



Competition and resource availability in an annual plant community dominated by an invasive species, *Carrichtera annua* (L. Aschers.), in South Australia

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Abstract

The last decade has seen spirited debates about how resource availability affect the intensity of competition. This paper examines the effect that a dominant introduced species, *Carrichtera annua*, has upon the winter annual community in the arid chenopod shrublands of South Australia. Manipulative field experiments were conducted to assess plant community response to changing below-ground resource levels and to the manipulation of the density of *C. annua*. Changes in the density of *C. annua* had little effect on the abundance of all other species in the guild. Nutrient addition produced an increase in the biomass of the most abundant native species, *Crassula colorata*. An analysis of the root distribution of the main species suggested that the areas of soil resource capture of *C. annua* and *C. colorata* are largely segregated. Our results suggest that intraspecific competition may be stronger than interspecific competition, controlling the species responses to increased resource availability. The results are consistent with a two-phase resource dynamics systems, with pulses of high resource availability triggering growth, followed by pulses of stress. Smaller plants were nutrient limited under natural field conditions, suggesting that stress experienced during long interpulse phases may override competitive effects after short pulse phases. The observed differences in root system structure will determine when plants of a different species are experiencing a pulse or an interpulse phase. We suggest that the limitations to plant recruitment and growth are the product of a complex interplay between the length and intensity of the pulse of resource availability, the duration and severity of the interpulse periods, and biological characters of the species.

Introduction

Recent years have seen a heated debate regarding the strength of competition in stressful environments. Some authors have argued that competition is minimal or non-existent under conditions of high environmental stress (Grime (1973, 1979); Mahmoud and Grime 1976; Grime and Hodgson 1987), while others suggested that the strength of competition is of equal magnitude in habitats of both high and low productivity (Newman 1973; Tilman 1980; Wilson and Tilman 1993). A more detailed understanding of the mechanisms that control competition intensity may clarify this argument.

Grime (1973, 1979) argued that in unproductive environments, competitive ability is far less important than differences in the ability of plants to conserve captured resources and to resist periods of stress. Plants that perform better in unproductive environments are stress tolerant rather than competitively superior (Grime and Hodgson 1987). However, evidence supporting this claim is scant.

Contrasting hypotheses concerning the importance of competition in habitats of low-productivity have been offered in place of Grime's early assumptions. Newman (1973) proposed that competition is equally intense along productivity gradients, but that it shifts from above to below ground competition in areas of low productivity. Tilman (1980) proposed a model

based on specific differences in the equilibrium point (R^*), a resource level at which vegetative growth and reproduction balances with the biomass losses suffered by the plant under given environmental conditions. When several species are limited by a single resource, the species with the lowest R^* for that resource is predicted to displace all other species (Tilman 1982). Thus, species with minimum resource requirements are superior competitors because they can lower the resource availability to levels at which other species cannot have positive net growth (Tilman 1990). A consequence of this model is that plants should compete strongly in habitats with low resource levels, and that plant community structure is largely determined by the extent of this competition (Chesson and Huntly 1997).

Fluctuating resource levels, produced by the temporal variability of abiotic conditions, have been assumed to be more important to competitive interactions between species than the effects of constant abiotic stress (Welden and Slausen 1986). It has been recently suggested that in arid zones plants experience two distinct temporal environments (Goldberg and Novoplansky 1997). The first, a pulse phase often of short duration, occurs when water and nutrient resources are readily available for uptake and utilisation into growth and reproduction. These pulses are separated by longer interpulse phases during which resource availability is greatly reduced and when most stress induced mortality occurs (Goldberg and Novoplansky 1997; Noy-Meir 1973). The severity and length of the interpulse phase determine the intensity of resource competition. As interpulse phases become of sufficient duration to cause substantial mortality, the intensity of competition during the pulse phases will be reduced (Goldberg and Novoplansky 1997). This hypothesis maintains the importance of competition in unproductive environments, but predicts that the effects of competition during pulses can be overridden by conditions experienced in the interpulse phase. On the other hand, after long pulses of high resource availability growth may lead to strong overlap of resource acquisition zones. As a consequence competition, and hence density dependent effects will be intense during the initial stages of the ensuing interpulse period. The two-phase resource model includes more complexity than the simpler preceding models of Grime (1973, 1979) and Tilman (1982, 1990), and can reconcile both arguments.

Individuals of a dominant species produce expanding zones of resource depletion, further limiting resource availability to other individuals with overlapping resource use zones (Grime 1979). Germination of some species may be inhibited by resource depletion caused by early emerging individuals which may capture large shares of available resources (Harper 1977), or by the release of CO_2 through root respiration of already established plants (Inouye 1980). Smaller seeded plants are more likely to experience reduced seedling recruitment resulting from density-dependent interactions with larger, more abundant species (Goldberg and Miller 1990).

