

DEFINING A PLANT'S BELOWGROUND ZONE OF INFLUENCE

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Abstract. The concept of a zone of influence, the area over which a plant alters the environment, forms the basis of many models of plant competition. Because of logistical difficulties, we actually know little about the sizes and shapes of zones of influence belowground. Here we advocate obtaining data on plants' belowground zones of influence, including the length and distribution of lateral roots, in order to understand better how plants respond to their abiotic soil environment and to other plants. We provide several examples from recent work. First, we present an analysis of a large global data set which shows that maximum lateral root spread correlates with canopy size but that, for a given canopy size, maximum lateral root spread is greater in arid environments and in coarse textured soils. Second, we use an experiment with the weedy annual *Abutilon theophrasti* to show how using nutrient analogs as tracers yields information about lateral root distributions within populations. In our experimental populations, the belowground zone of influence extended well beyond the closest neighboring plants. Overlap in zones of influence increased in nutrient patches. Third, we propose a new conceptual model of belowground zones of influence based on these and other data sets. The model assumes that the probability of resource uptake or competing with a particular neighbor declines with distance from the stem but that considerable uptake at great distances from the stem is still possible. It also allows for plasticity in root distributions as might occur in spatially heterogeneous soils. Finally, we suggest how better information on the shapes and sizes of belowground zones of influence will help develop a more predictive framework for understanding plant competition.

Key words: *belowground competition; canopy volume; lateral root spread; neighborhood models; soil resources.*

INTRODUCTION

Because plants are sessile, most of their environmental interactions take place within a restricted space. The area over which a plant takes up resources, produces chemical exudates, casts shade, sheds litter, or otherwise alters its environment is considered its zone of influence (Uranov 1965, Bonan 1993, Stohlgren 1993). Characterizing the zone of influence is important both because its size and shape determine the total pool of resources available to an individual and because overlap in zones of influence is necessary for facilitation or competition to occur (Czaran and Bartha 1992).

The zone of influence concept has been applied previously to belowground processes (Uranov 1965, Yastrebov 1996), and spatially explicit models based on this concept have examined competition for belowground resources (Mou et al. 1993, Biondini and Grygiel 1994, Huston and DeAngelis 1994, Biondini 2001). This approach should prove useful for predicting the outcome of competition as a function of the soil

environment, but it has been developed with little understanding of the actual spatial distribution of root systems, their activity under different abiotic conditions, or their architectural plasticity in the presence of neighboring plants.

To predict the outcome of plant interactions as a function of local soil conditions, neighborhood models have a long history aimed at understanding the strength and consequences of plant competition as a function of the spatial arrangement of aboveground plant parts. In some early models, the neighborhood simply consisted of the number of plant stems within a circular area of arbitrary radius, while later models incorporated information about neighbor sizes, proximity or angular dispersion (Ek and Monserud 1974, Mack and Harper 1977, Weiner 1982, 1984, Silander and Pacala 1985, Lindquist et al. 1994) or searched for the aboveground neighborhood size that best explains plant size variation (Pacala and Silander 1985). Distance-based predictors used in these models typically assume that plants are more effective at taking up resources closer to their stems, and the strength of neighbor interactions is often modeled to decline according to a predetermined function of distance (e.g., linear, hyperbolic;

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Weiner 1984, Pacala and Silander 1987, Yastrebv 1996, Zhang and Hamill 1997).

These modeling approaches reflect the fact that it is much easier to define a zone of influence aboveground than below. The size and spatial distribution of shoots are easily measured, and sources of temporal variation in aboveground zones of influences, such as changes in sun angle, are predictable. In contrast, belowground zones of influence, delimited by the spatial distribution of roots and their associated mycorrhizae, are likely to differ in both size and shape from their aboveground counterparts and are much more difficult to measure. Excavating roots carefully enough to reveal their connection to a particular plant is logistically challenging (Caldwell et al. 1996, Jackson et al. 1999). Excavations tend to miss many fine roots (Smit et al. 2000) that are most important for resource uptake (Passioura 1988, Robinson 2001). Excavations also may vary in efficiency as a function of root density (Cahill 2002), rarely reveal the spatial distribution of fungal hyphae, and do not provide information on which roots are currently active. Such data are better supplied through the application of tracers, as described below.

