

Context-dependent interactions between adult shrubs and seedlings in a semi-arid shrubland

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Abstract

Question: In semi-arid systems, rainfall gradients can cause plant-plant interactions to shift from negative to positive or vice versa. However, the importance of a second major abiotic factor, soil nutrients, has rarely been considered. We consider different combinations of both factors and ask: do net adult-seedling interactions become less competitive and more facilitative with increasing overall abiotic harshness?

Location: Succulent Karoo, Western Cape, South Africa.

Methods: We examined the interactions between seedlings and adult shrubs at two sites. Sites differ in rainfall, and each contain two habitats: Nutrient-rich mounds associated with underground termitaria and a relatively nutrient-poor matrix. We carried out a spatial pattern analysis of community-wide seedling-adult associations. We then conducted field and greenhouse experiments to test the effects of soil and the presence of neighbouring shrubs on the growth and survival of six seedling species.

Results: At the higher rainfall site, both competitive and facilitative effects of adults on seedlings were found but did not differ by habitat, despite the more benign conditions in the mound habitat. At the lower rainfall site, adult shrubs generally had neutral effects on seedlings in the matrix habitat. In the nutrient-rich mound habitat, however, adult shrubs had strong and consistently competitive effects on seedlings.

Conclusion: Seedling-adult interactions could not be predicted by a simple overall gradient of abiotic harshness, demonstrating the need for more complex, mechanistic models to predict plant-plant interactions. We suggest that rainfall and soil nutrients affect seedling-adult relations through their interactive effects on the life-history attributes of the species involved.

Keywords: Competition; Facilitation; Nurse-plant effect; Point pattern analysis; Succulent Karoo.

Nomenclature: Germishuizen & Meyer (2003).

Introduction

The direction and strength of plant-plant interactions can be context-dependent, varying with such factors as abiotic stress, predation pressure, life stage and the species involved (Grime 1973; Bertness & Callaway 1994; Goldberg & Novoplansky 1997; Callaway & Walker 1997; Callaway 1998). Recently, the role of abiotic stress in determining the relative importance of competition versus facilitation has come to the fore. A growing body of theory and empirical evidence suggests that competition may become relatively less important and facilitation relatively more important as abiotic conditions become more limiting (Bertness & Callaway 1994; Holmgren et al. 1997; Bruno et al. 2000; Callaway et al. 2002; Bertness & Ewanchuk 2002). However, while numerous studies have examined changes in the competition-facilitation interplay across gradients of single abiotic factors, few have examined these changes in the context of multiple factors (Holmgren et al. 1997; Ibáñez & Schupp 2001).

In arid and semi-arid systems, seedlings can experience both facilitative and competitive effects of neighbouring adult 'nurse' plants. Seedlings can benefit from reduced thermal stress or evapotranspiration (Franco & Nobel 1988; Greenlee & Callaway 1996), improved soil water conditions (Barnes & Archer 1999), elevated soil nutrients (Nobel 1989), and protection from herbivory (Ibáñez & Schupp 2001; Rebollo et al. 2005) provided by adult plants. Conversely, seedlings can also suffer from increased competition for light, soil water, or nutrients (Nobel 1989; Reichenberger & Pyke 1990; Holmgren et al. 1997). The net direction and strength of these interactions are thought to depend on site productivity (Bruno et al. 2003). While water availability in semi-arid environments has been shown to alter the net direction of plant-plant interactions (Greenlee & Callaway 1996; Tielbörger & Kadmon 1997; Kitzberger et al. 2000) the role of the second major productivity-related variable, soil nutrients, has rarely been addressed

in the context of the facilitation-competition interplay (Rebele 2000).

In the semi-arid Succulent Karoo shrubland of South Africa, productivity varies between plant communities within sites as well as among sites. Two distinct communities typically occur within a site: vegetation patches associated with termitaria and the surrounding matrix vegetation (Milton 1990; Midgley & Musil 1990; Esler & Cowling 1995). Patches overlying underground termitaria, known as *heuweltjies* (little hills) or mima-like mounds, are circular areas (10–20 m in diameter) where the soil is nutrient-enriched, more alkaline, and finer textured as a result of the foraging activity of the termite *Microhodotermes viator* (Milton & Dean 1990; Midgley & Musil 1990). Mounds are often preferentially grazed, colonized by herbivorous rodents, and disturbed by foraging aardvarks (*Orycteropus afer*) (Milton et al. 1992). Thus, vegetation dynamics on and off mounds have the potential to differ substantially, with consequences for seedling-adult interactions.

Here, we examine seedling-adult relations on termitaria and in the surrounding matrix vegetation at two sites that differ in rainfall. Specifically, we examine the hypothesis that the net effect of adult shrubs on seedlings becomes less strongly competitive and more facilitative with increasing overall abiotic harshness, e.g. from the on-mound habitat at the higher rainfall site to the off-mound habitat at the lower rainfall site. To test this, we examine community-wide patterns of seedling-adult shrub spatial associations. We then use greenhouse and field experiments involving a subset of species to test experimentally the effects of soil and neighbouring adult shrubs on seedling performance.

Methods

Study sites

Field data were collected from two sites in the Succulent Karoo, South Africa: the Tierberg Karoo Research Centre (33°10' S, 22°17' E), 30 km east of Prince Albert, and the Worcester Veld Reserve (33°39' S, 19°26' E), Worcester. Both sites are subject to low-level herbivory and disturbance by native wild animals. Soils are sandy loams or sandy clay loams, with soil on termite mounds 10–15% higher in clay fraction than soil on the surrounding matrix (Midgley & Musil 1990; Milton et al. 1992). On average (over 105 years), Prince Albert receives 172 ± 67 mm rain per year with an autumn (February–April) maximum while Worcester receives 269 ± 69 mm per year (over 125 years) with a winter (June–August) maximum (South African Weather Service). Plant productivity in South African semi-arid

regions increases linearly with increasing precipitation (Rutherford 1980). This is reflected in the higher vegetation cover at Worcester (70%), compared to 35% cover at Prince Albert. Shrubs at both sites are short-statured, but larger at Worcester (mean height ca. 50 cm, vs. ca. 30 cm at Prince Albert).

