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Positive and negative interactions between environmental conditions affecting *Cercocarpus ledifolius* seedling survival

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Abstract We evaluated the balance between positive and negative effects of environmental conditions on first-year seedling survival of the tree *Cercocarpus ledifolius* during two summers, 1996 and 1997. The experimental design was fully crossed with two levels of water, with and without supplementation, two levels of herbivory, with and without protection, and three major microhabitats, open interspaces, under the canopy of *Artemisia tridentata* shrubs, and under the canopy of mature *C. ledifolius* trees. Effects of drought and herbivory on seedling survival depended on the year. Water supplementation and herbivory protection during the dry summer of 1996 (27.7 mm) generally increased seedling survival. Additionally, survival tended to be greatest beneath *C. ledifolius* canopies. More important ecologically were the significant interactions. In 1996, water supplementation increased survival more with than without herbivory protection. The three-way interaction, treatment-microhabitat combination, was most important; by far the greatest survival was in the water supplementation and herbivory protection in the tree microhabitat. During the wet summer of 1997 (158.5 mm), neither water supplementation, herbivory protection, nor microhabitat were significant as main effects. The water-supplemented and herbivory-protected treatment again combined to yield highest survival, but this time in open interspaces rather than beneath trees. Our study shows how the importance of individual limiting factors and the relative favorableness of particular microhabitats appear to change across years depending on environmental conditions.

Keywords *Cercocarpus ledifolius* · Drought · Environmental variability · Facilitation · Herbivory

Introduction

The seedling stage is most affected by adverse conditions. Survival is strongly influenced by biotic and abiotic conditions (Sacchi and Price 1992). In particular, water is one of the major factors limiting seedling establishment in many ecosystems (Brown 1995). Internal water deficits during the seedling phase can prevent the plant from reaching the size necessary to survive future adverse conditions such as herbivory or continued drought (Kozlowski 1968; Brown 1995).

Another widespread hazard during establishment is herbivory, which is particularly detrimental when other constraints such as drought or limited nutrients reduce the ability to compensate for losses (Louda et al. 1990; Dunne and Parker 1999). Consequently, herbivory can directly and indirectly influence survival (Bullock 1991; De Steven 1991; Huntly 1991; Whitham et al. 1991; Karban and Strauss 1993; Mutikainen and Walls 1995), as well as alter the microhabitat pattern of new plant establishment (Jaksič and Fuentes 1980; Louda and Rodman 1996).

A third factor to consider is the effect of existing plants. Although potentially competitors of establishing seedlings, woody plants can facilitate recruitment beneath their crowns by ameliorating abiotic and biotic stresses (Jordan and Nobel 1981; Fuentes et al. 1984; Franco and Nobel 1988; Hunter and Aarssen 1988; Valiente-Banuet and Ezcurra 1991; Bertness and Callaway 1994; Berkowitz et al. 1995; Callaway 1995; Callaway and Walker 1997; Holmgren et al. 1997; Callaway and Pugnaire 1998; Weltzin and McPherson 1999; Rousset and Lepart 2000). Facilitation may be due to a variety of influences, such as reduced evapotranspiration and temperature (Callaway 1995), improved soil conditions and moisture retention (Joffre and Rambal 1988), increased nutrient availability (Jackson and

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Caldwell 1993; Stark 1994), and physical protection from herbivory, especially from larger mammals (Jaksič and Fuentes 1980; Bullock 1991). Under certain conditions, the benefits of facilitation can outweigh the negative effects of competition. It is the balance between negative and positive influences that determines the suitability of a site for establishment (Schupp 1995; Callaway and Walker 1997), and this balance may shift both spatially and temporally. In particular, it has been suggested that facilitation is more likely to outweigh interference in more stressful sites and/or years (Bertness and Callaway 1994; Callaway 1995; Greenlee and Callaway 1996; Callaway and Walker 1997; Kitzeberger et al. 2000).

The main objective of this work was to evaluate the effects of water limitation, herbivory, and facilitation by existing woody plants on early seedling recruitment of curl-leaf mountain mahogany (*Cercocarpus ledifolius* Nutt., Rosaceae). This is a patchily distributed species growing on hot, dry slopes throughout the Intermountain West of the United States that is exhibiting very limited population recruitment throughout its range. The following questions are of particular interest: (1) Is water a major limiting factor in seedling survival? (2) Does herbivory significantly reduce seedling survival? (3) With respect to seedling survival, do positive effects associated with growing under existing woody plants outweigh negative effects? (4) Does the balance between positive and negative effects on survival shift across years with changes in weather and stress? (5) Are there ecologically important interactions among the effects of water limitation, herbivory, and microhabitat on seedling survival?

