SEED BIOLOGY OF A RECENTLY INTRODUCED SPECIES, MYOPORUM LAETUM IN COMPARISON TO A SUCCESSFUL INVASIVE ALIEN, ACACIA CYCLOPS, IN THE SOUTHWESTERN CAPE, SOUTH AFRICA

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ABSTRACT

The invasive potential of Myoporum laetum, a tree recently introduced into the southwestern Cape, South Africa, was evaluated, by comparing various aspects of its seed biology with those of another bird-dispersed alien, Acacia cyclops which is a successful invader in this region. M. laetum has higher annual seed production, but lower soil-stored seed banks than A. cyclops. Both experience high seed predation, especially under parent canopies. M. laetum has a more persistant seed store and is able to germinate and establish in shade. Germination of untreated A. cyclops seeds was 23.3% and this increased to 47.4% after mild heat treatment. Untreated M. laetum seeds were completely dormant, but 3.3% germinated after acid treatment.

The high seed production, bird dispersal, persistant seed banks and ability to establish in shade, suggest that M. laetum could become invasive in thickets, such as existing acacia stands.

INTRODUCTION

A large number of woody alien species in the southwestern Cape, South Africa are invading the fynbos biome, to the extent that a "conservation crisis" exists (Macdonald and Jarman 1984). In addition to the control and management of alien plants, it is also essential to recognise new potential invaders. In the genus Myoporum, one species, M. serratum R. Br., is invasive in wetland areas of the southern Cape Peninsula (Knight 1986) and is proving difficult to control (Macdonald et al. 1985, Langley pers. com.). Another species, M. laetum Forst. f., has recently been introduced from New Zealand and is widely planted in the southwestern Cape. Thus, the invasive potential of M. laetum needs to be established at an early stage.

Critical both to control of presently invasive species and to the identification of potentially invasive species is the understanding of their seed biology (Milton and Hall 1981, Dean et al. 1986). Much work has been done on the seed biology of the major invasive species (Milton 1980, Holmes et al. 1987a). Seed production, predation, dispersal and storage have been identified as critical for the invasive success of an alien species. Seed production of invasive alien Acacia spp. in the southwestern Cape, is typically between 1100 and 7000 seeds/m^2/yr and may exceed 10 000 (Milton 1980). In their native habitats, seed production is controlled by a suite of predators, but introduction into a new country may free the plant of these predators and remove the control they have on seed production

(Dean et al. 1986). Dispersal of seeds, especially by birds, into uncolonized and predator-free habitats enhances the invasive ability of plants (Dean et al. 1986) and much of the success of Acacia cyclops has been attributed to bird dispersal (Glyphis et al. 1981, Knight 1988). Seeds which escape predation and remain dormant, represent a seed store that is either canopy stored (eg. Hakea spp.) or soil stored (eg. Acacia spp.). In the absence of heavy predation, a seed store many times larger than the annual seed production may accumulate (Dean et al. 1986). Plants with such large seed banks may be very difficult to eradicate (Holmes et al. 1987a). However, the invasive potential of plants with large reserves may only be realized in the presence of the appropriate germination cues (see Dean et al. 1988).

In this study, the invasive potential of M. laetum was investigated. In order to evaluate this potential, various aspects of the seed biology of M. laetum were compared to those of a successful invasive alien, Acacia cyclops, which is also bird-dispersed.

Study sites

Estimation of seed production, collection of ripe fruits and estimation of soil-stored seed bank of M. laetum was carried out at a site immediately adjacent to Rondevlei Bird Sanctuary on the Cape Flats (34° 03´20"S, 18° 29´30"E). Similar-sized trees have been planted along a roadside in a single row, approximately one canopy diameter apart (cover < 50%). The soil under the trees has been kept clear of grass, but there is a light cover of grass between the trees. Seeds of A. cyclops were collected at Muizenberg (34° 05´20"S, 18°29´45"E). Seed removal and seed decay experiments were carried out at Rondevlei Bird Sanctuary, in a mixed M. serratum/Acacia spp. thicket. This site has no ground cover other than leaf litter under the trees, but very thick grass in a number of small clearings.

