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COMPETITION BETWEEN ADULT AND SEEDLING SHRUBS OF *AMBROSIA DUMOSA* IN THE MOJAVE DESERT, NEVADA

Richard Hunter¹

ABSTRACT.—Seeds of the perennial shrub *Ambrosia dumosa* germinated in abundance following 11 days of rain during August 1983 at a study site in the northern Mojave Desert. Seedling establishment, growth, and reproduction were observed in natural vegetation and in an area that had been previously cleared of vegetation. For 5,527 *A. dumosa* seedlings, percent survival in April 1986 averaged 3% in the undisturbed vegetation and 58% in the denuded area. Seedlings occupying the cleared area had grown to sizes up to 0.1 m³ by October 1984; some produced flowers and fruit in the spring of 1985. Surviving seedlings in the undisturbed vegetation were all smaller than 0.001 m³ and did not reproduce. These pronounced differences in growth, survival, and reproduction associated with the presence or absence of adult shrubs demonstrated an intense competition that is incompatible with indications of mild competition from nearest-neighbor analyses. I therefore hypothesize that competition for water occurred, not by competition for water in two dimensions but by rapid use of a common resource, as if several people were drinking with straws from a common cup. This temporal mechanism would strongly favor adults over seedlings.

Attempts to detect the occurrence of "competition" in desert vegetation have depended largely on analyses of spacing and the distribution of shrub populations (reviewed recently by Fowler 1986, Ismail and Babikir 1986). Regular spacing has been taken to imply that competition has occurred in the past. However, neither pattern nor spacing with respect to neighbors has produced unequivocal evidence that competitive interactions have major effects in desert plant communities (Wallace and Romney 1972, Yeaton and Cody 1976, Ebert and McMaster 1981, Fonteyn and Mahall 1981, Phillips and MacMahon 1981, Wright 1982, Schlesinger and Jones 1984). Some workers have presented direct experimental evidence that competition for soil moisture occurred between desert shrubs by demonstrating that removal of shrubs resulted in statistically significant increases in the water potentials of remaining plants (Ehleringer 1984, Fonteyn and Mahall 1978, Robberecht et al. 1983). Though competition in deserts has thus been acceptably "proven," it would appear from these studies to be a minor process in shrub population dynamics producing subtle effects subject to considerable debate.

To assess the role of adult-seedling competition on seedling survival, growth, and reproduction, I compared seedling establishment in undisturbed vegetation with that in an adja-

cent area denuded of shrubs. Heavy rains in August 1983 over an area including several denuded areas resulted in germination of numerous seeds of the shrub *Ambrosia dumosa*, initiating the study.

STUDY SITE

The focus of the study was a 43 × 1,000-m area in Jackass Flats, Nevada (36°42'N, 116°24'W, 1,100 m altitude), cleared of vegetation by surface blading in 1979 (Major W. Jacobs, personal communication) for a purpose unrelated to this study. Prior to the *A. dumosa* germination, the denuded area supported a sparse population of the perennial grass *Oryzopsis hymenoides*. The abundant germination of *A. dumosa* appeared to be a highly localized event, extending approximately 1.3 km E, 3.3 km N, and 3–5 km S and W of the study site. The rain that caused germination fell almost daily 9–19 August 1983, totaling 99 mm at the nearest NOAA weather station 11 km away. That rainfall amount in such a short period was unprecedented in 23 years of record.

Soils in west Jackass Flats are sandy to a depth of at least 1 m (Romney et al. 1973, site 72). Natural plant cover consists largely of the shrubs *Larrea tridentata* and *A. dumosa*, together with sparse individuals of *Ceratoides lanata*, *Acamptopappus shockleyi*, and *O. hymenoides*.

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METHODS

In January 1984 a 100-m steel tape was laid at right angles to the long axis of the denuded area extending 25–32 m into undisturbed habitat on either side of the denuded plot. All seedlings were counted (but not measured) in a 1-m swath on one side of the tape. In addition, measurements were made of the heights, maximum widths, and the perpendicular widths of all mature shrubs (>10 cm in any dimension) and the grass *O. hymenoides* occurring in a 2-m swath centered on the tape. (The greater width was chosen to increase the number of individuals sampled for the sparser *O. hymenoides* and adults.) At subsequent censuses in October 1984, June 1985, and April 1986 all plants, seedling and adult, were measured and their reproductive states recorded. Seedlings that occurred in clusters were measured individually. The area covered by each shrub was calculated as an ellipse with the two radii equal to half of the two measured widths. Total cover was corrected for overlapping canopies. Shrub volume was estimated as the volume of an elliptical cylinder the height of the shrub.

