STUDIES ON AUSTRALIAN ACACIAS IN THE SOUTH WESTERN CAPE, SOUTH AFRICA

by

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requirements for the degree
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in the Department of Botany,
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ABSTRACT

The thesis comprises six papers dealing with aspects of the ecology of the exotic Acacias which are considered to be weeds in the South Western Cape. Topics covered are the origins and reasons for success of the Australian Acacias in the Cape, their phenology, reproductive biology, shade tolerance, litterfall and biomass. The implications of these findings for management are discussed in the general conclusion, and the raw data is tabulated in four appendices. The work is illustrated with 37 figures.

UITREKSEL

Hierdie tesis bevat ses verhandelings wat aspekte van die ekologie van die uitheemse Akasias, wat as pesplante in die Kaap beskou is, behandel. Aandag word aan die volgende ontwerpe gegee: die oorsprong en rede vir die sukses van die Australiese Akasias by die Kaap, hul fenologie, voortplantingsbiologie, skaduverdraagsaamheid, die afval van blare, takkies en peule, en hul biomasse. Die toepaslikheid van hierdie bevindings aan die bestuur van gebiede wat met akasia spesies besmet is, word in die algemene opsomming bespreek. Gegewens verskyn in tabel-vorm in die bylae. Die werk is met 37 tekeninge geïllustreer.

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INTRODUCTION

Despite Bolus' (1904) gloomy prediction that Australian Acacias and other woody exotics would struggle with the indigenous vegetation "for mastery of the whole area" of the Cape Peninsula, nothing was done to halt this process. There was little general awareness of the problem until the 1950's, when it was realised that indigenous species were being lost under thickets of exotic plants (Adamson, 1953), and alien shrubs were "choking our river courses" (Beyers, 1959). Bodies such as the 'Control of alien vegetation committee', aimed at publicising the problem, and organising volunteers to hack out alien plants, were started, and they have since multiplied.

In the 1960's and 1970's the number of publications (popular and scientific) dealing with the distribution, general ecology and control of alien plants was probably matched by the likewise exponential growth of the weed problem. Papers published during this period include: Schütte, 1960; Hall, 1961; Roux, 1961; Roux, 1964; Taylor, 1969; Wicht, 1971; Woods, 1974; Taylor, 1975; Boucher & Boucher, 1978; Marais, 1979; Hall, 1979; Stirton, 1978.

At present, research is being carried out at Universities in the Cape and Natal, as well as by the Botanical Research Institute, and Plant Protection Section of the Department of Agricultural Technical Services, and as part of the Fynbos Biome Research Program (S.A.N.S.P. 1978). The Department of Forestry and many Municipalities are actively involved in clearing thickets of Acacia and other pest plants, and the Department of Nature Conservation is bringing the problem to the attention of the public.

The exotic weed problem is not unique to the Cape, although it is particularly severe here. Australian shrubs, including Acacias, have become naturalised in the indigenous vegetation of California (Smith, 1979), Florida (Troop, 1979) and Mediterranean Europe (Tutin et al, 1968). South African shrubs, including Chrysanthemoides (Gray, 1976; P. Weiss, pers. comm.), Polygala (A.I.A.S., 1976), Lycium (Hughes, unpubl.) and Leucodendron argentum (Bridgewater, pers. comm.) are considered to be spreading excessively in some parts of Australia.

At the root of the problem in the Cape, is the fact that these fire-tolerant and prolific species were transported across that natural barrier of the Indian Ocean, and artificially propagated (Shaugnessy, unpubl.) in regions climatically well suited to them, and where they lacked the co-evolved predator/parasite complex normally controlling their numbers (Neser & Annecke, 1973; Van den Berg, 1977). Elton (1958) defined these factors as being chiefly responsible for the invasions of plants and animals which occurred throughout the world during the 19th and 20th centuaries.

The aims of this project, which deals in depth with a few aspects of the ecology of four Acacia species, are to provide a factual basis for the planning of biological and other control schemes, and to compare the behaviour of the exotics to that of the indigenous Fynbos (as far as this is known).

The four Acacia species involved are: A. cyclops A. Cunn. ex G. Don., A. longifolia (Andr.) Willd., A. saligna (Labill.) H. Wendl. and A. melanoxylon R.Br. The identification of the first three was confirmed by Dr. B. Maslin (Western Australian Herbarium), who studied a variety of material collected throughout the Cape (Maslin, pers. comm.). Duplicate specimens are housed in the Bolus Herbarium, University of Cape Town.

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Australian acacias in the S.W. Cape: pre-adaptation, predation and success

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1980
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Australian acacias in the S.W. Cape: pre-adaptation, predation and success

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ABSTRACT

Factors leading to the success of Australian acacias in the S.W. Cape are identified. Pre-adaptation at the genus, sub-genus and species levels, together with a stress-tolerant competitive strategy partly accounts for the invasive status of exotic acacias. Destruction of reproductive organs by indigenous pathogens and predators limits potential weeds in their natural habitat, but rarely in their place of adoption. Biological methods of controlling exotic acacias should prevent their dominance of, if not their spread through, S.W. Cape vegetation.

INTRODUCTION

The success of the exotic acacias in the S.W. Cape has, in the past, been attributed to their rapid establishment after fire, aided by nitrogen fixation and possibly allelopathy, (Roux & Middlemiss 1963), and to the recent deterioration of soil trace element status beyond the tolerence of indigenous vegetation (Schütte 1960). Recently van den Berg (1977) has found that the exotic acacias in the Cape have fewer natural enemies than in their place of origin.

This paper examines the contributions of pre-adaptation and predation to the success of exotic acacias and failure of African acacias to become part of the flora of the Fynbos Biome.

PRE-ADAPTATION

Genus Level

Through part of its range, (West and Central Australia, North Africa), the genus Acacia is associated with relatively coarse textured or sandy soils. Most of the species are nodulated, (Nakos 1977, Dancette et al 1969, Lange 1959, Grobbelaar et al 1975), and have associated mycorrhizae (Johnson & Michelini 1975, Barrow 1977). Acacia is therefore well adapted to the soils of the S.W. Cape which are sandy and poor both in trace elements (Schütte 1960) and major nutrients (Low 1978). Its distribution in warm arid zones suggests that acacia could withstand a summer drought.

According to Baker (1974), a genus with weed potential should produce large quantities of long lived seed and/or be capable of vegetative reproduction. Large seed crops are characteristic of the genus (Janzen 1969) and most Acacia species produce water-impermeable, dormant seed. The exceptions, which form only 'soft' seed, are among those which multiply by root suckering (Pedley 1978). Although most Acacia species are obligate

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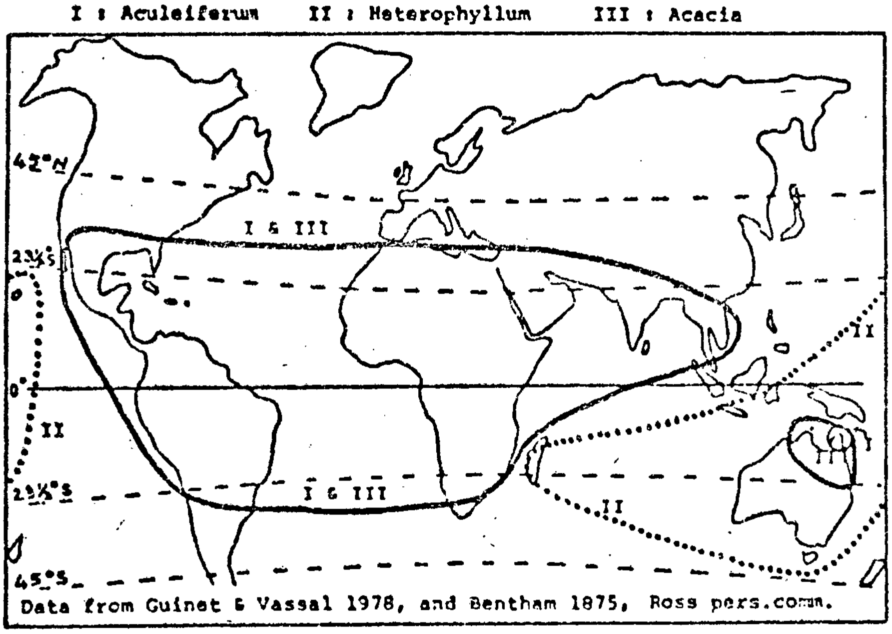

Data from Guinet & Vassal 1978, and Bentham 1875, Ross pers.comm.

FIGURE 1. Distribution of the subgenera of the genus Acacia.

outbreeders (Hopper & Maslin 1978, Moffett & Nixon 1967) they utilize generalised pollinators found throughout the tropical and temperate world - e.g., bees and flies (For. Comm. NSW 1975, Richards 1978).

Sub-genus Level

Guinet & Vassal (1978) define three subgenera within the genus Acacia. Two of these (Acacia and Aculeiferum (Vassal)) are widely dispersed in tropical and subtropical regions. The third subgenus, Heterophyllum (Vassal), (Phyllodineae DC), is confined to Australia and the Pacific Ocean islands.

Temperature apparently limits the distribution of Aculeiferum and Acacia (See Fig. 1), however it is not clear whether mean or minimum temperatures are critical, or whether germinating seeds and/or adult plants are affected.

The few species of subgenus Acacia endemic to Australia all occur in tropical north Australia (Guinet & Vassal 1978), and the subgenus Aculeiferum is represented in Australia by a single species in northern Queensland (Ross 1979). C4 grasses are also restricted to this part of Australia, and are replaced by C3 grasses to the South (Specht pers.comm.). That the African acacias, which all belong to subgenera Acacia and Aculeiferum, are limited to warmer habitats, is indicated by their replacement at higher altitudes by other woody genera (Walter 1968). A. karoo, the southern-most of the African acacias, and the only African acacia to have naturalised in Europe (Flora Europaea 1968), never forms

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part of the S.W. Cape plant communities, and within its range is confined to lower altitudes (Story 1952).

Acacia is thought to have originated in Central America and to have spread throughout Gondwanaland during the Mesozoic period (Guinet & Vassal 1978). However the genus only become prominent in pollen spectra of Africa, America, India and Australia during the Oligo-miocene - evidently in response to warmer, drier conditions (Axelrod & Raven 1978, Guinet & Vassal 1978, Lakhanpal 1970, Cookson 1954). Later climatic changes led to the disappearance of *Acacia* from the cold temperate Ukraine and New Zealand (Guinet & Vassal 1978) and its replacement of retreating Macchia genera in the Transvaal, as this region grew warmer and drier during the Holocene (Scott & Vogel 1978).

Despite the tropical origin of *Acacia*, and the present day subtropical and tropical distribution of two of the subgenera, the subgenus Heterophyllum (confined to Australia and the Pacific islands) has proliferated in extratropical Australia. More than half Australia's c.700 endemic *Acacia* species are confined to latitudes south of the Tropic of Capricorn (Hopper & Maslin 1978). In Queensland, subtropical *Acacia* species are replaced by temperate acacias at higher altitudes. (Pedley 1978). *Acacia* species richness is greatest in S.W. Australia - a region which like the S.W. Cape was subjected to climatic fluctuation throughout the Pleistocene-Recent period (Hopper & Maslin 1978).

The winter rainfall regime of the S.W. Cape is only about 18 000 years old (Axelrod & Raven 1978) and is clearly not the major factor determining the distribution of the characteristic and common genera of Capensis. These genera originated long before the climatic change took place, and have temperate affiliations (Coetzee 1978, Scott & Vogel 1978, Axelrod & Raven 1978). While their present distribution within the winter rainfall region is limited by drought on the west coast, they extend into the summer rainfall region on the south and east Cape coasts. The presence of Fynbos genera at high altitudes in the Drakensberg (Bews 1917) suggests that these genera are adapted to a temperate climate and oligo-tropic soils. There are exceptions, e.g. *Philippia* on the Tongaland coast, where edaphic factors appear to outweigh climatic factors (Moll pers.comm.).

The absence of the African acacias in the S. and S.W. Cape region may be attributed partly to edaphic factors but chiefly to the cool wet climate. This factor, rather than rainfall regime, distinguishes the region from the rest of Africa. Australian acacias of the Heterophyllum group, being pre-adapted to temperate conditions and leached soils (Gill 1961), have succeeded where the African groups have failed.

Species level

The Australian *Acacia* species were introduced selectively to the Cape, for specific purposes:- sand stabilization, silviculture, horticulture. Species from climatically and edaphically similar regions would obviously be preferred. With a few exceptions, the "aggressive" exotic acacias have remained with the Cape equivalent of their climatic/edaphic range in Australia.

All the exotic *Acacia* species spreading in the Cape have come from Australia between 25° and 40°S latitude. The same group of species has become naturalised where introduced in Europe between 35° to 45°N latitude (Flora Europaea 1968). Their success has been largely dependant on the establishment of the various species in suitable habitats. e.g., *A. pycnantha* has disappeared from the Cape Flats while *A. cyclops* and

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TABLE 1: Native and Exotic Habitats of Australian Acacias

SPECIES	NATURAL HABITAT	ADOPTED CAPE HABITAT	AUTHOR
A. cyclops	SW Austr. Recent and calcified dunes	W, SW, S Cape. Same as natural habitat and on sandstone	Seddon 1972 Bridgewater pers. comm.
A. saligna	SW Austr. coastal sand, and other substrates, esp. waterways & peaty depressions	W, SW, S&E Cape. All substrates, where adequate water is available	Maslin 1974 Bridgewater pers. comm.
A. longifolia	E & SE Austr. coastal forests, all substrates	SW,S,E Cape. Moister sites. Not on saline sand.	Bridgewater pers. comm.
A. pycnantha	SE & S Austr. silt and mudstones, forest precurser	shales and alluvium esp. moist sites	Bridgewater pers. comm.
A. melanoxylon	E, SE Austr. and Tasmania. Forest precurser on basalt and loam	Loamy soil in higher rainfall regions, esp. S. Cape	Howard 1974
A. mearnsii	E,SE Austr. and Tasmania shale, granite and sandstone	River courses in dry regions. Widespread in moist regions	Boucher 1978 Sherry 1971

A.saligna dominate the area: these three species were introduced together (Boucher & Stirton 1978).

GRIME'S THEORY

Grime (1977) postulated that there are three primary plant strategies: competitive, stress tolerant and ruderal, adapted to productive, unproductive and highly disturbed habitats, respectively. The characteristics of each group are presented below.

Competitive plants are fast growing and form a high dense canopy of mesophyll leaves. Copious litter is produced and tends to accumulate on the ground. Flowering and growth occur in clearly defined flushes. In reaction to stress (e.g. shading, drought) a competitive plant seeks to maximise production through morphological change.

Stress tolerant plants are slow growing, often with small sclerophyll leaves. Litter production is minimal, and flowering and growth do not always coincide with periods of maximum potential productivity. The plant lacks morphological plasticity, but survives stress by reducing growth and reproductive activity.

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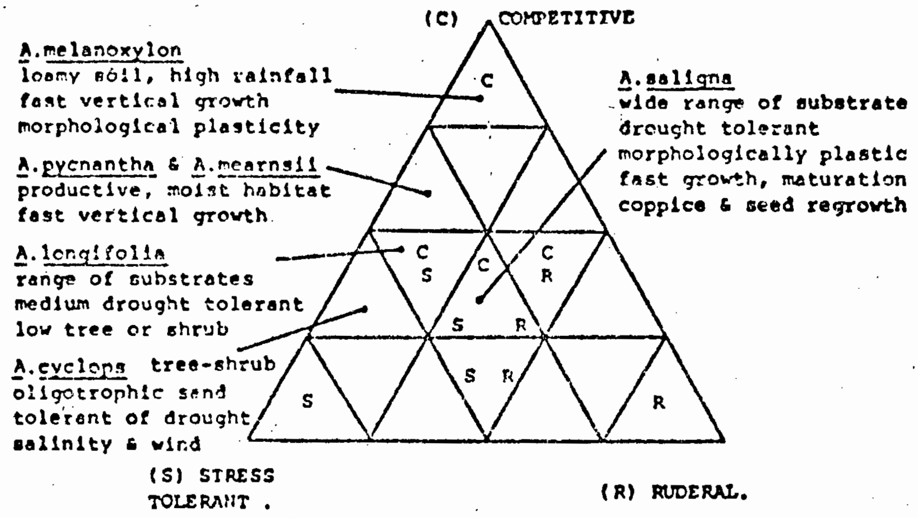

FIGURE 2. Probable position of exotic *Acacia* species in Grime's Triangle

Ruderal plants are fast growing, short lived herbs. Little litter is produced during the life span. Flowering occurs towards the end of the period favouring growth. In response to stress, all resources are diverted to seed production.

In general the exotic acacias fit the competitive plant model most closely. They all grow 1 - 2 metres during their first two years. Litterfall in an established acacia thicket is about 700g/m^2/p.a. (dry weight) - approximately three times as great as that of heathland and chaparral communities (Mooney & Rundel 1979). Most of the exotic acacias have a brief and clearly defined annual flowering season. While some growth occurs throughout the year, a dramatic flush occurs in spring (Milton unpubl. data).

A closer examination of the various species of exotic acacia suggests that a number of them have strategies intermediate between competitive and stress tolerant. (Fig. 2).

A. saligna, which regenerates both from seed and from coppice shoots, can survive frequent disturbance. This highly versatile plant has become naturalised around the Mediterranean sea, in California, and has assumed weed status even in E. Australia, where it has been introduced. In the Cape it occupies a wider range of habitats than the other exotics.

Grime (1977) visualises the structure of a community as dynamic. Early successional stages tend to be dominated by ruderals which are replaced by competitive plants. As the community matures further, a plant-imposed stress condition may develop through shading or binding of nutrients in living tissue. The climax community may have to be slower growing and more stress tolerant than its precursers.

The slow growth rate, small long-lived leaves and the virtual absence of ruderals in Fynbos suggests that this is a nutrient stressed vegetation (Martin 1966, Boucher 1977, pers. obs.). The mechanisms whereby acacias (relatively competitive plants) can become established in this stress tolerant vegetation appear to be as follows:-

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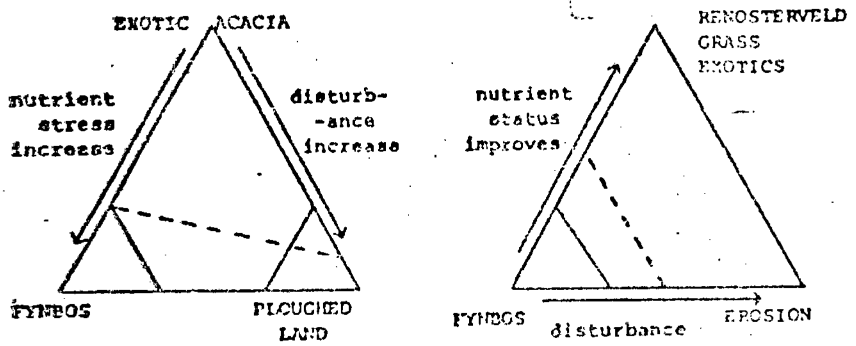


FIGURE 3. Resilience of Fynbos and Acacia communities.

1) Acacias first infest regions of relatively high productivity (watercourses, old lands, roadsides). They also encroach on Fynbos which is fire managed for grazing. This treatment prevents the accumulation of nutrients in the biomass and provides brief post burn periods of boosted K and P levels in the surface soil. (Bean 1962).
2) An established acacia changes its local environment by adding organic matter and nitrogen to the soil. The magnitude of this is indicated by crop harvests on old wattle lands (Orchard & Darby 1956, Sherry 1971, King 1939) and by the presence of ruderals and grasses in standing and cleared acacia thickets (Burgers pers. comm.)
3) Within five years, scattered stress-tolerant *A. cyclops* bushes, introduced by birds, have built up large stores of seed, and locally enriched the soil. After a second burn, single trees will be replaced by clumps of *A. cyclops*, and perhaps other exotic species less tolerant of nutrient stress.

Having boosted the nitrate content of soils, the acacias are unlikely to be succeeded by a stress tolerant vegetation such as Fynbos.

The resistance of an established community to an invading exotic species has been found to be inversely proportional to the diversity of the community (Harper 1965). Clements (1929) found that it was practically impossible to introduce *Typha* into a *Phragmites* community and vice versa. He concluded that modification or replacement of a climax association can only be brought about by mass migration aided by dramatic environmental change.

In the light of the above findings, one must conclude that

1) An *Acacia* species could be introduced into Fynbos (a diverse community) more easily than a Fynbos species could be introduced into an acacia thicket(monoculture).
2) Acacias, aided by burning and grazing, are modifying the environment to such an extent that they might be capable of replacing the existing climax.

Using Grime's (1977) model, acacias can be shown to be relatively flexible e.g., capable of exploiting productive habitats as well as of enduring considerable stress and disturbance. Fynbos lacks flexibility: repeated disturbance or nutrient addition may result in erosion, or replacement by a more eutrophic vegetation type. (Fig. 3)

TABLE 2: Seed density for two species in the S. Cape

Acacia cyclops (exotic)		*Chrysanthemoides monilifera* (indigenous)	
Intact seeds/m^2	Seed fragments/m^2	Intact seeds/m^2	Seed fragments/m^2
$\bar{x}$ = 2500	less than 1%	100-300	4000-6000

PREDATION

The plant communities of the Cape are not lacking in competitive species. These are particularly common in the early seral stages of sand dune and burn succession. Examples may include *Chrysanthemoides monilifera*, *Metalasia muricata*, *Anthospermum aethiopicum*, *Polygala myrtifolia*, *Sutherlandia frutescens*, *Virgilia oroboides* and *Montinia caryophyllacea* - all of which show most of the characters of the ideal competitive plant.

Chrysanthemoides monilifera was introduced to the coast of Victoria for stabilising sand. It soon naturalised, and now "competes strongly with and in places totally eliminates native dune species - particularly *Acacia longifolia*" (Gray 1976). This is a mirror image of the situation in the S and SW Cape. Here *A. cyclops* and *A. saligna* are replacing *Chrysanthemoides*. Casual obvservation suggests that, in the SW Cape, *C.monilifera* is heavily parasitised by gall forming insects, and that its seeds are cracked (by birds or rodents?). In Australia masses of intact seed lie beneath its relatively unblemished bushes. (Bridgewater pers.comm)

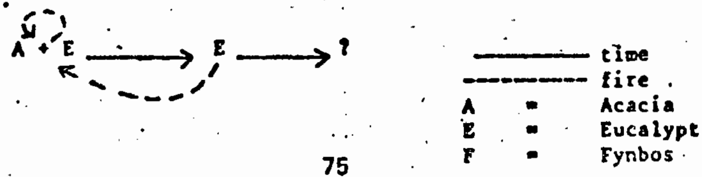
Preliminary seed counts support these observations. (Table 2.)

In Australia, at least 75% of the annual seed crop of some acacias (including *A. pycnantha*) is removed and buried or destroyed by ants (Majer 1978) Withers 1979). The seed crop is further reduced by fungi, birds, wasps, bugs and lepidopteran larvae(v.d.Berg 1977, Morellini 1977). In the SW Cape, rodents, certain bugs (Hemiptera), larvae of one species of Lepidoptera and germination destroy a total of less than a quarter of the annual seed crop (Shelton 1975, King 1976).

That predation of exotic acacia seed is below normal levels is indicated by the fact that the average seed densities under exotic acacia thickets is of an order of magnitude normally found only for ruderal communities (Thompson 1978). That there are enormous differences in the predation pressure exerted on Australian acacias, in their natural and in their adopted habitats, is indisputable.

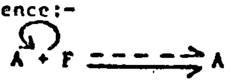
CONCLUSION

Noble and Slatyer (1977) presented the following model of the effects of time and fire disturbance on a seed regenerating mixed eucalypt/acacia community.



Fire, or the eventual death of the eucalypts, is required to restore the short-lived acacias to the community.

The situation in a mixed exotic acacia-fynbos community might follow this sequence:-



(no effective seed predation)

Aided by the ability to change their environment, by disturbance and by lack of effective seed predation, pre-adapted exotic acacias are likely to replace fynbos in all but the most stressed habitats. Fynbos, unlike eucalypt forest is unlikely either to outlive, or outshade exotic acacias: so that protection from fire alone, will not control exotic acacias.

(effective seed predation)

Reduction of disturbance, together with the effective predation of the exotic acacia seeds, may lead to the establishment of an equilibrium between exotic and indigenous vegetation.

It has been shown that the exotic acacias are competitive stress-tolerant species well adapted to the climatic and edaphic conditions of the Fynbos Biome. Lack of heavy seed predation has enabled them to succeed where indigenous species, with similar niches, have failed. The introduction of effective seed predators, while unlikely to halt the spread of the exotic acacias, should prevent their eventual dominance of all habitats suited to them.

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PHENOLOGY OF AUSTRALIAN ACACIAS IN THE S.W. CAPE, SOUTH AFRICA

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ABSTRACT

Australian Acacias introduced to the Cape about 145 years ago have become naturalised and are replacing indigenous vegetation over extensive lowland areas. Ecological studies were therefore carried out to provide a basis for their management and biological control. This paper describes their growth, litterfall, reproductive and nectar secretion phenology. Results indicate that growth and litterfall are seasonal events, but timing varies with species and site : reproductive phenology, on the other hand, is characteristic of a species, and varies little with time and place. Nectar secretion appears to be associated with both growth and flowering. Differences in the phenology of the study species in Australia and in the S.W. Cape are minor, and should prove no barrier to the introduction of organisms for biological control.

CONTENTS

INTRODUCTION

In the S.W. Cape, where the genus Acacia is represented only by scattered populations of Acacia karroo, Australian Acacias have attained weed status. They were introduced from the mediterranean climatic areas of Australia about 145 years ago for sand stabilization, wood and tan-bark production and horticulture, but are now replacing indigenous vegetation (Stirton, 1978). Of the thirteen species listed in Figure 11, the most troublesome species in the S.W. Cape are Acacia cyclops A. Cunn. ex G. Don., A. longifolia (Andr.) Willd., A. saligna De Wild., A. melanoxylon R.Br. and A. mearnsii De Wild.

The success of the Australian Acacias of the sub-genus Heterophyllum in the S.W. Cape, and in other regions with temperate and mediterranean type climates (Anon, 1977; Smith, 1979; Tutin et al, 1968; Anon, 1955; Le Roux, 1976) may partly be attributed to the fact that the sub-genus Heterophyllum is naturally distributed in cooler regions than the sub-genera Acacia and Aculeiferum (Milton, 1980). Of the African Acacias, all of which belong to the latter two sub-genera, only A. gummiferra (Quezel, 1978) and A. karoo (Robbertse, 1971) extend beyond 33° north or south latitude or into regions of mediterranean climate.

In the Cape, the exotic Acacia species generally occupy sites with edaphic and climatic conditions similar to those in their place of origin. A. cyclops occurs on deep coastal and alluvial sands. The ecological range of this species in the S.W. Cape appears to be wider than that in Australia, as the species also grows on shallow mountain soils derived from granite and sandstone. As in Australia, A. saligna is a pioneer species, most successful on moist or relatively nutrient-rich disturbed sites such as dune hollows, river banks, fire breaks, rubbish dumps and road verges.

It thrives on a wide variety of substrates, and coppices vigorously after fire and mechanical damage. *A. cyclops* and *A. saligna* have already replaced or infested much of the Coastal Macchia (Acocks Veld Type 47, Acocks 1953). *A. pycnantha* is restricted to clayey or silty soils in moist sites, and *A. mearnsii*, to river banks and gullies. *A. melanoxylon*, being limited to loamy soils and sheltered, humid sites, is not of much importance as a weed or crop in the S.W. Cape; but *A. longifolia*, which grows on both alluvial soil, sandstone and shale, has proved capable of replacing Mountain Fynbos in moist places.

In the S.W. Cape these Australian Acacias tend to form dense thickets up to 7 m in height. Other than in preventing soil erosion, such thickets have little to commend them. They are too tall and dense to be used by browsing animals in farming areas. They have a high transpiration rate which makes them undesirable in catchment areas, and in urban areas they rapidly take over unused land, thereby providing cover for undesirable elements.

Clearing of exotic Acacia thickets is carried out by a combination of mechanical, chemical and burning treatments - which, because of the large store of Acacia seed in the soil, must be repeated over many years. This sort of management is too costly to be applied in large areas of rugged territory or in marginal agricultural regions.

This paper reports on phenological studies that are part of a programme to provide a basis for the planning of effective management of the problem species of exotic Acacias in the S.W. Cape. Phenological information is required for the recognition of species in aerial photographs and satellite images, the timing of chemical or mechanical control measures, the selection of organisms for biological control and for the efficient harvesting of Acacia products for fodder or energy production.

Apart from its applications to management problems, phenology is of theoretical interest, particularly in mediterranean climatic regions which offer no ideal growing season.

METHODS

Site selection and description

Dense, mature, single-species stands, growing in habitats susceptible to infestation by the various Acacia species, were chosen for growth and litterfall studies. *A. longifolia*, *A. melanoxylon* and *A. saligna* study sites were on the University of Cape Town campus and at Hout Bay Forest Station (Figure 1). These sites are situated on the slopes of Table Mountain, on the Cape Peninsula. They lie on moderately sloping ground, 150 m above sea level. Both have medium textured, deep, red or yellow apedal, stoney soils (Hutton and Clovelly forms), with a clay content of 6 to 15% (Agricultural Technical Services, 1976; 1977). Weather stations near these sites (Kirstenbosch, Devils Peak, Newlands) receive 1 200 to 1 400 mm rain per annum (Weather Bureau 1965). In 1977, an exceptionally wet year, Kirstenbosch received 2 164 mm. The natural vegetation of the Peninsula is Fynbos, grading into forest on south-facing slopes and in moist gullies.

The Cape Flats, which lie due east of the rocky Peninsula, are almost totally covered by *A. cyclops* and *A. saligna* thickets. They once supported psammophilous fynbos on leached sands and limestone, grading into sclerophyll broad-leaved scrub nearer the coast, and ephemeral marsh

B

Figure 1. Map showing the positions of the study sites and weather stations on the Cape Peninsula and the Cape Flats. Inset Walter diagrams (Walter et al, 1975) give weather data for three stations during the study period.
(Weather data from Weather Bureau, 1965)

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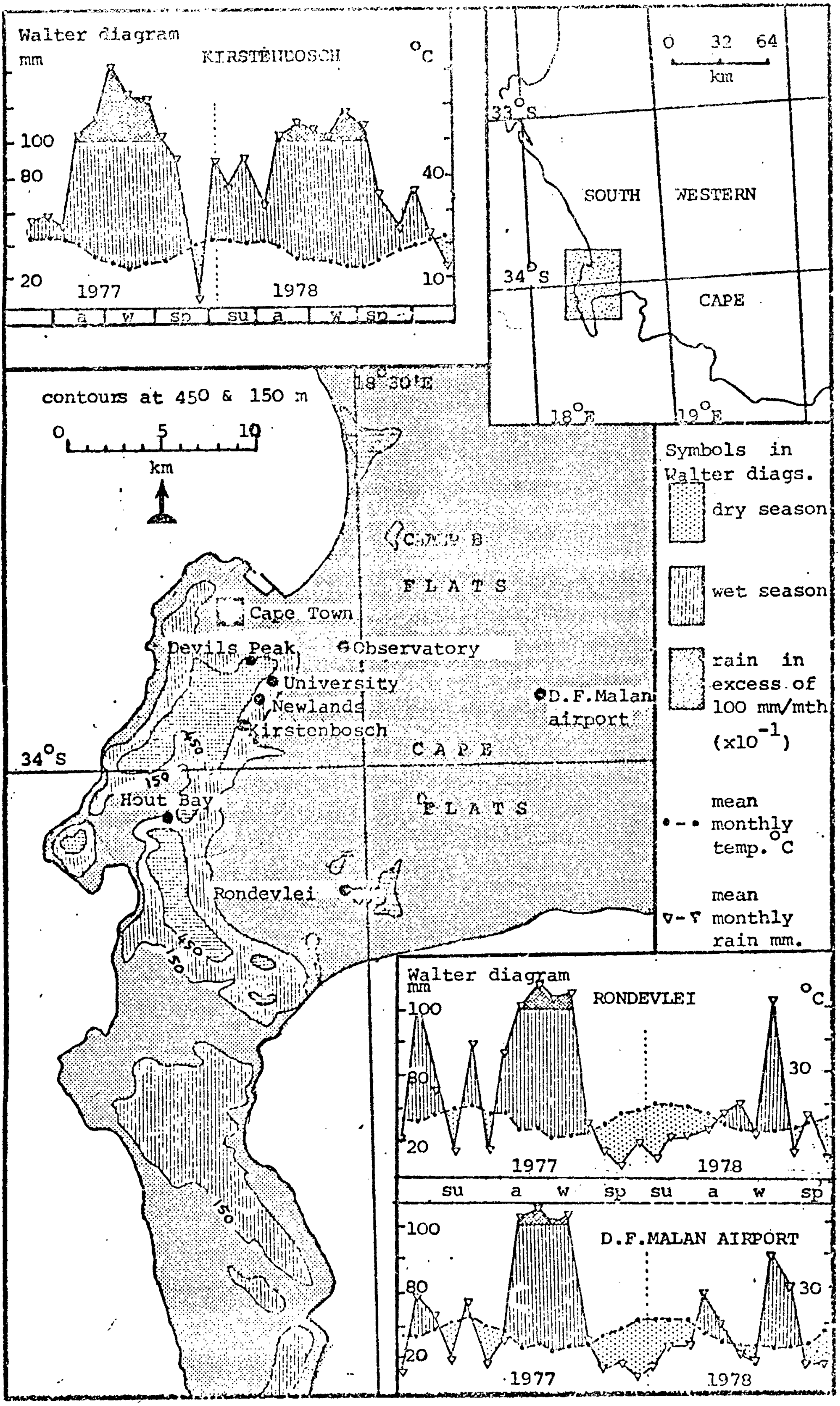
Walter diagram
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33°S
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CAPE
18°E
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km
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CAPE
FLATS
Cape Town
Devils Peak
Observatory
University
Newlands
Kirstenbosch
D.F.Malan airport
34°S
450
150
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CAPE
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Rondevlei
450
150
150
Symbols in Walter diags.
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wet season
rain in excess of 100 mm/mth (x10^{-1})
mean monthly temp. °C
mean monthly rain mm.
Walter diagram
mm
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100
80
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100
D.F.MALAN AIRPORT
80
30
20
1977
1978

communities in the dune hollows (Taylor, 1974). The Rondevlei Bird Sanctuary site was chosen as typifying the Cape Flats environment. It is situated on the shore of a brackish lake, about 15 m above mean sea level. Low dunes and marshy hollows are a feature of the generally flat topography. Regic, medium textured white sand (Fernwood form: Agricultural Technical Services, 1977) extends to a depth of about 25 m in most places but in some areas limestone dune cores are exposed (Henzen, 1973). The Cape Flats do not have the benefit of orographic rain, and receive about half as much rain as the mountainous regions. Rondevlei has a mean annual rainfall of 762 mm (Weather Bureau, 1965), however, the water table is near the surface throughout the year.

Mean monthly temperatures are similar at all sites, with monthly minima of 7 - 15°C and maxima of 17 - 26°C. Temperature extremes of 1.4°C and 35.5°C may occur on a few days in August and February respectively (Weather Bureau, 1965).

Growth phenology

Growth phenology was investigated by (1) destructive sampling of leader shoots, (2) non-destructive monitoring of leader shoots and (3) non-destructive monitoring of lateral shoots.

(1) Destructive sampling has been used to assess the seasonal production rate of a plant community (Specht & Rayson, 1957) and of individual species (Maconochie, 1975; Specht & Brower, 1975). Destructive sampling has the advantage of providing mass data, and avoiding continual interference with any particular plant. The techniques described in the above papers were not used in this study since

random clipping of 'new growth' was considered too crude, and because Acacias do not produce small leaves towards the end of their growing season or other markers of growth flushes.

Initially 400 shoots of each of the four study species were marked 10 cm from the shoot apex using red acrylic yarn attached with bitumen. Twenty shoots of each species were harvested monthly, and the following data recorded: shoot length, wet weight, dry weight, phyllode and lateral shoot number, and the presence of flower buds, nectar secretion and insect damage. After six months (May-October) this method was abandoned because seasonal differences in mass increment, leaf expansion and lateral shoot production were obscured by the rapid growth of woody tissue and lateral shoots. In addition to this, the shoots, now over a metre long, were cumbersome to process and were being damaged by the non-elastic markers which had cut into the vascular tissue.

Since mass increment, leaf expansion and lateral shoot production occur over the entire length of a shoot, monthly increments in these parameters are not comparable unless measured on shoots which had the same initial length at the beginning of each sampling period.

An improved sampling method, which provided the same range of data, was applied as from the sixth month. Twenty leader shoots of each of the study species (*A. cyclops*, *A. longifolia*, *A. melanoxylon* and *A. saligna*) were marked 20 cm below the apex. A further twenty shoots of equal length were cut, and wet and dry weight, phyllode and lateral shoot numbers were recorded. The latter sample acted as a standard measure of shoot parametres at the time of marking. Four weeks later the marked sample was harvested, a new set of shoots was measured and another standard sample cut. Monthly increments were calculated as follows:

M_1 , M_2 = measurements at times 1 & 2

mean M_2 - mean M_1 = I

I = monthly increment

Since different individuals were used at time 1 & 2, no standard error could be calculated on the monthly increment. However, the standard error of the sample mean at M_2 is given for every month (Figure 2) to show sample variability.

Data obtained by both methods were combined to give an unbroken set of increment readings for a fourteen month period.

(2) Non-destructive monitoring of leader shoots was carried out on 59 *A. longifolia* and 30 *A. melanoxylon* saplings, approximately 30 cm tall, and growing in a mixed stand on cleared land at UCT. An additional 20 *A. melanoxylon* saplings growing under the canopy of a nearby parent tree, were also marked and measured. The distance from the marker, (a numbered, split, celluloid bird-ring), to the apex of the terminal shoot was measured at monthly intervals. The method permitted calculation of the standard error on the mean monthly height increment. The population under the parent canopy provided a comparison of sapling growth in shade or competition, with that of growth in an open site.

(3) Non-destructive monitoring of lateral shoot growth was done by tagging a set of 20 lateral shoots (distributed over 4 - 6 bushes) for each of the four study species. Length, number and developmental stage of inflorescences and the activity of the phyllode nectaries were

recorded each month. Lateral shoot growth was slow, and in some species, particularly A. saligna, the lateral shoots tended to die after the pods had ripened. For this reason, the actual length increment data being unreliable, the percentage of marked shoots growing was used as an index of growth activity.

Other workers (Sommerville, 1977; Donnelly, 1977; Haynes, 1976) have also experienced problems with continual monitoring of shoots in the field, particularly shoot die-back and the change from apical to axillary bud growth.

Litterfall

Litterfall studies were designed to provide productivity data as well as quantified phenology data. A litter trap was adapted from the model used at Jonkershoek Forestry Station, Cape. It comprised a terylene net bag, 40 cm deep and 50 cm in diameter, suspended from a wire hoop attached to two metre-high iron fence droppers. The bottom corners of the bag were also tied to the droppers to prevent inversion of the bag in the wind. The equipment proved inexpensive and durable, and allowed the litter to dry rapidly, preventing decay. Ground traps including porous trays, tins and canvas sheets have been used for litterfall studies (Ashton & Frankenberg, 1976; Rogers & Westman 1977; Specht & Rayson, 1957; Hannon, 1958) but were rejected without trial in the present study as they were feared to be subject to interference from foraging animals, wind and rain.

The traps were placed about five paces apart, under single species thickets at the University, Hout Bay and Rondevlei sites, ten traps being alotted to each of the four Acacia species. The traps were emptied at monthly intervals. The litter was oven-dried at 90°C for 24 hr and sorted into the following categories: flowers, pods, seed, phyllodes, twigs and bark, unidentified matter, litter from other plant species and animal derived or inorganic debris. The last class was discarded, and the other classes all weighed individually.

Reproductive phenology

Five sources of data were used in this study:

a) Data from marked lateral shoots

b) Quantity of flowers, pods and seeds in monthly litterfall samples

c) Photographs of the exotic Acacias naturalised or planted in the S.W. Cape taken at monthly intervals

d) Notes made from 281 sheets of exotic Acacias housed at five S.W. Cape herbaria (BOL., NBG., CT., STE. and Williams Herbarium, Stellenbosch)

e) Field notes recording the first and last appearance of buds, open flowers, green and ripe pods on the various *Acacia* species

As these data could not be combined for quantitative analysis, and as numerous graphs are difficult to assimilate, bar charts providing a qualitative record of the phenology were constructed as illustrated by Dierschke (1972). The chart shows the type, but not the degree of activity taking place in any period.

Nectar secretion phenology

The percentage of shoots with active nectar glands was recorded during the growth studies. A more detailed study of nectar secretion was carried out on *A. longifolia* in July 1977 and July 1978. The degree of activity of phyllode glands on branches bearing either buds or open or withered flowers, was determined by nectar collection (Bentley,1977a). Branches were initially covered with plastic bags to reduce evaporation and to exclude nectivores, but this measure was found to be unnecessary for the purpose of obtaining comparitive estimates of activity. Nectar was collected from a known number of glands, using a 1 mm capillary tube. The length of the nectar-filled part of the tube was measured and the volume of nectar calculated (method communicated by S. Frost). The nectar composition was determined by gas-liquid chromatography and its concentration estimated using a refractometer.

RESULTS & DISCUSSION

Growth phenology

Monthly increments in the length, dry weight and phyllode number of the harvested leader shoots are presented in Figures 2A to 2E. The mean monthly increments of monitored leader shoots and the activity of lateral shoots are shown in Figures 3 and 6.

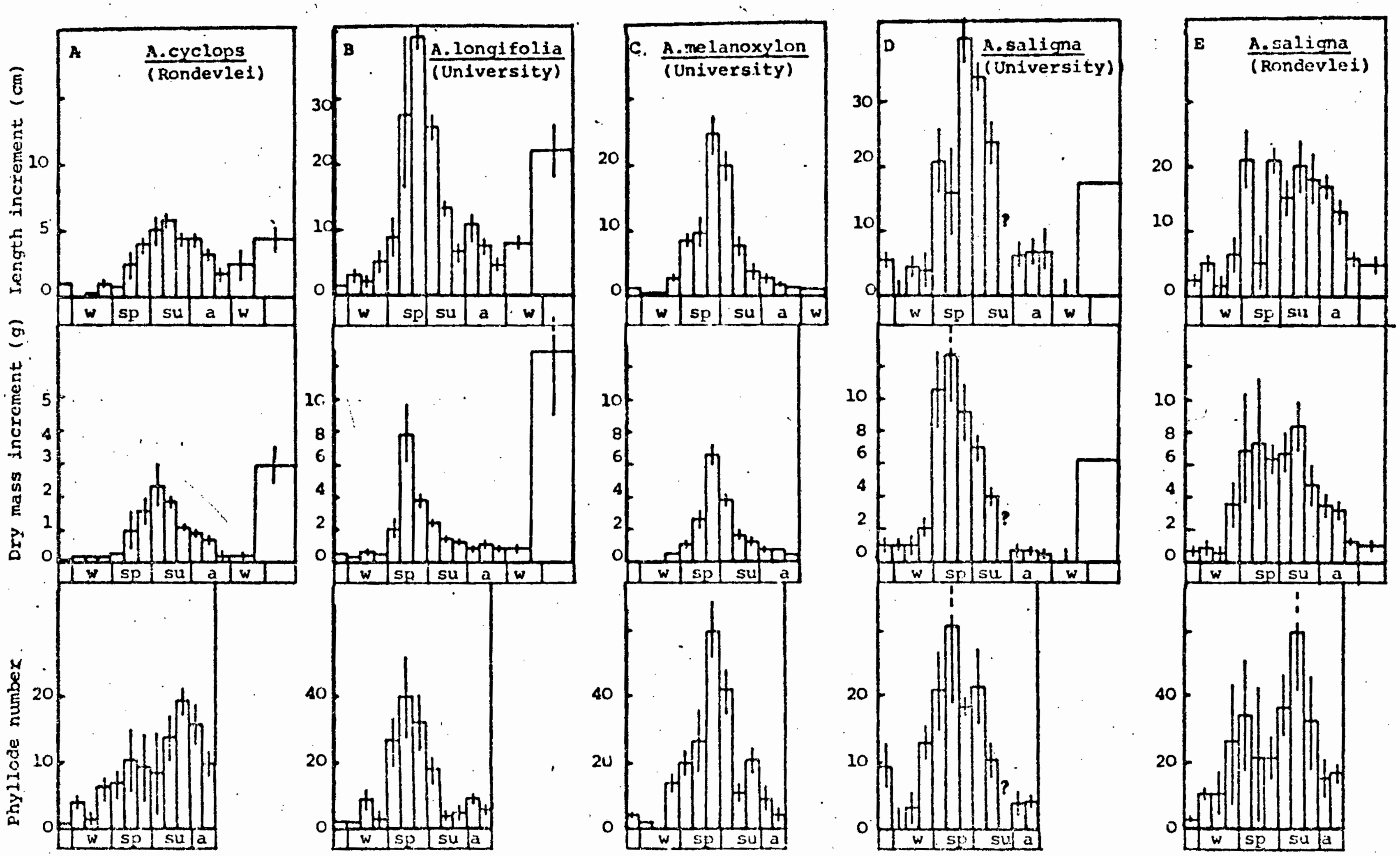
Leader-shoot growth, in terms of length and mass increment, began in the Austral spring month of September, peaked in November and December and ended in late summer (February) for *A. longifolia*, *A. melanoxylon* and *A. saligna* at the University site (Figures 2B, 2C and 2D). *A. cyclops* began its growth flush in October and continued to grow relatively rapidly until April (Figure 2A). *A. saligna*, at the Rondevlei site started to grow in August, but like *A. cyclops* at this site, continued to grow until April (Figure 2E).

In all species the rate of phyllode initiation increased about one month

Figure 2. Growth phenology of terminal shoots as determined by destructive sampling.

Standard error of the sample mean represented by vertical line :

w	sp	su	a
winter	spring	summer	autumn



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before shoot growth started, and declined before the end of the growing period (Figure 2A to 2E). The production of lateral shoots tended to coincide with the growing season, but was a highly variable parameter and is, therefore, not illustrated. Growth of all species was minimal during the winter when mean monthly temperatures fall below 15°C and there are fewer than 7.5 sunlight hours per day.

At the University site, periods of rapid and slow growth are well defined for all Acacia species. A. melanoxylon leader shoots show a clear-cut growth flush in late winter to early spring: little or no growth occurs from January to July (Figure 2C). This trend is emphasised in the non-destructive sample (Figure 3B). A. melanoxylon saplings growing beneath the canopy of a parent tree have an earlier and shorter growing season (July to October) as shown in Figure 3C. It is possible that competition for water limits growth of these saplings early in the dry season, when the surface soil is dried out by the roots of the older tree. The shaded saplings all bore pinnate leaves: this possible adaptation to low light intensity may have enabled them to start growing earlier in the season than the unshaded, phyllode-bearing sun plants.

Increments in length, phyllode number (Figure 2B) and lateral shoot number (not illustrated) for A. longifolia show a bimodal distribution, a major peak occurring in spring, and a minor one in autumn, a trend also seen the non-destructive sampling data (Figure 3A).

A. saligna shows a clear, spring growth-peak at the University site (Figure 2D). However, at Rondevlei, neither this species nor A. cyclops shows well defined growth flushes, the growth rate remaining fairly constant from early spring until mid-autumn (Figures 2A & 2E). The difference in the length of the

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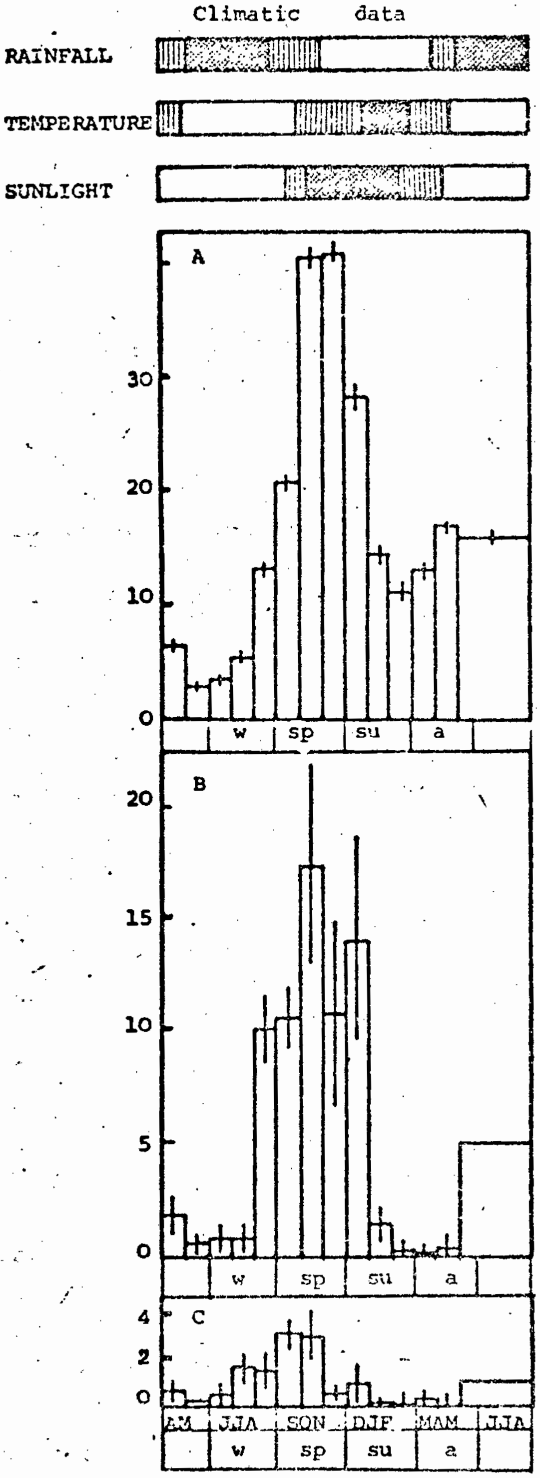
Figure 3. Growth phenology of terminal shoots as determined by repeated length measurements in the field. Standard error of the mean increment is represented by a vertical line on each bar of the histogram.



CODE	minimum monthly mean		
	RAIN mm	TEMP °C	SUNLT. hr/day
☐	5	12	4
▥	25	15	7½
▨	75	20	9

A. *Acacia longifolia*
saplings
unshaded site
(University)

B. *Acacia melanoxylon*
saplings
unshaded site
(University)

C. *Acacia melanoxylon*
saplings
beneath parent tree
(University)

growing season of A. saligna between the University and Rondevlei sites might be explained by the interaction of temperature (or light) with available soil moisture.

Linear regression equations relating monthly length increments to mean monthly temperatures show significant correlation for A. cyclops (r = 0.93) and A. saligna (r = 0.93) at Rondevlei (Figure 4). Correlation for A. saligna at UCT is not as good (r = 0.83), and there is no significant correlation between temperature and growth rate for the other two species at this site.

To ascertain whether there was a difference in water availability at the two sites, soil moisture was sampled in mid-summer. Analysis of cores taken from soil pits dug at Rondevlei in March showed that water, in quantities available to plants, was present at a depth of 20 cm on the lake shore where growth studies were carried out, and at a depth of 80 cm at a distance of thirty metres from the lake, in the thicket where the litter traps were set up. Acacia roots were present to a depth of at least 100 cm and therefore suffered no drought stress, even in the driest time of the year. The presence of marsh plants growing in association with the Acacias at the lake edge likewise indicated a perennial shallow water table.

This contrasted with the situation at the University site where, by March, the soil moisture content had dropped to below the permanent wilting point for plants growing on a clay-loam soil (12 - 13% moisture, dry weight basis, Daubenmire, 1947). Although the University site receives twice as much rain as the Rondevlei site, it has run-off drainage. The actual moisture available to plants growing in this site would probably fluctuate seasonally like the hypothetical soil moisture store shown on the Thornthwaite

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Figure 4. Regression of length increment on temperature, showing a linear relationship for the species at the Rondevlei site.

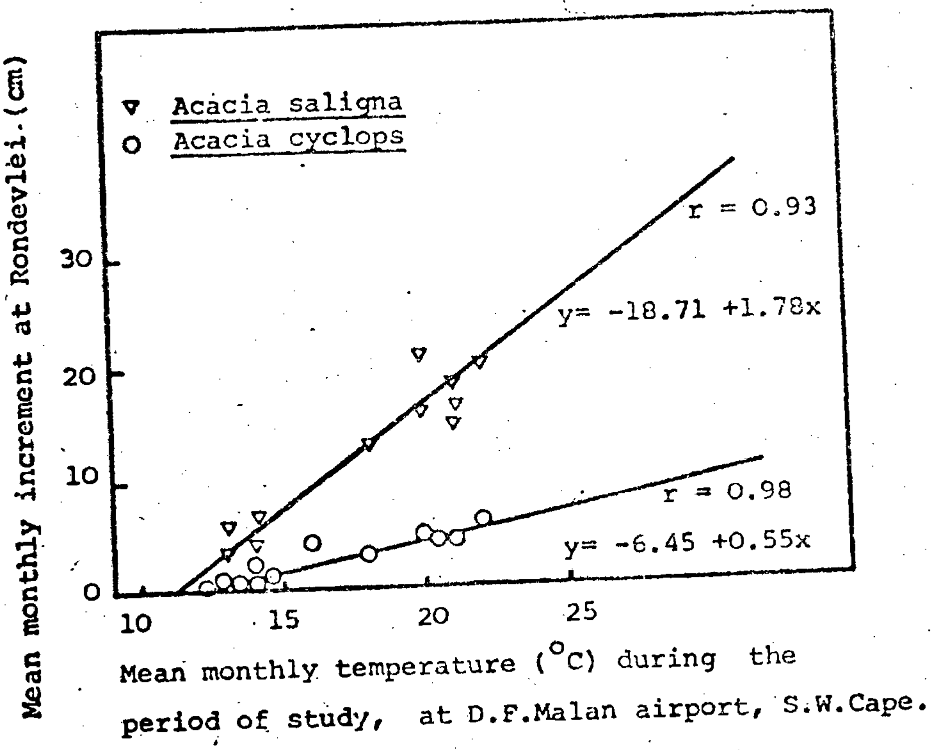


Figure 5. Growth periods of A. saligna at two sites in relation to the hypothetical soil moisture store. (Climatic data from Thornthwaite Associates, 1962).

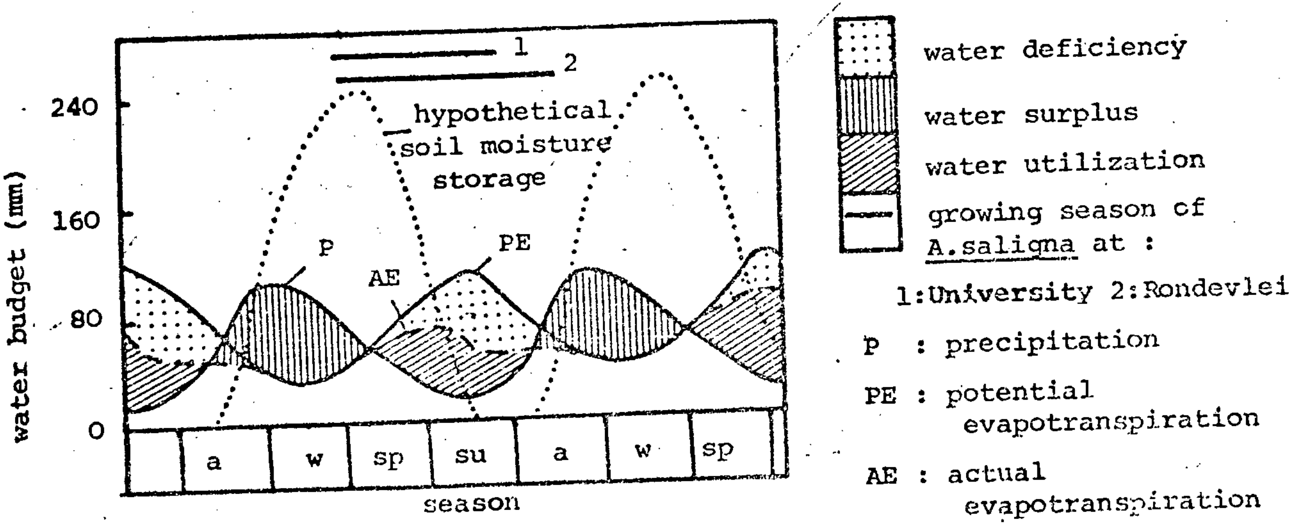


diagram (Figure 5).

Relative to the Thornthwaite diagram, A. saligna at both sites starts growing when the soil moisture store is at its maximum. At the University site, growth ceases when the hypothetical soil moisture store is depleted, but at the Rondevlei site, continues throughout the 'dry' season, stopping only when potential evapotranspiration (equated with temperature) falls in the autumn.

