PATTERNS OF ESTABLISHMENT OF *ACACIA CYCLOPS* CUNN. EX G.DON SEEDLINGS IN CONSOLIDATED AND UNCONSOLIDATED COASTAL SANDS.

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ABSTRACT

The ability of Acacia cyclops to invade a new habitat is closely associated with its seed biology. At Koeberg, the coastal drift sand areas were infested with dense monospecific thickets of A. cyclops whereas in the adjacent consolidated sands, the A. cyclops thickets were randomly dispersed between the indigenous West Coast Strandveld. In order to understand the mechanisms which make A. cyclops a more, or less effective invader, this project elucidated patterns of seed biology and seedling establishment in the coastal consolidated and unconsolidated calcareous sands.

In both the consolidated and unconsolidated sands, seed production, seedbank and soil moisture were similar. Vertical and horizontal distribution of seeds and seedlings, seed viability, seed removal and consumption, seedling root development and water potentials were however, significantly different between the sites. These differences were discussed with respect to the differential invasive capacity of A. cyclops in these soils. A. cyclops appears to be a light-demanding early successional shrub with a seed biology adapted to efficiently invade the disturbed unconsolidated sands.

INTRODUCTION

Originally introduced into South Africa from Australia for dune stabilization, shelterbelts and hedges in the south-western Cape (Shaughnessy 1980), *A. cyclops* A. Cunn.ex Don. has been ranked as the plant species currently posing the greatest threat to the strandveld vegetation type in the Fynbos Biome (McDonald and Jarman 1984). *A. cyclops* spreads over quartenary and tertiary deposits of calcareous sand on the coastal platform of the western and southern Cape that forms part of the Fynbos Biome (Rutherford and Westfall 1986), and occurs as a small leguminous tree or shrub which produce prolific quantities of hard coated impermeable seeds (Milton and Hall 1981). Its invasive success in the fynbos biome has been attributed to the following characteristics :

(a) \`Preadaptation' to edaphic and climatic conditions (Milton 1980).

(b) Lack of heavy seed predation (McDonald and Jarman 1984, Gill 1985).

(c) Disturbance regimes for which germination and establishment of the species are adapted (Jones 1963, Dean *et al*.1987).

(d) Long distance dispersal agents (Milton 1980, Glyphis *et al* 1981, Dean *et al*.1986, Knight 1988).

(e) Large annual seed crops (Milton 1980, Milton and Hall 1981, Gill and Neser 1984).

(f) Long-lived seeds (Milton 1980, Dean *et al*.1986)

Thus, the ability of *A. cyclops* to invade a new habitat is closely associated with its seed biology. Critical both to the control of *A. cyclops* as an invasive, or identification as a potentially invasive species then, is an understanding of their seed biology (Milton and Hall 1981, Dean et al. 1986).

An understanding of the mechanisms which make *A. cyclops* a more effective invader in different habitats and environments, would greatly contribute to the predictive modelling of its effects on other plants, and to the identification of higher risk conservational areas. This project aimed to elucidate different patterns of establishment of *A. cyclops* seedlings in the coastal sands and to predict their invasiveness in more consolidated sands supporting a dense indigenous assemblage.

METHODS

Site Description

This study was carried out at a 22.5ha nature reserve adjoining the Koeberg Nuclear Power Station which is owned, maintained and managed by Electricity Supply Commission (ESCOM). Two sites representing unconsolidated coastal sand and consolidated sand were selected.

The unconsolidated sand site was characterised by secondary trangressive dunes (see Tinley, 1985 for classification). The unconsolidated sand strip abutting the coastline comprised bands of low vegetated hairpin dunes colonized in areas cleared of *A. cyclops* by *Eragrostis cyperoides*. However, a major part of the coastal drift sand areas are usually colonized by dense monospecific thickets of A. cyclops.

The consolidated sands were characterised by deep calcareous sands, slightly weathered and poorly leached due to their youth and relatively low annual precipitation (Rutherford and Bosenberg 1987). Soils were classified as Fernwood soils (orthic A underlying regic sand). A mosaic of A. cyclops thickets occurred in a matrix of West Coast Strandveld ; on open to closed (40-90% cover) shrubland of mixed broad-leafed evergreen, deciduous and succulent elements together with smaller graminoids, annuals and geophytes (Moll et al. 1984).

Seed Production

Seedfall from A. cyclops trees was collected using 0.5m X 0.5m litter traps made of terylene mesh, and supported by 1m iron stakes. Five traps were arranged under mature plants in the consolidated and unconsolidated sand sites. These were emptied each month, and the collected seeds sorted, counted and weighed. The seed content of the leaf litter was measured by means of ten 0.5m X 0.5m quadrats under mature thickets at each site. All the litter lying on the surface of the soil was collected and the seeds contained in it were seperated and weighed in the laboratory.

Seed Bank

The vertical distribution of A. cyclops seed in the soil under a thicket at each site was investigated by excavation of ten 0.5m X 0.5m quadrats at varying depths (0 [litter]; 0-5cm; 5-10cm; 10-15cm; 15-20cm; 20-25cm; 25-30cm). Seed was seperated from soil and other organic matter by sieving and hand sorting.

The density of *A. cyclops* and its horizontal distribution relative to distance from the seed source was sampled at each site along a 6m transect running from the base of a mature tree out beyond the canopy. Measurements were taken at 1m intervals using a 0.25m X 25m quadrat, and counting the number of seeds and the number of germinated seeds/seedlings (litter and soil = 5cm depth). Germinated seeds were those whose radicles extended 1-2mm beyond the seed coat (cf. Pieterse and Cairns 1986).

