Factors affecting fruit set in Aizoaceae species of the Succulent Karoo

Gesine Pufal[a,*], Carolin Mayer[b], Stefan Porembski[a], Norbert Jürgens[b]

[a]*University of Rostock, Institute of Bioscience, Department of Botany, Wismarsche Straße 8, 18051 Rostock, Germany*
[b]*University of Hamburg, Biocentre Klein Flottbek and Botanical Garden, Hamburg, Germany*

Abstract

By reducing the number of flowers and fruits, intense grazing activities of domestic livestock are considered to have negative effects on the plant recruitment of perennial plants in the Succulent Karoo, South Africa. In the present study, the fruit set of six perennial species belonging to the Aizoaceae was investigated under two different grazing intensities. Two species (*Cheiridopsis imitans* and *Leipoldtia schultzei*) were examined more closely to determine whether factors other than grazing impact fruit production of these plants. Apart from reproductive output, the population structure of these two species was explored in heavily and slightly grazed areas.

For all investigated species, heavy livestock grazing was identified as a major threat to fruit production. Deviations from this pattern were recorded in a drought year, when harsh weather conditions reduced herd sizes dramatically and the usually high grazing pressure was alleviated. However, detailed analyses revealed that also other biotic factors can cause severe fruit and flower losses even exceeding that caused by grazing. Caterpillars of the noctuid moth, *Diaphone eumela*, and two rodent species, *Otomys unisulcatus* and *Rhabdomys pumilio*, proved to be further important herbivores of flowers and fruits. Experiments with caged plants, excluding livestock from grazing, confirmed though that livestock grazing definitely accounts for a continuous reduction of fruit production. Insufficient pollination success was another parameter reducing fruit set; however, this was almost exclusively observed under low grazing pressure.

Zusammenfassung

Allgemein wird angenommen, dass intensive Weidewirtschaft in der Sukkulenten-Karoo Südafrikas negative Effekte auf die Reproduktion und Verjüngung mehrjähriger Pflanzen hat, indem domestizierte Herbivoren die Zahl von Blüten und Früchten schmälern. In der vorliegenden Studie wurde der Fruchtansatz bei sechs perennierenden Arten der Aizoaceae unter zwei unterschiedlichen Beweidungsintensitäten untersucht. Ferner sollte die eingehendere Betrachtung zweier Arten (*Cheiridopsis imitans* und *Leipoldtia schultzei*) Aufschluss darüber geben, ob neben der Beweidung auch andere Faktoren die Fruchtproduktion dieser Pflanzen beeinflussen. Zusätzlich wurde in stark und gering beweideten Gebieten die Populationsstruktur dieser beiden Arten analysiert.

Für die untersuchten Arten erwies sich die Beweidung durch Nutzvieh als einer der wesentlichen Gründe für die Verringerung der Fruchtproduktion. Extreme Witterung in einem Dürrejahr führte zu Abweichungen von diesem Muster, da durch erheblich verringerte Weidetierbestände der sonst starke Beweidungsdruck nur geringfügig war.

---

*Corresponding author. Victoria University of Wellington, School of Biological Science, New Kirk Building, Wellington, New Zealand, Tel.: +64 4 463 8012.
E-mail address: gesine.pufal@vuw.ac.nz (G. Pufal).

Die detaillierten Untersuchungen zeigten allerdings, dass neben Beweidung andere biotische Faktoren noch größere Blüten- und Fruchtverluste verursachen können. Als Blüten- und Fruchtfresser erwiesen sich die Raupen des Nachtfalters *Diaphone eumela* (Noctuidae), sowie zwei Nagetierarten, *Otomys unisulcatus* und *Rhabdomys pumilio*. Experimente mit Pflanzen in Käfigen, die nur Nutzvieh ausschlossen, bestätigten jedoch, dass Beweidung durch Ziegen zweifellos für den kontinuierlichen Verlust von Früchten verantwortlich ist. Unzureichende Bestäubung verringerte ebenfalls den Fruchtansatz, spielte jedoch fast ausschließlich bei geringem Weidedruck eine Rolle.

Introduction

The Succulent Karoo Biome in South Africa is one of the most striking ecosystems in the world. With approximately 4850 plant species, of which 40% are endemic, it is one of the two arid regions that qualify as biodiversity hotspots (Hilton-Taylor, 1996). Aizoaceae, with most species being succulent dwarf shrubs, contribute about 20% to the flora of the Succulent Karoo (Cowling & Hilton-Taylor, 1999). Although this biome is so unique, less than 4% of the area are under protection (Lombard, 1995). Major threats to the biodiversity of the Succulent Karoo Biome are anthropogenic influences such as livestock grazing (Davis & Heywood, 1994). It is therefore necessary to investigate the impact of different land use practices on the flora and fauna as well as restoration possibilities to manage the conservation of biodiversity in the area.

For hundreds of years livestock herding has had a major impact on the landscape (Hoffman, Cousins, Meyer, Petersen, & Hendriks, 1999). Nowadays, the Succulent Karoo forms a mosaic of communally managed land and privately owned farms. On communal rangeland the stocking rates often exceed recommendations by the Department of Agriculture, leading to its degradation with altered vegetation and signs of erosion (Allsopp, 1999; Todd & Hoffman, 1999). Due to ongoing grazing pressure, the floristic diversity has severely been altered by a shift from perennial shrub vegetation to higher diversity and abundance of annuals and dominance of unpalatable shrubs (e.g. *Galenia africana*, Aizoaceae) (Todd & Hoffman, 1999). Commercial farms, on the other hand, often have the possibility of applying rotational grazing strategies with grazing forming a landscape that is considered near-natural.

