MODELING IMPACTS OF CO_2, OZONE, AND CLIMATE CHANGE ON TREE GROWTH

George E. Host[1], Gary W. Theseira[1], and J. G. Isebrands[2]

INTRODUCTION

Understanding the influence of ozone, CO_2, and changing climatic regimes on basic plant physiological processes is essential for predicting the response of forest ecosystems. To understand the relationships among these interacting factors, in the face of genetic and other environmental variability, requires a means of synthesis. Physiological process modeling provides one such tool: it allows the integration of diverse information from research, reflects the interactions among variables, and provides a direction for future research.

To model trace gas effects on aspen, we have adapted an existing growth process model for poplar known as ECOPHYS. ECOPHYS is a mechanistic whole-tree model that simulates growth of poplar in its establishment year (Host et al. 1990a, Isebrands et al. 1989, Rauscher et al. 1990). ECOPHYS uses the individual leaf as the primary biological unit of the model. Hourly solar radiation, temperature, and clonal (genetic) factors acting at the leaf level provide the major driving variables for plant growth. Canopy architecture is modeled by means of a three-dimensional geometric approach. By knowing leaf orientation patterns and tracking solar position over the course of the day, we calculate precise estimates of intercepted radiation, which in turn are supplied to a photosynthate production submodel. Photosynthates are distributed to various growth centers in the plant by means of a radiotracer-based model of carbon allocation (Dickson 1986). The amount of photosynthate arriving at a growth center, after respiratory losses are determined, is used to calculate biomass production and dimensional growth. The model has been subjected to extensive validations both in terms of photosynthesis (Host et al. 1990) and in regional predictions of biomass production (Host and Isebrands 1994).

Our current research has three major facets: the development of three-dimensional soil and root models to complement the existing above-ground portion of the model, the integration of existing trace gas response data into the model framework, and the scaling of the existing model in time and space; specifically to simulate the growth of an interacting population of trees for a number of years. These objectives will allow us to simulate impacts related to global change, and to provide input to models operating at larger temporal and spatial scales.

MODELING STRATEGIES AND APPLICATIONS

Soil Water and Nutrient Modeling

A three-dimensional soil water transport model was developed to provide a heterogeneous soil environment for root development. We currently simulate water movement in a 100 x 100 x 200 cm soil volume using variable-size cells (1-5 cm on a side). The use of different cell sizes allows the user to run the model under different levels of resolution. The soil model runs on an hourly times step and accounts for surface evaporation, capillary rise from a water table, water distribution from irrigation lines, and water uptake into a plant root system (Figure 1). The use of a three-dimensional model, vs. the traditional two-dimensional approach, allows us to simulate variability in moisture and nutrients in horizontal as well as vertical directions. The ability to simulate soil heterogeneity in the horizontal dimension is important not only for simulating differential growth of the canopy as a result of

[1]Research Associate and Postdoctoral Research Associate, respectively, Natural Resources Research Institute, University of Minnesota, Duluth, MN 55811.

[2]Project Leader and Research Plant Physiologist, USDA Forest Service, North Central Forest Experiment Station, Rhinelander, WI 54501.

vascularization between branches and root segments, but also for simulating competition for resources among plants. This latter aspect is important as we scale from the individual tree to the patch, as described below.

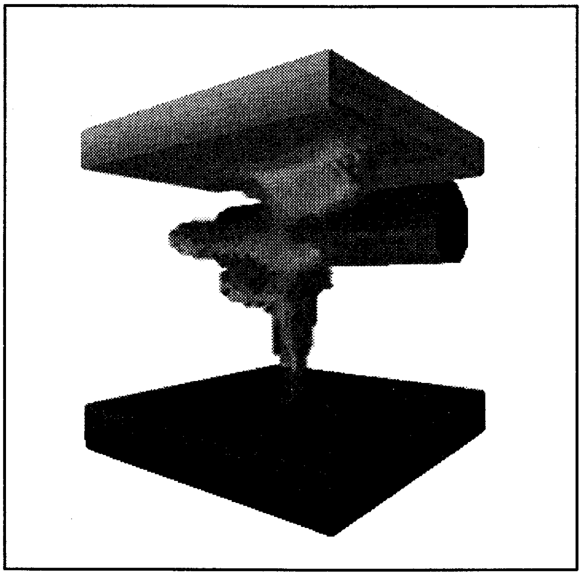

Figure 1. Visualization of a sample soil slab containing a plant root and a sub-surface irrigation line, derived from volumetric soil water content (wetter soil cells are rendered darker and drier cells lighter, while soil cells with moisture contents between 23 percent and 32 percent have been rendered transparent) following six hours of simulated soil water redistribution. The root system consists of a tap root and six lateral roots, four of which are visible as drier soil cells (lighter shade) extending left and right of the tap root. The irrigation line has wetted a cylindrical volume of soil cells (darker) located behind the tap root. The soil surface (top) has been dried by evaporation while the base of the soil slab (bottom) is being wetted by capillary rise from a water table.

