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LANDSCAPE DISTRIBUTION OF ORGANISMS AND THE SCALING OF SOIL RESOURCES

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Abstract.—We demonstrate that the competitive ability and landscape distribution of organisms can be affected by the interaction between their size and scaling properties and the scaling properties of the resources they consume. First, we prove that the landscape distribution of plants can be significantly affected by the interaction between their root lateral spread (RLS) and the scaling of soil N. Furthermore, we show that the nature of this interaction is highly dependent on the levels of soil N and plant age (adults or seedlings). We also demonstrate how the optimal RLS depends on the combination of soil N scaling properties at different levels of resolution. We made the ALLOCATE model spatially explicit for RLS and soil N scaling to analyze plant competition in a fractal environment. We show that, on the average, plants with low RLS and high root density (RD) dominate under low N stress, while plants with high RLS and low RD dominate at high N stress and that the scaling of soil N significantly controls the degree of dominance and the performance of seedlings. These results may cast some light regarding present disagreements as to which plant trait may be optimal in the competition for soil nutrients.

A generally accepted proposition in ecology is that the spatial variability of soil resources is one of the major determinants for the coexistence of plant species in a landscape (Grime 1979; Tilman 1988; Palmer 1992). Theoretical approaches such as landscape ecology and hierarchical theory have been developed to describe and analyze the nature and origin of spatial variability and the mechanisms of species coexistence (Milne 1991, 1992). Landscape ecologists have generally approached the subject by assuming that environmental variability can be described by the shape, number and distribution of homogeneous landscape components or "patches" (Palmer 1992). Burrough (1981) and Palmer (1988, 1992), *inter alia*, however, have shown that a wide variety of landscape and environmental variables of interest to ecology and ecological modeling vary continuously in space and thus can be modeled with the use of the basic mathematical structure of fractional Brownian motion.

Palmer (1992) used fractal geometry to simulate the spatial variability of continuous soil variables and study how the geometry of this variability (its fractal dimension) affects plant species coexistence and the plant richness of a landscape. He recognized, however, that, although the soil variables in question were con-

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tinuous in nature, the simulated landscape had to be homogeneous (and thus patchlike) at the microsite level (the smallest cell in the simulation). To avoid employing a patch base model, Palmer (1992) assumed that the microsite is the scale at which plants can physiologically integrate over the environment. The limitation of this approach, however, is that it assumes that all plants integrate soil resources over the same area and in the same manner (i.e., all plants have the same root lateral spread and root density). In nature, however, this is not the case, as plants do in fact have different root lateral spreads and root densities (Grime et al. 1988; Boot and Mensink 1990; Campbell et al. 1991). Thus, Palmer and Dixon (1990) have indicated the need to explore in further detail the ability of plants to integrate physiologically over an environment as related to their habitat breadth and the pattern of heterogeneity observed in nature.

The objective of this article is to explore plants' competitive ability and landscape distribution as affected by the interaction between the size and scaling properties of their root system and the scaling properties of the resources they use. In the first section, we develop a general theory to explore the relationship between the root area of plants and their landscape distribution. We accomplish this by analyzing the probability density function properties of resources that can be modeled with the use of integrated second-order stationary fractals. We expand this analysis in the second section by adding the root scaling properties of plants and use simulation modeling to explore how competition for soil nitrogen (N) in a fractal environment can affect plant community structure. We modify a simplified version of the ALLOCATE model (Tilman 1988), making it spatially explicit for root lateral spread and the scaling of soil mineralizable N.

PLANT ROOT AREA AND THE SCALING OF SOIL RESOURCES

Scaling is a term imbued with many shades of meaning. This ambiguity has prompted us to define certain terms more precisely as they are used in this article. We reserve the term *scale* for the exponent H (the dimension of the Brown zero set) that characterizes variables with fractal dimensions and defines the degree and type of spatial dependency. We use the term *extent* (denoted as A) to signify the maximum lag distance (space) for which the scaling factor H is operative. Beyond a distance A , the variables in question are spatially independent (in a statistical sense). For mathematical simplicity, we analyze only one-dimensional second-order stationary fractal models (stationary mean and variance), although the one-dimensional case can be extended to any dimension. The term *area* (denoted as a) will be associated with rectangles that have an infinitesimal width that, in essence, reduces area to length (double integrals are therefore replaced with one-dimensional integrals). This convention is also used in the section on plant competition in which root area is replaced with root lateral spread. Consequently, H is restricted to $0 < H < 1$.

To model landscape variables (soil N, soil texture, etc.), we followed the approach of Urban et al. (1987) and assumed that the value of a particular soil variable in a landscape, denoted as $Y(d)$, is the result of a combination of spatial

processes, denoted as $X(d)$, of similar grain but different extent (A 's) and scaling constants (H 's). Thus, $Y(d)$ has the following characteristics:

$$Y(d) = f(d) + \sum_{i=1}^{i=n} X_i(d), \quad (1)$$

where $f(d)$ is a deterministic function, $X_i(d)$ are random variables that have a normal distribution with $\xi[X_i(d)] = 0$ and $\text{variance}[X_i(d)] = \sigma_i^2$ for all i and d , d signifies any arbitrary point in the landscape, and $\xi[\]$ signifies the statistical expectation. Furthermore, for d_1 and d_2 the X_i 's have the following spatial relationships:

$$\xi\{[X_i(d_2) - X_i(d_1)]^2\} = 2 \left[\frac{d_2 - d_1}{A_i} \right]^{2H_i} \sigma_i^2 \quad \text{for } |d_2 - d_1| \leq A_i \quad (2)$$

$$\text{or } = 2\sigma_i^2 \quad \text{otherwise;}$$

$$\text{cov}[X_i(d_1)X_i(d_2)] = \left[1 - \left(\frac{d_2 - d_1}{A_i} \right)^{2H_i} \right] \sigma_i^2 \quad \text{for } |d_2 - d_1| \leq A_i \quad (3)$$

$$\text{or } = 0 \quad \text{otherwise;}$$

$$\text{cov}[X_i(d), X_j(d)] = 0 \quad \text{for } i \neq j \quad (4)$$

$$A_i < A_j \quad \text{for } i < j. \quad (5)$$

Values of H_i close to zero indicate spatial independence, whereas values of H_i close to one indicate total spatial dependency. Figure 1 shows an example of $Y(d)$ for the case of $n = 1$ and for different values of H , and figure 2A and B shows examples of the shape of equations (2) and (3) for the case of $n = 2$. Notice in figure 2 that, because of the constraints of equation (5), when the distance $|d_2 - d_1| < A_1$, the dominant scaling factor is H_1 , while, when $A_1 \ll |d_2 - d_1| < A_2$, H_2 dominates.

Organisms in general, and plants in particular, obtain their resources by integrating over a given area. Thus, the effective resource's variable for a given organism is not Y but rather the integration of the value of Y over the area or volume occupied by the organisms. Thus, for our particular analysis we define a new variable $W(d; a)$ as

$$W(d; a) = \int_d^{d+a} Y(d) = \int_d^{d+a} f(u) du + \sum_{i=1}^{i=n} Z_i(d; a), \quad (6)$$

where

$$Z_i(d; a) = \int_d^{d+a} X_i(u) du,$$

where d is a point in the landscape and a is the area over which an organism operates (e.g., area of the root system). The mean and variance for $W(d; a)$ are (see App. A for details)

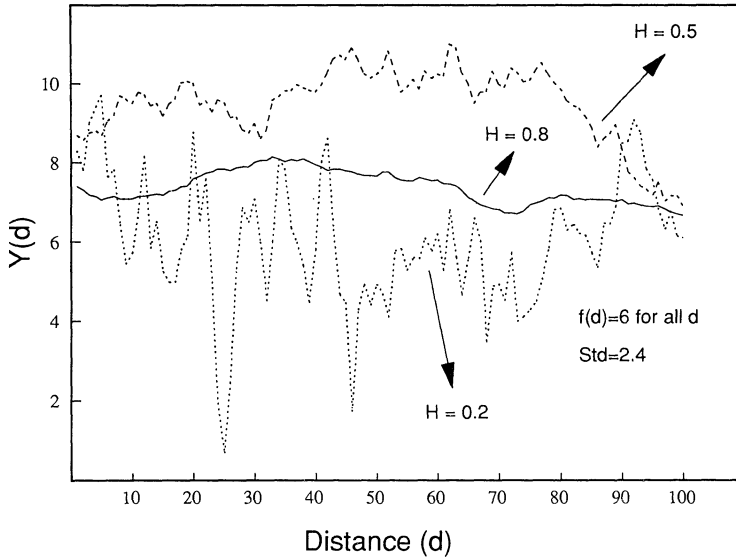


FIG. 1.—Example of a second-order stationary fractal variable $Y(d)$ (eq. [1]) that consists of a single spatial process $X(d)$, with $f(d) = 6$, and $\text{var}[X(d)] = \sigma^2 = 5.76$ for all d . Shown is the shape of $X(d)$ for three scaling constants $H = 0.2$, $H = 0.5$, and $H = 0.8$.

$$\xi[W(d; a)] = \int_d^{d+a} f(u) du \tag{7}$$

and

$$\text{var}[W(d; a)] = \sum_{i=1}^{i=n} \text{var}[Z_i(d; a)], \tag{8}$$

where $\text{var}[Z_i(d; a)]$ is a function of a , H , and the extent parameter A (App. A).
For $a \leq A_i$

$$\text{var}[Z_i(d; a)] = a^2 \left[1 - \frac{\left(\frac{a}{A_i}\right)^{2H_i}}{(2H_i + 1)(H_i + 1)} \right] \sigma_i^2. \tag{8a}$$

For $A_i < a < 2A_i$

$$\begin{aligned} \text{var}[Z_i(d; a)] = & (a^2 - A_i^2)\sigma_i^2 - \frac{2(a - A_i)}{2H_i + 1} \left[\frac{(a - A_i)^{2H_i+1}}{(2H_i + 2)A_i^{2H_i}} + A_i \right] \sigma_i^2 \\ & + \left[(2A_i - a)a - \frac{2A_i^{2H_i+2} - 2(a - A_i)^{2H_i+2}}{A_i^{2H_i}(2H_i + 1)(2H_i + 2)} \right] \sigma_i^2. \end{aligned} \tag{8b}$$

