New Phytologist

Research

Shifts from competition to facilitation between a foundation tree and a pioneer shrub across spatial and temporal scales in a semiarid woodland

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Received: *26 June 2006*
Accepted: *8 September 2006*

Summary

- Theoretical and empirical research has supported the hypothesis that plant–plant interactions change from competition to facilitation with increasing abiotic stress. However, the consistency of such changes has been questioned in arid and semiarid ecosystems.
- During a drought in the semiarid south-western USA, we used observations and a field experiment to examine the interactions between juveniles of a foundation tree (Pinyon pine, *Pinus edulis*) and a common shrub (Apache plume, *Fallugia paradoxa*) in replicated areas of high and low stress.
- The presence of *F. paradoxa* reduced *P. edulis* performance at low-stress sites, but had the opposite effect at high-stress sites. However, the intensity of the interactions depended on temporal variation in climate and age of *P. edulis*. Both above- and below-ground factors contributed to competition, while only above-ground factors contributed to facilitation.
- These results support the hypothesis that interactions can change from competition to facilitation as abiotic stress increases in semiarid environments. A shift from competition to facilitation may be important for the recovery of *P. edulis* and other foundation species that have experienced large-scale mortality during recent droughts.

Key words: climate change, competition, environmental stress, facilitation, foundation species, *Pinus edulis*, plant–plant interactions, removal experiment.

New Phytologist (2007) **173**: 135–145

doi: 10.1111/j.1469-8137.2006.01915.x

Introduction

Facilitation, the positive impact of one plant on another, has been shown to improve the recruitment, growth, and survival of the beneficiary species through shading, increased nutrient availability, and increased soil stability (see review by Callaway, 1995). Facilitation and competition both have been shown to be the net outcome of unbalanced positive and negative interactions, which can simultaneously occur between the same two plants (Aguiar & Sala, 1994; Holmgren *et al*., 1997; Holzapfel & Mahall, 1999; Maestre *et al*., 2003). The direction of net plant–plant interactions frequently changes in response to environmental conditions (Holzapfel & Mahall, 1999; Callaway *et al*., 2002; Maestre & Cortina, 2004) and several theoretical models predict that the relative importance of facilitation and competition should vary inversely across gradients of abiotic stress, with facilitation dominating under highly stressful conditions (Bertness & Callaway, 1994; Callaway & Walker, 1997; Brooker & Callaghan, 1998). In recent years, many field experiments have provided support for these models (Greenlee & Callaway, 1996; Bertness & Ewanchuck, 2002; Callaway *et al*., 2002; Maestre *et al*., 2003). However, there are a growing number of studies that do not support the predictions of the models (Kadmon & Tielbörger, 1999; Tielbörger & Kadmon, 2000; Pennings *et al*., 2003; Maestre & Cortina, 2004; Armas & Pugnaire, 2005;

Barchuk *et al.*, 2005). These opposing findings led to a recent review which questioned the generality of the theoretical models in arid and semiarid ecosystems, and suggested that new theoretical and empirical work was needed to better understand the role of facilitation in determining plant community structure and dynamics in these environments (Maestre *et al.*, 2005).

Using a meta-analysis of the current plant–plant interaction literature Maestre *et al.* (2005) concluded that the net effects of interactions between plants in arid and semiarid environments, either positive or negative, did not increase as abiotic stress increased. Lortie & Callaway (2006) then argued that the inconsistent findings observed by Maestre *et al.* (2005) were the result of the criteria used to select studies for the meta-analysis and statistical problems inherent in meta-analysis. In a commentary on the debate Michalet (2006) stated: 'Other studies, including both removal procedures and comparisons with open areas, are needed to understand better the relative parts of direct and complex interactions in arid ecosystems.' To address this debate, we examined the interactions between the juveniles of a foundation woodland tree species, pinyon pine (*Pinus edulis*), and a pioneer shrub species, Apache plume (*Fallugia paradoxa*), along a gradient of abiotic stress in a semiarid environment. Our findings address the current debate and add to this body of research in three ways.

First, we specifically address two aspects of the Maestre *et al.* (2005) meta-analysis that contributed to inconsistencies in the net direction of plant–plant interactions, as well as address a main issue on how best to measure stress within a site. Maestre *et al.* (2005) found that the nature of the relationships between plants depended both on the type of study (observational vs experimental) and on the plant performance variables measured (growth, survival, fecundity, etc.). Here, we include observational patterns of interactions between juvenile *P. edulis* growing in association with *F. paradoxa* compared with juvenile *P. edulis* growing in open space across replicated areas of high and low stress. We also conducted a field experiment to compare responses of juvenile *P. edulis* with its *F. paradoxa* associate left intact or removed. In all cases, we recorded both growth and mortality of the juvenile *P. edulis* to determine if the direction of the interaction was consistent across multiple response variables. Furthermore, we included a 'partial removal' treatment in which the above-ground portion of *F. paradoxa* was tied back, but the below-ground portion was left intact. This treatment allowed us to begin to understand the contribution of above-ground and below-ground influences on the interactions between *P. edulis* and *F. paradoxa*. Maestre *et al.* (2005) argued that abiotic variables can be good surrogates of biotic measurements of stress, while Lortie & Callaway (2006) suggested that examining variables associated with plant productivity was necessary to translate the effects of abiotic variables into a measure of stress. Here we have included both abiotic and biotic measures of stress within our sites and both appear to be in agreement.

Second, we examined the net interactions between the two species across a temporal stress gradient to determine if they were consistent with the findings across the spatial stress gradient. We used juvenile tree mortality as an indicator of interaction intensity to determine if the importance of competition or facilitation between *P. edulis* and *F. paradoxa* changed with *P. edulis* age. Previous studies have shown that such shifts in interactions are dependent on the life-history stage of one of the plants (Pugnaire *et al.*, 1996; Rousset & Lepart, 2000). In addition, a few studies have reported interaction shifts between species associated with changes in climate conditions across years (Belsky, 1994; Armas & Pugnaire, 2005) or within a single year (Holzapfel & Mahall, 1999; Pugnaire & Luque, 2001; Kikvidze *et al.*, 2006). Using mortality rates of juvenile *P. edulis* as an indication of interaction intensity, we used multiple surveys during the experiment to determine if interaction intensity changed throughout the year.