RESULTS

In January 1984 seedling density of *Ambrosia dumosa* ranged from 0 to 535/m². In the undisturbed vegetated area the seedlings were quite uniform in size and appearance. Individuals ranged up to 3 cm tall and lacked branches and expanding leaves. In the disturbed area they were somewhat larger and vegetative. They bore short branches and healthy green leaves and appeared to be actively growing. All but three new *A. dumosa* on the denuded area were less than 10 cm in any dimension. Remains of cotyledons, some still green, were apparent.

There were 5,527 *A. dumosa* seedlings in the first census. At the same time there were 15 *Larrea tridentata* and 3 *Acamptopappus shockleyi* seedlings. Ten of the *L. tridentata* and all *A. shockleyi* seedlings occurred in the undisturbed area; none of these survived to June 1985. Three of the 5 *L. tridentata* that germinated on the denuded area survived. Along the 2-m-wide transect there occurred 43 *Oryzopsis hymenoides* seedlings in the undisturbed area, 17 of which survived to June 1985, and 9 in the denuded area, 5 of

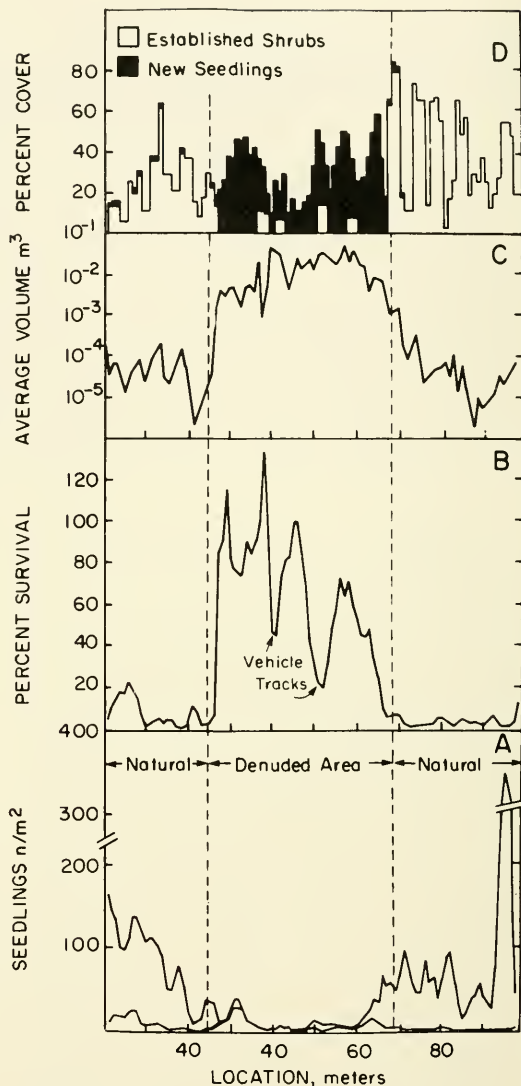


Fig. 1. Population characteristics of a cohort of *Ambrosia dumosa* seedlings spanning a 43-m-wide denuded area: A, density of seedlings in January and October 1984 (three meter moving average); B, percent survival in June 1985 (three meter moving average); C, average aboveground volumes; D, cover by seedlings and mature plants (*Larrea tridentata*, *A. dumosa*, and *Oryzopsis hymenoides*).

which survived. Cover by adult perennials in the undisturbed sections was by *A. dumosa* (10.5%), *L. tridentata* (7.1%), and other species (0.3%).

Ambrosia dumosa seedlings were more numerous in quadrats in the natural vegetation area than in quadrats located on the denuded area (Fig. 1A). They also were more dense on

TABLE 1. Logarithmic growth rates ($k = \ln(V_2/V_1)/dT$) and volume-doubling times (days) for *Ambrosia dumosa* seedlings and adults between September 1983 and October 1984.

Location (m)	Habitat	n	$k \pm \text{sem}$	Doubling time
0-25	Control	21	3.5 ± 0.2	72
26-30	West edge, scraped	5	7.5 ± 0.2	34
29-63	Central scraped	27	8.6 ± 0.2	29
64-68	East edge, scraped	3	7.6 ± 0.6	33
69-99	Control	23	3.2 ± 0.3	79
0-99	Control adults	28	0.6 ± 0.1	420

the edges than in the center of the denuded area. Many occurred near or in obstructions, such as around the bases of *O. hymenoides* clumps, around standing dead wood, in shallow depressions where litter and seeds collected (Reichman 1984), or in small sand deposits in the lee of dead twigs lying on the surface.