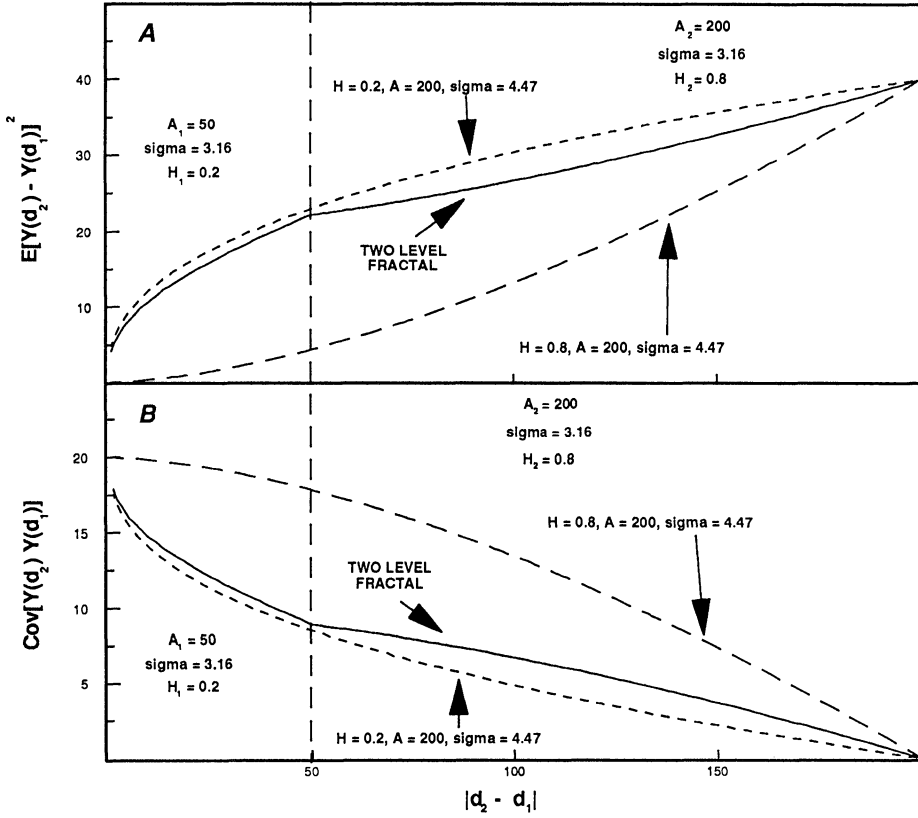


FIG. 2.—Distance function (A) and covariance function (B) for a variable that follows a second-order stationary fractal $Y(d)$ (eq. [1]) with $f(d) = 6$ for all d 's, and the sum of two spatial processes $X_i(d)$ with $\sigma_1 = \sigma_2 = 3.16$ for all d 's, $A_1 = 50$, $A_2 = 200$, $H_1 = 0.2$, and $H_2 = 0.8$. Shown for comparison are stationary fractal models $Y(d)$ that consist of only one spatial process $X(d)$, $A = 200$, $\sigma = 4.47$, and $H = 0.2$ or $H = 0.8$.

For $a \geq 2A_i$

$$\begin{aligned} \text{var}[Z_i(d; a)] = & 2A_i^2 \left[\frac{3}{2} - \frac{1}{2H_i + 1} \left(1 + \frac{1}{2H_i + 2} \right) \right] \sigma_i^2 \\ & + 2A_i(a - 2A_i) \left[1 - \frac{1}{2H_i + 1} \right] \sigma_i^2. \end{aligned} \tag{8c}$$

A cursory observation of these equations can show that the interrelationship among the scaling factor H , the area of integration (a), and the $\text{var}[Z_i(\cdot; \cdot)]$ is more pronounced for values of $a < 2A_i$. For large a 's ($a > 2A_i$) the $\text{var}[Z_i(\cdot; \cdot)]$ is a simple linear function of area (sum of independent random variables) that signifies that organisms with a size greater than $2A_i$ will "perceive" $Z_i(d; a)$ as a

TABLE 1

VALUES DERIVED FROM A LANDSCAPE IN WHICH THE LANDSCAPE PATTERN OF SOIL N FOLLOWS A SECOND-ORDER STATIONARY FRACTAL PATTERN $Y(d)$ WITH A SINGLE $X(d)$, $f(d) = \mu = 0.4$ OR 0.6 mg N FOR ALL d , $\sigma = 0.25$ AND SCALING VALUES FOR H OF $H = 0.2$ AND $H = 0.8$

H	$\xi[W(d; 10)]$	$SD[W(d; 10)]$	$P[W(d; 10) \geq 5]$
.2	4	1.85	.29
.8	4	2.41	.34
.2	6	1.85	.71
.8	6	2.41	.66

NOTE.—See text and eqq. (1)–(3). Here $\xi[W(d; 10)]$ and $SD[W(d; 10)]$ represent the mean and variance for the integrated values of $Y(d)$ over an area $a = 10$ (eq. 6); $P[W(d; 10) \geq 5]$ is the probability of finding an area $a = 10$ in which the amount of N is greater or equal to 5 mg (5 mg of N is the minimum requirement of the plant discussed in the text).

homogeneous “patchlike” structure. The spatial correlation of $W(d_1; a)$ and $W(d_2; a)$ for $d_1 \neq d_2$ is determined by the covariance functions (cov[]):

$$\text{cov}[W(d_1; a) W(d_2; a)] = \sum_{i=1}^{i=n} \text{cov}[Z_i(d_1; a) Z_i(d_2; a)]. \tag{9}$$

The equations for the $\text{cov}[Z_i(d_1; a) Z_i(d_2; a)]$ are shown in Appendix B.

We use five examples to underscore the relationship between the area of a plant root system and the scaling of the soil resources it uses. In all five examples, we assume that soil N is the most limiting factor for plant growth, and its landscape pattern follows equation (1). We want to analyze how the area of the root system interacts with the scaling (H_i) and extent (A_i) constants that characterize the landscape distribution of soil N to determine the probability that the plant will find a suitable habitat for growth.

In examples 1–3 (tables 1–3) the mean soil N in the landscape is a constant $f(d) = \mu$ for all d 's, and equation (1) has only one spatial process, $X(d)$, with scaling H and extent A . Example 1 represents the case of adult plants that have a fixed size that is less than the extent constant A . In this example we analyze how the scaling factor H and mean μ affect the probability that the plant can find a suitable habitat for growth in the landscape. The case of $\mu = 0.4$ mg of N represents a “poor” landscape, because the plant requirements per unit area (0.5 mg of N) are greater than μ , while the case $\mu = 0.6$ mg N represents a “rich” landscape. As table 1 shows, in poor landscapes the probability of a plant finding a suitable habitat for growth increases with H , while in richer landscapes it decreases with H .

Examples 2 and 3 represent the case of growing plants whose root systems are expanding in area. We analyze how the scaling factor H can affect the probability that the plant will find a suitable habitat for growth after reaching its full size contingent on whether the habitat in which the plant originally resides is poor

TABLE 2
 CONDITIONAL PROBABILITIES OF FINDING ADEQUATE
 RESOURCES FOR A PLANT THAT EXPANDS ITS ROOT SYSTEM
 FROM $a = 3$ TO $a = 6$

$W_0(d; 3)$	$P[W(d; 6) \geq 6 W_0(d; 3) = w_0]$	
	$H = .2$	$H = .8$
2	.19	.10
4	.81	.90

NOTE.—Here $W_0(d; 3)$ represents the amount of N (in mg) found in an area of size $a = 3$; $P[W(d; 6) \geq 6 | W_0(d; 3) = w_0]$ represents the conditional probability that a plant will find at least 6 mg of N when it expands its root system from the present area $a = 3$, where $W_0(d; 3) = w_0$ mg of N, to an area $a = 6$. The case of $W_0(d; 3) = 2$ represents a poor habitat (plant requirements for an area of $3 = 3$ mg of N), while $W_0(d; 3) = 4$ represents a rich habitat. Also, $H = 0.2$ and $H = 0.8$ are the two scaling factors used. Soil N follows a second-order stationary fractal pattern $Y(d)$ with a single $X(d)$, $f(d) = \mu = 1$ mg N for all d , $A = 10$, $\sigma = 1$ (see text and eqq. [1]–[3]). The extent constant is $A = 10$; thus the plant root system after expansion remains $a = 6 < A$.

TABLE 3
 CONDITIONAL PROBABILITIES OF FINDING ADEQUATE
 RESOURCES FOR A PLANT THAT EXPANDS ITS ROOT SYSTEM
 FROM $a = 7$ TO $a = 14$ IN SUCH A WAY THAT
 $A < a < 2A$

$W_0(d; 7)$	$P[W(d; 14) \geq 14 W_0(d; 7) = w_0]$	
	$H = .2$	$H = .8$
4	.39	.41
8	.62	.60

NOTE.—Here $W_0(d; 7)$ represents the amount of N (in mg) found in an area of size $a = 7$; $P[W(d; 14) \geq 14 | W_0(d; 7) = w_0]$ represents the conditional probability that the plant will find at least 14 mg of N when its root system expands from the present area $a = 7$, where $W_0(d; 7) = w_0$ mg of N, to an area $a = 14$. The case of $W_0(d; 7) = 4$ represents a poor habitat (plant requirements for an area of $7 = 7$ mg of N), while $W_0(d; 7) = 8$ represents a rich habitat. Soil N follows a second-order stationary fractal pattern $Y(d)$ with a single $X(d)$, $f(d) = \mu = 1$ mg N for all d , $A = 10$, $\sigma = 1$. The scaling values for H used are $H = 0.2$ and $H = 0.8$ (see text and eqq. [1]–[3]).

TABLE 4

CONDITIONAL PROBABILITIES OF FINDING ADEQUATE RESOURCES FOR A PLANT THAT EXPANDS ITS ROOT AREA FROM $a = 5$ TO $a = 10$ IN AN ENVIRONMENT IN WHICH THE SOIL N FOLLOWS A SECOND-ORDER STATIONARY FRACTAL PATTERN $Y(d)$ WITH TWO SPATIAL PROCESSES, $X_i(d)$, $i = 1, 2$

$W_0(d; 5)$	$P[W(d; 10) \geq 10 W_0(d; 5) = w_0]$	
	$H_1 = .2; H_2 = .8$	$H_1 = .8; H_2 = .2$
4	.20	.26
6	.80	.74

NOTE.—The model has two extent constants, $A_1 = 7.5$ and $A_2 = 15$, and $SD \sigma_1 = \sigma_2 = 0.4$. After expansion the root area of the plant (a) is such that $A_1 < a < 2A_1$ and $a < A_2$. Also, $W_0(d; 5)$ represents the amount of N (in mg) found in an area of size $a = 5$; $P[W(d; 10) \geq 10 | W_0(d; 5) = w_0]$ represents the conditional probability that the plant will find at least 10 mg of N when it expands from the present area $a = 5$, where $W_0(d; 5) = w_0$ mg N, to an area $a = 10$. The cases examined represent a poor landscape, with $f(d) = \mu = 0.4$ for all d and $W_0(d; 5) = 4$, and a rich landscape, $f(d) = \mu = 0.6$ for all d and $W_0(d; 5) = 6$ (the minimum requirements for the organism at size $a = 5$ is 5 mg N). We calculated the conditional probabilities for two combinations of scaling factors: $H_1 = 0.2$, $H_2 = 0.8$; and $H_1 = 0.8$, $H_2 = 0.2$. For more details, see text and eqq. (1)–(3).

(soil N below plant requirements) or rich (soil N above plant requirements). In both cases the original area of the root system is less than the extent constant A . In example 2 the area of the full-size plant (a) remains smaller than the extent constant A , while in example 3 the root area exceeds it $A < a < 2A$ (App. C shows how conditional probabilities are calculated). In example 2 the probability of finding a suitable habitat after root expansion decreases with H when the site in which the plant is residing is poor, while it increases when it is rich (table 2). In example 3, however, the results are reversed (table 3).