Materials and methods

Study species

Cercocarpus ledifolius is an evergreen shrubby tree of western North America (Davis and Brotherson 1991). Most stands of *C. ledifolius* have a pronounced absence of recruitment of new individuals (Scheldt and Tisdale 1970). Competition for water and soil resources and intense herbivory are thought to limit seedling establishment (Scheldt and Tisdale 1970). Schultz et al. (1996) suggested that the spatial distribution of *C. ledifolius* recruitment was influenced primarily by the presence or thickness of plant litter, root growth characteristics, presence of nurse plants, and herbivory, and that the distribution changed through the transition from current-year seedlings to immature saplings. Data on seedling establishment, survival, and growth are very sparse, however.

Study site

The study site, referred to as Swan Flat, is located in Logan Canyon (41° 57' N, 111° 28' W) within the Cache National Forest in northeastern Utah, USA. The elevation varies between 2,350 and 2,500 m and the slope of the southwest facing stand we used for experiments is about 35%. The climate is typical for the region, with most precipitation falling as snow during the cold wet winters supplemented by occasional storms during the hot dry summers.

The site is dominated by *C. ledifolius*, although Douglas fir (*Pseudotsuga menziesii*) is present as isolated individuals. Mountain big sagebrush (*Artemisia tridentata vaseyana*) and snowberry

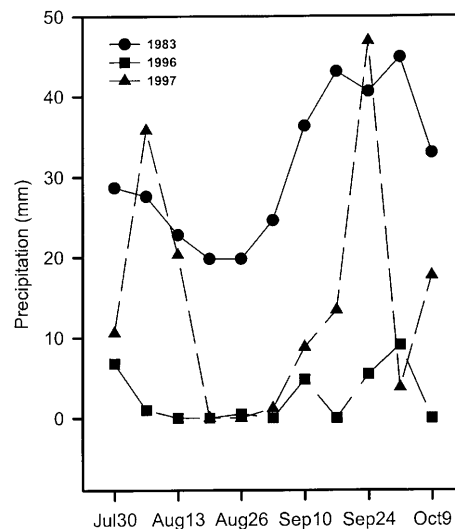


Fig. 1 Weekly precipitation (mm) during summer 1983 (estimated), 1996 and 1997

(*Symphoricarpos* spp.) are the most common shrubs. Except for current-year seedlings, which are briefly abundant in spring before massively dying off through the summer, very few *C. ledifolius* individuals with basal stem diameters <10 cm have been observed in the stand.

Field planting and data collection

The importance of water limitation, herbivory, and microhabitat for seedling survival were evaluated in a factorial experiment, with all treatments fully crossed.

Water treatments were (1) a control with natural water supply and (2) a water supplementation treatment. For this treatment, supplemental water was added weekly to equal the difference between estimated precipitation in the very wet 1983 El Niño year and actual precipitation recorded with a rain gauge in a clearing at the site. The goal was not to add a predetermined amount of water each week, but rather to add an amount of water calculated in the field that would, when combined with actual precipitation for the week, equal estimated 1983 precipitation for that week. This approach provided a fairly realistic mimic of both the quantity and temporal pattern of precipitation during an unusually wet summer. To obtain weekly estimates we first estimated monthly precipitation during 1983 from monthly precipitation maps (Jensen 1995) derived by interpolating data between climate stations. We then divided monthly precipitation among weeks using Logan, Utah (nearest available data, at the mouth of Logan Canyon, 1,600 m) data on the proportion of total monthly precipitation falling in a given week (Utah Climate Center, unpublished data). Weekly summer precipitation data for the two years of this study (actual) and for the reference year 1983 (estimated) are shown in Fig. 1. Total precipitation at the site during the study season was 27.7 mm in 1996, 158.5 mm in 1997, and 344.2 mm (estimated) in 1983.