Here, we call for more comprehensive measures of root distributions and root activity among competing plants and present data illustrating how belowground zones of influence may be affected by environmental conditions such as climate, soil texture, and the spatial distribution of nutrients. First, we enlarge and analyze a global data set of maximum lateral root spread and canopy size across climate and soil types to establish potential limits on the size of the belowground neighborhood (Schenk and Jackson 2002). Second, we describe our own work using nutrient analogs as tracers to examine functional root overlap and root system responses to spatial nutrient heterogeneity within populations of the weedy annual *Abutilon theophrasti*. Finally, we propose a new conceptual model for defining belowground zones of influence, based on understanding root distributions and the mechanisms by which plants interact with their soil environment, and use data from the tracer study to parameterize the model. The model does not assume that the uptake of belowground resources declines as a fixed, simple function of distance to plant stem as do traditional neighborhood models, and it incorporates plasticity in root distributions in response to the abiotic environment and other plants.

METHODS

Analyzing maximum lateral root spreads globally

Maximum lateral root spread determines the potential horizontal extent of a belowground zone of influence. Previous analyses of root distributions taken from root excavations reported in the literature have shown maximum lateral root spread to vary directly with canopy size (Schenk and Jackson 2002). Our analysis examined the allometric relationship between canopy size

and maximum lateral root spread as affected by climate and physical soil characteristics.

For this analysis, the data set of Schenk and Jackson (2002) was expanded ($n = 782$, usually one observation per species) to include observations from humid environments as well as water-limited systems. The data set includes measurements of lateral root spreads ($L_{\max,i}$), canopy heights (H_i), and canopy widths (W_i) for individual plants i . The lateral root spread of a plant is defined as the maximum linear distance (one-sided) reached by its roots, as measured from the stem base. Canopy volumes were estimated assuming an ellipsoid shape: $V_i = \pi H_i(W_i)^2/6$. Climatic conditions were characterized by mean annual precipitation (MAP) and an aridity index (MAP/PET), with PET being the mean potential evapotranspiration as calculated by the Penman-Monteith method, taken from the global 0.5° gridded data set of Choudhury (1997). The data were grouped into two aridity classes, arid (MAP/PET ≤ 0.2 , as defined by United Nations Environment Program [UNEP, 1992]) and semiarid to humid (MAP/PET > 0.2). Data were also grouped into two soil texture classes, coarse (gravel to loamy sand) or fine (sandy loam or finer), where such information was available ($n = 688$).

Allometric relationships between aboveground plant sizes and lateral root spreads were examined by reduced major axis (RMA) regression (Niklas 1994, Sokal and Rohlf 1995) of $L_{\max,i}$ against canopy volumes (V_i). The allometric equation used was

$$\log(L_{\max,i}) = a + b(\log[V_i]) \quad (1)$$

where a is the allometric constant and b is the allometric scaling factor. RMA regressions were calculated using the program PAST, version 0.65 (Øyvind Hammer, Paleontological Museum, University of Oslo, Norway). Allometric constants and scaling exponents were compared between aridity classes using ANCOVA. Effects of climate and soil texture on allometric relationships were analyzed in generalized linear models with $L_{\max,i}$ (log transformed) as the dependent variable, and with log-transformed V_i , aridity class, soil texture class, and all their possible interactions as independent variables using SYSTAT version 9.0 (SPSS, Chicago, Illinois, USA).