Seed production

Assuming trees to be circular in shape, all fruits were counted in a 1/32 arc from which the total per tree was estimated (see Knight 1988), for each of eight M. laetum trees. Projected canopy area was calculated from a mean of four radii for each tree. Seed production was then calculated as seeds per m^2 projected canopy. Comparative seed production estimates for A. cyclops were obtained from Milton (1980).

Seed removal

Post-fall removal of seeds was investigated using a "tray" or "cafeteria" experiment (Weiss 1983, Holmes et al. 1987a). Trays were constructed from 10 X 10cm polystyrene squares, in which depressions, 6cm in diameter and 0.5cm, deep were cut. Trays were covered with glued-on sand and partially buried to prevent displacement by wind. Each tray contained 25 fruits or arillate seeds. The following four treatments were used :

1. control
2. tray surface around indentation covered with grease to exclude invertebrates
3. tray placed inside 25cm high cage of 15mm wire mesh, closed at both top and bottom, to exclude vertebrates
4. tray with grease, placed inside cage to exclude both vertebrates and invertebrates

One set each of four trays (Figure 1) was placed under a canopy and in the open 3m away from the edge of the canopy. Four pairs of tray sets were used for each species. A. cyclops trays were set out under and adjacent to A. cyclops trees. As only one M. laetum tree was present at this site, the other three sets were set up under and adjacent to congeneric M. serratum trees. After 10 days, the number and condition of remaining seeds was noted.

Soil seed banks

Soil-stored seed of M. laetum was quantified 4 months after last

FIGURE 1. Arrangement of treatments in the "tray" experiment. From left to right, top row ; wire mesh + grease, wire mesh only, bottom row ; control, grease.

seed fall. Three successive 4cm-deep spits in 50 x 50cm quadrats were excavated under the canopy and 3m away, for five trees. Soil was sun-dried, sieved and hand-sorted. This gave seed counts for 0.25 m^2 areas (12cm depth) and an indication of the horizontal and vertical distribution of these seeds. Comparative data for soil seed banks of _A_. _cyclops_ from Rondevlei and nearby Cape Flats sites, were obtained from Milton (1980) and Holmes _et al_. (1987a).

Seed decay rate

Seeds were sowed into nylon bags and buried at 15cm depth (see Knight 1988). The period of burial included autumn and spring, the main periods of seed decay in the southwestern Cape (Holmes _et al_. 1987a). Four bags of 50 seeds were used each for _M_. _laetum_ and _A_. _cyclops._ After six months, bags were recovered and seeds classified as intact (hard), rotted or missing.

Seed viability

Freshly collected seeds of _M_. _laetum_ and _A_. _cyclops_ were tested for viability on moist filter paper and in soil.

Experiment 1

Seeds were treated as follows :

1. control
2. pericarp/aril removed (all subsequent treatments utilized seeds treated in this manner)
3. dry heat (60°C) for 1 hr (Jeffery _et al_ 1988)
4. seeds soaked in hydrochloric acid at pH2 for 2 hrs to

simulate passage through a bird gut (Glyphis *et al*. 1981)

5. 0°C overnight
6. -14°C overnight

Treated seeds were placed on moist filter paper in petri dishes with 5ml of a fungicide (benelate 0.75 g/l). 50 seeds were placed in each petri dish and three replicates were made for each treatment. Petri dishes were incubated in a growth chamber with day/night temperatures of 30°C/15°C. Germinated seeds were counted after each week. The experiment was discontinued after six weeks, two weeks after the last germination.