Percent survival in June 1985 is plotted in Figure 1B. Survival near the center of the disturbed area reached 100% in some quadrats and averaged 65%, whereas in the natural vegetation it averaged only 5% ($X^2 = 1461$, 1 d.f., $p < .0005$). Survival on the disturbed area appeared to taper off near the edges (Fig. 1B). A decrease in survival between 48 and 55 m was due to infrequent vehicle traffic (over which I had no control) crossing the transect. (Survival exceeding 100% in Figure 1B arose from small counting errors at the initial census due to clustering of seedlings and slight variations in repositioning the steel tape.)

By October 1984 there was a striking difference in seedling size between the disturbed and undisturbed plots (Fig. 1C). Within 14 months of germination, individual plants in the center of the disturbed area had reached nearly 0.1 m^3 in canopy volume, while none in the natural vegetation exceeded even 0.001 m^3 . Consequently, by October 1984 average cover on the disturbed area ($26 \pm 3\%$) exceeded cover in the natural vegetation of the undisturbed sections of the transect (18.6%) (Fig. 1D). In June 1985 and March 1986 cover was lower than in October 1984.

Logarithmic growth rates (Erickson 1976) were calculated for the period from germination to October 1974 (Table 1). They demonstrated what is visually apparent in Figure 1C: the growth of surviving seedlings was much slower in the control areas than on either the edges or center of the denuded strip.

Proportionally, growth of surviving seedlings in the control areas was more rapid than that of adults, but in absolute volume growth, adults (January–October 1984; $134 \text{ m}^3/\text{ha}$) far surpassed seedlings (germination–October 1984; $2.6 \text{ m}^3/\text{ha}$). Adult survival was 100% between January and October 1984, compared to 5% for seedlings.

In June 1985 there were 207 seedlings located between 31 and 62 m along the transect (the central denuded section), of which 31 had produced flowers and/or fruit. The mean volume of the reproductive plants was $.031 \text{ m}^3$ (s.e. = .004), and the smallest was 0.0016 m^3 . Slightly more than 50% (24 of 47) of the seedlings between 40 and 55 m flowered in 1985. All other seedlings along the entire transect remained nonreproductive.

DISCUSSION

Dominant shrub species in the Mojave Desert are long-lived (Johnson et al. 1975, Hunter et al. 1980, Vasek 1980), and turnover in established populations is correspondingly slow (Shreve and Hinckley 1937, Beatley 1980, Hunter et al. 1980, Goldberg and Turner 1986). Storm-initiated germination and subsequent high seedling mortality are typical (Went and Westergaard 1953, Sheps 1973, Friedman and Orshan 1975, Ackerman 1979, Ebert and McMasters 1981), though the densities I observed were extreme. The excellent survival I found on the denuded area has not been previously reported.

Denuded areas in the Mojave Desert normally require many years to regain even a semblance of original cover and diversity (Vasek et al. 1975, Romney et al. 1980, Wallace et al. 1980, Webb and Wilshire 1980). The rapid restoration of cover by a dominant species is evidently unusual but concurs with observations of Shreve (1942).

There were bare patches in the vegetated area several meters in diameter associated with slight improvements in survival (6 and 98 m; Fig. 1B); yet growth was not improved in those patches (Fig. 1C). In contrast, at the edge of the denuded area growth increased dramatically within 1 m (Fig. 1C). In other words, there was relative uniformity of growth and survival within the two areas and a sharp divergence at the boundaries. In order to explain the uniformity, I postulate that soil moisture levels in each of the two areas were relatively uniform, and that the differences in moisture content were due to plant transpiration in the vegetated area. Thus, the apparently patchy shrubs resulted in uniformly dry soil.