Seed viability

Germination trials of soil stored seeds of *A. cyclops* in both sites were carried out in a controlled environment chamber (12hrs light at 25° C ; 12hrs darkness at 20° C ; 90% moisture). One hundred seeds from each site were placed on moistened filter paper in petri dishes. After two weeks, germinated seeds were counted and removed. The remaining seeds were considered to be dormant and thus treated with two immersions in boiling water (cf. Milton 1980). The seeds were returned to the growth chamber, and after 30 days germinated seeds were counted. Remaining seeds were classified as `hard' or `soft' seeds. An additional 50 seeds from each site were treated with dry heat in a preheated oven at 60° C for five minutes (cf. Jeffrey *et al* 1988) and germinated as above. Germinated seeds were counted after 60 days.

Herbivory

Gross seed predation at the soil surface was measured using the method of Holmes _et al_ (1987) in which litterfall bags and trays of 0.5m X 0.5m horizontal area were placed under selected _A. cyclops_ trees at each site, and comparing the two types of trap after each month of seed fall (April - August).

Qualitative seed removal was monitored over the same period (april - august) in a `cafeteria' or `tray' experiment described by Weiss (1983) and Holmes _et al_ (1987). Polystyrene blocks measuring 10cm X 10cm with a circular depression in the center 0.5cm deep and 5cm in diameter, were prepared. The polystyrene plates were treated as follows:

(1) `Ant-proof'- Plate edges smeared with grease ; 20 seeds ; aril present .

(2) `Ant-proof - As above except seeds with aril removed.

(3) `Vertebrate-proof'- Plates enclosed in a cage of chicken mesh (15mm) ; 20 seeds ; aril present

(4) `Vertebrate proof'- As above except seeds with aril removed.

(5) Control - Plate edges smeared with grease and enclosed in chicken mesh to exclude all potential herbivores.

In the unconsolidated sand site, two replicate trays were placed on a dune free of infestation ; in an _A. cyclops_ thicket on top of a dune ; in a thicket half-way down a dune and ; in a thicket at the base of a dune. In the consolidated sand site, two replicate trays were placed in a mature A. cyclops thicket ; in a young thicket ; in indigenous Strandveld vegetation and ; in a 'gap' in the indigenous Strandveld (= potential site for invasion). Trays were partially buried to simulate natural conditions and to further prevent displacement by wind. At each site, seed removal was monitored after seven days.

Effect of light on germination

To establish the effect of light on germination of seeds from both sites, 40 seeds from each site were pretreated by manually chipping them at the micropylar end to ensure a maximum germination rate (cf McDowell 1981) and treated in a similar manner to that suggested by Milton (1980). Seeds were thus placed on moist filter paper in petri-dishes. Half of the treated seeds from each site were then immediately placed into a box which excluded the light. The remaining seeds were placed on the window sill where they were directly exposed to incident light. After seven, 14, 21 and 28 days, germinating seeds were removed and counted. Mean root:shoot ratios of seedlings were calculated for each treatment for each site.

Effect of light on seedling growth

Thirty locally collected A. cyclops seeds from consolidated and unconsolidated sands respectively were pretreated as above , and germinated in a controlled environment chamber (12hrs light at 25° C alternating with 12hrs darkness at 20° C). After ten days, the seedlings were planted in 500ml nursery plots with their respective soils used as a potting medium. A set of 30 plants (15 from consolidated sand and 15 from unconsolidated) were covered completely by black nylon shade cloth which was estimated to exclude 60-80% of the incident light. The other set were located in an unshaded open area. Seedlings were harvested at one,two and three month intervals after planting. Root and shoot were separated, oven dried at a 100°C for 24hrs and then weighed.

Plant moisture stress

Plant moisture stress of newly germinated seedlings (±15cm high), seedlings (±75cm high), young juveniles (±150cm high), juveniles (±400cm high), semi-adults (±1m high) and adults (>1m) were determined by pre-dawn and post-noon xylem pressure potentials of five replicates of each age category at each site using a Scholander-type pressure bomb (Model 1000 PMS instrument co. Oregon). Access to the the reserve was not possible, due to security considerations, for pre-dawn readings. Consequently readings were taken at a site next to the reserve which exhibited similar floristic and edaphic traits as the initial study site. Further, no young juveniles or juveniles were found in the consolidated sand site and readings were thus omitted for these age categories.

Moisture content of the soil was measured using a 503 Hydroprobe Nuclear Depth Moisture Gauge (Campbell Nuclear Corp. [CPN]). Two 3m aluminium tubes and three 3m aluminium tubes were driven into the soil at the consolidated and unconsolidated sand sites respectively. Tubes in the consolidated site were placed in close proximity to the *A. cyclops* thicket (depth = 120cm) and in the indigenous strandveld (depth = 135cm). Tubes in the unconsolidated sand site were placed on the top of a dune (depth = 200cm), half-way down a dune (depth = 270cm) and in a dune trough (depth = 210cm). Subsurface moisture in the soil was measured at depths of 15cm, 30cm, 45cm, 60cm, 90cm, 120cm, 150cm, 180cm, 210cm, 240cm, and 270cm where feasible.

Hydroprobe readings were taken over three months at monthly intervals (august-october). Prior to daily readings, standard counts were taken following which, the field counts were taken. Moisture content (in g/cc) was calculated by dividing the field count by the mean standard count to obtain a ratio. Moisture was thus determined by plotting this ratio on the Ratio Calibration Chart supplied by CPN.

RESULTS

Seed production

Biomass and number of seeds recorded for the seedfall and seedbank at each site decreased from april - august, whereas the number of seedlings/m increased (Table 1). The data suggests that *A.cyclops* seed production and seed store in the unconsolidated site declined more slowly than those of the consolidated site. Biomass and number of seed falling under the *A. cyclops* thickets at each site did not differ significantly ($P>0.05$) although differences recorded in seed production appear to be determined by stand age and topography. The seedbank under the canopy however, was significantly higher in the consolidated sand ($F=0.86$ $P<0.05$). Conversely, seedling emergence in the consolidated sand was significantly lower than that of the consolidated sand ($F=83.04$ $P<0.01$).

