BELOW-GROUND PROCESSES IN GAP MODELS FOR SIMULATING FOREST RESPONSE TO GLOBAL CHANGE

STAN D. WULLSCHLEGER [1], ROBERT B. JACKSON [2], WILLIAM S. CURRIE [3], ANDREW D. FRIEND [4], YIQI LUO [5], FLORENT MOUILLOT [6], YUDE PAN [7] and GUOFAN SHAO [8]

[1] *Environmental Sciences Division, Oak Ridge National Laboratory, Oak Ridge, TN 37831-6422, U.S.A.*
E-mail: wullschlegsd@ornl.gov
[2] *Department of Botany and Nicholas School of the Environment, Phytotron Building, Duke University, Durham, NC 27708, U.S.A.*
[3] *Appalachian Laboratory, Frostburg, MD 21532-2307, U.S.A.*
[4] *Center for Environmental Prediction, Rutgers University, New Brunswick, NJ 08901, U.S.A. at NASA Goddard Institute for Space Studies, New York, NY 10025, U.S.A.*
[5] *Department of Botany and Microbiology, University of Oklahoma, Norman, OK 73019-0245, U.S.A.*
[6] *Dynamique Réactionnelle des Ecosystèmes, Analyse spatiale et Modélisation Unit, CEFE-CNRS, F-34293 Montpellier cedex 5, France and Univ. Corse, Cevaren, 20250 Corte, France*
[7] *USDA Forest Service, Global Change Research, Newtown Square Corporate Campus, Newtown Square, PA 19073, U.S.A.*
[8] *Department of Forestry and Natural Resources, Purdue University, West Lafayette, IN 47907-1159, U.S.A.*

Abstract. Gap models have a rich history of being used to simulate individual tree interactions that impact species diversity and patterns of forest succession. Questions arise, however, as to whether these same models can be used to study the response of forest structure and composition under a changing climate. In contrast to many process-based models, gap models have traditionally been based on rather descriptive representations of species-specific growth processes. Opportunities now exist to expand upon these simple empirical relationships with more mechanistic descriptions of growth, the response of growth to environmental variables, and competition among species for available light, water, and nutrient resources. In this paper, we focus on several areas of below-ground research with the potential to improve the utility of gap models for predicting forest composition in response to a changing climate. Specific areas for model improvement include (1) improved descriptions of the soil environment for seed germination and subsequent seedling establishment, (2) multi-layer representations of soil water and nutrient availability, (3) more accurate information on biomass allocation to roots and root distribution within the soil profile, (4) improved treatment of inter- and intra-specific competition for available soil resources, (5) increased consideration of spatial processes as related to land-surface hydrology, and (6) improved attention to above- and below-ground interactions. This list is meant to stimulate discussion and provide guidance for future field research and model development. As an example of how increased attention to below-ground processes could help address intra-specific competition for water among trees of differing size classes, the gap model LINKAGES was modified to include a sub-model of multi-layered soil hydrology. It was then used to examine the impact of root distribution within soils on the simulated drought response of seedlings, saplings, and mature trees. An annual simulation of soil water content for a deciduous forest in eastern Tennessee showed that seedlings whose roots were restricted to the upper 20-cm of the soil experienced far more 'drought days' than did saplings and larger

trees that otherwise had access to deeper soil water reserves. We recognize that models of forest succession cannot include mechanistic detail on all potential below-ground processes and that there are obvious tradeoffs between model simplicity and more sophisticated parameterizations. We conclude, however, that feedbacks among global environmental change, seed germination and seedling establishment, above- and below-ground carbon allocation, root distribution within the soil profile, and soil water and nutrient dynamics will be critically important for predicting forest dynamics and ecosystem function in the 21st century. As a result, steps should now be taken to ensure that these processes are represented in future gap models.

1. Introduction

Simulation models are now routinely used to assess the response of terrestrial ecosystems to regional and global environmental change (VEMAP members, 1995; King et al., 1997; Neilson and Drapek, 1998; Pan et al., 1998; Potter et al., 1998). These models have historically varied in complexity from simple 'black box' representations of the biosphere (Oeschger et al., 1975) to highly detailed land-surface schemes operating in tandem with equally complicated global circulation models (Sellers et al., 1986; Foley et al., 1998). Experience has shown that the degree of complexity incorporated into such models is driven largely by how the model will be used and, as might be expected, there currently exists considerable diversity in the soil, plant, and atmospheric processes represented within specific models (Jackson et al., 2000).

Among the many categories of models used to simulate the potential response of ecosystems to climate change, individual-based models of forest succession or 'gap' models have both a unique history and application (Bugmann, 2001). The traditional emphasis of gap models in predicting species composition and successional dynamics under current climatic conditions has resulted in fairly simple parameterizations for a range of above- and below-ground processes compared to more detailed biophysical models (Shugart et al., 1992; Shugart and Smith, 1996). Many of these simplistic descriptions remain in current-day gap models, although there has been an increasing debate as to whether more mechanistic detail should be included in forest gap models (Pacala et al., 1993; Bugmann et al., 1996; Hurtt et al., 1998). Central to this debate is whether simple formulations included in many gap models can be used to study the response of forest structure and composition under a changing climate.

Attempts to incorporate stomatal, photosynthetic, and energy exchange dynamics into physiology-based models of forest succession have, for example, been successful (Martin, 1992; Friend et al., 1997). The below-ground components of gap models have not, however, benefited from the same degree of model improvement. Pastor and Post (1986) incorporated decomposition and nutrient cycling into LINKAGES and were among the first to demonstrate that both positive and negative feedbacks could impact patterns of forest succession given interactions

between species composition, litter quality, and above-ground productivity. More recent gap models such as HYBRID (Friend et al., 1997), FIRE-BGC (Keane et al., 1996) and 4C (Bugmann et al., 1997) have begun to include more sophisticated representations of below-ground processes, focusing on mechanistically improved descriptions of water and nutrient uptake, and whole-plant carbon allocation. However, such improvements are incomplete. As a result, there remains a need to consider the role of below-ground processes in gap models, and to evaluate the benefits and tradeoffs of such improved representations to model predictions of forest succession.

The goal of this paper, therefore, is to discuss which below-ground processes should be represented in gap models and to highlight why such processes are important in the context of species diversity, forest succession, and climatic change. Several areas for potential inclusion in gap models are identified (Sections 2 through 8), ranging from improved descriptions of the soil environment for seed germination (Section 2) to more accurate formulations of carbon allocation to roots (Section 5). In each section, consideration is given to how these processes can be represented in 'traditional' and physiology-based models of forest succession (cf. Bugmann, 2001). Incorporating specific empirical and/or mechanistic descriptions of critical below-ground processes in gap models may, in some instances, require information for which data do not exist. Therefore, the availability of data sets for model parameterization and validation are discussed and the role of future experimental studies are considered (Section 9). We conclude (Section 10) that the careful identification and judicious incorporation of below-ground processes into gap models will enhance the predictive capabilities of this category of ecosystem models and therein move us closer to our goal of better understanding how forest productivity and succession will be impacted by future changes in climate.

2. Environment of Regenerating Seedlings

Most conventional gap models introduce new individuals into the tree population as 'saplings' and thus avoid the need to simulate the many fine-scale processes associated with seed and seedling biology (Price et al., 2001; Bugmann, 2001). While this greatly simplifies the simulation of the regeneration process, studies have shown that the thermal environment of the soil surface and the availability of light, water, and nutrients can influence rates of seed germination. Species differences with respect to germination requirements or sensitivity to soil and climatic conditions can influence the successful recruitment of new individuals into a population and potentially alter the course of forest succession (Leishman et al., 1992).

The regeneration process in traditional gap models is driven by temperature, water, and the ability of seedlings to tolerate shade (Coffin and Lauenroth, 1990; Humphries et al., 1996; Mauchamp et al., 1994; Mouillot et al., 2001). In JABOWA (Botkin et al., 1972) and FORET (Shugart and West, 1977), as in other gap mod-

els, air temperature, soil water content, and light at the forest floor must exceed species-specific minima in order to ensure regeneration success (Price et al., 2001). Although threshold-type approaches have proven adequate for many applications, these simple representations of forest regeneration are being replaced in more physiology-based models (see Bugmann, 2001) by explicit consideration of reproductive biology, the germination process, seedling mortality, and the role that both climate and soil conditions play in determining these processes. For example, the gap model SIERRA (Mouillot et al., 2001) describes seed germination not only as a function of daily air temperature, but also considers the sensitivity of the germination process to soil water availability. Specifically, seed germination for a given species begins when air temperature exceeds a minimum threshold and when the water potential of the surface soil is above a fixed limiting threshold for at least five consecutive days. Although simple in concept, incorporating such a description of seed germination into traditional gap models requires that monthly simulations be replaced by daily time-step capabilities, that soils of a fixed depth (e.g., 1 m) be more finely divided into multiple soil depths including a shallow surface layer where seed germination and initial establishment take place, and that the water content of this uppermost soil layer be modeled as a dynamic function of prevailing climate and root distribution within the various layers (see Section 3; Multi-layer Soil Models and Water Availability). As demonstrated by the SIERRA model, the utility of such an approach is that seed germination becomes sensitive to intra-annual variation in temperature and precipitation, soil physical properties (e.g., sand, silt, clay) and their vertical distribution. Therefore, such a gap model is capable of representing interactions between climate and key below-ground plant and soil processes that have direct relevance to seedling establishment, forest regeneration, and global environmental change.

