Plants Integrate Information About Nutrients and Neighbors

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All organisms are challenged by the need to find patchy resources efficiently, resulting in the evolution of diverse foraging strategies (*1*). Plants exhibit a variety of behaviors in response to environmental stimuli (*2*), including altering the spatial distribution of their roots as a function of resource patchiness (*3*). Competitors also induce behavioral changes in plants, including increased (*4*) or decreased (*5*) root growth.

Because it is unknown whether plants synthesize these different types of information, we measured patterns of root growth of *Abutilon theophrasti* (Malvaceae) while manipulating both resource distributions and competition (*6*). Our goal was to determine whether root foraging behavior was an additive response to multiple forms of environmental information or whether plants used novel behaviors under different combinations of conditions.

A. theophrasti seedlings received one of six factorial combinations of soil heterogeneity (uniform, patch-center, and patch-edge) and competition treatments (alone versus with competition) (Fig. 1). In all treatments, one focal individual was planted on one side of the mesocosm. A second individual (of the same species) was planted on the opposite side (with competition), but not in the alone treatment. Soil nutrients were distributed homogenously throughout the soil [uniform (Fig. 1, A and D)], concentrated in a single patch in the middle of the mesocosm [patch-center (Fig. 1, B and E)], or concentrated in a single patch near the mesocosm edge on the outside of the focal plant [patch-edge (Fig. 1, C and F)]. Root distributions were recorded with a mini-rhizotron camera over 8 weeks of growth. We then removed the plant shoots and injected dyes of different colors into each root system. Root identity (focal versus competitor) was determined on the basis of color (*7*). We measured the distribution of the focal plant's roots in the soil; root and shoot biomass were also measured.

We analyzed presence or absence of focal plant roots in each location in the soil (Fig. 1, lines) and maximum rooting breadth (Fig. 1, bars) by using mixed models. In each analysis, soil heterogeneity and competition served as fixed effects and mesocosm as a random effect. For the presence-absence data, the model also included distance from stem as a fixed effect and mesocosm as a random effect.

The likelihood of a focal plant root occurring in a given soil location was influenced by a three-way interaction among distance from stem, heterogeneity, and competition ($P = 0.04$, table S1), whereas the maximum rooting breadth was influenced by an interaction between heterogeneity and competition ($P = 0.075$, table S2). When grown alone, plants adopted a broad rooting strategy regardless of the distribution of resources (Fig. 1, A to C), indicating that resource distributions alone did not alter root placement, consistent with prior work on *A. theophrasti* (*8*).

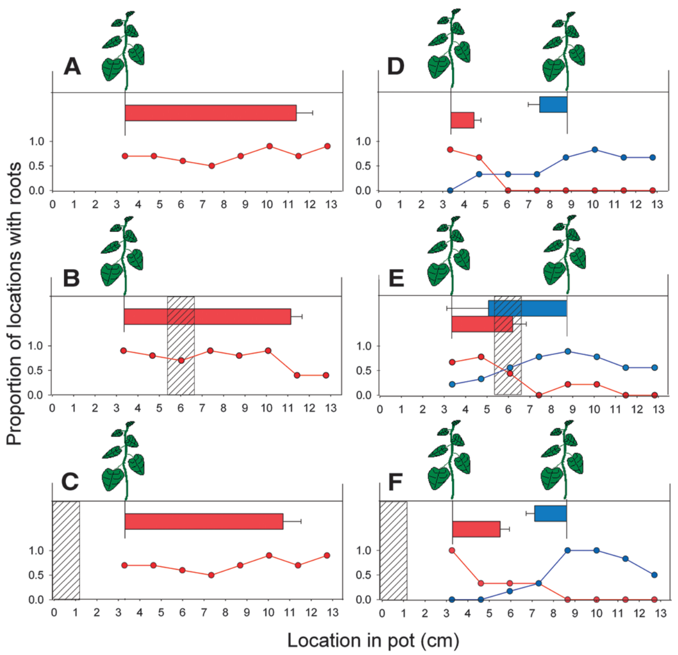

Fig. 1. The annual plant *A. theophrasti* was planted into six combinations of soil heterogeneity (uniform, patch-center, and patch-edge) and competition (alone versus with a competitor) treatments. (**A**) Alone uniform, (**B**) alone patch-center, (**C**) alone patch-edge, (**D**) competition uniform, (**E**) competition patch-center, and (**F**) competition patch-edge. Hatched areas denote nutrient patches (when present). Plant illustrations indicate the location of focal and competitor plants. Red data obtained from the focal plant; blue, data from the competitor (when present). The horizontal bars represent average root breadth (±1 SE), and the lines at the bottom of each frame indicate the proportion of replicates with focal plant roots in each location in the pot.

In contrast, competitors reduced both the likelihood of focal plant roots occurring far from the stem and focal plant rooting breadth, but these effects were moderated by nutrient distributions (Fig. 1 and table S2). In uniform soil with competition, plants had the most restricted root distribution (Fig. 1D), resulting in spatial soil segregation among the two plants. In the patch-center treatment with a competitor, plants had a broader root distribution (Fig. 1E), where plant roots overlapped in the patch and thus were not segregated. In the patch-edge treatment with competition, the root distribution of the focal plant roots was intermediate in breadth (Fig. 1E).

These data suggest root placement for this species is determined by a hierarchical set of decision rules dependent on presence or absence of a neighbor. First, if a plant grew alone, it adopted a broad foraging strategy that was agnostic with respect to resource distributions (Fig. 1, A to C). Second, if neighbors were present, a restricted foraging strategy was adopted that was modified by resource distributions (Fig. 1, D to F). This effect was most pronounced when nutrients were more abundant in the same direction as the competitor (Fig. 1, D to F).

Thus, plants nonadditively integrate information about both resource and neighbor-based cues in the environment. If such complex behaviors are widespread, they may influence spatial segregation and territoriality, niche differentiation and species coexistence, and the basic understanding of plant behavioral ecology.

References and Notes

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Supporting Online Material

www.sciencemag.org/cgi/content/full/328/5986/1657/DC1
Materials and Methods
Fig. S1
Tables S1 to S3
References

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