Spatial pattern analysis

Data for the spatial analysis were collected in the summer (December–March) of 2000–2001. Since it did not rain at the study sites during the summer of 2000–2001, summer sampling ensured that all seedlings surveyed had at least survived since the last rainfall (Worcester: mid-September; Prince Albert: early November). We did this to decrease the chances of observing patterns caused only by dispersal and increase the chances of observing patterns caused by favourable microsite conditions. At both sites, plots of 4 m × 4 m were established on six randomly selected mounds and six off-mound areas 10 m east of the edge of each mound. All shrubs within each plot were mapped and their species and canopy measurements (height and diameter in two axes) were recorded. Shrub volume was calculated from canopy measurements as if shrubs were ellipsoid in shape. Shrubs were divided into the categories 'adult' and 'juvenile' based on size, with size cut-offs determined by field observations of the minimum size of reproductive shrubs of each species. Spatial patterns of all juveniles, regardless of species, were considered together due to small sample sizes. Where one species had a strong representation, as with *Tripteris sinuata* in the Prince Albert off-mound habitat and *Mesembryanthemum guerichianum* in the Prince Albert on-mound habitat (Table 1), separate analyses were performed with these species alone and with all other species lumped together.

Spatial patterns of juveniles relative to adults were analysed using bivariate *O*-ring statistics (Wiegand et al. 1999; Wiegand & Moloney 2004). The *O*-ring statistic is a point-pattern statistic that considers the mean number of neighbours in a ring of radius r and ring-width of Dr around an individual, thus isolating specific distance classes. In this case, bivariate *O*-ring statistics measure the density of neighbouring juveniles as a function of distance from the centres of an average adult shrub, as detailed in Wiegand & Moloney (2004). Data from all six replicate plots were combined into one overall, mean function (Diggle et al. 1991; Schenk et al. 2003) of the bivariate *O*-ring statistic (see App. 1). To detect possible facilitation or competition between adult shrubs and juveniles, we contrasted our data to an antecedent condition null model (Wiegand & Moloney 2004) that randomizes the locations of the juveniles (because

they could potentially be found anywhere in the plot) and keeps the locations of the adult shrubs fixed (because their location did not change during juvenile establishment). Ninety-nine percent confidence envelopes were calculated from the highest and lowest values of $O(r)$ taken from 99 simulations of the null model.

Greenhouse experiment

Four species from each study site were chosen for experimental study. The selected species represent two dominant on-mound species and two dominant off-mound species from each site (Table 1). They included deciduous, leaf-succulent, and stem- and leaf-succulents. We conducted a greenhouse experiment to isolate the role of soil conditions on seedling growth. This was, primarily, a simple test of whether seedlings of all species could grow in all soil types. Seeds of the selected species were collected from the field. In March 2001, seeds were sown into individual tray cells containing soil from on- and off-mound habitats from the field sites at which those species occur naturally. Soil was collected from the top 10 cm of the soil profile. A total of 48 seedlings of each species were established in each of the two soil types (on- vs. off-mound). Seeds of *Ruschia caroli* had very low germination success in both soil types, and therefore this species could not be

used in either the greenhouse or field experiments (see below). Seeds of *Pteronia paniculata* also had low germination success, with sufficient replication only for the field experiment. Seedlings of the remaining species were allowed to grow for six months. Seedlings were watered so as to maintain a moderate level of drought stress (as assessed by visual indicators such as leaf wilt and chlorosis). Within each species an equal amount of water was applied to seedlings in both soil types. After six months, all plant stems were cut at the base, dried in a 70° C oven, and weighed. Where possible, roots were washed, dried, and weighed. The effect of on-mound vs. off-mound soil on biomass (total, or above-ground where root biomass was not measured) was analysed for each species using a *t*-test. Data were log-transformed when necessary to meet test assumptions. All analyses were carried out using JMP statistical software (Version 5.1, Anon. 2003).

Field experiment

We conducted a field experiment to evaluate habitat and microsite effects on transplanted seedlings. At each field site, eight paired on- and off-mound plots (4 m × 4 m each) were randomly selected. Each plot was divided into two equally sized subplots, one cleared of all above-ground vegetation by clipping and the other left

Table 1. Percentage of total cover and number of juveniles used in the spatial pattern analysis (Fig. 1) for each of the dominant shrub species, both on and off termite mounds, at each site. Experimental study species are indicated in bold.

	Percentage of total cover		Number of juveniles	
	On-mound	Off-mound	On-mound	Off-mound
Prince Albert				
<i>Psilocaulon junceum</i>	43	0	19	0
<i>Ruschia spinosa</i>	0	38	0	35
<i>Malephora lutea</i>	34	0	7	0
<i>Pteronia pallens</i>	3	24	9	5
<i>Tripteris sinuata</i>	2	12	16	271
<i>Galenia fruticosa</i>	0	10	0	11
<i>Mesembryanthemum guericchianum</i>	3	0	57	0
<i>Atriplex lindleyi</i>	2	0	37	0
<i>Hereroa latipetala</i>	0	2	0	11
Other species	13	13	3	15
Total			148	354
Worcester				
<i>Pteronia paniculata</i>	2	54	0	9
<i>Ruschia caroli</i>	14	28	0	31
<i>Pteronia incana</i>	31	0	6	0
<i>Euphorbia burmannii</i>	15	4	7	8
<i>Tylecodon paniculatus</i>	14	0	16	0
<i>Senecio junceus</i>	1	10	0	32
<i>Euphorbia mauritanica</i>	8	0	14	0
<i>Aloe microstigma</i>	2	0	8	0
Other species	13	4	12	11
Total			63	91

undisturbed. Seedlings were allowed to germinate and establish in the greenhouse as detailed above until June 2001, when they were transplanted to the field. *Tylecodon paniculatus* was transplanted in September 2001 due to its small size in June. Of each species 12 seedlings were transplanted into each subplot. Each species was transplanted only to the field site from which it was chosen as a representative species. Seedlings in the 'open' (cleared) treatment were planted in a grid with at least 20 cm of space between seedlings to avoid competition among seedlings. Seedlings in the 'neighbour plant' treatment were planted on the southern edge of the canopy of a randomly selected adult plant within the undisturbed subplot. Individuals of all dominant species in each habitat were used as neighbours; the species of the adult plant was recorded.

