

Root plasticity buffers competition among plants: theory meets experimental data

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Abstract. Morphological plasticity is a striking characteristic of plants in natural communities. In the context of foraging behavior particularly, root plasticity has been documented for numerous species. Root plasticity is known to mitigate competitive interactions by reducing the overlap of the individuals' rhizospheres. But despite its obvious effect on resource acquisition, plasticity has been generally neglected in previous empirical and theoretical studies estimating interaction intensity among plants. In this study, we developed a semi-mechanistic model that addresses this shortcoming by introducing the idea of compensatory growth into the classical-zone-of influence (ZOI) and field-of-neighborhood (FON) approaches. The model parameters describing the belowground plastic sphere of influence (PSI) were parameterized using data from an accompanying field experiment. Measurements of the uptake of a stable nutrient analogue at distinct distances to the neighboring plants showed that the study species responded plastically to belowground competition by avoiding overlap of individuals' rhizospheres. An unexpected finding was that the sphere of influence of the study species *Bromus hordeaceus* could be best described by a unimodal function of distance to the plant's center and not with a continuously decreasing function as commonly assumed. We employed the parameterized model to investigate the interplay between plasticity and two other important factors determining the intensity of competitive interactions: overall plant density and the distribution of individuals in space. The simulation results confirm that the reduction of competition intensity due to morphological plasticity strongly depends on the spatial structure of the competitive environment. We advocate the use of semi-mechanistic simulations that explicitly consider morphological plasticity to improve our mechanistic understanding of plant interactions.

Key words: *Bromus hordeaceus*; competition intensity; morphological plasticity; nutrient analogues; plant density; PSI (plastic sphere of influence); zone-of-influence model.

INTRODUCTION

Competition among plants is a primary factor controlling the performance of individuals in natural communities (Stoll et al. 2000). To understand and predict population and community dynamics, an estimation of competition intensity in a given system is essential. For example, the coexistence of species is mainly determined by intra- and interspecific interactions (Chesson 2000, Silvertown et al. 2001), but also community characteristics like productivity or invasibility are affected by interaction intensity (Hastwell and Huston 2001).

The intensity of competition between two or more plants is often quantified as the overlap of the individuals' canopy or root systems or, more generally,

the area of resource acquisition, represented by the individuals' area of influence (Czaran and Bartha 1992). The amount of overlap of these areas is determined by their size and shape, as well as by the overall plant density and spatial distribution. According to the symmetry of interactions (usually aboveground competition is considered to be asymmetric while belowground competition is considered to be symmetric), resources in the overlap areas are assigned to the individuals (e.g., Esther et al. 2008, May et al. 2009). This approach is the basis for common neighborhood concepts, assuming a circular area of influence centered on each individual, within which interactions with other plants occur.

In the zone-of-influence (ZOI) approach, the radius of the circle increases with plant size, while the competition strength is constant across the circle (Gates and Westcott 1978, Czaran and Bartha 1992, May et al. 2009). The field-of-neighborhood approach (FON) extends this idea by describing competition strength of an individual at a given point within the area of influence as a function of distance to the center (Berger and Hildenbrandt 2000, Berger et al. 2002, 2008). This extension allows

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calculating the division of resources in the overlap area in a more process-based manner, obviating the need for an a priori determination of the symmetry of interactions.

Both of these neighborhood concepts aim at sessile organisms and are based on the assumptions that (1) interactions of sessile organisms are restricted to immediate neighbors and (2) individuals cannot escape competitive interactions (Schneider et al. 2006). While the first assumption holds for most settings, the second one may often emerge as an oversimplification: plants show a high morphological plasticity in both root and shoot architecture (e.g., Sultan 2000), and are thus able to directly react to competitive environments (Brisson and Reynolds 1997).

In the context of morphology, *plasticity* can be defined as the developmental changes that follow the perception and integration of environmental information (Novoplansky 2002). A large body of literature exists focusing on plant species' perception of competitors by means of light quality and corresponding changes in shoot architecture (e.g., Schmitt et al. 1999, Tuccic et al. 2006, Bell and Galloway 2007). However, root plasticity is a common phenomenon in natural communities, as well (D'Antonio and Mahall 1991, Brisson and Reynolds 1994, Schenk et al. 1999, de Kroon and Mommer 2006), and there is evidence for a number of species that this plasticity allows individuals to avoid overlap of their rhizospheres, hereby buffering competition (Sorensen-Cothorn et al. 1993, Schenk et al. 1999, Casper et al. 2003). Unfortunately, this empirical evidence has not been satisfactorily considered in common modeling approaches addressing neighborhood competition.

In the field of modeling, to our knowledge, only two studies exist that focus on morphological plasticity: Brisson and Reynolds (1997) presented a general theoretical model that accounts for compensatory growth, and O'Brien et al. (2007) modeled root competition for space as an evolutionary game. Both studies showed that plasticity may play an important role for interaction intensity, but neither of them was parameterized or validated with experimental data. This may be problematic as soon as we are not only interested in the theoretical effects of morphological plasticity, but in quantitative forecasts of competition intensity.

In this study we attempt to fill the gap between theory and data by addressing the role of plasticity for interaction intensity with an approach combining a common-garden experiment with computer-based simulations. The simulation model of plant interactions is based on the field-of-neighborhood concept but extends this approach by allowing for plasticity in terms of compensatory growth. In the competition experiment, we estimated the belowground areas of influence of an annual grass species in the presence and absence of neighbors. Here, we adopted an approach of Martin et al. (1982), who used stable nutrient analogues as tracers

for measuring resource uptake at different distances to the plants' centers. Since the *area of influence* is defined as the zone of resource acquisition (Czaran and Bartha 1992), the amount of tracer uptake can be interpreted as a measure for the plant's competitive effect at the point of tracer injection (Casper et al. 2003).

