

Ecological field theory model: a mechanistic approach to simulate plant–plant interactions in southeastern forest ecosystems¹

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Ecological field theory, unlike many other vegetation modeling approaches, provides a basis to construct an individually based, spatially explicit, and resource-mediated model for mechanistic simulation of plant–plant interactions and vegetation dynamics. The model REGROW has been developed, based on ecological field theory principles, to simulate vegetation dynamics for northern hardwood forests. Using data from a current study of a southern pine system to calibrate a modified version of this model, SPGROW, we simulated growth of individuals for the first growing season in stands of loblolly pine (*Pinus taeda* L.) and sweetgum (*Liquidambar styraciflua* L.) seedlings and loblolly pine seedling – sweetgum sprout mixtures. SPGROW accurately simulated stand development at population and stand levels. However, less agreement occurred at the individual level between simulated and field survey values, possibly owing to lack of data on site heterogeneity and genetic variation. Plant interactions, which altered resource availability (light, water, and nutrients) to individual plants, played a major role in differentiating plant size in the model. Given its unique model structure and simulation accuracy, SPGROW has the potential to provide very detailed insight into the mechanisms of plant–plant interactions.

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Contrairement à plusieurs autres approches de modélisation de la végétation, la théorie écologique opérationnelle procure les fondements pour l'élaboration d'un modèle qui effectue une simulation mécaniste des interactions entre les plantes et de la dynamique de la végétation. Ce type de modèle est basé sur les individus, est spatialement explicite et tient compte de la ressource. Le modèle REGROW a été développé à partir des principes de la théorie écologique opérationnelle pour simuler la dynamique de la végétation dans les forêts feuillues nordiques. À l'aide de données provenant d'une étude en cours sur un système applicable au pin du sud et visant à calibrer une version modifiée de ce modèle, appelée SPGROW, nous avons simulé la croissance des individus pour la première saison de croissance dans des peuplements composés de semis de pin à encens (*Pinus taeda* L.) et de liquidambar (*Liquidambar styraciflua* L.) et de mélanges de semis de pin à encens et de rejets de liquidambar. SPGROW a simulé adéquatement le développement des peuplements au niveau du peuplement et de la population. Cependant, au niveau des individus, il y avait moins de concordance entre les valeurs simulées et les données d'un inventaire sur le terrain, possiblement à cause d'un manque d'information sur l'hétérogénéité du site et sur la variation génétique. Les interactions entre les plantes qui altèrent la disponibilité des ressources pour les plantes prises individuellement, telles la lumière, l'eau et les nutriments, ont joué un rôle important dans la différenciation de la dimension des plantes dans le modèle. Étant donné sa structure unique et la justesse de sa simulation, le modèle SPGROW peut fournir une compréhension très fine des mécanismes d'interaction entre les plantes.

[Traduit par la rédaction]

Introduction

Plant–plant interactions, specifically competition, strongly influence plant community dynamics and ecosystem structure. This is particularly true in the ecologically and economically important pine forests of the southeastern United States (Gjerstad and Barber 1987). Although these forests are among the most intensively managed ecosystems in North America (Vitousek and Matson 1984), little is known about the ecophysiological mechanisms that control plant interactions such as competition. Developing an understanding of these mechanisms and of plant interactions in general is important if forest management is to be based on sound ecological principles.

Recently, a conceptual model in which competitive effects are separated from competitive responses has been suggested as a theoretical foundation on which more mechanistic studies of resource competition can be developed (Bazzaz and Sipe 1987; Goldberg 1990). Plant–plant interactions are viewed as

a two-part process, i.e., the influence of the plant neighborhood (Weiner 1990) on resource availability (competitive effects) and the response of plants to available resources as determined by the physical environment modified by the neighboring plants (competitive response). This perspective provides several important features necessary to mechanistically approach competition.

First, competition is studied in relation to an individual and its spatially explicit interaction with neighboring plants. Plants are sedentary, and thus respond to proximity, size, and behavior of adjacent plants (Solbrig 1981; Silander and Pacala 1985; Weiner 1990). Second, resources within the domain of an individual plant are controlled by the structure of the neighborhood and the physical environment. Distribution of resources among plants within a neighborhood depends on the architecture of resource-acquiring organs (roots and leaves) as well as their physiological activities. Finally, the outcome of plant–plant interactions is driven by the neighboring plants' influence on resources and by acquisition of those resources by individual plants, rather than by the direct effect of neighbors on an individual.

Recently, several models based upon ecological field theory (EFT) have been developed to describe competitive effects and responses in an effort to understand the mechanisms of competitive interactions. These models predict individual plant

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response as a function of both neighborhood structure and resource availability (Wu et al. 1985; Walker et al. 1989; Mou 1991) with multiple resource limitations to plant growth quantitatively described by either continuous time Markovian mathematics (CTM) (Olson et al. 1985; Sharpe et al. 1985; Mou and Fahey 1993) or its improved form, integrated rate methodology (Wu et al. 1994). Use of the EFT approach allows for a model that is individually based, spatially explicit, and resource mediated. This paper (i) introduces EFT and its application to the study of competition in a forest ecosystem; (ii) contrasts the EFT approach to those used in other models; (iii) demonstrates the utility of the EFT-based model SPGROW in simulating plant–plant interactions among multiple life forms commonly associated in early successional southern pine forests; and (iv) discusses the deficiencies of this approach.

Model development and EFT model

Despite the short history of modeling in plant ecological research, a relatively large number of vegetation dynamic simulation models have been developed, such as JABOWA (Botkin et al. 1970; Botkin 1981), FOREST (Ek and Monserud 1974), FORET (Shugart and West 1977), ALLOCATE (Tilman 1988), neighborhood models (e.g., Weiner 1982, 1984), plant population dynamics models by Pacala and Silander (1985, 1987; Silander and Pacala 1985, 1990), and models derived from EFT. Some of these models greatly simplify plant–plant interaction in order to provide better detail on long-term community dynamics. Others, however, are designed to elucidate basic mechanisms underlying vegetation dynamics.

Because interactions among plants ultimately occur among individuals located within a neighborhood (Weiner 1990), and interactions are indirectly influenced by proximity and size of neighbors (Harper 1977; Solbrig 1981; Silander and Pacala 1985; Weiner 1982), the mechanisms of plant–plant interactions are obscured by ignoring local interactions among individual plants as a function of their relative locations and sizes (Huston et al. 1988; Silander and Pacala 1985). Furthermore, the competitive response of a plant is not directly to its neighbors (e.g., as in allelopathy); rather, the response is to resource availability (light, soil moisture, and nutrients) as determined by the abiotic environment and modified by the structure of the neighborhood (Bazzaz and Sipe 1987; Goldberg 1987, 1990). Thus, mechanistic models of competitive interactions should be individually based, spatially explicit, and resource driven.

Many earlier models used a statistical curve fitting approach, which has several inherent advantages (i.e., precise numerical and graphical representation of data). However, this approach suffers from a lack of generality, along with an inability to mechanistically represent the interactions (Sharpe and Rykiel 1991). Tilman (1988) developed a model ALLOCATE that simulates the behavior of grassland communities at the population level. Thus, its applicability to simulating interactions among individuals, particularly those differing in life form, may be limited. Models of forest succession, e.g., JABOWA (Botkin et al. 1970), FORET (Shugart and West 1977), and other gap models (Shugart 1984), are not spatially (horizontal) explicit at the scale of an individual seedling and sapling; therefore, no means exist for representing spatial heterogeneity in soil resources and the relative location of simulated plants. This limits the ability of these models to mechanistically describe

competitive effects and responses of individuals during early successional stages, when much of the stand structure is determined. Most gap models also treat individuals as the average of the population and do not account for size and proximity differences within neighborhoods. Pacala and Silander (1985, 1987) greatly improved the individually based property of their models by specifying relative locations of interacting individuals and the size of focal plants. However, their model, like all other neighborhood models, treat neighboring individuals at the population level. Although these models are effective in simulating vegetation dynamics at high levels of organization (community and landscape) and for longer periods of time, they may not be ideal in mechanistically simulating plant competition among multiple life forms, particularly during the early events of forest succession (i.e., during the first 5 years).