Seedlings were monitored monthly for growth and survival beginning in August 2001. Numbers of leaves and branches were counted until their large numbers became impractical to count (October or November 2001, for most species). Seedling survival was monitored until March 2002. Unfortunately, it did not rain at Prince Albert in the first month after seedlings were transplanted, so that all seedlings of *T. sinuata* died before any data could be collected on them. For *T. paniculatus* seedlings, which were transplanted at the end of the rainy season, growth was negligible and is therefore not reported here.

For each species, two-way split-plot ANOVAs were used to test the overall effects of habitat (on- vs. off-mound) and presence of an adult neighbour plant on growth and survival. Habitat and microsite (neighbour vs. open) were treated as fixed factors and block (plot pair) was treated as a random variable. We used the mean growth and proportional survival among seedlings within each subplot as the response variables. In order to isolate survival patterns caused by potential competitive or facilitative effects of neighbouring shrubs, only seedlings that apparently died from drought stress (as indicated by desiccated leaves and stems) were included in the survival analyses. Seedling mortality due to other causes was low (9% and 10% of total mortality at Prince Albert and Worcester, respectively). In order to meet the ANOVA assumption of homogeneity of variances, least squares were weighted by the reciprocal of factor level variances (Neter et al. 1996). All analyses were carried out using JMP statistical software (Version 5.1, SAS Institute; Anon. 2003). Since results for both growth traits were similar, we report only the results for the number of leaves.

Results

Spatial pattern analysis

At Prince Albert, seedlings in the off-mound habitat exhibited significant aggregation relative to adult plants at radii within the canopy of adult plants (Fig. 1a). Seedling density peaked at a density 170% greater than the density expected based on a random seedling distribution. A marginally significant trend in the same direction was detected when *Tripteris sinuata* was excluded from the analysis. This peak in seedling density was less (70% greater than expected) than the highly significant peak when *T. sinuata* was considered alone (200% greater than expected). This suggests that the proportional contribution of *T. sinuata* to community-wide aggregation was greater than the contribution of the remaining species, but that aggregation apparently did occur on a community-wide level.

In contrast, seedlings in the on-mound habitat at Prince Albert were significantly overdispersed relative to adult plants at scales below the mean adult shrub canopy radius (Fig. 1b). Seedling density was as much as 70% lower than expected density. Significant trends in the same direction were detected when *Mesembryanthemum guericchianum* was excluded from the analysis and when *M. guericchianum* was considered alone. The magnitude of overdispersion was similar in both cases (70% and 80% lower than expected, respectively) to the magnitude observed when all species were considered together.

At Worcester, seedlings were randomly distributed relative to adult plants at nearly all spatial scales, both off- (Fig. 1c) and on-mound (Fig. 1d). This lack of pattern was not simply due to lower sample sizes at Worcester. In the off-mound habitat at Worcester, seedling densities peaked at only 40% greater or less than the expected seedling density. In the on-mound habitat, two radii had relatively large effect sizes (90% greater and 80% lower density than expected), but no consistent trend of seedling aggregation or dispersion could be observed, and at most radii seedling density did not differ substantially from the expected density (Fig. 1d).

Greenhouse experiment

Seedlings of all species except *Ruschia caroli* could germinate and grow successfully in both soil types in a non-competitive greenhouse setting. *R. caroli* germinated poorly in both soil types. Across all established species except *Pteronia incana*, seedlings grew significantly faster in mound soil than in off-mound soil (Fig. 2). *P. incana* suffered from a severe aphid attack; results for this species may not reflect actual treatment effects on seedling performance.

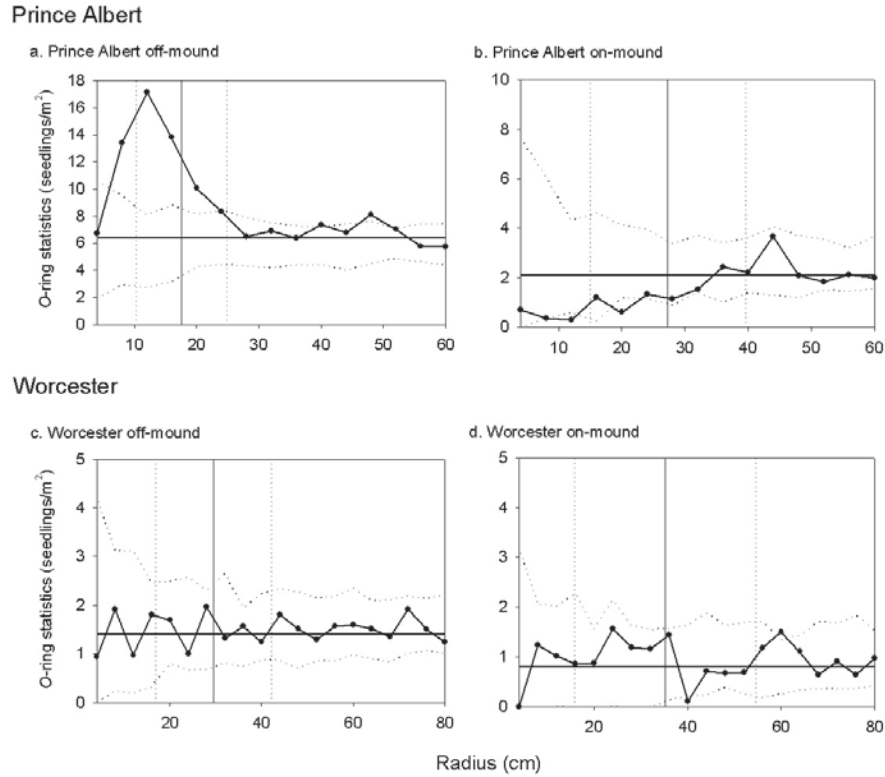


Fig. 1. Results of spatial pattern analysis of seedling association to adult plants for (a) Prince Albert off termite mound; (b) Prince Albert on-mound; (c) Worcester off-mound; (d) Worcester on-mound habitats. Observed O -ring statistics are given by a solid line, and dashed lines represent 99% confidence envelopes around $O(r)$ for a random pattern of seedlings. Solid vertical lines indicate the mean adult shrub canopy radii, and dashed vertical lines indicate the mean adult canopy radii ± 1 SD. The solid horizontal lines give the expected density of seedlings for a random pattern. Numbers of replicates are given in Table 1.

