The occurrence of seed-feeding Zulubius acaciaphagus (Hemiptera, Alydidae) and its effects on Acacia cyclops seed germination and seed banks in South Africa

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Following recent observations of an indigenous hemipteran Zulubius acaciaphagus feeding on alien Acacia cyclops seeds, we surveyed its occurrence and effects throughout the plant’s distributional range. Zulubius acaciaphagus occurred at all study sites, but when surveyed was most abundant at the north-western extreme of the plant’s distributional range, where the climate is hotter and drier. Intensity of feeding correlated positively with percentage seed rotted and negatively with percentage seed viability, but was not correlated with percentage spontaneous seed germination. Soil-seed density did not relate to alydid density, possibly because feeding intensity was low; mean maximum daily temperature and annual rainfall (or related factors) apparently have a major effect on seed density. Although Z. acaciaphagus destroyed up to 84% of the A. cyclops seed crop, detailed studies of the alydids’ population dynamics are required to assess its potential as a controlling agent of the alien invader.

Na aanleiding van onlangs waarnemings van ‘n inheemse halfverklikte Zulubius acaciaphagus wat op uitheemse Acacia cyclops-sade voed, is die voorkoms en gevolge daarvan oor die plant se hele verspreidingsgebied onder­soek. Zulubius acaciaphagus het in alle studiegebiede voorgekom, maar was tydens die ondersoek die volopste by die noordwestelike grens van die plant se verspreidingsgebied, waar die klimaat warmer en droër is. Die intensiteit van die voeding het positief met die persentasie verrotte saad gekorreleer en negatief met die persentasie saaddikte. Na die nie die persentasie spontane saadontkieming gekorreleer nie. Die digtheid van saad in die grond hou nie verband met die alydid-digtheid nie, maar is standorde wat deel uitmaak van die maksimum daalag die temperatuur en jaarlike reënval (of verwante faktore) waarskynlik ‘n groot invloed op saaddiktheid het. Alhoewel Z. acaciaphagus tot 84% van die A. cyclops-saad vernietig, word gedetailleerde ondersoek na die alydids’ populasiedynamika benodig om die potensiaal daarvan as beheeragt van die uitheemse indringers te bepaal.

Keywords: Acacia cyclops, alydids, distribution, seed bank, seed germination

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Introduction

Acacia cyclops A. Cunn. ex G. Don is a small evergreen tree, introduced into South Africa from Australia in the late 19th century for dune stabilization and shelterbelts (Shaughnessy 1980). It has become one of the most widespread alien invaders in the lowlands of the fynbos biome (Figure 1; Macdonald et al. 1985). Its invasive success is thought to be primarily due to a ‘preadaptation’ to climatic and edaphic conditions in the south-western Cape and to its ‘ecological release’ from pathogens and predators (Milton 1980). Although its seed production is similar in South Africa and Australia, seed banks are much larger in South Africa (Gill & Neser 1984). These large seed banks are a major obstacle to its successful control (Holmes et al. 1987b).

Acacia cyclops is attacked by many seed-feeding insect species in native western Australia, including nine hemip­terans (van den Berg 1980). Predation by a single species of hemipteran was found to account for the destruction of 25% of the seed crop (van den Berg, loc cit), and predation may thus explain the low seed banks found in Australia. Unlike chewing insect predators (e.g. Lepidoptera and Coleoptera), which consume whole seeds (Moore 1978), hemipterans puncture seeds (Underhill 1943) and may only kill seeds if the embryo is damaged (Janzen 1976). Hemipteran feeding punctures may break the water­ impermeable, seed-coat dormancy (Rolston 1978) of A. cyclops seeds (Neser 1984).

