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Root communication among desert shrubs

(competition/interference/self-nonself recognition/allelopathy/root exudates)

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ABSTRACT **Descriptive and experimental studies of desert shrub distributions have revealed important questions about the mechanisms by which plants interact. For example, do roots interact by mechanisms other than simple competition for limiting resources? We investigated this question using the desert shrubs *Ambrosia dumosa* and *Larrea tridentata* grown in chambers that allowed observation of roots during intraplant and intra- and interspecific interplant encounters. Two types of root "communication" were revealed. *Ambrosia* root systems appear to be capable of detecting and avoiding other *Ambrosia* root systems, whereas *Larrea* roots inhibit *Larrea* and *Ambrosia* roots in their vicinity.**

Horizontal distributions of desert plants have intrigued ecologists for many years and have been commonly interpreted in terms of competition, allelopathy, or protection (e.g., refs. 1–12). In the first experimental evaluation of such patterns Fonteyn and Mahall (11, 12) found no evidence for intraspecific interference for water among *Ambrosia dumosa* Payne (Asteraceae) shrubs, which have a clumped distribution, but *Ambrosia* shrubs in this same population routinely interfered with water availability to *Larrea tridentata* Cov. (Zygophyllaceae) shrubs, relative to which *Ambrosia* shrubs are distributed randomly. Why, then, do *Ambrosia* shrubs not interfere for water with each other? This question cannot be answered by simply invoking competition for limiting resources. We investigated other postulated mechanisms that could answer this question using specially designed root observation chambers in the laboratory. Our results suggest the existence of an unexplored complexity of root–root interaction mechanisms.

MATERIALS AND METHODS

Ambrosia plants grown from seed and small *Larrea* plants collected from the field were planted in flat, rectangular chambers filled with fine sand and oriented at a 45° angle so that positively geotropic roots would grow down along Plexiglas viewing windows covered with removable, opaque shutters (Fig. 1). The chambers were placed in a bright, warm greenhouse and the sand in them was kept continually moist and flushed with one-eighth strength Hoagland's solution every 8–10 days. After a period of establishment and growth, pairs of chambers were connected together, so that roots of a "test" plant would grow into the rhizosphere of a "target" plant. Elongation rates of all test plant roots visible through the viewing windows were calculated from measurements of length (to an accuracy of 0.1 mm) made at recorded times every 2 days. Elongation rates of target plant roots were not monitored, because at times of contact many were reorienting at 90° and/or touching the sides or ends of the chambers. We used *Ambrosia* and *Larrea* for test plants and live *Ambrosia* and *Larrea* roots for targets. Inert physical barriers of braided dacron line were used for control targets.

RESULTS

Rates of elongation of *Ambrosia* roots in the inert physical barrier control (PBC) experiments averaged 0.39 ± 0.10 mm/hr (mean ± standard deviation based on total number of roots) and were not affected by contact with the barriers (Fig. 2). In these experiments elongation rates of *Ambrosia* roots that touched sister roots of the same plant (0.39 ± 0.07 mm/hr) were not significantly different from those of roots that had no contact with sister roots (0.37 ± 0.08 mm/hr).

Roots of *Ambrosia* test plants, whose chambers were connected to chambers of *Ambrosia* target plants, elongated at the same rates as those in the PBCs when they never contacted target roots and before contact with target roots (Fig. 2). However, precipitous declines in elongation rates of *Ambrosia* test plant roots that touched live *Ambrosia* target roots occurred following such contact. Concurrently, other roots on the same test plants, but not in contact with target roots, continued to elongate at normal rates.

Rates of elongation of *Larrea* roots in the PBCs averaged 0.52 ± 0.17 mm/hr and were not affected by contact with the barriers (Fig. 3). *Larrea* roots very seldom touched sister roots from the same plant, and therefore effects of such contact could not be accurately measured.

Roots of *Larrea* (Fig. 3) and *Ambrosia* (Fig. 4) test plants, whose chambers were connected to chambers of *Larrea* target plants, showed linearly declining rates of elongation as they extended through the target chambers before and after and with or without contact with *Larrea* target roots.

Roots of *Larrea* test plants, whose chambers were connected to chambers of *Ambrosia* target plants, continued to elongate at rates insignificantly different from those measured in the PBCs regardless of any contact with *Ambrosia* target roots (Fig. 4).

DISCUSSION

The results of this study suggest some characteristics of the root "communication" mechanisms in *Ambrosia* and *Larrea*. Simple depletion of water or nutrients from around the roots is an unlikely explanation for our results in either case, because the sand in the chambers was continually moist and frequently flushed with nutrient solution. Furthermore, this possibility is inconsistent with the different responses by *Ambrosia* to intra- and interplant root contacts and with the lack of inhibition of *Larrea* test roots by *Ambrosia* target roots. In *Ambrosia* the occurrence of a measurable response only after contact suggests that interroot detection requires contact or that it is mediated by substances diffusing over a very short range. The reduction in *Ambrosia* root elongation after interplant, but not after intraplant, root contact suggests that this detection mechanism involves a capability of self-nonself recognition. The failure of test *Larrea* roots to

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Abbreviation: PBC, physical barrier control.