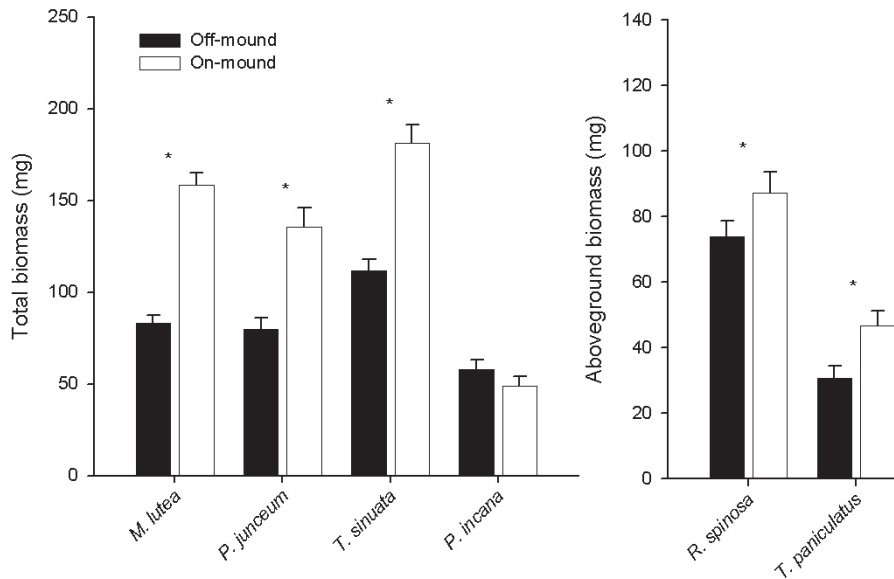


Fig. 2. Mean biomass (and SE) among greenhouse experiment seedlings, which were grown either in soil collected from termite mounds or from off-mound habitats. Significant differences ($\alpha = 0.05$) between on-mound and off-mound mean biomass are indicated with asterisks.

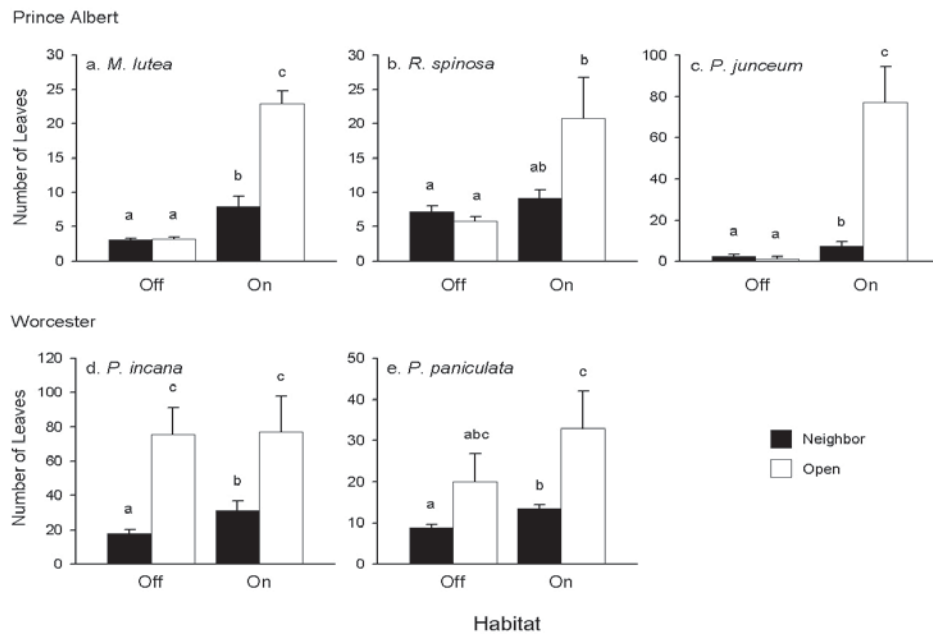


Fig. 3. Mean number of leaves (and SE) among field experiment seedlings, which were grown either on or off termite mounds and, within each of these habitats, either proximate to a neighbouring adult shrub ('neighbour' microsite) or in a cleared area ('open' microsite). Significant differences among different habitat-microsite combinations are indicated by different letters ($\alpha = 0.10$, due to small sample sizes: $n = 4$ for each habitat-microsite combination). See App. 2 for model results.