Livestock can affect plant recruitment directly by grazing or browsing flowers, fruits and seedlings (Milton & Dean, 1990) or indirectly with continuous grazing reducing plant fitness or the trampling preventing germination (Venter, 1962 in Esler, 1999). The present study investigates the fruit set of six Aizoaceae species under different grazing intensities.

Cheiridopsis imitans and *Leipoldtia schultzei* display different flowering strategies (steady state and big bang) and were therefore chosen for a detailed examination concerning the various influences on the development of fruits and their current population structure. The question was whether grazing is the major threat to the fruit set of indigenous species and, thus, their abundance and diversity in the Succulent Karoo or to what extent other factors also have an impact on the fruit production of perennial plants.

Materials and methods

The present study forms part of the botanical subproject (S06) of BIOTA Southern Africa (Biodiversity Monitoring Transect Analysis in Africa, www.biota-africa.org). Field investigations were conducted from 2002 to 2004 during the main flowering season (August–October).

Study site and study species

The study sites were established on two adjacent BIOTA observatories (standardised monitoring sites of $1 \, km^2$) in the Leliefontein Communal Reserve, Northern Cape. Leliefontein is situated on the Kamiesberg escarpment, which lies between 900 and 1500 m a.s.l. The whole region, known as Namaqualand, is characterised by a winter rainfall regime, Leliefontein receives about 150–250 mm precipitation annually (CV = 33%; Todd & Hoffman, 1999). High temperatures, low relative humidity and mostly no or very little cloud cover result in large annual and daily temperature fluctuations (Desmet & Cowling, 1999). The soils in Namaqualand are generally poor of nutrients and are rather infertile, but their nutrient content may vary depending on surrounding vegetation, rock cover and elevation (Allsopp, 1999; Carrick, 2003b; Petersen, Young, Hoffman, & Musil, 2004). Rainfall and temperature data were recorded by an automatic weather station (BIOTA) situated on the Leliefontein site and soil samples were taken on

different locations on both study sites (Pufal, unpublished data).

Namaqualand belongs to the Succulent Karoo Biome (Rutherford & Westfall, 1986) with succulents from many families (Cowling & Hilton-Taylor, 1999). The observatories are Leliefontein on communal rangeland (NW corner: 30.386S, 18.276E) with heavy browsing and grazing pressure by goats and wild living donkeys, and Remhoogte (NW corner: 30.935S, 18.276E), a commercial farm with very low browsing and grazing not affecting the experimental sites during the census. The farm has been stocked at or below the recommended carrying capacity of 0.083 small stock unit (SSU) per hectare for the past 40 years (T. Hoffman, personal communication). A strong fence-line contrast between the two sites is apparent.

Fruit set under different grazing intensities was investigated for the indigenous Aizoaceae species *Cheiridopsis denticulata*, *C. imitans*, *Ihlenfeldtia excavata*, *L. schultzei* (the latter two species incorporated in 2003), *Ruschia goodiae* and *Ruschia viridifolia*. The selection of these species was a mere practical decision, since they are (i) supposed to be insect pollinated and flower in spring (August until late October) (Struck, 1994a); (ii) their flowers are rewarding for livestock and they are therefore threatened by heavy grazing and (iii) sufficient individuals of each species with a manageable size for caging and flower counting occurred on both study sites. *C. imitans* and *L. schultzei* were randomly chosen and examined in more detail as part of a Diploma thesis.

Sampling methods

For each study species, 10 individuals from each of three clusters in each observatory were permanently marked in 2002 (*L. schultzei* was only added in 2003). Clusters (also referred to as populations) were defined as groups of individuals growing in close proximity to each other (with distances between individuals within clusters = 20 m, and distances between clusters 100–500 m). Additionally in 2003, 15 individuals of *C. imitans* and *L. schultzei* were permanently fenced with chicken wire on the heavily grazed site to prevent livestock grazing.

In each year, every 6–8 days, flowers and fruits of all marked individuals were counted and the number of damaged flowers recorded. The detailed examination of *C. imitans* and *L. schultzei* (beginning in 2003) allowed identification of different damage patterns. Caterpillars could be observed feeding on buds and flowers on several occasions. Since their specific feeding pattern was easily recognisable, such minor feeding damage on flowers was henceforth attributed to them. Left flower stalks on *C. imitans* were assumed to be the result of

rodents feeding on flowers. The rodents were identified by faeces and tracks around damaged plants as well as remains of "harvested" *C. imitans* flowers, matching the flower stalk, in a rodent burrow. Damage not only to flowers but also to other plant parts (leaves) was identified as grazing by livestock. Goats or donkeys show a similar feeding pattern, but since donkeys passed only very occasionally by the study area, damage by livestock is attributed to goats. Fruits were investigated and seeds counted. Flowers that wilted and developed a capsule containing only ovules but not seeds were regarded as not pollinated.

Fruit set (percentage of flowers developing into fruits) was calculated for all selected species as well as the percentages of the different kinds of damage to the flowers for *C. imitans* and *L. schultzei*. Individuals that did not flower during the census were omitted from analysis. All methods described above applied for individuals in clusters as well as for fenced-in individuals.

