

Competition for Soil Moisture Between Two Owens Valley Shrubs: The Roots of the Matter

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Abstract

Haplopappus cooperi and *Chrysothamnus teretifolius* (Asteraceae) are common shrubs living on alluvial fans in the Owens Valley, California. Analysis of spatial patterns revealed *Chrysothamnus* shrubs to be clumped and *Haplopappus* shrubs to be distributed randomly. With respect to each other, a random association existed between the two species. Shrub removal experiments, performed over one season, yielded unexpected data: *Haplopappus* predawn water potential was considerably altered by neighbors of either species, while *Chrysothamnus* water potential proved unaffected by neighbors. Since these results conflicted with published removal experiments, an excavation of the roots of these two species was performed. *Haplopappus* had a diffuse, shallow-root system; *Chrysothamnus* had a long tap root and produced its laterals deeper in the soil profile. Qualitative and quantitative comparisons of the two root systems helped explain the anomalous removal experiment data by revealing that the shallow-rooted shrubs were influenced by competition from neighbors, while the deeper-rooted ones were not.

Introduction

The extent to which desert perennials interact or compete for available moisture resources has been a research topic for decades. As is commonly the case in scientific investigations, the questions and answers become more complicated as more is learned about the system being studied. This study is no exception.

Early desert ecologists [Shreve, 1942] believed that abiotic factors had greater effects on shrubs than biotic factors. Later researchers realized that definite spatial arrangements of shrubs could be statistically determined; thus attention began to be

paid to the importance of biotic factors in structuring desert communities.

By the early seventies, many studies of plant distributions, such as those by Anderson [1971], Barbour [1969], and Beals [1968], concluded that perennials in desert communities could be distributed in one of three patterns. They could be: (1) positively associated, or "clumped;" (2) negatively associated, or "regular" in that there is at least a minimum amount of space between individuals; or (3) randomly associated.

Once a particular pattern was determined for the shrubs on a par-

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ticular site, hypotheses were made, and sometimes conclusions were drawn, on the degree of influence that neighbors had on a particular shrub species (see Woodell *et al.* [1969] and Yeaton and Cody [1976]). For example, on sites dominated by mature *Larrea tridentata* (Creosote Bush), Barbour [1969] and Woodell *et al.* [1969] found a regular pattern of distribution. This pattern was most pronounced on sites where water was most limiting [Woodell *et al.*, 1969]. Therefore, it was concluded that *Larrea* competed with members of its own species for water, at least when young. As shrubs grew, some neighbors died, and the resulting mature stand had evenly spaced *Larrea* shrubs. Fonteyn and Mahall [1981], in their classic removal experiment in a *Larrea/Ambrosia* community, did find evidence of competition for water between *Larrea* shrubs; removal of *Larrea* neighbors slightly increased the water status of remaining *Larrea*.

Further studies correlating above-ground distribution pattern with competition for water have proved ambiguous. Some have suggested that individuals within a clump compete with each other for available moisture. For example, Robberecht *et al.* [1983] found this to be the case for the desert bunchgrass, *Hilaria rigida*; and Ehleringer [1984] also came to this conclusion in his study of *Encelia farinosa*. However, although Fonteyn and Mahall [1981] observed *Ambrosia dumosa* to be clumped, they saw no improvement in water status when neighbors were removed around a monitored shrub.

In a recent paper, Cody [1986a] presented and analyzed data on shrub distributions at four sites in the Mojave Desert. He noted completely random distributions to be rare

and positive and negative associations to be common. In one analysis, Cody [1986a] showed *Acamptopappus sphaerocephalus* to be positively associated both with members of its own species and with *Hymenoclea salsola*. *Acamptopappus* was negatively associated with individuals of *Haplopappus cooperi*, *Opuntia ramosissima*, and *Salvia dorrii*. *Cassia armata*, *Ephedra nevadensis*, and *Thamnosia montanum* were all randomly associated with *Acamptopappus*.

Cody [1986a] suggests that such patterns emerge as shrubs grow older and larger. Species with roots that overlap or otherwise interfere would compete with each other, some shrubs would die, and a negative association would become apparent. Plants with shallow-root systems may fall into this category. Positively associated species have root systems that do not compete but are actually compatible with each other. Shrubs with long roots into moister, deeper soil layers where water is not limiting may be compatible.

The old method of determining degree of interaction based on above-ground distribution patterns alone suffers from a major flaw: it assumes similarities in below-ground morphologies. Cody's [1986a] suggestions and my evidence show that this is not the case.

