The ecological effect of *Acacia saligna* in a Sand Plain Fynbos ecosystem of the Western Cape, South Africa

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Declaration:

"I the undersigned, hereby declare that the work contained in this thesis is my own original work and that I have not previously in its entirety or in part submitted it at any university for a degree."

Signature:

Date:

Abstract

The invasive Australian acacia, *A. saligna*, is widespread in the Western Cape, South Africa, and is widely used by local communities. Not surprisingly, the introduction of the biological control agent, the fungus *Uromycladium tepperianum* in 1987 was received with mixed emotions. In an effort to determine the socio-economical and ecological impact of the fungus, the Department of Water Affairs and Forestry has commissioned a study, of which this thesis forms part.

For this thesis, a number of parameters, environmental as well as biological, were sampled, analyzed and compared with existing data from previous studies. The goal was to obtain a comprehensive estimation of the effect of *A. saligna* on a Sand Plain Fynbos community near Atlantis and to assess whether or not, the detrimental effect *A. saligna* has on plant biodiversity, has reached the stage where it has become irreversible. The floristic data confirmed results from earlier studies, that invasion of *A. saligna* in Fynbos communities induces a decline in plant diversity, especially in dense acacia thickets. This study mainly revealed structural changes rather than community shifts. The enrichment of the soil as noted by others authors was also confirmed for the study area. However, it was outside the scope of this study to determine the long-term effects of this enrichment on the Sand Plain Fynbos communities. Soil moisture content was sampled on three different occasions, in densely invaded and uninvaded study plots. The aim was to see if *A. saligna* had any influence on the availability of water in the upper soil. Contrary to expectations, moisture content under acacia stands was higher in spring and early summer in the top soil than in pristine fynbos. Pitfall traps were used to sample the arthropods that dwell the surface of the study area. For arthropods in general, the survey did not produce conclusive data, but spider species seem to be positively affected by the presence of *A. saligna*, probably due to the structural diversity they add to the fynbos. This study revealed that the full ecological impact of *A. saligna* on its environment is far from understood, mainly due to the richness and complexity of the fynbos communities and a lack of research about faunal aspect of the Fynbos ecosystem.

Abstrak

Die Australiese akasia, *A. saligna*, is wydverspreid in die Wes-Kaap , Suid-Afrika, en word dikwels gebruik deur die plaaslike gemeenskap. Dit is dan nie verbasend dat die invoering van die biologiese bestrydingsmiddel, die swam *Uromycladium Tepperianum* in 1987, met teenstrydige emosies ontvang is nie. In 'n poging om die sosio-ekonomiese en ekologiese impak van die swam te bepaal, het die Department van Waterwese en Bosboukunde 'n ondersoek aangevra waarvan diè tesis deel vorm. Vir diè tesis word 'n aantal parameters, omgewings sowel as biologies, geproef, geanaliseer en vergelyk met bestaande data van vroeër navorsing. Die doel van die studie is om te bepaal watter effek. *A. saligna* op 'n sandpleinfynbos gemeenskap naby Atlantis het en om sodoende vas te stel of die nadelige effek van *A. saligna* op die biodiversiteit onomkeerbaar is. Plantaardige data bevestig resultate uit vroeër studies dat *A. saligna* 'n afname in plant diversiteit, veral in digte akasiabosse, veroorsaak. In diè studie word getoon dat die toename van *A. saligna* strukturele veranderings in plaas van gemeenskaplike verskuiwings tot gevolg het. Die verryking van die grond, deur ander navorsers genoteer, word ook in diè studie bevestig. Dit is egter buite die veld van studie om die lang termyn gevolge van diè verryking van die grond op die sandpleinfynbosgemeenskap te beslis. Op drie verskillende geleenthede word die watergehalte van die grond getoets onder die akasiabosse en die fynbos. Die doel van die toetse is om vas te stel hoe *A. saligna* die beskikbaarheid van water in die boonste grondlaag beïnvloed. In teenstelling is hoër vogtigheidsvlakke in die boonste grondlaag onder die akasiabosse as onder die fynbos gevind gedurende lente en vroeë somer. Lokvalle is gebruik om monsters te neem van die antropodieë woonagtig op die oppervlak van die studiearea. Oor die algemeen is die opname vir die antropodieë onvoldoende. Dit is egter insiggewend dat die spinnekopspesies voordeel trek uit die aanwesigheid van *A. saligna*. Dit is waarskynlik omdat die akasia strukturele diversiteit aan die fynbos verleen. Die studie onthul dat die volle ekologiese impak van *A. saligna* op sy omgewing moeilik verstaanbaar is as gevolg van die diversiteit en kompleksiteit van fynbos asook 'n gebrek aan navorsing.

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- *Everyone I met during my stay in South Africa and who made me love the country even more.*
- *And last but not least, my parents, they are the best...*

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*"Science can only ascertain what is but not what should be,
and outside of its domain, value judgments of all kinds remain necessary."*

Albert Einstein (1879-1955)

Chapter 1

Introduction

When the Australian *Acacia saligna* was first introduced into South Africa around 1845 (Shaughnessy, 1980), nobody probably realized that this tree would cause a controversy 150 years later. This tree is currently one of the most problematic plant invaders in South Africa, capable of outcompeting the indigenous vegetation completely especially vegetation in the Cape Floristic Region (Macdonald & Jarman, 1984).

However, even at present *A. saligna* has a certain economic and possibly ecological value and its recent biological control has caused many heated discussions between representatives of different interest groups. Conservationists mention the dramatic impact of invasion by this tree on the indigenous plant communities and the consequent reduction in stream flow in invaded catchment areas. Smallholders and subsistence farmers on the other hand feel threatened by the applied biological control program and criticize the fact that no proper environmental or socio-economic impact study was done before the irrevocable decision was made to release the biological control agent, the rust fungus *Uromycladium tepperianum* in *A. saligna* infested areas in the Cape.

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1.1 *Acacia saligna, the port jackson willow* (Mimosaceae: Acacia Mil)

1.1.1 Classification

<u>Scientific name</u>: *Acacia saligna* (Labill.) H. Wendl.

Synonyms: *Acacia cyanophylla* (Lindl.), *A. falcata* (Willd.)

(Roux, 1961; Shaughnessy, 1980; NAS, 1980).

<u>Common names</u>: port jackson willow, golden wreath wattle, blue-leaved wattle,

orange wattle (Boucher & Stirton, 1978; NAS, 1980).

1.1.2 Description

Acacia saligna is a dense bushy shrub, usually 2-5 m tall. Occasionally it grows to treelike proportions up to 10 m tall, with a single main stem. The tree has no real leaves but leaflike structures (phyllodes) that can be up to 20 cm long and 5 cm wide. These long phyllodes and the pendant branches give the trees its common name port jackson willow. The tree produces an abundance of round, bright yellow flowers in spring (August till October). After maturation, the dark brown and flattened seeds drop from the tree and are often buried by ants shortly thereafter (Roux, 1963; Boucher & Stirton, 1978; NAS, 1980, Holmes, 1990).

1.1.3 Ecology

Acacia saligna is native to the south-western corner of western Australia. In its native habitat, the summer temperatures range from about 23-26°C, winter temperatures from 4-9°C. The plant is intolerant of frost and grows best where the winter and summer means are between 13°C and 30°C respectively. This tree grows from sea level to about 300 m altitude, with isolated occurrences at higher elevations. Particularly drought hardy, it grows where annual rainfall is as low as 250 mm, though it does better where the annual rainfall is 350-600 mm and grows well where rainfall is as high as 1 000 mm per annum. Under natural conditions, *A. saligna* grows mainly on sandy, coastal plains, but is found from swampy sites and riverbanks to low, often granitic, rocky hills and coastal slopes. It occurs on poor acidic or calcareous sands, under the most dry and adverse soil conditions, in moderately heavy clays and a range of podzols (NAS, 1980).

Fig. 1.1: *Acacia saligna*, the port jackson willow, in full bloom.

Fig. 1.2: Phyllodes, blossoms and seed pods of *Acacia saligna*

1.1.4 History of Acacia saligna *in South Africa*

It is uncertain in which year *Acacia saligna* was introduced into South Africa. It was possibly imported around 1833, included in a shipment of Australian *Acacia* species (Boucher & Stirton, 1978; Shaughnessy, 1980). It was referred to in a letter by Baron von Ludwig in 1835. Other official records by the colonial secretary John Montague show that "port jackson trees" were imported around 1845 and it is possible that specimens of *A. saligna* were only brought in at that time (Roux, 1961; Boucher & Stirton, 1978, Shaughnessy, 1980). With the evidence available, it is impossible to reconstruct this period with accuracy, the chief difficulty being nomenclature (Roux, 1961). It appears that different forms of *A. saligna* were introduced to the Cape Town Region and that the people responsible for the import treated them as different species. Subsequently, the differences between the forms were not easily recognized and no distinction was made between them (Shaughnessy, 1980). A common denominator for these different 'species' was the common name "port jackson willow".

The main reason for importing foreign tree species into the Cape was the threat posed by drift sands on the Cape Flats. The increasing human pressure on the Flats destroyed the indigenous vegetation, which resulted in the destabilization of the dune fields (Stirton, 1978). When the first hard road across the Flats was completed in 1845, it was in danger of being covered with sand (Roux, 1961; Shaughnessy, 1980). It was not until 1876, however, that large-scale, successful sand binding activities got underway when an effective method was discovered to grow trees on the bare sand. Refuse from Cape Town was collected and spread out over the sown seeds which resulted in a high success rate (Roux, 1961). *A. saligna* was the most successful species and most of the official plantations were made up of this tree (Shaughnessy, 1980). At this point seeds were being distributed as far as Port Elizabeth and Durban (Shaughnessy, 1980). Because of its active promotion, *A. saligna* was soon widespread and its economic value began to decrease as other tree species made their introduction for more specific needs. Plantations were abandoned and the tree slowly started to break away from the areas where it had been planted (Roux, 1961; Boucher & Stirton, 1978).

The current distribution is by no means due to natural spread as *A. saligna* seed was sold to the public as late as 1975 (Hall & Boucher, 1977), long after it had been recognized as an invading species (Marloth, 1908 ex Boucher & Boucher, 1978). It is estimated that in the undisturbed Sand Plain Fynbos vegetation, it would take about 170 years for aliens to develop 100% cover following their first appearance, and about 125 years for 50% cover (Boucher, 1984). In Sand Plain Fynbos under cultivation or grazing, alien invasion is up to twice as fast (Boucher, 1984).

1.1.5 Uses of Acacia saligna

Port jackson was initially planted because of its excellent sand binding activities but it had many other uses, which increased its value. The tree was used as timber for construction, fencing posts and for firewood (Shaughnessy, 1980). Depending on the site, the tree yields 1.5-10 m^3 ha^{-1} of wood per year (NAS, 1980). Because of the suitability of the bark as a tanning agent large government plantations produced more than half a million kilogram of bark between 1890 and 1910 (Boucher & Stirton, 1978). Another use for this acacia was as nurse plants to shelter other economic species during their developmental stages (Shaughnessy, 1980).

Presently, many other uses are cited such as for shade, as windbreaks, for ornamentation, soil enrichment, fodder, soil binding and for mulch (NAS, 1980). The most important of today's uses are probably as firewood and animal fodder (NAS, 1980) Regrowth of established bushes is so good that they can be completely grazed off without harming the plants. Although the value of the plant as animal fodder is contested by some (Cowling, 1992; Donnelly & Morris, 1992; Degen *et al.*, 1997), others claim it is indispensable for their survival (Armstrong, 1992a, b; Combrink, 1992). The importance of port jackson in the present day economy will not be clear until an extensive study into its use is performed. Only then can a realistic cost-benefit analysis be made. The Department of Water Affairs and Forestry (DWAF) is currently funding such an extensive study of which this thesis forms a part.

1.1.6 Current distribution

In its country of origin, *Acacia saligna* occurs in the Winter Rainfall Region of south-western Australia (Boucher & Stirton, 1978; Milton & Hall, 1981). In South Africa, it now occurs from Clanwilliam on the West Coast to Port Elizabeth in the southeast (Hall & Boucher, 1977; Richardson *et al.*, 1992; Morris, 1999) (Fig 1.3). It occupies large areas of farm and conservation land and is still spreading. It is mostly restricted to the coastal areas with a rainfall of more than 250 mm but just as in Australia, it spreads inland along riverbanks (Boucher & Stirton, 1978; Anonymous, 1993). The tree has established itself in the following South African vegetation types according to Boucher & Stirton (1978): Mountain Fynbos, Sand Plain Fynbos, Eastern Succulent Karoo, Grassveld and the Karoo. In 1991, its spread was considered uncontrolled over most of its range (Morris 1991).

Acacia saligna has been introduced into many countries for much the same reason that it was initially introduced into the Cape. It has been planted in Uruguay, Mexico, Israel, Iran, Iraq, Jordan, Syria, Greece, Cyprus and many North African countries (NAS, 1980).
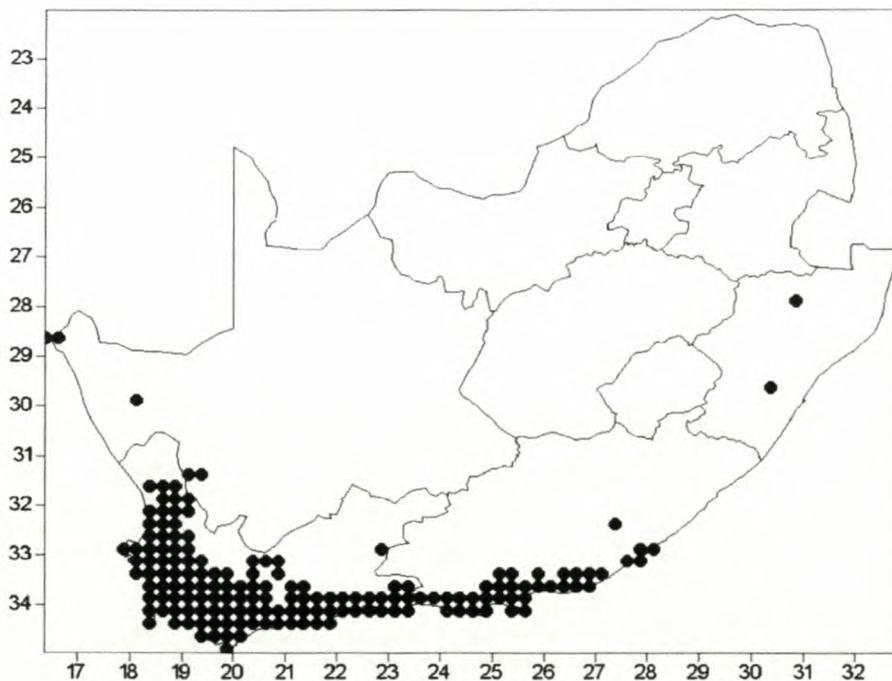
Fig. 1.3: Distribution of *Acacia saligna* in South Africa (Morris, 1999).
(drawn by L. Henderson, PPRI, Pretoria).

1.1.7 Mechanical and chemical control of A. saligna

A variety of mechanical and chemical control measures are available for the control of *A. saligna* (McVeigh, 1990; Morris, 1991). The most efficient method is the physical removal of the tree, roots and all. Ringbarking to soil level is another option. The use of fire is only partially successful as the tree resprouts and germinates readily after a fire. The use of herbicides on seedlings can be successful if the seedlings are not too big. Herbicide application on cut stumps can prevent a tree from resprouting but is only moderately successful. The estimated costs of clearing thickets of different densities ranged on average from R 526 to R 2 408 per ha, depending on the clearing method used (based on 1986 prices) (Macdonald & Wissel, 1989).

1.1.8 Biological control of A. saligna

The biological control of *A. saligna* will be discussed under section 1.3.2.

1.2 The ecology of fynbos and Acacia saligna

Fynbos is usually characterized by the presence of proteoid shrubs which form an overstorey of highly variable density. Ericoid shrubs and restioid hemicryptophytes together usually form the understorey. The whole is the result of the climate and low-nutrient soils. The factor that differentiates this Biome from the adjacent ones is fire, being both a mineralizing agent and a disturbance (Macdonald & Richardson, 1986). Invading species seem to make use of this 'invasion window' created by fire (or any other disturbance in the case of *A. saligna*) to enter the community and proliferate (Richardson & Van Wilgen, 1992; Richardson & Cowling, 1992). All successful aliens have one thing in common: a short juvenile period and a massive seed production (Rejmanek & Richardson, 1996). In addition to these qualities, port jackson resprouts and its seeds germinate rapidly after fire, giving it access to the nutrient pool created by the fire (Richardson *et al.*, 1992).

By 1985, 20% of the fynbos was estimated to be invaded by one alien or another and the invasive trees and shrubs are thought to have exerted the greatest ecological effects on the Biome (Macdonald & Richardson, 1986). Over the whole Biome, ranked abundance of seven invading species was positively correlated with agricultural lands, especially *A. saligna*, suggesting that artificially modified environments are most prone to invasion (Richardson *et al.*, 1992). Invasion of fynbos by *A. saligna* causes a reduction in local diversity and in the cover and frequency of remaining species (Richardson *et al.*, 1989; Holmes & Cowling, 1997a). The relatively high absolute growth rate of *A. saligna* compared to overstorey proteoids, combined with its ability to grow to a height of three meters or more, enables it to overtop the indigenous vegetation and monopolize the light source (Holmes & Cowling, 1997a). The presence of water-soluble antibiotic substances produced by the *Acacia* has been demonstrated but it is not clear whether these play a significant role in competition between the exotic and the indigenous vegetation (Roux & Middlemis, 1963; Jones *et al.*, 1963). Furthermore, *Acacia* species increase the organic matter and nitrogen contents of the soil. The result is a decrease in C:N ratio and possibly (persistent) detrimental effects to the indigenous vegetation with a shift in the microbiological communities in the soil (Roux & Warren, 1963; Witkowski, 1991; Stock *et al.*, 1995). The impact of *Acacia* infestations on soil chemical status is considerably greater than that of fire or season (Musil & Midgley, 1990).

Fynbos guild structure does not remain constant between uninvaded and long invaded stands, confirming that certain guilds cope better with invasion. Vertebrate dispersed species are over-represented in old invaded stands (Holmes & Cowling, 1997a). Although all indigenous vegetation regenerates less successfully in *Acacia*-infested stands (Musil, 1993), Holmes & Cowling (1997a) feel that irreversible damage to the fynbos has not yet occurred. The clearing method implemented is probably crucial to the restoration process, but whereas fire is the appropriate management tool in fynbos, the high fuel loads in dense *Acacia* thickets can sterilize the soil after a fire as mentioned by Macdonald *et al.* (1989) and the best way to return to fynbos can be a 'hands off' approach as suggested by the PPRI (Anonymous, 1987) or alternatively by using active restoration methods including the use of heat and smoke treatments of the soil to actively stimulate germination (Jeffery *et al.*, 1988; De Lange & Boucher, 1990; Van Wilgen *et al.*, 1992).

Heat treatment by means of fire has the dual effect of stimulating fynbos species to germinate as well as the seeds of *A. saligna*. This can easily lead to the exotic species outcompeting the

germinating fynbos species (Jeffery *et al.*, 1988). Non-burning may be considered to keep the *Acacia* seed dormant and thus reduce competition for germinating indigenous species. Smoke treatments have the advantage that unlike heat treatments, they only stimulate the germination of indigenous species and not of *Acacia* seeds (De Lange & Boucher, 1990). Over time, the *Acacia* seed bank will decline and if there is no seed input from mature trees the fynbos will be able to recover.

The establishment of a suitable method to enhance restoration of fynbos in the dying port jackson stands is a prerequisite if a proper solution is to be found for the socio-economic and environmental problem that port jackson has become in South Africa.

1.3 Biological pest control

1.3.1 Description

The term 'biological control' was first used to signify the use of natural enemies to control insect pests. Its scope has expanded during the years to include any 'biological' method such as genetic manipulation to prevent damage by pest species. In the strict sense however, biological control can be defined as the use of natural enemies for the control of animal or plant populations (Wilson & Huffaker, 1976). The goal is not complete eradication of the pest but rather to reduce the pest population to an acceptable level, allowing survival of both pest and control organism (Samways, 1981).

Biological control (biocontrol) is not a new concept, centuries ago the Chinese were said to have introduced ant nests into barns to combat the insects that fed on the stored products. More recently and on a larger scale there is the case of the introduction of the mongoose into the West Indies in the nineteenth century to control the booming rat population (Simmonds *et al.*, 1976). A more unlucky attempt was made in South Africa by Cecil Rhodes when he introduced the European starling (*Sturnus vulgaris*) in 1899 to control insect plagues (MacLean, 1993). The birds themselves are now rated as a pest species.

A common characteristic of these early examples of biological control is the haphazard way in which the introductions were made. Many were ineffective or produced negative side effects. Very few of the control species were host specific but immediate economic gain often blurred common sense (Simmonds *et al.*, 1976).

Biological control has gained in popularity over the last 100 years as many successful introductions have been undertaken against pests in different areas of the world. The relatively new concept of using plant pathogens for weed control fits in perfectly in this context. Many introduced weeds have proved to be good targets for biological control, especially where they have become dominant species (Greathead, 1995) because they provide the control agent with a stable environment in which to develop. After the USA and Australia, South Africa is the third most active country in biological control of weeds (Olckers, 1999). Since the first biological control measures in 1913, more than 85 species of biocontrol agents have been released onto some 47 weed species in South Africa (Olckers, 1999).

Benefits derived from successful biological control are often quite obvious for everybody to see. They are cheap, require only an initial investment and control continues indefinitely without maintenance. These characteristics have created somewhat of a paradox: demands for control often come from farmers but the industry has little inclination to provide (classical, or genetically unmodified) biological control agents because they are commercially unattractive. In many instances, biological control has been used where alternatives were not feasible and control programs are carried out by governments or organizations using public funds (Greathead, 1995). Furthermore, many biological control projects do not produce any substantial success. The ones that do are generally considered big winners, but the lack of a methodology to calculate the benefits in economic terms makes it more difficult to justify the necessary research (Cullen & Whitten, 1995).

In the long term, the use of biocontrol is very sensible. It reduces the need for chemicals and hence delays the build up of resistance against those chemicals so that they can still be used in emergency situations (Samways, 1981). All introduced organisms however present a potential hazard, especially if the control agent is to be permanently established and it is without question that the decision to release an agent should not be made lightly.

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Possible negative effects include damage to non-target organisms as the most serious risk (Greathead, 1995). This emphasizes the need for host-specific control agents. Conflicts of interest form another possible drawback of biocontrol as a control agent can virtually never be contained or eradicated once it has been released and established.

1.3.2 Biocontrol of A. saligna

Back in 1908, people already started noticing that Australian acacias were outcompeting indigenous vegetation (Marloth, 1908 ex Boucher & Boucher, 1978). In 1943, the first control operation was set up in the Cape of Good Hope Nature Reserve, but at least till the early 1980's, these control operations were utterly ineffective, due to a lack of systematic action and follow-up (Macdonald *et al.*, 1989). In the Cape Peninsula, the occurrence of port jackson has stabilized since 1976, mainly because there is a balance between the clearing operations and the infestation of new sites (Moll & Trinder-Smith, 1992).

The method of clearing is a controversial subject as different clearing methods can be used to achieve different goals. Many factors have to be taken into consideration when clearing port jackson thickets. The slash and burn technique combined with regular follow-ups has been propagated as the most effective technique to fight port jackson (Holmes *et al.*, 1987a) but other authors maintain that the complete physical removal of the tree is the most effective means (McVeigh, 1990; Morris, 1991). Chemical treatment of low density infestations has not received much attention although it is a low disturbance technique that does not promote *Acacia* seed germination.

Although the high fuel load of dense *Acacia* thickets can cause the soil to be sterilized and become bare for a long time after a fire (Macdonald *et al.*, 1989) a follow up period of at least ten years is necessary in order to prevent re-infestation from soil stored *Acacia* seeds (Macdonald & Jarman, 1984). Mainly for this reason, at present, clearing operations, performed under the Working For Water Project are not yet economically viable when only the gain in runoff water is considered as the economic benefit (Marais, 1998). Not surprisingly, the biological control of *A. saligna* can be extremely cost effective in the way that after introduction of the fungus, no further action is needed (Versfeld *et al.*, 1998),

although in some cases restoration methods are advisable (Holmes & Cowling, 1997a, b). It is unfortunate that in most cases, *Acacia saligna* does not occur in pure stands but often in combination with other invasive species. In these areas the biological control is unlikely to result in a reduction of the clearing costs (Marais, pers comm.). The biological control of port jackson will be most cost-effective in those areas where there is no direct economical incentive to initiate clearing operations.

In the case of *A. saligna*, the initiative to release the control agent *Uromycladium tepperianum* was taken by the Plant Protection Research Institute (PPRI) in 1987, in response to requests by higher authorities reacting to pressure from bodies such as farmers unions, nature conservation bodies and municipalities (Fig. 1.4) (Donnelly & Morris, 1992). At this moment, this former highly problematic invader is to be considered under complete biological control (Olckers, 1999) *i.e.* no other control measures are necessary to maintain the port jackson population at acceptable densities.
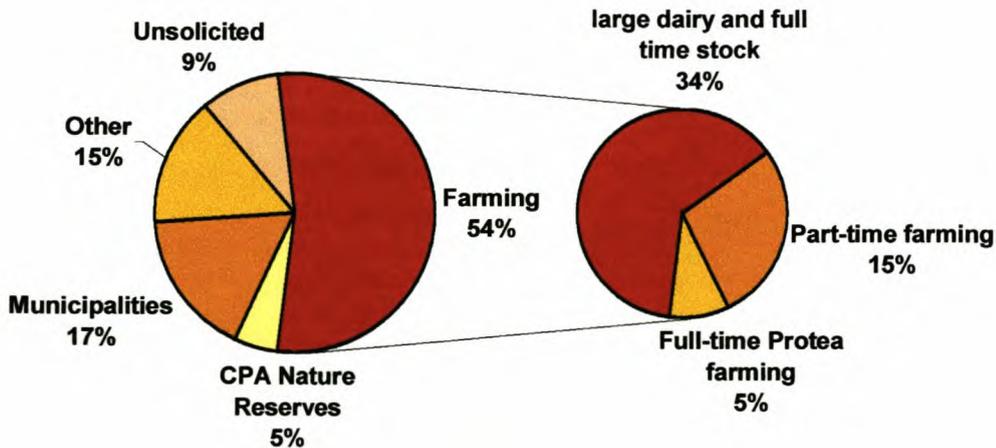
Fig. 1.4: Requests from various parties for the release of the biological control
agent (Donnelly & Morris, 1992).

The decision to release the fungus was not taken lightly but was the last option to control an invader where all other methods, chemical and mechanical had failed (Anonymous, 1993). Although the release of a control agent is irrevocable, it is critical for people to understand that biological control never seeks complete eradication of the pest species, merely a reduction in population numbers. There is no reason to fear that port jackson will disappear entirely from South Africa. Their gradual decline in numbers will create favourable conditions for other, more desirable plants to recover, so that indigenous plants will become more abundant in between the remaining *A. saligna* plants and ensure the continuation of diverse plant communities (Anonymous, 1987).

1.4 The biology of the *Acacia* gall rust, *Uromycladium tepperianum*

In southwestern Australia where port jackson is indigenous, it is attacked and limited by the gall-forming rust fungus *Uromycladium tepperianum*. This rust causes galling on stems, branches, phyllodes and reproductive organs and the formation of witches' brooms on branches of *A. saligna* (Gathe, 1971; Morris, 1987) (Fig. 1.5). On *A. saligna*, the infection is limited to the location of spore germination, as the tree is quite effective in restricting the parasite (Gathe, 1971). The first symptoms generally appear three to six months after infection. Galls are produced in an annual cycle and large numbers of wind-dispersed teliospores which infect the trees are produced on the surface of the galls (Burges, 1934). The fungus is autoecious (all spore types develop on one single host) and has a microcyclic (uncomplicated) life cycle, producing only two spore states, spermatia and teliospores (Morris, 1991).

U. tepperianum has been recorded on over 100 *Acacia* species and experiments with African *Acacia* species showed symptoms of infection developing on the seedlings of three indigenous species but the development of the fungus appears to cease after a few months. *U. tepperianum* appears to have distinct genotypes, distinguishable at host species level (*formae speciales*). Normal galls only develop on the specific hosts (Morris, 1987). *U. tepperianum* was said to be present in South Africa as early as 1934 (Burges, 1934) with *A. decurrens*

acting as host species. It might be due to the distinct genotypes that *U. tepperianum* did not attack *A. saligna* before the release of a host specific genotype in 1987.

It has become apparent that the galls are hosts to a number of parasites themselves. These parasites are most likely local as the chances of the initial *U. tepperianum* inoculum being contaminated are minimal (Morris, 1999). Morris (1999) mentions an unidentified moth and several fungi affecting the galls. In this study two different types of unidentified larvae were observed excavating the galls. The tunnelling of larvae inside the galls does not appear to affect sporulation, despite the damage it causes to the galls (Morris, 1999).

More concerning is the presence of several parasitic fungi on the galls. They interfere with and reduce teliospore production by *Uromycladium tepperianum*. The high prevalence of these and possibly other organisms could slow down the spread of *U. tepperianum* (Morris, 1999), and subsequently the decline of the *A. saligna* populations.

Fig. 1.5: Gall formation by *Uromycladium tepperianum* on *Acacia saligna* (Morris, 1997).

1.5 Objectives of this study

The objectives of this study are twofold:

- To gather information about the possible biological and physical effects of *Acacia saligna* on the Coastal Fynbos ecosystem. The goal was to collect a wide range of information in one study area as opposed to the several existing publications that focused on specific issues such as plant species richness or soil nutrient status.

- To determine, by means of a literature study and own data, whether *A. saligna* could cause irreversible changes to a coastal Sand Plain Fynbos ecosystem in the Western Cape, South Africa. In addition, an assessment of the present and potential future status of *A. saligna* in this habitat will be made.

Fig. 1.6: The effect of a severe infection by *U. tepperianum* on an *A. saligna* population.

Chapter 2

Description of the study area

2.1 Location and description

The selected study area is located south of Mamre (33°31' S; 18°29' E), and is demarcated by Silwerstroomstrand Road in the north and the N 307 in the west. Opposite the study area, on the other side of the N 307 lies the Mamre Nature Garden.

The site is approximately 12 km inland from the Atlantic Ocean, and 40 km north of Cape Town. The area surveyed is about 100 ha in extent and comprises Sand Plain Fynbos vegetation as well as pockets of *Acacia saligna* stands of varying density. No other alien invasive trees apart from *A. saligna* occur in the area.

Mamre was established in 1808 as a mission station, housing the remnants of the Hottentot tribes of the region (Boucher, 1981). At present it is a relatively small community of mainly coloured people. The much larger town of Atlantis lies a few kilometers to the south, within walking distance. From aerial photographs it is clear that the study area has been exposed to a high degree of human influence for at least the last fifty years. Small trails used to cover the whole area but in recent years they seem to have been more and more abandoned. The outskirts of Mamre have at present reached the boundaries of the study area.

