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Association With Mature Plants Protects Seedlings From Predation in an Arid Grassland Shrub, *Gutierrezia microcephala*

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Summary. Survivorship of *Gutierrezia microcephala* (Compositae) seedlings was studied in an undisturbed arid grassland and in experimental plots where various components of the natural vegetation were removed following seed germination. The major causes of seedling mortality were herbivore damage from the specialist grasshopper, *Hesperotettix viridis*, and drought stress associated with competition from established plants. The relative intensity of these mortality factors varied strongly with seedling size. Large seedlings had higher overall survivorship but were most likely to be killed by defoliation; most small seedlings died of drought stress.

In plots where all perennial grasses were removed (leaving established *G. microcephala* plants), seedling survivorship was 5 times greater than in undisturbed vegetation. Surviorship in plots where both grasses and mature *G. microcephala* were removed was slightly poorer than in undisturbed vegetation due to a large increase in mortality from defoliation. From May–August, when the herbivore *H. viridis* was abundant, seedling survivorship was better in the immediate vicinity of mature conspecific plants than in plots lacking mature *G. microcephala*, both in the presence and absence of perennial grasses. These results provide a counter example to theories predicting that the impact of specialist herbivores on seedling recruitment is greatest in the vicinity of parent plants.

Introduction

Localized attack on seeds and juvenile plants by specialist herbivores that center their foraging activity at mature trees has been proposed by Janzen (1970) and Connell (1971) as a mechanism that could promote low density and regular spacing in tropical tree populations. Attempts to test this mechanism as a cause of spatial patterns in tropical forests have yielded equivocal results (Connell 1979; Hubbell 1979); and Hubbell (1980) has criticized the importance of this process in relation to tropical forest structure. However, the question of how herbivores affect the spatial pattern of reproduction in plant populations remains an important issue, and has been poorly studied outside of tropical forest communities.

This study examines the impact of herbivory by a specialist grasshopper on seedling recruitment of a composite shrub, *Gutierrezia microcephala. G. microcephala* is a common, widely distributed plant in arid grasslands of southwestern North America. It is a small shrub (maximum height or canopy diameter less than 1 m) and is generally considered to be a successional species among the perennial, vegetatively reproducing grasses that form the potential dominant vegetation at mid elevations in this region (Shantz 1917; Whitfield and Anderson 1938). In contrast to many perennial grasses, *G. microcephala* reproduces solely by seed, and thus seedling ecology is of key importance in its population dynamics. Several authors have noted a relationship between establishment of *Gutierrezia* populations and local vegetation disturbances such as grazing, erosion, and trampling (Shantz 1917; Solbrig 1960). *G. microcephala* is poisonous to cattle and it forms extensive stands in many areas subject to heavy grazing (Clements 1920). However, little is known about conditions affecting reproduction of *G. microcephala* within communities not subject to chronic human disturbances.

I studied a population of *G. microcephala* in a grassland that had been protected from cattle grazing for about 30 years. In this region, mature *G. microcephala* plants commonly harbor an important native herbivore, *Hesperotettix viridis* (Orthoptera:Acrididae). *H. viridis* is only rarely observed feeding on seedlings; grasshoppers spend the majority of their time feeding and roosting in the canopies of large established plants, and do not appear to have any specific preference for seedlings. Yet grasshoppers may have a profound impact on reproduction in *G. microcephala* since even minor amounts of feeding can be fatal to a seedling.

It is difficult to predict the type of site most favorable for seedling survival in the presence of herbivores. Bare areas might be more favorable for seedlings than dense, undisturbed vegetation due to competition for moisture. However, seedlings may be more easily discovered by herbivores in relatively open areas than when growing interspersed among other plants. Alternatively, shade could be important in reducing drought stress on vulnerable young plants (Steenbergh and Lowe 1969), yet the shade of conspecifics might also yield a lethal rain of herbivores (Janzen 1971). In order to understand how herbivory and other causes of seedling mortality vary with vegetation background, I studied seedling survivorship in small plots where the composition of established vegetation was experimentally altered. The relationship between seedling size and the intensity of different mortality factors was also examined for seedlings in undisturbed vegetation.