Some mechanistically based models have been developed to simulate the influence of the environment on physiological processes of individual leaves (reviewed by Reynolds and Acock 1985) or of individual plant organs (Hall 1979; Chartier and Prioul 1976; Deans and Ford 1983; Henderson 1981; Ford et al. 1987a, 1987b). These models provide very detailed insight into the mechanisms that influence many physiological processes. However, the significance of such detail may be lost when the models simulate higher level vegetation dynamics (Shugart 1984). Moreover, these models often require detailed data that seriously constrain the simulation of plant–plant interactions at the scale of a plant neighborhood, particularly when the neighborhood is composed of plants that differ in life form.

EFT combined with CTM allows for spatially explicit models of resource availability as influenced by neighborhood structure and simulates the influence of multiple-resource limitations on individual plant growth (Wu et al. 1985, 1994; Sharpe et al. 1985; Olson et al. 1985; Walker et al. 1989; Mou and Fahey 1993). EFT provides an approach for studying neighborhood relationships in which the spatial interactions among plants are functions of proximity, size, and plant structural features (architecture and morphology) as they influence resource availability (Walker et al. 1989; Mou 1991).

The EFT modeling approach consists of two distinct portions to calculate interactive (competitive) effects and responses. In the first EFT portion, spatial variation in resource availability is calculated based on site resource availability and neighborhood structure. Resource availability to each individual plant is also calculated in this EFT portion. A second portion of the model evaluates the growth rate of each individual plant and its dimensional changes based upon its resource acquisition.

Rather than using an index of neighborhood structure, e.g., distance of neighbors and focal plant size, EFT explicitly evaluates the influence of plants on the available resources within their domains as determined by geometric representation of root and crown architecture. EFT then distributes resources at each location to each individual plant present within that location. Therefore, plants interact only when their domains overlap and interact only within the overlapped region. The intensity of the effect of a plant (either positive or negative) on a resource at any given location within the plant's domain depends on plant size, the distance from that location to the center of the plant, the plant's physical (i.e., morphological and architectural) characteristics, and related species'

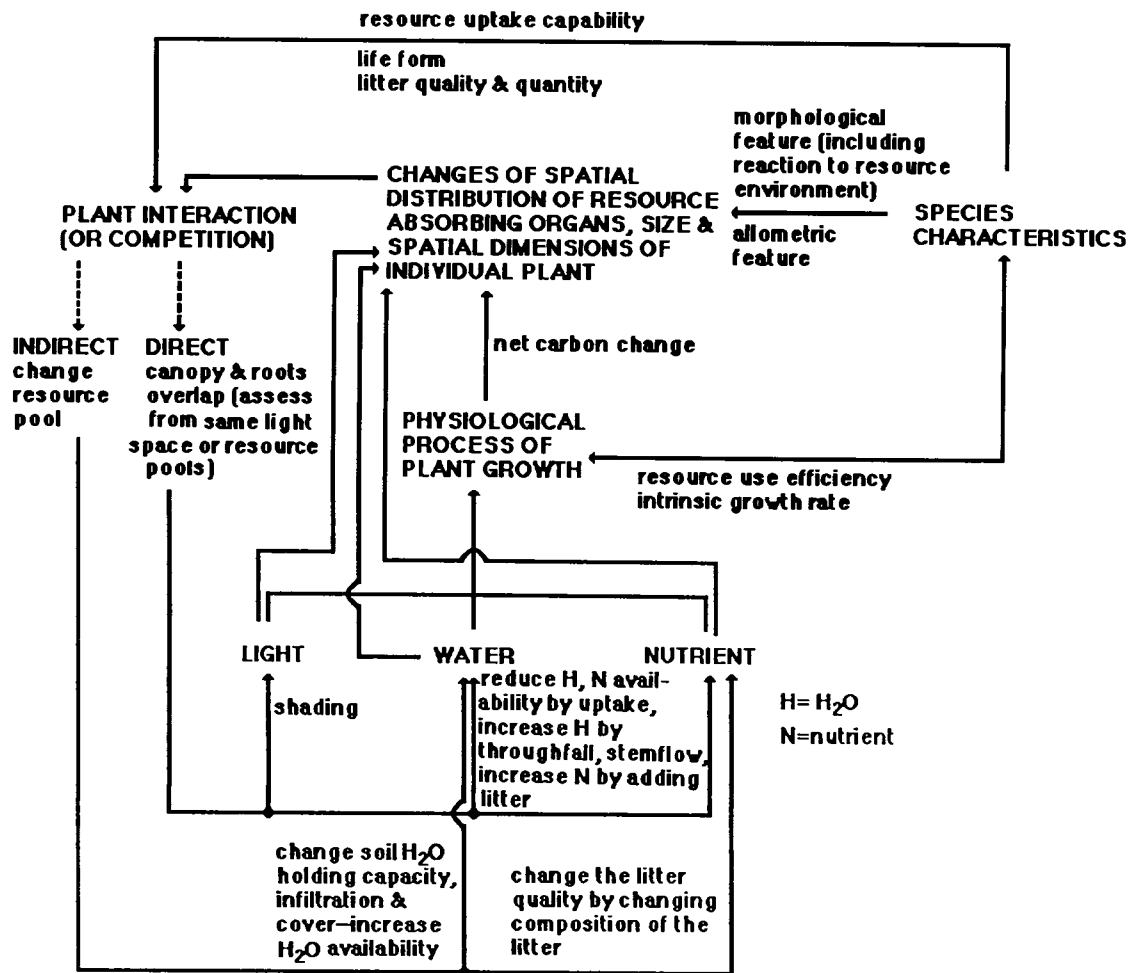


FIG. 1. A flowchart of the conceptual structure of SPGROW.

(physiological) characteristics. The different effects of canopy, stem, and roots on site resource availability are calculated separately and then summed to estimate total plant effect. Under noninteracting situations (without overlapping plant domains), soil resources available to a plant from a given location within its domain depend on the resources supplied from the substrata. However, under interacting situations, if the resource availability from that location is not sufficient to fully meet the requirements of interacting plants, then resources are partitioned to interacting individuals based upon their influence intensity. The final soil resource availability (water or nutrient) for each individual is calculated by summing and normalizing the available resources to that plant at all locations within its domain. Light availability for any individual plant is determined based upon its height, leaf distribution, and the height of interacting neighbors.

The resources (light, water, and nutrients) acquired by an individual are then introduced into a CTM equation to calculate growth. In our model, each unit of resource acquired by various species will differentially affect growth rates depending upon species resource use efficiency characteristics.

In this way, the model treats competitive effects and responses separately, with each closely interacting with the other through time. Although this theory and modeling approach are data intensive, they provide general guidance for studying plant–

plant interactions more mechanistically, and they resolve some difficult problems inherent in neighborhood approaches.

This modeling approach has been successfully applied to simulations of vegetation dynamics in an Australian woodland (Walker et al. 1986, 1989; Penridge et al. 1987; Walker and Dowling 1991). The model REGROW was also developed using this approach to simulate early successional changes in a northern hardwood forest at Hubbard Brook Experimental Forest, New Hampshire. In REGROW, a grid system (each cell is 10 × 10 cm) was developed to represent spatial resource heterogeneity, relative locations, and domains of influence (Mou and Fahey 1993). The basic logic of the model system is shown in Fig. 1. Spatially explicit site resource availability at each point in space and time is evaluated as a function of physical site factors, such as organic matter content, precipitation, and groundwater table. Resource levels are then modified through the influence of plants (canopy, stem, and root) at a particular location within a plant's or a group of plants' domain(s).