Within the 100 ha large study area, 40 smaller plots (each 50 m^2) were selected according to their degree of *A. saligna* infestation (Fig. 2.2). Each plot was demarcated and assigned to one

of the follwing categories: no *A. saligna* infestation, >25 %, >50% or >75% *Acacia* cover. Ten plots were initially selected in each category but by the end of the study some of the plots had been lost due to the disappearance of the markers. The plots were spread out over the whole of the area as evenly as possible to reduce the risk of pseudo-replication (Hurlbert, 1984).
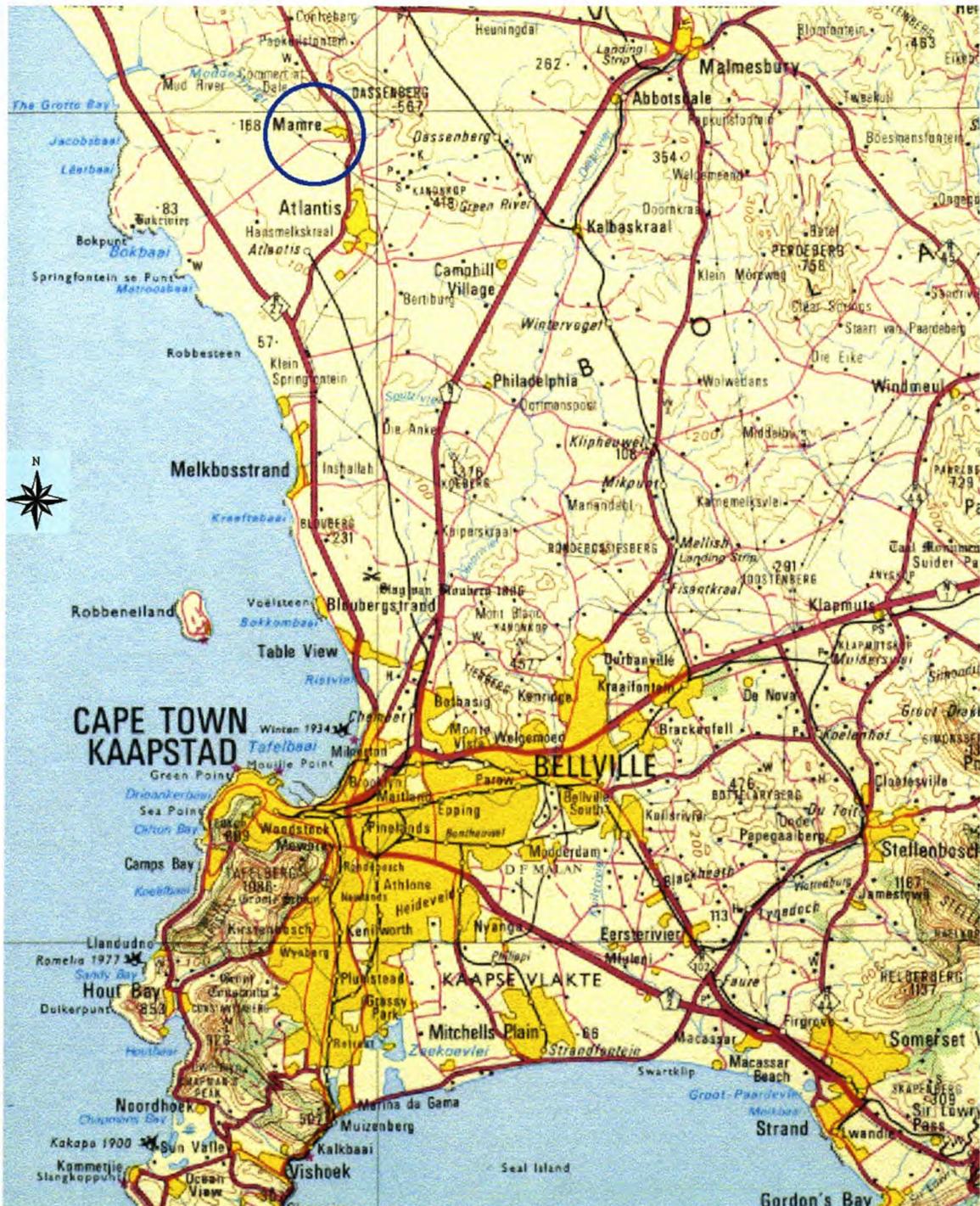
Fig 2.1: Location of the study area in the Western Cape coastal region.

Fig. 2.2: Spatial distribution of the sampling plots over the research area. Detailed information on each plot is available in Appendix B.

2.2 Vegetation

2.2.1 Description

The western Cape coastal foreland vegetation was categorized by Boucher (1987) in seven classes following major floristic differences. The three most common veld types in the region (Acocks, 1953), West Coast Strandveld (Veld Type 34), Coastal Renosterveld (Veld Type 46) and Coastal Fynbos (Veld Type 47) all fall within one class, the *Ehrhartetae-calycinae* (Boucher, 1987). Structurally they are dominated by shrubs although grasses can play an important part in the early successional stages. The vegetation found in the study area is classified by Boucher (1987) as belonging to the order *Ehrharto-Phylicetalia cephalanthae*.

Sand Plain Fynbos (also called Coastal Fynbos) (Rebelo, 1996) occurs on leached acid sandy soils, which accumulate from the *in situ* weathering of granites and sandstones, or as wind blown accumulations of sand from rivers, estuaries or on leached maritime dunes. The sands vary in depth from less than a metre to more than 70 meters (Boucher, 1983). It tends to be confined to deep acid sands (Rebelo, 1996).

To the north, Sand Plain Fynbos extends into Namaqualand and to the east it does not extend beyond False Bay, although similar inland vegetation occurs on aeolian sands in the Breede River valley (Boucher, 1987). Altitude ranges of this Veld Type are from 0-300 meter and for rainfall from 300-500 per annum (Acocks, 1953). A subdivision of the Coastal Fynbos was suggested by Acocks (1953) and presented by Moll *et al.* (1984). An extensive classification of the different plant communities on the south-western coast is presented by Boucher (1987). In the study area, the type of Sand Plain Fynbos is *Phylica cephalantha – Thamnochortus punctatus* Shrubland (Boucher & Shepherd, 1988). This can be further subdivided in specific communities and it appears that the *Thamnochortus punctatus – Leucospermum parile* Shrubland best represents the basic matrix of the environmental variation, present in the Sand Plain Lowland Fynbos (Boucher & Shepherd, 1988).

The western Coastal Fynbos was defined by Moll *et al.* (1984) as Sand Plain Lowland Fynbos with the following characteristics: open to closed (25-90% canopy cover), low to mid-high, graminoid shrublands. This Veld Type is dominated by ericoid leaved shrubs. (Boucher, 1983; Rebelo, 1996). The vegetation is typically Asteraceous and Proteoid Fynbos and does not differ structurally from equivalent Mountain Fynbos types, although very few species are shared (Rebelo, 1996). Sand Plain Fynbos is far more uniform in composition than Mountain Fynbos, possibly because of the uniformity of the sandy plains in contrast to the variety of niches present in the folded mountains of the Cape (Boucher, 1983).

Coastal Fynbos is characterized by the presence of *Erica mammosa* (ninepin heath), *Phylica cephalanha* (starface), *P. stipularis* (baboonface), *Thamnochortus obtusus* and *T. punctatus* (sandveld thatching reed) (Boucher, 1983). Restionaceae are always prominent in this vegetation while Ericaceae and Proteaceae are often less conspicuous. All the communities constitute complete Fynbos communities as they always include at least two of the three families mentioned above (Boucher, 1987). Some component species of the western Coastal Fynbos are apparently out of phase with their environment in that they grow during the dry summer period. A high proportion of the species have very small or reduced leaves, a low proportion of succulence and the perennial herbaceous flora is largely hard and stiff with reduced leaves and photosynthetic stems. These conditions are possibly an adaptation to the low nutrient status of the substrate where it is advantageous to utilize the meagre nutrient resources efficiently, as soon as they become available (Boucher, 1983). Annual herbs and geophytes occur throughout, but they do not assume the same proportions as are found in either the Coastal Renosterveld or the West Coast Strandveld. The low nutrient status of the substrate is probably responsible for the virtual absence of the invasive European annual flora. In contrast, the vegetation is very susceptible to invasion by trees and tall shrubs from the Australian heathlands (Boucher, 1983).
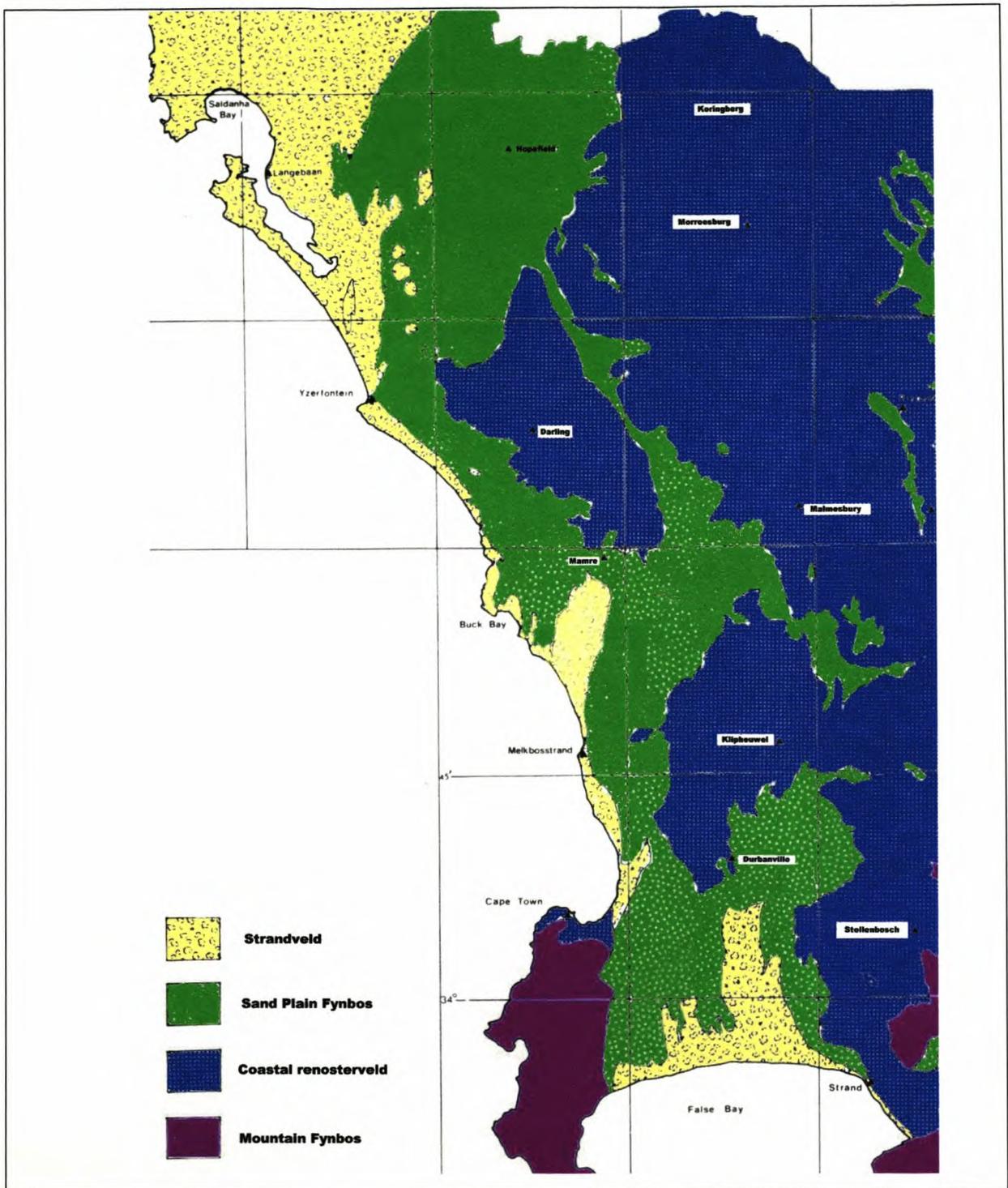
Fig. 2.3: Distribution of the vegetation types in the southwestern Cape.

2.2.2 Conservation status

Some 50% of the original vegetation type is said to be left (Rebelo, 1996). In some areas, urbanization is transforming the Sand Plain Fynbos. Elsewhere it is used for grazing, but the carrying capacity is low. Some small holdings are transforming the natural vegetation to poor pasture, mainly for horses (Rebelo, 1996). Sand Plain Fynbos is unsuited to wheat growing and there is thus more of it left than is the case with the adjacent Coastal Renosterveld. The communities are however not in a satisfactory state. The remaining vegetation is threatened by the fast expanding centres such as of the Cape Metropolitan Region and only a mere 1.4% of the existing vegetation type is under conservation (Jarman, 1986).

2.3 Geomorphology, geology and soils

2.3.1 Geology and geomorphology

The basic outline of the Western Cape coastline was created during the break-up of Gondwanaland, about 130 million years ago (Rogers, 1982). This was the start of a long period of marine transgressions and regressions that took place under the changing climatic conditions of the time. Continental drift and the consecutive shifts in sea currents played a large part in these climatic conditions and in the geomorphology of the coastal lowlands (Odendaal, 1983). The geology of the west coast lowlands is dominated by late Pre-Cambrian sandstones and limestones of the Malmesbury Supergroup, intruded locally by granites of the Cape Granite Suite (Fry, 1987). Most of the coastal lowlands are blanketed by Pleistocene aeolian sediments of the Bredasdorp Formation (Rogers, 1982; Odendaal, 1983). The sediment deposits vary from limestone to calcareous dune sands to acid sands and were deposited nearby the shifting coastline. In the more southern parts of the West Coast, periods of higher rainfall induced mobilization of soluble components in the sand deposits (Odendaal, 1983).

2.3.2 Soils

A. South African classification

The soils in the study area are leached aeolian sands and are classified as belonging to the Fernwood Form (Fw), Fernwood Series (McVicar *et al.*, 1977). The soils are acidic (pH(KCL) 4.0–5.4), low in nutrients and have a low organic matter content (0.4-0.9 %) (Lambrechts & Fry, 1988).

B. International classification

The above soil form is correlated to international nomenclature, in the FAO-Unesco nomenclature, as the Major Soil Group (MSG) Arenosols. Due to the low CEC of the soils around Mamre (Musil & Midgley, 1990), this MSG can be described at soil unit level as a Ferralic Arenosol (Aro). Using the USDA soil taxonomy system this soil type would classify under the order of Entisols (McVicar *et al.*, 1977; Driessen & Dudal, 1991).

The soils in the study area were not entirely uniform and the South African classification system was sometimes limited in providing an appropriate classification. Some soils resembled the Clovelly Soil Form to a varying extent. These difficulties with proper soil classification were also noted by Lambrechts & Fry (1988).

2.4 Climate

The southwestern Cape is a Winter Rainfall Area with warm and dry summers and cool and relatively wet winters. The southernmost extremity of the coastal lowlands of the Western Cape Province, that is southwards of Melkbosstrand, can be classified as having a humid climate. The rest of the coastal lowlands has a cool steppe or semi-arid character (CSa/BSk – Köppen classification). This classification takes into account the ratio between

precipitation and water loss through evaporation (Nieman, 1982). The mean annual temperature for the region (14-17°C) is lower than expected for these latitudes and the mean annual rainfall varies from 500 mm in the south to 150 mm in the north (Schulze, 1965). The rainfall in the southwestern Cape can be highly variable due to variations in the landscape (Fig. 2.4 & 2.5). The main reason for the relatively low temperatures and precipitation is the dominance of the South Atlantic subtropical anticyclone (Nieman, 1982). The subsiding air in the high-pressure system inhibits rainfall over the west coast. In addition, the surface circulation of the anticyclone results in south easterly winds almost parallel to the coast (Fig. 2.6). These winds cause upwelling of cold sub Antarctic water which cools the overlying air. Wind speeds often exceed the 5 m/s threshold for active displacement of dry, medium-sized sand grains and exposed soils are susceptible to wind erosion (Odendaal, 1983). Evaporation from the ocean supplies enough moisture to saturate the cool air, producing radiation fogs moving in from the sea over the coastal lowlands (Nieman, 1982). Fogs are more frequent during the colder months and the condensation from the fogs is probably a major source of moisture for the vegetation. Due to the fogs, sunshine duration over the western coastal lowlands is 70% less than expected. The climatic data for the Mamre area is summarized in Table 2.1 (data from Agricultural Research Council, Stellenbosch).

Table 2.1: Summary of climatic data for the Mamre area (recorded at the Philadelphia
Police Station).

Altitude: Longitude: Latitude:
76 m   18°35' E   33°40' S

longterm summary of average monthly rainfall (in mm) for 78 years ending in 1998

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
total	8.5	9.9	12.4	29.5	54.7	66.6	65.6	56.6	33	21.2	13.8	9.6
maximum	77	59	76.2	146	241	204	173	188	99	83	74.8	56.7
minimum	0	0	0	0	0.5	2.3	6.5	8.8	1.5	0.2	0	0

longterm summary of average daily temperature (in °C) for 25 years ending in 1998

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
average	22.5	22.8	21.4	18.6	15.4	12.7	11.6	12.2	13.9	16.4	19.3	21.3
high	32	33.4	30.2	27.9	22.7	18	19.1	19.6	21.9	27.9	31.7	32.6
low	15.9	15.8	13.6	11.6	9.6	6.8	6.1	7.2	7.8	10	12	13.9

longterm summary of monthly evaporation (in mm) for 25 years ending in 1998

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
total	276	227	202	117	67.2	43.3	42.6	62.3	92	161	219	260
ave/day	9.5	8.4	6.6	4	2.2	1.5	1.5	2	3.1	5.3	7.4	8.8

longterm summary of monthly sunshine (in hrs) for 25 years ending in 1998

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
total	326	279	270	213	178	158	163	196	208	264	284	316
ave/day	10.7	10.2	8.8	7.2	5.8	5.3	5.5	6.4	7	8.6	9.6	10.2

RAINFALL ISOHEYTS

- - -	150 mm
	< 200 mm
	200 – 300 mm
	300 – 400 mm
	400 – 500 mm
	500 – 1 000 mm
	1 000 – 2 000 mm
	> 2 000 mm

0   10   20   30   40 km

SOURCE : 1 : 250 000 Rainfall Map
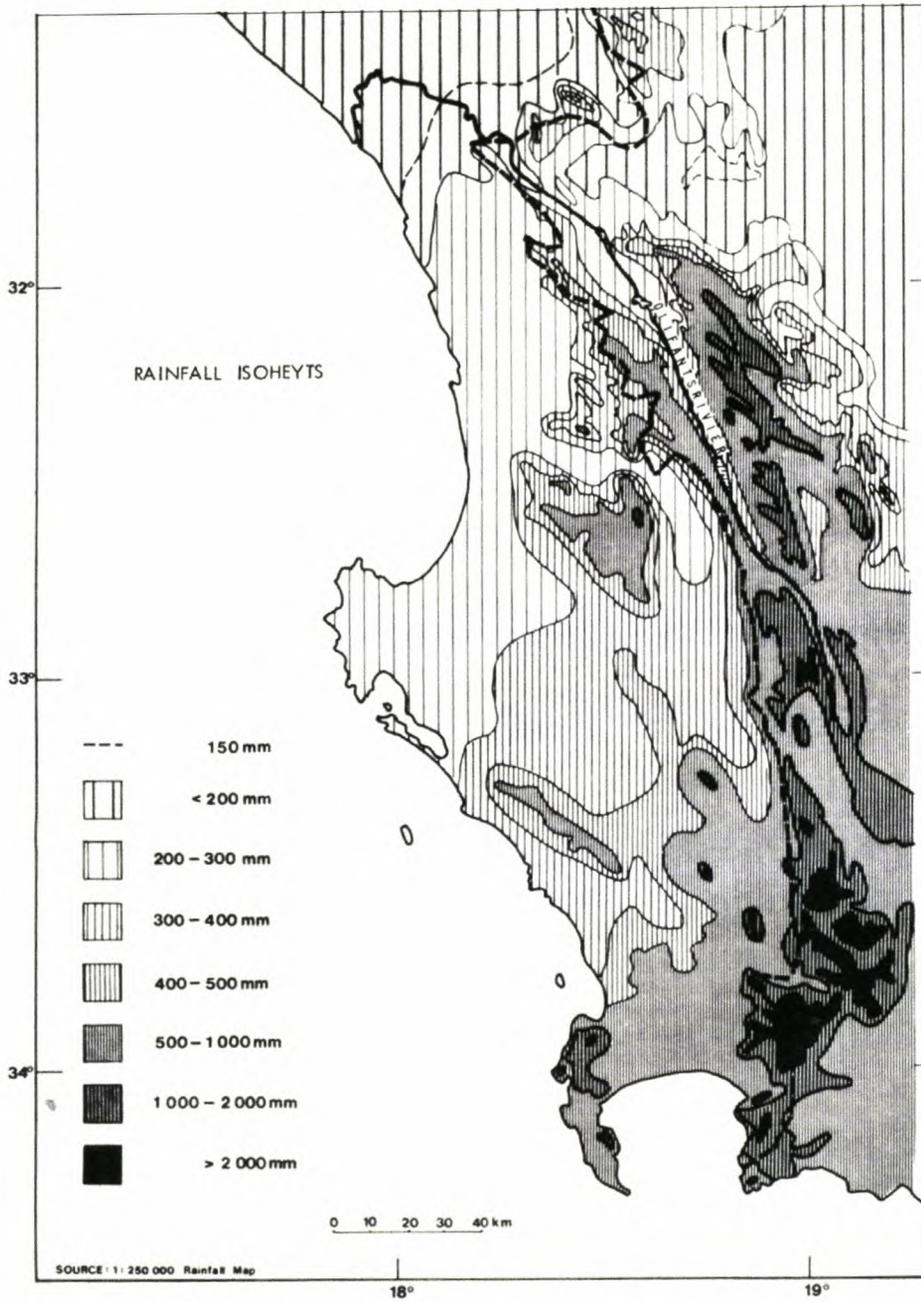
Fig. 2.4: Annual average rainfall distribution in the southwestern Cape, South Africa.

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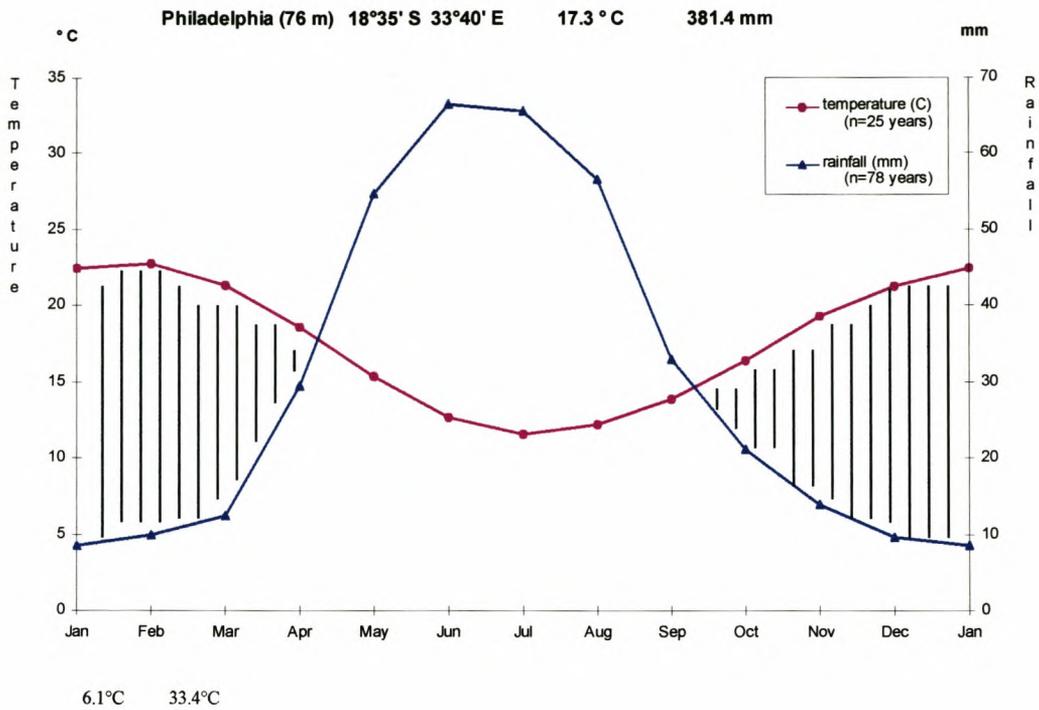
Fig. 2.5: Klima diagram for Philadelphia, approximately 15 km south east of Mamre.
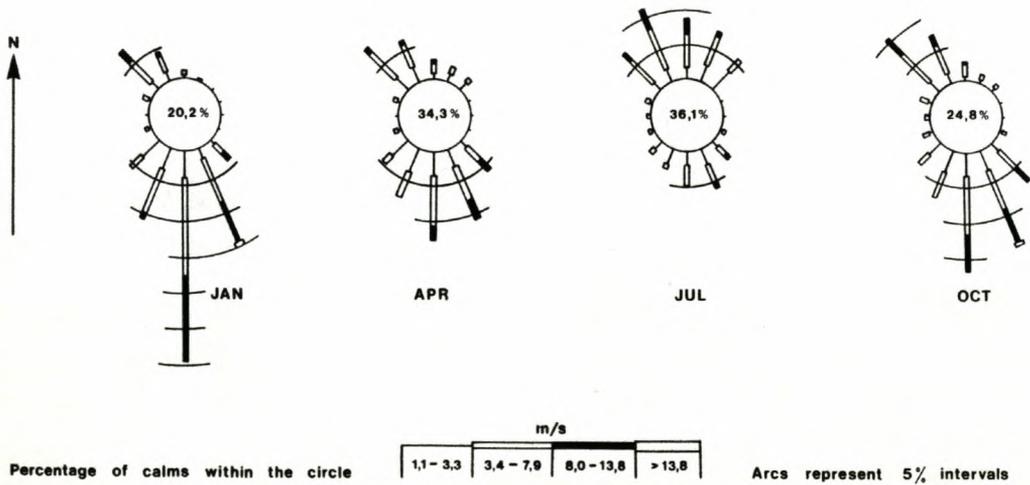
Fig. 2.6: The prevailing winds in the Mamre area in the different seasons. (data from Schulze, 1965).

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Chapter 3

Impact of *Acacia saligna* on soil chemical status

The invasion of Sand Plain fynbos by *Acacia saligna* causes a disturbance in the soil chemical status that is greater than the seasonal or post-fire variation (Musil & Midgley, 1990). Due to the increased availability of nutrients, the composition of the fynbos communities can shift to more nutrient-demanding species (Witkowski & Mitchell, 1989). Determining the extent of the nutrient changes that occur under different stages of *A. saligna* invasion, is a first step towards successful restoration of the Sand Plain fynbos communities.

3.1 Methods

3.1.1 Sampling procedure

The sampling took place during June and July 1999. Ten soil samples were taken in each of the 50m² plots at 1 m intervals, using a soil auger from both the topsoil (0-10 cm) and the deeper soil (40-50 cm). Any litter present was removed before taking the sample. After

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sampling, the topsoil samples from each plot were mixed together to provide a bulk sample for the plot. The samples from the deeper soil were also bulked. Each sample was air-dried and stored in open plastic bags until they were analysed (Tan, 1996).

3.1.2 Soil analyses

The following chemical properties were analysed in each soil sample (Loock, 1990):

- pH

pH was measured using a calibrated pH meter in a soil suspension 1 mol dm^{-3} KCl. Potassium chloride is used to mask variation in salt concentration of the samples. The accuracy of the pH meter is 0.05 pH units.

- Resistance

Resistance was measured using an electrode placed in soil moistened with de-ionised water. Resistance is a function of the salt concentration in the soil and is inversely proportional to the salt concentration.

- Organic carbon

Organic material in the soil was oxidised by treatment with a hot mixture of $K_2Cr_2O_7$ and sulphuric acid. The excess dichromate was titrated with iron (II) ammonium sulphate hexahydrate. The reduced dichromate is equivalent to the organic C present in the sample.

- Phosphorus

Phosphorus was extracted using the Bray - 2 method. This procedure extracts acid soluble, absorbed (or available) and reserve phosphates present in the soil. The total inorganic phosphate in the extract is determined by an automated colorimetric analysis.

- Iron

The content of free Fe oxides in the samples was determined using sodium dithionite with sodium citrate at pH 7.3 for extraction and an absorption spectrophotometer for concentration readings.

- Na, K, Ca, Mg

An ammonium acetate solution (1 mol dm^{-3}) served as extractant for these exchangeable and water soluble cations. After extraction, concentrations were determined using an atomic absorption spectrophotometer.

- Inorganic nitrogen

Inorganic nitrogen (NH_4^+, NO_3^-) in soils was extracted using a 1 mol dm^{-3} KCl solution. Concentration was determined through the colorimetric method using a continuous flow analyser. The values for NH_4^+ and NO_3^- were added to obtain total nitrogen.

3.1.3 Statistical analyses

For each variable, the null hypotheses was tested that there was no difference between the variable values in the different density classes. Additionally, the pairwise comparisons of the mean variable level was performed for the four different density classes using the Tukey Method of multiple comparisons (Neter *et al.*, 1991) to establish which values were significantly different from the others. Not all the sample sizes were equal per density class as two of the uninvaded plots were lost when the markers that marked the plots disappeared. The Tukey Test handles this problem in a conservative way *i.e.* the significance limit will be actually lower than 0.05.

3.2 Results

3.2.1 Topsoil

The null hypothesis was rejected for all the measured chemical properties in the topsoil, except for NO_3-N. In general, all the measured values increased with increasing *Acacia* cover. Resistance decreased with increasing cover density. Most increases were only significantly different between the highest density class and the uninvaded Sand Plain Fynbos. Phosphorous and Fe concentration varied significantly in between density classes but this did not seem to be related to the degree of *Acacia* cover. The carbon content of the soil was only elevated in the densely invaded plots. The results are summarized in Table 3.1. and Fig. 3.1. It was assumed that the increased nutrient levels are caused by *A.saligna* presence because the fynbos communities in the study area were all typical of nutrient-poor, acidy sandy soils (see chapter 6).

3.2.2 Deep soil

In general, the chemical soil properties of the deeper soil followed the trend set in the topsoil, however differences between invade and uninvaded plots were less significant than in the topsoil. Significant differences were mostly between the two most extreme cases *i.e.* the uninvaded fynbos and plots with the highest degree of *A. saligna* cover (>75%).