Lastly, our study is important because it focused on a foundation tree species during a long-term drought. Surprisingly few studies have focused on the importance of facilitation in a foundation tree species. For example, in their meta-analysis tests for net effects on growth and survival across stress gradients, Maestre *et al.* (2005) included only three studies for which the target plant was a foundation tree species (but see Barchuck *et al.*, 2005). Dayton (1972) defined a foundation species as a single species that defines much of the structure of a community by creating locally stable conditions for other species, and by modulating and stabilizing fundamental ecosystem processes (see review by Ellison *et al.*, 2005). Several studies have shown that *P. edulis* affects a diverse community of organisms from microbes to vertebrates (Whitham *et al.*, 2003) as well as affecting important ecosystem processes (Chapman *et al.*, 2003; Schuster *et al.*, 2005). Therefore, monitoring shifting interactions between *P. edulis* and abundant shrubs is important for understanding the distribution and stability of the third largest vegetation type in the United States, of which *P. edulis* is a codominant (West, 1984). Furthermore, an ongoing drought in the south-western USA has affected the survival of *P. edulis* (Ogle *et al.*, 2000; Mueller *et al.*, 2005) across a large geographic region (Breshears *et al.*, 2005). Gitlin *et al.* (2006) showed *P. edulis* to be a good 'barometer of change' for plant responses to drought and there is considerable evidence that many plant species will expand or contract their ranges in response to climate change (Parmesan & Yohe, 2003; Gitlin *et al.*, 2006). Abrupt shifts in interactions among plants from competition to facilitation, and vice versa, might provide a partial mechanism for these shifts and be critical in the recovery of important foundation species and their associated communities (Brown *et al.*, 2001).

We used this system to test the following specific hypotheses: interactions between juvenile *P. edulis* and *F. paradoxa* shift from negative to positive with increasing stress; there are both above- and below-ground components to the interactions between juvenile *P. edulis* and *F. paradoxa*; the intensity of facilitative and competitive interactions with *F. paradoxa* decreases with age of juvenile *P. edulis*; the intensity of facilitative and competitive interactions between juvenile *P. edulis* and *F. paradoxa* changes seasonally with temporal variation in environmental stress.

Materials and Methods

Site description and determination of stress gradient

All research was conducted near Sunset Crater National Monument, 33 km north-east of Flagstaff, AZ, USA. Soils in this area are dominated by 1200-yr-old cinder deposits (Houk, 1995) that include basaltic ash, cinders and lava flows and belong in the US Department of Agriculture Soil Taxonomic Sub-Group of Typic Ustorthents. This area averages < 400 mm of precipitation yr^{-1}, approximately evenly divided between summer rainfall and winter rain and snow. Dominant trees were pinyon pine (*Pinus edulis* Engelm) and one-seed juniper (*Juniperus monosperma* Engelm) at lower elevations, and *P. edulis* and ponderosa pine (*Pinus ponderosa* P. & C. Lawson) at higher elevations. Apache plume (*Fallugia paradoxa* D. Don) was the most abundant intercanopy species at all elevations but vegetation cover was relatively low with large areas of bare ground. The distributions of *P. edulis* and *F. paradoxa* overlap significantly across the south-western United States (Elmore & Janish, 1976) and interactions between the two species are likely to be common. In fact, at all of our study sites, *F. paradoxa* averaged only 22–27% of available habitat, yet > 60% of all juvenile *P. edulis* in the sites were associated with *F. paradoxa* (Stulz, 2004).

Previous studies have shown this cinder environment to be more stressful than surrounding sandy-loam soil sites (Cobb *et al.*, 1997; Swaty *et al.*, 1998). However, to determine if spatial stress gradients existed within the cinder fields, four low-elevation (1725–1800 m) and four high-elevation (2050–2250 m) sites were examined across a series of cinder cones within a 5 km radius of Sunset Crater National Monument. Here we define stress as abiotic environmental factors (temperature, precipitation, elevation, etc.) that reduce the growth and/or survival of plants. The four sites were paired such that one member of each pair occupied the highest and lowest elevations, respectively, in which *P. edulis* typically occur in the cinder fields near Sunset Crater. We hypothesized that the high-elevation sites would be less stressful than the low-elevation sites based on previous correlations between elevation and stress in semiarid environments (Allen & Breshears, 1998; Xu *et al.*, 2004).

To estimate environmental stress within our sites, we measured two abiotic factors (soil temperature and soil moisture) and two plant performance factors (average annual stem growth of mature *P. edulis* and mature *P. edulis* mortality). Soil temperature was recorded at 15 cm depth (Barnant thermocouple thermometer, type K) at 10 randomly chosen areas of bare ground (hereafter called open) and 10 randomly chosen points under *F. paradoxa* at each site in August of 2003. This date was used to capture the spatial scale stress differences present at the end of the experiment. At the same time, gravimetric soil moisture content was quantified by collecting 15-cm-deep soil samples at the 10 points under *F. paradoxa* at each site. Soil samples were then weighed, dried at 105°C for 48 h, and reweighed. To determine if differences in stress between high- and low-elevation sites could be attributed to variation in soil texture (Donahue *et al.*, 1983), the soil samples were sieved through a 2 mm screen to measure the fine earth vs coarse fragment fraction of the sample. Previous studies in these cinders have shown that particle size is closely tied to numerous micro- and macronutrients (Cobb *et al.*, 1997).

To assess mature *P. edulis* performance we examined average annual stem growth (1999–2003) of 10 randomly selected mature *P. edulis* trees at each site by randomly selecting five shoots per tree and measuring each year's growth with digital calipers. We also quantified mature *P. edulis* mortality at all eight sites. *P. edulis* mortality was the result of a region-wide drought that began in 1996 and continues in 2006 (Ogle *et al.*, 2000; Breshears *et al.*, 2005; Mueller *et al.*, 2005). Stand-level mortality is a good indicator of overall site stress as it is correlated with decreased stem and trunk growth, increased branch dieback and reduced foliage density (Swaty *et al.*, 2004). We assessed mature *P. edulis* mortality by running four random 50 m transects at each site in 2003. The first 25 mature (taller than 2 m and sexually reproductive) *P. edulis* trees encountered along transects were designated as living or dead. All stress variables were individually compared between high- and low-elevation sites using *t*-tests.

