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# Competition and herbivory influence growth and survival of shrubs on old fields: Implications for restoration of renosterveld shrubland

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**Abstract**

**Question:** How does competition by grasses, grazing by indigenous large herbivores, and their interaction affect the establishment, growth and survival of transplanted native woody and herbaceous seedlings on an abandoned agricultural field?

**Location:** West Coast Renosterveld, Cape Floral Region, South Africa.

**Methods:** Indigenous shrub seedlings were planted in different treatments, where either grass competition or herbivory or both were manipulated. Survival, growth and canopy cover of the seedlings were measured on a monthly basis over 14 months, and compared between treatments.

**Results:** Experimental transplanting of indigenous shrubs into an old field showed that most of the plants investigated competed for resources with grasses on the field, and competition negatively affected the seedlings throughout the experiment. Mortality was higher, and growth was reduced for seedlings exposed to grass competition. Herbivory alone had no significant impact on the target species with the exception of *Olea europaea* ssp. *africana*. There was no significant interaction between competition and herbivory.

**Conclusion:** Reduction of herbaceous competition significantly accelerates shrubland recovery on abandoned agricultural fields in renosterveld.

**Keywords**: Mediterranean shrubland; *Olea europaea* ssp. *africana*; South Africa; Succession; Vegetation dynamics.

**Abbreviations:** NPNW = Not protected from herbivory and not weeded; NPW = Not protected from herbivory and weeded; PNW = Protected from herbivory and not weeded; PW = Protected from herbivory and weeded.

**Nomenclature:** Germishuizen and Meyer (2003).

## Introduction

For many years ecologists have debated the relative importance of competition and herbivory in influencing the distribution and abundance of plants in natural communities (Parker & Salzman 1985). Competition from neighbouring plants and herbivory can influence the growth, survival and reproduction of individual plants, and consequently the sizes of plant populations (Gurevitch et al. 2000). Competitor removal experiments (Robberecht et al. 1983) and herbivore exclosure experiments (Rausher & Feeny 1980; Louda 1983) clearly demonstrate that plant success can be affected by either process acting alone. Field observations further suggest that manipulation of plant neighbours and herbivore densities frequently have synergistic or substitutive effects on plant performance, e.g., the removal of plant neighbours may either relax or intensify herbivory.

The interactive effect of herbivory and plant competition may arise through two major routes. First, rates of herbivory may increase or decrease when the abundance of plant neighbours, or some factor correlated with plant abundance, is altered (Holt & Lawton 1994). Secondly, herbivory might increase or decrease the competitive effect of one plant on another by impacting on plant regrowth ability (Willis et al. 1998). For natural plant populations, little is known about the relative impact of these forces, or about the nature of interactions between them.

Renosterveld is a species-rich shrubland type that is confined to lowlands on fertile soils in the winter rainfall region of the Western Cape, South Africa. Most of this vegetation type has been replaced by agriculture (vines, olives, wheat), and the remainder is highly fragmented (Kemper et al. 1999). In some cases, land owners have abandoned crop production to use the land for conservation, tourism and game farming. Restoration of abandoned fields has potential to improve the conservation status of renosterveld shrubland by increasing the sizes of fragments or establishing links among fragments (Krug et al. 2004). However, natural succession of shrubland onto abandoned fields appears to take many decades.

The aim of this study is thus to explain the apparent slow return of indigenous renosterveld vegetation onto abandoned fields. Three hypothetical causes of slow vegetation return are seed limitation, competition from dominant herbaceous plants and herbivory by ungulates that are attracted to the grass-dominated old fields. Shiponeni (2003) demonstrated that the return of wind and dung-dispersed indigenous plant species to old fields in this vegetation type does not seem to be limited by seed availability. In this paper, we therefore examine the importance of competition and herbivory on establishment, growth and survival of shrub seedlings transplanted onto an old field in the mesic, winter rainfall region of South Africa. We address the following questions:

1. How does competition affect survival and growth of renosterveld seedlings?
2. What is the impact of herbivory on the survival and growth of the seedlings?
3. Do interaction effects between competition and herbivory exist, and how do these interactions effect the survival and growth of the transplanted seedlings; in other words: how do the effects of herbivore damage of the seedlings depend on whether competitors are present or absent, and *vice versa*?