Table 3.1: *Statistical comparison of soil chemical properties in plots with different densities of Acacia saligna at the Mamre study site (winter 1999).*

Mean chemical soil status in different density classes

			density class (% cover)					null hypothesis P value
			0	25+	50+	75+		
Topsoil	pH	(KCl)	4.8375(a)	4.94(a)	5.09(a,b)	5.37(b)	***	P<0.0003
Deepsoil	pH		4.95(a)	4.98(a)	5.04(a)	4.9125(a)		P<0.8558
Topsoil	Resist.	(Ohm)	12173.75(a)	7860(b)	7821(b)	4613(c)	***	P<0.0001
Deepsoil	Resist.		12246.25(a)	10711(a)	10475(a)	6070(b)	***	P<0.0010
Topsoil	C	(%)	0.4125(a)	0.51(a,b)	0.48(a,b)	0.7(b)	***	P<0.021
Deepsoil	C		0.3375(a)	0.29(a)	0.33(a)	0.3375(a)		P<0.6988
Topsoil	P		3.25(a,b)	1.6(a)	1.8(a)	4.2(b)	**	P<0.0012
Deepsoil	P	(mg/kg)	1.875(a,b)	0.9(b)	1.2(a,b)	2.25(a)	*	P<0.0156
Topsoil	Fe		14.8125(a)	11.46(a,b)	8.37(b)	13.69(a)	**	P<0.0012
Deepsoil	Fe		11.8375(a,b)	10.12(b,c)	6.63(c)	15.825(a)	***	P<0.0001
Topsoil	Na		0.03375(a)	0.038(a)	0.036(a)	0.082(b)	***	P<0.0006
Deepsoil	Na		0.02375(a)	0.034(a)	0.031(a)	0.0787(b)	***	P<0.0003
Topsoil	K		0.0175(a)	0.025(a)	0.027(a,b)	0.04(b)	**	P<0.0022
Deepsoil	K		0.0125(a)	0.01(a)	0.009(a)	0.0225(b)	***	P<0.0002
Topsoil	Ca	(cmol/kg)	0.60375(a)	0.856(a)	0.987(a)	1.549(b)	***	P<0.0008
Deepsoil	Ca		0.37125(a)	0.392(a)	0.506(a)	0.57(a)		P<0.0489
Topsoil	Mg		0.0775(a)	0.164(a)	0.174(a)	0.464(b)	***	P<0.0001
Deepsoil	Mg		0.04875(a)	0.086(a)	0.097(a)	0.215(b)	***	P<0.0001
Topsoil	Svalue		0.7325(a)	1.083(a)	1.224(a)	2.135(b)	***	P<0.0003
Deepsoil	Svalue		0.45625(a)	0.522(a)	0.642(a,b)	0.8862(b)	***	P<0.0005
Topsoil	NH4-N		0.17625(a)	1.052(b)	0.737(a,b)	1.032(b)	*	P<0.0237
deepsoil	NH4-N		0.1875(a)	0.528(a,b)	0.646(a,b)	0.76(b)	*	P<0.0310
Topsoil	NO3-N	mg/kg	0.5225(a)	0.662(a)	0.64(a)	0.944(a)		P<0.2908
deepsoil	NO3-N		0.3675(a)	0.332(a)	0.456(a)	0.605(a)		P<0.4003
Topsoil	total N		0.69875(a)	1.714(b)	1.377(a,b)	1.976(b)	**	P<0.0091
deepsoil	total N		0.555(a)	0.86(a)	1.102(a)	1.365(a)		P<0.3127

Significance level *** P< 0.001, ** P<0.01, * P<0.05
Values across colums with any letter in common are not significantly different at P<0.05 (Tukey test).
Values are the means of 10 replicates.
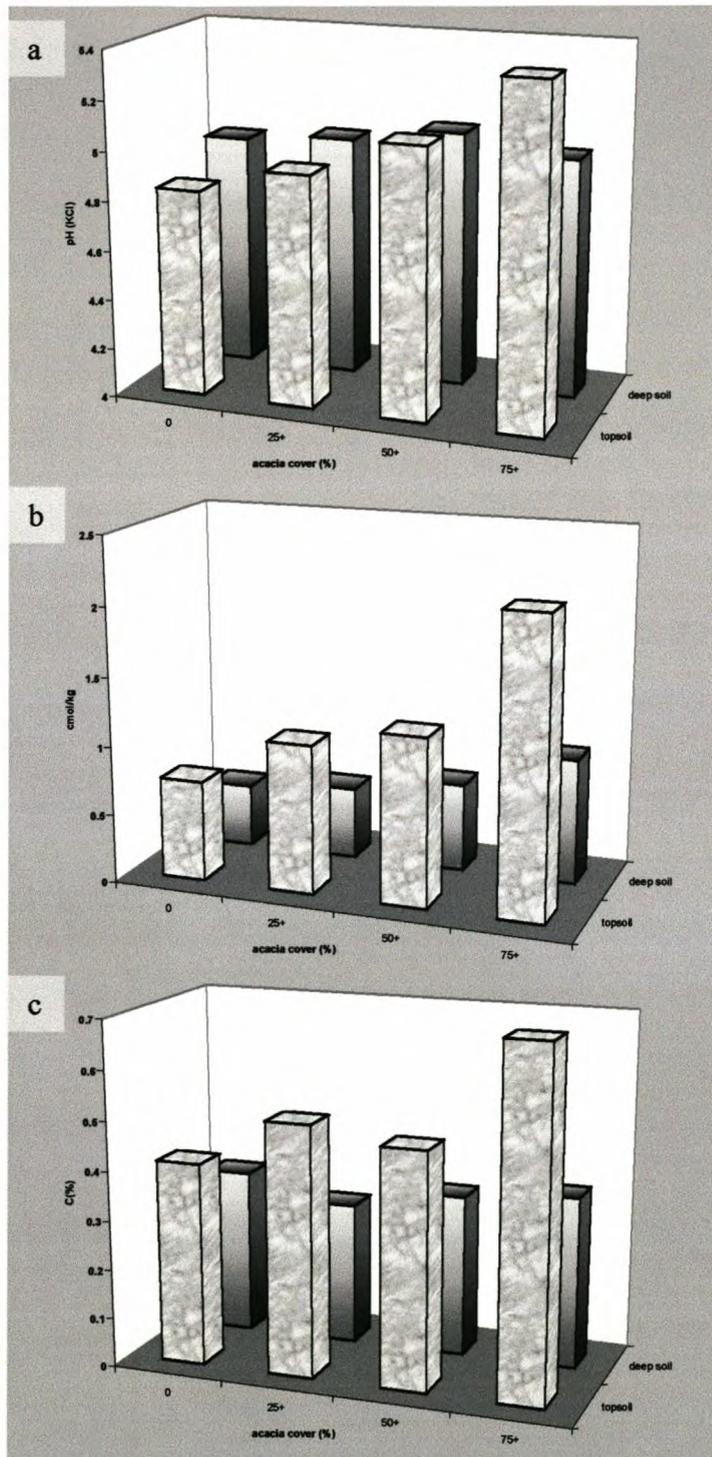
Fig. 3.1: Differences in soil nutritional status under varying degrees of *Acacia saligna* cover. (a) pH (KCl), (b) Exchangeable cations (Na, K, Ca and Mg) in cmol/kg, (c) total carbon content (%).
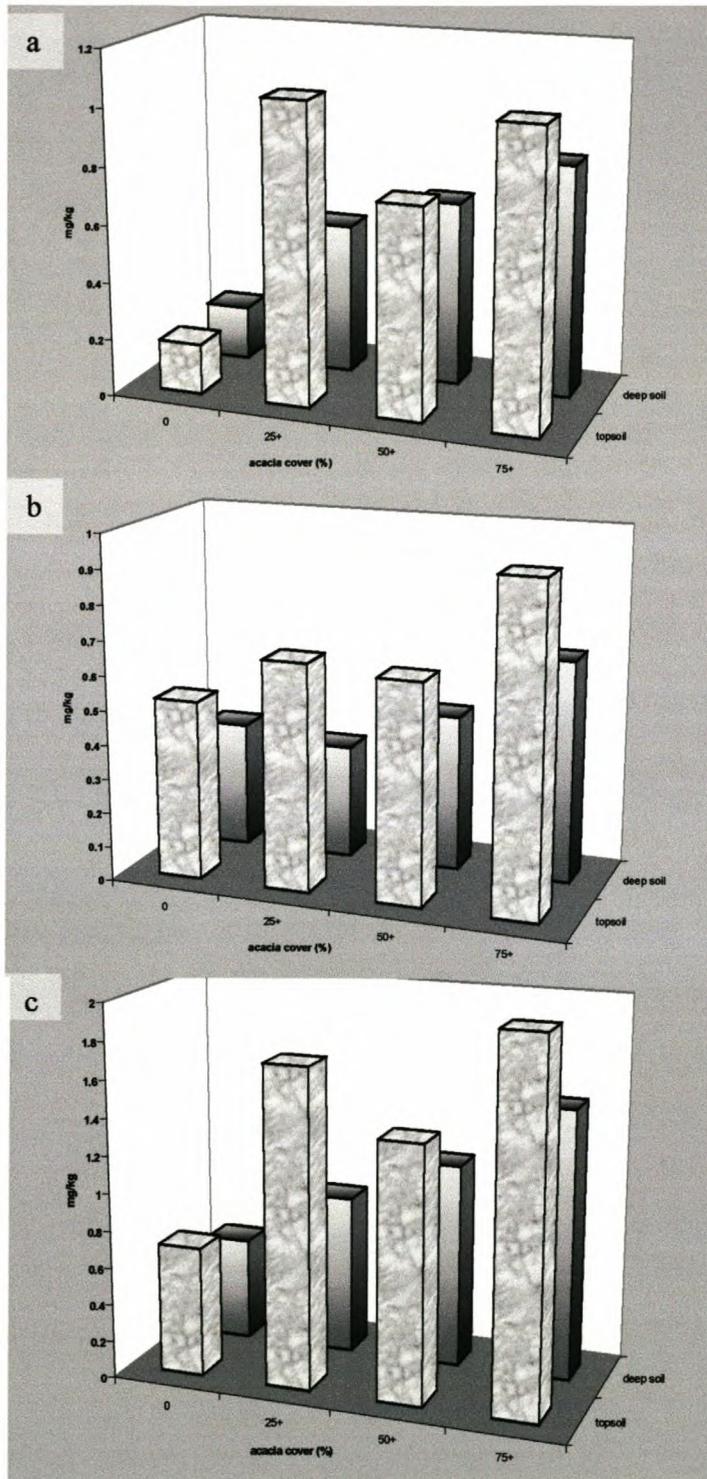
Fig. 3.2: Differences in soil nutritional status under varying degrees of *Acacia saligna* cover. (a) NH_4^+ (mg/kg), (b) NO_3^- (mg/kg) and (c) total nitrogen (mg/kg).

3.3 Discussion

3.3.1 General

The impact of *Acacia* infestation on soil chemical status has been found to be greater than that of fire or seasonal differences (Musil & Midgley, 1990). It has been known for some time that some Australian *Acacia* species have nitrogen-fixing capabilities (Roux & Warren, 1963) but their impact on the soil chemical status reaches much further than that (Musil & Midgley, 1990; Witkowski, 1991; Musil, 1993). Many of the chemical elements under investigation here, increased at least twofold in densely invaded fynbos compared to uninvaded fynbos sites.

The pH in the topsoil of densely invaded *A. saligna* stands was higher than in uninvaded or lightly invaded (>25% cover) fynbos (P<0.05). This confirms the results of Musil & Midgley (1990) but not of Musil (1993). This discrepancy is probably due to the fact that these authors did not differentiate between *A. saligna* stands of different densities.

Musil & Midgley (1990) detected significant differences in soil pH between different seasons with the soil becoming more acidic in autumn, winter and spring. This might be explained by the higher precipitation and the processes associated with the seasons (*i.e.* differences in leaching, atmospheric nutrient input and increased microbiological activity). The seasonal difference seems less in dense *Acacia* stands, possibly because the phyllodes and the litter intercept the rainfall before it reaches the ground and allow more time for evaporation. In the deep soil the difference in pH is not present.

The same trend as observed for pH can be observed in the soil carbon content. The highest values occur in the densely invaded plots, while the least invaded and uninvaded plots do not differ significantly. The higher organic content can be attributed to the high litter production of *A. saligna*. About half the canopy mass is renewed annually (Milton, 1980). The litter accumulates on the ground and in mature thickets the dry weight of the

litter layer exceeds that of the living canopy (Milton, 1980). The nitrogen content of *Acacia* litter is about three times as great as that of fynbos species, resulting in a low C:N ratio which favours bacterial decomposition (Milton, 1980). The turnover time for *Acacia* litter is about 8-9 years compared to 13-15 years for sclerophyll shrubs (Milton, 1980). However it seems that the mineralisation rate for *A. saligna* litter is not as high as would be expected. Stock *et al.* (1995) found, in their study of the West Coast Strandveld, that the mineralisation rate was higher in the West Coast Strandveld than in fynbos, probably due to a richer environment favouring bacterial decomposition. After invasion by *Acacia cyclops* (rooikrans), the mineralisation rates were even higher. In the more nutrient poor Sand Plain Fynbos on the other hand, the mineralisation rates are low, even after invasion by *A. saligna*. The reason why similar invasive species in similar climatic conditions produce different effects in West Coast Strandveld and Sand Plain Fynbos is uncertain. It may be that decomposer communities in the nutrient poorer environment of the fynbos are not equipped to keep up with enhanced (and qualitatively different) litter input from the port jackson or that port jackson specifically produces chemical compounds which restrict decomposition (Stock *et al.*, 1995). It has been shown that seedlings of *A. saligna* produce antibacterial substances (Jones *et al.*, 1963). And these substances could remain in the plant throughout its life.

A. saligna is capable of accumulating phosphorous, probably due to the presence of mycorrhiza (Barrow, 1977). The phosphorous content of *A. saligna* litter exceeds that of litter from the indigenous vegetation by a factor of 2 to 4 (Milton, 1980; Witkowski & Mitchell, 1987). The estimated potential annual input is between 0.442-0.92 g and 0.019 g P m^{-2} yr^{-1} for *A. saligna* and Sand Plain Fynbos respectively (Milton, 1980; Mitchell *et al.*, 1986). In this way, invasion by *A. saligna* can increase the P content in the soil. The experimental data found in the literature however are sometimes contradictory (Musil & Midgley, 1990; Witkowski, 1991; Musil, 1993). This study found that P concentrations were no different between uninvaded and densely invaded fynbos. The significant difference occurred between the densely and low and medium density *Acacia* stands. In contradiction to Milton (1980), Witkowski (1991) found that the P concentrations of abscised leaves of certain fynbos species by far exceed those in abscised *A. saligna*

leaves. The unexpected low P content of the soil under low and medium density *A. saligna* stands can be attributed to a high P demand by *A. saligna* as suggested by Musil & Midgley (1990). Witkowski (1994) showed that *A. saligna* seedlings respond positively to P additions.

The explanation for the high value in densely invaded plots might be the fact that *Acacia* stand density usually increases with time post invasion. Dense stands are generally older which leaves ample time for P to accumulate. Older (mature) trees also produce more reproductive parts, which contribute about 30% to the litter (Milton, 1980) compared to 1.5% for recently matured trees (Witkowski, 1991). Reproductive parts contain higher concentrations of N and P (Witkowski, 1991) so that young stands have not yet reached their full nutrient enrichment potential.

Low-density stands are generally recent invasions and could consequently have a negative P balance. P concentrations tend to vary seasonally as demonstrated by Musil & Midgley (1990), with values being highest in winter and spring. This can both be attributed to increased mineralisation rates of litter under conditions of improved soil moisture (Read & Mitchell, 1983) and the amount of P input through precipitation (Brown *et al.*, 1984). The atmospheric input per annum can be as high as the yearly input by the litterfall of Sand Plain Fynbos (Mitchell *et al.*, 1986). P concentrations in both topsoil and deeper soil were correlated, with the deep soil values being about half of the values for the topsoil.

All the other macro-elements under investigation (Na, K, Ca, Mg) occurred in significantly higher concentrations in the most densely invaded plots, both in the topsoil and in the deeper soil (except Ca). Compared to uninvaded Sand Plain Fynbos, dense *Acacia* stands had a three-fold and two-fold increase in the combined concentration of these four elements in topsoil and deep soil respectively. *A. saligna* increases the nitrogen content of the soil and depends on symbiotic N_2-fixing bacteria in its root nodules to supply sufficient nitrogen in the nutrient poor soils of the lowland Sand Plain Fynbos (Roux & Warren, 1963; Stock *et al.*, 1995). The potential input through litter is up to 10.5

g m^{-2} yr^{-1}, nine times as high as for fynbos communities (Milton, 1980) and about 50 times the atmospheric input of total nitrogen for the area (Stock & Lewis, 1986a). The results from this study also indicate elevated nitrogen levels (both NH$_4$-N and NO$_3$-N) associated with *Acacia* invasion. However the values were not as significantly different as for other chemical variables. As in the case of phosphorous, this can be due to a low net nitrogen mineralisation rate (Stock *et al.*, 1995) or to seasonal differences in soil nitrogen content due to increased leaching with the onset of the winter rains (Musil & Midgley, 1990). Most of the nitrogen is in the form of NH$_4$-N except in the uninvaded plots. The nitrogen concentrations in the deeper soil layer were relatively high but this might be the result of nitrogen from the surface soil being washed down into deeper soil layers (Stock & Lewis, 1986b).

Seasonal variations in soil nutrient status are observed for most chemical properties in Sand Plain Fynbos and are the result of a number of factors. Atmospheric input through precipitation is highly correlated with rainfall patterns (Stock & Lewis, 1986a). Alternatively, nutrients can easily be leached from the acid, sandy soils with low organic content that constitute most of the soils of Sand Plain Fynbos. Rainfall is an important factor in the mineralisation processes and microbial degradation is often limited by a lack of soil moisture (Stock & Lewis, 1986b; Musil & Midgley, 1990; Stock *et al.*, 1995). The rains also trigger a growth response in the fynbos community resulting in an increased uptake of minerals at a time when input from litter is at a minimum (Milton, 1980). Nitrifying bacteria are responsible for conversion of NH$_4$-N to NO$_3$-N. These organisms favour a specific temperature and moisture regime and are most active during spring and autumn in Mediterranean-type ecosystems (Schaefer, 1973), resulting in maximum concentration of NO$_3$-N in these seasons (Stock & Lewis, 1986b).

3.3.2 Effects of increased nutrient availability in fynbos

Infestations of *A. saligna* in Sand Plain Fynbos could render the environment less suitable for the indigenous species through nutrient enrichment of the soil (Witkowski &

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Mitchell, 1987) because plants adapted to low nutrient conditions do not always compete successfully on fertilized soils (Specht, 1963). It is true that indigenous plant forms regenerate less successfully in *Acacia* infested stands (Holmes & Cowling, 1997a; Musil, 1993) and reduced seed yields have been reported for certain Proteaceae in response to nitrogen addition (Witkowski, 1990a). Many other factors, however, come into play apart from soil nutrient status when affecting regeneration. Shading by *Acacia* trees may affect seed production and the thick litter layer could prevent seed penetration to the soil surface (Milton, 1980; Musil, 1993). In contrast to observation in similar heathlands around the world, indigenous plant forms show no or little response to higher nutrient levels in *Acacia* stands and seedling mortality was not affected. This is in accordance with the general principle that plants from infertile sites, which have low growth rates and low nutrient absorption rates are usually unresponsive to changes in nutrient availability (Musil, 1993). Skewed shoot : root length ratios (up to 20% higher for Restioids) in *Acacia* stands reflect shading, rather than nutrient availability (Musil, 1993).

The limiting element in Sand Plain Fynbos is nitrogen and other nutrients rather than phosphorous (Witkowski, 1989a, b). Nitrogen addition results in increases in the live vegetative cover of annuals, graminoids and restioids (Witkowski, 1989b; Witkowski & Mitchell, 1989). These plants seem more plastic in their response to nutrient increase than slow growing, stress tolerant evergreen shrubs (Witkowski, 1989a). After clearing, the early succession in former *Acacia* stands is dominated by grasses and exotics (Milton, 1980) whereas in pure fynbos it is dominated by Restionaceae and coppicing shrubs (Hoffman *et al.*, 1987). Litter tends to become more nutrient rich with elevated nutrient availability but much of the nutrients are immobilized in the litter layer rather than returned to the soil (Witkowski, 1989b, Stock *et al.*, 1995).

Plant mortality is not enhanced under increased nutrient input and it can be said that this vegetation type is resilient to changes in nutrient status. Chronically high nutrient inputs will however eventually lead to a shift in species composition with an increase in ephemeral, nutrient demanding species (Witkowski, 1989a).

3.3.3 Long-term effects of invasion on soil nutrient status

Frequent fires are a characteristic feature of fynbos ecosystems and have a significant influence on soil chemical status (Stock & Lewis, 1986b; Musil & Midgley, 1990). The elevated nutrient levels in post-fire fynbos are transient and disappear within a year (Musil & Midgley, 1990). *Acacia* invaded fynbos shows the same high nutrient levels as post-fire fynbos, although the impact of *Acacia* invasion is far more significant. When dense *Acacia* infestations are cleared, the elevated nitrogen status of the soil may be short-lived (Witkowski, 1991) since the sandy soils present under most of this vegetation type are incapable of storing large quantities of nitrogen (Witkowski *et al.*, 1990).

Burning after removal or die-off of *A. saligna* will destroy the litter layer in which much of the nutrients are stored (Milton, 1980; Witkowski, 1989b; Stock *et al.*, 1995). Any long-term effects due to the slow degradation of *Acacia* litter would be eliminated (Musil & Midgley, 1990). Nutrient concentrations increase temporarily after a fire but a large amount of the most important element, N, is lost by volatilisation (between 20.4 and 158 kg ha^{-1}) (Van Wilgen & le Maitre, 1981).

In short, the absence of any detrimental effects of nutrient enrichment by *A. saligna* on seedling survival and growth of indigenous taxa (Musil, 1993), and the short-term effects of nutrient additions in the sandy soils of the Sand Plain Fynbos when the nutrient source is removed (Stock & Lewis, 1986b; Musil & Midgley, 1990) suggests that the impact of *A. saligna* on the soil chemical status is temporary and revocable after removal of the trees. It seems unlikely that the increased nutrient status of the soil is a persistent condition that could severely restrict re-establishment of indigenous species as feared by Stock *et al.* (1995).

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Chapter 4

Impact of *Acacia saligna* invasion

on soil moisture

4.1 Methods

On three different occasions (August, September and November), soil core samples were taken in the densely invaded (>75% *Acacia* cover) and in the uninvaded plots. The samples were taken from both the topsoil (0-10 cm, three samples) and the deeper soil (30-40 cm, three samples), and were evenly spread on the length axis of the plot. The samples were stored in airtight plastic bags for transport, weighed and dried in an oven for 24 hours at 105 °C. Then they were weighed again in order to calculate the amount of water stored in the soil. No samples were taken in the plots that had a 25% and 50% *Acacia* cover due to practical restriction to handle a large number of samples at the same time.

The first two sampling sessions occurred five days after a period of rainfall (in August and September respectively), when the average daily temperature ranged from 8.4 °C to 15.9 °C. The third sampling took place in November, after a thirty day period of no rainfall, during which the average daily temperature ranged from 14.4 °C to 25.6 °C. No samples were taken in summer and autumn because it was impossible to use the soil auger to take samples during these seasons. The soil was too dry and showed no consistency, which rendered the soil auger

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ineffective. The soil analysis results were analyzed using the SAS Program and the Tukey Test for comparison of the treatment levels.

4.2 Results

Due to the large variations (Fig. 4.1 & 4.2) within plots of the same invasion status there was no significant difference in soil moisture content of top soil and deep soil between invaded and uninvaded plots in August. In September, the deep soil in the invaded plots was significantly drier than in the uninvaded plots. Although not significant, the trend during August and September is that the topsoil is moister in invaded plots while the deep soil is moister under uninvaded Sand Plain Fynbos. In November, when rainfall is less frequent, soil moisture levels are significantly higher in invaded plots, in both topsoil and deep soil. In the invaded plots, the soil moisture has not dropped to significantly lower levels compared to August and September as is the case in the uninvaded plots.

Soil moisture levels in summer are expected to be comparable to, or even lower than the values measured in November. The discrepancy in soil moisture level between *Acacia saligna* stands and uninvaded Sand Plain Fynbos probably disappears as the dry season progresses.

4.3 Discussion

Alien invasive trees are often reported to use valuable water in excessive quantities (Marais, 1998; Versfeld *et al.*, 1998). This has been the main economic argument for control (Marais, 1998), together with the threat of invasion to plant species richness (Richardson *et al.*, 1989). The increase in streamflow after clearing of wattle and pines along a riverbank has been proven by Dye and Poulter (1995). Some of this increase however is due to the clearing operation and is not due to the removal of alien vegetation as such. Clearing riverbanks of indigenous fynbos vegetation would also result in an increased stream flow, although possibly not to the extent recorded by Dye and Poulter (1995). Immelman *et al.* (1973) provide data from Jonkershoek and Stellenbosch which shows that mature fynbos vegetation reduces

vegetation reduces stream flow to nearly the same extent as a pine plantation. *In situ*, *A. saligna* could therefore have an influence on the soil moisture level as shown in Fig. 4.2.

Contrary to expectations when soil moisture samples were taken, soil moisture levels were higher in the topsoil of invaded plots. These increased levels were not correlated with the higher carbon content of the soil in invaded stands. More likely, this result can be attributed to a shelter effect from the acacias. The trees reduce wind speed and solar radiation at ground level and the litter layer provides an insulating layer where relative humidity is high, further reducing evaporation. In the November survey, this shelter effect became even more apparent when the solar radiation intensified and the southeasterly wind started blowing. In Sand Plain Fynbos the ground is often bare and exposed to the elements.

Another feature of *Acacia* thickets is the higher leaf surface area compared to Fynbos vegetation. During the winter months when fogs occur frequently, the higher surface area of these thickets enables them to trap more water in the form of condensation.

Any effects of water consumption by the acacias only become apparent in the deeper soil, which tends to be drier during the wetter months under the *Acacia* thickets. According to Milton (1980), *A. saligna* is variable in its growing season and at sites where water can be a limiting factor, growth may start as soon as August. Whereas at other sites, the growth season is more generally correlated with temperature. The network of superficial roots of *A. saligna* could be responsible for preventing rainfall water from percolating to deeper soil layers. Any precipitation is retained in the topsoil and used for early growth. This process will contribute to the lowering of the water table because of a reduced percolation from the winter rains.

In late spring the situation is rather different with the soil moisture in uninvaded fynbos being considerably lower throughout the profile compared to the August and September values. The evaporation and the low water retention capabilities of the sandy soil could be factors in the drying of the soil, which is slower under *Acacia* thickets. Also, in the dry season *A.saligna* might depend more on its taps roots to draw water from the deeper soil (watertable), leaving the moisture in the upper soil untouched.

The differences in soil moisture in the different plots are likely to influence the composition and the activity of the soil microflora and microfauna (Dr. A. Botha, pers comm., University of Stellenbosch, Dep of Microbiology). The microorganisms in soil in a Mediterranean climate are adapted to temporary water deficits (Schaeffer, 1973) but different organisms function optimally at specific moisture levels. It seems from this study that *Acacia* thickets provide a more stable environment for microorganisms in comparison to the more extreme conditions prevalent in the soils of uninvaded Sand Plain Fynbos. This also means that the decomposition and mineralization processes can continue longer under *Acacia* stands, enhancing the already elevated nutrient status of the soil.

The soil moisture sampling in this study was not continued long enough to make inferences for the whole year. Preferably the moisture status of the soil should be monitored for several years, and under standard conditions. Sampling on pre-set dates can return biased results in the event of rain. Temperature studies could be valuable to obtain a more complete picture of the microclimate prevalent in the different vegetation types.

Finally, care should be taken when interpreting these results. Although *A. saligna* is drought resistant, it prefers moist habitats and its spread is often linked with rivers and riverbanks (Boucher & Stirton, 1978). The possibility remains that the increased moisture availability in the *Acacia* thickets is not due to the presence of the trees, but that the trees are present because the sites, as such, are wetter. The high variability within the samples of the same vegetation type, suggests that there is no single, easy explanation for the difference in moisture availability between uninvaded Sand Plain Fynbos and invaded Sand Plain Fynbos.
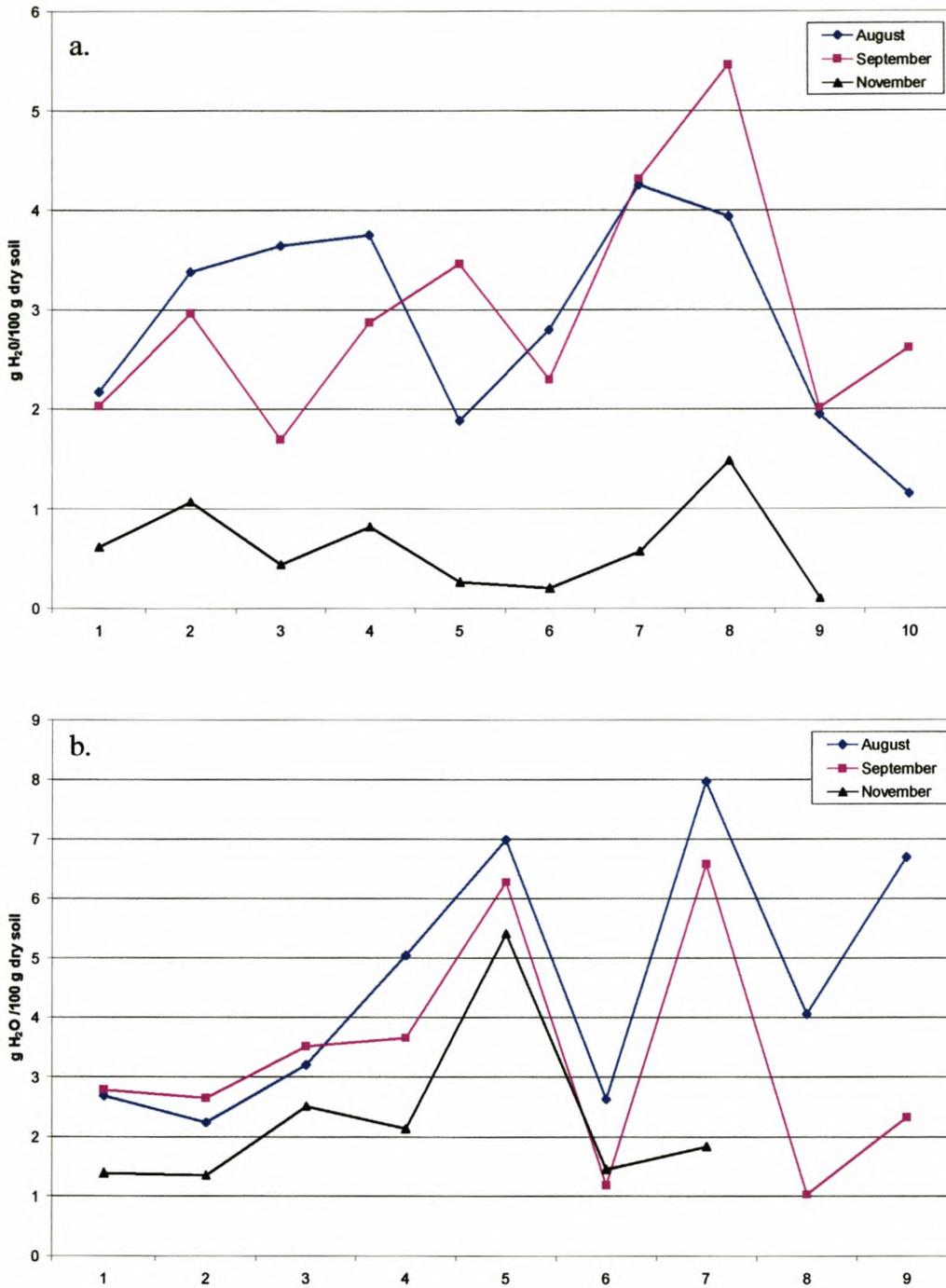
Fig. 4.1: Soil moisture levels of the topsoil in different plots of (a) uninvaded and (b) invaded Fynbos with an *Acacia saligna* cover of more then 75%.
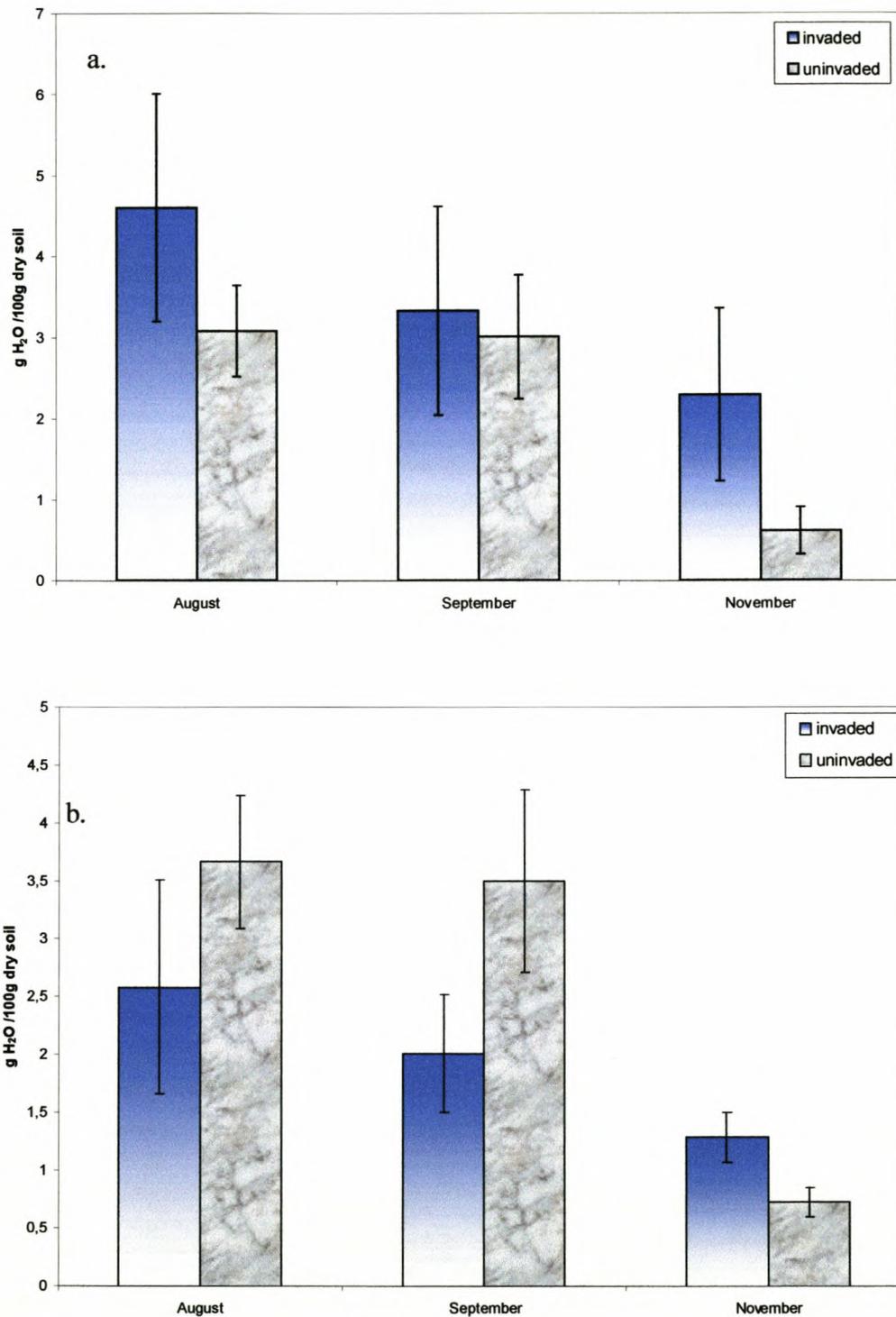
Fig. 4.2: Mean soil moisture content of (a) the topsoil (0-10 cm) and (b) the deeper soil (30-40 cm) under invaded and uninvaded fynbos. Error bars indicate 95% confidence interval. In November, the moisture content under *Acacia* is significantly greater than in uninvaded plots.