Recently, an alydid bug (Zulubius acaciaphagus Schaffner, Alydidae: Alydinae) has been observed feeding on the canopy-held seeds of A. cyclops in South Africa. Although initial observations of Z. acaciaphagus on A. cyclops were made in 1975 (Schaffner 1987), it is uncertain when initial colonization of A. cyclops by Z. acaciaphagus (c.f. Strong 1974) occurred. Zulubius acaciaphagus has been shown to markedly decrease the viability of A. cyclops seeds, and may possibly reduce the rate of seed accumulation in the soil (Holmes et al. 1987a). Little is known about the distribution of Z. acaciaphagus and the extent of its attack on A. cyclops seeds in South Africa. In this paper we investigate the distribution of alydids on A. cyclops and assess the effects alydids have on A. cyclops seeds and seed banks.

Field sites and Methods

Studies were made between 27 December 1986 and 10 January 1987 at 16 sites supporting dense (i.e. canopy cover > 90%) stands of mature A. cyclops throughout the plant’s distributional range (Figure 1). At each site, 10 trees were selected at random to assess alydid presence and seed damage. The proportion of deformed seeds (i.e. those with a shrunk or depressed appearance), which might be the result of alydid feeding on developing seeds, was deter­mined by inspecting 100 seeds in newly dehisced pods on each tree. The number of feeding turrets (c.f. Gill 1985) per seed was recorded for 100 undeformed seeds on each tree. The density of Z. acaciaphagus adults and nymphs from each tree was determined as follows: dehisced pods contain­ing seeds were carefully removed from randomly selected branches, placed into plastic bags and sprayed with insecticide. Any Z. acaciaphagus present were sorted into adults, large nymphs (2 mm long), and small nymphs (< 2 mm long) and expressed as a proportion of seeds collected (112–732 seeds, or ca. 50 pods, per tree). Although the overwintering behaviour of alydids adults is not known, mature seeds are available on A. cyclops trees for 5 months (Knight 1986) beginning in October, with developing seeds available prior to this (pers. obs). Alydids populations should thus have attained seasonal abundance by the time of this study.
Stand density and demography of *A. cyclops* were estimated at each site by measuring all stem diameters (at 0.1 m above ground) in a 10-m × 10-m plot. Trees were classified into <3-cm, 3–5-cm, 6–20-cm, and >20-cm stem diameter categories. Wood biomass was estimated from stem diameters using regression equations from Milton & Siegfried (1981). Density of seeds in the soil was determined by extracting 50 random soil cores (50 mm diameter × 150 mm deep) within the 10-m × 10-m plot.

Germination trials
Undeformed seeds collected from the 10 trees at the 16 sites were tested for percentage spontaneous germination (germination) and percentage decay (rotting) as follows: four replicates of 25 seeds each per tree were placed in 9-mm sterile, plastic petri-dishes, containing filter paper moistened with 6 ml benomyl solution [0.022% (m/v) active ingredient, c.f. Clemens et al. 1977]. Seeds were germinated in a controlled environment with a 12-h photoperiod at 25°C alternating with 20°C. Germinated seeds [those with radicals extending 1–2 mm beyond the seed coat (Pieterse & Cairns 1986)] and rotted seeds were counted and removed over a period of 26 days. Remaining seeds were considered to be dormant and were manually chipped at the micropylar end to ensure a maximum germination rate (McDowell & Moll 1981), and incubated for a further 14 days to determine percentage viability (viability).

Soil-stored seeds from 12 sites (seeds from four sites were not tested) were also subjected to germination trials, as described above with four replicates of 25 seeds each per site. In addition, four replicates of 25 seeds classified as deformed were tested for viability.

Data analysis
The importance of selected site factors in determining soil-stored seed and alydid densities, and germination response of fresh seed, was tested by stepwise multiple linear regression analysis (SMLRA, BMDP2R, Dixon 1985) using means from each of the 16 sites. Climatic data were taken from the nearest weather station (Appendix 1). Infestation level of *A. cyclops* at each study area was extracted from Macdonald et al. (1985) (Figure 1).