## Methods

The study was carried out on Elandsberg Private Nature Reserve (EPNR), north of Wellington in the Western Cape Province of South Africa (33°24''17' S and 33°29''8' S, and 18°58''30' E and 19°05''10' E, 80-460 m a.s.l). The site receives a mean annual rainfall of 687 mm, of which 77% falls in the frost-free cool season (April-September). Daily temperatures average 12.2 °C in winter and 23.8 °C in summer (Anon. 1984). Soils are fine textured, moderately fertile being derived from sedimentary rock of the Malmesbury series.

The reserve currently covers 3900 ha of natural veld, including low mountain fynbos, renosterveld shrublands, and small patches of taller scrub forest in fire-protected habitats along riparian corridors, among boulders and on termitaria. The renosterveld portion, ca. 1000 ha, is the largest remaining patch of West Coast Renosterveld in the Cape floristic region (von Hase et al. 2003). Indigenous large herbivores (seven antelope species and two zebra species) were re-introduced in the reserve in 1972 (Mike Gregor pers. comm.).

The field where this study was conducted, was used for cultivation of oats (*Avena sativa*) from 1960 until 1985, then oversown with European pasture grasses, and used for livestock grazing until 1987 when all agricultural activity was abandoned, and the field was incorporated into the reserve (Mike Gregor pers. comm.). The field is dominated by introduced European grasses and herbaceous plants, and differs from the natural vegetation not only in the degree of woody cover but also in the relative abundance of the herbaceous species. The open grassy area of the old field is dominated by the perennial African lawn grass, *Cynodon dactylon* in summer, and introduced European grasses (*Briza maxima, B. minor, Bromus diandrus, B. pectinatus, Lolium* spp., *Poa annua, Vulpia myuros*) after winter rainfall (Shiponeni 2003). Renosterveld species that have colonized the field include the shrubs *Dicerothamnus rhinocerotis* and *Helichrysum* spec. (*Asteraceae)*, *Hermannia* spec. (*Sterculiaceae*) and *Thesium* spec. (*Santalaceae*), and an indigenous perennial forb, *Leysera gnaphalodes* (*Asteraceae*). All large game species present in the reserve have access to the site.

A field experiment was conducted to understand the role of herbivory and competition on plant establishment on abandoned agriculture lands. Treatments were:
P-W: Protected from large herbivores and weeded to remove grass (assumes no herbivory by large mammals);
P-NW: protected from large herbivores and not weeded (assumes no herbivory but active grass competition);
NP-W: Not protected and weeded (assumes exposure to herbivory by large mammals but no grass competition);
NP-NW: Not protected and not weeded (assumes exposure to herbivory and grass competition).

Each treatment (0.64-$m^2$ plots) was replicated five times. Throughout the results section of this paper the various treatments will be referred to by acronyms given above.

Grass biomass was removed in the weeded plots at ground level using a short-handled spade, taking care to not to disturb the soil. The competition effect was estimated by comparing survivorship, growth, and canopy area of the target plants in weeded and unweeded plots under herbivore exclusion. Large herbivores were excluded by positioning wire cages (80 cm × 80 cm × 40 cm, 10 mm mesh size) over selected plots. Smaller mammals (e.g. rodents) and insects were not prevented from entering the cages. The effect of herbivory by large mammals was determined by comparing survivorship, growth, and canopy area of target plants in protected and unprotected plots, without competition. The combined effects of competition and herbivory were determined by comparing survivorship, growth, and canopy area of target plants in unprotected and unweeded plots vs. protected weeded plots.