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Chapter 5

Seedbank and viability of

Acacia saligna seed

Although seeds are most abundant in the topsoil (Milton, 1980), the activity of dune mole-rats (*Bathyergus suillus*) could cause a high turnover of the soil, causing young seeds to be buried, and older seeds to be brought back to the surface. In the context of alien eradication, the deeply buried seeds can cause re-infestation in the long term.

5.1 Methods

Seed samples were collected from all the plots during July and August. A sample was taken from the topsoil (0-10 cm) and from the deeper soil (40-50 cm) from the centre of each plot using a soil corer (Ø 4.5 cm).

To obtain a more detailed picture of the vertical distribution of acacia seeds, four 600 cm^2 samples were taken, every five cm, in four different soil pits, up to a depth of 60 cm. The pits were randomly selected under the canopy of dense *A. saligna* thickets.

Before treatment, the seeds were stored in air-dry soil. Afterwards, the seeds were sieved from the soil using a sieve with a mesh size of 710 µm and separated manually from the remaining residue. The seeds from all plots were put together. Only visibly undamaged seeds were used for further treatment. The seeds were placed in paper bags and exposed to dry heat in a pre-heated oven at 100 °C for 30 minutes. According to Jeffery *et al.* (1988), this method is suited to ensure a high percentage of germination within a few days. Following the heat treatment, the seeds were air-cooled to room temperature and placed into plastic petri dishes, containing filter paper moistened with 6 ml of a fungicide solution (Funginex, 0.38 g/l active ingredient). Twenty seeds were placed in each petri dish and the experiment was replicated ten times. After preparation, the petri dishes were placed into a germination chamber with a 12-12 hour photoperiod and a 16-25°C temperature regime. As a control, a batch of ten seeds was placed in the fungicide solution without prior heat treatment.

In an alternative treatment, seeds were chipped manually at the distal end of the seed to break the seed coat and placed into petri dishes under the same conditions as described for the heat-treated seeds. Four replicates of twenty seeds were tested. As a control, a batch of seeds was clipped but not treated with a fungicide solution.

5.2 Results

5.2.1 Seed bank size

In the densely invaded *A. saligna* stands, seed bank densities in the top 10 cm of the soil ranged from virtually zero to 5 600 seeds m^{-2} with a mean of 2 400 seeds m^{-2}. In the lightly infested plots, seed densities ranged from undetectable to 1 800 seeds m^{-2}. No seeds were found in the uninvaded plots. Seed densities in the deep soil (40-50 cm) were much lower, as was expected. At this depth, seeds were only detected in high-density stands. Seed density averaged 500 seeds m^{-2}.

5.2.2 Distribution

Three profiles showed a density of a few hundred seeds m^{-2} on the surface although the profiles were taken under the canopy of dense *A. saligna* stands. The fourth profile, taken under an old tree (Ø > 25 cm) showed a steep decline in seed density in the top ten centimeters of the soil from 2 400 to 260 seeds m^{-2}, and a slow decline deeper in the profile. Very few seeds are found deeper than 20 cm. In one soil pit, the seed density was greatest at a depth of 15-20 cm, suggesting that a local influence is concentrating the seeds.

Wherever there was a substantial litter layer under the port jackson stands, many seeds were found in this layer. They were however not included in the study because strictly speaking, they are not yet part of the soil seed bank. Unburied seeds have a high incidence of predation, loss to fire, or microbiological attacks than buried seeds due to higher exposure and contribute less to the long-term persistence of a species.

5.2.3 Germination trials

The heat treatment returned little results, with only 13% germination after six weeks. Since the heat treatment did not produce the expected results, an alternative method was used to stimulate germination. In a second experiment, clipping the seed coat resulted in a rapid absorption of water and a swelling of the seeds, as was visible by the further cracking of the seed coat. The first seed germinated after two days, but by two weeks a mere 13% had germinated. After 43 days, 30% of the seeds had germinated. One of the control dishes that contained clipped seeds but no funginex showed a 25% germination after 4 days. Thereafter, the remaining seeds suffered from a fungal attack and were destroyed. Due to time constraints, and considering the slow rate of germination, the germination trial was ended after 60 days.

5.3 Discussion

5.3.1 Seed bank size and distribution

The number of seeds under the *A. saligna* thickets is surprisingly low in comparison to the normal seed yield of an average tree in the Western Cape which can be up to 10 000 per m^2 (Milton, 1980; Milton & Hall, 1981). The vertical distribution of the *A. saligna* seeds is similar to that recorded by Milton (1980) in one case only (Fig. 5.2) and the number of seeds obtained from equivalent volumes of soil in this study is much lower. This is probably due to the relatively young age of the port jackson trees. As shown by Milton & Hall (1981) and Morris (1997), juvenile stands of port jackson do not have the normal seed bank size of 10 000 seeds per m^2. Although the impact of the fungus on the seed production of the tree is yet unknown (Morris, 1997) and the seed production per year can be erratic due to circumstances, the number of seed in the soil at Mamre might be low for three reasons:

1. Age of the trees

As mentioned above, young trees are not able to produce the same amount of seed as fully mature trees. Although old trees occur spread out over the study area, they are rare and often in a very poor condition, being heavily infected by the fungus. Furthermore they are likely to be singled out by the local community for timber or firewood. It may be that since the release of the fungus, the average age of the port jackson trees has been reduced, with a concomitant reduction in seed production.

2. Infection by Uromycladium tepperianum

The fungus attacks the reproductive tissue of *A. saligna* trees (Morris, 1987, 1991) and infected trees form fewer flowers and pods (Morris, 1987). Many of the seed bank studies performed on *A. saligna* were performed before the release of the fungus or before it became as widespread as it is today (Milton, 1980; Milton & Hall, 1981; Holmes, 1988). During a five-year study on infected trees, Morris (1997) observed that the size of the seed bank

seemed to stabilize after infection. The Mamre study site is situated close to the original point of release of the fungus. Therefore it can be assumed that the area has been infected for about ten years. If the control agent truly has an effect on the seed output, then it is only natural that the observed seed bank size at the Mamre site is as low as it is at present, even under the dense *Acacia* stands. Even as stressed trees are sometimes known to produce more seeds as a survival mechanism, this would be counterproductive for the port jackson as the fungus can easily attack the reproductive tissue and this would place the tree under additional stress.

3. Fire

Germination of *Acacia saligna* seed is stimulated by heat (Milton & Hall, 1981; Jeffery *et al.*, 1988) and up to 70% of the viable seeds germinate in the months following a fire (Holmes, 1988). Germinating seeds are effectively removed from the seed bank. In most of the sample plots, young trees (up to 10 mm diameter) constituted the bulk of the trees present. The high incidence of fire in these thickets (natural or man-induced) prevents the build-up of the seed bank, both by stimulating germination and by destruction of seeds. The evidence for the latter is that the soil cores from many plots contained more burned seeds turned to charcoal than undamaged ones. The high fuel load of the *Acacia* thickets (Van Wilgen & Richardson, 1985), littered with dead and dying trees, causes intense fires that destroy even the seeds of the *A. saligna*.

A possible theory explaining the small seed bank sizes most likely includes the three above mentioned factors. From aerial photographs is it known that the study site was already invaded by port jackson as early as 1967. Atlantis was non-existent and the outskirts of Mamre did not reach the study site as they do now. Many trails are visible on the photographs and the area was probably used for grazing and as a source for wood as it is today. During all the time since invasion and since the last fire, the acacias had time to build up a large seed bank, as stands of mature trees can have seed bank sizes of up to 212 000 seeds per m^2 (Morris, 1997). Since the introduction of the fungus however, seed production could have decreased and the older trees disappeared, possibly more rapidly due to increased human population pressure. The younger stands that replaced the old trees are incapable of producing enough seeds to keep the seed bank at its high level, especially because the fungus infects a high percentage of the sexually mature trees. A reconstruction of the history of land use at the

nearby Fynbos Biome study site at Pella (Brownlie & Mustart, 1988), revealed that the burning regime in the area was often as short as 3-4 years. Since the Mamre study site bears marks of human presence over the whole of the area, it can be assumed that fire incidence is higher than it would be under strictly natural circumstances for uninvaded Sand Plain fynbos. This could explain the absence of old *A. saligna* stands and the low frequency of *Protea repens* which has a juvenile period of three years and is often dominant in mature Sand Plain Fynbos (Boucher & Shepherd, 1988).

Further investigation is needed to determine whether the low seed bank size is related to a low seed production. Previous studies that estimated seed bank sizes in *A. saligna* stands were often performed on more fertile soils, which would allow the trees to put more resources into seed production. If seed production is low, predation pressure from rodents on seeds can be relatively high (Holmes, 1990).

The soil stored seed bank is an important factor contributing to the persistence of *A. saligna* after initial invasion (Holmes, 1988). Unlike *A. cyclops*, *A. saligna* seeds have a low decay rate (Holmes, 1989a), requiring follow up periods of up to ten years after clearing (Holmes, 1988).

Little is known about the long term survival of *A. saligna* seeds but about 45% of the annual seed production is normally eliminated during the first year in the absence of predation. In the second year after the seedfall, another 15% is eliminated (Holmes, 1989a). Rodents can potentially consume the entire *Acacia* seed crop if *Acacia* invasion does not alter (lower) the rodent population densities found in fynbos (Holmes, 1990) but Milton (1980) suggests that rodents take only an estimated 1% of the available seed per year. Ants remove seed from the litter layer because they are attracted by the aril on the seed of *A. saligna*. They do not destroy the seed but are responsible for its burial. This behaviour takes the seed out of the predators' reach and is partly responsible for the maintenance of the soil seed bank (Holmes, 1990). The penetration of the seed in the soil is helped by the burrowing activities of the locally abundant mole-rat (*Bathyergus suillus*), other mammals, snakes and burrowing insects which are common in sandy areas (Milton, 1980). In one soil pit, the density of the seeds increased at a depth of 15-20 cm, adding proof to the burrowing theory.

Only in the densely invaded thickets were there seeds present at a depth of 30-40 cm. Since the density of the invading trees is a time dependent factor (the thickets becomes more dense over time) this may suggest that it takes a long time (several years) for seeds to reach these depths. No experiments were performed to determine the viability of seeds buried at different depths but *A. saligna* seeds obtained in this study sometimes germinated in the soil samples taken at 30-40 cm depth while they were being air-dried. This means that seeds buried at these depths are still viable and can germinate without any other stimulus than exposure to light. The inherent germination inhibition by the hard seed coat was gradually broken down over time in these particular seeds while the seed was buried in the soil.

The absence of seeds in the uninvaded plots confirms earlier observations by Milton (1980) that seeds are mostly deposited in the canopy shade, with little lateral distribution.

5.3.2 Germination trials

The water impermeable seed coat has been established as the major reason for dormancy in *Acacia* seeds (Cavanagh, 1980). Seed treatment to enhance germination is aimed at breaking this dormancy by rendering the seed coat permeable. Numerous techniques are used to achieve this goal. 'Dry' treatments such as heat, scarification, chipping or temperature fluctuations or 'wet' treatments such boiling or treatment with acids or solvents have all been used with varying degrees of success (Clemens *et al.*, 1977; Cavanagh, 1980; Milton, 1980; Holmes *et al.*, 1987b; Jeffery *et al.*, 1988). Although Jeffery *et al.* (1988) obtained a high germination percentage using dry heat treatment, it was discarded in this study due to an apparent low success rate. The control batch which was not treated, did not germinate either so it can be assumed that the heat treatment was not the cause for the low germination rate.

The degree of seed dormancy may vary from year to year and between stands (Cavanagh, 1980; Jeffery *et al.*, 1988). This perhaps explains why the heat treatment of the *A. saligna* seeds did not provide a satisfactory germination rate. Secondary dormancy, possibly involving the embryo, could explain why seeds will not germinate after the breaking of the seed coat (Clemens *et al.*, 1977) and is believed to become a more dominant factor in older seed

(Aveyard, 1968 ex Cavanagh, 1980). It has not been established how long *A. saligna* seeds remain viable in the soil but Holmes *et al.* (1987a) found viable seeds in the soil up to 8 years after clearing. Unfortunately they probably underestimated the degree of viability because they assumed seeds not to be viable if they did not germinate within two weeks of chipping the seeds. This present study shows that even after chipping and rapid imbibition of the seeds it can take considerable time (even up to four weeks) for the seeds to germinate when they are placed in a fungicide solution. There is a possibility that the fungicide used in the experiment has a negative effect on germination as a germination peak as observed by Milton (1980) and Jeffery *et al.* (1988) did not occur.

Acacia saligna is a tree from a fire-prone environment and is well adapted to fire, unlike *A. cyclops,* with which it often is interspaced. Germination of *A. saligna* seeds is stimulated by fire and up to 70% of the seed bank can germinate after a fire (Holmes, 1990). The seeds of *A. saligna* can tolerate higher temperatures than indigenous heat promoted species (Jeffery *et al.*, 1988) probably in adaptation to the higher fuel loads and hotter fires experienced in invaded vegetation. Apart from a better heat tolerance the seeds of *A. saligna* respond fast to stimulation, making them highly successful competitors. Although again it is noted that the present study found an abnormally high degree of dormancy in the *Acacia* seeds collected from the study area. Further germination trials should be conducted to determine the viability of the *Acacia* seeds.. Likewise, it would be interesting to test the different effects of chemical products (*e.g.* fungicides) on the viability of the seeds.
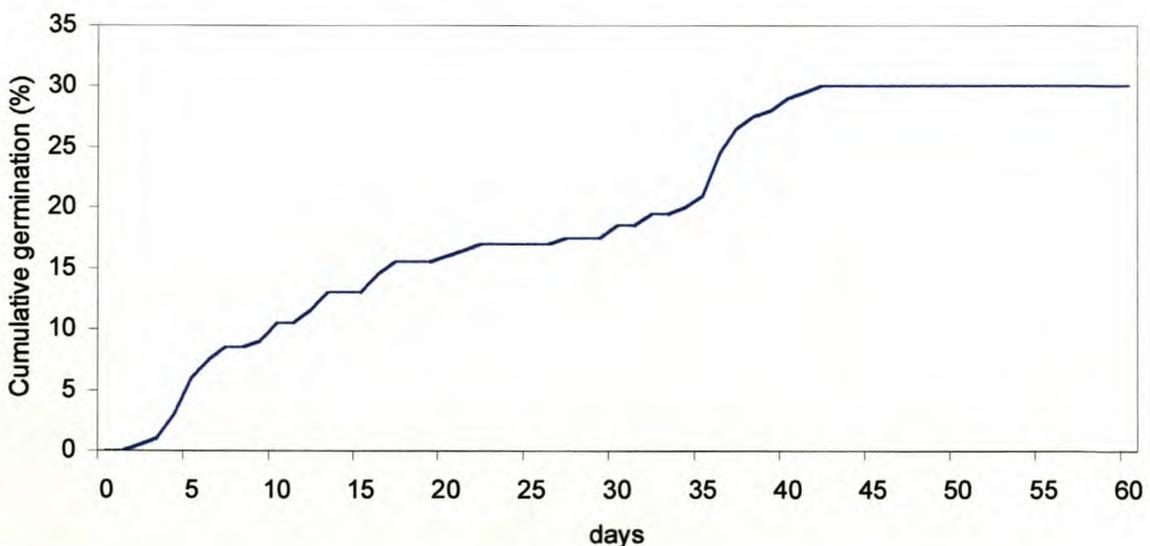
Fig. 5.1: Cumulative germination of clipped *A. saligna* seeds in a 0.38g/l Funginex solution. After 43 days, a peak of 30% germination was reached.
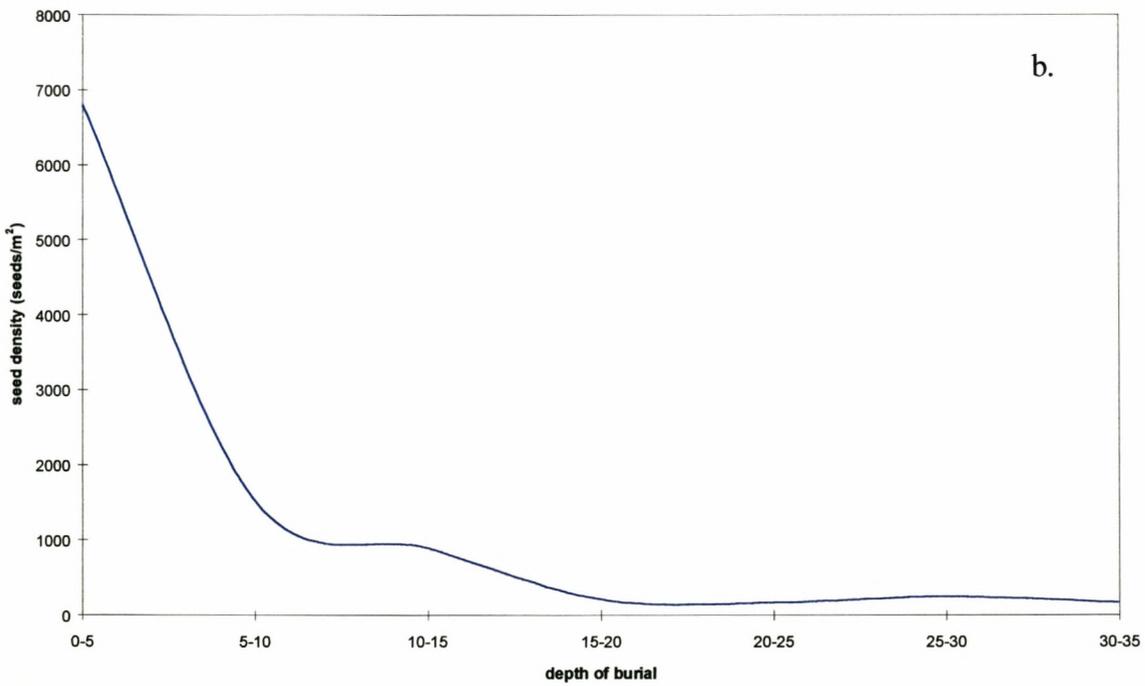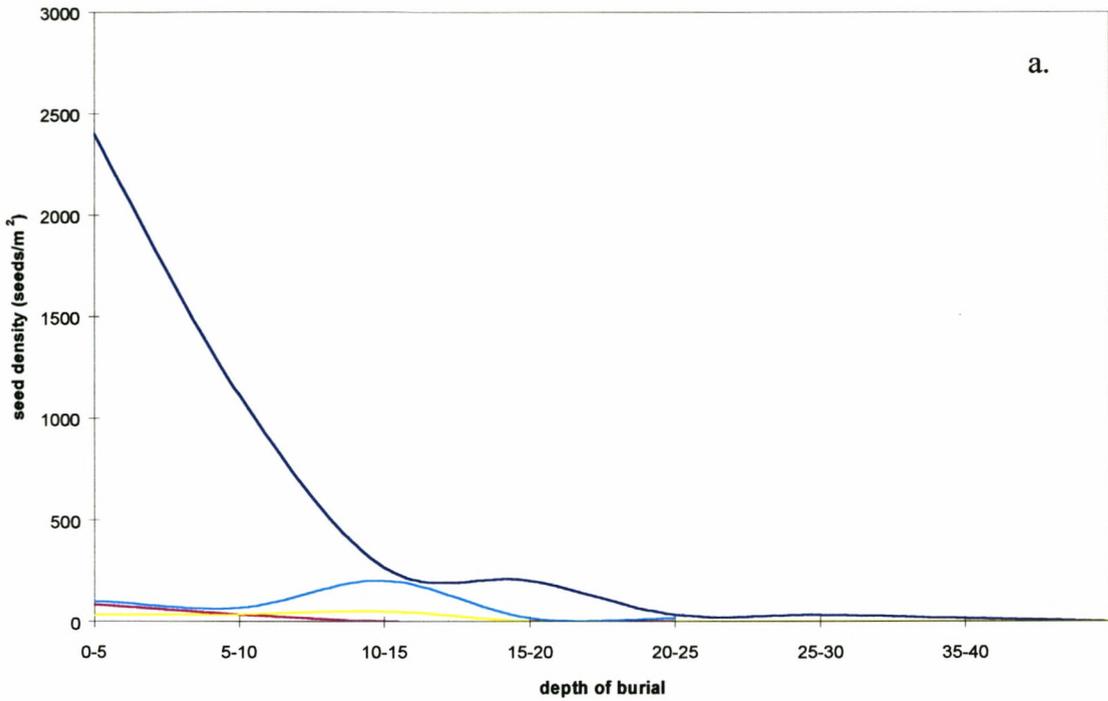
Fig. 5.1: (a)Vertical distribution of *Acacia saligna* seeds in the soil in four different soil pits (own data) and (b) the distribution under a Cape Flats thicket (Milton, 1980).

Chapter 6

Impact of the present *Acacia* population on the Sand Plain Fynbos Communities

Acacia saligna forms dense stands in agricultural and conservation areas (Morris, 1997). Over time it causes severe reduction in species richness and a shift in community structure in Fynbos vegetation (Richardson & Van Wilgen, 1986; Holmes & Cowling, 1997a). Despite this awareness, there has been surprisingly little research on vegetation dynamics following *A. saligna* invasion. Most studies, including this one offer a snapshot picture of what is a flowing biological process. In the long run however, many static and well-documented observations can create a good impression of the bigger process.

Since the introduction of the biological control agent *Uromycladium tepperianum*, the Plant Protection Research Institute (PPRI) has set up a monitoring program to evaluate the success of the agent, quantitatively. This study aims at complementing the PPRI programme and to introduce ordination methods to help to determine the impact of *A. saligna* invasion on Sand Plain Fynbos communities objectively. Ordination is a useful tool that gives added value to syntaxonomic classification and helps with the interpretation of vegetation data (Deall & Theron, 1990). It has been shown that plant communities often relate strongly to soil geology (McDonald, 1987).

In this study, Principal Components Analysis (PCA), Detrended Correspondence Analysis (DCA) and Canonical Correspondence Analysis (CCA) were used to test this theory on Sand Plain Fynbos vegetation, in relation to invasion by *A. saligna*.

6.1 Methods

6.1.1 Study sites

During March 1999, the study area was visited repeatedly and a total of 40 small plots, each 50 m^2 in size were chosen for closer examination. The plots were subjectively selected according to uniformity and crown cover density of the *A. saligna* trees and were assigned to the following density classes: 0% cover, 25–50%, 50–75% and 75–100% *A. saligna* crown cover. The plots that were free of *A. saligna* were located approximately three times the height of the nearest trees, distant from them, in order to minimize the influence exerted by the trees on the uninvaded plots. In practice this resulted in a distance of ± 15 meters. The grid location of the center of each plot was recorded with a GPS system (Trimble Pathfinder XRS) with sub-meter accuracy, in order to allow monitoring in the following years.

6.1.2 Health status and structure of the A. saligna population

In the plots that were invaded by *A. saligna*, the stem diameters of the trees were recorded at 10 cm above ground level and a visual estimate was made of the number of galls on individual trees. This was done in accordance with the monitoring method used by the Plant Protection Research Institute (PPRI) (Morris, 1997) so that comparisons could be drawn between their data and that recorded during this study. In dense *Acacia* stands, a transect was made to estimate the stem density. The transects were two meters wide and contained a minimum of 100 trees. The length of the transects varied with stem density. In the plots with an *Acacia* cover between 25% and 75%, all the trees were measured because the plots often contained less than 100 individuals. After recording in the field, the trees were grouped into size classes to

reflect the population age structure. In comparison, the trees are also pooled according to the number of galls they bear.

6.1.3 Sand Plain Fynbos Communities

In each of the 40 plots, the vegetation was sampled by recording the identity of species and by making an estimate of their respective canopy cover. The plot size (5m x 10m) is entirely adequate for this kind of vegetation except under a limited number of circumstances (very sparse or very homogenous) (Boucher, 1987), which where not encountered during this study. The percentage cover was categorized according the Braun-Blanquet scale. Reference specimen material of the species encountered during the study are stored in a field herbarium located at the University of Stellenbosch, Department of Botany. The vegetation data were used to classify the Sand Plain Fynbos communities in each of the sample plots. The classification was based on the identification key presented by Boucher (1987) and which was refined by Boucher & Shepherd (1988). This classification makes use of differential species to distinguish between plant communities.

6.1.4 Ordination techniques

The CANOCO (Ter Braak & Šmilauer, 1998) software package was used to perform Canonical Correspondance Analysis (CCA), Detrended Correspondence Analysis (DCA) and Principal Component Analysis (PCA) analyses on the data. CCA is defined as a method of direct ordination with the resulting ordination being a product of the variability of the environmental data as well of the variability of the species data (Kent & Coker, 1992). DCA finds axes of variation within the species data only. It mathematically levels out distortion caused during the analysis. PCA, another ordination technique is less suited for floristic analysis but is a very effective method to produce an ordination of plots, based on environmental variables alone (Kent & Coker, 1992). In all the analyses, the default options for the program variables were used. With the PCA, the environmental data was centered and standardized by the program, prior to analysis. In the analysis of the floristic data, the plant species that could not be identified to species level were excluded. Similarly,

Oxalis species were also excluded because they occurred in almost every vegetation plot in similar abundance and this tended to confound the underlying variation between the plots. As for the environmental variables, the choice was made to include only the chemical properties of the soil and the *Acacia* cover. The ordination techniques were used as a tool to find a relationship between quantifiable environmental variables and the variation of the vegetation in the field.

6.2 Results

Species richness in the sample plots was approximately the same for the uninvaded fynbos and for the invaded plots, up to an *Acacia* canopy cover of 75%. A significant reduction in species richness only occurred in the class with the highest *Acacia* cover (> 75%). (Tukey-test, P < 0.05). The uninvaded plots have a higher variance in species richness than the *Acacia* infested plots. The highest number of species was found in plot 20 (uninvaded), with 33 species. The lowest number was found in (the densely invaded) plot 33, with only two identifiable species.

Only two communities were identified using the described identification key: the *Diastella proteoides – Berzelia abrotanoides* Mid-high Open Shrubland and the *Thamnochortus punctatus – Leucospermum parile* Mid-high Open Shrubland. Both communities occur in the area but their boundaries could not be distinguished due to the paucity of data, particularly in the invaded stands.

The results of the different ordination techniques that were applied to the raw data will be presented and discussed in the next paragraph.

6.3 Discussion

The higher variance in species richness in uninvaded plots is due to the high difference in post-fire age of the uninvaded plots. The plots were selected to provide a good cover of the variation in the vegetation through the study area and included mature as well as recently burned areas. The age difference within the other classes of infestation is smaller because plots with a specific *A. saligna* cover are more even-aged. Although the average number of species is only significantly lower for the highest density class, there is a trend for species numbers to decrease with increasing *Acacia* cover (Figure 6.1). The species numbers are underestimated because only species that were identifiable were included in the analysis. Furthermore the sampling took place during early winter, and did not include many geophytes and annuals, which grow and flower (flowers are necessary for identification purposes) at different times of the year.

The reduction in species richness of indigenous plants, as witnessed in this study, is one of the major problems associated with the presence of dense stands of alien trees in the Fynbos Biome (Richardson *et al.*, 1989). Similarly, cover and frequency of indigenous plants decline with each stage of invasion, which was also noted by Holmes & Cowling (1997a). The mean number of species in the uninvaded plots is about twice as high as in the sample plots with more than 75% *A. saligna* cover. This ratio is low in comparison with the ratios of 4:1 and 3:1 recorded in other publications (Richardson & Van Wilgen, 1986; Richardson *et al.*, 1989). But the lack of a standard plot size in previous studies conducted in the Fynbos is responsible for the inability to compare results between studies. The 50 m^2 plots are suited for Sand Plain Fynbos communities under most circumstances (Boucher, 1987) but might be unsuited to correctly represent the abundance of species in densely invaded Fynbos. A larger plot size would probably give a more realistic result under dense *Acacia* stands where there is a low frequency and cover of indigenous plants. Indeed, invasion of Fynbos by alien trees has often caused a significant reduction in species richness on a small scale (Richardson *et al.*, 1989). Indigenous vegetation does not survive in its complete form under *A. saligna*. Observations suggest that this vegetation cannot tolerate the shade from dense stands, that *A. saligna* locally dries out the soil (although this was

contradicted by this study) and that heavy litter fall from the trees affects natural vegetation growth (Boucher & Shepherd, 1988).

It is important to stress that these reductions in species richness, as observed by this study, are only local extinctions. Of all the known extinctions in the Fynbos Biome, none can attributed exclusively to the influence of alien plants (Richardson *et al.*, 1989). These data also do not reflect any species present in the plots in the form of seed. As observed by Homles & Cowling (1997), species disappear more quickly from the vegetation than from the seed bank, in invaded fynbos. So the possibilty remains that even densily invaded sites, can be (partially) restored from the seedbank.
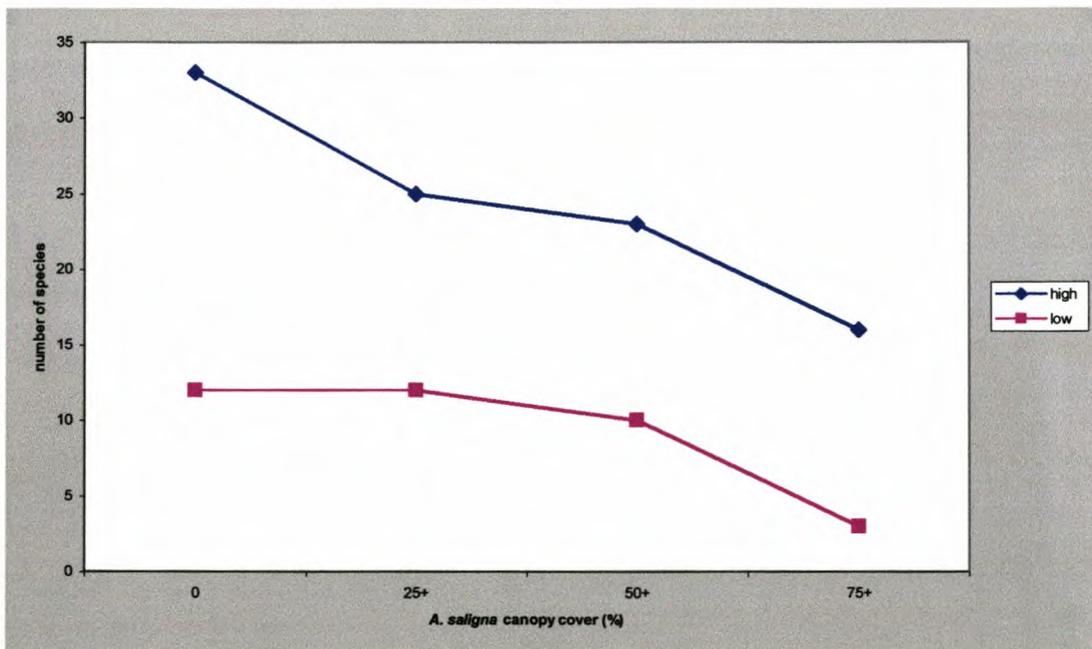
Fig. 6.1: Highest and lowest absolute number of species found per plot within each class of *A. saligna* cover. When looking at these extremes, we can see more clearly the potential impact of *A. saligna* on Sand Plain Fynbos communities under different degrees of infestation. In Fig. 6.2, this trend is less clear due to the variation (inherent to Fynbos) within plots of the same infestation class.
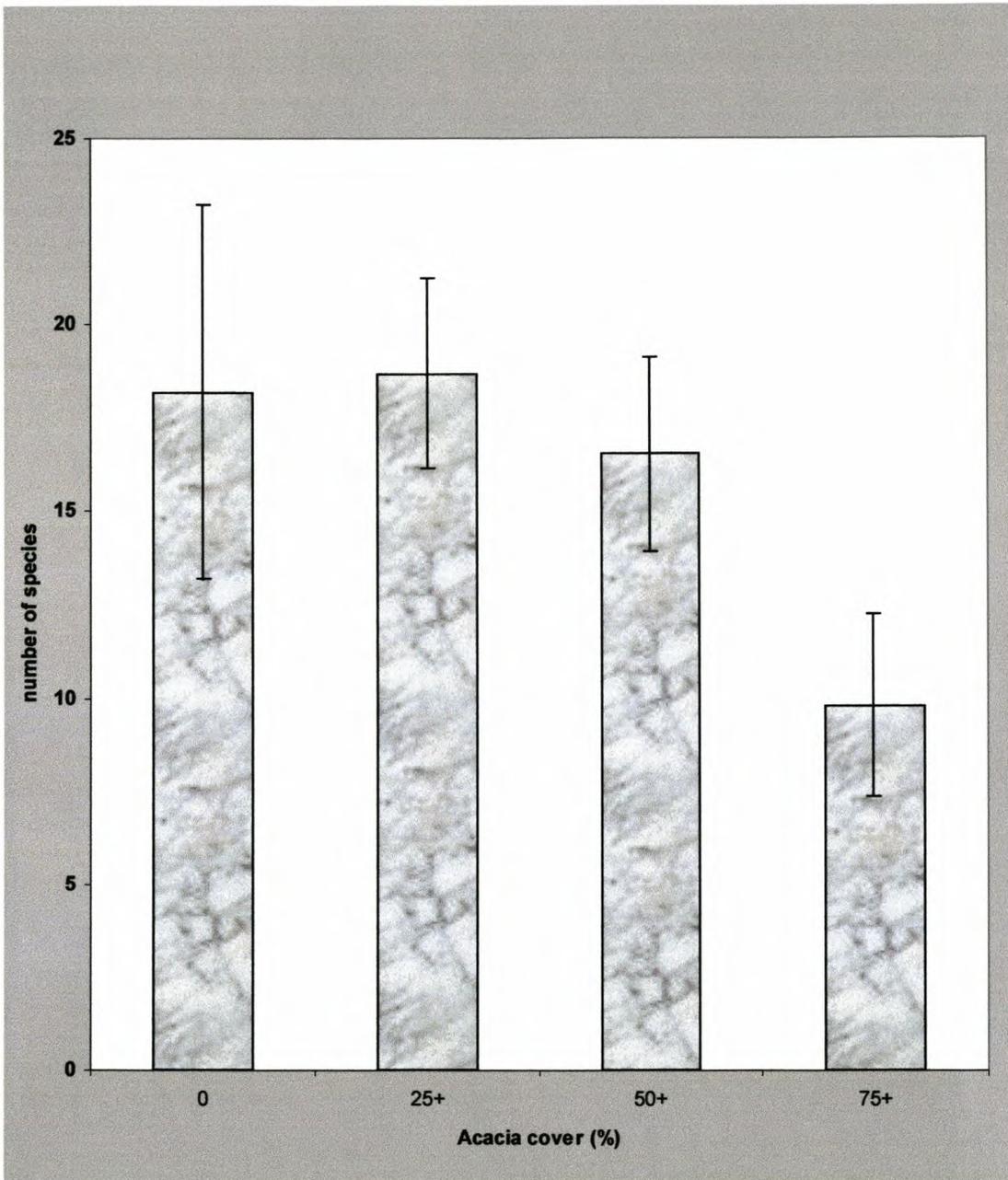
Fig 6.2: Average species richness in Sand Plain Fynbos vegetation under different degrees of *Acacia saligna* cover. Error bars indicate 95% confidence intervals.