Root Growth Modeling

The ECOPHYS root growth model maintains roots of various orders in three-dimensional space. Root architecture is based on a highly relaxed fractal algorithm utilizing a monopodial branching pattern and is coded using a free tree structure (Figure 2). Overall root growth is governed by hourly translocation from the shoot. Branch roots may be formed at any radial position about the main axis of a parent root for which there is a corresponding vascular bundle. Initiation angles of branch roots with respect to parent roots vary randomly along a probability distribution as do changes in direction of growth of any root apex. The growth rate of root apices and the frequency of branch initiation are regulated by soil strength. Root geotropic response in poplar is strongly correlated to root order and is taken into account in the simulation. To simulate fine root turnover, a proportion of terminal higher order roots are 'killed' and replaced by new growth at each time step.

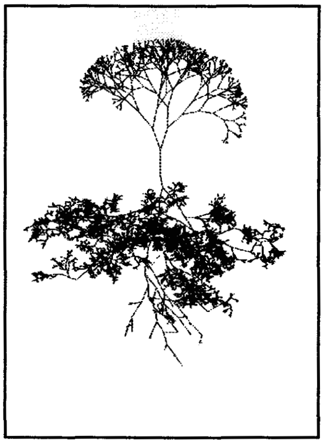

Figure 2. Two-dimensional rendering of a three-dimensional mathematical root model after 72 time steps, given a constant photosynthate input.

Trace Gas Modeling

Working with aspen and hybrid poplars, we have developed a mechanistic individual tree process model of the plant growth response to altered CO_2 and ozone concentrations. This modeling work has been done in close cooperation with field and growth chamber experiments. Specifically, we developed a mechanistic model for the A/Ci response by incorporating our existing light response model with the CO_2 model proposed by Weber et al. (1985), adding parameters for carboxylation efficiency and CO_2 saturation rates. A mechanistic understanding of stomatal conductance does not exist; we follow the assumption of Ball et al. (1982) that plants maintain a relative constant ratio of internal to ambient CO_2 levels.

Submodels have been developed to simulate the effects of ozone on leaf longevity, and effective leaf area; direct effects of ozone on photosynthesis have proven more problematic, as the interactions between ozone and CO_2 are nonlinear (Coleman et al. In review).

Scaling

Scaling ECOPHYS into a second season of growth requires the ability to simulate branch growth and development. Our strategy for growing branches is based on the concept of branch autonomy, which states that branches essentially operate like first year shoots: they translocate carbon to their own internodes, and those of the lower stem and roots, but do not translocate upwards to other leaves or branches (Isebrands 1983). In addition, leaves on branches maintain the same genetically-determined photosynthetic characteristics. Patterns of internode expansion and growth are the same as in the first year shoot. As a result, our original ECOPHYS model, which simulates the growth of a first year shoot, coupled with a branch architecture algorithm, can be used to simulate the growth of a branched poplar tree.

To scale to branches requires that ECOPHYS be translated into an object-oriented format. There are several reasons for this translation. To accommodate the exponential increase in the number of leaves and branches that occur in the second and subsequent growing seasons requires that the model run in a language that can access extended computer memory. Second, object-oriented data structures can be organized hierarchically, and relate much more to the natural organization of biological systems, rather than the array-based structure of traditional programming languages. Finally, object-oriented languages are much easier to maintain and debug that procedure-based languages.

When the recoding is complete, the current aboveground ECOPHYS model will become an 'object' within the multi-year model. This 'ECOPHYS object' will have all the components of the original model (a population of leaves and internodes, coupled with photosynthate production and transport rules), plus new information on branch location, angle, and an expanded carbon allocation matrix that describes carbon transport within a branched structure. The object-oriented ECOPHYS will thus be able to grow an individual tree into the second and subsequent growing seasons. This approach will also allow us to simulate interactions within a small population of trees.