Example 4 also represents plants that are expanding in size in a landscape in which the mean soil N is also a constant ($f(d) = \mu$ for all d 's). The difference, however, is that equation (1) is now the sum of two spatial processes, $X_i(d)$, with scaling H_i and extent A_i , $i = 1, 2$ ($A_1 < A_2$). The initial root area of the plants is less than A_1 , while after expansion to their full size (a) it is such that $A_1 < a < 2A_1$ and $a < A_2$. As in examples 2 and 3, we condition the probabilities of finding a suitable habitat for growth on the amount of N available for the plant before expansion (see App. D for details). Table 4 shows the results. In poor original habitats the probability of finding a suitable habitat on expansion increases when $H_1 > H_2$, while for the case of rich original habitats the results are reversed. Examples 1–4 clearly indicate that both the scaling factors H_i as well as the size of the plant vis-à-vis the extent parameters A_i can have a significant impact on the probability of plants finding suitable habitats for growth and thus their landscape distribution patterns. This implies that any disturbance that changes H , A , or both

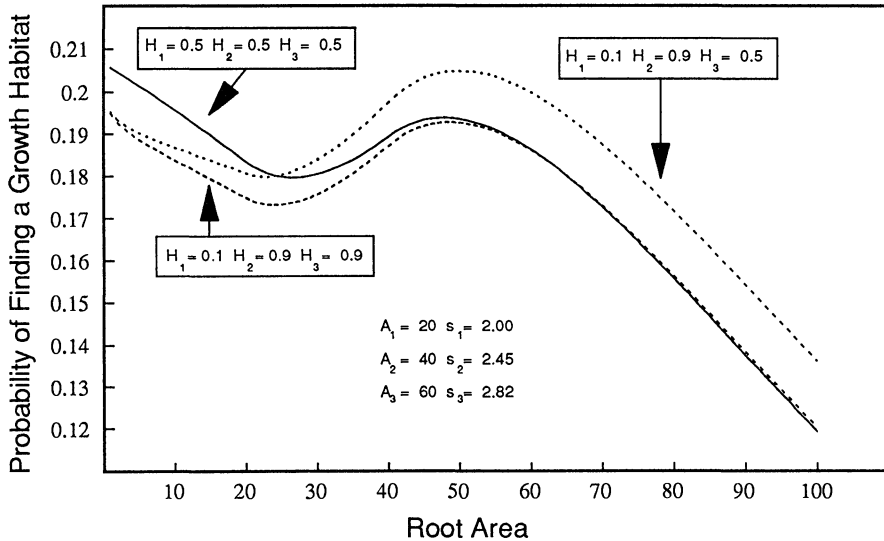


FIG. 3.—Probability for plants with different root areas to find an adequate site for growth in a landscape in which soil N follows a second-order stationary fractal pattern $Y(d)$ that consists of the sum of three spatial processes, $X_i(d)$, $i = 1, 2, 3$ (see text and eq. [1]–[3]) that have the extent A , SD s , and scaling factors shown in the graph.

can significantly enlarge or restrict the spatial distribution and habitat breadth of plants.

In the last example we regard a landscape in which the pattern of soil N is the result of the sum of three spatial processes, $X_i(d)$ (eq. [1]), and the mean soil N in the landscape, $f(d)$, is no longer a constant. For this landscape pattern of soil N, we determined which plant size (measured by its root area) has the highest probability of finding a growth habitat for the different combination of scaling factors H_i , $i = 1, \dots, 3$. The extent and standard deviation constants used are $A_1 = 20$, $A_2 = 40$, $A_3 = 60$, $\sigma_1 = 2.0$, $\sigma_2 = 2.45$, and $\sigma_3 = 2.82$, while $f(d)$ has the form

$$\begin{aligned}
 f(d) &= 4.33 \quad \text{for } 0 \leq d \leq A_1 \\
 f(d) &= 4.33 + \frac{1.73(d - A_1)}{A_2 - A_1} \quad \text{for } A_1 < d \leq A_2 \\
 f(d) &= 6.06e^{-0.0085(d - A_2)} \quad \text{for } A_2 < d \leq 100.
 \end{aligned} \tag{10}$$

Figure 3 shows that, when $f(d)$ is no longer a constant, different combinations of scaling factors that are dominant at different extents can significantly affect the landscape distribution of plants with different root areas by affecting their probability of finding a suitable habitat for growth. These results have implications in the development of landscape models because they outline a mechanism

by which disturbances of different sizes may differentially affect the landscape distribution of a variety of organisms by altering the scaling patterns of soil resources at different extents.

PLANT COMPETITION IN A FRACTAL ENVIRONMENT

In the previous section, we discussed in general theoretical terms how the interrelationship between plant root area and the scaling of soil resources can affect the probability distribution of growth habitats. In this section, we use simulation models to explore in more detail the same relationship within the context of plant competition for soil resources (N in this case). The specific areas of interest are, first, how the scaling of soil N affects the probability distribution of growth habitats for plants with two different strategies for scaling of root biomass to area (we will use Grime's [1979] root lateral spread concept): (1) large root lateral spread but low root density and (2) small root lateral spread but high root density. Second, we will determine how the scaling of N resources plus different levels of N supply rates (a proxy for the rate of N mineralization) affect the outcome of competition between the two plants outlined in the first interest area. Finally, we will study how the interactions among the scaling of soil N, N supply rates, plant growth rates, biomass allocation to roots, and the scaling of root biomass to root lateral spread can affect plant community composition.

Model Description

The model we developed was based on a simplified version of the ALLOCATE model for plant competition developed by Tilman (1988, chaps. 4–8) and modified so as to include the two parameters of interest: root lateral spread and scaling of soil N. In this simplified version, the ALLOCATE model consists of the following set of equations:

$$\frac{dB_i}{dt} = B_i \left[\frac{r_i PR_i R}{\frac{PR_i}{(1 - PR_i)} R + K_i} - \text{RESP}_i \right] \quad (11)$$

$$\begin{aligned} \frac{dR}{dt} = \text{NSR} \left\{ S - R - \sum_{i=1}^{i=n} B_i [(1 - PR_i) \gamma a_i + PR_i \gamma b_i] \right\} \\ - \sum_{i=1}^{i=n} B_i \left[\frac{r_i PR_i R}{\frac{PR_i}{(1 - PR_i)} R + K_i} \right] [\gamma a_i (1 - PR_i) + \gamma b_i PR_i], \end{aligned} \quad (12)$$

where B_i , PR_i , r_i , RESP_i , γa_i , and γb_i represent total plant biomass, fraction of plant biomass allocated to roots, maximum growth rate, respiration rate, N content per unit of leaf biomass, and N content per unit of root biomass for plant i ,

respectively; K_i is the half saturation constant for plant N uptake; while S , R , and NSR represent the total soil N, available soil N, and N supply rate, respectively. Although Tilman (1988) uses the term *respiration*, the constant RESP is in reality a mortality rate. We made two additional modifications to this version of the ALLOCATE model. First, we did not differentiate between leaf and stem biomass because for simplicity we assumed no differences in the species we modeled. The ALLOCATE model includes competition for light (a shading effect). This term was not included in the model because our only interest was competition for soil N. Furthermore, Tilman (1990) has shown that for the first 40 yr N competition rather than light competition is the major factor controlling succession in the tall-grass prairie.

The ALLOCATE model does not include either plant spatial dimensions (e.g., root lateral spread, root area, or root volume) or soil N scaling properties. We therefore modified the model to make it spatially explicit. Root lateral spread was modeled with the use of a simple allometric relationship of the form

$$RLS_i = \alpha_i(\text{PR}_i B_i)^{\beta_i}, \quad (13)$$

where RLS_i represents the root lateral spread of plant i , while α_i and β_i represent scaling constants. From this equation we can calculate root biomass density (RBD_i) as

$$\frac{\text{PR}_i B_i}{RLS_i} = \frac{\text{PR}_i B_i}{\alpha_i(\text{PR}_i B_i)^{\beta_i}} = \alpha_i^{-1}(\text{PR}_i B_i)^{1-\beta_i} = \alpha_i^{-1} \left[\left(\frac{RLS_i}{\alpha_i} \right)^{1/\beta_i} \right]^{1-\beta_i};$$

thus,

$$RBD_i = \alpha_i^{-1/\beta_i} RLS_i^{1/\beta_i - 1}. \quad (14)$$

With this information we made equation (11) spatially explicit by replacing the ratio $\text{PR}_i:(1 - \text{PR}_i)$ with RBD_i and R with the integration of available soil N over the RLS_i of the plant in question:

$$\frac{dB_i}{dt} = B_i \left[\frac{r_i(1 - \text{PR}_i)RBD_i \int_d^{d+RLS_i} R(u; t) du}{RBD_i \int_d^{d+RLS_i} R(u; t) du + K_i RLS_i} - \text{RESP}_i \right], \quad (15)$$

where $R(u; t)$ is available soil N at time t at landscape location u , while the interval $(d_i, d_i + RLS_i)$ represents the landscape location of the root system of the plants in question. Thus, the available N for plant i is the product of root density multiplied by the available soil N in the $(d_i, d_i + RLS_i)$ interval. In this equation K_i is now the half saturation constant for plant N uptake per unit of RLS_i .

The equation for the change with time of available soil N per unit area for all points in the landscape was constructed from equation (12) by replacing S with

TABLE 5

PLANT PARAMETERS USED IN THE SIMULATION MODEL

Sp	RLS	<i>r</i>	PR	Biom	α	β	<i>K</i>	RESP	γ_a	γ_b
1	8.76	.36	.17	25	1	1.5	41.0	.007	.1	.059
2	34.02	.25	.42	25	1	1.5	8.0	.007	.1	.059
3	59.55	.17	.61	25	1	1.5	2.0	.007	.1	.059
4	86.11	.10	.78	25	1	1.5	.3	.007	.1	.059
5	97.96	.07	.85	25	1	1.5	.1	.007	.1	.059
6	4.25	.36	.17	25	1	1.0	41.0	.007	.1	.059
7	10.50	.25	.42	25	1	1.0	8.0	.007	.1	.059
8	15.25	.17	.61	25	1	1.0	2.0	.007	.1	.059
9	19.50	.10	.78	25	1	1.0	.3	.007	.1	.059
10	21.25	.07	.85	25	1	1.0	.1	.007	.1	.059
11	2.38	.36	.17	25	1	.6	41.0	.007	.1	.059
12	4.10	.25	.42	25	1	.6	8.0	.007	.1	.059
13	5.13	.17	.61	25	1	.6	2.0	.007	.1	.059
14	5.94	.10	.78	25	1	.6	.3	.007	.1	.059
15	6.26	.07	.85	25	1	.6	.1	.007	.1	.059

NOTE.—For details on how these parameters were calculated, see App. E. Here RLS represents root lateral spread (sensu Grime 1979); *r* is the daily growth rate; PR is the proportion of biomass allocated to roots. Biom is the maximum biomass that each plant can attain; *K* is the half saturation constant for N uptake; RESP is the daily respiration rate; γ_a and γ_b represent the crude protein – N content per unit of biomass of leaves and roots.