The combined experimental and modeling approach allowed us to (1) parameterize the model with data from real plants, (2) investigate the interplay among three key factors determining the amount of overlap of rhizospheres (plant density, spatial distribution of individuals and morphological plasticity), and (3) quantitatively forecast the consequences of the experimentally detected root plasticity for interaction intensity in scenarios of different competitive environments. Moreover, as a first step towards an understanding of the impact of plasticity on community dynamics, we calculated the spatial variance of root competition. Spatial variance can give an impression about the amount of unoccupied space, e.g., for germination or the survival of weak competitors, and the expected size inequality of competing plants.

METHODS

Experimental approach

Our study species was the annual grass *Bromus hordeaceus*, a common species in dry grasslands of central Europe (see Plate 1). It is relatively small, develops a homogeneous rhizosphere, is fast growing and germinates throughout the year (Jäger and Werner 2002, Waisel et al. 2002).

To gain information on the shape, strength, and plasticity of the grasses' belowground zones of influence, we measured uptake of a nutrient tracer at different distances to the plants' centers for both single and competing individuals. The tracer we chose for this study was lithium (Li), which is a stable nutrient analogue to potassium and particularly applicable to measure root activity due to its low detection limit and high resolution (Casper et al. 2003).

In July 2007, an area of 4 × 6 m in an experimental garden of Potsdam University, Germany, was dug up to a depth of 0.6 m. The obtained soil was sieved, and treated with a PN fertilizer to increase the likelihood that potassium was the only limiting nutrient. Before refilling the cavity with the treated soil, it was enclosed with a wire netting to prevent intrusion by moles and mice. To ensure uniform and gentle irrigation, the area was covered with a rain shelter and equipped with a micro-drip system (Gardena GmbH, Ulm, Germany). The plot was split into six subplots of 2 × 2 m each, and seeds of *B. hordeaceus* originating from the same seed family were sown in a design that allowed for 18 replicates for each of the following 12 constellations (see also Fig. 1):

(1)–(3) single individuals with tracer application at 3, 6, or 9 cm distance, respectively;

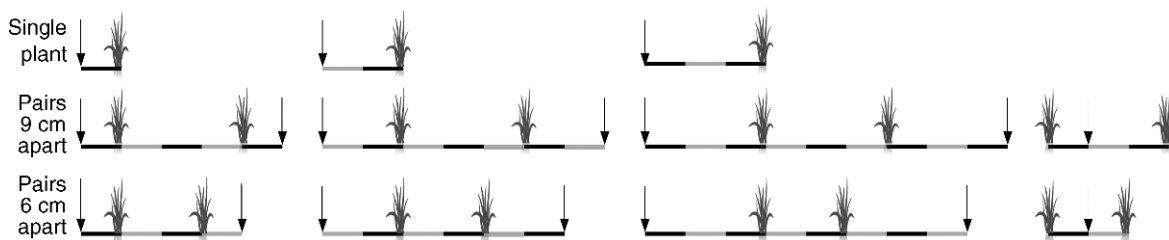


FIG. 1. Experimental design of the competition experiment using the annual grass *Bromus hordeaceus*. One unit on the measuring scale denotes 3 cm, and arrows indicate locations of tracer injection (lithium chloride, LiCl).

(4)–(8) pairs of individuals growing at a distance of 9 cm with tracer application either between competitors (3 cm distance and 6 cm distance, respectively) or at 3, 6, or 9 cm distance at the competitor-averted side; and

(9)–(12) pairs of individuals growing in a distance of 6 cm with tracer application either between competitors (3 cm distance among plants) or at 3, 6, or 9 cm distance at the competitor-averted side.

This resulted in a total of 54 single individuals (3 distances \times 18 replicates), 45 pairs with 9 cm distance (2 distances between competitors \times 18 replicates + 3 distances at averted side \times 18 replicates = 90 individuals = 45 pairs), and 36 pairs with 6 cm distance (1 distance between competitors \times 18 replicates + 3 distances at averted side \times 18 replicates = 72 individuals = 36 pairs) distributed over the six subplots as balanced as possible. The distance between replicates was \sim 35 cm.

Four weeks after germination, 10 mL of 0.2 mol/L lithium chloride (LiCl) was applied following the above design and using a syringe to create a nearly continuous vertical column of tracer in the upper 10 cm of soil. After 14 days the aboveground parts of all plants were harvested, dried for 48 h at 80°C, and weighed separately. We analyzed \sim 0.2 g dry mass per plant with flame emission spectroscopy for tracer concentrations and the resulting values were extrapolated to total uptake of Li for each individual.

Statistical analysis

Based on the measured uptake of lithium we tested two hypotheses: (1) the uptake of lithium decreases linearly with distance from the plant center (this model was tested against an alternative model with a unimodal response) and (2) the individuals' uptake is lower between competitors than at the competitor-averted side.