Methods

The study was conducted from May–Aug. 1979 (with a final census of plant survivorship in May 1980) in the Bernalillo watershed of the Cibola National Forest, Sandoval Co., New Mexico. The study area was an arid grassland at 1,700 m elevation that had been protected from commercial grazing and other

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human disturbances for about 30 years. Perennial vegetation on the area was strongly dominated by *Gutierrezia microcephala* and the native grasses *Hilaria jamesii, Sporobolus cryptandrus, Bouteloua eriopoda,* and *Muhlenbergia torreyi.* Scattered individuals of juniper (*Juniperus monosperma*) and cholla cactus (*Opuntia imbricata*) were the only plants of an arborescent growth form on the site. The *Gutierrezia* population on this site has been referred to as *G. sarothrae* in a previous publication (Parker and Root 1981); however, reexamination of specimens from this population has shown that achenes of disc flowers were invariably aborted, a distinguishing character of *G. microcephala* (Solbrig 1960).

Germination of *G. microcephala* occurs in the early spring from seed disseminated in the previous autumn. Occasional new seedlings appeared in early May as censuses were conducted, but the bulk of seedlings had germinated earlier. *G. microcephala* seedling density is highly variable between years and probably depends on the amount of winter and early spring precipitation, as in other desert plants (Beatley 1974). Rainfall measured at a nearby weather station from Jan.–May 1979 was more than 100% above the normal amount for this period (60 mm), which may explain why extensive *G. microcephala* germination occurred in this year. In 4 years of observations on this study area, seedlings were completely absent in 2 years and present at mean densities of approximately 3–4 per m^2 in the other two years.

On 15–16 May 1979, after the bulk of seed germination, a strip transect 2×30 m was laid out and the area was exhaustively searched for seedlings. Seedlings were individually marked with numbered stakes (placed 10 cm from the seedling) and their positions were mapped in the plot; for each seedling the following information was recorded: height (measured to the nearest cm), the distance to the nearest mature *G. microcephala* plant (canopy edge), and the distance to and species identity of the nearest perennial grass plant. Seedlings were recensused at 3 week intervals (6 June, 27 June, 18 July, and 8 Aug.) and their heights measured if still alive. Dead seedlings were classified as dying of either defoliation or drought stress. A seedling was considered to have died of defoliation if all of its leaves had been chewed off at the time of death. Lethal feeding damage by *H. viridis* is highly characteristic in that grasshoppers leave numerous tiny feeding scars on the stem of a seedling after devouring its leaves. Seedlings commonly produced new leaves during the summer if only partially damaged; however, I never observed new leaf production by totally defoliated seedlings. If an entire seedling was missing, it was also classified as a death due to defoliation; these amounted to 6.5% of all marked seedlings. Seedlings whose leaves were mostly intact at the time of death were assumed to have been killed by drought stress. Unlike herbivore damage, it is harder to attribute a specific cause of mortality to seedlings that merely turned brown and withered up. However, due to the hot, arid climate of this region (Houghton 1972), it is reasonable to interpret non-herbivore related deaths as due to drought stress, intensified by competition from established plants. Although many seedlings probably suffered from both water stress and herbivore damage, this classification attempts to evaluate the relative importance of these two mortality factors as a cause of each seedling death by using specific morphological criteria. Seedlings dying between 8 Aug. 1979 and May 1980 were not assigned to a mortality category because I was not able to observe them near the time of death. Consequently, all analyses of causes of mortality in this study refer only to the period between May–Aug. 1979, during which 94% of all seedling deaths occurred.