In 2004, distances to the nearest neighbour of each marked individual were measured within the clusters of *C. imitans* and *L. schultzei*. All nearest neighbour plants were classified as seedling, juvenile, flowering, non-flowering or dead. Juveniles were plants with more than two leaf pairs lacking signs of past or present flowering. Non-flowering plants showed evidence of previous but not present flowering (e.g. old fruits or stalks). Individuals with only dry leaves left and no signs of new growth were supposed to be dead. Furthermore, within a radius of 1 m around every marked plant, all individuals were counted and categorised as described above.

Results

Fruit set—all study species

In 2002, the fruit set of the investigated species *R. viridifolia*, *R. goodiae*, *C. imitans* and *C. denticulata* was significantly higher on the site with low grazing pressure (Fig. 1A). In the following year, *C. imitans* showed a significantly higher fruit set on the heavily grazed site, whereas all other species did not express significant differences in the fruit set between both land use systems (Fig. 1B). *R. viridifolia* and *L. schultzei* could not be analysed in 2003 since these species did not come to fruiting during the field campaign due to a delayed onset of flowers. In the last year of the study, the fruit set of all examined species was again significantly higher on land with low grazing pressure, with the species *R. goodiae*, *R. viridifolia*, *L. schultzei* and *Ihlenfeldtia excavata* delivering highly significant results (Fig. 1C).
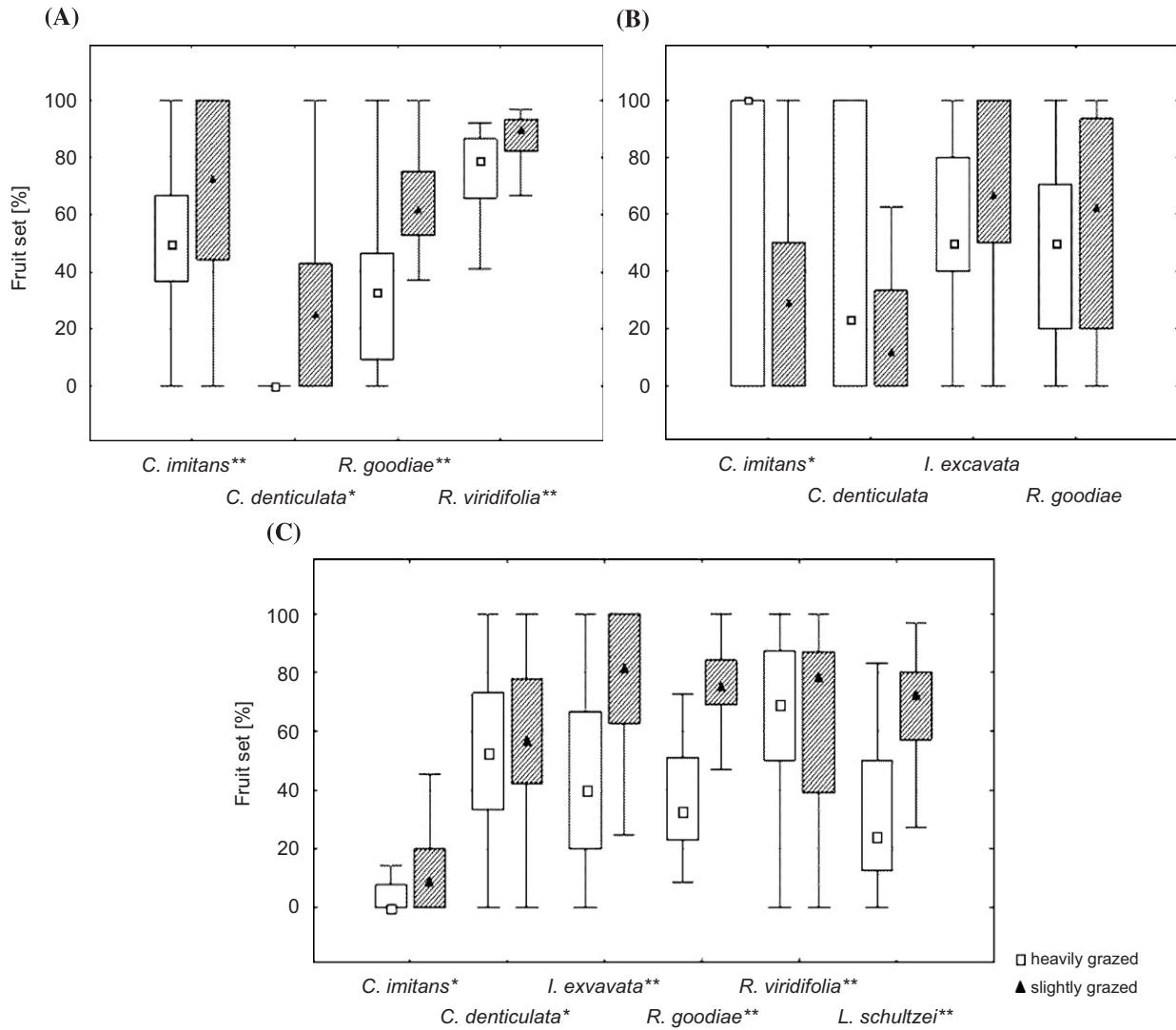
(A)

(B)

(C)

Fig. 1. Fruit set of the examined species in (A) 2002, (B) 2003 and (C) 2004. Significant differences between heavily and slightly grazed sites are marked with $*p < 0.05$ and $**p < 0.01$.