Local conditions greatly influence plant community structure. Soil patches with high organic matter content in arid ecosystems are associated with topographic depressions (Ludwig and Tongway (1995, 1997, 1997)) and perennial shrubs and trees (Romney et al. 1978; Facelli and Brock (2000, 2000)). The strong localized effect of perennial woody plants on soil properties has been documented in a variety of systems (Belsky 1992; Callaway et al. (1991, 1996); Gutierrez et al. 1993; Maranon and Bartolome 1993; Parker and Muller 1982; Facelli and Brock 2000). Decomposition of plant litter in these areas aids soil moisture retention and increases microbial activity resulting in high rates of organic turnover which effectively produce "fertility islands" (Garner and Steinberger 1989). Higher concentrations of soil nitrogen are retained in these sites than in the bare soil adjoining the islands (Garner and Steinberger 1989). Surface applications of nitrogen on bare soil, outside these sites, can simulate island soil fertility to some extent, provided natural precipitation is adequate to make soluble forms of nitrogen available to the resident plants (Romney et al. 1978).

By manipulating both resource availability and the density of a dominant ephemeral species in an arid environment, the relative intensity of competition in the local ephemeral plant community can be assessed. In this paper we aim to determine the intensity of competition exerted by an introduced species, *Carichtera annua*, on the winter annual plant community in the chenopod shrublands of arid South Australia. We addressed the following specific issues: a) What is the competitive effect of *C. annua* on the rest of the annual plant community, and b) How does soil resource availability affect the response of native annual species to *C. annua*?

Methods

The project was conducted at Middleback Research Centre, 20 km northwest of Whyalla, South Australia (32°57' S, 137°24' E). The climate is arid (annual rainfall 230 mm) with mild winters and hot summers. Soils are predominantly brown calcareous earths with clay-loam texture, and calcium carbonate accumulated at variable depths. The pH is slightly alkaline, and nutrient availability is low (Crocker 1946). The dominant vegetation is a chenopod dominated shrubland with a sparse overstorey of *Acacia papyrocarpa* (species names follow Jessop and Toelken (1986)). The system supports a wide diversity of short-lived annual plants, both native and introduced. The annual plant community is dominated by the exotic herb, *Carrichtera annua* (Ward's Weed). Common native ephemeral species include *Sclerolaena* sp., *Crassula colorata*, *Wahlenbergia stricta*, *Tetragonia tetragonoides* and the grass species *Danthonia caespitosa* and *Stipa nitida*. In years with abundant autumn rainfall ephemeral species are an important component of the plant community.

Experimental sites were located inside a permanent fenced enclosure (104 m × 92 m), erected some 20 years prior to this study. The enclosure was designed to prevent sheep and rabbit browsing, leaving kangaroos as the main source of grazing pressure. Field observations were made on a monthly basis from May to September. The rainfall during this period was above monthly average throughout winter and spring, following an extremely dry summer period.

Root depth

The aim of this part of the study was to characterize the root systems of the four more abundant ephemeral taxa (*C. annua*, *Sclerolaena* sp., *C. colorata* and the two dominant grasses combined (*S. nitida* and *D. caespitosa* which could not be differentiated at the time of the sampling). Five individuals representing each taxa were randomly selected. The soil under each of those individuals was extracted using a 50 mm diameter soil corer to a depth of 20 cm to extract intact root systems, with only little root mass loss due to soil disruption.

Density manipulation

Density manipulation experiments were carried out in ten split-plot quadrats (1 m × 3 m). Each quadrat was split into three 1 m × 1 m plots. Quadrats were located in open, unshaded areas away from remnant mounds left by dead perennial plants within an enclosure. The sites were selected to contain regular densities of *C. annua*, as determined by visual estimates of remaining dead adult plants. One of three density treatments (see below) was randomly assigned to each 1 m × 1 m plot within each quadrat, so that each quadrat contained three different density treatments and each density treatment was replicated ten times. Sampling was conducted in the central 50 cm × 50 cm area within each plot, leaving a 25 cm buffer zone to minimise edge effects.

The treatments (density decreased, density increased, and control) involved manipulation of the density of remnant fruit-bearing dead stems of *C. annua* remaining from the previous growing season. As recruitment of *C. annua* is dependent on short distance (a few cm) seed dispersal from fruits borne on dead, fruit-bearing plants remnant adult plants rather than from the soil seedbank or seed redistribution (Guterman (1993, 1989)), manipulating adult density was expected to change potential recruitment. This method was used in preference to removing or scattering *C. annua* seeds, because a) it simulates better the natural process, and b) it minimises the effects of seed predation by ants and other seed foraging insects. Under rain-induced circumstances, *C. annua* seeds are released from the fruit and the wetted seed exudes a mucilaginous coat aiding its adherence to the soil. This mucilaginous layer probably limits predation by ants. The increased density treatment involved doubling the number of fruit bearing dead stems. The density of *C. annua* within each plot was recorded, and then the number of stems required was collected from the field and "planted" at random within the plot. A hole was made in the soil with a nail and a stem placed into the hole. In the decreased density treatment half of the stems present were randomly removed from each assigned plot. The control treatment involved leaving the density of extant stems of *C. annua* untouched. To account for possible disturbance effects caused in the increased density treatment, holes were made at random in the other plots.