Feeding responses of grasshoppers to seedlings of different sizes were studied in June 1981 by enclosing 4th instar *H. viridis* nymphs over groups of seedlings using wire screen cages. Small areas (25 cm diameter) containing 5–8 *G. microcephala* seedlings were chosen; the height of each seedling was recorded and all non-seedling vegetation was removed by clipping. Ten nymphs were then added to a cylindrical cage (30 cm diameter by 40 cm high) placed over the seedlings. Six replicate cages were used and nymphs in each cage were repeatedly censused (at intervals of 0.75–2 h) in order to observe whether perching behavior of grasshoppers was related to seedling size. Grasshoppers feed intermittently while perched on a plant, so perching sites should be well correlated with feeding sites. At the end of 24 h each seedling was assigned to one of 4 damage categories: (6) 0–10% defoliation. (2) 10–50% defoliation. (3) 50–90% defoliation. (4) greater than 90% defoliation. A proper null hypothesis is that seedling choice by nymphs is proportional to seedling height, rather than the less strict null H_0 that feeding site selection is independent of seedling size (seedling height is highly correlated with shoot dry weight, $R^2 = 0.88$, $N = 41$). The null hypothesis that grasshopper perch site selection was linearly proportional to seedling height was tested as follows: the total number of perch observations of grasshoppers on seedlings in each cage was divided by the sum of seedling heights to obtain the expected number of perch observations per cm seedling size. The height of each seedling in a cage was multiplied by this index to obtain the expected number of perch observations per seedling; after grouping seedlings into 3 size classes the observed and expected number of perch observations were compared using a log-likelihood ratio test (Sokal and Rohlf 1969).

The influence of vegetation composition on seedling survivorship was studied by selectively removing different components of established vegetation in 3 treatments. In each treatment, all *G. microcephala* seedlings were first marked in a square 3×3 m area and then the composition of established vegetation was altered in a 5×5 m area centered on this plot, thus avoiding edge effects at the treatment boundaries. The treatments were as follows: (1) Grass removal. All perennial grasses in the plot were clipped at ground level and removed from the plot, leaving all mature *G. microcephala* and other plant species (which were always a minor component). (2) *Gutierrezia* removal. All mature *G. microcephala* plants were clipped at ground level and removed, leaving the perennial grasses. (3) Total removal. Both mature *G. microcephala* and grasses were removed from the area, leaving only seedlings and a few scattered annuals. Some of the grasses occasionally resprouted from roots; these shoots were removed during censuses of seedlings throughout the summer. *G. microcephala* almost never resprouted from root crowns; the few sprouts observed were also removed. Great care was taken to remove plants without disturbing the roots or shoots of remaining plants; it took 4–8 hours to selectively weed a single 25 m^2 area. Three plots each of grass removal and *Gutierrezia* removal, and two plots of total removal, were prepared. All plots were within 30 m of the control seedling strip transect, and the plots were separated from each other by at least 3 m of undisturbed vegetation. The plots were initiated during May 17–21 and seedlings were censused throughout the summer on the same dates as control seedlings.

Results

1. Seedling Environments

Mature plants of both *G. microcephala* and perennial grasses play a major role in the environment of almost every *Gutierrezia*

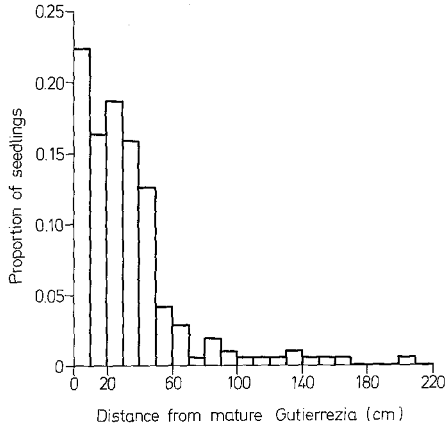

Fig. 1. Distance of seedlings from canopy of nearest mature *G. microcephala* ($n = 215$)

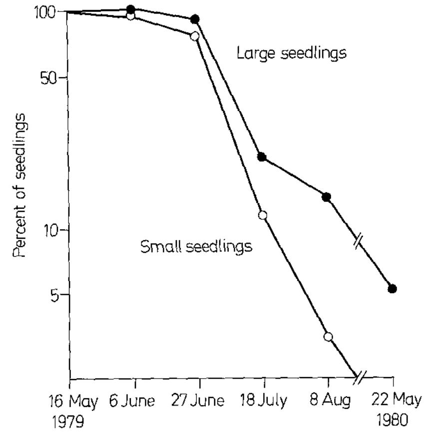

Fig. 2. Normalized survivorship curves of *G. microcephala* seedlings classified according to size on 16 May 1979. Large seedlings were those $\geqq 3$ cm (initial $n = 118$); small seedlings were those less than 3 cm ($n = 97$). A 2×2 contingency table was used to compare mortality rates within each census interval; test statistics for the 5 intervals were then pooled (Snedecor and Cochran 1967, p 255). Mortality rates were significantly greater for small seedlings ($p < 0.001$)