Seedbank

The vertical distribution of *A. cyclops* seed at both sites is illustrated in Figure 2. Most of the seed (C-82.7% ; UC-68.7%) lies in or below the litter for the first 5cm. A high proportion (28.1%) of seeds in the unconsolidated sand occur at the 5-10cm depth which may suggest that these seeds have been buried by the constant shifting of loose sand in these coastal sands. Seeds at depths of 20cm in the consolidated sands may be attributed to the intensive mole rat (*Bathyergus sullius*) activity noted in this area.

Month	Site	Total seed mass (seedfall) g/m^2 /month	Total seed mass (litter) g/m^2 /month	Seedfall under canopy no/m^2/month	Seedbank under canopy no/m^2/mnth	Seedlings/m^2 under canopy
April	C	2,177±0.75	30.35±8.6	139.3±39.4	2015.5±341.2	9.2±6.1
	UC	1.587±0.26	17.42±7.2	105.8±36.1	1716.1±287.2	27.3±6.7
May	C	0.98±0.31	25.51±8.3	67.6±27.3	1209.6±260.5	7.1±4.6
	UC	0.74±0.23	12.63±2.9	49.6±13.6	1242.3±186.3	29.9±8.2
June	C	0.45±0.11	21.15±4.1	34.2±9.9	1410.8±192.1	6.8±4.0
	UC	0.55±0.18	10.37±1.8	37.0±9.3	891.7±200.9	31.6±4.7
July	C	0.11±0.02	13.8±3.8	6.9±2.5	906.0±216.8	11.3±3.9
	UC	0.17±0.06	9.31±2.5	11.1±3.6	606.2±92.7	39.2±13.1
August	C	0.02±0.002	15.11±2.7	3.3±1.0	1007.3±167.1	14.5±7.6
	UC	0.23±0.04	11.8±3.1	15±4.5	807.0±105.5	34.4±8.9

Table 1. Total biomass, number of seeds and seedling density relative to the monthly fall of *A. cyclops* seed in the consolidated (C) and unconsolidated sand (C) sites

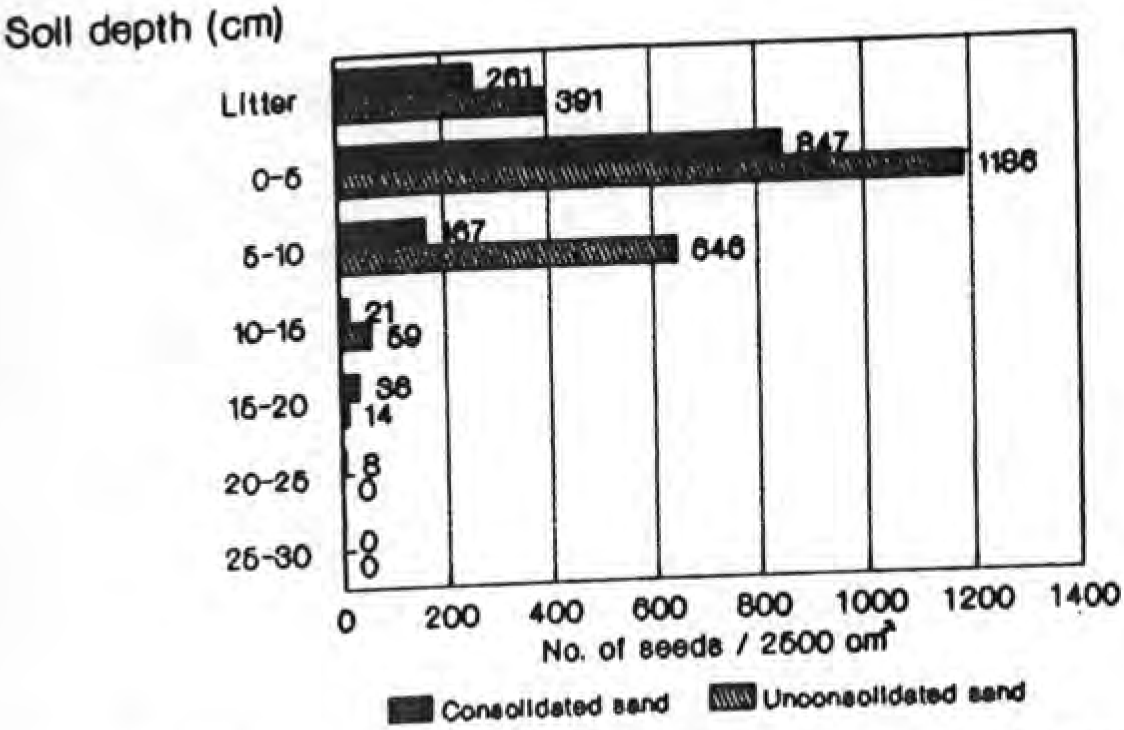

Figure 1. Vertical distribution of A. cyclops seed excavated from the consolidated and unconsolidated sand sites.