Correlation analysis (BMDP6D, Dixon 1985) was employed to test effects of alydid density and feeding intensity (% seeds with at least one turret) on seed germination response, using data from 10 trees at each site. Clumping of feeding turrets was investigated by Chi-squared testing deviations from the Poisson distribution (Zar 1974). Differences in germination response between fresh and soil-stored seeds were tested by the Mann–Whitney U Test (Siegel 1956).

**Results**
*Zulubius acaciaphagus* adults or nymphs were found at 14 of the 16 sites investigated (Figure 2), but all life-cycle stages were sampled only at Klipfontein and East London. However Klipfontein, in the extreme north-west, supported over 100 times the density of any other site. No other *Zulubius* species was collected. There was evidence of alydid feeding at all 16 sites, but only the three north-westerly sites (Klipfontein, Fairvlei and Koeberg) had more than 25% of seeds with feeding turrets (Figure 3). Alydid density was positively correlated with mean maximum daily temperature and negatively correlated with mean annual precipitation (r = 0.557, r = 0.506, respectively; P < 0.05). Mean maximum daily temperature explained 31% of the inter-site variation in alydid density (Table 1).

At an inter-site level, average germination of fresh seeds was positively correlated with mean average daily temperature (r = 0.501, P < 0.05), which accounted for 25% of the variation (Table 1). Seed rotting was positively correlated with alydid large nymphs and small nymphs (r = 0.889 and r = 0.823 respectively, P < 0.001), which accounted for 85% of the inter-site variation (Table 1). Alydid density, feeding intensity and site factors such as precipitation and temperature, accounted for 97% of the variation in seed rotting (Table 1). Viability was not correlated with any variable at an inter-site level.

Estimated density of soil-stored seeds ranged from 28 seeds m⁻² near East London to 11 400 seeds m⁻² at Arniston (Figure 4). Soil-stored seed density was not correlated with any measure of alydid or plant density, but was negatively correlated with mean maximum daily temperature (r = -0.597, P < 0.05). Mean maximum daily temperature and annual precipitation accounted for 50%
of the inter-site variation in seed density (Table 1). Numbers of *Z. acaciaphagus* adults, large nymphs and small nymphs and their visible effects — percentage deformity and turrets (analysed for 10 trees per site) — were all

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**Figure 2** Density of *Zulubius acaciaphagus* adults, large nymphs and small nymphs on *Acacia cyclops* at 16 sites in South Africa (drawn to a square root scale). Stippled = small nymphs; striped = large nymphs; solid = adults; numbers are mean alydids per 10 000 seeds ± S.D., n = 10 samples.

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**Figure 3** Density of alydid feeding turrets (% seeds with turrets) on *Acacia cyclops* seeds at 16 sites in South Africa (drawn to a square root scale). Stippled = 1 turret per seed; striped = 2–3 turrets per seed; solid = 4 or more turrets per seed; numbers are mean percentage turrets ± S.D., n = 10 samples.
significantly correlated among each other (Table 2). The distribution of alydid feeding turrets on seeds at the three sites with the highest feeding intensity was highly clumped (mean = 1,147, S.D. = 1,636; P < 0.05, Chi-squared test).

Germination of fresh seeds was low (Table 3), and was not correlated with alydid density or feeding intensity (Table 2). Within sites, seed rotting during the first 26 days of the germination trials was positively correlated with alydid density (Table 2). Seed viability showed significant (P < 0.05) negative correlations with all measures of alydid density except the density of small nymphs (Table 2). All seeds classified as deformed were non-viable.

Seed germination and viability were significantly lower in fresh seeds than in soil-stored seeds at six and nine of the 12 sites respectively (Table 3). Rotting in the first 26 days was significantly higher in fresh seeds than in soil-stored seeds at eight of the 12 sites (Table 3).