Mortality and growth of juvenile *P. edulis* in association with *F. paradoxa*

To determine if juvenile *P. edulis* performance was affected by association with *F. paradoxa*, we quantified mortality and shoot growth of juvenile *P. edulis* growing in the open and in association with *F. paradoxa* across the four pairs of sites. Juvenile *P. edulis* were characterized as < 40 mm basal trunk diameter (BTD), shorter than 1 m in height, < 35 yr old (calculated by counting bud scale scars), and nonreproductive. To measure mortality, juvenile *P. edulis* growing in the open and in association with *F. paradoxa* were recorded as living or dead in August 2003. To quantify plant growth, stem growth for 2002 was recorded on any living juvenile *P. edulis* by measuring the growth of five randomly selected lateral stems per plant and averaging them. A total of 245 juveniles at low-elevation sites and 258 juveniles at high-elevation sites were measured with regard to mortality. A total of 177 juveniles at low elevation and 179 juveniles at high elevation survived and were used for analysis of stem growth. Average percentage mortality and average stem length of juvenile *P. edulis* per site were compared using a two-way ANOVA with *F. paradoxa* presence and elevation as the independent variables, followed by Tukey's multiple comparison tests.

Experimental examination of *P. edulis–F. paradoxa* association

To test our observational findings we performed a shrub manipulation experiment at one of the high- and low-stress site pairs. We located 180 juvenile *P. edulis* trees growing in association with *F. paradoxa* (90 at the high-elevation site and 90 at the low-elevation site) and three treatments were implemented evenly. We compared juvenile *P. edulis* with intact *F. paradoxa* ($n = 30$ per site, control group) with juvenile *P. edulis* whose associated *F. paradoxa* was removed by severing all shoots at ground level ($n = 30$ per site, removal group). Because *F. paradoxa* with their tops removed died, this treatment effectively eliminated the effects of above-ground shading and below-ground root activity. We also included a partial 'removal' in which the above-ground portion of the associated *F. paradoxa* was tied back using twine and steel rebar ($n = 30$, tie-back group). This treatment eliminated shade for the juvenile *P. edulis*, but allowed them to interact with living roots of *F. paradoxa*. This third treatment allowed us to assess the relative contribution of above- and below-ground factors of competitive and facilitative interactions. The size of the *F. paradoxa* associate was consistent across the treatments within a site (Stulz, 2004). The experiment was initiated in June 2002 and monitored through the end of the summer in 2003.

On 12 August 2003 stem growth for the year 2002 was measured on any juvenile *P. edulis* possible (some had died before any 2002 growth occurred or had died and blown away before census) using the method described above. At the end of August 2003, final mortality of juvenile *P. edulis* in each treatment was recorded and differences in mortality between treatments at each site were tested using a chi-square test. Individual Fisher's exact tests were then performed to compare mortality of the control group (*F. paradoxa* left intact) with the two experimental treatments (removal and tie-back groups). Differences in 2002 stem growth were tested using a two-way ANOVA with treatment and elevation as the independent variables, followed by Tukey's multiple comparison tests.

Size and temporal effects on manipulated *P. edulis–F. paradoxa* associations

To test if the intensity of facilitative and competitive interactions between juvenile *P. edulis* and *F. paradoxa* decreased with increasing *P. edulis* age, we used logistic regression to determine if pre-experimental BTD and height of juvenile *P. edulis* were correlated with mortality in each of the experimental treatments. We used mortality of juvenile *P. edulis* as a surrogate for interaction intensity.

We also examined if the intensity of facilitative and competitive interactions between *P. edulis* and *F. paradoxa* changed temporally, by monitoring mortality rates throughout the length of the experiment. This was achieved by recording the cumulative mortality of juvenile *P. edulis* in each of the treatments on eight different observation dates during the experiment. We tested for differences in mortality of *P. edulis* between treatments at three distinctive time periods: rapid responses (first 12 wk, ending late September 2002, from the beginning of the experiment until the first fall rains), fall/winter responses (October 2002–March 2003, from first fall rains until the last winter snowfall), and spring/summer responses (April 2003–August 2003, from the last snowfall until the end of the experiment), using chi-square tests. Individual Fisher's exact tests were then performed to compare mortality of the control group (*F. paradoxa* left intact) with the two experimental treatments (removal and tie-back groups) for each of the three time periods. We also used a region-wide climatic index (Palmer Drought Severity Index, PDSI) to examine if seasonal changes in interaction intensity were related to temporal variation in overall climatic conditions. PDSI is a weighted measure of overall abiotic and climatic conditions broken down into 350 regions throughout the United States, and is calculated based on precipitation and temperature data, as well as the local available water content (AWC) of the soil (Palmer, 1965; Alley, 1984). It has a value of zero to indicate normal conditions, while values above zero indicate moister than average conditions and values below zero indicate drier than average conditions. Our study sites were all located in Arizona region two, and weekly PDSI measures were obtained from NOAA's website (www.cpc.noaa.gov) for the entire duration of the experiment. We calculated an average PDSI value for each of the three distinctive time periods described above. Because both sites occur in Arizona region two, the same value of PDSI was used at both the spatially high and low-stress sites as an indicator of the overall climatic conditions, or overall stress, being experienced across the entire study site.

Results

Elevation and stress

In support of our elevation-based stress hypothesis, we found that low-elevation sites were more stressful than high-elevation sites for all the biotic and abiotic variables we examined (Table 1). Soil temperature was significantly higher and soil moisture was significantly lower at low-elevation sites, both in open areas as well as under *F. paradoxa*. However, these difference in soil abiotic stress where not the result of difference in soil particle size distribution ($t_4 = 0.82$, $P > 0.05$).

Consistent with the finding that low-elevation sites suffer greater abiotic stress, the biotic measures of stress show a similar pattern. Mature *P. edulis* mortality was significantly higher and average stem growth of mature *P. edulis* was significantly lower at the low-elevation sites (Table 1). Given the large differences in the stress variables between elevations, hereafter we refer to high-elevation sites as low stress and low-elevation sites as high stress.