Measuring the distribution of root function using tracers

Maximum lateral root spread is only part of the size or shape of a plant's zone of influence, as additional information is needed on the placement and activity of roots in different directions. Because physically uncovering roots and determining individual plant ownership where they intermingle is difficult, we used uptake of stable nutrient analogs to (1) estimate a plant's belowground zone of influence in the presence of competing plants, and (2) identify changes in the belowground zone of influence with changes in the spatial

distribution of nutrients. Isolated plants often proliferate roots in nutrient patches (Drew and Saker 1975, Fitter 1994, Casper and Jackson 1997), and we wanted to know whether similar root system plasticity occurs among potentially competing individuals. The information we acquired on root distributions enabled us to parameterize our model by estimating the probability that a plant's roots intercept a point at a given distance from the stem.

Tracers are ideally suited to measure root function in different locations and to identify overlap in zones of influence among co-occurring plants. Various types of tracers have been used extensively to examine vertical and horizontal root extensions (Hall et al. 1953, Dansgaard 1964, Fox and Lipps 1964, Fitter 1986, Marmolos et al. 1995) but have been used less to illuminate the belowground structure of populations or communities. Stable nutrient analogs, as applied in our study of *A. theophrasti*, can be especially useful because they are present in much lower concentrations in plant tissues and in the soil than many stable isotopic tracers (such as ^{15}N), and therefore have lower detection limits and higher resolution. Different tracers can be used in the same population or community, allowing lateral root spread to be measured simultaneously in multiple directions, and thus determine shape parameters of the belowground zone of influence.

Populations of *A. theophrasti* were established in an outdoor garden by transplanting one-week-old seedlings into regular grids of nine rows of nine plants spaced 6 cm apart. Plants were omitted in locations 2 and 6 in rows 3 and 6, and after four weeks, one of four tracers, consisting of 0.2 M chloride salts of Cs, Li, Rb, and Sr, was randomly assigned to each of these four locations. Cs and Sr are analogs for K, and Li and Rb are analogs for Na and Ca, respectively. For each location, a syringe was used to inject 2 mL of tracer at 2-cm incremental depths (a total of 10 mL) to create a nearly continuous vertical column. In our experiment, plants took up only Sr and Rb. Spatially paired populations were assigned either of two nutrient treatments. This was done by preparing the soil before planting to a depth of 15 cm and adding 33.6 g of slow-release fertilizer either evenly throughout the 60×60 cm plot—the homogeneous nutrient treatment—or divided among four 6 cm wide, 15 cm deep cylindrical patches centered on the points of tracer injection—the heterogeneous nutrient treatment. Two weeks after tracer injection, all plants except those around the perimeter of each population were harvested, dried, and weighed. The portion of each plant produced since the time of tracer application, as estimated based on growth in a marked subset of the plants, was analyzed for tracer concentrations. Within a set of paired plots, uptake of a particular tracer was indicated by levels higher (one-tailed *t* test; $P < 0.01$) than those found in the 10 plants that were most distant from a point where that tracer had been injected (≥ 38.4 cm). Tracers moved hori-

zontally in the soil less than 3 cm. Differences between nutrient treatments in the number or locations of plants taking up tracer indicate root system responses to nutrient patches. Results are based on four replicate populations of each nutrient treatment (see Casper et al. 2000 for methodological details).

RESULTS AND DISCUSSION

Analyzing maximum lateral root spreads globally

Maximum lateral root spreads $L_{\max,i}$ were strongly related to aboveground canopy sizes V_i ($P < 0.001$) and yielded the following regression: $\log(L_{\max,i}) = 0.458 + 0.451(\log[V_i])$ ($r^2 = 0.528$). The slopes, i.e., the allometric scaling factors, were different ($P < 0.0001$) between the two aridity classes. Plants from arid environments tended to have larger lateral root spreads relative to canopy size than plants from semi-arid and humid environments. This difference is most pronounced in larger, woody plants (Fig. 1). Soil characteristics also had an effect on the allometric scaling factor, with plants growing on soils of coarse texture tending to have larger lateral root spreads for a given canopy size than those growing on soils of finer textures. This is indicated by the significant interaction ($P < 0.05$) between canopy size and soil texture in the generalized linear model (Table 1). These results suggest the prediction that, all else being equal, belowground zones of influence will be bigger in coarse than in fine textured soils.

