

REPORT

PLANT SCIENCE

The exploitative segregation of plant roots

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Plant roots determine carbon uptake, survivorship, and agricultural yield and represent a large proportion of the world's vegetation carbon pool. Study of belowground competition, unlike aboveground shoot competition, is hampered by our inability to observe roots. We developed a consumer-resource model based in game theory that predicts the root density spatial distribution of individual plants and tested the model predictions in a greenhouse experiment. Plants in the experiment reacted to neighbors as predicted by the model's evolutionary stable equilibrium, by both overinvesting in nearby roots and reducing their root foraging range. We thereby provide a theoretical foundation for belowground allocation of carbon by vegetation that reconciles seemingly contradictory experimental results such as root segregation and the tragedy of the commons in plant roots.

A root system's ability to obtain soil resources essential for growth and survival determines a plant's yield and is highly influenced by competition with other plants' roots (1). However, we have few observations of intact root systems in soil and lack a comprehensive theory for root system responses to their environment (2). Agricultural technologists need to understand the mechanisms by which plants compete belowground to design and breed ideal cultivars (3). Understanding the response of these cultivars to different plant densities is crucial to

optimize crop resource-use efficiency and maximize food production (4). Additionally, plant roots represent a large carbon pool that stores approximately a third of the world's phytomass (5), and understanding how roots respond to belowground competition is critical to predict vegetation carbon uptake and to design strategies to mitigate climate change (6). Here, we develop a game-theoretic model that predicts how one plant's roots will respond to roots of nearby plants. We also present a dataset describing spatial distributions of root density for individual plants, and how

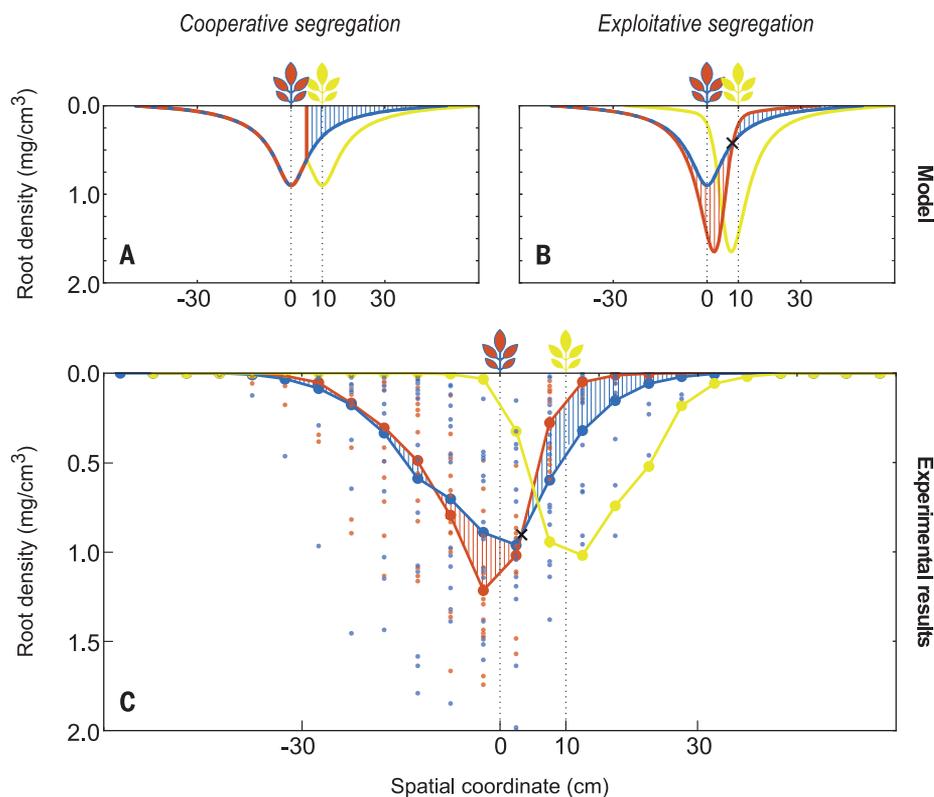
these respond to competition, confirming model predictions.

Plants can sense soil resources (7) and the presence of nonself (8) and nonkin roots (9) and respond phenotypically to these stimuli (10). However, published data have been contradictory about the direction of the belowground plastic responses to the presence of competitors and unclear about the mechanisms. Studies of changes in vertical or horizontal root foraging ranges often conclude that neighboring plants tend to minimize the overlap between their root systems (root segregation) (11). A second group of studies examines the effect of competition on the total carbon allocated to roots (12). Among these, some report a decrease in plants' allocation of carbon to roots (13, 14), presumably in accordance with root segregation; others report an increase (15–17); and still others find no significant effect (18, 19). Neither of these approaches is complete. The former considers only the foraging range but neglects the distribution of root density within that range,

