
Phenological process models based on carbon productivity at the leaf and branch levels, and their effects on Aspen tree architecture

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ECOPHYS is a complex computer model that simulates the growth of hybrid poplar and aspen trees. Its primary purposes are to identify major physiologically-based factors that influence tree growth and to predict how interactions among them and with the external environment will affect growth (Isebrands et al., 2000). ECOPHYS' capabilities and submodels of various tree ecosystem processes continue to evolve. Currently ECOPHYS simulates aspen growth in the Free-Air CO₂ and O₃ Enrichment (Aspen FACE) experiment in Rhinelander, WI, <http://www.aspenface.mtu.edu>. The main objective of the Aspen FACE experiment is to examine, for predictive purposes, the effects of elevated CO₂ and O₃ on ecological interactions of northern hardwood forests (Dickson et al., 2000).

In this paper we describe ECOPHYS phenological process models for bud break, leaf drop, branch abscission, bud set, and bud survival and vigor. These models are of the same type and include randomness and fading memory components. The leaf-drop algorithm described in Martin et al. (2001) is a predecessor of these models, though it does not include fading memory. Each of these models is based on local photosynthate productivity within the tree at the leaf or branch level, as well as genetic factors and field data (Ceulemans et al., 1996, Isebrands et al., 2001, Karnosky et al., 1999, Lenz et al., 2003, Noormets et al., 2001, Pieters et al., 1999). Within ECOPHYS, leaf-level photosynthate productivity is based on leaf area and photosynthetic rate. Photosynthetic rate is determined by a number of factors including levels of O₃ and CO₂, light, temperature, and RH, as well as N and H₂O availability and leaf age. Our phenological process models are responsive to these variables via photosynthate productivity.

In developing these models we have applied phenological and growth data from the Aspen FACE site received from Jud Isebrands and Evan McDonald through personal communications in 2002. The phenological data, organized according to aspen clone and treatment, include bud break, bud set, and end-of-season leaf senescence start dates and rates for 1999 and 2000. The growth data includes stem height and stem diameter measurements for 1998 and 2000, and leaf area measurements for 2000. Stem height and stem diameter modified averages for 1999 were obtained from Isebrands et al., (2001).

We have used as input Aspen FACE environmental data obtained from Warren Heilman and Jaak Sober for the years 1998, 1999, and 2000. These were obtained via personal communications and from <http://www.aspenface.mtu.edu>.

The bud-set algorithm described below assumes that branch productivity can predict bud set adequately for tree and patch level simulation of growth and competition. It applies to all branches except for short shoots which set bud right away. At the start of the growing season, stored carbohydrates are distributed to buds according to their bud-strength, which is based on the previous year's growth. If a bud's strength falls below a user-determined threshold, the bud grows into a short shoot which sets bud immediately. For all other green wood, our bud-set algorithm initiates branch by branch bud set based on ECOPHYS' simulated branch-level productivity. This results in bud-set dates that vary from branch to branch, producing determinate and indeterminate branches.

Within ECOPHYS there is branch-level positive feedback between growth and productivity. Branch growth is based on the branch's productivity, and longer branches with larger leaf area are more productive. The longer and stronger branches are among those that set bud relatively late and so have a longer season in which to grow in length and leaf area. They are winners in the competition among branches for light and other resources.

Our model allows for a low-productivity branch to set bud late due to randomness and/or a change in competition such as a branch dying that previously shaded it. We include randomness to take account of unmodelled factors that may prevent bud set.

Our model assumes that branches that set bud early do so because they are not productive enough to keep growing new leaves and internodes while meeting their maintenance needs. Except for the spring distribution of over-winter storage, ECOPHYS' green branches rely only on the productivity of their own leaves to survive and grow. The amounts of photosynthate available to the young internodes determine how rapidly they grow in length. The amounts available to young leaves determine how much they grow in area. Thus in ECOPHYS the abundance of photosynthate within the branch determines its growth. The consequences of too little photosynthate in the branch over time are setting bud early, possibly followed by branch death.