Long-term climate data do not exist for the site. Therefore, in order to give a better climatic context to these two study years we selected four northern Utah weather stations to represent regional weather trends. We compared 1996 and 1997 mean June–September temperature and total June–September precipitation to long term averages (Table 1). Although this does not completely correspond to the study season, July–October, it is representative of summer conditions. Temperature did not appear to differ between 1996 and 1997, both of which were at or slightly above the long-term mean (Table 1). In contrast, precipitation was well below the long-term mean (43–53%) in 1996 and well above the long-term

Table 1 Regional weather summary based on four weather stations. Stations are: Logan-Utah State University, station no. 425186, records from 1893 to 2000, west of the study site; Trenton, station no. 428828, records from 1976 to 2000, southwest of the site; Laketown, station no. 424856, records from 1910 to 2000, southeast of the site; and Woodruff, station no. 429595, records from 1948 to 2000, southeast of the site. Data cover the 4-month period June through September. Temperatures are means, where

Station	Mean June-September temperature (°C)			Total June-September precipitation (mm)		
	Average	1996	1997	Average	1996	1997
Logan	19.8	20.5	20.1	99.1	47.5	172.2
Trenton	17.8	17.7	18.4	108.7	47.0	196.1
Laketown	15.8	16.3	15.9	87.4	50.8	177.8
Woodruff	14.2	14.6	14.7	93.7	48.3	241.0

mean (174–257%) in 1997 (Table 1). Thus 1996 and 1997 represented very dry and wet years, respectively.

Herbivory treatments also included two levels, (1) with and (2) without protection from aboveground insect and vertebrate herbivores combined. For insect protection, we sprayed a dilution of synthetic pyrethrin insecticide (InterCept-H & G, 2 ml/l water) on seedlings once per week; at the same time we sprayed control seedlings with the same amount of water. Water sprayed in this treatment was too small to affect the water supplementation treatment. For mammal protection, we covered plots with a 1-cm mesh hardware cloth cage (30 × 30 cm). The cage slightly (~10%) reduced light, and did not affect soil temperature (mean±SEM, 23.8±0.4°C and 23.5±0.4 outside and inside a cage in the open microhabitat at 1340 hours MST on 22 May 2001; $n=10$, $F_{1,18}=0.458$, $P=0.507$).

Three microhabitats were used: (1) “open,” in open interspaces between woody vegetation, a mosaic of bare soil and herbaceous vegetation; (2) “shrub,” beneath *A. tridentata* canopies; and (3) “tree,” beneath *C. ledifolius* canopies. These three microhabitats differed in important characteristics such as light, litter accumulation, and soil development (Table 2) that were similar for open and shrub soils, and considerably higher for tree soils. Both shading and litter increased from open interspaces to shrubs and especially to trees. In summary, while the shrub microhabitat differed only marginally in some respects from open interspaces, the tree microhabitat differed dramatically in characteristics that are expected to have positive effects on seedling recruitment (i.e., greater nutrient and organic C concentrations) as well as characteristics that may have positive effects, negative effects, or both (e.g., greatly increased shading and litter accumulation).

Seedlings were started in a greenhouse. We germinated seeds with cold moist stratification (1–4°C) on filter paper for 10–12 weeks (Kitchen and Meyer 1990), kept the germinated seeds at 15°C for a week and then transplanted them into Lännen Paperpots (2.8 cm diameter × 10 cm deep), one-third of which were filled with soil from each of the three microhabitats collected from the study site. At approximately 6 weeks we transplanted them into the field (early July), with seedlings grown in a given microhabitat's soil being planted into that microhabitat. At this time, transplanted seedlings were similar to natural seedlings in size (3–4 cm) and number of leaves (3–5).

For each of the 12 treatment combinations at each of 10 sites we planted 10 seedlings in a 30×30 cm quadrat for a total of 1,200 seedlings (10 seedlings × 3 microhabitats × 2 water treatments × 2 herbivory treatments × 10 replicate sites). Sites were separated by ~50 m along a transect perpendicular to the slope. For 1 week we watered all seedlings every other day and covered them with a light mesh cloth (Plant Guard) to reduce loss to transplant shock. Afterwards, we removed the cloth and only watered the plants under the water supplementation treatment. When we added water we also reapplied insecticide (2 ml of the mixture / 30×30 cm square) for the herbivory protection treatment, sprayed herbivory