Plant counts were undertaken monthly from late autumn (May) to early spring (September), including all emergent seedlings within the 50 cm × 50 cm zone

in each plot. In the reduced density plots, newly emergent *C. annua* were counted and half of the new recruits removed monthly, so each cohort of emergents had its density manipulated only once.

At the end of September all plants within the 50 cm × 50 cm plots were harvested at ground level using secateurs. Plants were dried for 24 h at 80 °C and weighed. Total shoot biomass and number of individuals of each species per plot were recorded. The number of *C. annua* fruits per plant was counted following drying. As variation of seeds/pod is minimal in this species (Facelli and Temby (in press)) fruit number is a good estimator of reproductive output.

Nutrient manipulation

Twenty four 2 m × 1 m split-plot quadrats (selected as above) were established, each containing two 1 m × 1 m plots. A factorial arrangement of two factors (nutrient availability and presence of *C. annua* were imposed at two levels each (nutrients added or not, and *C. annua* removed or not). Twelve of the twenty-four quadrats were selected at random to receive nutrient supplementation. In early June, two months after the first seedlings emerged, the nutrient addition quadrats received 37 g of controlled slow-release, nitrogen-rich fertiliser (Osmocote™, Scotts Aust. Pty Ltd) (N:P:K = 15:5:10). This treatment was intended to simulate nutrient-rich conditions such as those beneath dead *A. papyrocarpa* (Facelli and Brock 2000). Application followed seedling establishment, as fertiliser pellets often absorb water, reducing moisture available to newly germinated plants. A second application was made in late August. All remnant fruit bearing stems of *C. annua* were removed from one plot in each of the twenty four quadrats, while the other plot was left untouched. In addition, newly emerged *C. annua* were removed from assigned plots during the monthly counts of newly emerged seedlings running from May to September. At the end of September all plants within the 50 cm × 50 cm zones were harvested, sorted by species, and treated as described for the density manipulation study.

Data analyses

Root depth data were not normally distributed and was analyzed using non-parametric Kruskal-Wallis test. Data from the density manipulation experiment were analyzed using a one-way ANOVA and Kruskal-Wallis' non-parametric test when ANOVA assump-

tions were not met. The data from the nutrient manipulation experiment were analysed using two-way ANOVA and Welch ANOVA when data were heteroscedastic. The Shannon-Weaver Index of Diversity (Shannon 1948) was calculated leaving out *C. annua*, to determine whether the absence/presence treatment influenced community diversity. By excluding *C. annua* from the presence treatment plots it allowed the diversity of the remaining community to be directly compared to the diversity of the standing community in the absence plots.

Results

Most emergent species identified were present only in a small number of plots: 60% of all species were found in less than 6 plots. Thus they were considered as one group (minor species) for most data analyses. Included in this group were: *Wahlenbergia stricta*, *Tetragonia tetragonoides*, *Medicago minima*, *Brachycome lineariloba*, *Erodium cygnorum*, *Erodium cicutarium*, *Vittadinea* sp., *Sisymbrium erysimoides* and *Calotis hispidula* as well as four species which could not be readily identified. Taxa considered individually in the analyses were *C. annua*, *Sclerolaena* sp., *Crasula colorata* and the combined grasses group of *Danthonia caespitosa* and *Stipa nitida*.

Root depth

The roots of *C. annua* were significantly deeper than all other species ($\Pi^2 = 14.57$, $P < 0.01$), while no difference was found between *Sclerolaena* sp. and the combined grasses group ($P > 0.05$) (Figure 1). The root system of *C. colorata* was quite shallow with the main tap root rarely extending deeper than 0.6 cm. Some adventitious roots may have penetrated deeper, however, the retrieval technique applied could not remove entire, unbroken sections of these roots.