Plots were set up in two rows parallel to the natural vegetation. Treatments were distributed in a stratified design, with unprotected and protected treatments paired. Six indigenous plant species commonly found in the renosterveld areas at Elandsberg were selected for use in the experiment. Four of these were low shrubs typical of open renosterveld shrubland (Acocks 1998; Low & Rebelo 1998): *Athanasia trifurcata* and *Relhania fruticosa* (*Asteraceae*), wind-dispersed, microphyllous shrubs; *Leucadendron corymbosum* (*Proteaceae*), wind-dispersed, mesophyll shrub; and *Salvia chamelaeagnea* (*Lamiaceae*), dung-dispersed, mesophyll shrub. *Olea europaea* ssp. *africana* (*Oleaceae*), is a small evergreen tree of fire refuge habitats such as drainage lines, boulder screes and large termite mounds. *Crassula glomerata* (*Crassulaceae*), an annual succulent understorey forb, is the sixth species incorporated in the experiment, as seedlings germinated naturally from the soil seed bank. Its palatability to large mammals is not known. The species were expected to differ in palatability to large herbivores, as well as in life form. Nomenclature follows Germishuizen & Meyer (2003).

Seedlings matched for size (3 - 5 cm in height) were used in the experiment because this study focused on plant performance, rather than seedling emergence. Seedlings were grown in the nursery and at the age of approximately four months were transplanted into the 20 treatment plots. In total 25 marked seedlings were planted in each plot: five seedlings of *A. trifurcata*, *C. glomerata*, *L. corymbosum* and *R. fruticosa* each, four seedlings of *O. europaea* ssp. *africana* and one single seedling for *S. chamealeagnea*. The number of seedlings was determined by germination success in the nursery. Unfortunately, no rain fell for two weeks after seedlings were transplanted, so that some of the seedlings died after the first data collection, as treatment plots were not watered after transplantation. Seedlings were monitored monthly for 14 months, starting the first month after transplantation. The following parameters were recorded: number of surviving plants per species, and height, and canopy area of each seedling. The survivorship of transplanted seedlings was calculated as the mean number of surviving seedlings per species and per treatment. To compare seedling growth and canopy area between treatments, average values per species per plot were calculated. These average values were then used for further analysis, thus regarding one treatment plot as a replicate. Therefore, each treatment was replicated five times.

The effects of treatment on the growth of each species were tested separately, and differences in means were illustrated graphically using a significance level of $p < 0.05$. Canopy areas were log transformed to reduce inequality of variance in the raw data, and to ensure that the data met the requirements for the parametric tests. A two-factor analysis of variance tested the main effects of herbivory and competition and their interaction on measured plant parameters, viz plant height, and canopy area, in each species. A Scheffé *post-hoc* test was conducted to determine significant effects of competition in protected treatments and of herbivory in weeded treatments, as well as to separate significant differences between treatments (STATISTICA 6.1, StatSoft, Inc.; Anon. 2003). Canopy area was calculated using the following formula for an ellipse (Bronstein & Semendjajew 1991):

$$\text{Cover} = (\pi/4) \quad canopy1 \quad canopy2 \qquad (1)$$

where *canopy*1 and *canopy*2 are two perpendicular diameters of the plant as seen from above.

Seedling survival at the end of the treatment is the proportion of seedlings that survived relative to the total number of seedlings planted. Proportions were arcsine transformed to conduct a two-factor analysis of variance to test for differences in the proportions of seedlings that survived between the four different treatment combinations. The Scheffé test was used as *post-hoc* test to determine significant effects of competition in protected treatments and of herbivory in weeded treatments, as well as to separate significant differences between pairs of treatments. (STATISTICA 6.1; Anon. 2003).