Experiment 2

Viability was tested in soil collected from the Rondevlei site. Treatments were as in experiment one, except that treatment five was replaced by acid treatment, followed by 60°C for one hour to simulate heating at the soil surface following bird dispersal (Glyphis *et al*. 1981). Fifty seeds were placed in soil-containing trays and three replicate trays were used per treatment. Trays were kept in the greenhouse (day/night temperature approximately 25 °C/20°C) and soil was kept moist throughout the experiment. Germinated seeds were counted each week. As all *M. laetum* seedlings observed in the field had germinated in shade and no germination had occurred after eight weeks in the experiment, shade cloth, providing 75% shade was placed over the *M. laetum* trays. There were not sufficient replicate trays to have unshaded, as well as shaded treatments. The experiment was maintained for 18 weeks.

Seed removal and germination data was analysed, using one- and two-way Chi-square tests and calculating standardized deviates (obs.freq.- exp.freq.)/sqrt(exp.freq.).

RESULTS

Seed Production

Annual seed production of M. laetum is shown in Table 1, along with comparative data for A. cyclops, A. saligna and A. melanoxylon. The range for M. laetum of 3129-6819 seeds/m^2 falls between that of A. cyclops and A. saligna. A. melanoxylon data is incomplete, but its seed production is clearly much greater than that of the other species (Milton 1980).

Seed Removal

Wire cages had a significant ($P<0.01$) effect in reducing seed removal of M. laetum and seed removal outside cages was almost total (Table 2). A large quantity of seed fragments indicated that rodent seed predators were responsible for most seed removal. Seed removal was higher under canopies than in the open ($P<0.05$). Very little removal of M. laetum seed from inside cages occurred, but chewed pericarps showed that small rodents had been able to pass through the 15mm mesh. No significant seed removal by invertebrates was observed

Removal of A. cyclops seed was high in all treatments (Table 2). This, as shown by the seed debris inside and outside cages was the result of high rodent predation, including animals small enough to pass through the 15mm wire mesh. This obscured any possible effect of invertebrates in seed removal, although much ant activity was observed around remaining arillate seed.

TABLE 1. Seed Production of *M. laetum* and three *Acacia* species, based on representative fruit counts for *M. laetum* and pod masses for *Acacia* spp.

Species	Projected canopy area (m^2)	Seeds per tree	Seeds per m^2 proj. canopy	Data Source
M. laetum				
1.	3.63	20480	5641	own data
2.	4.91	15360	3129	"
3.	4.91	22080	4498	"
4.	3.63	15040	4142	"
5.	3.63	24160	6654	"
6.	3.80	25920	6819	"
7.	5.31	30560	5756	"
8.	3.98	20160	5070	"
A. cyclops				
1.	16.00	48312	3019	Milton (1980)
2.	12.50	17160	1373	"
3.	4.90	9557	1950	"
4.	12.60	25758	2044	"
		446-11630		Glyphis (Milton 1980)
A. saligna	4.97	48563	10562	Milton (1980)
A. melanoxylon		250000		"

TABLE 2. **Seed removal of *M. laetum* and *A. cyclops* after 10 days, from under canopies of parent trees and in the open**

Species	Cover	Number of seeds removed (out of 25) Ctr	Gr	Wire	Gr + Wire
M. laetum					
1.	canopy	23	21	0	1
	open	20	15	2	0
2.	canopy	24	18	0	0
	open	18	16	0	0
3.	canopy	25	25	0	0
	open	16	20	0	0
4.	canopy	25	25	0	0
	open	25	25	0	0
A. cyclops					
1.	canopy	25	25	8*	10*
	open	25	24	0	0
2.	canopy	25	25	0	0
	open	25	25	25*	24*
3.	canopy	25	25	16*	23*
	open	25	25	25*	25*
4.	canopy	25	25	19*	25*
	open	25	25	25*	25*

Treatments : Ctr = control ; Gr = grease around edge of tray to exclude invertebrates ; Wire = tray inside 15mm wire mesh cage to exclude vertebrates ; Gr + Wire = tray with grease inside wire cage to exclude both vertebrates and invertebrates.