Branch-level Bud-set algorithm

Let d denote a day during the growing season that is at least 15 days after spring bud break. For each simulated green-wood branch that has not yet set bud, consider the amount of photosynthate produced by that branch on day d . Let $PB(d)$ denote the quantity of photosynthate remaining in branch B on day d after all transport of photosynthate, and growth and maintenance processes have occurred throughout the tree. The following bud-set algorithm is based on a rolling weighted average of $PB(d)$ taken over the current and previous 14 days. When this rolling weighted average falls below a specified threshold value, then bud set may occur, depending on the value of a random number as described below.

The fading memory weights used are based on the assumption that productivity of the branch on any given day in the past becomes less and less important in determining bud-set as time goes on. Furthermore, productivity occurring 15 days or more before in the past has no direct influence at all on whether or not bud set occurs on the current day.

We model this using a fading-memory function of the form $w(t) = Ae^{\alpha t}$, where A and α are positive constants. The value of α is chosen to achieve the desired rate of fading. The equation

$A \sum_{t=-14}^0 e^{\alpha t} = 1$ is solved to determine the value of A . A typical pair of parameter values is $\alpha = 0.2$ and $A = 0.191$.

Let d denote a day during the growing season at least 15 days after bud break. The weighted average net branch photosynthate over the current and previous 14 days is given by

$$PaB(d) = A[PB(d) + e^{-\alpha}PB(d-1) + e^{-2\alpha}PB(d-2) + \dots + e^{-14\alpha}PB(d-14)].$$

Denote the threshold value for $PaB(d)$, below which the branch may set bud, by τ . If $(PaB(d) - \tau) \geq 0$ then the branch will not set bud on day d . Define $K = (PaB(d) - \tau) \cdot \delta$. Here δ is a scaling factor affecting the likelihood that a weak branch, that is a branch B such that $(PaB(d) - \tau) < 0$, will set bud. Nominal parameter values are $\delta = 5$ and $\tau = 0.1$. If the value of δ is increased, the likelihood of bud set is increased. A positive value of τ indicates that a branch may set bud even though it maintains a positive $PaB(d)$.

Let ξ denote a uniform random number between 0 and 1. Whether or not branch B sets bud on day d is determined by the following logic:

If $K \geq 0$ the branch does not set bud. If $K < 0$ and $\xi > 1 - e^K$ the branch does not set bud. However, if $K < 0$ and $\xi \leq 1 - e^K$ then the branch sets bud. The inclusion of ξ simulates uncertainty and variability due to unmodelled dynamics. The probability that a branch sets bud when $PaB(d) < \tau$ is $1 - e^K$.

There are some branches for which the $K < 0$ condition necessary for bud set does not occur prior to a final bud-set date. These are indeterminate branches. They continue to grow in length and width until a user-specified final bud-set date.

Architectural influences

Phenological process models of bud break, leaf drop, branch abscission, bud set, and bud survival and vigor greatly influence the architecture of an ECOPHYS -simulated tree over multiple years of growth. These models are also designed to simulate competition among trees growing in a patch. Our models respond to competition for resources among leaves and branches via the branch or leaf photosynthate productivity response to this competition. The leaves and branches may be on the same tree or distributed among trees within a patch. Within ECOPHYS, leaf and branch productivity is

computed on a daily basis over multiple growing seasons. Our phenological process models also operate on a daily time scale. This results in dynamic feedback among productivity and phenological processes. This feedback results in interdependencies among process and productivity responses. These daily interactions result in seasonal and multi-year growth and competition patterns that can not fully be explained by considering the processes one at a time.

However, it is still worth considering the architectural influences of varying one process model while keeping the other process models the same. Figure 1 shows a sample screen shot of an ECOPHYS simulation of an aspen tree in the third year of growth. One can observe from this picture that branch abscission of older wood as well as green wood has occurred. The tree appears to have normal architecture but if the branch abscission routine is turned off, the tree grows into a thick broom during the next year of growth. However, if branch abscission is made overly aggressive, the simulation will produce a thin 16 year-old tree with hardly any branches, even in the absence of competition from other trees.

The survival and vigor of buds determine how many and where new branches sprout and how much over-winter stored carbon each emergent branch receives. In our model, bud survival and vigor is determined by the previous year's post bud-set productivity of the leaf from which the bud grew. A vigorous bud, one that appears where there was a highly productive leaf, receives a large amount of over-winter storage relative to other buds. When such a bud breaks, the emerging branch initially grows longer and stronger than do emergent branches from buds with less carbohydrate because early growth is determined by this stored carbohydrate. When branches rely on their own productivity, a branch from a strong bud may build on its strong growth start. A branch from a weaker bud often falls further behind as it is shaded by more vigorous branches.