Longer maximum lateral root spread found for arid climates may be related to the low plant density typically found there. Wide-spreading roots enable plants to take up water from bare interspaces between individual plants (Walter 1963). The observation that lateral roots extend farther from the stem base in coarse than in finer soils lends support to the suggestion made by Sperry et al. (1998) and Jackson et al. (2000) that plants of a given canopy size need larger root systems in coarse textured soils because such soils offer larger resistance to water flow and have smaller water-holding capacities. Coarse soils may also offer less impedance to root growth, enabling plants to explore a larger soil volume.

Measuring the distribution of root function using tracers

Examining results from the experiment with *A. theophrasti*, several features of belowground population structure were described by the capacity of plants to acquire tracers from discrete injection points. Roots of many plants extended well beyond immediate neighbors, with a maximum spread of 32 cm (Fig. 2). Root systems also responded to nutrient patches; twice as many plants took up tracer when nutrient patches were centered on the points of tracer injection (Fig. 2). Although the introduction of nutrient patches increased the probability that a given plant intercepted the soil

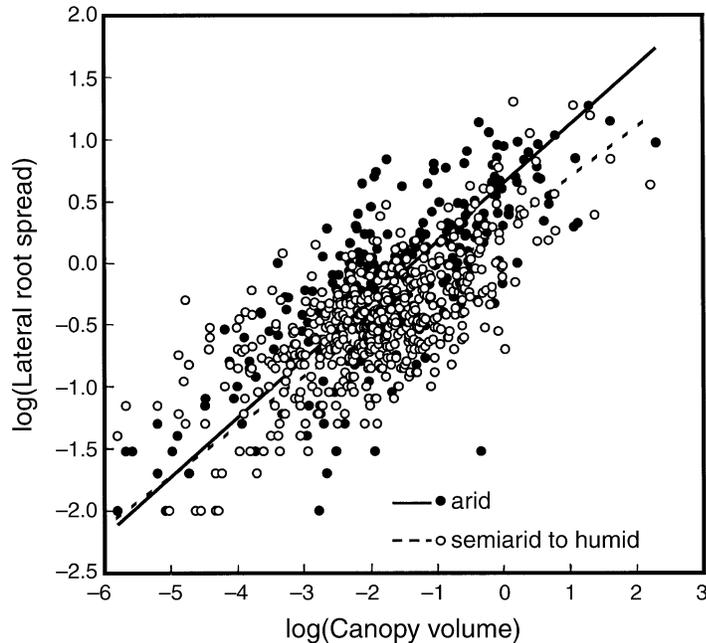


FIG. 1. Allometric relationships between aboveground canopy volume and maximum lateral root spread. The regression lines and equations are based on reduced major axis regressions performed on log-transformed data, using the general equation $\log(L_i) = a + b(\log[V_i])$, with L_i expressed in meters and V_i in cubic meters.

space marked by tracer and consequently increased the number of overlapping root systems in that space, the overall spatial distribution of plants taking up tracer was similar in the two treatments (Fig. 2). In both the homogeneous and heterogeneous nutrient treatments, roughly 55% of all plants taking up tracer were located within 10 cm of the tracer. The fact that plants equidistant from Sr and Rb sometimes took up one but not the other suggests that the root systems are spatially asymmetric (Casper et al. 2000).

Despite the concentration of roots in nutrient patches, plants growing in heterogeneous soil did not apparently acquire more nutrients than plants in homogeneous soil. Soil treatment affected neither mean plant biomass ($F_{1,3} = 0.859$, $P = 0.422$) nor the sizes of the largest plants as measured by the biomass of each of the four largest plants in each population ($F_{1,3} = 5.568$, $P = 0.099$). However, the sizes of the largest plants varied considerably among populations (7.68–13.57 g for the single largest plant), and both block (representing the pairs of homogeneous and heterogeneous soil treatment plots; $F_{3,24} = 3.664$, $P = 0.026$) and the interaction between soil treatment and block ($F_{3,24} = 5.21$, $P = 0.007$) were significant in ANOVA. Results are consistent with prior studies with *A. theophrasti*, where the spatial distribution of nutrients did not affect population level productivity but had subtle effects on plant size hierarchies within the populations (Casper and Cahill 1996, 1998).