Detailed analysis of fruit set in *C. imitans* and *L. schultzei*

Factors limiting the fruit set of *C. imitans* in 2003 were the caterpillars of *Diaphone eumela* (Noctuidae) and two rodent species (*Otomys unisulcatus*, *Rhabdomys pumilio*), with both factors having a significantly higher influence on the slightly grazed site (Table 1). The strength of impact of the two factors could not be compared statistically on the slightly grazed site since the factors "caterpillar" and "rodents" correlated ($r_s = -0.44$, $p < 0.05$). On the heavily grazed site, where the two factors did not correlate ($r_s = -0.08$, $p = 0.749$), the influence of rodents on the fruit set was not different from that of *D. eumela* on fruit development (MWU: $Z = 0.59$, $p = 0.554$).

In 2004, flowers of *C. imitans* and *L. schultzei* were lost due to *D. eumela* caterpillars, rodents, livestock

Table 1. Fruit set (%) and total damage (%) to flowers of *C. imitans* in 2003, caused by different factors and comparison of their strength for the two sites with Mann–Whitney U-tests (Z and p-values given)

	Heavily grazed	Slightly grazed	Z	P
n	63	183		
Fruit set	90.5	47.5	4.06	$<0.0001***$
D. eumela	1.6	30.6	-4.42	$<0.0001***$
Rodents	7.9	21.9	-2.58	$0.01*$

Also given is the total number of flowers for all observed individuals (30) per site.

grazing and a lack of pollinators to varying proportions (Table 2). In contrast to 2003, feeding damage due to *D. eumela* was equal for *C. imitans* individuals on both

Table 2. Fruit set (%) and total damage (%) to flowers of *C. imitans* and *L. schultzei* in 2004, caused by different factors and comparison of their strength for the two species with Mann–Whitney-U-tests (Z and p-values given)

	Heavily grazed				Slightly grazed			
	C. imitans	*L. schultzei*	Z	p	*C. imitans*	*L. schultzei*	Z	P
n	91	1058			184	4746		
Fruit set	16.5	31.5	−3.84	**0.0001*****	17.9	73.5	−5.71	**<0.0001*****
D. eumela	40.7	54.4	0.22	0.822	27.2	7.2	1.83	0.07
Goats	20.9	4.2	−0.33	0.743	0	0		
Rodents	22.0	0	2.41	**0.016***	45.7	0	5.11	**<0.0001*****
Not pollinated	0	9.9	−4.49	**<0.0001*****	9.2	19.4	−3.25	**0.001****

Also given is the total number of flowers for all observed individuals (30) per site and species, respectively.

sites (MWU: $Z = 1.32$, $p = 0.186$), whereas flowers of *L. schultzei* were distinctly more often destroyed by caterpillars in the heavily grazed area (MWU: $Z = 4.74$, $p < 0.001$). Grazing by livestock had a major impact on the Leliefontein observatory and the number of flowers lost due to grazing differed significantly between the sites for both species (MWU: *C. imitans*: $Z = 2.55$, $p < 0.05$, *L. schultzei*: $Z = 3.81$, $p < 0.001$). *O. unisulcatus* and/or *R. pumilio* only fed on flowers of *C. imitans* and had a significantly higher impact on the slightly grazed site (MWU: $Z = -3.98$, $p = 0.001$). Flowers of both species remained significantly more often non-pollinated on the slightly grazed site (MWU for *C. imitans*: $Z = -2.91$, $p < 0.005$, *L schultzei*: $Z = -4.0$, $p < 0.001$) in comparison to the heavily grazed site, where for example all *C. imitans* flowers were pollinated. Since all factors correlated on the slightly grazed site ('rodents' and 'not pollinated': $r_s = -0.52$, $p < 0.01$, '*D. eumela*' and 'not pollinated': $r_s = -0.63$, $p < 0.005$), as well as '*D. eumela*' and 'goats' on the heavily grazed site ($r_s = -0.71$, $p < 0.001$), further statistical comparisons of the intensity of all factors were not performed. Influences on the fruit set of *L. schultzei*, however, did not correlate within one site and Fig. 2 shows differences between the strength of all factors for each land use system. When comparing the different factors for the two species within each observatory, some varied significantly in their strength (Table 2).

Exclusion of livestock

In 2003, no grazing activities were observed in the usually heavily grazed area where individuals of *C. imitans* had been marked and fenced in. Therefore, the influence of grazing could not be compared between unprotected and caged plants in this particular year. In 2004, the fruit set of protected *C. imitans*-individuals ("protected individuals") was significantly
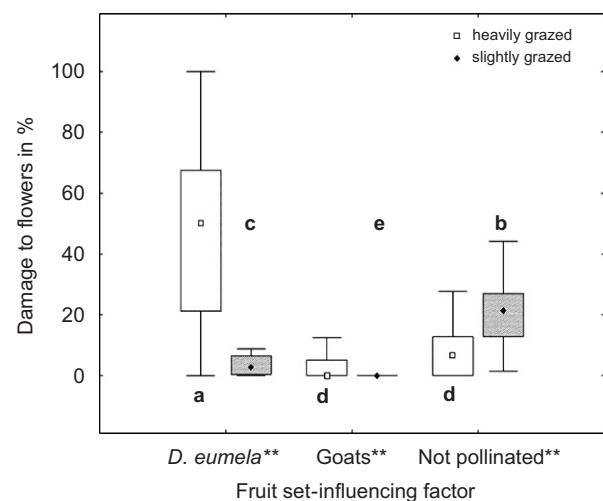

Fig. 2. Influences on the fruit set of *L. schultzei* on both observatories in 2004. Highly significant differences between the sites are indicated with **. (Comparison of the strength of the factors within each site: Boxes that share the same letter do not differ significantly from each other.)

higher ($Q_1 = 11.11\%$; $Q_2 = 20\%$; $Q_3 = 40\%$) compared to unprotected plants ($Q_1 = 0.0\%$; $Q_2 = 0.0\%$; $Q_3 = 7.69\%$; MWU: $Z = 2.92$, $p < 0.005$). Comparing the different factors that prevented flowers of caged and free individuals from developing into fruits, grazing ("goats") was the only impact that was significantly higher for individuals without protection (MWU: $Z = -2.03$, $p < 0.05$; Fig. 3A).