For testing the first hypothesis, we used data from individually growing plants and from tracer uptake at the competitor-averted sides. Two linear mixed-effects models (with block as random factor) were fitted using a maximum-likelihood approach, the first one assuming a linear relationship between the explanatory variable "distance" and the response variable "uptake," and the second one fitting an exponential term allowing for a unimodal relationship. The quality of the models was compared by resulting AIC values. We estimated 95%

confidence intervals for the predicted values by building the variance-covariance matrix from the variables and model parameters, extracting the variance to calculate the standard error, and multiplying the standard error of the predicted data with Student's *t* values for the 0.025 and 0.975 quantiles.

For testing the second hypothesis, three subsets of the data were analyzed separately: (1) uptake of competitors growing at 6 cm distance and tracer injection at 3 cm, (2) uptake of competitors growing at 9 cm distance with tracer injection at 3 cm distance, and uptake of competitors growing at 9 cm distance with tracer injection at 6 cm. For each set, two linear mixed-effects models were fitted with one including information about the position of tracer injection (between competitors vs. competitor-averted side) and the other one only estimating the overall mean of tracer uptake. The significance of the explanatory factor "position" was tested using a likelihood ratio test.

Since the data of Li uptake were positively skewed, they were log-transformed prior to analysis and a visual check of normality and homoscedasticity of errors was performed. In the case of unbalanced data subsets due to missing values, data points were sampled randomly to obtain the same number of observations for all treatments. Confidence intervals were calculated as described above. We used the statistical package R, version 2.10.1 (R Development Core Team 2009) and the additional package "nlme" version 3.1-96 (Pinheiro et al. 2009) for all analyses.

Modeling approach

The plastic sphere-of-influence (PSI) model developed in this study is a rule-based, spatially explicit simulation tool emulating the development of plants' individual areas of influence in response to their competitive environment. It accounts for different degrees of morphological plasticity and calculates resulting competition intensities. From a conceptual point of view, it is closely related to the field-of-neighborhood (FON) approach by Berger and Hildenbrandt (2000; see also Berger et al. 2002, 2008), however, the model in its current version has no temporal dimension, i.e., the simulations display a snapshot in time.

Each individual is characterized by its coordinates on a simulated grid and a surrounding circular area of

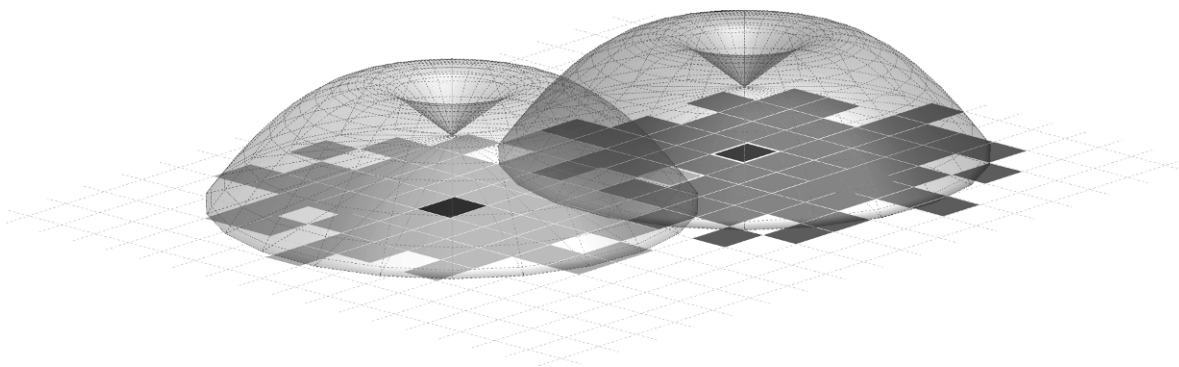


FIG. 2. Schematic illustration of the PSI (plastic sphere-of-influence) approach. Individuals are characterized by their location on the simulated grid (coordinates of the central black cell). The potential root space is determined by the radius of the surrounding sphere of influence; the realized root space (light gray cells for the individual on the left, dark gray cells for the individual on the right) is a probabilistic function of the intensity of the sphere of influence (height of the “kernel”) and the intensity of spheres of influence of potential competitors.

influence within which the plant is principally able to gather resources (see Fig. 2). The intensity of influence within this area is described as a function of distance from the center, the PSI function, which in our case was parameterized with empirical data.

In contrast to FON models, in the PSI approach, only a certain fraction of the cells within the individual’s sphere of influence is actually occupied by the plant and belongs to the realized root space. Which cells these are is a stochastic function of (a) the intensity of the sphere of influence at the location of the cells (cells with higher intensity of influence have a higher probability of being occupied) and (b) the presence and relative influence of competitors, since each cell can be occupied by only one single individual. Thus, cells with a low occupancy probability will generally stay free in the absence of competitors, but can serve as “fall-back regions,” if cells with high intensities of influence are occupied (competition). In that case, the realized root space can attain noncircular shapes, the phenomenon we observe as *morphological plasticity*.

To implement this approach in a simulation model, several computational steps are necessary. After plants are randomly distributed on the simulated grid (*initialization*), each individual is assigned a preliminary root space within its sphere of influence independent of the presence of neighbors (*preliminary root space*). Cells that are occupied by more than one individual are then stochastically assigned to one of the competitors as a function of the plants’ relative influences in the respective cells (*competition*). In case an individual lost cells due to competition, it can compensate for the loss by occupying new cells within its sphere of influence according to the number of lost cells, their distances to the plant’s center, and the assumed degree of plasticity (*compensatory growth*). The competition intensity is then calculated based on the difference between the realized number of cells per individual and the maximum possible number, i.e., assuming a scenario without any competition (*belowground competition intensity*). In the

following sections the single implementational steps are explained in more detail.