* rodents able to get inside cage

Soil seed bank

Total number of seeds per m under canopies of five *M. laetum* trees is shown in Table 3, along with comparable data for *A. cyclops* and four other *Acacia* spp. Only a single seed was found in one of the five quadrats excavated 3m away from the *M. laetum* trees. The mean seed bank of *M. laetum* was lower than that of *A. cyclops* and very much lower than those of the other *Acacia* spp. The ratio of mean annual seed production to mean seed bank m was 0.2 for *M. laetum*, compared to 1.0 for *A. cyclops* (Dean *et al.* 1986).

Vertical distribution of seeds of *M. laetum* and *A. cyclops* is shown in Figure 2. Although no *M. laetum* seeds were found on the soil surface, the vertical distribution of seeds of these two species was similar, the highest percentage of the seed bank at 4-8cm depth.

Seed decay rate

The rate of decay of *A. cyclops* seeds was very much higher than that of *M. laetum* (Table 4). While 76-88% of *A. cyclops* seeds had rotted or were missimg after 6 months, only 0-4% of *M. laetum* seeds were missing.

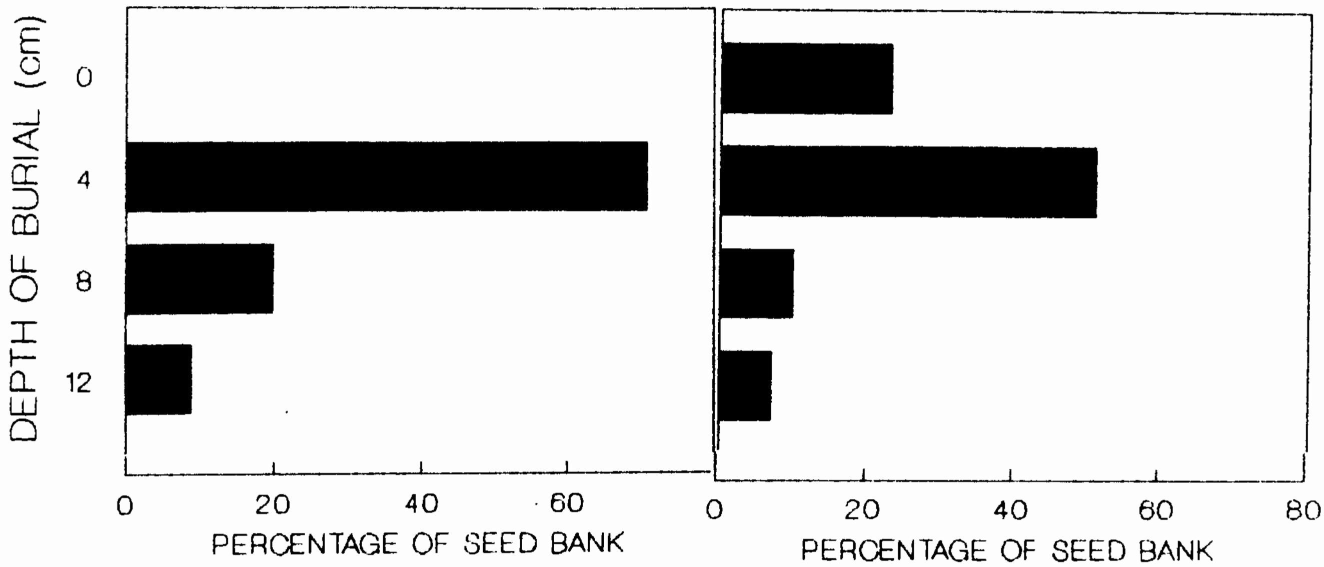
Germination

Experiment 1.