S(*u*) (where *S*[*u*] is the total amount of soil N at location *u* in the landscape), *R* with *R*(*u*; *t*), and *B_i* by *B_i* per unit of RLS_{*i*}. The equation is

$$\frac{\partial}{\partial t}R(u; t) = NSR[S(u) - R(u; t)] - NSR \left[\sum_{i=1}^{i=n} \frac{B_i}{RLS_i} (\gamma a_i(1 - PR_i) + \gamma b_i PR_i) I_{(d_i, d_i + RLS_i)}(u) \right] - \sum_{i=1}^{i=n} \frac{B_i}{RLS_i} \left[\frac{r_i(1 - PR_i) RBD_i \int_{d_i}^{d_i + RLS_i} R(u; t) du}{RBD_i \int_{d_i}^{d_i + RLS_i} R(u; t) du + K_i RLS_i} (\gamma a_i(1 - PR_i) + \gamma b_i PR_i) I_{(d_i, d_i + RLS_i)}(u) \right], \tag{16}$$

where *d_i* is the location of the plant *i* in the landscape and the indicator function *I*_(INT)(*u*) is one when *u* belongs to the interval INT and zero otherwise. In this case, INT is the interval (*d_i*, *d_i* + RLS_{*i*}).

Model Parameters

Total soil N in the landscape (*S*[*u*]) was modeled by equation (1) with the use of a single spatial process, *X*(*d*), with an extent constant *A* = 300 cm, *f*(*u*) = 6, and var(*X*[*u*]) = 5.76 for all *u*'s. The scaling effects were investigated with the use of two scaling parameters: *H* = 0.2 and *H* = 0.8. We used three nutrient supply rates: 0.001529, 0.000343, and 0.000092, which represent the maximum, average, and minimum N supply rates, respectively, needed to sustain adult plants in the absence of inter- or intraspecific competition (table 5). Because the

model involves both inter- and intraspecies competition, these NSRs represent different levels of N supply stress.

Parameters for all the plants used in the different model runs are shown in table 5. The values for the r_i , PR_i , and K_i were selected to have as close a resemblance as possible to the available experimental data (see App. E for details). We selected three different β values to scale root biomass to RLS ($\beta = 0.6, 1, 1.5$ with $\alpha_i = 1$ for all i 's). This resulted in root lateral spreads ranging from 2.38 cm ($\beta = 0.6, PR = 0.17$) to 97.96 cm ($\beta = 1.5, PR = 0.85$) and root densities ranging from 3.4 g cm^{-1} ($\beta = 0.6, PR = 0.85$) to 0.22 g cm^{-1} ($\beta = 1.5, PR = 0.85$). The maximum attainable biomass was the same for all species. In all cases the maximum root lateral spread was less than the extent constant A .

For objectives 1 and 2, we simulated 1,000 individual patches with 150 plants per patch (75 for each plant for objective 2). The patches were simulated in groups of five for 1,000 d and repeated 200 times. For each simulation, only the central patch was sampled to avoid edge effects. In the case of objective 1, we sampled the central plant of the central patch.

For objective 3, we modeled nine contiguous patches with a total of 150 plants per patch (10 for each of the 15 species randomly located within the patch). Simulations were run for 1,000 d and repeated 100 times. Only the central patch for each run was sampled at the end of each simulation for statistical analysis to avoid edge effects. Two simulation strategies were used: the first provided an unlimited supply of N until all plants reached their full (adult) biomass and was followed by the impositions of the different N supply constraints (NSRs) for 1,000 d; in the second strategy, all plants were started as seedlings (seedlings are plants with a biomass equal to 10% of the adult biomass) and the N supply constraints were applied at the start. These two strategies were designed to study whether soil N scaling factors combined with N supply rates have different impacts when applied to already established communities as opposed to a situation in which the adult vegetation has been removed and plants are reestablishing via seedlings. We used the second strategy to explore in further detail the problem of root expansion discussed in example 2 (table 2) of the previous section with the addition of root density and within the context of intra- and interspecific competition.

Model Results

Probability distribution of growth habitats for plants with two different scalings of root biomass to root lateral spread.—We used two plants for comparison: species 2 and 12 of table 5. These plants have the same r , $RESP$, PR , K , and α but differ in their scaling of root biomass to root lateral spread. Species 2 has a $\beta_2 = 1.5$, which results in a root lateral spread of 34 cm and a root density of 0.31 g cm^{-1} . Species 12 has a $\beta_{12} = 0.6$, which results in a root lateral spread of 4 cm and a root density of 2.6 g cm^{-1} . The plants were grown in monocultures (no interspecific competition) and were supplied with unlimited N until they reached their full size, after which the N supply rate was reduced for 1,000 d to $NSR = 0.000343$ (average level). At the end of the 200 simulations, we determined the percentage of patches at which the central plant biomass was at least 80% of the full-size plant (thereafter referred to as adult plants).

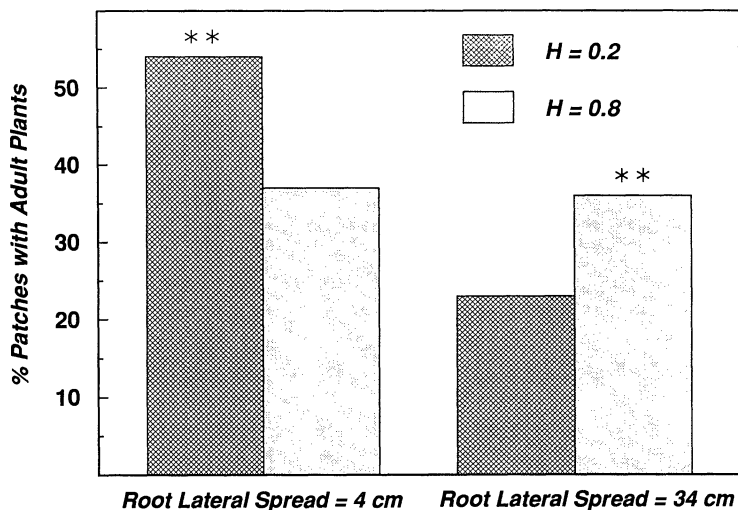


FIG. 4.—Percentage of patches with adult plants (biomass $\geq 80\%$ of maximum biomass) after a 1,000-d simulation (monoculture, no interspecific competition) for two species with different root lateral spreads (RLS) and root densities (RD): species 12 (table 5) with RLS = 4 cm and RD = 2.6 g cm^{-1} and species 2 (table 5) with RLS = 34 cm and RD = 0.31 g cm^{-1} . Total soil N followed a second-order stationary fractal model $Y(d)$ (eq. [1]) that consists of only one spatial process $X(d)$ with $A = 300 \text{ cm}$, $f(d) = 6$ for all d , $\sigma = 2.4$, and $H = 0.2$ or $H = 0.8$. The N supply rate used was $\text{NSR} = 0.000365$ (see text for more details). Two asterisks represent significant differences (within each species) between $H = 0.2$ and $H = 0.8$ at $P < .01$.

Figure 4 shows the results. The scaling of soil N had indeed a significant impact in the percentage of patches with adult plants (an index of the ability of plants to withstand the imposition of a nutrient supply stress). Species 2, with its extensive root system and low root density, had a significantly higher ($P < .01$) percentage of adult plants at soil N scaling of $H = 0.8$ than at $H = 0.2$ (36% vs. 23%). The results were the contrary for species 12 characterized by a small root lateral spread, high-density root system. The percentage of adults was 54% for $H = 0.2$ and 37% for $H = 0.8$ ($P < .01$).

The results for species 2 ($\beta = 1.5$) can be explained directly by the increase in the coefficient of variation (C.V.) for $S(u)$ when H changes from 0.2 to 0.8. In a nutrient-poor environment a large C.V. results in an increase in the probability of finding adequate growth habitats. For species 12 ($\beta = 0.6$), however, the explanation cannot be extrapolated from the changes in C.V. since the C.V. does not significantly change with the changes of H . This leaves us with only a heuristic explanation. Plants with small-root lateral spread but high root densities may be able to exploit the “cracks” (high peaks and valleys) that characterize the pattern of soil resources at low H values (see fig. 1).

Competition between plants with an extensive low-density root system versus plants with a small high-density root system.—To explore this objective, we ran competition simulations between plants 2 and 12 and 5 and 12. We used the case

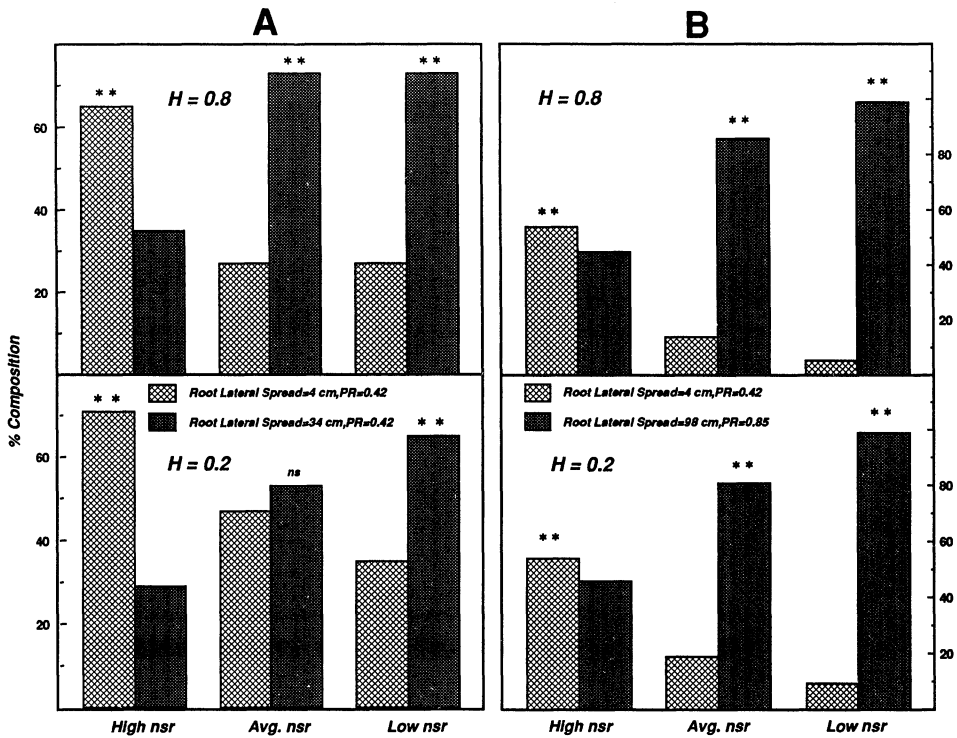


FIG. 5.—Average percentage composition of 200 patches after a 1,000-d simulation of intra- and interspecific competition among three species with different root lateral spreads (RLS) and root densities (RD): species 12 (table 5) with RLS = 4 cm and RD = 2.6 g cm^{-1} , species 2 (table 5) with RLS = 34 cm and RD = 0.31 g cm^{-1} , and species 5 (table 5) with RLS = 98 cm and RD = 0.26 g cm^{-1} . Total soil N followed a second-order stationary fractal model $Y(d)$ (eq. [1]) that consists of only one spatial process $X(d)$ with $A = 300 \text{ cm}$, $f(d) \approx 6$ for all d , $\sigma = 2.4$, and $H = 0.2$ or $H = 0.8$. The species were grown under three different N supply rates: high (NSR = 0.001529), average (NSR = 0.000343), and low (NSR = 0.000092); see text for more details. *A*, Results of competition between species 12 and species 2; *B*, results of competition between species 12 and species 5. Two asterisks represent significant differences between plants with RLS of 4 cm and RLS of 34 cm or plants with RLS of 4 cm and RLS of 98 cm at $P < .01$; *ns* = no difference.

of plant 5 versus 12 to analyze the combined effects of the allometric root scaling constant β and biomass allocation to roots on species competition. All simulations were given an unlimited supply of N until they reached adult size and then were grown for 1,000 d with three N supply rates: high (NSR = 0.001529), average (NSR = 0.000343), and low (NSR = 0.000092).