## Results

Species in the control treatment (PW) however showed higher survival than in the other treatments, except for *R. fruticosa* where only 20% (SE =15) of the original seedlings survived (Table 1). Grass competition reduced the survival of all target species; the effect was only significant for *L. corymbosum* (Scheffé *post-hoc* test, $p = 0.05$). Seedling survival was also negatively affected by herbivory. Except for *R. fruticosa*, where survival rates where higher than in the control, all species show reduced survival when exposed to herbivory. In *O. europaea* ssp. *africana*, seedlings survived better when protected from grazing, regardless of weeding. Survival of *L. corymbosum* was significantly improved by weeding, but not by protection from herbivory ($p < 0.05$; $F_{3,16} = 6.966$), while *C. glomerata* survived best where protected and weeded ($p < 0.05$; $F_{3,16} = 4.471$; Table 1).

### *Seedling height and canopy cover*

The average height and canopy cover of seedlings at the age of 14 months exposed to grass competition and herbivory was compared for each of the six species (Table 2 and Table 3, respectively). Removal of grass biomass has a direct effect on the seedling height and canopy area of all target species (Table 2, Fig. 1, and Fig. 2), indicating that grass competed with the transplanted seedlings.

**Table 1.** Mean % survival at 14 months for each of the target species planted on experimental plots. Mean ± SE, *df* = 3 (four treatments) and $n = 20$ (plots) for all species. (Factors influencing shrub growth and establishment in each of the four treatments. PW = protected from herbivory and weeded to remove competition; PNW = protected and not weeded; NPW = not protected and weeded; NPNW = not protected and not weeded). Letters indicate significant differences between columns. ($F_{(3,16)}$ for each species and $F_{(3,96)}$ for all species). Significance: * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

| | Treatment | | | | | |
|---|---|---|---|---|---|---|
| Species | No herbivory, no competition (PW) | Herbivory only (NPW) | Competition only (PNW) | Herbivory and Competition (NPNW) | *F*-value | *P*-value |
| *Athanasia trifurcata* | 0.96 ± 0.40 | 0.60 ± 0.20 | 0.47 ± 0.22 | 0.34 ± 0.18 | 2.163 | 0.132 |
| *Crassula glomerata* | 0.96 ± 0.04a | 0.68 ± 0.08ab | 0.62 ± 0.08ab | 0.56 ± 0.11b | 4.471 | 0.018* |
| *Leucadendron corymbosum* | 0.96 ± 0.04a | 0.80 ± 0.08ab | 0.51 ± 0.09b | 0.57 ± 0.07b | 6.966 | 0.003** |
| *Olea europaea* ssp. *africana* | 0.60 ± 0.15 | 0.30 ± 0.05 | 0.45 ± 0.09 | 0.35 ± 0.10 | 1.600 | 0.228 |
| *Relhania fruticosa* | 0.20 ± 0.15 | 0.44 ± 0.23 | 0.08 ± 0.04 | 0.04 ± 0.04 | 1.588 | 0.231 |
| *Salvia chamelaeagnea* | 0.90 ± 0.10 | 0.80 ± 0.20 | 0.40 ± 0.24 | 0.60 ± 0.24 | 1.156 | 0.356 |
| All species combined | 0.76 ± 0.06a | 0.60 ± 0.06ab | 0.42 ± 0.06bc | 0.41 ± 0.06c | 6.527 | 0.004** |