6.3.1 Ordination

The PCA performed on the environmental data set confirms the results that are presented in Chapter 3. As shown in Figure 6.3, the distinction between the sampling plots, based on the environmental data is greatest between the uninvaded plots and the plots with a high percentage of *Acacia* cover (> 75%), although there are some outliers. These outliers could be both the result of minor historical or environmental differences between the plots that have a prominent effect on the resulting vegetation, but no direct cause for these outliers could be identified.

It must be noted that this ordination does not demarcate any vegetation communities, as no floristic data was used in the analysis.

The eigenvalues are values that represent the relative contribution of each axis to the explanation of the variation in the data set (Kent & Coker, 1992). In Figure 6.3 the eigenvalues for the X-axis is 0.441, for the Y-axis 0.160. In Figure 6.4, a bi-plot is presented, showing the eigenvector values for the properties that make up the environmental data. The direction of the arrow indicates the direction in which the value of the variable increases most rapidly, the length of the arrow represents the rate of change. The scale of the arrows is different from the scale of the axes. PCA results of this kind are extremely valuable when they are interpreted alongside a floristic ordination of the same plots but carried out with a different ordination technique (Kent & Coker, 1992). In our case, the PCA results were compared with those obtained from the DCA technique, discussed later in this chapter. From the comparison it emerges that the vegetation does not exactly reflect the gradients in environmental variables (soil nutrients and *Acacia* cover). However, the vegetation structure (on which the DCA is based) of the uninvaded plots is again set apart from the invaded plots in the DCA (Figure 6.6). In all the plotted diagrams, the primary and secondary axis explained most of the variation. When other combinations of axes where plotted against each other, the two-dimensional plot showed less distinctive patterns.
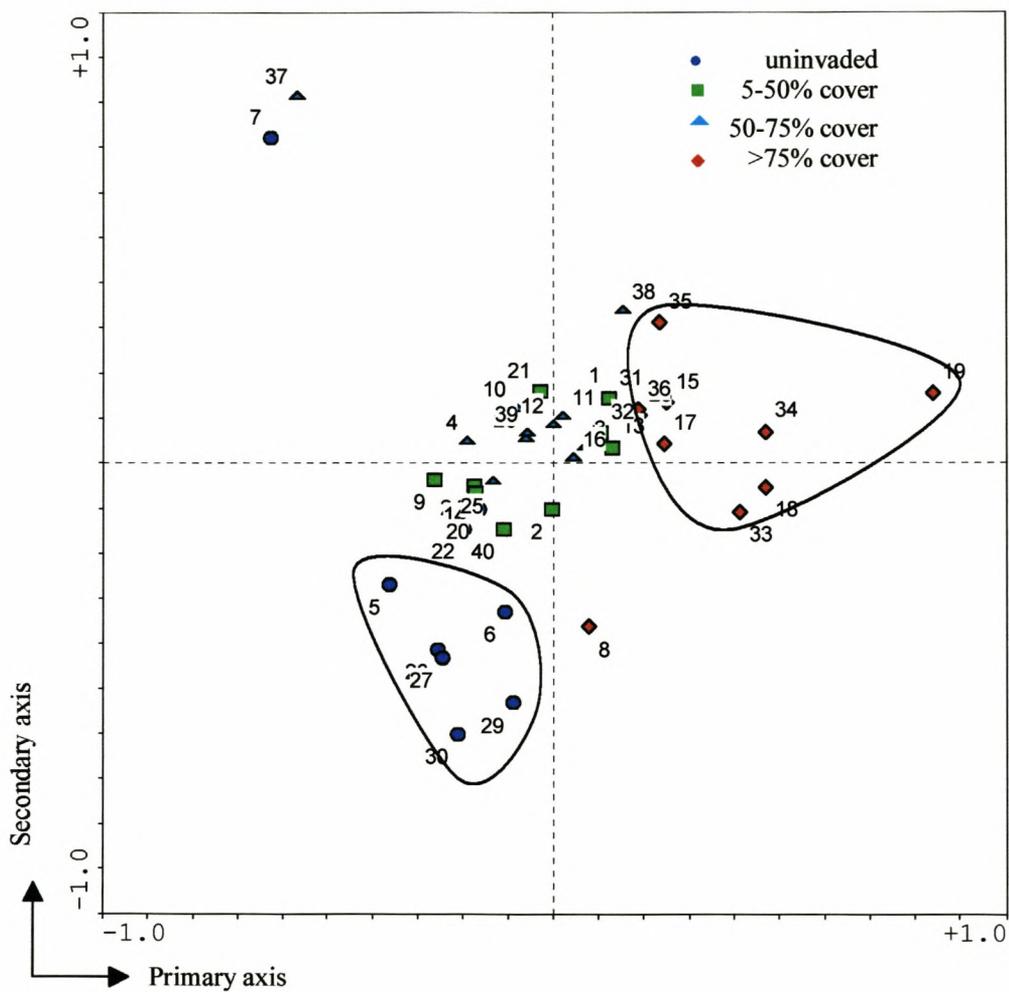
Fig. 6.3: Ordination of the plots (PCA), based on the available environmental data. The parameters used are displayed in Fig. 6.4. the pattern of invaded and uninvaed plots is circled.
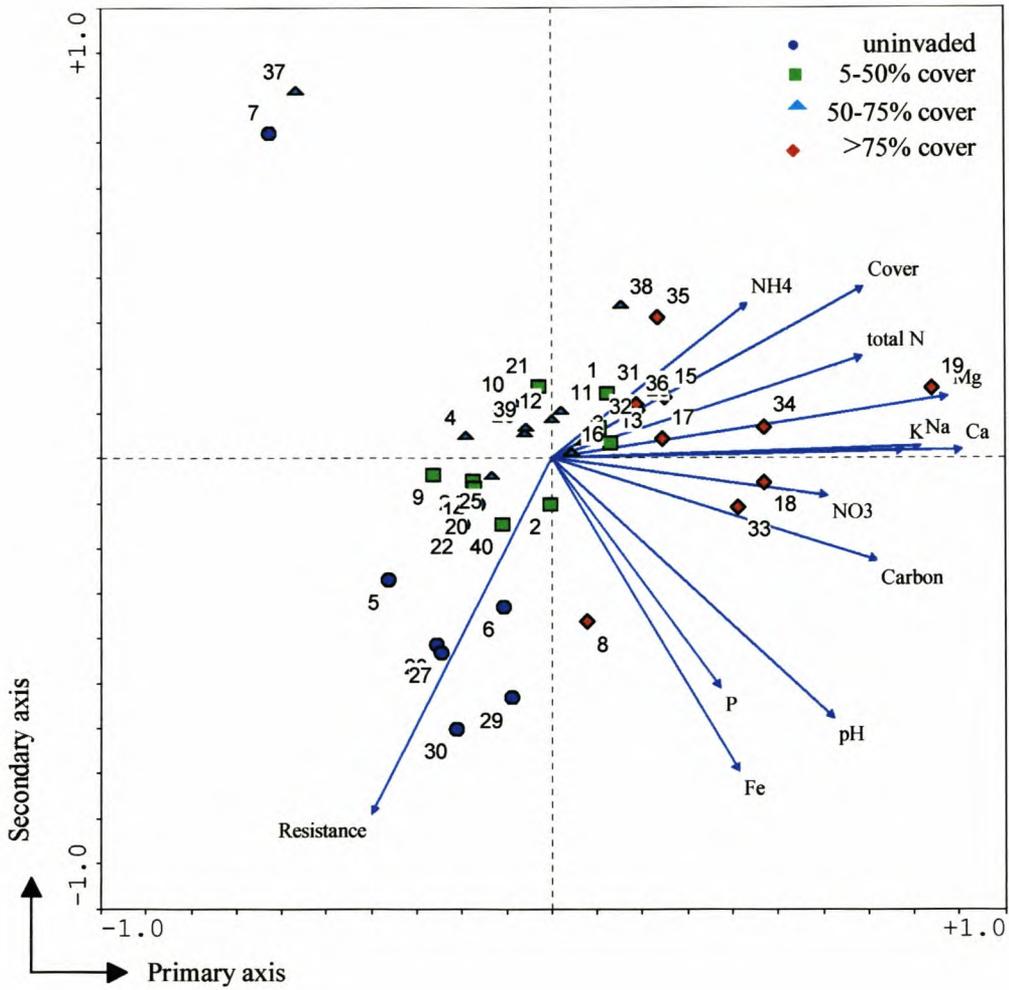
Fig. 6.4: Ordination of the plots (PCA), based on the available environmental data. The variables that make up this data are superimposed to visualize their contribution to the explanation of the variance between the plots.

In the study area, two different types of communities were identified using the identification key presented by Boucher (1987). This hierarchical key makes use of differential species to distinguish between plant communities. For further reference however, the terminology used by Boucher & Shepherd (1988) will be used to distinguish between the two identified communities because the latter study was at a more detailed scale than the reconnaissance survey of Boucher (1987) and therefore

closely resembled the present study. The altered composition of the indigenous vegetation under *A. saligna* prevents accurate identification, especially because invasion is sometimes correlated with previous disturbances (Boucher & Shepherd, 1988).

Although only two communities were identified, the differences between plots in terms of species presence and abundance are apparent both in the field and in the data. As suggested by Deall & Theron (1990), ordination by DCA was superimposed *a posteriori* on the species data as a control on whether the classification was confirmed by a mathematical and objective ordination technique.

As shown in Figure 6.5, The *Diastella proteoides – Berzelia abrotanoides* Mid-high Open Shrubland is not distinguished from the *Thamnochortus punctatus – Leucospermum parile* Mid-high Open Shrubland by DCA. Both communities occur in the area but their boundaries could not be distinguished due to the paucity of data, particularly in the invaded stands. This failure to discriminate between these communities is to be expected considering that the samples under dense *A. saligna* stands were often relatively poor in species richness and because of intrinsic qualities of DCA (see explanation below). First of all, Fynbos vegetation is continuous (McDonald, 1987) which makes it intrinsically difficult to draw community boundaries, and the communities in the research area are quite similar. Furthermore, the effect of the invasion by *A. saligna* could also confound the data and hence the classification of the communities as shown in Figure 6.5. The *Thamnochortus punctatus – Leucospermum parile* Shrubland is described by Boucher & Shepherd (1988) as being a typical community representing Sand Plain Fynbos. It is the general widespread background community in the area and is not one indicative of specialized variations. It occurs on uniform, flat sandy soils that offer little opportunities for specialization. The *Diastella proteoides–Berzelia abrotanoides* Shrubland is confined to inconspicuous seasonal drainage lines (Boucher, 1987; Boucher & Shepherd, 1988). The Sand Plain Fynbos communities were classified by Boucher (1987) using differential species, whereas the nature of DCA is to group plant communities according to their similarities (Hill, 1996). This difference in approach and the overlap between the *D. proteoides–B. abrotanoides* and *T. punctatus–L. parile* Shrublands causes them to be grouped together. Another important feature of DCA is

that the axes are scaled in terms of average standard deviation of species turnover (SD) (Kent & Coker, 1992). Along a gradient, a species appears and disappears over a distance of about 4SD. This means that a complete species turnover occurs in about 4SD, while a 50% change in composition occurs in 1 SD or slightly more. In Figures 6.5 and 6.6, all the plots are situated within 4SD of each other, suggesting a high species overlap between plots. Boucher (1987) mentions the failure of DECORANA, a software package similar to CANOCO, to reveal any meaningful ecological coincidences, probably because differences in ages in the vegetation masked the obvious patterns.
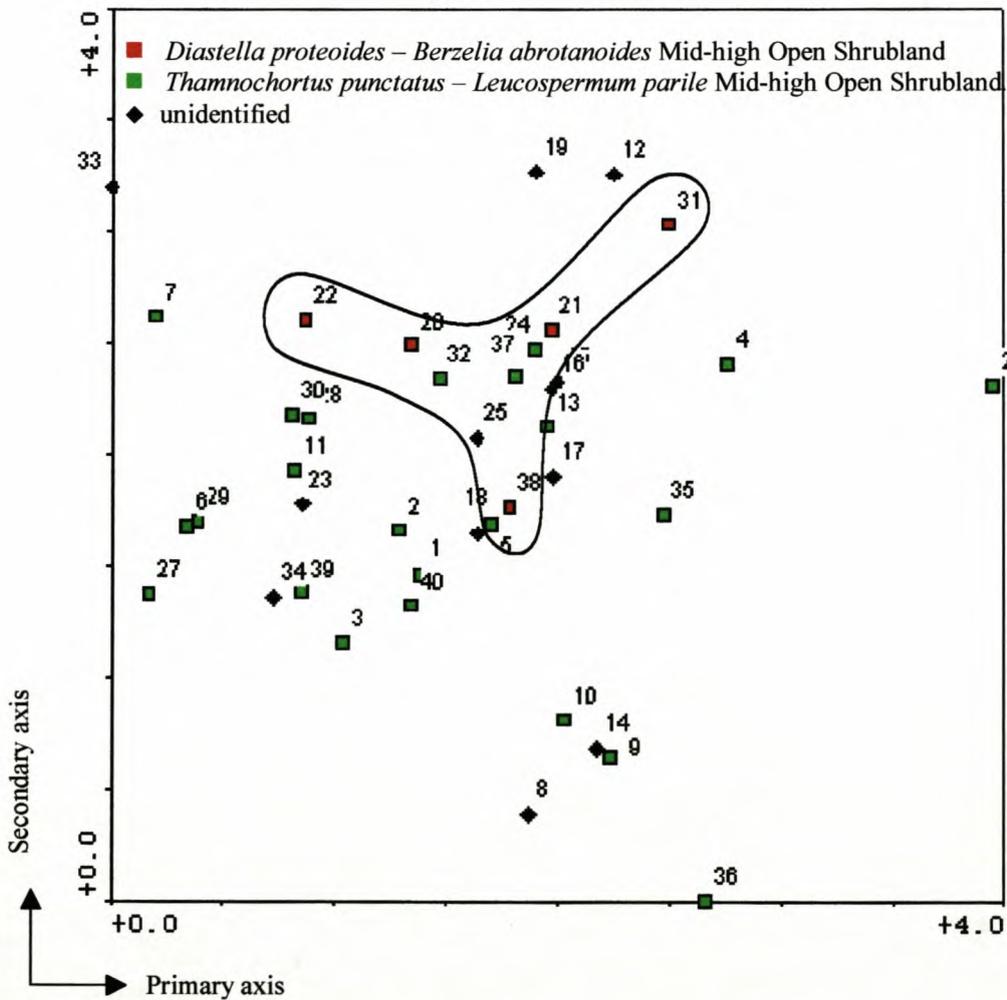
Fig. 6.5: DCA ordination of the floristic data, indicating the two different communities present in the research area. The five *D. proteoides–B. abrotanoides* communities are encircled.
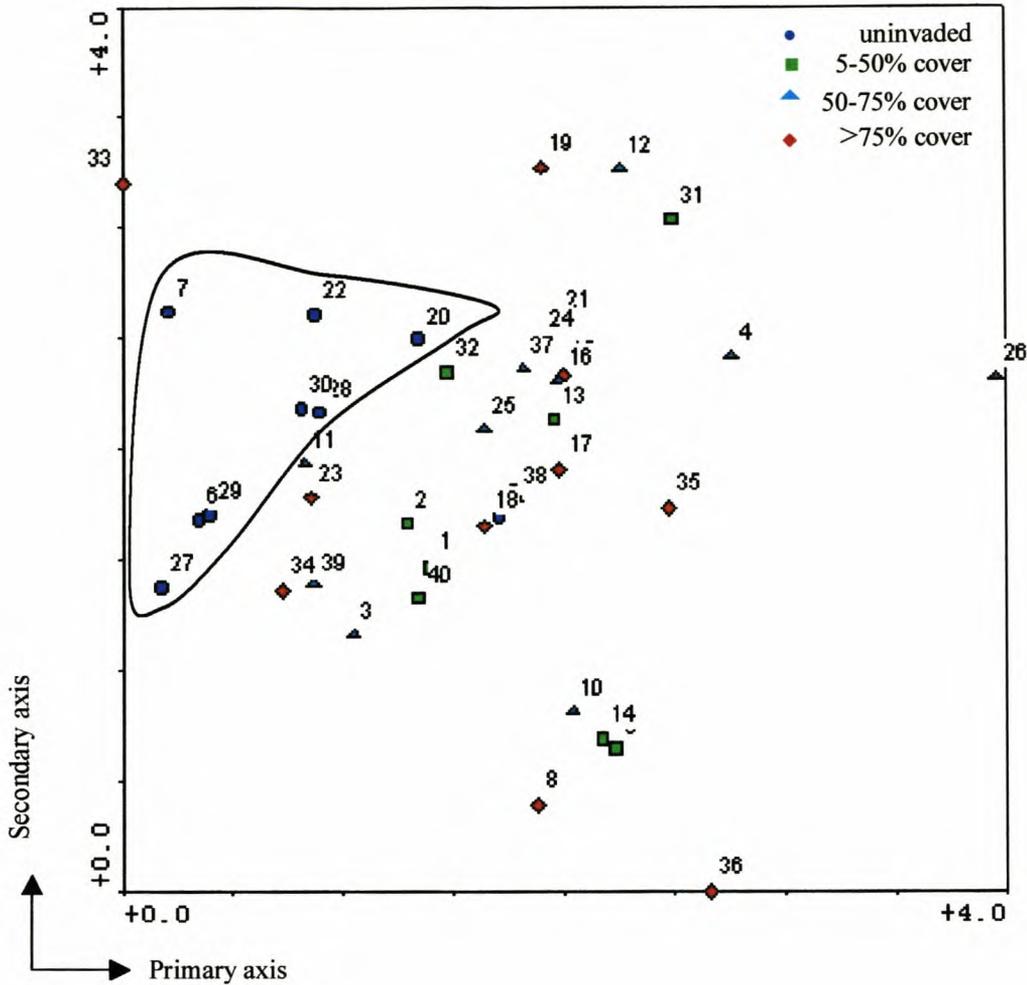
Figure 6.6: DCA ordination of the floristic data, indicating the influence of the *Acacia* cover on the variation in the data. The uninvaded plots are encircled.

If we classify the same ordination of plots according to the degree of *A. saligna* cover we can find that there is a tendency for the uninvaded plots to be distinguished from the rest except for one plot (No. 5, see Fig. 6.6). This signifies the large impact invasion of *A. saligna* has on the plant communities in the research area. *A. saligna* invasion does not as such cause a shift in the type of community but rather a structural change within a community that can be picked up with ordination techniques. For instance the total percentage cover of indigenous species in densely invaded stands was negligible in most plots.

From the floristic data we can deduce that fires have been frequent in this area. Very short fire intervals (3–4 years) benefit sprouting shrubs and most perennial

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hemicryptophytes to the detriment of the slow maturing obligatory reseeders. Restionaceae are overwhelmingly present in this kind of vegetation. The only widespread Ericaceae in this vegetation are also coppicing species (e.g. *E. mammosa*). The obligatory reseeding Proteaceae, *Leucospermum parile* is well adapted to this disturbance regime and can become abundant (Boucher 1987). Although the uninvaded plots are more or less grouped together, the ordination technique does not seem to distinguish between the different degrees of *Acacia* invasion. This means that there is a large degree of variation in the data that is not readily explained by the degree of *A. saligna* crown cover. One major aspect of invasion that was not measured during this research was the light penetration through the vegetation canopy. Results by Holmes & Cowling (1997a) show that *Acacia* canopies in long invaded stands intercept more light than in recently invaded stands even when both stands have a similar canopy cover. This is because long invaded stands had denser canopies. In all cases and at all heights, the acacia's intercept more light than fynbos species. Holmes & Cowling (1997a) further note a relationship between community guild structure and age of invasion. The distribution of species among growth forms is similar between uninvaded and recently invaded plots, but changed in the long invaded stands. The most significant change noted by Holmes & Cowling (1997a) was the presence of proportionally more vertebrate dispersed species in long invaded stands. In this study, the bird dispersed *Rhus* species, was also found more likely to occur in invaded fynbos but increased likelyhood was not statistically different (t-test, p = 0.24).

In a way the age of invasion and the *Acacia* canopy cover are related. In a fire-prone environment, such as the research area, the abundance of a fire-adapted species such as *A. saligna* will increase with every fire. The decision to classify the research plots according to *Acacia* canopy cover and not on age of invasion was based on the assumption that fires in this region are so frequent that individual *A. saligna* trees do not have the time to develop large canopies. A high canopy cover would thus be the result of a high abundance of trees, which would be the result of a population built up over a few fire-cycles.

By imposing environmental variables upon the axes of ordination, the ecological interpretability of vegetation data can be enhanced (Deal & Theron, 1990). This is

applicable in indirect gradient analysis where environmental data is superimposed *a posteriori* on the ordination, but is more valuable in direct gradient analysis (Kent & Coker, 1992). In CCA, the environmental data is used to explain the variation in the data. Figure 6.7 displays the ordination results when this ordination technique is applied to the field data of this study. The first two axes that explain most of the variation have eigen values of respectively 0.311 and 0.276. These axes are picked by CANOCO and have no intrinsic value but after closer examination they turn out to be highly correlated to the main environmental variables ($R^2 > 0.9$). Together, these first two axes explain 27.7 % of the variation within the data, which indicates that the species-environment is more complicated than that shown here and cannot be attributed to just the few variables used in this analysis. To explain the complexity of a fynbos community, a multi-dimensional model is required. In this case, a four-dimensional ordination manages to explain 49% of the variation.

The distribution of Fynbos communities is strongly correlated to soil geology and to a lesser extent, with soil moisture status (McDonald, 1987; Richards *et al.*, 1995). Most of the environmental variables under investigation here are considered to be influenced by *A. saligna* invasions and vary greatly during the year (Musil & Midgley, 1990). Furthermore, fires also influence the nutrient status of the soil during the period when recruitment takes place. Further research should focus on whether and how nutrient enrichment in Sand Plain Fynbos communities influences the floristic composition and structure of these vegetation types. Experiments by Witkowski (1989a & b) have indicated possible effects but were rather too short-term to detect fundamental changes.
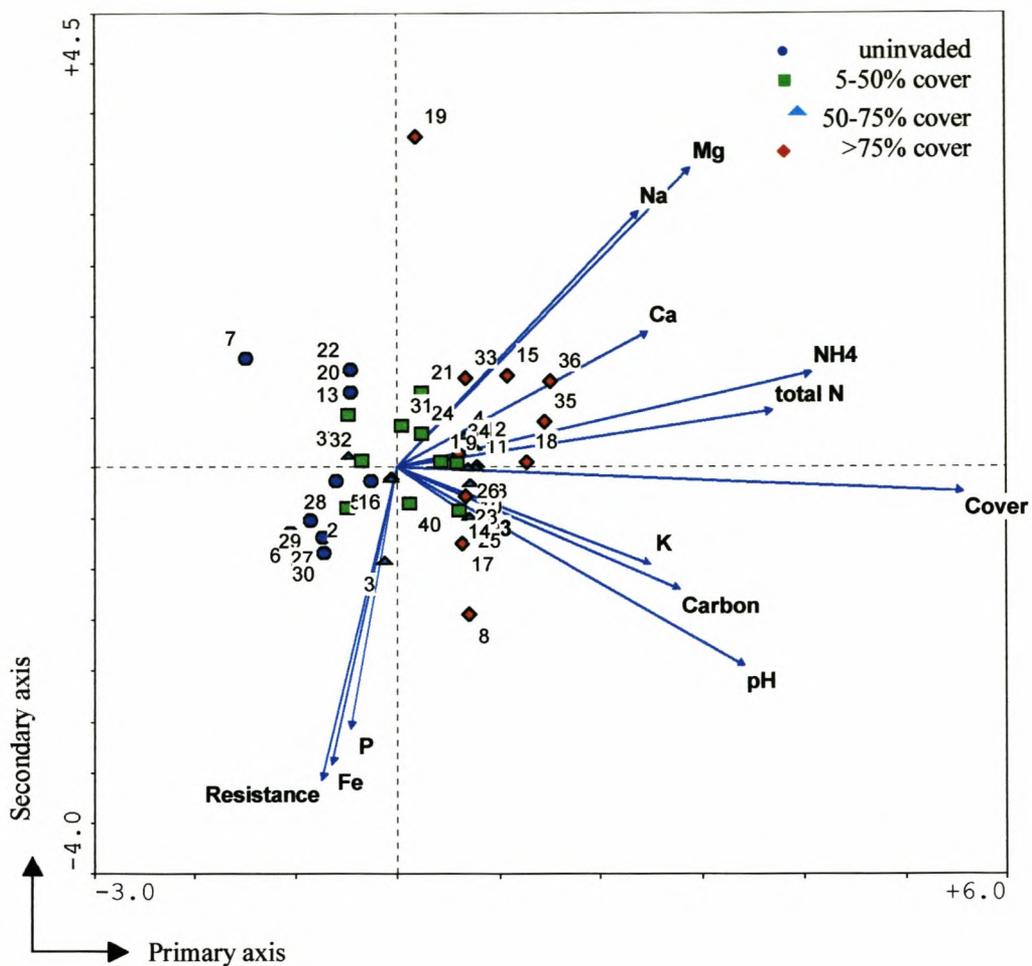
Fig. 6.7: Bi-plot of the Canonical ordination of the floristic and environmental data. The direction and length of the arrows indicate the contribution of the environmental variables in the variation of the floristic data.

Fig. 6.8: A typical view of the research area. The foreground is dominated by restioids, the clumps in the centre are *Phylica cephalantha* shrubs while *A. saligna* is visible in the background.

Much of the variation in the ordination is explained by variables that are in one way or another related to the *Acacia* canopy cover. But it could be that the true causes of the variation are other factors that are also associated with *A. saligna* but that are not included in the analysis. Soil moisture status, shade and protection from winds are some of them. In this matter CCA is a tool that creates questions as well as provides answers.

Alien invasion invariably results in a loss of indigenous species with increasing alien canopy cover (Richardson & Van Wilgen, 1986; Richardson *et al.*, 1989; Holmes & Cowling, 1997a). It appears that the process of degradation can be reversed by removal of the alien vegetation, especially when alien canopy closure has not yet been attained (Richardson *et al.*, 1989, Holmes & Cowling, 1997a). Even in *Acacia* thickets a few fire cycles old, representatives of all major Fynbos growth forms persist as soil stored propagules (Holmes & Cowling, 1997b).

The big issue, however, is which clearing method to use? The common technique of burning the vegetation might result in sterilization of the soil of both exotic and indigenous species, as observed by Macdonald *et al.* (1989). The solution suggested by the Plant Protection Research Institute (Anonymous, 1987), *i.e.* to wait for a natural recovery of the indigenous vegetation in between the dying acacia's has not been backed up by research. Morris (1997) recorded an 80% reduction in *A. saligna* stem density after eight years of infection with *Uromycladium tepperianum*. However he makes no mention of recovering Fynbos vegetation at these sites.

Although recovery is said to be possible, the mechanisms are not yet completely clear. At this moment it is not known how long soil-stored propagules of different Fynbos species persist in the soil, nor the role that dispersal plays in the recovery process. Especially in long-invaded stands, active restoration is likely to be necessary to speed up the recovery process. Restoration techniques could include reseeding (Holmes & Cowling, 1997b) as well as smoke-promoted germination of Fynbos seeds (De Lange & Boucher 1990; Brown, 1993).

6.3.2 Acacia saligna *population status*

The *A. saligna* thickets, although homogenous at first sight, display a large variation in composition when they are classified according to diameter classes. Some plots have many emerging seedlings, which make up to 50% of the population. Especially in the densest thickets regeneration is high. The low light penetration does not inhibit germination in *A. saligna* (Milton, 1980) and under mature thickets the seed input is high ensuring massive germination, even without the stimulating effect of a fire. Nevertheless survival of the seedlings is low as shown by the number of dead trees in these plots. Intraspecific competition, a phenomenon also observed by Witkowski (1994) in a controlled environment, is likely to be an important factor in the early life stages of *A. saligna*. It could even be more important than infection by *U. tepperianum*. Morris (1997) found that young seedlings are prone to infection and that trees in small size classes generally die off at a higher rate than the larger trees. He attributed this to rapid infection after germination. In the present study, few of the dead seedlings found in the plots bore galls. It could be that they were nonetheless

infected as galls generally only appear after a few months. Considering the available information, the combined effect of a high intraspecific competition under a dense canopy and the possible stress of infection are believed to be the cause of the low survival rate of the seedlings.

The differences in *Acacia* community composition become even more apparent in the 25–50% and the 50–75% canopy cover classes. Some plots have up to five times more trees than other plots, but are nevertheless categorized as having the same *Acacia* canopy cover. However, in general the tree density increases with increasing crown cover. Canopy cover was chosen over stem density as a method of classification because it is quicker to estimate in the field and because the projected canopy of an *A. saligna* directly demarcates its area of influence. Shading, litter production and seed fall are highest directly under the tree.

Few trees in the study exceed a diameter of 50 mm (at 10 cm above soil level) and even less have grown larger than 100 mm. Old trees often bear hundreds of galls (Morris, 1997) and it is likely that trees die before their time from the ever increasing amount of stress inflicted by the fungus as the trees grow older. In the study area the *A. saligna* infestation consists of fairly young, even-aged, thickets of varying density. Whether this is caused by the fungus, short fire cycles or systematic cutting of larger trees is unclear. But it can hardly be denied that this situation diminishes the economic value of *A. saligna*. The size of the wood makes it unsuitable for timber and the accessibility of the thickets is very low.