Figure 5A and B shows the results. The interplay between NSR and scaling of soil N complicates the picture that emerged from the previous single-species model. At high NSR species 12 ($\beta = 0.6$) was always dominant ($P < .01$), but its dominance declined from an average of 69% to an average of 54% when the biomass allocation to roots of the competing species ($\beta = 1.5$) increased from

0.42 to 0.85 (fig. 5A vs. B). On the average, species 12 composition was significantly higher ($P < .01$) under a soil mineralizable N scaling of $H = 0.2$ than under $H = 0.8$ (50% vs. 38% when competing with species 2 and 25% vs. 22% when competing with species 5). At low N, NSR species 2 and 5 were the dominants ($P < .01$), and, on the average (for all NSR), their percentage in the community was higher ($P < .01$) under $H = 0.8$ than under $H = 0.2$ (60% vs. 48% for species 2 and 77% vs. 74% for species 5).

In addition to the interplay among β , NSR, and H , these results also suggest two other patterns. First, there is a positive relationship between root scaling patterns and biomass allocation to roots. In general, the results suggest that, in order to compete effectively for soil resources at all N supply levels, species with a root allometric scaling factor of $\beta > 1$ must also allocate substantial amounts of biomass to their root system. Second, our results indicate an ability to substitute root density ($\beta < 1$) for biomass allocation to roots (high PR) at the high end of the N supply scale (lower N stress).

Competition among plants that differ in growth rate, root biomass, and the scaling of biomass to root lateral spread.—In this set of simulations, we used all 15 species shown in table 5. We first looked at the case in which nutrient supply constraints are imposed in a mature community in which all species have reached adult size. As in the case of the two-species model, plant community composition was affected by the N supply rates, the scaling of soil N, and the root lateral spread of the different plants (fig. 6). Plants with a root lateral spread of less than 10 cm had a significant ($P < .01$) decline in community composition when progressive nutrient stresses were applied: from a high of 34% in the high NSR to a low of 9% in the low NSR. Furthermore, the change in the scaling of soil N from $H = 0.2$ to $H = 0.8$ significantly ($P < .01$) decreased their composition at average and low NSR (–26% and –31%, respectively). Plants with root lateral spread greater than 25 cm showed a different behavior. Their composition was unaffected by changes in NSR ($P > .05$), but at the lower NSR a change in the soil N scaling resulted in a significant ($P < .01$) increase in their composition (+13%). Finally, plants with root lateral spread in the 10–25-cm range significantly increased their composition when NSR was changed from high to average ($P < .01$) but were unaffected by changes in the scaling of soil N. This could result from the fact that all the plants in this category have $\beta = 1$, which means that root density is unaffected by root lateral spread.

While average responses are shown in figure 6, there were also variations in the responses of the different species within each group. At that level, species have a similar response to the ALLOCATE model; that is, dominance was correlated with biomass allocation to the root system (PR). For example, while at the low NSR plants with a root lateral spread of less than 10 cm declined in aggregate by –31% when H was changed from 0.2 to 0.8, the decline was –55% for plants with a PR = 0.42 (root density = 2.56 g cm⁻¹) and –23% for plants with a PR = 0.78 (root density = 3.28 g cm⁻¹).

We also examined the case of nutrient supply constraints applied to seedlings growing (and thus expanding in size) in a fractal environment. While species composition at high NSR was similar in both adult- and seedling-based models

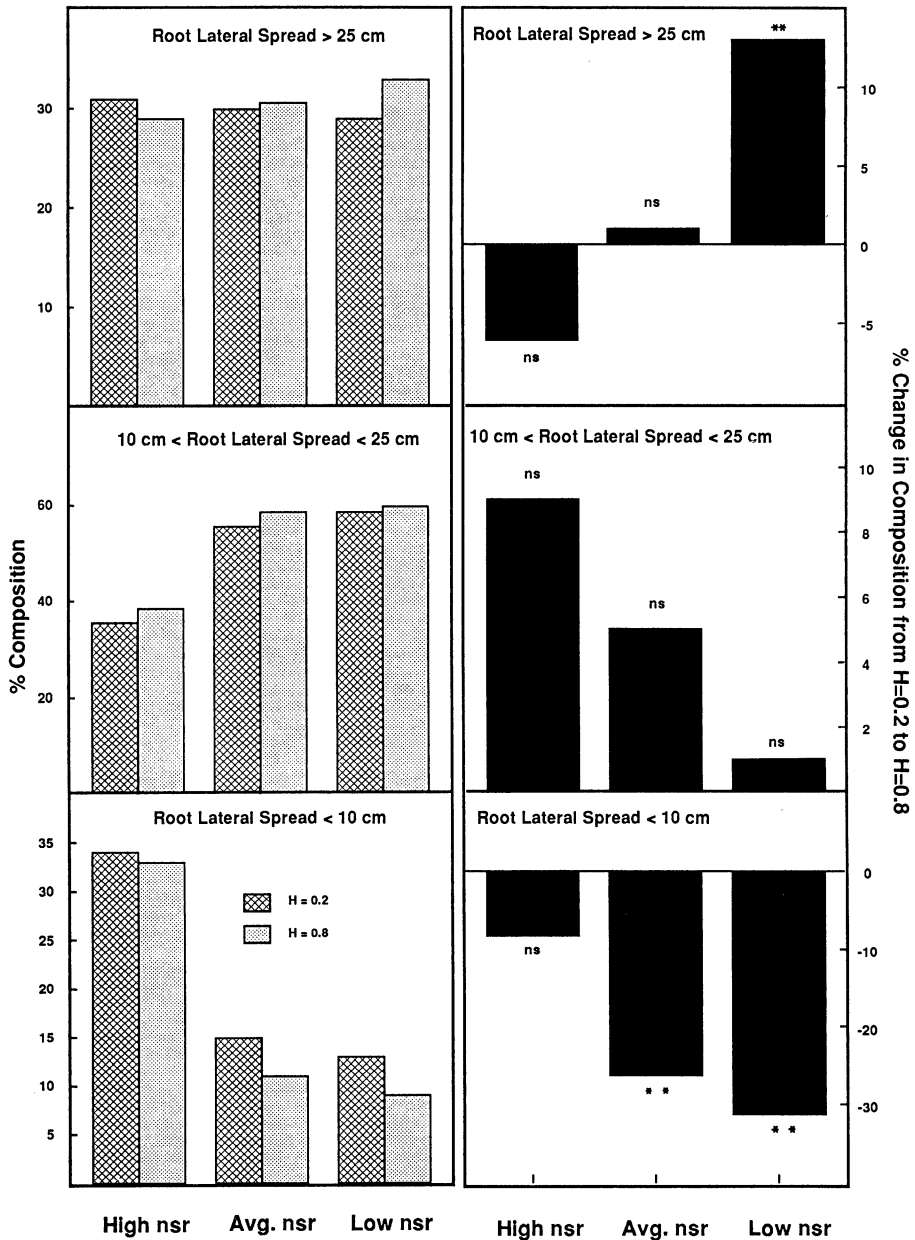


FIG. 6.—The results of 1,000 d of intra- and interspecific competition in an established community (all adult plants) composed of the 15 plants shown in table 5 and growing in an environment in which total soil N followed a second-order stationary fractal model $Y(d)$ (eq. [1]) that consists of only one spatial process $X(d)$ with $A = 300$ cm, $f(d) = 6$ for all d , $\sigma = 2.4$, and $H = 0.2$ or $H = 0.8$. All plants were first provided with an unlimited supply of N until they reached their full (adult) biomass; this was followed by the imposition of three different N supply constraints (NSRs) for 1,000 d: high (NSR = 0.001529), average (NSR = 0.000343), and low (NSR = 0.000092); see text for more details. The left side of the graph shows percentage composition of groups of plants with three distinct root lateral spreads. The right side of the graph shows the percentage change in composition when the scaling of total soil N is changed from $H = 0.2$ to $H = 0.8$. Two asterisks represent significant differences between $H = 0.2$ and $H = 0.8$ at $P < .01$; ns = no difference.

(figs. 6 and 7), at the lower end of NSR the results were not symmetric. In the adult-based model, species with a root lateral spread of less than 10 cm decreased their composition to an average of 12% for the average and low NSR, while in the seedling-based model the average value was 29%. The opposite was true for species with a $10 < \text{RLS} < 25$ cm: in the adult model the average species composition at average and low NSR was 50% versus 43% in the seedling-based model. For species with $\text{RLS} > 25$ cm, there was a smaller change in species composition between adult and seedling models: an average of 30% for average and low NSR in the adult models to 25% in the seedling-based model. This difference in behavior resulted from the interplay among the conditional distribution of growth habitats associated with organisms that are expanding in a fractal environment (see table 2) and the differences in root densities. Because of intra- and interspecific competition for soil available N, all NSR rates in the model represent different levels of N stress, which indicates that many seedlings will be surrounded by areas with NSR that are lower than plant requirements. This means the "N obstacle" that a plant needs to overcome will be higher for plants that must expand over large areas. Conversely, because plants with high RLS capture resources over large areas the requirements of N per unit area decline.

SUMMARY AND CONCLUSIONS

In the first part of this article, we explored in general theoretical terms the interaction between the root area of a plant and the scaling (H) of soil N and how this interaction may affect the landscape distribution of plants. First, we considered a landscape in which soil N can be modeled with the use of only one scaling (H) and extent constant (A) and in which the mean for soil N is a fixed constant ($f[d] = \mu$ for all d ; see eq. [1]).

For an adult plant with a fixed root area inhabiting a poor landscape (average resources below plant requirements), the probability of finding a suitable habitat increases with the scaling factor H , while in richer landscapes the results are the opposite: the probabilities of finding a suitable habitat decreased with H (table 1). These results strongly indicate that a small change in the scaling of soil N can significantly affect the spatial distribution of plants and thus landscape patchiness.

For seedlings whose root systems are expanding in area, the results depended heavily on whether, as it expands, the root area remains smaller than the extent constant (A), or it expands beyond it. When plant root area remained within the bounds of the extent constant A (table 2), the results were opposite to the ones found for the case of adults (table 1). If the organism was originally residing in a poor site, its probability of finding a suitable habitat after root expansion was inversely related to the scaling factor H (the opposite was true for rich original habitats). These results indicate that population level response to changes in the scaling and total pools of landscape resources may depend heavily on the mixture of organism sizes (seedling vs. adult plants in our case).