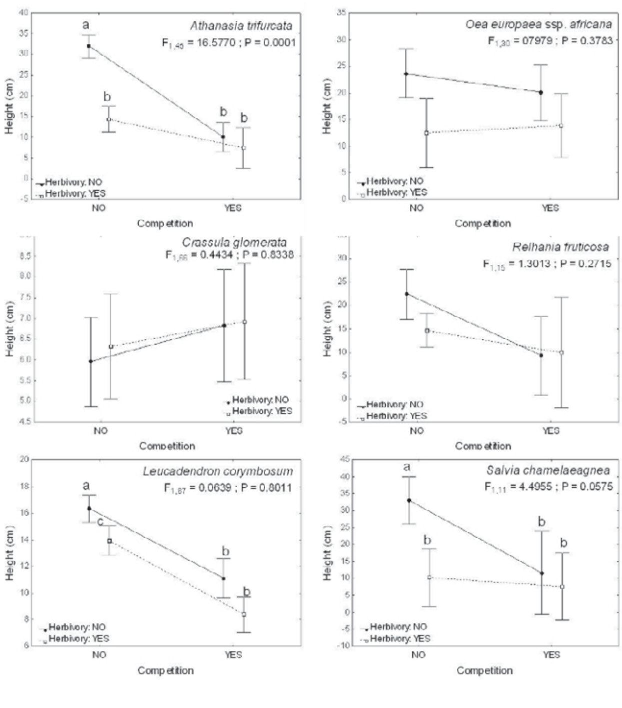


**Fig. 1.** Interaction effect of grazing and grass competition on the average height at the end of treatment of species. Solid line = protected, and dotted line = exposed to vertebrate herbivory. Different letters above error bars indicate significant differences between treatments. Vertical bars indicate standard deviations from the mean.

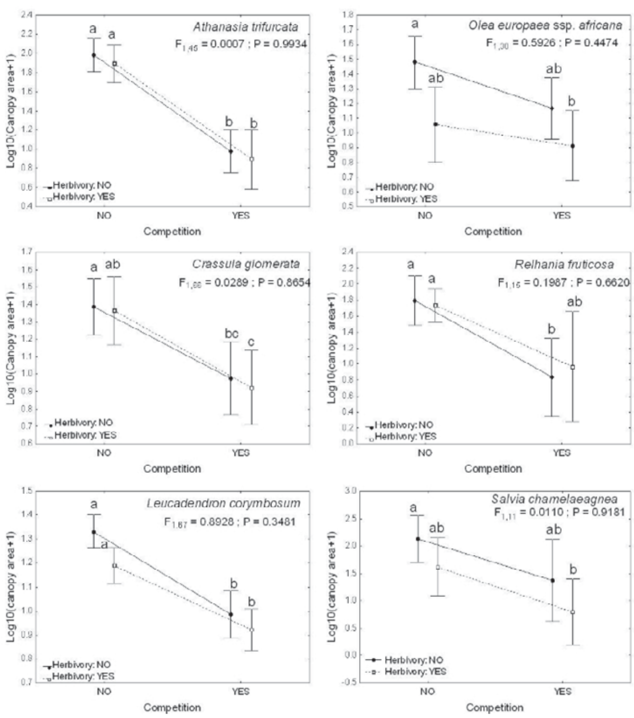


**Fig. 2.** Interaction of grazing and grass competition on the average canopy area at the end of treatment of species. Solid line = protected, and dotted line = exposed to vertebrate herbivory. Different letters indicate significant differences between treatments. Vertical bars indicate standard deviations from the mean.

**Table 2.** Mean height (± SD) and mean canopy cover (± SD) of seedlings exposed to competition (PNW) and protected from competition (PW) under the exclusion of herbivory. *p*-values obtained through Scheffé *post-hoc* tests. Significance: * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

| Species / Treatments | Variable (cm) | PW (No competition) Mean ± SD (*N*) | PNW (Competition) Mean ± SD (*N*) | *p*-values | |
|---|---|---|---|---|---|
| *Athanasia trifurcata* | Height | 32.028 ± 7.645 (18) | 10.090 ± 3.597 (11) | **0.000** | *** |
| | Canopy | 1.979 ± 0.455 (18) | 0.980 ± 0.192 (11) | **0.000** | *** |
| *Crassula glomerata* | Height | 5.958 ± 2.714 (24) | 6.833 ± 1.997 (15) | 0.795 | |
| | Canopy | 1.385 ± 0.233 (24) | 0.976 ± 0.233 (15) | **0.029** | * |
| *Leucadendron corymbosum* | Height | 16.333 ± 3.137 (24) | 11. 125 ± 2.336 (12) | **0.000** | *** |
| | Canopy | 1.330 ± 0.169 (24) | 0.984 ± 0.203 (12) | **0.000** | *** |
| *Olea europaea* ssp. *africana* | Height | 23.625 ± 10.295 (12) | 20.055 ± 7.405 (9) | 0.780 | |
| | Canopy | 1.481 ± 0.418 (12) | 1.170 ± 0.307 (9) | 0.175 | |
| *Relhania fruticosa* | Height | 22.400 ± 7.741 (5) | 9.250 ± 4.596 (2) | 0.087 | |
| | Canopy | 1.792 ± 0.349 (5) | 0.833 ± 0.088 (2) | **0.024** | * |
| *Salvia chamelaeagnea* | Height | 33.000 ± 10.752 (6) | 11.750 ± 1.767 (2) | **0.007** | ** |
| | Canopy | 2.124 ± 0.429 (6) | 1.366 ± 0.405 (2) | 0.335 | |

