Association of three succulent plant species with woody canopy in the mixed bushveld, South Africa

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Succulents are an important component of the mixed bushveld. Although the nurse plant syndrome is known from arid areas, association of succulents with woody canopy has ot been studied in non-arid areas. The study was done in two phases, the first being to confirm the existence of an association and the second being to investigate a possible cause of the association. The three species studied were all significantly associated with woody canopy. All of the relatively small (0–1m) *Euphorbia ingens* plants and most of the relatively small (0–0.5m) *Aloe marlothii* and *Opuntia vulgaris* plants encountered were beneath woody canopy. There was a very strong significant association between being damaged by fire and growing between woody canopies for all three species. Fires are likely to be lethal to any plants of the study species that are shorter than about 1 m. In any area where fires are frequent there are likely to be fewer young plants of the study species between woody canopies than there will be within the protection of a bush clump.

Key words: *Euphorbia ingens*, *Aloe marlothii*, *Opuntia vulgaris*, bush clumps, fire.

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Introduction

An understanding of the association of a species with other species or other environmental factors helps us to explain the distribution of that species. This is basic to ecology. The relationships and interactions between various species also help to predict future changes in vegetation, especially in relation to environmental change and invasions by alien plants.

Euphorbia ingens E. Meyer ex Boiss (Euphorbiaceae) is a large, much-branched succulent spiny tree, up to about 10 m tall with a rounded crown. It is usually part of deciduous woodland, being most common on rocky outcrops and termitaria, but also occurs in grassland (Palgrave 1984). This species produces capsular fruits which burst when ripe, dispersing the seeds. It is susceptible to frost and also to fungus attack when growing in wet conditions (Barkhuizen 1978).

Aloe marlothii Berger (Liliaceae) is a medium tall tree, 2–4 m high (Van Wyk & Smith 1996). It has long, broad, succulent leaves with spines at the margins. The leaves are closely packed at the stem apex. The stem is covered with dead leaves, which are thought to provide some protection from fire (Jordan 1996). Large numbers of 10 mm diameter capsular fruits are produced.

Opuntia vulgaris Mill. (Cactaceae) is a sprawling shrub, up to 5 m tall. The leaves are very reduced and there are spines on the large succulent cladodes. Reproduction is both vegetative and by seed. It produces edible obovoid fruits, about 60 mm long, each containing many seeds (Palgrave 1984). These fruits are eaten by frugivorous birds and mammals, which distribute the seeds.

Succulents are an important component of the mixed bushveld. Their properties of drought resistance and modest habitat requirements allow them to prosper in this, often harsh, range type. Bond (1983) and Jordan (1996) both provide some indication that fire is probably one of the most important factors causing succulent mortality in the bushveld.

Aloe marlothii is a remarkably successful species and is widespread and common. It provides an excellent comparison with the other species that were studied. The fruits of *Opuntia vulgaris* are harvested by rural people for consumption themselves and sale. There is also potential for producing cochineal dyes from this species. *Opuntia vulgaris* is an alien invader species, introduced from South America. It is a declared weed in South Africa that has been identified as a threat to indigenous diversity (Wells *et al.* 1986). It effectively removes patches of land from grazing and at late stages of invasion this species may severely reduce grazing potential and accessibility of range for livestock.

There are 73 southern African species of *Euphorbia* and 75 southern African species of *Aloe* classified as threatened in the red data list for plants in this sub-continent (Hilton-Taylor 1996). Application of my results to these related endangered species will help the prediction of their distribution and population biology.

This study will help to predict the results of management practices including fire and bush clearing on large succulent plants. People making decisions on alien plant control programmes will also benefit.

The study will give some idea of the relevance of methods based on random distribution of successful seedlings and saplings.

Association of one species of succulent plant, the saguaro, *Carnegiea gigantea* (syn. *Cereus gigantea*), with various woody plants has been determined by Niering *et al.* (1963), Steenbergh & Lowe (1969) and Vandermeer (1980). In these studies it was the protection from herbivory and frost damage and the more favourable microclimate in the shade of other woody plants (and any other shading structure) that were put forward as allowing far more saguaro plants to survive there than elsewhere. In South Africa, Compton (1929) noticed that dwarf succulents grew at the bases of certain shrubs in the Karoo. Yeaton & Esler (1990) found that "mound-building species of the Mesembryanthemaceae" in the Karoo acted as "sites of establishment for seedlings of several species of woody shrubs" and Beukman & Vlok (1991) showed that an arid fynbos tussock species played a similar role. Milton (1995) however, found that proximity to mature perennials reduced both survival and growth of Karoo annuals and perennials.