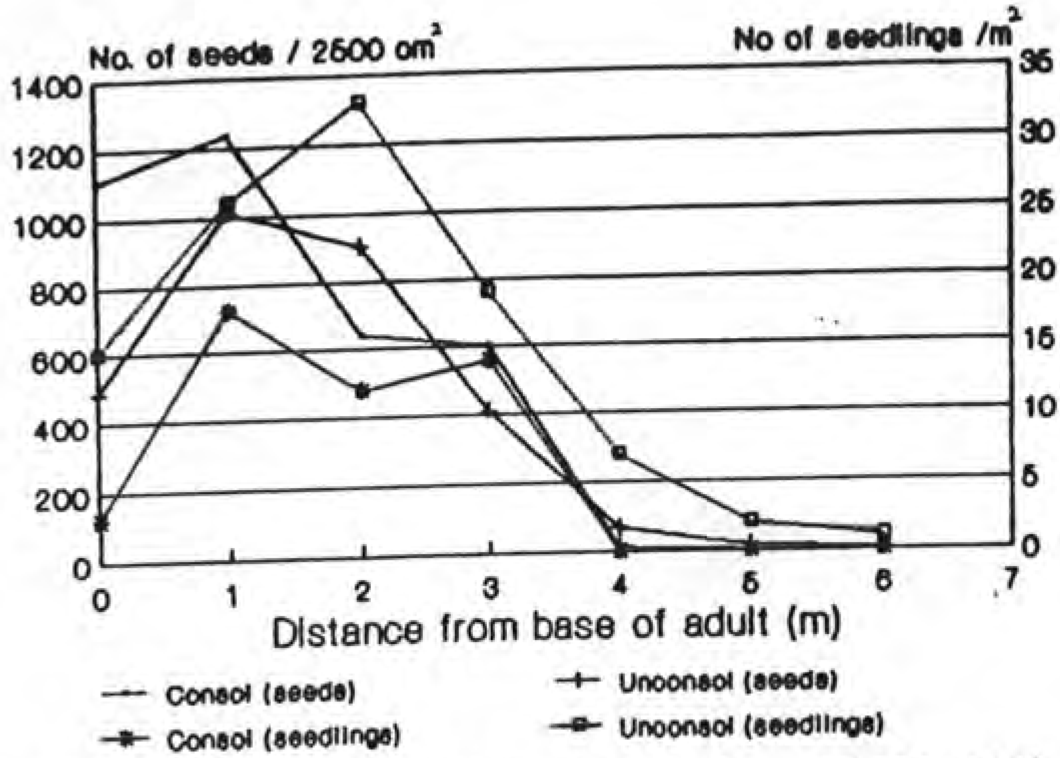

Figure 2. Horizontal distribution of A. cyclops seed and seedlings with increasing distance from the parent plant in the consolidated and unconsolidated sand sites.

The effect of distance from the parent tree on the density of fallen seed and emergence of seedlings is illustrated in Figure 2. Most seeds fall in the canopy shadow within 1 metre from the base of the adult trunk, and the most emergent seedlings occur $<$ 2m from the trunk base. Significantly higher densities of seedling and seeds were recorded beyond the adult plant canopy ($x=2.7$m from base) in the unconsolidated sand (seedling $F=0.74$ $P<0.05$; seeds $F=0.58$ $P<0.05$) compared to the consolidated sand. The spread of these seeds and consequent seedling establishment appears to be dependant on wind, soil, or water movement, or transport by birds or mammals.

Seed viability

Prior to hot water treatment (HWT), seeds from the unconsolidated stand exhibited a high capacity for germination compared to seeds from the consolidated sand (Table 2). Seed germination in seeds from both sites were significantly enhanced by the HWT ($r=-0.49$ $P<0.05$). Percentage hard and bad seeds from the unconsolidated sand were, 5 and 13 times respectively, lower than those from the consolidated sand. Simulation of dry heat resulted in similar germination rates for both sites.

Herbivory

Quantitative predation experiments (Table 3) showed that seed removal by vertebrates and invertebrates constituted a potential 85.54% loss to the seedbank in the consolidated sand compared to an extremely low 19.83% in the unconsolidated sand site.

Table 2. Results of percentage viability tests on *A. cyclops* seeds from consolidated and unconsolidated sands (*HWT= hot water treatment)

Site	% hard	%bad	Pretreatment germination	Post-2 X *HWT	5 mins @ 100 C
C	14	13	8	65	28
UC	3	1	17	79	21

Figure 3. Germination rate of *A. cyclops* seeds from consolidated and unconsolidated sands in light and darkness after seven,14, 21 and 28 days incubation

Table 3. Mean number of *A. cyclops* seeds per m^2 in litter bags and open trays five months after litter fall in both consolidated and unconsolidated sands.

Treatment	Mean no. of seeds / 5 months / m^2	
	Consolidated sand	Unconsolidated sand
Bags (no predation)	346	232
Tray (predation)	49	186
% Loss	85.84	19.83

Table 4. Qualitative seed removal by ants and rodents at selected sites in the consolidated and unconsolidated sands

Site description	% Seeds Removed			
	Ant-proof (aril)	Ant-proof (no aril)	Rodent-proof (aril)	Rodent-proof (no aril)
1.Consolidated				
Mat. thicket	72.5±6	15±2	20±	0
Y. thicket	100	32±4	45±10	5±1
Strandveld	100	46±8	60±12	5±1
`Gap'	100	39±12	55±6	5±2
2.Unconsol.				
Open dune	0	0	0	0
Infested top	15±4	0	0	0
Infested mid	2±1	0	0	0
infested bot	20±5	0	0	0

Qualitative predation experiments (Table 4) revealed similar trends. Both ants and rodents (predominantly the striped field mouse *Rhabdomys pumilio*) are important seed movers and seed consumers respectively in the consolidated site. The red-coloured funicle of *A. cyclops* was a favoured item in the diet of both the ants and rodents as reflected by the significantly different (ant-proof F=39.73 P<0.01 ; rodent proof F=21.07 P<0.01) predation rates of seeds with and without the funicle. Predation in the unconsolidated sand site was virtually non-existent with only occasional predation (2-20%) of *A. cyclops* seeds in the infested dunes.