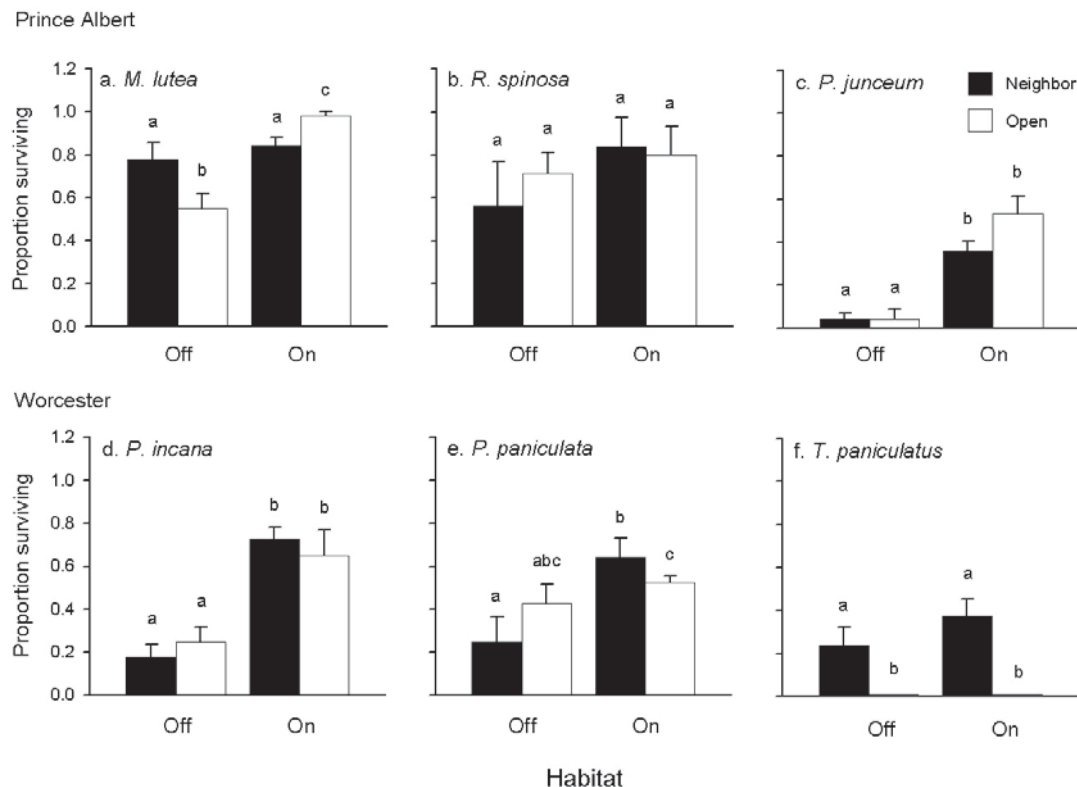


Fig. 4. Proportional survival of field experiment seedlings, which were grown either on or off termite mounds and, within each of these habitats, either proximate to a neighbouring adult shrub ('neighbour' microsite) or in a cleared area ('open' microsite). Significant differences among different habitat-microsite combinations are indicated by different letters ($\alpha = 0.10$, due to small sample sizes: $n = 4$ for each habitat-microsite combination). See App. 3 for model results.

Field experiment

At Prince Albert, there was an overall trend among the species to have more leaves in the on-mound habitat than in the off-mound one (Fig. 3a-c; App. 2). Seedlings generally had more leaves when grown in the open than when grown in proximity to adult neighbours, but this effect was found to depend on habitat (significant or marginally significant habitat by microsite effect) for all species (Fig. 3a-c; App. 2). In the off-mound habitat, none of the three species showed significant differences between the two microsites. In contrast, seedling growth on the mounds was significantly greater in the open microsite than in the nurse plant microsite for two of the three species, with the third species, *R. spinosa*, showing a strong trend in the same direction (Fig. 3b).

At Worcester, habitat did not affect seedling growth, while seedlings had significantly more leaves in the open microsite than in the neighbour microsite (App. 2). Seedlings in the open microsites had more leaves in both the off-mound and on-mound habitats (Fig. 3d-e).

Seedling survival trends differed substantially among species (Fig. 4; App. 3). At Prince Albert, all three species had significantly or marginally significantly higher survival in the on-mound habitat than in the off-mound habitat. Effects of neighbour plants on survival, however, were only detected for one species, *M. lutea*. For this species, survival in the on-mound habitat was higher in the open microsite, suggesting suppression by adult shrubs, whereas in the off-mound habitat, survival was higher in the nurse plant microsite (Fig. 4a). At

Worcester, results were similarly species-dependent. In the on-mound habitat, both *P. paniculata* and *T. paniculatus* survival was higher among seedlings growing proximate to adult shrubs. In the off-mound habitat, only *T. paniculatus* survival depended on microsite, with survival significantly higher among seedlings growing next to adult shrubs.

Discussion

Seedlings in semi-arid systems have been shown to benefit from proximity to adult plants (Franco & Nobel 1988; Nobel 1989; Flores & Jurado 2003). A growing body of evidence, however, indicates that the net balance between competition and facilitation may be conditional (Holmgren et al. 1997; Tielbörger & Kadmon 1997; Kitzberger et al. 2000; Callaway et al. 2002). Current facilitation theory (Bertness & Callaway 1994; Bruno et al. 2003) and Grime’s (1973, 1979) theory of plant life-history strategy both suggest that competition should be relatively less important and facilitation more important in environments with high abiotic stress. Conversely, Tilman (1985, 1988) has argued that the intensity of competition should stay constant along stress gradients (but does not consider facilitation in his model). Here, we examined seedling-adult interactions at two sites and in two habitats within each site: the more nutrient-rich termite mound habitat and the less nutrient-rich off-mound matrix. Our results demonstrate the complex outcomes of these different conditions in a

Table 2. Summary of spatial pattern analysis and field experiment results indicating suppressive, facilitative, or neutral effects of adult shrubs on shrub seedlings. Seedling-adult relations are compared between two sites and, within each site, between seedlings growing on and off termite mounds. Results are presented by seedling species. Parentheses indicate non-significant but large magnitude trends in the direction of the interaction indicated.

	Prince Albert		Worcester	
	On-mound	Off-mound	On-mound	Off-mound
Field spatial pattern				
All species combined	Suppression	Facilitation	Neutral	Neutral
<i>Mesembryanthemum guerichianum</i>	Suppression			
<i>Tripteris sinuata</i>		Facilitation		
Other species (mostly those below)	Suppression	(Facilitation)	Neutral	Neutral
Field experiment - growth				
<i>Malephora lutea</i>	Suppression	Neutral		
<i>Ruschia spinosa</i>	(Suppression)	Neutral		
<i>Psilocaulon junceum</i>	Suppression	Neutral		
<i>Pteronia incana</i>			Suppression	Suppression
<i>Pteronia paniculata</i>			Suppression	(Suppression)
Field experiment - survival				
<i>Malephora lutea</i>	Suppression	Facilitation		
<i>Ruschia spinosa</i>	Neutral	Neutral		
<i>Psilocaulon junceum</i>	Neutral	Neutral		
<i>Pteronia incana</i>			Neutral	Neutral
<i>Pteronia paniculata</i>			Facilitation	Neutral
<i>Tylecodon paniculatus</i>			Facilitation	Facilitation

natural system (Table 2). In general, a simple gradient of abiotic harshness is not sufficient to predict the outcome of plant-plant interactions in this system.

Seedlings generally performed better on the mounds than in the surrounding matrix. In the greenhouse, seedlings were larger in mound soil than in off-mound soil, and the higher productivity of the mound habitat manifested itself in the general tendency for seedlings to achieve larger sizes and have higher survival rates in this habitat under field conditions. These results verify that abiotic conditions are more favourable on the mounds than in the matrix, probably due to the combination of higher soil nutrient levels and higher water-holding capacity in the finer textured soils (Midgley & Musil 1990).

