.com/doi/abs/10.1002/ecs2.1893>
- [37] D. C. Chojnacky, L. S. Heath, J. C. Jenkins, Updated generalized biomass equations for North American tree species, *Forestry: An International Jour-*

- nal of Forest Research 87 (1) (2014) 129–151. doi:10.1093/forestry/
510 cpt053.
URL <http://dx.doi.org/10.1093/forestry/cpt053>
- [38] C. Eloy, M. Fournier, A. Lacointe, B. Moulia, Wind loads and competition
for light sculpt trees into self-similar structures, Nature Communications
8 (1) (2017) 1014. doi:10.1038/s41467-017-00995-6.
515 URL <https://doi.org/10.1038/s41467-017-00995-6>