**Table 1** Results of stepwise multiple linear regression analysis. Significance levels are P < 0.1

| Dependent variables | Soil-seed density | Alydid density | Germination (fresh seeds) | Rotting (fresh seeds) |
|---------------------|-------------------|----------------|--------------------------|-----------------------|
| Independent variables | r²                | Independent variable | r²                | Independent variable | r²        |
| tmax                | -0.356            | tmax             | 0.310                   | tavg                 | 0.251     |
| pptan               | -0.145            |                 |                         |                       |           |
| densl               | 0.105             |                 |                         |                       |           |
| Overall regression equation | 0.606 | 0.310 | 0.251 | 0.972 |

Abbreviations are as follows: tmax = mean maximum daily temperature; pptan = annual precipitation; densl = density of stems, diameter < 3 cm; tavg = average daily temperature; alln = large nymphs; alsn = small nymphs; turr = % seeds with turrets; infllev = infestation level; pptsu = summer precipitation; def = % deformed seeds

**Discussion**

There is evidence of *Z. acaciaphagus* throughout the distributional range of *A. cyclops* in South Africa, but it is most abundant in hotter and drier environments. The species shows no relationship to *A. cyclops* density or demography.

Alydids apparently cause an increase in rotting and a decrease in viability of *A. cyclops* seeds. Whilst alydid feeding may break water-impermeable, seed-coat dormancy (Neser 1984) this appears to cause rotting rather than increased germination. Although damage to the embryo may be required to kill a seed (Janzen 1976), any puncture may introduce bacterial and fungal pathogens (Janzen 1971), which may lead to rotting in moist environments. Furthermore, hemipterans can be vectors of fungi (Green & Palm-bald 1975). This is supported by the high correlation between seed rotting and alydid density. The correlation

**Figure 4** Density of soil-stored *A. cyclops* seeds at 16 sites in South Africa; numbers are mean seeds m⁻² ± S.E., n = 50 samples.
would also deplete the seed bank. Especially those exposed to warm surface temperatures following removal of the stand, germinate more readily and hence the lower rotting of soil-stored seeds.

Factors (including those mentioned) appear to encourage seed bank decay. The large decreases measured in year after the felling of mature stands (Holmes et al. 1987b) may be related to the low density of alydids present at most sites. Higher temperatures and rainfall (or related factors) appear to encourage seed bank decay. The large variation in alydids density may reflect the low density of alydids present at most sites. Higher temperatures and rainfall (or related factors) may increase rotting of seeds in the soil.

The finding that soil-seed density is not correlated with the production of viable seeds (Waloff & Richards 1977; Schaefer 1980; Louda 1982; Harley 1985), yet few studies have demonstrated that they can influence plant recruitment (Louda 1982; De Steven 1982). Assuming that all rotted and seed deformity in this study was the result of alydid feeding, Z. acaciaphagous destroyed on average only 16% of the A. cyclops seed crop, compared to an equivalent alydid species in Australia which kills about 25% of the seed crop (van den Berg 1980). However, at Klipfontein, 84% of the seed crop was destroyed, indicating that alydids may have the potential to reduce the invasiveness of A. cyclops. Furthermore, since alydids populations increase through spring and summer, late maturing seeds are predisposed to greater attack (Gill 1985).

The wide variation in alydids pre-dispersal seed attack, both within and between sites, highlights the difficulties in assessing the extent of seed loss to the plant species (Auld 1983; New 1983). The intensity of feeding reported here falls within the range for native seed predators and their hosts (Janzen 1971). Alone it may not be sufficient to reduce A. cyclops populations, but it may curtail the plant’s invasiveness by reducing the number of viable seeds dispersed into ‘safe sites’ (c.f. Harper 1977). Costs of clearing operations would then decrease as a result of the lower rate of recruitment.

If the colonization of A. cyclops by Z. acaciaphagous is recent, as suggested by Holmes et al. (1987a), then the rate of accumulation of A. cyclops seeds in the soil should decrease over the next decade. A detailed study of Z.
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