Wu et al. (1985) developed six equations (eqs. 1–6 of Table 1; see Appendix for variable definitions) that serve the following functions in the model: (i) determine the spatial effect of an individual plant on each specific resource (light, water, and nutrients); unique effects due to roots, stem, and canopy are calculated separately (eqs. 1–3 of Table 1); (ii) calculate the

TABLE 1. Important equations of EFT in calculating plant influence on site resource availability, residual resources, and resource availability to individual plants (Wu et al. 1985; Mou et al. 1991)

$$\begin{aligned}
 [1] \quad P_{Rir} &= \frac{b_i + c_i \exp[-\mu_i |r - r_i|]}{1 + \exp[\beta_i [(r - r_i)^2 - a_i^2]} \\
 [2] \quad P_{Cir} &= P_{C0i} \exp[-\phi_i (r - r_i)^2] \\
 [3] \quad P_{S\bar{r}} &= \exp[-z_i |r - r_i|] \\
 [4] \quad H_y &= H_{y-1} (1 - h_R P_{Ry}) (1 - h_C P_{Cy}) (1 + h_S P_{Sy} \pi P_{C0k} / \partial_y) \\
 [5] \quad N_y &= N_{y-1} (1 - n_R P_{Ry}) (1 + n_C P_{Cy}) (1 + n_S P_{Sy} \pi P_{C0k} / \partial_y) \\
 [6] \quad l_y &= l_{y-1} (1 - P_{Cy}) \\
 [7] \quad H_i &= \left(\sum_{r=0}^{a_i} P'_{Rir} H_{0r} \right) / \left(\sum_{r=0}^{a_i} \sum_{k=1}^n P_{Rkr} \right) \\
 [8] \quad N_i &= \left(\sum_{r=0}^{a_i} P'_{Rir} N_{0r} \right) / \left(\sum_{r=0}^{a_i} \sum_{k=1}^n P_{Rkr} \right) \\
 [9] \quad P'_{R\bar{r}} &= P_{R\bar{r}} / \left(\sum_{k=1}^n P_{Rkr} \right) \\
 [10] \quad l_i &= \sum_{x=1}^n A_{Lx} V_x \\
 [11] \quad A_{Lx} &= W_{LKx} / W_{LK} \\
 [12] \quad V_x &= V_0 \exp(-kx) \\
 [13] \quad k &= \ln(1/m_x) / -mx \\
 [14] \quad \Delta W / \Delta t &= W_{LK} \Omega q(l_i H_i N_i) / (l_i H_i + l_i N_i + N_i H_i) \\
 &\quad - 1 / \{1 + \exp[\Delta H_L / g(1/T_{1/2L} - 1/T)] + \exp[\Delta H_L / g(1/T_{1/2H} - 1/T)]\} W_{LB} \\
 [15] \quad \Omega &= ((W_n / W_0)^{1/n} - 1 + R_i W'_{LB}) / (rkr)
 \end{aligned}$$

residual resource availability (light, water, and nutrients) after plant uptake at each site (eqs. 4–6 of Table 1).

These equations use general morphological patterns (root, stem, and canopy) to determine their effects on resources in a spatially explicit manner. Both water and nutrient availability (soil resources) are affected by canopy, roots, and stems, and the calculated value for each resource at any particular location may be influenced by many individuals. The difference between the original site soil resource availability and the total plant effect (positive or negative) is the residual soil resource availability. The residual soil resource levels are calculated by eqs. 4 and 5 in Table 1 (note that the stem influence on water and nutrients is related to the canopy volume calculated as $\pi P_{C0k} / \partial_y$). Light availability at the ground level is influenced only by the canopy, slope, aspect, and latitude.

Other equations (7, 8, and 10 of Table 1) developed by Mou (1991) calculate resource availability (water, nutrients, and light) for each individual plant at each simulation time step. Calculations for water and nutrient availability for each plant were accomplished by summing the resource partitioned to the plant based upon its relative influence intensity at each location (eq. 9) within its domain (eqs. 7 and 8). Light avail-

ability to any individual (eq. 10) is estimated by summing the products of relative leaf proportion (eq. 11) and relative light intensity (eq. 12) as described by Beer's law (eq. 13) for each canopy layer.

After resource availability to each individual is determined in the EFT portion of the model, the plant growth portion of the model simulates growth rate and dimension changes for each plant. CTM is a quasi-physiological simulation of the photosynthesis process (see eq. 14 in Table 1) and is described in detail by Olson et al. (1985), Wu et al. (1994), and Mou (1991). For each time step, changes in plant size and dimension due to growth determine the pattern of subsequent plant interactions and resource availability. Iteration of the steps will simulate plant interaction and overall vegetation dynamics through time.

In this model exercise, we used the model REGROW as the basic frame for simulating a loblolly pine (*Pinus taeda* L.) – sweetgum (*Liquidambar styraciflua* L.) system. The modified version of REGROW is referred to as SPGROW to indicate its origin and application to southern pine forest stands. We kept the basic structure and equations of REGROW as described above, but several modifications were made. First, modifications were incorporated to alter canopy effects for an ever-

green tree species relative to deciduous trees. Second, to more mechanistically simulate canopy effect on light, we represented the change in canopy shadow cast throughout the growing season, which is a function of the slope, location (latitude), time (both diurnal and seasonal), and the height of the plant (Campbell 1977). Consequently, the cast was enlarged to an ellipse and moved to the north of the plant, which contrasts the vertical projection of the canopy by directly applying eq. 2 in Table 1. Therefore, corresponding changes were made so that light competition in SPGROW was only from neighbors to the south. Finally, rather than using a consistent ratio of leaf mass / total mass, leaf biomass changes over the growing season were simulated by using a modified sine curve and a modified normal curve for loblolly pine and sweetgum, respectively, based on literature results and our own field observation. In addition, the module for forest floor dynamics was idled in SPGROW since there was no forest floor accumulation before the trees were planted. The purpose of the simulation was to (i) demonstrate the model's capability for handling population dynamics in early successional vegetation in the southeastern United States and (ii) delineate limitations that future improvements must address.

Model simulation

Data set and model parameterization

Loblolly pine, the most common species in the southern pine ecosystem, is a fast growing timber species and consequently has been extensively planted throughout the South. Sweetgum, a common associate of loblolly pine, regenerates from seedlings or stump and root sprouts and may quickly dominate early successional sites (Miller et al. 1991). To test the degree to which SPGROW could simulate pine-sweetgum interactions with only allometric data and other limited information plus some data from the literature, we used three plots from an ongoing field study located at the E.V. Smith Research Center of Auburn University. To parameterize the model, we used information from the E.V. Smith study, such as local weather data (including precipitation, potential and actual evaporation, and temperature) and soil organic matter content (see below).

The E.V. Smith Research Center is located near Shorter, Ala., about 40 km east of Montgomery, Ala. Soils are of the Malbis series (fine-loamy, siliceous, thermic, Typic Hapludults), a typical soil for the Upper Coastal Plain of Alabama. The land has been continuously cultivated. The mean annual precipitation during 1987-1992 was 1024 mm, with a typical drought period from late July to October, when less than 20% of annual precipitation occurred. Mean annual evaporation (pan evaporation) was 1063 mm, and the highest evaporation was during the drought period. Mean maximum air temperatures in July and January were 33°C and 13°C, respectively. Mean minimum air temperatures were 20°C and 2°C in July and January, respectively.