A conceptual model of belowground zones of influence

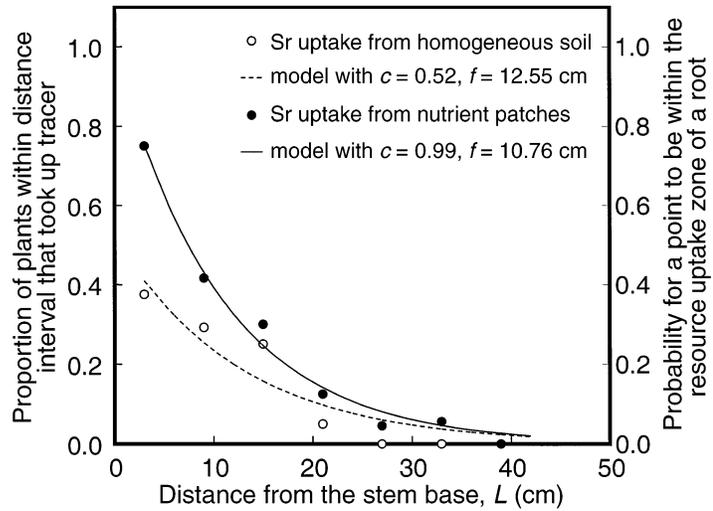
Taken together, the two data sets discussed above indicate that a plant's zone of influence, and the number of neighbors with which it interacts belowground, depend on local and global environmental conditions. Here, we propose a conceptual model that accounts for such environmental influences and their effects on the probability that given locations in the soil are within the zone of influence of one or more roots. In this

TABLE 1. Statistical parameters of a generalized linear model (GLM) of lateral root spread (log transformed) as a function of aboveground canopy size (log transformed), aridity class (arid vs. semiarid to humid), and soil texture class (coarse vs. medium to fine).

Source	ss	df	F	P
Canopy size	48.728	1	353.465	<0.0001
Aridity	8.097	1	58.736	<0.0001
Soil texture	0.062	1	0.447	0.504
Canopy size × aridity	0.944	1	6.851	0.009
Canopy size × soil texture	0.550	1	3.992	0.046
Aridity × soil texture	0.012	1	0.090	0.765
Canopy size × soil texture × aridity	0.018	1	0.131	0.718
Error	93.743	680		

Note: The r^2 -value of the GLM was 0.582.

FIG. 2. Proportion of all *Abutilon theophrasti* plants that took up Sr tracer as a function of distance from the injection point. Filled circles represent plants in populations where a patch of fertilizer was centered on the points of tracer injection. Open circles represent plants in populations where the same quantity of fertilizer was evenly distributed. Curves were fit using Eq. 2. Parameters from that equation for the best fits are listed in the legend (homogeneous treatment, adjusted $r^2 = 0.818$, $df = 6, 6$, $F = 36.26$; heterogeneous treatment, adjusted $r^2 = 0.982$, $df = 6, 6$, $F = 403.49$). Parameter c was significantly different between the two fits ($P < 0.05$), while parameter d was not.



model, roots are treated as discrete entities. In contrast to previous models (e.g., Weiner 1984, Pacala and Silander 1987, Zhang and Hamill 1997), this model does not assume that the absolute amount of resource uptake within an individual root system declines as a simple function of distance from the stem, but assumes instead that the probability of resource uptake from a particular soil location and the probability of competing with a particular neighbor is a function of the distance from the stem. This model accounts for the fact that plants are capable of taking up large quantities of resources at great distances from the stem and allows for patchiness and stochasticity in root placement.