“average” is the mean of the 4 monthly means calculated over the entire period of record and “1996” and “1997” are means of the 4 months in the given year. Precipitation values are totals, where “average” is the sum of the four monthly means calculated over the entire period of record and “1996” and “1997” are sums of the 4 months in the given year. Data are from Western Regional Climate Center (2001) (<http://www.wrcc.dri.edu>)

Table 2 Summary of the major environmental differences among microhabitats (Ibáñez et al. 1999; E.W. Schupp, unpublished data). Soil characteristics are from analyses of the surface soil samples from a representative pedon of each microhabitat type. Litter samples are from 30×30 cm samples, $n=10$. Available soil water capacity was calculated as the ratio between centimeter of water/centimeter of soil multiplied by the horizon depth and by 1–percent rock fragments. Percentage of full sun is the mean value of 10 photosynthetic active radiation measurements with respect to elevated readings from large clearings (measurements were made between 13:56 and 14:43 MST on 22 May 2001 with a LI-COR LI-250 light meter with a LI-190sA Quantum sensor)

Variable	Microhabitat		
	Open	Shrub	Tree
Surface soil characteristics			
Phosphorus (mg/g)	7.20	6.10	14.00
Nitrogen (%)	0.31	0.33	0.90
Organic carbon (%)	2.67	2.95	8.99
Litter dry mass (kg/m ²)	0.12	0.27	2.50
Available water capacity (cm)	4.47	11.08	12.63
Percentage of full sun (%)	99.1	30.8	5.8

control plants with water, and recorded survival. The experiment continued through summer and early fall until snowfall for 12 weeks (from 22 July to 9 October). The experiment was replicated in 1996 and 1997.

Statistical analysis

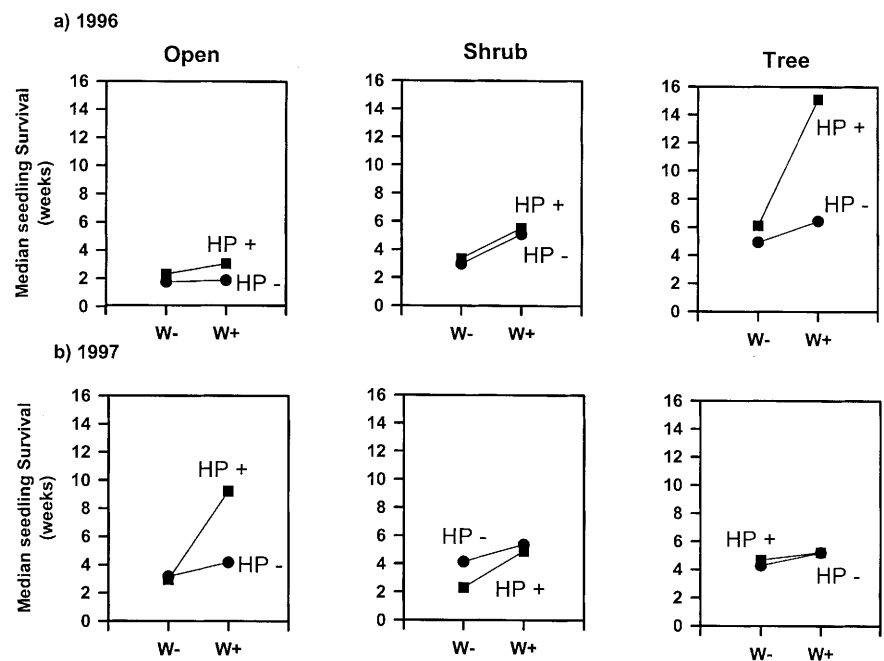
Statistical analysis was performed using a failure-time approach, which measures the time to failure (death) of each individual (Fox 1993). We used the LIFEREG procedure (SAS 1990), which produces estimates of parametric regression models with censored survival data using the method of maximum likelihood. A log logistic distribution was used because it gave the highest likelihood value. The significance of treatments and interactions for survival time were evaluated with a Log Likelihood model comparing median survival values predicted from the survival curves (phat, or predicted time to 50% mortality) for each treatment.