No seeds of *M. laetum* germinated in any treatment on filter paper, but all seeds were still hard after 6 weeks. While

TABLE 3. **Mean soil seed banks and seed bank range for *M. laetum* and five *Acacia* species.**

Species	Seed Bank (seeds/ m^2)	Mean Seed Bank (seeds/ m^2)	Data source
M. laetum			
1.	1608		own
2.	152		"
3.	2596		"
4.	572		"
5.	700		"
		1126	
A. cyclops	28-5899	2031	Milton (1980)
10% cover		76	Holmes *et al* (1987
42% cover		1579	"
72% cover		1095	"
100% cover		5170	"
A. saligna	10152-13792	11920	Milton (1980)
A. longifolia	2110-13182	7646	"
A. melanoxylon	2967-94511	48739	"
A. mearnsii		38340	"



<u>Myoporum laetum</u> <u>Acacia cyclops</u> (Milton 1980)

FIGURE 2. Vertical distribution of seeds of <u>M. laetum</u> under individual trees and <u>A. cyclops</u> under a thicket on the Cape Flats.

TABLE 4. Number of seeds of *M. laetum* and *A. cyclops* intact, rotting or missing after burial at 15cm depth, for six months

Species	seeds intact	seeds rotting	seeds missing
M. laetum			
1.	50	0	0
2.	48	0	2
3.	50	0	0
A. cyclops			
1.	10	0	40
2.	12	32	6
3.	11	2	37
4.	6	0	44

4.7±4.6% of untreated A. cyclops seeds germinated, significantly higher germination ($p<0.05$) occurred with heat (9.3±3.1%) and a smaller, but not significant increase occurred with acid treatment (6.7±4.2%) (Table 5). Latest germination ocurred after 4 weeks and by six weeks, all A. cyclops seeds had begun rotting.

Experiment 2.

After eight weeks, no germination of M. laetum seeds had occurred. A further eight weeks, with 75% shade resulted in 3.3 ± 2.3% germination of acid-treated seeds. No further germination had taken place when the experiment was discontinued after 18 weeks.

Much higher germination of A. cyclops occured in soil than on filter paper, in the first experiment. 23.3 ± 10.1% of untreated seeds germinated while significantly higher germination ($p<0.01$) occurred in heat treated seeds (47.4 ± 5.0%) (table 6). Smaller, non-significant increases occurred in seeds with the aril removed (29.3 ± 7.6) and acid and heat in combination (29.3 ± 17.0). The process of removal of arils may have resulted in scoring of those seeds. Germination after freezing was significantly lower than the control ($p<0.05$) No further germination of A. cyclops occurred after 11 weeks.

TABLE 5. The effect of various treatments on germination of *A. cyclops* and *M. laetum* on moist filter paper in petri dishes

	Acacia cyclops	*Myoporum laetum*
Treatment		
Control	4.7 ± 4.6	0
Pericarp/aril removed	2.0 ± 2.0	0
60°C	9.3 ± 3.1	0
Acid	6.7 ± 4.2	0
0 C	2.0 ± 2.0	0
-14°C	3.3 ± 2.3	0

TABLE 6. The effect of various treatments on germination of *M. laetum* and *A. cyclops* in soil

Treatment	*Acacia cyclops*	*Myoporum laetum*
Control	23.3 ± 10.1	0
Pericarp/aril removed	29.3 ± 7.6	0
60°C	47.3 ± 5.0	0
Acid	24.0 ± 5.3	3.3 ± 2.3
Acid + 60°C	29.3 ± 17.0	0
-14°C	17.3 ± 13.3	0

Seed production

M. laetum produces a relatively large fruit crop, comparable to the major invasive *Acacia* spp. This size may be the result of the absence of natural pre-fall seed predators, as is thought to be the case with these *Acacia* spp. (Dean *et al.* 1986). The importance of seed quantity alone, however, is probably less than that of the actual seedling survival rate (Kruger *et al.* 1986), as large seed production may be effectively neutralized by heavy post-fall seed predation, low germination rate or a low success rate of seedling establishment. A possible advantages of high seed production by alien species, is the saturation of seed predators and the introduction of as many different genotypes as possible (Kruger *et al.* 1986).