seedling. Only 5% of all seedlings on the control plot occurred at a distance greater than 20 cm from a perennial grass plant. Also, only one seedling out of 215 occurred at a distance greater than 2 m from the canopy of a mature conspecific, and 96.3% of the seedlings were within 1 m of an established *G. microcephala* plant (Fig. 1). The proximity of most seedlings to mature *G. microcephala* is a composite result of overlapping seed dispersal zones around individual plants, and thus reflects the spatial pattern of mature plants as well as seed dispersal distances. However, it is consistent with the apparently limited dispersal potential of *G. microcephala* seeds. The genus *Gutierrezia* is characterized by a highly reduced pappus, unlike many members of the tribe Astereae which have a well developed capillary pappus for wind dispersal (Solbrig 1960).

2. *Mortality of Seedlings in Relation to Intial Size*

Seedling height in undisturbed vegetation on 16 May ranged from 1–7 cm (mean = 2.8 cm). Variation in size may have been due either to differences in early growth conditions or to differences in time of germination among these plants. Seedlings were pooled into two size classes according to whether their size on 16 May was above or below the mean; survivorship curves for these two groups of seedlings are shown in Fig. 2. In both groups mortality was most severe during late June–early July; however, mortality rates were consistently higher for seedlings initially below the mean size and none of these seedlings survived their first year of life. The early July peak in seedling death rates for both size classes of seedlings corresponds to the end of the early summer dry season in this area, which might be a period of maximum water stress. Also, most *H. viridis* individuals reach adulthood during this time, probably resulting in a period of severe feeding intensity on seedlings. In Fig. 3 the fraction of seedlings dying of drought stress or defoliation (to 8 Aug.) is shown as a function of seedling size on 16 May. The relative proportion of mortality due to defoliation or drought stress is significantly different among the size classes (log-likelihood ratio test, $G = 27.302$, $p < 0.001$). Defoliation was a more significant cause of mortality for large seedlings and drought stress was more significant for small seedlings.

A greater intensity of herbivore damage to large seedlings was also observed in cage experiments where nymphs of *H. viridis* were offered seedlings of a range of sizes (Table 1). Nymphs were observed perching on small seedlings significantly less often than expected if frequency of perching was directly proportional to seedling height ($G = 12.32$, $p < 0.005$). This method of recording nymphal behavior does not distinguish between reduced discovery rate vs. reduced tenure on small seedlings

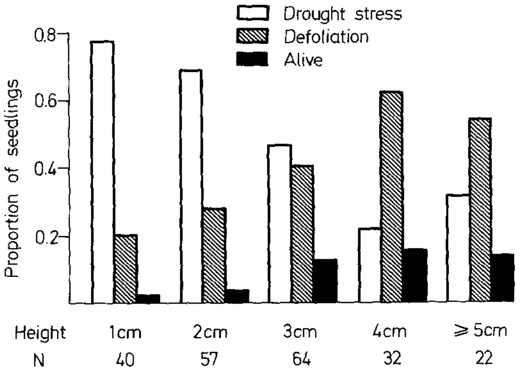

Fig. 3. Proportion of *G. microcephala* seedlings dying of drought stress or defoliation, or alive on 8 Aug. as a function of size on 16 May

Table 1. Perching and feeding behavior of *H. viridis* nymphs on *G. microcephala* seedlings of different sizes

	Seedling height (cm)		
	1.0–2.9	3.0–4.3	4.4–8.6
Number of seedlings	11	12	13
Number of observations of nymphs perched on seedlings	3	31	39
Number of perch observations expected if linearly proportional to seedling height	12.75	26.5	33.75
Proportion of seedlings more than 50% defoliated in 24 h	0.454	0.833	0.769

Table 2. Survivorship of *G. microcephala* seedlings exposed to different vegetation backgrounds for one year. Annual survivorship rate varied significantly among the treatments ($G = 30.388$, 3 *df*, $p < 0.001$); survivorship was highest in the grass removal treatment and did not vary significantly among the remaining 3 treatments ($G = 0.913$, 2 *df*, $p > 0.50$)