Even after seed germination, the upper soil layer continues to be the primary source of water for the developing seedling. The soil water content of this layer can, like light, be a major determinant of seedling survival. Shallow root development in the first year of growth for some species can induce high seedling mortality, either directly by drought or indirectly by competition with grasses and herbs for available water (Casper and Jackson, 1997). Estimating root distribution and soil water content of the upper soil layers (see Section 3; Multi-layer Soil Models and Water Availability) during the first few months after seed germination may be an excellent proxy for seedling survival. The gap model SIERRA (Mouillot et al., 2001) considers the impact of soil moisture on seedling mortality by subjecting a cohort of developing seedlings to increased mortality when soil water potential during a 60 day post-germination period falls below a species-specific threshold. Similarly, the germination and survival of seedlings in the gap model 4C (Bugmann et al., 1997) depend on light, temperature, and soil water status, although in the current version of this model seed germination is responsive only to light (Price et al., 2001).

Events like fire and other natural disturbances can modify the availability of

nutrients at the soil surface and this too can potentially induce changes in seedling regeneration (Trabaud et al., 1985; Tyler, 1995). Gap models that include a fire response for vegetation generally use only empirical estimates of fire effects on post-fire seed germination according to ecosystem type and species (Keane et al., 1996; Mouillot et al., 2001). Nutrient effects on seed and seedling biology are likely to be important in some cases and, like soil water content, should be evaluated as a determinant of seedling establishment and forest regeneration in gap models. Unfortunately, neither traditional nor physiology-based gap models have addressed the sensitivity of seed germination and regeneration to soil nutrient availability. One approach to representing this phenomenon in gap models such as LINKAGES, and other models that explicitly consider nutrient cycling, would be to link seedling establishment with available soil N. This could be done by making post-germination mortality an inverse function of the N growth-reduction modifier (see Pastor and Post, 1986). Since either a growth modifier or available soil N is already calculated in many traditional and physiology-based gap models, maximum seedling survival following seed germination could be represented to occur under optimum soil N conditions and, under less optimal conditions, rates of seedling survival could fall to zero below a minimum species-specific threshold of available soil N. This approach is analogous to how growth modifiers for light, temperature, water, and N are already used in gap models.

In considering how soil water status and/or nutrient availability influence seed and seedling biology, and the sensitivity of such processes to changes in climate, it is important to ask whether data are available either from field surveys or manipulative experiments for the purpose of model parameterization or validation. According to Price et al. (2001), several studies have addressed how soil temperature and drought impact seed germination (Black and Bliss, 1980; Livingston and Black, 1987) and data from these studies are sufficient to begin identifying broad consequences for seedling establishment. Weltzin and McPherson (2000) recently investigated, for example, the response of woodlands and semi-desert grasslands to changes in regional precipitation and concluded that increased rates of seedling emergence and establishment associated with enhanced summer precipitation were sufficient to facilitate down-slope shifts in the woodland-grassland ecotone. Less information is available in terms of describing the relative sensitivity of seed germination and regeneration to soil nutrients. As a result, there is a clear need for both comparative (Holl, 1999) and multifactor experimental (Broncano et al., 1998) studies that are designed to examine the response of seed germination and subsequent seedling survival to soil nutrient availability.

3. Multi-layer Soil Models and Water Availability

Soil water is a primary limitation to the growth of trees in many locations of the world for at least part of the growing season. Moreover, one of the most important

aspects of global change for ecosystems will be changes in land-surface hydrology, particularly as a result of intra-annual variation in the timing and amount of precipitation (Kattenberg et al., 1996). However, despite the observation that competition among plants for water and nutrients is just as important in determining forest dynamics as competition for light, few gap models have been developed that treat below-ground competition with sufficient spatial and temporal detail to capture these complex processes.

The level of detail needed in gap models for describing soil water and nutrient availability, and competition among individuals for these resources, should reflect the hydrologic and/or physiological objectives of individual modeling groups. Nonetheless, we believe that a priority should be placed on 1) incorporating multi-layered soils into gap models, 2) allowing seedlings, saplings, and mature trees to occupy distinct soil layers, thus having access to different amounts of soil water and nutrient resources, 3) improving the mechanistic detail (i.e., biomass allocation) with which below-ground processes like root distribution and soil water extraction are described, and 4) replacing monthly formulations of forest water balance with sub-models that operate at a daily time step resolution. Fortunately, some of these improvements are already being made. For example, the Thornthwaite and Mather (1957) soil water balance equation that is used to calculate monthly evapotranspiration in many traditional gap models has been replaced in more physiology-based models with sub-models that range in complexity from a revised monthly bucket approach as in FORCLIM (Bugmann and Cramer, 1998) to highly temporally resolved models like HYBRID (Friend et al., 1997) and EXE (Martin, 1992). These latter two gap models describe stomatal control of transpiration as a function of temperature, relative humidity, and soil water potential, and EXE (Martin, 1992) explicitly considers how transpiration is modified by soil water content as estimated for roots distributed in multiple soil layers. Recent modifications to LINKAGES have also included replacing the Thornthwaite and Mather (1957) equation with an energy combination approach (Shuttleworth and Wallace, 1985) and incorporating 12 soil layers for calculation of 'patch' water balance (Wullschleger, unpublished results). In this modified version of LINKAGES, the water content of each soil layer is determined by a standard 'bucket' methodology that uses daily transpiration, soil evaporation, precipitation, and canopy interception to quantify changes in soil water content. The approach is not computationally intensive, yet the daily time-step allows one to easily compare modeled estimates of soil water content with field data; something that has not been possible with earlier versions of this or other monthly time-step gap models (see Section 9; Model Validation and Data Needs). Comparative simulation studies showed that this increased level of detail is important for predicting the effects of climatic change on species composition (Bugmann et al., 2001).

Although several traditional and physiology-based gap models include multiple soil layers, most do so for the purpose of better estimating evaporation and the effects of water-deficits on transpiration (Martin, 1992). Little consideration is

given, however, to how this spatial detail could be used to represent the effects of soil moisture on different species or size classes of a single species that might otherwise differ in their root distribution within the soil profile. One generic approach to representing competition among individuals for water in physiology-based gap models would be to allow shallow rooted life-forms such as grasses (Coffin and Lauenroth, 1990) or seedlings to root only to a limited soil depth, whereas the roots of saplings and mature trees would occupy progressively deeper soils. Soil water content could then be tracked by depth-increment, 'drought days' and annual growth modifiers calculated separately for each size class (see Bugmann (2001) for a discussion of drought days in gap models), and maximum growth potentials adjusted accordingly. More complicated schemes might involve relating the extent of root distribution to tree height, diameter, or leaf area, or solving for an optimized depth of rooting based on soil texture and climate (Kleidon and Heimann, 1998). This optimization scheme has been implemented in a global biosphere model and could be incorporated into either traditional or physiology-based gap models. One benefit of implementing such an 'optimized' approach to root development would be a more dynamic representation of roots within the soil profile, allowing roots to be distributed to potentially greater soil depths than might otherwise be specified by a fixed coefficient approach. As a result, trees would have increased access to deep soil water reserves, thus limiting the negative impacts of drought on growth.

As an example of how one of the simpler root distribution approaches might be used to represent competition for available water among seedlings, saplings, and mature trees, the gap model LINKAGES was modified to include a multi-layer sub-model of soil hydrology and roots distributed *a priori* to one of three soil depths (Wullschleger, unpublished results). An annual simulation of soil water content for a deciduous upland oak forest in eastern Tennessee showed that seedlings whose roots were restricted to the upper 20-cm of the soil experienced far drier soils than did saplings whose roots were allowed to extend to a depth of 50-cm, and larger trees whose roots were distributed throughout the 142-cm soil profile (Figure 1). For a 200-day growing season, seedlings were simulated to accumulate 64 'drought days' compared to 38 drought days for saplings and no drought days for large trees. These results suggest that in an average year (1993) seedlings of many species would experience little or no growth, a condition that within the context of LINKAGES would lead to increased rates of mortality for small stature vegetation.