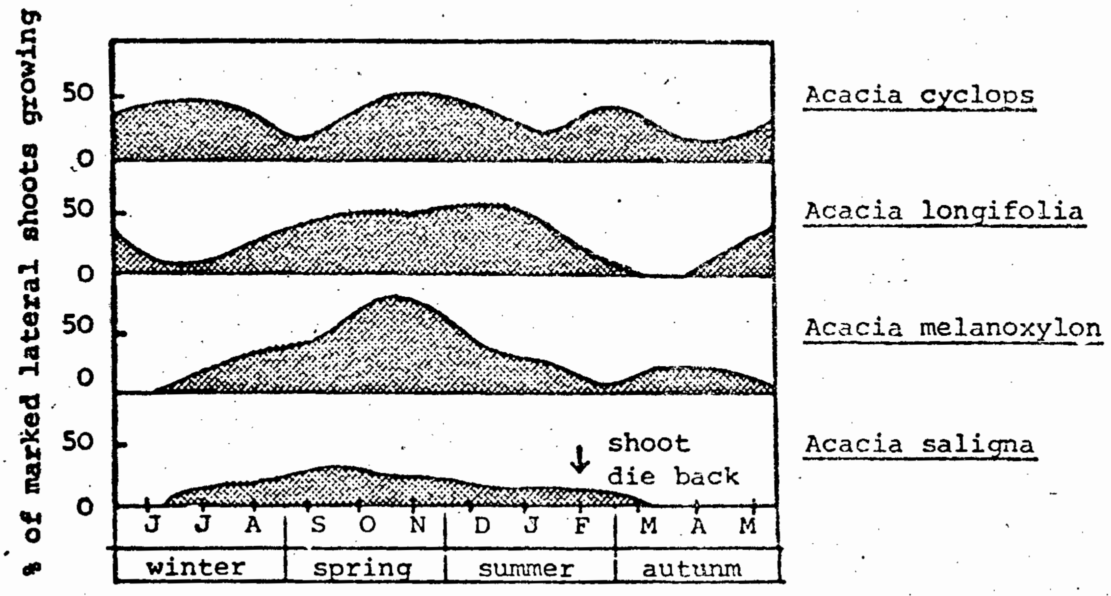
These results indicate that when Acacia growth is not limited by water availability, it is linearly correlated with mean monthly temperature, over the range 12°C to 22°C.

The fact that different growth patterns were obtained for different species at the same site suggests that Acacia species vary in their response to given conditions. This is illustrated by comparison of the flushing behaviour of A. melanoxylon (Figure 3B) with the more gradual increase and decrease in the growth rate of A. longifolia (Figure 3A).

Regardless of the differences in the responses of individual species, it is postualated that in run-off situations, such as the University site, growth is limited alternately by soil moisture and temperature (sunlight). In run-on sites such as Rondevlei, growth is limited by temperature (sunlight) alone. Acacias growing along river courses, around lakes and dams and on the coast may be expected to have longer growing seasons and to grow more rapidly than those on well drained slopes. The implication of this is that, in a summer drought climate, run-on situations may be most susceptible to infestation by woody weeds such as Acacias which grow best when temperatures exceed 15°C.

B

Figure 6. Lateral shoot growth : approximate curves (fitted by eye) showing the percentage of marked shoots growing each month.



Australian Acacias

The length extension of lateral shoots was very slow. The following trends were observed (Figure 6): A. cyclops grew throughout the year, with minima in August, January and April. There appears to be little apical dominance in this species. A. longifolia grew rapidly in spring, but produced a secondary growth flush in the autumn, (April - June). A. melanoxylon grew rapidly in the spring (September - December) only. A. saligna lateral shoot growth could not be charted for an entire year because the shoots died at the end of the summer fruiting season. For all species, lateral shoot growth showed the same general trends as leader shoot growth.

Acacia growth phenology compared with that of Australia and the Pacific

Acacias growing under a wide variety of climatic regimes have been found to grow in seasonal flushes rather than at a steady rate. The spring and summer growing season identified in this study, has been recorded in arid South and central Australia (Maconochie & Lange 1970; Maconochie, 1973), in the sclerophyll forest of South Australia (Maconochie, 1975), in the wetter winter rainfall climate of Victoria (Ashton, 1975a) and S.W. Australia (Majer, 1979), in the warm temperate rainfall transition zone of Queensland (Wetherall, 1966; Tunstal, in Specht & Brower, 1975), and even in the non-seasonal climate of Hawaii (Lanner, 1965).

The ability of some Acacia species to extend their growing seasons well into summer where water is available, or to produce a second growth flush in response to rain, has been noted in the present study for A. saligna and A. longifolia. Elsewhere it has been found that in warm temperate climates Acacias can maintain some growth throughout the year (Lanner, 1965; Winkworth, 1973; Maconochie, 1973). This enables them to respond to unseasonal increases in rainfall or temperature (Maconochie, 1973; Wetherall, 1966; Connor et al, 1971). Acacias cease to grow when temperatures fall to zero (Connor et al, 1971; Ashton, 1975a). The resemblance of the bimodal growth of A. harpophylla to the net photosynthetic index, is indicative of its ability to respond to favorable temperature and moisture conditions (Connor et al, 1971).

Physiologically Acacia is well adapted to hot dry climates. When late summer drought causes negative turgor pressures in the phyllodes (Hellmuth, 1971) water-use efficiency is improved, and the rate of photosynthesis does not decrease. Photosynthesis is, however, reduced to less than 50% of the maximum when temperatures fall outside the range 16°C to 35°C (Van den Driessche et al, 1971).

The present study has confirmed that Acacia growth is limited by temperatures below 15°C or less than 7.5 hours of sunshine per day. In addition to their response to environmental conditions, the various species appear to have innate characteristic growth rhythms.

Acacia growth phenology compared with that of plant communities in mediterranean-type climatic regions

Kruger (in press) found that the growing seasons of the various components of the Fynbos were staggered, a feature possibly facilitating resource partitioning on nutrient poor soils. However, most of the growth activity of Fynbos and of Australian Heath occurs during the dry summer (Sommerville, unpubl.; Specht, 1975; Levyns, 1964). In other Mediterranean vegetation types in Chile, California, Europe as well as in the coastal shrublands of the South West Cape, growth activity reaches a peak in spring and declines in summer (Mooney & Parsons, 1973; Specht, 1973; Rundel, 1977;

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Montenegro et al, 1979; Sommerville, unpubl.).

If as suggested by Specht (1975) spring growing shrubs have an advantage over summer growing shrubs in competition for limited water and nutrients, then the exotic Acacias would have an advantage over Fynbos, but not over coastal shrubland. On the other hand, the flexibility of species such as *A. cyclops* and *A. saligna* may enable them to continue growing after the indigenous spring-growing shrubs have slowed down.

Litterfall phenology

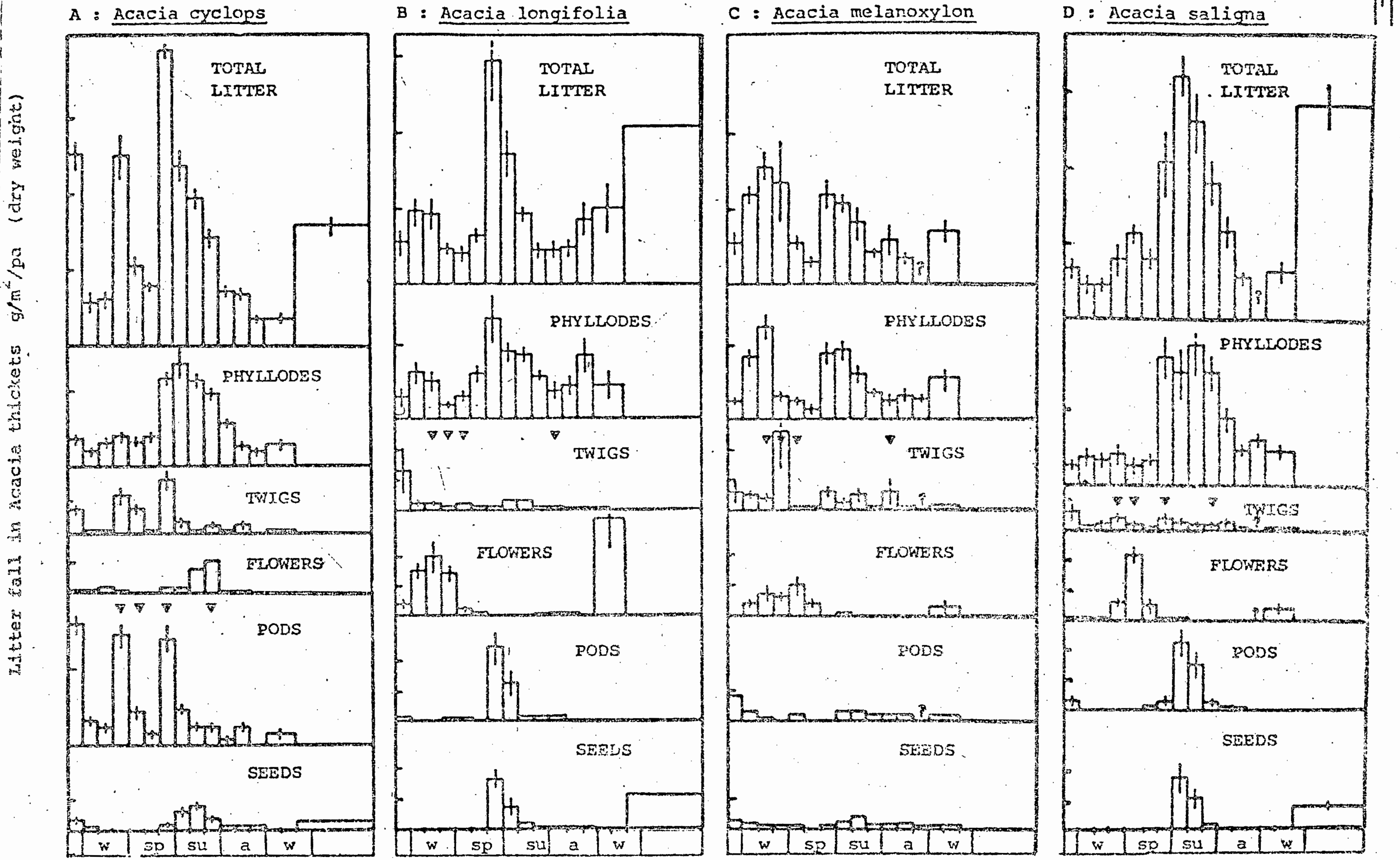
The litterfalls of *A. longifolia* and *A. melanoxylon* were studied at the University site, *A. cyclops* at Rondevlei and *A. saligna* at both Rondevlei and Hout Bay sites. The total monthly litterfall, and that of the various components is presented in the form of histograms (Figure 7).

Litter fell throught the year but showed distinct seasonal trends in all the study species. These trends reflect the seasonal fall of phyllodes which formed the major single litter component for all species (Table 1).

Table 1. Components of falling Acacia litter (Period May 1977 - April 1978)

Species	Total Litter kg/ha/pa Dry mass	Phyllodes %	Wood %	Flowers %	Pods %	Seed %
A. cyclops	9687	39.0	11.3	1.4	35.5	5.3
A. longifolia	5426	61.7	2.6	10.6	16.0	8.3
A. melanoxylon	5030	63.3	26.5	6.7	0.5	0.3
A. saligna	8042	60.8	10.0	8.7	12.1	8.0

Figure 7. Litter-fall phenology based on analysis of monthly collections of falling litter. Standard error of mean



B

Australian Acacias

Phyllode fall

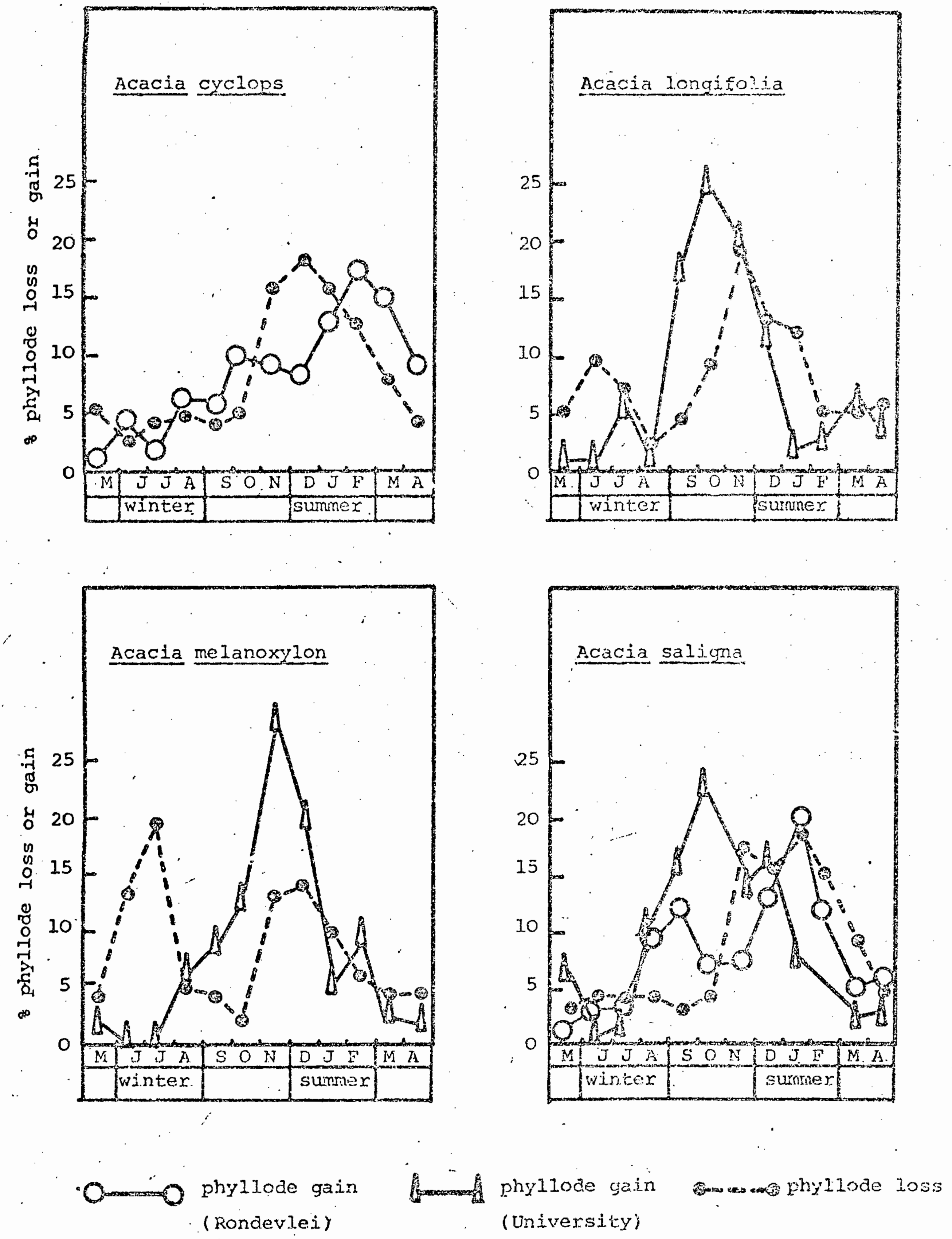
Phyllode fall is clearly not a random event in the evergreen Acacias. For A. cyclops and A. saligna, phyllode fall peaked in the summer (November to March see Figure 7A - 7D). Bimodal peaks in the rate of foliage fall were recorded for A. longifolia and A. melanoxylon: a summer peak (November to January) and a winter peak (June and July) as shown in Figurer 7B and 7C.

The annual march of phyllode gain and loss is illustrated in Figure 8. Loss and gain peaks tend to co-incide in the early summer. Simultaneous growth (or production) and foliage fall peaks have been recorded for Acacias in Australia. Tunstal (in Specht & Brower, 1975) found that growth and leaf-fall of A. harpophylla both peaked in summer (November to January). In A. pycnantha and two other South Australian Acacias, peak rates of phyllode production (Maconochie & Lange, 1970; Maconochie, 1975), a pattern also observed for A. dealbata in Victoria (Ashton, 1975 a & c). In central Australia, peak foliage losses occurred during periods of maximum growth as well as during drought stress (Maconochie, 1973).

Corresponding spring and summer growth and foliage fall peaks have been recorded in other Australian sclerophyll genera (Specht & Brower, 1975; Hannon 1958; Attiwill et al, 1978; Rogers & Westman, 1977; Ashton, 1975 a & c) and plant communities (Specht & Rayson, 1957; Specht, 1975; Jones, 1968; Groves, 1965). In mixed coastal scrub near Sydney, N.S.W., and in Eucalypt forest near Brisbane, Queensland, leaf-fall occurred throughout the year with an early summer maximum (Maggs & Pearson, 1977; Birk, 1979). Spring growth and litterfall peaks have also been recorded in the Californian Chapparral (Mooney, 1977) and in the Quercus ilex forests of mediterranean France (Lossaint, 1973).

B

Figure 8. Monthly phyllode loss and gain as a percentage of yearly totals in phyllode number increment (terminal shoot growth data) and mass falling phyllodes (litterfall data).



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In the Fynbos, growth and leaf-fall peaks appear to co-incide later in the summer (November to February), (Kruger, in press). Indigenous species growing in association with the Acacias in the study sites (Rhus, Solanum, Euclea, Asparagus) dropped their leaves mainly between January and April. In two S.W. Cape shrubland communities, Renosterveld and Strandveld (Acocks Veld Types 46 and 34) leaf-fall peaks in late summer, and does not appear to co-incide with the growth peak which occurs in moist weather (Sommerville unpubl.).

Bimodal peaks in leaf-fall are considered to be less common than single peaks, but have been recorded for a Eucalypt, a fern and an understory Acacia species in the coastal forests of Queensland (Rogers & Westman, 1977; Birk, 1979).

Continual foliage loss throughout the year with maxima during periods of water stress and growth, as observed in the exotic Acacias, appears to be the pattern typical of leaf-fall phenology in evergreen sclerophyll vegetation in mediterranean type climates. Foliage loss during drought stress may be interpreted as a means of reducing the transpiration rate (Jones, 1968; Kozlowski, 1973; Hanes, 1965). Losses during or immediately following periods of active growth may be the consequence of internal nutrient cycling, a strategy advantageous on oligotrophic soils such as those in parts of Australia and the S.W. Cape. There is apparently no literature dealing with internal nutrient cycling in the Fynbos, but there is Australian evidence for significant withdrawal of phosphorous, nitrogen and potassium from Eucalyptus and Acacia leaves before abscission (Specht & Groves, 1966).

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Wood fall

Wood, a category including twigs and bark, is generally a minor and extremely variable component of the monthly and yearly litterfall. In May, August and November 1977, wood fall of *A. cyclops*, *A. saligna* and *A. melanoxylon* exceeded that of any other months (Figure 7A, C, D). Comparison of wood fall with rainfall and wind velocity data recorded close to the study sites, suggests that major losses of woody material occurred in response to the first heavy winter rain, and to wind gusts exceeding 15 m sec^{-1}. This apparent correlation is most clearly seen in an old *A. cyclops* thicket growing at the windy Rondevlei site.

The results of the present study are similar to those of Ashton (1975c), who found that twig and branch fall in a Eucalypt forest in Australia, was highly variable and related to the incidence of storms.

Flower fall

Flowering is strictly seasonal in all species studied, however, in those species in which inflorescence buds develop four to five months before the flowering season, there is a continual rain of aborted buds increasing up to the time of the major fall of withered flowers. Flowerfall occurs in winter in *A. longifolia* followed in sequence by *A. saligna* and *A. melanoxylon* and finally *A. cyclops* in early summer. *A. cyclops* produces occasional out of season flowers, and a very minor flowering flush appears to have occurred in this species in July 1977 (Figure 7A).

No attempt was made in this study to separate the flowering stages represented in the litter samples, and the category "flowers" includes inflorescences at all stages of development. That quantified, detailed information on flowering stages can be extracted from litter samples has been demonstrated by Ashton (1975b) in a study of Eucalyptus phenology.

Pod fall

The pod fall of A. longifolia and A. saligna occurs over a six week period, three to four months after pollination (equated here with the fall of withered flowers). The seeds of these species have small, grey-white funicles unlikely to attract frugivorous dispersers. The seeds are never presented to potential dispersers while on the tree, since the pods are both deciduous and dehiscent.

The pods of A. cyclops are not deciduous: they disintegrate on the tree over a period of three to four years. Their fall pattern resembles that of the twigs, 65% of the total annual pod fall occurring during the three wet or windy months referred to before. A. melanoxylon set so little fruit at the study site that no clear pod fall pattern emerged. The fall of the pods throughout the year indicates that this species has non-deciduous pods. Both A. cyclops and A. melanoxylon have black seeds surrounded by coiled red arillate funicles. Pods which split open when ripe, but remain on the tree, allow year-round presentation of these attractive seeds to dispersers. Bird dispersal has in fact been recorded for both species in South Africa (Middlemiss, 1963; Glyphis, 1976; Phillips, 1928).

Seed fall

Seed fall co-incides with pod fall in the species with deciduous pods, but peaks in the dry summer for all Acacia species studied. Dry season seed fall appears to be a feature of the genus Acacia in Africa and Australia but this will be discussed below.

Reproductive phenology

The reproductive phenology of the exotic Acacias in the S.W. Cape was studied so that by comparison with the literature, it would be possible to determine whether the timing of reproductive events was fixed for a species, or whether it altered when a species was grown in another country under slightly different environmental conditions.

Five stages in the reproductive phenology of A. cyclops, A. longifolia, A. melanoxylon and A. saligna are illustrated in Figure 9. Analysis of litterfall data and monitoring of the lateral shoots gave similar estimates of the peak in flowering and seedfall. The former method provided a larger sample but the latter method had the advantage of dealing with living rather than aborted structures. The timing and duration of selected reproductive stages is presented in Table 2.

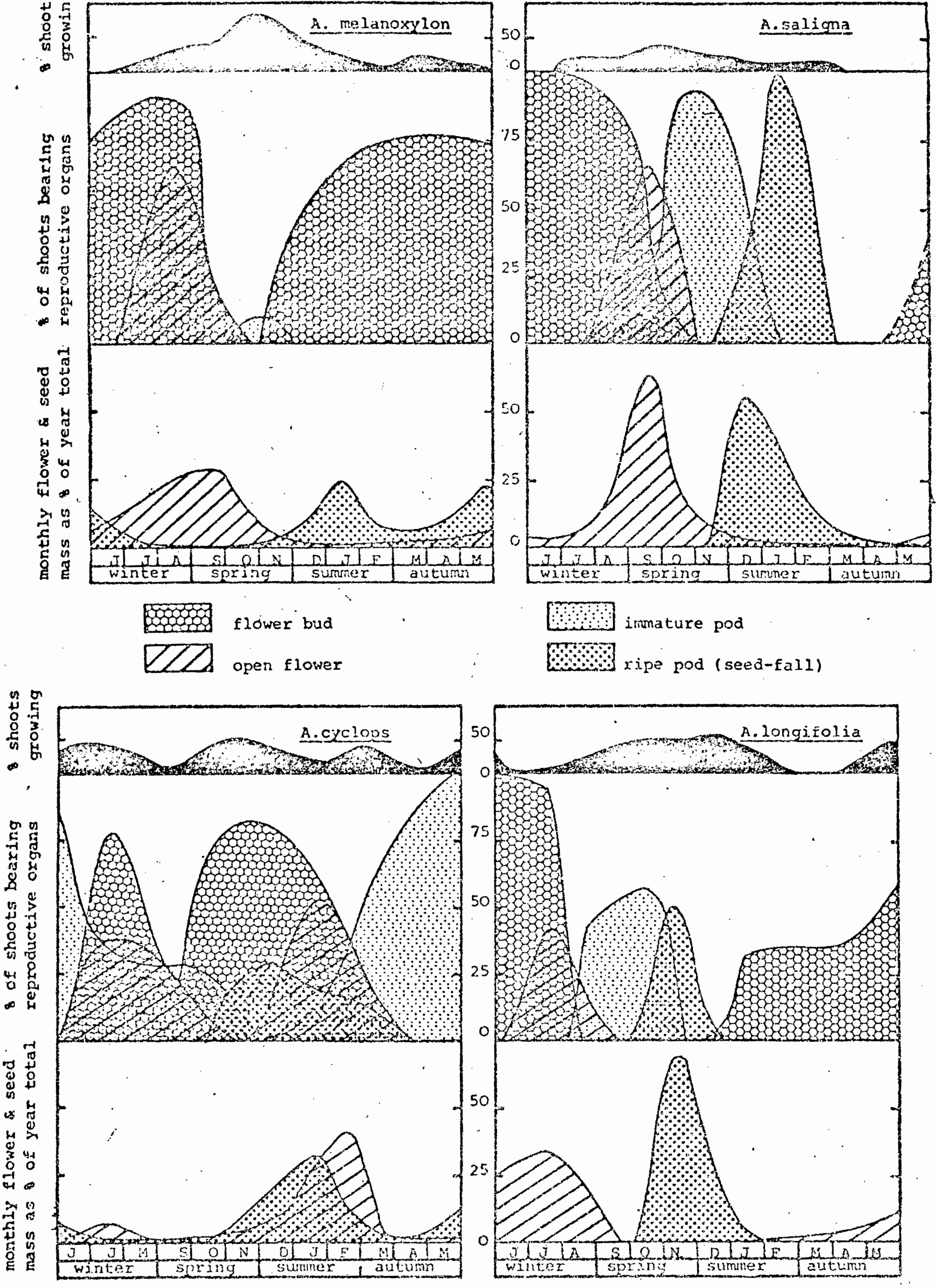
Table 2. Reproductive phenology of four exotic Acacia species

Species	time of flower bud formation	duration of flower bud growth	time of anthesis	duration of pod growth	time of seed-fall
A. melanoxylon	Nov.	9 mth	Aug.-Sept.	4 mth	Dec.-Apr.
A. longifolia	Feb.	5 mth	July	4 mth	Nov.
A. saligna	May	4 mth	Aug.-Sept.	4 mth	Dec.
A. cyclops	Oct.	3 mth	Dec.-Feb.	12 mth	Dec.-Feb.

The inflorescence buds of A. melanoxylon, A. longifolia and A. saligna are differentiated in the axils of phyllodes produced during the previous season's growth, and they gradually increase in size until shortly before the early

B

Figure 9. Approximate curves for the seasonal amounts of reproductive activity of four Acacia species in the S.W. Cape, based on field observation of lateral shoots and analysis of falling litter.



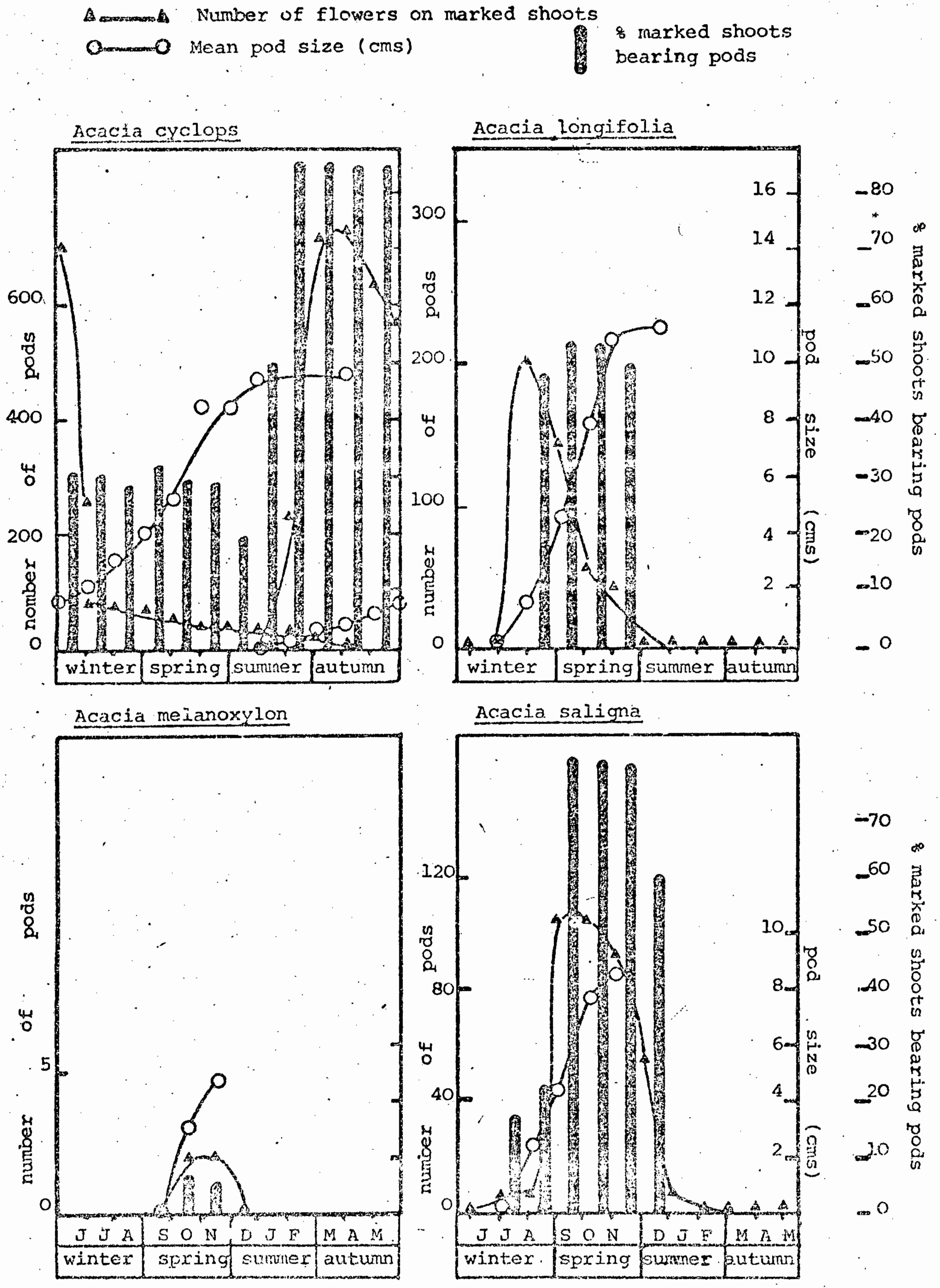
spring flowering season, when they swell rapidly. The inflorescences of A. longifolia are sessile. They are usually born in pairs in the phyllode axils, but on old trees up to six inflorescences have been observed, crowded into a single axil. The flower heads of A. melanoxylon and A. saligna are generally grouped in a racemose manner, but during the growing season A. saligna shoots may produce solitary flower heads in the axils of newly formed phyllodes. These have no dormancy, but grow fast, opening within a few weeks of their formation. Anthesis of the spring flowering Acacia species was clearly defined and brief. No open flowers were recorded out of season during field studies or seen on herbarium specimens (Figure 9 & 11).

The inflorescence buds of A. cyclops are differentiated singly or in pairs in phyllode axils near the tips of growing shoots, in spring. They develop rapidly to open in summer. Most buds are produced during the peak growing season (October to January), but a few buds or flowers may be found at any month of the year. Both litterfall and lateral shoot data suggest that A. cyclops had a second burst of flowering in the winter 1977. No second peak was recorded in 1978, however examination of herbarium material suggests that a brief winter flowering season is not an unusual occurrence in this species.

Few of the winter or out of season flowers of A. cyclops produce fruit. Pods formed during the summer grow slowly to mature in the following summer (Figure 10). The pods of the spring - flowering species all grow rapidly, increasing in length by more than two centimetres per month. By mid-summer of the same year, they are mature, and dehisce. The pods of A. longifolia and A. saligna are then shed, while those of A. melanoxylon remain on the tree. Figure 10, which shows the number of pods on marked shoots, together with their size, indicates that pods are continually being aborted,

B

Figure 10. Monthly pod development of four exotic Acacia species, based on monthly measurements of lateral shoots.



and only a few, (estimated to be between 6 and 58%) reach maturity. Pod bearing was well synchronised among marked shoots of each species. The reason for the very high abortion rate of A. melanoxylon flowers is not known, since anthesis occurred, and pollinators were seen on the flowers. Most of the tagged A. melanoxylon trees were fairly young (less than 10 yr).

Reproductive phenology of thirteen exotic Acacias in the S.W. Cape

The reproductive phenologies of thirteen exotic Acacia species are summarised in the form of a chart (Figure 11). The chart is designed to serve as a rapid reference to the expected reproductive state of the various species at any time of the year, but not to the degree of activity. Five easily recognisable stages are charted, and the species have been arranged according to the date of appearance of the first open flowers.

The species represented on the chart can be grouped according to their reproductive phenology as follows:

a) Winter to spring flowering species with slow inflorescence development and rapid pod maturation (nos. 1 - 9)

b) Late spring to summer flowering species with slow pod maturation but rapid inflorescence development (nos. 10 - 13)

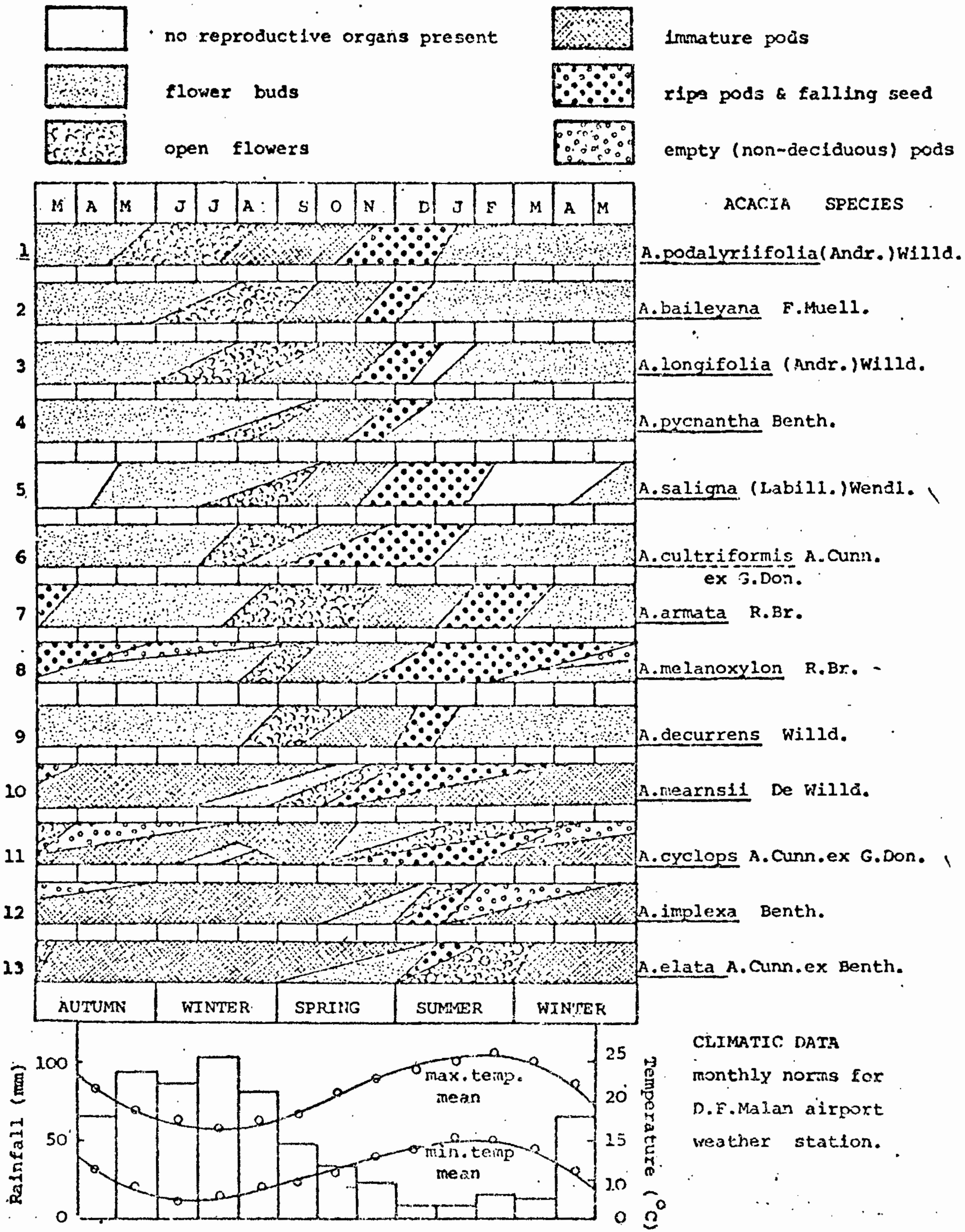
c) Species which flower intermittently throughout the year or have more than one flowering season (no. 11)

d) Species with persistent pods (nos. 8, 11, 12)

e) Species with deciduous pods (nos. 1 - 7, 9, 10, 13)

All species shed their seed during the summer.

Figure 11. Summary chart of the reproductive phenology of thirteen species of Australian Acacias in the S.W. Cape, with the chief seasonal climate features.



CLIMATIC DATA
monthly norms for
D.F.Malan airport
weather station.

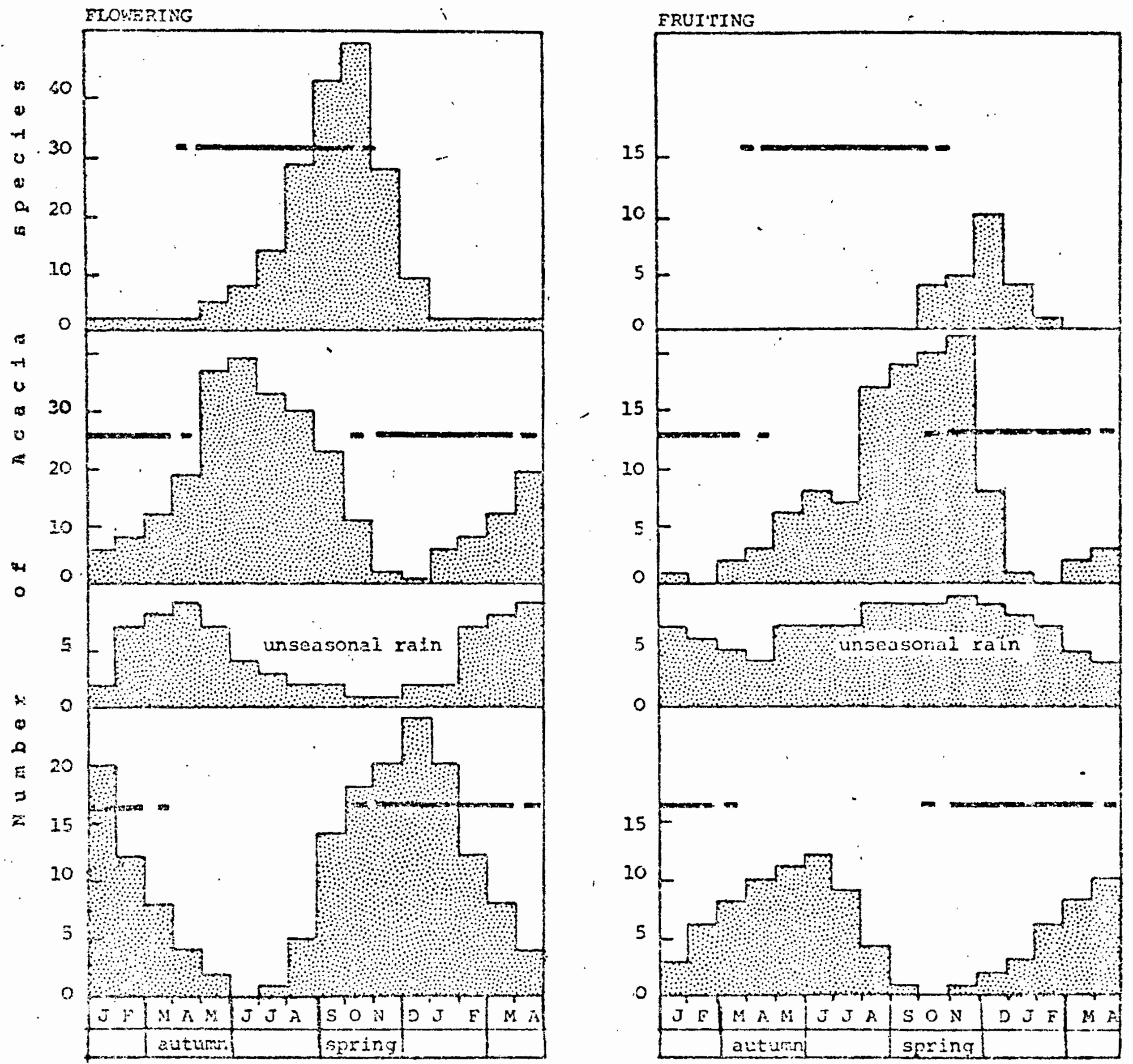
Australian Acacias

Comparison of reproductive phenology with other members of the genus Acacia

The trends noted in the Australian Acacias in the S.W. Cape have been recorded in the literature for other members of the same genus. Inflorescence differentiation occurs six months before anthesis in the spring-flowering African Acacias, but the buds remain small until the warmer weather when they expand rapidly (Robbertse & Vorster, 1974). The buds of A. albida and A. karoo, which open in late summer, are formed in spring, and have no dormant period (Robbertse & Vorster, 1974; Story, 1952). These two types of inflorescence growth are represented in the S.W. Cape by A. longifolia and A. cyclops respectively.

The timing of the flowering season has been shown to be a species characteristic (Figure 11), but may sometimes be altered slightly by climatic factors. Anthesis tends to occur later in cool regions than in warm ones, so that in Australia a wave of Acacia flowering appears to sweep from north to south. The autumn and winter flowering of Acacias in Queensland and the Northern Territory (Pedley, 1978; Davies, 1976; Tindale, 1970, 1972; Preece, 1971) is followed by winter and spring flowering in N.S.W. and S.W. Australia (Forestry Comm. N.S.W., 1975; Maslin, 1974, 1977) and spring flowering in Victoria (Ewart, 1930; Coleman, 1935; Derrick, 1966). This shift can also be recognised in the performance of a single species under different conditions. Acacia leiocalyx and A. melanoxylon flower earlier in Queensland than they do in N.S.W. and Victoria (Pedley, 1978; Ewart, 1930), and the flowering of A. koa is delayed at high altitudes (Lanner, 1965). The ability of A. baileyana to flower and set seed is apparently a function of temperature. This species flowers earlier and sets fewer seeds on the coastal plain near Sydney than it does on the plateau at an altitude of 600 m (Newman, 1934). In South Africa A. baileyana aborts its buds near Cape Town (100 m) but flowers and

Figure 12A. **Flowering and fruiting times of members of the genus *Acacia* in their natural habitats.**



DISTRICTS & REFERENCES

S.E. & S.W. Australia
Maslin, 1974 - 1977
Tindale, 1970; 1975
Ewart, 1930

N.E. & Central Australia
Maslin, 1974
Tindale, 1970; 1972; 1975
Pedley, 1978

Mid W. & E. Australia
Tindale, 1970; 1975
Davies, 1976

Africa
Carr, 1976
Von Breitenbach, 1965
Van Wyk, 1972

▬ ▬▬▬▬ ▬ RAIN

B

fruits prolifically near Pretoria (1 370 m) in the Transvaal.

Most African Acacias are spring and summer flowering, the start of the flowering season apparently co-inciding with that of the rainy season (Figure 12A). Some Acacia species have been found to flower intermittently, or to have secondary bursts of flowering, in response to unseasonal rainfall or temperature increases (Pedley, 1978). These opportunistic flowerers are particularly common in arid regions including the Namibia and northern Cape area (Carr, 1976) and West Australia (Davies, 1976). Opportunistic flowering is also a feature of Acacia species with very wide distribution ranges, such as A. aneura in Australia (Preece, 1971) and A. karoo in Southern Africa (Story, 1952). Among the exotic Acacias in the S.W. Cape, only A. cyclops seems to have a flexible flowering phenology, but as is the case with A. aneura, the minor flowering peak produces little if any fruit (Preece, 1971).

Records of fruiting seasons for the summer rainfall regions of Africa and for various parts of Australia are presented in Figure 12A. An outstanding feature of the fruiting phenology of Acacia is that, regardless of whether flowering occurs in a wet, intermediate or dry season, the pods of the majority of species ripen during a dry season. Fruit ripening shows no marked peak where rainfall is unseasonal.

The rate of fruit maturation appears to be timed to the production of ripe fruit in the dry season. Among the exotic taxa, it has been noted that the summer (dry season) flowering species have slow-growing pods which take about a year to mature. In Zimbabwe-Rhodesia the pods of early (spring) flowering species (anthesis preceeding the summer rain), may take up to a year to mature, whereas those of the late flowering species ripen within four to six months (Müller, pers comm). The net result is that most

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Acacias shed seed in the dry season ie. summer in Mediterranean climates and winter in summer rainfall regions.

Dry-season ripening of fruit may facilitate the drying and hardening of the seed testa. Mature but soft Acacia seed will absorb water and germinate (Story, 1952; Milton, unpubl. data), but hardened seed is water-impermeable and remains dormant until the seed coat is damaged. Hard seed thus has a longer shelf-life than fresh seed (Nixon, pers comm) and in its natural habitat, dormancy is essential for success in the fire-pioneer niche many Acacia species occupy, in both Africa and Australia.

Pod persistence has been noted in three of the exotic Acacias (A. cyclops, A. implexa, A. melanoxylon) all of which have red or orange arillate funicles, suggesting that the seeds are dispersed by fructivores. Another Australian Acacia which bears its seed on fleshy orange funicles (A. oswaldii) also has persistent pods (Pedley, 1978). (See figure 15).

A. victorae and A. aneura in arid West Australia bear persistent pods, but their seed funicles are inconspicuous. The year-round rain of seed is nevertheless attractive to emus and other large ground-feeding herbivores (Davies, 1976). Davies (1976) speculates that, were all the seed to be shed at one time, it would rapidly be removed by invertebrates. On the basis of funicle morphology, Berg (1975) postulated that about 300 of the 500 species of Australian Acacia considered, are dispersed by ants. Persistent pods, by providing a predictable food source for vertebrates, may ensure long distance dispersal by vertebrates rather than short distance dispersal by ants. Asynchronous ripening of seeds within pods of A. karoo (Story, 1952) may be a means by which this and other African Acacia species achieve dispersal by mammals. (Some seeds are hard and indigestible while the remainder and the pod itself are still succulent enough to be attractive to a browsing or foraging mammal).

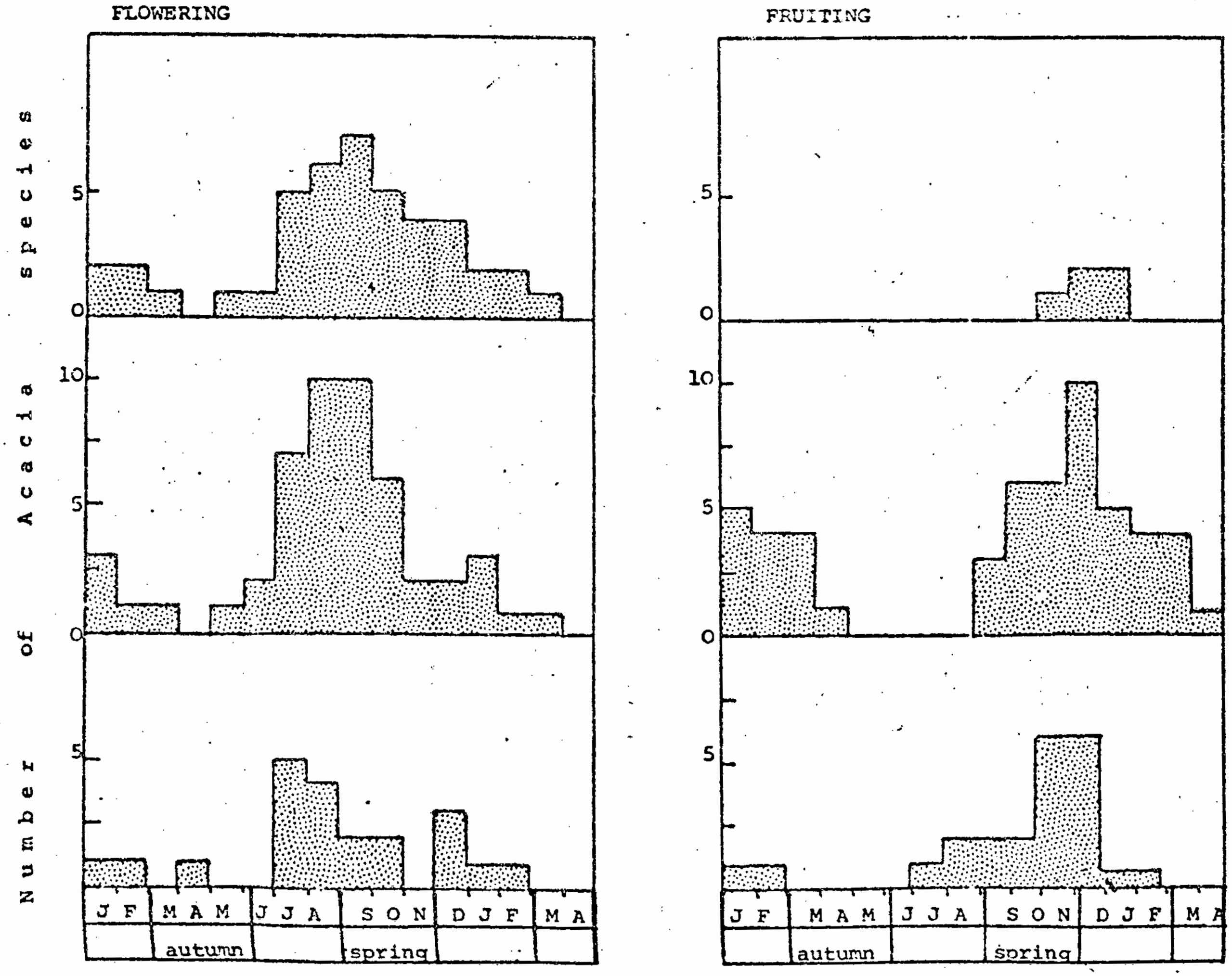
Stability of reproductive phenology

If the results of the present study are to be applied to management and biological control problems in the Cape and in other parts of Southern Africa in the future, it is necessary to know how much the phenology of a particular species could shift in response to environmental factors. Information derived from herbarium specimens and graphed in Figure 12B indicates that the phenology of the exotic Acacias does not vary much between the summer and the winter rainfall regions in South Africa. Field observations suggest that some species, including A. longifolia and A. podalyriifolia, may flower a few weeks later on the Transvaal highveld than they do in the Cape and in Natal.

That reproductive phenology is not a direct response to environmental conditions is indicated by the fact that certain individual A. mearnsii trees are always late flowering and others always early: this difference is so ridgedly fixed that it is impossible to cross-pollinate such trees (K. Nixon, pers. comm.).

Available information (Fig 12B; Appendix Table) gives no reason for concluding that the exotic Australian Acacias in South Africa have altered their phenology since introduction. Some species appear to flower slightly earlier (in terms of calendar dates) in the S.W. Cape than they do in Australia: these are A. cyclops, A. decurrens, A. mearnsii, A. pycnantha and A. saligna. However available information is not accurate enough to state this with certainty.

Figure 12B. Flowering and fruiting times of exotic Acacias in the South African winter & summer rainfall regions and in their places of origin in Australia.



DISTRICTS & REFERENCES

In natural habitat in Australia

Seddon, 1972; Maslin, 1974
Ewart, 1930; Moss, 1965.
Anon, 1935; Pedley, 1978
Forde & Ford, 1978
(winter rain)

As exotics in the S.W.Cape

own data &
herbarium records

(winter rain)

As exotics in the S.Cape, Natal & Transvaal

own data &
herbarium records
(summer rain)

Australian Acacias

There is some evidence that anthesis of the Australian Acacias is triggered by temperature. This includes the north to south sequence of flowering of the majority of Australian Acacias, the delay in flowering with increasing altitude (Lanner, 1965) and the fact that the flowering time of A. melanoxylon in the S.W. Cape (34^oS) is more similar to that in Victoria (35^oS) than to that further north in Queensland (Appendix).

It is concluded that the reproductive phenology of the various Acacia species is fairly stable. Selection (natural or silvicultural) could shift the flowering time of a population to any point within the range for the species. Flowering or seed set may fail to occur when the species is planted in a climatic regime for which its phenology is not adapted. Under such circumstances, the species is unlikely to become naturalised. Climatic conditions may be one of a number of factors limiting the success of A. podalyriifolia and A. baileyana in the S.W. Cape.

Acacia reproductive phenology compared with that of Mediterranean type vegetation

Table 3 indicates that spring is the peak flowering time for plant communities in mediterranean type climates, however there is no season when all species are in the non-flowering stage, in such a community. Flowering activity at all seasons is a feature of the Cape Fynbos (Cody & Mooney, 1978; Kruger, in press). The tall woody species of the Fynbos and Chapparal flower in winter or early spring, as opposed to the hemicryptophytes and herbs which flower at the beginning of summer (Rycroft, 1950; Kruger, in press; Mooney & Parsons, 1973; Levyns, 1929). That temperature triggers the flowering of Fynbos species is suggested by the difference in the timing of flowering in similar communities on north and south facing slopes of the Jonkershoek valley (Rycroft, 1950; Van der Merwe, 1966), and variation in the flowering time of Protea cynaroides L. over its geographical range (Vogts, 1972).

The June to September flowering time of the majority of the exotic Acacias precedes the main burst of flowering in the Fynbos, but co-incides with the flowering of many of the larger proteoid shrubs. Acacia flowers attract large numbers of bees, flies and wasps, but it is not known whether this could affect the numbers of pollinators visiting indigenous species.

The little information available on the fruiting phenology of mediterranean type vegetation indicates that in California, Chile, S.W. Australia and in the S.W. Cape the majority of species produces ripe fruit in summer (Mooney et al, 1974; Milewski & Davidge, in press; Sommerville, unpublished; Van der Merwe, 1966). Few species bear fleshy fruit in the Fynbos, but fruiting species dominate forest and coastal scrub. Those which bear ripe fruit in autumn and winter may provide birds with an alternative food source when insects are in short supply. The replacement of large stretches of coastal scrub with exotic Acacias appears to have reduced the bird diversity in these areas (H. Langley, pers. comm.). Acacia cyclops, with its red funicles and persistent pods, attracts large flocks of starlings and doves. These birds later perch on tall indigenous shrubs as far as 500 m from the seed source, and deposit the Acacia seed in their droppings. (Glyphis & Milton, unpublished)

The reproductive phenology of a Fynbos community seems to be determined by its age, floristic composition (Sommerville, unpubl.), so that the comparison of a few exotic species with entire communities is of limitied value. The reproductive phenology of the exotic Acacias is similar to that of the woody elements of the Fynbos. It is not known whether the Acacias compete with indigenous plant communities for pollinators and dispersers.

Table 3. Flowering seasons of mediterranean-type vegetation

Reference	Community	No. of species	% of total species in flower			
			WINTER	SPRING	SUMMER	AUTUMN
Groves, 1965	Heath, Victoria	122	24	56	34	21
Specht & Rayson, 1957	Heath, S. Austr.	102	7	34	10	9
Milewski & Davidge	Heath, Perth, W.A.	60	27	75	5	12
Mooney et al,[1] 1974	Chapparal, California		6	55	45	16
"	Israel		12	63	26	10
"	Mattoral, Chile		3	46	40	5
" ex Adamson & Salter, 1952	Fynbos, Cape Penin.		16	46	30	22
Milton ex[2] Adamson & Salter, 1952	Strandveld False Bay	92	24	53	26	13
Rycroft, 1950	Fynbos (N)* Jonkershoek	298	22	36	16	10
v.d. Merwe, 1966	Fynbos (S)* Jonkershoek	448	28	30	18	13
Sommerville, unpublished	21 yr montane Fynbos	50	26	37	22	29
"	5 yr montane Fynbos	61	21	27	21	28
"	Coastal Fynbos	17	35	39	14	14
"	Mature Strandveld	44	29	40	19	9
"	Immature Strandveld	52	28	33	11	12
"	Coastal Renosterveld	32	5	21	10	8
Olivier, 1979	Karoo, Worcester	273	25	30	5	7

* (N) = north and (S) = south facing slope

Data extracted from Adamson & Salter (1952) by [1]Mooney et al and [2]Author

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Nectar secretion phenology

All the exotic Acacias examined bore glands either on the rachis, in the case of the pinnate-leaved species, or on the phyllode base or margin. The position of the glands in the Acacia species discussed is illuatrated in Figure 13.

The presence of a drop of secretion at the gland mouth, taken as indicating gland activity, was recorded during growth studies on lateral and terminal shoots to establish whether nectar secretion coincided with flowering or growth. Results are presented graphically in Figure 14. The glands of A. cyclops, while obvious on very young phyllodes, are minute and possibly vestigal on fully expanded phyllodes. No gland activity was recorded on the tagged A. cyclops shoots studied, but an active gland was seen in the field on one occasion. Additional observations were carried out on A. longifolia to determine whether nectar output was related to the developmental state of the flowers (see Table 4).