Table 1 Abiotic and biotic stress variables measured at high-elevation and low-elevation cinder soil sites near Sunset Crater National Monument in northern Arizona, USA. Values are mean (± 1 SE)

Variable (test used and *P*-value)	High elevation/low stress ($n = 4$ sites)	Low elevation/high stress ($n = 4$ sites)
Soil temperature bare ground (°C) ($n = 10$) ($t_4 = 6.88$, $P < 0.0001$)	12.4 (0.30) a	15.1 (0.25) b
Soil temp-under *Fallugia paradoxa* (°C) ($n = 10$) ($t_4 = 5.81$, $P < 0.0001$)	10.4 (0.28) a	12.7 (0.26) b
Soil moisture (%) ($n = 10$) ($t_4 = 3.74$, $P < 0.001$)	6.0 (0.68) a	3.1 (0.37) b
Soil particle size > 2 mm (%) ($n = 10$) ($t_4 = 0.82$, $P > 0.05$)	50.0 (5.15) a	44.8 (3.76) a
Average annual stem growth of mature *Pinus edulis*, 1998–2003 (mm) ($n = 10$) ($t_4 = 7.12$, $P < 0.001$)	39.8 (2.13) a	28.6 (3.87) b
Mature *P. edulis* mortality (%) ($n = 100$) ($t_4 = 9.79$, $P < 0.0001$)	10.8 (2.95) a	58.3 (4.35) b

All replicates for each variable were averaged within a site. Site averages were tested between elevations using a *t*-test. Different letters represent significant differences between high and low elevations ($P < 0.05$).

Mortality and growth of juvenile *P. edulis*

In agreement with our hypothesis, we found that the performance of juvenile *P. edulis* in association with *F. paradoxa* was enhanced (i.e. facilitation) at high-stress sites, while it was negatively affected at low-stress sites (i.e. competition). Importantly, these patterns were consistent across four pairs of observational sites. Mortality and stem growth of juvenile *P. edulis* both showed a highly significant interaction between site stress and growing environment ($P < 0.0001$ for both), indicating that the performance of juvenile *P. edulis* in open and nursed environments differed across elevations. At high-stress sites, the average mortality of juvenile *P. edulis* growing in the open was six times higher than those growing in association with *F. paradoxa* ($F_{3,12} = 31.72$, $P < 0.0001$; Fig. 1a). Furthermore, when juvenile *P. edulis* survived in the open, their stem growth was only 50% of the growth of *P. edulis* growing in association with *F. paradoxa* ($F_{3,12} = 44.22$, $P < 0.001$; Fig. 1b).

In contrast, at the low-stress sites, the mortality of juvenile *P. edulis* growing with *F. paradoxa* was over two times greater than that of *P. edulis* growing in the open ($F_{3,12} = 31.72$, $P < 0.0001$; Fig. 1a). Similarly, stem growth of *P. edulis* in association with *F. paradoxa* was reduced by 48% compared with that of *P. edulis* growing in the open ($F_{3,12} = 44.22$, $P < 0.0001$; Fig. 1b).

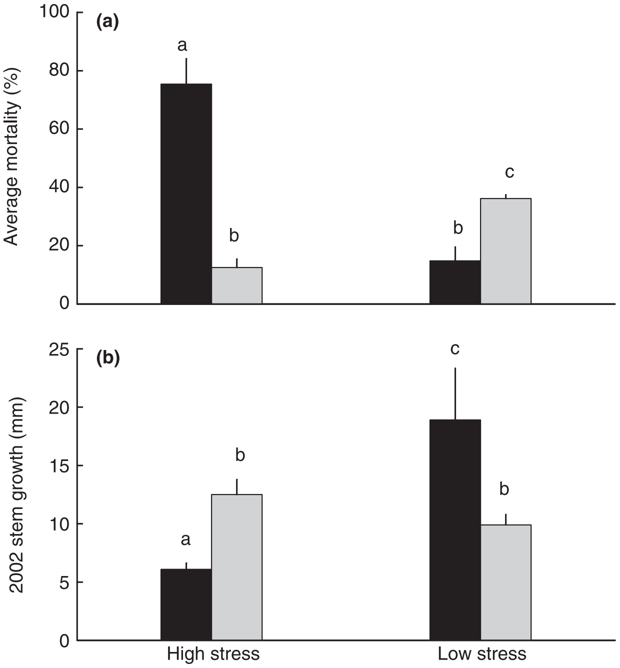

Fig. 1 Average mortality (a) and average 2002 stem growth (b) per site of juvenile *Pinus edulis* growing in the open (black columns) and in association *with Fallugia paradoxa* (grey columns) ($n = 4$ sites per stress level). Error bars represent 1 SE and different letters indicate significant differences between locations ($P < 0.05$).

Experimental alteration of *P. edulis–F. paradoxa* association

Experimental manipulation of *F. paradoxa* confirmed the patterns found in our observational studies. At the high-stress site, mortality of juvenile *P. edulis* differed significantly among treatments ($\chi^2 = 31.48$, $P < 0.0001$; Fig. 2a). Only 20% of *P. edulis* with intact *F. paradoxa* died, while the removal and tie-back of *F. paradoxa* resulted in 66.7 and 90% mortality, respectively. The mortality of juvenile *P. edulis* in the two experimental treatments (removal and tie-back groups) was significantly greater than *P. edulis* mortality in the control group (results of individual Fisher's exact tests not shown). Also, average stem growth of juvenile *P. edulis* with intact