Based on these abiotic conditions and the predictions of facilitation theory, the net effect of neighbouring plants would be expected to be more strongly competitive on the mounds than in the off-mound matrix within each site. Results from the Prince Albert site support this prediction, since seedlings were suppressed by adult shrubs in the on-mound habitat but not in the off-mound habitat. In the on-mound habitat, seedlings of all species grew more than twice as large when in the open than when in proximity to an adult shrub, and survival was generally higher in the open microsite. The results of the field experiment are consistent with the community-wide pattern of seedling dispersion away from adult plants that was detected in the spatial pattern analysis. Thus, the collective evidence suggests that adult shrubs in the on-mound habitat have strong competitive effects on seedlings.

Conversely, in the off-mound habitat there was no evidence that adult shrubs suppress seedling growth or survival. Evidence for facilitation was similarly scant. In this habitat, however, experimental results contrast with the community-wide patterns of seedling spatial aggregation around adult shrubs. Seedling aggregation is not merely attributable to short-distance seed dispersal, since in only 17% of the cases was the closest adult neighbour a conspecific. It is possible that aggregation was caused primarily by the seed-trapping effects of adult shrubs. Alternatively, it is possible that facilitation plays an important role in this habitat only in certain cases, e.g. for particular species, such as *T. sinuata*, which was strongly represented in the spatial pattern data; or shortly after seedling emergence, when soil remains moist around shrub islands longer than it does in the open (Flores & Jurado 2003); or in years of lower precipitation than the year in which the experimental study was conducted (Greenlee & Callaway 1996).

While net seedling-adult interactions were divergent in the two habitats at Prince Albert, these interac-

tions were similar across both habitats at the Worcester site, consistent with Tilman's (1985, 1988) theory of constant competitive intensity. Both on and off the mounds, seedling growth was limited by proximity to adult shrubs. Moreover, the magnitude of this effect was similar in both habitats (Fig. 3). Seedlings growing next to adult neighbours had fewer leaves and branches and exhibited the tall, spindly morphology characteristic of light-limited plants. Conversely, seedling survival was higher under nurse shrubs in several cases. Similar results, wherein adult shrubs had competitive effects on seedlings in terms of growth but facilitative effects in terms of survival, were found by Kitzberger et al. (2000) in a Patagonian steppe system. These contrasting effects observed at Worcester may be due to a trade-off between reduced thermal stress and reduced light availability under nurse plants (Holmgren et al. 1997). Such contrasting effects may, additionally, explain the lack of significant spatial associations between seedlings and adult shrubs at the community level.

Results across the two sites are also equivocal in their support of our predictions. We expected the net seedling-adult interaction to be most strongly competitive at the higher rainfall, higher cover Worcester site than at the lower rainfall Prince Albert site. Precipitation over the course of the field experiment (10 months) totalled 275 mm at Worcester and 159 mm at Prince Albert, consistent with the long-term averages for these sites. Although differences between the two sites cannot be attributed solely to precipitation, it is likely that lower rainfall translates to higher abiotic stress at the Prince Albert site, given the great importance of precipitation in semi-arid systems. Thus, the off-mound habitat at Prince Albert may be considered the most harsh of the various site-habitat combinations in terms of abiotic conditions. As predicted, competition was least evident here relative to other site-habitat combinations. Interestingly, however, competition was most consistently seen in the on-mound habitat at the same site, not at the more productive Worcester site. This suggests that a simple gradient of abiotic harshness is not sufficient to predict the outcome of plant-plant interactions in this system, contrary to the results of other single-gradient studies (Callaway et al. 2002; Bertness & Ewanchuk 2002).

Although our results only partially support the facilitation and Grime models of plant-plant interactions, they also only partially support Tilman's model of constant competitive intensity. A possible explanation for these results is that adult plant life-history characteristics determine the effects of these shrubs on seedlings. Goldberg & Novoplansky (1997) postulate that, where resources such as rainfall are pulsed in their availability,

competition is weak only when plant performance during interpulse phases is independent of plant performance during pulses and when the interpulse phase is critical in determining lifetime plant fitness. These assumptions appear to be met for the Prince Albert matrix species and Worcester matrix and mound species, which tend to be long-lived and slow-growing (Midgley & van der Heyden 1999; Wiegand et al. 2000), but not for the short-lived, fast-growing Prince Albert on-mound species (Milton 1990; Esler & Cowling 1995). In the latter habitat, shrub fitness appears to be contingent upon rapid growth and reproduction before the next potentially fatal drought period (Esler & Cowling 1995) or animal disturbance (since animal disturbance is considerably more likely on the mounds than in the matrix [Milton et al. 1992]). If such shrubs are able to acquire water and nutrients rapidly when these resources become available, these species are likely stronger competitors than their more stress-tolerant counterparts.

Although life-history strategy has long been predicted to affect plant competitive ability (Grime 1979), it has not been considered in the context of the competition-facilitation balance. Moreover, facilitation has generally not been included in Tilman's model, despite its potential to alter the net direction or strength of plant-plant interactions even if competitive intensity does remain constant. In order to develop a mechanistic model of plant-plant interactions in arid and semi-arid systems, we must refine our understanding of both the effects of life-history strategy on these interactions and the effects of interactions among abiotic gradients on plant life-history strategies. Such a mechanistic understanding is fundamental to predicting community maintenance or change under varying abiotic conditions.

Acknowledgements. We are grateful to the Western Cape Department of Agriculture for permission to work at the Worcester Veld Reserve and Hannes Botha for his assistance at this site. We thank Pieter Harmse, Richard Dean, Katharina Niemeyer, Lee Simons, and Stella Ndlhovu for assistance with field and greenhouse experiments. We also thank the South African Weather Service for rainfall data. This manuscript benefited from comments by Truman Young, Mikaela Huntzinger, Fabio Scarano, and several anonymous reviewers. This research was funded by a Fulbright Student Scholarship and Percy Sladen Memorial Fund grant to C. Riginos and by University of Stellenbosch and National Research Foundation (South Africa) research grants to S.J. Milton.