Although the nurse plant syndrome is known from arid areas (Niering *et al.* 1963; Steenbergh & Lowe 1969; Vandermeer 1980) and the association of *Panicum maximum* with woody canopy because of the concentration of nutrients under woody plants has been described (Bosch & Van Wyk 1970), association of succulents in non-arid areas has not been studied. In the past, most models of community changes, invasions and population fluctuations have assumed a random distribution for successful propagules. One of the purposes of this paper is to confirm an observation that this, at least in some cases, is not valid.

The following hypotheses were tested for each species:

- the number of plants growing under woody canopy is greater than would be expected for a random distribution;
- the proportion of plants growing under woody canopy that were damaged by fire would be lower than expected assuming random damage.

Study area

The study area is in the sourish mixed bushveld (Acocks 1953), at the foot of the Strydpoort mountains in eastern Northern Province, South Africa. The altitude is 1380 m to 1520 m and the aspect is south south-east. The winters are fairly cold and dry and frost is common. The annual rainfall is 350 mm to 650 mm per annum. The land has steep-sided gneiss ridges separated by narrow valleys. The soil on the ridges is a shallow sandy loam, whereas the soil of the valley bottoms is clayey.

The vegetation is an open savanna, with *Acacia caffra* the dominant tree, in a fairly tall and dense grass sward dominated by *Cymbopogon plurinodis*, *Themeda triandra*, *Elionurus muticus* and *Hyparrhenia* spp. *Acacia caffra*, *Combretum molle*, *Dombeya rotundifolia*, *Peltophorum africanum*, *Euphorbia ingens*, *Acacia karroo*, *A. gerrardii* var *gerrardii*, *A. burkei*, *A. permixta*, *Faurea saligna*, *Maytenus senegalensis*, *Ficus thoningii*, *Acacia robusta* subsp. *robusta*, *Schotia brachypetala*, *Acacia davyi*, *Dovyalis zeyheri*, *Ormocarpum trichocarpum*, *Diospyros lycioides* subsp. *sericea* and *Carissa bispinosa* are common woody plants in the study area.

The study area is used for cattle grazing and is burned about once every three years when conditions allow.

Methods

This study was done in two phases, the first being to confirm the existence of an association and the second being to investigate a possible cause of the association. The first phase of the study was done on the farm Lowlands (23°58'S, 29°50'E). The beginning point and direction of a transect were randomly chosen. Sampling points were placed every 30 m along the transect. When the boundary of the property was reached then another transect was started 60 m from and parallel to the previous transect and sampling was continued. At each sampling point the distance to the nearest woody plant was measured. The canopy diameter in the direction of the sampling point and perpendicular to this were also measured. Then the distance from the sampling point to and height of the nearest individual of each of the study species were measured and a record was made whether the plant was growing beneath woody canopy or between woody canopies.

The proportion of plants occurring beneath woody canopy was calculated for each of the study species. An estimate of density of woody plants per hectare was then calculated according to density = 10 000/(2 x mean distance)² (Cottam & Curtis 1956). The mean canopy area estimate was calculated as mean canopy area = (½ mean diameter)². The canopy cover was calculated by multiplying the estimate of woody plant density with the estimate of mean canopy area (Cottam & Curtis 1956). In a population in which the plants are randomly distributed the proportion occurring beneath woody canopy would be expected to be equal to the percentage canopy cover expressed as a proportion.

The log-likelihood ratio test of goodness of fit (*G*-test), as described by Sokal & Rohlf (1995), was used to test whether any deviation of the observed proportion from the expected was significant. According to Sokal & Rohlf (1995) this test has several advantages over the chi-square test. As the test was one-tailed, the null-hypothesis of random distribution of plants was rejected if $P < 0.05$.

The second phase of the study was done on communal land (5 km north of Lowlands) that had been burned in September 1997. The beginning and direction of a 1.3 km-long 20 m-wide continuous transect were randomly chosen. The heights, whether they were under woody canopy or not and whether they had been killed, were damaged or were undamaged by the fire was recorded for all individuals of the three study species within the transect.

The association of damaged plants (and later, killed plants) with growing between woody canopies was tested for each species with a *G*-test (Sokal & Rohlf 1995). Once again, the null-hypothesis of no association was rejected if $P < 0.05$.