Seed removal

The high vertebrate removal of both *M. laetum* and *A. cyclops* seeds cannot be clearly distinguished into the effects of birds and of rodent seed predators. However, the large quantity of seed debris and high frequency of chewed pericarps suggests that the latter are predominant. As mammalian herbivores are absent from New Zealand (Carlquist 1965), predation of seed by rodents is an "unnatural" factor for *M. laetum*. The chief predator is probably *Rhabdomus pumilio*, as this animal has been shown to be the main seed predator in *Acacia* thickets on the Cape Flats, consuming a large proportion of the annual seed crop (David 1980). Animals small enough to pass through the 15mm wire mesh were probably juvenile _R. pumilio_, or _Mus minutoides_, which is also present in such thickets (David 1980). As the time of the seed removal experiment was shortly after the annual population peak of _R. pumilio_ (David 1980), large numbers of juveniles were probably responsible for the ineffectiveness of the wire mesh in excluding vertebrates. The higher seed predation under canopies is evidence of the seed shadow effect described by Janzen (1972). Seed predators are attracted by the high seed densities under parent canopies, with the result that the chance of survival of seeds falling under the parent canopy is extremely poor. In such cases, dispersal of seeds away from the parent is almost essential for successful reproduction (Janzen 1972). It is important to note that heavy predation of seeds may not prevent invasion by an alien plant, if even a very small number of seeds escape predation (Kruger _et al_. 1986).

One of the most successful ways of escaping seed predators and one which makes control extremely difficult, is bird dispersal (Dean _et al_. 1986). Although this seed removal experiment could not distinguish the dispersal effects of birds, the evidence of establishment of _M. laetum_ in a _M. serratum/Acacia_ spp. thicket at the study site and documented bird dispersal of _M. serratum_ (Knight 1986), which has very similar fruits, suggests that birds may play an important role in dispersal of _M. laetum_. Establishment of seedlings of bird dispersed species usually occurs in or around bushes or trees supplying food or used as perches by the seed-dispersing birds (Glyphis _et al_. 1981, Kruger et al. 1986). As M. laetum, unlike A. cyclops (Milton 1980), is able to establish in shade (pers.obs), bird dispersal into shaded sites may be more important for M. laetum. The highly localised seed banks of M. laetum, under canopies, suggests that little short-range dispersal occurs (i.e. to within a few meters outside the canopy). The quantity of seed which is dispersed further than this, eg. by birds, was not estimated in this experiment.

Soil seed bank

The lower ratio of seed stored to seed produced, together with the lower mean seed bank of M. laetum suggests that soil-stored seed is of less importance to M. laetum than to A. cyclops. However two factors must be considered. Firstly, Holmes et al. (1987a) showed that at 100% cover of A. cyclops, the proportion of seeds consumed by predators was lower because of limited nesting sites for rodents and the rate of seed bank accumulation increased. Thus much higher seed banks of M. laetum could possibly accumulate in a high density population

Secondly, the large seeds bank of various Acacia spp. measured by Milton (1980) are the result of accumulation over seven to more than 25 years. The M. laetum seed banks measured in this experiment could not have accumulated over more than five years. Thus the persistence of seeds in the soil is of great importance.

Soil seed banks are a serious problem in the control of invasive alien plants, for example, the large seed banks of Acacia spp. in the southwestern Cape, have been a serious obstacle in the way of their eradication (Milton and Hall 1981). Clearing of thickets and the resulting heating of the soil leads to mass germination of seeds (Dean et al. 1986). This may, however be of less importance to M. laetum, if it requires shade for germination and establishment, as observations in the field suggest.