6.3.3 Health status of A. saligna *thickets*

The fungus *U. tepperianum* was introduced into the vicinity of the research area in 1987 (Morris, 1997). It is safe to say that the "disease" has been established here for at least ten years. This results in a high degree of infection throughout the *A. saligna* population. The number of galls on a tree tend to be correlated with the size of the tree, expressed in stem diameter, which becomes clear from Figures 6.10–6.12. The largest trees have up to 200 galls but the majority of the trees contain between one and ten galls. The group of uninfected trees consisted mainly of seedlings and

young trees up to 10 mm in diameter. Living, uninfected seedlings are rare in the plots with more than 75% canopy cover. In the more open *Acacia* thickets, most of the seedlings are uninfected. This discrepancy can be explained by the microenvironment that exists within the dense thickets. First of all there is a high input of fungal spores from the surrounding trees. Secondly, the humidity within the dense vegetation is higher than in the open air, which creates a more suitable environment for infection. When the canopy cover is less than 75%, the number of uninfected trees largely coincides with the number of trees in the size class up to 10 mm diameter. Morris (1997) points out that although infection of young trees can be rapid after a fire, it is restricted by the low incidence of possible infection sites. As soon as the tree reaches sexual maturity, gall numbers increase due to the infection of inflorescences.

The estimate of the number of galls on each tree in this study is conservative. Burges (1934) claims that gall formation by *U. tepperianum* on *A. saligna* is confined to the immediate area of infection. However, in this study it was often difficult to make a distinction between individual galls as a number often appeared to have united to form one long gall. They were considered to be a single gall whenever there was doubt about the exact number forming the combined infection.

An attempt was made to link the number of galls to the apparent health status of the tree but in practice it turned out to be impossible to find any easy measurable parameters (*i.e.* degree of defoliation) that gave an indication of the health of a tree while at the same time corresponding to the number of galls. There was an enormous individual variation between trees. This is illustrated in Figure 6.9, where two similar trees with approximately the same amount of gall formation are shown next to each other. One tree suffers from a high degree of defoliation while the other one still has a full, healthy crown. The reason for this difference is unclear. It is possible that genetic variability of the acacia's could result in an improved resistance of some individuals, or some trees might have slightly deeper roots giving access to more groundwater than its neighbour. In any case this is an observation which deserves further investigation.

Fig. 6.9: Two similar *Acacia saligna* trees, bearing approximately the same number of galls. The tree on the left suffers severe defoliation while the tree on the right appears healthier.
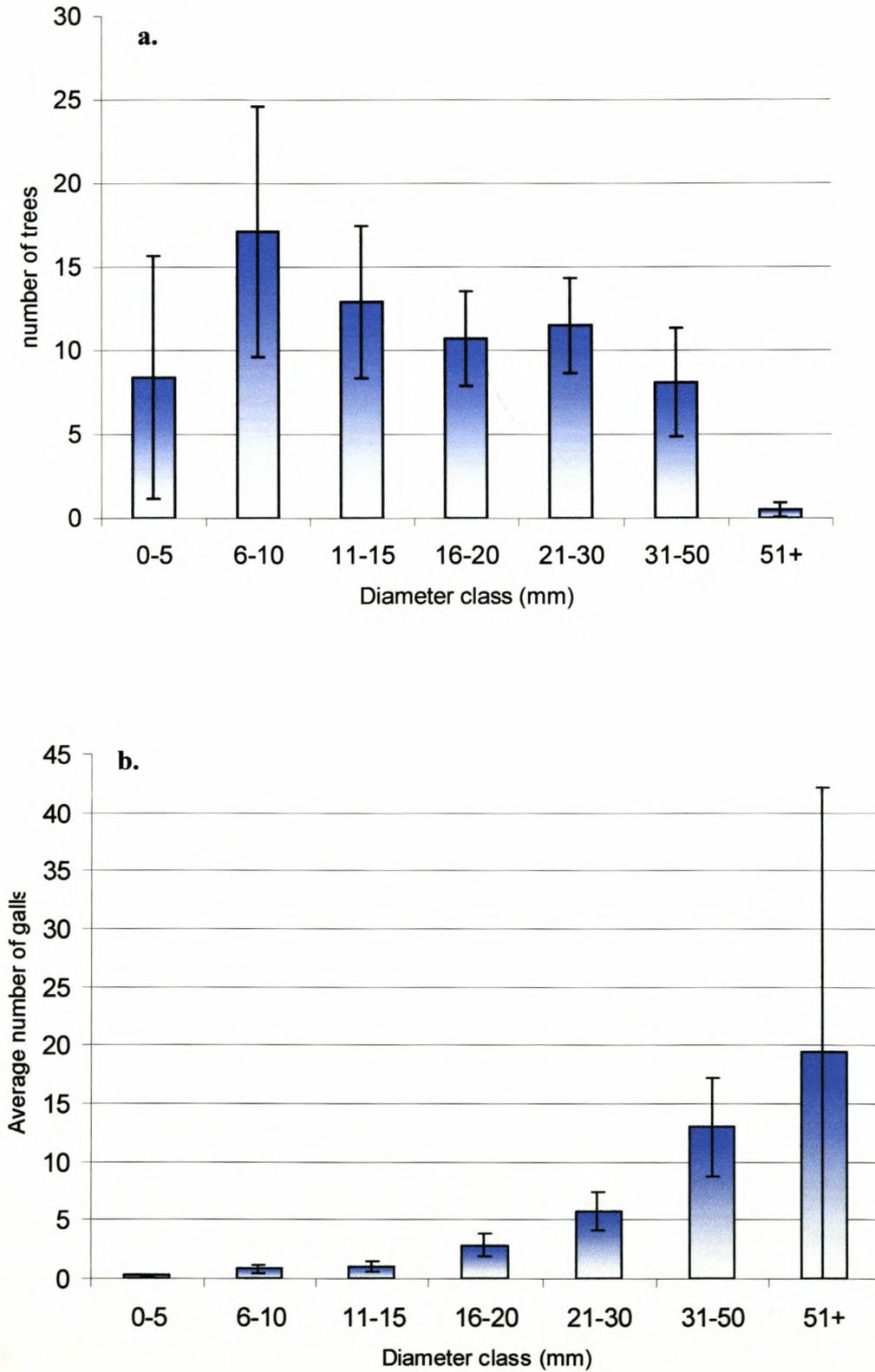
Fig. 6.10: (a) *Acacia saligna* population structure according to stem diameter and (b) average number of galls in each diameter class. *Acacia* canopy cover in these plots is between 25% and 50%. Error bars indicate 95% confidence intervals.
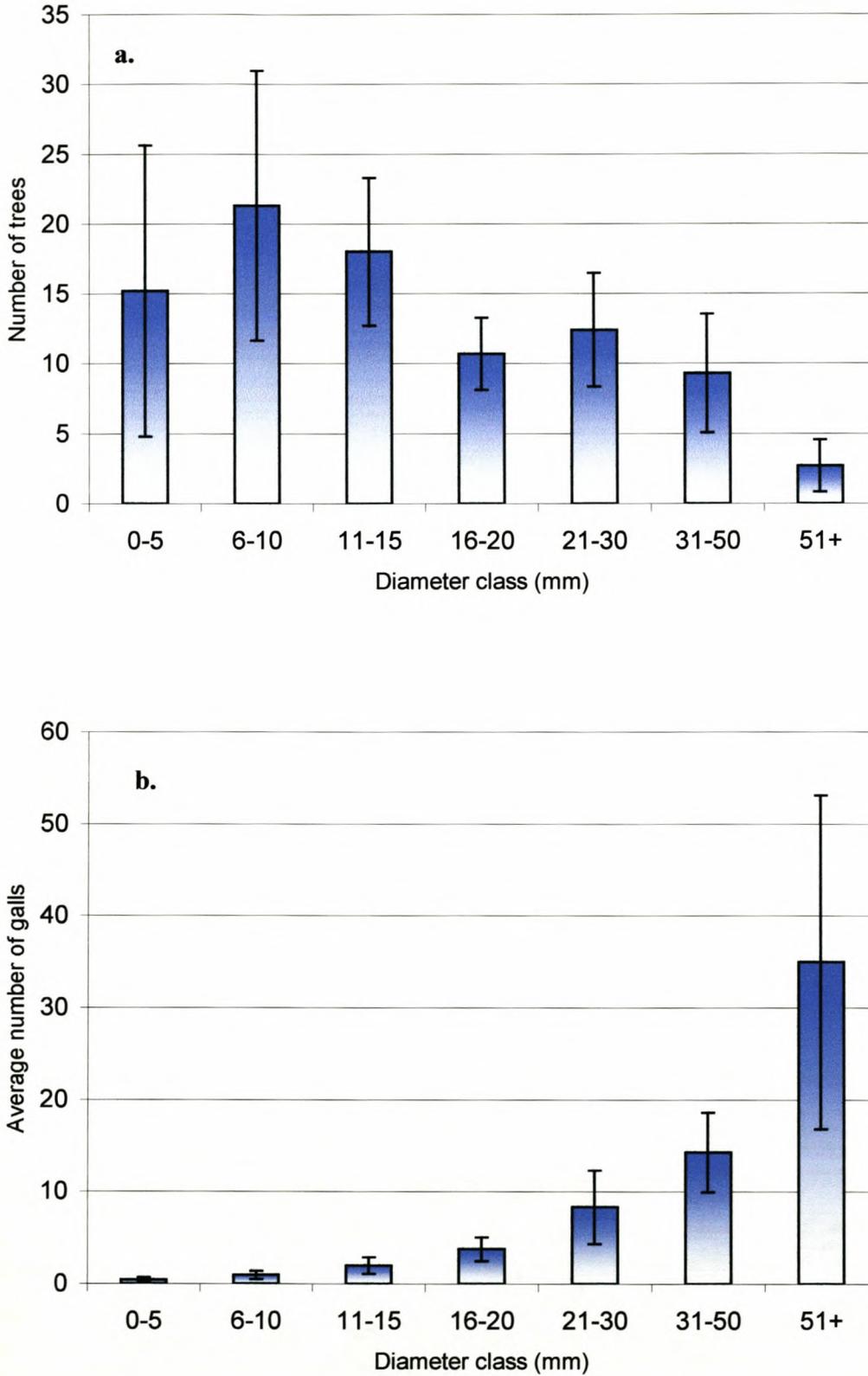
Fig. 6.11: (a) *Acacia saligna* population structure according to stem diameter and (b) average number of galls in each diameter class. *Acacia* canopy cover in these plots is between 50% and 75 %. Error bars indicate 95% confidence intervals.
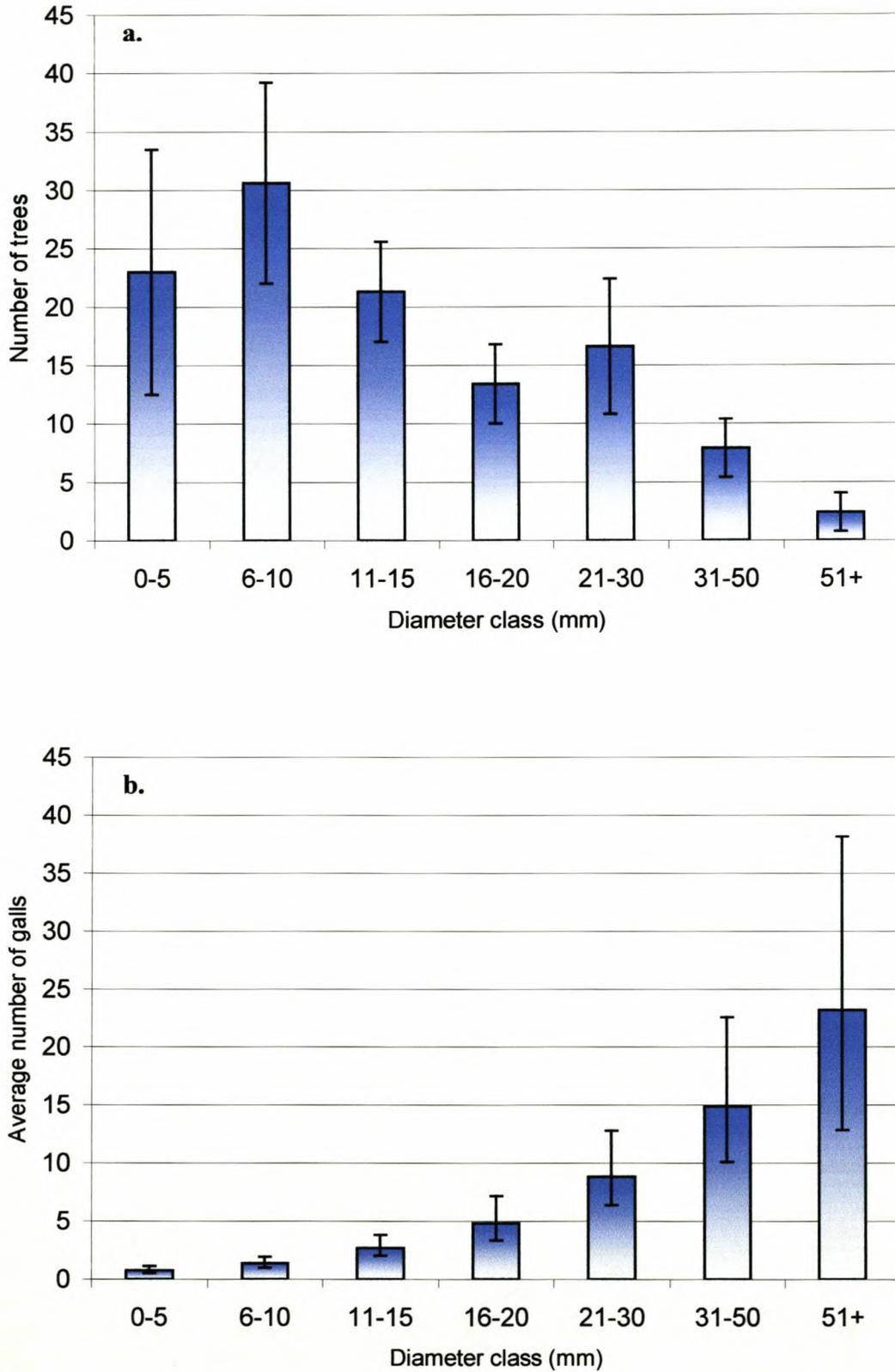
Fig. 6.12: (a) *Acacia saligna* population structure according to stem diameter and (b) average number of galls in each diameter class. *Acacia* canopy cover in these plots is between > 75 %. Error bars indicate 95% confidence intervals.

Chapter 7

Epigaeic invertebrates associated with *Acacia saligna* invasion

Invertebrates, by virtue of their small size, are able to exploit very small and specific features within the environment. These features are known as microhabitats (Ausden, 1996). Furthermore, soil and litter invertebrates are a large and crucial component in the functioning of ecosystems (Majer & Greenslade, 1988). A study aimed at assessing the environmental impact of *Acacia saligna* on the invertebrate community could provide insights that might otherwise be overlooked.

7.1 Methods

During September 1999, epigaeic invertebrates were sampled in the vegetation plots using pitfall traps. Pitfall traps can be used to sample any species that is sufficiently mobile to enter the trap, but specifically for active, surface-living invertebrates in low vegetation (Ausden, 1996). This method is less suited for sampling the *Acacia* invaded Fynbos. But since intercomparison of different sampling techniques is not possible due to method-specific biases (Ausden, 1996), one general sample method had to be used. Pitfalls are a cheap and easy method for catching large numbers of invertebrates with a minimum of effort. Biases are

towards abundant and active species and are also influenced by the nature of the ground cover (Majer & Greenslade, 1988; Ausden, 1996). The trapping results may not reflect the true density of a species (Majer & Greenslade, 1988) and are therefore not used as such in this study.

Five traps were placed in each vegetation plot during the month of September. They consisted of plastic cups (Ø six cm, height nine cm), placed in the ground at two-meter intervals and partially filled with a preservant (ethelene glycol) to prevent decay or predation of the captured specimens (Majer & Greenslade, 1988). The cups were emptied after seven days and the arthropods present were sorted and identified by the University of Stellenbosch, Department of Entomology, under supervision of Dr H. Geertsema.

The results were analysed using the CANOCO software package (Ter Braak, 1998). Detrended correspondences analysis (DCA) was applied to Arachnida and the other arthropod taxa, as well as to the combined data. Because of the biases of the trapping technique towards certain species, the analysis was made not only on the abundance data, but on presence/absence data as well, in order to eliminate the weight of abundant species on the analysis. The standard options of the CANOCO program were used, and no species or samples were excluded from the analysis.

7.2 Results

The presence of *A. saligna* does not cause a significant reduction in the number of arthropod species captured, nor in the number of individuals present in the traps (P>0.05). The average number of invertebrate species captured in the uninvaded Fynbos plots is 8.375 (SD 3.04). The number of individuals trapped averages 67 (SD 34.16). In the plots with the highest density of *Acacia* cover, the number of species and individuals averages respectively 5.8 (SD 1.75) and 30.5 (SD 28.2). Due to the large variation within *Acacia* cover classes, these numbers are not significantly different (t-test, P > 0.05). There is however a tendency for the maximum and minimum number of specimens to drop with increasing *Acacia* cover (Fig. 7.1). If a distinction is made between the Arachnida and the other arthropoda, the data

portraits a slightly different situation. For the Arachnida, there is no significance difference in the number of species trapped in the different *Acacia* density classes but there is a significantly higher (t-test, $P < 0.05$) number of individuals in the uninvaded Fynbos than in the most dense (> 75% cover) *Acacia* invaded plots. (10.875, *SD* 4.1 *vs.* 3.7 *SD* 2.94). Again these numbers should be interpreted with caution as the high standard deviation indicates sub-optimal sampling.   When we compare the number of Arachnida in uninvaded plots to the invaded plots (all invasion stages combined), the difference is again significant (10.875 *vs* 5.51, t-test, $P < 0.05$).The data for the insects do not indicate a change in the number of species or number of individuals trapped.

In total 1 766 individuals were captured, of which 1 530 belonged to the other arthropoda and 236 to the Arachnida. Of the other arthropoda the *Scarabaeidae* were most numerous with two species and 1 139 individuals. The *Carabidae* was the second most common family represented by four species and 174 individuals. The other arthropoda were not identified to species level. In the Arachnidae group, the two most common species were *Caponia capensis* (74 individuals) and an unidentified *Cydrela* species (78 individuals). Another common species was *Hirriusa bidentatus* (28 individuals).
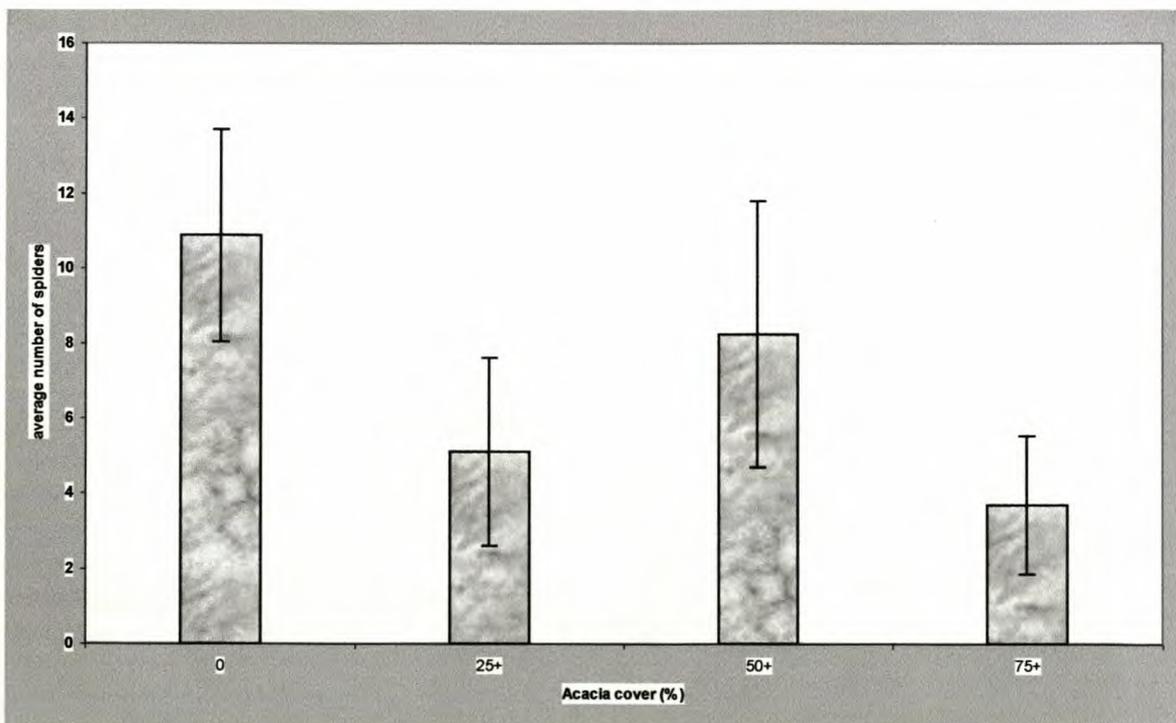
Fig 7.1: The average number of spiders trapped in relation to the increasing *Acacia saligna* cover. Error bars indicate 95% confidence intervals.

The spatial ordination of the sampling plots extracted more qualitative information from the raw data. It did not prove to be fruitful to enter all the data for the analysis. The numerical dominance of a handful of species blurred out any possible distinction between the plots. When all species were given equal weight, by turning the raw data into presence/absence data, a grouping of the uninvaded plots, distinctive from the invaded plots, appears (Fig. 7.2).

If the data for the group of the Arachnida and other arthropoda are analysed separately, we see that only the spider group is sensitive to *A. saligna* invasion. The spider species trapped in the uninvaded Fynbos are to a large extent different from those trapped in *Acacia* invaded plots. In a spatial ordination this results in the grouping of the uninvaded plot (Fig. 7.4). The insect group is much less sensitive to the presence of *Acacia* trees and the DCA is not able to distinguish the different degrees of infestation by means of the presence/absence of the trapped insects (Fig 7.3).
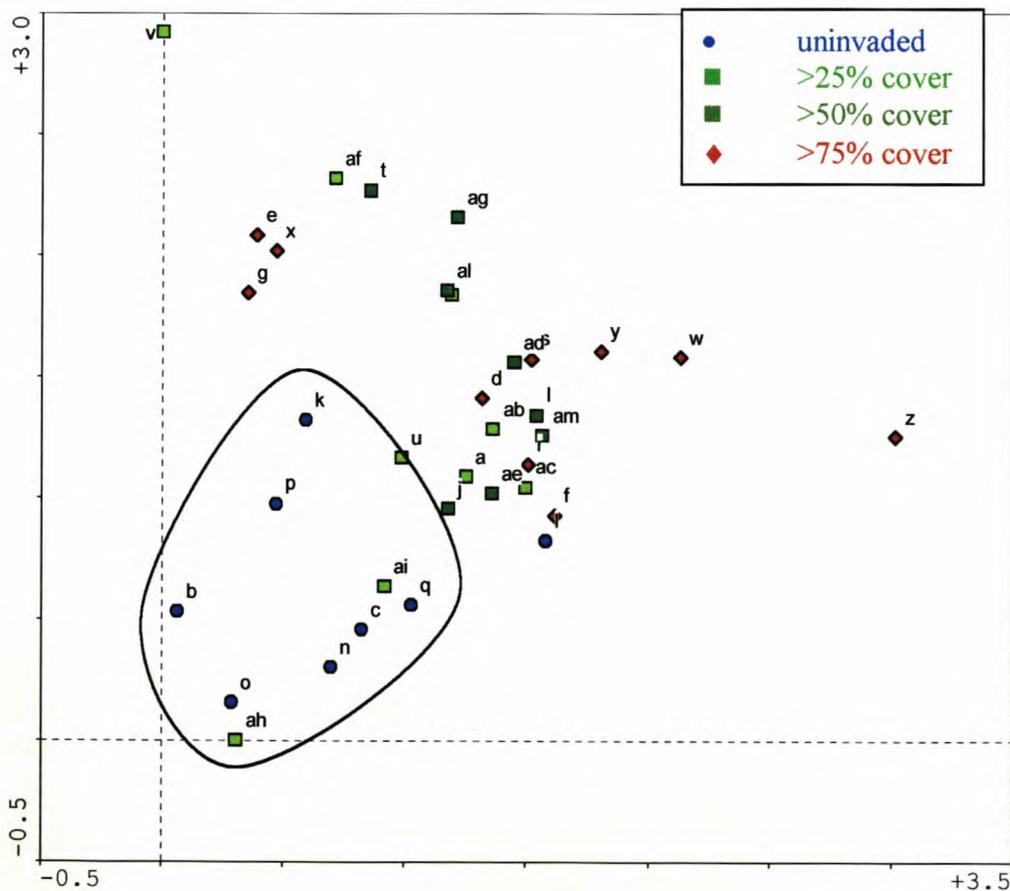
Fig 7.2: Spatial representation of the DCA on the presence/absence data for all the trapped invertebrates. Most of the uninvaded plots are grouped together.
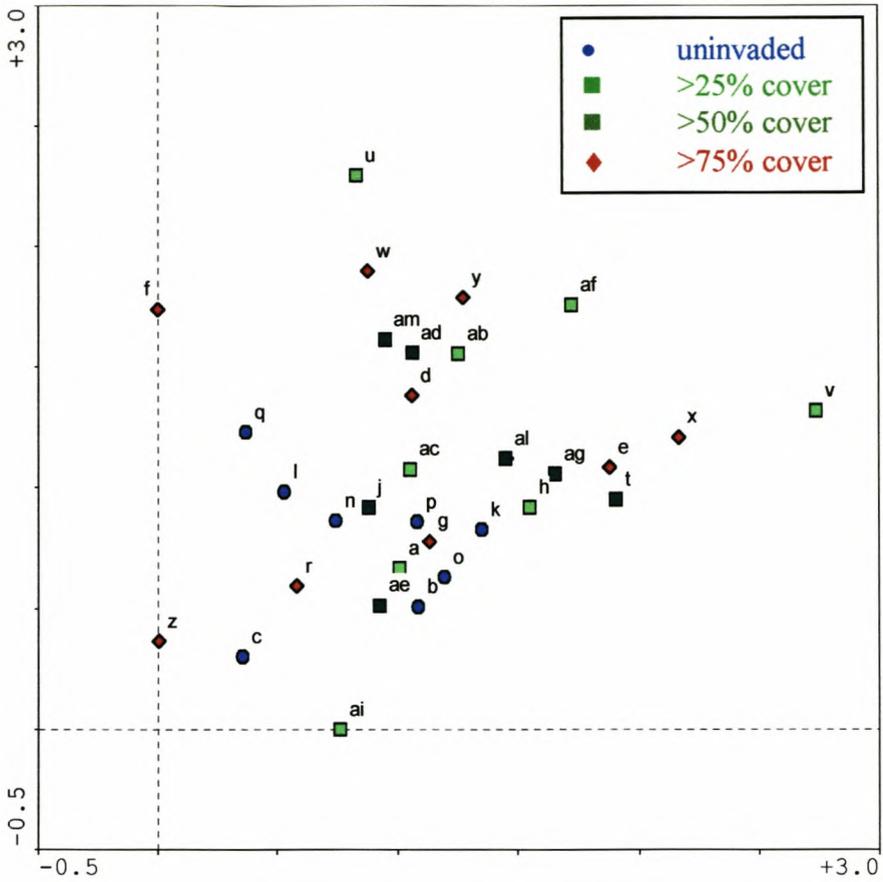
Fig 7.3: Spatial representation of the DCA on the presence/absence data for the trapped invertebrates, other than Arachnida. No distinct grouping is evident.
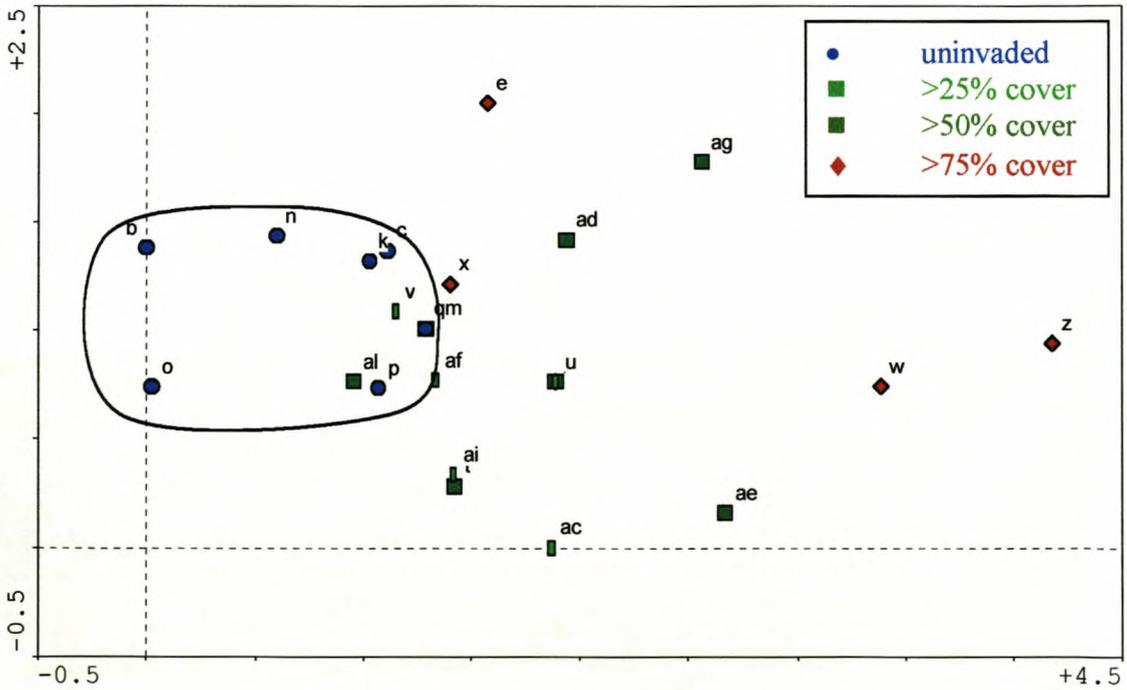
Fig 7.4: Spatial representation of the DCA on the presence/absence data for the trapped invertebrates, other than Arachnida. The uninvaded plots are circled.

7.3 Discussion

There are few data on soil and litter invertebrates in the Fynbos Biome (Majer & Greenslade, 1988). So it becomes difficult to compare the results from this study to other similar studies. Besides the results of any study on arthropods is biased beforehand by the objective and the trapping method used. In this case, the use of pitfall traps most likely underestimated the number of species present in the *A. saligna* invaded plots. First of all the increased amount of litter under the acacias, compared to pure Fynbos, impedes the movement of soil invertebrates and renders the pitfall traps less effective. Secondly, the *Acacia* canopy shields the traps from the large number of flying insects (*e.g.* the *Scarabaeidae*), also lowering their chances of being trapped. Thirdly, the arthropods inhabiting the trees' canopy have little chance of being trapped. There is proof that *A. saligna* is host to a number of insects which might not occur in pristine Fynbos, *e.g.* the unidentified larvae found feeding on the galls induced by *Uromycladium tepperianum* on *A. saligna* (Morris, 1999; pers. obs.). Furthermore, the sampling in this study only took into account a small portion of the potential annual variation within the invertebrate communities.

The theory exists that 'architecturally more complex' plants, such as trees, attract more arthropod species than plants that have smaller above-ground parts, such as most Sand Plain Fynbos species (see Strong *et al.*, 1984). The reason for the increased species richness is said to be the horizontal (young plants *vs.* old plants) and vertical stratification of herbivores withing tree species. This theory however has not been proven in all studies (Fowler, 1985). Especially because the *A. saligna* does not attain full maturity when attacked by *U. tepperianum*, the structural impact of the trees on a vegetation type does not reach its full potential. The effect of *A. saligna* on the non-epigaeic invertebrates could not be determined by this study. An increase in structural complexity, together with a higher plant diversity in ageing Fynbos, is cited by Schlettwein (1984) as a possible reason for the higher diversity in ant and leafhopper communities in older stands. Donnelly (1983) discovered an ant species richness, positively correlated with plant species richness in Jonkershoek Valley (Stellenbosch, South Africa). As mentioned in the previous chapter, *A. saligna* invasion has a negative effect on the overall plant species richness and diversity in the Sand Plain Fynbos. The effect on the arthropod habitat is thus twofold: a increase in structural diversity, which can have a positive effect on biodiversity, especially in a mixed vegetation (Waltz &

Whitham, 1997) and a decrease in biodiversity through the suppression of the original Fynbos vegetation.