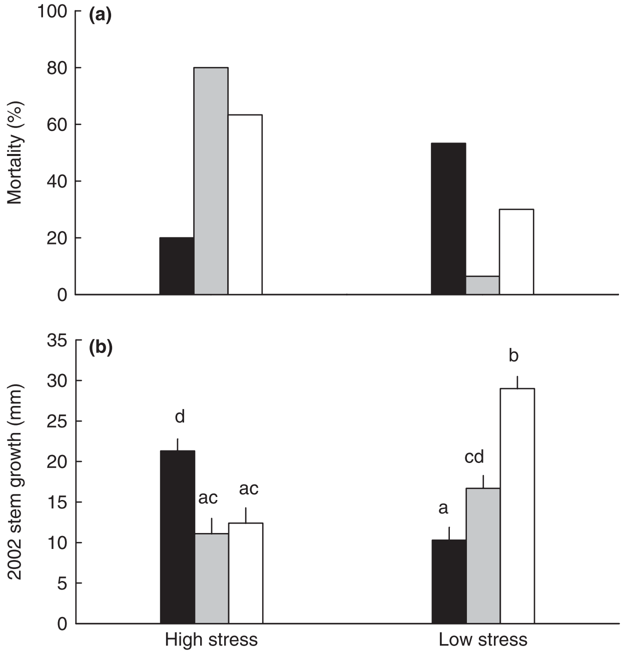

Fig. 2 Mortality (a) and average 2002 stem growth (b) of juvenile *Pinus edulis* that had their *Fallugia paradoxa* left intact (black columns), removed (white columns), or tied back (grey columns) ($n = 30$ juveniles per treatment). Error bars for growth represent 1 SE and different letters indicate significant differences between treatments ($P < 0.05$).

F. paradoxa associations was nearly two times greater than stem growth of *P. edulis* in the removal or tie-back groups ($F_{5,139} = 20.4$, $P < 0.0001$; Fig. 2b).

At the low-stress site, mortality of juvenile *P. edulis* again differed significantly among treatments ($\chi^2 = 12.07$, $P < 0.01$; Fig. 2a). Here, *P. edulis* with intact *F. paradoxa* experienced 53.3% mortality, compared with only 30 and 6.7% mortality in the removal and tie-back groups, respectively. Mortality of juvenile *P. edulis* with intact *F. paradoxa* was significantly greater than that of *P. edulis* with *F. paradoxa* tied back and showed a marginally significant increase over the mortality of *P. edulis* with *F. paradoxa* removed (results of individual Fisher's exact tests not shown). Consistent with our mortality findings, we also found that the growth of *P. edulis* with *F. paradoxa* intact was reduced by 50% when compared with *P. edulis* in the tie-back group, and by 33% compared with *P. edulis* with *F. paradoxa* fully removed ($F_{5,139} = 20.4$, $P < 0.0001$; Fig. 2b). Stem growth of juvenile *P. edulis* showed a highly significant interaction between site stress and treatment ($P < 0.0001$ for both), suggesting the magnitude of differences in stem growth among treatments was dependent on site stress.

Size and temporal effects on experimental mortality

Contrary to our hypothesis, at the high-stress site facilitative benefits remained constant for all sizes of *P. edulis* measured. The probability of juvenile *P. edulis* mortality was not significantly correlated with *P. edulis* height or BTD when *F. paradoxa* associates were left intact ($R^2 = 0.033$, $P > 0.05$ and $R^2 = 0.153$, $P > 0.05$, respectively), removed ($R^2 = 0.096$, $P > 0.05$ and $R^2 = 0.076$, $P > 0.05$, respectively) or tied back ($R^2 = 0.118$, $P > 0.05$ and $R^2 = 0.017$, $P > 0.05$, respectively).

In contrast, at the low-stress site, juvenile *P. edulis* mortality was inversely correlated with *P. edulis* size when *F. paradoxa* was completely removed. We found *c.* 30% of *P. edulis* mortality could be explained by pre-experimental *P. edulis* height ($R^2 = 0.208$, $P < 0.05$; Fig. 3a), and 21% of *P. edulis* mortality could be explained by pre-experimental *P. edulis* BTD ($R^2 = 0.288$, $P < 0.05$; Fig. 3b), with smaller *P. edulis* more likely to die in each case. *P. edulis* trees that died in the removal group were 44% shorter and had 38% smaller BTD than those that lived. However, juvenile *P. edulis* mortality was not significantly correlated with *P. edulis* height or BTD when *F. paradoxa* associates were left intact ($R^2 = 0.084$, $P > 0.05$ and $R^2 = 0.058$, $P > 0.05$, respectively) or tied back ($R^2 = 0.127$, $P > 0.05$ and $R^2 = 0.124$, $P > 0.05$, respectively).

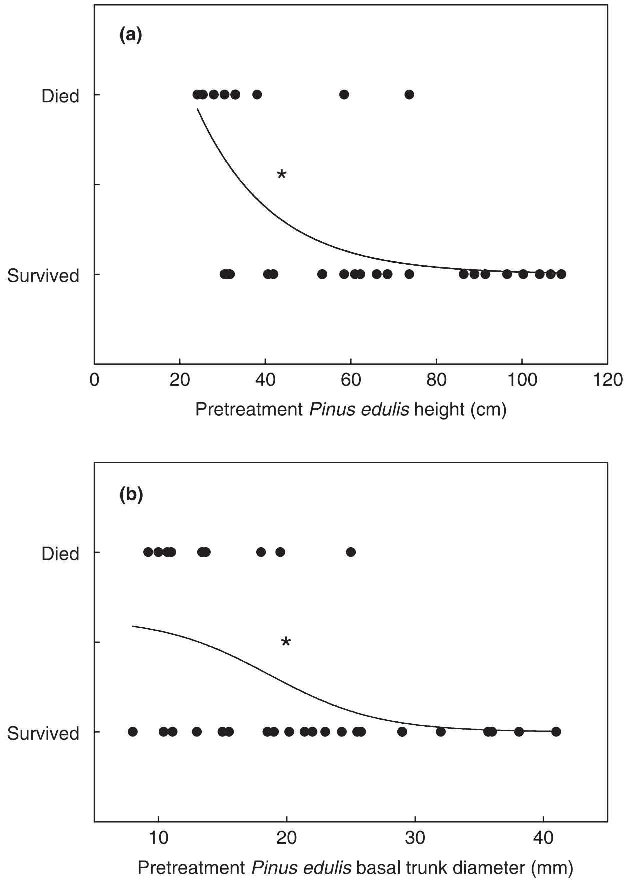

Fig. 3 Logistic regression of the relationship between mortality of juvenile *Pinus edulis* with *Fallugia paradoxa* removed at the low-stress site and pretreatment *P. edulis* height (a) and basal trunk diameter (b). *, significant correlation between the two variables ($P < 0.05$).