This example simulation with the gap model LINKAGES shows the importance of differential root distribution among size classes as a determinant of drought susceptibility. Clearly, larger trees are able to access greater soil volumes and deeper soil water reserves than do seedlings and saplings. Plant excavation studies coupled with hydrogen and oxygen isotopic analyses are beginning to provide the type of data needed in order to quantify root distribution and differential soil water access by depth for various size classes of trees (Schulze et al. 1996; Snyder and Williams, 2000; Weltzin and McPherson, 1997). A stable isotope analysis conducted in a
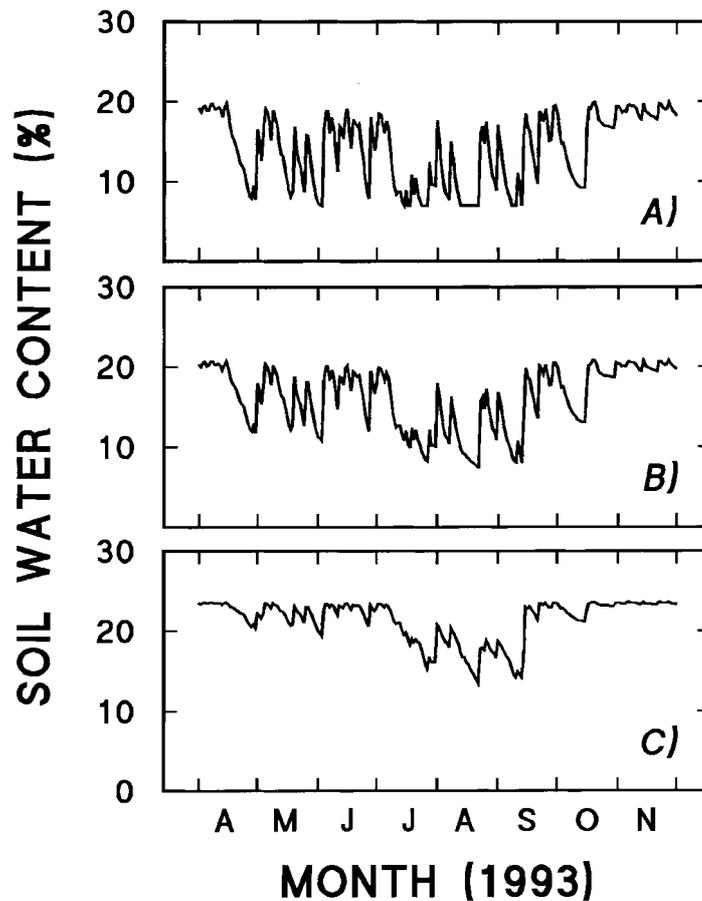
Figure 1. Soil water content as simulated with the gap model LINKAGES after modification to include a multi-layer soil compartment. Root distribution for (a) seedlings was restricted to the upper 0–20 cm compartment, whereas (b) saplings occupied the 0–50 cm compartment, and (c) mature trees had access to the entire 142-cm soil profile.

temperate savanna by Weltzin and McPherson (1997) concluded that both sapling and mature *Quercus emoryi* Torr. trees acquired water from soil depths greater than 50-cm, whereas one- and two-year-old seedlings used water from between 20 and 35-cm. By comparison, two-month-old seedlings extracted water primarily from the upper 15-cm soil profile. Gap models do not, however, explicitly consider the ecological significance of these size-class distinctions to water utilization, drought sensitivity, species recruitment, regeneration, or forest succession. Thus, an increase in the complexity with which roots are treated spatially within soils would go a long ways towards addressing the balance between above- and below-ground complexity in gap models (see Section 8; Above- and Below-Ground Interactions).

4. Biogeochemistry, Nutrient Competition, and Global Change

The biogeochemical cycles of C and N are closely linked in terrestrial ecosystems. In temperate and boreal forests, soil N availability has historically limited tree growth (Vitousek and Howarth, 1991) and continues to do so today in many locations (Fenn et al., 1998). Therefore, plant competition for soil N is a key factor in determining a species' success within an ecosystem. Traditional gap models represent competition for soil N through the use of growth modifiers and by classifying species as being either N tolerant or intolerant (Bugmann, 2001). While a simple growth-reduction factor for N is probably sufficient for many applications, it does not capture the true interactions of limiting factors, and thus the true mechanisms of plant competition. Therefore, physiology-based gap models have implemented other ways of treating competition for nutrients. In the algorithms currently used in HYBRID (Friend et al., 1997), N demand is calculated for each tree; N demand is greater either for larger trees that have the potential for greater absolute growth, or for trees with greater N concentrations in plant tissues. Nitrogen demand is summed for all trees on the plot, and total demand is compared against N availability as calculated by a soil sub-model. If demand is greater than availability, a factor is calculated by dividing availability by summed demand. This factor is then multiplied by N demand for each tree and used to calculate realized N uptake by each tree. As implemented in HYBRID, such an algorithm considers all plants on the plot to be equal *relative* competitors for N, but unequal *absolute* competitors for N. Between trees with similar tissue N concentrations, this algorithm creates a positive feedback between size and nutrient uptake. This feedback allows larger trees to suppress the growth of smaller trees which is, in fact, a realistic facet of plant competition.

While soil N availability is a major determinant of plant competition and productivity, soil N availability is itself strongly controlled by the amount and chemistry of decomposing litter. The fundamental relationships among litter chemistry, decomposition, and nutrient cycling have been reported extensively, and indeed rates of decay and net N release to available soil pools have been related to the initial concentration of N and lignin in litter (Melillo et al., 1982; Aber et al., 1990). The central role of litter C and N chemistry in litter decomposition suggests that changes in the litter quality, whether such changes occur due to shifts in species composition or in direct response to global change, could lead to altered rates of decomposition and altered soil N availability (reviewed by Peñuelas and Estiarte, 1998).

Individual species clearly differ in litter chemistry, and such differences are important to decomposition and soil N availability. Tree species appear to associate with particular regimes of nutrient availability, reflected in turn by litter quality; for example, species adapted to low fertility soils often have litter characterized by high lignin and low N concentrations. Relationships like these have been interpreted as species responses to abiotic factors (Reich et al., 1997) or alternatively

as plant-soil feedbacks in nutrient availability mediated by litter quality (Hobbie, 1992; Ferrari, 1999). An intermediate interpretation would be that nutrient cycles are constrained by abiotic factors, but that the species occupying a site can perpetuate high or low soil availability of N through interactions between litter production, litter chemistry, and rates of decomposition.

There is evidence that because of these species-specific differences in litter quality, marked shifts in species composition due to climate change will likely be amplified by a feedback through the N cycle over what might otherwise be expected from considering the direct effects of climate change on growth processes alone. Post and Pastor (1996) used the gap model LINKAGES to simulate the impact of warming on the nutrient dynamics of mesic forests in northeastern Minnesota and observed that the present-day mixed spruce-fir/northern-hardwood forest would be replaced in a future warmer climate by a more productive northern hardwood forest (Figure 2). The higher N and lower lignin content of litter typical of northern-hardwoods like sugar maple were shown to enhance soil N availability which amplified the effect of warming on productivity (Figure 2a). Conversely, forests growing on drier, sandy soils responded to warming differently. Under conditions of a warming climate, the simulated mixed spruce-fir/northern-hardwood forest was replaced by a stunted pine-oak forest with productivity rates more typical of savannas (Figure 2b). This response was explained by higher lignin and lower N concentration of oak and pine litter that ultimately reduced decomposition, N mineralization, and overall N availability (Post and Pastor, 1996). These examples clearly indicate that if climate change alters species composition, then positive and negative feedbacks on forest productivity as mediated through the N cycle are possible.

Interactions among decomposition, N availability, and species composition such as those described above for LINKAGES would not be possible in gap models without a representation of below-ground processes. The question of including multiple soil layers in gap models (see Section 3; Multi-layer Soil Models and Water Availability) will also need to be considered in terms of biogeochemical processes. There is a tradeoff between increased mechanistic realism, at a price of greater parameterization (assuming the necessary below-ground data are available), and the need for additional fine-scale assumptions. Arguing in favor of multiple soil layers is the fact that N turnover could be represented more realistically, because N turnover rates are much greater in upper soil horizons. Responsiveness to aspects of global change could then be captured more realistically, because biogeochemistry in the forest floor is sensitive to changes in litter quality or N deposition compared with mineral soils alone or with whole soils (Currie, 1999). However, the algorithm described earlier (e.g., HYBRID) for modeling plant competition for soil N, though simple in one soil layer, becomes quite complex in a multi-layered soil. Plant demand would need to be partitioned between soil layers or other assumptions made concerning differential competition among plant roots for nutrients in different soil layers. In other words, the inclusion of below-ground competition for avail-
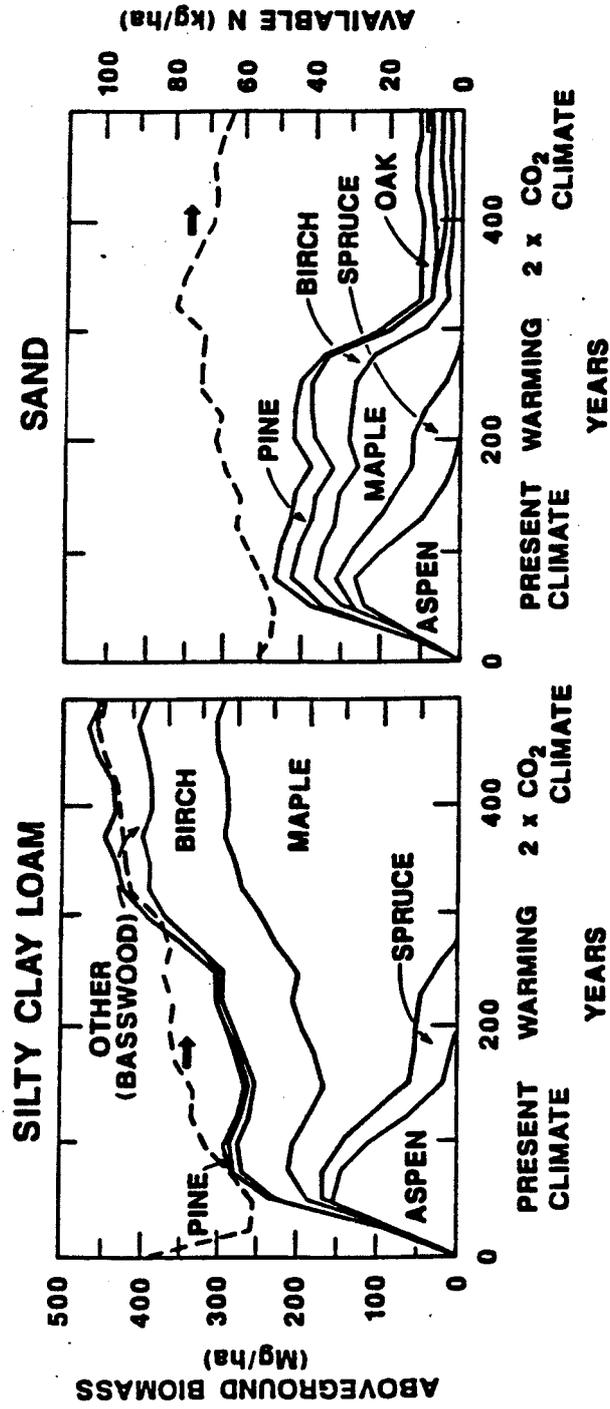
Figure 2. Predicted changes in forest composition, biomass, and nitrogen availability in response to two-fold increase in atmospheric CO_2 (warmer, drier climate). Simulations were completed for two soil types in northeastern Minnesota. The biomass for a species is represented by the vertical distance between the solid lines bounding the area labeled for a species. Available nitrogen is indicated by the dashed line associated with the scale at the right. Reproduced from Pastor and Post (1988).