Initialization.—The underlying grid consists of 1000×1000 cells of 1 mm^2 , leading to a total area of 1 m^2 . Edge effects are avoided by implementing toroidal boundary conditions, i.e., the upper and lower edge, as well as the left and right edge, of the grid are merged. For model parameterization (estimation of θ_1 and θ_2 , which determine the shape of the PSI function), plant positions are determined according to the design of the common-garden experiment. For subsequent simulation experiments, plants are distributed randomly with varying density and different degrees of aggregation (AC; spatial autocorrelation with a scale of 10 cm).

Preliminary root space.—Each individual is assigned a circular sphere of influence determined by the PSI-function. The PSI function, which gives the probability for a cell to be occupied by a plant’s rhizosphere, shows a unimodal shape according to the nutrient uptake as measured in the experimental approach. Our heuristic parameterization ψ of the PSI function is given by

$$\psi_{\text{occ}}(d) = \begin{cases} \alpha + d\theta_1 - d^\beta\theta_2 & \text{for } 0 \leq d \leq d_0 \\ 0 & \text{otherwise} \end{cases}$$

where d denotes the distance of the cell to the center of the plant and d_0 is the distance at which the function equals 0, i.e., the radius of the base area. The constants $\alpha=0.5$ and $\beta=2.9$ were chosen by modeling the shape of the function such that it roughly describes the observed values of tracer uptake. Parameters θ_1 and θ_2 were fitted to the observed data as described in *Parameterization*, below.

To construct the preliminary root space, cells within the sphere of influence, which are not already assigned by the individual itself, but which may be assigned by other individuals, are chosen randomly and allocated to the preliminary root space with probability ψ_{occ} . The search for cells is continued until $\text{cells}_{\text{max}}$ (the maximum number of cells a plant can occupy in case there is no competition from other individuals) = 7000 cells is

obtained. Due to the equal probability for each cell within the sphere of influence to be chosen but its actual allocation to the preliminary root space as a function of the probability ψ_{occ} , the resulting pattern of occupied cells follows approximately the shape of the PSI function. Another effect of the random-search algorithm is that the developing root space is not necessarily continuous. Note however, that we do not intend to model the distribution of roots themselves but the pattern of their uptake activity.

Competition.—In cells that are assigned to more than one individual, competition occurs. Competition is implemented as a stochastic process in which the probability to win and finally occupy a cell is given by the relation of the ψ values of each of the competitors at the considered location.

Compensatory growth.—For each individual plant, the total distance of all cells lost due to competition is summed and stored in the simulation model. This “distance credit” is used for randomly assigning free cells in the sphere of influence and occupying them with probability ψ_{occ} until either the total distance of the compensatory cells balances the distance credit or no free cells are left in the individual’s sphere of influence. In case of recurring competition in the cells that were assigned for compensatory growth by more than one individual, the competition–compensation cycle is repeated until there is no overlap of cells anymore. Since plasticity may be limited by abiotic as well as biotic factors (Valladares et al. 2007, Gianoli and Palacio-Lopez 2009), we introduce a parameter DP specifying the degree of plasticity. This is implemented by dividing the initial distance credit by 3/DP, and defining the maximum degree of plasticity to be 3. For example, if DP = 1.5, then new cells can be occupied during compensatory growth only until half of the distance credit is depleted.

Belowground competition intensity.—As a measure of belowground interaction intensity, the average difference between the realized and the potential size of the root space is calculated. The standardized value of interaction intensity ranges between 0 (no competition) and 1 (strong competition) and is analogous to the RNE index (relative neighbor effect; Markham and Chanway 1996):

$$\text{RNE} = \frac{\text{potential size} - \text{realized size}}{\text{potential size}}.$$

In addition to competition intensity, we also measured the variance of competition intensity (as the number of individuals that compete for one cell) across the area as well as the total number of non-occupied cells at the end of the searching procedure.

Parameterization

For the parameterization of the interaction kernel, the experimental set-up was reproduced in the model: one single or two competing individuals growing at either 6

or 9 cm distance were simulated. At the 12 positions of tracer injection, the numbers of occupied cells were recorded in a measurement area of 10×10 cells to account for slight diffusion of tracer in the soil. The resulting values were scaled to the order of magnitude of tracer uptake:

$$\text{scaled uptake}_i = \text{occupied cells}_i \left(\frac{\text{mean uptake}}{\text{mean occupied cells}} \right)$$

where i denotes the point of tracer injection. The mean number of occupied cells and the amount of mean uptake are average values for 10 simulation runs and 18 experimental replicates, respectively. After standardization, the level of similarity between observed and predicted values did not depend on the absolute number of occupied cells in the single measurement areas, but on their relative amount of occupied cells compared to the other measurement areas. For each combination of the two kernel parameters θ_1 and θ_2 the negative log-likelihood for observing the found experimental data, assuming correct underlying model parameters, was estimated. The parameter set leading to the maximum likelihood was detected using a simulated annealing algorithm implemented in the “optim” function of the statistical package R (R Development Core Team 2009) following Belisle (1992).

Scenarios

Based on the above model, we simulated scenarios with each combination of the following parameter values: (1) plant density from 10 to 150 plants per 1 m^2 in steps of 10; (2) degree of plasticity DP from 1 to 3 (maximum plasticity) in steps of 0.5; and (3) level of autocorrelation AC between plants from -0.4 (regularity) to 0.4 (aggregation) in steps of 0.2. Each of the resulting 375 combinations was replicated 10 times.