The response pattern was different when the plant root area after expansion exceeded the extent constant A (table 3). In this case, only small differences were found between H values. There are, however, interesting comparisons to be made

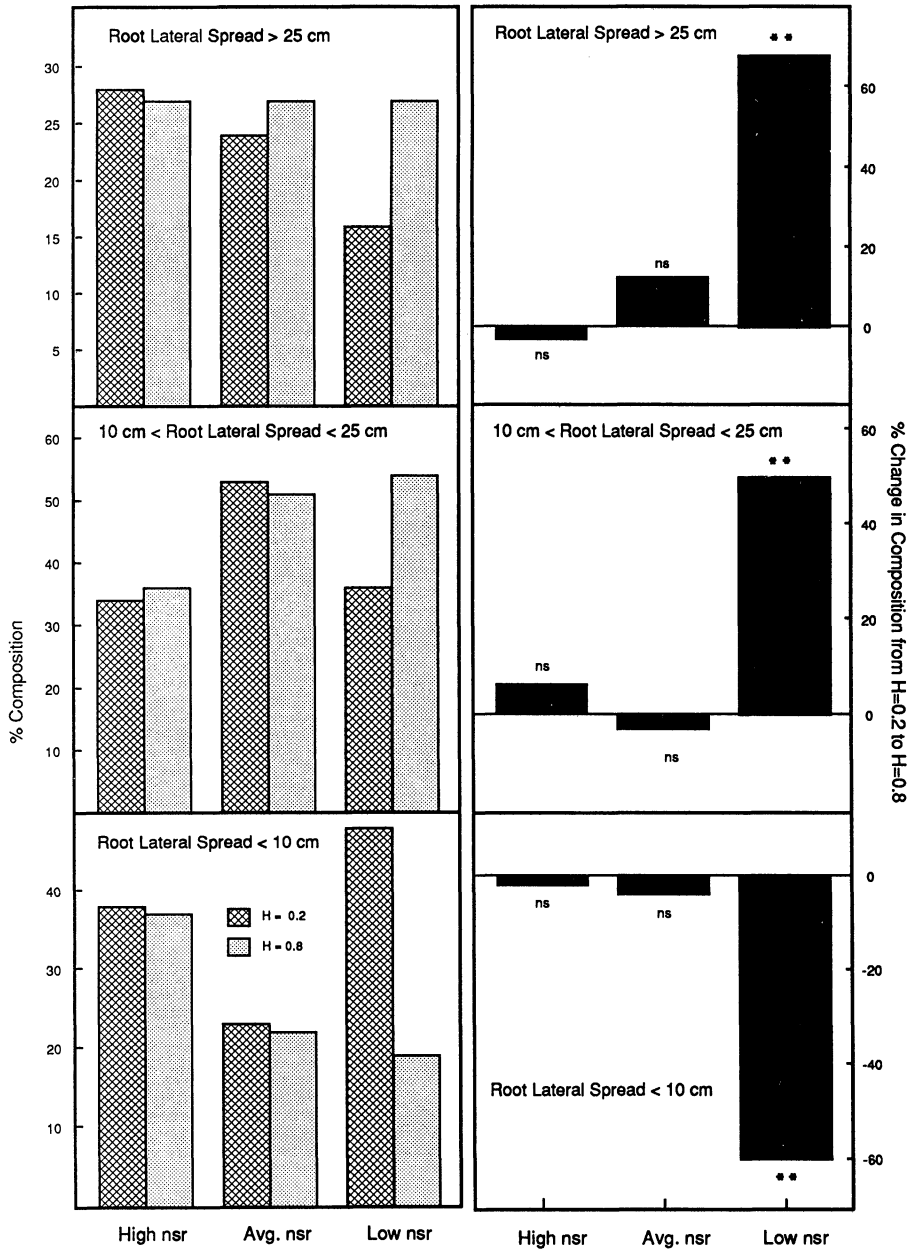


FIG. 7.—The results of 1,000 d of intra- and interspecific competition in a community of seedlings composed of the 15 plants shown in table 5 and growing in an environment in which total soil N followed a second-order stationary fractal model $Y(d)$ (eq. [1]) that consists of only one spatial process $X(d)$, with $A = 300$ cm, $f(d) = 6$ for all d , $\sigma = 2.4$, and $H = 0.2$ or $H = 0.8$. The seedlings were subjected to three different N supply constraints (NSRs) and allowed to grow for 1,000 d: high (NSR = 0.001529), average (NSR = 0.000343), and low (NSR = 0.000092) (see text for more details). The *left side* of the graph shows percentage composition of groups of plants with three distinct root lateral spreads. The *right side* of the graph shows the percentage change in composition when the scaling of total soil N is changed from $H = 0.2$ to $H = 0.8$. Two asterisks represent significant differences between $H = 0.2$ and $H = 0.8$ at $P < .01$; ns = no difference.

between plants with root area (a) that is less than the extent constant A and plants with $A < a < 2A$. If a plant originally resides in a poor site, the ability to expand its root system beyond the extent constant A becomes a significant advantage because it increases the probability of finding suitable habitats for growth (0.39 vs. 0.19 for $H = 0.2$ and 0.41 vs. 0.10 for $H = 0.8$; tables 2 and 3). If the organism, however, originally resides in a rich site, the size of the extent constant A may indeed become a barrier for expansion (0.81 vs. 0.62 for $H = 0.2$ and 0.90 vs. 0.60 for $H = 0.8$; tables 2, 3). These differences need to be taken into account when analyzing the landscape effect of disturbances that break the extent of the spatial autocorrelation of soil variables.

We then expanded our theoretical analysis to the case in which the mean of soil N in the landscape is no longer a constant and in which the pattern of soil N is the result of the sum of three spatial processes, $X_i(d)$ (eq. [1]), with a combination of different scaling constants, H_i . We used this model to determine whether there is an optimal root area for plants that have the same soil N requirements but inhabit landscapes with different combinations of scaling constants (H_i , $i = 1, \dots, 3$). We found that the optimal root area for a plant to succeed may in fact be significantly influenced by the combination of scaling constants of the different spatial processes (fig. 3). These results have implications in the development of models designed to predict which organisms may be more susceptible to disturbances that alter the value of the scaling constants that control the landscape patterns of soil resources at different extents.

We analyzed the effect of resource scaling in plant species competition by making the ALLOCATE model (Tilman 1988) spatially explicit. Soil N was modeled with the use of second-order stationary fractals, and plants were spatially dimensioned with the use of the root lateral spread concept (Grime 1979). We derived the following conclusions from the analysis of model outputs: First, in monocultures, adult plants with low RLS but high root densities are better suited to withstand a nutrient stress (N in this case) than plants with a high RLS and low root densities when the scaling of soil N is low: $H < 0.5$ (fig. 4). For $H > 0.5$, however, the results were exactly the reverse (fig. 4).

Second, in the presence of intra- and interspecific competition (fig. 5), plants with low RLS and high root density were dominant only under low nutrient stress, but their dominance was significantly reduced when the scaling factor H was near one. At high N, stress conditions plants with large RLS and low root densities were dominant, and their dominance was magnified when the scaling factor H was near one. These two results may cast some light on the theoretical dispute between Tilman (1982, 1988) and Grime (1979) as to which plant trait may be optimal in the competition for soil nutrients: the ability to capture nutrients rapidly, which in our context would be associated with high root density, or the ability to withstand low nutrient supply rates, which in our context would be associated with high RLS.

Finally, we also ran large-scale simulations involving species with different RLS, biomass allocation to roots, root densities, and growth rates (table 5) that were competing in a landscape characterized by different soil N scaling properties and NSR. The general trends of the results of the two species model discussed

above were also observed in a multispecies model, with an added role played by the allocation of biomass to roots (see figs. 6 and 7). The results were also heavily dependent on whether the nutrient stress was applied to adult plants or seedlings. Seedlings of plants with low RLS and high root density do much better when competing with seedlings of plants with high RLS and low root density than adults competing with adults (figs. 6, 7). This interplay between plant traits, age, and the scaling of soil resources may add another tier of explanation to the observation that species that are dominant as adults and that sometimes tend to become even more dominant when nutrient or water stress is applied cannot successfully compete as seedlings in secondary succession. A typical example is the case of *Bouteloua gracilis* in the short-grass prairie, a plant with a large root system and large allocation of biomass to roots (Redente et al. 1990) that is dominant in undisturbed communities but has a low probability for establishment in disturbed areas in which the surface vegetation has been removed (Coffin and Lauenroth 1990). Coffin and Lauenroth (1990) have related these low establishment probabilities to the presence or absence of optimal growing conditions (in particular, sequence of rainfall events) and the physiological and morphological characteristics of *B. gracilis*, and they have developed detailed and complex models to account for the observed patterns. Our results relating biomass allocation to roots, RLS, root density, and the scaling of soil resources to the ability of seedlings versus adults to compete can add a complementary and certainly more parsimonious explanation to the phenomenon.

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APPENDIX A

MEAN, VARIANCE, AND PROBABILITY DENSITY FUNCTION OF THE INTEGRATED FRACTAL PROCESS $Z(d; a)$ DESCRIBED BY EQUATION (6) OF THE TEXT

Since $X(d)$ is a Gaussian process, then $Z(d; a)$ is also a Gaussian process. To establish that, we need to remember that W_1, \dots, W_n have a joint normal distribution if they can be represented as

$$W_i = \sum_{j=1}^m a_{ij} U_j \quad i = 1, \dots, n,$$

where $U_j, j = 1, \dots, m$ are independent and normally distributed random variables. It follows then that any set of partial sums of W_1, \dots, W_n are also jointly normal. Now $Z(d; a)$ can be written as a limit of a sum: Define

$$\Delta_n x = \frac{a}{n} \text{ with } x_k = d + k\Delta_n x \text{ for } k = 1, 2, \dots, n.$$

Then

$$\int_d^{d+a} X(u) du \approx \lim_{n \rightarrow \infty} \sum_{k=1}^n X(x_k) \Delta_n x.$$

Thus it will also be normally distributed.