The following statistical approach provides a theoretical framework for estimating the belowground zone of influence: For any given location l in the soil one determines the probability P_l that it is within the zone of influence of a plant. For an individual plant (i), the density of roots typically declines with distance from the stem and will reach zero beyond the maximum lateral root spread $L_{max,i}$. Therefore, the probability for any location in the soil to be within the zone of influence of a root from that plant will also be a function of distance from the stem. Such probability functions can be determined horizontally and vertically; we illustrate the approach for the horizontal dimension and project the zones of influence around roots within the upper layers of the soil onto a horizontal plane. Zone-of-influence probability functions may have different shapes, but exponential declines with distance from the stem are likely. In consequence, the following model may be used to calculate the probability $P_{l,i}$ for any location l to be part of the belowground zone of influence of a plant i . Similar calculations could in principle be applied to hyphae of mycorrhizal fungi. $P_{l,i}$ is a function of the distance L_i from the stem base of the plant within the maximal lateral extent $L_{max,i}$ of the root system:

$$P_{l,i} = \max[1, c(\exp[-L_i/f])] \quad (2)$$

$$P = 0 \quad \text{for } L_i > L_{max,i}$$

where c is a constant characterizing overall root density within the zone of influence, and f is a shape parameter characterizing the relationship between root length density and distance to the stem (see Fig. 3). Note that the probability distribution for the placement of roots is symmetric around the stem base, but this does not mean that actual root systems will typically be symmetric.

Other variables may further influence $P_{l,i}$, including soil characteristics at that location (e.g., structure, nutrient concentration, water content, presence of toxins, presence of roots from other plants, or presence of other soil organisms). Such factors may be incorporated into the model by multiplication with additional variables, as demonstrated here for a general parameter characterizing nutrient availability N_i :

$$P_{l,i} = \max[1, c(\exp[-L_i/f]N_i)] \quad (3)$$

$$P = 0 \quad \text{for } L_i > L_{max,i}$$

This additional parameter accounts for the fact that root placement is often nonrandom and can respond to resource gradients, thereby increasing the probability for nutrient-rich soil locations to become part of a plant's belowground zone of influence. Furthermore, the model can be extended to account for spatial correlation within root systems. Living roots are connected, which means that locations adjacent to those known to be part of a belowground zone of influence will have a higher probability of also being inside this zone.

In addition to these factors, $P_{l,i}$ may also be decreased (Schenk et al. 1999) or increased (Gersani et al. 1998, Robinson et al. 1999) if roots from a competitor j are already present in the location, which could be ac-

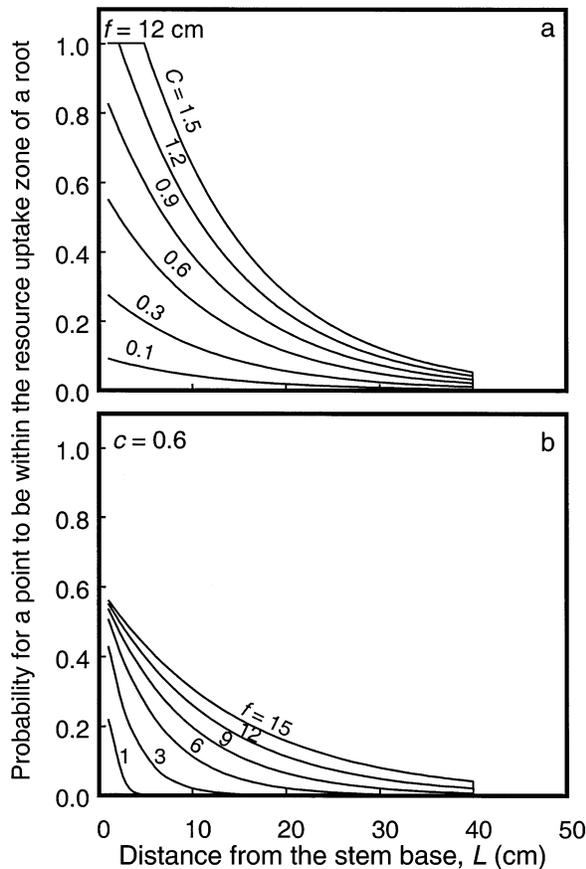


FIG. 3. Models of the probability for a point within the upper 10 cm of soil and at a given distance from the stem to be within the resource uptake zone of a root (curves calculated by Eq. 2), depicting different shapes of belowground zones of influence. In (a), the shape parameter f in Eq. 2 is held constant, while c varies; in (b), c is held constant, while f varies.