able nutrients in multiple soil layers would require the introduction of additional hypothetical formulations for which, unfortunately, few data are available.

Finally, relatively little is known about the effects of elevated CO_2 concentration, temperature, and N deposition on litter chemistry. It was widely believed that growth of plants at high CO_2 will lead to reduced N concentration of leaf litter and that this would have significant consequences for N cycling. Rastetter et al. (1991) concluded from simulations with an ecosystem model that interactions between the C and N cycles provided a negative feedback in both arctic tundra and temperate forests exposed to atmospheric CO_2 enrichment. A critical assumption of these simulated results was that the growth of plants at elevated CO_2 produced litter with a C-to-N ratio higher than that of ambient-grown plants, which subsequently reduced N mineralization in the soil and decreased the amount of N available for plant uptake. Recent analyses, however, suggest that while a lower N concentration of green leaves is a rather consistent response to elevated CO_2 concentration, this reduction is not always seen in leaf litter (Norby and Cotrufo, 1998). Gap models that include an adequate representation of N cycling and appropriate interactions with the C cycle would prove useful for evaluating the significance of this litter quality assumption at the ecosystem scale. In this regard, a sensitivity analysis with gap models would be useful for determining if additional field data or experiments are needed to resolve whether a CO_2-induced impact on litter chemistry (if any) would be important to decomposition, nutrient cycling, productivity, and ultimately to forest succession.

5. Biomass Allocation to Roots

Biomass allocation between roots and shoots (often expressed as root/shoot ratio) is one of the most important processes regulating plant growth. It is a process that has largely been ignored in many traditional gap models, although allocation is beginning to be included in physiology-based models such as an early version of HYBRID (Friend et al., 1993), where below-ground allocation of biomass was described as a fixed ratio between foliage and fine root C mass. In other gap models, as in 4C (Bugmann et al., 1997) and FIRE-BGC (Keane et al., 1996), dynamic allocation schemes are based on principles such as the pipe model theory, the functional balance between root and leaf activity, and mass balance approaches (see Bugmann, 2001). Nonetheless, the consequences of below-ground allocation for water uptake and nutrient acquisition, and the need for such detail in gap models cannot be over-emphasized (Norby et al., 2001). Hurtt et al. (1998) recently argued that our ability to model long-term plant performance continues to be limited by our inability to model plant resource allocation. Allocation of biomass is known to influence rates of plant productivity, the biophysical properties of vegetative canopies that have direct relevance to plant-climate interactions, and competition among species for above- and below-ground resources, and thus for forest succession.

Given that allocation of biomass to above- and below-ground organs is important, three important questions arise; 1) how does one model such a dynamic process, 2) what data sets are available from which to quantify this process and the apparent sensitivity of below-ground biomass allocation to environmental variables, and 3) what additional experimental studies are required in order to better understand the fundamental mechanisms controlling above- and below-ground allocation. Clearly the experimental and modeling communities have struggled with these questions for years. As indicated earlier, allocation in some gap models has been described using a functional balance approach (see Bugmann, 2001). This model of allocation, developed by Brouwer (1962), proposes that in a given environment, total root function (e.g., water or nutrient uptake) should be balanced by total shoot function (e.g., canopy C gain). The functional balance approach was implemented by Thornley (1972) to describe above- and below-ground allocation of photosynthate during vegetative plant growth. Various versions of the functional balance concept have been integrated into crop and forest growth models. However, recent quantitative tests have indicated that the functional balance model cannot explain CO_2-induced changes in allocation (Luo et al., 1994), thus raising doubts as to whether this model can adequately represent allocation in a future, higher CO_2 world. Fortunately, there are other concepts and/or models that can be used to predict biomass allocation, including resource balance (Field et al., 1992), N productivity (Ågren, 1985; Ågren and Ingestad, 1987), source-sink regulation (Stitt, 1991), optimality (Hilbert, 1990), growth/photosynthesis balance (Luo et al., 1994), and coordination (Reynolds and Chen, 1996). None of these allocation schemes, however, have so far been implemented in either traditional or physiology-based gap models.

In order to preserve the simplicity of gap models, simple but effective biomass allocation modules are needed. Although fixed coefficients or allometric relationships are used in existing gap models to link below-ground biomass allocation to either tree diameter or leaf area, future models must be dynamic in that allocation above- and below-ground should be responsive to environmental variables like water, nitrogen, and light. Such an approach would ensure that appropriate above- and below-ground interactions are represented. Simple phenomenological approaches like the one implemented in a global carbon model by Friedlingstein et al. (1998) should be derived from empirical data at the patch scale. These concepts could then be incorporated in gap models. Such an approach would only make sense, however, if roots served an explicit function in gap models (other than detracting from above-ground biomass) such as water and/or nutrient uptake. For example, assuming that the role of roots in water uptake was appropriately modeled, e.g., using a scheme similar to the one by Friedlingstein et al. (1998), water-limited conditions would promote carbon allocation to roots, which would serve to minimize water deficits through enhanced root development and greater water uptake. Such a positive feedback is in broad agreement with experimental evidence. We note, however, that not all modeling schemes reflect this dynamic response of

below-ground carbon allocation to drought. For example, gap models that estimate allocation of carbon to roots based on fixed coefficients or allometric equations applied to stem diameter predict a response opposite to the one described above; that is, soil resource limitations that negatively impact above-ground productivity also negatively impact below-ground allocation of biomass.

Physiology-based gap models could take advantage of the simple Friedlingstein et al. (1998) allocation scheme, but because of their presumed ability to handle additional levels of complexity, mechanistic models of forest succession might better implement one of the more advanced allocation schemes. Of the more detailed allocation models available, the N productivity method, either alone or in combination with other approaches, may be the simplest to implement (Ågren, 1985). In order to predict the effects of elevated CO_2 on biomass allocation, Luo et al. (1994) combined the N productivity scheme with growth observations and derived a simple equation that represented what they termed the growth/photosynthesis balance. Using this equation, these authors were successful in predicting the ratio of root to total plant dry mass (i.e., root fraction) from the sensitivity of photosynthesis and relative growth rate to elevated CO_2 concentration. Implementing other allocation schemes (e.g., source-sink, optimality, etc.) in gap models would require a number of parameters that are much more difficult to obtain, including specific root and shoot activities and detailed physiology of C assimilation and respiration.