Removal experiments have yielded interesting, yet ambiguous, results in the past, but none have gone to the actual zone of competition, the roots, to add support to their theories. In this ongoing study, I have compared water relations of two Owens Valley shrubs, *Haplopappus cooperi* and *Chrysothamnus teretifolius*. In order to test Cody's [1978] proposed

idea that competition occurs among and between the two study species, I have performed a controlled shrub removal experiment. Also, I have excavated roots of these species in order to better understand the role of root systems in desert shrub interactions.

Study Site and Study Organisms

A research site was chosen on an east-facing alluvial fan on the west side of Owens Valley approximately 8 km northwest of Big Pine, California. *Haplopappus* and *Chrysothamnus* (both Asteraceae) were codominants on the site, each accounting for over 30 percent of total shrub cover. *Poisson* analyses of quadrat data showed *Haplopappus* to have a random distribution and *Chrysothamnus*, a clumped distribution relative to members of their own species. The two species were distributed randomly relative to each other.

Haplopappus and *Chrysothamnus* are two closely related genera. Systematic affinities between the two are currently being debated (J. Morefield, pers. comm., 1987). Intergeneric hybrids are not uncommon in nature.

In an earlier study of four species of *Haplopappus* and *C. teretifolius* in the Mojave Desert, Cody [1978] noted that all the shrubs had similar habitat and resource requirements, and he suggested that there was competition between them.

Materials and Methods

For the removal experiment, 48 shrubs (24 of each species) were chosen to be central shrubs of the 48 experimental plots. Shrubs chosen were surrounded within a 1.8 m

radius by at least three individuals of both species. Following measurements of all shrubs in a plot, one of the following treatments was applied around the central shrub: (1) all neighbor shrubs were removed, (2) *Haplopappus* shrubs (only) were removed, (3) *Chrysothamnus* shrubs were removed, and (4) no shrubs were removed (control). Removals were completed in early April, 1986, after which I monitored predawn xylem pressure potential (XPP) at regular intervals throughout the field season using a pressure bomb (see Scholander [1965]). One branchlet was cut from each central shrub for XPP determination, and the six measurements per treatment for the species were averaged.

Root systems of three shrubs were exposed by digging trenches with a backhoe. A more careful excavation of roots was then done by hand. Root systems were sketched, measured, described, and photographed.

In order to make a quantitative analysis of the root biomass, I removed 1/4 litre root and soil samples from the vertical face of the trench. Samples were taken at 20-, 40-, 60-, 80-, and 100-cm depths along the main-root axis and at 25-, 50-, and 75-cm distances out from the main axis (for all depths except 100 cm). Samples were dried, then roots were separated from soil using an "elutriator" (apparatus described by Groeneveld [1985]). Roots were then dried and weighed. Samples taken from distances greater than 0 cm from the main axis at each depth were combined to make 1/2 litre. For example, both the 25-cm "distance" samples taken at 20-cm depth were combined and elutriated as representative of that soil region. Biomass measurements

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were then divided by two to give root biomass per 1/4 litre of soil.

Results and Discussion

Results for XPP of central shrubs in the removal experiment appear in Figure 1. There was no significant effect of neighbor removal on central *Chrysothamnus* shrubs. There was a general trend toward lower XPP as the season became hotter and drier, yet *Chrysothamnus* shrubs appeared not to be competing with each

other or with *Haplopappus* individuals for their water needs. *Haplopappus*, however, showed a dramatic response to absence of neighbors. Control shrubs exhibited a much lower XPP than central shrubs in plots where any or all neighbors were removed. *Haplopappus* water potential was obviously affected by presence of both *Haplopappus* and *Chrysothamnus* neighbors which appeared to compete with it for available moisture. An analysis of root morphologies helped explain the outcome