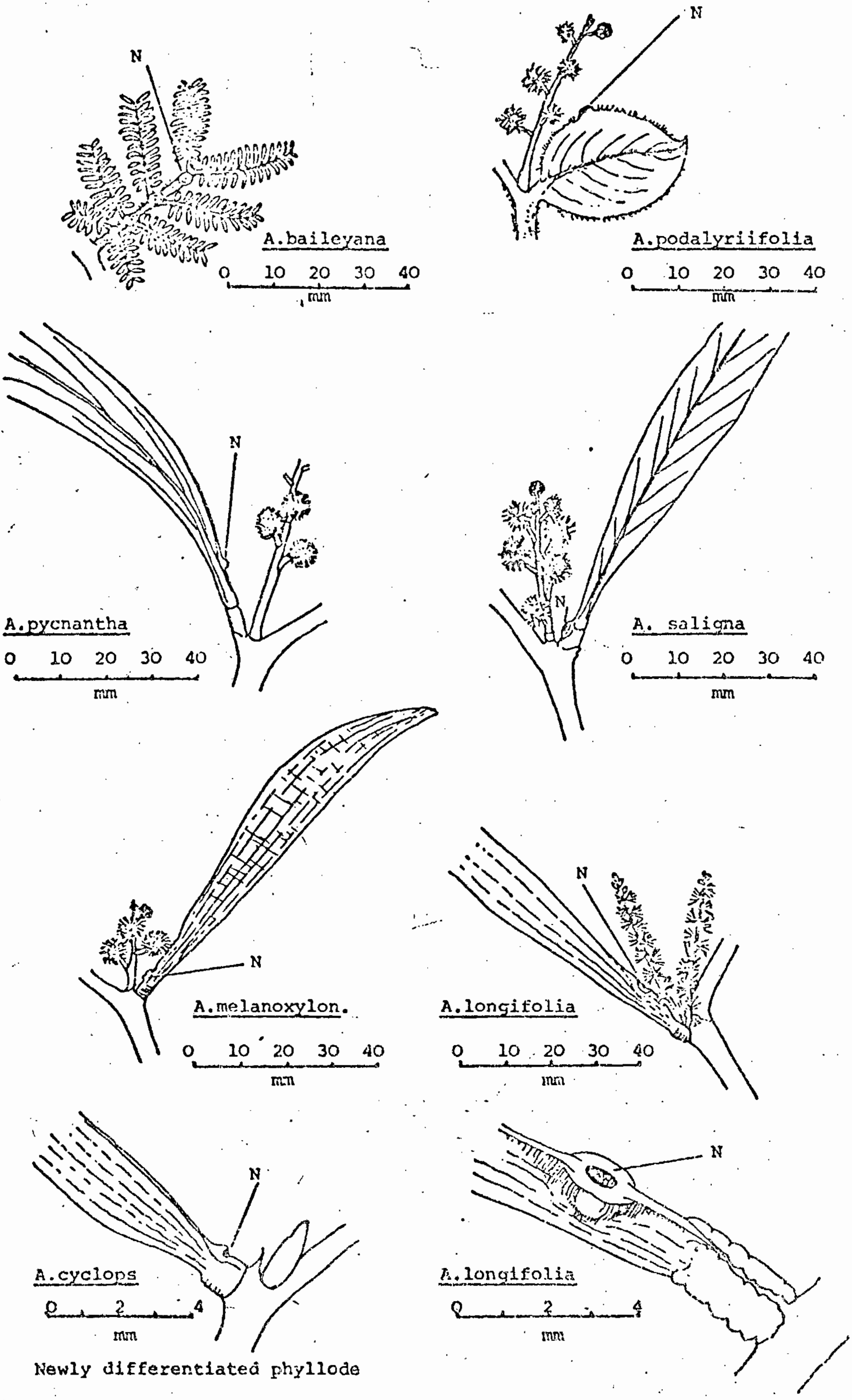
Nectar secretion and flowering

No nectar secretion was observed on the phyllode glands of lateral shoots of A. saligna. Figure 14 shows that the phyllode glands of A. melanoxylon only secreted nectar during the months when lateral shoots bore open flowers. A. longifolia secreted nectar intermittently at a low rate, but activity reached a clear peak during anthesis (July to September). Table 4 shows that the number of active glands and the volume of nectar secreted is greater on shoots bearing open flowers than on those bearing buds or withered flowers.

B

Figure 13. The position of extra-floral nectaries on some exotic Acacia species in the S.W. Cape.

N : extra-floral nectary



A.baileyana

A.podalyriifolia

A.pycnantha

A. saligna

A.melanoxylon.

A.longifolia

A.cyclops

A.longifolia

Newly differentiated phyllode

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Table 4. Nectar secretion on flowering shoots of *A. longifolia*

Date	Time bagged before assessed	Parameter	Developmental stage of the flowers		
		*	BUD	OPEN	WITHERED
22.7.1977	--	percent phyllodes with active glands	5.9 (4.4)	62.7 (20.9)	--
19.7.1978	1 hr		11.0 (6.3)	84.6 (3.7)	14.6 (10.7)
21.7.1977	5 hr	nectar volume per shoot ul	5.8 (1.7)	17.9 (4.7)	--
19.7.1978	1 hr		0.7 (0.5)	8.4 (1.7)	1.4 (1.1)

* means and standard errors for samples of 10 shoots with approximately 20 phyllodes each.

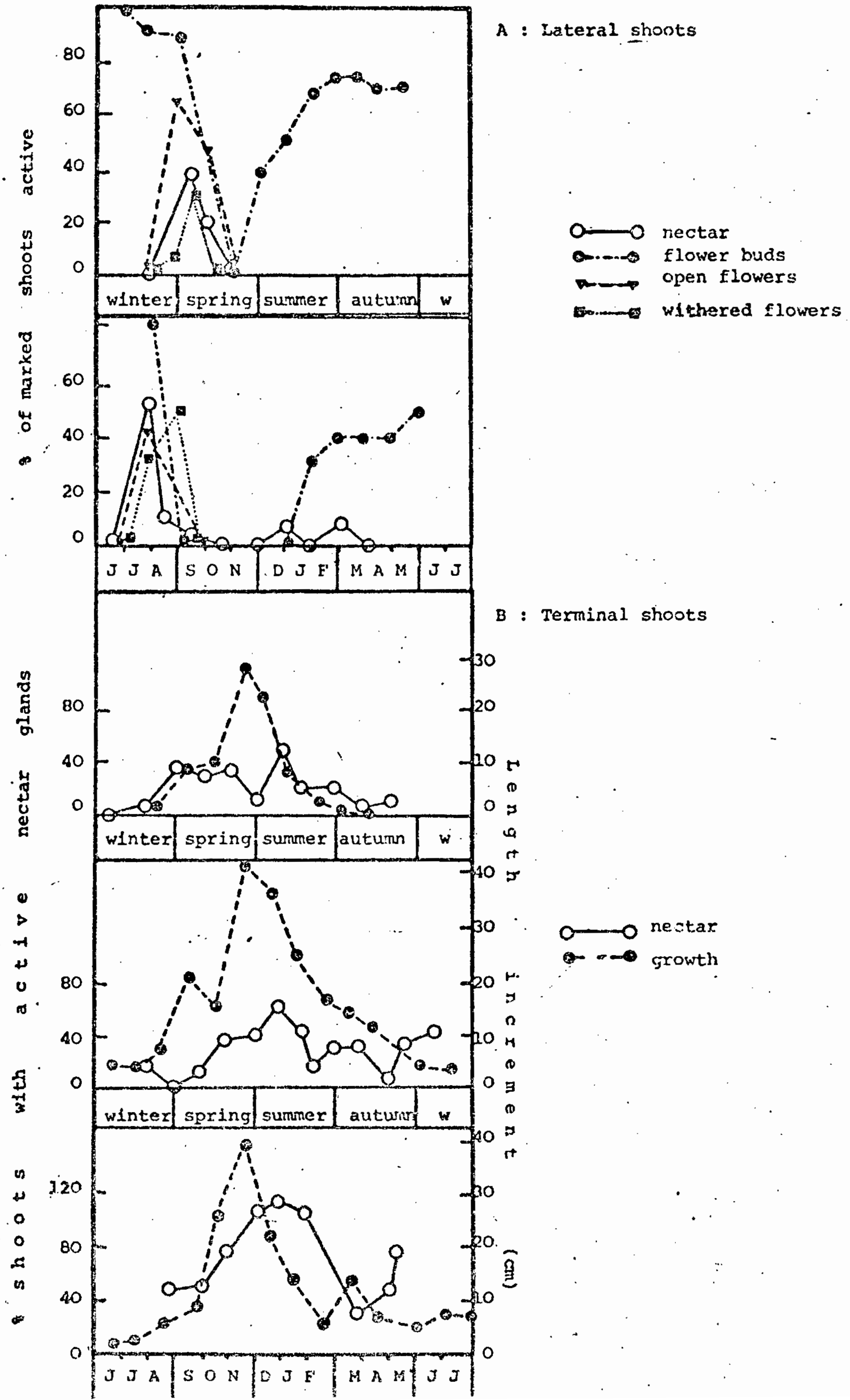
Figure 14A shows that nectar secretion is associated with anthesis in *A. longifolia* and *A. melanoxylon*. *A. podalyriifolia* phyllodes with open flowers in their axils also had actively secreting glands, but no quantitative data was collected for this species.

The flowers of Acacias, although bright yellow and often scented, are of the papaver type (Vogel, 1978), and bear no nectar. The secretion of nectar by nearby extra-floral nectaries, may act as an additional attractant to pollinators. Insects observed on flowering branches of Acacias may be grouped as follows:

(1)	eaters of pollen and nectar	(bees, beetles)
(2)	nectar feeders	(wasps, ants, flies, coccinellids)
(3)	predators	(spiders, mantids, assassin flies)

B

Figure 14. Activity of extra-floral nectaries relative to A: flowering and B: growth. The percentage of lateral and terminal shoots with active phyllode nectaries was recorded monthly.



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Birds including White-eyes (Zosterops pallidus Swainson) and Cisticola species have been observed, possibly preying on these insects.

That Acacias are not wind pollinated has been inferred from the structure of the pollen grain (Coetzee, 1955), from the fact that little of the pollen becomes airborne (Moss, 1965; Vogel, 1978), from the high degree of outcrossing in isolated trees (Li, 1978), and from the attraction most Acacia species have for bees (Phillips, 1928,; Anon, 1935). Pollinators may be essential for the survival of the Acacia species since selfed flowers of A. mearnsii, A. decurrens and A. koa produce very few pods or fertile seeds (Moffet, 1956; Lanner, 1965) and the majority of about 50 species recently investigated in Australia are obligate outbreeders (Hopper & Maslin, 1978).

Although bees would probably be attracted to Acacias for their abundant nutritious pollen alone, they also sip nectar. The nectar comprises 50% glucose, 37% fructose and 12% sucrose, by volume (gas-liquid chromatographic analysis). The concentration of freshly secreted nectar is between 50% and 60% sucrose equivalents. The secretion of a low volume of highly concentrated nectar is typical of an insect pollinated plant (S. Frost, pers. comm.). Due to evaporation the glands are sometimes blocked by crystalised sugar towards the end of summer. Insects which might otherwise have been unlikely to visit flowering Acacias (ants, flies, wasps, coccinellids) are attracted to this sugar-rich nectar. These insects, most of which are large enough to act as pollen vectors, brush against the flowers in their attempts to reach the nectar at the phyllode base, or to evade voracious crab-spiders.

Although Bentley (1977a) found that, in the case of Bixa orellana L., nectar secretion by extra-floral nectaries during the flowering season attracted ants which protected the flower buds from predation, its function in

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flowering Acacias appears to be the attraction of pollinators. This has been suggested by Ford & Forde (1976), who noted that A. pycnantha was probably pollinated by birds attracted either to the nectar secreted during the flowering season, or to the insects feeding on it. Finding that nectar exudation was at its greatest during anthesis, in two Acacia species in S.W. Australia, but greater during vegetative or seedling growth of other species, Lamont (1978; 1979) concluded that extra floral nectaries were a vestige of the tropical ancestors of Acacias. The nectaries of modern Australian Acacias may have lost their ancestral function, but there appears to be a web of interactions between nectaries, Acacias, insects and birds, varying with species and season (Lamont, 1978; 1979).

Nectar secretion and growth

Nectar secretion by phyllode glands on the leader shoots is greater during spring and summer than during autumn and winter (Figure 14B) and appears to co-incide with the period of rapid growth. The apparent correllation between nectar secretion and growth cannot be proven statistically, but are supported by casual field observations.

The nectar flands of A. longifolia, A. melanoxylon and A. saligna become functional soon after the phyllode is differentiated. The glands of fully expanded phyllodes further down the growing shoot, appear to be less active. The fact that year-old phyllodes on flowering branches have active glands suggests that the glands do not atrophy as the phyllode matures, but become dormant when nectar secretion is of no benefit to the plant. Bentley (1977b) in her review of literature dealing with extrafloral nectaries stated that nectaries cease to function when the organ with which they are associated matures. My observation that nectaries on mature (year old) Acacia phyllodes are revitalised during flowering is new, and tends to support the hypothesis that nectaries are pollinator attractants, or have a dual function.

The secretion of nectar by the vegetative parts of a plant may have a protective function as the nectar attracts ants, the presence of which is said to discourage herbivores (Bentley, 1976; 1977; Janzen, 1966; Majer, 1979).

In an attempt to relate herbivory to growth phenology, the number of harvested terminal shoots showing insect damage was recorded every month. The data is presented in Table 5.

Table 5. Percent herbivore damage to terminal shoots (n = 20 shoots per species/mth)

	Month												
Species	M	J	J	A	S	O	N	D	J	F	M	A	$\bar{x}$
A. cyclops	60*	88	64	71	63	73*	95*	100	50	55	70	35	71
A. long.	92*	85	100	67	94	82	19	75*	76	95*	95	100*	82
A. melan.	83*	85*	80	95	63	61	20	88	100	100*	100*	100*	81
A. saligna	92	83	76	71	57	82*	52*	50*	74	75	61	70	70

* severe damage to individuals ________ growing season

Terminal shoots were damaged throughout the year, and there was no clear pattern of herbivory. New (1979), in a study of the phenology of Coleoptera on four Acacia species near Melbourne, found that the numbers of most phytophageous beetles peaked in spring and summer, and yet, for the four species of Acacia studied in the Cape, the lowest rates of herbivore damage occurred during their growing seasons. An explanation of this trend is that during the growing season the Acacias outgrew their predators, but the latter destroyed much of the production as the growth rate diminished.

Phytophageous insects such as weevils, katydids, locusts, phasmids and lepidopteran larvae are abundant in crowded stands of young seedlings in the S.W. Cape. These young plants actively secrete nectar, and the nectaries are visited by ants, flies and coccinellids. Although mature trees are occasionally infested by tree hoppers and large Lepidopteran larvae (*Pachypasa capensis* (L.)), phytophageous insects are generally less abundant on these.

Observations made in the present study, although not quantified, provide evidence both for and against the protectionist role of extra-floral nectaries. Similar observations have been made by other authors. The following observations which support the protectionist theory, are reinforced by the present study:

(1) nectaries are most active on new foliage, and their activity decreases as the foliage matures (Majer 1979; Bentley, 1977b).

(2) peak nectar secretion co-incides with peak growth (Majer, 1979).

(3) ants, and other insects which might deter herbivores, such as wasps, flies and coccinellids, are attracted to the nectar. (Bentley, 1977b; Majer, 1979; Lamont, 1978).

Unsubstantiated observations which refute the protectionist hypothesis are that ants introduce *Icerya* and other scale insects to Acacias, and that active glands are selectively eaten by phytophageous insects. The fact that nectary activity co-incides with anthesis in some Acacia species suggests that the nectar serves to attract pollinators (Ford & Forde, 1976; Lamont, 1978; Lamont, 1979), but the two functions are not mutually exclusive.

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Major (1977) found that of six Acacia species examined in S.W. Australia, only A. saligna had obvious nectar glands and secreted nectar. Since herbivores were more abundant and diverse on this species than on the other, he concluded that the other species had some other herbivore deterrent (such as the presence of cyanides in the foliage). Lamont (1979) found that in some Acacia species nectar secretion co-incided with flowering, while in other it occurred only on growing shoots and seedlings.

Lamont (1979) states that "... extrafloral nectaries are clearly a vestige of tropical (mesophytic) ancestors.", and would be maladaptive in drought and nutrient-poor habitats. If these glands are a relict, it is not surprising that they have almost disappeared in species found in drought and nutrient stressed habitats (A. cyclops), but have retained some function in species found in moister habitats. This function is not necessarily their original one.

A single phyllode gland may serve two functions in some Acacia species. While the phyllode is expanding it secretes nectar which may have a protectionist function. It then becomes dormany until open flowers are produced in the phyllode axil, whereupon it again secretes nectar, possibly as a pollinator attractant. Phenological evidence presented in Figure 1-A & B and in Table 5 suggests that for A. longifolia and A. melanoxylon nectar secretion may serve both protectionist and pollinator attractant functions, but for A. saligna it probably serves the former function alone. The new growth of A. cyclops, a species found in arid areas and coastal sand, is protected by a sticky, varnish-like substance (soluable in ethyl acetate), and this species does not appear to have active phyllode glands.

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Phenological sequence

The main phenological events occur in the following sequence in A. longifolia, A. melanoxylon and A. saligna:

winter & early spring : flowering
spring & summer : growth of terminal, lateral shoots and pods
maximum phyllode fall
late summer : shedding of pods and seed
autumn : second growth spurt in some species
appearance of inflorescence buds in axils of spring phyllodes

The litterfall of A. melanoxylon is distinctly bimodal, with peaks in mid summer and mid winter. Nectar production is associated with growth and anthesis.

The sequence observed for A. cyclops is unlike that of the other species.

late spring : shoot growth and inflorescence formation
pods ripen and open
maximum phyllode fall
summer : flowers open
shoot growth continues
seed shed
autumn & winter : slow growth of shoots and pods
spring : pod and shoot growth rate increases

The nectar glands of A. cyclops are very small and rarely active. This may be considered an adaptation to drought or nutrient stress. It is tentatively suggested that the protective and pollinating functions of the insects which nectar attracts, are taken over by birds in A. cyclops.

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Flowers and newly opened pods, about 20 cm below them in the canopy, are borne simultaneously on A. cyclops. Flocks of starlings and other birds congregate in the trees at this time to eat the seeds: it is probable that they also take phytophageous insects and transport pollen.

The growth phenology of the exotic Acacias, other than A. cyclops is more similar to that of the Californian Chapparal and the Australian Eucalypts than it is to Australian Heath and Cape Fynbos (Specht & Rayson, 1957; Rundel, 1977; Westman, 1978; Kruger, in press). In most Mediterranean vegetation, however, flowering succeeds growth, and as in the case of A. cyclops, flowers are borne on the current seasons shoots (Evans, 1972; Rundel, 1977; Mooney et al, 1974).

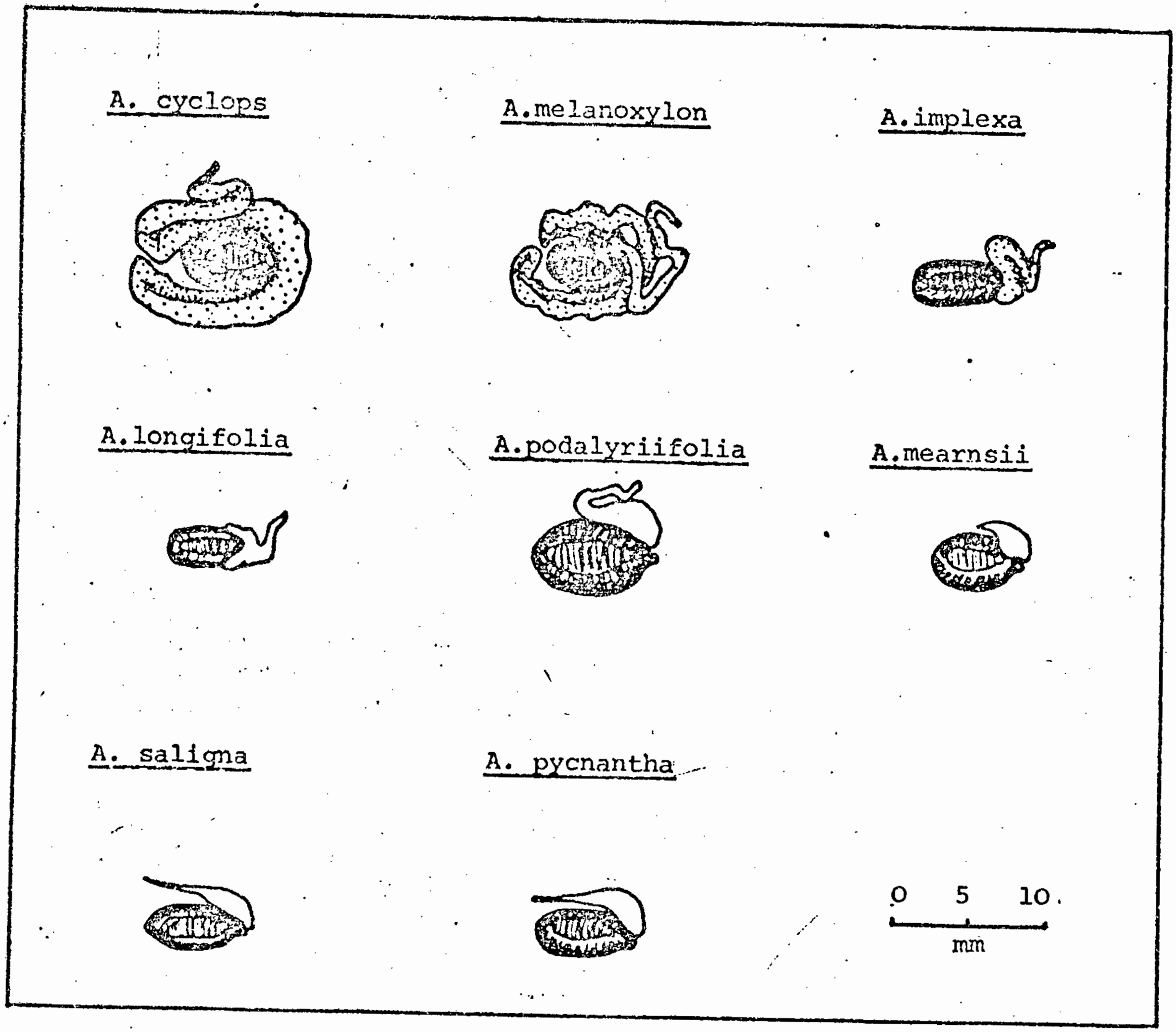
Most production (reproductive and vegetative) of the Acacias occurs when temperatures are high, but the soil moisture not depleted. The slow growth of the lateral shoots may indicate that some competition for photosynthesates is occurring between vegetative and reproductive structures at this time.

In all 13 Acacia species examined, the reproductive structure formed in the autumn remained dormant until the following spring or summer. This implies that both vegetative growth and the development of inflorescences and pods of Acacias are limited by cold temperatures.

The reproductive sequence of Fynbos species is poorly known, but leaf-fall appears to be the only event which is synchronised for the whole community. The early growth flush of the majority of exotic Acacias, which utilises the optimal period for growth, may give these plants some competitive advantage over late growing Fynbos species. It is also possible that this feature could be exploited for the selective removal of exotic plants from fynbos

B

Figure 15. Seed and funicle morphology of eight Australian Acacia species exotic in the S.W. Cape. Numbers 1 to 3 have persistent (non-deciduous) pods.



APPLICATIONS

The phenological information presented in this paper can be employed in distribution mapping, control and utilization of the exotic Acacias. Practical applications discussed here have not been tried in the field, so should be treated with caution.

Phenological charts can aid in the identification of plant species on aerial photographs (Sayn-Wittgenstein, 1961). Trees with showy flowers or autumn colours show up clearly, but filters can be used in addition to emphasise colour differences, and infra-red film will differentiate actively growing species. Since the exotic Acacias generally form dense thickets and start to grow earlier than most plant communities in the S.W. Cape, it should be possible to plot their distribution on infrared photographs taken in September. Exotic Acacias have also been found to have a unique signature on satellite images of arid Fynbos and coastal scrub taken in January (S. Lane, pers. comm.)

Most of the exotic Acacias produce masses of yellow flowers. Comparison of a colour photograph with Figure 11 should make it possible to determine which species is in flower. Where information on the relative abundance of Acacia species in a mixed stand is required, photographs should be taken near the beginning of the flowering period of the earlier flowering species. Photographs taken over the Cape Peninsula in July, September and October should result in good distribution maps of A. longifolia, A. saligna and A. melanoxylon respectively. A. cyclops, which is not conspicuous when in flower could be plotted from infrared images.

Distribution mapping of weeds is necessary for planning control measures, release of organisms for biological control and for monitoring the effects of treatments on the distribution of the various species.

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The use of herbicides for elimination of woody weeds in mountain water-catchments and in nature reserves cannot be recommended. Preliminary trials (D. Donnelly, unpublished) have shown that indigenous vegetation is damaged by wide-range systemic herbicides, but that more selective herbicides containing 2,4,-D and 2,4,5-T contaminate the soil for at least six months. Repeated use of any herbicide favours species which have mobile seed (ruderals) or large stores of dormant seed in the soil. Exotic Acacias, which have more stored undamaged seed than indigenous vegetation would be favoured.

Herbicides may, however, prove useful in urban areas and road reserves. The transport of systemic herbicides to the roots is greatest just before the end of the growing season, and many mature perennials are most susceptible when carbohydrate reserves are low (Muzik, 1970). The *Acacia* species generally grew in spring and summer: autumn and winter should then be the most effective seasons for herbicide treatment. This is borne out by the successful control of 16 000 ha of *A. dealbata* in Victoria with a single winter aerial application of 2,4,5-T (Flinn & Hopmans, 1977). Treatment of Eucalypts (which have a growth rhythm similar to that of the *Acacia* species) in May have proved more effective than December treatments, in N.S.W., Australia (Truman, 1970).

On the basis of the growth phenology reported in this paper, it is suggested that *A. melanoxylon* be treated with herbicide during the summer, while the other species would probably be most effectively controlled by autumn or winter treatments.

Mechanical damage should be most effective when the carbohydrate stores are low ie. following a growth flush, but prior to the build-up of photosynthesates. A. saligna is said to be killed by late summer destruction with a bush whacker (R.D. Parker, pers. comm.) but there would appear to be no published work on this subject.

Burning of Acacias seems wasteful, and on poor, unstable sand, is inadvisable. Although it is not considered economically feasible at present to use wattle (A. mearnsii) slash for methane production or for fodder (Goodricke, 1978; Wattle Research Institute, 1978), improved harvesting efficiency and the rising costs of other fuels and fodders, may make this a proposition in the near future.

Acacia foliage is used as a drought fodder in Australia. Analysis of the foliage of Australian and African species shows that it has a high crude protein content, but a rather low calorific value (Everist, 1969; Radwanski & Wickens, 1967). For this reason Acacia fodder should be supplimented with some energy-rich substance such as molasses (Everist, 1969). In the S.W. Cape, farmers grazing goats on A. saligna dominated veld supplement their diet with maize meal (Mundell, 1977).

While food analysis indicates that Acacia fodder is very similar to lucerne hay with regard to its protein, carbohydrate, fibre and ash content (Everist, 1969; Van der Merwe, 1970), its palatability varies with species and with the age of the foliage. A. mearnsii has been found to be unpalatable because of the tannins in the leaves (Goodricke, 1978). Other species eg. A. aneura, have high flavonoid or saponin content in the young leaves, but become more palatible as the foliage matures (Pedrotti & Fox, 1979). The palatibility of A. cyclops and A. saligna appears to vary in this way, since local farmers say that goats prefer older and wilted phyllodes to fresh young growth (C. Uys; H. Sharp, pers. comms.).

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Prior to abscission, N, P, and Mg are reabsorbed from the foliage of tropical legumes including Acacia (Ernst, 1975). Reabsorbtion has also been found to occur in Acacias in Australian Heathland (Specht & Groves, 1966). Mature leaves contain more fibre and more carbohydrate, but only about half as much crude protein as young Acacia leaves (Everist, 1969). The ideal time for harvesting Acacia forage must be when the foliage is mature but not old. During harvest the weather should be dry as the green forage may otherwise be spoilt by mildew (Goodricke, 1978).

Seeds and pods of A. cyclops and A. saligna are selected and eaten by primates, rodents and goats. The seeds contain more than 25% crude protein. Similar values have been obtained for the seeds of A. albida and for lupin seed (King, 1976; Van der Merwe, 1970). Grinding of the seed is advisable since it would enable stock to obtain maximal nutritional benefit and would also prevent dispersal of intact seed in the faeces. The pods of A. longifolia and A. melanoxylon are ready for harvesting in November, and those of A. cyclops and A. saligna, in December.

It may be possible to combine mechanical control with harvesting of fodder and fuel, in mid-summer. Bush cutting of Acacia in mid-summer is not only damaging to the bushes, but will supply pods, seed and mainly fully expanded phyllodes less than six months old (the previous year's foliage having fallen in early summer). The slash could be separated into fodder, and unpalatable material for methane production.

There appears to have been little or no change in the phenology of the Australian Acacias since their introduction to the S.W. Cape about 145 years ago. This means that control methods applied in Australia should have similar effects here, and the organisms imported for biological control should require little adjustment. Phenological similarities alone however are no guarentee of success in biological control. Colonising weed species can undergo genetic changes and form races within as few as 60 years (Wilson, 1965). Acacias have been established in the S.W. Cape for over a centuary. It was found that in the case of Hakea, genetic or morphological differences were more important in determining the success of the weavil introduced to control it, than the climatic similarity of the region from which the weavil originated (Kluge, 1979).

CONCLUSION

Phenological studies of the Australian Acacias in the S.W. Cape could be used as an aid in their mapping, control and utilization. For control, which is the greatest priority, field trials are required to test the effect of summer harvesting and winter spraying on Acacia stands. Manual and mechanical harvesting methods should be compared with regard to costs and product quality, and Acacia fodder should be subjected to palatibility tests. It would appear that Acacias start to grow earlier in the year than most Fynbos species: if this difference could be exploited, selective removal of Acacias from mixed stands might be possible. As regards phenology, the prospects for biological control look bright, but a historical and genetic study of local populations is now a priority.

Of less practical value than the other phenological studies described in this paper was the investigation of the activity of extra-floral nectaries. This revealed that nectar secretion is periodic and associated in some species with growth, and in others with both flowering and growth. Glands do not atrophy as phyllodes age, and in some species may have a protectionist role when young, but function chiefly to attract pollinators in the following year, when they bear inflorescences in their axils.

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APPENDIX

Flowering and fruiting times of some Australian Acacias in their natural habitats in Australia and in South Africa

Species	Flowering Season Australia	Flowering Season S. Africa	Difference (months)	Fruiting Season Australia	Fruiting Season S. Africa	Reference
A. armata	Aug. - Oct.	Aug. - Oct.	0	?	Jan. - Mar.	Ewart 1930
A. baileyana	Jul. - Aug. Jun. - Jul.	Jul. - Sept.	0	Dec.	Nov. - Dec.	Anon 1935 Newman 1934
A. cyclops	Dec. - Feb. Dec.	Oct. - Feb.	+1	Nov. - Dec.	Oct. - Feb.	Seddon 1977 Cambage 1925
A. cultriformis	?	Jul. - Sept.		?	Nov. - Jan.	
A. dealbata	Jul. - Sept. Aug. - Sept.	Jun. - Sept.	+1	?	Aug. - Oct.	Ewart 1930 Anon 1935
A. decurrens	Sept. - Oct.	Aug. - Oct.	+1	?	Dec. - Jan.	Ewart 1930
A. elata	Dec. - Jan.	Jan. - Feb.	0	?	Jan.	Pedley 1978, Ewart 1930
A. longifolia	Jul. - Sept. Sept. - Nov.	Jun. - Sept.	0	summer	Nov. - Dec.	Pedley 1978, Hazard et al 1977 Ewart 1930
A. mearnsii	Nov. - Dec.	Aug. - Nov.	+3	Nov. - Dec.	Nov. - Feb.	Ewart 1930, Cambage 1925
A. melanoxylon	Jul. - Oct. Nov. - Mar.	Aug. - Sept.	0	all year	Dec. - Apr.	Ewart 1930 Pedley 1978
A. podalyriifolia	May - Jul.	May - Jul.	0	?	Nov. - Dec.	Moss 1965
A. pycnantha	Sept. - Nov.	Jul. - Sept.	+2	?	Dec.	Ewart 1930 Ford & Forde 1977
A. saligna	Aug. - Oct.	Jul. - Sept.	+1	Nov. - Jan.	Nov. - Dec.	Maslin 1974

+ = earlier in South Africa than in Australia

C

REPRODUCTIVE BIOLOGY OF AUSTRALIAN ACACIAS IN THE SOUTH WEST CAPE, SOUTH AFRICA

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KEY WORDS

Acacia

reproduction

seed-bank

weed control

fire

Cape

Australia

germination

Australian Acacias

ABSTRACT

Australian Acacias have attained weed status in the Cape Province, South Africa. This study shows that in the Cape these exotic plants are pollinated but lack effective seed predators. They drop 1 100 to 7 000 seeds/m^2/annum, and have a seed-bank about two to five times this magnitude about 95% of which is dormant. Viability does not appear to decrease with age. The large reproductive output, and existing stores of Acacia seed, are seen as critical aspects of the control of infestations. A review of the literature, and an evaluation of management methods currently employed in the Cape, are used together with the results of this study to suggest strategies for the control of Australian Acacias in the Cape.

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CONTENTS

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INTRODUCTION

For the past century, Australian Acacias have been widely planted in regions with tropical, warm temperate and mediterranean-type climates. Being drought tolerant and fast growing, they are a valuable source of firewood and forage in arid regions (National Academy of Sciences, 1979). In the S.W. Cape, various species were planted for sand stabilization, for tannin production, wind breaks, fire wood, timber and horticulture (Stirton, 1978). Although none of the African Acacia species form part of the fynbos flora of the region, all the introduced Australian species of the section Heterophyllum grow well in the S.W. Cape, and a number of them have naturalised and are spreading onto disused land and into natural vegetation. Members of the section Heterophyllum are apparently better adapted to cooler climates than are species in other sections of the genus Acacia (Milton, 1980).

The seeds of nearly all Acacia species are dormant until the water-impermeable testa is damaged by heat or abrasion. Seed longevity and dormancy is possibly a product of evolution in ecosystems subject to occasional hot fires. Acacias have a very large potential annual seed crop but this is depleted in their natural habitat by parasites and predators. Bruchid beetles are one of the major seed destroyers of the non-Australian Acacias. In Australia the reproductive potential of the indigenous Acacias is reduced at the flower stage by gall-forming fungi and wasps, and seed is destroyed by bugs, moth larvae, ants and some beetles (Van den Berg, 1977; Sherry, 1971; New, 1979). Very few of the predators of the seed of the non-Australian Acacias have made use of the seed of the exotic Australian species.

Their tolerance of cool conditions together with their large output of dormant seed and relative freedom from predators, has enabled the Australian Acacias to become naturalised in many of the warm temperate and mediterranean regions where they have been introduced. Some of the species are now regionally viewed as problem plants: in the S.W. Cape these include A. cyclops A. Cunn. ex G. Don, A. longifolia (Andr.) Willd., A. mearnsii De Wild., A. melanoxylon R.Br., A. pycnantha Benth. and A. saligna (Labill.) Wendl. (Stirton, 1978).

The long-term solution to both maintaining the useful functions of the Acacias and controlling their abundance appears to be the limitation of their reproductive capacity. This paper describes the reproductive biology of the Australian Acacia species naturalised in the S.W. Cape, and suggests various means of depleting their seed-bank and of reducing regeneration.

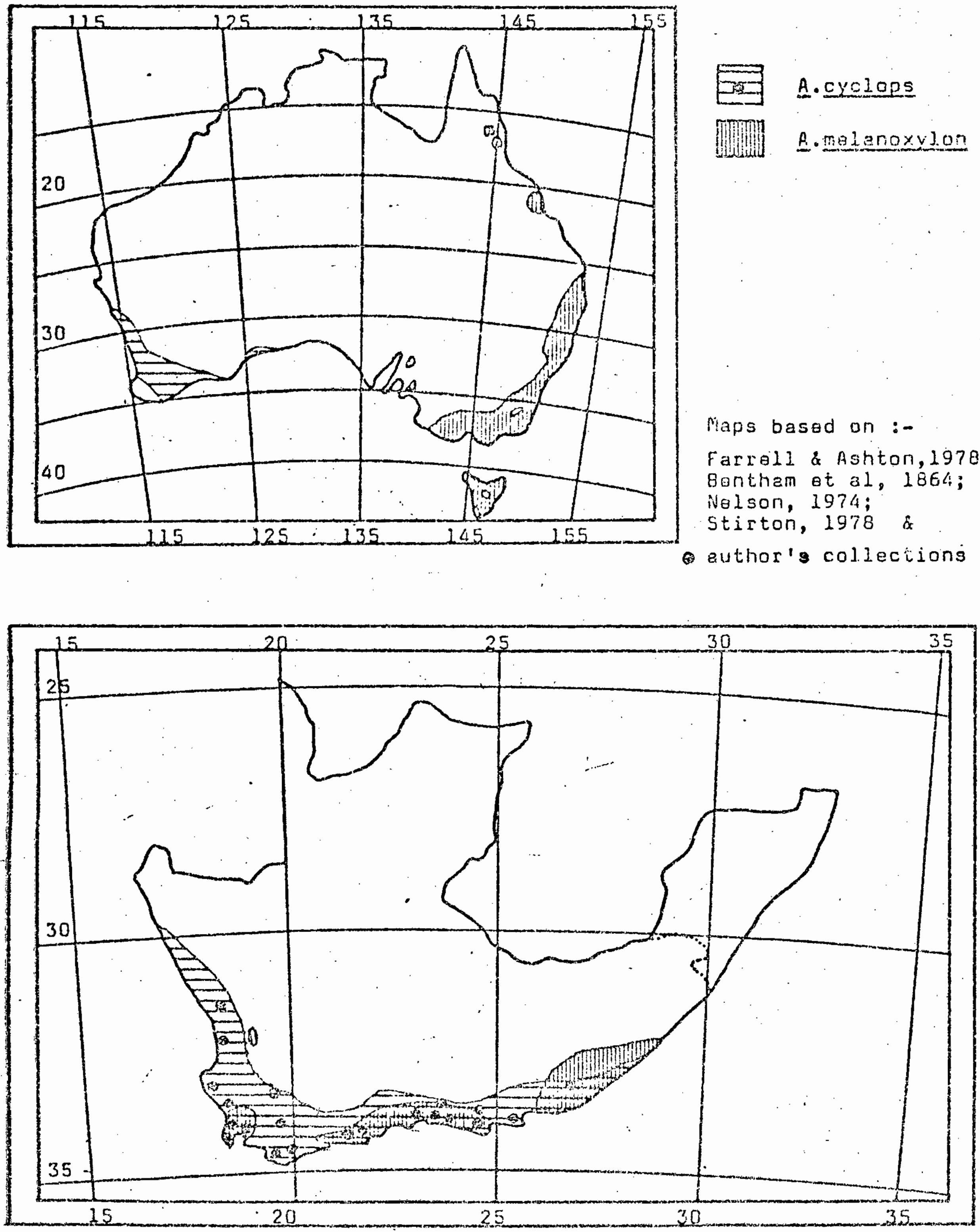
METHODS

Four Australian Acacia species which have attained weed status in the Cape were selected for detailed study. They are A. saligna and A. cyclops from south-western West Australia, and A. longifolia and A. melanoxylon from the south-eastern and eastern coasts of Australia. These species are all distributed in winter rainfall regions, although the distribution of A. melanoxylon extends into summer rainfall regions to the north and south.

In addition, pollination trials were carried out on A. podalyriifolia, an eastern Australian species, widely used as a garden subject in South Africa. This species is of interest in that it sets few seeds in the S.W. Cape, and is not yet considered to be a weed in this region.

The distribution of the major study species in Australia and in South Africa is shown in Figure 1, and climatic data for both regions is illustrated in Figure 2. It will be seen that the climate of the S.W. Cape is similar to that of the regions of origin of the introduced Acacia species. Edaphic

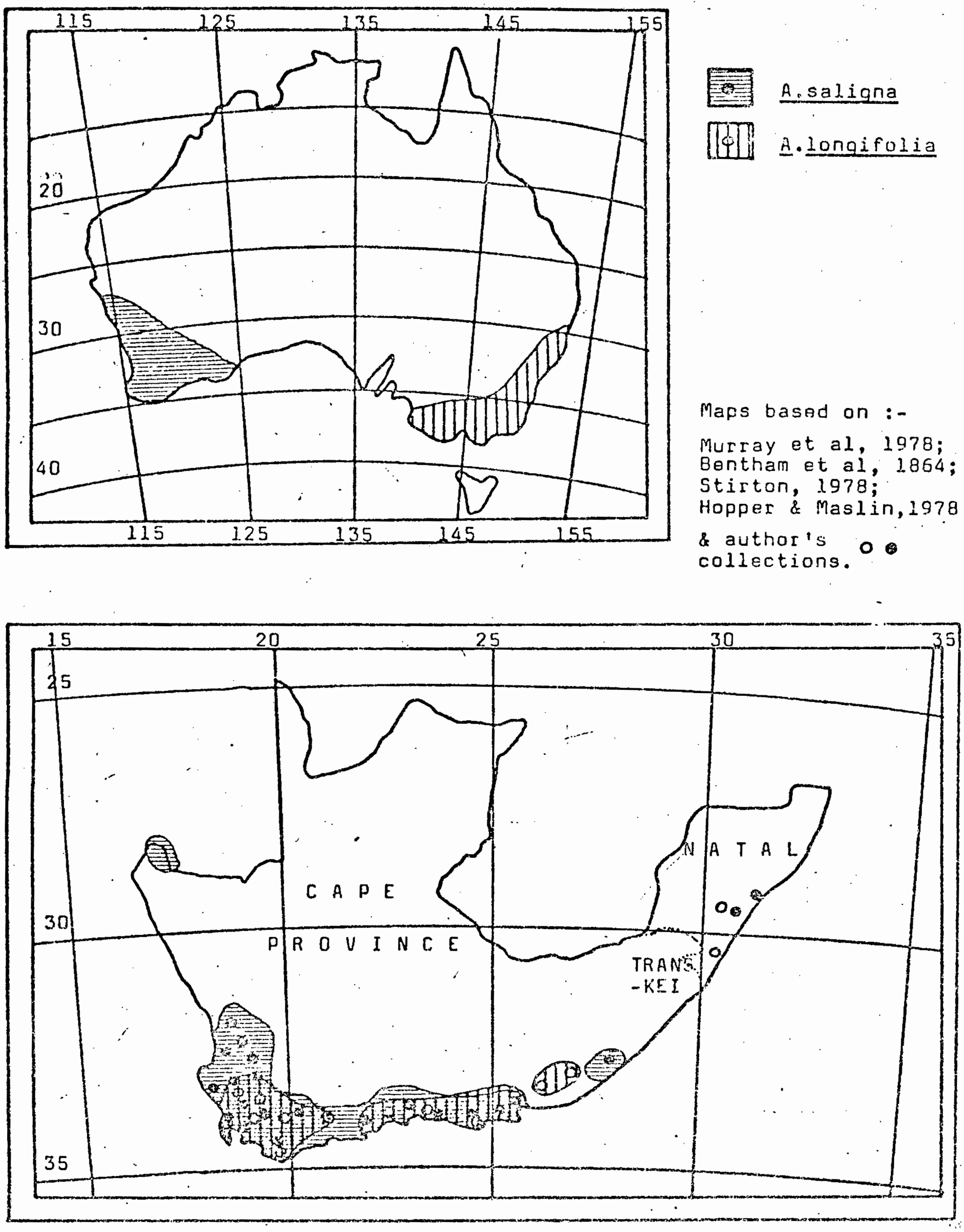
Figure 1A. Natural distribution of A.cyclops and A.melanoxylon in Australia and the present extent of infestations in the Cape Province, South Africa.



Maps based on :-

Farrell & Ashton, 1978;
Bentham et al, 1864;
Nelson, 1974;
Stirton, 1978 &
⊗ author's collections

Figure 1B. Natural distribution of A.longifolia and A.saligna in Australia and the present extent of infestations in the Cape Province, South Africa.



Maps based on :-

Murray et al, 1978;
Bentham et al, 1864;
Stirton, 1978;
Hopper & Maslin, 1978
& author's collections. ○ ●

Figure 2A. Climatic data for the natural habitats of the Australian Acacia species mentioned in this study.

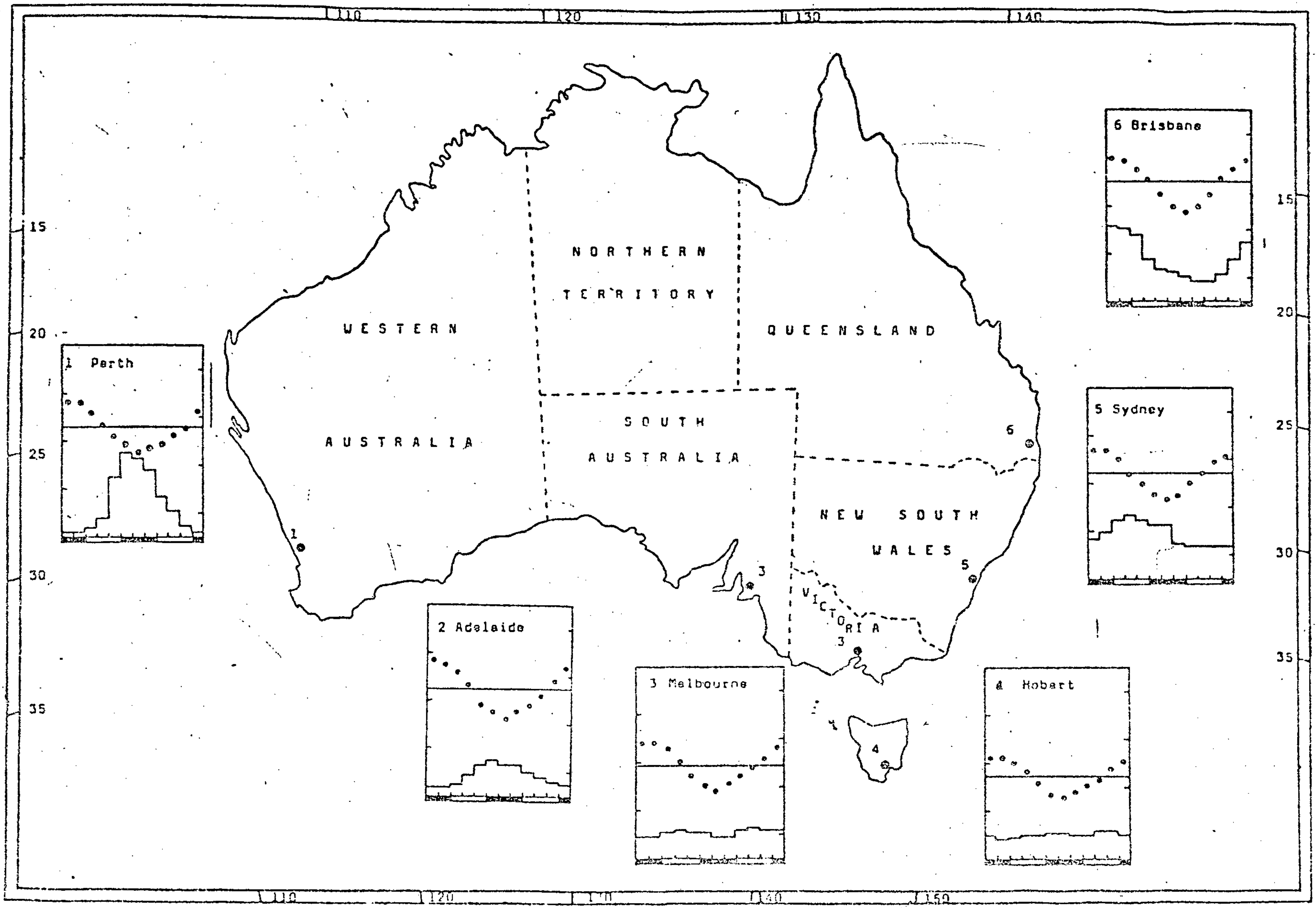
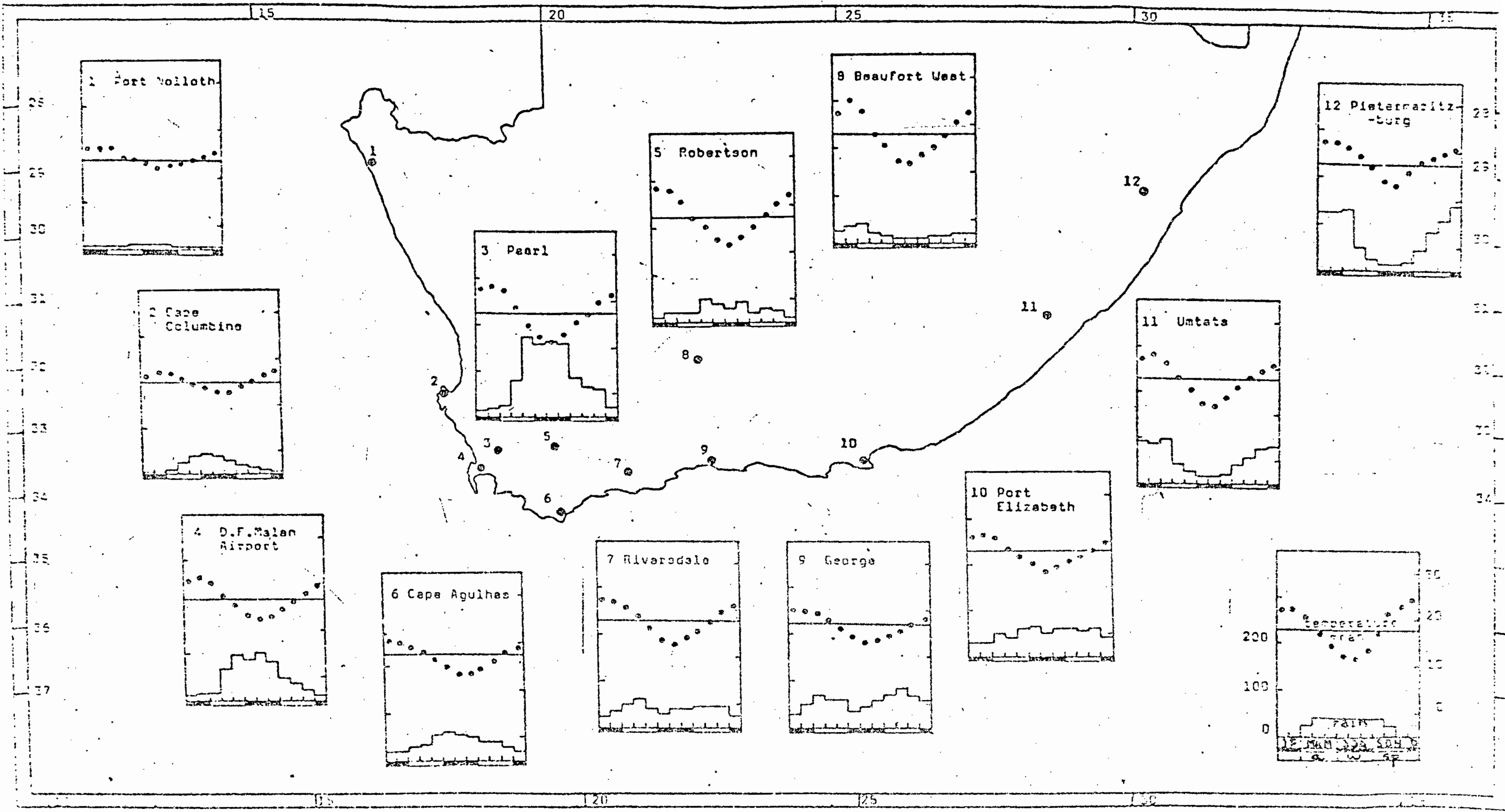


Figure 2B. Climatic data for the adopted habitats of the Australian Acacias studied in the S. W. Cpae, South Africa



factors too are comparable. On both continents, *A. cyclops* occurs on deep leached, saline or lime rich sand, but in the S.W. Cape, it has extended its distribution onto the sandstone derived rocky soils of the fold mountains. *A. saligna* occurs on a wide variety of substrates, wherever water is available; *A. longifolia* is found mainly on alluvial sand, but also on clay-loam on moist mountain slopes. *A. melanoxylon* grows best in sites potentially capable of supporting forests: in fullies, along rivers and on the coastal mountain ranges of the Southern Cape, which receive both winter and summer rain.

Choice of study sites

Most of the research was carried out in the vicinity of Cape Town. All the study species are common in the area, but *A. melanoxylon* does not appear to grow as well here as it does in the Knysna region. This was a drawback in obtaining comparable information, and for this reason some species have received more attention than others. Additional information on seed banks was obtained from Stellenbosch, Villiersdorp and the Knysna region in the southern Cape. All sites mentioned in this paper are shown on the map (Figure 3).

Flowering efficiency

The aim of the study was to determine whether pollinators or climatic factors were limiting the reproduction of Australian Acacias in the S.W. Cape. This was done by comparing records of fruiting success for Acacias growing in their natural habitat with data obtained for Acacias in an adopted habitat.

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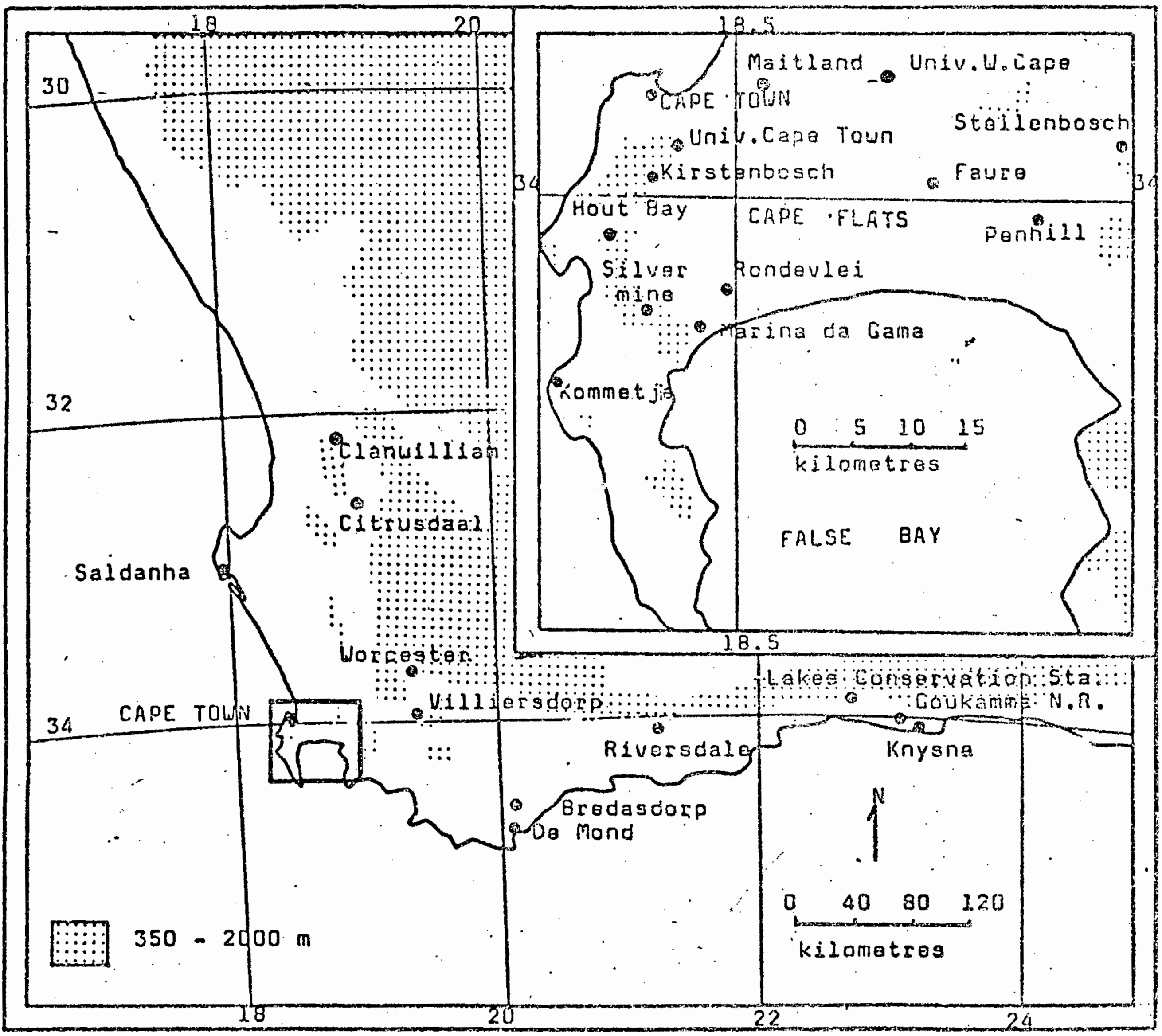
FIGURE 3. Study sites and weather stations in the Cape.



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The results should also serve as a basis for comparison after the introduction of organisms for biological control. Data were derived from two sources:

(1) Lateral shoots bearing inflorescence buds were marked. Monthly counts of flowers, pods and seeds were made, and flowering and fruiting success were calculated from these data.

(2) Entire A. cyclops and A. saligna trees were harvested, divided into various components and weighed. The average numbers of inflorescences, green or ripe pods per cubic metre of canopy were calculated, and subsequent changes were taken as an indication of the abortion rate of the various reproductive structures. Data obtained by this method were assumed to give a rough assessment of flowering efficiency.

Seed production

Seed production may be estimated by direct counts of pods on a living canopy (Phillips, 1928; Glyphis, unpubl), by harvesting and weighing the pods (Janzen, 1969; Wickens, 1969) or by collection of the seed falling on a known area (Donald, 1959; Ashton, 1975). Since the latter two methods were already being employed on other aspects of this study of Acacia ecology, they were chosen to provide seed production data.

(1) All mature pods were removed from felled trees, weighed, and the average number per cubic metre and per projected metre of canopy was calculated from the weight. This figure was multiplied by the average number of seeds per pod to obtain estimates of seed production.

(2) Falling seed was collected using circular, 50 cm diameter litter traps made of terylene mesh, and supported on 1.5 m iron stakes.