To assess the above and below ground interactions among individual trees, we will simulate a block or patch of trees growing under uniform spacing. We envision simulating an interaction block of 16 trees in a 4 x 4 matrix, and planted under a range of typical planting densities (e.g. 2 to 4 m spacings). Trees within the block will shade each other as a function of size, leaf arrangement, branch architecture and solar angle. In addition, they will compete below ground in the three-dimensional soil matrix described previously. To scale to a field plantation level, this patch of trees can be considered a random sample within a particular soil type. To simulate growth within a plantation consisting of several soil types, the model can be run independently for each individual soil type, and area-weighted estimates of growth calculated to characterize the plantation as a whole (Figure 3).

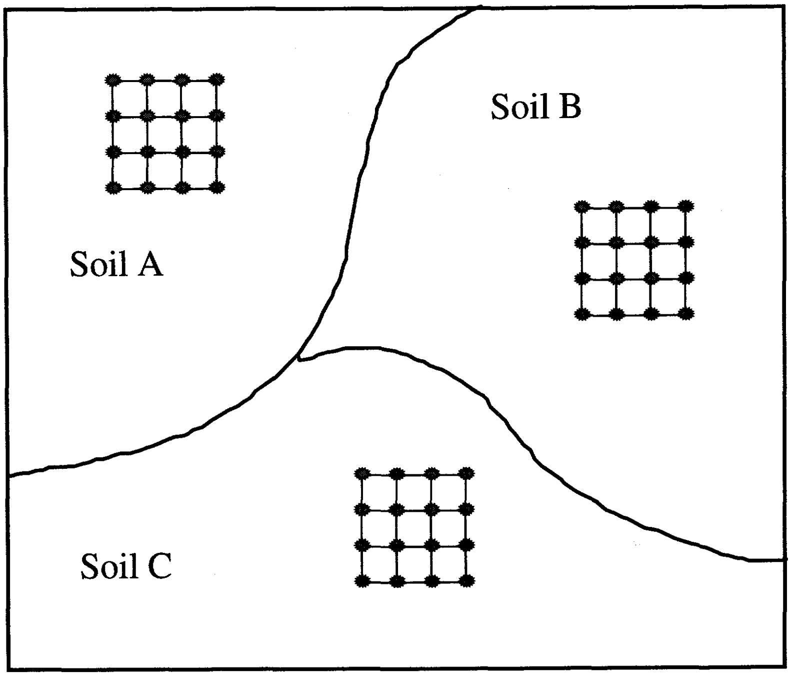

Figure 3. The scaled ECOPHYS patch model as random samples within a field consisting of three soil types.

Model Applications

One of the foremost applications of physiological process models to climate change is the prediction of growth differences, and one of the foremost challenges is the development of realistic detailed climatic change scenarios. One resolution to this challenge is the use of existing, high resolution climatic data. In the Lake States, the growing seasons of 1988 and 1992 were the warmest and coldest years in 100 years of record. We collected hourly solar radiation and temperature data from a weather station in northern Wisconsin, USA, and used these as inputs to ECOPHYS. At this site, air temperatures averaged 2 °C higher and cumulative radiation was 30 percent greater in 1988 compared with 1992. These weather data were used to simulate one growing season's photosynthesis and growth in two *Populus* clones: *P. Eugenei*, a clone characterized by a strongly vertical leaf display and a long growing season, and *P. Tristis*, a planophile clone with an early bud set date. For *P. Eugenei*, photosynthesis was 85 percent greater in 1988 compared with 1992 (Host and Isebrands, In review). Leaf area and total biomass showed increases of 70 percent and 56 percent, respectively, between these years. The patterns were similar for *P. Tristis*, but the differences were less pronounced. These simulations indicate that differences in seasonal weather patterns observed over a few years can account for large but clonally-specific differences in photosynthesis and biomass production in the early growth of *Populus*.

CONCLUSIONS

Modeling at the scale of detailed physiological processes fills an important niche in the hierarchy of spatial scales required to understand global change. We have described the essential components of a modeling effort designed to understand interactions among soil, root, and shoot systems, plant response to trace gases, and the scaling of detailed physiological processes in time and space. In addition, we present an application of the model using 100 yr climatic extremes recorded over the past decade. The development and use of process models not only provides an integration of existing research, it also focuses research questions related to uncertain future conditions.

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