To characterize $Z(d; a)$, we need only to determine its mean and variance. First, $Z(d; a)$ is a Gaussian process, which means we can use Lebesgue's theorem of dominated convergence (Shiryayev 1984, p. 185) to interchange expectation and integration. Mean:

$$\xi[Z(d; a)] = \xi \left[\int_d^{d+a} X(u) du \right] = \int_d^{d+a} \xi[X(u)] du = 0.$$

Variance:

$$\begin{aligned} \text{var}[Z(d; a)] &= \text{cov}[Z(d; a)Z(d; a)] = \text{cov} \left[\int_d^{d+a} X(u) du \int_d^{d+a} X(s) ds \right] \\ &= \int_d^{d+a} \int_d^{d+a} \text{cov}[X(u)X(s)] ds du \\ &= \int_d^{d+a} \int_d^{d+a} \left[1 - \left(\frac{|u-s|}{A} \right)^{2H} \right] \sigma^2 I_{(|u-s| \leq A)} ds du, \end{aligned}$$

where $I_{(|u-s| \leq A)} = 1$ when $|u-s| \leq A$ and 0 otherwise. That generates three cases. First, $a < A$:

$$\text{var}[Z(d; a)] = \int_d^{d+a} \int_d^{d+a} \left[1 - \left(\frac{|u-s|}{A} \right)^{2H} \right] \sigma^2 du ds = a^2 \left[1 - \frac{a^{2H}}{A^{2H}(2H+1)(H+1)} \right] \sigma^2.$$

Second, $A \leq a \leq 2A$:

$$\begin{aligned} \text{var}[Z(d; a)] &= \int_d^{d+a-A} \int_d^{s+A} \left[1 - \left(\frac{|u-s|}{A} \right)^{2H} \right] \sigma^2 du ds \\ &\quad + \int_{d+a-A}^{d+A} \int_d^{d+a} \left[1 - \left(\frac{|u-s|}{A} \right)^{2H} \right] \sigma^2 du ds \\ &\quad + \int_{d+A}^{d+a} \int_{s-A}^{d+a} \left[1 - \left(\frac{|u-s|}{A} \right)^{2H} \right] \sigma^2 du ds. \end{aligned}$$

Thus,

$$\begin{aligned} \text{var}[Z(d; a)] &= \frac{(a^2 - A^2)\sigma^2}{2} - \frac{\sigma^2(a-A)}{2H+1} \left[A + \frac{(a-A)^{2H+1}}{A^{2H}(2H+2)} \right] \\ &\quad + \sigma^2 \left[(2A-a)a - \frac{2A^{2H+2} - 2(a-A)^{2H+2}}{A^{2H}(2H+1)(2H+2)} \right] \\ &\quad + \sigma^2 \left\{ \frac{(a^2 - A^2)}{2} - \frac{(a-A)}{2H+1} \left[A + \frac{(a-A)^{2H+1}}{A^{2H}(2H+2)} \right] \right\} \end{aligned}$$

and

$$\begin{aligned} \text{var}[Z(d; a)] &= \sigma^2 \left\{ (a^2 - A^2) - \frac{2(a - A)}{2H + 1} \left[A + \frac{(a - A)^{2H+1}}{A^{2H}(2H + 2)} \right] \right\} \\ &\quad + \sigma^2 \left[(2A - a)a - \frac{2A^{2H+2} - 2(a - A)^{2H+2}}{A^{2H}(2H + 1)(2H + 2)} \right]. \end{aligned}$$

Finally, $a > 2A$:

$$\begin{aligned} \text{var}[Z(d; a)] &= \int_d^{d+A} \int_d^{s+A} \left[1 - \left(\frac{|u - s|}{A} \right)^{2H} \right] \sigma^2 du ds \\ &\quad + \int_{d+A}^{d+a-A} \int_{s-A}^{s+A} \left[1 - \left(\frac{|u - s|}{A} \right)^{2H} \right] \sigma^2 du ds \\ &\quad + \int_{d+a-A}^{d+a} \int_{s-A}^{d+a} \left[1 - \left(\frac{|u - s|}{A} \right)^{2H} \right] \sigma^2 du ds. \end{aligned}$$

Thus,

$$\begin{aligned} \text{var}[Z(d; a)] &= \sigma^2 A^2 \left[\frac{3}{2} - \frac{1}{2H + 1} \left(1 + \frac{1}{2H + 2} \right) \right] \\ &\quad + 2A\sigma^2(a - 2A) \left[1 - \frac{1}{2H + 1} \right] + \sigma^2 A^2 \left[\frac{3}{2} - \frac{1}{2H + 1} \left(1 + \frac{1}{2H + 2} \right) \right] \end{aligned}$$

and

$$\text{var}[Z(d; a)] = 2\sigma^2 A^2 \left[\frac{3}{2} - \frac{1}{2H + 1} \left(1 + \frac{1}{2H + 2} \right) \right] + 2\sigma^2 A(a - 2A) \left[1 - \frac{1}{2H + 1} \right].$$

APPENDIX B

COVARIANCE BETWEEN $Z(s; a)$ AND $Z(d; a)$ WHERE $s < d$

The $\text{cov}(Z[s; a], Z[d; a])$ is calculated using an approach similar to the one used to estimate the $\text{var}(Z[d; a])$ in Appendix A. What changes, however, is the limits of integrations. The $\text{cov}(Z[s; a], Z[d; a])$ is calculated as follows:

$$\begin{aligned} \text{cov}[Z(s; a), Z(d; a)] &= \text{cov} \left[\int_s^{s+a} X(u) du \int_d^{d+a} X(y) dy \right] \\ &= \int_d^{d+a} \int_s^{s+a} \text{cov}[X(y)X(u)] du dy \\ &= \int_d^{d+a} \int_s^{s+a} \left[1 - \left(\frac{|u - y|}{A} \right)^{2H} \right] \sigma^2 I_{(|u-y| \leq A)} du dy, \end{aligned}$$

where the indicator function $I_{(\cdot)}$ is as defined in Appendix A. The bounds imposed in the limits of integration ($I_{(|u-y| \leq A)} = 1$) generate six distinct cases, with the integrals to be solved being of the general form

$$\begin{aligned} \text{cov}[Z(s; a), Z(d; a)] &= \int_{l\text{-limit}_1}^{u\text{-limit}_1} \int_{l_1(y)}^{u_1(y)} \left[1 - \left(\frac{|u - y|}{A} \right)^{2H} \right] \sigma^2 du dy \\ &\quad + \dots + \int_{l\text{-limit}_n}^{u\text{-limit}_n} \int_{l_n(y)}^{u_n(y)} \left[1 - \left(\frac{|u - y|}{A} \right)^{2H} \right] \sigma^2 du dy. \end{aligned}$$

Here l -limit _{i} and u -limit _{i} , $i = 1, \dots, n$, are lower and upper limits for y within the interval 0 to a , and $l_i(y)$ and $u_i(y)$ are functions of y of the form $l_i(y) = y - A$ and $u_i(y) = y + A$, with the constraint that $(d - s) \leq l_i(y)$ and $u_i(y) \leq (d - s + a)$. The limits of integration depend on the $|d - s|$, the size of the area (a), and the extent (A). The six cases are, first, $|d - s + a| < A$. There is only one integral to solve with the limits of integration:

$$0 \leq y \leq a \quad \text{and} \quad l_1(y) = (d - s) \leq u \leq u_1(y) = (d - s + a).$$

The covariance then is

$$\text{cov}[Z(s; a), Z(d; a)] = \sigma^2 \left\{ a^2 - \frac{[(d - s + a)^{2H+2} + (d - s - a)^{2H+2} - 2(d - s)^{2H+2}]}{A^{2H}(2H + 1)(2H + 2)} \right\}.$$

The second case is $(d - s) \leq A \leq (d - s + a)$ and $2(d - s) \leq a \leq 2A$. There are three integrals to solve, with the limits of integration as

$$0 \leq y \leq d - s + a - A \quad \text{and} \quad l_1(y) = (d - s) \leq u \leq u_1(y) = y + A;$$

$$d - s + a - A \leq y \leq d - s + A \quad \text{and} \quad l_2(y) = (d - s) \leq u \leq u_2(y) = d - s + a;$$

and

$$d - s + A \leq y \leq a \quad \text{and} \quad l_3(y) = y - A \leq u \leq u_3(y) = d - s + a.$$

The covariance then is

$$\begin{aligned} \text{cov}[Z(s; a), Z(d; a)] = & \sigma^2 \left\{ a^2 - A^2 \left[1 + \frac{2}{(2H + 1)(2H + 2)} \right] \right\} \\ & + \sigma^2 (d - s)^2 \left[\frac{2(d - s)^{2H}}{A^{2H}(2H + 1)(2H + 2)} - 1 \right] \\ & + \sigma^2 \left[a(2A - a) - 2A \frac{(a - A)}{2H + 1} \right]. \end{aligned}$$

The third case is $(d - s) \leq A \leq (d - s + a)$, $2(d - s) \leq a$, and $2A \leq a$. There are three integrals to solve, with the limits of integration as

$$0 \leq y \leq d - s + A \quad \text{and} \quad l_1(y) = (d - s) \leq u \leq u_1(y) = y + A;$$

$$d - s + A \leq y \leq d - s + a - A \quad \text{and} \quad l_2(y) = y - A \leq u \leq u_2(y) = y + A;$$

$$d - s + a - A \leq y \leq a \quad \text{and} \quad l_3(y) = y - A \leq u \leq u_3(y) = d - s + a.$$

The covariance then is

$$\text{cov}[Z(s; a), Z(d; a)] =$$

$$\begin{aligned} & \sigma^2 \left[(d - s + a + A)(s - d + A) + \frac{(d - s + a - A)^2}{2} - \frac{(d - s - A)^2}{2} \right] \\ & - \sigma^2 \left\{ \frac{A(d - s + a - A)}{2H + 1} + \left[\frac{(a - A)^{2H+2} - (d - s)^{2H+2}}{A^{2H}(2H + 1)(2H + 2)} \right] + \frac{A(A + s - d)}{2H + 1} \right\} \\ & - \sigma^2 \left\{ \left[\frac{A^{2H+2} - (d - s)^{2H+2}}{A^{2H}(2H + 1)(2H + 2)} \right] - 2A(a - 2A) \left[1 - \frac{1}{2H + 1} \right] \right\}. \end{aligned}$$

The fourth case is $(d - s) \leq A \leq (d - s + a)$, $a \leq 2(d - s)$, and $a \leq 2A$. There are two integrals to solve, with the limits of integration as

$$0 \leq y \leq (d - s + a - A) \quad \text{and} \quad l_1(y) = (d - s) \leq u \leq u_1(y) = (y + A)$$

and

$$(d - s + a - A) \leq y \leq a \quad \text{and} \quad l_2(y) = (d - s) \leq u \leq u_2(y) = (d - s + a).$$

The covariance then is

$$\begin{aligned} \text{cov}[Z(s; a), Z(d; a)] &= \sigma^2 \left[\frac{a^2}{2} - \frac{(d - s - A)^2}{2} - \frac{A(d - s + a - A)}{2H + 1} + a(s - d + A) \right] \\ &\quad - \sigma^2 \left[\frac{A^{2H+2} + (d - s - a)^{2H+2} - 2(d - s)^{2H+2}}{A^{2H}(2H + 1)(2H + 2)} \right]. \end{aligned}$$

The fifth case is $0 \leq A \leq (d - s)$ and $(d - s + A) \leq a$. There are two integrals to solve, with the limits of integration as

$$(d - s - A) \leq y \leq (d - s + A) \quad \text{and} \quad l_1(y) = (d - s) \leq u \leq u_1(y) = (y + A)$$

and

$$(d - s + A) \leq y \leq a \quad \text{and} \quad l_2(y) = (y - A) \leq u \leq u_2(y) = (y + A).$$

The covariance then is

$$\text{cov}[Z(s; a), Z(d; a)] = 2A(a - d + s) \left(1 - \frac{1}{2H + 1} \right) \sigma^2.$$

Finally, the sixth case is $0 \leq A \leq (d - s)$ and $(d - s - A) \leq a \leq (d - s + A)$. There is only one integral to solve, with the limits of integration as

$$(d - s - A) \leq y \leq a \quad \text{and} \quad l_1(y) = (d - s) \leq u \leq u_1(y) = (y + A).$$