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Ten traps were arranged at 10 m intervals under mature single-species thickets of each of the Acacia species studied. The annual seed production was estimated from the twelve-month sum of the mean numbers of seeds collected per unit area per month.

Seed-bank

The vertical distribution of Acacia seed in the soil under a thicket and an isolated tree was investigated by excavation of half-metre-square quadrats in 4 or 5 cm spits. Spit depth was kept constant at each level by the use of a spirit level. Seed was separated from sand and other organic matter by sieving and hand sorting.

The density of Acacia seed and its horizontal distribution relative to topography and distance from a seed source, were sampled using a soil corer, 15 cm deep and 7½ cm in diameter. The sampling was carried out in conjunction with studies of stand density, size-class distribution and seedling germination. A 5 X 5 m plot was selected in an Acacia stand, or on land cleared of Acacias. All living Acacia trees within the plot were counted and arranged in size classes according to stem diameter. Counts of Acacia seedlings present in five randomly distributed ¼ m square quadrats were made, and a record kept of canopy height, cover, associated species and site factors. Seed in the litter was sampled by removing and sorting all unconsolidated litter from ten randomly distributed ¼ m square quadrats in each study plot. Seed in the soil was estimated by taking five soil cores at regular intervals along ten transects through each plot, the surface litter having been first removed. The 50 core samples were then bulked to give 10 samples of five cores each. The samples were roughly sieved in the field, and further sieved and hand sorted in the laboritory, to extract all Acacia seeds. After counting, germination trials were run on all the seeds collected from each plot.

In addition to this systematic collection of soil samples, additional cores were taken under isolated trees, or during management studies. Although these samples are smaller, and soil and litter were both samples with the core, the results are comparable, and are listed in Appendix I.

Viability tests

Germination tests on soil-stored Acacia seed were carried out in a growth chamber, under constant conditions. (Temperature 20 - 25°C, humidity 90 - 100%, day length 12 hr). Seeds were placed on moist filter paper in covered petri-dishes. After eight days, germinated seeds were removed, and the remaining seeds treated by brief immersion in boiling water. The seeds were then returned to the growth chamber. For two weeks after the hot water treatment, germinating seeds were removed and counted daily, and thereafter at weekly intervals. A second hot water treatment was required to break the dormancy of <u>A. cyclops</u> seed.

Additional germination tests were carried out on freshly collected seed, laboratory stored seed, and seed collected from bird droppings.

Field germination counts

Counts of germinating seedlings were made during the winter, under thickets, and at various intervals after Acacia thickets had been cleared or burned. Depending on seedling density, quadrats of ¼ m, 1 m, 2 m and 5 m square were used.

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Pollination trials

The unopened inflorescences on a number of A. longifolia and A. podalyriifolia A. Cunn. shoots were counted, and covered with numbered terylene mesh bags (mesh size ½ mm). As most of the insects that pollinate Acacias are large, and as very little pollen becomes airborne, mesh bags greatly reduce cross-pollination (Sherry, 1971 : 356). The open inflorescences of another set of shoots (on the same set of trees) were cross pollinated by brushing them with flowers from other trees, and likewise bagged. The inflorescences on a third set of shoots were counted, and the tagged shoots were left uncovered for pollination to occur naturally.

When the pods were almost mature, pod counts were made on all three sets of shoots, and the effect of self, cross and open pollination on fruit set was assessed.

RESULTS & DISCUSSION

Flowering efficiency

Estimates of flowering efficiency, based on the number of pods produced per inflorescence and per flower, are presented in Table 1. Between 0.4% and 36% of the inflorescences bear pods, and less than 1% of the flowers of any of the Acacia species studied, produced mature pods. These are comparable with values obtained for open pollinated A. koa in Hawaii (Lanner, 1965) and A. karoo in the eastern Cape (Story, 1952), where 0.007% and 0.3% (respectively) of the flowers set fruit.

As shown in Table 1, the stage at which most reproductive organs are lost differs with species. The large losses of A. melanoxylon buds and flowers at the University site may partly be attributed to the age of the trees: ten of the twenty marked trees were about eight years old, and were flowering for the second time only. None of these trees set any fruit. Climatic or site factors may also have been responsible for the high abortion rate. In a damp, sheltered valley, only ten km from the University, A. melanoxylon trees are heavily laden with pods every year, as are trees growing in the moister Southern Cape region.

That environmental factors affect fruit set has been observed by Newman (1934) for A. baileyana F. Muell. in Australia. At the coast (altitude 50 m), this shrub flowers early and fails to set fruit, but it sets abundant fruit on the plateau (altitude 600 m). A. baileyana appears to behave in the same way in South Africa. Specimens planted in the University garden (altitude 150 m) abort all their buds every year, but in Pretoria (altitude 1500 m) the species flowers prolifically and sets fruit. African Acacias may require warm temperatures to set fruit, for although A. karoo, planted in the Royal Botanical Garden of Victoria, flowers, it never sets fruit (Ross, unpubl.).

Data derived from monitoring of lateral shoots and tree harvesting indicate that losses of immature A. cyclops pods are very high (85 - 95%). Most of these losses occurred a few months after fertilization and may be the result of competition among the pods on a peduncle for nutrients or space. There are, on average, 46 flowers per inflorescence, but the mean number of mature pods is 3.3 (error on the mean: 20%) per inflorescence.

Another factor affecting the degree and timing of the loss of reproductive structures is pollination. In Acacia, pollen cells are grouped into sixteen-celled pollinia, four to eight pollinia in each anther (Sherry, 1971; Coetzee, 1955). Although some pollen becomes airborne (Moss, 1965) most of it remains on the anthers until detatched by pollinators (Vogel, 1978), mainly bees, but also by flies and wasps that appear to be attracted to the nectar secreted by extrafloral nectaries during anthesis of a number of species (Milton, in prep.). A. cyclops and A. pycnantha may be partly bird

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Table 1. Flowering and fruiting success of selected Acacia species

Species & Date source	Inflor. bud no.	% lost	No open inflor.	% lost *	Juvenile pod no	% lost	Mature pod no	Inflorescences (flowers) which bear pods %
A. cyclops	261	49	133	10	706	(86)	(95)**	13 (0.3)
lateral shoot	...	..	...	..	90	(63)***	33	....
A. cyclops m^3 1	...	..	...	..	111504	95	5490	....
canopy 2	...	..	...	..	42016	95	1950	....
3	...	..	...	..	14731	94	930	....
A. longifolia lateral shoot	481	63	178	61	200	73	54	11 (0.2)
A. longifolia pollinat. trial	827	..	...	..	...	..	281	34 (0.6)
A. podalyriifolia pollin. trial	247	..	...	..	...	..	33	14 (0.6)
A. melanoxylon lateral shoots	447	82	79	97	2	0	2	0.4 (0.01)
A. saligna	262	44	149	60	105	42	61	23 (0.6)
lateral shoot	1168				407	53	193	17 (0.4)
A. saligna m^3 canopy	2021	..	...	..	...	..	209	10 (0.3)
A. koa	207	36	132	77	30	100	0	0.0 -
Hawaii	125	27	91	96	4	75	1	0.8 -
Lanner, 1965	356	35	230	84	36	94	2	0.6 -
A. dealbata Natal Philp et al 1946	...	..	...	..	1062	21	842	....
A. karoo E. Cape Story, 1952	16000	..	...	..	....	..	3200	20 -

* (1- number of inflorescences bearing juvenile pods ÷ number of mature inflorescences) x 100

** Loss of juvenile pods from July 1977 to November 1977

*** calculated number based on previous years losses from July - Nov (63%) and current years loss from March to July, 1978.

pollinated (Milton in prep; Ford & Forde, 1976).

Most of the fifty Australian Acacia species investigated in a recent study were found to be obligate out-breeders (Hopper & Maslin, 1978). Self pollination is known to result in a higher rate of pod abortion than cross pollination in A. decurrens Willd. (Philp & Sherry, 1946). Moffet (1956) recorded a seed set of 19.5% in selfed flowers as opposed to 48.2% in open pollinated flowers. Li (1978) found that an Acacia tree 100 m from the nearest conspecific individual was largely cross pollinated.

In an attempt to determine whether cross pollination was a limiting factor in the pod yield of exotic Acacias in the S.W. Cape, pollination experiments were carried out on A. longifolia and A. podalyriifolia growing on the University campus. The results are presented in Table 2.

Table 2. Results of pollination experiments

Type of pollination	self	open	cross
A. longifolia			
mean no. fruit/inflor.	0.11	0.35	0.49
standard error of mean	0.04	0.08	0.15
A. podalyriifolia			
mean no. fruit/inflor.	0.05	0.14	0.07
standard error of mean	0.02	0.09	0.05

The fruit set of the open and cross pollinated flowers of A. longifolia was significantly higher (level of significance 0.01) than that of self pollinated flowers. Fruit set of A. podalyriifolia was generally rather low, but fruit set of cross-pollinated flowers was not significantly different to that of open-pollinated flowers. Both trials indicate that lack of cross pollination is not a limiting factor in the reproduction of these exotic Acacia species at the University site. The observed poor pod crop on A. podalyriifolia may be due to either environmental factors or an inherited trait. Although A. longifolia generally sets abundant fruit at the University site, yields appear to be chronically low on certain individuals and on parts of the tree that receive little sun.

Seed production

The annual seed production of the four Acacia species studied, estimated by the harvesting of pods and from litter-fall data, are presented in Tables 3A and 3B respectively.

Table 3A. Seed production of Australian Acacias in the S.W. Cape based on pod masses of individual harvested trees

Species	Canopy Vol. m^3	Pods per tree	Seeds per tree	Estimated seeds per m^3 canopy	Estimated seeds per m^2 projected canopy	Data source
A. saligna	20.7	4336	48563	2341	10562	trees felled at Faure 1977 - 1978
A. cyclops 1	16.0	5490	48312	3019	3019	
" 2	25.1	1950	17160	648	1373	
" 3	7.4	1086	9557	1291	1950	
" 4	27.7	2927	25758	930	2044	
A. cyclops	....	....	446 - 11630	...	63 - 1645	Glyphis (unpubl.) Rondevlei
A. cyclops	....	5343	.....	...	....	Linder (unpubl.) Faure
A. melanoxylon	....	....	250000	...	(2500)	Phillips (1928) S. Cape

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Table 3B. Seed production of the Australian Acacias in the S.W. Cape based on litter-fall data (number/m^2/annum).

Species	Year	Fallen Seeds/m^2	% Error on mean	Site
A. cyclops	1977	1197 (mean)	13	Rondevlei
	1978	1113 (ave.)	-	"
A. longifolia	1977	2923 (mean)	18	University
	1978	7381 (ave.)	-	"
A. melanoxylon	1977	66 (mean)	19	University
	1978	10 (ave.)	-	"
A. saligna	1977	5443 (mean)	11	Rondevlei
	1978	5032 (ave.)	-	(mature stand)
	1977	530 (mean)	31	Houtbay (sapling stand)
A. melanoxylon	1959	2400 - 3200	-	S. Cape, Donald, 1959

The difference in the calculated seed production and the measured seed fall per unit area may be attributed both to method and to differences in the sites and the ages of the thickets from which data were collected.

Acacia longifolia and A. saligna have about three times the annual seed output of A. cyclops. These species produce smaller seeds that A. cyclops, and lack the energy-rich arillate funicle of A. cyclops. The combined seed and funicle energy of A. saligna (21.88 K J/g) is less than half that of A. cyclops (55.62 K J/g) according to King (unpubl.). The energy demand of the reproductive structures may have some bearing in the differences in the size of the seed crops of the two species.

A. melanoxylon produced fewer than 100 seeds per square metre at the University site, due to the abortion of buds and flowers. In the S. Cape, where this species grows better, seed production is in the order of 2 000 to

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3 000 seeds per square metre per annum, (Donald, 1959), a value very similar to that obtained for A. cyclops. It is interesting that the seeds and funicles of these two species are morphologically similar, and both species are dispersed by birds.

The calculated seed yield of an average sized, mature, exotic acacia is in the order of 9.5 to 48.5 x 10^3 seeds per annum. This is comparable with figures given for African Acacias : A. karoo in the E. Cape produces 2.4 to 29.2 x 10^3 seeds per tree per annum (Story, 1952), and an average sized A. albida, 27.7 x 10^3 seeds per tree per annum (Radwanski & Wickens, 1967)*. Seed crops of South American Acacias studied by Janzen (1969) were generally smaller (0.08 to 6.6 x 10^3 seeds/tree/annum).

Seed-bank

Two to eight percent of new, ripe Acacia seeds will imbibe water and germinate (Preece, 1971; Beadle, 1940; Welsh, unpubl.; Larsen, 1964; Floyd, 1966). A mean of 2.3% (n=7; SEM=0.6) of freshly fallen seed from the study species germinated without treatment. It may then be assumed that a large proportion of the annual seed crop is incapable of immediate germination, and that this 'hard' seed will be stored in the soil until dormancy is broken by damage to the seed testa.

The object of this research into the distribution, quantity, viability, longevity, rates of increase and decrease and of germination of the seed-bank was to provide a basis for monitoring the effects of various management techniques, including biological control, on Acacia thickets and their seed-banks.

*Ross (1979) Calcuclated that a single A.caffra tree in Natal had a crop of 45.0 x 10^3 seeds.

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Vertical and horizontal distribution of seed in the soil

The vertical distribution of A. saligna seed in Cape Flats sand under a thicket at the Penhill site, is illustrated in Figure 4.

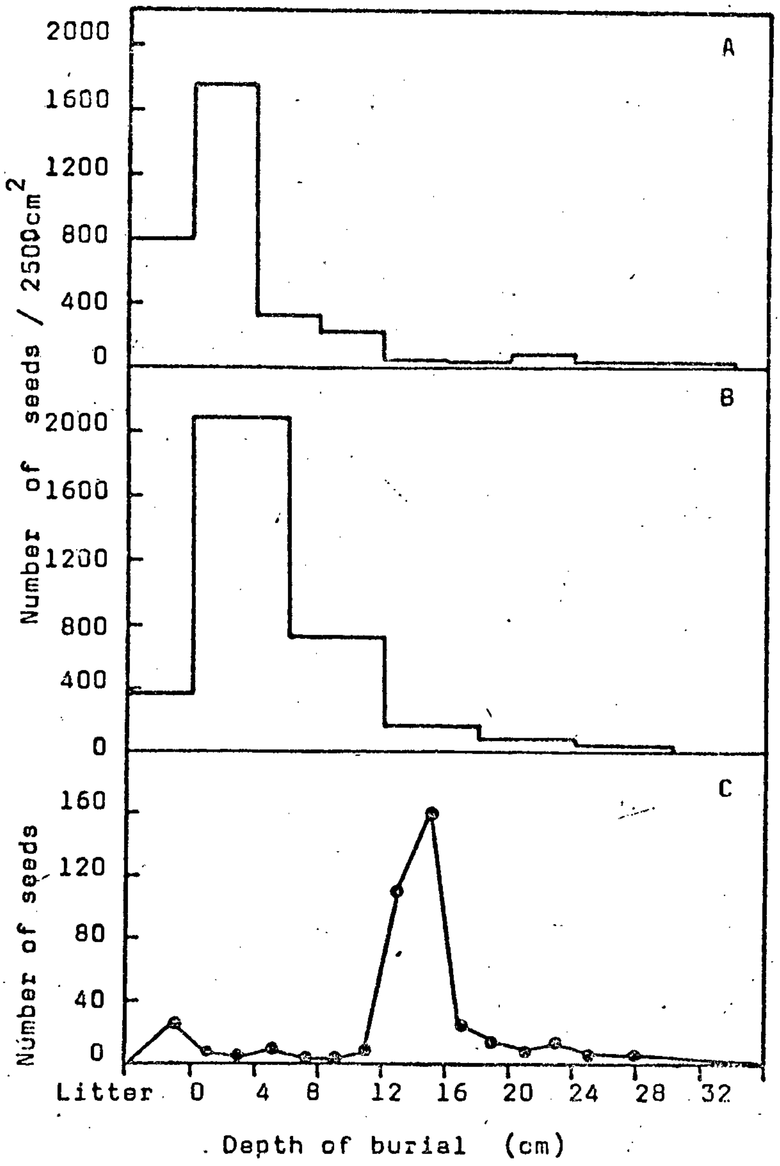
Most of the seed lies below the litter, within the upper 8 cm soil. Below this depth, seed density decreases sharply, but some seed is found to a depth of at least 35 cm in loose, sandy soil. The mean calculated seed store for four samples randomly located on the ¼ ha Penhill site was 11916 seeds per square metre (to 15 cm). The low standard error of the mean (6.8%), indicates that horizontal distribution of seed on level ground under an Acacia thicket is very even. This was confirmed by data from other sites, where the mean standard error within a set of samples was 36% (n = 16 sites, Appendix I).

These results contrast with those of Majer (1978), who found that the distribution of Acacia (and other legume) seed germinating after fire, in West Australia, was highly clumped. He was able to relate this to the storage of seed in ant nests, 15 to 21 cm below the soil surface. Ants remove up to 70% of fallen Acacia seed in established Acacia woodlands in some parts of Australia, and this results in very uneven vertical and horizontal distribution of seed (Withers, 1978; Majer, 1978). Of the Australian Acacias investigated by Berg (1975), 60% had swollen white, oil-rich funicles attractive to ants.

In the S.W. Cape, I have observed the Argentine ant (Iridomyrmex humilis) moving A. saligna seed, but judging by the quantity and even distribution of seed in the soil, ants are of little importance in the distribution of seed. As indicated in Figures 4A & B, seed gradually moves down through the litter into the soil. Penetration of seed to depths of 35 cm or more in sand is probably aided by the activities of burrowing animals, particularly the large

C

FIGURE 4. Vertical distribution of _Acacia saligna_ seed in the soil under a thicket on the Cape Flats, and of Acacia seed in an ant nest in Yalgorup Park, Western Australia.



Vertical distribution of _A. saligna_ seed excavated from sandy soil at the Penhill study site, 5 months after the last seedfall.

Vertical distribution of _A. saligna_ seed excavated from sandy soil at the Penhill study site, 10 months after the last seedfall.

Vertical distribution of Acacia seed in an ant-heap in Western Australia.

(Majer, 1978)

dune mole-rat (Bathyergus sullius), but also other burrowing mammals, snakes, frogs and insects which are common in sandy areas such as the Cape Flats. Seed appears to be more shallowly distributed in clay soil.

Topography affects the local seed store density, because seeds roll or wash down-slope. This results in the concentration of seed at the bases of dunes or slopes, and in drainage lines and in river valleys. Table 4 shows that seed is concentrated down-slope.

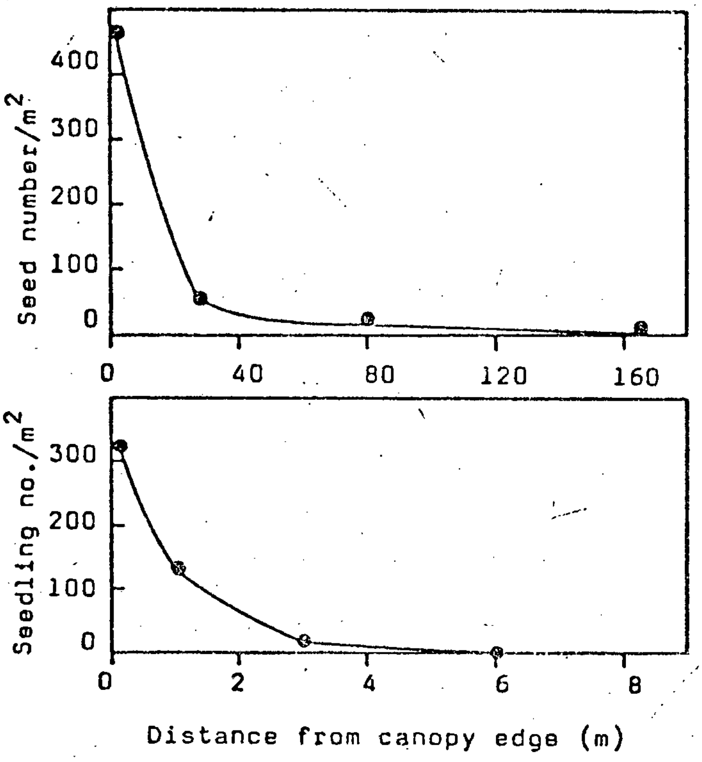
Table 4. The effect of a gradient on the density of Acacia seed and seedlings

Species	Site	Slope angle degrees	Slope length metre	Position on slope	Seed/m^2	Seedlings/m^2
A. cyclops	Goukamma	30	20	top	0 (0)*	
				bottom	1489 (90)	
A. saligna	Goukamma	30	20	top	1985 (71)	
				bottom	4113 (51)	
A. longifolia	University	20	10	top	343	8
				-3		27
				-5		44
				-7		72
				bottom	7026	94

* % error on the mean

The effect of distance from the parent tree canopy on the density of fallen seed and on post-fire seedling regeneration is illustrated in Figure 5. Most of the seed falls within the canopy shadow. The spread of Acacias into uninfested areas is therefore dependent on soil or water movement, or

FIGURE 5. Effect of the distance from the parent canopy on the density of fallen seed or seedling regeneration of exotic Acacias in the Cape.



Change in the density of A. melanoxylon seed with distance from the parent canopy. canopy. Tree height Tree height : 30m.

(Donald, 1959)

Change in the density of A. longifolia seedlings with distance from the parent canopy. Tree height : 3m. Counts made 2 months after a fire.

transport by man, birds and other animals. Glyphis & Milton (in prep.) found that birds transport A. cyclops seed in large quantities over distances of at least 100 m. and deposit most of it around the emergent bushes on which they perch.

Quantity of seed stored in the soil

Estimates of seed density for all sites sampled are given in Appendix I. The size of the seed bank appears to be determined by the amount of seed produced annually, by the duration of seed dormancy, by stand age and management as well as by topography, distance from seed source and predation. The ranges and mean sizes of the seed banks for the various species studied are given in Table 5.

Although the recorded seed-bank may be up to 30 times as great as the annual seed fall, it is generally less that three times the annual fall. This may be attributed to the continual loss of seed through predation, decay and germination, the last being the most important factor for exotic Acacias. Field counts (Table 6) and laboratory trials (Table 8) indicate that only 20% to 40% of A. cyclops seeds will remain dormant after one to two years of storage, the remainder will germinate, given favorable conditions. On one occasion 714 A. cyclops seedlings per square metre were counted during the rainy season in a thicket at the Rondevlei site, where the seed-store was known not to exceed 2 500 seeds per square metre. The other exotic Acacia species studied appear to have both a greater seed-production and a longer period of seed dormancy, and consequently accumulate large seed-banks more rapidly.

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Table 5. Seed bank relative to annual fall of seed, and predicted accumulation time

Species and sites (from appendix I)	Seed-fall/ m^2/pa. seed no.	Seed-bank/ m^2:range seed no.	Seed-bank/ m^2:mean seed no.	Seed-bank/ seed-fall ratio	Estimated time to store mean bank ** (years)	Estimated time to store 10000 seeds (years)
A. cyclops 1,2,3,4,5,17	1197 (13)* 1113	28 - 5899		1.70	11	34
A. saligna (mature) 8,9,10,11,14	5443 (11) 5032	10152 - 13792	11920	2.19	8	8
A. saligna (juv.) 13 & Houtbay	530 (31)	-	145	0.27	less than 5	-
A. longifolia 18,19	2923 (19) 7381	2110 - 13182	7646	2.62	7	8
A. melanoxylon Donald, 1959	3218	2967 - 94511	(48739)	1 - 29 (15)	min. 25	-
A. mearnsii 20	-	-	38340	-	-	-

* % error on mean given in parenthesis

** the time taken for the accumulation of the mean seed-bank for the species was calculated as follows:

B = bank; AI = annual input (from Fig. 6); Y = years from germination to maturity (about 10 for *A. melanoxyl*

and 5 years for the other species). B ÷ AI + Y = Accumulation time (years).

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Rodents take only an estimated 1% of the available seed in mixed A. cyclops and A. saligna thickets on the Cape Flats (King, unpubl.; Shelton, unpubl.). Alydidae (seed-sucking bugs) may reduce the crop of viable seeds in A. cyclops when they are exceptionally abundant. This appears to have occurred at site 17 (Appendix I) an isolated infestation along a farm road running through fynbos in the Bredasdorp area. The bugs also feed on the seeds of A. mearnsii and A. melanoxylon.

The rate of seed accumulation could not be accurately calculated from the available information. The time taken for a given seed-bank to accumulate was estimated from the losses known to occur at various stages between seed production and incorporation in the seed-bank (Figure 6). Figure 6, a model of seed production, loss and accumulation for three Acacia species, shows how a relatively low seed production and high germination rate lead to far slower rates of seed accumulation in A. cyclops than in the other two species.

Seed production and store are also dependent on the age of the Acacia trees, because, although a two year old sapling can set a few pods, large crops are not produced until the trees are over five years old (older in the case of A. melanoxylon). The rate of seed accumulation appears to increase until the trees are about 30 years old, and then to level off. A seed-bank of about 10^3 seeds/m^2 is expected under a mature A. cyclops thicket, and in the order of 10^4 for well established A. saligna, A. longifolia and A. mearnsii thickets (Appendix I : 6-12, 14, 18-20, 30, 31) and for A. melanoxylon plantations and thickets in the S. Cape (Donald, 1959).

The pattern of seed accumulation is complicated by land management history. The size and condition of the stumps of felled trees, together with the size and density of trees in the present stand may give some indication of the age of the infestation, but growth rings are considered to be of little use in aging Acacias (Wick, 1970; Lanner, 1965; Wickens, 1969).

After an Acacia thicket has been cleared, the rate at which the seed store declines will depend on the agents of seed destruction. In the S.W. Cape these include rodents, insects, fire and factors stimulating germination. Table 6 related the size of the seed bank to management practices and to the time elapsed since removal of seed bearing trees.

Table 6. Effects of clearing and burning on the seed-bank

Species	Sample number	Seeds/m^2 initial	Treatment	Time(mth) elapsed	Seeds/m^2 final	Percent decrease
A. cyclops	28	1565 (15)*	clear	12	886 (36)*	43
A. cyclops	27	1565 (15)	clear/burn	12	108 (36)	93
A. cyclops	25**	2523 (39)	clear	2	1761 -	30
A. cyclops	22,23	"	clear	12	454 (22)	82
A. cyclops	21,24	"	clear	24	442 -	82
A. saligna	9	11861 (7)	clear	10	13792 -	0
A. saligna	10	"	clear	15	10152 (32)	14
A. saligna	23**	9268 (11)	clear	12	8763 (43)	5
A. saligna	24,21	"	clear	24	3970 (37)	57
A. saligna	15,16	?	clear/burn	12	2694 (16)	?
A. saligna				30	1373 (33)	49***

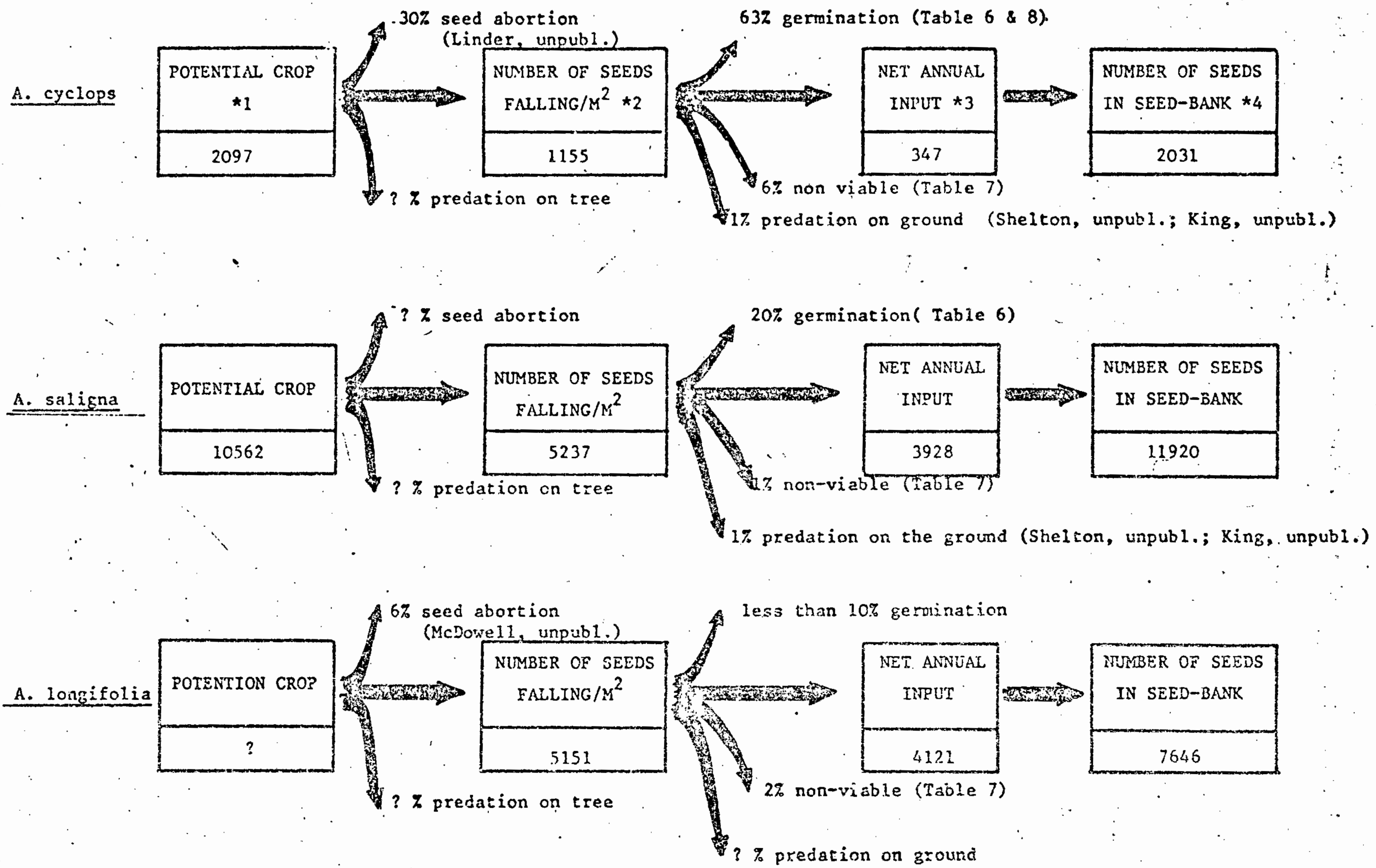
* percent error on the mean

** figures in Appendix I represent seed of both species

*** % decrease over 18 month period

Figure 6. Models of estimated seed production, loss & accumulation for three exotic *Acacia* species in the Cape.

(data source : *1 : Table 3A ; *2 : Table 3B ; *3 : calculated ; *4 : Table 5)



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The data in Table 6 suggest that A. saligna seed stores decline more slowly after clearing than those of A. cyclops. This may be due to differential predationof the seed of the two species; however the Striped Field Mouse (Rhabdomys pumilio) which is abundant in newly felled Acacia thickets, shows no preference for A. cyclops seed over A. saligna seed in laboratory tests (Shelton, unpubl.). Alternatively, A. cyclops may have a shorter period of dormancy than A. saligna: preliminary tests indicate that about 60% of old seed (minimum age 2 yr) will germinate without treatment (see Table 8). A. mearnsii seed-banks also decrease slowly. Regeneration densities of 5 000 and 1 483 trees/ha were recorded on old wattle lands in Natal when they were left fallow after 20 and 44 years of maize cultivation respectively (Sherry, 1971).

Fire, which kills seed in the upper layers of the soil, and stimulates germination of more deeply buried seed, is probably the most rapid means of reducing the store of dormant seed.

Many Australian authors refer to the storage of Acacia seed under climax forest and in old pastures, and of its importance in the regeneration of Acacia after fire (Cambage, 1926; Cunningham & Cremer, 1965; Howard, 1974; Farrel & Ashton, 1978; Gilbert, 1959; Withers, 1978; Majer, 1978), but few quantitative assessments of the seed-bank have been made. Barbour & Lange (1967) found no A. longifolia (syn. A. sophorae)seed in the top-soil of a coastal site dominated by this species, but A. myrtifolia seed was abundant (5000 - 10000 seeds/m^2). Howard (1974) found 15.5 seeds/m^2 (1.4 seeds/ft^2) to a depth of 10 cm in a 60 year old A. melanoxylon forest in Tasmania: but this figure is probably an under-estimation since the seed store was calculated from seedlings appearing in soil samples which received no heat treatment. Other estimates of stored seed have been based on counts of seedlings after burning or clearing. They confirm that in their natural habitats in Hawaii and Australia, Acacia seed-banks are one to three orders of magnitude smaller than they are for exotic Acacias in South Africa (Cunningham & Cremer, 1965; Purdie, 1977; Scowcroft & Wood, 1976).

The mean seed-bank densities for exotic Acacias in the S.W. & S. Cape (2×10^3 to 4×10^4 seeds/m^2) lie within the range of seed densities found in pastures, old-lands and other disturbed areas supporting annual herbs and grasses. The mean seed density to 20 cm for 24 such sites was 13736 seeds/m^2 (SEM = 3345) (Thompson, 1978). Seed-banks of this magnitude are very unusual for woody species. The mean seed density of 21 samples from woody communities (listed in Thompson, 1978), was 1224 seeds/m^2 (SEM = 278). Large stores of dormant seed are characteristic of early seral species (Thompson, 1978; Harper, 1977).

The Australian Acacias generally act as early successional species, replacing Eucalypts and other climax forest species temporarily after fire. In the Cape, where their seed-bank exceeds that recorded in Australia, and may be greater than that of indigenous dune pioneers (Appendix I : 33-37), there are no taller, woody species to replace them. The seed bank is therefore a major obstacle to the removal of exotic Acacias from indigenous vegetation.

Viability, germination & destruction

Viability

Viability of Acacia seed extracted from the soil was tested by germinating seed under constant conditions. The results summarised in Table 7 show that the seed of the exotic Acacias in the S.W. Cape is at least 87% viable. Prior to hot water treatment (HWT), only 4.8% of the seeds were able to absorb water and germinate. These results are typical of the results of germination tests carried out on the seeds of Australian and African Acacias

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(Appendix II).

Table 7. Summarised results of viability tests on the seed of exotic Acacias extracted from soil in the S.W. and S. Cape.

Species	No. of tests	Total seeds	Pretreatment germination %	Post-HWT % germination	% bad seed	% hard seed
A. cyclops	4	513	9.2 (3.6)*	87 (3.0)**	6.2 (2.0)	7.0 (1.8)
A. longifolia	4	869	2.0 -	97 (0.3)	1.5 (0.9)	1.8 (0.6)
A. melanoxylon	1	191	not recorded	70 -	0 -	30.0 -
A. saligna	13	9700	3.6 (1.3)	83 (3.0)	1.0 (0.2)	16.5 (3.8)
all tests	22	11273	4.8 (1.3)	87.3 (2.2)	2.3 (0.5)	11.1 (2.6)

* = standard error of the mean ** = two HWT's applied to *A. cyclops* seed

HWT = Hot water treatment

Germination rate

The mean rate of germination for all trials run in the growth chamber is illustrated in Figure 6. 4.8% of the seeds germinated during the first week, before treatment with hot water. 47% had germinated within a week of receiving hot water treatment, 70% had germinated within two weeks of treatment, and after six weeks a mean of 87% germination was attained for 12 samples run simultaneously. 6% of the seed rotted, and 7% remained hard and dormant.

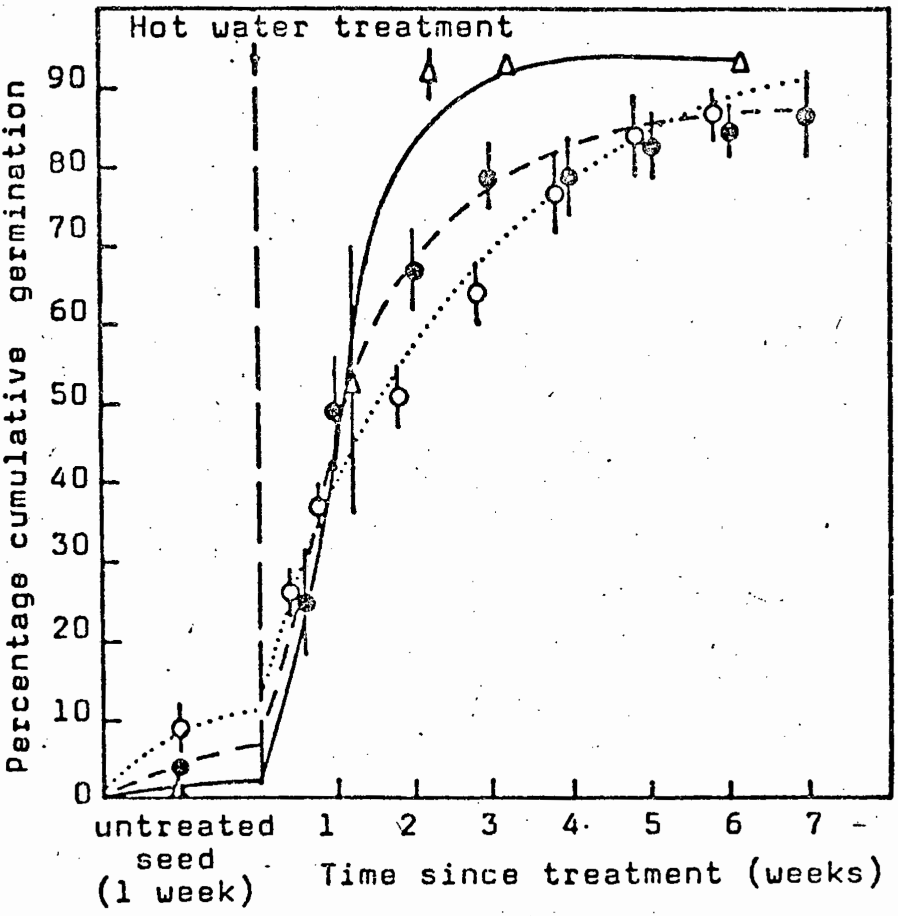
Acacia seed dormancy is enforced by the water-impermeable seed coat. The permeability of the testa appears to vary with seed age, species and the degree and type of damage that it may be subjected to, and this in turn affects the germination rate.

82% of *A. saligna* seed removed from an unopened, ripe pod, and still soft enough to be dented with the thumb nail, germinated within ten weeks, whereas only 2% of hard seed collected from the ground at the same site had germinated within this period. Similarly, Story (1952) found that green and soft coated A. karoo seed germinated without treatment. The formation of a water-impermeable testa requires a period of after-ripening, and this may have been one of the selective pressures resulting in the dry season ripening of pods in the winter and summer rainfall regimes of both Africa and Australia (Milton in prep.).

Figure 7 shows that the germination rates of the various species differed. This may be a function of the effect of hot water on the testas of the various species. The dormancy of A. longifolia was broken by the standard hot water treatment, and ten replicate samples of A. longifolia seed reached an average of 92% germination within two weeks of treatment. On the other hand, only 21% of the A. cyclops seed germinated after hot water treatment. (Tests were run concurrently in the same growth chamber). Six weeks after repetition of the treatment (HWT), a total of 87% of the A. cyclops seed had germinated. Dormancy of this species appears to be more effectively broken by scarification, aging and digestive processes (see Appendix II and Table 8). As this species is a coastal dune pioneer, it is possible that these processes are more important in breaking dormancy in the field, than fire. Results of pilot tests carried out to determine the effects of various treatments on the dormancy of A. cyclops seed are given in Table 8. The tests were carried out between March and June, 1979.

C

FIGURE 7. Cumulative germination of Acacia seed samples under growth chamber conditions.



·····○······· *A.cyclops* (4 samples, 513 seeds)

– –●– – *A.saligna* (11 samples, 8990 seeds)

——△—— *A.longifolia* (4 samples, 869 seeds)

Vertical bar represents the standard error on the mean.

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Table 8. The effect of various treatments on the dormancy of *A. cyclops* seed

Seed source and treatment	Seed number	% germination after 2 weeks	% germination after 6 weeks
hardened new seed taken from open pods, March, 1979	50	0	2
as above, twice hot water treated	50	0	78
seed passed by birds (sample 1)	50	4	32
seed passed by birds (sample 2)	36	0	36
seed sieved from the soil minimum age of 2 years	50	0	64
seed hot water & acid treated then stored for 2 years	50	88	92

Passage through the gut of a bird broke the dormancy of about one third of the *A. cyclops* seeds tested. The implications of this are that seed deposited in indigenous vegetation by birds may accumulate for some years before the first seedlings are large and common enough to be noticed.

Light does not affect the germination of *A. aneura* seed (Preece, 1971) and results in Table 9 indicate that this holds true for *A. longifolia* and *A. saligna* in the S.W. Cape. Light does however affect seedling morphology. As shown in Table 9, darkness promotes hypocotyl elongation at the expense of root development. Seedlings growing in the dark develop a broad flange of tissue between the hypocotyl and the root. This may prevent the seed from being pushed deeper into the soil by the force of the upward growing hypocotyl. No flange developed between the root and hypocotyl regions of seedlings growing in the light. Seedlings take about a month to grow a 10 cm long hypocotyl. Seeds germinating below 10 cm in the soil would probably be unable to produce a hypocotyl long enough to reach the surface before their energy was expended.

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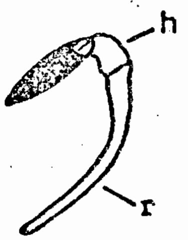
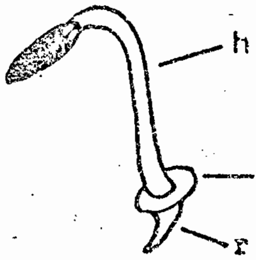
The practical value of this experiment is its application to fire management. A slow hot fire would destroy more Acacia seed than a rapid fire because, as well as killing seed near the soil surface, it could stimulate germination of seed buried too deep to emerge.

Table 9. The effects of light on Acacia seed germination and development

Light regime	Daylight		Darkness	
Species	*A. saligna*	*A. longifolia*	*A. saligna*	*A. longifolia*
Number of seeds tested	100	100	100	100
% germination at 4 weeks	65	100	60	96
Root length range mm	44 - 21	72 - 41	42 - 11	21 - 19
Hypocotyl length range	40 - 3	25 - 4	110 - 42	100 - 66
Mean root length ÷ mean hypocotyl length	3.86	4.63	0.40	0.25
S.E. of mean ratio	(1.13)	(0.90)	(0.27)	(0.05)
Illustration of seedling morphology h = hypocotyl f = flange r = root				

Aging and longevity

Since no better means was found for dating excavated seed, it was assumed that seed age was correlated with depth of burial. It is acknowledged, however, that burrowing animals may disturb the stratigraphy. The germination rates of *A. saligna* seed excavated from various depths at the Penhill site are compared in Table 10. The following trends are evident:

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(1) after nine months storage, seed from all depths germinated more rapidly

(2) seed from the litter and the upper layers of soil germinated more slowly than seed extracted from depths of over 9 cm below the soil surface

(3) seed extracted from depths of over 25 cm below the surface germinated most rapidly

(4) few 'soft', immediately water-permeable seeds were found at depths greater than 8 cm

(5) depth of burial or 'age', did not affect seed viability

Table 10. The effect of seed 'age' on the germination rate of A. saligna seed excavated from the Penhill site.

Seed source and minimum age	Spit depth cm	Percentage germination			
		Untreated seed	Days after hot water treatment 4	14	42
Penhill (A) (test 1) minimum age 6 mth	litter	18	4	46	64
	0 - 8	4	5	42	77
	9 - 24	1	18	42	80
	25 - 32	0	35	70	74
Penhill (A) (test 2) minimum age 10 mth	litter - 8	-	31	89	-
	9 - 24	-	38	82	-
	25 - 28	-	46	88	-
Penhill (B) minimum age 15 mth	litter - 5	4	18	83	96
	6 - 15	1	27	84	95
	16 - 26	0	30	74	99

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Although old A. saligna seeds remain viable, they appear to lose vigour. Seedlings developing from seed excavated from below 24 cm depth had poorly developed roots and thin shoots in comparison with seedlings from seed found in the upper layers of soil. The seedlings from the 'oldest' seeds grew slowly, and most of them had failed to shed the seed from the first leaf after about one month.

In Australia many of the Acacia species are fire weeds (Floyd, 1976; Cunningham & Cremer, 1965). As most species are relatively short-lived, (30 - 70 years), they cannot outlive the climax Eucalyptus or rain forest species, but survive in the form of dormant seed (Noble & Slatyer, 1977; Howard, 1974). Even though climax forests may take two to four hundred years to develop, Acacias appear again after catastrophic fires. Even-aged stands of A. melanoxylon and A. dealbata in Tasmania and Victoria are the result of such fires (Farrell & Ashton, 1978; Gilbert, 1959; Howard, 1974).

Gilbert (1959) found that only one generation of Acacia dealbata is produced when a climax forest is destroyed by fire. This probably also applies to other Acacia species, as Acacia species are absent from African and Australian forests a century or more in age (Weisser & Marques, 1979; Howard, 1974; Cunningham & Cremer, 1965). Although the seed-bank (as indicated by the post-fire germination density) is greatest in living Acacia stands, Acacia seedlings appear in burned and cleared forests of two to five hundred years old, in the order of thousands and tens of thousands per hectare (Gilbert, 1959; Howard, 1974; Cunningham & Cremer, 1965).

The seed of A. binervata, a species favoured by short rotation burning, remains viable for less than 30 years, (Floyd, 1976), but this case is probably an exception rather than the rule.

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The ecological position of Acacia species such as A. dealbata, A. melanoxylon, A. mearnsii and A. pycnantha in Australian Eucalypt and rain forests may be compared with that of leguminous tree species commonly found in marginal and disturbed areas of the indigenous forests of the S.W. and S. Cape, particularly Podalyria species and Virgilia oroboides (Berg) Salter.

Virgilia resembles the exotic Acacia species in its relatively short lifespan (60 years) and its large store (500-2000 seeds/m^2) of dormant seeds buried to a depth of at least 10 cm in the soil under forests and mats of groundcover which exclude the light. Virgilia seed is also long-lived, being 95% viable after 33 years in the soil (Phillips, 1926).

Laboratory tests have shown that Virgilia oroboides can compete successfully with Acacia longifolia, overtopping it within 2 weeks, and by maintaining this height advantage for at least 9 weeks, shading and stunting the root development of the Acacia (McDowell, 1979). Field trials at present in progress, suggest that in moist, potential forest sites, Virgilia could out-compete A. longifolia (Rycroft, pers.comm.). The propagation of indigenous species similar to exotic species in morphology and life history, was proposed by Bridgewater & Kaeshagen (1978), as a means of containing exotics in Australia. The idea is worthy of investigation in the S.W. Cape.

REVIEW OF AGENTS RESPONSIBLE FOR THE DISPERSAL, GERMINATION AND DESTRUCTION OF ACACIA SEED

Abiotic agents

Fire

Acacias, in general are light demanding, pioneer shrubs and trees with long-lived, dormant seed produced in large quantities. Features such as this could have been selected in an ecological regime where occasional fires destroyed the tall, forest vegetation that tended to replace the Acacias. Occasional fires may still be necessary for the continued existance of some members of this genus: others occupy habitats unsuitable for climax forest, and the longevity of the seeds of some species may enable them to replace climax species as these die of old age (Cunningham & Cremer, 1965; Farrell & Ashton, 1978; Gilbert, 1959; Majer, 1977; Noble & Slatyer, 1977; Withers & Ashton, 1977; Howard, 1974; Purdie, 1977; Preece, 1971; Weisser & Marques, 1979).

In the sub-climax Acacia communities of arid and coastal areas, it is unlikely that seed longevity would be as important for survival as rapid germination. It is not surprising then that the African Acacias, particularly A. albida, which occurs throughout the African savannas, appear to have a higher percentage of 'soft' seed than most of the Australian species (Appendix II). A. harpophylla F. Muell. and A. argyrodendron Domin., both of which dominate the scrub in parts of semi-arid Queensland, are exceptional among Australian Acacias in that their seed is thin-coated, and retains its viability for only a few months. Both these species, like many of the African species, regenerate after the frequent fires by coppicing and root suckering (Pedley, 1978; Coaldrake, 1971).

In Africa and Australia it has been found that Acacia population desities can be manipulated by controlling fire frequency and intensity. Seed viability of many Acacia species is reduced by being heated in the soil to 100°C for five minutes or more (Floyd, 1966, 1976). Temperatures of this magnitude occur in the top 2.5 cm of sandstone-derived soil during natural forest fires (Beadle, 1940), and a slow, hot fire killed all Acacia seed to this depth, and stimulated germination from 8.5 cm below the soil surface (Floyd, 1966; Cunningham & Cremer, 1965).

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Where Acacia seeds are deeply buried in ant nests (Majer, 1978) or are covered by a thick carpet of litter (Donald, 1959), very little germination occurs unless there is a hot burn. A succession of cool fires, such as are used in the management of Eucalypt plantations in West Australia, can lead to the disappearance of the Acacia understory (Bridgewater, pers.comm.).

In African Acacia savanna, the annual production and death of the grass understory makes it possible to achieve hot burns annually. This type of management favours grass and herbs at the expense of woody perennials, and is used to increase the carrying capacity of the land for grazing animals (Adams, 1967; Joubert, 1966; Pratt & Knight, 1971; Story, 1952; West, 1965.

In Australia, short rotation (1-3 year) burns of Acacia-dominated communities can only be achieved artificially by spraying the saplings with desiccant (Cunningham & Cremer, 1965). Whereas short-rotation burns reduce the density of Acacia populations, medium-frequency burns (15-50 years) result in denser stands of many of the seed-regenerating species (Floyd, 1976; Cunningham & Cremer, 1965). Where fires are only occasional (100-500 years), Acacias are present in the community as living trees for less than a century, and as dormant seed for the remainder of the cycle. (Gilbert, 1959; Howard, 1974; Cunningham & Cremer, 1965).

If fire could be excluded from climax vegetation throughout the lifetime of the Acacia seed, Acacias would, theoretically, disappear from the community (Noble & Slatyer, 1977). It is unlikely that this often occurs in practice since the fall of forest trees opens up the canopy sufficiently for Acacia seedlings to become established (Gilbert, 1959; Withers, 1978).
The low stature of Fynbos, and the patchiness of coastal bush, make it unlikely that fire exclusion alone would prohibit the reestablishment of

exotic Acacias in these communities in the S.W. Cape.

The management practices that have been found effective in the reduction of Acacia density in Australia are

(1) hot burns followed by Acacia-selective grazing (Floyd, 1966, 1976; Cunningham & Cremer, 1965),

(2) cool burns (Bridgewater, pers.comm.),

(3) short-rotation burns (Cunningham & Cremer, 1965) and

(4) exclusion of fire (Noble & Slatyer, 1977).

Germination of Acacia seed after fire is generally more prolific than after soil-turning or clearing. This may however, not apply to sites where the majority of the Acacia seed is old (climax forest, pasture), as Acacia seed dormancy is apparently broken by aging or weathering. At all local sites investigated, fire was found to be more effective than clearing in inducing germination and reducing the seed store. The effects of fire and clearing on germination at local sites are listed in Table 11. 26% of the A. cyclops seed germinated after the fire, and an additional 67% appears to have disappeared, probably having perished in the fire or died subsequent to germination. A. cyclops seed reserves decline more rapidly than those of A. saligna after clearing possibly because their dormancy is more rapidly broken by aging. The number of seedlings counted on cleared land was higher than that counted under thickets (level of significance 0.01), and seedling survival in thickets appeared to be minimal.

In the Cape, where the distribution of Acacia seed in soil is very even, both hot and cool fires will result in massive seedling germination. Hot burns however destroy more seed than cool burns. Fynbos vegetation subject to fire management should be searched for Acacias some months before being burnt. The Acacias should be felled and the branches stacked over the stump to ensure a localised hot burn. Burnt areas should be checked for Acacia regeneration within a year of the fire, and weeded, as the density of exotic Acacias are likely to increase under a burning regime. Natural areas from which fire is excluded should also be checked periodically since fire exclusion is no guarentee against import and establishment of Acacias in low, sparse or clumped vegetation.

Of the management practises found effective in Australia for reducing the density of Acacia stands or removing them from a position of dominance, all but the first noted above would be impractical or ineffective in the S.W. Cape. A hot burn, followed by destruction of all seedlings would seem to be the most rapid and certain way of removing Acacia thickets and their seed.

Wind

The prevailing wind can influence the pattern of fall of Acacia seed around the parent tree (Story, 1952), and could possibly cause seed to blow into streams and onto moving vehicles. However it is a minor agent in Acacia seed dispersal.

By splitting or toppling A. cyclops, A. longifolia and A. saligna trees between 30 and 40 years old, the wind brings about a continual patchwork regeneration of Acacia thickets in the Cape. Gaps in the canopy are soon colonised by Acacia saplings and grasses, making it improbable that the Acacia thicket as a whole will become senescent and gradually be replaced by shade tolerant indigenous vegetation.

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Table 11. The effect of clearing and burning on the germination of the seed of exotic Acacia seed in the Cape.

Site and Species	Time (mth) since treatment	seed/m^2 *	Thicket		Cleared			Burned		
			Seedlings per sq m	Percent germin.	Seedlings per sq m	Percent germin.	Percent remain	Seedlings germin.	Percent germin.	Percent remain
Silvermine A. longifolia A. saligna	2	-	107 (22)**	-	336	-	-	3284 (650)	-	-
Penhill A. saligna	3	11917 (811)	14 (9)	less than 1	175 (101)	1	86	2388 (9612)	20	-
Rondevlei A. cyclops	12	1571 (330)	46 (10)	3	13 (5)	1	56	409 (53)	26	7
Goukamma A. cyclops	12	2523 (983)	0.1	less than 1	10	less than 1	18	-	-	-
Goukamma A. saligna	12	9268 (1019)	10	less than 1	23	less than 1	94	-	-	-
University of Cape Town A. longifolia	12	2110 (696)	0	0	50 (16)	2	-	-	-	-

* Data from Appendix I

** Figures in parenthesis are standard errors of the mean

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Water

Although A. saligna seedlings can utilize excess water (Fox & Wallman, 1979) prolonged waterlogging kills A. cyclops and A. saligna trees. The seed, which is water impermeable, is not affected by long periods of immersion in fresh or salt water (Cambage, 1924; Rolston, 1978). Moving water is an important dispersal agent for the exotic Acacias in the S.W. Cape. Phillips (1928) reported that A. melanoxylon had spread at least 20 miles (33 km) along a stream bank within 13 years of its establishment in a single upstream plantation. In the S. and S.W. Cape, A. mearnsii, A. longifolia and A. melanoxylon are constantly being carried into nature reserves by the rivers (P. Cattell & P.C. van Rooyen, pers. comms.). In the drier W. Cape, A. saligna and A. cyclops often line the stream banks of industrial and farming areas. Even the seasonal rivers of the Cedarberg (2000 m) are infested with A. saligna which has spread from plants introduced to the scattered mountain farms.

During a survey of the benthic fauna of a local estuary, exotic tree seeds, in densities of about 60 seeds/m^2, were found in the bottom sediments. They included A. cyclops, A. saligna, A. longifolia, A. mearnsii and Albizia lophthantha - all species which are common in the river catchment. As the seeds were found to be viable, silt dredged from this and other estuaries with weed infested catchments, is a carrier of invasive species.

Thickets of Acacias along river banks and lake margins are not only undesirable as a source of infection, but also because they fall and clog waterways (Cattell, pers.comm.), alter the habitat for terrestrial and aquatic animals, and probably have high interception and evapotranspiration rates (van der Zel, 1979).

Dispersal of the dune-colonising species, A. cyclops and A. saligna, by currents and high tides, has not been documented, but is likely.

Biotic agents

Seed destruction and dispersal

The seed of African Acacias is chiefly distributed by large mammals, which feed on the pods. These are indehiscent, and generally contain seeds in various stages of maturity. Some of the seeds are digested by the animal, the remainder are passed intact with the dung (Palmer & Pitman, 1972; Story, 1952; Bews, 1917; Radwanski & Wickens, 1967). Small mammals (Sief el Din & Obeid, 1971), and birds (Wickens, 1969) destroy fallen seed and unripe pods, but insects, particularly Bruchid beetles, destroy the greater part of the annual seed crop of the American (Janzen, 1965) and African Acacia species (Seif el Din & Obeid, 1971; Story, 1952; Wickens, 1969; Southgate, 1978). Other common seed-destroying insects include Lamellicorn beetles, which feed on green pods, Chalcid wasps which parasitise the seed, and a Hemipteran, Nariscus sp., which sucks out the seed contents (Story, 1952). All these insects occur on A. karoo, the distribution of which partly overlaps that of the exotic Acacias in the Cape.

Australian Acacias differ from those in other parts of the world with regard to their dispersers and predators. The seeds of the Australian Acacia species are generally smaller than those of the American and African species and have more elaborate funicles (Guinet & Vassal, 1978). Most Australian Acacia seeds have swollen white funicles no larger than the seed itself. These attract ants which gather up 50 - 90% of the annual seed crop, feeding on some of it, and burying the remainder in their nests (Berg, 1975; Majer, 1978; Withers, 1978). A few of the Australian Acacia species with non-deciduous pods, have a showy, red, arillate funicle which probably attracts birds (van der Pijl, 1969) such as Lorikeets and Pigeons (Pedley, 1978).