Competition (PNW) was the most important factor affecting the growth of *A. trifurcata*, *L. corymbosum*, and *S. chamelaeagnea*. Seedlings were significantly smaller in non-weeded (PNW) plots than on plots were grass was removed (PW): *A. trifurcata* (Scheffé *post-hoc* test, $p < 0.001$), *L. corymbosum* ($p < 0.001$), and *S. chamelaeagnea* ($p = 0.007$) (Table 2). A significant reduction in canopy cover as a response to grass competition was observed for *A. trifurcata* (Scheffé *post-hoc* test, $p < 0.001$), *L. corymbosum* ($p < 0.001$) and *R. fruticosa* ($p = 0.024$).

The growth of *O. europaea* ssp. *africana*, a tree usually growing on nutrient rich soil of underground termitaria, was not affected by grass competition (Table 2), but seedlings were smallest in unprotected, weeded plots (Fig. 1). *C. glomerata* does not show a clear response to competition. While seedlings that are exposed to competition are taller than those growing in grass-free areas, although not significantly (Scheffé *post-hoc* test, $p = 0.795$), canopy cover is significantly reduced under competition (Scheffé *post-hoc* test, $p = 0.029$).

Herbivory also has an effect on seedling height and canopy cover, but not as pronounced as grass competition (Table 3, Figs. 1 and 2). Seedlings of *A. trifurcata* (Scheffé *post-hoc* test, $p < 0.001$), *L. corymbosum* ($p = 0.027$), and *S. chamelaeagnea* ($p = 0.008$) exposed to herbivores (NPW) were significantly smaller than protected seedlings at end of treatment, while canopy cover was only slightly reduced. Thus, those species benefit from protection. No significant effect of exposure to herbivores was found on the height and canopy cover of *C. glomerata* and *R. fruticosa*, and it appeared that herbivores avoided these species. Although both height and canopy cover *O. europaea* spp. *africana* were lower in those seedlings exposed to herbivory, the effect was not significant (Scheffé *post-hoc* test: height, $p = 0.067$, cover, $p = 0.075$).

In general, grazing and competition had statistically independent effects for most species. Only in *A. trifurcata* was there a significant interaction ($p < 0.01$; $F_{(1,45)} = 16.56$), between grazing and grass competition.

**Table 3.** Mean Height (± SD) and mean canopy cover (± SD) of seedlings exposed to herbivory (NPW) and protected from herbivory (PW) under the exclusion of competition. *p*-values obtained through Scheffé post-hoc tests. Significance as in Table 2.