Effects of density manipulation

The manipulations of density of *C. annua* resulted in a significant reduction of densities in the reduced density plots ($F = 9.83$, $P < 0.01$), but there was no significant difference between the control and the increased density treatment plots. Per plot and per plant fruit production by *C. annua* were not influenced by density manipulations ($F = 0.50$, $P = 0.61$, and $F = 1.61$, $P = 0.223$ respectively). Plot and plant shoot

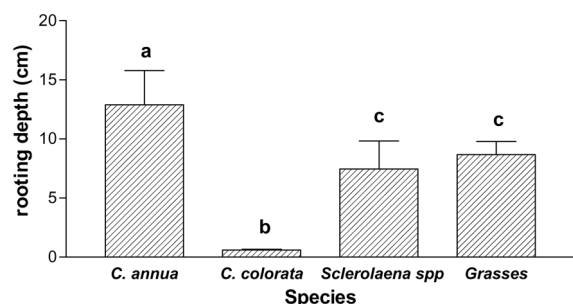


Figure 1. Rooting depth of the four major species in field enclosures. Means and standard deviations given. Different letters indicate significant differences at ($\alpha = 0.05$).

biomass of *C. annua* did not differ across density treatments ($F = 1.13$, $P = 0.342$ and $F = 0.96$, $P = 0.39$ respectively) (Figure 2). However, the power of both tests was low (Power = 0.223 and Power = 0.194 respectively) because of high variability amongst plots. Observations of plots prior to harvest indicated that the leaves and branches of *C. annua* in some increased density treatment and control plots had a distinct purple colouration, suggesting a probable plant nitrogen deficiency. This colouration was not observed in the reduced density treatments or in increased density or control plots with lower *C. annua* densities.

Manipulation of *C. annua* density did not have any detectable effect on the densities of *Sclerolaena* sp., *C. colorata*, combined grasses, and minor species (Kruskal-Wallis test, $\Pi^2 = 3.76$, $P = 0.152$; $\Pi c^2 = 0.32$, $P = 0.851$; $\Pi^2 = 1.81$, $P = 0.404$; and $\Pi^2 = 2.06$, $P = 0.357$ respectively). Variability in plant abundance for most species was rather large. The mean total number of plants per plot (excluding *C. annua*) was similarly unaffected by density treatments ($\Pi^2 = 1.34$, $P = 0.513$) (Figure 3).

Mean shoot biomass per plot and per plant were not affected amongst other species under the imposed density regimes. *Sclerolaena* sp. *C. colorata*, grasses, the minor species and total biomass (excluding *C. annua*) showed no significant differences across treatments. The mean total shoot biomass and the grasses were only marginally non-significant with a trend toward a higher biomass in the reduced density treatment plots (Table 1).

Effects of nutrient manipulation

Per plot and per plant fruit production of *C. annua* were not affected by fertiliser application ($F = 2.59$,

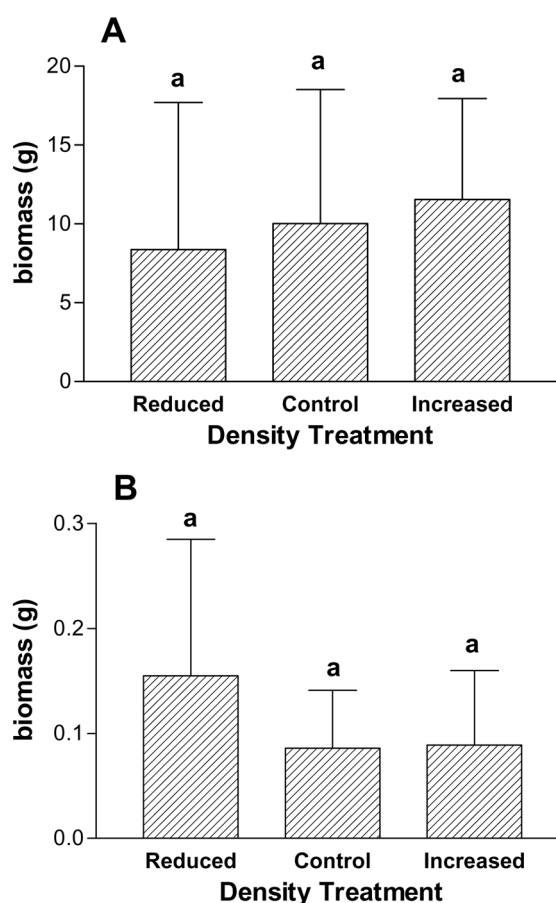


Figure 2. Shoot biomass of *C. annua* per plot (A) and per plant (B) under three imposed density regimes. Means and standard deviations given. No significant difference in biomass exists between treatments at $\alpha = 0.05$.

Table 1. Results of a non-parametric Kruskal-Wallis comparisons of mean shoot biomass per plot and per plant under three imposed *Carrichtera annua* density regimes. (numbers in bold indicate marginally significance).