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Two of the exotic Acacia species in the S.W. Cape, A. cyclops and A. saligna, have arillate funicles, and are bird dispersed (Glyphis, unpubl.; Glyphis & Milton, in prep; Middlemiss, 1963; Phillips, 1928; Winterbottom, 1970). Other dispersers of the exotic Acacia species in South Africa are man and other primates (P. Cattell, pers.comm.; Davidge, 1976; Middlemiss, 1963), large mammals (Phillips, 1928; Ridley, 1930), rodents and ants (Phillips, 1928), all of which my own observations have confirmed.

In Australia, the potential seed crop of the Acacias appears to be reduced at the flowering stage rather than mainly after seed formation. A gall-rust, Uromycladium tepperanum McAlpine, which attacks Albizia and Acacia species in west and east Australia, has many species-specific strains (Gathe, 1971; Van den Berg, 1977). A. saligna populations in West Australia may be 80 to 90% infected with this fungus (Morrellini, unpubl.; Van der Berg, 1977) which also attacks A. cyclops and A. longifolia (Gathe, 1971). The flowers and vegetative buds of some of the species, including A. longifolia, may also be heavily parasitised by wasps (van der Berg, 1977), and in arid West Australia, flocks of birds have been known to destroy whole crops of unripe pods (Davies, 1976).

Although Bruchid beetles are insignificant as Acacia seed parasites in Australia (New, 1979; Pedley, 1978), the ripe seed may be destroyed by parrots and other seed-eating birds (Preece, 1971; Davies, 1976), ants (Majer, 1978; Withers, 1978), Chalcid wasps (Preece, 1971), Hemiptera and funicle mining Lepidopteran larvae (van der Berg, 1977).

In the S.W. Cape, few animals or pathogens make use of the flower, pod, and seed production of the exotic Acacias. Most are generalists, using the resource when it is abundant: seed eating birds, rodents (King, unpubl.; Shelton, unpubl.), baboons (Davidge, 1976), Vervet monkeys, and goats which can apparently digest most of the seed (Anon., 1975). An as yet unidentified funicle-mining Lepidopteran larva (Glyphis, unpubl.) is associated with A. cyclops throughout the present range of the exotic, as is a seed feeding Hemipteran (Heteroptera, Alydidae, one or two undescribed species), apparently homologous to Acacia seed bugs in Australia and America, (S. Neser, pers.comm.). This bug was also observed to feed on the unfallen seed of A. melanoxylon and A. mearnsii: all of which Acacia species have slowly developing or non-deciduous pods. If the small seed store at the Bredasdorp site was in fact the result of the abundance of these hemiptera on the trees, the bug may play an increasingly important role in the control of A. cyclops providing that its own predators do not increase as well. In Natal, various boring beetles, weavils, and heteroptera of minor importance have been found on the pods of A. mearnsii (Hepburn, 1966).

Many generalised herbivores eat the young phyllodes of the exotic Acacias. These include a variety of Orthoptera, weavils, Phasmida, Hemiptera such as Pentatomids and myrids, Lepidopteran larvae, especially Lasiocompidae, Geometridae and Lycaenidae, as well as buck and domestic stock. Of these, probably only the Lappet moth (Pachypasa capensis) and browsing mammals ever severely defoliate the problem Acacias in the S.W. Cape. Severe defoliation can reduce the seed crop for the year in which it occurs (Rockwood, 1974).

Seedling destruction

Permanent removal of Acacias from sites they occupied necessitates destruction of dormant seed in the soil. The most obvious way to do this is to make it germinate, and then to remove the seedlings. Herbicides, flame-throwers, cultivation and manual weeding are used at present, but a more selective, more economical method, less destructive to other plants and animals, is required. The use of pathogens, predators and plant competition should be considered.

Acacia seedlings, particularly when crowded and growing in the shade, are susceptible to fungal attack. 74% of A. cyclops seeds germinating under the parent canopy at the Rondevlei site, had died, apparently of fungal attack, within one month of germination. Likewise, Scowcroft et al (1976) found that 50% of the seedlings of A. koa germinating after a fire on Hawaii, were killed within a year of germination by root-crown (Calonectria) and other fungi, and fungal infection caused the deaths of A. pycnantha seedlings germinating in their natural habitat in Victoria (Withers, 1978).

Wire-worms, white grubs and cut-worms (larval Coleoptera and Lepidoptera) are commonly found in the soil where Acacia seeds are germinating, and it is reported that these, together with termites, destroy A. mearnsii seedlings in South African nurseries (Hepburn, 1966; Wattle Research Institute, 1975; Sherry, 1971). Snails (Helix aspera) destroyed seedlings of the study species grown in containers at the University of Cape Town nursery, and snails and slugs feed on the seedlings of indigenous Acacias as well (Brown & Booysen, 1967). Older seedlings are eaten by generalist phytophageous insects, hares (Sherry, 1971) and larger browsing mammals.

Selective browsing of the seedlings of Acacia species in preference to those of other genera has been reported from both Africa and Australia, and is probably related to the nutritional value of these nodulated plants. Goats, cattle, buck, hare and their marsupial counterparts have been found to take Acacia seedlings in preference to those of other forest, savanna heathland or coastal shrubs, and can reduce their density relative to the other species (Story, 1952; Sherry, 1971; Cowling, unpubl.; Seif el Din & Obeid, 1971; Donald, 1959; Preece, 1971; Cunningham & Cremer, 1965).

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Acacia seedlings are light demanding. They do not survive under dense vegetation or in artificial shade, and even A. melanoxylon, a relatively shade-tolerant species, can be out-competed by fast-growing indigenous species if it is selectively grazed (Donald, 1959). If plant competition on sites cleared of Acacias could be increased by sowing fast growing grasses or shrubs, or by the addition of fertilizer, Acacia seedlings could be shaded out.

The economic and practical feasibility of using selective grazing and plant competition in the control of Acacia have yet to be tested on the exotic Acacias in the S.W. Cape, but they have proved successful on a small scale in Australia (Cunningham & Cremer, 1965) and are the basis of grassland savanna management in Africa.

CONCLUSION

A summary of the relevant findings serves to introduce some suggestions for the management of exotic Acacias in the S.W. Cape. It is emphasised that all management methods proposed here still require field testing: they are not well tried techniques suitable for application on a large scale.

Although less than one percent of the flowers produce mature pods, the seed production of A. cyclops is in the order of 1000 to 3000 seeds/per m^2 of projected canopy area per annum, and that of A. saligna, A. longifolia and A. melanoxylon at suitable sites in the order of 3000 to 10000 seeds/m^2/annum.

Seed stores for all species investigated were one and a half to three times as great as the annual seed-fall, and under old thickets, were up to five times as large as the annual seed crop. Losses of seed from the soil are chiefly due to germination. Seed accumulates relatively slowly under thickets of A. cyclops, which has smaller seed crops and a shorter period of dormancy than the other Acacia species studied.

The seed was evenly distributed in thickets on level ground, but concentrated in hollows and drainage lines on uneven ground. Very little seed extends beyond the projected canopy area of isolated trees. Most of the seed is found beneath the litter in the upper 8 cm of soil, but in loose sandy ground, may be found to a depth of at least 36 cm.

Seed extracted from the soil was at least 85% viable, and viability did not appear to diminish with age. Processes which make the testa water-permeable, including heating, abrasion and aging, break the seed dormancy. The testa of A. cyclops seed may be broken down more rapidly by aging than that of the other Acacia species. Fire is more effective than clearing in inducing mass germination.

Management suggestions

Since A. cyclops seed dormancy appears to be broken by two or three years of aging, burning is not required to ensure complete germination. Burning destroys litter and humus, and so is best avoided in coastal areas with loose sand. When A. cyclops thickets in such areas are cleared, fire should be excluded, and its seedling regeneration weeded out annually. On large tracts of land and in areas isolated from indigenous vegetation, it may be necessary to supplement the indigenous seed supply by sowing such species as Ehrharta villosa, Ehrharta calycina, Chrysanthemoides monilifera, Metalasia muricata, Myrica cordata and Rhus species, all of which have previously been used by the Forestry and Roads Departments of the Cape Province with some success for stabilization work (Walsh, 1968; Matthaei, 1976).

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At the Goukamma Nature Reserve in the Southern Cape, felled A. cyclops was stacked in rows. These acted as wind-breaks, while the shade they cast prevented A. cyclops seedlings from becoming established beneath them. The open ground between the rows was rapidly colonised by annual forbs and creeping dune grasses. A. cyclops seedlings, which germinated in large numbers between the brush rows, were removed by hand weeding of the accessible open strips. Numerous Striped Field Mice (Rhabdomys pumilio) were observed in the brush rows for about a year after clearing, and as these mice fed on Acacia seed both under and between the brush rows, they are thought to have contributed to the relatively rapid reduction of seed at this site. This method, devised by the warden of the Goukamma Nature Reserve, appears to be leading to the reestablishment of indigenous bush on steep coastal sand dunes.

For the permanent removal of A. longifolia, A. mearnsii, A. melanoxylon or A. saligna from a site, fire exclusion and weeding would probably be inadequate except in the special case of indigenous forest or a small area of intensively managed land, such as Kirstenbosch Gardens. Here clearing followed by mulching and frequent weeding led to the reestablishment of indigenous Fynbos within thirteen years on 200 ha of land once infested with alien plants including these four Acacia species (Marais, 1979 & unpubl.).

Of the other Australian methods found to reduce Acacia density, short rotation burning is impractical in dense stands because of the greenness of the saplings and the cost of using a desiccant spray, and in cases of light infestation, because the recovery time of the larger Fynbos species is possibly longer than that of most Acacia species. The use of cool, rapid burns is also unsuitable here becuase of the even, shallow distribution of seed in the soil, and because this method is likely to favour A. saligna which coppices strongly after fire.

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For maximum Acacia seed destruction, and for stimulation of the most deeply buried seed, fires should be as slow and as hot as possible. This can be achieved in the case of dense infestations by felling the Acacias four to six months before the burn, and spreading the felled trees evenly over the cleared area. A spring burn is recommended as this would kill coppice shoots, root suckers and seedlings which have grown during the winter, while stimulating mass germination of deeply buried seed, most of which should die during the dry summer.

Where isolated Acacias occur in patches of natural vegetation, it is recommended that these be felled some months before burning, and the branches placed over the seed shadow of the felled bushes. This should result in hot spots in the generally cool Fynbos fire (Taylor & Kruger, 1978; Martin, 1965) which will kill or stimulate germination of the majority of Acacia seeds. All indigenous vegetation managed on a burning rotation should be checked within two years of the fire for Acacia regeneration, and weeded if necessary.

Spraying of Acacia seedlings with Paraquat (1,1'- dimethyl -4,4'- bipyridylium dichloride), while they still bear only pinnate juvenile leaves, followed by annual weeding for three or four years, has led to the replacement of exotic Acacia thickets with indigenous pioneer species at some sites on the Cape Peninsula mountain chain.

As alternatives to the use of herbicides in water catchments, recreation areas and nature reserves, selective grazing and fertilization should be considered.

Acacias boost the nitrogen status of soils (Sherry, 1971), and this favours grasses and cereal crops when the Acacia thickets are cleared. Although

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the nodulation of Acacia saligna seedlings grown in pots was increased by the addition of nitrogen (ammonium sulphate) (Fox & Wallman, 1979), nodulation of plantation trees (A. mearnsii) decreases as soil nitrogen increases (Hallsworth, 1958). Acacias respond to phosphorous addition (Barrow, 1977; Schönau, 1971; Sherry, 1971:216) but not to nitrogenous fertilizers (Schönau, 1971). Fertilizer appears to increase the competitive abilities of non-nodulated plants relative to Acacia. This is well illustrated by Muir's (1977) observation that Acacias are less prominent in vegetation receiving leachate from fertilised farmland, than in otherwise identical vegetation receiving no extra nutrients.

Fertilization is unlikely to favour Fynbos plants, many of which respond poorly to fertilizers (FFTRI, 1972) or which, like Australian sclerophyll may become mesophytic and less drought resistant in response to fertilizer (Specht, 1973). It may favour annuals and grasses, some of which are known to compete strongly with Acacia. These include Cynodon dactylon and Eragrostis curvula (Sherry, 1971), which are commercially available, and grow well in the S.W., S. and E. Cape (Dawson & van Wyk, 1979). In coastal areas, Ehrharta villosa and E. calycina would be more successful. Depending on the form of land use planned, shrubby species could later be sown to replace waning grass cover. The use of annual species such as Lolium rigidum and Avena species may be preferable where eventual return to indigenous vegetation is desired.

Selective browsing of Acacia leading to its failure to dominate the community has been observed in Australia (Cunningham & Cremer, 1965; Preece, 1971), Hawaii (Scowcroft & Wood, 1976), Kenya (Pratt & Knight, 1971) and for exotic A. melanoxylon in the forests of the Southern Cape (Donald, 1959). It is possible that fertilization may magnify this effect by further boosting the nutritional value of Acacias, as well as increasing competition from the grasses and other non-nodulated plants. Fertilising has been found useful in the eradication of bramble from open areas, because in response to fertilizers, bramble (Rubus sp.) produces soft, nutrient-rich new shoots after clearing. These are browsed off by cattle, and reinfestation is prevented by sowing of Eragrostis grass (Haigh, in press).

Taxonomically, the exotic Acacias in the S.W. Cape still fall well within the limits for the species in Australia (Maslin, pers.comm.), and there is no evidence that significant changes have occurred in their phenology (Milton, in prep.). Biological control using imported Australian organisms should then theoretically be possible where the environment is suitable for them. The ideal form of control in the South African situation, would be the reduction of the reproductive potential of the exotic Acacias. This would permit the continued use of Acacia species for wood, bark, stabilization and ornament, without their being a threat to indigenous vegetation and a costly nuisance on vacant land.

To this end experiments are now being carried out on an Australian wasp, Trichologaster acacia-longifolia, which parasitises apical and inflorescence buds of Acacia longifolia (Van den Berg, 1980), and other seed-destroying insects and pathogens are being selected for further study.

The general conclusion reached after completing the present study of the reproductive biology of the Australian Acacias in the Cape, is that their vast output of dormant seed and the build-up of this in the soil in the absence of adequate predation, is they key to their success, and must be controlled if these plants are to supplement rather than reduce the economic and aesthetic value of the land.

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APPENDIX 1A Estimates of the exotic Acacia seed-bank and its viability in the S.W. and S. Cape, South Africa

* core dimensions : 7.5 cm diameter, 15 cm long

** core dimensions : 7 cm diameter, 7 cm long

*** germination after hot water treatment

**** germination with no form of prior treatment

Sample	Site	Species	Site description	Sample size	Seed number per sq m	% error of mean	minimum % viability ***
1	Rondevlei	A. cyclops	Thicket, c 30 yr	50 cores*	1571	21	89
2	Kommetjie	A. cyclops	Seed shadow of very old tree	9 cores	5899	32	—
3	Rondevlei	A. cyclops	Thicket c 30 yr	10 cores	2244	39	—
4	Rondevlei	A. cyclops	Thicket c 30 yr	10 cores	1136	26	—
5	Rondevlei	A. cyclops	Thicket c 30 yr	10 cores	1306	41	—
6	Coukamma	A. cyclops & A. saligna	Thicket c 40 yr	9 cores	10773	52	—
7	Coukamma	A. cyclops & A. saligna	Thicket c 40 yr	15 cores	10311	91	—
8	Penhill	A. saligna	Young stand, long history of infestation. 5 mth cleared	1/4 m^2 to 32 cm deep	12652	—	86
9	Penhill	A. saligna	As above, 10 mths after clearing of Acacias	1/4 m^2 to 25 cm deep	13792	—	97
10	Penhill	A. saligna	As above, 15 mths after clearing of Acacias	50 cores	10152	32	91
11	Penhill	A. saligna	Adjacent to above site, not cleared. 8 mth after seedfall	50 cores	11070	18	94
12	Faure	A. saligna	7 yr old thicket, land has history of infestation	50 cores	7586	31	78

APPENDIX 1A   Estimates of the exotic Acacia seed-bank and its viability in the S.W. and S. Cape, South Africa

* core dimensions : 7.5 cm diameter, 15 cm long

** core dimensions : 7 cm diameter, 7 cm long

*** germination after hot water treatment

**** germination with no form of prior treatment

Sample	Site	Species	Site description	Sample size	Seed number per sq m	% error of mean	minimum % viability ***
13	Marina da Gama	A. saligna	Thicket, 4 yr old, recent introduction to natural site	50 cores	145	30	91
14	Stellenbosch	A. saligna	Seed shadow of isolated, very old tree, clay soil	1/4 m^2 to 5 cm deep	11932	--	--
15	Univ. of W. Cape	A. saligna	One yr after clearing and burning old stand	100 cores	2694	16	86
16	Univ. of W. Cape	A. saligna	As above, 2½ yr after clearing and burning	14 cores	1373	33	--
17	Bredasdorp	A. cyclops	Thicket, medium aged, small & surrounded by natural veg.	10 cores	28	100	--
18	Univ. of Cape Town	A. longifolia	Thicket c 20 yr. Clay slope.	50 cores	2110	33	98
19	Villiersdorp	A. longifolia	Thicket, medium aged, sandy river bank	5 cores	13182	32	--
20	Villiersdorp	A. mearnsii	Very old thicket, alluvial sand	5 cores	38340	35	--
21	Goukamma	A. cyclops & A. saligna	Thicket, c 40 yr. Cleared 2 yr ago.	9 cores	2070	--	--
22	Goukamma	A. cyclops	Dune thicket, c 40 yr, cleared 1 yr ago.	9 cores	667	65	--
23	Goukamma	A. cyclops & A. saligna	Dune thicket, c 40 yr, cleared 1 yr ago	19 cores	9217	42	--
24	Goukamma	A. cyclops & A. saligna	Dune thicket, c 40 yr, cleared 2 yr ago	19 cores	4424	36	--
25	Goukamma	A. cyclops & A. saligna	Dune thicket, c 40 yr, cleared 2 mth ago.	5 cores	2726	--	--

APPENDIX 1A Estimates of the exotic Acacia seed-bank and its viability in the S.W. and S. Cape, South Africa

* core dimensions : 7.5 cm diameter, 15 cm long

** core dimensions : 7 cm diameter, 7 cm long

*** germination after hot water treatment

**** germination with no form of prior treatment

Sample	Site	Species	Site description	Sample size	Seed number per sq m	% error of mean	minimum % viability ***
26	Lakes Nature Reserve	A. cyclops	New infestation in natural vegetation. c 7 yr old.	8 cores	303	44	—
27	Rondevlei	A. cyclops	Thicket c 30 yr. Cleared and burned 1 yr ago.	50 cores	108	36	94
28	Rondevlei	A. cyclops	Thicket, c 30 yr. Cleared 1 yr ago.	50 cores	886	36	78
29	Maitland Cemetary	A. saligna	Presently under grass. 100 yr of recurrent thickets	1/4 m^2 to 16 cm deep	108	—	—
30	Shelton unpubl.	A. cyclops & A. saligna	Cape Flats, old thicket	4 x 1/4 m^2 surface	4020 - 9046	6	—
31	King unpubl.	A. cyclops & A. saligna	Cape Flats, old thicket	litter & 2 cm soil	201 -	14 - 8	—
32	Donald 1959	A. melanoxylon	Plantations & infestations in indigenous forest, Knysna	1/4 m^2 x 7 A1 horizon	2860 - 94420	—	90

APPENDIX IB Estimates of the seed bank of indigenous dune shrubs in a coastal Nature Reserve in the S.S.W. Cape.

33	De Mond	Sideroxylon inerme	Old trees, probably over 100 yr, leeward dunes	10 cores**	1416	28	****less than 1%
34	De Mond	Chrysanthemoides monilifera	Single species stand, seaward dune	15 cores	301	31	"
35	De Mond	Myrica cordifolia	Sprawling mat, dune hollow	5 cores	602	—	1%
36	De Mond	Euclea racemosa	Old thicket on leeward dune	10 cores	0	0	—
37	De Mond	Passerina rigida	Mature plant seed shadow seaward dune	5 cores	1386	—	c25

APPENDIX II. . The effect of various treatments on the dormancy of Acacia seed

HWT = hot water treatment

- = not tested

+ = effective in inducing germination

* = mean of up to ten species tested

** = mean of more than ten species tested

Species	Untreated % germin.	Percentage germination in response to treatment						Author
		HWT	fire dry-heat	cold	percussion abrasion	digestion acid	age	
A. cyclops	0	0	-	92	92	4	-	Welsh, unpubl.
	17	-	-	-	-	22	-	Glyphis, unpubl.
	1	15	-	-	92	34	-	Jones, 1963
A. decurrens	2	62	98	-	-	-	-	Beadle, 1940
	-	75	-	-	-	-	-	Osborne, et al 1931
	2	89	-	-	-	-	-	Larsen, 1964
A. elata	6	36	-	100	96	0	-	Welsh, unpubl.
	-	80	-	-	37	-	-	Clements et al
	2	48	-	-	-	-	-	Larsen, 1964
A. longifolia	-	96	-	-	96	-	-	Clements, et al
	5	-	100	-	-	-	-	Floyd, 1976
	0	72	-	-	-	-	-	Larsen, 1964
A. mearnsii	6	14	-	92	98	16	-	Welsh, unpubl.
	-	88	-	-	-	-	-	Osborn, et al
	-	99	-	-	-	-	-	Poggenpoel, 1978
A. melanoxylon	0	0	-	92	76	0	-	Welsh, unpubl.
	0.5	99	-	91	22	-	-	de Zwaan, unpubl.
	-	-	+	-	+	+	-	Phillips, 1928
	0	50	-	-	-	-	-	Farrell et al, 1978
A. pycnantha	-	100	-	-	-	-	-	Withers, 1978
	2	40	-	-	-	-	-	Larsen, 1964
A. saligna	6	64	-	-	96	90	-	Jones, 1963
	6	51	-	-	-	-	-	Larsen, 1964
Australian spp.	2	-	-	-	-	-	+	Preece, 1971
	8**	57	-	-	-	-	-	Larsen, 1964
	2*	-	99	-	-	-	-	Floyd, 1966
	12*	-	83	-	35	-	-	Floyd, 1976
A. karoo	9	63	47	-	89	-	-	Story, 1952
	24	-	-	0	53	56	-	Brown et al, 1967
A. albida	90 slow	90 slow	poor	-	95 rapid	90 slow	90 slow	Wickens, 1969
African spp.	40*	-	-	-	77	77	-	Brown et al, 1969
	-**	+	+	-	+	+	-	Carr, 1976

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EFFECTS OF SHADING ON NURSERY GROWN ACACIA SEEDLINGS

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ABSTRACT

This paper describes the effects of shading on four species of phyllodinous Australian Acacias (Mimosoideae) naturalised in the S.W. Cape: A. cyclops A. Cunn. ex G. Don., A. longifolia (Andr.) Willd., A. melanoxylon R.Br. and A. saligna (Labill.) Wendl. The seedlings compensated for reduced light intensity by retaining their juvenile leaves longer, and by producing larger, more horizontally orientated leaves or phyllodes. The stems of the shaded plants were etiolated and their root area, and root and shoot dry masses were less than those of plants grown in full sunlight. Although the seedlings of all four species survived for fifteen months in 75% shade, A. melanoxylon was more shade-tolerant than the other species. Shading, achieved by the use of "smother crops" or by heaps of brushwood, may prove effective in the control of Acacia regeneration, provided that at least 90% light reduction can be obtained.

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INTRODUCTION

Some of the Australian Acacia species introduced to South Africa during the mid nineteenth centuary have become naturalised, and are now considered to be problem plants on disused land and in the indigenous vegetation of the South Western Cape (Taylor, 1975; Hall & Boucher, 1977). After the removal of unwanted Acacia thickets by fire or felling, the regeneration is generally controlled by herbicide treatment, slashing or weeding. An economical control program, less damaging to the remaining indigenous plants and to the environment, is needed.

Methods suitable for controlling shrub encroachment in grasslands, such as the use of browsing animals, or annual burns, cannot be considered for use in the shrubby Fynbos which often grows in shallow soil on steeply sloping ground. In their natural habitats in Australia or in Africa, there is very little Acacia seedling regeneration beneath the canopy of mature Acacia trees (Howard, 1974; Obeid & Seif el Din, 1970). There is also little or no regeneration under thickets of plantations of Acacias growing as exotics (Donald, unpubl.; Milton, unpubl.), and Acacia seedlings rarely survive under closed canopies of grasses (Brown & Booysen, 1967) or other genera of trees or shrubs (Roux & Middlemiss, 1963; Gilbert, 1959; Howard, 1974; Noble & Slatyer, 1977).

Lack of Acacia seedling regeneration under a canopy could be due to either enforced dormancy, or to low seedling survival rates. The latter is more acceptable since Acacia seeds can germinate in the dark (Preece, 1971), and numerous seedlings have been observed under the deep shade of Acacia thickets during the rainy season although few survive.

A number of factors may be responsible for the death of Acacia seedlings growing beneath taller plants : competition for water and nutrients, competition for light, susceptability to pathogens or inhibition by chemicals released by the roots or litter of the dominant plants. Although there is evidence that A. longifolia seed germination is inhibited by the litter of its own and other species, this is not considered to be the major factor causing poor regeneration under plant cover (McDowell, unpubl.). Except in cases where water availability is the limiting factor, root competition is probably not responsible for the death of Acacia seedlings. The fact that heaps of brushwood control Acacia regeneration as errectively as cover provided by living trees (Milton, unpubl.) supports this premise, and indicates that the failure of seedlings to survive under a canopy is directly or indirectly the result of shading. This is not unexpected in the genus Acacia, where most of the species are heliophilous members of the early seral stages of succession (Weisser & Marques, 1979; Brown & Booysen, 1967; Noble & Slatyer, 1977; Pedley, 1978).

If shade could be used to control regeneration, it would have the advantage of disturbing the soil and remnant vegetation less than would mechanical methods. Shading has been used successfully to control an alien weedy grass, Stipa trichotoma Nees, in New Zealand (Wells, 1977), and is recommended for the control of Baccharis halimifolia L (Asteraceae), a woody perennial weed, in Australia

(Panetta, 1977).

This study is concerned soley with the effects of shade on Acacia seedling growth and morphology : predation, competition and allelopathy were eliminated or equalised as far as was possible.

METHODS

The Effect of light on germination

Two hundred seeds of A. longifolia and two hundred of A. saligna were pretreated by pouring boiling water over them and letting them steep until the water cooled. They were then placed on moist filter paper in petri-dishes. Half of the treated seeds of each species were then immediately placed into a box which excluded the light. The remaining seeds were placed on a window sill. After 6, 11 and 28 days, germinating seeds were removed and counted. The aim of this experiment was to find out whether the germination of these species was affected by light.

Nursery experiment

Locally collected Acacia seed was pretreated with hot water, as before, and germinated in controlled environment chamber (temperature 22 - 25°C; 12 hous daylight). After seven days, 80 seedlings of each species were planted in one-litre nursery bags. Clay loam was used as the potting medium for A. longifolia (Andr.) Willd. and A. melanoxylon R.Br., but A. cyclops A. Cunn. ex G. Don. and A. saligna (Labill.) Wendl. were planted in sand collected on the Cape Flats : these are the types of substrate normally found in the habitats infested by the respective Acacia species. Both media had been sieved to facilitate the extraction of the root system.

The nursery bags were arranged in two sets, each set comprising two rows of 20 plants each for each of the four species. The rows were randomly arranged with respect to one another, and the whole set was surrounded by sand-filled 'blank' nursery bags, so that the roots of the plants in the outside rows would not be heated more than those of the inner rows. Plastic sheets under the containers prevented the Acacia roots from growing down into the ground, or the grass roots from penetrating the nursery bags.

One set of plants was covered by black nylon shade-cloth which excluded 75% of the incident light. This was stretched over a one metre high frame, and reached the ground on all four sides. The other set of seedlings was located in an open area where it would not be shaded by trees or buildings.

After eight months, some of the A. cyclops and A. saligna seedlings were transplanted into five-litre containers. For this reason, their height and mass at 10 and 15 months is not comparable with that of the other two species which were still growing in one-litre bags.

Measurement of parameters

Seedlings were harvested at 3, 4, 6, 8, 10 and 15 months after germination. The data collected at each harvest is tabulated in

Table 1. As the seedlings grew, some of the parameters became too time-consuming to measure, while the measurement of others became possible.

Root systems were extracted by washing the decanted plant over 1 mm plastic mesh. Root length was estimated by a method adapted from Rowse & Phillips (1974). Washed roots were spread out on a plastic sheet on which a grid of black lines, one or two centimeters apart, had been printed, and the root/grid-line intersections were counted. An estimate of root length was obtained from an equation (1) based on Rowse & Phillips (1974).

$$L = \tfrac{1}{2}\pi \,.\, D/2 \,.\, N \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots(1)$$

where L is the estimated root length; D is the size of the grid squares and N is the number of root/grid-line intersections. This method gave results which compared favourably with results obtained by the tedious method of measuring each rootlet with dividers and a ruler. The root surface area was calculated from estimated root length, using the formula for the surface area of a cylinder. The average size of a photosynthetic organ (based on five sets of measurements per plant) was calculated using equation 2.

$$L \,.\, B \,.\, C \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots(2)$$

where L is the length, and B the breadth of the photosynthetic organ, and C is a factor estimated to compensate roughly for its non-rectangular shape: 0.5 for the fusiform phyllodes of <u>A. saligna</u>,

TABLE 1. Parameters measured at each seedling harvest.[2]

Parameters	Age at harvest (months) 3	4	6	8	10	15
shoot length (cm)	*	*	*	*	*	*[1]
shoot dry mass (g)	*	*	*	*	*	*
total foliage area (cm^2)	*	*	*	*		
pinnate leaf number	*	*	*	*	*	*[1]
intermediate leaf number	*	*	*	*	*	
phyllode number	*	*	*	*	*	*[1]
root surface area (cm^2)	*	*	*			
root dry mass (g)	*	*	*	*	*	
nodule number	*	*	*	*		
nodule dry mass (g)				*	*	
foliage moisture content (%)					*	
stem moisture content (%)					*	
root moisture content (%)					*	
lateral shoot number					*	*[1]
leaf or phyllode size (cm^2)					*	*[1]
leaf or phyllode inclination (deg)					*	*
internode length (cm)					*	*[1]
basal circumference (cm)						*[1]
replicate number per species and treatment	5	5	5	2	2	5

[1] data gathered from only *A. longifolia* and *A. melanoxylon* in 15th month

[2] results are tabulated in Milton, 1980, unpublished thesis

0.6 for pinnate leaves, and 0.7 for phyllodes of A. cyclops, A. longifolia and A. melanoxylon.

The total photosynthetic area was calculated by multiplying the mean leaf or phyllode size by the number of these organs on the plant. This statistic probably represents only half the actual photosynthetic area, because the dorsal and ventral surfaces of phyllodes appear to be identical.

In assessing the orientation of a leaf or phyllode, inclination, but not rotation was measured (Figure 1). The angle between the axis of the leaf or phyllode and the vertical gave an indication of verticality, 0° being vertical, and 90°, horizontal. This measurement was independent of stem angle, an important consideration in the case of lateral branches and tilted leader shoots.

After all other parameters had been measured, root and shoot were separated, oven-dried at 100°C for 24 hr, and then weighed.

Relative growth rate (RGR)

RGR was calculated using equation 3, taken from Evans (1972).

$$\mathrm{RGR} = \frac{\log e \;\; {}_1W - \log e \;\; {}_2W}{{}_2T \; - \; {}_1T} \quad \ldots\ldots\ldots\ldots(3)$$

where ${}_2W$ and ${}_1W$ are the dry weights at the beginning and end of the harvesting period ${}_1T$ to ${}_2T$, and the units are grams g^{-1} month $^{-1}$.

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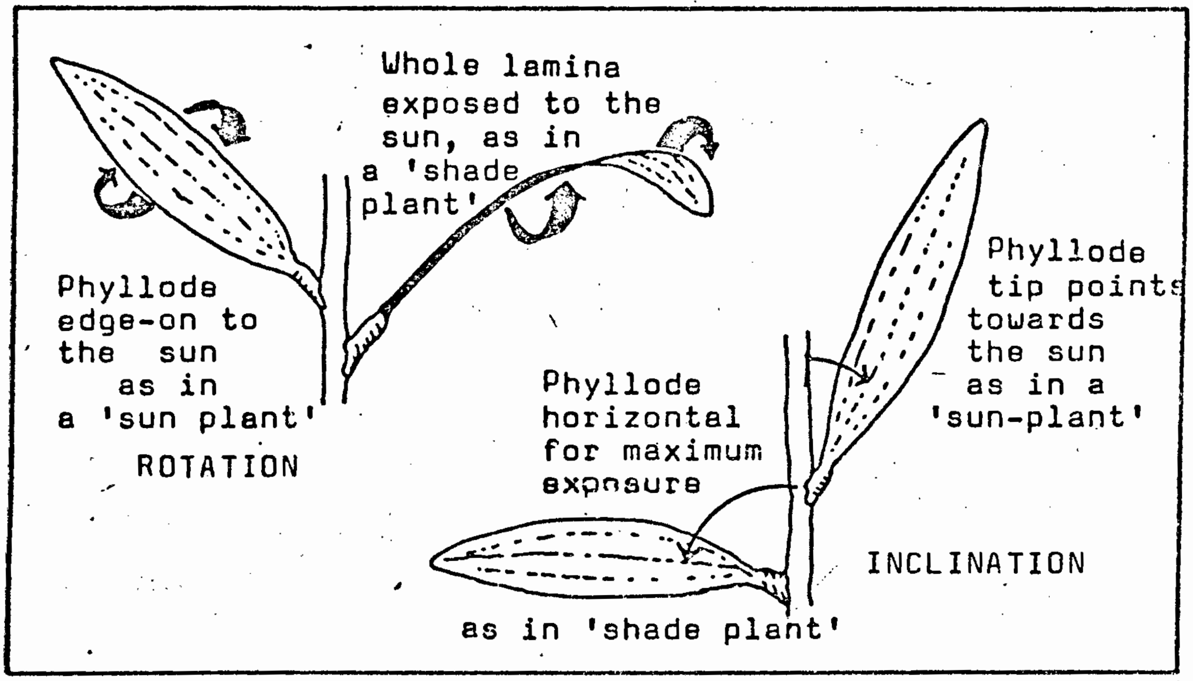
Figure 1. Foliage orientation, showing: ROTATION with phyllode (a) edge-on to the sun and (b) with lamina facing the sun, and INCLINATION with phyllode (a) near horizontal and (b) near vertical.



Field studies

The relative light intensity under the shade of an isolated tree and under heaps of brushwood was measured using a camera light meter (Sekonic Studio model). Paired measurements were made, a few seconds apart in time, in shade and in the open. Light intensity in the shade was calculated by dividing the shade reading by that obtained in the open, and is given as a percentage.

Measurements of the height of A. melanoxylon seedlings growing under a parent tree and in the open were made at monthly intervals over a period of 18 months. These results are of interest as the possible occurrence of allelopathy, competition, predation and drought stress could not be controlled in the field.

RESULTS

Effects of light on germination

The results of a pilot experiment (Table 2A) show that the germination rates of A. saligna and A. longifolia were similar in light and in darkness. These results support those of Preece (1971) in Australia, who found that A. aneura Benth seed germinates equally well with and without light. It is therefore probable that shade prevents the establishment rather than the germination of Acacia seed. Light exclusion does, however, affect the morphology of the seedlings. 28-day old A. longifolia seedlings growing in the dark had a mean shoot/root ratio 4.00 compared with a ratio of 0.22 for seedlings growing in the light. In the absence of light, most of the available energy is channelled into shoot growth, and it is possible

TABLE 2A. Germination of Acacia seeds in light and in darkness

Days from HWT*	6				11				28			
Species	*A. saligna*		*A. longifolia*		*A. saligna*		*A. longifolia*		*A. saligna*		*A. longifolia*	
Treatment	0**	●	0	●	0	●	0	●	0	●	0	●
% seeds germinating (n = 100)	23	16	38	73	47	37	86	94	65	60	100	96

* HWT = Hot water treatment

** 0 = light; ● = darkness

TABLE 2B. Dry mass (g) of Acacia seedlings at 10 months in two container sizes (n = 1)

Species	*A. cyclops*		*A. saligna*	
Treatment	Sun	Shade	Sun	Shade
1 litre container	4.0	0.8	5.1	6.6
5 litre container	5.8	2.2	16.3	10.9

that these etiolated seedlings, with their poorly developed root systems, are more likely to suffer moisture stress than those growing in a light environment.

Effect of container size on dry-mass production

Dry-matter production was affected by the size of the containers in these nursery trials, since the only available nutrients were those available in the potting media. The dry masses at 10 months, of *A. cyclops* and *A. saligna* seedlings transplanted into five-litre containers at the age of 8 months, and those grown in one-litre containers, is compared in Table 2B. Two months after transplanting, the seedlings in the larger containers were two to eleven grams (dry weight) heavier than seedlings remaining in their original containers. Since *A. longifolia* and *A. melanoxylon* seedlings were not transplanted, comparisons between species are not valid after 8 months.

Comparison of the growth rates of four Acacia species

Analysis of variance of shoot length and total dry mass data showed significant differences between the species during their first six months of growth. These differences were more marked in the sun-plants than in plants grown in the shade (Tables 3A & 3B).

At three months, *A. saligna* was significantly shorter, and had produced less dry mass than the other species, while *A. cyclops* initially had more robust seedlings in both shade and sun treatments.

TABLE 3A. Shoot-length means (cm), for six harvests

Shared superscripts indicate that values within a single row do not differ significantly at the 5% level.

* implies interspecies difference significant at the 5% level, and ** a difference significant at the 1% level. 0 = sun, θ = shade treatment.

Seedling age mth.	Sample size	Treatment	*A. cyclops*	*A. longifolia*	*A. melanoxylon*	*A. saligna*	Signif.
3	5	0	3.4^{a}	2.3^{ab}	2.1^{b}	1.2	**
3	5	θ	4.3	2.4^{a}	2.7^{a}	1.5	**
4	5	0	4.6^{a}	2.0	3.5^{a}	1.1	**
4	5	θ	5.9	2.8^{a}	3.8^{a}	3.0^{a}	**
6	5	0	12.2^{a}	5.6^{b}	8.1^{b}	9.2^{ab}	*
6	5	θ	17.3^{a}	6.9^{a}	16.1^{a}	10.9^{a}	ns
8	2	0	23.5^{a}	24.8^{a}	37.5^{a}	28.9^{a}	ns
8	2	θ	43.5^{a}	44.2^{ab}	61.0^{b}	59.5^{b}	*
10	2	0	36.5^{a}	31.0^{a}	39.5^{a}	36.0^{a}	ns
10	2	θ	67.0^{a}	36.0^{a}	59.0^{a}	65.0^{a}	ns
15	5	0	-	31.0^{a}	36.5^{a}	-	ns
15	5	θ	-	45.5^{a}	54.0^{a}	-	ns

TABLE 3B. Total dry mass of Acacia seedlings at six harvests

All symbols as in Table 3A.

Seedling age mth.	Sample size	Treatment	*A. cyclops*	*A. longifolia*	*A. melanoxylon*	*A. saligna*	Signif
3	5	○	0.075^{b}	0.069^{bc}	0.042^{ac}	0.042^{ac}	*
3	5	●	0.038^{a}	0.027^{a}	0.031^{a}	0.034^{a}	ns
4	5	○	0.182^{a}	0.101^{b}	0.088^{b}	0.211^{a}	**
4	5	●	0.084^{a}	0.049^{a}	0.082^{a}	0.072^{a}	ns
6	5	○	1.530^{a}	0.800^{b}	0.510^{b}	2.020^{a}	**
6	5	●	0.470^{a}	0.310^{a}	0.490^{a}	0.670^{a}	ns
8	2	○	7.66^{a}	4.77^{a}	6.58^{a}	6.95^{a}	ns
8	2	●	2.63^{a}	3.25^{a}	4.98^{a}	7.48^{a}	ns
10	2	○	16.31^{a}	6.62^{a}	9.12^{a}	19.10^{a}	ns
10	2	●	7.45^{a}	4.31^{a}	3.98^{a}	11.99^{a}	ns

By the age of six months, A. saligna was as tall and as productive as A. cyclops, and had overtaken the other two species.

A. longifolia was the least productive of the four species in both treatments but A. cyclops appeared to have been more severely affected by shading, the dry mass of the shade plants being less than half that of the sun-plants from the age of four months onwards. The large increment in A. cyclops and A. saligna dry mass between the eighth and tenth months is the result of the transplanting of these two species into larger containers at eight months, and not to some intrinsic factor.

The relative growth rates (RGR) and the monthly height increment of naturally established Acacia seedlings, growing inland on the University of Cape Town Campus or at a coastal site about 10 km away, are listed in Table 4. A. saligna had the most rapid growth followed by A. longifolia and A. melanoxylon respectively. The growth of A. cyclops appeared to be slower than the other species, but as it has a shrubby growth form, and shows little apical dominance, its growth is not directly comparable with that of the other Acacias. On coastal dunes and cliffs, A. cyclops is capable of forming a dense, hedge-like, dwarf thicket, less than 30 cm in height. In more protected sites, A. cyclops and the other Acacia species overtop the indigenous vegetation within about two years (Figure 2). Having a rapid rate of growth and a greater final height than the majority of species in Fynbos and coastal shrub communities, the Acacias maintain their dominance, and eventually suppress the indigenous vegetation, which appears to be light demanding.

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Figure 2. Cumulative height growth of *Acacia saligna* and *A. longifolia* seedlings, and Fynbos shrubs after fire. (Data from a single 100 m^2 plot on the burned lower north-facing slopes of the Constantiaberg, Cape Peninsula).

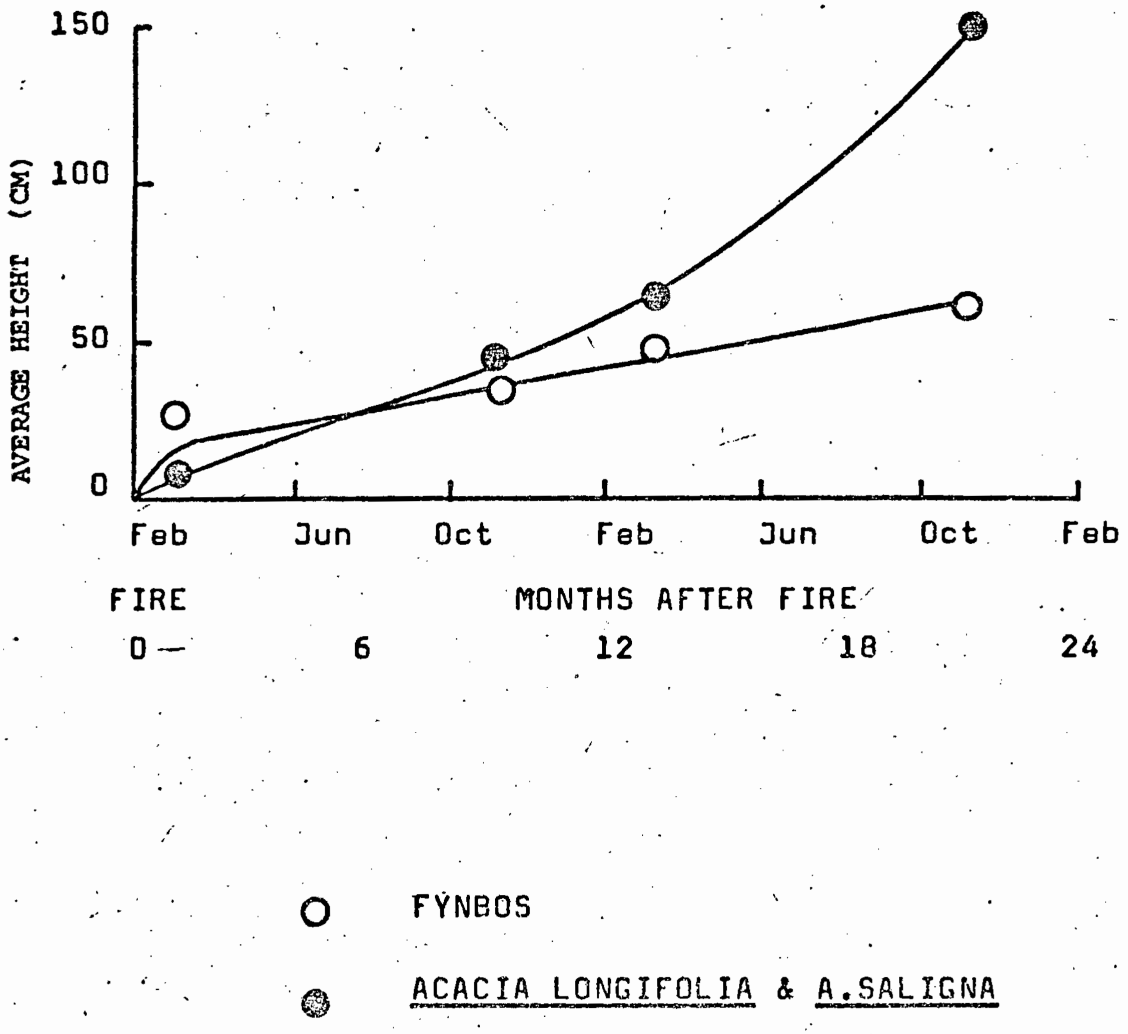

TABLE 4. Growth of Acacia seedlings in the field during their second year

Species	*A. cyclops*[1]	*A. longifolia*	*A. melanoxylon*	*A. melanoxylon*	*A. saligna*	*A. saligna*
Site	coastal	inland	inland	inland[2]	coastal	inland
RGR(g/g/month)	0.284	0.342	0.306	0.043	0.449	0.443
Height incr. (cm/mth)	3.6	13.6	7.7	1.7	13.1	14.8
Tot. height at 2 yr (cm)	-	213	142	29	207	225

1 : age unknown

2 : deep shade (10% normal sunlight)

The reduced RGR and height increments of A. melanoxylon seedlings growing in the deep shade cast by the parent canopy, suggest that Acacia seedlings are also light demanding (Table 4).

The effects of shading on the growth habit and morphology of Acacia seedlings

Figures 3 and 4 illustrate the differences between Acacia seedlings grown in full sunlight and those grown in one quarter sunlight. Shade-plants are taller and have retained their apical dominance for longer than plants grown in the open. The latter often develop prostrate or slanted leader shoots, and have many lateral shoots near the stem base. The stems of sun-plants are red or yellow when young, rapidly becoming brown and woody with age : but those of shade-plants remain green and pliable.

In the open, A. melanoxylon develops its first phyllodes at eight months, whereas in the shade it bears only pinnate leaves until it is about one year old. A. cyclops, A. longifolia and A. saligna seedlings develop their first phyllodes at about four months, whether grown in the sun or the shade, but the juvenile, pinnate foliage, which has normally been lost by six months is retained for up to ten months in the shade.

The foliage of shade-plants is a light, grassy green, their laminae thin textured, broad, and in the case of A. saligna, undulating : those of sun-plants are relatively narrow, leathery and dark green, glaucous or tinged with red. The phyllodes and leaves

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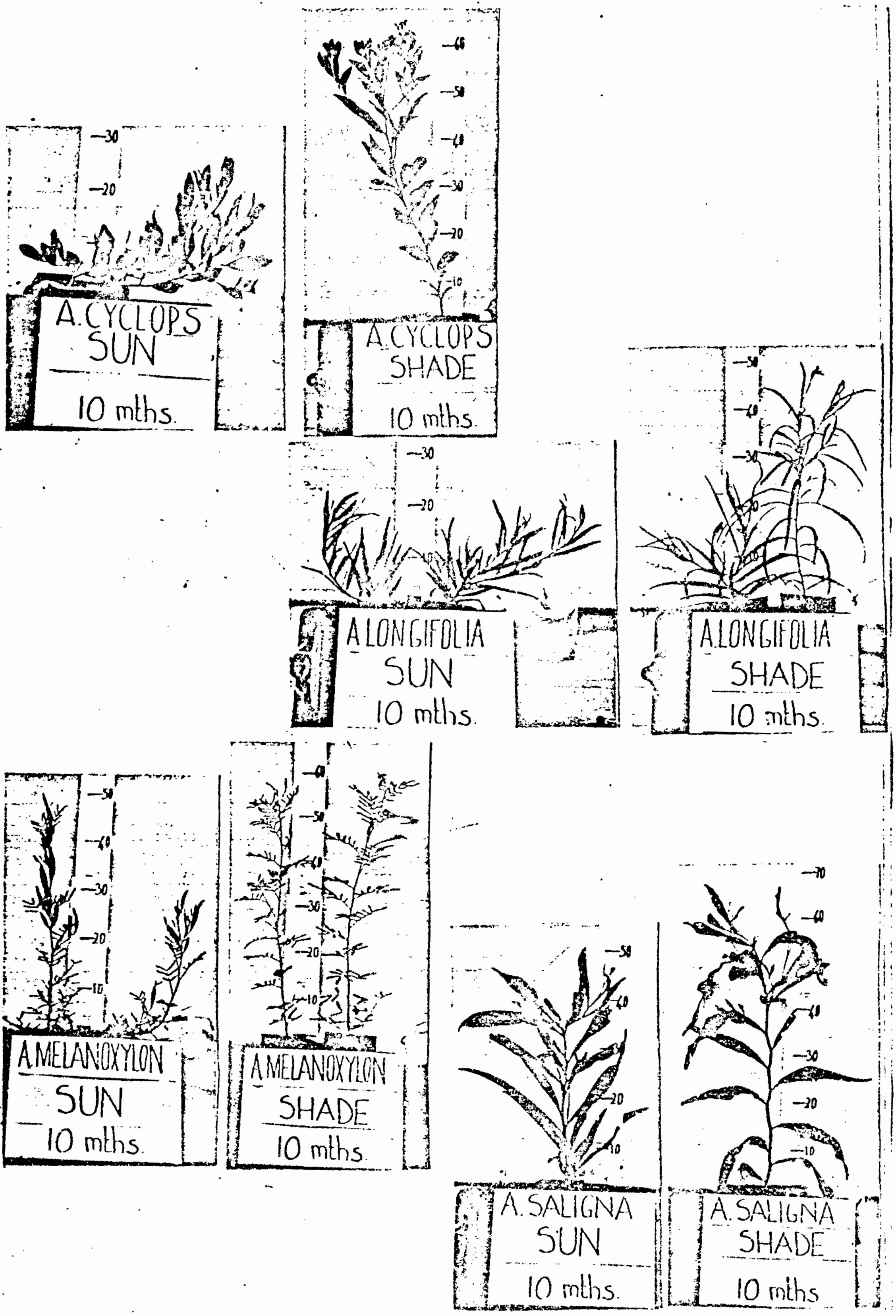
Figure 3. Sun- and shade-plants of four Acacia species, photographed at ten months. Sun-plants are shorter and more branched. They have more phyllodes, and these are held stiffly, edge on to the sun, in a near vertical position.



of all species are held almost vertical in sun-plants, but in the shade, tend to droop, or to be held out horizontally (Figure 3). Notice that the phyllodes of the sun-plants are generally seen broadside on, while many shade-plant phyllodes are presented edge-on to the camera. Phyllodes can apparently be rotated so as to present only their margins to the sun (sun-plants) or the entire upper surface of the lamina (shade-plants).

Poor root development was a feature of shaded plants of all species and was obvious from the first harvest until the last at ten months. The effects of shading on the root systems of three and four months old Acacia seedlings are illustrated in Figure 4. Notice also the advanced development of nodules and phyllodes on the sun-plants.

Quantitative assessment of differences between seedlings grown in sun and shade

Analysis of varience tests were carried out on all parameters measured at each harvest. The results, summarised in Tables 5 to 8, show how often foliage, stem, root and dry mass parameters were found to differ significantly between treatments.

Foliage characters (Table 5)

The orientation and mean surface area of photosynthesising organs, and the numbers of pinnate (juvenile) leaves were significantly affected by shading in a relatively high percentage of samples.

Figure 4. The effects of shading on the early development of the root system of Acacia seedlings.

Note the relative scarcity of lateral roots and nodules on shaded plants.

FULL SUNLIGHT

75 % SHADE (1/4 SUNLIGHT)

4 month old A.longifolia

3 month old A.cyclops

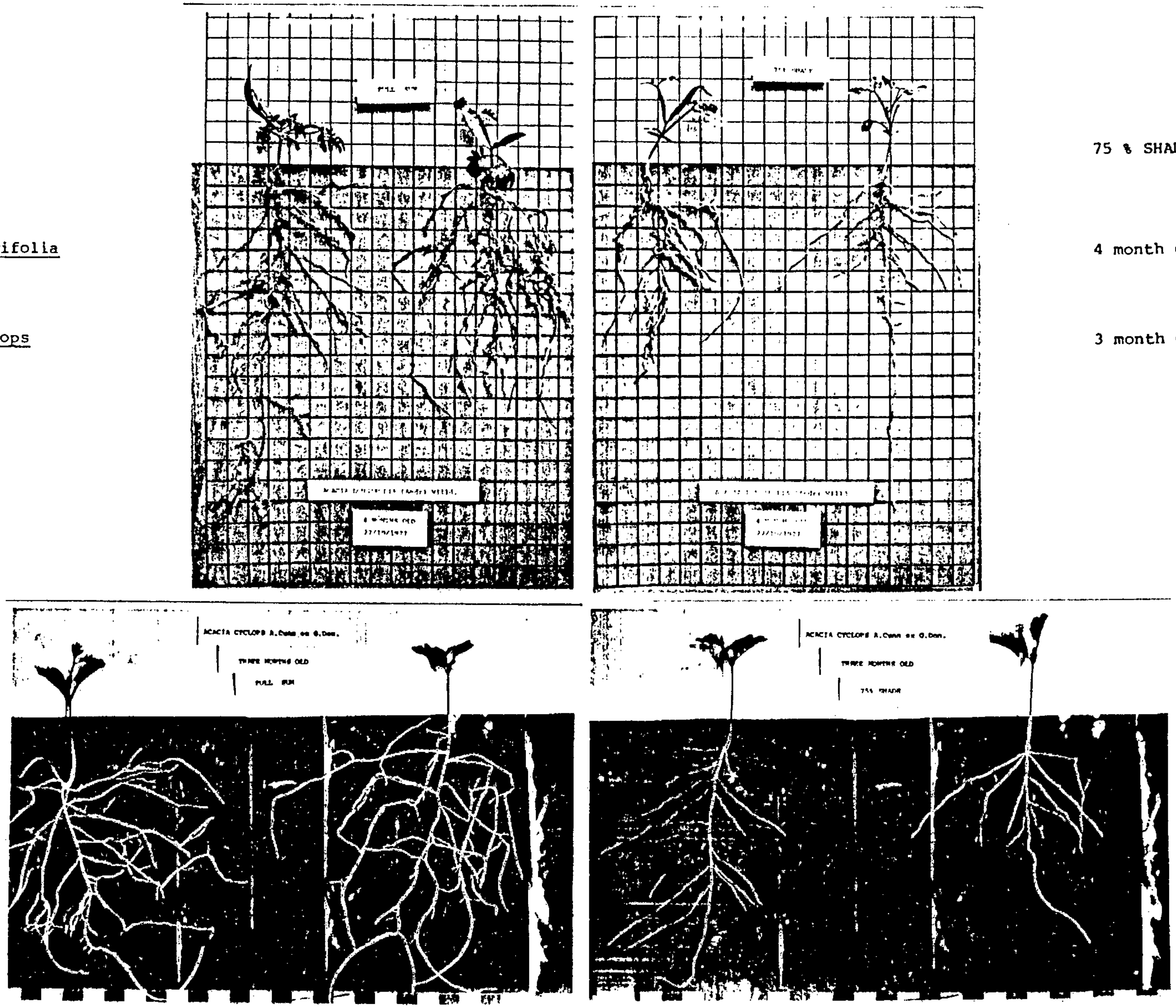


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TABLE 5. .. Results of analysis of varience (one way) tests on foliage parameters (see note below)

Parameter	A. cyclops		A. longifolia		A. melanoxylon		A. saligna		Data[3] sets tested	% tests signif
	Sun[1] trend	Tests[2] signif	Sun trend	Tests signif	Sun trend	Tests signif	Sun trend	Tests signif		
Phyll./leaf size	+>-	1/5	+/-	1/6	-	4/6	+/-	2/5	22	36
Phyll./leaf number	+	1/5	+	2/6	+>-	2/6	+/-	0/5	22	23
Phyll./leaf area tot.	+	2/5	+/-	0/6	-	0/6	+/-	1/5	22	14
Pinnate leaf no.	+>-	2/5	+>-	2/6	+>-	3/6	+/-	1/5	22	36
Phyllode number	+	1/5	+	0/6	+	1/6	+/-	0/5	22	9
Verticality	+	1/2	+	1/2	+	1/2	+	1/2	8	50
Data sets tested	27		32		32		27		118	-
% of tests signif.	30		19		34		19		-	26

Note: 1 The table should be read as follows: "the monthly means of sun-grown plants tend to '+' be larger, '-' be smaller, or '+/-' to show no consistent trend relative to shade-grown plants. '+>-' suggests a reversal of the trend with time.

2 This fraction represents the number of variance tests which indicated significant differences (at 5% level) between treatments, and the total number of data sets tested: hence 1/5 shows that the effects of treatment differed significantly in only one of five sets of data tested.

3 The final two columns show the total number of data sets tested for each parameter, and the percentage of these tests which showed significant differences between treatments.

Phyllodes and leaves were consistently held at an angle closer to the vertical in sun-plants than in shade-plants, the mean stem/phyllode angle being 23° and 44° respectively (with a standard error of 10%). Sun plants initially had a greater number of juvenile leaves, but did not retain them for as long as did the shade plants. Phyllode number was a highly variable parameter, but tended to be greater in full sunlight.