Results

The maximum distance between the sampling point and the nearest plant was somewhat higher for *Opuntia vulgaris* than for *Euphorbia ingens* and *Aloe marlothii* (171 % and 145 % respectively), but not overwhelmingly so (Table 1). This supports the observation made in the field that the whole study area is roughly uniformly infested with the alien invader, *Opuntia vulgaris*.

Euphorbia ingens and *Aloe marlothii*, as characteristic components of the mixed bushveld vegetation type, are well represented in the samples at 5% and 6% of woody plant density respectively. *Opuntia vulgaris*, makes up a smaller component of the woody vegetation at 2% of woody plant density (Table 1).

The proportions of the samples of each of the three study species that were observed to be growing under woody canopy were all much higher than those expected under the null hypothesis of random distribution relative to woody canopy (Table 1). The three species were significantly associated ($P \leq 0.005$ for all three) with woody canopy (G=304.7, 115.7 & 193.6 respectively).

All of the relatively small (0–1 m) *Euphorbia ingens* plants and most of the relatively small (0–0.5m) *Aloe marlothii* and *Opuntia vulgaris* plants were beneath woody canopy (Table 1). The proportions of small plants beneath woody canopy were about the same as the proportions of all plants beneath woody canopy for all three species.

In the second phase of the study, as in the first, the strong association of the three study species with woody canopy was evident (Table 2). Indeed, not a single *Euphorbia ingens* plant less than 1m tall was found between woody canopies. Very few *Euphorbia ingens* and *Aloe marlothii* and no *Opuntia vulgaris* at all were killed by the fire. There was a very strong significant association between being damaged by the fire and growing between woody canopies for *Euphorbia ingens* (n = 121, G = 22.5, P <0.001); *Aloe marlothii* (n = 154, G = 33.6, P <0.001) and *Opuntia vulgaris* (n = 95, G = 6.5, P <0.05). There was no significant association between being killed and growing between woody canopies for any of the study species (P > 0.05).

Discussion

The significant association that I found of the three study species with woody canopy shows that some factor is either causing a non-uniform distribution of successful propagules or favouring plants that become established there. The observation that the proportions of small plants that were under woody canopy were about the same as those for the whole populations is an indication that the factors causing the association, whatever they may be, act on the young life stages of the plants. This observation is also an indication that the succulents do not eventually outcompete and kill their nurse plants,

Table 1

Parameter estimates for the woody vegetation as a whole and specifically for each of the three study species, based on a sample of 120 points. The first height class is 0-1 m for Euphorbia ingens *and 0-0.5 m for* Aloe marlothii *and* Opuntia vulgaris

	Woody vegetation	*Euphorbia ingens*	*Aloe marlothii*	*Opuntia vulgaris*
Maximum distance (m)	5.1	32.1	38.0	55.0
Mean distance (m)	1.63	7.44	6.77	11.56
Density (individuals/ha)	943	45	55	19
Canopy cover (%)	18.7	-	-	-
Observed proportion under woody canopy	-	0.92	0.63	0.77
Expected proportion under woody canopy	-	0.22	0.22	0.22
Mean height (m)	1.76	2.81	1.91	1.01
Maximum height (m)	9.2	9.2	5.9	3.1
Minimum height (m)	0.1	0.2	0.2	0.1
Minimum height between canopy	-	1.5	0.4	0.2
Total number of plants in first height class	-	12	8	29
Proportion of plants in first height class under woody canopy	-	1.00	0.75	0.76

as is often the case in Arizona and the Karoo (Vandermeer 1980; Yeaton & Esler 1990).

The cause of the phenomenon could be one or more of several factors. There could be some micro-environmental condition under woody canopy that favours the survival and growth of the study species. A possibility is concentrations of nutrients under woody canopy like those described by Bosch & Van Wyk (1990) and Griffioen & O'Connor (1990). Another possibility is higher levels of soil moisture and cooler conditions because of the shading effect of woody canopy. This was the primary factor given for driving the nurse plant syndrome of saguaro (*Carnegiea gigantea*) described by Niering *et al.* (1963); Turner *et al.* (1966); Steenberg & Lowe (1969) and Vandermeer (1980).