Species	Per Plot		Per Plant	
	χ^2	P	χ^2	P
<i>Sclerolaena</i> spp.	2.8816	0.2367	1.2000	0.5488
<i>Crassula colorata</i>	0.2268	0.8928	0.4808	0.7863
Grass species	1.0355	0.5958	5.5543	0.0622
Minor species	2.0845	0.3527	4.0571	0.1315
Total No. of Plants	5.5411	0.0626	3.8478	0.1460

$P = 0.122$ and $F = 0.40$, $P = 0.531$ respectively), suggesting that the reproductive output of *C. annua* was not nutrient limited. The abundance, plot biomass and plant biomass of *C. annua* were similarly unaffected by the application of fertiliser ($F = 1.06$, $P = 0.315$; F

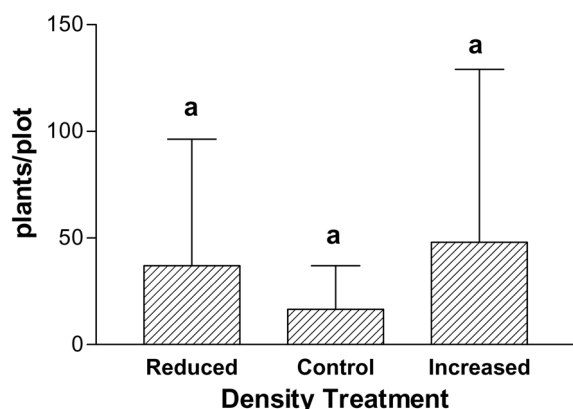


Figure 3. Total abundance of plant species (excluding *Carrichtera annua*) under three imposed density treatments. Means and standard deviations given. No significance was detected $\forall = 0.05$. Note, however the large variability.

= 3.06, $P = 0.094$ and $F = 0.60$, $P = 0.445$ respectively).

The presence of *C. annua* had no effect upon the abundance of the major and grouped species. Fertiliser application significantly increased the density of *C. colorata* and the total abundance of ephemeral plants (excluding *C. annua*) (Figure 3, Table 2). There were no significant interaction terms between treatments. Difference in *C. colorata* abundance between nutrient treatments was evident from July (Figure 4).

The presence of *C. annua* had no effect upon plot shoot biomass of any of the taxa analysed (Table 3). Shoot biomass per plot of *C. colorata* and grasses was significantly higher in fertilised plots. For all others, shoot biomass was unaffected by the nutrient supplement.

The presence of *C. annua* had no effect upon average shoot biomass per plant for any of the species and groups of species (Table 4). The shoot biomass per plant for *Sclerolaena* sp. was significantly reduced in plots where *C. annua* had been removed. Fertiliser only increased per plant shoot biomass of *C. colorata* ($p < 0.05$). The interaction term for *Sclerolaena* sp. was marginally non-significant.

Low power of interaction terms for all tests reflected the high variability within same treatment plots for the collected data. Increased replication of treatments may have made observed and moderately non-significant differences more apparent.

Removal of *C. annua* did not affect diversity at any stage of the study (Table 5). Species diversity was significantly higher in non-fertilised plots than in fertilised plots in early September ($F = 9.58$, $P = 0.004$),

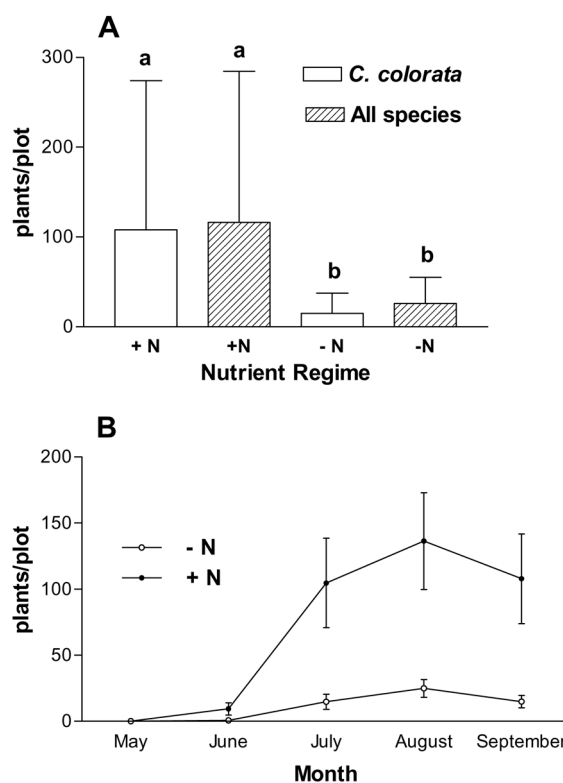


Figure 4. A) Abundance of *Crassula colorata* and all plants in plots with nutrients added or not. Means and standard deviations given. Different letters indicate significant differences in abundance at $\forall = 0.05$. B) Abundance of *Crassula colorata* in plots with nutrients added or not over the course of the study. Means and standard error means are given. Asterisks indicate dates when differences are significantly different ($\forall = 0.05$.)

but by late September the difference had disappeared. The increase in *C. colorata* mentioned above is likely to have produced the decline in diversity in the fertilized plots because of increased dominance over other species which failed to increase in numbers. The decline of *C. colorata* by late September, the end of its life cycle, may have eliminated the diversity difference between nutrient treatments.