The ongoing study is a complete factorial design of an addition series experiment to investigate plant competition among three species (loblolly pine, sweetgum, and broomsedge (*Andropogon virginicus* L.)) representing three life forms at various densities and combinations. The dimensions of each plot were approximately 5 × 9 m, and each plot was further divided to 44 subplots of 1 m². Plants were randomly arranged within the subplot depending on the density and species combination arrangement. Sweetgum seedlings (1-0) were planted

TABLE 2. Site resource availability and average air temperature for each time step

Time step	Water	Light	Nutrient	Temperature (°C)
1	3.00	0.35	0.50	8.6
2	3.00	0.22	0.55	12.4
3	3.00	0.30	0.58	12.7
4	3.00	0.43	0.61	13.8
5	3.00	0.48	0.65	14.1
6	2.80	0.54	0.70	15.5
7	2.50	0.49	0.77	14.7
8	3.00	0.65	0.85	15.9
9	2.80	0.82	0.83	22.4
10	2.50	0.65	1.10	20.5
11	2.08	0.76	1.20	22.4
12	2.07	0.91	1.20	26.0
13	1.83	1.00	1.15	26.6
14	1.14	0.91	1.10	27.7
15	1.10	0.79	1.05	26.1
16	0.99	0.88	0.99	26.5
17	0.89	0.83	0.80	28.1
18	0.80	0.72	0.80	27.8
19	0.75	0.77	0.73	25.8
20	0.89	0.61	0.75	20.8
21	0.80	0.53	0.74	18.3
22	0.70	0.48	0.70	14.3
23	0.86	0.39	0.69	13.7
24	1.30	0.24	0.65	14.2
25	1.80	0.21	0.60	10.7
26	2.50	0.24	0.54	12.3

NOTE: Information from 1991 was used to make this table. The time step count was from Julian day 1 to 365, and each 14 days was one time step (the Julian day 365 was put into the last time step). Growing season started at the 5th time step for both species and ended at the 20th time step for loblolly pine and the 19th time step for sweetgum.

1 year prior to pine planting and cut after the first growing season to stimulate resprouting to mimic a typical artificial regeneration practice of planting pines into a forest composed of sweetgum rootstocks. Bare-root loblolly pine seedlings were planted from late January through February of 1990.

Plot 105, plot 108, and plot 98 were arbitrarily selected for this simulation exercise. Within each plot, exact locations of all the individuals and their initial and final biomass were measured. Mean soil organic matter content for each plot was determined as described by Perry (1993). Plot 105 was a pure sweetgum seedling plot with a density of 1 seedling/m². Plot 108 was a pure pine seedling plot with a density of 2 seedlings/m², while plot 98, a mixture of pine seedlings and sweetgum sprouts, had a density of 1 sweetgum rootstock sprout + 1 pine seedling/m².

A local weather station provided detailed weather data on a daily basis. These data were averaged on a biweekly basis to fit a model simulation with a time step of 2 weeks (Table 2). Soil water availability in each time step was evaluated by subtracting mean evaporation from precipitation and then adding the water budget from the previous time step (Table 2). Because continuous field light measurements were not available, the ratio of mean evaporation of each time step to the annual maximum evaporation (the best indicators of light conditions available) was used to determine the light availability of each time step above the canopy. Also, solar declination angle was used to modify available light throughout

TABLE 3. Regression models of total weight versus plant dimensions for the two species used in this modeling exercise

Dimensions(Y)	Model*	r ²
Loblolly pine		
Leaf wt. (g)†	Y = 0.176X (X > 500 g) Y = 0.466X (X < 100 g)	
Stem wt. (g)†	Y = 0.473X (X > 500 g) Y = 0.209X (X < 100 g)	
Root wt. (g)†	Y = 0.351X (X > 500 g) Y = 0.325X (X < 100 g)	
Crown diam. (m)	ln(Y) = 0.348 ln(X) + 2.200	0.885
Root diam. (m)	ln(Y) = 0.432 ln(X) + 1.484	0.810
Height (cm)	ln(Y) = 0.380 ln(X) + 2.936	0.929
Crown length (cm)	ln(Y) = 0.354 ln(X) + 2.664	0.937
DBH (cm)	ln(Y) = 0.777 ln(X) - 5.004	0.932
Basal diam. (cm)†	ln(Y) = 0.829 ln(X) - 3.301(X > 500 g) ln(Y) = 0.988 ln(X) - 3.090(X < 100 g)	0.956 0.998
Sweetgum		
Leaf wt. (g)†	Y = 0.160X (X > 500 g) Y = 0.260X (X < 100 g)	
Stem wt. (g)†	Y = 0.298X (X > 500 g) Y = 0.248X (X < 100 g)	
Root wt. (g)†	Y = 0.542X (X > 500 g) Y = 0.492X (X < 100 g)	
Crown diam. (m)	ln(Y) = -0.444 ln(X) + 1.290 (seedling) ln(Y) = -0.534 ln(X) + 0.902 (sprouts)	0.913 0.983
Root diam. (m)	ln(Y) = -0.604 ln(X) + 0.257	0.849
Height (cm)	ln(Y) = -0.372 ln(X) + 2.814 (seedling) ln(Y) = -0.336 ln(X) + 2.612 (sprouts)	0.893 0.956
Crown length (cm)	ln(Y) = -0.440 ln(X) + 2.216	0.929
DBH (cm)	ln(Y) = -0.762 ln(X) - 5.061	0.881
Basal diam. (cm)	ln(Y) = -0.835 ln(X) - 3.852	0.958

*X, total weight (in grams).

†When plant biomass was 100 and 500 g, a linear interpolation was used to estimate dimensions.

TABLE 4. A list of constants used in SPGROW

Parameter	Loblolly pine	Sweetgum
β	0.5	0.9
b	0.4	0.4
c	0.3	0.7
μ	1	1
φ	1.6	0.55
z	13.0	15.0
P _{C0}	0.9	0.75
Leaf N concn. (‰)	1.321	1.460
Root density (g/cm ³)	0.0153	0.0487
Ω	0.072	0.035
q	0.85	0.91
P _R	0.82	0.85
P _C	0.15	0.10
P _S	0.03	0.05
k	2.50	1.40
ΔH _H (kcal·mol ⁻¹)		100
ΔH _L (kcal·mol ⁻¹)		40
T _{1,2L} (°C)		15
T _{1,2L} (°C)		55

NOTE: One kilocalorie = 4.19 kJ.

TABLE 5. Comparison between the model simulation and a field survey (stand)

	Final mass (g)			Error (%)*
	Initial mass (g)	Field survey	Simulation	
Plot 98 (loblolly pine; 2 seedlings/m²)				
Sum	187.85	5 275.25	5 334.08	1.01
Mean	3.91	109.90	111.13	1.01
SD	1.61	24.93	53.82	115.88
Plot 105 (sweetgum; 1 individuals/m²)				
Sum	313.43	9925.45	9931.89	0.01
Mean	13.06	413.56	413.83	0.01
SD	5.56	169.63	177.29	1.05
Plot 108 (1 loblolly pine + 1 sweetgum/m²)				
Loblolly pine				
Sum	109.20	2 883.80	3 042.80	5.51
Mean	4.55	120.16	126.78	5.51
SD	1.72	49.69	65.07	30.95
Sweetgum				
Sum	12 035.0	18 639.0	17 171.0	-7.88
Mean	501.5	776.6	715.5	-7.88
SD	195.3	413.9	174.8	-57.77

*Error is calculated by the following: 100 × (dry weight_{simulation} - dry weight_{field survey}) / dry weight_{field survey}