In support of our hypothesis, seasonal changes in the importance and/or intensity of facilitative and competitive interactions (as measured by juvenile *P. edulis* mortality) were observed during the experiment (Fig. 4). At the high-stress site, significant differences among treatments in juvenile *P. edulis* mortality existed during the rapid response period ($X_2^2 = 11.396$, $P < 0.01$; Fig. 4a) and the spring/summer period ($X_2^2 = 16.094$, $P < 0.001$; Fig. 4a). In both cases *P. edulis* mortality rates in both experimental treatments (removal and tie-back groups) were significantly higher than the controls (results of individual Fisher's exact tests not shown). The rapid response period and the spring/summer period both occurred during extremely harsh environmental stress conditions, with average PDSI values of –4 and –3.18, respectively. However, more moderate environmental stress conditions (average PDSI = –1.72) during the fall/winter period resulted in no significant differences between treatments in juvenile *P. edulis* mortality ($\chi^2 = 4.636$, $P > 0.05$; Fig. 4a).

In contrast, at the low-stress site significant differences among treatments in juvenile *P. edulis* mortality occurred only during the fall/winter period ($\chi^2 = 20.758$, $P < 0.0001$, Fig. 4b) when environmental stress conditions were more moderate (average PDSI = –1.72). The *P. edulis* mortality of the control group was significantly higher than either experimental group (results of individual chi-square comparisons not shown). At this site, we found no differences among treatments in juvenile *P. edulis* mortality during the rapid response period ($\chi^2 = 5.506$, $P > 0.05$; Fig. 4b) or the spring/summer period ($\chi^2 = 1.218$, $P > 0.05$; Fig. 4b) when harsher environmental stress conditions existed throughout the region (average PDSI = –4 and –3.18, respectively).

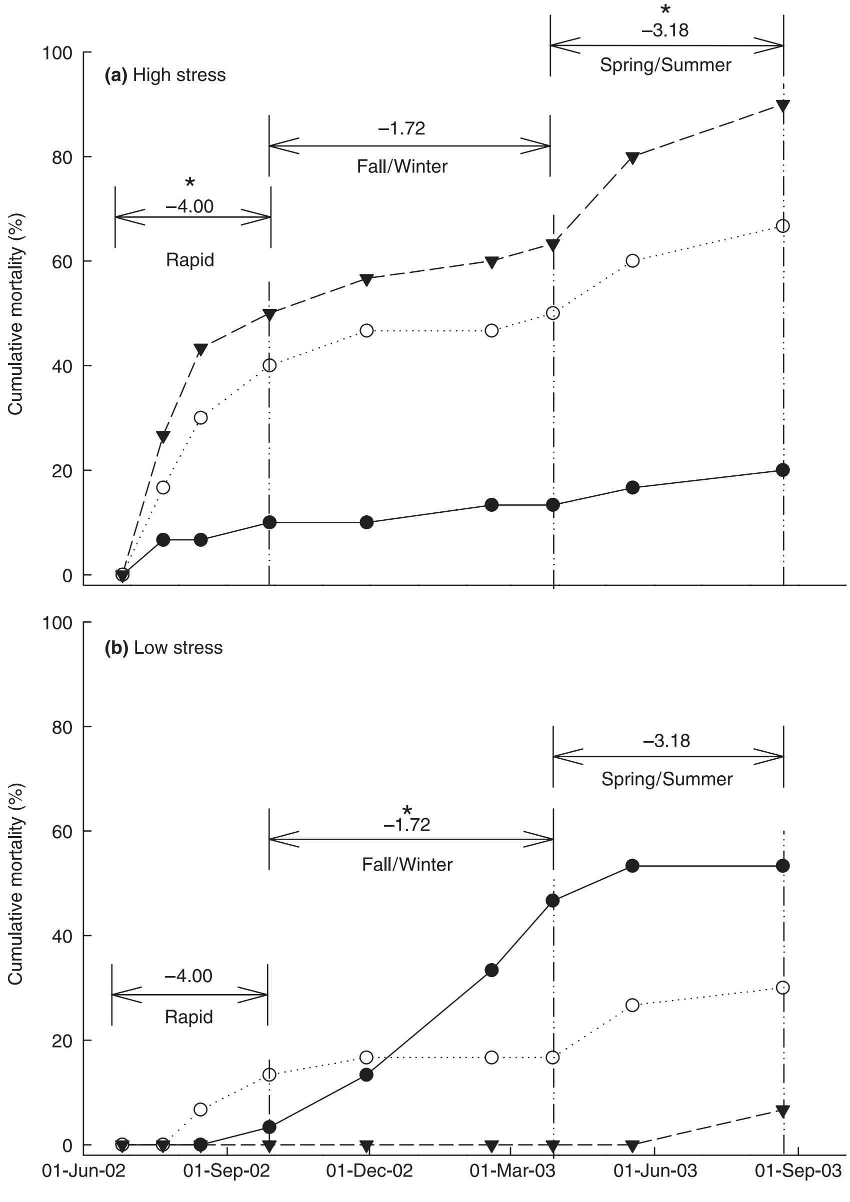

Fig. 4 Cumulative total mortality of juvenile *Pinus edulis* with *Fallugia paradoxa* intact (black circles), removed (white circles) or tied back (triangles) ($n = 30$ juveniles for all treatments) throughout the experiment at the high-stress site (a) and low-stress site (b). Seasonal differences of *P. edulis* mortality between treatments were tested on three dates represented by vertical lines: 25 September 2002 (rapid responses), 28 March 2003 (fall/winter responses) and 22 August 2003 (spring/summer responses). *, significant differences in observed mortality between treatments during the time periods represented between arrows ($P < 0.05$), and the average Palmer Drought Severity Index value for each time period is shown above the arrow.

Discussion

Changes in plant–plant interactions along a spatial stress gradient

Our observational and experimental data both demonstrated that plant–plant interactions shifted from facilitation at high-stress sites to competition at low-stress sites, and that these patterns were consistent across two plant performance parameters (survival and growth; Figs 1, 2). These findings are consistent with the hypothesis posed by Bertness & Callaway (1994) that the importance of facilitation would increase, and the importance of competition would decrease, with increases in stress. Maestre *et al.* (2005) found the nature of plant–plant interactions in arid and semiarid regions could differ in experimental and observational studies. For example, observational studies showed higher growth in the presence of neighbors at high and low stress, while experimental studies showed lower growth in the presence of neighbors at both stress levels (Maestre *et al.*, 2005). However, our results were consistent for growth and mortality measures in both the observational and experimental components of our study.