I therefore propose, as a generalization, that in deserts, though shrub aboveground biomass is relatively patchy, soil moisture is relatively uniform. This could arise through rapid equilibration of soil water pools, depending on relatively rapid hydraulic conductivity through soils and roots (Richards and Caldwell 1987). It could also arise through uniform withdrawal of soil moisture by shrubs, but that mechanism is contradicted for wet soil by data of Cable (1977) and Fernandez and Caldwell (1975) on the spatial aspects of moisture withdrawal and root growth. Probably, as soil goes from wet (near 0 MPa) to dry (near 5.0 MPa), the mechanism producing uniformly available soil moisture would switch from equilibration by water movement to relatively uniform withdrawal by shrubs. Nevertheless, whatever the mechanism, this hypothesis relates significantly to current research on desert plant ecology, which attempts to infer competition by spatial analysis of aboveground biomass.

Went (1973), observing density-dependent growth of desert ephemerals, proposed that plants share rather than compete for resources, each individual growing in proportion to its share of the available resources. A less teleological view is that they had equal capabilities for resource utilization, thus making competition ineffective rather than absent. This is reasonable for desert ephemerals, which all start at a given time as seeds and then germinate and grow rapidly to maturity. My hypothesis is similar, except that it involves both adults and seedlings. It appears that though they shared a common pool of

water, seedlings had a much greater probability of drought-induced mortality. They had less biomass to "store" water, smaller root systems, and were less self-shading. Their small size was, therefore, a probable cause of the differential mortality (see e.g. Cook 1979, Paine 1976, and Sebens 1982 on size-related mortality). The result was that adults utilized the majority of the resource, and, although seedlings grew proportionately faster than adults while water was available, they failed to become established because of their small size.

I offer no plausible alternative hypothesis to explain the large differences in growth and survival between seedling populations on and off the denuded site. Browsing damage was apparent on a few *A. dumosa* seedlings and on many *O. hymenoides*, but it was almost totally restricted to the denuded sections (Hunter 1987). The possibility of competition between seedlings did occur, but only on the denuded area, where seedling cover averaged $26 \pm 3\%$ (s.e.) in October 1984. In the vegetated areas, seedling cover was then only $0.7 \pm 0.1\%$, while adult cover was 17.9% (Fig. 1D). To suggest that fertility or soil compaction might cause such major differences would be specious. Fertilizers have had little effect in the Mojave Desert without added water (Romney et al. 1978, Lajtha and Schlesinger 1986). There was no evidence of soil disturbance other than a slight compaction in the denuded area. Allelopathic interactions have been suggested for both *A. dumosa* (Muller 1953) and *L. tridentata* (Knipe and Herbel 1966), with some positive effects seen in the lab. But a study by Wallace and Romney (1972) showed positive association of *A. dumosa* with 17 species, *L. tridentata* with 12 species, and negative association with only 2 and 1 species, respectively. That, together with the improved growth of annuals under *A. dumosa* canopies (Muller 1953), implies that allelopathy is not significant in the field.

An analogy to my hypothesis is several people drinking a single soda, each with his own straw. The soda disappears at a rate proportional to the number of drinkers and their drinking rates, but independent of the distances between them. Similarly, my hypothesis suggests the evidence from spatial analysis for competition among desert shrubs is incomplete. Of what importance is distance

between neighbors if root systems overlap, if soil water flows at significant rates, if a neighbor is orders of magnitude smaller, or has a different phenological pattern? I would argue that distance to the nearest neighbor is of minor importance. Of more relevance would be the sum of biomasses of neighboring plants, as in studies by Fowler (1984) and McAuliffe (1984), or modelled by Weiner and Conte (1981). But even that addition would ignore competitive aspects that are temporally determined or that are related to vertical rather than horizontal spacing, and would therefore be incomplete.

There is some circumstantial evidence for my hypothesis. The improved survival of seedlings under adult canopies (Friedman and Orshan 1975), the high percentage survival of individuals in clusters of seedlings (this paper, Ebert and McMasters 1981), the finding of only contagious distributions in the Qatari Desert (Ismail and Babikir 1986), and the weak correlation between distance to neighbor or neighbor's size and mortality (Yeaton and Cody 1976, Howe and Wright 1986) all suggest distance between neighbors is of only slight competitive importance in undisturbed desert.

I do not mean to suggest that competition is totally unrelated to horizontal spacing. There have been limited successes at inferring competitive interactions using analyses of spacing (Fowler 1986). The findings that larger (older?) shrubs are regularly spaced, while small ones are random (Phillips and MacMahon 1981, Cody 1986), suggest small effects operating over long periods of time. They could be effects of spatial patterns of moisture use by shrubs and of differences between species in phenologies and root distribution patterns. I suggest these are all small variations on a nearly uniform background of intense competition for water that is largely independent of plant spacing.

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