Effect of light on germination and seedling growth

Seeds of *A. cyclops* from each site germinated equally well over 28 days (Figure 3). Germination rates between the light and dark treatments for each site were however significantly different (C/F=5.37 P<0.05 ; UC/F=5.89 P<0.05). Germination of soil stored seed in *A. cyclops* is thus generally enhanced by the presence of light. The effect of light on seedlings grown in full sunlight and those grown in 20-40% light is shown in Table 4. No significant difference between sites was recorded (P>0.05) but shoot/root drymass ratios were consistently and significantly larger (C:F=12.75 P<0.01 ; UC:F=19.21 P<0.01) in shade-grown plants, implying that shoot development proceeds at the expense of root development when light is limited. Over the 3 month growth period, the shoot/root dry mass ratio increases as the seedling grows, suggesting that root growth takes precedence during the early stages of seedling growth.

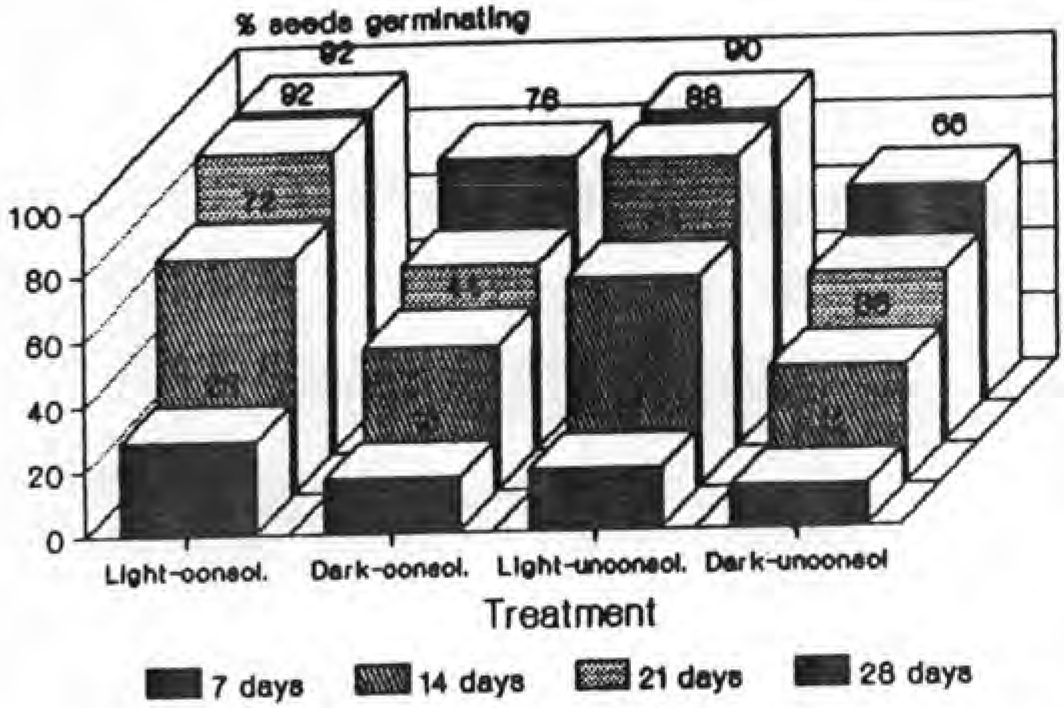

Figure 3. Germination rate of A. cyclops seeds from consolidated and unconsolidated sands in light and darkness after seven, 14, 21 and 28 days incubation

Table 4. Mean total dry mass and shoot/root dry mass ratio for A. cyclops seedlings grown in the light (100%)(O) and shade (20-40%)(●) in consolidated (C) and unconsolidated (UC) sand sites. (* denotes significant difference (P<0.05) between treatments)

Time (months)	Site	Treatment	Mean total dry mass (g)	Shoot/root dry mass ratio
1	C	O	0.041*	1.49*
		●	0.019	2.01
	UC	O	0.036*	0.81*
		●	0.013	1.86
2	C	O	0.059*	1.73
		●	0.023	2.15
	UC	O	0.063*	0.92*
		●	0.027	2.07
3	C	O	0.082*	1.68
		●	0.031	2.26
	UC	O	0.13 *	1.05*
		●	0.044	2.14

Plant moisture stress

Moisture content of the soil is depicted in Figure 4 (a-e). Soil moisture content generally decreased from August to September in all the sites, and is consistent with the rainfall patterns for the area. Maximum soil moisture for the consolidated site was at a depth of 90 (Aug-Sept) - 120cm (Oct), and for the unconsolidated site at a depth of 150 (Aug-Sept) - 180cm (Oct). Soil moisture at each depth was however not significantly different between the sites (P>0.05). A. cyclops plants at both sites thus appear to have equal amounts of water potentially available to them. In the consolidated site this water may however be bound in an inaccessible form or the plants may possess an inadequate rooting system to extract it. This is reflected by the significantly higher post-noon water potential readings for newly-germinated seedlings (t=15.88 P<0.01) seedlings (t=7.64 P<0.01) and semi-adults (t=6.71 P<0.01) (Figure 5). Post-noon readings were similar between the age categories in both sites.