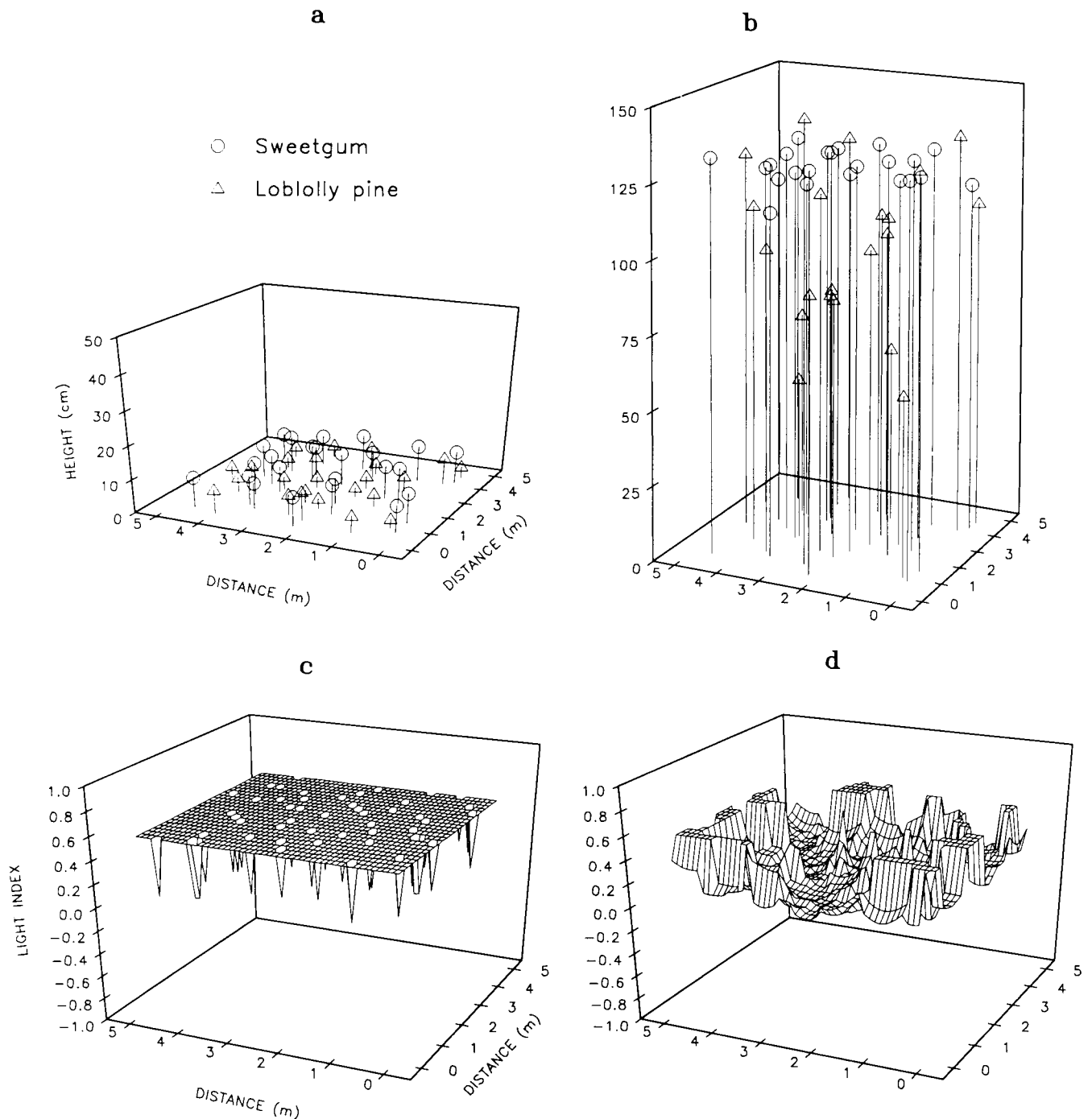


FIG. 2. Spatial graphs (for plot 108) showing the initial and final (*a* and *b*) plant distributions, (*c* and *d*) light availability at the ground level, (*e* and *f*) water residual availability, and (*g* and *h*) nutrient residual availability.

the growing season. These two factors were equally weighted (Table 2). Literature results (Vitousek and Matson 1985) relating soil organic matter content, temperature, and soil moisture were used to evaluate availability of soil nitrogen (the most limiting nutrient at the site) for each time step (Table 2). Biweekly averages of solar elevation angle and solar declination angle were calculated for canopy cast computation.

To parameterize allometric relations that determine plant influential domains, more than 30 individual plants of various sizes for each modeled species were excavated on sites close to the Auburn University campus. The basal diameter, DBH

(if the plants were tall enough), height, crown diameter, crown length, root system radius, root depth, radial growth, and height growth of these plants were measured. Subsequently, they were separated by leaves, roots, and stems to determine oven-dry (60°C) mass. Regression relationships were established between total plant mass and each dimension. These factors were similarly regressed against aboveground plant biomass (Table 3).

We assumed symmetry in all directions for a plant influence on site (except for light). The influence intensity is based upon the constants β , b , c , μ , ϕ , and z in the EFT equations. Values

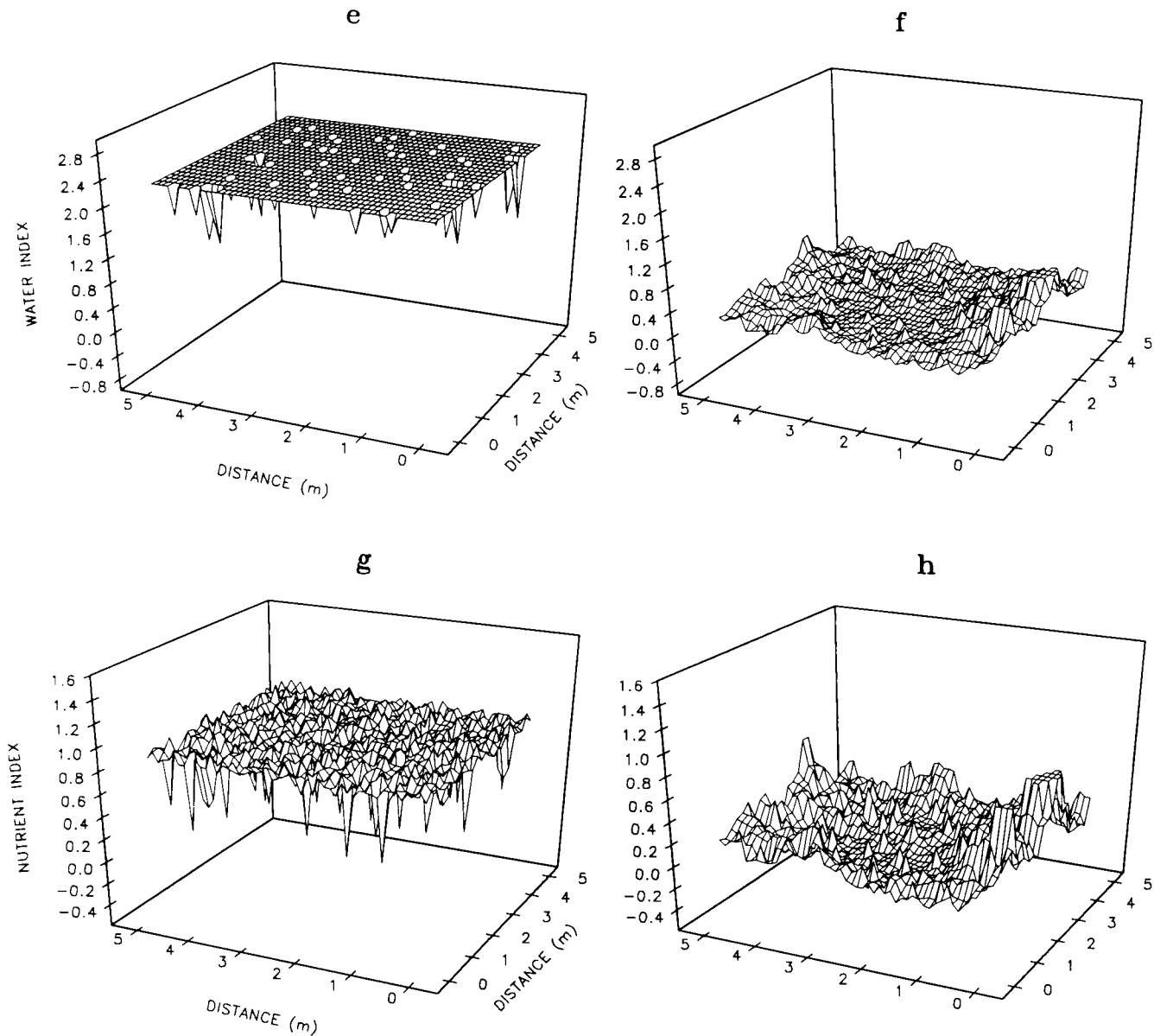


FIG. 2 (concluded).

for these constants (Table 4) were determined based upon the allometry data and general plant morphology. The highest root densities close to the stem and the average root density at the extended region of the root system determine c and b , respectively. However, β , μ , ϕ , and z were estimated by general observation of the species owing to lack of detailed information. Usually, the z value is large since the stem influence on resources diminishes quickly as distance from stem increases. Considering that sweetgum has smoother bark and is mostly multitemmed owing to its sprouting origin, we assumed that the stem effect may extend further, thus we gave sweetgum a lower z value, which will reduce the diminishing rate of stem influence (eq. 3 in Table 1). Higher leaf mass / total mass ratio and less dramatic seasonal change in leaf mass resulted in a higher ϕ value for loblolly pine. Increased root mass close to the stem for sweetgum (P. Mou, unpublished data) led to a higher sweetgum β value. The leaf vertical distribution and canopy light reduction coefficient of each species

was also estimated from field observation. The weighting factors used in eqs. 4 and 5 (Table 1) were arbitrarily assigned because of lack of information (Table 4).