Results

Results of the survival analysis differed between the two years of study. In 1996, all main effects and all interac-

Table 3 Results from the survival analysis of seedling survival during the summers of 1996 and 1997. Log Likelihood for Log logistic in 1996=-1,038.56, and in 1997=-1,099.40

Variable	df	1996				1997			
		Estimate	SE	Chi-squared	P	Estimate	SE	Chi-squared	P
Intercept	1	2.79	0.19	226.67	0.0001	0.04	0.26	0.03	0.0001
Site	9			79.50	0.0001			66.23	0.0001
Microhabitat	2			74.84	0.0001			4.62	0.0994
Water	1			12.80	0.0003			0.72	0.3956
Herbivory	1			8.36	0.0038			0.30	0.5834
Site×Microhabitat	18			68.72	0.0001			56.14	0.0001
Site×Herbivory	9			55.00	0.0001			19.01	0.0906
Site×Water	9			34.29	0.0001			19.65	0.0202
Microhabitat×Water	2			12.72	0.0017			10.03	0.0066
Microhabitat×Herbivory	2			16.75	0.0002			7.20	0.0273
Water×Herbivory	1			12.25	0.0005			0.19	0.6659
Microhabitat×Water×Herbivory	2			8.69	0.0130			5.24	0.0730
Scale parameter	1	0.41	0.01			0.68	0.02		

Fig. 2 Predicted median seedling survival during the growing season (1996 and 1997) in the three microhabitats, *open*, *shrub*, and *tree*, with (W^+) and without (W^-) water supplementation, and with (HP^+) and without (HP^-) herbivory protection

tions were statistically significant (Table 3; Fig. 2a). The significant interactions make interpretations of main effects problematic, but not meaningless. There is a tendency for survival to increase (1) from open to shrub to tree microhabitats, (2) with water supplementation, and (3) with herbivory protection (Fig. 2a). As the significant two-way interactions demonstrate, however, these main effects were not consistent. For example, while watering tended to increase survival beneath trees and shrubs, it had virtually no effect in open microhabitats, thus the significant microhabitat \times water interaction. Similarly, the combination of water supplementation with herbivory protection tended to increase survival much more than either water supplementation or herbivory protection alone, yielding the significant water \times herbivory interaction. Ultimately most important, however, was the sig-

nificant 3-way interaction demonstrating that the strength of the water \times herbivory interaction varied with microhabitat; there was a weak to non-existent interaction in open and shrub microhabitats, and a very strong interaction in the tree microhabitat. The result was unusually high survival in the treatment combination of water supplementation with herbivory protection in the tree microhabitat.

Overall, 19% of the seedlings were alive at the end of the summer of 1996 (Fig. 3). Although the mortality rate was greatest during the first month, significant mortality continued through the summer in this very dry year.

During 1997, the site effect was highly significant and the main microhabitat effect was marginally significant, while all interactions except water \times herbivory were significant or nearly significant ($P < 0.10$; Table 3; Fig. 2b).

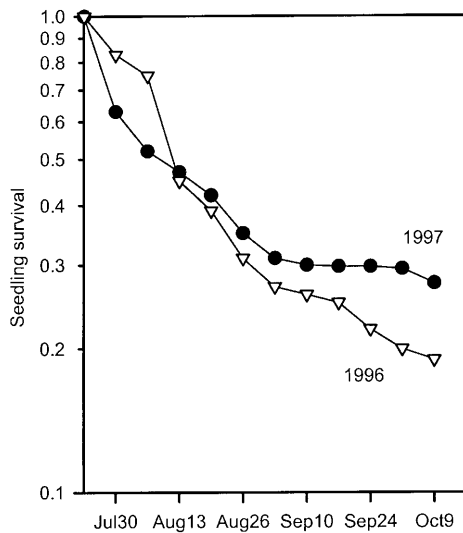


Fig. 3 Weekly seedling survival percentage during the summers of 1996 and 1997

As the statistical results suggest, interpretable patterns were less obvious than in 1996. As in 1996, however, a single treatment stood out; highest survival was again found with the combination of water supplementation and herbivory protection, but in the open rather than the tree microhabitat in this wetter year.

Overall, 27.5% of the seedlings survived the 1997 summer (Fig. 3). As in 1996, the mortality rate was greatest in the first month, but in contrast to 1996, mortality had virtually ended by mid-August.

A note of caution should be added with respect to between-year comparisons. Due to small seedling size and tough grayish leaves it was at first difficult to confidently determine if a seedling was dead. As a result, during roughly the first half of 1996 we used a more conservative approach than at other censuses, thus overestimating early 1996 survival. Consequently, neither early parts of the survival curves nor estimated median survival times (since they depended on the curves) should be compared between years. This conservative approach in early 1996 does not, however, affect either overall patterns of survival across treatment combinations within a year or overall proportions surviving until the end of the year; thus, these results can be qualitatively compared between years.