counted for by an additional parameter in Eqs. 2 or 3. Such competitive effects could be studied by testing the hypothesis that the probability of any soil location to contain roots of two plants, i and j , is equal to P_i (i and j) = $P_i \times P_j$, which is true if $P_i \times P_j$ are independent of each other.

We applied this conceptual model to the *Abutilon* system described above, by using the tracer experiments to parameterize Eq. 2 (Fig. 2). In this experiment, soil locations were represented by tracer injection points, which were surrounded by *Abutilon* plants spaced at various distances from these points. All plants for the homogeneous and heterogeneous nutrient treatments, respectively, were divided into groups by their distance to the injection points, with a group containing all plants within the same 6-cm distance increment (0–6 cm, 6–12 cm, 12–18 cm, . . . , 36–42 cm). We determined the proportion of plants within each group that took up tracer. These proportions were plotted against the distances between tracer injection points

and plant stems, resulting in a graph of $P_{i,j}$ as a function of $L_{i,j}$, as in Eq. 2. We then fitted the equation to these data. Note that these data characterize the average belowground zone of influence for the tested *Abutilon* populations, because they were gathered by measuring many plants spaced at various distances from a given injection point.

In the homogeneous nutrient treatment, there was a total probability of $P_{i,j} = 0.11$ for any given soil location within the maximum root spread of an individual *Abutilon* plant (32 cm) to be within the belowground zone of influence of that plant, or, in other words, the zone of influence of an average *Abutilon* plant covered ~11% of the area within its maximum root spread. $P_{i,j}$ was >0.3 for distances 0–6 cm and declined to $P = 0$ at distances >24 cm from the stem (Fig. 2). Tracer within the small area close to the stem was thus most likely to be taken up, but the distribution of tracer uptake within the population revealed that the majority of tracer (~75%) was taken up from the much larger area between 12 and 30 cm from the stems of individual plants.

Nutrient-enriched locations in the heterogeneous soil treatment were about twice as likely to supply tracer to the plants than the nonenriched locations in the homogeneous soil treatment (Fig. 2). This information could, in principle, be used to estimate the magnitude of parameter N_i in Eq. 3, but overall soil nutrient availability in these experiments was not quantified. Competitive effects on root placements could not be quantified, because all plants in these regularly spaced arrays were equally subjected to intraspecific competition.

In conclusion, the probabilistic model outlined can be used to formulate and test explicit hypotheses about shapes and sizes of belowground zones of influence and the variables that affect them, including interactions with resources and other plants. Once the factors that determine the shapes and sizes of belowground zones of influence are quantified, they could be incorporated into predictive models of plant performance.

Belowground zones of influence and competition

Maximum lateral root spread defines the boundary of the zone of influence or the soil space from which a plant gathers resources, but the distribution of roots within this space greatly affects the degree of overlap in zones of influence among competitors and the extent of competition and resource partitioning. Overlapping zones of influence determine the set of plants that make up the competitive neighborhood. The amount of overlap in the lateral distribution of roots in the upper soil layers, where nutrient concentrations are usually highest (Sposito 1989, Jobbágy and Jackson 2001), may be particularly important for root competition. Co-occurring plant species can sometimes reduce competition for water by partitioning soil space vertically (Fernandez and Caldwell 1975, Sala et al. 1989, Ehleringer et

al. 1997), but this option may be less available in competition for nutrients (but see McKane et al. 2002). Temporal partitioning of root activity may also occur even if root systems physically overlap (Gebauer and Ehleringer 2000, McKane et al. 2002). For these reasons, it is particularly important to measure root function—not just the physical presence of roots.