Treatment	Number of plots	Initial number of seedlings	Percent surviving 1 year	
			Mean	Range
Control	3[a]	215	2.79%	2.47–3.19%
Mature *Gutierrezia* removed	3	138	2.17%	0 –4.26%
Perennial grasses removed	3	143	14.69%	12.50–18.60%
Total removal	2	149	1.34	0 –1.89%

[a] Control plot divided into 3 areas (2 × 10 m) in order to calculate range of % survivorship

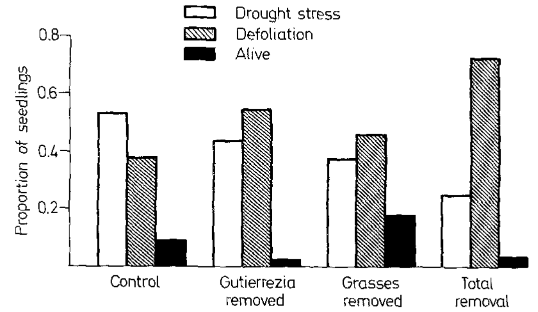

Fig. 4. The influence of vegetation background on the proportion of *G. microcephala* seedlings dying of drought stress or defoliation, or alive on 8 Aug. The number of seedlings in each treatment is given in Table 2

as underlying mechanisms. However, observations on incidence of nymphal perching behavior correspond well to the level of defoliation of these seedlings after 24 h. Over half of the small seedlings (less than 3.0 cm) escaped severe defoliation, whereas 80% of seedlings greater than 3.0 cm in height were severely damaged ($G = 4.138$, $p < 0.05$). Thus, under controlled conditions where seedlings of a range of sizes were equally available to foraging grasshoppers, large seedlings suffered disproportionate damage despite the longer period of feeding necessary to defoliate them.

3. The Influence of Vegetation Background on Seedling Survivorship

Mortality rates over the first year of life in different vegetation backgrounds are shown in Table 2. Seedling survivorship was highest in plots where mature *G. microcephala* plants were present and perennial grasses had been removed; there was a 5-fold increase in survivorship in these plots relative to seedlings in undisturbed vegetation. Survivorship in the other two vegetation manipulation treatments was not significantly different from controls.

During the period from May–Aug. when the herbivore *H. viridis* was abundant, the removal of mature *G. microcephala* resulted in a significantly higher rate of mortality due to defoliation, both for treatments with perennial grasses present (control vs. *Gutierrezia* removal, $G = 8.941$, $p < 0.005$) and for treatments with grasses removed (grass removal vs. total removal, $G = 21.205$, $p < 0.001$; see Fig. 4). Defoliation was particularly severe in the total removal plots, accounting for 74% of all seedling deaths.

Discussion

1. Size and Survivorship

Recent reviews of seedling biology have stressed the importance of timing of germination and seedling size as critical factors determining the fate of seedlings; larger seedlings generally have better survivorship and begin to reproduce sooner than smaller seedlings of the same cohort (Cook 1979, 1980). Most studies of seedlings in natural populations have also found that drought stress (compounded by competition) and herbivory are the major causes of mortality, as in this study. However, the interaction between seedling size and survivorship is not well understood in situations where both drought stress and herbivory are simultaneously important. The results of the present study suggest that the intensity of different mortality risks may vary strongly with seedling size. Even though large seedlings had an overall survivorship advantage, they were more likely to be killed by herbivore damage than small seedlings. The combined risks of drought stress and herbivory thus create a 'dilemma' for seedling *G. microcephala*. Large shoot size may be advantageous in generating photosynthetic products necessary for building an adequate root system, yet it may also result in a higher probability of severe damage to the seedling by leaf-feeding herbivores. Size-dependent herbivory on seedlings could result in selection for more conservative shoot growth rates and increased allocation to root growth if herbivores are a consistent source of seedling mortality.