The ratio of leaf mass to total plant mass for loblolly pine fluctuates around an average value (McCarthy and Skaggs 1992; Dalla-Tea and Jokela 1991; Sionit et al. 1985) that can be accurately described by a sine curve with a coefficient to control the amplitude of the fluctuation. The dynamics of this ratio for sweetgum, a deciduous tree, follow a different pattern and can be described by a modified normal curve that simulates a quick leaf mass increase to the maximum in the early growing season and a gradual decrease after July.

We assumed that outer bark and stem or root heartwood were dead tissue. Sapwood was assumed to have 10% living parenchyma tissue. Based upon our allometric data, we estimated the ratio of living mass to total plant mass. This ratio will decrease as plants grow. However, since our simulation covered only one growing season and plants were generally

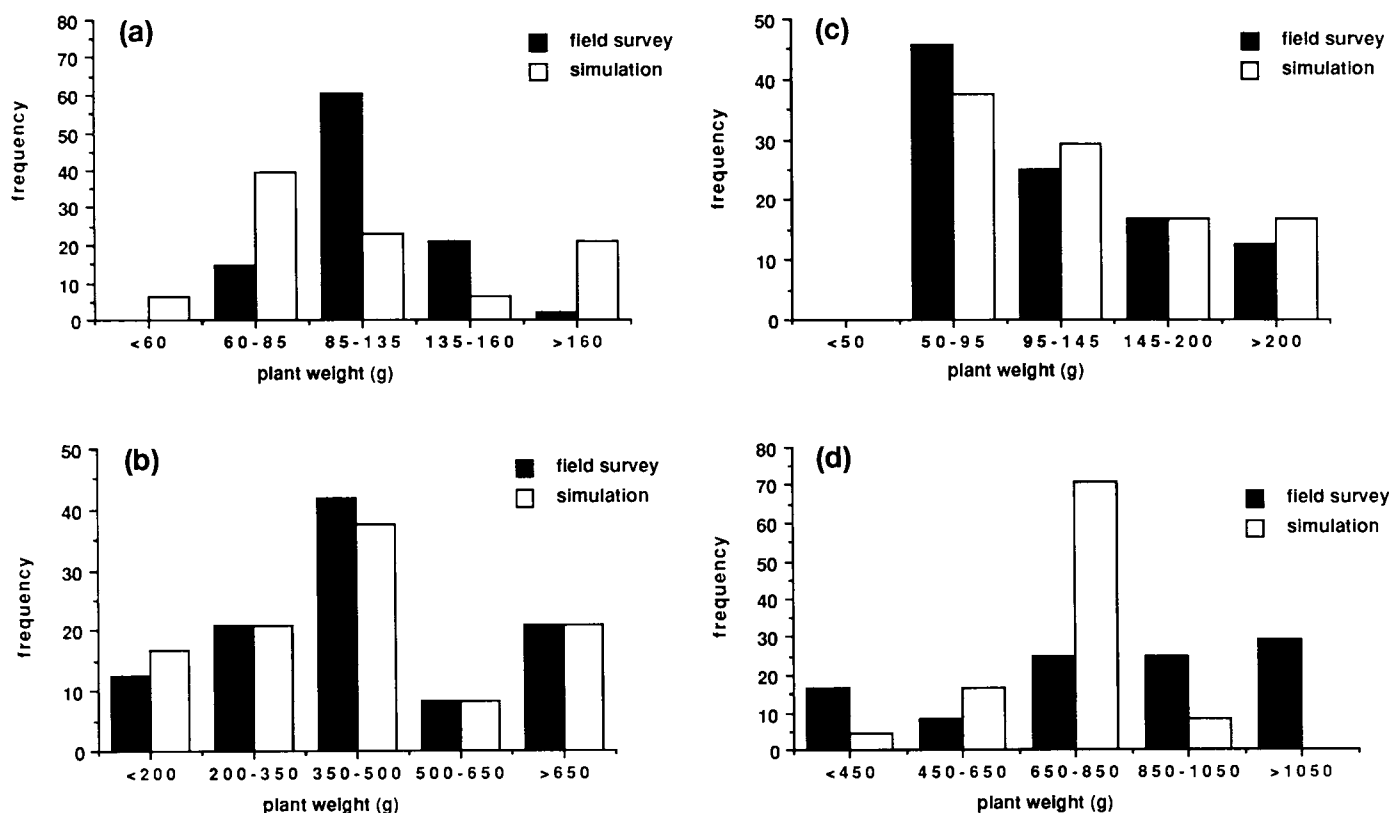


FIG. 3. Plant size frequency comparison between model simulation and field survey results. (a) Plot 98, pure loblolly pine stand. (b) Plot 105, pure sweetgum stand. (c) Plot 108, loblolly pine population. (d) Plot 108, sweetgum population.

small. we classified all plants into three classes: (i) plants weighing less than 100 g, (ii) those weighing more than 500 g, and (iii) those weighing between 100 and 500 g. For class 1, we assumed 100% of their mass to be alive. For class 2, 45% and 55% of the total plant mass was assumed to be alive for loblolly pine and sweetgum, respectively. For class 3, the ratio changed linearly from 100% to 45% for loblolly pine and from 100% to 55% for sweetgum plants based on the weight of each individual. Plant respiration was estimated by Sharpe's (1983) analytical equation (the second part of growth eq. 14 in Table 1) and was applied to live mass.

The final two calibrations for the model were the "intrinsic growth factor", Ω , (eq. 15 in Table 1), and the "unknown factor", q . To estimate Ω , first, we determined n , the total number of time steps in a growing season. Sweetgum started to grow in mid-March and ended in mid-October, and loblolly pine began growth in mid-March and ended in late-October. We arbitrarily set each time step as 2 weeks, so that n in this model equals 15 for sweetgum and 16 for loblolly pine. Second, we selected a few individuals from each species (from plots not used in the final simulation) with the highest known W_n/W_0 ratios, and calculated the mean W_n/W_0 ratios among them to represent the highest growth rate of the two modeled species. A representative individual for each species was determined by using the average ratios. Third, we ran the model for each of these representative individuals with q being set as unity to get values of kr , R_n , W'_{LB} and r (Appendix) of that plant for all the time steps. These values were then averaged among time steps and introduced into eq. 15 (Table 1) for computing an initial Ω . Finally, the final Ω value was deter-

mined, for each species, by iteratively running the model for that plant to adjust Ω until final mass was accurately estimated. After Ω was determined in this way, it was used as a constant in all subsequent simulations (Table 4). Furthermore, all the parameters, constants, and site data used in determining Ω were not subjected to change in the subsequent model simulation. These Ω values were not only species specific, but also site specific.