RESULTS

Experimental approach

Individual *Bromus hordeaceus* plants took up between 0.08 and 4.32 g of Li during the two weeks following the application. The highest uptake ($0.95 \text{ g} \pm 0.25 \text{ g}$; mean and 95% CI) was measured at intermediate distances of 6 cm. Toward the plants’ centers, the uptake of Li decreased only slightly, whereas at 9 cm distance, the uptake was considerably lower (Fig. 3a). Comparison between a linear and a unimodal model predicting tracer uptake confirmed this observation in that there was a slightly better AIC value for the unimodal model (342.12 vs. 343.13). However, a large fraction of unexplained variance remained in the data so that 95% confidence intervals on the predicted uptake comprise a range of up to $\pm 30\%$ of predicted values (Fig. 3b).

Results from competing individuals showed no obvious differences in tracer uptake at 3 cm distance between competitors as compared to the competitor-averted side. However, a significantly lower tracer

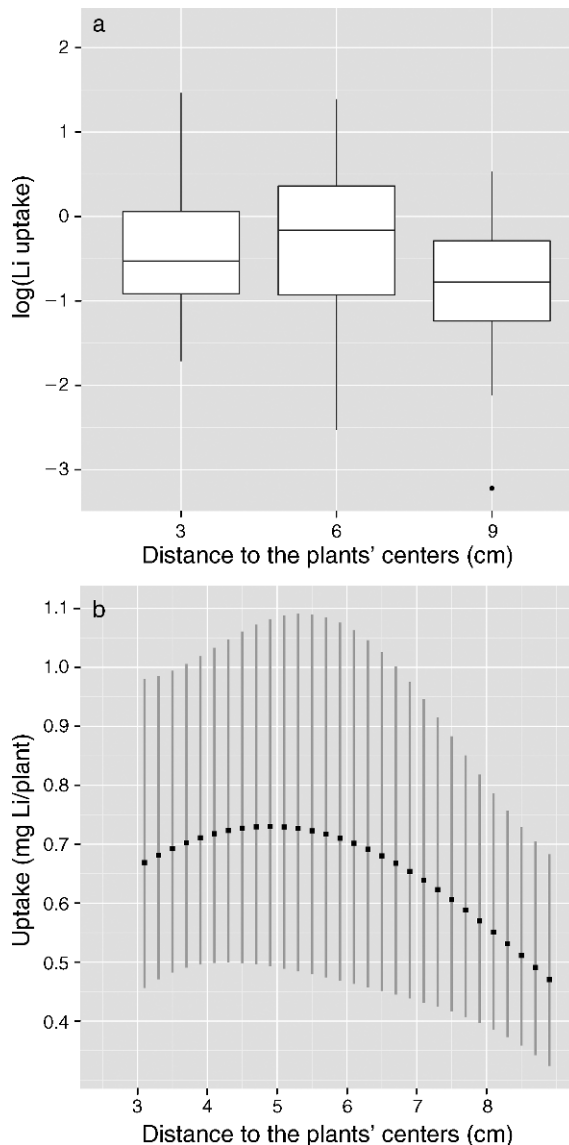


FIG. 3. Lithium uptake. (a) Uptake of Li is dependent on distance to the plants' centers based on data for single individuals and for competing plants at the competitor-averted side (i.e., the side opposite to the competitor). The horizontal line in the center of the box is the median; whiskers extend to the most extreme data point ≤ 1.5 times the interquartile range from the box, and the dot denotes an outlier. (b) Uptake predicted by the fitted model. Gray bars indicate 95% confidence intervals for predictions (see *Methods: Statistical analysis* for details).

uptake was found in the direction toward the competitor than at the averted side when Li was injected at 6 cm distance (likelihood ratio = 5.74, $df = 3$, $P = 0.017$; see Fig. 4), indicating that individuals were growing away from their competitors.

Modeling approach

The optimization of the parameters of the PSI function resulted in a value of 0.079 for θ_1 and a value

of 0.0012 for θ_2 . The function shows a unimodal shape of uptake of an individual plant in depending on the injection distance with a maximum value at a distance of around 5 cm and a decrease to zero at a distance of 12 cm.

The predictions of the parameterized model for tracer uptake fitted the observed values for the single points of tracer injection relatively well ($R^2 = 0.48$, pairwise t test: $t_{(11)} < 0.001$, $P = 1$). The relative neighbor effect (RNE), reflecting the competition intensity, was zero for the model runs simulating the experimental conditions with two competing plants, independent of whether the distance among competitors was 6 or 9 cm.

In simulations with more than two plants, the RNE increased linearly with the density of plants (results not shown), and nonlinearly with decreasing plasticity and increasing spatial autocorrelation among plants (see Fig. 5). The effect of plasticity on competition was strongest at an intermediate plant density of 100 plants on the simulated grid (steepest decrease of the RNE with increasing plasticity) and independent of the degree of aggregation of plants (the slopes of the five different degrees of autocorrelation were almost the same).