Shade-plants of A. cyclops differed significantly from sun-plants in 30% of the data sets tested. They tended to have smaller phyllodes and a reduced total photosynthetic area. The opposite trends were observed in A. melanoxylon, where the significant differences represent compensations for shading such as larger, pinnate leaves and a greater total photosynthetic area.

In the other two species, the phyllode sizes and total foliage areas differed significantly between treatments on occasion, but there was no consistent trend. Shading appeared to have had little effect on any of the foliage parameters of A. saligna except phyllode orientation, but the foliage of this species may have differed significantly in unmeasured parameters such as phyllode texture and colour.

Stem characters (Table 6)

The stems of the sun-plants of all four Acacia species were shorter than those of the shade-plants, the difference being significant in 45% of the data sets tested. Other stem parameters also show constant

TABLE 6. The results of analysis of variance tests on stem parameters (interpretation as in Table 5)

Parameter	*A. cyclops*		*A. longifolia*		*A. melanoxylon*		*A. saligna*		Data sets tested	% tests signif
	Sun trend	Tests signif	Sun trend	Tests signif	Sun trend	Tests signif	Sun trend	Tests signif		
Stem length	-	3/5	-	1/6	-	3/6	-	3/5	22	45
Internode length	-	0/1	-	1/2	-	0/2	-	1/1	6	33
Basal circumference			+	1/1	+	0/1			2	50
Lateral shoot number	+	0/1	+	0/2	+	1/2	+	0/1	6	17
Data sets tested		7		11		11		7	36	-
% tests signif.		43		27		36		57	-	39

trends for all species, but due to the small number of replicates, these differences are seldom significant.

The long internodes, small basal circumference and paucity of lateral shoots in shade plants suggest that they are etiolated, and that they retain apical dominance for longer than sun-plants.

The stem characters of A. saligna are more markedly affected by shading than those of the other three species.

Root characters (Table 7)

For all species tested, the root surface area of shade-plants was less than that of plants grown in the sun, the difference being significant in 58% of the sets of data tested ($P = 0.05$). This trend was particularly marked in A. cyclops, where the surface area of the shade-plant roots was significantly less than that of the roots of sun-plants, at every harvest ($P = 0.01$).

Nodule number was a highly variable character, and showed no clear reaction to treatment. On the other hand, the dry mass of nodules was consistently, if not significantly, higher in plants growing in full sunlight.

TABLE 7. The results of analysis of variance tests on root parameters (interpretation as in Table 5)

Parameter	*A. cyclops*		*A. longifolia*		*A. melanoxylon*		*A. saligna*		Data sets tested	% tests signif
	Sun trend	Tests signif	Sun trend	Tests signif	Sun trend	Tests signif	Sun trend	Tests signif		
Root surface area	+	3/3	+	1/3	+	2/3	+	1/3	12	58
Nodule number	+	0/4	+/-	1/4	+/-	0/4	+/-	0/4	16	6
Nodule dry mass	+	0/2	+	0/2	+	1/2	+	0/2	8	13
Data sets tested		9		9		9		9	36	-
% tests signif.		33		22		33		11	-	25

TABLE 8. Results of analysis of varience tests on seedling dry mass (interpretation as in Table 5)

Parameter	*A. cyclops*		*A. longifolia*		*A. melanoxylon*		*A. saligna*		Data sets tested	% tests signif
	Sun trend	Tests signif	Sun trend	Tests signif	Sun trend	Tests signif	Sun trend	Tests signif		
Root dry mass	+	4/5	+	5/5	+	2/5	+	2/5	20	65
Shoot dry mass	+	4/6	+	2/6	+/-	0/6	+/-	1/6	24	29
Total dry mass	+	4/5	+	5/5	+	0/5	+/-	2/5	20	55
Data sets tested		16		16		16		16	64	-
% tests signif.		75		75		13		31	-	48

Dry matter production (Table 8)

Root dry mass was, without exception, lower in shaded plants of all species than in their sun-grown counterparts. In 65% of all the sets of data tested, this difference was significant, making root dry mass the most sensitive to shading of all the parameters measured.

Total dry mass was significantly greater for sun-plants in over half the samples, but shoot dry mass was significantly affected in only 29% of the data sets.

In all species there was a tendency for the total dry mass of the sun-plants to exceed that of the shade plants, but while this trend was highly significant in A. cyclops and A. longifolia seedlings of almost all ages, and in four and six month old A. saligna seedlings, it was never significant in A. melanoxylon.

Shoot/Root drymass ratio (Table 9)

The shoot/root drymass ratio is consistently larger in shade-plants, implying that shoot development proceeds at the expense of root development when light is limited. Treatment differences in the shoot/root ratio were more marked in A. saligna and A. melanoxylon, which maintained good shoot growth in the shade, than in A. cyclops and A. longifolia, where shading reduced both shoot and root production.

For all four species, and under both treatments, the shoot/root dry-mass ratio increases as the seedlings grow. Other authors have

TABLE 9. Mean shoot/root dry-mass ratios for each harvest.[1]

Age at harvest (months)	A. cyclops		A. longifolia		A. melanoxylon		A. saligna	
	Sun	Shade	Sun	Shade	Sun	Shade	Sun	Shade
3	1.72	2.37	0.87	1.06	0.87	1.57	1.12	1.03
4	2.00	2.61	0.79	1.16	1.03	1.11	1.13	2.78
6	2.19	2.69	1.26	2.50	0.97	1.49	1.44	2.63
8	2.35	4.93	1.86	3.21	1.80	2.62	1.65	2.18
10	2.29	3.78	1.82	2.93	1.04	2.49	1.27	2.67
Significance between months	*	ns	**	**	**	**	ns	ns

[1] Significant differences between treatments are underlined ($P = 0.05$).

Significant differences between months are indicated as follows:

ns = not significant

* = significant at 0.05 level

** = significant at 0.01 level

also found that root growth takes precedence over shoot growth during the early stages of seedling growth (Panetta, 1977; Withers, 1979), and it has been suggested that, by stunting the root system, shading causes moisture stress which leads to the death of seedlings.

The relationship between total photosynthetic area and total dry mass

Shading affects both the photosynthetic area and the dry mass of Acacia seedlings. The increase or decrease in the total photosynthetic area (TPA) or in the total dry mass (TDM) of a shade-plant relative to a sun-plant was calculated as follows:

$$\Delta x = \frac{x^2 - x^1}{x^1} \quad . \qquad \ldots\ldots\ldots(4)$$

where Δx = difference in TPA or TDM between shade- and sun-plants relative to sun-plants

x^1 = TPA or TDM of a sun-plant

x^2 = TPA or TDM of a shade-plant

The regression of mean Δ TDM values on mean Δ TPA values obtained by equation (4), arranged the species linearly, in order of their relative 'efficiency' in shade. The linear relationship was not unexpected, as photosynthetic area and dry mass are linearly related (Evans, 1972).

If the shade-plants are used as a basis for comparison (equation 5), the species were arranged in the opposite order, or according to their ability to maximise production in full sunlight (Figure 5).

$$\Delta x = \frac{x^1 - x^2}{x^2} \quad \ldots\ldots\ldots\ldots\ (5)$$

where Δx = difference in TPA or TDM between sun- and shade-plants relative to shade-plants

x^1 and x^2 as in equation (4)

The relationship between Δ TPA and Δ TDM appeared to be weakly linear when all the actual data points were used, ($r = 0.58$ for equation (4); $r = 0.62$ for equation (5)); but was strongly linear when average values for each species were used ($r = 0.99$ for equation (4); $r = 0.92$ for equation (5)).

In order to illustrate area/mass relationships within as well as between species, all the data for each species are plotted, as well as mathematically fitted curves based on species means (Figure 5).

A. melanoxylon, a species in which shade-plants were found to have a larger total photosynthetic area than sun-plants, suffers minimal fall-off in dry matter production when growing in the shade. Conversely, A. cyclops, which maintains a large foliage area in full sunlight, may reach its maximum productivity when growing in the open, whereas A. melanoxylon, which produces less photosynthetic area in full sunlight than it does in shade, may prove less productive in the open than in partial shade.

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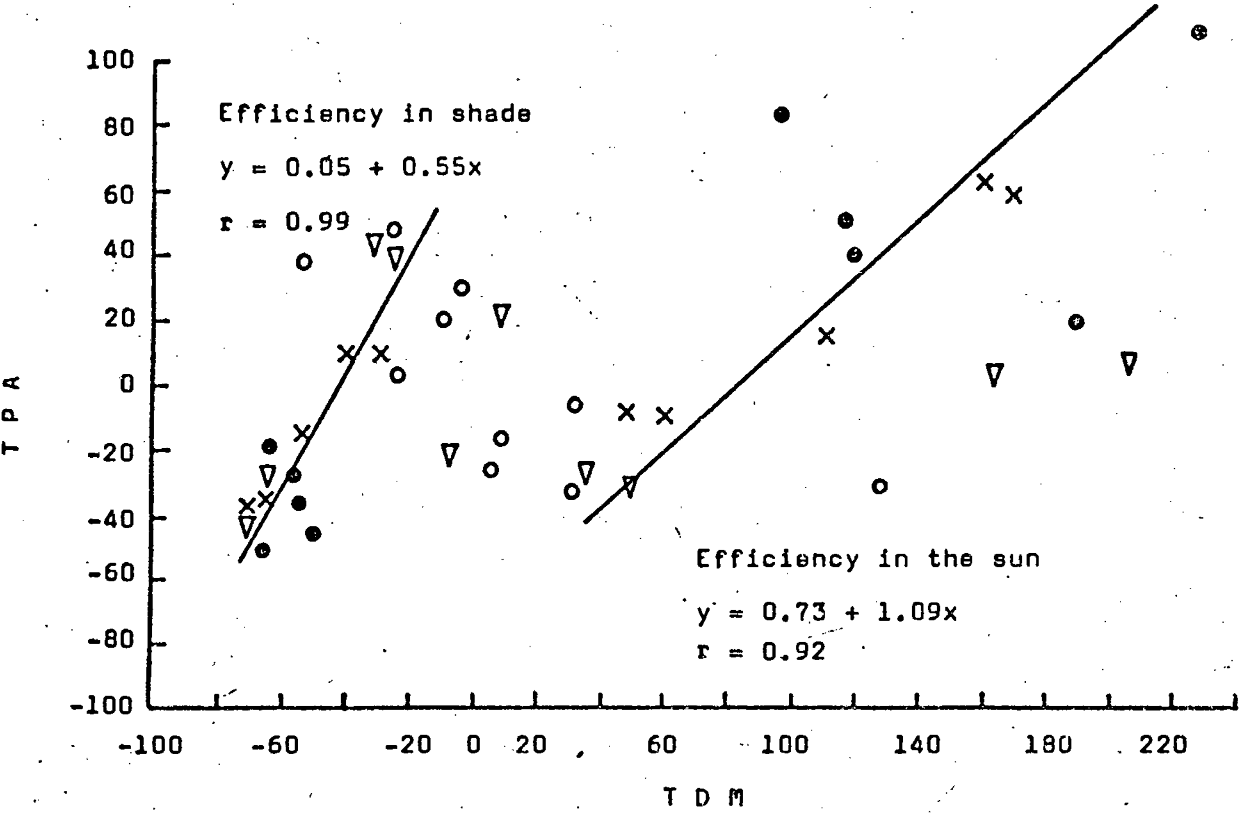
Figure 5. Relative sun and shade 'efficiency' of four species of Acacia as illustrated by the relationship between Δ TDM and Δ TPA values (equations 4 and 5). Data are given in full in the appendix. Curves are fitted to the mean values for each species.

● <u>A. cyclops</u> ∇ <u>A.longifolia</u> o <u>A.melanoxylon</u> × <u>A.saligna</u>

* For data and calculations, see Appendix.



TPA was very variable in A. saligna and A. longifolia, but within these species there was a tendency for large relative TPA reductions to be correlated with large relative TDM reductions.

Although A. melanoxylon was not always the most productive of the four species, in absolute terms, when grown in the shade (Table 3), its ability to maintain production in reduced light at a level similar to that in full light, indicates that it is the most shade tolerant of the four Acacia species examined in this study.

DISCUSSION

If one accepts the theory of natural selection, one would expect that the shade tolerance limits of a species would enable it to function most efficiently in its normal ecological niche. When forced to grow outside its optimal range of light intensity, a plant can compensate by increasing or decreasing the size of its leaves, the amount of chlorophyll they contain or the angle at which they intercept the light.

Table 10 summerises the effects of shading on the growth habit, morphology and dry mass of the seedlings of the four Acacia species examined in this study, and compares these with results quoted in the literature for other plant species and genera.

Acacia seedlings react to shading in much the same way as seedlings of other kinds of plants. In moderate shade, they tended to produce fewer, larger, thinner leaves, orientated so as to intercept

TABLE 10: Summary of shade-plant characteristics relative to those of sun-plants. The symbols +; =; -; indicate increase, equality or decrease of a parameter in a shade-plant relative to that of a sun-plant. Symbols in parenthesis are based on observations only. Blanks indicate a lack of information.

Species	*Acacia cyclops*	*Acacia longif.*	*Acacia melanox.*	*Acacia saligna*	*Acacia pycnantha*	Deciduous hardwoods	Eucalypt spp.	*Impatiens parviflora*	*Baccharis halimifolia*	General
Seral stage	early	mid	late	early	mid	late	late	late	early	-
height	+	+	+	+	+	+	+			+
Leaf/phyllode size	-	=	+	=	+	+	+/-	+	+	+
Juvenile leaf no.	+	+	+	+	+		+			+
Leaf thickness	(-)	(-)	(-)	(-)	-		-	-	-	-
Leaf/phyll no.	-	-	-	=			-		-	
Verticality	-	-	-	-	-		-			-
Total foliage area	-	=	+	=	+		=/-			
Total chlorophyll	pale	pale	pale	pale			-/+			+
Lateral shoot no.	-	-	-	-		-	-			-
Stem base girth	(-)	-	-	(-)						-
Internode length	+	+	+	+			+			
Photosynthetic rate								-		
Relative growth rate	-	=	=	-	-			-	-	
Shoot dry mass	-	-	=	=	-	-				-
Root dry mass	-	-	-	-	-	-			-	-
Shoot/root ratio	+	+	+	+	+			+	+	+
Nodule dry mass	-	-	-	-	=					-
Nodule number	-	-	=	=	+					-
Moisture content	+	+	+	+						
Root surface area	-	-	-	-						-
Source of data	this study				Withers 1979	Logan 1965	Cameron 1970	Evans 1972	Panetta 1977	Daubenmire 1947

the maximum amount of light, and were generally etiolated and unbranched. The RGR and dry matter production of shaded seedlings was relatively low, and their root systems were reduced and poorly nodulated.

The results of extreme light reduction are not listed in Table 10. When light is reduced beyond the limits for a particular species, rates of respiration and photosynthesis are reduced so that the compensating morphology can no longer be maintained. Smaller leaves are produced, the growth rate decreases, and the plant remains dwarfed or dies without reproducing itself (Cameron, 1970; Ashton & Frankenberg, 1976; Withers, 1979; Evans, 1972, Panetta, 1977).

Species differ greatly in their tolerance of shade. Acmena smithii Merrill & Perry, a climax rain forest species, is scorched in full sunlight and grows normally in 22% daylight (Ashton & Frankenberg, 1976). Most plant species require more light than this for normal growth.

The results of Withers (1979) show that the survival rate of plants declines when they can no longer compensate for reduced light by increasing their photosynthetic area. The degree of shading at which leaves and total leaf areas are smaller, rather than larger than those produced by the species in daylight, may indicate the shade tolerance of the species.

Reduction in leaf area occurs below 42% daylight in Eucalyptus spp. seedlings (Cameron, 1972; Withers, 1979), below 8% in the seedlings of Acacia pycnantha, an understory shrub in Eucalypt woodland (Withers, 1979) and below 2% for the seedlings of Acmena smithii growing beneath the parent canopy in tall, closed forest (Ashton & Frankenberg).

Acacia cyclops, a shrub from the coastal dunes of S.W. Australia (Seddon, 1972) was the least shade-tolerant of the four species examined in this study. In 25% daylight it had smaller phyllodes and significantly less total photosynthetic area than it had in the open. A. cyclops also failed to retain its juvenile leaves in the shade, and its phyllodes were never held at an angle greater than 30° from the vertical. The inability of A. cyclops to compensate for reduced light is reflected in the extreme differences in root and shoot drymass between sun- and shade-grown seedlings.

It was because of its role as a pioneer on exposed dunes that A. cyclops was introduced to the Cape for drift-sand stabilization (Stirton, 1978). Although few of its seedlings survive for more than a few months under the parent canopy (7.5 ± 2.2% daylight), under heaps of brushwood (5.8 ± 1.9% daylight) (Milton, unpubl.) or under dense indigenous scrub (Roux & Middlemiss, 1963), seedlings, originating from seed brought in by birds, can survive in open areas between bush-clumps (Glyphis, Milton & Seigfreid, in prep.).

A. melanoxylon, which was found to be the most shade-tolerant of the four Acacias studied (figure 5), produced only pinnate leaves in the shade, and these were held at an average angle of 50° from the vertical. This member of the preclimax sere of the coastal forests of eastern Australia and Tasmania (Farrell & Ashton, 1978), suffers very little loss in dry matter production when grown in 25% daylight. It requires a minimum of only 20% daylight for normal growth (Donald, unpubl.) and can survive in 8% daylight (Phillips, 1928). The remarkable difference in the growth rates of this relatively shade-tolerant species in an open site and under the deep shade of a parent canopy (10% daylight), is illustrated in Figure 6.

Although A. melanoxylon seedlings are suppressed by tall, climax rain-forest (Howard, 1974; Ashton & Frankenberg, 1976), in Australia, and likewise by the indigenous forests of the S. and S.W. Cape (Phillips, 1928; Donald, unpubl.), they can become established in marginal and disturbed forest.

Figure 5 indicates that A. longifolia and A. saligna are more tolerant of shade than A. cyclops, but less so than A. melanoxylon. The natural habitat of A. longifolia is scrub forest of S.E. Australia (Ewart, 1930; Murray et al, 1978). A. saligna is endemic to south western Australia where it grows in dune hollows and along water courses (Maslin, 1974) generally further from the coast than A. cyclops (Abbott, pers. comm.). Where moisture is available, A. saligna appears to favour clearings (Morellini, unpubl.), and it grows on wasteland, and along roadsides in urban areas (Milewski, pers. comm.). In the S.W. Cape, A. saligna also grows best in moist and disturbed sites. On flat, sandy areas, the survival of young A. saligna seedlings appears to be better in partial shade, those in full sunlight dying of desiccation during the dry summer.

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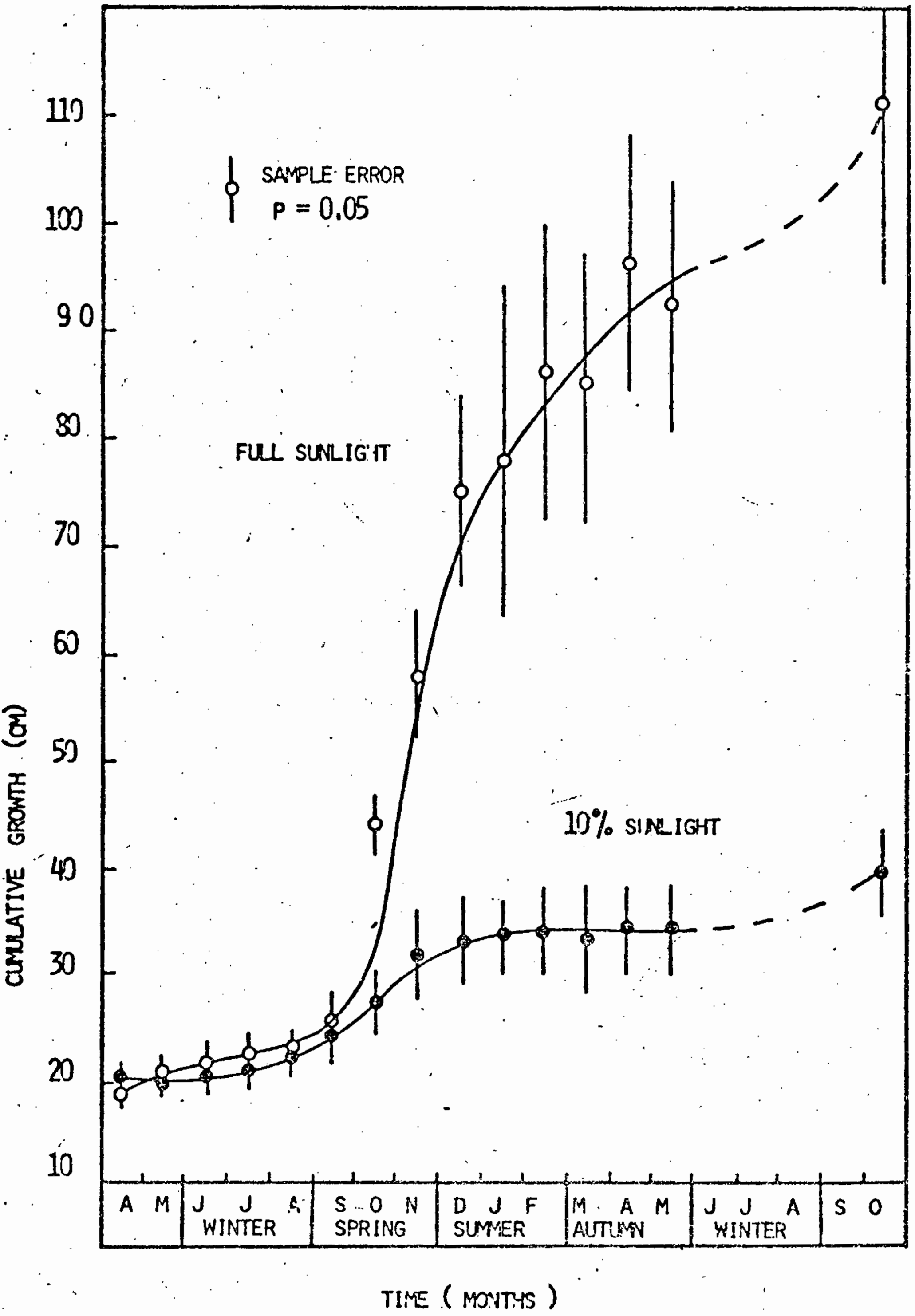
Figure 6. Height growth of self-established *A. melanoxylon* seedlings in the field, showing the effect of deep shade on the growth rate of seedlings.



Both A. longifolia and A. saligna showed considerable variation in their reaction to shading, and indications are that they grow most rapidly in moist, open or semi-shaded habitats. It is possibly the generalist strategy of these species which has enabled them to become naturalised in a variety of habitats in Natal and the Cape where they have been introduced.

CONCLUSION AND MANAGEMENT IMPLICATIONS

The seedlings of all the Acacia species tested survived for 15 months in 25% daylight, and by this time had reached a height of 60 cm. A reduction of more than 75% of incident light would be necessary for the suppression of any of these species.

Field observation suggest that 90% to 95% light reduction is adequate for the control of A. cyclops and A. saligna and probably also A. longifolia, since seedlings of this species also fail to become established in thickets. Light should be reduced by a minimum of 95% for the control of A. melanoxylon. Heavy shading not only reduces the rate of photosynthesis and respiration (Evans, 1972) but by stunting the root system, probably causes the seedling to experience drought stress (Panetta, 1977). Shaded acacia seedlings seem to be more prone to 'damping off' and to attack by Icerya purchasi than those growing in the open, but the validity of this observation has not been tested.

Shading can be achieved after felling by stacking the brushwood into heaps one to two metres high. Although the open areas between these stacks must be kept weeded of Acacia, this control method has the additional advantage of encouraging large populations of rodents to build up under the brushwood. These feed on Acacia seed both in the shelter and in the open. Tall brushwood heaps also offer perches for birds, a potential source of indigenous seed. To avoid mass germination of Acacia seed lying dormant in the soil, once indigenous vegetation has been re-established, it is essential to exclude fire for many years, perhaps for over a centuary. In mountain catchment areas this may conflict with Forestry Department policy, which prescribes burning of the vegetation on a 10 to 15 year rotation (Kruger, 1977).

It may also be possible to provide adequate shade by establishing 'smother crops'. Ideally these should be fast-growing, easily established from seed, and unlikely to pose an additional threat to indigenous vegetation. Pioneer grasses, such as <u>Avena fatua</u> L. and <u>Ehrharta villosa</u> Schult.f. grow very vigorously on sites recently cleared of Acacias. Early seral grasses could be further encouraged by nitrogen fertilization, which has no beneficial effect on the growth of Acacia species (Specht, pers. comm.; Schönau, 1971).

Partial shading of the semi shade-tolerant species, <u>A. longifolia</u> and <u>A. saligna</u>, should be avoided, as this could facilitate their establishment.

The problem of the spread of <u>A. melanoxylon</u> into indigenous forest has not been solved, but will probably be reduced by low intensity exploitation of indigenous trees. It is Forestry Department policy to lop selected timber trees before felling them, so as to cause minimal damage to neighbouring trees (M. Cameron, pers. comm.).

Although the nursery experiment provided information on the relative shade tolerance of the four Acacia species tested, clearer results might have been obtained by measuring a smaller number of variables over a larger number of replicates. Parameters, such as root mass and area or leaf area and orientation, which require time-consuming preparation or numerous measurements, could have been measured less frequently and on larger samples. The use of five litre containers, and a shade cloth frame over two metres in height is recommended for shade tolerance experiments on Acacia species which are to be continued for a year or more.

The exploitation of shade-intolerance has promise as an alternative to chemical control of Acacia pest plant control in the S.W. Cape. Field trials should now be carried out to identify suitable smother crops. These should be fast-growing, easily established, but preferably incapable of extensive self-propagation unless they are indigenous species. In addition a 'smother crop' should be able to exclude a minimum of 90% of the daylight within a few months of germination.

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APPENDIX. TPA & TDM data for Figure 5

Species	Age	TPA (cm^2)			TDM (g)			Equation 4		Equation 5	
		Sun	Shade	Diff.	Sun	Shade	Diff.	TPA	TDM	TPA	TDM
<u>A. cyclops</u>	3	5	3	2	0.075	0.038	0.037	-0.45	-0.49	0.83	0.97
	4	9	6	3	0.182	0.084	0.089	-0.36	-0.54	0.56	1.17
	6	94	45	49	1.530	0.470	1.060	-0.52	-0.69	1.09	2.25
	8	222	185	37	6.700	2.600	4.070	-0.16	-0.66	0.20	1.91
	10	1257	887	370	16.310	2.450	8.860	-0.29	-0.54	0.42	1.19
	$\bar{x}$							-0.36	-0.58	0.62	1.50
<u>A. longifolia</u>	3	3	2	1	0.069	0.027	0.042	-0.39	-0.61	0.65	1.56
	4	5	4	1	0.101	0.049	0.052	-0.15	-0.51	0.18	1.06
	6	49	31	18	0.800	0.310	0.490	-0.36	-0.63	0.57	1.67
	8	204	224	20	4.770	3.250	1.520	0.10	-0.31	-0.09	0.45
	10	624	684	60	6.620	4.310	2.310	0.10	-0.38	-0.09	0.60
	$\bar{x}$							-0.14	-0.49	0.24	1.07
<u>A. melanoxylon</u>	3	2	3	1	0.042	0.031	0.011	0.50	-0.26	-0.33	0.35
	4	7	8	1	0.088	0.082	0.006	0.18	-0.07	-0.15	0.07
	6	58	74	16	0.510	0.490	0.020	0.28	-0.04	-0.22	0.06
	8	198	206	8	6.580	4.980	1.600	0.04	-0.24	-0.04	0.32
	10	380	531	151	9.120	3.980	5.140	0.40	-0.56	-0.28	1.29
	$\bar{x}$							0.28	-0.23	-0.20	0.41
<u>A. saligna</u>	3	3	4	1	0.042	0.034	0.008	0.40	-0.25	-0.29	0.33
	4	14	9	5	0.211	0.078	0.133	-0.33	-0.62	0.05	1.62
	6	116	67	49	2.020	0.670	1.350	-0.42	-0.66	0.07	2.01
	8	265	331	66	6.950	7.480	1.350	0.24	0.08	-0.20	-0.07
	10	665	998	333	19.100	11.990	7.110	0.50	-0.37	-0.33	0.59
	$\bar{x}$							0.08	-0.36	-0.14	0.91

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LITTERFALL OF THE EXOTIC ACACIAS
IN THE SOUTH WEST CAPE

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ABSTRACT

Litter-fall under thicket of Australian Acacias naturalised in the Cape averages 704 g/m^2/pa (dry weight). This is comparable with the litter-fall recorded in sub-tropical and warm temperate Eucalypt forests in Australia, but is three times as great as the litter-fall of evergreen scrub in winter rainfall regimes. Acacia litter comprises about 60% foliage and about 25% reproductive structures, and, according to the literature is rich in phosphorous and has a low carbon/nitrogen ratio. The ground beneath an Acacia thicket is covered by a layer of litter with a dry mass equal to about 1/5 of the living biomass, or three times the mass of the annual litter-fall. Plants adapted to low soil nutrient levels do not compete successfully on fertilised soils (Specht, 1963), and it is suggested here, that, by enriching the soil, Acacias make the environment less suitable for indigenous Fynbos plants.

CONTENTS

INTRODUCTION

A number of species of exotic Australian Acacias are replacing the Fynbos and coastal shrub communities of the south western Cape, South Africa. The indigenous vegetation is dominated by small-leaved sclerophyll evergreen shrubs - a structural type characteristic of nutrient-poor substrates in Mediterranean climate regions (Beadle, 1966; Loveless, 1962; Specht, 1963; Mooney, 1977). Its low productivity is indicated by its low standing crop (Kruger, 1977), long-lived leaves (Kruger, 1980; Kruger, 1979) and the paucity of fallen litter (Kruger, 1977; Glyphis, 1976; H.P. Linder, unpubl.; Milton, unpubl.). The exotic Acacias are taller and faster growing than the indigenous vegetation, and within a few years cover the ground with a thick litter layer.

The aim of this paper is to compare the litter production and accumulation of exotic Acacia thickets to that of Mediterranean sclerophyllous vegetation similar to Fynbos. Hypotheses, as to the relative productivity and nutrient turnover of exotic and indigenous vegetation, which arise from this comparison, can be tested when the litterfall studies at present being carried out as part of the Fynbos Biome research project (S.A.N.S.P., 1978) have been completed.

METHODS

All the data used in this paper were collected in mature self-established thickets of exotic Acacias on the Cape Peninsula or the adjacent Cape Flats, in the S.W. Cape, between March, 1977 and

November 1978. They comprise quantitative assessments of the masses of the canopy, the annual litterfall and the ground litter layer.

Canopy weight

Nine A. cyclops and seven A. saligna trees of various stem diameters were measured, felled, divided into foliage, twigs and branches exceeding 20 mm in diameter, and then weighed in the field. Each of the components was subsampled, and the dry weight/wet weight ratio of the sub-sample was used to estimate the dry weight of the entire tree. The weight of canopy per unit area (ie. excluding wood and branches over 20 mm in diameter) was calculated as follows:

$$\frac{\text{canopy weight} \quad (g)}{\text{canopy area} \quad (m^2)}$$

Canopy cover was assumed to be continuous. Total biomass per unit area was the product of total tree mass, and tree density per hectare.

Annual litterfall

Ten terylene mesh bags attatched to wire hoops 0.5 m diameter and mounted on metal legs were set out under each of the following Acacia species to catch falling litter: A. cyclops Cunn. ex G. Don., A. longifolia (Andr.) Willd., A. melanoxylon R.Br. and A. saligna (Labill.) Wendl. Litter was collected at monthly intervals between May, 1977 and April, 1978, dried at 90°C for 24 hours and weighed. The standard error on the mean monthly weight of the litter of each species never exceeded 10% so that the sum of the monthly means is considered to be a good estimate of the litter production of selected Acacia thickets over the 12 month study period.

Ground litter layer

Ground litter was sampled during the winter of 1978. All litter within ten random 1/16 m^2 quadrats in each thicket was collected, dried and weighed. Although the distribution of the litter was sometimes patchy due to molehills and depressions on the ground, the mean for each study site is used as an estimate of the dry weight of the litter layer at steady state for a particular species.

Decomposition rate

This was not studied in the field, but was calculated from the litterfall and litterlayer data, using Olson's (1963) equation (2).

$$K = L/X_{ss} \quad . \quad . \quad . \quad . \quad . \qquad (2)$$

where L = annual litterfall (g/m^2); X_{ss} is the litter on the ground at steady state, inclusive of the current year's litterfall (g/m^2); and K is the decomposition constant.

The time taken for 95% of the steady state litter to accumulate or to decay was estimated with the use of equation 3 (Olson, 1963).

$$3/K = T_{95\%} \quad . \quad . \quad . \quad . \quad . \qquad (3)$$

where K is the decay constant, and $T_{95\%}$ is the 95% decay or accumulation time.

RESULTS

Biomass of Acacia thickets in the S.W. Cape (Table 1A) is about ten times greater than that of Fynbos (Kruger, 1977) and other mediterranean type vegetation (Mooney, 1977) which have biomasses of 15 - 30 tons/ha. Since the annual litter-fall of Acacias is comparable to that of other communities on a percentage biomass basis (Table 1B), their actual litter output greatly exceeds that of most shrublands (Table 3).

In a mature, healthy thicket, very little of the Acacia litter is woody. Most of it origenates from the canopy (which makes up less than 20% of the total biomass) and consists chiefly of phyllodes (Table 2). Flowers, pods and seed together constitute about 30% of the litter and twigs, unidentifiable plant fragments and caterpillar fras are variable minor components.

About half the canopy mass is renewed annually. The litter accumulates on the ground, and, in a mature thicket, the dry weight of the litter-layer exceeds that of the living canopy.

The annual litter-fall of the four species studied (averaging 704 g/m^2/pa) is comparable with that of forests in the sub-tropical and warm temperate regions of S.E. Queensland, New South Wales, Victoria and South Australia (Table 3). The litter-fall of evergreen scrub communities in Mediterranean regions is about 200 g/m^2/pa (Mooney, 1977), which falls short of the annual litter-fall for warm temperate regions (550 g/m^2/pa; Bray & Gorham ex Birk, 1979) and even of cool temperate regions (300 - 400 g/m^2/pa;

TABLE 1A. Biomass and canopy weight of exotic Acacias (t/ha dry weight)

Vegetation	Biomass	% error	(n)	Canopy weight	% error	(n)
<u>A. cyclops</u>	131	4	(5)	22	18	(9)
<u>A. saligna</u>	135	10	(4)	12	21	(7)
Fynbos a	11 - 26	12	(9)	-	-	-
Fynbos b	18					
British heath c	24					

a = Kruger, 1977; b = Kathan, unpubl.; c = Chapman, 1967

TABLE 1B. Litterfall and Litter-layer relative to biomass and canopy weight

Vegetation	Litter-fall as a % of Biomass	Litter-fall as a % of Canopy weight	Litter-layer as a % of Biomass	Litter-layer as a % of Canopy weight
<u>A. cyclops</u>	7.4	43.5	21.2	125.0
<u>A. saligna</u>	6.0	68.0	15.5	177.3
Fynbos	-	-	18.5	-
Mediterranean a	10.1	-	-	-
British heath b	12.9	-	71.0	-

a = calculated from data in Mooney, 1977. b = Chapman, 1967

TABLE 2. Components of annual litter-fall of exotic Acacias in the S.W. Cape

Components	*A. cyclops*	*A. longifolia*	*A. melanoxylon*	*A. saligna*
Total litter (g/m^2)	968	543	503	804
Flowers %	1.4	10.6	6.7	8.7
Pods %	35.5	16.0	0.5	12.1
Seed %	5.3	8.3	0.3	8.0
Twigs %	11.3	2.6	26.5	10.0
Unident. & fras %	7.7	0.8	2.7	10.4
Phyllodes %	39.0	61.7	63.3	60.8

Kozlowski, 1973). This low productivity has been attributed to the summer drought which limits photosynthesis, and to the poverty of the soils (Mooney, 1977; Specht, 1973). The S.W. Cape, where high productivity Acacias are replacing low productivity heath- and shrub-land, without the assistance of additional nutrients, provides a natural experiment for the study of differences in the growth and nutritional strategies of these plants.

The ground litter-layer of the Acacia thicket weighed between 1400 and 2 800 g/m^2, which is fairly average by world standards (Table 3, column 3), but greatly exceeds the 99 - 495 g/m^2 recorded in mature montane Fynbos (Kruger, 1977). That there is a marked difference in the accumulation of litter under exotic Acacias and indigenous vegetation is clearly seen in the field. Under Acacia thickets, the litter layer forms a carpet 20 - 40 mm deep, unbroken except where disturbed by moles. Under Fynbos and other indigenous communities, the litter is thin and patchy. Litter covers an average of 15% of the soil surface under Fynbos on Table Mountain, Cape Peninsula (n = 31; Glyphis, 1976), 12% under coastal bush (n = 50; Milton, unpubl.) and 5% under the dry Fynbos on Piquetberg, S.W. Cape (n = 36; H.P. Linder, unpubl.).

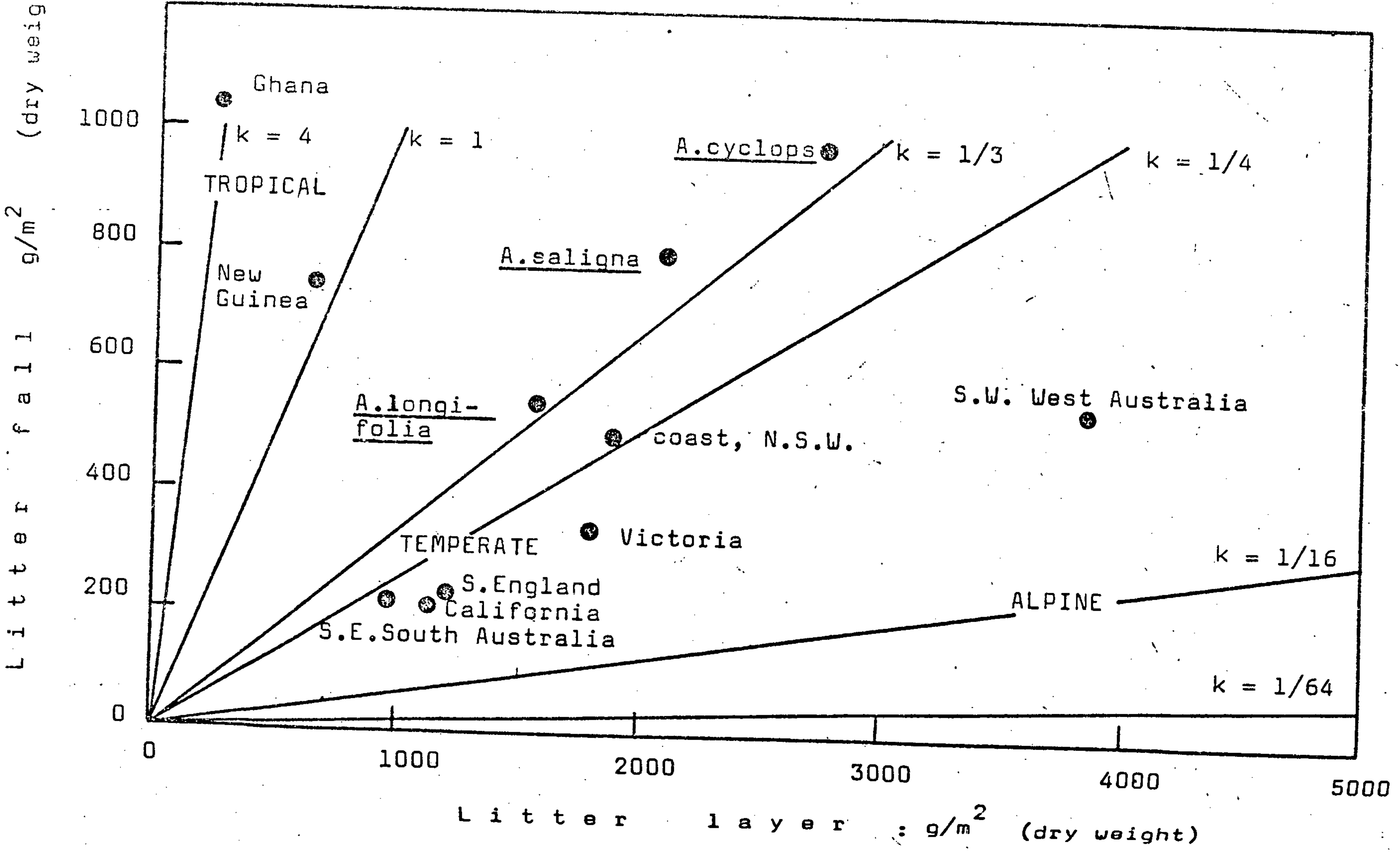
The mass of the annual litterfall of Acacias in the S.W. Cape was equal to about one third of the mass of the ground litter, giving the decomposition constant a value of between 0.326 and 0.384. When litter-fall and ground litter dry weights of the exotic Acacias are plotted on Olson's (1963) graph, which shows the relationship between these parameters for a wide range of plant communities, the line (representing 'K') lies realistically between 'K' for tropical

TABLE 3. Litter fall, accumulation and decay for plant communities in tropical, temperate and Mediterranean climate regions

Plant community	Locality	Litter -fall 'L'	Litter layer 'X'	Decay const. K=L/X	95% decay time 3/K yr	Author
Tropical forest	Ghana	1050	226	4.650	0.65	Nye, 1961 ex Edwards, 1977
Tropical forest	New Guinea	755	646	1.200	2.5	Edwards, 1977
Subtropical rain forest	Queensland	913	1168	0.782	3.8	Plowman, 1979
Rain forest	South Australia	782	1408	0.556	5.4	Ashton & Frankenberg, 1976
Subtropical wet sclerophyll	Queensland Australia	887	2179	0.407	7.4	Plowman, 1979
A. cyclops	exotic acacias in the S.W. Cape South Africa	968	2781	0.348	8.6	this study
A. longifolia		543	1570	0.346	8.7	this study
A. saligna		804	2096	0.384	7.8	this study
A. melanoxylon		503	-	-	-	this study
Eucalypt forest	Victoria, Australia	776	2225	0.349	8.6	Ashton, 1975
Eucalypt forest	S.E. Queensland	640	2700	0.238	12.6	Rogers & Westman, 1977
Eucalypt forest	West Australia	550	3873	0.142	21.1	Hatch, 1955 ex Rogers & Westman, 1977
Coastal scrub	New South Wales	490	1900	0.258	11.6	Maggs & Pearson, 1977
Eucalypt forest	Victoria, Australia	356	1825	0.163	18.4	Attiwill, 1968
Gymnosperm forest	N. hemisphere	370	-	-	-	Kozlowski, 1973
Angiosperm forest	N. hemisphere	320	-	-	-	Kozlowski, 1973
Pine forest	S.E. U.S.A.	-	-	0.250	12.0	Olson, 1963
Pine forest	Minnesota	-	-	0.063	47.6	Olson, 1963
Alpine conifers	California	-	-	0.009	333.3	Olson, 1963
Quercus forest	France	390	1140	0.342	8.7	Lossaint, 1973
Quercus garrigue	France	230	-	-	-	Lossaint, 1973
Chaparral	California	282	1359	0.208	14.4	Mooney, 1977
Mediterranean type scrub	World average	200	-	-	-	Mooney, 1977
Evergreen scrub	California	83-213	-	-	-	Mooney & Rundel, 1979
Sclerophyll open forest	Adelaide, S. Australia	233	980	0.238	12.6	Lee & Correll, 1978
Evergreen scrub	Chile	160	-	-	-	Cody & Mooney, 1978
Heathland	South Australia	136	-	-	± 2	Specht & Rayson, 1957
Fynbos	S.W. Cape	-	99-495	-	-	Kruger, 1977
Dry heath	S. England	288	1294	0.223	13.5	Chapman, 1967

Values calculated (where necessary) from data in the papers cited

Figure 1. Decomposition rates of the litter (*k*) of exotic Acacia thickets in the S.W.Cape compared with that of other plant communities, based on Table 3 & Olson, 1963.



regions (which can exceed 1.00) and 'K' of about 0.25 for temperate regions (Figure 1).

The time taken for 95% of the steady litter state to accumulate or to decay is estimated to be between 7 and 9 years for exotic Acacias in the S.W. Cape. This is slightly faster than that in temperate and boreal conifer forests or Chaparral. Kruger's (1977) data show that litter under Fynbos may have reached a stable mass within six years : but, even if Fynbos litter were to decay as rapidly as it fell (which is unlikely in a mediterranean climate), this would not account for the paucity of the litter-layer. As in other Mediterranean shrub communities, the lack of litter on the ground must be attributed to the very low litter-fall values.

DISCUSSION

The nitrogen and phosphate content of the leaves and bark of Australian Acacias exceeds that of other mediterranean sclerophyll vegetation, and is 2 - 4 times as great as that in Fynbos plants (Table 4). This difference is also reflected in the protein content of Acacia shoots, which is about three times as high as that of browseable shrubs sampled in plant communities of the Fynbos Biome (Table 5). Since the average annual litter-fall of exotic Acacia thickets in the S.W. Cape (704 ∓ 110 $g/m^2/pa$) is three times greater than values cited for mediterranean sclerophyllous bush (Table 3), the annual nitrogen and phosphate input by Acacia litter should be about nine times as great, per unit area, as that of fynbos communities.

TABLE 4. Nitrogen and phosphorous levels in Acacias, Fynbos and other Mediterranean plant communities

Vegetation & Plant part analysed	Locality	C/N ratio	% N	% P	Litter fall g/m^2	Author
Acacia dealbata leaf litter	Victoria, Australia	10.1	2,03	0,06		Ashton, 1975
Eucalypt litter	same site as above	23,3	1,14	0,07	776	Ashton, 1975
Garrigue	France	-	0,96	0,03	230	Lossaint, 1973
Coastal scrub	N.S.W., Australia	-	0,85	0,04	490	Maggs & Pearson, 1977
Melaleuca marsh	S.W. West Australia	-	0,79	0,02	430	Congdon, 1979
Sclerophyll forest	South Australia	-	0,46	0,02	233	Lee & Correll, 1978
Chaparral	California	-	0,5-0,2	0.06-0,02	83-213	Mooney & Rundel, 1979
Fynbos Proteaceae	S.W. Cape	-	0.58	0.04	-	Low, 1978
Fynbos Ericaceae	S.W. Cape	-	0,63	0.03	-	Low, 1978
Fynbos Restionaceae	S.W. Cape	-	0.49	0.01	-	Low, 1978
Fynbos Protea leaves	S.W. Cape	-	0,70	0,03	-	F.F.T.R.I., 1972
Acacia baileyana bark	N.S.W., Australia	87.5	0.48	-	-	Hannon, 1958
Acacia longifolia bark	N.S.W., Australia	78.0	0,50	-	-	Hannon, 1958
Acacia maidenii bark	N.S.W., Australia	55.7	0.79	-	-	Hannon, 1958
Non-legumes	Site as above	270.0	0,18	-	-	Hannon, 1958

TABLE 5. Protein and phosphorous content of Australian Acacias and plant communities in the S.W. Cape

	Plant community	% Protein	% P	Author
S.W. Cape	Coastal dune scrub	6.03 ± 0.14	0.03	Joubert & Stint, 1979b
S.W. Cape	Coastal Fynbos	3.80 ± 0.51	0,03	Joubert & Stint, 1979b
S.W. Cape	False Fynbos	3.51 ± 0.12	0,02	Joubert & Stint, 1979b
S.W. Cape	Mountain renosterbos	4.36 ± 0.60	0,05	Joubert & Stint, 1979b
S.W. Cape	*Acacia karroo* (marginal, in hot, arid, river valleys)	15.07	0.13	Joubert & Stint, 1979b
Australia	Australian Acacias mean for 12 species	15,19 ± 1.03	0,13	Everist, 1969

Assuming a N content of 1.5% and a P content of 0.13%, Acacia litter would contribute 10.5 g/m^2 N and 0.92 g/m^2 P to the soil each year, as compared with 2.2 g/m^2 N and 0.08 g/m^2 P in Garrigue (Lossaint, 1973), 2.8 g/m^2 N and 0.28 g/m^2 P in chaparral (Mooney & Parsons, 1973), 1.0 g/m^2 N and 0.03 g/m^2 P in sclerophyll forest, South Australia (Lee & Correll, 1978), and 4.4 g/m^2 N and 0.19 g/m^2 P in dry sclerophyll bush, N.S.W., Australia (Maggs & Pearson, 1977).

The rapid decay of Acacia litter (8 - 9 years) relative to that of sclerophyll scrub (13 - 15 years; Table 3) might be explained by the fact that the low carbon/nitrogen ratio of Acacias (Table 4) favours microbial activity (Birk, 1979; Ashton, 1975).

Apart from the nitrogen added to the soil by the litter, the activity of the symbiotic bacteria in Acacia nodules fixes nitrogen, changing the soil nitrogen status (Nakos, 1977; Langkamp et al, 1979). The total input of nitrogen to an <u>A. mearnsii</u> plantation has been estimated to be in the order of 20 g/m^2/pa (180 lb/acre/pa; Hallsworth, 1958). Acacias, probably due to the presence of mycorrhiza, are also able to accumulate phosphorous (Barrow, 1977).

There is evidence that the addition of nutrients to oligotrophic, sclereophyll ecosystems upsets the water balance of the plant community, killing species with strong summer growth rhythms (Specht, 1973). This results in the opening up of the sclerophyll community, and an increase in the number of annuals and spring-growing exotic perennials (Specht, 1963; 1973; 1975). It follows that Fynbos communities, which also have a summer growth rhythm (J. Sommerville, unpubl.;

Kruger, 1980), are found on some of the most nitrogen and phosphorous deficient soils in the world (Low, 1978), and probably conserve nutrients by storage and internal cycling, (Specht, 1963; Kruger, 1979), will not be able to compete on a nutrient enriched substrate.

The growth strategy of Acacias appears to differ from that of South African and Australian heathland communities, in that the Acacias grow from early spring until growth is limited by water shortage in late summer, or by cold in early winter (Milton, in prep.), and Acacias rapidly recycle living and dead organic matter.

There can be little doubt that Acacias make the soil increasingly unsuitable for Fynbos plants. This is demonstrated by the difference in the successional sequence after fire in pure and Acacia dominated Fynbos : the former is dominated by Restionaceae and coppicing shrubs, the latter by grasses (Pentaschistis, Plagiochloa, Ehrharta, Briza, Avena) and exotic forbs (Phytolacca, Lactuca, Conyza, Senecio spp., Sonchus spp.).

CONCLUSION

Their evolution in a temperate climate (Milton, 1980), their early and extended growing season (Milton, in prep.), their height, and their freedom from effective predators and pathogens in the S.W. Cape have all contributed to the success of the Australian Acacias in the Fynbos Biome. This paper has shown that another important factor in favour of the Acacias is their ability to maintain a high rate of litter-fall and litter turn over, and by so to boost the nitrogen and phosphorous status of the soil. This nutrient enrichment may be one of the factors enabling the exotic Acacias, once introduced to an area, to maintain a hold among indigenous shrubs, and eventually to change, degrade and replace the original vegetation.

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BIOMASS OF AUSTRALIAN ACACIAS IN THE SOUTH WESTERN CAPE, SOUTH AFRICA

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ABSTRACT

Dimention analysis was carried out on thickets of the Australian exotics, Acacia cyclops Cunn. ex G. Don. and A. saligna (Labill.) Wendl. A set of regression equations relating stem diameter to mass was used to estimate the above ground biomass at 14 sample sites. The mean estimated biomass of 104 t/ha (dry weight) is about three times that of indigenous Fynbos vegetation, and is made up of 61% wood, 9% bark, 26% twig, 10% foliage and green twigs, and, during the summer, up to 17% pods. The trees are between five and ten metres in height and grow at an average density of 5200 trees/ha. Since the value of Acacia products is low, and harvesting, preparing and transporting is expensive, it is not possible at present to finance Acacia clearing operations by the sale of Acacia products.

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CONTENTS

INTRODUCTION

Although, in places, the Acacias still serve the function for which they were imported from Australia - holding unstable sand, their spread is generally seen as counterproductive, reducing as it does the farming and recreational value of land, and ousting indigenous vegetation.

An estimated 3 000 km^2 of flat and gently sloping land in the Cape is infested by _Acacia cyclops_ and _A. saligna_ (Taylor, 1975), and these and other exotic Acacias are becomming ever more common in mountainous areas as well. Hall (1979) found that Acacias were the major problem in 23% of the threatened habitats of rare plants.

Direct use of Acacias for goat farming has failed because the sale value of the animals did not meet the cost of fencing and food supplements (C. Uys; H.W. Sharp, pers. comms.). Clearing of the Acacia thickets to replace them with indigenous vegetation, pasture or crops is not economic where the soil is poor, so that much of the infested land remains unused.

If a market for Acacia products were developed, it is possible that the sale of these would help to finance clearing operations. Photosynthetic tissue, pods, bark, twigs and stem wood all have some potential value as animal feeds, fuels (including alcohols, methane and charcoal), chemicals (including tannins and acetone), (W.R.I., 1978; Goodricke, 1978) or fibers.

Before the economic feasibility of exploiting usable Acacia products can be gauged, it is necessary to estimate the total Acacia biomass per unit area, and its distribution in the various components of a tree. The aim of this study is to construct regression equations which relate the masses of Acacia products to an easily measured dimention, and to investigate the biomass yield of typical exotic Acacia thickets in the Cape.

METHOD

Acacia thicket biomasses were estimated by means of dimension analysis. This method, in which allometric relationships for trees of various sizes are applied to the size distribution in the stand, is considered to be the best one for estimating the standing crop of woody stands over 2 - 5 years in age (Madgwick, 1970; Whittaker & Marks, 1975). It has been successfully applied to temperate forest (Satoo, 1970; Whittaker & Woodwell, 1968), Eucalypt forest (Attiwill, 1979), African savanna-woodland (Huntley, 1977) and to Black Wattle plantations (Schönau, 1978).

The three steps required for dimention analysis are:

1. Sampling of individual trees
2. Recording stand characteristics
3. Use of data obtained (steps 1 & 2) to estimate stand biomass

Sampling individual trees

Between February and November, 1978, nine A. cyclops Cunn. ex G. Don. and seven A. saligna (Labill.) Wendl. ranging from 20 - 160 mm in diameter[1] (a range covering most of the trees in the study area) were felled at Faura School for Boys, on the Cape Flats, 20 km S.E. of Cape Town. After the stem diameter and circumference[1], total tree height, canopy height and diameter had been measured the trees were divided up into the following components:

a. wood exceeding or equal to 20 mm diameter
b. twigs or branches (live or dead) less than 20 mm in diameter
c. green matter (including foliage, young shoots and immature fruits)
d. mature or fully grown pods

All components were weighed in the field using 20 and 5 km Persola spring balances. The dry weight/wet weight ratio was calculated from subsamples of each component which were analysed in the laboritory. Estimates of pod number per unit weight and of the bark mass/wood mass ration were also obtained from subsamples.

An additional five A. saligna trees were sampled at Olifantsbosch, a coastal site in the Cape Point Nature Reserve. At this site, only diameter, canopy volume, tree height and wet weight of two components (wood over 20 mm diameter and all residual biomass) was recorded. Two year old A. longifolia seedlings were harvested in the University grounds on the lower slopes of Table Mountain for the collection of

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[1] Measured 10 cm above ground level

basal diameter, height and total wet weight statistics.

The relation ship between stem diameter (or circumference) and the wet and dry weights of the components (a, b, c, d) was calculated by regression analysis, and a set of idealised curves drawn for the prediction of component weight from stem diameter.

Stand characteristics

Plots were layed out in a number of pure and mixed stands of A. cyclops, A. longifolia and A. saligna in the south western and southern Cape. Every tree within a plot was assigned to a stem diameter[1] size class (class interval = 2 cm), and the number of trees in each class was recorded. Percentage projected canopy cover, average tree height, the approximate age of the stand, percentage projected cover by species other than Acacias, and the soil type were also recorded.

Estimation of standing crops

The total biomass (or mass of a component) per unit area of an Acacia stand was calculated using the equation (1) given by Satoo (1970).