Two ways are possible to calibrate the model to determine q , the unknown factor in eq. 14 (Table 1), i.e., calibration at an individual level or at the community (or population) level. The former is accomplished by running the model to simulate a single individual, and q is adjusted until predicted and actual field values are equal. An average q value is then calculated for a few individuals of the same species and is used in model simulation. Alternatively, one may use a population or a community as the base to adjust q . We used another two plots of pure pine and pure sweetgum (not used in simulation) to adjust q values for both species. Values of q close to 1 for both species (Table 4) indicated that (i) the model captured most of the key factors influencing plant growth or (ii) errors inherent in the simulation are compensating within the model structure.

Results and discussion

We used the model to perform a 1-year simulation for these three plots. Table 5 shows simulation results compared with the field survey values at both the plot level and individual plant level. Figs. 2a-2h indicate spatial distribution of individual plants, light availability, at the ground level, soil water

TABLE 6. Error frequency for individual plants

Error ranges (%)	Plot 98 Loblolly pine		Plot 105 Sweetgum		Plot 108			
	No. of individuals	Percent frequency	No. of individuals	Percent frequency	Loblolly pine		Sweetgum	
					No. of individuals	Percent frequency	No. of individuals	Percent frequency
<10	6	12.5	5	20.8	6	25.0	4	16.7
10–30	12	25.0	7	29.2	10	41.7	9	37.5
30–50	21	43.8	7	29.2	5	20.8	6	25.0
50–100	8	16.7	2	8.3	3	25.0	1	4.2
100–4000	1	2.0	3	12.5				
>4000							3*	12.5
Total	48	100.0	24	100.0	24	100.0	24	100
Minimum		5.0		2.0		5.0		1
Maximum		196.0		251.0		73.0		18 867*

*Several sweetgum individuals failed to sprout until very late in the growing season and thus had a large error range in the simulation versus field survey.

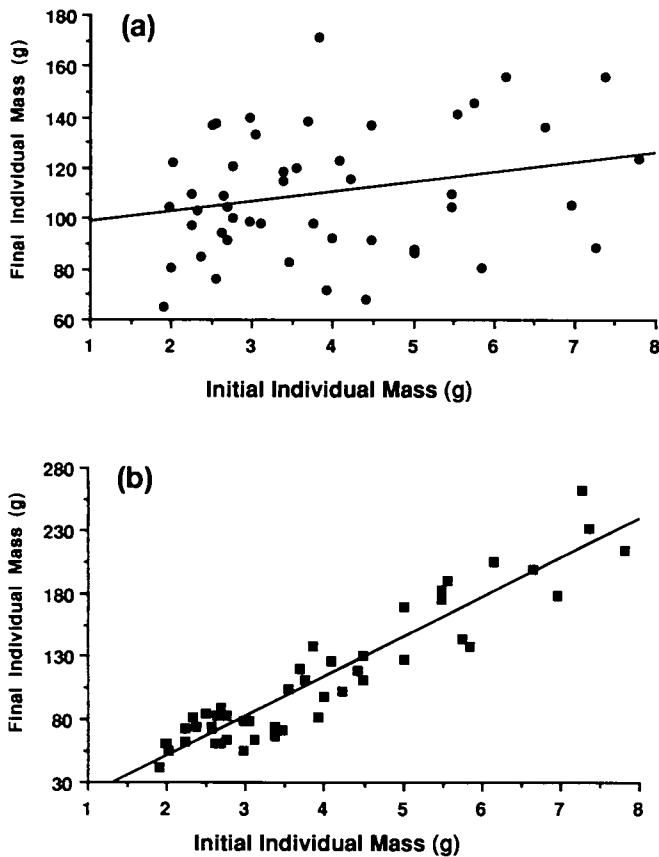


FIG. 4. Scatter graph comparison between simulation and field survey for the relationship between initial mass and final mass. (a) Result from field survey. (b) Result from simulation.

availability, and nutrient availability as influenced by plants at the initial and final stage of the simulation. Plots of resource availability during the simulation period (not shown) demonstrate tremendous resource spatial heterogeneity created when plants initially interact and show a trend toward decreased heterogeneity and resource availability as plants grow and interactions become more intense. These trends were also

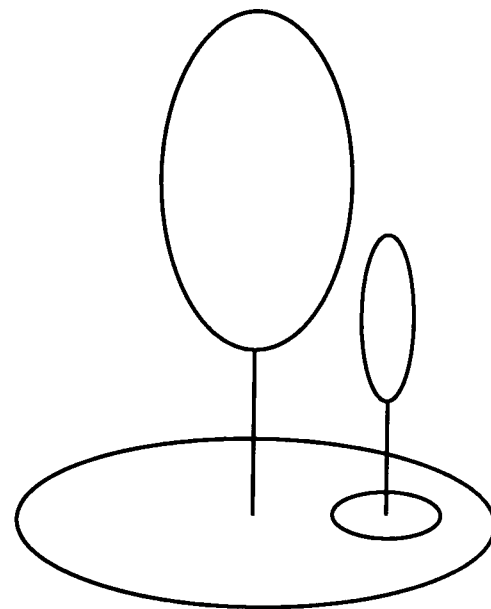


FIG. 5. Illustration of asymmetric competition on soil resources due to plant size differences.

reflected in the simulation for northern hardwood forests with the model REGROW (Mou and Fahey 1993).

Generally, simulated results closely agreed with the field survey at the plot level. Total biomass errors for plots 105, 98, and 108 were only 0.01%, 1.1%, and 6.1%, respectively. Population biomass errors at the plot level for plot 108 were 5.51% and 7.75% for loblolly pine and sweetgum, respectively. Other plot-level indicators such as mean individual mass and standard deviation of the mass were also similar between simulation and survey values, except for standard deviations of individual pine mass in plot 98 and sweetgum mass in plot 108 (Table 5, Fig. 3). However, for particular individuals, large differences between the simulation and experimental data were observed, especially in plot 108 (Table 6).

Young loblolly pine seedlings were obviously suppressed by the sweetgum sprouts. Average final biomass of pine seedlings was 12% smaller in the presence of sweetgum (plot 108)

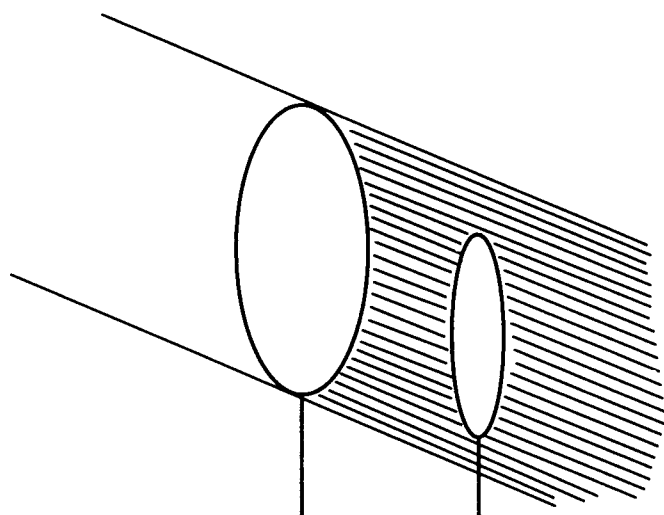


FIG. 6. Illustration of asymmetric competition on light due to plant size differences and relative position to light source.

than in pure culture (plot 98), even though soil fertility (as measured by soil organic matter content) was 10% higher in the mixed sweetgum–pine plot than in the pure pine plot. This effect of sweetgum on pine is not unexpected, since the simulated and actual final total biomass of sweetgum after one growing season was more than five times higher than that of loblolly pine. Since sweetgum sprouts were so much larger than pine and competition tended to be asymmetric (Weiner 1990), the effect of pine on sweetgum was not examined in this simulation.

Because light and water were uniformly distributed within plots at time zero, and the nutrient (nitrogen) was randomly distributed around a mean with limited deviation, final plant sizes were not affected by the variation in site resource availability. Instead, final sizes were the result of initial seedling size and the effects of plant–plant interactions. The positive slope of the regression line in Fig. 4*b* shows the influence of initial plant size, while the variation about the regression indicates a neighborhood effect. The divergence between initial size and final size for plants was much greater in plot 105 than in plot 98 because of the larger size of sweetgum seedlings and, consequently, more intensive interactions among plants. The relationship between initial and final sizes in the field survey was much weaker (Fig. 4*a*).