2. Seedling Survivorship in Different Vegetation Backgrounds

The 5-fold increase in seedling survivorship in plots where perennial grasses alone were removed suggests that competitive interactions with grasses have a critical influence on seedling recruitment. However, this competitive release was realized only in the presence of mature *G. microcephala*: there was little difference in survivorship between plots with only grasses present and totally bare plots, due to a compensatory increase in herbivore impact when grasses were removed. That seedling survivorship was best in sites of low grass density among established *G. microcephala* plants does not imply a lack of competition with mature *G. microcephala* (see below); these areas merely provided the greatest number of 'safe sites' in terms of both competitive interactions and relative protection from herbivory.

Seedlings growing in bare areas several meters from mature *G. microcephala* suffered a greater intensity of herbivore damage than seedlings within stands of conspecifics; this unusual result can be explained in terms of herbivore movement behavior. *H. viridis* adults have functional wings, yet spontaneous flights are rare, and the primary mode of locomotion for both nymphs and adults is hopping between bushes. Both nymphs and adults are also sometimes seen walking on the ground in early morning when ground temperatures are not too high. The mean hop length for adults is on the order of 1 m, and within patches of host plants, most moves are hops directly between the canopies of neighboring plants, with only limited time spent on the ground. However, in an area lacking mature *G. microcephala*, as in the total vegetation removal plots, successive moves on the ground are likely to bring a grasshopper in repeated contact with small seedlings. This is supported by the following observations. When 20 marked adult *H. viridis* were released on the ground in the center of one of the grass removal plots, all but one jumped directly into the canopy of a nearby *G. microcephala* plant within one minute of release. However, grasshoppers released in one of the total removal plots walked slowly on the ground, repeatedly changing directions and pausing to climb small fragments of dead vegetation. More than half of the marked animals released in the plot containing mature *G. microcephala* were still present after 10 h, whereas no marked animals could be found in the total vegetation removal plot. Local vegetation structure thus influences both the mode and speed of travel through an area. The absence of mature plants seems to increase the relative amount of time spent on the ground even though it also increases the rate at which grasshoppers abandon an area. As a result, seedlings may be encountered by herbivores at a higher rate in bare patches several meters from established plants than when growing within a stand of conspecifics, even though more herbivores are present in the latter situation.

The spatial scale of the experiment is important to these results. At very long distances from sources of herbivores, seedling survivorship would probably be higher than in small open areas immediately adjacent to intact vegetation, as Whelan and Main (1979) found concerning grasshopper invasion of burn areas in Australia. Also, on a very local scale, competitive interactions with adult plants might act to reduce seedling survivorship. Due to extremely high mortality among seedlings, the available data are inadequate for examining this process, but the following comparison is suggestive: for seedlings on the control plot, less than 1% (1/110) of those within 25 cm of a mature *G. microcephala* plant survived for 1 year, while 5.3% (4/76) of those between 26–50 cm survived.

Variation in herbivore impact between years is also important in understanding spatial patterns of reproduction in *G. microcephala*. If heavy seed germination occurred in a year of low herbivore abundance, local competitive interactions with established plants (both *G. microcephala* and perennial grasses) would probably control seedling survivorship, favoring establishment in bare areas (bare sites had the lowest overall seedling survivorship in the year of this study when herbivores were abundant). *H. viridis* population densities sufficient to create a severe impact on seedlings occurred in 3 out of 4 years of observations in this area. Since seedling densities were likewise variable between years, the long term importance of herbivores in governing *G. microcephala* seedling recruitment depends on whether seed germination and high herbivore population densities tend to occur in the same years. The nature of covariance between seedling and herbivore densities can only be understood through long term study; this is an important area for future research.

In conclusion, seedling recruitment in *G. microcephala* seems to be determined by a complex interaction between plant competition, drought stress, and herbivore impact. In years when herbivores are abundant, recruitment does not vary in a simple manner with distance from conspecifics as predicted by the hypothesis of Janzen (1970) and Connell (1971). The limited dispersal capacity of seeds coupled with the high density adult plant population ensures that virtually every seedling will grow within a few meters of a source of herbivores (Fig. 1). Yet the searching behavior of the herbivore *H. viridis* results in a reversal of the predicted probability of discovery within this span of distances; seedlings growing out in the open away from mature *G. microcephala* suffer a greater intensity of attack by herbivores than those growing directly among mature plants. Herbivores may thus act to restrict seedling recruitment to areas within patches of mature *G. microcephala* in this system.

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