At low plant density, autocorrelation (AC) had a stronger effect on interaction intensity at lower levels of plasticity, whereas at a high density, the effect of

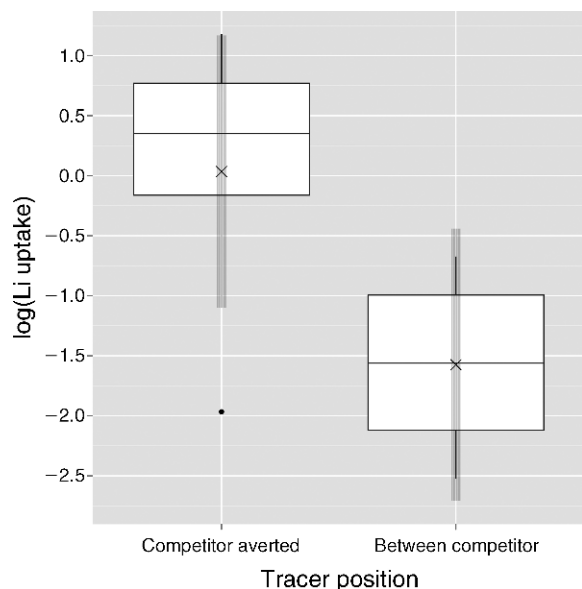


FIG. 4. Uptake of Li at 6 cm distance between competitors and at competitor-averted side. Box-and-whisker plots represent measured data, with whiskers extending to the most extreme data point ≤ 1.5 times the interquartile range from the box; the horizontal line in the center of the box is the median; the dot denotes an outlier. The "X" symbols indicate predicted uptake values, and gray bars show 95% confidence intervals for predictions (see *Methods: Statistical analysis* for details). We expected plants to take up more Li at the competitor-averted side because we expected roots to be directed away from the competition, with this effect stronger when competitors grow in greater proximity.

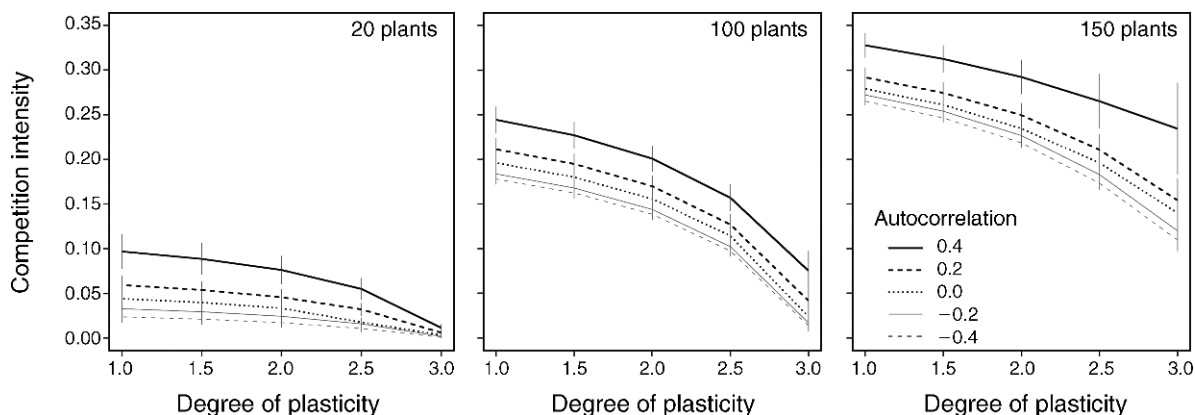


FIG. 5. Competition intensity is dependent on the degree of plasticity, autocorrelation of plants, and density of plants. Error bars indicate \pm SD. The degree of plasticity is the standardized difference between the realized and the potential size of the simulated root space. Competition intensity is analogous to relative neighbor effect (RNE).

autocorrelation among plants was stronger assuming higher levels of plasticity.

As expected, compensatory growth reduced the number of free cells in the simulated patch, i.e., plants could use available space more efficiently, an effect that became larger with increasing density (Fig. 6). Moreover, from more uniform ($AC = -0.4$), over random ($AC = 0$) to aggregated patterns ($AC = 0.4$), the percentage of free cells at highest densities increased around 15% for compensatory plants but $<10\%$ for non-compensatory plants. The variance in competition intensity (measured as the number of plants that compete for the same cell) increased with density and was generally higher when compensatory growth was suppressed. Only in simulations with aggregated patterns, the impact of plasticity on the variance in competition intensity clearly increased with the number of plants.

DISCUSSION

The combination of the experimental and modeling approach we present here provides a novel methodological framework for estimating root plasticity and predicting belowground competition intensity for scenarios of different plant densities and spatial patterns. With the introduction of plasticity into interaction models and the confrontation of these models with experimental data we make a step toward a more mechanistic understanding of belowground competition, which will be especially important for scaling-up from individual interactions to community dynamics. In the following sections we discuss the experimental results as well as the simulated scenarios in more detail.

The basic shape of the plastic sphere of influence

In contrast to the widely accepted assumption of decreasing nutrient uptake with increasing distance to the plants' centers (Weiner 1984, Pacala and Silander 1987, Yastrebv 1996, Zhang and Hamill 1997, Casper

et al. 2003), we found a unimodal response of root activity with a maximum at intermediate distances. Excavations of a few randomly selected plants showed that root spread was mainly lateral, so that root tips, which are known to have the highest uptake rates (Robinson 2001), were absent from areas close to the plants' centers. Since resource depletion is a main driver of belowground competition, this finding emphasizes the importance of differentiating between the physical presence of roots and their actual activity for understanding and predicting competition intensity (Casper et al. 2003).