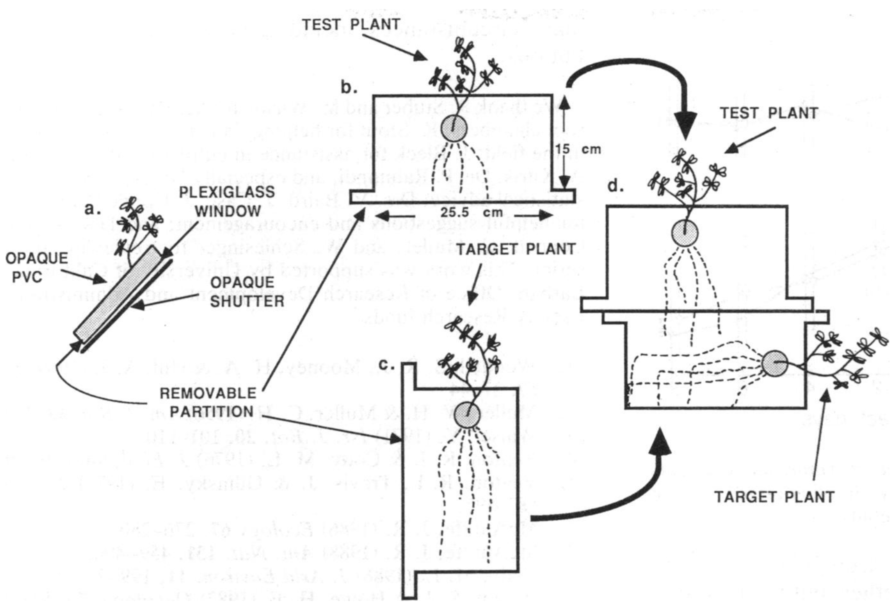

FIG. 1. Root chamber design and arrangement. (*a*) Side view of construction and orientation. PVC, polyvinyl chloride. (*b* and *c*) Face views of test and target chambers and plants. (*d*) Face view of test and target chambers connected (partitions removed). Roots inside chambers are diagramed with dashed lines.

respond to target *Ambrosia* roots suggests the mechanism involves some degree of taxonomic specificity.

The inhibitory mechanism of *Larrea* roots appeared to be fundamentally different from that of *Ambrosia*, because contact was not required, inhibition occurred over distances of centimeters, and the inhibition was not species specific. Therefore the mechanism probably involves the release of a readily diffusible, generally inhibitory substance by *Larrea* roots into the soil. Allelopathy in *Larrea* has been suspected since 1828 (14), and *Larrea* has become well known for its production of a large, diverse array of secondary compounds (15), but firm evidence of allelopathy in this species has not been previously presented.

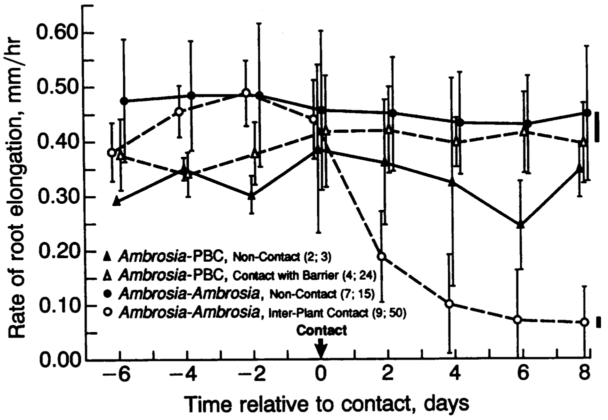

FIG. 2. Rates of elongation of *Ambrosia* test roots before and after contact (arrow at day 0) with PBCs or living *Ambrosia* target roots. The "0" day for noncontact roots was taken to be the average day of contact for sister contact roots of approximately the same age on the same plant. Treatments are designated as follows: test roots-target type, with or without contact with target (number of test plants [= number of test/target pairs]; total number of roots). Measurements were made simultaneously on each day but are offset in the figure for clarity. Noncontact roots were on the same test plants as contact roots within target types. Since variation existed among plants and among roots on a plant, and different plants had different numbers of measurable roots in particular categories, means and error bars (two standard errors shown on either side of the mean) were calculated as follows: (*i*) variances among plants (s_P^2) and among roots on a plant (s_R^2) were estimated as shown in a single classification analysis of variance (ANOVA) with unequal sample sizes (13); (*ii*) means for treatments and dates were estimated using the weighted averages of the plant means: (root elongation rates averaged per test plant × weight): the weights are W_i/W, where $W_i = 1/(s_P^2 + s_R^2/n_i)$, n_i = number of roots measured on plant *i*, and W = sum of W_is; (*iii*) standard errors of these estimates of the means $= 1/\sqrt{W}$. In addition, a repeated-measures ANOVA, based on n = number of test plants, with root elongation rates averaged per test plant, was used to test for differences among treatments (*Ambrosia*, PBC, noncontact: could not be analyzed in this way because of the small n number). By this test, treatments whose final means (day 8) do not share a bar (right end of figure) were statistically different ($P < 0.05$).