Seed Decay

As mentioned above, the ability to store seeds in the soil for long periods allows for the accumulation of very large seed banks. A. cyclops differs from other Acacia spp. in that it has a much slower rate of seed bank accumulation which results from a high germination rate and rapid decay (Milton 1980). This is apparently the result of feeding of alydid bugs which may occur at very high densities in A. cyclops stands (Holmes et al. 1987b). Small feeding holes are made in the testa, causing the seeds to imbibe water in the soil and either germinate or rot, while only undamaged seeds remain as a seed store (Holmes et al. 1987b). Holmes et al. (1987a) showed that seed decay of A. cyclops (measured as seed loss through germination and rotting) was 94-100% in the first year, compared to 40-52% for A. saligna. Although this experiment observed decay over only six months, it included most of the time in which rotting of seeds occurs (Holmes et al. 1987a). Thus the decay rate of 74-88% for A. cyclops is in agreement with Holmes et al. (1987a). In contrast to this, however is the 0-4% loss for M. laetum over the same period. This suggests that M. laetum may rank among the more persistant Acacia spp., such as A. saligna and possess the ability to accumulate a large seed bank. An important point to be noted here, is that M. laetum seeds were not tested for viability after the experiment. Thus what proportion of this seedbank is capable of germination at any stage, remains unknown.

Germination

While 23.3 ± 10.1% of A. cyclops seed germinated in soil without any treatment, dormancy of M. laetum was apparently complete. The lower germination of A. cyclops on filter paper in the first experiment was probably the result of rapid decay caused by the high temperature and humidity. The response of seeds to various treatments, appears to reflect their natural habitats. A. cyclops is predominantly a dune species (Gill 1985) and dormancy is broken by mild heat, as might be experienced from solar heating at the soil surface in exposed sites (Gill 1985, Jeffery et al. 1988). The lack of effect of acid treatment in breaking dormancy, in agreement with the results of Glyphis et al. (1981) and suggest that this effect of bird dispersal is not required by A. cyclops for germination. The decreased germination, resulting from freezing suggests that seeds lying on the soil surface may be vulnerable to frost.

M. laetum, as a forest species, does not germinate in response to temperature extremes, but, unlike A. cyclops, appears completely dependant on bird dispersal to provide the acid treatment, necessary for germination. The effect of acid soaking of seeds in breaking dormancy is probably through the leaching of germination inhibitors from the seed coat (Dean _et al_. 1986). As all _M_. _laetum_ seeds were shaded after eight weeks, it is not possible to ascribe this germination after 16 weeks to the effect of shade and not simply to the result of a further eight weeks time in the soil. However, the observation of seedlings under the _M_. _serratum/Acacia_ spp. thicket suggests a requirement of cool, moist conditions , such as would be provided by shade, for germination.

Summary

Many of the differences between the seed biology of _M_. _laetum_ and _A_. _cyclops_ are the result of their differing natural habitats _M_. _laetum_, a forest species relies heavily on bird dispersal, requiring acid treatment of its seeds for germination and cool, moist, shaded conditions for germination and establishment. _A_. _cyclops_, on the other hand is a dune species and requires mild heat, such as heating of exposed soil to break dormancy and does not establish under heavy shade (Milton 1980).

Rodent seed predation of both species appears to be high, especially under canopies, but high seed production and bird dispersal result in the escape of sufficient seeds to allow the formation of a soil seed store. _A_. _cyclops_ shows rapid germination and rotting of seeds, with the result that few seeds remain dormant after two years and accumulation of the seed bank is very slow (Milton 1980). Although a smaller proportion of the annual _M_. _laetum_ seed crop enters the seed bank, these seeds show

strong persistance. This, together with the significantly large seed bank observed under individual trees, suggests that M. laetum possesses the ability to accumulate a very large soil-stored seed bank.

The most important points to emerge from this study, regarding the invasive potential of M. laetum are the evidence of successful bird dispersal, the ability to establish in existing thickets and the apparent potential to accumulate a large, persistant seed bank.

An unknown factor which could be important in terms of future invasive species, is that of the possibility of M. laetum/M. serratum hybrids. As possible hybrid plants were observed at Rondevlei (pers. obs.), this requires investigation.

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