In evaluating the various carbon allocation schemes that one might consider implementing in gap models, it becomes evident that the data requirements of these models are high. As a result, a combination of data compilation and experimental studies are needed in order to provide the fundamental knowledge that will enable biomass allocation above- and below-ground to be represented in physiology-based gap models. At a minimum, two types of data activities will be required to facilitate the incorporation of biomass allocation schemes into gap models. First, data sets that quantify root and shoot biomass, and root-to-shoot ratios, should be compiled for various size classes of trees (e.g., seedlings and mature trees). These data should come from plants grown under field conditions and exposed to prevailing soil water, nutrients, and climate. Norby et al. (2001) noted that large databases are likely to be available on the independent and interactive effects of environment variables on growth and physiology of herbaceous plants and tree seedlings (e.g., greenhouse and growth chamber studies). However, it was emphasized that factorial experiments designed to investigate the interactive effects of elevated temperature, rising ozone, altered patterns of precipitation, and increased nitrogen deposition are practically nonexistent for mature trees. Conducting such studies and interpreting the results in a modeling context will be a challenge for plant scientists. Secondly, although root-to-shoot ratios may be a relative measure of biomass allocation above- and below-ground, we recognize that that these simple indices do not reveal much about the mechanisms that regulate biomass allocation. To test the functional balance concept, for example, specific activities of shoots and roots (i.e., mass-based, whole-shoot photosynthetic rate and whole-root nutrient or water uptake rates) and

root and shoot biomass should be simultaneously measured. Detailed studies such as these will likely be confined to the laboratory or greenhouse. To our knowledge, no single experiment has been undertaken to measure these components in order to test the functional balance concept under elevated CO_2 concentration, either alone or in combination with temperature. Studies like these should be given priority as the relative direction of biomass allocation above- and below-ground is likely to impact plant productivity and response to a changing climate.

6. Below-Ground Storage of Carbon and Nutrients

Gap models are increasingly including disturbance regimes that are known to influence species composition and patterns of forest succession. As a result, it will become increasingly necessary to consider whether below-ground processes might also impact the recovery of a given species from a natural disturbance. For example, large roots act as storage organs for nutrients in many tree species. These roots can survive disturbances in some species, and new stems grow from buds along roots. Species vary in the degree to which they are able to grow root sprouts and in the stimulation needed to induce sprouting (Oliver and Larson, 1996). Compared to species with high growth rates and nutrient demand, species adapted to low resource supply accumulate larger storage of carbohydrates and nutrients, and may have an advantage for sprouting and growth of new leaves after disturbances. Therefore, the benefit of storage should be measured in terms of fitness and this should incorporate probabilities of survival and reproduction over the life of the individual (Chapin et al., 1990).

Traditional gap models include 'sprouting' as one means of introducing new individuals into an existing tree population. How many sprouts are introduced depends on whether adequate radiation is available at the forest floor, whether a tree of a given species died in the preceding year and a stump is, therefore, available, and the average number of sprouts for the species in question. For example, in the model LINKAGES, 59 out of 72 tree species have the potential to initiate sprouts, with some species (e.g., red maple, aspen, pin cherry) capable of initiating multiple sprouts per stump. The actual number of sprouts initiated in the model is modified by the light, degree day, and soil water growth multipliers. Nonetheless, the concept of sprouting as a regeneration mechanism means that species capable of prolific sprouting (e.g., early-succession species) are at a distinct advantage in terms of occupying a site following a disturbance. For this reason alone, it is important that sprouting be incorporated into gap models (Price et al, 2001).

Under conditions of elevated atmospheric CO_2 and altered climate, below-ground storage of C and nutrients will likely affect and be affected by biogeochemical changes in ecosystems. For example, higher CO_2 concentrations could increase C production and allocation to roots as shown in some experiments (Delucia et al., 1999). Successional responses to altered fire regimes also depend on below-

ground storage, and studies suggest that nutrient storage is critical for determining the successional rate of disturbed forests (e.g., Aber and Driscoll, 1997). Thus, with projected changes in disturbance regimes and below-ground C and nutrient storage in the future, the interactions between these factors will likely affect successional dynamics and species composition in forests.

7. Spatial Processes and the Lateral Flow of Water

All gap models assume that the forest floor in a patch is flat. This assumption simplifies model structure by ignoring runoff from one patch to another. It also, by definition, eliminates the possibility that microsite differences in soil water content or nutrient availability will be modeled in a realistic manner. However, a landscape or catchment is more complex than an isolated patch because spatial considerations such as lateral flow of water, topography, site aspect, and differences in vegetation water use are important (Hatton et al., 1992).

Based on existing scenarios of climate change, many regions of the world will experience higher temperatures and altered rates of precipitation. Higher temperatures will directly affect forest ecosystems through effects on plant physiology, but indirect effects such as higher water demand may have a greater impact on some water-sensitive forest ecosystems (Stakhiv and Major, 1997). As the water balance of forest ecosystems becomes increasingly important, assumptions about lateral flow of water will also become more important. Moreover, the incorporation of spatially-explicit processes in gap models will provide an opportunity to more realistically simulate nutrient re-distribution from one patch to another. This will be particularly important in forests on fragmented landscapes.

At the landscape scale, there are many situations where spatial processes among patches will play important roles in forest growth and succession. This was shown by Hatton et al. (1992) who used a spatially-explicit hydroecological landscape model of water, carbon, and energy balances (Topog-IRM) to simulate the direct effects of a two-fold increase in CO_2 concentration on catchment water yield, soil moisture status, and tree growth. These authors showed that (among other effects) the size and duration of 'wet' areas within catchments would, due to CO_2-induced reductions in stomatal conductance and transpiration, increase under conditions of elevated CO_2 concentrations. Since mesic areas are critical to maintaining biological diversity at the landscape-level, Hatton et al. (1992) concluded that the inclusion of spatial processes in ecological models would be an important tool for inferring the impact of global environmental change on species distribution and landscape biodiversity. Price et al. (2001) similarly recognized how disturbances such as fire, harvesting, storm damage, and flooding can result in the formation of microsites. These authors concluded that such areas could be important for determining seed dispersal, germination, and ultimately forest composition after a disturbance.

8. Above- and Below-Ground Interactions

Attempts to incorporate more detailed below-ground processes into gap models will need to take into account the multiple interactions that arise when dealing with plants and soils. Norby et al. (2001) emphasize that many above-ground processes are influenced by soil resource availability and that to understand inter- and intra-specific competition there is a need to focus on how plants affect local conditions through water and nutrient uptake. This concept is implied by the illustrations that we have used: soil moisture influences seed germination and seedling mortality; root distribution within the soil profile impacts competition among species and/or size classes for water and nutrients, with implications for above-ground productivity; and soil resource availability influences carbon allocation below-ground, which in turn has the potential to alter forest growth. Not only are many of these interactions important to above-ground productivity, but they also have direct implications for mortality and regeneration (Keane et al., 2001; Price et al., 2001).

The incorporation of below-ground detail into traditional and physiology-based gap models will require that increased attention also be given to the above- and below-ground interactions that occur at the ecosystem level. Many times, these interactions lead to an equilibrium between the available resources and the potential use of this resource, as can be observed in the interaction between simulated leaf area index (LAI) and water availability in biogeochemical models (Running and Coughlan, 1988; Running and Gower, 1991). The link between water availability and LAI illustrates the concept of hydroecological equilibrium in the natural soil-vegetation system (Eagleson, 1982; Hatton et al., 1997). This equilibrium highlights not only the limitation of forest productivity on dry sites, but also the feedback of a decreasing leaf biomass in order to limit, in the following year, transpirational water losses. Because of this, spatio-temporal variations in LAI are observed that correspond to different microclimates and soil water availabilities (Running, 1984). For example, due to increased water availability, valley bottoms and north facing slopes have a higher LAI than do ridge tops. Moreover, the inter-annual variations of LAI in Mediterranean landscapes illustrate the constant adjustment of foliage leaf area to site water availability. These adjustments effectively constrain transpiration in the following year. The same kind of equilibrium can be observed in areas of low nutrient availability where the balance between LAI, litter fall, and litter decomposition can be a factor limiting forest productivity. As with water availability, both litter fall and litter decomposition are related to the current climate (Couteaux et al., 1995). Therefore, changes in below-ground processes and their interaction with above-ground processes at the ecosystem scale should be taken into account when considering potential feedbacks in relation to climate change.

9. Model Validation and Data Needs

Our discussion to this point has focused on a limited suite of below-ground processes that we feel are likely candidates for incorporation into gap models. We have indicated why these processes are important at the plant and ecosystem scale, and have suggested ways in which they could be represented in traditional and physiology-based models of forest succession. It is recognized, however, that in dealing with the species-specific nature of gap models, few data sets are available for model parameterization and validation. Such a deficiency is a concern not only as it relates to the incorporation of below-ground processes into gap models, but also as applied to questions that address above-ground processes, regeneration, and mortality (Keane et al., 2001; Norby et al., 2001; Price et al, 2001). Not surprisingly, this lack of appropriate data sets for model parameterization and validation has been a source of considerable frustration, as evidenced by the statements of Rastetter (1996):

> Although the prospect for testing (ecosystem) models is grim, these models are likely to remain a vital part of any evaluation of the responses to changes in global climate and carbon dioxide because the alternatives are worse. It would be fool hardy to plunge blindly into the future without some attempt to evaluate the global consequences of human activities.

While the sentiments expressed by Rastetter (1996) are understandable, Aber (1997) argues that ecology is a data-rich field and that there are very few areas of ecology for which no validation data exist. Regarding the incorporation of below-ground processes in gap models, relevant data sets are beginning to emerge especially as they relate to maximum rooting depth of vegetation (Canadell et al., 1996), root distribution within soil profiles (Jackson et al., 1996), and fine root biomass, surface area, and nutrient contents (Jackson et al., 1997). Such data sets may prove useful for model development, but probably more so for establishing general patterns of response rather than for species-specific parameterizations of gap models.