However, since the confidence in the unimodal relationship between resource uptake and the distance to the plants' centers is relatively low and in contrast to the assumptions of previous studies, more experimental investigations are needed to test whether this is a more general pattern among species and abiotic conditions. If so, current competition models may need to be revised in the light of that finding.

Root plasticity and its effects on competition intensity

Plants showed a noticeable response to the presence of competitors in the location of nutrient uptake: uptake was significantly reduced in proximity to other individuals and increased at the competitor-averted side. Similar results were found by a number of other studies on morphological plasticity. A classical example is the work by Muller (1946), who found for the semi-desert shrub *Parthenium argentatum* no horizontal overlap of roots with those of conspecific neighbors, but much greater lateral root spread into unoccupied soil. Similar "territoriality" of a whole range of species has been reviewed by Schenk et al. (1999).

In general, our simulations show that the ability to avoid overlapping areas of influence has considerable consequences for the outcome of plant-plant interactions. Belowground competition intensity is reduced, since root biomass is distributed more homogeneously in

space and areas of high competition pressure can be equalized. This is in accordance with the simulation study of Brisson and Reynolds (1997), which shows that compensatory plants utilize the available space more efficiently and respond with higher growth rates. Similarly, forest models that allow for plastic development of tree canopies predict that plasticity affects tree performance (Vincent and Harja 2008), the size structure of simulated tree populations (Umeki 1997) and overall productivity by reducing competitive interactions (Sorensen-Cothorn et al. 1993).

Interactive effects of density, distribution and degree of plasticity

As expected, increasing values of plant density and autocorrelation and decreasing degrees of plasticity all intensify competition among plants. More interesting findings derive from the complex interactions among these factors for predicting the consequences of competition. If compensatory growth is intense due to high degrees of plasticity, the effect of initial plant distribution has a less pronounced effect on competition intensity compared to scenarios without compensatory growth or lower degrees of plasticity. The higher overlap of root space due to local aggregation in positively autocorrelated distributions can be mitigated by the ability to redirect root growth to areas of lower competition intensity. Extrapolating this result to subsequent population dynamics, density-dependent mortality would be lower when compensatory growth is possible. A similar result was presented by Brisson and Reynolds (1997): in their simulated scenarios, the change from a clumped to a regular distribution of individuals due to density-dependent mortality was delayed in plants with plastic root growth compared to non-compensatory plants. Stoll and Bergius (2005) showed a similar result not only for simulated but also for experimental plant populations, using genotypes of *Arabidopsis thaliana* with different shoot plasticity: five weeks after sowing, genotypes with reduced plasticity showed more uniform patterns compared to the wild types. The neglect of the strong influence of morphological plasticity in forecasting competition intensity might be a reason why the often-assumed high relevance of spatial correlation of pattern of plants could not be supported by experimental studies (e.g., Huston and DeAngelis 1987, Bonan 1991).

Finally, we also found a noticeable three-way interaction: depending on plant density, the effect of autocorrelation on competition intensity either increases with decreasing degrees of plasticity (at low densities), or decreases with decreasing degrees of plasticity (at high densities). The underlying mechanism of this pattern is likely to be the stronger promotion of clumped individuals at low densities than more uniformly distributed plants, since there is more need to alleviate areas of competition. At high densities, increasing plasticity reduced competition intensity for more uni-

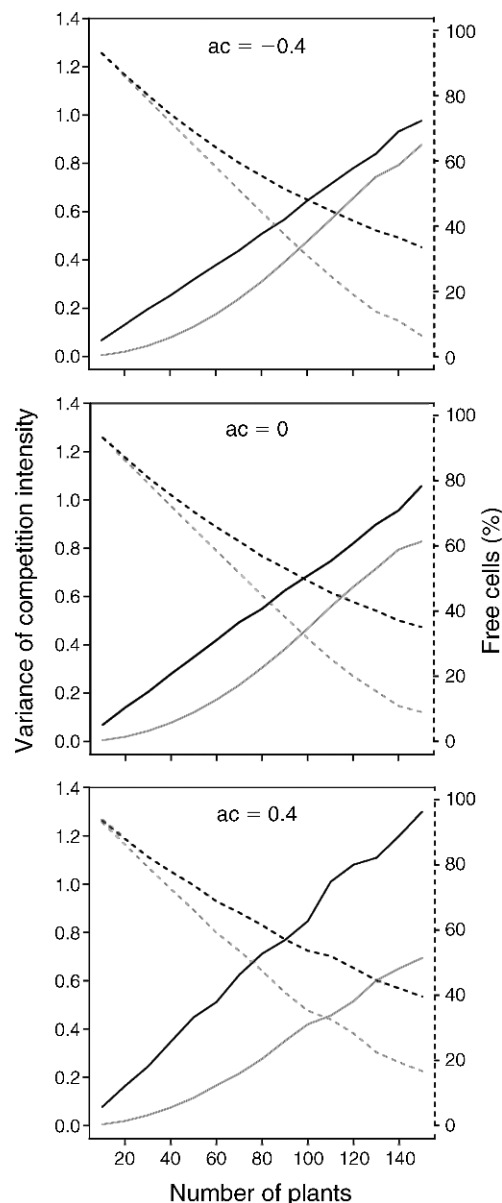


FIG. 6. Variance in competition intensity across area (solid lines) and number of free cells (dashed lines) with full morphological plasticity (gray) and without plasticity (black) for three degrees of autocorrelation (AC).

formly distributed plants more strongly than for aggregated plants, because the possibility for realizing compensatory growth is higher.