| Species / Treatments | Variable (cm) | PW (No competition) Mean ± SD (*N*) | PNW (Competition) Mean ± SD (*N*) | *p*-values | |
|---|---|---|---|---|---|
| *Athanasia trifurcata* | Height | 32.028 ± 7.645 (18) | 14.392 ± 5.762 (14) | **0.000** | *** |
| | Canopy | 1.979 ± 0.455 (18) | 1.891 ± 0.392 (14) | 0.932 | |
| *Crassula glomerata* | Height | 5.958 ± 2.714 (24) | 6.323 ± 1.952 (17) | 0.0979 | |
| | Canopy | 1.385 ± 0.442 (24) | 1.336 ± 0.339 (17) | 0.999 | |
| *Leucadendron corymbosum* | Height | 16.333 ± 3.137 (24) | 13.925 ± 2.066(20) | **0.027** | * |
| | Canopy | 1.330 ± 0.169 (24) | 1.189 ± 0.171 (20) | 0.063 | |
| *Olea europaea* ssp. *africana* | Height | 23.625 ± 10.295 (12) | 12.500 ± 5.666 (6) | 0.067 | |
| | Canopy | 1.481 ± 0.418 (12) | 1.058 ± 0.079 (6) | 0.075 | |
| *Relhania fruticosa* | Height | 22.400 ± 7.741 (5) | 14.636 ± 4.528 (11) | 0.128 | |
| | Canopy | 1.792 ± 0.349 (5) | 1.732 ± 0.327 (11) | 0.999 | |
| *Salvia chamelaeagnea* | Height | 33.000 ± 10.752 (6) | 10.375 ± 4.589 (4) | **0.008** | ** |
| | Canopy | 2.124 ± 0.429 (6) | 1.611 ± 0.657 (4) | 0.461 | |

## Discussion

This study was designed to examine the effects of grass competition, herbivory by indigenous large herbivores, and the combined effect of these two factors on the growth and survival of seedlings of indigenous Renosterveld shrubs on an abandoned agricultural field. The results clearly indicate the importance of grass competition and the effect of herbivory on renosterveld species establishing on abandoned agricultural lands. Both herbivory and competition by grasses had an effect on the survival and growth of the transplanted renosterveld species. However, species responded differently to both treatments. In most cases, survival and growth of plants were reduced more in the competition treatment than the herbivory treatment. These results support the suggestion of Goldberg (1987) and Miller & Werner (1987) that the response to competition may be highly species-specific. The results indicate that most of the target plants competed for resources where the grass biomass was left intact in the treatment i.e. on the non-weeded plots.

The combined effects of competition and herbivory are poorly studied (e.g. van der Wal et al. 2000). Gurevitch et al. (2000) performed a meta-analysis of the relative effects of competition and herbivory on survival and growth of five plant species. They found that plant growth was affected equally by competition and herbivory, and that there was no significant interaction. In our results, competition has more impact on the plants than herbivory, and there is no significant interaction effect between the two factors.

Our finding that competition had a greater effect than herbivory on all variables measured in the field is inconsistent with the expectation that herbivory would have a greater effect on target plant performance (Augustine & McNaughton 1998). Plants that are not surrounded by grass biomass experience less competition for resources such as light, nutrients and water, than plants where grass biomass is left intact (Reader et al. 1994). This notion is supported by old-field experiments of Bonser & Reader (1995) who report that competition will increase with increasing productivity. The relevance of this for restoration of old fields in renosterveld shrubland is that interventions such as grass control may be necessary at high rainfall and fertile sites, but not at arid sites or on infertile soils. This hypothesis remains to be tested. The growth and survival of *A. trifurcata*, *C. glomerata*, *L. corymbosum*, *R. fruticosa* and *S. chamalaeagnea*, all common species of low open renosterveld shrubland vegetation, are likely to be impacted by competition. *O. europaea* ssp. *africana*, an evergreen tree associated protected habitats such as drainage lines, termitaria and boulder scree, is more likely to be impacted by herbivory than competition.

Presumably the broad-leaved seedlings of *O. europaea* ssp. *africana* are better competitors for light than microphyllous shrubs. Moreover, the root system of *O. europaea* ssp. *africana* might be developed and well established in an earlier stage than those other transplanted species, thus, this species is better equipped to compete with grass.