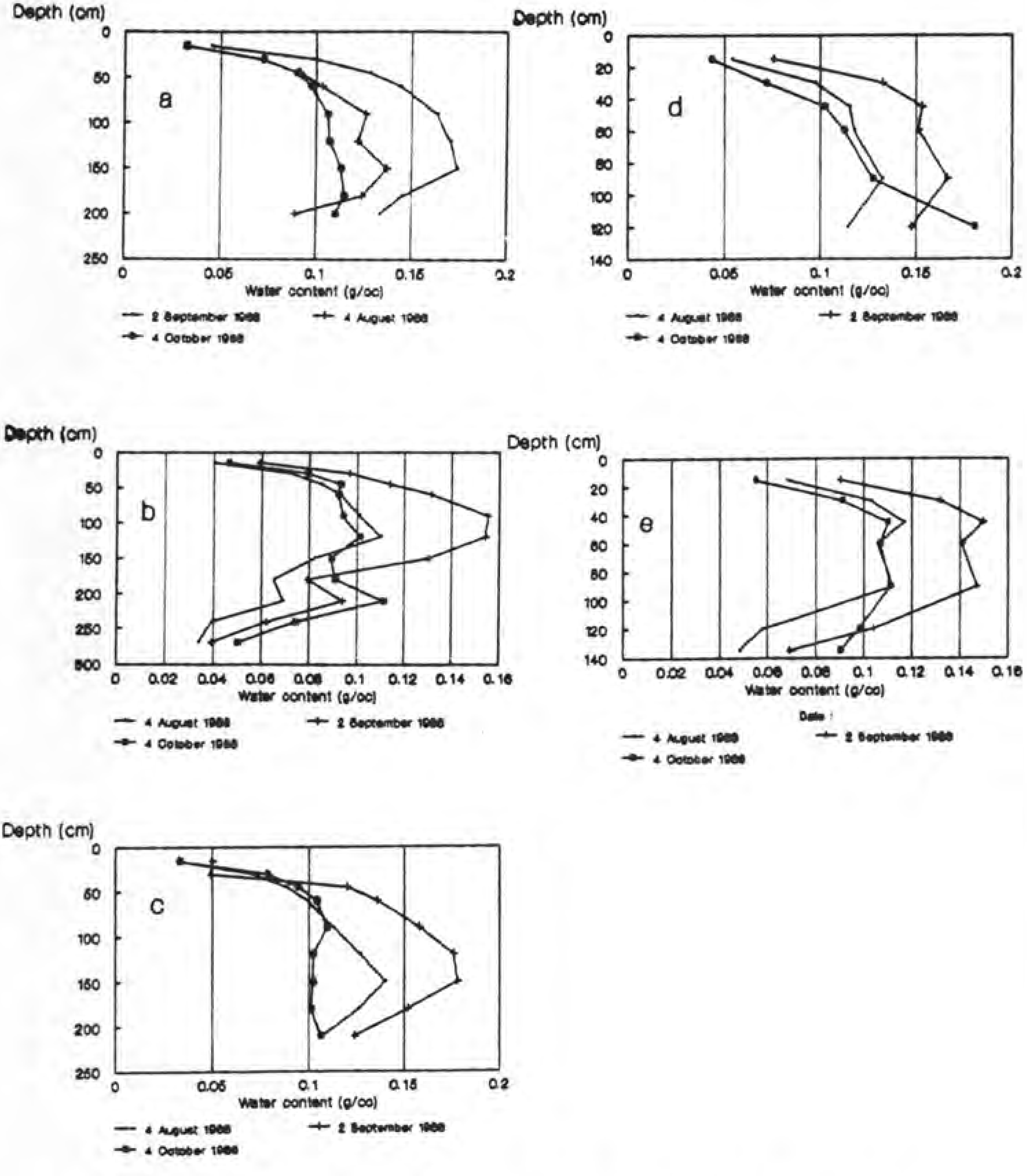

Figure 4 (a-e). Plant moisture content of the soil at selected sites in the unconsolidated (a-c) and consolidated sands (d-e).

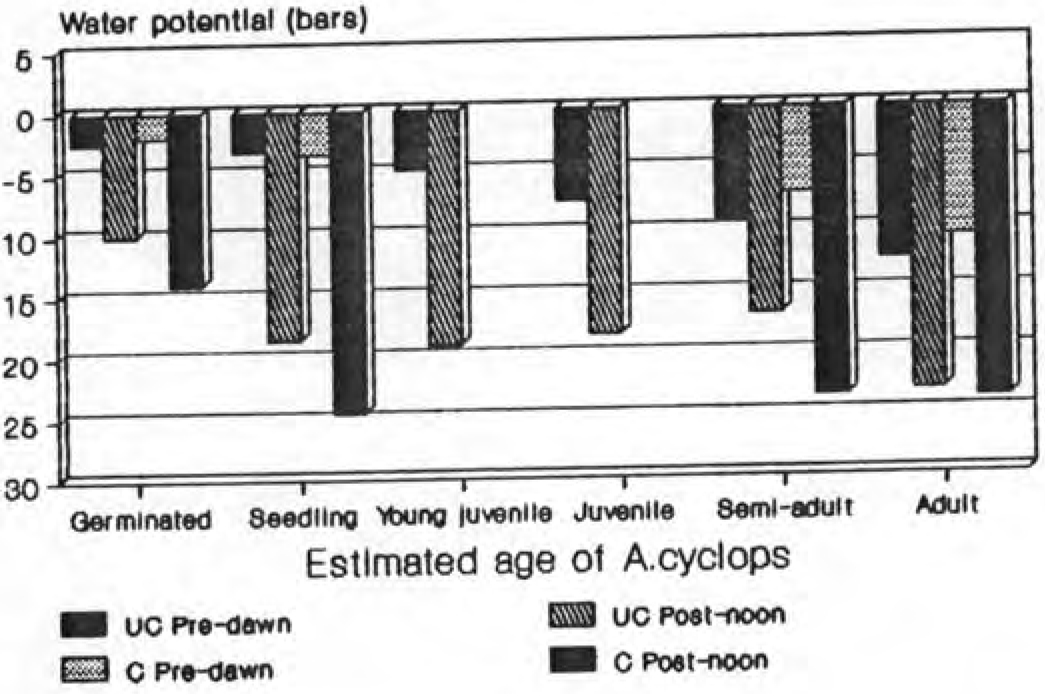

Figure 5. Water potential of plants of different age categories in the consolidated and unconsolidated sands.

DISCUSSION

Figure 6 summarizes the relative biotic and abiotic stresses encountered in the consolidated and unconsolidated sands and confirms that *A. cyclops* is a light-demanding early successional shrub with a seed biology adapted to efficiently invade badly disturbed areas. It appears however, to be less successful in invading mature indigenous Strandveld vegetation in the consolidated sand, undisturbed by man.