Aboveground vs. belowground plasticity

In the presented interaction model we simulated the activity, plasticity, and competition of roots. Since during our experiment the grasses hardly shaded each other, we believe that the model adequately captured competitive interactions between study individuals. However, when comparing the findings from such a system with studies on above-ground competition or



PLATE 1. Two competing individuals of the study species *Bromus hordeaceus*. In the foreground is part of a micro-drip system for irrigation. Photo credit: K. Schiffers.

applying the model to shoot plasticity, we have to account for the different characteristics of above- and belowground interactions.

Aboveground competition is assumed to be asymmetrical, i.e., larger competitors gain disproportionately more resources than smaller ones. This leads to a higher variance in individual performance compared to symmetric competition and eventually to higher density-dependent mortality. Since plasticity in growth reduces not only the intensity but also the asymmetry of competition (Schwinning and Weiner 1998, Stoll et al. 2002), the effect of plasticity on competition intensity will be relatively larger compared to belowground competition, particularly when focusing on mortality as the response to above-ground competition. This implies that the importance of plasticity on competition intensity will depend on the specific combination of aboveground/belowground interactions and the measure of plant performance. However, the qualitative results of the simulations should also apply to the effects of plasticity, density, and spatial pattern on aboveground competition.

Effects of plasticity on the spatial variability of competition intensity

The spatial variability of competition intensity can give a first impression of the degree of variability in the plants' individual fitness. As expected, our results show that the variability of competition intensity increases with the density of plants and is generally lower for scenarios with compensatory growth. Accordingly, the number of free cells is also lower when compensatory

growth is high. In line with these results, Brisson and Reynolds (1997) found compensatory plants to better utilize the available space and to cover ~20% more of the total area than non-compensatory plants. They conclude that, due to plasticity, more plants are able to survive or grow in a specified area. Here, we want to argue that it is important to distinguish between the density of plants and the density of total biomass. Total biomass will be definitely higher when plants are able to respond plastically, since space is used more effectively. However, for the survival and establishment of weak competitors and thus for the number of plants, the effect of plasticity can have contrasting outcomes. On the one hand, a more regular distribution of roots of already-present plants can have a positive effect on species that can deal with intermediate levels of competition intensity, since the area of high competition intensity is reduced. On the other hand, survival and establishment of weak competitors will be hampered by the reduced availability of competition-free space. That means that the effect of plasticity of one species might mediate coexistence with another species of intermediate competitive strength, while it hampers coexistence with species with low competitive strength.

A comparison between scenarios of regular, random and aggregated distributions of plants shows that, despite very similar outcomes for regular and random patterns, positive autocorrelation clearly increases variability in competition intensity for non-compensatory plants. However, the variability for simulations allowing plastic responses to neighbors is decreased compared to negative autocorrelation.

Toward a stronger link between models and data

The use of nutrient tracers as presented here proved to be a valuable method to gain information on plants' belowground areas of influence. In combination with process-based models and parameter-optimization procedures such as simulated annealing, theoretical work and experimental data on interaction intensity can progressively approach each other.

While our study is a first step toward this goal, a high level of uncertainty remains regarding model structure and parameters, due to the strong variability of experimentally obtained data and the general lack of a comprehensive understanding of root plasticity. We therefore advocate for further studies using a similar approach for filling existing knowledge gaps while avoiding the difficulties encountered in our work. Here, we list some suggestions.

The high amount of unexplained variance in the uptake of nutrient tracer was most likely caused by inhomogeneous irrigation during the experiment and consequential drift of tracers. Despite the installation of a micro-drip system, we observed strong differences in soil moisture during the two weeks of tracer application. For future studies, we thus recommend growing plants in a greenhouse for better control of abiotic conditions, in particular uniform soil water content.

The random search of cells to be occupied in the individuals' spheres of influence, the assumption that the number of cells is linearly related to plant performance, and the mode in which the limits of plasticity are defined are simplified model assumptions. By refining these assumptions stepwise and comparing model quality by means of accuracy and simplicity future studies could increase the predictive power of such simulations.

In addition, the interaction model would benefit from validation with independent data. Simulation scenarios could be reproduced in experimental setups to compare resulting values for the relative neighbor effect. We intended to do so in our study, however the reduction of size due to the presence of neighbors was negligible for both competition scenarios. While this is in accordance with the outcome of the simulated realization of the experiment, in terms of model validation a value of zero is generally unfortunate, since it can result from a whole range of parameter combinations. Thus, a design with higher plant densities would be a valuable source of information for validating the sphere-of-influence model.

CONCLUSIONS

The qualitative effect of morphological plasticity in reducing competition intensity among plants has been shown by a number of experimental and theoretical studies. The approach introduced in our present work advances these studies in two respects. First, we investigated how plasticity interacts with two other main factors determining the overlap area of competing individuals and showed that the effect of plasticity is highly dependent on the competitive environments in

terms of the density and spatial distribution of plants. Second, by parameterizing the model with experimental data, we made a step from qualitative statements toward quantitative predictions of competition intensity. Such predictions are essential for understanding and forecasting changes on higher organizational levels, such as populations and communities. Moreover, quantitative predictions are necessary for the application to management or conservation-related case studies, like the increasing employment of plant population modeling in the field of environmental-change research (Jeltsch et al. 2008). In general, the conclusions of our study substantiate the position of Weiner et al. (2001:448), who state: "What most limits the usefulness of zone of influence models may not be their simple mechanisms of competition but their absence of plasticity."

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