When we trace growth of each plant throughout the simulation, relationships among the interacting plants can be seen. For instance, the asymmetric nature of competition for resources among interacting plants of different sizes was demonstrated. The resource domain of a small plant may be completely overlapped by that of a larger neighboring individual; however, only a small portion of the resource domain of the large neighbor is influenced by the small plant (Fig. 5). Therefore, the competitive responses due to resource depletion from the overlapped region is much more severe for the small than for the large individual, particularly if the large individual is able to meet its resource requirements in the portion of its domain that is not shared by other plants. Size difference also contributed to asymmetric light competition owing to overshadowing by large neighbors. In addition, relative locations of neighboring plants to the sun can also cause an asymmetric effect

(Fig. 6; i.e., taller trees to the south of shorter trees have a greater effect on light).

The remarkable accuracy of the simulation at the stand level, by SPGROW, may have resulted from a number of factors, including (i) the resource-driven nature of the model; (ii) the fact that leaf area was used as the base in computing plant productivity in this simulation rather than the potentially less accurate method of using relative growth rate with total mass as the base; (iii) the calibration procedure that incorporated both individual- and stand-level attributes; and (iv) the short simulation period.

Several factors may have contributed to the poorer precision of the simulation at the individual level. First, resources within each plot were uniformly distributed in the model, but may be considerably more heterogeneous in nature. The lack of spatially explicit data for soil water and nutrient availability constrained a more realistic simulation regarding site heterogeneity. Earlier REGROW simulations for northern hardwood forests in central New Hampshire confirmed a significant influence of site heterogeneity on plant growth simulation (Mou 1991). Second, many sources of variation within populations were not explicitly incorporated in this model. Genetic variation may account for an unknown portion of the divergence between initial individual biomass and final size (Fig. 4). In addition, herbivory and other damage may influence growth, but these were not included in the model (however, we did not observe any significant herbivory damage to plants in our experiment). Third, the current model is not well suited to simulate the plant sprouting process, which may have influenced the simulation results of plot 108. All sweetgum seedlings in this plot were cut to the ground during the previous winter; the stumps sprouted during the next growing season. The model simulation covered the first growing season after cutting and randomly assigned an initial biomass, corresponding to typical 1-year-old seedlings, for each stump. Lastly, our limited data regarding plant dimensions (specifically belowground parts) and plastic responses related to various physical and biological environments constrain this model. We used an oversimplified plant allometry approach to delineate the domains of each resource-foraging organ. Such simplifications, in all likelihood, reduced the accuracy of the simulation for individual plants. Nevertheless, reasonably precise simulation of mean tree interference was obtained.

Conclusion

Suitability of EFT model

EFT models focus on individual plants and simulate plant growth directly through resource acquisition, which depends largely upon the morphology of the individual plants, environmental factors that influence resource availability, and plant interactions. This feature enables the simulation of plant community dynamics in an individually based, spatially explicit, and resource-driven manner, all of which are important attributes of a mechanistic model of plant–plant interactions.

SPGROW was able to simulate accurately the growth of sweetgum and pine at the stand level, despite relatively limited data. We expect that more accurate simulation may be achieved by further parameterization of the model and by model-structure improvement. We also ran the model by modifying site heterogeneity patterns. Such treatment had marginal change in results at the population and community levels, but did alter

the growth rate of individuals. This feature of the model will be useful in future studies to explore plant interactions and the relationships between population or community dynamics and site heterogeneity.

As a complex model system, SPGROW can greatly assist in (i) integrating different levels of biological organizations along ecological hierarchies; (ii) organizing information on plant interactions and vegetation succession; (iii) delineating the deficiencies within the knowledge base; and (iv) providing a theoretical base on which field experiments may be designed. Because of the complexity of plant interactions, it is impossible to use field studies exclusively to investigate all factors involved. With limited experimental data, this model may be able to simulate experiments with settings and conditions impossible to do in the field owing to time and funding constraints. Furthermore, this type of model provides mechanistic insight into plant-plant interaction, a feature lacking in many other endeavors (Bazzaz and Sipe 1987).

Acknowledgments

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Appendix

TABLE A1. Symbols and notations used in this article

Name	Description	Unit
P_R	Plant root influence on resources	Unitless
b^*	Uniform root influence in extended domain	Unitless
c^*	Additional root influence to b at stem location	Unitless
μ^*	Root influence reduction coefficient near periphery	cm^{-2}
β^*	Root influence reduction coefficient near stem	cm^{-1}
a	Periphery radius of root domain	cm
i	Subscript representing i th individual	
r	Vector indicating spatial location	
P_C	Plant canopy influence on resources	Unitless
P_{C0}	Maximum plant canopy influence on resources	Unitless
ϕ^*	Canopy influence reduction coefficient	cm^{-2}
P_S	Plant stem influence on resources	Unitless
z^*	Stem influence reduction coefficient	cm^{-1}
H_y	Water availability at any given site after access by y individuals	Unitless
H	Water availability, lower case h with R, C, or S indicating weighting factors for root, canopy, and stem	Unitless
N_y	Nutrient availability at any given site after access by y individuals	Unitless
N	Nutrient availability, lower case n with R, C, or S indicating weighting factors for root, canopy, and stem	Unitless
H_i	Water availability for i th individual plant	Unitless
H_{0r}	Site water availability without any plant effect	Unitless
N_i	Nutrient availability for i th individual plant	Unitless
N_{0r}	Site nutrient availability without any plant effect	Unitless
P_{Rir}	Root influence of plant i at r	Unitless
P_{Rkr}	Root influence of plant k at r	Unitless
P'_{Rir}	Proportion of the total root influence of plant i at r	Unitless
l_i	Light availability to plant i	Unitless
A_{Lx}	Relative importance of leaf at x th layer to whole tree leaves	Unitless
V	Normalized light intensity determined by Beer's law	Unitless
W_{Lk}	Leaf dry mass	g
V_0	Normalized light intensity determined above canopy	Unitless
k^*	Light intensity reduction coefficient used in Beer's law	Unitless
x	Representing x th canopy layer relative to canopy depth	$\text{cm} \cdot \text{cm}^{-1}$
l_{mx}	Relative light intensity at mx to the top of the canopy	%
mx	Distance from the top of the canopy	cm
W	Plant dry mass	g
Ω^*	Plant intrinsic growth rate	t^{-1}
q^*	Unknown factors affecting plant growth	Unitless
g^*	Gas constant	$1.987 \text{ cal} \cdot \text{K}^{-1} \cdot \text{mol}^{-1}$
ΔH_H^*	Enthalpy of activation for high temperature	$\text{kcal} \cdot \text{mol}^{-1}$
ΔH_L^*	Enthalpy of activation for low temperature	$\text{kcal} \cdot \text{mol}^{-1}$

TABLE A1 (concluded)

Name	Description	Unit
$T_{1/2L}^*$	Low temperature at which the biochemical activity is one-half of the maximum	°C
$T_{1/2H}^*$	High temperature at which the biochemical activity is one-half of the maximum	°C
T	Ambient temperature	°C
W_{LB}	Plant living mass	g
n	Number of time steps of a growing season in model simulation	Unitless
W_n	Total plant mass at the end of n th time step (in this simulation W_n represents total plant mass at the end of growing season)	g
W_0	Total plant mass at the start of the growing season	g
R_i	Respiration factor (calculated from eq. 14)	g/g
W'_{LB}	Ratio of living mass to total plant mass	g/g
r	Ratio of leaf mass to total plant mass	g/g
kr	The average value of $(I_i H_i N_i) / (I_i H_i + I_i N_i + N_i H_i)$ in eq. 14 of all time steps during the whole simulation period	Unitless
t	Time	

*These values are constants.