The presence of *A. saligna* has the additional effect of enriching the soil with nutrients. This chronic, positive stress on the naturally nutrient poor Sand Plain Fynbos may indirectly influence the arthropod communities in this area. This enrichment eventually causes a shift in plant species towards grasses and exotics (Milton, 1980). If the overall productivity of an ecosystem increases, the vegetation can support a larger biomass of arthropods (Kirchner, 1977), even though plant species richness may go down. One should be careful however when using biomass as a measure of 'richness'. As demonstrated by Schlettwein (1984), a few large specimens can dramatically alter the outcome of the biomass sampling. Biomass was not used in this study for this reason. Indeed it would have influenced the outcome as there was a tendency for the trapped individuals in the dense *Acacia* stands to be larger, probably due to better cover and lower predation.

The high variance of the numeric results in this study, make an estimation of population parameters for the invertebrate species impossible, as well as a correlation between arthropod abundance and *A. saligna* cover. This is the result of inadequate sampling but other more extensive studies (Kirchner, 1977; Donnelly, 1983; Schlettwein, 1984; Majer & Greenslade, 1988) faced the same problems. Fact is that the arthropod population is so numerous and diverse, with many rare species (Kirchner, 1977; Donnelly, 1983) it takes enormous amounts of effort to gather and analyse a representative sample. In the Fynbos Biome, the situation is even more difficult due to the complete lack of precise, comparable data. This problem was partially circumvented by using qualitative data (presence/absence) instead of quantitative data. This approach proved to work for the Arachnida, because these are mostly ground-dwelling predators and they are thus suitable for trapping with pitfall traps. It is thus not surprising that the correspondence analysis of the presence/absence data for spiders did produce some results, contrary to the same analysis on the insect data. One can cautiously conclude that *A. saligna* invasion, does cause a shift in the spider communities in Sand Plain Fynbos. For the other arthropoda, the results are inconclusive, maybe due to inadequate sampling but it might well be that they are less sensitive to the *Acacia* cover. After all many species are very mobile and can move in and out of vegetation patches at will. Only in large stretches of homogenous vegetation can one really detect changes in their community structure.

Table 7.1: Invertebrate species captured with pitfall traps in Sand Plain Fynbos (Mamre, South Africa).

Arachnida

Presence/absence in plots with *Acacia* cover (%)

			0	>25	>50	>75
1.	Agelenidae	*Maimuna deserticola* Simon	+			
2.	Amaurobiidae	*Obatala armata* Lehtinen	+			
3.	Caponiidae	*Caponia capensis* Purcell	+	+	+	+
4.	Gnaphosidae	*Asemesthes montanus* Tucker	+			
5.	Gnaphosidae	*Asemesthes* sp.	+			+
6.	Gnaphosidae	*Trachyzelotes jaxartensis* Kroneberg				+
7.	Gnaphosidae	*Zelotes* sp.	+	+		+
8.	Lycosidae	*Proevippa hirsuta* Russell-Smith			+	+
9.	Lycosidae	*Proevippa* sp.		+		+
10.	Lycosidae	*Pseudevippa* sp.			+	
11.	Lycosidae	*Trabea varia* Purcell	+			
12.	Miturgidae					+
13.	Nemesiidae	*Hermacha* sp.	+			
14.	Oxyopidae	*Oxyopes* sp.		+		
15.	Palpimanidae	*Diaphorocellus* sp.	+			
16.	Phildromidae	*Hirriusa bidentatus* Lawrence	+		+	
17.	Pholcidae	*Smeringopus* sp.				+
18.	Phyxelididae			+		
19.	Salticidae	*Stenaelurillus* sp.	+			
20.	Scytodidae	*Scytodes* sp.		+		
21.	Zodariidae	*Cydrela* sp.	+	+	+	+
22.	Zodariidae	*Diores* sp.	+	+		
23.	Zodariidae	*Psammoduon* sp.	+	+	+	+

Other arthropoda

			0	>25	>50	>75
1.	Archaeognatha			+		
2.	Carabidae	4 species	+	+	+	+
3.	Chilopoda		+	+	+	+
4.	Curculionidae		+			+
5.	Diplopoda	2 species	+	+	+	+
6.	Isopoda			+		
7.	Lampyridae		+	+		+
8.	Lygaeidae					+
9.	Pentatomidae			+	+	
10.	Scarabaeidae	2 species	+	+	+	+
11.	Schorpionidae		+		+	+
12.	Tenebrionidae	3 species		+		

87
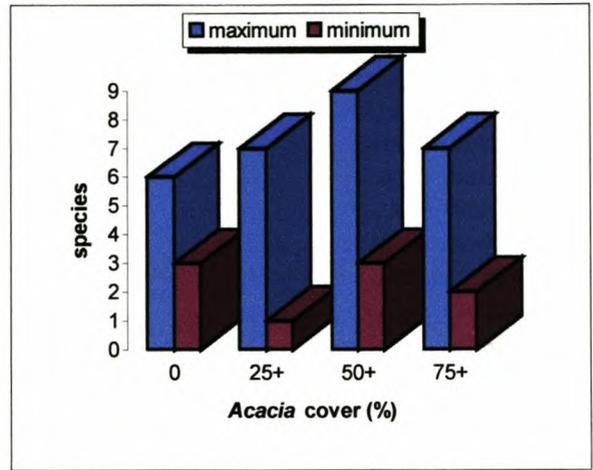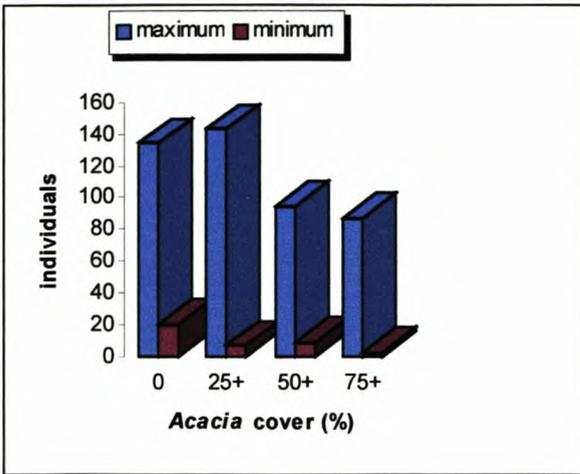
Fig. 7.5: Maximum and minimum number of individuals (left) and species (right), other than Arachnidae, trapped in the sampling plots. For average numbers, see Appendix C.
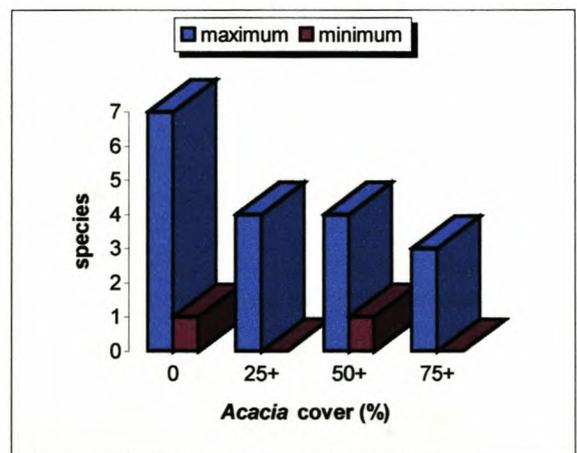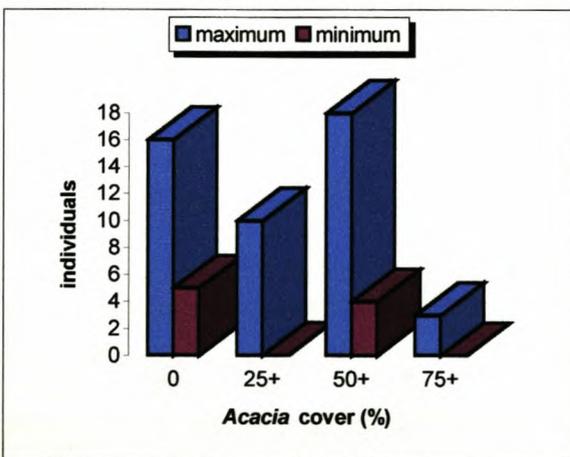
Fig. 7.6: Maximum and minimum number of individuals (left) and species (right), of Arachnidae, trapped in the sampling plots. For average numbers, see Appendix C.

Chapter 8

Conclusions

8.1 Ecological impact

It is a fact that *A. saligna* invasion of Fynbos vegetation causes a severe reduction in species richness. From an ecological point of view it is one of the major problems associated with the alien invasions in the Fynbos Biome (Richardson *et al.*, 1989). Other immediate problems include a shift in guild structure and lower fertility and reproduction of the indigenous vegetation. This study did not disclose any clear shifts in the vegetation communities in Sand Plain Fynbos, probably because the communities are the result of older, geological influences. In fact, a light infestation with *A. saligna* actually adds structural diversity to the Sand Plain Fynbos. When the infestation becomes denser, the detrimental impact on the biodiversity becomes problematic. There is of course the visual 'pollution' that even a single *A. saligna* tree causes in the low Fynbos vegetation.

Several factors have been identified as possible causes for the disappearance of Fynbos vegetation after invasion. Among them the increased nutrient input, the heavy litter fall, the shift in fire cycle or the high water consumption of *A. saligna*. Fact is that the Fynbos ecosystem is so complicated that it is very difficult to single out one causal factor. The higher nutrient status of the soil under *Acacia* thickets could be a factor, especially in the sandy soils

on which Sand Plain Fynbos occurs. This is a problem that should disappear after the removal of the acacias. As for the water consumption of *A. saligna*, and its possible long-term effect on the groundwater level, there is little information. This study seems to indicate that the *Acacia* cover and litter create a moister environment by preventing the topsoil from drying out rapidly in summer.

A. saligna invasion does not as such cause a shift in the type of community but rather a structural change within a community that can be picked up with ordination techniques. For instance the total percentage cover of indigenous species in densely invaded stands was negligible in most plots. Alien invasion invariably results in a loss of indigenous species with increasing alien canopy cover (see also Richardson & Van Wilgen, 1986; Richardson *et al.*, 1989; Holmes & Cowling, 1997a). The presence of *Acacia saligna* is a severe problem for the indigenous fynbos vegetation, but it's positive effects shouldn't be overlooked either. The main danger comes from the fact that the tree forms dense thickets after a few fire cycles. But in many cases man has promoted the invasion through prior disturbance of the Fynbos. The damage done by *A. saligna* doesn't seem to have reached an irreversible situation at this stage. Fynbos vegetation can remain dormant in seed banks for long periods, and all it takes to restore it is the removal of the *Acacia* thickets. To determine the best approach for restoration is beyond the scope of this study, but there are several ways to speed up the process, for instance through smoke-induced germination. The fungus *Uromycladium tepperianum* will definitely reduce the need for costly management techniques, but it will never make the port jackson disappear completely. If however the fungus succeeds in lowering the tree's reproductive potential, it will be easier to control.

From this study, it is unclear weather or not the fungus is having an impact on the *A.saligna* population in the area. There is no apparent relationship between the number of galls on a tree and health status parameters (*i.e.* defoliation). Furthermore, there is no historic vegetation data for the study area to make comparisons with the present situation. The number of seeds in the seedbank is low, compared to results from other studies, but there is no proof that the *Acacia* seed production is actually lowered. Frequent fires can also contribute to keeping the seedbank size down.

More than a decade after it's release, the fungus is slowly getting established throughout the Western Cape and it is now itself under attack from other organisms. A number of

unidentified larvae have been sighted feeding on the fungus' galls (Morris, 1999; pers. obs.). It is unclear how this trend will affect the fungus's capability to attack *A. saligna*. Considering *A.saligna*'s wide range of qualities which make a species a succesful invader (see Rejmánek & Richardson, 1996), it is unlikely that *U. tepperianum* alone will succeed in reversing the invasion of fynbos by *A. saligna*. But the time might be right to rethink the old management techniques and make optimal use of the biocontrol agent to reduce clearing costs.

One aspect about *A. saligna* invasion that was not investigated in this study is the increased fire hazard, occurring from the relatively higher fuel load of *Acacia* thickets. It is likely that both fire frequency and intensity are altered after invasion, thus disturbing the natural fire regime of the Fynbos communities. Although the fuel load is increased, *A. saligna* stands do not burn easily under normal weather conditions (Van Wilgen & Richardson, 1985). The reason for this is twofold: first of all the moisture content of *A. saligna* foliage is much higher than that of fynbos species. Secondly most of the biomass is located in the canopy, out of reach of the fuel bed. Using the Rothermel fire model Van Wilgen & Richardson (1985) came to the conclusion that fire in *A. saligna* invaded areas has a lower rate of spread and a lower fire intensity under most weather conditions. Only under extreme conditions will the fuel stored in the canopy ignite resulting in fires that are more difficult to control. And that are potentially more damaging.

But circumstances in the field have changed and the most important evolution is the introduction of *U. tepperianum*. The impact the fungus is having on the trees has increased the fuel load in terms of dead trees and branches. These create a bridge between the fuel bed and the canopy. Rejuvenation is also more abundant under dying trees and these seedlings add even more to the fuel load. It was apparent that intense fires occur in the study areas as many *Acacia* seeds in the seed bank were completely charred. The presence of *A. saligna* in this type of vegetation could result in more frequent burns. In the long run, the frequency and intensity of the fires will promote vegetation that is stuck in an early post-fire succession phase and the extinction of more slowly reproducing species. The low presence of *Protea repens* in this area (no individuals occurred in the sample plots) could be a first sign of this evolution.

Despite the negative effects of *A. saligna* on the vegetation in the study area, it remains unclear how the fauna responds to the presence of the trees. A small number of trees will be

beneficial to both micro and macro fauna. A port jackson tree adds structural diversity to the low Sand Plain Fynbos vegetation. It provides perching places for birds, shelter for arthropods (*e.g.* increased litter cover), and a food source (seeds) for rodents. These are in fact aspects of alien invasion in Fynbos that have been greatly ignored in scientific studies so far. Since the port jackson will never be eradicated, it is time to use its presence as a means to increase our knowledge of the Fynbos ecosystem as a whole.

8.2 Future research

A positive side effect of the *A. saligna* invasion is that it has increased our knowledge of the Fynbos ecosystem, and it has disclosed just as many gaps in our knowledge.

- Shading is often cited as a main cause in the reduction of species richness after *Acacia* invasion, yet there has been no research on the effect of shading on Fynbos. With shade nets it would be very simple to simulate different degrees of *Acacia* infestation and to monitor the changes that take place in the Fynbos.

- Year round monitoring of changes in soil moisture and soil nutrient status are needed to comprehend the natural cycles that occur in Fynbos, and the relative impact of port jackson on these cycles.

- The evolution and maybe recovery of Fynbos vegetation under infected *A. saligna* stands should be investigated, and the policy towards clearing should be adapted to make maximum use of the fungus as a biological control agent. Together with this we need to know to what extent the fungus limits the trees' capacity to become invasive.

- There is insufficient knowledge concerning the biodiversity of the Fynbos Biome, other than floral richness. Any research concerning Fynbos should take a more holistic approach in order to be able to make the right and informed decisions concerning the future of the Fynbos ecosystem.

References

ACOCKS, J. P. H. 1953. Veld types of South Africa. *Mem. Bot. Surv. S. Afr.* 57.

ANONYMOUS. 1987. A fungus released to help control port jackson "willow". *Plant Protection News* No. 8.

ANONYMOUS. 1993. Biological control of the Port jackson willow - Was it warranted? *Plant Protection News* No. 31.

ARMSTRONG, G. 1992a. A necessary evil? *Veld & Flora* 78(1): 10-13.

ARMSTRONG, G. 1992b. And never the twain shall meet? - Port Jackson. *Veld & Flora* 78(3): 93-94.

AUSDEN, M. 1996. Invertebrates. In: *Ecological Census techniques - A handbook.* (ed. W. J. Sutherland) Cambridge University Press. Pp: 139-177.

BARROW, N. J. 1977. Phosphorous uptake and utilization by tree seedlings. *Austr. J. Bot.* 25(6): 571-584.

BOUCHER, C. 1981. Lowcon Field Excursion Guide. In: *Proceedings of a symposium on coastal lowlands of the Western Cape* (ed. E. Moll). University of the Western Cape, Cape Town. pp.:73-89.

BOUCHER, C. 1983. Floristic and structural features of the coastal foreland vegetation south of the Berg River, Western Cape Province, South Africa. *Bothalia* 14(3&4): 669-674.

BOUCHER, C. 1984. Patterns of invasion by larger woody alien species in selected areas of the Fynbos Biome, South Africa. Report on a study tour to Australia from 2 August to 9 September 1984.pp: 40-43. Department of Agriculture and Water Supply, Stellenbosch.

BOUCHER, C. 1987. A phytosociological study of transects through the Western Cape Coastal Foreland, South Africa. Ph.D. Thesis, University of Stellenbosch, Stellenbosch.

BOUCHER, C. & BOUCHER, D. A. 1978. Uitheemse plante bedreig die Kaapse Weskus. *Elsenburg J.* 2(1): 1-11.

BOUCHER, C. & MOLL, E. J. 1981. South African Mediterranean shrublands, In: *Mediterranean-type shrublands* (eds F. di Castri, D. W. Goodall & R. L. Specht) Elsevier, Amsterdam.

BOUCHER, C. & SHEPHERD, P. A. 1988. Plant communities of the Pella site. In: *A description of the Fynbos Biome project intensive study site at Pella.* (ed. M. L. Jarman). S. Afr. Nat. Sci. Prog. Rep. No. 33: 38-76. CSIR, Pretoria.

BOUCHER, C. & STIRTON, C. H. 1978. *Acacia saligna.* In: C. H. Stirton (ed.) *Indringerplante, mooi maar gevaarlik.* Cape Dept. Nature and Environmental Conservation, Cape Town.

BROWN, A. C. 1993. Promotion of germination of fynbos seeds by plant derived smoke. *New Phytology* 123: 575-583.

BROWN, G., MITCHELL, D. T. & STOCK, W. D. 1984. Atmospheric deposition of phosphorus in a coastal fynbos ecosystem of the south-western Cape, South Africa. *J. Ecol.* 72: 547-551.

BROWNLIE, S. & MUSTART, P. 1988. History of recent land-use and management implications. In: *A description of the Fynbos Biome project intensive study site at Pella.* (ed. M. L. Jarman). S. Afr. Nat. Sci. Prog. Rep. No. 33: 10-29. CSIR, Pretoria.

BURGES, A. 1934. Studies in the genus *Uromycladium* (Uredineae). 1. General introduction, the anatomy of the galls, and the cytology of the vegetative mycelium and pycnia of *Uromycladium tepperianum* (Sacc.) McAlp. On *Acacia stricta* Willd. *Proc. Linn. Soc. N. S. Wales* 59: 212-228.

CAVANAGH, A. K. 1980 A review of some aspects of the germination of acacias. *Proc. Roy. Soc. Vic.* 91: 161-180.

CLEMENS, J., JONES, P. G. & GILBERT, N. H. 1977. Effect of seed treatments on germination in *Acacia. Austr. J. Bot.* 25: 269-276.

COMBRINCK, P. C. 1992. Port Jackson - friend or foe? *Veld & Flora* 78(3): 94.

COWLING, R. M. 1992. Definitely an unnecessary evil. *Veld & Flora* 78(2): 63-64.

COWLING, R. M., KIRKWOOD, D., MIDGLEY, J. J. & PIERCE, S. M. 1997. Invasion and persistence of bird dispersed, subtropical thicket and forest species in fire prone coastal fynbos. *J. Veg. Sci.* 8: 475-488.

CULLEN, J. M. & WHITTEN, M. J. 1995. Economics of classical biological control: A research perspective. In: *Biological control - Benefits and Risks* (eds. H. M. T. Hokkanen & J. M. Lynch).

Cambridge University Press, Cambridge. pp.: 270-276.

DE LANGE, J. H. & BOUCHER, C. 1990. Autecological studies on *Audouinia capitata* (Bruniaceae). I. Plant-derived smoke as a seed germination cue. *S. Afr .J. Bot.* 56(6): 700-703.

DI CASTRI, F. & MOONEY, H. A. (eds) 1973. Mediterranean type ecosystems: origin and structure. Springer-Verlag, Berlin.

DEALL, G. B. & THERON, G. K. 1990. Ordination as a tool for substantiating and interpreting floristic classifications: a case study. *Bothalia* 20(2): 223-227.

DEGEN, A., BLANKE, A., BECKER, K., KAM, M., BENJAMIN, R. W. & MAKKAR, P. S. 1997. The nutritive value of *Acacia saligna* and *Acacia salicina* for goats and sheep. *Animal Science* 64: 253-259.

DONNELLY, D. 1983. Comparison of community structure of the epigaeic invertebrate fauna, with particular reference to ants and beetles, between Fynbos sites under different management practices. M.Sc. Thesis, University of Stellenbosch, Stellenbosch.

DONNELLY, D. & MORRIS M. J. 1992. Port Jackson biocontrol: dispelling the myths. *Veld & Flora* 78(2): 62.

DRIESSEN, P. M. & DUDAL, R. (eds) 1991. The major soils of the world. Agricultural University Wageningen, Wageningen.

DYE, P. & POULTER, T. 1995. Clearing invasive trees in riparian zones increases streamflow. CSIR, Pretoria.

FOWLER, S. V. 1985. Differences in insect species richness and faunal composition of birch seedlings, sapling and trees: the importance of plant architecture. *Ecol. Ent.* 10: 159-169.

FRY, M. St. L. 1987. A detailed characterization of soils under different fynbos-climate-geology combinations in the South-western Cape. M.Sc. Thesis, University of Stellenbosch, Stellenbosch.

GATHE, J. 1971. Host Range and symptoms in Western Australia of the gall rust *Uromycladium tepperianum. J. Roy. Soc. W. Austr.* 54: 114-118.

GREATHEAD, D. J. 1995. Benefits and risks of classical biological control. In: *Biological control - Benefits and Risks* (eds. H. M. T. Hokkanen & J. M. Lynch). Cambridge University Press, Cambridge 54-63.

HALL, A. V. & BOUCHER, C. 1977. The threat posed by alien weeds to the Cape Flora. In: Proceedings of the Second National Weeds Conference of South Africa. Balkema, Cape Town. Pp. 35-45.

HILL, T. R. 1996. Description, classification and ordination of the dominant vegetation communities, Cathedral Peak, Kwazulu-Natal Drakenberg. *S. Afr. J. Bot.* 62(5): 263-269.

HOFFMAN, M. T., MOLL, E. J. & BOUCHER, C. 1987. Post fire succession at Pella, a South African Lowland Fynbos site. *S. Afr. J. Bot.* 53(5): 370-374.

HOKKANEN, H. M. T. & LYNCH, J. M. Biological control: Benefits and Risks. Cambridge University Press, Cambridge.

HOLMES, P. M. 1988. Implications of alien *Acacia* seed bank viability and germination for clearing. *S. Afr. J. Bot.* 54(3): 281-284.

HOLMES, P. M. 1989a. Decay rates in buried alien *Acacia* seed populations of different density. *S. Afr. J. Bot.* 53(3): 299-303.

HOLMES, P. M. 1989b. Effect of different clearing treatments on the seed bank dynamics of an invasive Australian shrub, *Acacia cyclops*, in the Southwestern Cape, South Africa. *For. Ecol. Manag.* 28: 33-46.

HOLMES, P. M. 1990. Dispersal and predation of alien *Acacia* seeds: effects of season and invading stand density. *S. Afr .J. Bot.* 56(4): 428-434.

HOLMES, P. M. & COWLING, R. M. 1997a. The effects of invasion by *Acacia saligna* on the guild structure and regeneration capabilities of South African fynbos shrublands. *J. Appl. Ecol.* 34: 317-332.

HOLMES, P. M. & COWLING, R. M. 1997b. Diversity, composition and guild structure relationships between soil-stored seed banks and mature vegetation in alien plant invaded South African Fynbos Shrublands. *Plant Ecology* 133: 107-122.

HOLMES, P. M., DALLAS, H. & PHILLIPS, T. 1987a. Control of *Acacia saligna* in the Southwestern Cape - Are the clearing treatments effective? *Veld & Flora* 73(3): 98-100.

HOLMES, P. M., MACDONALD, I. A. W. & JURITZ, J. 1987b. Effects of clearing treatment on seed banks of the alien invasive shrubs *Acacia saligna* and *A. cyclops* in the southern and southwestern Cape, South Africa. *J. Appl. Ecol.* 24: 1045-1051.

HUFFAKER, C. B. & MESSENGER, P. S. 1976. Theory and practice of biological control. Academic Press, London.

HURLBER,T S. H. 1984. Pseudoreplication and the design of ecological field experiments. *Ecol. Mons.* 54(2): 187-211.

IMMELMAN, W. F. E., WICHT, C. L. & ACKERMAN, D. P. 1973. Ons groen erfenis. DWAF, Pretoria.

JARMAN, M. L. 1986. Conservation priorities in lowland regions of the fynbos biome. *S. Afr. Nat. Sci. Prog. Rep.* No. 87.

JEFFERY, D. J., HOLMES, P. M. & REBELO, A. G. 1988. Effects of dry heat on germination in selected indigenous and alien legume species in South Africa. *S. Afr. J. Bot.* 54(1): 28-34.

JONES, R. M., ROUX, E. X. & WARREN, J. M. 1963. Studies in the autecology of the Australian *Acacias* in South Africa. III. The production of toxic substances by *Acacia cyclops* and *A. cyanophylla* and their possible ecological significance. *S. Afr. J. Sci.* 59: 295-296.

KENT, M. & COKER, P. 1992. Vegetation description and analysis. A practical approach. Wiley & Sons, Chichester. 363 pp.

KIRCHNER, T. B. 1977. The effects of resource enrichment on the diversity of plants and arthropods in a shortgrass prairie. *Ecol.* 58: 1334-1344.

KRUGER, F. W., MITCHELL, D. T. & JARVIS, J. U. M. (eds) 1983. Mediterranean-type ecosystems. The role of nutrients. *Ecological studies* 43.

LAMBRECHTS, J. J. N. & FRY, M. 1988. Soils of the Pella site. In: *A description of the Fynbos Biome project intensive study site at Pella.* (ed. M. L. Jarman). S. Afr. Nat. Sci. Prog. Rep. No. 33: 33-37. CSIR, Pretoria.

LE MAITRE, D. C., VAN WILGEN, B. W., CHAPMAN, R. A. & McKELLY, D. H. 1996. Invasive plants and water resources in the Western Cape Province, South Africa: modelling the consequences of a lack of management. *J. Appl. Ecol.* 33: 161-172.

LOOCK, A. (ed.) 1990. Handbook of standard soil testing methods for advisory purposes. Soil Science Society of South Africa, Pretoria.

MACDONALD, I. A. W. 1984. Is the Fynbos Biome especially susceptible to invasion by alien plants? A re-analysis of the available data. *S. Afr. J. Sci.* 80: 369-377.

MACDONALD, I. A. W., CLARK, D. L. & TAYLOR, H. C. 1989. The history and effects of alien plant control in the Cape of Good Hope Nature Reserve, 1941-1987. *S. Afr. J. Bot.* 55(1): 56-75.

MACDONALD, I. A. W. & JARMAN, M. L. 1984. Invasive alien organisms in the terrestrial ecosystems of the Fynbos Biome. *S. Afr. Nat. Sci. Prog. Rep.* No 85

MACDONALD, I. A. W. & RICHARDSON, D. M. 1986. Alien species in the terrestrial ecosystems of the Fynbos Biome. In: *The ecology and management of biological invasions in Southern Africa.* (eds Macdonald, I. A. W., F. J. Kruger & A. A. Ferrar). Oxford University Press, Cape Town. Pp. 77-91.

MACDONALD, I. A. W. & WISSEL, C. 1989. Costing the initial clearance of alien *Acacia* species invading fynbos vegetation. *S. Afr. J. Plant Soil* 6(1): 39-45.

MACDONALD, I. A. W. & WISSEL, C. 1992. Determining optimal clearing treatments for the alien invasive shrub *Acacia saligna* in the southwestern Cape, South Africa. *Agr. Eco. Env.* 39: 169-186.

MACLEAN, G. L. (ed.) 1993. Roberts' birds of Southern Africa. John Voelcker Bird Book Fund, Cape Town.

MAJER, J. D. & GREENSLADE, P. 1988. Soil and litter invertebrates. In *Mediterranean-type ecosystems: A data source book.* (ed. Specht R. L.) Kluwer Academic Publishers, Dordrecht.

MARAIS, C. 1998. An economic evaluation of invasive alien plant control programs in the mountain catchment areas

McDONALD, D. J. 1987. Ordination by detrended correspondence analysis (DCA) of the vegetation of Swartboschkloof, Jonkershoek, Cape Province. *Bothalia* 17(1): 121-129.

McVEIGH, S. 1990. Chemical control for port jackson willow. *Farmers Weekly* 80010, p.26.

McVICAR, C. N., DE VILLIERS J. M., LAMBRECHTS, J. J. N., LOXTON, R. F., MERRYWEATHER, F. R. LEROUX, J., VERSTER E., VAN ROOYEN, T. H. & VON HARMSE, H. J. 1977. Soil Classification. A binomial system for South Africa. Department of Agricultural Technical Services, Pretoria.
of the Western Cape Province, South Africa. Ph. D. Thesis, University of Stellenbosch, Stellenbosch.

MIDGLEY, J. J. 1989. Season of burn of serotinous fynbos Proteaceae: A critical review and further data. *S. Afr. J. Bot.* 55(2): 165-170.

MILTON, S. J. 1980. Studies on the Australian acacias in the South Western Cape, South Africa. M. Sc. Thesis, University of Cape Town, Cape Town.

MILTON, S. J. & HALL, A. V. 1981. Reproductive biology of Australian acacias in the south-western

Cape Province, South Africa. *Trans. Roy. Soc. S. Afr.* 44(3): 465-485.

MITCHELL, D. T., COLEY, P. G. F., WEBB, S. & ALLSOPP, N. 1986. Litterfall and decomposition processes in the Coastal Fynbos vegetation, south-western Cape, South Africa. *J. Ecol.* 74: 977-993.

MOLL, E. J., CAMPBELL, B. M., COWLING, R. M, BOSSI, L, JARMAN, M. L. & BOUCHER, C. 1984. A description of major vegetation categories in and adjacent to the Fynbos Biome. *S. Afri. Nat. Sci. Prog. Rep* No. 83.

MOLL, E. J. & TRINDER-SMITH, T. 1992. Invasion and control of alien woody plants on the Cape Peninsula Mountains, South Africa - 30 years on. *Biol. Conser.* 60: 135-143.

MORRIS, M. J. 1987. Biology of the *Acacia* gall rust, *Uromycladium tepperianum. Plant Pathology* 36: 100-106.

MORRIS, M. J. 1991. The use of plant pathogens for biological weed control in South Africa. *Agric. Ecosyst. Environ.* 37: 239-255.

MORRIS, M. J. 1997. Impact of the gall-forming rust fungus *Uromycladium tepperianum* on the invasive tree *Acacia saligna* in South Africa. *Biological Control* 10: 75-82.

MORRIS, M. J. 1999. The contribution of the gall-forming rust fungus *Uromycladium tepperianum* (Sacc.) McAlp. to the biological control of *Acacia saligna* (Labill.) Wendl. (Fabaceae) in South Africa. *Afr. Entomol. Mem.* 1: 125-128.

MUSIL, C. F. 1991. Seed bank dynamics in Sand Plain Lowland Fynbos. *S. Afr. J. Bot.* 57(3), 131-142.

MUSIL, C. F. 1993. Effect of invasive Australian *Acacia*s on the regeneration, growth and nutrient chemistry of South African Lowland Fynbos. *J. Appl. Ecol.* 30: 361-372.

MUSIL, C. F. & MIDGLEY, G. F. 1990. The relative impact of invasive Australian acacias, fire and season on the soil chemical status of a Sand Plain Lowland Fynbos community. *S. Afr. J. Bot.* 56(4): 419-427.

NATIONAL ACADEMY OF SCIENCES. 1980. Firewood crops. Shrub and tree species for energy production. National Academy of Sciences, Washington, DC.

NETER, J., WASSERMAN, W. & KUTNER, M. H. 1990. Applied linear statistical models. 3rd edition. Irwin Inc., Boston.