Discussion

We failed to detect any strong competition effect of *C. annua*, the introduced dominant species in this community, on the recruitment and growth of other species, suggesting that it may not compete strongly for below-ground resources. We also found evidence of different root structures that may result in reduced overlap of resource depletion zones among the vari-

Table 2. Results of two-way ANOVA for the abundance of major and grouped species under imposed removal and nutrient regimes (numbers in bold indicate significance). Power of the interaction term for all tests given.

Species	Nutrient Regime		<i>C. annua</i> Removal		Interaction Term		Power of Interaction
	F	P	F	P	F	P	
<i>Sclerolaena</i> spp.	2.416	0.127	2.416	0.127	0.114	0.737	0.0626
<i>Crassula</i>	10.74	0.002	0.774	0.384	0.038	0.858	0.0536
Grasses	0.012	0.914	0.128	0.722	1.536	0.222	0.2281
Minor Species	1.844	0.181	1.534	0.222	0.080	0.778	0.0589
Total No. Plants	5.580	0.023	2.785	0.102	0.004	0.953	0.0504

Table 3. Results of a two-way ANOVA for the shoot biomass per plot of the major and grouped species under imposed removal and nutrient regimes (numbers in bold indicate significance). Power of the interaction terms for all tests given.

Species	Nutrient Regime		<i>C. annua</i> Removal		Interaction Term		Power of Interaction
	F	P	F	P	F	P	
<i>Sclerolaena</i> spp.	0.234	0.631	0.398	0.531	0.393	0.534	0.0941
<i>C. colorata</i>	7.203	0.010	0.187	0.668	0.036	0.850	0.0540
Grasses	4.952	0.031	0.369	0.547	0.544	0.465	0.1115
Minor Species	1.187	0.282	2.772	0.103	0.245	0.623	0.0773
Total No. of Plants	0.983	0.327	2.751	0.104	0.118	0.733	0.0631

Table 4. Results of a two-way ANOVA for the shoot biomass per plant of the major and grouped species under imposed removal and nutrient regimes (numbers in bold indicate significance). Power of the interaction terms for all tests given.

Species	Nutrient Regime		<i>C. annua</i> Removal		Interaction Term		Power of Interaction
	F	P	F	P	F	P	
<i>Sclerolaena</i> spp.	1.906	0.186	6.865	0.019	4.370	0.053	0.5018
<i>C. colorata</i>	27.31	0.000	0.136	0.715	0.648	0.428	0.1218
Grasses	3.671	0.063	0.812	0.373	0.785	0.381	0.1390
Minor Species	0.494	0.487	0.154	0.698	0.000	0.990	0.0500
Total No. of Plants	0.337	0.565	0.018	0.895	0.023	0.882	0.0525

Table 5. Shanon-Weiner's diversity index of the ephemeral community under experimental removal and nutrient regimes (numbers in bold indicate significance). There were no significant interaction terms between treatments.

Month	Removal	Control	Fertilized	Not Fertilized
June	0.41 ± 0.48	0.32 ± 0.46	–	–
July	0.87 ± 0.51	0.59 ± 0.48	0.76 ± 0.55	0.71 ± 0.48
August	0.71 ± 0.40	0.61 ± 0.47	0.57 ± 0.37	0.75 ± 0.48
Early September	0.67 ± 0.48	0.64 ± 0.40	0.48 ± 0.33	0.83 ± 0.47
Late September	0.68 ± 0.38	0.55 ± 0.35	0.52 ± 0.35	0.71 ± 0.36

ous species (i.e. niche differentiation). During conditions of low environmental stress, desert plants may coexist with limited competition.

Root system length varied considerably amongst the studied species. Smaller species, such as *C. colorata* appear to use water and nutrients from only the very upper soil layers. These species are likely to be

more dependent on regular rainfall events than larger species that can access deeper soil resource reserves following local depletion of topsoil supply. Larger annual species are less likely to suffer nutrient or water limitation to the same extent as smaller species during unfavourable periods. During periods of extreme resource limitation the roots of *C. colorata* are

unlikely to be able to access deeper nutrient reserves, which may result in high mortality or low reproductive output.