For *L. schultzei* on the other hand, fruit set did not differ significantly between protected ($Q_1 = 0.00\%$; $Q_2 = 33.41\%$; $Q_3 = 44.44\%$) and unprotected individuals ($Q_1 = 12.5\%$; $Q_2 = 24.38\%$; $Q_3 = 50\%$). Similar to the results for *C. imitans,* however, the impact of livestock on the fruit set was the only factor being significantly higher for unprotected individuals (MWU: $Z = -2.31$, $p < 0.05$; Fig. 3B).
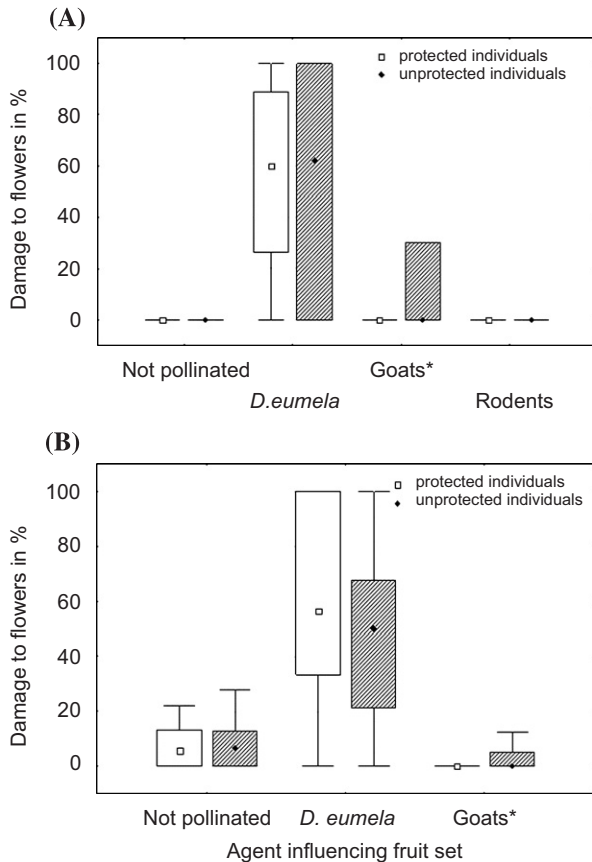
(A)

(B)

Fig. 3. Influences on the fruit set of (A) *C. imitans* and (B) *L. schultzei* comparing protected ("caged") and unprotected ("free") plants. Significant differences are marked with *.

Table 3. Number of nearest neighbours in age categories for *C. imitans* and *L. schultzei* under both land use systems in 2004

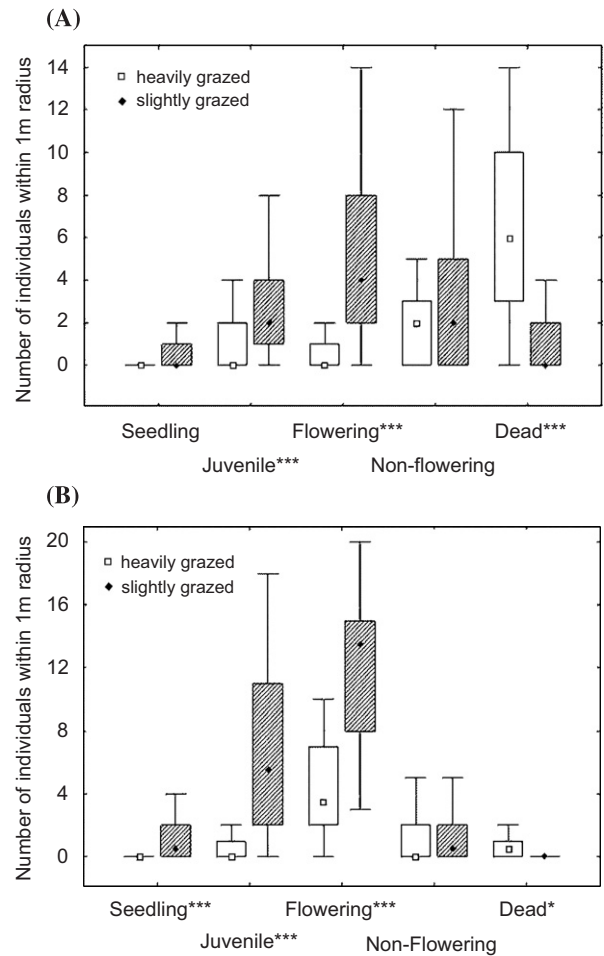|	Heavily grazed		Slightly grazed	
	C. imitans	*L. schultzei*	*C. imitans*	*L. schultzei*
Seedling	0	1	0	15
Juvenile	5	3	10	12
Flowering	2	17	12	3
Non-flowering	5	3	6	0
Dead	17	6	2	0

(A)

(B)

Fig. 4. Number of individuals in age categories within a 1 m radius around marked (A) *C. imitans* and (B) *L. schultzei* individuals in 2004. Compared are individuals in heavily and slightly grazed areas. Significant differences are marked with*.