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Fig. 1. Spatial distribution across one horizontal dimension of root density in solitary plants and pairs of interacting individuals separated by a distance $d = 10$ cm. The y axis measures root density, not depth. (A to C) Results from the mathematical model solved under (A) Pareto conditions and (B) an ESS equilibrium, and (C) empirical results. Orange lines (and circles) correspond to a focal plant that is interacting with a neighbor (yellow), and blue lines (and circles) correspond to solitary plant, both centered at the zero spatial coordinate. Areas shaded with vertical bars indicate the differences between the root systems of the solitary and the focal interacting plants at each distance from their insertion to the substrate, orange bars indicate local root overproduction, and blue bars indicate local root underproliferation of the focal interacting plant. The black cross indicates the position of the shifting point (S). In (c), small circles represent the data, large circles represent the mean root density at a given spatial coordinate, and lines represent linear interpolations between the means. See materials and methods (supplementary material) for details.



and the latter ignores the spatial distribution of roots. Few have considered both features of root systems together [but see (20)].

Theoretical studies have added to the confusion in the literature. Some modeling studies rely on simple optimization, in which roots are assumed to equalize average nutrient uptake per unit rooting effort across space (21). Others incorporate game theory (22) and predict that plants will engage in a belowground tragedy of the commons (23–25) *sensu* Hardin (26) and should thus overallocate to roots in the presence of a neighbor. Game-theoretical approaches, like the empirical ones, have generally not looked simultaneously at total allocation and spatial distribution [but see (27)].

We developed a spatially explicit game-theoretical framework describing plant competition for a soil resource (supplementary materials). Our model explicitly incorporates soil resource dynamics and a distance-dependent foraging cost. The fitness cost of accessing a soil patch at a distance from the stem accounts for the cost of proliferating and maintaining absorbing roots inside the patch and transporting roots from the patch to the stem. Game-theoretic equilibrium solutions can be obtained either by assuming that plants adopt the strategy that produces the highest possible fitness for the collective (cooperative equilibrium) or by maximizing their competitive ability [evolutionary stable strategy (ESS)] (28). Cooperative fitness maximization implies that plants should collectively maximize resource uptake per unit of root cost (a fitness surrogate). To do so, they would need either to directly recognize nonself roots and their cost to the neighbor or to have been artificially selected to deploy roots that maximize collective production given a fixed spatial pattern of individuals. This strategy represents a potential target for crop optimization. In the ESS, each individual plant maximizes its own uptake per unit cost. This is the plant strategy that presumably evolves by natural selection.

To analyze the phenotypical response of plants to competition, we compared root spatial distributions predicted by a model of a solitary plant (bell-shaped root distribution centered at the insertion to the substrate) and a plant facing a neighbor. When plants in competition were assumed to follow a cooperative strategy (Fig. 1A), root behavior showed cooperative segregation; that is, each plant withdrew from any location where it sensed nonself roots having lower exploitation costs. However, when plants were assumed to embrace an ESS, the model predicted exploitative segregation; that is, the range of the root system was shortened on the side facing a neighbor, but plants locally overproliferated roots close to their own insertion point (Fig. 1B; see supplementary materials for representations in three dimensional soil). The