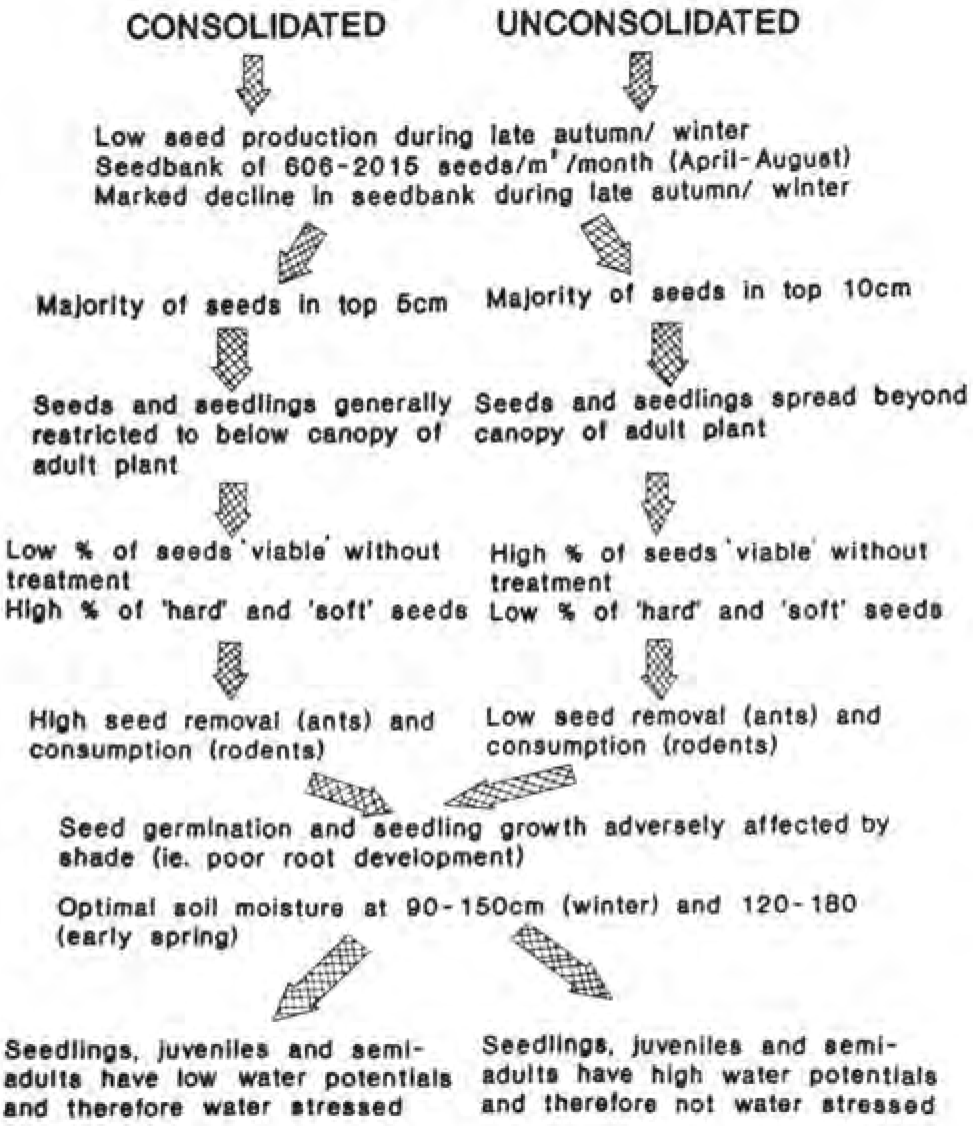

Figure 6. Model summarising the relative biotic and abiotic stresses encountered by *A. cyclops* in the consolidated and unconsolidated sands.

Seedbank and seed production

Seedbanks in mature monospecific thickets of *A. cyclops* in the Cape range from 1800-2000 seeds/m (Milton 1980). Values recorded in this study for the seedbanks of both consolidated and unconsolidated sands generally fall within this range, although predation, decay and germination may account for the marked decline of seeds in the seedbank during this period (April-August) which follows the reported time of seedfall (late spring/early summer) (Milton 1980).

Seed production in the Cape is reported to be in the range of 1500-3000 seeds/m^2 (Gill and Neser 1984). Peak seedfall of *A. cyclops* in the south-western Cape occurs during late spring and early summer (November-April) (Milton 1980) and this may account for the significantly lower seedfall recorded during the study period, for both sites. Differences in seedfall and seedbanks of *A. cyclops* between the consolidated and unconsolidated sand may be attributed to different ages of the thickets, topography and management history (ie. alien control measures). The *A. cyclops* stands in both sites thus appear to be characterised by high seed production and a large seed bank.

Seed distribution

Changes in seed distribution with the soil depth indicates an early loss of seed from the litter to the surface soil (0-5cm) and occassional penetration to depths of 20cm. This may be aided by the activities of burrowing animals, such as the dune mole-rat, in the consolidated sand, or burial by constantly shifting sands in the coastal sands. Holmes *et al*. (1987) found that although seeds of A. cyclops germinated optimally from a depth of 5cm in the field, seedlings can emerge from depths down to 15cm. Losses via rotting however, increased with depth of burial. Thus, seeds from both sites should be equally adept at germination to depths of 15cm. Seed densities however, were considerably larger in the top 10cm of the unconsolidated sand signifying a lower seed removal or predation.

The increased horizontal spread of A. cyclops seed and seedlings into uninfested areas in the unconsolidated sand appears to be attributed to lower predation rates ; soil or water movement ; transport by birds, man or other animals and ; disturbance regimes to which germination and establishment of the seeds are adapted. The bulk of seed in both sites falls under the adult canopy where germination and establishment are likely to be inhibited due to shading and intra-specific competition.