For models of belowground competition it is clearly insufficient to assume that belowground zones of influence are of a fixed, circular shape. For example, in a sparse, natural, herbaceous community in Florida shrubland, plants took up tracer over distances of up to 97 cm, with a mean of 51 cm, but in many cases more distant plants took up tracer while closer plants did not (Hawkes and Casper 2002). Excavations of all but the finest roots in woody species often reveal root systems shaped as irregular polygons that overlap less with neighbors than would circular systems with the same areas (Brisson and Reynolds 1994, Mou et al. 1995). Such shapes may result from responses of root growth to soil resource availability or from direct root avoidance mechanisms, which to date have been found mostly in water-limited environments (Mahall 1998). There is ample evidence that belowground competition can affect the shape of root systems (Schenk et al. 1999), and, conversely, that asymmetric shapes of root systems influence the magnitude of competition (Brisson and Reynolds 1997).

Future directions

More information on the plasticity of belowground zones of influence is needed before we can apply our probabilistic model to other systems and compare its predictive power to more traditional models that assume fixed zones of influence. Better data on how root systems respond to different resource conditions and under different neighbor densities are necessary to determine the probability of root placement at different distances from the stem. For example, at the moment we are unable to say how belowground zones of influence and neighborhood sizes should change with even simple changes in population structure, such as plant density. Plant size decreases with increases in density, but how do root features and the zone of influence change with plant size? Within a population, do smaller, subordinate plants produce shorter lateral roots as suggested by the interspecific comparisons in our global data set? Or do they produce fewer laterals without altering their length?

Much recent work on the design of whole root systems (Einsmann et al. 1999, Johnson and Biondini 2001, Wijesinghe et al. 2001) has been motivated by Campbell et al.'s (1991) study showing a tradeoff in the scale and precision of root foraging. They demonstrated that species with larger root systems, as measured by biomass, were less able to proliferate roots in nutrient patches. Whenever the subject of interest is really the spatial area over which a plant forages, we

suggest that the zone of influence is a more appropriate measure than biomass. This is because the storage function of roots may contribute greatly to biomass, and storage biomass may vary independently of fine root biomass (Casper et al. 1998). Moreover, depending on the scale of nutrient heterogeneity, the size and shape of the zone of influence may be as important as precision in enabling plants to access nutrient patches.

Many studies examining plant responses to nutrient patches have worked with isolated, potted plants, and we need to know whether their findings extrapolate to competing individuals (Hutchings and de Kroon 1994, Robinson et al. 1999, Fransen et al. 2001). At least in populations of *A. theophrasti*, more individuals actively taking up nutrients from the same vertical column of soil where nutrients are locally elevated, but productivity does not increase. The results are consistent with Gersani et al.'s (1998, 2001) idea that higher nutrient levels are balanced by the production of more roots until nutrient availability is roughly the same in the different microhabitats. If this commonly occurs, nutrient heterogeneity could alter the shape of the zone of influence but little affect the outcome of competition among plants with the ability to proliferate roots in patches.

In summary, we think that characterizing the size, shape, and plasticity of the belowground zone of influence, using methods that directly assess root activity, such as tracers, holds much more promise than measures of root biomass, root/shoot ratio, or even total root surface area (Gleeson and Tilman 1990, Aerts et al. 1991, Cahill and Casper 2000, Johnson and Biondini 2001) in helping us understand the strength of belowground interactions in plant communities. For plants with the same root/shoot ratio, for example, many short lateral roots may make plants stronger belowground competitors with nearest neighbors, while more sparse systems with longer lateral root spread may enable plants to search over longer distances and locate pockets where nutrients are elevated or competing roots are absent. Characterizing the belowground zone of influence should be done in a field setting, both with and without neighbors, where lateral root growth is not constrained by the size of a pot. Armed with such information, our approach should have numerous applications, enabling us to make predictions about the nature of plant interactions under different abiotic conditions and with changes in the number and identities of neighboring plants.

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