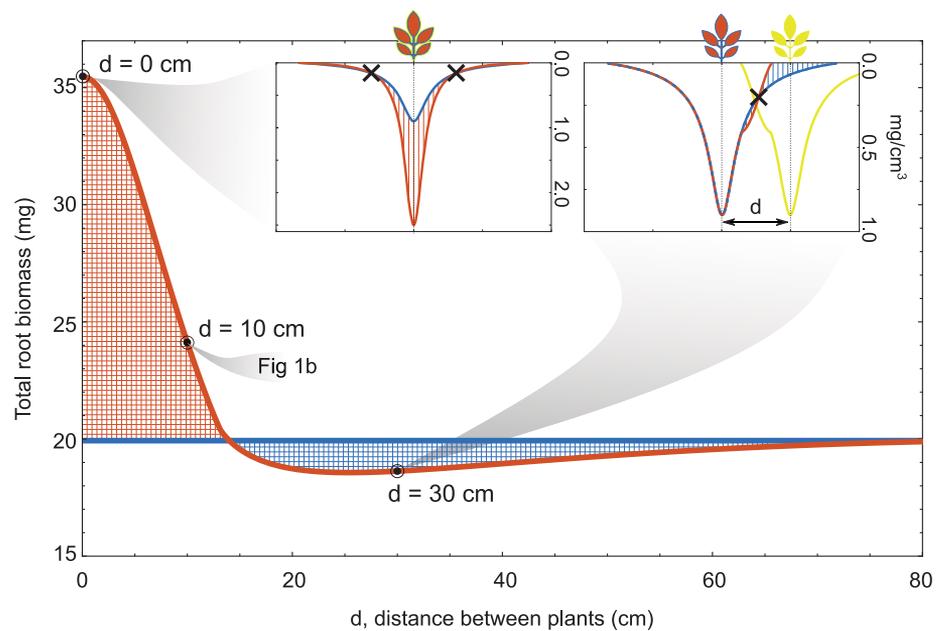


Fig. 2. ESS model prediction of a plant's total root biomass (integral of the spatial distribution of root density). The blue line indicates a solitary plant and the orange line indicates a focal interacting plant, at increasing distance from an interacting neighbor (d , centimeters). The orange-hatched area indicates an increase and blue-hatched area a decrease in total plant root biomass as a response to the presence of the neighbor at each distance. (Insets) The root density distribution in space of plants at $d = 0$ cm (maximum total biomass increase) and at $d = 30$ cm (total biomass decreases). Insets' color codes, abscissa axis values, and model parameterization are the same as in Fig. 1. See materials and methods (supplementary material) for details.

shifting point S defines the distance from the plant-shoot insertion to the substrate at which the strategy shifts from root overproliferation to underproliferation. Both the over- and underproliferation predicted by the ESS simply optimize a plants' resource economy when in competition and do not require direct sensing of nonself roots.

For a solitary plant, the benefit of proliferating roots in a given location decelerates as local root density increases, because, even within a single plant's root network, individual root branches compete with one another for the same resource. As roots proliferate, the solitary plant gains more total resource but also steals more resource from itself. When a neighbor is present, two opposing forces are at work: (i) Some of the stolen resource comes from the neighbor, promoting overproliferation. (ii) Increased proliferation of a neighbor's roots depletes soil resource, promoting underproliferation. The cost of growing a unit of absorbing root surface increases with distance from the plant because the root surface must be connected to the stem by a xylem conduit. When the local cost of roots is low, force (i) dominates and plants should overproliferate roots. However, in locations far from a focal plant but close to its neighbor, force (ii) dominates, leading to local underproliferation by the focal plant.

Exploitative segregation can explain seemingly contradictory results reported in the literature. When two competing plants are very close to each other, plants should respond to competition by increasing biomass allocation to roots (Fig. 2) and should exhibit a root tragedy of the commons. However, as plants are set farther apart, local underproliferation in distant areas compensates for local overproliferation near the plant, resulting in a slight decrease in total root allocation. Also, as in the literature, such plants should exhibit range segregation by decreasing the total spatial spread of their root systems.

We tested these predictions in a greenhouse experiment using a traditional cultivar variety of pepper plant (*Capsicum annuum* L. var. *luesia*, Solanaceae) (supplementary materials). Plants were grown in gutters alone or paired with a competitor located at 10-cm distance. Root systems of competing individuals were stained in situ with different colors, and the spatial distribution of root density of each plant was mapped in the horizontal axis of the gutter. We thereby obtained data integrating spatial information and plant allocation strategy.

We did not observe a root tragedy of the commons at that given plant-plant distance, as there were no significant differences in total root biomass ($t = -0.9422$, $P = 0.3573$), shoot:root ratio ($U = 116$, $P = 0.9025$), or reproductive

yield ($t = -0.6177$, $P = 0.5417$) between solitary and competing plants. We detected evidence for root segregation, as we found significant differences ($t = -5.3362$, $P < 0.0001$) between the observed root overlap in interacting plants (20 cm of overlap) and the expected overlap between solitary-like distributed root systems (40 cm). Plants exhibited an exploitative segregation response to competitors (Fig. 1c) as predicted by the ESS equilibrium of our model. Each plant overproliferated roots near to its own stem and underproliferated roots closer to its neighbor's stem than to its own. Both of these effects are statistically significant: overproliferation of roots with increasing competitor root density ($F = 11.6013$, $P < 0.001$) and negative interaction between length and competitor root density ($F = 58.2655$, $P < 0.001$). This negative interaction indicates that plants responded to competitor root density by shifting from local overproliferation at low transporting lengths to underproliferation as the transporting length between the plant shoot and the soil patch increased.

We thus demonstrated experimentally the predictions of our ESS model: Plants do both locally overproliferate roots near their stem and reduce their foraging range when it overlaps with a neighboring root system. By integrating root allocation and spatial information, the exploitative segregation theory reconciles hypotheses that have been largely considered

contradictory: root segregation and the tragedy of the commons.

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SUPPLEMENTARY MATERIALS

science.sciencemag.org/content/370/6521/1197/suppl/DC1
Materials and Methods
Figs. S1 to S16
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Data and Code S1
MDAR Reproducibility Checklist

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Competitive roots

Much of the world's plant biomass exists out of sight underground in the form of roots. Cabal *et al.* developed a theoretical model and tested it empirically to explain the rules that govern root growth (see the Perspective by Semchenko). Plants adjust how and where their roots grow according to how close neighboring—and competing—plants might be. The model extracts some of the rules about how root balls differ when grown close to neighboring plants compared with being grown in the absence of competition.

Science, this issue p. 1197; see also p. 1167

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