References

- Barnes, P.W. & Archer, S. 1999. Tree-shrub interactions in a subtropical savanna parkland: Competition or facilitation? *J. Veg. Sci.* 10: 525-536.
- Bertness, M.D. & Callaway, R.M. 1994. Positive interactions in communities. *Trends Ecol. Evol.* 9: 191-193.
- Bertness, M.D. & Ewanchuk, P.J. 2002. Latitudinal and climate-driven variation in the strength and nature of biological interactions in New England salt marshes. *Oecologia* 132: 392-401.
- Bruno, J.F., Stachowicz, J.J. & Bertness, M.D. 2003. Inclusion of facilitation into ecological theory. *Trends Ecol. Evol.* 18: 119-125.
- Callaway, R.M. 1998. Are positive interactions species-specific? *Oikos* 82: 202-207.
- Callaway, R.M. & Walker, L.R. 1997. Competition and facilitation: a synthetic approach to interactions in plant communities. *Ecology* 78: 1958-1965.
- Callaway, R.M., Brooker, R.W., Choler, P., Kikvidze, Z., Lortie, C.J., Michalet, R., Paolini, L., Pugnaire, F.I., Newingham, B., Aschehoug, E.T., Armas, C., Kikodze, D. & Cook, B.J. 2002. Positive interactions among alpine plants increase with stress. *Nature* 417: 844-848.
- Diggle, P.J., Lange, N. & Benes, F.M. 1991. Analysis of variance for replicated spatial point patterns in clinical neuroanatomy. *J. Am. Stat. Assoc.* 86: 618-625.
- Esler, K.J. & Cowling, R.M. 1995. The comparison of selected life-history characteristics of Mesembryanthema species occurring on and off Mima-like mounds (*heuweltjies*) in semi-arid southern Africa. *Vegetatio* 116: 41-50.
- Flores, J. & Jurando, E. 2003. Are nurse-protégé interactions more common among plants from arid environments? *J. Veg. Sci.* 14: 911-916.
- Franco, A.C. & Nobel, P.S. 1988. Interactions between seedlings of *Agave deserti* and the nurse plant *Hilaria rigida*. *Ecology* 69: 1731-1740.
- Germishuizen, G. & Meyer, N.L. 2003. *Plants of southern Africa: an annotated checklist*. Strelitzia 14, National Botanical Institute, Pretoria, SA.
- Goldberg, D.H. & Novoplansky, A. 1997. On the relative importance of competition in unproductive environments. *J. Ecol.* 85: 409-418.
- Grime, J.P. 1973. Competitive exclusion in herbaceous vegetation. *Nature* 242: 344-347.
- Grime, J.P. 1979. *Plant strategies and vegetation processes*. J. Wiley & Sons, Chichester, UK.
- Greenlee, J.T. & Callaway, R.M. 1996. Abiotic stress and the relative importance of interference and facilitation in montane bunchgrass communities in western Montana. *Am. Nat.* 148: 386-396.
- Holmgren, M., Scheffer, M. & Huston, M.A. 1997. The interplay of facilitation and competition in plant communities. *Ecology* 78: 1966-1975.
- Ibáñez, I. & Schupp, E.W. 2001. Positive and negative interactions between environmental conditions affecting *Cercocarpus ledifolius* seedling survival. *Oecologia* 129: 543-550.

- Kitzberger, T., Steinaker, D.F. & Veblen, T.T. 2000. Effects of climatic variability on facilitation of tree establishment in Northern Patagonia. *Ecology* 81: 1914-1924.
- Midgley, G.F. & Musil, C.F. 1990. Substrate effects of zoogenic soil mounds on vegetation composition in the Worcester-Robertson valley, Cape Province. *S. Afr. J. Bot.* 56: 158-166.
- Midgley, G.F. & van der Heyden, F. 1999. Form and function in perennial plants. In: Dean W.R.J. & Milton S.J. (eds.) *The Karoo: ecological patterns and processes*, pp. 91-106. Cambridge University Press, Cambridge, UK.
- Milton, S.J. 1990. Life styles of plants in four habitats in an arid Karoo shrubland. *S. Afr. J. Ecol* 1: 63-72.
- Milton, S.J. & Dean, W.R.J. 1990. Mima-like mounds in the southern and western Cape: are the origins so mysterious? *S. Afr. J. Sci.* 86: 207-208.
- Milton, S.J., Dean, W.R.J. & Kerley, G.I.H. 1992. Tierberg Karoo Research Center: History, physical environment, flora, and fauna. *Trans. R. Sci. S. Afr.* 48: 15-46.
- Neter, J., Kutner, M.H., Nachtsheim, C.J. & Wasserman, W. 1996. *Applied linear statistical models*. 4th. ed. McGraw-Hill, Boston, MA, US.
- Nobel, P.S. 1989. Temperature, water availability, and nutrient levels at various soil depths: consequences for shallow-rooted desert succulents, including nurse plant effects. *Am. J. Bot.* 76: 1486-1492.
- Rebele, F. 2000. Competition and coexistence of rhizomatous perennial plants along a nutrient gradient. *Plant Ecol.* 147: 77-94.
- Rebollo, S., Milchunas, D.G. & Noy-Meir, I. 2005. Refuge effects of a cactus in grazed short-grass steppe. *J. Veg. Sci.* 16: 85-92.
- Reichenberger, G. & Pyke, D.A. 1990. Impact of early root competition on fitness components of four semiarid species. *Oecologia* 85: 159-166.
- Rutherford, M.C. 1980. Annual plant production-precipitation relations in arid and semi-arid regions. *S.Afr. J. Sci.* 76: 53-56.
- Schenk, H.J., Holzapfel, C., Hamilton, J.G. & Mahall, B.E. 2003. Spatial ecology of a small desert shrub on adjacent geological substrates. *J. Ecol.* 91: 383-395.
- Tielbörger, K. & Kadmon, R. 1997. Relationship between shrubs and annual communities in a sandy desert ecosystem: a three-year study. *Plant Ecol.* 130: 191-201.
- Tilman, D. 1985. The resource-ratio hypothesis of plant succession. *Am. Nat.* 125: 827-852.
- Tilman, D. 1988. *Plant strategies and the dynamics and structure of plant communities*. Princeton University Press, Princeton, NJ, US.
- Wiegand, T. & Moloney, K.A. 2004. Rings, circles, and null-models for point pattern analysis in ecology. *Oikos* 104: 209-229.
- Wiegand, T., Milton, S.J., Esler, K.J. & Midgley, G. 2000. Live fast, die young: estimating size-age relations and mortality pattern of shrubs species in the semi-arid Karoo, South Africa. *Plant Ecol.* 150: 115-131.
- Wiegand, T., Moloney, K.A., Naves, J. & Knauer, F. 1999. Finding the missing link between landscape structure and population dynamics: a spatially explicit perspective. *Am. Nat.* 154: 605-627.