[1] 10 cm above ground level

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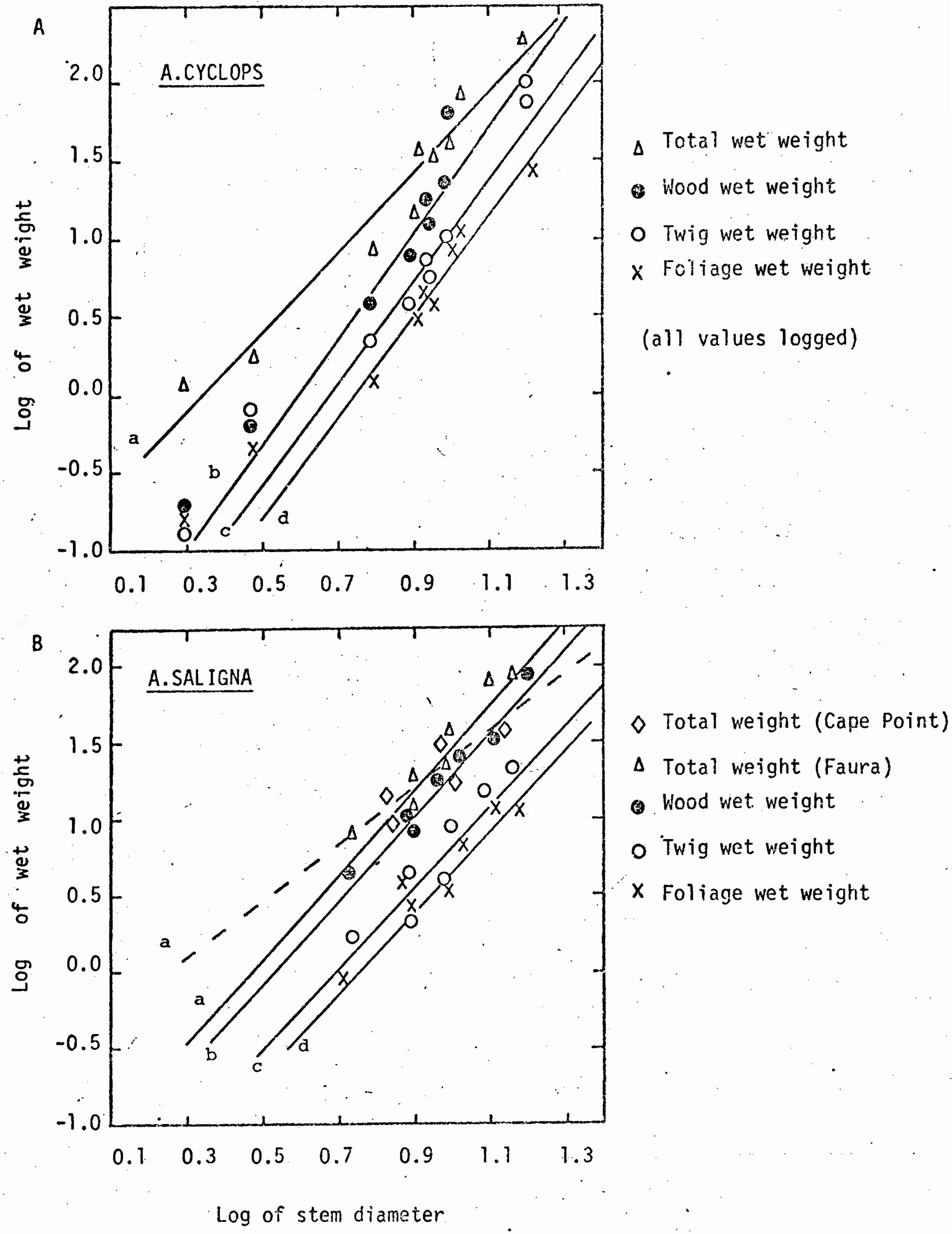
Figure 1. Regression of the log of total wet weight, and wood, twig and foliage wet weight on the log of stem diameter.



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Regression equations for Figure 1

A.CYCLOPS Regression of log wet weight on log stem diameter

a	$\log y = -0.87 + 2.53 \log x$	$SE(y) = 0.15$	$r = 0.98$
b	$\log y = -2.03 + 3.43 \log x$	$SE(y) = 0.12$	$r = 0.97$
c	$\log y = -2.35 + 3.40 \log x$	$SE(y) = 0.15$	$r = 0.96$
d	$\log y = -2.35 + 3.19 \log x$	$SE(y) = 0.09$	$r = 0.98$

A.SALIGNA (Faura) Regression of log wet weight on log stem diameter

a	$\log y = -1.18 + 2.68 \log x$	$SE(y) = 0.06$	$r = 0.99$
b	$\log y = -1.37 + 2.67 \log x$	$SE(y) = 0.04$	$r = 0.99$
c	$\log y = -1.82 + 2.62 \log x$	$SE(y) = 0.15$	$r = 0.94$
d	$\log y = -1.92 + 2.60 \log x$	$SE(y) = 0.13$	$r = 0.93$

A.SALIGNA (Cape Point)

a	$\log y = -0.45 + 1.86 \log x$	$SE(y) = 0.11$	$r = 0.93$

a	regression of total wet weight on stem diameter	(log kg/ log cm)
b	regression of wood wet weight on stem diameter	"
c	regression of twig wet weight on stem diameter	"
d	regression of foliage wet weight on stem diameter	"

$$W = (w' n) \quad . \quad . \quad . \quad . \qquad (1)$$

where W is the total biomass (or mass of a particular component) per unit area; w' is the total (or component) weight of an average member of the size class; n is the number of trees per unit area in the size class 'n'. w' was read of the idealised regression curve (Figure 1) and n is listed in Table 1.

RESULTS

Regression of mass on stem diameter

The biomass of the two Acacia species was strongly correllated with their stem diameters. This applied to both the dry and wet weight of the whole tree and of its component parts (wood, twigs and foliage). Although the relationship was clearly curvilinear, an exponential curve tended to overestimate, and a power curve to underestimate the biomass of the larger trees. The relationship between the logs of diameter and mass values was linear, and gave biomass estimates very close to actual measured values over the entire range of stem diameters. The correllation between diameter and to toal biomass was $r = 0.98$ for A. cyclops and $r = 0.99$ for A. saligna at the Faura site. (See equations for Figure 1).

The value of double log linear regression for predicting biomass from a stem dimention, which has been pointed out by Madgwick, (1970) Satoo (1970) and Whittaker & Marks (1975), is confirmed yet again by these results.

From Figure 1B it can be seen that the slope of the regression line

Table 1. Total wet weight of individual trees in nine stem diameter classes. (Values derived from regression equations, Figure 1).

Diameter class median (cm).	Wet weight (kg) A.cyclops (Faura)	 A.saligna (Faura)	 A.saligna (Cape Point)
1.5	0.4	0.2	0.6
3.5	3.3	1.8	3.5
5.5	11.2	5.6	7.9
7.5	25.1	14.1	14.1
9.5	47.9	25.1	22.4
11.5	75.9	41.6	31.6
13.5	112.2	75.9	44.7
15.5	158.5	100.0	56.2
17.5	208.9	131.8	63.1

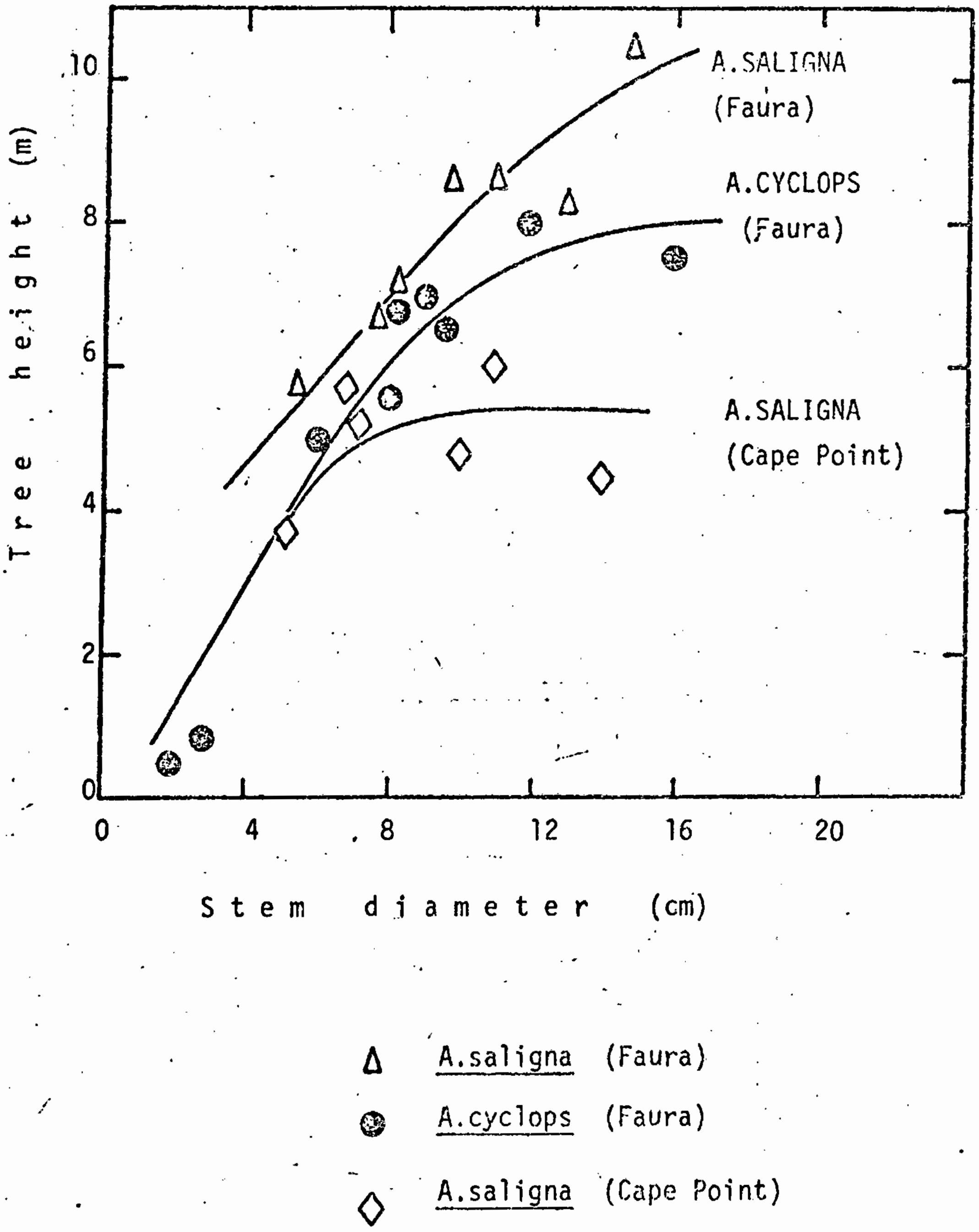
for A. saligna at the Cape Point site differs from that of the Faura sample. The correllation between mass and diameter was weaker for the trees sampled at Cape Point than for the Faura samples, (r = 0.93). These differences can be attributed to the location of the Cape Point site on exposed coastal dunes. Tree height appeared to be limited by wind-pruning, so that, for trees 4 - 5 m in height, stem diameter increments were not reflected in height increments, and the plants remained shrubby rather than tree-like in appearance. Figure 2 illustrates the relationship between diameter and height at the coastal and inland sites.

Size class distribution and stand biomass

It is necessary to sample the frequency distribution of the diameter size classes present in a thicket in order to make a realistic assessment of the biomass of that thicket. The product of the mass of a tree of average diameter, and tree density per unit area is unlikely to give a dependable estimate of the biomass of a thicket because the distribution of both tree quantity and mass in size classes is strongly skewed (Figure 3). Another complicating factor is that the thickets are often associations of two or more Acacia species differing in their diameter/mass relationship and in the allocation of biomass to stem and canopy.

The biomass of each of nine stem diameter class medians (class interval = 2 cm) was read off Figure 1A & B, and is listed in its antilog form in Table 1. These values were used to estimate the biomass contribution of each size class and species within a stand,

Figure 2. Relationship between tree height and stem diameter. *



* Curves are fitted by eye.

and ultimately the total stand biomass per unit area . . (2).

$$B = (f^1b^1, \quad f^2b^2 \quad ..... \quad f^nb^n) \quad . \quad . \quad . \qquad (2)$$

where B is the estimated stand biomass/unit area;

f^1, f^n is the frequency of trees in diameter size classes 1 - n;

b^1, b^n is the biomass for diameter size classes 1 - n (Figure 1).

The diameter size class distribution of trees in 14 Acacia stands in the S. and S.W. Cape was sampled during the course of this study. Despite the variation in habitat, stand age and species composition, the standard error was only 12% of the mean estimated wet weight of a mature Acacia thicket : 173 metric tons/ha (Table 2). Stem diameters ranged from below 1 cm to over 16 cm. Although only 2% of all measured trees exceeded 16 cm in diameter, theirs was the largest single contribution (38%) to the total stand biomass (Figure 3).

After clearing ro fire, Acacias regenerate from seed in large numbers. Densities of up to 3 million seedling/ha were recorded nine months after a fire on the Cape Peninsula. The young stands grow rapidly, and apparently by means of competition, thin themselves out, until, after five years, their densities are similar to that a mature stands (Figure 4). Numerous seedlings less than 1 cm in diameter (and generally under 10 cm in height) may be present in mature stands, particularly during the rainy season. Casual field observation as well as ciameter class distribution records (Table 2) suggest that some seed germinates every year, but that seedlings have very little chance of survival under the mature canopy. For this reason, seedlings of less than 1 cm in diameter were considered to be

Figure 4. Change in stand density and biomass of Acacia thickets with time compared with change in biomass of Fynbos and heath with time.

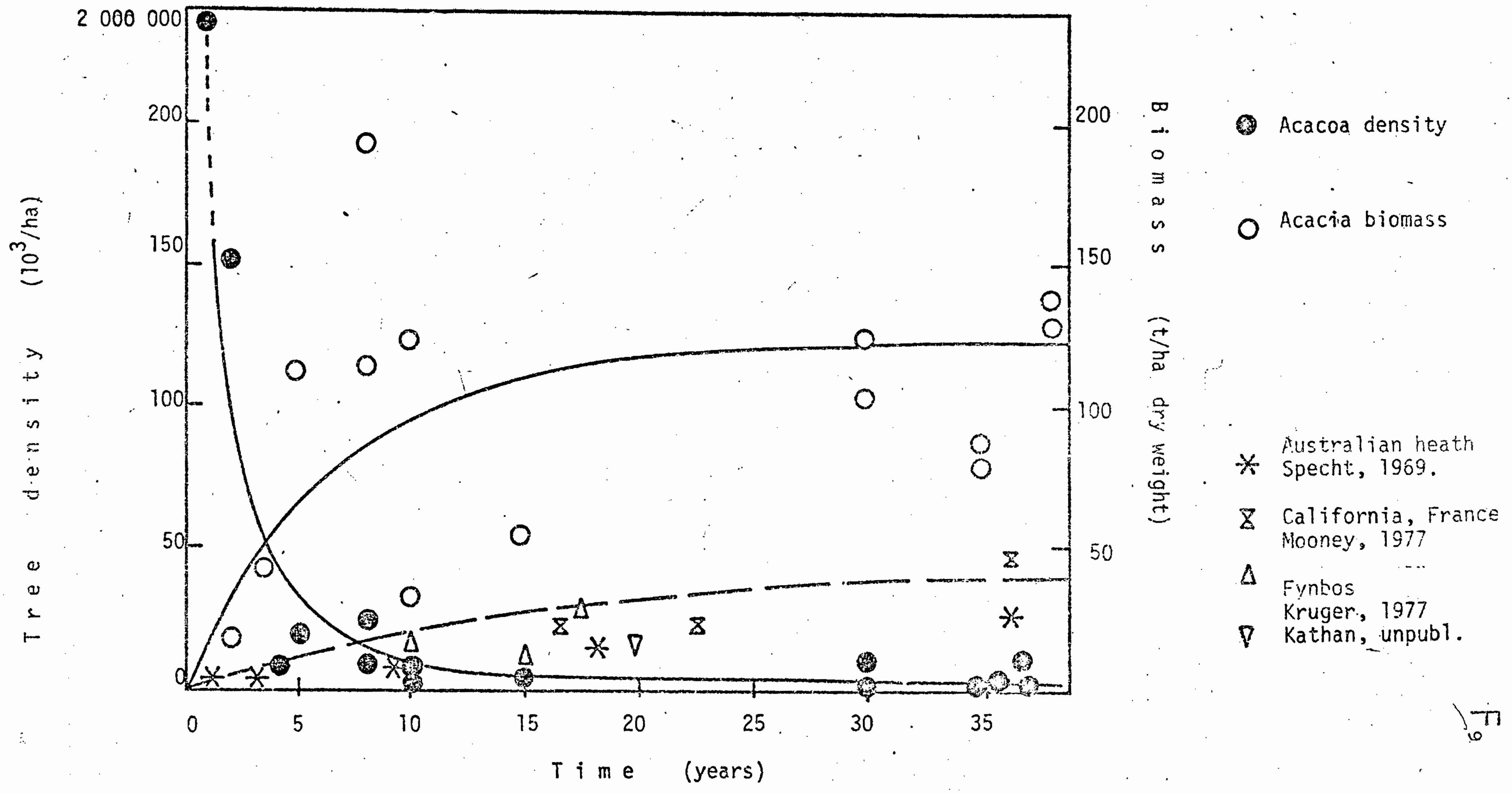


Table 2 Stand characteristics for exotic Acacia thickets in the Southern and South Western Cape, South Africa.

C = A.cyclops; L = A.longifolia; M = A.melanoxylon; S = A. saligna U.C.T. = University of Cape Town; Rondevl. = Rondevlei ; Bredas. = Bredasdorp.

Species	L & S	L & M		S	C & S		C & S		S	S	S	C	C	S	L	C	C	C & S		C & S			
Site description																							
Locality	Houtbay	U.C.T		Cape Pt.	Rondevl.		Paura		Paura	Penhill	Penhill	Rondevl.	Marina		U.C.T.	Bredas.	Bredas.	Goukamma		Goukamma			
Dist. from sea (km)	6.0	6.0		0.5	4.5		4.5		7.5	9.0	9.0	4.5	1.0		6.0	5.0	5.0	2.0		2.0			
Soil texture^1	c.l.	c.l.		s.l.	s.		s.		s.l.	s.l.	s.l.	s.	s.		c.	lime.s.	lime.s.	s.		s.			
Stand age (yr)	0.75	2		4	35		35		8	10	10	35	5		15	? 30	? 30	35		35			
Stand height (m)	0.25	2.5		5	7		7		7	7	7	7	9		6	5.5	7	8		6			
Canopy cover (%)	85	80		90	70		60		30	30	70	55	85		40	55	70	55		80			
Cover by other spp.^{2}	1	30		1	1		2		3	11	10	4	5		5	22	9	1		1			
Plot area (m^2)	1	1		75	100		100		25	25	25	25	25		25	50	50	25		25			
Distribution of Acacias in stem diameter classes																						Total seedling number in class	% of total
under 1 cm	372	-	-	-	-	-	40	-	46	-	-	-	82	-	-	-	-	150	75	3	120	667	70
1 - 2 cm	-	5	10	7	4	-	40	-	30	5	5	-	30	-	2	2	11	-	-	-	-		
3 - 4 cm	-	-	-	15	3	-	15	1	11	2	-	5	-	2	8	2	15	1	-	-	-	75	8
5 - 6 cm	-	-	-	21	7	-	1	3	8	-	-	6	-	5	2	6	2	1	1	-	-	63	7
7 - 8 cm	-	-	-	13	7	-	-	-	6	-	-	10	-	1	-	4	2	1	-	-	-	44	5
9 - 10 cm	-	-	-	7	4	-	-	5	7	-	-	5	-	7	-	1	2	2	-	-	-	40	4
11 - 12 cm	-	-	-	1	2	-	-	3	1	-	-	-	-	2	1	1	3	-	-	-	-	14	1
13 - 14 cm	-	-	-	-	-	-	-	3	2	-	-	-	-	2	1	2	-	-	-	3	1	14	1
15 - 16 cm	-	-	-	-	-	-	-	2	3	-	-	-	-	-	-	2	-	1	-	-	-	8	1
over 16 cm	-	-	-	-	7	2	-	5	-	1	4	-	-	-	1	1	2	-	-	-	-	23	2
Density																						Mean density (C.V. %)	
Number/ plot	372	5	10	64	34	2	96	22	114	8	9	26	112	19	10	21	37	155	76	6	121	no./ha	
Total no./ha	3720000	150000		8533	3600		15733		45600	3200	3600	10400	52400		4000	4200	7400	92800		50800		32304	(36)
No.over 1 cm/ha	0	150000		8533	3600		15733		27200	3200	3600	10400	19600		4000	4200	7400	2800		1600		18324	(56)
No.over 2 cm/ha	0	0		7600	3200		5067		15200	1200	1600	10400	7600		3200	3800	5200	2800		1600		5257	(21)
No.over 4 cm/ha	0	0		5600	2900		2933		10800	400	1600	9400	6800		2000	3400	2200	2400		1600		3926	(22)
Biomass																						Mean biomass (C.V. %)	
kg/ plot (wet weight)	1.3*	3*		594	2335		1432		825	136	528	574	468		221	1049	868	315		337		t/ha	
t/ha (wet weight)	0.14	30		79.2	233.5		190.9		330.0	54.4	211.2	229.6	187.2		88.4	209.8	173.6	126.0		134.8		173	(12)
t/ha (dry weight)	0.05	18		47.5	140.1		114.5		198.0	32.6	126.7	137.8	112.3		53.0	125.9	104.2	75.6		80.9		104	(12)

1 : c = clay; l = loam; s = sand. 2 : % projected cover of plot area * actual weight of harvested seedlings. (All other mass values are based on regression equations).

ephemoral, and are excluded from the stand density values plotted in Figure 4.

Dry weight/Wet weight ratios

The dry weight/wet weight (DW/WW) ratios of the wood, twigs, foliage and pods of A. cyclops and A. saligna are given in Table 3. All components of A. cyclops trees have a significantly higher dry mass per unit fresh weight than A. saligna (P = 0.01). The low moisture content of A. cyclops (34%) may be one of the factors enabling it to grow in drier, windier habitats, and closer to the shore than A. saligna. The higher specific density of its wood explains why Rooikranz[1] is more popular than Port Jackson[2] as a fuel.

Distribution of the biomass in the tree components

The contribution of wood, bark, twigs, foliage and pods to the total above ground biomass of an Acacia tree (on both wet and dry weight bases) is listed in Table 4. These values can be used in conjunction with dimention/mass regression equations, class frequency distribution data and DW/WW ratios, to predict how much of a particular product a stand could yield.

The biomass distribution pattern of an average Acacia thicket has been worked out in this way, using data from the regression equations

[1, 2] local vernacular names for [1] A. cyclops and [2] A. saligna

TABLE 3. Dry weight/wet weight ratios for *A. cyclops* and *A. saligna* in the South Western Cape

	Wood over 2 cm. diam.	Brown twigs	Foliage & green twigs	Pods	Total for tree
A. cyclops $\bar{x}$ (C.V.%)	0.685 (1.6)	0.727 (4.1)	0.429 (2.6)	0.380 (-)[1]	0.660 (1.6)
				0.906 (1.3)[2]	
A. saligna $\bar{x}$ (C.V.%)	0.610 (3.4)	0.470 (2.3)	0.361 (4.4)	0.320 (-)[1]	0.534 (2.7)
Average for both species	0.648	0.599	0.395	0.350[1]	0.597
Difference between species	0.075	0.257	0.068	0.060	0.126
Level of significance	**	**	**	-	**

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1 : Mature green pods, November

2 : Non-deciduous, ripe pods

** Significance level 0.01

Table 4. Distribution of biomass in the above ground parts of A.cyclops and A.saligna in the S.W. Cape

A. Wet weight basis (WW)

		Wood & bark	Brown twigs	Foliage	Pods
A.cyclops (Faura)	$\bar{x}$ (SE)	47.6 (5.1)	31.1 (5.0)	16.8 (1.8)	22
A.saligna (Faura)	$\bar{x}$ (SE)	63.6 (2.5)	20.7 (1.7)	15.4 (1.0)	5
A.saligna (Cape Point)	$\bar{x}$ (SE)	45.0 (4.0)	55.2 (4.0)		-
Average		55.6	25.9	16.1	14

B. Dry weight basis (DW)

(Faura)		Wood & &bark	Bark	Twig	Foliage	Pod
A.cyclops	$\bar{x}$	50.2	5.7	34.3	10.9	17
	(SE)	(5.6)	(0.5)	(5.5)	(1.1)	-
A.saligna	$\bar{x}$	72.4	11.3	18.0	9.8	3
	(SE)	(2.1)	(1.6)	(1.5)	(0.8)	-
Average		61.3	8.5	26.2	10.4	10

C. Significant differences in the distribution of components.

	Wood	Twig	Foliage
A.cyclops & A.Saligna at Faura (DW)	**	*	ns
A.cyclops & A.saligna at Faura (WW)	*	ns	ns
A.saligna at Faura & Cape Point (WW)	**	**	

* significant at 0.05 level ; ** 0.01 level ; ns not significant

(Figure 1) and from Tables 2, 3 and 4. The mean biomass distribution for the two species is used in these calculations since A. cyclops and A. saligna are equally common in the lumped data from Table 2[1]. The results of this calculation are presented in Figure 5. Wood makes up the major portion of wet and dry biomass, twigs contribute about 25% and foliage contributes only 10% to the total dry mass ie. about 11 t/ha.

There are significant differences in biomass partitioning both between species and between sites (Table 4). When they are growing under similar conditions, A. cyclops is more finely divided (ie. more highly branched) than A. saligna, the large diameter wood fraction contributing 48% to the wet weight of the former, but 64% to that of the latter. At the more exposed coastal site A. saligna is more shrub-like, with large gauge wood making up only 45% of the wet mass.[2]

The large twig component of A. cyclops suggests that wood production per tree of given diameter is less for this species than for A. saligna. This is not the case however, because the low wood volume is off-set by its high density.

DISCUSSION

The above ground biomass of exotic Acacia thickets in the Cape is comparable with that of forests in subtropical arid regions (120 t/ha),

[1] A. cyclops, 45%; A. longifolia, 3%; A. saligna, 52%

[2] The age of the stand (4 yr) might be partly responsible for this.

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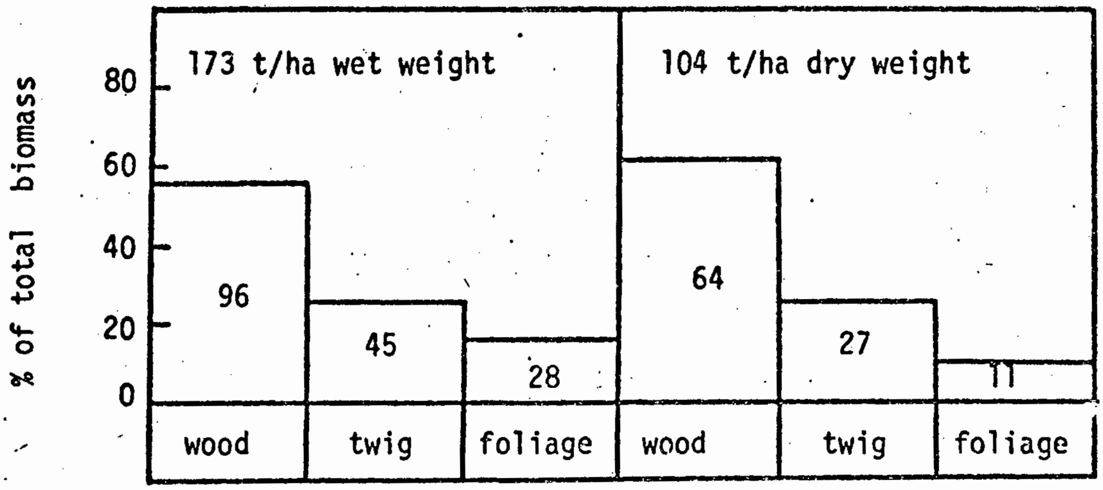
Figure 5. Distribution of biomass, on a wet and dry weight basis, in an average, mixed A.cyclops and A.saligna thicket in the Cape.



while the biomass of the indigenous Fynbos is typical of low shrub communities in these regions ie. 20 - 35 t/ha (Robin et al, 1975).

Fynbos and similar mediterranean-type shrublands in France and Australia mature slowly relative to the Acacia species studied, and when mature, seldom attain a biomass of over 40 t/ha (Figure 4). This means that after a fire, regenerating Acacias rapidly outgrow Fynbos plants and maintain this position of dominance.

Previous papers in this series (Milton & Moll; Milton a & b, all in prep.) have shown that Acacias differ from Fynbos species in their phenology and rates of growth and biomass turnover. The moisture content of A. cyclops (34%) and A. saligna (47%), however, is comparable with that of Fynbos (42 - 49%, Kathan, unpubl.; 32 - 44%, Kruger, unpubl.) and Australian heath (30 - 42%, Specht, 1969).

Allocation of biomass in the exotic Acacias is similar to that of small trees in temperate regions (Whittaker & Woodwell, 1968; Satoo, 1970). In larger trees, more of the biomass is allocated to the wood, while in shrubs more is allocated to twigs and foliage.

The relationship between tree number and stem diameter in the Acacia thickets is negati-e and exponential (Figure 3). A similar relationship exists in the indigenous forests of the Southern Cape (Van Laar & Leward, 1973).

The total above ground biomass of exotic Acacia thickets in the S.W. and S. Cape (104 t/ha) is comparable with the 110 - 148 t/ha (dry weight) estimated biomass of Black wattle plantations in Natal (Schönau, 1978). The distribution of the biomass, however, differs, in that wood greater than 2 cm in diameter makes up 50 and 72% of the dry weight of A. cyclops and A. saligna (respectively), but accounts for 77 - 80% of the dry weight of A. mearnsii[1] plantation trees (Schönau, 1978). Foliage contributes only 5% to the total plantation biomass.

Self established thickets of exotic Acacias were found to have a mean density of 5267 (CV = 21%) trees/ha, which is crowded relative to the densities at which Acacias are grown under plantation conditions (1280 - 1440 trees/ha; Schönau, 1978). The wild thickets are generally between 5 and 10 m in height - considerably shorter than plantation trees, which at the age of 10 years had a breast height diameter of 12.5 cm and averaged 17.5 m in height (Schönau, 1978).

All these differences suggest that self-established Acacia thickets in the S.W. Cape are going to be more difficult to harvest and will produce less wood than plantation trees.

Recently the Wattle Research Institute has investigated the feasibility of using residual plantation biomass for fodder or fuel.

Although in Australia many Acacia species are used as a drought fodder, it is necessary to supplement this fodder with a high calory feed and mineral licks (Everish, 1969). Leaves and twigs or A. mearnsii, which were gathered by hand (using secaters), dried, and ground in a hammer mill, were found to contain 5.7% tannin and were

[1] A. mearnsii de Willd. = Black Wattle

unpalatable to sheep. Despite its high protein content (18%), the Acacia fodder had a low digestibility, and its was concluded that the quality of the fodder did not warrent the costs of its collection and processing (Goodricke, 1978).

Harvesting and chipping of plantation biomass for use in the production of methane, alcohol, acetone or yeast, or simply for heating water to drive steam engines, is capital intensive. For example, in order to produce methanol economically, it would be necessary to supply one million tons/p.a. from a radius of 100 km on a sustained yield basis. For the production of ethanol by fermentation, cheap byproducts of the sugar industry (such as molassis) should be readily available (W.R.I., 1978).

Clearly, felling and elimination of the non-uniform self-established Acacia thicket in the S. and S.W. Cape does not meet the prerequisites for the production of methane, alcohol or yeast on a commercial basis, and the necessity of hand gathering would add to the production costs of Acacia fodder.

CONCLUSION

Although, at present, there appears to be little possibility of financing the clearing of Acacia thickets in the Cape, on a large scale, with revenue from the sale of the products, the outlook is not entirely dismal. Brush chippers are already being used by some municipalities for the demolition of Acacia thickets. Research into the best way of using these chips without further dispersing Acacia seed is needed. It also seems worthwhile to carry out research on the use of Acacia chips in small scale methane digesters, charcoal burners and composters for small-holdings, and on the effects of processing methods on the palatibility and food value of Acacia forage.

The high productivity of Acacias on soils generally considered to be very infertile, is probably attributable to their ability to accumulate nitrogen and phosphorous, greatly enriching the soil (Milton, b), and so possibility of growing vegetables on ploughed strips through Acacia thickets should be investigated, as a means of making the best of a bad situation.

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GENERAL CONCLUSIONS

The Australian Acacia species studied are well suited to the climatic and edaphic conditions of the Cape. They all produce much viable seed which accumulates in the soil (10 000 seeds/m^2 being typical of the seed store under mature trees) since very little of the seed is destroyed by predators or pathogens.

Three Acacias differed from most Fynbos plants in that they grew from spring until autumn (soil moisture permitting), and flowered in winter. *A.cyclops* , with its summer growth peak, resembled the Fynbos in its growth phenology. The annual litterfall (700 g/m^2) and the standing biomass (100 t/ha) of Acacia thickets is about four times as high as that of Fynbos. Acacias regenerating from seed overtop Fynbos within nine months and maintain a 2 - 4 m height advantage.

The management suggestions that follow are based on the findings reported in the thesis papers as well as on discussion and casual observation. Three phases of management are discussed.

Phase 1 : *Clearing operatios.*

a) Mechanical clearing. Trees should be felled as close to the ground as possible. Coppice regrowth of *A.saligna* saplings can be minimised if they are cut when carbohydrate stores are at their lowest ie. summer. Large isolated *A.saligna* trees can also be killed by ring-barking.

The low sale value of Acacia products combined with high labour and fuel costs make commercial exploitation of wild Acacia thickets unfeasible at present, but the materials could be used for fire wood, forage or methane production on a small scale. The best season for effective bushcutting or felling, and for the manufacture of forage from foliage and pods, is summer.

In coastal and other areas with strong winds and sandy soils, Acacia debris should not be burned, but should be stacked in parallel heaps, not more than ten metres apart. In this way rodent predation of the seed is encouraged, seedlings germinating under the brushwood are mostly shaded out, annual weeding operations in the open rows is facilitated, and the exposed soil is protected from wind erosion.

b) Burning. This is the most rapid means of depleating stored Acacia seed, but it is not recommended for use in lightly infested Fynbos or where the soil is likely to be eroded.

Should the burning of lightly infested Fynbos be unavoidable (on a fire break, grazing land or in a fire-managed catchment area), Acacias should be felled some months before the planned burn, and the debris of each tree stacked over its own stump, thereby causing a 'hot spot' in the fire which should destroy Acacia seed and coppice shoots. Planned or accidental burns in Acacia infested Fynbos should be checked, and the area weeded within 9 months of the fire (ie. before Acacias have overtopped the Fynbos). Thereafter, biennial checks are recommended.

For maximum destruction of buried Acacia seed on densely infested land, a very hot fire is needed. This can be achieved by felling the trees during the winter, spreading out the debris as evenly as possible, and burning it in the spring or summer when the wood is quite dry.

c) Herbicides are not recommended. They are expensive, non-specific, less effective than mechanical clearing and most have some residual effect in soil or water.

Systemic herbicides should be applied at the end of the growing season so that they are transported to the roots ie in the summer for the spring-growing A.melanoxylon and in autumn for species with longer growing seasons. Roundup decays rapidly in the soil and thus is safer than other herbicides, but it must not be forgotten that it is a general herbicide, killing Fynbos plants as well as Acacia saplings.

A 5 % Roundup solution, or a mixture of 245-T and diesoline applied to the freshly cut stump prevents regrowth of A.mearnsii and A.saligna (D.Donald, pers comm.), and these herbicides have been found to decay more rapidly in the soil than Tordon.

Phase 2. Regeneration control.(in dense infestations)

Within 1 - 2 months of a fire it is neccessary to remove the seedlings which come up in densities of many hundreds/m^2. This can be done by spraying the area with the herbicide Paraquat , but since the use of herbicides favours ruderals and species with large stores of seed in the soil, this treatmnet should not be repeated. Seedlings can also be removed by hoeing. The use of highly competitive plants such as grasses hes been found effective in suppressing regeneration along river courses and on sand dunes.

It is neccessary to weed the cleared area again about six months after the initial seedling flush, and then to weed annually or biennially. The weeding operation is useless if the roots are not pulled out, because seedlings of all the Acacia species can regrow if they are broken off at soil level.

Phase 3. Re-establishment and maintainance of natural vegetation.

After clearing dense Acacia infestations it may be advisable to sow the seed of alternative ground covers, particularly if the infested area is large and isolated from sources of indigenous seed. Grasses such as Ehrharta, Pentaschistis ans Eragrostis, and indigenous Asteraceae (eg. Metalasia, Chrysanthemoides, Helichrysum) are recommended as pioneers. These are fast growing and appear to compete better on nitrogen enriched soils than do other Fynbos shrubs and Restionaceae.

Fire should be excluded from the area during, and for as long as possible after the reestablishment period. Small indigenous browsing buck may be useful in the area once a good cover has been established, because they selectively brouse tender Acacia shoots, apparently in preference to indigenous plants.

A dense stand of indigenous vegetation is less likely to be infested by exotic plant.species than a patchy one : but it is not immune to infestation, and should be checked periodically. It would appear that moist, frost-free areas, particularly if they are frequently burned, grazed or in close proximity to roads , are very susceptible to Acacia infestation.

Biological control of Acacias by means of imported seed-destroying insects, is at present being investigated by Plant Protection (D.A.T.S.). This, if it succeeds, will contain, but not eliminate the Acacia problem. Since Australian Acacias growing in the S.W. Cape do not seem to differ significantly from those growing in their place of origin, with regard to morphology (Maslin, pers.comm.) or their phenology, these features should not present problems for the introduced insects.

Further research is needed, and as can be seen from the list that follows, not all of it is botanical.

1. Field trials to compare the effectiveness of burning, brushcutting, stacking or removing debris, herbicide treatment and plant competition in the eradication of Acacia thickets and re-establishment of indigenous vegetation.
2. Cost/benefit analysis of methods currently employed.
3. Monitoring the rate of decline in density of soil stored viable Acacia seed on land cleared or burned on a known date (eg. Goukamma Nature Reserve).
4. Investigation of smother crops and pioneers for rapid revegetation of cleared Acacia thickets.
5. Study of the feasibility of strip farming in Acacia thickets
6. Economics of Small scale use of Acacia products.
7. Detailed taxonomic study aimed at the recognition of possible ecotypes of the most prominent Acacia problem species, and comparison with Australian material. This information is needed when insects for biological control are being selected and introduced , and would also be of theoretical interest in the field of weed biology.

APPENDIX

TERMINAL SHOOT GROWTH : DESTRUCTIVE SAMPLING A. CYCLOPS APPENDIX 1A

DATE	STATISTIC	PARAMETER					% DAMAGE TM=apex missing		n SAMPLE SIZE
		length cms	dry mass grams	percent moisture	phyllode number	Lat.shoot number			
3/5/77	$\bar{x}$	10.00	0.33	64	10.00	?	?		27
	SEM	0.00	0.03		0.22				
MAY 3/6/77	$\bar{x}$	10.90	0.38	64	11.08	3.21	Total	64	24
	SEM	0.17	0.03		0.78	0.28	Insect	52	
	INCR	0.90	0.05		1.08	-	TM	12	
	CUMUL	10.90	0.38		11.08	3.21	Wind	4	
JUN 1/7/77	$\bar{x}$	10.90	0.47	66	15.25	4.88	Total	79	24
	SEM	0.22	0.03		0.89	0.20	Insect	79	
	INCR	0.00	0.09		4.17	1.23	TM	4	
	CUMUL	10.90	0.47		15.25	4.88	Wind	4	
JUL 1/8/77	$\bar{x}$	10.97	0.64	62	16.90	4.04	Total	70	24
	SEM	0.20	0.24		1.23	0.38	Insect	45	
	INCR	0.07	0.17		1.65	-0.84	TM	8	
	CUMUL	10.97	0.64		16.90	4.04	Wind	8	
AUG 4/9/77	$\bar{x}$	12.15	0.81	62	23.50	4.83	Total	79	24
	SEM	0.31	0.06		1.65	0.38	Insect	70	
	INCR	1.18	0.17		6.60	0.79	TM	4	
	CUMUL	12.15	0.81		23.50	4.83	Wind	12	
SEPT 4/10/77	$\bar{x}$	12.90	1.10	66	30.40	5.92	Total	75	24
	SEM	0.49	0.15		2.42	0.37	Insect	58	
	INCR	0.75	0.29		6.90	1.09	TM	8	
	CUMUL	12.90	1.10		30.40	5.92	Wind	12	
OCT 2/11/77	$\bar{x}$	15.44	2.07	58	40.90	7.00	Total	76	25
	SEM	1.12	0.62		5.26	0.57	Insect	68	
	INCR	2.54	0.97		10.50	1.08	TM	4	
	CUMUL	15.44	2.07		40.90	7.00	Wind	8	
standard 2/11/77	$\bar{x}$	20.00	2.23	59	56.30	8.75	Total	100	20
	SEM	0.00	0.16		4.59	0.62	Insect	100	
NOV 3/12/77	$\bar{x}$	24.08	3.81	61	66.05	8.68	Total	90	10
	SEM	0.61	0.36		5.12	0.74	Insect	90	
	INCR	4.08	1.58		9.75	-0.07			
	CUMUL	19.52	3.65		50.65	6.93			
standard 3/12/77	$\bar{x}$	20.00	2.56	58	47.25	6.65	Total	100	10
	SEM	0.00	0.30		7.10	0.61	Insect	100	

TERMINAL SHOOT GROWTH : DESTRUCTIVE SAMPLING   A. CYCLOPS   APPENDIX 1A

DATE	STATISTIC	PARAMETER					% DAMAGE		n SAMPLE SIZE
		length cms	dry mass grams	percent moisture	phyllode number	Lat. shoot number	TM=apex missing		
DEC 2/1/78	x̄	25.28	4.94	56	55.67	5.11	Total	100	9
	SEM	1.02	0.70		7.74	0.70	Insect	100	
	INCR	5.28	2.38		8.42	-1.54			
	CUMUL	24.80	6.03		59.07	5.39			
standard 2/1/78	x̄	20.00	1.64	57	20.39	3.67	Total	44	18
	SEM	0.00	0.13		1.50	0.42	Insect	44	
JAN 2/2/78	x̄	26.20	2.73	57	34.76	5.76	Total	48	21
	SEM	0.42	0.21		3.07	0.57	Insect	48	
	INCR	6.20	1.09		14.37	2.09			
	CUMUL	31.00	7.12		73.44	7.48			
standard 2/2/78	x̄	20.00	1.28	58	18.05	3.74	Total	32	19
	SEM	0.00	0.07		1.19	0.42	Wind	5	
FEB 2/3/78	x̄	24.62	2.36	58	37.15	6.95	Total	60	20
	SEM	0.40	0.13		2.08	0.41	Insect	55	
	INCR	4.62	1.08		19.10	3.21	Wind	5	
	CUMUL	35.62	8.20		92.54	10.69			
standard 2/3/78	x̄	20.00	1.39	56	20.65	4.15	Total	70	20
	SEM	0.00	0.07		1.32	0.37	Insect	60	
MAR 10/4/78	x̄	24.50	2.27	62	37.05	6.35	Total	70	20
	SEM	0.62	0.13		3.00	0.75	Insect	70	
	INCR	4.50	0.88		16.40	2.20			
	CUMUL	40.12	9.08		108.94	12.89			
standard 10/4/78	x̄	20.00	1.40	60	25.45	5.10	Total	50	20
	SEM	0.00	0.07		1.35	0.43	Insect	50	
APR 4/5/78	x̄	23.30	2.13	56	35.16	7.37			
	SEM	0.38	0.10		2.47	0.72	Total	32	19
	INCR	3.30	0.73		9.71	2.27	Insect	32	
	CUMUL	43.42	9.81		118.65	15.16			
standard 4/5/78	x̄	20.00	1.57	56	23.00	4.40	Total	60	10
	SEM	0.00	0.19		2.78	0.92	Insect	60	
MAY 2/6/78	x̄	21.75	1.73						10
	SEM	0.42	0.36						
	INCR	1.75	0.16						
	CUMUL	45.17	9.97						

TERMINAL SHOOT GROWTH : DESTRUCTIVE SAMPLING   A. CYCLOPS   APPENDIX 1A

DATE	STATISTIC	PARAMETER					% DAMAGE TM=apex missing	n SAMPLE SIZE
		length cms	dry mass grams	percent moisture	phyllode number	Lat.shoot number		
standard 2/6/78	$\bar{x}$	20.00	1.41			3.90		10
	SEM	0.00	0.22			0.60		
JUN & JUL 25/7/78	$\bar{x}$	25.00	1.88			7.20		9
	SEM	1.82	0.17			1.10		
	INCR	5.00	0.47			3.30		
	½ INCR	2.50	0.24			1.65		
	CUMUL	50.17	10.44			(18.46)		
standard 25/7/78	$\bar{x}$	20.00	1.01			6.80		5
AUG & FEB 13/2/79 (6½ mths)	$\bar{x}$	49.60	20.80			14.80		5
	SEM	5.85	4.64			2.54		
	INCR	29.60	19.79			8.00		
	INCR ÷ 6.5	4.55	3.04			1.23		
	CUMUL	79.77	30.23			(26.46)		

TERMINAL SHOOT GROWTH : DESTRUCTIVE SAMPLING   A. LONGIFOLIA   APPENDIX 1B

DATE	STATISTIC	PARAMETER					% DAMAGE TM-apex missing		n SAMPLE SIZE
		length cms	dry mass grams	percent moisture	phyllode number	Lat.shoot number			
25/5/77	$\bar{x}$	10.00	0.38	74	9.00	0.00	?		25
	SEM	0.00	0.05		0.36	0.00			
MAY 28/5/77	$\bar{x}$	11.60	0.75	71	10.80	0.20	Total	92	25
	SEM	0.28	0.05		0.85	0.14	Insect	65	
	INCR	1.60	0.37		1.80	0.20	Other	48	
	CUMUL	11.60	0.75		10.80	0.20			
JUN 27/6/77	$\bar{x}$	14.35	0.88	72	12.40	0.20	Total	96	25
	SEM	0.94	0.06		0.84	0.14	Insect	48	
	INCR	2.75	0.13		1.60	0.00	Other	44	
	CUMUL	14.35	0.88		12.40	0.20			
JUL 26/7/77	$\bar{x}$	16.40	1.44	71	21.40	1.09	Total	87	23
	SEM	0.99	0.13		2.86	0.37	Insect	30	
	INCR	2.05	0.56		9.00	0.89	Other	57	
	CUMUL	16.40	1.44		21.40	1.09			
AUG 28/8/77	$\bar{x}$	21.40	1.86	71	24.70	1.64	Total	96	25
	SEM	2.02	0.22		2.98	0.41	Insect	24	
	INCR	5.00	0.42		3.30	0.55	Other	80	
	CUMUL	21.40	1.86		24.70	1.64			
SEPT 26/9/77	$\bar{x}$	30.20	4.05	72	52.25	4.14	Total	100	22
	SEM	3.44	0.70		7.61	0.77	Insect	55	
	INCR	8.80	2.18		27.55	2.50	Other	73	
	CUMUL	30.20	4.05		52.25	4.14			
OCT 26/10/77	$\bar{x}$	58.13	11.92	72	91.70	5.95	Total	100	19
	SEM	14.80	2.20		13.80	1.08	Insect	47	
	INCR	27.93	7.87		39.45	1.81	Other	73	
	CUMUL	58.13	11.92		91.70	5.95			
standard 27/10/77	$\bar{x}$	20.00	0.52	81	12.96	0.84	Total	4	25
	SEM	0.00	0.04		0.94	0.22	Insect	4	
NOV 27/11/77	$\bar{x}$	59.96	4.22	71	44.60	3.04	Total	19	27
	SEM	1.63	0.41		9.19	0.66	Insect	19	
	INCR	39.96	3.71		31.64	2.22	Other	4	
	CUMUL	98.09	15.62		123.34	8.15			
standard 27/11/77	$\bar{x}$	20.00	0.45	88	12.30	0.25	Total	15	20
	SEM	0.00	0.11		0.45	0.14	Other	0	

TERMINAL SHOOT GROWTH : DESTRUCTIVE SAMPLING **A. LONGIFOLIA** APPENDIX 1B

DATE	STATISTIC	PARAMETER					% DAMAGE	n SAMPLE SIZE
		length cms	dry mass grams	percent moisture	phyllode number	Lat.shoot number	TM=apex missing	
DEC 29/12/77	$\bar{x}$	46.10	2.89	73	30.50	1.35		20
	SEM	1.87	0.18		3.55	0.52		
	INCR	26.10	2.44		18.20	1.10		
	CUMUL	124.19	18.06		141.54	9.25		
standard 29/12/77	$\bar{x}$	20.00	0.63	77	13.10	0.25		21
	SEM	0.00	0.06		0.46	0.14		
JAN 27/1/78	$\bar{x}$	33.60	1.94	65	16.95	0.05		21
	SEM	1.31	0.11		0.86	0.05		
	INCR	13.60	1.31		3.85	-0.02		
	CUMUL	137.79	19.37		145.39	9.05		
standard 27/1/78	$\bar{x}$	20.00	0.84	70	12.95	0.25		20
	SEM	0.00	0.08		0.54	0.14		
FEB 27/2/78	$\bar{x}$	26.60	2.14	66	18.40	0.70		20
	SEM	1.39	0.14		1.92	0.32		
	INCR	6.60	1.30		5.45	0.45		
	CUMUL	144.39	20.67		150.84	9.50		
standard 27/2/78	$\bar{x}$	20.00	1.17	64	12.05	0.05		20
	SEM	0.00	1.06		5.26	0.05		
MAR 27/3/78	$\bar{x}$	31.20	1.96	66	21.05	0.65		20
	SEM	1.70	0.12		1.84	0.28		
	INCR	11.20	0.78		9.00	0.60		
	CUMUL	155.59	21.45		159.84	10.10		
standard 27/3/78	$\bar{x}$	20.00	0.83	69	13.30	0.20		20
	SEM	0.00	0.08		0.51	0.20		
APR 27/4/78	$\bar{x}$	27.76	1.91	70	19.45	0.40		20
	SEM	1.13	0.11		1.21	0.15		
	INCR	7.76	1.08		6.15	0.20		
	CUMUL	163.35	22.53		165.99	10.30		
standard 27/4/78	$\bar{x}$	20.00	0.72	75	13.47	0.00		19
	SEM	0.00	0.05		0.35	0.00		
MAY 1/6/78	$\bar{x}$	24.72	1.54					10
	SEM	0.92	0.08					
	INCR	4.72	0.82					
	CUMUL	168.07	23.35					

TERMINAL SHOOT GROWTH : DESTRUCTIVE SAMPLING A. LONGIFOLIA APPENDIX 1B

DATE	STATISTIC	PARAMETER					% DAMAGE TM=apex missing	n SAMPLE SIZE
		length cms	dry mass grams	percent moisture	phyllode number	Lat.shoot number		
standard 1/6/78	$\bar{x}$	24.72	1.54					10
	SEM	0.92	0.08					
JUN & JUL 25/7/77	$\bar{x}$	40.80	3.24			1.67		9
	SEM	2.14	0.44			1.13		
	INCR	16.08	1.70			1.67		
	½ INCR	8.04	0.85			0.87		
	CUMUL	184.15	25.05			11.97		
standard	$\bar{x}$	20.00	0.64			1.80		5
	SEM	0.00	0.09			0.97		
AUG - FEB	$\bar{x}$	168.70	87.32			8.33		3
	SEM	25.40	29.03			4.41		
	INCR	148.70	86.68			6.53		
	INCR ÷ 6.5	22.88	13.34			1.00		
	CUMUL	332.85	111.73			18.50		

TERMINAL SHOOT GROWTH : DESTRUCTIVE SAMPLING A. MELANOXYLON

APPENDIX 1C

DATE	STATISTIC	PARAMETER					% DAMAGE		n SAMPLE SIZE
		length cms	dry mass grams	percent moisture	phyllode number	Lat.shoot number			
25/5/77	$\bar{x}$	10.00	0.49	69	9.23	?	?		26
	SEM	0.00	0.40		0.40				
MAY 28/5/77	$\bar{x}$	10.66	0.60	67	13.84	3.08	Total	76	25
	SEM	0.25	0.04		1.73	0.47	Insect	60	
	INCR	0.66	0.11		4.61				
	CUMUL	10.66	0.60		13.84	3.08			
JUN 27/6/77	$\bar{x}$	10.77	0.78	65	14.12	2.17	Total	83	24
	SEM	0.30	0.08		1.68	0.49	Insect	63	
	INCR	0.11	0.18		0.28	-0.91	Other	20	
	CUMUL	10.77	0.78		14.12	2.17			
JUL 26/7/77	$\bar{x}$	10.73	0.87	62	14.00	1.96	Total	71	24
	SEM	0.30	0.10		2.09	0.34	Insect	54	
	INCR	-0.04	0.09		-0.12	-0.21	Other	21	
	CUMUL	10.73	0.87		14.00	1.96			
AUG 25/8/77	$\bar{x}$	13.15	1.16	65	28.10	4.04	Total	91	23
	SEM	0.60	0.15		3.72	0.64	Insect	87	
	INCR	2.42	0.29		14.10	2.08	Other	26	
	CUMUL	13.15	1.16		28.10	4.04			
SEPT 26/9/77	$\bar{x}$	21.70	2.11	68	48.10	7.30	Total	65	20
	SEM	1.27	0.23		4.52	0.75	Insect	65	
	INCR	8.55	0.95		20.00	3.26	Other	5	
	CUMUL	21.70	2.11		48.10	7.30			
OCT 26/10/77	$\bar{x}$	31.18	4.61	70	75.53	9.42	Total	63	19
	SEM	2.65	0.72		10.47	1.29	Insect	57	
	INCR	9.48	2.50		27.43	2.12	Other	5	
	CUMUL	31.18	4.61		75.53	9.42			
standard 27/10/77	$\bar{x}$	20.00	1.04	76	30.92	6.00	Total	0	25
	SEM	0.00	0.08		2.38	0.35			
NOV 27/11/77	$\bar{x}$	45.75	7.61	68	90.75	14.05	Total	20	20
	SEM	2.33	0.63		7.35	0.88	Insect	20	
	INCR	25.75	6.57		59.83	8.05			
	CUMUL	56.93	11.18		135.36	17.47			
standard 27/11/77	$\bar{x}$	20.00	1.02	74	22.30	5.10	Total	10	20
	SEM	0.00	0.06		1.75	0.31	Insect	10	
DEC 29/12/77	$\bar{x}$	39.97	4.84	69	65.04	9.76	Total	88	17
	SEM	2.54	0.52		7.04	0.79	Insect	88	
	INCR	19.97	3.82		42.74	4.66	Other	-	
	CUMUL	76.90	15.00		178.10	22.13			

TERMINAL SHOOT GROWTH : DESTRUCTIVE SAMPLING A. MELANOXYLON APPENDIX 1C

standard 27/1/78	$\bar{x}$	20.00	1.26	71	30.00	5.75	Total	40	20
	SEM	0.00	0.11		2.41	0.36	Insect	40	
JAN	$\bar{x}$	27.51	2.98	63	41.30	6.95	Total	100	20
	SEM	1.02	0.20		3.53	0.47	Insect	100	
	INCR	7.51	1.72		11.30	1.20			
	CUMUL	81.41	16.72		189.40	23.33			
standard 27/1/78	$\bar{x}$	20.00	1.30	67	19.75	4.45	Total	95	20
	SEM	0.00	0.09		1.46	0.31	Insect	95	
FEB 27/2/78	$\bar{x}$	23.70	2.67	61	41.00	6.56	Total	100	9
	SEM	1.40	0.29		4.21	0.77	Insect	100	
	INCR	3.70	1.37		21.25	2.11			
	CUMUL	88.11	18.09		210.65	25.44			
standard 27/2/78	$\bar{x}$	20.00	1.76	62	30.45	6.10	Total	95	20
	SEM	0.00	0.14		1.74	0.43	Insect	95	
MAR 27/3/78	$\bar{x}$	22.40	2.37	62	39.10	7.67	Total	100	18
	SEM	0.69	0.15		3.63	0.75	Insect	100	
	INCR	2.40	0.61		8.65	1.57	Other	17	
	CUMUL	90.51	18.70		219.30	27.01			
standard 24/3/78	$\bar{x}$	20.00	1.66	62	33.40	5.20	Total	100	20
	SEM	0.00	0.07		2.72	0.59	Insect	100	
APR 27/4/78	$\bar{x}$	21.60	2.23	64	37.15	7.10	Total	100	20
	SEM	0.30	0.10		1.74	0.49	Insect	100	
	INCR	1.60	0.57		3.75	1.90	Other	15	
	CUMUL	92.11	19.27		223.05	28.91			
standard 27/4/78	$\bar{x}$	20.00	1.98	59	28.84	4.84	Total	100	19
	SEM	0.00	0.12		1.92	0.59	Insect	100	
MAY 1/6/78	$\bar{x}$	20.87	2.28						10
	SEM	0.50	0.10						
	INCR	0.87	0.31						
	CUMUL	92.98	19.58						
standard 1/6/78	$\bar{x}$	20.87	2.28						10
	SEM	0.50	0.10						
JUN & JUL 27/7/78	$\bar{x}$	21.10	2.25			8.80			10
	SEM	0.45	0.10			0.83			
	INCR	0.23	-0.03			3.96			
	½ INCR	0.12	-0.01			1.98			
	CUMUL	93.21	19.55			32.87			