Even under circumstances where validation data sets are not readily available, independent experimental results can often be found for comparison against intermediate variables predicted by the model (Aber, 1997). The addition of increased physiological detail to gap models may be one way of more easily validating intermediate output from the models without focusing solely on the end product of the simulation such as total biomass, species composition and/or stems per hectare. Norby et al. (2001) indicated that the fast time scale of more mechanistic gap models opens up the potential for comparing predictions of carbon and water fluxes to data from the expanding network of eddy covariance towers (e.g., AmeriFlux). For example, this was an important motivating force behind modifying LINKAGES from a monthly to a daily time-step model and in efforts to improve the mechanistic detail with which transpiration and soil water extraction were described (Wullschleger, unpublished results). Having incorporated such changes into LINK-

AGES there is increased confidence that model calculations of soil water content, seasonal patterns of drought, and 'drought days' (if any) are represented in a temporally resolved manner. One should realize, however, that a simple validation of intermediate model output against short-term data does not necessarily imply that long-term processes like nutrient cycling, leaf area index, and feedbacks to species composition and forest dynamics are being reliably predicted (Rastetter, 1996).

Finally, gap models have historically been used for site-specific and regional predictions of forest productivity, and more recently to simulate forest response to climatic change (Shugart et al., 1992; Shugart and Smith, 1996). In this capacity, the focus has been on evaluating climate-induced changes in total biomass and species composition. Less emphasis, however, has been placed on whether gap models can help identify specific plant and soil processes that govern forest structure and composition, and therein, contribute to the improved design of field experiments and monitoring studies (Price et al., 2001). Friend et al. (1997) touched on this when they concluded that the development of mechanistic gap models '*can highlight key areas of plant physiology, soil dynamics, and overall ecosystem behavior where our knowledge needs to be increased through experimental work*'. A sensitivity analysis where individual model parameters are changed by some percentage (e.g., 10%) and subsequent changes in various output variables are quantified would be one way in which gap models could provide useful insights on the below-ground processes that influence forest productivity. Friend et al. (1997) completed a sensitivity analysis for HYBRID and, from a list of 76 model parameters, concluded that phenology, photosynthesis, and foliage/fine root carbon and nitrogen partitioning were among the more important determinants of ecosystem carbon balance. Such an approach is valuable in terms of identifying gaps in our knowledge and for highlighting areas where additional field experiments may be needed. These authors noted, however, that the results of a sensitivity analysis must be viewed in the context of the particular climate used, and therefore cautioned that the ranking of important model parameters might change under a future climate scenario. This cautionary note provides yet another reason for why model development and field studies should be closely linked as we address issues of forest response to global change.

10. Conclusions and Recommendations

The historic omission of below-ground processes in gap models was partly a consequence of the goals and interests of the developers of the models. In addition, there was – and to a large extent remains – a lack of sufficient data on below-ground processes and species-specific differences for model initialization, validation, and performance testing of the models (Oja and Arp, 1996). This lack of information poses a serious obstacle to incorporating below-ground processes in gap models and thereby threatens our goal of better understanding how forest productivity

and succession will be impacted by future changes in climate. Fortunately, novel measurement techniques for determining the spatial distribution of roots in soil (Hruska et al., 1999; Linder et al., 2000), large-scale field experiments, and data compilation activities (Canadell et al., 1996; Jackson et al., 1996) are beginning to yield information that in the near future will enable the improved representation of below-ground processes in models of various categories. In terms of gap models, there is now a tendency to replace the earlier, simple formulations of growth (Norby et al., 2001), mortality (Keane et al., 2001), and regeneration (Price et al., 2001) with increasingly detailed and mechanistic approaches, and it is generally recognized that below-ground processes not represented in earlier models should now be included. In this paper, we have tried to highlight likely areas where existing gap models could be improved by adding either new below-ground processes, thereby expanding the predictive capabilities of this class of models, or including improved spatial and/or temporal treatment of existing processes. Foremost among the ideas presented for gap model improvement, we believe that *immediate* gains in how individual species are represented can be realized by 1) replacing single-layered soils with multiple soil layers, 2) allowing seedling, sapling, and mature tree roots to occupy distinct soil layers and, thus, have differential access to soil water resources, and 3) describing seed germination and/or regeneration as a function of surface soil characteristics (e.g., temperature and/or soil water potential). These improvements will require modest model revision and a survey of published data and ongoing field experiments. Appropriate methodologies are available to initially guide such additions to gap models. More effort will be required, however, as modelers strive to add detail to how biomass is dynamically allocated to roots *versus* shoots in gap models, and how biomass allocation to roots influences water and nutrient acquisition. Few of the allocation schemes discussed earlier lend themselves to easy incorporation into gap models, and there will need to be close coordination between modelers and experimentalists to decide what information is required in order to successfully add this level of complexity. The same can be said for adding water and nutrient uptake characteristics to roots, and for adding spatially-explicit detail to the distribution of water and nutrients within the soil profile.

Finally, as below-ground detail is added to gap models, there will be a growing need to evaluate the significance of alternative formulations in terms of the simulated forest dynamics and, ultimately, the predictive power of gap models (Bugmann et al., 1996; cf. Badeck et al., 2001; Shao et al., 2001; Bugmann et al., 2001). The inclusion of key below-ground processes, particularly competition among size classes for water and biomass allocation schemes, may ultimately improve model behavior, but such detail will come at the price of increased parameterization efforts and increased model complexity.

Acknowledgements

References

Aber, J. D.: 1997, 'Why Don't We Believe the Models?', *Bull. Ecol. Soc. Amer.* July, 232–233.

Aber, J. D. and Driscoll, C. T.: 1997, 'Effects of Land Use, Climate Variation and N Deposition on N Cycling and C Storage in Northern Hardwood Forests' *Global Biogeochem. Cycles* **11**, 639–648.

Aber, J. D., Melillo, J. M., and McClaugherty, C. A.: 1990, 'Predicting Long-Term Patterns of Mass Loss, Nitrogen Dynamics, and Soil Organic Matter Formation from Initial Fine Litter Chemistry in Temperate Forest Ecosystems', *Can. J. Bot.* **68**, 2201–2208.

Ågren, G. I.: 1985, 'Theory for Growth of Plants Derived from the Nitrogen Productivity Concept', *Physiol. Plant.* **64**, 17–28.

Ågren, G. I. and Ingestad, T.: 1987, 'Root: Shoot Ratio as a Balance between Nitrogen Productivity and Photosynthesis', *Plant Cell Environ.* **10**, 579–586.

Badeck, F.-W., Lischke, H., Bugmann, H., Hickler, T., Hönninger, K., Lasch, P., Lexer, M. J., Mouillot, F., Schaber, J., and Smith, B.: 2001, 'Tree Species Composition in European Pristine Forests: Comparison of Stand Data to Model Predictions', *Clim. Change* **51**, 307–347.

Black, R. A. and Bliss, L. C.: 1980, 'Reproductive Ecology of *Picea mariana*(Mill) BSP, at Tree Line Near Inuvik, Northwest Territories, Canada', *Ecol. Monogr.* **50**, 331–354.

Botkin, D. B., Janak, J. F., and Wallis, J. R.: 1972, 'Some Ecological Consequences of a Computer Model of Forest Growth', *J. Ecol.* **60**, 849–872.

Broncano, M. J., Riba, M., and Retana, J.: 1998, 'Seed Germination and Seedling Performance of Two Mediterranean Tree Species, Holm Oak (*Quercus ilex*L.) and Aleppo pine (*Pinus halepensis*Mill.): A Multifactor Experimental Approach' *Plant Ecology* **138**, 17–26.

Brouwer, R.: 1962, 'Nutritive Influences on the Distribution of Dry Matter in the Plant', *Netherlands J. Agri. Sci.* **10**, 399–408.

Bugmann, H.: 2001, 'A Review of Forest Gap Models' *Clim. Change* **51**, 259–305.

Bugmann, H. and Cramer, W.: 1998, 'Improving the Behaviour of Forest Gap Models Along Drought Gradients', *For. Ecol. Manage.* **103**, 247–263.

Bugmann, H. K. M., Xiaodong, Y., Sykes, M. T., Martin, P., Linder, M., Desanker, P. V., and Cumming, S. G.: 1996, 'A Comparison of Forest Gap Models: Model Structure and Behaviour', *Clim. Change* **34**, 289–313.

Bugmann, H., Grote, R., Lasch, P., Lindner, M., and Suckow, F.: 1997, 'A New Forest Gap Model to Study the Effects of Environmental Change on Forest Structure and Functioning', in Mohren, G.

M. J., Kramer, K., and Sabaté, S. (eds.), *Global Change Impacts on Tree Physiology and Forest Ecosystems*, Kluwer Academic Publishers, pp. 255–261.

Bugmann, H. K. M., Wullschleger, S. D., Price, D. T., Ogle, K., Clark, D. F., and Solomon, A. M.: 2001, 'Comparing the Performance of Forest Gap Models in North America', *Clim. Change* **51**, 349–388.