Population structure

For *C. imitans* the mean distance to the nearest neighbour on the heavily grazed site ($Q_1 = 9$ cm; $Q_2 = 16$ cm; $Q_3 = 32$ cm) was not significantly different from that on the slightly grazed site ($Q_1 = 6$ cm; $Q_2 = 14$ cm; $Q_3 = 33$ cm; MWU: $Z = 0.50$, $p = 0.617$). On the other hand, *L. schultzei* showed highly significantly larger distances to the nearest neighbour on the heavily grazed site ($Q_1 = 15$ cm; $Q_2 = 20$ cm; $Q_3 = 30$ cm) compared to the slightly grazed site ($Q_1 = 8$ cm; $Q_2 = 12$ cm; $Q_3 = 21$ cm; MWU: $Z = 3.39$, $p < 0.001$). A detailed age classification for the nearest neighbours of all marked individuals of *C. imitans* and *L. schultzei* is presented in Table 3.

For both species, the density of juveniles and flowering individuals within a 1 m radius around marked plants was significantly higher on land with low grazing pressure (Fig. 4). Seedlings of *L. schultzei* were also distinctly more abundant on the slightly grazed site. Non-flowering individuals of both species were equally abundant under either land use system although dead plants were significantly more frequent on the site with heavy grazing pressure.

Discussion

The results of this study clearly confirmed that livestock grazing reduces the reproductive output of plants by decreasing fruit set (see also Milton, 1992; 1994; Riginos & Hoffman, 2003; Todd & Hoffman, 1999). In two out of three consecutive years, three

investigated Aizoaceae species showed a lower fruit set on communal rangeland with high grazing pressure compared to privately managed land with minimal grazing. These findings were further substantiated by results from exclosure experiments for two species, *C. imitans* and *L. schultzei*, since grazing significantly reduced the fruit set of unprotected control plants compared to caged plants.

In 2003, no significant differences in fruit production could be detected for five of the species when compared between both land use systems. *C. imitans* even had a higher fruit set in the area with heavy grazing. It is assumed that the relief from grazing pressure accounted for the assimilation of results. The recommended stocking rates for the Leliefontein community are 0.083 SSUs per hectare but the long-term average (1971–2004) lies at 0.173 SSU/ha. In 2003, stocking rates of the entire Leliefontein community declined tremendously (0.050 SSU/ha) at the end of the year in comparison to the beginning of the year (0.143 SSU/ha; T. Hoffman, unpublished data). The extensive loss of animals was due to the harsh weather conditions in 2003, when after a long dry period, heavy rains and freezing temperatures occurred and a lot of goats died shortly before the census started. Thus, the observed plants were not grazed since animals were not abundant in the area.

On the other hand, the detailed analysis of *C. imitans* and *L. schultzei* revealed that besides livestock grazing, also other biotic factors can also inhibit fruit development substantially. The caterpillars of *D. eumela* turned out to be another destructive herbivore of flowers of both examined plant species. The abundance of this insect (in terms of percentage of damaged flowers) varied distinctly between years and sites. Its occurrence had an almost epidemic character on the slightly grazed site in 2003, accounting for half of the loss of *C. imitans*-flowers. Also other insects might have an impact on the fruit set of the investigated plant species, but only little is known about the invertebrate community of the Paulshoek area (Seymour & Dean, 1999). To date, for the Succulent Karoo, *D. eumela* has not even been denoted in the literature or in museums (Picker, Griffiths, & Weaving, 2002), but the caterpillars are well known among people of the local community (F. Claasen, personal communication). In general, it is assumed that with higher complexity of the landscape, as given on the private farm (Todd & Hoffman, 1999), the number of seed predators and pollinators increases (Steffan-Dewenter, Münzenberg, & Tscharntke, 2001). Also phytophagous and/or florivorous arthropods have been reported to occur in higher abundances under low grazing intensities (Cagnolo, Molina, & Valladares, 2002; Dennis, Young, & Gordon, 1998; Fay, 2003; Gibson, Brown, Losito, & McGavin, 1992; Hutchinson & King, 1980; Kruess & Tscharntke, 2002), which serves

as a possible explanation for the increased occurrence of *D. eumela* on the slightly grazed site in 2003. On the other hand, in 2004, the abundance of this caterpillar was equal on the two study sites concerning proportion of flowers destroyed on *C. imitans*, while its impact on *L. schultzei* was significantly greater on flowers of the heavily grazed site. However, insect populations are known to oscillate distinctly among years, often due to climatic variations (Mayer & Kuhlmann, 2004; Roubik, 2001).

Other herbivores, at least for flowers of *C. imitans*, were most likely two rodent species, *O. unisulcatus* and *R. pumilio*. These two species have previously been reported in the area with significantly higher abundances on the slightly grazed site, probably due to the larger shrub cover (Joubert & Ryan, 1999). These findings could be confirmed in this study, in terms of proportions of flowers eaten by the rodents, which was definitely greater on the site with low grazing pressure. No flowers or fruits of *L. schultzei* were eaten by rodents, though. The fruits of this species are much smaller and grow high above the ground compared to fruits of *C. imitans*. *Leipoldtia* fruits seem to be out of reach for small mammals apart from offering a less-rewarding food resource for them.