TERMINAL SHOOT GROWTH : DESTRUCTIVE SAMPLING A. SALIGNA(RV) APPENDIX 1D

DATE	STATISTIC	PARAMETER					% DAMAGE	n SAMPLE SIZE
		length cms	dry mass grams	percent moisture	phyllode number	Lat.shoot number		
2/5/77	$\bar{x}$	10.00	0.24	82	6.00	0.00		28
	SEM	0.00	0.02		0.20	0.00		
MAY 3/6/77	$\bar{x}$	12.27	0.86	77	8.33	0.25	100	12
	SEM	0.53	0.08		0.58	0.18		
	INCR	2.27	0.62		2.33	0.25		
	CUMUL	12.27	0.82		8.33	0.25		
JUN 1/7/77	$\bar{x}$	17.00	1.66	76	18.10	3.25	75	12
	SEM	1.78	0.38		2.31	0.98		
	INCR	4.73	0.80		9.77	3.00		
	CUMUL	17.00	1.66		18.10	3.25		
JUL 1/8/77	$\bar{x}$	18.83	2.14	77	28.17	3.83	58	12
	SEM	2.32	0.49		7.35	1.20		
	INCR	1.83	0.48		10.07	0.58		
	CUMUL	18.83	2.14		28.17	3.83		
AUG 4/9/77	$\bar{x}$	25.60	5.72	78	54.40	6.82	100	11
	SEM	3.11	2.32		18.47	2.29		
	INCR	6.77	3.58		26.23	2.99		
	CUMUL	25.60	5.71		54.40	6.82		
SEPT 4/10/77	$\bar{x}$	40.77	12.60	79	88.70	11.00	50	7
	SEM	12.55	3.55		17.86	2.90		
	INCR	15.17	6.88		34.30	4.18		
	CUMUL	40.77	12.60		88.70	11.00		
OCT 2/11/77	$\bar{x}$	51.19	19.71	72	110.00	10.58	100	12
	SEM	4.61	4.00		23.30	1.80		
	INCR	10.42	7.11		21.30	-0.42		
	CUMUL	51.19	19.71		110.00	10.58		
standard 2/11/77	$\bar{x}$	20.00	1.64	78	13.30	1.00	70	10
	SEM	0.00	0.20		1.40	0.37		
NOV 3/12/77	$\bar{x}$	41.47	8.04	75	34.90	4.70	80	10
	SEM	2.34	1.00		6.55	1.21		
	INCR	21.47	6.40		21.60	3.70		
	CUMUL	72.66	26.11		131.60	14.28		
standard 3/12/77	$\bar{x}$	20.00	1.30	77	12.80	2.33	55	9
	SEM	0.00	0.24		2.43	0.65		

x

TERMINAL SHOOT GROWTH : DESTRUCTIVE SAMPLING **A. SALIGNA(RV)** APPENDIX 1D

DATE	STATISTIC	PARAMETER					% DAMAGE	n SAMPLE SIZE
		length cms	dry mass grams	percent moisture	phyllode number	Lat.shoot number		
DEC 2/1/78	$\bar{x}$	35.60	7.98	75	50.60	6.60		10
	SEM	4.20	1.58		9.27	1.68	80	
	INCR	15.60	6.68		37.80	4.27		
	CUMUL	88.26	32.79		169.40	18.55		
standard 2/1/78	$\bar{x}$	20.00	1.10	76	13.10	1.70		10
	SEM	0.00	0.11		1.34	0.50	0	
JAN 2/2/78	$\bar{x}$	40.03	9.49	77	72.56	7.67		9
	SEM	3.77	1.87		18.73	1.94	44	
	INCR	20.03	8.39		59.56	5.97		
	CUMUL	108.29	41.18		228.96	24.52		
standard 2/1/78	$\bar{x}$	20.00	1.10	76	17.89	2.78		9
	SEM	0.00	0.19		3.51	0.72	22	
FEB 2/3/78	$\bar{x}$	38.00	5.63	77	51.88	6.13		8
	SEM	3.88	1.30		13.52	2.22	88	
	INCR	18.00	4.53		33.99	3.35		
	CUMUL	126.29	45.71		262.95	27.87		
standard 2/3/78	$\bar{x}$	20.00	0.95	79	12.10	1.10		10
	SEM	0.00	0.09		0.91	0.59	80	
MAR 2/4/78	$\bar{x}$	36.80	4.41	75	27.00	2.56		9
	SEM	1.66	0.55		6.02	1.26	33	
	INCR	16.80	3.46		14.90	1.46		
	CUMUL	143.09	49.17		277.85	29.33		
standard 2/4/78	$\bar{x}$	20.00	1.17	76	12.90	1.20		10
	SEM	0.00	0.25		1.89	0.59	30	
APR 4/5/78	$\bar{x}$	33.80	4.51	77	30.30	3.20		10
	SEM	2.15	0.45		3.67	0.57	40	
	INCR	13.80	3.34		17.40	2.00		
	CUMUL	156.89	52.51		295.25	31.33		
standard 4/5/78	$\bar{x}$	20.00	1.35	73	11.80	0.00		5
	SEM	0.00	0.19		0.80	0.00	80	
MAY 2/6/78	$\bar{x}$	26.25	2.56			0.33		4
	SEM	1.48	0.19			0.33		
	INCR	6.25	1.21			0.33		
	CUMUL	163.14	53.72			31,66		
standard 2/6/78	$\bar{x}$	20.00	1.31			0.00		5
						0.00		

TERMINAL SHOOT GROWTH : DESTRUCTIVE SAMPLING   A. SALIGNA(RV)   APPENDIX 1D

DATE	STATISTIC	PARAMETER					% DAMAGE	n SAMPLE SIZE
		length cms	dry mass grams	percent moisture	phyllode number	Lat.shoot number		
JUN & JUL 25/7/78	$\bar{x}$	29.86	3.31			1.60		5
	SEM	2.19	0.45			0.81		
	INCR	9.86	2.00			1.60		
	½ INCR	4.93	1.00			0.80		
	CUMUL	173.00	55.72			33.26		
standard 25/7/78	$\bar{x}$	20.00	2.36			2.40		5
	SEM	0.00	0.58			1.12		

TERMINAL SHOOT GROWTH : DESTRUCTIVE SAMPLING **A. SALIGNA (UCT)**

DATE	STATISTIC	PARAMETER length cms	 dry mass grams	 percent moisture	 phyllode number	 Lat.shoot number	% DAMAGE	n SAMPLE SIZE
25/5/77	$\bar{x}$	10.00	0.24	82	6.00	0.00		28
	SEM	0.00	0.02		0.20	0.00		
MAY 28/5/77	$\bar{x}$	15.60	0.93	80	15.46	2.46		13
	SEM	1.25	0.13		3.45	1.00	85	
	INCR	5.60	0.69		9.46	2.46		
	CUMUL	15.60	0.93		15.46	2.46		
JUN 27/6/77	$\bar{x}$	15.87	1.56	77	14.75	2.40		12
	SEM	2.12	0.26		3.21	0.66	100	
	INCR	0.27	0.63		-0.71	-0.06		
	CUMUL	15.87	1.56		14.75	2.40		
JUL 26/7/77	$\bar{x}$	20.19	2.21	78	17.40	1.77		13
	SEM	2.47	0.43		3.25	0.62	69	
	INCR	4.32	0.65		2.65	-0.63		
	CUMUL	20.19	2.21		17.40	1.77		
AUG 25/8/77	$\bar{x}$	24.50	4.14	71	31.10	3.42		24
	SEM	2.51	0.84		4.66	0.67	88	
	INCR	4.31	1.93		13.70	1.65		
	CUMUL	24.50	4.14		31.10	3.42		
SEPT 26/9/77	$\bar{x}$	46.10	14.63	75	53.00	5.00		23
	SEM	4.69	2.60		6.84	0.86	57	
	INCR	21.60	10.49		21.90	1.58		
	CUMUL	46.10	14.63		53.00	5.00		
OCT 26/10/77	$\bar{x}$	62.67	27.50	75	84.87	7.00		15
	SEM	7.03	5.69		12.97	1.35	93	
	INCR	16.57	12.87		31.87	2.00		
	CUMUL	62.67	27.50		84.87	7.00		
standard 27/10/77	$\bar{x}$	20.00	0.92	83	7.73	0.40		15
	SEM	0.00	0.08		0.75	0.24	27	
NOV 27/11/77	$\bar{x}$	60.10	10.10	72	26.70	2.90		15
	SEM	3.87	1.49		1.77	1.04	33	
	INCR	40.10	9.18		18.97	2.50		
	CUMUL	102.77	36.68		103.81	9.50		
standard 27/11/77	$\bar{x}$	20.00	0.70	80	7.00	0.60		10
	SEM	0.00	0.10		0.15	0.34	50	

TERMINAL SHOOT GROWTH : DESTRUCTIVE SAMPLING **A. SALIGNA(UCT)** **APPENDIX 1B**

DATE	STATISTIC	PARAMETER length cms	dry mass grams	percent moisture	phyllode number	Lat.shoot number	% DAMAGE	n SAMPLE SIZE
DEC 27/12/77	$\bar{x}$	54.40	7.70	75	29.30	4.20		10
	SEM	1.70	0.80		5.40	1.10	50	
	INCR	34.40	7.00		22.30	3.60		
	CUMUL	137.17	43.68		126.11	13.10		
standard 29/12/77	$\bar{x}$	20.00	0.71	78	8.82	1.30		11
	SEM	0.00	0.06		0.38	0.37	36	
JAN 27/1/78	$\bar{x}$	44.30	4.71	74	19.30	1.70		10
	SEM	2.94	0.44		3.11	1.18	100	
	INCR	24.30	4.00		10.48	0.40		
	CUMUL	161.47	47.68		136.59	13.50		
standard 27/1/78	$\bar{x}$	20.00	0.64	79	8.70	0.50		10
	SEM	0.00	0.07		0.54	0.40	50	
FEB 27/2/78	$\bar{x}$							
	SEM							
	INCR							
	CUMUL							
standard 27/2/78	$\bar{x}$	20.00	1.40	72	6.10	0.90		10
	SEM	0.00	0.56		0.84	0.48	100	
MAR 24/3/78	$\bar{x}$	26.52	1.92	74	9.44	1.11		9
	SEM	1.68	0.22		1.17	0.34	100	
	INCR	6.52	0.52		3.34	0.21		
	CUMUL	167.99	48.20		139.93	13.71		
standard 24/3/78	$\bar{x}$	20.00	1.02	72	5.27	0.00		11
	SEM	0.00	0.11		0.39	0.00	91	
APR 27/4/78	$\bar{x}$	26.60	1.65	77	9.40	0.80		10
	SEM	1.78	0.20		1.14	0.20	100	
	INCR	6.60	0.63		4.13	0.80		
	CUMUL	174.59	48.83		144.06	14.51		
standard 27/4/78	$\bar{x}$	20.00	0.95	77	6.25	0.25		8
	SEM	0.00	0.20		0.62	0.25		
MAY 1/6/78	$\bar{x}$	26.32	1.23					5
	SEM	3.09	0.41					
	INCR	6.32	0.28					
	CUMUL	180.91	49.11					

TERMINAL SHOOT GROWTH : DESTRUCTIVE SAMPLING **A. SALIGNA(UCT)** APPENDIX 1B

DATE	STATISTIC	PARAMETER					% DAMAGE	n SAMPLE SIZE
		length cms	dry mass grams	percent moisture	phyllode number	Lat.shoot number		
standard 1/6/78	$\bar{x}$	26.32	1.23	77				5
	SEM	3.09	0.14					
JUN & JUL 24/7/78	$\bar{x}$	25.10	1.21			0.80		5
	SEM	3.78	0.29			0.37		
	INCR	-1.20	-0.02			0.55		
	½ INCR	-0.60	-0.01			0.28		
	CUMUL	179.69	49.09			15.06		
standard 25/7/78	$\bar{x}$	20.00	0.72			0.00		2
	SEM	0.00	0.17			0.00		
AUG - FEB 9/2/79	$\bar{x}$	134.00	41.40			12.00		1
	SEM							
	INCR	114.00	40.69			12.00		
	INCR ÷ 6.5	17.50	6.26			1.85		
	CUMUL	293.69	89.77			27.06		

LITTERFALL DATA **A. CYCLOPS** APPENDIX 2A

DATE & STATISTIC	FLOWER MASS	POD MASS	SEED NUMBER X10^{-3}	SEED MASS	LEAF MASS	TWIG MASS	OTHER SPECIES MASS	TOTAL MASS ACACIA
MAY 1977								
sample $\bar{x}$ (g)	0.01	15.70	32.30	1.37	3.71	3.00	0.36	25.20
SEM	0.004	1.49	4.63	0.22	0.37	0.52	0.08	1.96
kg/ha	0.50	799.4	1645	69.8	188.9	152.7	18.3	1283.1
SEM	0.20	75.87	236	11.2	18.8	26.5	4.1	99.8
JUN 1977								
sample $\bar{x}$ (g)	0.01	3.12	11.40	0.36	1.86	0.37	0.40	6.05
SEM	0.01	0.50	2.32	0.07	0.25	0.04	0.01	1.22
kg/ha	0.50	158.9	580	18.3	94.7	18.8	20.4	308.0
SEM	0.31	25.5	118	3.6	12.7	2.0	0.5	62.1
JUL 1977								
sample $\bar{x}$ (g)	0.02	2.51	1.80	0.06	3.14	0.42	0.19	6.39
SEM	0.01	0.35	0.49	0.02	0.54	0.16	0.05	0.89
kg/ha	10.2	127.8	92	3.1	159.9	21.4	9.7	325.4
SEM	0.5	17.8	25	1.0	27.5	8.2	2.5	45.3
AUG 1977								
sample $\bar{x}$ (g)	0.03	14.37	2.00	0.06	4.02	4.92	0.59	25.04
SEM	0.01	1.86	0.77	0.01	0.51	0.87	0.17	2.76
kg/ha	1.5	731.7	102	3.1	204.7	250.5	30.3	1274.9
SEM	0.5	94.7	39	0.2	26.0	44.3	8.7	140.5
SEPT 1977								
sample $\bar{x}$ (g)	0.005	4.26	0.30	0.005	3.18	1.52	0.26	10.52
SEM	0.002	0.54	0.15	0.003	0.34	0.38	0.07	1.21
kg/ha	0.3	216.9	15	0.3	161.9	77.4	13.2	535.6
SEM	0.01	27.5	8	0.1	17.3	19.4	3.6	61.6
OCT 1977								
sample $\bar{x}$ (g)	0.003	1.43	0.20	0.003	3.76	0.23	0.20	7.91
SEM	0.002	0.27	0.13	0.002	0.42	0.08	0.07	0.74
kg/ha	0.15	72.8	10	0.15	191.4	11.7	10.2	402.7
SEM	0.10	13.8	7	0.10	21.4	4.1	3.6	3.8
NOV 1977								
sample $\bar{x}$ (g)	0.17	13.65	15.90	0.80	11.56	7.00	0.86	38.25
SEM	0.14	1.81	4.61	0.25	0.97	1.11	0.42	3.90
kg/ha	8.7	695.0	810	40.7	588.6	356.4	43.8	1947.6
SEM	2.0	92.2	235	12.7	49.4	56.5	21.4	19.9
DEC 1977								
sample $\bar{x}$ (g)	0.23	4.58	49.10	2.21	13.47	1.48	0.37	23.72
SEM	0.08	0.73	10.18	0.51	1.62	0.35	0.18	2.01
kg/ha	11.7	233.2	2500	112.5	685.8	75.4	18.8	1207.7
SEM	4.1	37.2	520	25.5	82.5	17.8	0.9	102.3
JAN 1978								
sample $\bar{x}$ (g)	0.79	2.55	74.30	3.16	11.37	0.41	0.21	19.23
SEM	0.16	0.44	14.31	0.53	0.90	0.18	0.09	1.42
kg/ha	40.2	129.8	3783	160.9	578.9	20.9	10.7	979.1
SEM	8.2	22.4	729	27.0	45.8	9.2	4.6	72.3

LITTERFALL DATA **A. CYCLOPS**

APPENDIX 2A

DATE & STATISTIC	FLOWER MASS	POD MASS	SEED NUMBER X10^{-3}	SEED MASS	LEAF MASS	TWIG MASS	OTHER SPECIES MASS	TOTAL MASS ACACIA
FEB 1978								
sample $\bar{x}$ (g)	0.11	2.31	38.20	1.40	9.28	0.99	0.20	14.08
SEM	0.02	0.35	7.56	0.03	0.90	0.27	0.07	1.18
kg/ha	56.1	117.6	1945	71.3	472.5	50.4	48.9	716.9
SEM	1.0	17.8	385	1.5	45.8	13.8	3.6	60.1
MAR 1978								
sample $\bar{x}$ (g)	0.004	0.85	9.10	0.30	5.53	0.16	0.30	7.12
SEM	0.002	0.23	2.23	0.08	0.39	0.05	0.12	0.63
kg/ha	0.20	43.3	463	15.3	281.6	8.1	15.3	362.5
SEM	0.10	11.7	114	4.1	19.9	2.5	6.1	32.1
APR 1978								
sample $\bar{x}$ (g)	0.008	2.26	8.60	0.28	2.82	0.93	0.25	6.74
SEM	0.003	0.30	0.97	0.04	0.19	0.43	0.08	0.52
kg/ha	0.40	115.1	438	14.3	143.6	47.4	12.7	343.2
SEM	0.15	15.3	50	2.0	9.7	21.9	4.1	26.5
MAY 1978								
sample $\bar{x}$ (g)			10.60	0.33	1.90			3.62
SEM			2.72	0.09	0.60			0.26
kg/ha			540	16.8	96.7			184.6
SEM			139	4.6	30.6			13.2
JUN & JUL 1978								
sample $\bar{x}$ (g)	0.0	2.28	5.75	0.15	5.10	0.28	0.18	6.87
SEM		0.59	1.11	0.07	1.39	0.24	0.08	0.97
kg/ha		116.1	293	7.6	259.7	14.3	9.2	349.8
SEM		30.0	56	3.6	70.8	12.2	4.1	49.4
AUG 78 - JAN 79								
sample $\bar{x}$ (g)			202.3	14.0				86.5
SEM			21.9	?				5.0
kg/ha			10300	713				4400
SEM			112	?				250
12 MONTH TOT	131	3441	12382	510	3775	1090	252	9688
kg/ha $\bar{x}$	10.9	287.0	1032	42.0	314.6	90.8	21.0	807.3
SEM	5.3	80.9	345	14.9	60.8	31.6	3.8	152.7
15 MONTH TOT	131	3557	13215	527	4132	1104	261	10221
21 MONTH TOT	-	-	23515	1240	-	-	-	14621

COMPONENTS AS PERCENT OF YEARS TOT	FLOWER	POD	SEED	PHYLLODE	TWIG
	1.35	35.52	5.26	38.97	11.25

MONTHLY TOTAL	M	J	J	A	S	O	N	D
	13.24	3.18	3.36	13.16	5.53	4.15	20.11	12.47
AS PERCENT								
	J	F	M	A	M	JJ	A-J	
OF ANNUAL TOT	10.10	7.41	3.75	3.54	1.90	3.61	45.42	

LITTERFALL DATA **A. LONGIFOLIA** APPENDIX 2B

DATE & STATISTIC	FLOWER MASS	POD MASS	SEED NUMBER X10^{-3}	SEED MASS	LEAF MASS	TWIG MASS	OTHER SPECIES MASS	TOTAL ACACIA MASS
MAY 1977								
sample $\bar{x}$ (g)	0.74	0.12	0.00	0.00	2.95	1.26	2.90	5.07
SEM	0.12	0.05			1.17	0.81	0.89	1.94
kg/ha	37.7	6.1			150.2	64.2	147.7	258.2
SEM	6.1	2.6			59.6	41.2	45.3	98.8
JUN 1977								
sample $\bar{x}$ (g)	3.07	0.02	0.00	0.00	6.20	0.19	10.67	9.48
SEM	0.74	0.01			1.43	0.06	7.95	1.96
kg/ha	156.3	1.0			315.7	9.7	54.3	482.7
SEM	37.7	7.1			72.8	3.1	40.5	99.8
JUL 1977								
sample $\bar{x}$ (g)	3.89	0.00	0.00	0.00	4.89	0.17	1.59	8.96
SEM	1.06				1.02	0.09	0.33	1.90
kg/ha	198.1				249.0	8.7	81.0	456.2
SEM	54.0				51.9	4.6	16.8	96.7
AUG 1977								
sample $\bar{x}$ (g)	2.77	0.08	0.00	0.00	1.75	0.12	1.10	4.68
SEM	0.38	0.04			0.23	0.04	0.25	0.48
kg/ha	141.0	4.1			89.1	6.1	56.0	238.3
SEM	19.4	2.0			11.7	2.0	12.7	24.4
SEPT 1977								
sample $\bar{x}$ (g)	0.40	0.08	0.00	0.00	2.97	0.14	0.94	3.59
SEM	0.17	0.02			0.51	0.06	0.17	0.62
kg/ha	20.4	4.1			151.2	7.1	47.9	182.0
SEM	8.7	1.0			26.0	3.1	8.7	31.6
OCT 1977								
sample $\bar{x}$ (g)	0.08	0.05	0.00	0.00	5.77	0.08	0.65	6.29
SEM	0.08	0.02			0.67	0.06	0.23	0.72
kg/ha	4.07	2.5			293.8	4.1	33.1	320.3
SEM	4.07	1.0			34.1	3.1	11.7	36.7
NOV 1977								
sample $\bar{x}$ (g)	0.00	8.80	370.0	6.13	12.91	0.12	0.74	28.80
SEM		1.81	59.7	1.10	3.47	0.04	0.08	4.88
kg/ha		448.1	18839	312.1	657.3	6.1	37.7	1466.4
SEM		92.2	3040	56.0	176.7	2.0	4.1	248.5
DEC 1977								
sample $\bar{x}$ (g)	0.00	4.65	197.00	2.65	8.62	0.30	1.39	16.75
SEM		1.74	61.79	1.08	1.45	0.10	0.96	3.13
kg/ha		236.8	10030	134.9	438.9	15.3	70.8	852.9
SEM		88.6	3146	55.0	73.8	5.1	48.9	159.4
JAN 1978								
sample $\bar{x}$ (g)	0.03	0.43	5.50	0.06	8.25	0.29	0.51	9.07
SEM	0.02	0.19	1.82	0.02	0.73	0.06	0.06	0.80
kg/ha	1.5	21.9	280	3.1	420.1	14.8	26.0	461.8
SEM	1.0	9.7	92	1.0	37.2	3.1	3.1	40.7
FEB 1978								
sample $\bar{x}$ (g)	0.04	0.12	0.70	0.005	3.52	0.03	4.07	4.15
SEM	0.02	0.05	0.05	0.003	0.45	0.02	1.09	0.47
kg/ha	2.0	6.11	35	0.3	179.2	1.5	207.2	211.3
SEM	1.0	2.55	2	0.2	22.9	1.0	55.5	23.9

LITTERFALL DATA **A. LONGIFOLIA** APPENDIX 2B

DATE & STATISTIC	FLOWER MASS	POD MASS	SEED NUMBER X10^{-3}	SEED MASS	LEAF MASS	TWIG MASS	OTHER SPECIES MASS	TOTAL ACACIA MASS
MAR 1978								
sample $\bar{x}$ (g)	0.12	0.55	0.30	0.003	3.65	0,09	4.05	4.29
SEM	0.04	0.03	0.30	0.003	1.45	0.05	0.76	1.47
kg/ha	6.1	28.0	15	0.2	185.8	4.6	206.2	218.4
SEM	2.0	1.5	15	0.2	73.8	2.6	38.7	74.9
APR 1978								
sample $\bar{x}$ (g)	0.14	0.03	0.10	0.001	4.23	0.02	1.00	4.82
SEM	0.07	0.02	0.10	0.001	1.25	0.01	0.19	1.28
kg/ha	7.1	1.5	5	0.05	215.4	1.0	50.9	245.4
SEM	3.6	1.0	5	0.05	63.7	0.5	9.7	65.2
MAY 1978								
sample $\bar{x}$ (g)			0.20	0.002	8.18			
SEM			0.20	0.002	2.40			
kg/ha			10	0.1	416.5			(427)
SEM			10	0.1	122.2			
JUN & JUL 1978								
sample $\bar{x}$ (g)	12.73	0.00	0.00	0.00	8.82	0.04	2.26	21.59
SEM	5.10				4.00	0.03	1.41	5.04
kg/ha	648.2				449.1	2.0	115.1	1099.0
SEM	259.7				203.7	1.5	71.8	256.6
AUG 1978 - JAN 1979								
sample $\bar{x}$ (g)			1449	24				120
SEM								
kg/ha			73802	1222				6110
SEM								
12 MONTH TOT	571.	760	29205	451	3345	143	1019	5392
kg/ha $\bar{x}$	47.6	63.4	2433.8	37.5	279.0	11.9	84.9	449.3
SEM	21.0	39.9	1706.7	27.3	46.3	4.9	18.8	107.3
15 MONTH TOT	1219	760	29215	451	4211	145	1134	6918
21 MONTH TOT	-	-	103017	1673	-	-	-	13028

COMPONENTS AS PERCENT OF YEARS TOT	FLOWER	POD	SEED	PHYLLODE	TWIG
	10.58	16.03	8.31	61.67	2.64

MONTHLY TOTAL AS PERCENT OF ANNUAL TOT								
	M	J	J	A	S	O	N	D
	5.09	8.90	8.41	4.39	3.61	5.90	27.03	15.72
	J	F	M	A	M	JJ	A-J	
	8.51	3.89	4.03	4.52	7.92	20.38	113.32	

LITTERFALL DATA **A. MELANOXYLON** APPENDIX 2C

DATE & STATISTIC	FLOWER MASS	POD MASS	SEED NUMBER $X10^{-3}$	SEED MASS	LEAF MASS	TWIG MASS	OTHER SPECIES MASS	TOTAL ACACIA MASS
MAY 1977								
sample $\bar{x}$ (g)	0.06	0.16	3.20	0.06	2.43	2.61	1.70	5.51
SEM	0.02	0.07	1.03	0.03	0.37	1.64	0.40	1.64
kg/ha	3.1	8.1	162	3.1	123.7	132.9	86.6	280.5
SEM	1.0	3.6	52	1.5	18.8	83.5	20.4	83.5
JUN 1977								
sample $\bar{x}$ (g)	0.81	0.06	1.20	0.03	8.32	2.12	2.05	11.75
SEM	0.18	0.02	0.05	0.01	0.98	0.56	0.78	1.13
kg/ha	41.2	3.1	61	1.5	423.6	107.9	104.3	598.3
SEM	9.2	1.0	3	0.5	50.0	28.5	39.7	57.5
JUL 1977								
sample $\bar{x}$ (g)	1.34	0.02	0.20	0.002	12.04	1.74	1.12	15.40
SEM	0.53	0.01	0.13	0.001	1.64	0.58	0.24	1.76
kg/ha	68.2	1.00	10	0.10	613.0	88.6	57.0	784.1
SEM	27.0	0.51	10	0.05	83.5	29.5	12.2	89.6
AUG 1977								
sample $\bar{x}$ (g)	1.20	0.00	0.20	0.003	3.03	10.19	3.36	13.29
SEM	0.30		0.13	0.001	0.61	4.96	1.10	5.57
kg/ha	61.1		10	0.20	154.3	518.8	171.1	676.7
SEM	15.2		6	0.05	31.1	252.8	56.0	283.6
SEPT 1977								
sample $\bar{x}$ (g)	2.03	0.04	0.20	0.003	2.70	0.49	2.43	5.55
SEM	0.63	0.03	0.13	0.001	0.18	0.21	0.66	0.68
kg/ha	103.4	2.4	10	0.20	137.5	24.9	123.7	282.6
SEM	32.1	1.5	6	0.05	9.2	10.7	33.6	34.6
OCT 1977								
sample $\bar{x}$ (g)	0.86	0.010	0.00	0.00	1.38	0.41	2.45	3.02
SEM	0.32	0.005			0.24	0.12	0.64	0.52
kg/ha	43.8	0.50			70.3	20.9	124.7	153.8
SEM	16.3	0.25			12.2	6.1	32.6	26.5
NOV 1977								
sample $\bar{x}$ (g)	0.02	0.00	0.50	0.005	8.73	2.56	9.28	11.75
SEM	0.01		0.31	0.003	1.52	0.74	3.48	1.98
kg/ha	1.0		25	0.2	444.5	130.3	472.5	598.3
SEM	0.5		15	0.2	77.4	37.7	177.2	100.8
DEC 1977								
sample $\bar{x}$ (g)	0.07	0.07	2.60	0.04	9.04	1.00	7.74	10.68
SEM	0.03	0.04	1.19	0.02	1.01	0.33	2.89	1.35
kg/ha	3.6	3.6	132	2.0	460.3	50.9	394.1	543.8
SEM	1.6	2.0	60	1.0	51.4	16.8	147.2	68.7
JAN 1978								
sample $\bar{x}$ (g)	0.13	0.06	3.00	0.07	5.96	1.98	4.71	8.20
SEM	0.05	0.05	1.34	0.03	0.95	0.65	0.70	1.94
kg/ha	6.6	3.1	152	3.6	303.5	100.8	239.8	417.5
SEM	2.6	2.6	68	1.5	48.4	33.1	35.6	98.8
FEB 1978								
sample $\bar{x}$ (g)	0.02	0.04	1.20	0.02	3.61	0.31	3.23	4.40
SEM	0.01	0.02	0.47	0.01	0.54	0.09	0.83	0.57
kg/ha	1.0	2.0	61	1.0	183.8	15.8	164.5	224.0
SEM	0.5	1.0	24	0.5	27.5	4.6	42.3	29.0

LITTERFALL DATA **A. MELANOXYLON** APPENDIX 2C

DATE & STATISTIC	FLOWER MASS	POD MASS	SEED NUMBER X10^{-3}	SEED MASS	LEAF MASS	TWIG MASS	OTHER SPECIES MASS	TOTAL ACACIA MASS
MAR 1978								
sample $\bar{x}$ (g)	0.07	0.03	0.70	0.02	2.60	2.57	4.97	5.77
SEM	0.02	0.03	0.30	0.01	0.59	1.93	1.94	1.85
kg/ha	3.6	1.5	35	1.0	132.4	130.9	253.1	293.8
SEM	1.0	1.5	15	0.5	30.0	98.3	98.8	94.2
APR 1978								
sample $\bar{x}$ (g)	0.05	0.04	0.30	0.03	2.93	0.13	7.79	3.46
SEM	0.02	0.04	0.15	0.02	0.47	0.05	6.45	0.49
kg/ha	2.5	2.0	15	1.5	149.2	6.6	396.7	176.2
SEM	1.0	2.0	7	1.0	23.9	2.6	328.4	25.0
MAY 1978								
sample $\bar{x}$ (g)			0.44	0.010	4.75			
SEM			0.24	0.004	0.91			
kg/ha			22	0.5	241.9			(242)
SEM			12	0.2	46.3			
JUN & JUL 1978								
sample $\bar{x}$ (g)	1.56	0.05	0.34	0.007	11.35	0.92	1.08	13.89
SEM	1.04	0.05	0.34	0.007	2.30	0.42	0.21	2.76
kg/ha	79.4	2.5	17	0.4	577.9	46.8	55.0	707.2
SEM	53.0	2.5	17	0.4	117.1	21.3	10.7	140.5
AUG 1978 - MAY 1979								
average		0.1	1.2	0.1	28.3	1.7	35.0	32.5
kg/ha		5.1	61	5.1	1440.0	61.0	1782.1	1654.8
12 MONTH TOT	339	27	677	14	3196	1331	2589	5030
kg/ha $\bar{x}$	28.3	2.3	56	1.2	266.3	111	215.8	419.0
SEM	10.0	0.6	17	0.3	50.9	39.6	39.7	61.5
15 MONTH TOT	418	30	716	15	4016	1378	2644	5979
21 MONTH TOT	-	35	777	20	5457	1439	4426	7634

COMPONENTS AS PERCENT OF YEARS TOT	FLOWER	POD	SEED	PHYLLODE	TWIG
	6.7	0.5	0.3	63.3	26.5

MONTHLY TOTAL	M 5.59	J 11.89	J 15.59	A 13.46	S 5.63	O 3.06	N 11.89	D 10.82
AS PERCENT OF ANNUAL TOT	J 8.31	F 4.45	M 5.84	A 3.50	M 4.81	JJ 14.06	A-J	

LITTERFALL DATA   *A. SALIGNA*   APPENDIX 2D

DATE & STATISTIC	FLOWER MASS	POD MASS	SEED NUMBER X10^{-3}	SEED MASS	LEAF MASS	TWIG MASS	OTHER SPECIES MASS	TOTAL ACACIA MASS
MAY 1977								
sample $\bar{x}$ (g)	0.10	1.08	9.33	0.16	2.63	2.38	1.02	6.85
SEM	0.03	0.54	5.28	0.10	0.73	1.14	0.50	1.32
kg/ha	5.1	55.0	870	8.1	133.9	121.2	51.9	348.8
SEM	1.5	27.5	268	5.1	36.7	58.0	25.5	67.2
JUN 1977								
sample $\bar{x}$ (g)	0.27	0.00	0.00	0.00	3.63	0.39	0.77	4.45
SEM	0.06				1.15	0.17	0.62	1.20
kg/ha	13.7				184.8	19.9	39.2	226.6
SEM	3.1				58.6	8.7	31.6	61.1
JUL 1977								
sample $\bar{x}$ (g)	0.22	0.01	0.44	0.008	3.25	0.87	0.48	4.51
SEM	0.05	0.01	0.24	0.005	0.77	0.39	0.25	0.88
kg/ha	11.2	0.5	22	0.4	165.5	44.3	24.4	229.6
SEM	2.6	0.5	12	0.3	39.2	19.9	12.7	44.8
AUG 1977								
sample $\bar{x}$ (g)	2.33	0.005	0.00	0.00	3.77	1.76	0.28	7.86
SEM	0.38	0.005			1.16	0.64	0.10	2.19
kg/ha	118.6	0.3			192.0	89.6	14.3	400.2
SEM	19.4	0.3			59.1	32.6	5.1	111.5
SEPT 1977								
sample $\bar{x}$ (g)	8.52	0.004	0.00	0.00	2.41	0.59	0.27	10.94
SEM	1.16	0.002			1.13	0.39	0.10	1.26
kg/ha	433.8	0.2			122.7	30.0	13.7	557.1
SEM	59.1	0.1			57.5	19.9	5.1	64.2
OCT 1977								
sample $\bar{x}$ (g)	2.19	0.54	0.00	0.00	3.17	0.23	0.54	7.78
SEM	0.70	0.18			0.93	0.05	0.18	1.41
kg/ha	111.5	27.5			161.4	11.7	27.5	396.1
SEM	35.6	9.2			47.4	2.6	9.2	71.8
NOV 1977								
sample $\bar{x}$ (g)	0.03	1.27	3.00	0.06	16.42	1.64	1.91	20.53
SEM	0.02	0.45	2.00	0.04	2.93	0.60	0.77	4.04
kg/ha	1.5	64.7	152	3.1	836.0	83.5	97.3	1045.3
SEM	1.0	22.9	101	2.0	149.2	30.6	59.3	204.2
DEC 1977								
sample $\bar{x}$ (g)	0.001	8.89	367.9	6.94	14.60	0.93	1.20	31.36
SEM	0.001	2.44	121.5	2.24	3.20	0.25	0.45	3.33
kg/ha	0.5	352.6	18732	353.4	743.3	47.4	61.1	1596.7
SEM	0.5	124.2	6186	114.6	162.9	12.7	22.9	169.6
JAN 1978								
sample $\bar{x}$ (g)	0.001	5.92	217.30	4.40	18.17	0.78	1.65	29.38
SEM	0.001	1.88	78.27	1.56	3.95	0.26	0.64	4.51
kg/ha	0.5	301.4	11064	224.0	925.2	39.7	84.0	1495.9
SEM	0.5	95.7	3985	79.4	201.1	13.2	32.6	229.6
FEB 1978								
sample $\bar{x}$ (g)	0.001	0.97	32.60	0.63	14.82	0.75	2.22	17.54
SEM	0.001	0.32	14.25	0.29	3.10	0.17	1.05	3.23
kg/ha	0.05	49.4	1659	32.1	754.6	38.2	113.0	893.1
SEM	0.05	16.3	725	14.8	161.9	8.7	53.5	164.5

LITTERFALL DATA **A. SALIGNA** APPENDIX 2D

DATE & STATISTIC	FLOWER MASS	POD MASS	SEED NUMBER X10^{-3}	SEED MASS	LEAF MASS	TWIG MASS	OTHER SPECIES MASS	TOTAL ACACIA MASS
MAR 1978								
sample $\bar{x}$ (g)	0.001	0.37	13.40	0.27	8.73	1.16	1.17	11.44
SEM	0.001	0.12	5.43	0.09	1.71	0.39	0.51	2.27
kg/ha	0.05	18.8	682	13.7	444.5	59.1	59.6	582.5
SEM	0.05	6.1	274	4.6	87.1	19.9	26.0	115.6
APR 1978								
sample $\bar{x}$ (g)	0.00	0.08	1.11	0.02	4.54	0.46	0.50	5.31
SEM		0.04	0.61	0.01	0.70	0.31	0.17	0.74
kg/ha		4.1	56	1.0	231.2	23.4	25.5	270.4
SEM		2.0	31	0.5	35.6	15.8	8.7	37.7
MAY 1978								
sample $\bar{x}$ (g)			0.00	0.00	5.52			
SEM					0.94			
kg/ha					304.7			(305)
SEM					47.9			
JUN & JUL 1978								
sample $\bar{x}$ (g)	3.47	0.00	0.00	0.00	8.82	0.38	0.12	12.67
SEM	1.20				1.90	0.15	0.10	2.82
kg/ha	176.7				449.1	19.3	6.1	645.1
SEM	61.1				96.7	7.6	5.1	143.6
AUG 1978 - JAN 1979								
sample $\bar{x}$ (g)			988.6	16.0				182.0
SEM			98.9	1.6				20.2
kg/ha			50319	814				9267
SEM			5034	82				1028
12 MONTH TOT	696	975	32833	636	4896	608	612	7275
kg/ha $\bar{x}$	58.0	81.2	2726	53.0	408.0	50.7	51.0	606.3
SEM	35.4	41.5	1711	32.9	90.8	9.4	9.6	153.9
15 MONTH TOT	(873)	(975)	32833	636	(5650)	(627)	(618)	8225
21 MONTH TOT			83152	1450				17492

COMPONENTS AS PERCENT OF YEARS TOT	**FLOWER**	**POD**	**SEED**	**PHYLLODE**	**TWIG**
	8.91	12.48	8.14	62.68	7.78

MONTHLY TOTAL AS PERCENT OF ANNUAL TOT	M	J	J	A	S	O	N	D
	4.80	3.12	3.16	5.50	7.66	5.44	14.36	21.95
	J	F	M	A	M	JJ	A-J	
	20.56	12.27	8.01	3.71	4.19	8.87	127.38	

APPENDIX 3 A

NECTAR PRODUCTION AND COMPOSITION OF A. LONGIFOLIA

Method 1 21.7.1977 12-17 hrs S.A.S.T.

Nectar droplets collected from phyllode glands after branches had been covered with plastic bags for five hours.

Table Nectar volume per approx 30 cm branch (mm^3)

STATISTIC	BUD	OPEN FLOWERS
n	10	11
$\bar{x}$	5.81	17.86
s^2	27.4	244.5
$s_{\bar{x}}$	1.66	4.7

Method 2 22.7.1977 10.30-12.00 hrs S.A.S.T.

Nectar droplets collected from phyllode glands on branches with buds and open flowers. Branches were not sleeved in plastic beforehand.

Table Gland Activity

BRANCH	BUDS ONLY			OPEN FLOWERS		
NUMBER	NO. PHYLLODES	% ACTIVE	NOTE	NO. PHYLLODES	% ACTIVE	NOTE
1	32	?	one ant	12	92	
2	20	5		23	?	many ants
3	41	0		25	4	
4	27	0		13	100	
5	23	0		22	50	
6	21	40		13	100	
7	26	8	large buds	22	64	
8	22	0		24	13	fungus in gland
9	20	0		19	89	
10	25	0	ants tending soft scale	21	52	
n	10	9		10	9	
$\bar{x}$	25.7	5.9		19.4	62.7	
$s_{\bar{x}}$		4.4			20.9	

APPENDIX 3C

Method 3 19.7.1978 14.00-15.00 hrs S.A.S.T.

A. longifolia branches, at three stages of flowering, were covered with plastic bags for one hour. Nectar was collected in micro-capillary tubes and the percent activity and volume of nectar secreted, was assessed.

Table Nectar Gland Activity and Flowering Stage

BRANCH NUMBER	BUDS			OPEN			WITHERED		
	NO. PHYLLODES	% ACTIVE	NECTAR VOL. mm^3	NO. PHYLLODES	% ACTIVE	NECTAR VOL. mm^3	NO. PHYLLODE	% ACTIVE	NECTAR VOL. mm^3
1	36	28	?	32	100	5.7	12	0	0.0
2	36	0	0.0	28	61	10.0	16	0	0.0
3	34	12	1.6	16	81	spilt	14	0	0.0
4	23	0	0.0	22	86	1.6	19	37	3.1
5	16	0	0.0	14	86	12.6	20	0	0.0
6	15	0	0.0	27	93	6.3	14	0	0.0
7	16	4	3.1	14	93	12.6	13	0	0.0
8	9	55	?	5	60	6.3	17	94	9.4
9	16	0	0.0	12	83	1.6	13	0	0.0
10				20	90	14.1			
11				11	82	18.9			
12				11	100	3.1			
$\bar{x}$	22.0	11.0	0.67	17.6	86.6	8.4	15.3	14.6	1.4
$s_{\bar{x}}$	3.5	6.3	0.46	2.4	3.7	1.7	0.9	10.7	1.1

NECTAR COMPOSITION **A. LONGIFOLIA**

Nectar samples collected 19.7.1978 at 15.00 hrs were analysed by gas-liquid-chromatography, at UCT Botany Department by R. Cowling.

Concentration of sugars : approx 400 mg/ml

Composition	Glucose	50%
	Fructose	37%
	Sucrose	12%

Data summary for seedling shading experiments.

Parameter	Species	Age mth	Sun-plants Mean	Sun-plants (n)	Sun-plants C.V.	Shade-plants Mean	Shade-plants (n)	Shade-plants C.V.	[1]Signif.
Shoot length (cm)	A.cyclops	3	3.5	5	35	4.3	5	5	ns
		4	4.6	5	21	5.9	5	9	*
		6	12.2	5	9	17.3	5	17	***
		8	23.5	2	9	43.5	2	10	*
		10	36.5	2	10	67.0	2	46	ns
	A.longifolia	3	2.3	5	24	2.4	5	28	ns
		4	2.0	5	26	2.8	5	10	**
		6	5.6	5	38	6.9	2	49	ns
		8	24.8	2	14	44.2	2	13	ns
		10	31.0	2	5	36.0	2	64	ns
		15	31.2	5	14	45.5	5	30	ns
	A.melanoxylon	3	2.1	5	17	2.8	5	17	*
		4	3.5	5	21	3.9	5	25	ns
		6	8.1	5	34	16.1	5	53	ns
		8	37.5	2	9	61.0	2	0	**
		10	39.5	2	23	59.0	2	2	ns
		15	36.5	5	10	54.5	5	27	*
	A.saligna	3	1.2	5	14	1.5	5	10	***
		4	1.1	5	60	3.0	5	32	***
		6	9.2	5	46	10.9	5	55	ns
		8	28.9	2	8	59.5	2	4	***
		10	36.0	2	43	65.0	2	0	ns
Shoot dry mass (g)	A.cyclops	3	0.04	5	34	0.03	5	15	**
		4	0.12	5	32	0.06	5	17	***
		6	1.05	5	22	0.34	5	26	****
		8	5.38	2	20	2.12	2	4	ns
		10	11.40	2	37	5.95	2	77	ns
		15	15.74	5	18	8.44	5	35	****
Shoot dry mass (g)	A.longifolia	3	0.03	5	32	0.01	5	46	**
		4	0.04	5	34	0.03	5	31	ns
		6	0.45	5	40	0.20	5	70	ns
		8	3.07	2	4	2.43	2	6	*
		10	4.25	2	15	3.20	2	4	ns
		15	8.10	5	22	7.00	5	63	ns
	A.melanoxylon	3	0.02	5	10	0.02	5	32	ns
		4	0.05	5	31	0.04	5	30	ns
		6	0.26	5	39	0.29	5	36	ns
		8	4.18	2	14	3.60	2	2	ns
		10	4,65	2	17	2.85	2	37	ns
		15	5.70	5	6	6.10	5	44	ns
	A.saligna	3	0.02	5	68	0.02	5	6	ns
		4	0.11	5	47	0.05	5	32	*
		6	1.17	5	52	0.49	5	59	ns
		8	4.25	2	12	5.13	2	8	ns
		10	10.70	2	74	8.75	2	35	ns
		15	45.73	5	44	20.65	5	33	ns
Mean[1] leaf or phyllode size (cm^2)	A.cyclops	3	1.9	5	52	1.3	5	29	ns
		4	2.1	5	21	2.0	5	36	ns
		6	10.4	5	18	5.2	5	15	****
		8	8.7	2	11	10.3	2	28	ns
		10	17.7	2	10.	19.7	2	37	ns
	A.longifolia	3	0.9	5	43	0.8	5	84	ns
		4	1.0	5	16	1.2	5	28	ns
		6	2.8	5	36	3.3	2	42	ns
		8	5.5	2	19	7.6	2	27	ns
		10	9.6	2	26	12.9	2	1	ns
		15	7.3	5	16	13.4	5	19	***

Level of significance * = 0.5; ** = 0.25; *** = 0.1; **** = 0.05

1 length x breadth x shape factor (see Methods, Paper 4)

Parameter	Species	Age mth	Sun-plants Mean	Sun-plants (n)	Sun-plants C.V.	Shade-plants Mean	Shade-plants (n)	Shade-plants C.V.	Signif.
Mean leaf or phyllode size (cm^2)	A.melanoxylon	3	0.4	5	29	0.7	5	39	ns
		4	1.1	5	36	1.6	5	36	ns
		6	2.9	5	28	6.2	5	26	****
		8	3.7	2	40	10.1	2	28	**
		10	7.1	2	12	16.1	2	11	**
		15	6.7	5	16	17.9	5	30	****
	A.saligna	3	0.6	5	23	0.8	5	13	*
		4	1.6	5	24	1.3	5	25	ns
		6	13.5	5	30	6.1	5	42	***
		8	19.6	2	10	17.9	2	2	ns
		10	21.5	2	27	38.4	2	13	ns
Pinnate leaf number	A.cyclops	3	2.8	5	30	2.2	5	21	ns
		4	4.0	5	0	3.0	5	24	**
		6	3.2	5	26	4.6	5	19	*
		8	0.5	2	142	3.5	2	61	ns
		10	0.5	2	142	2.0	2	0	ns
	A.longifolia	3	3.8	5	12	2.6	5	21	***
		4	4.0	5	18	3.4	5	34	ns
		6	4.4	5	26	4.0	2	0	ns
		8	1.0	2	141	4.5	2	47	ns
		10	0.0	2	0	4.0	2	0	****
		15	0.0	5	0	0.0	5	0	ns
	A.melanoxylon	3	4.2	5	20	3.8	5	22	****
		4	6.6	5	8	5.4	5	28	ns
		6	19.8	5	19	12.0	5	16	****
		8	27.5	2	54	20.5	2	3	ns
		10	35.5	2	2	32.5	2	37	ns
		15	9.2	5	81	19.8	5	25	*

Parameter	Species	Age mth	Sun-plants Mean	Sun-plants (n)	Sun-plants C.V.	Shade-palnts Mean	Shade-palnts (n)	Shade-palnts C.V.	Signif.
Pinnate leaf number	A.saligna	3	5.0	5	14	5.2	5	87	ns
		4	6.4	5	21	6.0	5	29	ns
		6	1.4	5	109	5.0	5	32	***
		8	0.0	2	0	1.5	2	47	ns
		10	0.0	2	0	0.0	2	0	ns
Phyllode number	A.cyclops	3	0.0	5	0	0.0	5	0	ns
		4	0.4	5	138	0.0	5	0	ns
		6	5.8	5	22	4.0	5	31	ns
		8	25.0	2	11	14.5	2	5	*
		10	70.5	2	39	43.0	2	23	ns
	A.longifolia	3	0.0	5	0	0.0	5	0	ns
		4	1.0	5	71	0.4	5	136	ns
		6	13.0	5	29	5.5	2	64	ns
		8	36.0	2	28	25.0	2	62	ns
		10	65.0	2	33	49.0	2	32	ns
		15	84.6	5	20	71.8	5	71	ns
	A.melanoxylon	3	0.0	5	0	0.0	5	0	ns
		4	0.0	5	0	0.0	5	0	ns
		6	0.0	5	0	0.0	5	0	ns
		8	25.5	2	31	0.0	2	0	*
		10	18.0	2	63	0.5	2	142	ns
		15	32.4	5	51	26.8	5	51	ns
	A.saligna	3	0.0	5	0	0.0	5	0	ns
		4	2.2	5	50	1.0	5	71	ns
		6	7.2	5	37	6.0	5	26	ns
		8	13.5	2	26	18.5	2	27	ns
		10	31.0	2	68	26.0	2	44	ns

Parameter	Species	Age mth	Sun-plants Mean	Sun-plants (n)	Sun-plants C.V.	Shade-plants Mean	Shade-plants (n)	Shade-plants C.V.	Signif.
Total leaf + phyllode number	A.cyclops	3	2.8	5	30	2.2	5	21	ns
		4	4.4	5	13	3.0	5	24	***
		6	9.0	5	22	8.6	5	21	ns
		8	25.5	2	8	18.0	2	16	ns
		10	71.0	2	38	45.0	2	22	ns
	A.longifolia	3	3.8	5	12	2.6	5	21	***
		4	5.0	5	14	3.8	5	34	ns
		6	17.6	5	22	9.5	2	37	*
		8	37.0	2	31	29.5	2	60	ns
		10	65.0	2	33	53.0	2	29	ns
		15	84.6	5	20	71.8	5	71	ns
	A.melanoxylon	3	4.2	5	20	3.8	5	22	ns
		4	6.6	5	8	5.4	5	28	ns
		6	20.0	5	18	12.0	5	17	****
		8	53.0	2	13	20.5	2	4	**
		10	53.5	2	20	33.0	2	39	ns
		15	41.6	5	31	46.6	5	44	ns
	A.saligna	3	5.0	5	14	5.2	5	9	ns
		4	8.6	5	21	7.0	5	17	ns
		6	8.6	5	46	11.0	5	20	ns
		8	13.5	2	26	18.5	2	27	ns
		10	31.0	2	68	26.0	2	44	ns
Total[1] foliage surface area (cm^2)	A.cyclops	3	11	5	27	6	5	11	ns
		4	18	5	10	11	5	5	**
		6	185	5	9	827	5	8	**
		8	444	2	14	361	2	9	ns
		10	2559	2	33	1046	2	40	ns
Total foliage surface area (cm^2)	A.longifolia	3	7	5	20	4	5	31	ns
		4	11	5	13	8	5	7	ns
		6	101	5	22	68	2	53	ns
		8	384	2	6	408	2	25	ns
		10	1190	2	5	1242	2	34	ns
		15	1248	5	15	2015	5	39	ns
	A.melanoxylon	3	3	5	16	5	5	17	ns
		4	14	5	16	16	5	8	ns
		6	115	5	12	152	5	18	ns
		8	386	2	19	410	2	18	ns
		10	769	2	22	1085	2	34	ns
		15	554	5	15	1812	5	31	ns
	A.saligna	3	6	5	13	8	5	3	*
		4	28	5	20	18	5	15	ns
		6	243	5	28	137	5	24	ns
		8	536	2	25	410	2	18	ns
		10	1455	2	62	2053	2	39	ns
Foliage inclination (degrees from the vertical)	A.cyclops	10	18.0	2	8	29.0	2	5	**
		15	21.6	5	33	29.0	5	36	ns
	A.longifolia	10	27.8	2	22	50.8	2	19	ns
		15	14.8	5	20	40.6	5	24	***
	A.melanoxylon	10	20.3	2	19	58.0	2	24	ns
		15	15.9	5	20	41.7	5	25	****
	A.saligna	10	31.5	2	11	49.0	2	9	*
		15	34.7	3	37	50.7	3	8	ns

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[1] Includes both dorsal & ventral surfaces

Parameter	Species	Age mth	Sun-plants Mean	Sun-plants (n)	Sun-plants C.V.	Shade-plants Mean	Shade-plants (n)	Shade-plants C.V.	Signif.
Inter-node length (mm)	A.cyclops	10	18	2	0	21	2	2	ns
	A.longifolia	10	11	2	13	17	2	3	*
		15	13	5	14	16	5	11	ns
	A.melanoxylon	10	18	2	0	22	2	5	ns
		15	17	5	13	22	5	10	ns
	A.saligna	10	19	2	14	36	2	8	*
Lateral shoot number	A.cyclops	10	6.5	2	8	6.0	2	0	ns
	A.longifolia	10	6.5	2	8	6.5	2	8	ns
		15	6.2	5	19	4.4	5	42	ns
	A.melanoxylon	10	17.0	2	6	3.0	2	0	***
		15	7.8	5	12	7.2	5	23	ns
	A.saligna	10	5.5	2	27	3.5	2	43	ns
Basal stem circum-ference (mm)	A.longifolia	15	28	5	7	21	5	9	*
	A.melanoxylon	15	28	5	5	23	5	9	ns
Moisture content (%)	Mean of 4 Acacia species								
Foliage		10	66.4	8	1	73.9	8	2	*
Stem		10	55.0	8	4	57.4	8	4	ns
Root		10	78.8	8	3	73.9	8	5	ns

Parameter	Species	Age mth	Sun-plants Mean	Sun-plants (n)	Sun-plants C.V.	Shade-plants Mean	Shade-plants (n)	Shade-plants C.V.	Signif.
Root surface area (cm^2)	A.cyclops	3	25	5	30	12	5	23	****
		4	63	5	29	31	5	31	***
		6	224	5	8	99	5	27	****
	A.longifolia	3	16	5	39	11	5	35	ns
		4	47	5	24	24	5	18	****
		6	145	5	46	62	5	62	ns
	A.melanoxylon	3	12	5	21	7	5	46	**
		4	32	5	33	20	5	18	*
		6	107	5	29	76	5	33	ns
	A.saligna	3	30	5	18	17	5	23	ns
		4	97	5	13	30	5	62	****
		6	172	5	19	140	5	37	ns
Root dry mass (g)	A.cyclops	3	0.03	5	36	0.01	5	17	***
		4	0.06	5	20	0.03	5	36	****
		6	0.48	5	9	0.13	5	32	****
		8	2.28	2	11	0.51	2	58	**
		10	4.91	2	26	1.50	2	66	ns
	A.longifolia	3	0.04	5	47	0.01	5	43	**
		4	0.06	5	38	0.02	5	35	**
		6	0.35	5	11	0.11	2	100	****
		8	1.65	2	3	0.83	2	36	***
		10	2.37	2	8	1.11	2	14	**
	A.melanoxylon	3	0.02	5	33	0.01	5	42	*
		4	0.05	5	28	0.04	5	33	ns
		6	0.26	5	35	0.14	5	71	ns
		8	2.40	2	34	1.38	2	10	ns
		10	4.47	2	8	1.13	2	27	**

Parameter	Species	Age mth	Sun-plants			Shade-plants			Signif.
			Mean	(n)	C.V.	Mean	(n)	C.V.	
Root dry mass (g)	A.saligna	3	0.02	5	20	0.02	5	12	ns
		4	0.10	5	29	0.03	5	64	****
		6	0.57	5	58	0.18	5	44	****
		8	2.70	2	37	2.36	2	8	ns
		10	8.40	2	74	3.24	2	28	ns
Nodule number	A.cyclops	3	2.4	5	112	0.2	5	225	ns
		4	2.0	5	50	1.4	5	81	ns
		6	3.9	5	43	3.4	5	94	ns
		8	5.5	2	90	4.5	2	110	ns
	A.longifolia	3	7.4	5	55	3.8	5	82	ns
		4	8.6	5	24	4.6	5	45	**
		6	12.6	5	78	14.5	2	5	ns
		8	32.5	2	67	45.5	2	36	ns
	A.melanoxylon	3	3.0	5	125	1.2	5	108	ns
		4	7.4	5	31	4.0	5	61	ns
		6	12.2	5	41	21.8	5	66	ns
		8	32.5	2	15	27.5	2	23	ns
	A.saligna	3	1.8	5	114	1.8	5	121	ns
		4	2.0	5	0	1.8	5	47	ns
		6	6.6	5	50	4.6	5	73	ns
		8	25.5	2	97	38.5	2	64	ns
Nodule dry mass (g)	A.cyclops	8	0.27	2	62	0.06	2	83	ns
		10	0.56	2	11	0.25	2	60	ns
	A.longifolia	8	0.18	2	3	0.08	2	25	ns
		10	0.27	2	13	0.16	2	28	ns

Parameter	Species	Age mth	Sun-plants			Shade-plants			Signif.
			Mean	(n)	C.V.	Mean	(n)	C.V.	
Nodule dry mass (g)	A.melanoxylon	8	0.29	2	24	0.06	2	50	ns
		10	0.32	2	2	0.13	2	15	**
	A.saligna	8	0.22	2	14	0.13	2	23	ns
		10	0.35	2	44	0.24	2	54	ns
Whole plant dry mass (g)	A.cyclops	3	0.08	5	35	0.04	5	5	***
		4	0.18	5	27	0.08	5	23	****
		6	1.53	5	17	0.47	5	26	****
		8	7.66	2	18	2.63	2	15	*
		10	16.31	2	34	7.45	2	75	ns
	A.longifolia	3	0.07	5	39	0.03	5	37	***
		4	0.10	5	34	0.05	5	31	**
		6	0.80	5	26	0.30	2	80	*
		8	4.80	2	2	3.30	2	5	****
		10	6.90	2	7	4.30	2	1	***
	A.melanoxylon	3	0.04	5	29	0.31	5	36	ns
		4	0.09	5	41	0.08	5	32	ns
		6	0.51	5	43	0.49	5	55	ns
		8	6.58	2	21	4.98	2	5	ns
		10	9.12	2	13	3.98	2	34	ns
	A.saligna	3	0.04	5	38	0.03	5	12	ns
		4	0.21	5	39	0.08	5	41	***
		6	2.02	5	37	0.67	5	53	***
		8	6.95	2	22	7.48	2	8	ns
		10	19.10	2	74	11.99	2	33	ns