Our results may explain several field observations. The precipitous reduction of elongation of test *Ambrosia* roots following contact with target *Ambrosia* roots and the concurrent continuation of elongation of other roots on the same test plant appear to constitute a detection and avoidance mechanism that would, in effect, redirect root elongation into soil not occupied by roots of neighboring *Ambrosia* plants. Thus, with this mechanism the soil volume competitively utilized by root systems of neighboring, "clumped" *Ambrosia* shrubs would be much smaller than if the roots were distributed irrespectively of each other. This may explain the lack of interference among these shrubs in the field (11, 12).

The finding of inhibition of *Larrea* test roots by nearby *Larrea* target roots supports the suggestion by several work-

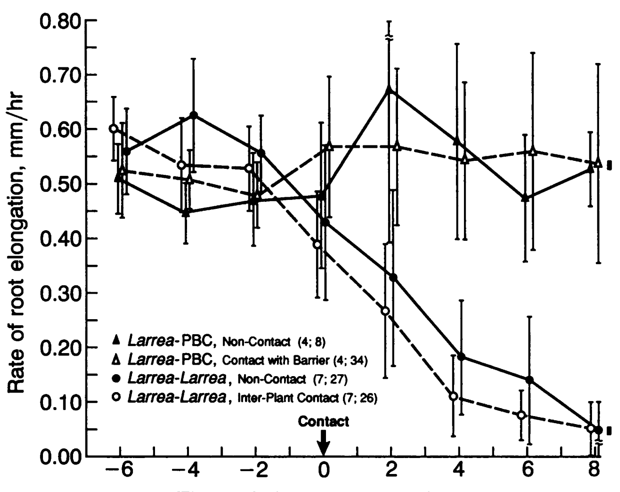

FIG. 3. Rates of elongation of *Larrea* test roots before and after contact (arrow at day 0) with PBCs or living *Larrea* target roots. See Fig. 2 legend for details.

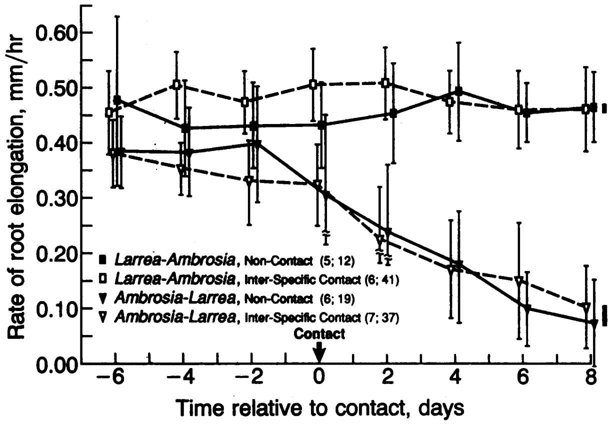

FIG. 4. Rates of elongation of *Larrea* or *Ambrosia* test roots before and after contact (arrow at day 0) with living target roots of the other species. See Fig. 2 legend for details.

ers (1, 4, 16) that *Larrea* shrubs may strongly interfere with each other when growing closely together, but the nature of the mechanism has not been demonstrated previously. The inhibition of elongation of roots of one *Larrea* entering soil near roots of another *Larrea* could strongly limit soil volumes and therefore quantities of water available to one or both plants.

The findings that *Larrea* test roots grew freely through soil occupied by *Ambrosia* target roots, and that *Ambrosia* test roots grew at reduced rates into soil occupied by *Larrea* target roots, fit with the discovery that these species commonly interfere with each other's water availability in the Mojave Desert (11, 12). Our results suggest this interference may be mechanistically asymmetrical. *Ambrosia* shrubs may interfere with *Larrea* primarily by means of competition for limiting resources, whereas *Larrea* shrubs may interfere with *Ambrosia* largely through root-mediated allelopathy. Both mechanisms could result in reduced water availability.

There is little information in the literature about communication among roots. Root exudates appear to mediate host recognition in some vascular plant root parasites (17–21), and there are inconclusive indications that root exudates are involved in "soil sickness" (e.g., refs. 22–27). Our work with *Larrea* may represent the strongest evidence to date for root-mediated allelopathy, and our results with *Ambrosia* strongly suggest that root–root detection and avoidance systems exist. The fact that we found a form of root communication in each of the two species we investigated suggests the paucity of information in the literature does not reflect the occurrence of such phenomena in the field. Interactions among roots may be very complex (28), and the simple models of competition for limiting resources commonly applied may provide insufficient explanations for many circumstances, including intracommunity plant distributions.

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