While neighbour removal is used commonly to measure competition (e.g. Aarssen & Epp 1990). Campbell et al. (1991) have questioned the use of removal experiments to study competition because nutrient supply in removal plots may increase from the decomposition of dead roots of neighbours, which are usually not removed completely. Consequently, the increase in canopy area due to grass removal may be greater in weeded plots than in non weeded plots due to the nutrient release from the decomposition of roots. Our experiments did not control for this effect.

Cages were used to exclude the effect of large herbivores on all target species. Where cages were used there was a significant increase in height at the end of the treatment, especially for *A. trifurcata, L. corymbosum, O. europaea* ssp. *africana and S. chamelaeagnea*. The reason for this could be that the protected plants lost less tissue to herbivores, but also due to the trampling effect, which can inflict mortality on plant seedlings (Salihi & Norton 1987). Results of monthly monitoring indicated that unprotected plants showed obvious signs of herbivory, such as cropped stems and damaged leaves, and were also trampled.

The experiment was conducted for large herbivores, but we did not attempt to determine what type of herbivores actually removed tissue. We assumed that small mammals (rodents), insects (grasshoppers), and molluscs (snails, slugs) caused equal damage to plants inside and outside the protective cages.

Since the target species differ in terms of palatability to large herbivores and in competitive ability, some plants will survive with grasses around them and some will not. Many authors have suggested that invertebrate herbivory effects are likely to be most conspicuous when grazed plants are competing with other plants for resources, since differential herbivory can provide a competitive advantage to the least damaged plants (Bentley & Whittaker 1979). Selective grazing by large herbivores and target species palatability were not considered but this certainly had an effect on the results. However, a positive correlation has been found between competitive ability and palatability for species in grassland area (Crawley 1990). This finding is consistent with the prediction of competitor release of unpalatable species when exposed to grazing (Pacala & Crawley 1992).

In the field *A. trifurcata, O. europaea* ssp. *africana* and *S. chamelaeagnea* were strongly grazed and browsed while *L. corymbosum, R. fruticosa* and *C. glomerata* did not show any signs of herbivory. The surprising lack of effect that herbivory had on seedlings of some species might be due to their small size. Many studies have recognized that less apparent species will be more difficult for large herbivores to find than taller plant species (O'Connor 1992). In the case of selective herbivory, however neighbouring species might reduce the grazing pressure on palatable plants by making them less obvious, which might ameliorate the direct grazing effects, as was shown in the study by Mulder & Ruess (1989) on *Triglochin palustris*.

Our results showed no interaction effect between herbivory and competition on the average height at the end of treatment for all but one of the target species (*A. trifurcata)*. The height of plants at the end of treatment was taller in weeded and protected treatments than in the weeded and non-protected treatments. One could argue that grass removal might enhance the rate of herbivory, as the target plants were easily found by herbivores in the non-protected environment. Canopy area showed no significant difference for interaction for all the target species. The herbivory impact increased in non-weeded plots. Presumably, herbivory damage increased because plots with more biomass which were not protected attracted more herbivores, due to the great plant cover and food availability. Leibold (1996) predict that grazing pressure increases with increasing productivity.

Consequently, our results are consistent with the assumption that the individual effects of herbivory and competition from neighbouring plants are independent rather than interactive, with each factor reducing the performance of each plant. A possible reason for independent effects of herbivory and competition on the shoots of target species might be that herbivores have little effect on the competitive ability of some target plants if the plant is already at the bottom of competitive hierarchy. On sites where water is not a limiting factor Richardson et al. (1996) found that growth of juvenile plants was most restricted by tall, fast growing competitors. In contrast, in dryland areas, herbaceous broad-leaved weed species were shown to have the most detrimental influence on juvenile plant growth (Richardson et al. 1993).

Another possibility is that the competitive balance between renosterveld species and the grass biomass may be unaffected by herbivory if herbivores feed on both the renosterveld species and grass biomass. It might be also that the presence of the grass biomass may not affect the ability of target renosterveld species to escape detection by herbivores if herbivore density is high in the old field or if herbivores use visual plus olfactory cues to locate the target plants.

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