Table 2

The effects of a fire on Euphorbia ingens, Aloe marlothii *and* Opuntia vulgaris *based on a 1.3 km-long 20 m-wide transect*

Euphorbia ingens

Height class	Beneath woody canopy: Alive Undamaged	Beneath woody canopy: Alive Damaged	Beneath woody canopy: Killed	Between woody canopies: Alive Undamaged	Between woody canopies: Alive Damaged	Between woody canopies: Killed	Total
0-0.5	7	5	0	0	0	0	12
>0.5-1	9	3	1	0	0	0	13
>1-2	8	2	1	1	6	1	19
>2-3	12	8	0	2	5	0	27
>3	31	10	0	2	6	1	50
Total	67	28	2	5	17	2	121

Aloe marlothii

Height class	Beneath woody canopy: Alive Undamaged	Beneath woody canopy: Alive Damaged	Beneath woody canopy: Killed	Between woody canopies: Alive Undamaged	Between woody canopies: Alive Damaged	Between woody canopies: Killed	Total
0-0.3	8	3	1	2	5	1	20
>0.3-0.6	10	6	0	1	3	0	20
>0.6-1.2	9	7	2	1	10	1	30
>1.2-1.8	24	1	0	16	15	2	58
>1.8	19	0	2	1	3	1	26
Total	70	17	5	21	36	5	154

Opuntia vulgaris

Height class	Beneath woody canopy: Alive Undamaged	Beneath woody canopy: Alive Damaged	Beneath woody canopy: Killed	Between woody canopies: Alive Undamaged	Between woody canopies: Alive Damaged	Between woody canopies: Killed	Total
0-0.3	16	0	0	7	3	0	26
>0.3-0.6	5	5	0	6	7	0	23
>0.6-1.2	7	6	0	3	7	0	23
>1.2-1.8	5	1	0	0	3	0	9
>1.8	6	4	0	3	1	0	14
Total	39	16	0	19	21	0	95

A second possibility is that the seeds of the study species are concentrated under woody plants. This could be caused by defecation of seeds by frugivorous birds and mammals from perches in woody canopy for *Opuntia vulgaris*, which has fruits readily eaten by these animals. This may be valid for *Opuntia vulgaris*, but is not a plausible explanation for the association of *Euphorbia ingens* and *Aloe marlothii*, neither of which produces fruits palatable to these animals. As the association in the sample of *Opuntia vulgaris* was not the strongest of the three species it is unlikely that this explanation is valid for this species either. The seeds of *Euphorbia ingens* and *Aloe marlothii* may be concentrated beneath woody canopy because it traps them and retains a higher concentration than between canopies.

A third possibility is that of shrubs protecting seeds or seedlings of the study species from being eaten or trampled by animals. The study species are succulent, spiny and probably not very palatable however, and this explanation is also not likely.

A fourth possible explanation is that woody canopy reduces the growth of grasses by competition and attraction of cattle to shade (and thus higher trampling and grazing pressure). Reduced grass growth will decrease the amount of competition that grass offers to the study species and also reduce the fine-fuel load and thus the heat of fires when the area burns. The study area burns fairly often and all three of the study species are vulnerable to being burned to death.

This fourth possible explanation was investigated further in the second phase of the study. The hypothesis, that being damaged by fire is associated with growing between canopies, is accepted for the study species. This association thus provides a plausible explanation for the phenomenon described in the first phase of the study. Fires are likely to be lethal to any plants of the study species that are shorter than about one metre. In any area where fires are frequent there are likely to be much fewer young plants of the study species between woody canopies than there will be within the protection of a bush clump.

The methodology employed in this study was reasonably effective and unbiased. One source of bias may have been not finding small plants in areas with few individuals of one or more of the study plants. This bias would probably be towards making a type II error (i.e. towards a finding of no association when one did, in fact, exist) and thus does not much weaken the support for my conclusions.

This study is a first step in that it establishes that the three succulent species studied are associated with woody canopy and puts forward a plausible explanation. It does not finally eliminate other factors that may contribute to the phenomenon however.

The results of this study have some applications for management and conservation. The densities of *Opuntia vulgaris* in the study area are probably not yet a cause for concern as the indigenous plant species diversity is unlikely to have been reduced as yet. The phenomenon of clumping of succulent and woody plants means that the dynamics of populations of these plants may be determined to a large extent by the existing woody vegetation. Measures to control the noxious weed *Opuntia vulgaris* should be concentrated where there are bush clumps to harbour it. Another implication is that burning is probably not going to be effective in combatting *Opuntia vulgaris* invasion. This is because there is unlikely to be a high mortality of young plants in a bush clump.

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