The manipulation of the density of *C. annua* had little effect on the density of other species, with the exception of *Sclerolaena* sp., indicating a lack of strong competition between *C. annua* and the other ephemeral species. The roots of *C. annua* extend significantly deeper into the soil than the rest of the species in the community, suggesting that they occupy somehow different soil niches (Wilson 1988). Root niche separation often reduces the intensity of competition amongst desert species (Fowler 1986; Sala et al. 1989). On the other hand *C. annua* is also noted to be an opportunistic species, germinating abundantly after brief rainfall events (Loira and Noy-Meir 1979). Early emergence may secure the capture of a disproportionate share of environmental resources (Ross and Harper 1972; Harper 1977; Inouye 1980; Bergelson and Perry 1989) and may reduce establishment of late establishing species. Thus preemption, rather than direct competition may be the dominant density dependent effect.

Shoot biomass of *C. annua* per plot was the same in all treatments. This implied that a few large individuals and many smaller ones occupied halved plots, and higher density treatment plots probably supported uniformly smaller individuals. This intra-specific control of the biomass of *C. annua* may have then resulted in the same level of interspecific competition on the other species, because competition in plants is likely to be a function of biomass rather than the number of individuals (Goldberg and Werner 1983). Reproductive output appeared also to be similar for all treatments. However, high variation in fruit numbers within halved treatment plots indicates that larger individuals produced most fruit, whilst smaller plants contributed few or none at all. This reinforces our view that density treatments had more effect on an intraspecific than an interspecific competition. Indeed, it has been observed previously that interspecific competition is weaker than intraspecific competition in determining plant growth and fecundity in annual plant species in arid environments (Yeaton and Cody 1976; Yeaton et al. 1977). Another indication that interference between individuals of *C. annua* was more intense at higher densities is suggested by the purple colouration of shoots in the more crowded plots. This colouration is commonly caused by excess carbohydrate buildup under N limitation, due to a breakdown in the synthesis of amino acids and other

nitrogen compounds (Marschner 1995) and may have been caused by high resource depletion in the rooting zone at higher densities.

Separation of root niches may have also contributed to the small response of the ephemeral community to different abundances of *C. annua*. Recruitment of all species was unaffected by changes to *C. annua* abundance. This interpretation would be consistent with the concept of vacant niches existing within plant assemblages (Elton 1958). *Carrichtera annua* may be able to occupy space at increasing densities without substantially affecting the native residents. The importance of niche differentiation in plant communities is still unresolved. While the traditional equilibrium models of coexistence as well as more recent models (Tilman 1982) are based on niche separation, the experimental evidence supporting niche differentiation in resource uptake is still scant (Crawley 1990). While some studies found strong experimental evidence of niche separation (e.g. Grime and Curtis (1976) and Berendse (1983), Sala et al. (1989), Jacobs and Sheley (1999)) these constitute a minority, and the several other studies found evidence of broad niche overlap (e.g. Mahdi et al. (1989)).

The results from the nutrient addition study reinforces the evidence of low competitive effect of the dominant *C. annua* on the ephemeral community. Differences in rooting depth may have reduced the effects of direct root competition and lends further support to the findings that *C. annua* competes more strongly at an intra-specific level for below-ground resources. There may be very little root niche overlap amongst the studied ephemeral species. It is also possible that nutrient and water resources in the field enclosure were simply not limiting. There is no evidence that competitive exclusion or reduction in total shoot biomass per plot for any major or grouped species occurred in the presence of *C. annua*. The recorded rainfall during the study suggests that there was high water availability, and nutrient pulses are known to strongly correlate with pulsed water supply (Goldberg and Novoplansky 1997).

The response of *C. colorata* to nutrient supplementation, however, suggests that nutrient availability may be a limiting factor in the growth and abundance of smaller ephemeral species. Under increased nutrient supply, *C. colorata*'s abundance and shoot biomass per plot and per plant were significantly higher. Recruitment of certain species can be promoted by increased nitrate concentrations (Fenner 1985). The noted increase in shoot biomass implies that growth

of *C. colorata* is nutrient limited under natural field conditions. Goldberg and Novoplansky (1997) stated that competitive effects amongst plants during a favourable pulse phase could be overridden by the conditions experienced during the interpulse phase. The high recorded rainfall during the study suggests frequent water pulses, indicating that the system was unlikely to be severely water stressed. However, nutrient pulse frequency in the observed plots was probably quite low. All experimental plots were situated in open, exposed areas, characterized by lower levels of nutrients, which became concentrated around the bases of perennial woody plants (Facelli and Brock (2000, 2000)). Given the very low topsoil nutrient content in open areas small, shallow rooted plants, such as *C. colorata*, may be severely nutrient stressed. The more extensive root systems of larger species, such as *C. annua* and *Sclerolaena* spp., may be able to extract larger amounts of available soil nutrients from below the root zone of *C. colorata* because water persists longer in deeper layers of soil.