Our finding that competitive interactions increased with elevation was consistent with other studies along an elevational gradient conducted in arid and semiarid environments. At a low-elevation, high-stress site, Pugnaire & Luque (2001) showed increased performance of five associated understory plants growing under the experimentally planted leguminous shrub, *Retama sphaerocarpa*. They observed the opposite pattern in their high-elevation, low-stress site. Also, a recent study by Cavieres *et al.* (2006) showed that positive interactions between an alpine plant community and the nurse cushion plant *Laretia acaulis* were more common at lower elevations. These findings are not surprising as water stress is usually higher at the lower end of an elevational gradient in arid environments. In contrast, many studies of montane regions located in temperate, boreal or arctic climates have shown that facilitation increased with elevation (Callaway, 1998; Choler *et al.*, 2001; Cavieres *et al.*, 2002) because positive interactions stem from the ability of neighbors to protect the target species from extreme cold. In a study of 11 alpine sites that included 115 species over a large geographic range, Callaway *et al.* (2002) showed that the removal of neighbors had a positive effect at less stressful, lower elevation sites and a negative effect at more stressful, higher elevation sites in all but one site. This site was located in the Sierra Nevada mountains of Spain, which have a semiarid Mediterranean climate. These results suggest that plant–plant interactions along elevational gradients in arid and semiarid environments may be particularly complex because of opposing water and temperature stress gradients. The results also argue that more complex models than those currently available may be needed in these environments.

Above- and below-ground contributions to interactions

Previous literature has shown that facilitation (Callaway, 1995) and competition (Connell, 1983) can involve both above– and below-ground interactions. A few recent studies have attempted to partition net interactions between plants into both above- and below-ground, positive and negative contributions (Holzapfel & Mahall, 1999; Maestre *et al.*, 2003). Results from *F. paradoxa* manipulations at our high-stress site, where juvenile *P. edulis* from the tie-back group and removal group showed similar performance (Fig. 2), suggest that alteration of the above-ground environment is the most important benefit of facilitation. Juvenile *P. edulis* with *F. paradoxa* tied back did not receive any measurable benefit from retaining the nurse plant's root structure, as mortality and growth did not differ between the removal and tie-back treatments. These findings are consistent with those from a review by Holmgren *et al.* (1997) in which the provision of shade was the most important mechanism for facilitation.

In contrast, results of our tie-back experiment under low stress suggest that interacting plants compete for both above- and below-ground resources. Results from manipulations showed that shading of juvenile *P. edulis* by *F. paradoxa* and the *F. paradoxa*'s ability to acquire below-ground resources are presumably both important mechanisms contributing to the competitive interaction (Fig. 2). Juvenile *P. edulis* released from both above- and below-ground competition (removal group) had significantly higher growth than those released from only above-ground competition for light (tie-back group), and both had higher growth rates than *P. edulis* trees that were not released from either above- or below-ground competition (control group with intact *F. paradoxa*). Thus, along with a shift in the main net interaction (i.e. facilitation vs competition) across spatial stress gradients, it appears that the relative importance of above- and below-ground interactions also changes.

Results from this experiment need to be interpreted with caution, owing to two caveats of the tie-back treatment: tie-back of *F. paradoxa* did not completely eliminate shading effects as some focal *P. edulis* still experienced shade in the early morning, or late in the afternoon depending on tie-back position; and tie-back of *F. paradoxa* and compression of their branches resulted in a reduction of leaf area exposed to the sun, causing unknown alterations to the below-ground environment. Future experiments that include a fourth treatment (i.e. full removal followed by addition of shade to mimic only the above-ground effects of *F. paradoxa*) in a full-factorial design would allow further exploration of the relative importance of above- and below-ground factors.

Shifting interactions with *P. edulis* age

At high-stress sites, our observations and experiments argue that facilitation of *P. edulis* by *F. paradoxa* is important from seedling establishment until at least *c.* 35 yr of age (40 mm BTD, our largest size) as we found no differences in *P. edulis* performance based on *P. edulis* size. This is consistent with the finding that across all low-elevation, high-stress sites, *F. paradoxa* only accounted for approx. 20% of the available habitat, but > 60% of all juvenile *P. edulis* trees were found in association with *F. paradoxa* (Stulz, 2004). In addition, at a site very similar to ours, Callaway *et al.* (1996) found that establishment of a closely related pine species was dependent on association with a nurse plant.

In contrast, at our low-stress sites we found evidence that competition with *F. paradoxa* was strongest with older, larger *P. edulis* trees (Fig. 3). Here, mortality of *P. edulis* with *F. paradoxa* removed correlated significantly with both *P. edulis* height and basal trunk diameter. These findings suggest that, at the low-stress site, the association with *F. paradoxa* may be beneficial to *P. edulis* seedlings, but that the relationship may shift to competition as juvenile *P. edulis* age. These results are consistent with other studies that have shown that the balance of interactions between plants can change depending on life-history stage of one of the species involved (Walker & Vitousek, 1991; Chapin *et al.*, 1994; Pugnaire *et al.*, 1996; Hastwell & Facelli, 2003). For example, Rousset & Lepart (2000) found that colonizing oaks had greater positive interactions with neighbors early in development, but then turned to competition as the oaks aged. Further experimentation is needed to determine if the interaction between *F. paradoxa* and *P. edulis* is facilitative under low stress at the seedling stage, but switches to competition at the juvenile stage.

As juvenile *P. edulis* age and mature, their association with shrubs is likely to shift to competition, even in high-stress conditions. In an observational and experimental study at one of our high-stress sites, McHugh & Gehring (2006) showed that above- and below-ground growth of mature *P. edulis* was strongly negatively affected by shrubs, including the dominant species, *F. paradoxa.* Furthermore, *P. edulis* survival was positively associated with low shrub density (McHugh, 2004). Combined with our experiment, these studies argue for a life-stage shift in interactions from facilitation to competition between *P. edulis* and abundant shrubs as the tree ages. The opposing effects of *F. paradoxa* on juvenile and mature *P. edulis* indicate that interactions with *F. paradoxa* are likely to have a powerful impact on the occurrence and age class distribution of *P. edulis*, especially under drought conditions.