Canadell, J., Jackson, R. B., Ehleringer, J. R., Mooney, H. A., Sala, O. E., and Schulze, E.-D.: 1996, 'Maximum Rooting Depth for Vegetation Types at the Global Scale', *Oecologia* **108**, 583–595.

Casper, B. B. and Jackson, R. B.: 1997, 'Plant Competition Underground', *Ann. Rev. Ecol. Syst.* **28**, 545–570.

Chapin III, F. S., Schulze, E., and Mooney, H. A.: 1990, 'The Ecology and Economics of Storage in Plants', *Ann. Rev. Ecol. Syst.* **21**, 423–447.

Coffin, D. P. and Lauenroth, W. K.: 1990, 'A Gap Dynamics Simulation Model of Succession in a Semiarid Grassland', *Ecol. Modelling* **49**, 229–266.

Couteaux, M. M., Bottner, P., and Berg, B.: 1995, 'Litter Decomposition, Climate and Litter Quality', *Trends Ecol. Evol.* **10**, 63–66.

Currie, W. S.: 1999, 'The Responsive C and N Biogeochemistry of the Temperate Forest Floor', *TREE* **14**, 316–320.

Delucia, E. H., Hamilton, J. G., Naidu, S. L., Thomas, R. B., and Andrews, J. A.: 1999, 'Net Primary Production of a Forest Ecosystem with Experimental CO_2 Enrichment', *Science* **284**, 1177–1179.

Eagleson, P. S.: 1982, 'Ecological Optimality in Water Limited Natural Soil Vegetation Systems. 1: Theory and Hypothesis', *Water Resour. Res.* **18**, 325–340.

Fenn, M. E., Poth, M. A., Aber, J. D., Baron, J. S., Bormann, B. T., Johnson, D. W., Lemly, A. D., McNulty, S. G., Ryan, D. F., and Stottlemeyer, R.: 1998, 'Nitrogen Excess in North American Ecosystems: Predisposing Factors, Ecosystem Responses, and Management Strategies', *Ecol. Appl.* **8**, 706–733.

Ferrari, J. B.: 1999, 'Fine-scale Patterns of Leaf Litterfall and Nitrogen Cycling in an Old-growth Forest', *Can. J. For. Res.* **29**, 291–302.

Field, C. B., Chapin III, F. S., Matson, P. A., and Mooney, H. A.: 1992, 'Responses of Terrestrial Ecosystems to the Changing Atmosphere: A Resource-Based Approach', *Ann. Rev. Ecol. Syst.* **23**, 201–235.

Foley, J. A., Levis, S., Prentice, I. C., Pollard, D., and Thompson, S. L.: 1998, 'Coupling Dynamic Models of Climate and Vegetation' *Global Change Biol.* **4**, 561–579.

Friedlingstein, P., Joel, G., Field, C. B., and Fung, I. Y.: 1998, 'Toward an Allocation Scheme for Global Terrestrial Carbon Models' *Global Change Biol.* **5**, 755–770.

Friend, A. D., Shugart, H. H., and Running, S. W.: 1993, 'A Physiology-Based Model of Forest Dynamics', *Ecology* **74**, 792–797.

Friend, A. D., Stevens, A. K., Knox, R. G., and Cannell, M. G. R.: 1997, 'A Process-Based, Terrestrial Biosphere Model of Ecosystem Dynamics (Hybrid v3.0)' *Ecol. Modelling* **95**, 249–287.

Hatton, T. J., Salvucci, G. D., and Wu, H. I.: 1997, 'Eagleson's Optimality Theory of an Ecohydrological Equilibrium: Quo Vadis?' *Func. Ecol.* **11**, 665–674.

Hatton, T. J., Walker, J., Dawes, W. R., and Dunin, F. X.: 1992. 'Simulations of Hydroecological Responses to Elevated CO_2 at the Catchment Scale', *Aust. J. Bot.* **40**, 679–696.

Hilbert, D. W.: 1990, 'Optimization of Plant Root: Shoot Ratios and Internal Nitrogen Concentration', *Ann. Bot.* **66**, 91–99.

Hobbie, S. E.: 1992, 'Effects of Plant Species on Nutrient Cycling' *TREE* **7**, 336–339.

Holl, K. D.: 1999, 'Factors Limiting Tropical Rain Forest Regeneration in Abandoned Pasture: Seed Rain, Seed Germination, Microclimate, and Soil', *Biotropica* **31**, 229–242.

Hruska, J., Cermak, J., and Sustek, S.: 1999, 'Mapping Tree Root Systems with Ground-Penetrating Radar', *Tree Physiol.* **19**, 125–130.

Humphries, H. C., Coffin, D. P., and Lauenroth, W. K.: 1996, 'An Individual-Based Model of Alpine Plant Distribution', *Ecol. Modelling* **84**, 99–126.

Hurtt, G. C., Moorcroft, P. R., Picala, S. W., and Levin, S. A.: 1998, 'Terrestrial Models and Global Change: Challenges for the Future', *Global Change Biol.* **4**, 581–590.

Jackson, R. B., Canadell, J., Ehleringer, J. R., Mooney, H. A., Sala, O. E., and Schulze, E.-D.: 1996, 'A Global Analysis of Root Distribution for Terrestrial Biomes', *Oecologia* **108**, 389–411.

Jackson, R. B., Mooney, H. A., and Schulze, E.-D.: 1997, 'A Global Budget for Fine Root Biomass, Surface Area, and Nutrient Contents', *Proc. Nat. Acad. Sci.* **94**, 7362–7366.

Jackson, R. B., Schenck, H. J., Jobbagy, E. G., Canadell, J., Colello, G. D., Dickinson, R. E., Field, C. B., Friedlingstein, P., Heimann, M., Hibbard, K., Kicklighter, D. W., Kleidon, A., Neilson, R. P., Parton, W. J., Sala, O. E., and Sykes, M. T.: 2000, 'Belowground Consequences of Vegetation Change and their Treatment in Models', *Ecol. Appl.* **10**, 470–483.

Kattenberg, A. et al.: 1996, 'Climate Models – Projections of Future Climate', in Houghton, J. T., et al. (eds.), *Climate Change 1995. The Science of Climate Change*, pp. 285–357.

Keane, R. E., Morgan, P., and Running, S. W.: 1996 'Fire-BGC – A Mechanistic Ecological Process Model for Simulating Fire Succession on Coniferous Forest Landscapes of the Northern Rocky Mountains', USDA Forest Service, Intermountain Research Station, p. 122.

Keane, R. E., Austin, M., Field, C., Huth, A., Lexer, M. J., Peters, D., Solomon, A., and Wyckoff, P.: 2001, 'Tree Mortality in Gap Models: Application to Climate Change', *Clim. Change* **51**, 509–540.

King, A. W., Post, W. M., and Wullschleger, S. D.: 'The Potential Response of Terrestrial Carbon Storage to Changes in Climate and Atmospheric CO_2', *Clim. Change* **35**, 199–227.

Kleidon, A. and Heimann, M.: 1998, 'A Method of Determining Rooting Depth from a Terrestrial Biosphere Model and its Impact on the Global Water and Carbon Cycle', *Global Change Biol.* **4**, 275–286.

Leishman, M. R., Hughes, L., French, K., Armstrong, D., and Westoby, M.: 1992, 'Seed and Seedling Biology in Relation to Modelling Vegetation Dynamics Under Global Climate Change', *Aust. J. Bot.* **40**, 599–613.

Linder, C. R., Moore, L. A., and Jackson, R. B.: 2000, 'A Universal Molecular Method for Identifying Underground Plant Parts to Species', *Molecular Ecol.* **9**, 1549–1559.

Livingston, N. J. and Black, T. A.: 1987, 'Water-Stress and Survival of 3 Species of Conifer Seedlings Planted on a High Elevation South-Facing Clear-Cut', *Can. J. For. Res.* **17**, 1115–1123.

Luo, Y., Field, C. B., and Mooney, H.A.: 1994, 'Predicting Responses of Photosynthesis and Root Fraction to Elevated CO_2: Interactions Among Carbon, Nitrogen, and Growth', *Plant Cell Environ.* **17**, 1194–1205.

Martin, P. H.: 1992, 'EXE: A Climatically Sensitive Model to Study Climate Change and CO_2 Enrichment Effects on Forests', *Aust. J. Bot.* **40**, 717–735.

Mauchamp, A., Rambal, S., and Lepart, J.: 1994, 'Simulation Dynamics of a Vegetation Mosaics: A Spatialized Functional Model', *Ecol. Modelling* **71**, 107–130.

Melillo, J. M., Aber, J. D., and Muratore, J. F.: 1982, 'Nitrogen and Lignin Control of Hardwood Leaf Litter Decomposition Dynamics', *Ecology* **63**, 621–626.

Mouillot, F., Rambal, S., and Lavorel, S.: 2001, 'A Generic Process-Based Simulator for Mediterranean Landscapes (SIERRA): Design and Validation Exercises', *Forest Ecol. Manage.* **147**, 75–97.