Another parameter diminishing fruit set in 2004 was the lack of pollination success, however, almost exclusively on the slightly grazed site. It has already been hypothesised that there are too few pollinators for too many flowers in Namaqualand (Cohen & Shmida, 1993; Moldenke, 1976; Struck, 1994b, 1995). Thus, it is assumed that the fewer flowers present on the heavily grazed site (Mayer & Pufal, unpublished data) had a better chance of getting pollinated than flowers blooming at higher densities under low grazing pressure. Due to very dry weather conditions from May until July 2003, the flower occurrence on both sites was much lower than in normal years (Mayer & Kuhlmann, 2004; Mayer & Pufal, unpublished data). The plants developed fewer buds, which also flowered later than usual. Therefore, all observed flowers on both study sites received sufficient visits by pollinating insects.

Precipitation affected flower development in 2004, when after fairly good rainfall earlier this year plants could produce considerable amounts of buds. However, later that year, insufficient rains in August and September caused the withering of a large number of buds, which dramatically reduced the number of flowers on both study sites (Pufal, unpublished data). The climatic conditions had therefore a direct effect on the flower set but influenced the fruit set only indirectly, e.g. the abundance of herbivorous insects or a sufficient pollination success due to lower numbers of flowers.

Investigations on the population structure confirmed a long-term impact of grazing (Milton, 1994; Milton, Dean, Du Plessis, & Siegfried, 1994) for *C. imitans* and *L. schultzei*

with plants growing under heavy grazing pressure showing failure in recruitment. Here, distinctly less juvenile and flowering individuals were found on the site with intense grazing compared to lightly grazed land. The decline in fruit production due to ongoing grazing pressure is supposed to result in lowered seed availability, which in turn reduces the number of seedlings and the chances for seedling establishment (see also Carrick, 2003a, 2003b; Riginos & Hoffman, 2003; Todd, 2000). The thesis of Milton et al. (1994) regarding a shift in age structure to older age classes and an increase in dead plants due to intense grazing could also be proved for the two examined species, since significantly more dead plant individuals were recorded under heavy grazing pressure (see also Riginos & Hoffman, 2003). Obviously, continuous grazing of plants slowly reduces the plant's fitness eventually leading to the death of individuals (Milton, 1994; Todd & Hoffman, 1999).

Conclusions

In this study, heavy livestock grazing was identified to be a major threat to fruit production of perennial Aizoaceae species in Namaqualand. However, in contrast to this widely accepted hypothesis, the present observations also showed that the variation in the fruit set of plants also depends on other biotic factors that can—under extreme climatic conditions—even cause higher fruit and flower losses. The present results demonstrate that the system of plant reproduction in interaction with the influencing biotic factors in the Succulent Karoo is highly dynamic and hardly predictable. Further research on the dynamics of the influencing parameters, especially indirect of precipitation fluctuations within and between years, could provide better insights into this dynamic system.

For conservation of *C. imitans* and *L. schultzei* and other Aizoaceae species, management strategies are needed that promote a healthy population structure. Since livestock fed only on flowers of the investigated species, it might be practicable to avoid grazing during flowering time in areas where both species are abundant. In areas with only a few plant individuals, rehabilitation could possibly be promoted by sowing seeds under unpalatable or spinescent refuge plants to prevent grazing of flowers in the later adult stage.

Acknowledgements

References

Allsopp, N. (1999). Effects of grazing and cultivation on soil patterns and processes in the Paulshoek area of Namaqualand. *Plant Ecology*, *142*, 179–187.

Cagnolo, L., Molina, S. I., & Valladares, G. R. (2002). Diversity and guild structure of insect assemblages under grazing and exclusion regimes in a Montane grassland from Central Argentina. *Biodiversity and Conservation*, *11*, 407–420.

Carrick, P. J. (2003a). Competitive and facilitative relationships among three shrub species, and the role of browsing intensity and rooting depth in the Succulent Karoo, South Africa. *Journal of Vegetation Science*, *14*, 761–772.

Carrick, P. J. (2003b). Different landuse options produce a gradient of plant richness at a single location in Namaqualand: the pattern and the processes. In: *Proceedings of the VIIth international rangelands congress* (pp. 177–187). Durban, South Africa.

Cohen, D., & Shmida, A. (1993). The evolution of flower display and reward. In M. K. Hecht, R. J. MacIntyre, & M. T. Clegg (Eds.), *Evolutionary Biology*, Vol. 27 (pp. 197–243). New York: Springer.

Cowling, R. M., & Hilton-Taylor, C. (1999). Plant biogeography, endemism and diversity. In W. J. D. Dean, & S. J. Milton (Eds.), *The Karoo-Ecological patterns and processes* (pp. 42–56). Cambridge: Cambridge University Press.

Davis, S. D., & Heywood, V. H. (1994). *Centres of plant diversity: A guide and strategy for their conservation*. Oxford: Oxford University Press.

Dennis, P., Young, M. R., & Gordon, I. J. (1998). Distribution and abundance of small insects and arachnids in relation to structural heterogeneity of grazed, indigenous grasslands. *Ecological Entomology*, *23*, 253–264.

Desmet, P. G., & Cowling, R. M. (1999). Biodiversity, habitat and range-size aspects of a flora from a winter-rainfall desert in north-western Namaqualand, South Africa. *Plant Ecology*, *142*, 23–33.