Causes of seedling mortality are not known. Although slight herbivore damage was evident, probably from insects and/or mollusks, there was little evidence of entire or nearly entire consumption: few seedlings “disappeared.” Instead, they desiccated and died in place. Such an observation alone does not isolate the cause of death, however, since seedling death is probably frequently due to interacting rather than individual effects. For example, even mild herbivory may increase the likelihood of dying from water stress.

To summarize, in both years, survival in most treatment combinations was fairly similar with the exception

of a single treatment standing out with unusually high survival (Fig. 2). In both years, the combination of water supplementation and herbivory protection was required to yield this high level of survival. Years differed, however, in which microhabitat this occurred: tree microhabitat in 1996 and open microhabitat in 1997.

Discussion

The effects of water availability, herbivory, existing woody vegetation, and their interactions varied between years. Annual patterns of precipitation may affect both quantitative and spatial dynamics of the population by influencing patterns of germination and seedling survival (Kozłowski 1968), and by altering the balance between facilitation and interference (Greenlee and Callaway 1996). Berkowitz et al. (1995) observed variation between years in the degree of facilitation of tree seedlings by shrubs and herbs, and suggested that net effects of intact communities on the survival of tree seedlings cannot be conclusively demonstrated with one year’s results. Our study supports this idea.

Is water a major limiting factor for seedling survival?

In our study seedling recruitment was limited by water availability. Overall seedling survival was greater in the wetter year (1997) and water supplementation enhanced survival more in the drier year (1996). Although in both years we supplemented water to equal estimated 1983 weekly precipitation (total summer precipitation 321 mm), this treatment effect was not likely equivalent in the two years. Supplemental watering in 1997 with above-average precipitation likely came close to simulating an exceptionally wet year, while supplementation in the very dry 1996 summer may have in reality only simulated a moderately wet year. This is important for interpretations below.

Does herbivory significantly reduce seedling survival?

Herbivory has been suggested as another major cause of seedling mortality for *C. ledifolius* (Scheldt and Tisdale 1970). Kraft (1960) reported 14 species of insects on *C. ledifolius* trees in Oregon, but Dealy (1975) rarely observed seedling herbivory by insects in the cotyledon stage and not at all in older stages. Consumption of green leaves by rodents, however, has been reported by Hammer and Maser (1973), and Scheldt and Tisdale (1970). In our study, herbivory protection increased survival during the dry summer of 1996, when herbaceous biomass in the stand was relatively low due to the scarcity of water. The increased survival due to herbivory protection was especially large beneath *C. ledifolius*. This may be due to the tree acting as a source of *C. ledifolius* herbivores (Edwards and Gillman 1984). Alternatively, it

may be due to the more favorable environmental conditions under trees allowing seedlings to benefit from release from herbivory, while seedlings in other microhabitats were so stressed that few survived, protected or not. There was no evidence shrub canopies physically sheltered or hid *C. ledifolius* seedlings from herbivores, as has been suggested in other studies (Bullock 1991; Callaway 1995; García et al. 2000). In open interspaces, survival was so low overall, probably because of drought stress, that possible differences could not be observed. In 1997, when high precipitation produced greater vegetation growth in the stand, herbivory protection was not significant overall, although it appeared beneficial in open interspaces where seedlings were perhaps more exposed to herbivores.

Although a case could be made that water limitation had a slightly greater effect than herbivory, the overwhelming evidence is that neither stress is operating in isolation. The interaction between water supplementation and herbivory protection was apparently not due to water supplementation increasing herbivory; water supplementation did not increase surrounding vegetation or *C. ledifolius* seedling size, which could have attracted herbivores. Instead, it appears survival was determined by strong interactions among stresses. Water supplementation greatly increased seedling survival only when coupled with herbivory protection in the appropriate microhabitat, and herbivory protection greatly increased seedling survival only when coupled with water supplementation in the appropriate microhabitat. These interactions are the key result of this study.

Do positive effects associated with growing under woody species outweigh negative effects on seedling survival? Do these effects shift across years?