Neilson, R. P. and Drapek, R. J.: 1998, 'Potentially Complex Biospheric Responses to Transient Global Warming', *Global Change Biol.* **4**, 505–521.

Norby, R. J. and Cotrufo, M. F.: 1998, 'A Question of Litter Quality', *Nature* **396**, 17–18.

Norby, R. J., Ogle, K., Curtis, P. S., Badeck, F. W., Huth, A., Hurtt, G. C., Kohyama, T., and Peñuelas, J.: 2001, 'Aboveground Growth and Competition in Forest Gap Models: An Analysis for Studies of Climatic Change', *Clim. Change* **51**, 415–447.

Oeschger, H., Siegenthaler, U., Schotterer, U., and Gugelmann, A.: 1975, 'A Box Diffusion Model to Study the Carbon Dioxide Exchange in Nature', *Tellus* **27**, 168–192.

Oja, T. and Arp, P. A.: 1996, 'Nutrient Cycling and Biomass Growth at a North American Hardwood Site in Relation to Climate Change: FORSVA Assessments', *Clim. Change* **34**, 239–251.

Oliver, C. D. and Larson, B. V.: 1996, *Forest Stand Dynamics*, John Wiley and Sons, New York, p. 520.

Pacala, S. W., Canham, C. D., and Silander, J. A.: 1993, 'Forest Models Defined by Field-Measurements. 1. The Design of a Northeastern Forest Simulator', *Can. J. For. Res.* **23**, 1980–1988.

Pan, Y. D., Melillo, J. M., McGuire, A. D., Kicklighter, D. W., Pitelka, L. F., Hibbard, K., Pierce, L. L., Running, S. W., Ojima, D. S., Parton, W. J., and Schimel, D. S.: 1998, 'Modeled Responses of Terrestrial Ecosystems to Elevated Atmospheric CO_2: A Comparison of Simulations by the Biogeochemistry Models of the Vegetation/Ecosystem Modeling and Analysis Project (VEMAP)', *Oecologia* **11**, 389–404.

Pastor, J. and Post, W. M.: 1986, 'Influence of Climate, Soil-Moisture, and Succession on Forest Carbon and Nitrogen Cycles', *Biogeochemistry* **2**, 3–27.

Pastor, J. and Post, W. M.: 1988, 'Response of Northern Forests to CO_2-Induced Climate Change', *Nature* **334**, 55–58.

Peñuelas, J. and Estiarte, M.: 1998, 'Can Elevated CO_2 Affect Secondary Metabolism and Ecosystem Function?', *TREE* **13**, 20–24.

Post, W. M. and Pastor, J.: 1996, 'LINKAGES – An Individual-Based Forest Ecosystem Model', *Clim. Change* **34**, 253–261.

Potter, C. S., Davidson, E. A., Klooster, S. A., Nepsted, D. C., de Negreiros, G. H., and Brooks, V.: 1998, 'Regional Application of an Ecosystem Production Model for Studies of Biogeochemistry in Brazilian Amazonia', *Global Change Biol.* **4**, 315–333.

Price, D. T., Zimmermann, N. E., van der Meer, P. J., Lexer, M. J., Leadley, P., Jorritsma, I. T. M., Schaber, J., Clark, D. F., Lasch, P., McNulty, S., Wu, J., and Smith, B.: 2001, 'Regeneration in Gap Models: Priority Issues for Studying Forest Response to Climate Change', *Clim. Change* **51**, 475–508.

Rastetter, E. B.: 1996, 'Validating Models of Ecosystem Response to Global Change', *BioScience* **46**, 190–198.

Rastetter, E. B., Ryan, M. G., Shaver, G. R., Melillo, J. M., Nadelhoffer, K., Hobbie, J. E., and Aber, J. D.: 1991, 'A General Biogeochemical Model Describing the Responses of the C and N Cycles in Terrestrial Ecosystems to Changes in CO_2, Climate and N Deposition', *Tree Physiol.* **9**, 101–126.

Reich, P. B., Grigal, D. F., Aber, J. D., and Gower, S. T.: 1997, 'Nitrogen Mineralization and Productivity in 50 Hardwood and Conifer Stands on Diverse Soils', *Ecology* **78**, 335–347.

Reynolds, J. F. and Chen, J. L.: 1996, 'Modelling Whole-Plant Allocation in Relation to Carbon and Nitrogen Supply: Coordination Versus Optimization: Opinion', *Plant and Soil* **186**, 65–74.

Running, S. W.: 1984, 'Microclimate Control of Forest Productivity: Analysis by Computer Simulations of Annual Photosynthesis/Transpiration Balance in Different Environments', *Agric. For. Meteorol.* **32**, 267–288.

Running, S. W. and Coughlan, J. C.: 1988, 'A General Model of Forest Ecosystem Processes for Regional Applications. I. Hydrological Balance, Canopy Gas Exchange and Primary Production', *Ecol. Modelling* **42**, 125–154.

Running, S. W. and Gower, S. T.: 1991, 'FOREST-BGC: A General Model of Forest Ecosystem Processes for Regional Applications: II. Dynamic Carbon Allocation and Nutrient Budgets', *Tree Physiol.* **9**, 147–160.

Schulze, E. D., Mooney, H. A., Sala, O. E., Jobbagy, E., Buchman, N., Bauer, G., Canadell, J., Jackson, R. B., Loreti, J., Oesterheld, M., and Ehleringer, J. R.: 1996, 'Rooting Depth, Water Availability, and Vegetation Cover Along an Aridity Gradient in Patagonia', *Oecologia* **108**, 503–511.

Sellers, P. J., Mintz, Y., Sud, Y. C., and Dalcher, A.: 1986, 'A Simple Biosphere Model (SiB) for Use Within General Circulation Models', *J. Atmos. Sci.* **43**, 505–531.

Shao, G., Bugmann, H., and Yan, X.: 2001, 'A Comparative Analysis of the Structure and Behavior of Three Gap Models at Sites in Northeastern China', *Clim. Change* **51**, 389–413.

Shugart, H. H. and Smith, T. M.: 1996, 'A Review of Forest Patch Models and their Application to Global Change Research', *Clim. Change* **34**, 131–153.

Shugart, H. H. and West, D. C.: 1977, 'Development of an Appalachian Deciduous Forest Succession Model and its Application to Assessment of the Impact of the Chestnut Blight', *J. Environ. Manage.* **5**, 161–179.

Shugart, H. H., Smith, T. M., and Post, W. M.: 1992, 'The Potential for Application of Individual-Based Simulation Models for Assessing the Effects of Global Change', *Annu. Rev. Ecol. Syst.* **23**, 15–38.

Shuttleworth, W. J. and Wallace, J. S.: 1985, 'Evaporation from Sparse Crops-An Energy Combination Theory', *Quart. J. R. Met. Soc.* **111**, 839–855.

Snyder, K. A. and Williams, D. G.: 2000, 'Water Sources Used by Riparian Trees Varies among Stream Types on the San Pedro River, Arizona', *Agricul. For. Meteorol.* **105**, 227–240.

Stakhiv, E. Z. and Major, D. C.: 1997, 'Ecosystem Evaluation, Climate Change and Water Resources Planning', *Clim. Change* **34**, 167–177.

Stitt, M.: 1991, 'Rising CO_2 Levels and their Potential Significance for Carbon Flow in Photosynthetic Cell', *Plant Cell Environ.* **14**, 741–762.

Thornley, J. H. M.: 1972, 'A Model to Describe the Partitioning of Photosynthate during Vegetative Plant Growth', *Ann. Bot.* **36**, 419–430.

Thornthwaite, C. W. and Mather, J. R.: 1957, 'Instructions and Tables for Computing Potential Evapotranspiration and the Water Balance', *Publ. Climatol.* **10**, 183–311.

Trabaud, L., Michels, C., and Grosman, J.: 1985, 'Recovery of Burnt *Pinus halepensis* Mill. Forests. II. Pine Reconstitution after Wildfire', *For. Ecol. Manage.* **13**, 137–179.

Tyler, C. M.: 1995, 'Factors Contributing to Postfire Seedling Establishment in Chaparral: Direct and Indirect Effects of Fire', *J. Ecol.* **83**, 1009–1020.

VEMAP members: 1995, 'Vegetation Ecosystem Modeling and Analysis Project – Comparing Biogeography and Biogeochemistry Models in a Continental-Scale Study of Terrestrial Ecosystem Responses to Climate Change and CO_2 Doubling', *Global Biogeochem. Cycles* **9**, 407–437.

Vitousek, P. M. and Howarth, R. W.: 1991, 'Nitrogen Limitation on Land and Sea – How Can It Occur', *Biogeochemistry* **1**, 87–115.

Weltzin, J. F. and McPherson, G. R.: 2000, 'Implications of Precipitation Redistribution for Shifts in Temperate Savanna Ecotones', *Ecology* **81**, 1902–1913.

Weltzin, J. F. and McPherson, G. R.: 1997, 'Spatial and Temporal Soil Moisture Resource Partitioning by Trees and Grasses in a Temperate Savanna, Arizona, U.S.A.', *Oecologia* **112**, 156–164.