Esler, K. J. (1999). Plant reproduction ecology. In W. R. J. Dean, & S. J. Milton (Eds.), *The Karoo-ecological patterns and processes* (pp. 123–144). Cambridge: Cambridge University Press.

Fay, P. A. (2003). Insect diversity in two burned and grazed grasslands. *Environmental Entomology*, *32*(5), 1099–1104.

Gibson, C. W. D., Brown, V. K., Losito, L., & McGavin, G. C. (1992). The response of invertebrate assemblies to grazing. *Ecography*, *15*(2), 166–176.

Hilton-Taylor, C. (1996). Patterns and characteristics of the flora of the Succulent Karoo Biome, Southern Africa. In L. J. G. Van der Maesen, X. M. Van der Burg, & J. M. Van Medenbach de Rooy (Eds.), *The biodiversity of African plants* (pp. 58–72). Dordrecht: Kluwer Academic Publishers.

Hoffman, M. T., Cousins, B., Meyer, T., Petersen, A., & Hendriks, H. (1999). Historical and contemporary land use and the desertification of the Karoo. In W. R. J. Dean, & S. J. Milton (Eds.), *The Karoo. Ecological patterns and processes* (pp. 257–273). Cambridge: Cambridge University Press.

Hutchinson, K. J., & King, K. L. (1980). The effects of sheep stocking level on invertebrate abundance, biomass and energy utilization in a temperate, sown grassland. *Journal of Applied Ecology, 17*, 369–387.

Joubert, D. F., & Ryan, P. G. (1999). Differences in mammal and bird assemblages between commercial and communal rangelands in the Succulent Karoo, South Africa. *Journal of Arid Environments, 43*, 287–299.

Kruess, A., & Tscharntke, T. (2002). Contrasting responses of plant and insect diversity to variation in grazing intensity. *Biological Conservation, 106*(3), 293–302.

Lombard, A. T. (1995). The problems with multi-species conservation: Do hot spots, ideal reserves and existing reserves coincide? *South African Journal of Zoology, 30*, 146–163.

Mayer, C., & Kuhlmann, M. (2004). Synchrony of pollinators and plants in the winter rainfall area of South Africa—observations from a drought year. *Transactions of the Royal Society of South Africa, 59*(2), 55–57.

Milton, S. J. (1992). Effects of rainfall, competition and grazing on flowering of *Osteospermum sinuatum* (Asteraceae) in arid Karoo rangeland. *Journal of the Grassland Society of Southern Africa, 9*(4), 158–164.

Milton, S. J. (1994). Growth, flowering, and recruitment of shrubs in grazed and in protected rangeland in the arid Karooo, South Africa. *Vegetation, 111*, 17–27.

Milton, S. J., & Dean, W. R. J. (1990). Seed production in rangelands of the southern Karoo. *South African Journal of Science, 86*, 231–233.

Milton, S. J., Dean, W. R. J., Du Plessis, M. A., & Siegfried, W. R. (1994). A conceptual model of arid rangeland degradation. *Bioscience, 44*(2), 70–76.

Moldenke, A. R. (1976). California pollinator ecology and vegetation types. *Phytologia, 34*, 304–361.

Petersen, A., Young, E. M., Hoffman, M. T., & Musil, C. F. (2004). The impact of livestock grazing on landscape biophysical attributes in privately and communally managed range lands in Namaqualand. *South African Journal of Botany, 70*, 777–783.

Picker, M. D., Griffiths, C., & Weaving, A. (2002). *Field guide to insects of South Africa*. Cape Town: Struik Publishers.

Riginos, C., & Hoffman, M. T. (2003). Changes in population biology of two succulent shrubs along a grazing gradient. *Journal of Applied Ecology, 40*(4), 615–625.

Roubik, D. W. (2001). Ups and downs in pollinator populations: when is there a decline? *Conservation Ecology, 5*(1), 2 [online] URL: ⟨http://www.consecol.org/vol5/iss1/art2/⟩.

Rutherford, M. C., & Westfall, R. H. (1986). Biomes of Southern Africa—an objective categorization. *Memoirs of the Botanical Survey of South Africa, 54*, 1–98.

Seymour, C. L., & Dean, W. R. J. (1999). Effects of heavy grazing on invertebrate assemblages in the Succulent Karoo, South Africa. *Journal of Arid Environments, 43*, 267–286.

Steffan-Dewenter, I., Münzenberg, U., & Tscharntke, T. (2001). Pollination, seed set and seed predation on a landscape scale. *Proceedings of the Royal Society of London, 268*, 1685–1690.

Struck, M. (1994a). Flowering phenology in the arid winter rainfall region of southern Africa. *Bothalia, 24*(1), 77–90.

Struck, M. (1994b). Flowers and their insect visitors in the arid winter rainfall region of southern Africa: observations on permanent plots. Insect visitation behaviour. *Journal of Arid Environments, 28*, 51–74.

Struck, M. (1995). Land of blooming pebbles: flowers and their pollinators in the Knersvlakte. *Aloe, 3&4*, 56–64.

Todd, S. (2000). Patterns of seed production and shrub association in two palatable Karoo shrub species under contrasting land use intensities. *African Journal of Range and Forage Science, 17*, 22–26.

Todd, S. W., & Hoffman, M. T. (1999). A fence-line contrast reveals effects of heavy grazing on plant diversity and community composition in Namaqualand, South Africa. *Plant Ecology, 142*, 169–178.