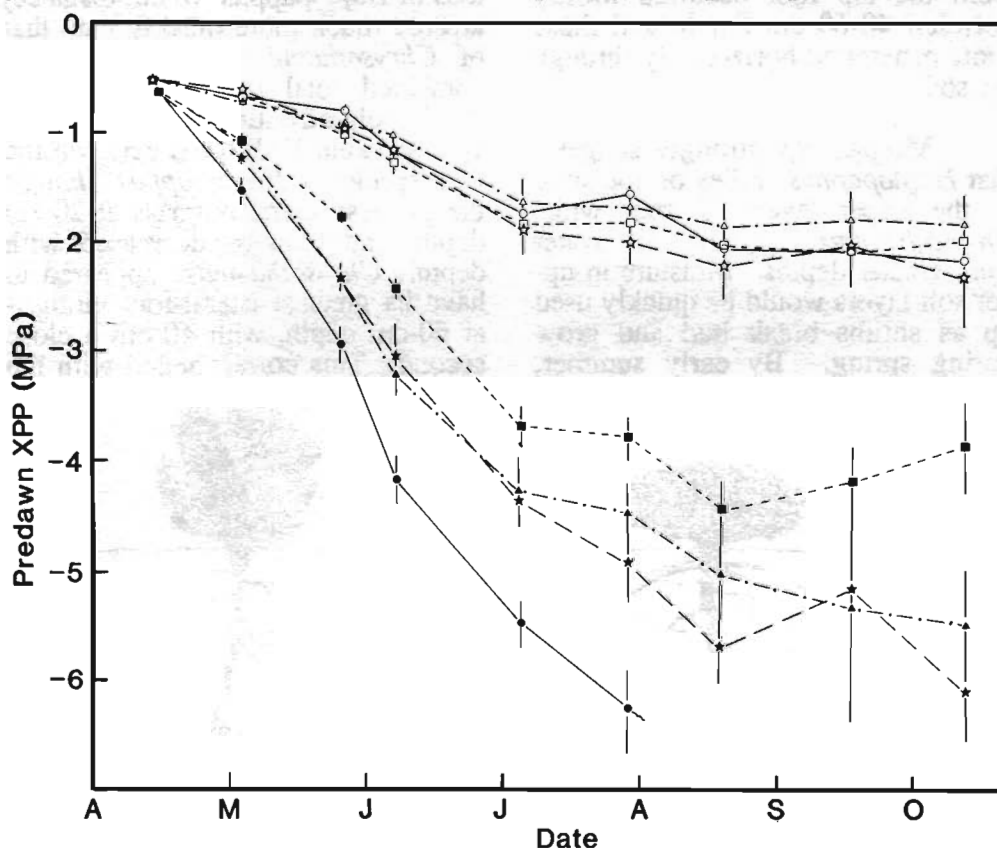


Figure 1. Seasonal trends of predawn water potential (XPP) for both *Haplopappus* and *Chrysothamnus* and all treatments used in the removal experiment. Months are marked along the abscissa, and predawn XPP, in MPa, along the ordinate. Open symbols represent plots in which *Chrysothamnus* was the central shrub, closed represent *Haplopappus* plots. Symbols correspond to the following treatments: squares = all neighbors removed, triangles = *Chrysothamnus* neighbors removed, stars = *Haplopappus* neighbors removed, circles = control, no neighbors removed. Each symbol represents the average of six branchlets, one from each of the six central shrubs receiving that treatment. Standard error bars are included.

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of the removal experiment. Root systems of representative shrubs are diagrammed in Figure 2. *Haplopappus* had a shallow root system that branched heavily almost immediately beneath the canopy and spread laterally into upper soil layers. The maximum depth to which *Haplopappus* roots could be reliably traced was 12 m. *Chrysothamnus* had a long tap root which was traced as deep as 17 m, where it was still as much as 14 mm in diameter. Lateral emergence from the tap root occurred mostly between 40-60 cm depth, and these roots penetrated horizontally through the soil.

Morphology strongly suggests that *Haplopappus* relies on moisture in the upper layers of soil, while *Chrysothamnus* obtains its water from greater depths. Moisture in upper soil layers would be quickly used up as shrubs break bud and grow during spring. By early summer,

Haplopappus must rely entirely on water in relatively shallow regions of the soil, where roots of other *Haplopappus* shrubs, as well as some roots of *Chrysothamnus*, occur and compete. *Chrysothamnus* continues to tap deeper soil where moisture is more abundant.