Seed viability

A. cyclops are hard-seeded species whose seeds only germinate when the water impermeable testa is damaged by heat, abrasion or decay (Dean et al. 1986). This hard testa ensures protection from fungal attack and water inbibition thus allowing it to remain dormant and viable for two or more years (Milton 1980). Viability tests in this study revealed that dormancy of a relatively high percentage of seeds from the unconsolidated sand sites has been broken. It is hypothezised that abrasion in the coarse grained sand and/or exposure to moderate, fluctuating soil temperature of the exposed dune sand surfaces (cf. Jeffrey et al. 1988) and/or exposure to solar radiation (cf. Rolston, 1978) may stimulate germination without the traditionally recognized (McDonald and Jarman 1984) stimulus of a single high temperature treatment in the form of fire. The extremely high percentage of `bad' seeds in the consolidated sand suggests that seeds may have been damaged by a local seed sucking bug, Zulubius acaciaphagus. Holmes and Rebelo (1988) found that the intensity of feeding by Z. acaciaphagus is positively correlated with percentage seed rotting and negatively with percentage seed viability.

Herbivory

The energy rich seeds (18.91-22.98 KJ/g : King 1976), and funicle with a high energy content, are a favoured item (27-81% : David 1980) in the diet of the seed eating R. pumilio. The influence of R. pumilio and other consumers may be responsible for the marked decline in seed in the litter of the consolidated site. The enlarged red funicles are also attractive to frugivorous birds (Knight 1988) but bird-activity during the period of study was negligible. Seed removal by ants was significant in the consolidated sand although only seeds with funicle attached were generally removed. Seed removal and predation was negligible or non-existent in the unconsolidated sand and may be attributable to the lack of habitat for these animals as well as extremes of temperature, drought conditions and wind experienced in this area during the spring and summer months.

Effect of light on germination and seedling growth

Few hard-seeded species are shade tolerant and seedlings germinating under dense cover have been shown to become etiolated and die (Milton 1980). The effects of light on germination and seedling growth reported here substantiate this observation. Shade prevents both the germination and establishment of *A. cyclops*. Light exclusion further affects the morphology of the seedlings. In the absence of light, most of the available energy is channeled into shoot growth, and it is possible as Milton (1980) suggests, that these etiolated seedlings with their poorly developed root systems, are more likely to suffer moisture stress than those growing in a light environment. Root growth normally takes precedence over shoot growth during the early stages of seedling growth and it has been suggested by Withers (1979) that, by stunting the root system, shading causes moisture stress which leads to the death of seedlings. The inability of *A. cyclops* to compensate for reduced light is reflected in the extreme differences in root and shoot drymass ratios between sun- and shade-grown seedlings. Thus, in the consolidated sand *A. cyclops* appear to be incapable of surviving for more than a few months under the parent canopy, or under the dense indigenous scrub. Further, should seeds manage to fall in a 'gap' in the inmdigenous scrub, this is likely to be rapidly consumed by *R. pumilio*. Seed germination and seedling growth in the unconsolidated sand however, is enhanced by low apparent predation rates, available open areas exposed to high incident light and subsequent decreased moisture stress.

Plant moisture stress

During the drying phase of the soil recorded in this study the flow of water from the soil into the root becomes a complex function of shoot-water potential, the distribution of roots and of soil water and the properties of the various resistances (Paleg and Aspinall 1981). The amount and rate of water uptake depends on the ability of the roots to absorb water from the soil with which they are in contact, as well as on the ability of the soil to supply and transmit water towards the root at a rate sufficient to meet the transpiration requirements of the plant. These in turn depend on the properties of the plant (rooting density, depth and rate of root extension as well as the physiological ability of the plant to increase its own water suction sufficiently to continue drawing water from the soil at the rate needed to avoid wilting) and properties of the soil (eg. wetness relationships and conductivity). Jeffrey (1987) contends that the key characteristic of soil water is the quantity of plant available water used by the vegetation. Sutcliffe (1979) further notes that this water availability (which is also a function of plant and soil properties) has important effects on the distribution of plants. The results then exhibit an apparent paradox in that soil moisture in both the consolidated and unconsolidated sands is similar both in distribution and content but the absence of juvenile plants in the consolidated sands and the significantly higher post-noon water potentials of newly-geminated and young seedlings than the unconsolidated sand confirms the postulate that the seedlings in the consolidated sands are moisture stressed. The moisture stress then does not appear to be due to the available water in the soil, rather it appears to be due to poor root development and consequent accesibility to soil stored water. As mentioned above this poor root development in the consolidated sands is correlated to shading effects. These shading effects may be due to shading from the parent plant or by the dense indigenous Strandveld vegetation.

Summary

The relative abilities of A. cyclops to invade coastal sands appears to be closely correlated with their seed biology and seedling establishment. In the consolidated sands A. cyclops plants are more stressed than their counterparts from the unconsolidated sands. These stresses then affect their invasive capacity in these habitats. This project has identified some of these stresses in consolidated sands and they include :

(a) Seeds generally require an external stimulus to germinate eg. fire. The Strandveld vegetation however is generally more fire-resistant than the Fynbos vegetation occurring in close proximity.

(b) Seed distribution is restricted vertically to shallow depths and horizontally to within the adult canopy.

(c) Seeds are subject to intensive predation and to a lesser extent, removal.

(d) Seed rotting is more prevalent and may be attributable to a local seed-sucking bug and/or fungal infections.

(e) Seed germination and seedling growth are significantly inhibited by shade conditions.

(f) Seedlings have a poor root development and this thus results in water stress and subsequent wilting after a relatively short period of growth.

Conversely, the *A. cyclops* growing in the unconsolidated sands have circumvented these stresses due to the unstable nature of the dune environment to which *A. cyclops*, as an early successional species, is strongly adapted.

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