Temporal patterns in the intensity of plant–plant interactions

Our results also suggest that the intensity of interactions between two species can change seasonally throughout the year (Fig. 4) and can be related to changes in overall environmental stress conditions of the region. Furthermore, our results support earlier studies showing temporal switches in the net direction of interactions (Greenlee & Callaway, 1996; Pugnaire & Luque, 2001). For example, Kikvidze *et al.* (2006) recently showed that interactions between two dominant grassland species and their associated communities switched from competition during the early part of the growing season when conditions were favorable, to facilitation during the late part of the growing season when the site became more xeric. In this study, we found the intensity of net interactions seen across spatial stress scales (using mortality rates as an indicator of interaction intensity) strengthened or weakened during different time periods throughout the experiment. Facilitative affects of *F. paradoxa* on juvenile *P. edulis* at the high-stress site were strongest in the early part of the experiment, at the end of a record-level drought (rapid responses), and again during the warm dry period at the end of the experiment (spring/summer period; Fig. 4a – note the inflection point between rapid increases in mortality seen early on, and low rates of mortality seen through the middle portion of the study). Both of these time periods corresponded to periods of harsh region-wide environmental stress conditions (average PDSI = −4 and −3.18, respectively). In contrast, competitive affects of *F. paradoxa* on juvenile *P. edulis* at the low-stress site were strongest during the cooler, wetter period (at the end of the record dry year) at the middle of the experiment (fall/winter period; Fig. 4b – this time note the inflection point between low rates of mortality early on and the rapid accumulation of mortality seen over the winter months) when region-wide stress conditions were more moderate (average PDSI = −1.72). These findings add to a growing body of evidence that shifts in plant–plant interactions are correlated not only with changes in stress across spatial scales but with changes in stress conditions (such as temperature and moisture) across temporal scales as well (Belsky, 1994; Holzapfel & Mahall, 1999; Kikvidze *et al.*, 2006).

The results of our experiment suggest that spatial and temporal stress interacted to generate the final net interactions seen at low- and high-elevation sites. Not including temporal changes in plant responses to interactions could have resulted in very different conclusions. For example, if mortality of *P. edulis* had been recorded only after the ‘rapid response’ period, we would have concluded that *F. paradoxa* was facilitative under high stress but had no effect on *P. edulis* performance under low stress. Conversely, if mortality of *P. edulis* had been recorded only after the ‘fall/winter’ period, we would have concluded that *F. paradoxa* was competitive under low stress but had no affect on *P. edulis* performance under high stress. Mortality in some of our treatment groups was nearing 100% by late August 2003, making it impossible for our experiment to continue. However, we argue that long-term field experiments that are monitored at multiple times are needed in future studies to examine shifting interactions across spatial scales. Interactions between spatial and temporal scales that influence the net interactions between plants, such as seen in this study, may help to explain why several recent studies do not support the hypothesis that plant–plant interactions switch from competition to facilitation as stress increases (Kadmon & Tielbörger, 1999; Tielbörger & Kadmon, 2000; Pennings *et al.*, 2003; Maestre & Cortina, 2004; Armas & Pugnaire, 2005; Barchuk *et al.*, 2005). Including temporal shifts in future studies and theoretical models may also help resolve the debate about the role of environmental stress in determining the nature of interactions between plants in arid and semiarid environments, and may help to explain some of the inconsistencies in the nature of plant–plant interactions in dry environments (Maestre *et al.*, 2005).

Importance of shifting interactions involving a foundation species

Shifts in interactions, such as those observed in this study, add to a growing body of evidence demonstrating that interactions are strongly context-dependent, and that increasing the scale of a study (i.e. time, species, landscape) results in frequent reversals in the sign of an interaction (Bailey & Whitham, 2006). Documenting such shifts involving foundation species becomes increasingly important because foundation species define major vegetation types and influence the distribution and abundance of many dependent community members. Because *P. edulis* is a dominant tree in the third largest vegetation type in the United States (West, 1984), and supports approx. 1000 associated community members (Whitham *et al.*, 2003), we expect that the switch from competition to facilitation could affect the distributions of other associated community members from microbes to vertebrates (Brown *et al.*, 2001).

Understanding shifts in plant–plant interactions through time becomes increasingly important in the face of global climate change, especially when involving a foundation tree species. The 2001 report by the International Panel on Climate Change predicts increased frequency and severity of drought in the south-west United States over the next several decades (IPCC, 2001). Our findings suggest that, as drought pressure increases abiotic stress in the region, facilitation will become the more common interaction between juvenile *P. edulis* and *F. paradoxa*. We predict that *P. edulis* recruitment will be increasingly restricted to associations with *F. paradoxa*, resulting in a tighter linkage in the distribution of these species. However, close association with *F. paradoxa* is detrimental to mature pinyons (McHugh, 2004; McHugh & Gehring, 2006), so it is difficult to predict the full effect of the interaction of these two species on pinyon populations. Because *P. edulis* is a good 'barometer of change' for plant responses to drought (Gitlin *et al.*, 2006), our results suggest that shifts from competition to facilitation, and vise versa, may help to explain the ability of plants to expand or contract their ranges in response to climate change (Parmesan & Yohe, 2003; Gitlin *et al.*, 2006). Shifts towards facilitation may also play a critical role in postdrought recovery of important foundation species and their associated communities (Brown *et al.*, 2001) as well as buffer further vegetation changes in arid and semiarid regions.

Acknowledgements

We thank B. Sthultz, K. Kennedy, B. Mueller, K. Simonin, A. Stone, A. Foley, K. Haskins, A. and K. Goforth, J. Bosch, N. and S. Stulz and members of the Whitham and Gehring lab groups. CMS also thanks Steve Kimock for the muse. Funding was provided by NSF grants DEB-0236204, DEB-0087017 and DEB0415563. Special thanks to the Sunset Crater National Monument and the United States Forest Service staff for their cooperation.

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