Nutrient stress often has more adverse effects on plant growth than water stress (Harper 1977). Plants have very limited ability to cache nutrients taken up during pulses of high resource availability, as high nitrogen and phosphorous concentrations can be toxic. Smaller plants may be subject to long nutrient interpulse intervals, not in phase with their larger neighbours which can access deeper soil reserves (Figure 5). The duration and severity of these interpulse periods may override the species' competitive response during the nutrient pulse phases associated with frequent rainfall events. The elevated surface nutrient availability caused by fertiliser application probably resulted in higher *C. colorata* root mass, which may have allowed *C. colorata* to continue to draw water resources even as the water level moved down the soil profile (Figure 5). In plants in low nutrient sites root elongation may have been insufficient to maintain contact with the receding wet soil level, leading to increased stress. In contrast, larger neighbouring plants would be able to maintain root elongation allowing access to deeper water and nutrient resources throughout. *C. colorata*'s productivity was limited by low nutrient supply, indicating that stress may have been more important than competitive interactions with neighbouring plants in determining its response to the soil environment. A larger deeper rooted species, such as *C. annua* may be able to continue to elongate roots to maintain access to the re-

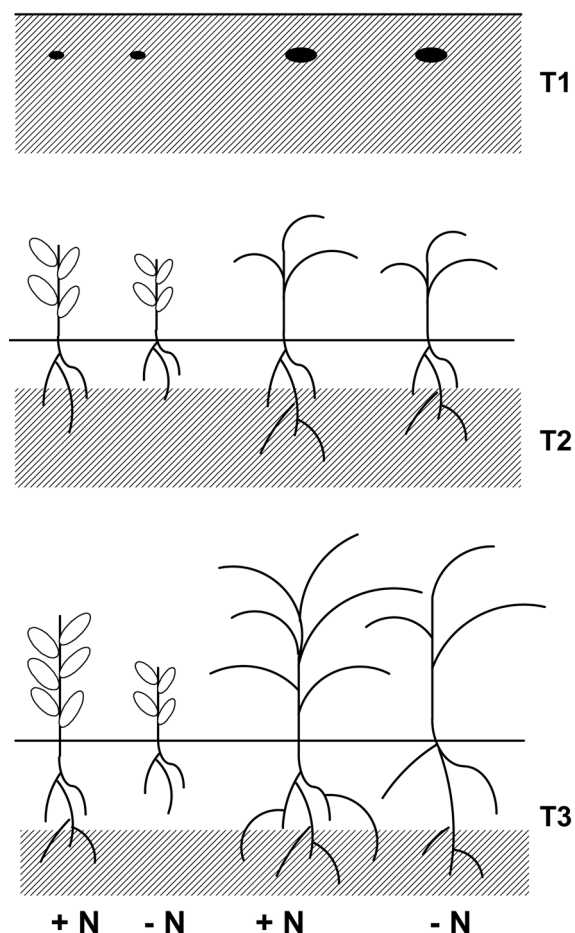


Figure 5. Representation of the assumed root dynamics of *Crasula colorata* (left) and *Carrichtera annua* (right) under high (+ N) and low (- N) nutrient availability from the time a rainfall event triggers germination (T1). The shaded section represents the zone of the soil with water available. As the wet front recedes (T2), the root extension of small, nutrient limited plants is unable to keep up their root elongation (T3), and the plant eventually dies. Nutrient limited individuals of larger plant species may keep up root extension longer with drying conditions

ceding wet soil area even in low nutrient sites (Figure 5).

Lower diversity in the nutrient supplemented plots was due more to the large increase in *C. colorata* abundance rather than to competitive exclusion of any species as suggested by Goldberg and Miller (1990). The results of this study show that nutrient status has a significant effect upon ephemeral plant community composition. In nutrient-poor soils, the growth of smaller species is restricted, limiting their contribution to the plant community. Goldberg and Novoplansky (1997) two-phase resource hypothesis appears to

hold, but the level of resource availability which constitutes a "pulse" phase seems to be species dependent, probably a function of plant size, structure, and physiology. On open, bare patches of soil, *C. colorata* produces a low shoot biomass and is present in lower numbers than on more fertile soils where its productivity has been shown to increase. In open areas, *C. colorata* probably experience very short pulse intervals, in comparison to other species. Similar pulse phases do not appear to be shared by the larger species, which exhibited no significant change in biomass or abundance between nutrient treatments. Pulse and interpulse phases may be species specific, and overlap amongst the entire ephemeral community may only occur under conditions of abundant resource availability, or during periods of severe resource depletion such as in an extended drought.

Our results suggest that density dependent effects of *C. annua* may be predominantly intraspecific. Interspecific competition may, however become more important after long pulses of resource availability end, when plants have achieved high densities and large sizes, and resources become limiting. The dynamics and interactions operating in this system may thus be quite complex, because the time when a pulse ends will be different for the various species. Overall community structure may be determined both by stress effects during interpulse periods, and by the competitive effects that occur during periods with long or frequent pulses.

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