Dynamic branch by branch bud set affects tree architecture as follows. Each green-wood branch continues to grow in length until it reaches bud set. After bud set the branch only grows in diameter. Our bud-set algorithm simulates branches achieving bud set at varying times during the growing season. Branches that maintain adequate productivity do not set bud until the final bud-set date. A branch with highly productive leaves grows longer faster and produces larger leaves than do other branches, taking more of limited resources and consequently contributing to the slower growth of other branches, and possibly their early bud-set and even abscission. Dynamic bud-set also influence architecture over multiple years in that the green wood that it influences becomes brown wood later on. The brown-wood branches then influence the location of resulting green-wood branches.



Figure 1. Third-year ECOPHYS tree

References

- Ceulemans, R., B.Y. Shao, X.N. Jiang, and J. Kalina. (1996). First- and Second-year aboveground growth and productivity of two *Populus* hybrids grown at ambient and elevated CO₂. *Tree Physiology* **16**:61-68.
- Dickson, R.E., K.F. Lewin, J.G. Isebrands, M.D. Coleman, W.E. Heilman, D.E. Riemenschneider, J. Sober, G.E. Host, D.R. Zak, G.R. Hendrey, K.S. Pregitzer, and D.F. Karnosky. (2000). *Forest Atmosphere Carbon Transfer and Storage (FACTS-II) The Aspen Free-air CO₂ and O₃ Enrichment (FACE) Project: An Overview*.
- Isebrands, J. G., G. E. Host, K.E. Lenz, G. Wu, H. W. Stech. 2000. Hierarchical, parallel computing strategies using Component Object Model for process modelling responses of forest plantations to interacting multiple stresses. In: (R.J.M. Ceulemans, F. Veroustraete, V. Gond, and J.B.H.F. Van Rensbergen eds.) *Forest Ecosystem Modeling, Upscaling, and Remote Sensing*, SPB Academic Publishing, The Hague, The Netherlands. pp 123-135.
- Isebrands, J.G., E.P. McDonald, E. Kruger, G. Hendrey, K. Percy, K. Pregitzer, J. Sober and D.F. Karnosky. (2001). Growth responses of *Populus tremuloides* clones to interacting elevated carbon dioxide and tropospheric ozone. *Environmental Pollution*. Vol. 115 No. 3, pp. 359-371.
- Karnosky, D.F., B. Mankovska, K. Percy, R.E. Dickson, G.K. Podila, J. Sober, A. Noormets, G. Hendrey, M.D. Coleman, M. Kubiske, K.S. Pregitzer, and J.G. Isebrands, (1999). Effects of tropospheric O₃ on trembling aspen and interaction with CO₂: Results from an O₃-Gradient and a FACE experiment. *Water, Air, and Soil Pollution* **116**: 311-312.
- Lenz, K., K. Roskoski, H. Stech, and G. Host. (2003) Analysis of Aspen FACE Phenological, Morphometric and Growth Data for 1998 – 2000. Univ. of Minnesota Duluth, Math. and Stat. Dept. Tech Report #2003-10.
- Martin, M.J., G.E. Host, K.E. Lenz, J.G. Isebrands. (2001). Simulating the growth response of aspen to elevated ozone: a mechanistic approach to scaling a leaf-level model of ozone effects on photosynthesis to a complex canopy architecture. *Environmental Pollution*. **115**:425-436.
- Noormets, A., E.P., McDonald, R.E. Dickson, E.L. Kruger, A. Sober, J.G. Isebrands, D.F. Karnosky, 2001. The effect of elevated carbon dioxide and ozone on leaf- and branch-level photosynthesis and potential plant-level carbon gain in aspen. *Trees* **15**:262-270.
- Pieters, G.A., M.E. Van Den Noort, and J.A. Van Nijkerken, 1999. Growth adaptation of leaves and internodes of poplar to irradiance, day length and temperature. *Tree Physiology* **19**, 933-942.