Received 13 December 2004;

Accepted 3 June 2005.

Co-ordinating Editor: V.D. Pillar.

For App. 1, 2 & 3, see *JVS/AVS Electronic Archives*;
www.opuluspress.se/pub/archives/index.htm

App. 1. Following the notation in Wiegand & Moloney (2004) (Eq. 11), the numerical estimator of the bivariate O -ring statistic $O_{12}(r)$ is calculated as:

$$\hat{O}_{12}^w(r) = \frac{\frac{1}{n_1} \sum_{i=1}^{n_1} \mathbf{Points}_2 [R_{1,i}^w(r)]}{\frac{1}{n_1} \sum_{i=1}^{n_1} \mathbf{Area} [R_{1,i}^w(r)]} \quad (\text{A1})$$

where n_1 is the number of points of pattern 1, $R_{1,i}^w(r)$ is the ring with radius r and width w centered in the i th point of pattern 1, $\mathbf{Points}_2[X]$ counts the points of pattern 2 in a region X , and the operator $\mathbf{Area}[X]$ determines the area of the region X .

To integrate the data of N different replicates into a single function, we extended the formula for one replicate (eq. A1) and calculated, for each spatial scale r , the average number of points of pattern 2 over all N replicates and the average area over all N replicates:

$$\hat{O}_{12}^w(r) = \frac{\frac{1}{N} \left(\frac{1}{n_1^1} \sum_{i^1=1}^{n_1^1} \mathbf{Points}_2 [R_{1,i^1}^w(r)] + \dots + \frac{1}{n_1^N} \sum_{i^N=1}^{n_1^N} \mathbf{Points}_2 [R_{1,i^N}^w(r)] \right)}{\frac{1}{N} \left(\frac{1}{n_1^1} \sum_{i^1=1}^{n_1^1} \mathbf{Area} [R_{1,i^1}^w(r)] + \dots + \frac{1}{n_1^N} \sum_{i^N=1}^{n_1^N} \mathbf{Area} [R_{1,i^N}^w(r)] \right)} \quad (\text{A2})$$

where i^j is the i th point of pattern 1 and replicate j and n_1^j is the number of points of pattern 1 and replicate j .

App. 2. Results of ANOVAs for number of leaves among seedlings planted on and off termite mounds ('on' versus 'off' habitat), both proximate to neighbouring adult plants ('neighbour' microsite) and in cleared areas ('open' microsite). See also App. 3.

	Source of variation	SS	df	F	p
Prince Albert					
<i>Malephora lutea</i>	Block	2.2	3	0.67	0.626
	On/Off	103.3	1	97.41	0.002
	Neighbour/open	39.2	1	68.64	<0.001
	On/Off*Nbr/Open	37.8	1	66.06	<0.001
	Error	3.4	6		
<i>Ruschia spinosa</i>	Block	4.9	3	7.35	0.068
	On/Off	7.6	1	8.26	0.026
	Neighbour/Open	2.8	1	2.63	0.156
	On/Off*Nbr/Open	4.4	1	4.09	0.089
	Error	6.5	6		
<i>Psilocaulon junceum</i>	Block	2.4	3	1.21	0.440
	On/Off	21.4	1	15.19	0.007
	Neighbour/Open	15.3	1	10.55	0.018
	On/Off*Nbr/Open	16.3	1	11.25	0.015
	Error	8.7	6		
Worcester					
<i>Pteronia incana</i>	Block	3.0	3	0.59	0.664
	On/Off	0.3	1	0.29	0.602
	Neighbour/Open	15.69	1	17.77	0.006
	On/Off*Nbr/Open	0.2	1	0.22	0.656
	Error	5.3	6		
<i>Pteronia paniculata</i>	Block	2.8	3	0.91	0.530
	On/Off	2.3	1	2.23	0.182
	Neighbour/Open	7.1	1	6.84	0.040
	On/Off*Nbr/Open	0.5	1	0.50	0.507
	Error	6.2	6		

App. 3. Results of ANOVAs for survival among seedlings planted on and off termite mounds ('on' versus 'off' habitat), both proximate to neighbouring adult plants ('neighbour' microsite) and in cleared areas ('open' microsite).

	Source of variation	SS	df	F	p
Prince Albert					
<i>Malephora lutea</i>	Block	0.6	3	0.21	0.882
	On/Off	18.2	1	18.32	0.017
	Neighbour/Open	0.6	1	0.57	0.479
	On/Off*Nbr/Open	10.3	1	9.37	0.022
	Error	6.6	6		
<i>Ruschia spinosa</i>	Block	6.9	3	7.55	0.066
	On/Off	1.5	1	3.69	0.095
	Neighbour/Open	0.1	1	0.19	0.676
	On/Off*Nbr/Open	0.4	1	0.53	0.492
	Error	4.5	6		
<i>Psilocaulon junceum</i>	Block	2.4	3	2.26	0.260
	On/Off	57.8	1	94.56	<0.001
	Neighbour/Open	2.8	1	1.95	0.212
	On/Off*Nbr/Open	2.8	1	1.95	0.212
	Error	8.7	6		
Worcester					
<i>Pteronia incana</i>	Block	8.5	3	6.61	0.078
	On/Off	35.4	1	88.12	<0.001
	Neighbour/Open	0.0	1	0.01	0.939
	On/Off*Nbr/Open	0.8	1	2.42	0.170
	Error	2.1	6		
<i>Pteronia paniculata</i>	Block	2.6	3	0.51	0.700
	On/Off	7.7	1	4.98	0.088
	Neighbour/Open	0.1	1	0.11	0.753
	On/Off*Nbr/Open	2.8	1	2.62	0.157
	Error	6.4	6		
<i>Tylecodon paniculatus</i>	Block	0.0	3	0.19	0.899
	On/Off	1.3	1	1.60	0.252
	Neighbour/Open	26.3	1	27.73	0.002
	On/Off*Nbr/Open	1.3	1	1.40	0.282
	Error	5.7	6		