During very dry summers such as 1996, the microenvironments created by shrub, and especially by tree canopies, appear to favor seedling survival even though survival was very low for all treatments without water supplementation. The tree canopy and its associated litter layer apparently provided a moister, less stressful environment than the rest of the community during this dry summer, although conditions were clearly still very stressful. If as we suspect water supplementation in the dry year only simulated a moderately wet year, our results suggest that trees may also be beneficial in such moderate years, especially if combined with low levels of herbivory. Treatments without water supplementation in the wetter 1997 year also support this contention.

Although not as good as the tree microhabitat, shrub appeared to be a more favorable environment than open interspaces, in moderate wet and dry years. The shrub canopy likely reduces evapotranspiration and the deeper soil depth under shrubs than in open interspaces (Ibáñez et al. 1999) provides for greater water storage. Additionally, *Artemisia* may increase the availability of water near the surface via "hydraulic lift" and nocturnal release

(Caldwell et al. 1991), providing seedlings growing under shrubs with water otherwise unreachable by seedling roots. Jaindl et al. (1993) found *C. ledifolius* to be a strong competitor for available water. These results are not unexpected. There is extensive evidence from arid regions that shrubs and trees can act as nurse plants and facilitate establishment beneath their crowns (Jordan and Nobel 1981; Fuentes et al. 1984; Franco and Nobel 1988; Valiente-Banuet and Ezcurra 1991; Callaway 1992).

In very wet years, however, represented by water supplementation in 1997, the most favorable microsite for seedling survival was open interspaces as long as herbivory was excluded. De Jong and Klinkhamer (1988) similarly found a greater benefit of water supplementation in open interspaces than beneath vegetation and suggested that in water-limited environments plants are more likely to colonize exposed microhabitats during wet summers. Our results indicate that the balance between facilitation and interference can shift from a net positive effect of *C. ledifolius* crowns to a net negative effect when abiotic and biotic stresses are greatly reduced. In very wet, relatively cool years with little herbivory, benefits of growing in the open appear to outweigh benefits of growing beneath trees. Open interspaces probably provide suitable light conditions and reduced competition that would enhance survival compared to the other two microhabitats. Additionally, pathogens in the litter beneath trees may be a greater problem in wetter years. During wet years, seedlings of this deep-rooted species (Dealy 1975) should be able to have access to soil moisture all summer long, even in the open; long-term survival is less certain, however.

Longer-term effects of microhabitats

In seedling and sampling stages, beyond those studied here, the shrub microhabitat may constitute the most favorable microhabitat for *C. ledifolius*. Schultz et al. (1996) observed how established seedlings, juveniles, and immature individuals were preferentially found in an adjacent *A. tridentata* community rather than beneath *C. ledifolius* canopies, where competition with larger trees probably outweighs facilitation. Under the shrubs, in addition to greater soil depths (Ibáñez et al. 1999) and water supplies (Caldwell et al. 1991) than in the open microhabitat, the relative unpalatableness of the nurse plant might prevent browsing (McAuliffe 1986), which may be more important for these older individuals than for current-year seedlings. In the long-term, however, it seems that mature individuals may benefit most from growing within or adjacent to tree patches. On these slopes, where a water table is unreachable, perhaps only these deep soils with high organic carbon content can capture and hold enough water to maintain larger individuals through dry summers (Ibáñez et al. 1999). Additionally, the greater nutrient supply in tree soils relative to open and shrub soils likely also benefit adults (Table 2).

Are there ecologically important interactions among the effects of water limitation, herbivory, and microhabitat on seedling survival?

As stressed throughout this discussion, interactions are the key to understanding *C. ledifoliosus* survival, and are the key result of this study. Although significant main effects were interpretable in a general sense, the true effect of each could only be understood in the context of interactions. Similarly, the outcome of interactions depended on the year.

Conclusions

Variations in habitat favorableness from year to year suggest that the role of nurse plants during recruitment of curl-leaf mountain mahogany is complex and influenced by the environment. Trees as nurse plants appear to exert a crucial positive influence on current-year seedlings during dry to moderate summers. In very wet summers, however, open interspaces may provide a more suitable microhabitat if the seedlings can escape herbivory, while trees and shrubs may be more suitable with intense herbivory. Consequently, the balance appears to be influenced by an interaction between weather, herbivory and the environmental characteristics of the microhabitat. Additionally, microhabitat favorableness may change as recruits pass through successive life stages. These longer-term scenarios of patch dynamics deserve more detailed attention.

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