The covariance then is

$$\begin{aligned} \text{cov}[Z(s; a), Z(d; a)] &= \\ &\sigma^2 \left[(A - d + s)(a - d + s + A) + \frac{a^2}{2} - \frac{(d - s - A)^2}{2} - \frac{A(a - d + s + A)}{(2H + 1)} \right] \\ &\quad + \sigma^2 \left[\frac{A^2}{(2H + 1)(2H + 2)} - \frac{(d - s - a)^{2H+2}}{A^{2H}(2H + 1)(2H + 2)} \right]. \end{aligned}$$

APPENDIX C

CONDITIONAL PROBABILITIES FOR $W(d; a)$ AS DEFINED IN EQUATION (6)

As shown in Appendix A, $Z(s; a)$, and thus $W(s; a)$, has a normal distribution. This signifies that $W(s; a)$ and $W(d; a)$ ($s < d$) have a joint multivariate normal distribution. If we define $W_1 = W(s; a)$ and $W_2 = W(d; a)$, then the parameters of the multivariate distribution are

$$\begin{aligned} \mu_{W_1} &= \int_s^{s+a} f(u) du \quad \text{and} \quad \mu_{W_2} = \int_d^{d+a} f(u) du \\ \sigma_{W_1}^2 &= \text{var}[W(s; a)]; \quad \sigma_{W_2}^2 = \text{var}[W(d; a)] \\ \rho &= \frac{\text{cov}[W(s; a), W(d; a)]}{\sqrt{\text{var}[W(s; a)]} \sqrt{\text{var}[W(d; a)]}}. \end{aligned}$$

The conditional distribution of $W(d; a)$ given $W(s; a) = w_0$ is univariate normal, with the following parameters (Mood et al. 1974, p. 167):

$$\mu_{(W_2|W_1=w_0)} = \mu_{W_2} + \frac{\rho\sigma_{W_2}}{\sigma_{W_1}}(\mu_{W_1} - w_0)$$

and

$$\sigma_{(W_2|W_1=w_0)}^2 = \sigma_{W_2}^2(1 - \rho^2).$$

APPENDIX D

CONDITIONAL DISTRIBUTION ASSOCIATED WITH DOUBLING THE SIZE AND CROSSING EXTENT BOUNDARIES (TABLES 3 AND 4)

Assume a situation in which the variable of interest has a second-order stationary fractal structure of the following form (for the case of only one spatial process $X_2(d) \equiv 0 \forall d$):

$$Y(d) = f(d) + X_1(d) + X_2(d) \quad H_1 \neq H_2 \quad \text{and} \quad 2A_1 < A_2.$$

Furthermore, assume that the process in question ($W[\cdot; \cdot]$) integrates over an area of size $= a[W(d; a)]$ such that $0.5A_1 < a < A_1$. Let us assume that the process $W(\cdot; \cdot)$ doubles in size: $W(s; a')$, $a' = 2a$ and thus $A_1 < a' < A_2$. We want to calculate the conditional probability of $W(s; a')$ given $W(s; a) = w_0$.

We can construct $W(s; a')$ as $W(s; a') = W(s; a) + W(s + a, a)$, that is, as the sum of two nonoverlapping $W(\cdot; \cdot)$ variables. As a consequence,

$$P[W(s; a') \leq w | W(s; a) = w_0] = P[W(s; a) + W(s + a; a) \leq w | W(s; a) = w_0],$$

so

$$P[W(s; a') \leq w | W(s; a) = w_0] = P[W(d; a) \leq w - w_0 | W(s; a) = w_0],$$

where $d = s + a$. Using the equations for the multivariate normal distributions, the values for A_1, A_2, a , and a' in question, we have

$$\begin{aligned} \mu_{W_1} &= \int_s^{s+a} f(u) du \quad \text{and} \quad \mu_{W_2} = \int_d^{d+a} f(u) du \\ \sigma_{W_1}^2 &= \text{var}[W(s; a)] = \text{var}[W(d; a)] = \sigma_{W_2}^2 = a^2(\sigma_1^2 + \sigma_2^2) \\ &= \frac{\sigma_1^2 a^{2H_1+2}}{A_1^{2H_1}(2H_1 + 1)(H_1 + 1)} - \frac{\sigma_2^2 a^{2H_2+2}}{A_2^{2H_2}(2H_2 + 1)(H_2 + 1)}. \end{aligned}$$

Given that $A_1 < a' < 2A_1 < A_2$, we can use the covariance equations from Appendix B for H_1 and H_2 and the fact that in our case $d - s = a$. Therefore,

$$\begin{aligned} \text{cov}[W(s; a), W(d; a)] &= \sigma_1^2 \left[A_1 \left(2a - \frac{A_1}{2} \right) - a^2 - \frac{(2a - A_1)A_1}{2H_1 + 1} \right] \\ &\quad - \left[\frac{A_1^{2H_1+2} - 2a^{2H_1+2}}{A_1^{2H_1}(2H_1 + 1)(2H_1 + 2)} \right] \sigma_1^2 \\ &\quad + a^2 \sigma_2^2 \left[1 - \frac{a^{2H_2}(2^{2H_2+1} - 1)}{A_2^{2H_2}(2H_2 + 1)(H_2 + 1)} \right]. \end{aligned}$$

Thus,

$$\rho = \frac{\text{cov}[W(s; d), W(d; a)]}{\text{var}[W(s; a)]}.$$

With these values we can calculate the conditional mean and variance of W_2 given $W_1 = w_0$, using the equations for the conditional distribution shown in Appendix C. With that, then, we can calculate the appropriate probabilities.

APPENDIX E

ESTIMATION OF THE r , PR, AND K PARAMETERS USED IN THE SPECIES COMPETITION MODEL

We selected values for the r (maximum rate of growth), PR (fraction of biomass allocated to roots and rhizomes), and K (half saturation constant) parameters that have a close resemblance with the available experimental data. In order to do that we proceeded as follows.

First, we selected PR values that followed the patterns of root plus rhizome biomass allocation of the five species (*Agrostis scabra*, *Agropyron repens*, *Poa pratensis*, *Schizachyrium scoparium*, and *Andropogon gerardii*) shown in table 1 of Tilman and Wedin (1991). The PR values selected for the simulations run in the main text were 0.17, 0.42, 0.61, 0.78, and 0.85.

Second, the r values for the model were generated as follows. We first assumed for simplicity that the aboveground biomass of plants was composed entirely of leaves. This assumption is reasonable because the objective of this model is not to test the effects of leaf-to-shoot ratios in plant growth. We subsequently ran a regression between the $(1 - LF) = PR$ and weekly RGR_{\max} data shown in figure 4.7 of Tilman (1988) and rescaled the RGR_{\max} from weekly to daily values (LF is biomass allocation to leaves, and RGR_{\max} is maximum growth rate). The resulting equation is

$$r = 0.4276 - 0.419 * PR.$$

The corresponding r values for the PR values used in the simulations (see above) are 0.36, 0.25, 0.17, 0.1, and 0.07.

Third, to estimate the K values associated with each pair of r , PR values, we used the following approach. We began by rescaling the X - and Y -axes of the data presented in figure 4A of Tilman (1990) that relate the equilibrium concentration of $NO_3^- - N$ in soil solution under a monoculture (R^*) of the five species discussed above (Y -axis) to their respective root biomass (X -axis). We rescaled R^* by dividing each R^* by R_{\max}^* , thus generating relative R^* (RR^*) in the 0–1 range. The X -axis was rescaled to relative values by replacing the root biomass with the corresponding PR values for the species in question (table 1 of Tilman and Wedin 1991).

We then ran a regression between the RR^* and PR. The resulting equation was

$$RR^* = 0.5 * \exp(0.185 - 3.466 * PR) \quad r^2 = 0.92.$$

Now the equivalent for R^* in equation (15) of the text was derived as follows. First we solved equation (15) for the total amount of resources needed at equilibrium:

$$\frac{dB_i}{dt} = B_i \left[\frac{r_i(1 - PR_i)\alpha_i^{-1/\beta_i} RLS_i^{1/\beta_i - 1} \int_d^{d+RLS_i} R(u; t) du}{\alpha_i^{-1/\beta_i} RLS_i^{1/\beta_i - 1} \int_d^{d+RLS_i} R(u; t) du + K_i RLS_i} - RESP_i \right] = 0$$

$$\int_d^{d+RLS_i} R(u; t) du = \frac{K_i RLS_i^{2-1/\beta_i} \alpha_i^{1/\beta_i} RESP_i}{r_i(1 - PR_i) - RESP_i}.$$

Now, the R^* discussed above is a dimensionless value because it corresponds to the equilibrium solution for the ALLOCATE model, which (see main text) is itself dimen-

sionless. To calculate a comparable R^* value for equation (15), we first need to take the partial derivative with respect to root lateral spread of the resources equilibrium equation

$$\frac{\partial}{\partial RLS_i} \left[\int_{RLS_i} R(u; t) du \right] = R^*(u; t) = \frac{K_i \left(2 - \frac{1}{\beta_i} \right) RLS_i^{1-1/\beta_i} \alpha_i^{1/\beta_i} RESP}{r_i(1 - PR_i) - RESP_i}.$$

Therefore, $R^*(u; t)$ is both a function and β_i and root lateral spread (RLS_i) for species i . Now, when $\beta_i = 1$ root lateral spread is directly proportional to root biomass; this indicates, for example, that the root lateral spread of a plant with a biomass of two is equal to the root lateral spread of two plants with biomasses of one, respectively. The concentration of root biomass per unit area is a constant, and the nutrient requirements per unit area are therefore independent from area. Thus, the case $\beta_i = 1$ is the closest equivalent to the R^* of the ALLOCATE model. Therefore, given the fact that we used $\alpha_i = 1$ for all i 's, we have that

$$R^*(u; t) = R^* = \frac{K_i RESP_i}{r_i(1 - PR_i) - RESP_i}, \beta_i = 1, \alpha_i = 1 \forall i.$$

If we fix the K for the species with the highest PR to an arbitrary value K_{n0} (where $n0$ is the index for the species with the highest PR), we can then create the following set of equalities:

$$\frac{R_i^*}{R_{n0}^*} = \frac{K_i RESP_i}{r_i(1 - PR_i) - RESP_i} \frac{r_{n0}(1 - PR_{n0}) - RESP_{n0}}{K_{n0} RESP_{n0}} = \frac{RR_i^*}{RR_{n0}^*} = \frac{e^{0.185 - 3.466PR_i}}{e^{0.185 - 3.466PR_{n0}}}.$$

Thus,

$$K_i = \frac{e^{0.185 - 3.466PR_i} (r_i(1 - PR_i) - RESP_i) K_{n0} RESP_{n0}}{e^{0.185 - 3.466PR_{n0}} (r_{n0}(1 - PR_{n0}) - RESP_{n0}) RESP_i}.$$

In the simulations run in this article, we chose a constant $RESP_i = 0.007$ for all i 's and a $K_{n0} = 0.1$; for computational purposes, we rescaled all the other values of K by half. Thus, in our particular case,

$$K_{n0} = 0.1$$

$$K_i = 0.5 \frac{e^{0.185 - 3.466PR_i} (r_i(1 - PR_i) - RESP_i) K_{n0}}{e^{0.185 - 3.466PR_{n0}} (r_{n0}(1 - PR_{n0}) - RESP_{n0})} \text{ for } i \neq n0.$$

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