Quantitative analyses of root biomass agreed with observed morphologies. Values for biomass appear in Table 1. First, the main-root axis of *Haplopappus* (0 cm distance) tapered much more quickly than that of *Chrysothamnus*. Secondly, the combined total of laterals at each depth (column entitled "Total Minus 0 cm" in Table 1) differed between the two species. *Haplopappus* showed the greatest lateral biomass at 20-cm depth, and biomass decreased with depth. *Chrysothamnus* appeared to have its greatest lateral-root biomass at 60-cm depth, with 40 cm a close second. This corresponded with the

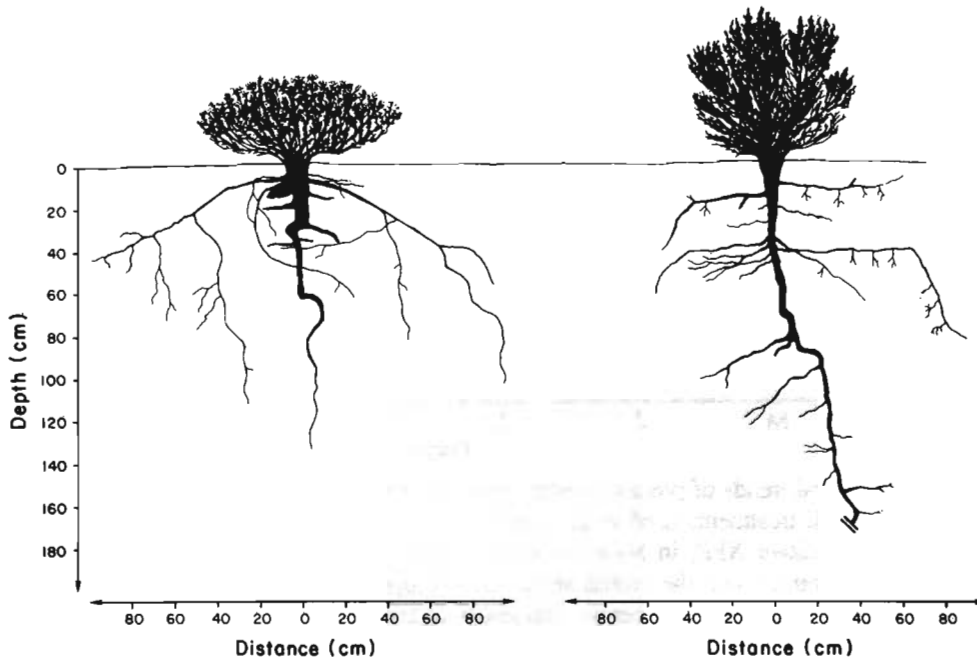


Figure 2. Diagrammatic sketches of root systems representative of *Haplopappus* (left) and *Chrysothamnus* (right) shrubs. Drawings by Christina Weber-Johnson.

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Table 1

Haplopappus cooperi (H.c.) and *Chrysothamnus teretifolius* (C.t.) root biomass in g per 1/4 litre soil for shrubs illustrated in Figure 2. Final column is the total of the lateral roots only, that is, the total sampled root biomass at the given depth excluding the main-root (0 cm) sample.

	Depth (cm)	0	25	50	75	Total	Total minus 0 cm
<i>H.c.</i>	20	3.856	1.459	0.140	0.131	5.586	1.730
	40	1.173	0.266	0.259	0.141	1.839	0.666
	60	0.763	0.087	0.059	0.145	1.054	0.291
	80	0.291	0.118	0.063	0.095	0.567	0.276
	100	0.155					
<i>C.t.</i>	20	37.826	0.126	0.097	0.152	38.201	0.375
	40	14.042	0.329	0.117	0.062	14.550	0.508
	60	7.163	0.214	0.195	0.119	7.691	0.528
	80	6.449	0.090	0.059	0.113	6.711	0.262
	100	6.039					

observed lateral root proliferation from the tap at 50-cm depth.

Conclusions

My preliminary study supports Cody's [1986a] hypothesis that clumped species can be compatible. *Chrysothamnus* had a deep tap root and access to regions of soil where water was not limiting. In the removal experiment, this shrub species proved not to be affected by presence of neighbors. *Haplopappus* was randomly distributed on the site. Its root system was shallower and thus dependent on moisture in upper soil layers. As upper soil layers dry, *Haplopappus's* ability to obtain adequate moisture was significantly affected by presence of neighbors.

The results I obtained, along with those of others, lead to the conclusion that studies of above-ground

spacing patterns alone do not provide sufficient information to allow adequate assessment of below-ground phenomena, such as competition for water. Root morphology of desert shrubs varies from species to species yet appears to be fairly constant among members of a particular species [Cody, 1986b; Groeneveld, 1986]. More studies of roots should be done to determine if root morphology correlates with above-ground spacing patterns and results of removal experiments; only then can we devise a comprehensive theory of competition for water between desert perennials.

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