NIEMAN, W. A. 1982. Climate of the coastal lowlands of the Western Cape. In: *Proceedings of a symposium on coastal lowlands of the Western Cape*

(ed. E. Moll) University of the Western Cape, Cape Town pp: 11-15.

ODENDAAL, J. P. le G. 1983. Die ontstaan en ontwikkeling van die kusvlakte van suidwes Kaapland: 'n geomorfologiese ondersoek. Ph. D. thesis, University of Stellenbosch, Stellenbosch.

OLCKERS, T. 1999. Biological control of weeds in South Africa (1990-1998): Introduction. *Afr. Entom. Mem.* 1: 1-2.

READ, D. J. & MITCHELL, D. T. 1983. Decomposition and mineralization processes in mediterranean-type ecosystems and heathlands of similar structure. In: *Mediterranean-type ecosystems. The role of nutrients.* (Kruger F. W., Mitchell D. T. & Jarvis J. U. M. (Eds)) *Ecological studies.* Vol. 43.

REBELO, T. 1996. The Vegetation of South Africa, Lesotho and Swaziland. Dept. of Environmental Affairs and Tourism, Pretoria.

REJMÁNEK, M. & RICHARDSON, D. M. 1996. "What Attributes Make Some Plant Species More Invasive?" *Ecology,* 77(6): 1655-1661.

RICHARDS, M. B., COWLING, R. M. & STOCK, W. D. 1995. Fynbos plant communities and vegetation-environment relationships in the Soetanysberg hills, Western Cape. *S. Afr. J. Bot..* 61(1): 298-305.

RICHARDSON, D. M. & COWLING, R. M. 1992. Why is Mountain Fynbos invasible and which species invade? In: *Fire in South African Fynbos.* (eds B. W. van Wilgen, D. M. Richardson, F. J. Kruger & H. J. van Hensbergen) *Ecol. Stud.* 93.

RICHARDSON, D. M., MACDONALD, I. A. W. & FORSYTH, G. 1989. Reductions in plant species richness under stands of alien trees and shrubs in the Fynbos Biome. *S. Afr. For. J.* 149: 1-8.

RICHARDSON, D. M., MACDONALD, I. A. W., HOLMES, P. M. & COWLING, R. M. 1992. Plant and animal invasions. In: *The ecology of Fynbos: nutrients, fire and diversity.* (ed. R. M. Cowling) Oxford University Press, Oxford.271-304.

RICHARDSON, D. M. & VAN WILGEN, B. W. 1986. Effects of thirty-five years of afforestation with *Pinus radiata* on the composition of mesic Mountain Fynbos near Stellenbosch. *S. Afr. J. Bot.* 52: 309-315.

RICHARDSON, D. M. & VAN WILGEN, B. W. 1992. Ecosystem, community and species response to fire in Mountain Fynbos: conclusions from the Swartboskloof experiment. In: *Fire in South African Fynbos.* (eds B. W. van Wilgen, D. M. Richardson, F. J. Kruger & H. J. van Hensbergen) *Ecol. Stud.* 93.

ROGERS, J. 1982. Geological history of the Western Cape's coastal lowlands. In: *Proceedings of a symposium on coastal lowlands of the Western Cape* (ed. E. Moll) University of the Western Cape, Cape Town.

ROUX, E. R. 1961. History of the introduction of Australian acacias on the Cape Flats. *S. Afr. J. Sci.* 57: 99-102.

ROUX, E. R. & MIDDLEMIS, E. 1963. Studies in the autecology of the Australian acacias in South Africa. I. The occurrence and distribution of *Acacia cyanophylla* and *A. cyclops* in the Cape Province. *S. Afr. J. Sci.* 59: 268-294.

ROUX, E. R. & WARREN, J. L. 1963. tudies in the autecology of the Australian acacias in South Africa. II. Symbiotic nitrogen fixation in *Acacia cyclops*, A. Cunn. *S. Afr. J. Sci.* 59: 294-295.

SAMWAYS, M. J. 1981. Biological control of pests and weeds. The Camelot Press, Southampton.

SCHAEFER, R. 1973. Microbial activity under seasonal conditions of drought in Mediterranean-type climates. In *Mediterranean-type ecosystems - Origin and structure* (eds F. DiCastri & H. A. Money). Springer-Verlag, Berlin.

SCHLETTWEIN, C. D. G. 1984. Comparison of insect biomass and community structure between Fynbos sites of different ages after fire with particular reference to ants, leafhoppers and grasshoppers. M.Sc. Thesis, University of Stellenbosch, Stellenbosch.

SCHULZE, B. R. 1965. Climate of South Africa, part 8: general survey. *W.B.* 28, Government Printer, Pretoria.

SHAUGHNESSY, G. L. 1980. Historical ecology of alien woody plants in the vicinity of Cape Town. Ph. D. thesis, University of Cape Town, Cape Town.

SIMMONDS, F. J., FRANZ, J. M. & SAILER, R. I. 1976. History of biological control. In: *The theory and practice of biological control.* (eds Huffaker C. B. & P. S. Messenger) Academic Press, London. Pp.: 17-39.

SPECHT, R. L. 1963. Dark Island heath (Ninety-mile Plain, South Australia) VII. The effect of fertilizers on composition and growth 1950-1960. *Austr. J. Bot.* 11: 67-94.

STIRTON, C. H. 1978. Alien invaders. Beautiful but dangerous. Cape Dept. Nature and Environmental Conservation, Cape Town.

STOCK W,. D. & LEWIS, O. A. M. 1986a. Atmospheric input of nitrogen to a Coastal Fynbos

ecosystem of the south-western Cape Province, South Africa. *S. Afr. J. Bot.* 52: 273-276.

STOCK, W. D. & LEWIS, O. A. M. 1986b. Soil nitrogen and the role of fire as a mineralizing agent in a South African Coastal Fynbos system. *J. Ecol.* 74: 317-328.

STOCK, W. D., WIENAND, K. T. & BAKER, A. C. 1995. Impacts of invading N2-fixing *Acacia* species on patterns of nutrient cycling in two Cape ecosystems: evidence from soil incubation studies and ^{15}N natural abundance values. *Oecologia* 101: 375-382.

STRONG, D. R., LAWTON, J. H. & SOUTHWOOD, T. R. E. 1984. Insects on plants. Community patterns and mechanisms. Blackwell Scientific Publications, Oxford.

TAN, K. H. 1996. Soil sampling, preparation, and analysis. Marcel Dekker, Inc., New York.

TER BRAAK, C. J. F. & ŠMILAUER, P. 1998. CANOCO Reference Manual and User's Guide to *Canoco for Windows.* Software for Canonical Community Ordination (version 4). Centre for Biometry Wageningen (Wageningen, NL) and Microcomputer Power (Ithaca NY, USA), 352 pp.

VAN WILGEN, B. W., BOND, W. J. & RICHARDSON, D. M. 1992. Ecosystem management. In: *The ecology and management of biological invasions in Southern Africa.* (eds Macdonald, I. A. W., F. J. Kruger & A. A. Ferrar). Oxford University Press, Cape Town. Pp. 345-371.

VAN WILGEN, B. W. & LE MAITRE, D. C. 1981. Preliminary estimates of nutrient levels in fynbos vegetation and the role of fire in nutrient cycling. *S. Afr. For. J.* 119: 24-28.

VAN WILGEN, B. W. & RICHARDSON, D. M. 1985. The effects of alien shrub invasions on vegetation structure and fire behaviour in South African Fynbos Shrublands: A simulation study. *J. Appl. Ecol.* 22: 955-966.

VERSFELD, D. B., LE MAITRE, D. C. & CHAPMAN, R. A. 1998. Alien invading plants and water resources in South Africa: a preliminary assessment *WRC Report* TT 99/98. CSIR, Pretoria.

WALTZ, A. M. & WHITHAM, T. G. 1997. Plant development affects arthropod communities: opposing impacts of species removal. *Ecol.* 78(7): 2133-2144.

WILSON, F. & HUFFAKER, C. B. 1976. The Philosophy, Scope, and Importance of Biological Control. In: *The theory and practice of biological*

control. (eds. Huffaker C. B. & P. S. Messenger) Academic Press, London. Pp.: 3-16.

WITKOWSKI, E. T. F. 1989a. Response to nutrient additions by the plant growth forms of Sand Plain Lowland Fynbos, South Africa. *Vegetatio* 79: 89-97.

WITKOWSKI, E. T. F. 1989b. Effects of nutrient additions on litter production and nutrient return in a nutrient-poor Cape fynbos ecosystem. *Plant & Soil* 117: 227-235.

WIKOWSKI, E. T. F. 1990a. Nutrient limitation of inflorescence and seed production in *Leucospermum parile* (Proteaceae) in the Cape fynbos. *J. Appl. Ecol.* 27:148-158.

WITKOWSKI, E. T. F. 1990b. Growth and competition between seedlings of *Protea repens* and the alien invasive, *A. saligna*, in relation to nutrient availablility. *Func. Ecol.* 5: 101-110.

WITKOWSKI, E. T. F. 1991. Effects of invasive alien acacias on nutrient cycling in the coastal lowlands of the Cape Fynbos. *J. Appl. Ecol.* 28: 1-15.

WITKOWSKI, E. T. F. 1994. Growth of seedlings of the invasives, *Acacia saligna* and *A. cyclops*, in relation to soil phosphorus. *Austr. J. Ecol.* 19: 290-296.

WITKOWSKI, E. T. F. & MITCHELL, D. T. 1987. Variations in soil phosphorus in the Fynbos Biome, South Africa. *J. Ecol.* 75: 1159-1171.

WITKOWSKI, E. T. F. & MITCHELL, D. T. 1989. The effects of nutrient additions on above-ground phytomass and its phosphorus and nitrogen contents of Sand Plain Lowland Fynbos. *S. Afr. J. Bot.* 55(2): 243-249.

WITKOWSKI, E. T. F., MITCHELL, D. T. & STOCK, W. D. 1990. Response of a Cape Fynbos ecosystem to nutrient additions. *Acta Oecologia* 11: 311-326.

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APPENDIX A

Plant species checklist (name, plot number)

Acrosanthes teretifolia Eckl. & Zeyh., 1,
Agathosma species, 38,
Anthospermum galioides Rchb.f. ssp. galioides, 16,
Anthospermum species, 11, 15, 23,
Aristea dichotoma (Thunb.) Ker Gawl., 1, 2, 3, 6, 12, 24, 25,
Aspalathus albens L., 1, 6, 7, 15, 20, 27, 28, 29, 30, 39,
Aspalathus attenuata R.Dahlgren, 21,
Aspalathus capensis (Walp.) R.Dahlgren, 27,
Aspalathus divaricata, 12, 13, 24, 31, 32,
Aspalathus microphylla DC., 3,
Aspalathus species, 8, 24,
Asparagus capensis, 5, 9, 14,
Asparagus capensis L. var. capensis, 1, 3, 18, 35, 36, 38, 39,
Asparagus rubicundus P.J.Bergius, 23, 25,
Asparagus species, 12, 30,
Berzelia abrotanoides (L.) Brongn., 22,
Calopsis viminea (Rottb.) H.P.Linder, 2, 5, 7, 11, 12, 16, 17, 21, 25, 30,
Cannomois parviflora (Thunb.) Pillans, 3, 11, 29,
Cassytha ciliolata Nees, 20, 22,
Chondropetalum nudum Rottb., 20, 21, 22, 38,
Chondropetalum species, 31,
Cliffortia drepanoides Eckl. & Zeyh., 12,
Cliffortia falcata L.f., 1, 2, 4, 10, 11, 13, 24, 26, 30, 31, 32, 35, 36, 37, 40,
Cliffortia polita Weim., 30,
Cliffortia polygonifolia, 8, 9, 10, 25, 29, 38,
Cliffortia ruscifolia L. x theodori-friesii Weim., 4, 26,
Clutia africana Poir., 12, 19, 38,
Clutia polifolia Jacq., 3, 8,
Clutia species, 18,
Crassula setulosa, 22,
Cryptadenia grandiflora (L.f.) Meisn., 20, 37,
Diosma aspalathoides Lam., 22,
Diosma oppositifolia L., 13, 20, 21, 22, 29, 30, 32, 40,
Diosma species, 13, 36,
Ehrharta species, 19, 24, 26,
Ehrharta villosa, 4, 12, 21, 26,
Erica coarctata, 24, 40,
Erica mammosa L., 13, 20, 39,
Erica species, 31,
Eriospermum species, 7,
Euchaetis scabricosta I.Williams, 2, 22,
Ficinia deusta (P.J.Bergius) Levyns, 22,
Ficinia species, 2, 17, 27,
Grisebachia plumosa, 2, 9, 10, 12, 13, 20, 21, 24, 32, 38, 40,
Grisebachia plumosa Klotzsch ssp. eciliata E.G.H.Oliv., 11, 23,
Helichrysum indicum (L.) Grierson, 7,
Heliophila species, 22,
Ischyrolepis monanthos (Mast.) H.P.Linder, 5, 7, 12, 13, 20, 21, 22, 23, 24, 28,
Isolepis marginata (Thunb.) A.Dietr., 6,
Leucadendron species, 9, 11, 12, 19, 39, 40,

Leucospermum hypophyllocarpodendron (L.) Druce ssp. canaliculatum (H.Buek ex Meisn.) Rourke, 1, 6, 11, 14, 20, 22, 23, 24, 25, 27, 29, 31, 32, 35, 38, 39, 40,
Macrostylis villosa, 24, 25,
Macrostylis villosa (Thunb.) Sond. ssp. minor I.Williams, 32,
Metalasia muraltiifolia DC., 36, 38,
Metalasia muricata (L.) D.Don, 4, 17, 21, 24, 26, 31, 35, 37, 40,
Microloma sagittatum (L.) R.Br., 15,
Muraltia species, 10,
Othonna filicaulis Jacq., 9,
Othonna species, 1, 2, 3, 8, 9, 10, 11, 12, 13, 30, 36, 38, 39,
Oxalis luteola Jacq., 9, 10, 12, 14, 16, 24, 25, 31, 32, 35, 36, 37, 38,
Oxalis polyphylla, 5, 10, 14, 17, 25, 40,
Oxalis polyphylla Jacq. var. alba Salter, 6,
Oxalis species, 11, 13, 32,
Oxalis versicolor, 3, 4, 5, 7, 8, 9, 10, 11, 12, 13, 15, 16, 26, 27, 28, 29, 30, 34, 39,
Passerina ericoides L., 27, 40,
Passerina filiformis L., 7,
Passerina vulgaris Thoday, 1, 2, 4, 5, 10, 14, 16, 18, 19, 20, 21, 23, 25, 26, 28, 37,
Pelargonium myrrhifolium, 23,
Pelargonium oenothera (L.f.) Jacq., 31, 32,
Pelargonium species, 37,
Pelargonium triste (L.) L'H,r., 3, 10, 34, 39,
Pentaschistis species, 20, 26, 37,
Phylica abietina Eckl. & Zeyh., 26,
Phylica cephalantha Sond., 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 20, 21, 22, 23, 24, 25, 27, 28, 29, 30, 31, 32, 34, 38, 39, 40,
Phylica ericoides, 36,
Phylica gracilis (Eckl. & Zeyh.) D.Dietr., 24, 28, 31,
Phylica imberbis, 31,
Phylica species, 2, 3, 30, 31, 33, 36, 40,
Phylica stipularis L., 7, 11, 12, 16, 21, 22, 25, 29, 30, 32, 40,
Poa species, 5,
Prismatocarpus species, 21,
Putterlickia pyracantha (L.) Szyszyl., 30,
Restio filiformis Poir., 29,
Restio species, 2, 6, 8, 20, 22, 23, 25, 32,
Rhus laevigata, 1, 3, 5, 9, 12, 13, 14, 15, 16, 20, 25, 26, 30, 38, 39,
Rhus laevigata L. var. laevigata fo. cangoana Moffett, 7, 18, 19, 23, 24, 28, 33,
Rhus species, 8, 34,
Rumex species, 10, 15, 28, 39,
Ruschia species, 7, 9, 12, 13, 27, 30, 39,
Salvia africana-caerulea L., 6, 23, 34,
Salvia lanceolata Lam., 27,
Salvia species, 2, 9, 11, 12, 30, 37, 38,
Serruria fasciflora Salisb. ex Knight, 1, 2, 3, 10, 14, 21, 22, 32, 35, 36, 40,
Serruria species, 20, 38,
Staavia radiata (L.) Dahl, 20, 22, 31, 37, 38,
Staberoha cernua (L.f.) T.Durand & Schinz, 3, 7, 11, 17, 20, 27, 28, 39, 40,
Staberoha distachyos (Rottb.) Kunth, 2, 3, 7, 11, 13, 27, 28, 37, 38, 39, 40,
Stoebe bruniades (Rchb.) Levyns, 12,
Struthiola leptantha Bolus, 6, 9, 15, 20, 22, 28, 31, 34,
Thalassodendron species, 20,
Thamnochortus erectus (Thunb.) Mast., 1, 9, 10, 13, 14, 17, 23, 24, 40,
Thamnochortus obtusus Pillans, 1,
Thamnochortus punctatus Pillans, 5, 8, 9, 10, 14,
Thamnochortus species, 7, 8, 15, 17, 20, 23, 24, 27, 28, 29, 31, 32, 38,
Thamnochortus sporadicus Pillans, 2, 5, 6, 39, 40,
Thesium virgatum Lam., 15,
Tribolium uniolae (L.f.) Renvoize, 11, 19, 21, 24, 31,
Ursinia anthemoides, 20,

APPENDIX B

Relevé checklist and Braun-Blanquet table

```
=> Relevé number: 1

Nr. table in publ.              : AB
Cover abundance scale           : Braun/Blanquet (old)
Relev, area (m2)                : 50.00
Altitude (m)                    : 195
Cover tree layer (%)            : 25-50
Lat                             : 333122.24
Long                            : 182845.01
```

Acrosanthes teretifolia	+	Passerina vulgaris	+
Aristea dichotoma	+	Phylica cephalantha	2
Aspalathus albens	2	Rhus laevigata	+
Asparagus capensis v. capensis	+	Serruria fasciflora	+
Cliffortia falcata	+	Thamnochortus erectus	+
Leucosperm hypophyllo s. canalicula	+	Thamnochortus obtusus	+
Othonna species	+	Willdenowia sulcata	2

```
=> Relevé number: 2

Nr. table in publ.              : AC
Cover abundance scale           : Braun/Blanquet (old)
Relev, area (m2)                : 50.00
Altitude (m)                    : 195
Cover tree layer (%)            : 25-50
Lat                             : 333122.11
Long                            : 182843.45
```

Aristea dichotoma	+	Phylica species	+
Calopsis viminea	+	Restio species	+
Cliffortia falcata	+	Salvia species	+
Euchaetis scabricosta	+	Serruria fasciflora	1
Ficinia species	+	Staberoha distachyos	1
Grisebachia plumosa	+	Thamnochortus sporadicus	2
Othonna species	+	Willdenowia sulcata	2
Passerina vulgaris	+	Zygophyllum spinosum	+
Phylica cephalantha	3		

```
=> Relevé number: 3

Nr. table in publ.              : AD
Cover abundance scale           : Braun/Blanquet (old)
Relev, area (m2)                : 50.00
Altitude (m)                    : 195
Cover tree layer (%)            : 50-75
Lat                             : 333122.57
Long                            : 182841.96
```

Aristea dichotoma	+	Phylica cephalantha	3
Aspalathus microphylla	+	Phylica species	+
Asparagus capensis v. capensis	+	Rhus laevigata	+
Cannomois parviflora	1	Serruria fasciflora	2
Clutia polifolia	+	Staberoha cernua	1
Othonna species	+	Staberoha distachyos	1
Oxalis versicolor	+	Willdenowia sulcata	1
Pelargonium triste	+	Zygophyllum spinosum	+

```
=> Relevé number: 4

Nr. table in publ.              : J
Cover abundance scale           : Braun/Blanquet (old)
Relev, area (m2)                : 50.00
Altitude (m)                    : 195
```

```
Cover tree layer (%)        : 50-75
Lat                         : 333139.13
Long                        : 182905.06
```

Cliffortia falcata	+	Oxalis versicolor	2
Cliffortia ruscifolia	+	Passerina vulgaris	+
Ehrharta villosa	+	Phylica cephalantha	2
Metalasia muricata	+		

=> Relevé number: 5

```
Nr. table in publ.          : K
Cover abundance scale       : Braun/Blanquet (old)
Relev, area (m2)            : 50.00
Altitude (m)                : 195
Cover tree layer (%)        : 0
Lat                         : 333139.62
Long                        : 182904.83
```

Asparagus capensis	+	Phylica cephalantha	2
Calopsis viminea	+	Poa species	+
Ischyrolepis monanthos	1	Rhus laevigata	+
Oxalis polyphylla	+	Thamnochortus punctatus	+
Oxalis versicolor	+	Thamnochortus sporadicus	1
Passerina vulgaris	+		

=> Relevé number: 6

```
Nr. table in publ.          : L
Cover abundance scale       : Braun/Blanquet (old)
Relev, area (m2)            : 50.00
Altitude (m)                : 195
Cover tree layer (%)        : 0
Lat                         : 333141.49
Long                        : 182858.04
```

Aristea dichotoma	+	Restio species	+
Aspalathus albens	4	Salvia africana-caerulea	+
Isolepis marginata	+	Struthiola leptantha	+
Leucosperm hypophyllo s. canalicula	2	Thamnochortus sporadicus	1
Oxalis polyphylla	+	Zygophyllum spinosum	+
Phylica cephalantha	2		

=> Relevé number: 7

```
Nr. table in publ.          : M
Cover abundance scale       : Braun/Blanquet (old)
Relev, area (m2)            : 50.00
Altitude (m)                : 195
Cover tree layer (%)        : 0
Lat                         : 333142.79
Long                        : 182856.18
```

Aspalathus albens	2	Phylica stipularis	1
Calopsis viminea	+	Rhus laevigata	2
Eriospermum species	+	Ruschia species	+
Helichrysum indicum	+	Staberoha cernua	+
Ischyrolepis monanthos	2	Staberoha distachyos	1
Oxalis versicolor	+	Thamnochortus species	+
Passerina filiformis	+	Willdenowia arescens	1
Phylica cephalantha	2	Zygophyllum spinosum	+

=> Relevé number: 8

```
Nr. table in publ.          : S
Cover abundance scale       : Braun/Blanquet (old)
Relev, area (m2)            : 50.00
Altitude (m)                : 195
Cover tree layer (%)        : 75-100
Lat                         : 333153.02
Long                        : 182856.49
```

Aspalathus species	1	Restio species	2
Cliffortia polygonifolia	+	Rhus species	+
Clutia polifolia	+	Thamnochortus punctatus	1
Othonna species	+	Thamnochortus species	1
Oxalis versicolor	+	Ursinia species	+
Phylica cephalantha	1		

=> Relevé number: 9

```
Nr. table in publ.        : AH
Cover abundance scale     : Braun/Blanquet (old)
Relev, area (m2)          : 50.00
Altitude (m)              : 195
Cover tree layer (%)      : 25-50
Lat                       : 333134.23
Long                      : 182835.96
```

Asparagus capensis	+	Phylica cephalantha	1
Cliffortia polygonifolia	+	Rhus laevigata	+
Grisebachia plumosa	+	Ruschia species	+
Leucadendron species	+	Salvia species	+
Othonna filicaulis	+	Struthiola leptantha	1
Othonna species	+	Thamnochortus erectus	2
Oxalis luteola	+	Thamnochortus punctatus	2
Oxalis versicolor	+	Zygophyllum species	+

=> Relevé number: 10

```
Nr. table in publ.        : AG
Cover abundance scale     : Braun/Blanquet (old)
Relev, area (m2)          : 50.00
Altitude (m)              : 195
Cover tree layer (%)      : 50-75
Lat                       : 333128.16
Long                      : 182844.45
```

Cliffortia falcata	+	Passerina vulgaris	+
Cliffortia polygonifolia	+	Pelargonium triste	+
Grisebachia plumosa	1	Phylica cephalantha	3
Muraltia species	+	Rumex species	+
Othonna species	+	Serruria fasciflora	1
Oxalis luteola	+	Thamnochortus erectus	2
Oxalis polyphylla	+	Thamnochortus punctatus	2
Oxalis versicolor	+	Zygophyllum species	+

=> Relevé number: 11

```
Nr. table in publ.        : AL
Cover abundance scale     : Braun/Blanquet (old)
Relev, area (m2)          : 50.00
Altitude (m)              : 195
Cover tree layer (%)      : 50
Lat                       : 333143.66
Long                      : 182836.04
```

Anthospermum species	+	Oxalis versicolor	+
Calopsis viminea	+	Phylica cephalantha	2
Cannomois parviflora	1	Phylica stipularis	+
Cliffortia falcata	+	Salvia species	+
Grisebachia plumosa	+	Staberoha cernua	1
Leucadendron species	+	Staberoha distachyos	1
Leucosperm hypophyllo s. canalicula	+	Tribolium uniolae	+
Othonna species	+	Ursinia species	+
Oxalis species	+	Zygophyllum spinosum	+

=> Relevé number: 12

```
Nr. table in publ.        : AM
Cover abundance scale     : Braun/Blanquet (old)
Relev, area (m2)          : 50.00
Altitude (m)              : 195
Cover tree layer (%)      : 50-75
Lat                       : 333146.08
```

Long	: 182837.14		
Aristea dichotoma	+	Othonna species	+
Aspalathus divaricata	1	Oxalis luteola	+
Asparagus species	+	Oxalis versicolor	+
Calopsis viminea	1	Phylica cephalantha	2
Cliffortia drepanoides	+	Phylica stipularis	+
Clutia africana	+	Rhus laevigata	+
Ehrharta villosa	+	Ruschia species	+
Grisebachia plumosa	+	Salvia species	+
Ischyrolepis monanthos	+	Stoebe bruniades	+
Leucadendron species	+	Willldenowia species	1

=> Relevé number: 13

Nr. table in publ.	: AJ
Cover abundance scale	: Braun/Blanquet (old)
Relev, area (m2)	: 50.00
Altitude (m)	: 195
Cover tree layer (%)	: 25-50
Lat	: 333140.43
Long	: 182834.35

Aspalathus divaricata	+	Oxalis species	+
Cliffortia falcata	+	Oxalis versicolor	+
Diosma oppositifolia	+	Phylica cephalantha	+
Diosma species	+	Rhus laevigata	2
Erica mammosa	+	Ruschia species	+
Grisebachia plumosa	1	Staberoha distachyos	1
Ischyrolepis monanthos	2	Thamnochortus erectus	1
Othonna species	+	Ursinia species	+

=> Relevé number: 14

Nr. table in publ.	: AI
Cover abundance scale	: Braun/Blanquet (old)
Relev, area (m2)	: 50.00
Altitude (m)	: 195
Cover tree layer (%)	: 25-50
Lat	: 333134.61
Long	: 182837.64

Asparagus capensis	+	Phylica cephalantha	2
Leucosperm hypophyllo s. canalicula	+	Rhus laevigata	+
Oxalis luteola	+	Serruria fasciflora	2
Oxalis polyphylla	+	Thamnochortus erectus	3
Passerina vulgaris	1	Thamnochortus punctatus	3

=> Relevé number: 15

Nr. table in publ.	: R
Cover abundance scale	: Braun/Blanquet (old)
Relev, area (m2)	: 50.00
Altitude (m)	: 195
Cover tree layer (%)	: 75-100
Lat	: 333154.02
Long	: 182855.25

Anthospermum species	+	Rhus laevigata	1
Aspalathus albens	+	Rumex species	+
Microloma sagittatum	+	Struthiola leptantha	+
Oxalis versicolor	+	Thamnochortus species	2
Phylica cephalantha	1	Thesium virgatum	+

=> Relevé number: 16

Nr. table in publ.	: T
Cover abundance scale	: Braun/Blanquet (old)
Relev, area (m2)	: 50.00
Altitude (m)	: 195
Cover tree layer (%)	: 50-75
Lat	: 333154.07
Long	: 182844.33

Anthospermum galioides s. galioides	+	Phylica cephalantha	3
Calopsis viminea	+	Phylica stipularis	2
Oxalis luteola	+	Rhus laevigata	3
Oxalis versicolor	+	Willdenowia sulcata	2
Passerina vulgaris	1		

=> Relevé number: 17

```
Nr. table in publ.          : E
Cover abundance scale       : Braun/Blanquet (old)
Relev, area (m2)            : 50.00
Altitude (m)                : 195
Cover tree layer (%)        : 75-100
Lat                         : 333115.06
Long                        : 182859.47
```

Calopsis viminea	+	Thamnochortus erectus	1
Ficinia species	+	Thamnochortus species	+
Metalasia muricata	1	Willdenowia sulcata	2
Oxalis polyphylla	+	Zygophyllum sessilifolium	+
Staberoha cernua	+		

=> Relevé number: 18

```
Nr. table in publ.          : F
Cover abundance scale       : Braun/Blanquet (old)
Relev, area (m2)            : 50.00
Altitude (m)                : 195
Cover tree layer (%)        : 75-100
Lat                         : 333118.04
Long                        : 182900.15
```

Asparagus capensis v. capensis	+	Passerina vulgaris	+
Clutia species	+	Rhus laevigata	+

=> Relevé number: 19

```
Nr. table in publ.          : G
Cover abundance scale       : Braun/Blanquet (old)
Relev, area (m2)            : 50.00
Altitude (m)                : 195
Cover tree layer (%)        : 75-100
Lat                         : 333119.91
Long                        : 182859.49
```

Clutia africana	+	Passerina vulgaris	+
Ehrharta species	+	Rhus laevigata	+
Leucadendron species	+	Tribolium uniolae	+

=> Relevé number: 20

```
Nr. table in publ.          : B
Cover abundance scale       : Braun/Blanquet (old)
Relev, area (m2)            : 50.00
Altitude (m)                : 195
Cover tree layer (%)        : 0
Lat                         : 333118.88
Long                        : 182902.83
```

Aspalathus albens	+	Restio species	+
Cassytha ciliolata	+	Rhus laevigata	+
Chondropetalum nudum	1	Serruria species	+
Cryptadenia grandiflora	+	Staavia radiata	+
Diosma oppositifolia	1	Staberoha cernua	+
Erica mammosa	+	Struthiola leptantha	+
Grisebachia plumosa	+	Thalassodendron species	+
Ischyrolepis monanthos	+	Thamnochortus species	1
Leucosperm hypophyllo s. canalicula	+	Ursinia anthemoides	+
Passerina vulgaris	+	Willdenowia sulcata	+
Pentaschistis species	+	Zygophyllum species	+
Phylica cephalantha	2		

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=> Relevé number: 21

```
Nr. table in publ.            : A
Cover abundance scale         : Braun/Blanquet (old)
Relev, area (m2)              : 50.00
Altitude (m)                  : 195
Cover tree layer (%)          : 25-50
Lat                           : 333115.08
Long                          : 182903.55
```

Aspalathus attenuata	+	Passerina vulgaris	1
Calopsis viminea	+	Phylica cephalantha	4
Chondropetalum nudum	1	Phylica stipularis	+
Diosma oppositifolia	+	Prismatocarpus species	+
Ehrharta villosa	+	Serruria fasciflora	+
Grisebachia plumosa	1	Tribolium uniolae	+
Ischyrolepis monanthos	+	Willdenowia species	+
Metalasia muricata	+		

=> Relevé number: 22

```
Nr. table in publ.            : C
Cover abundance scale         : Braun/Blanquet (old)
Relev, area (m2)              : 50.00
Altitude (m)                  : 195
Cover tree layer (%)          : 0
Lat                           : 333117.38
Long                          : 182902.49
```

Berzelia abrotanoides	+	Phylica cephalantha	2
Cassytha ciliolata	+	Phylica stipularis	+
Chondropetalum nudum	+	Restio species	+
Crassula setulosa	+	Serruria fasciflora	+
Diosma aspalathoides	+	Staavia radiata	+
Diosma oppositifolia	1	Struthiola leptantha	+
Euchaetis scabricosta	+	Willdenowia species	+
Ficinia deusta	+	Willdenowia sulcata	+
Heliophila species	+	Zygophyllum species	+
Ischyrolepis monanthos	+	Zygophyllum spinosum	+
Leucosperm hypophyllo s. canalicula	1		

=> Relevé number: 23

```
Nr. table in publ.            : D
Cover abundance scale         : Braun/Blanquet (old)
Relev, area (m2)              : 50.00
Altitude (m)                  : 195
Cover tree layer (%)          : 75-100
Lat                           : 333116.14
Long                          : 182958.98
```

Anthospermum species	+	Phylica cephalantha	1
Asparagus rubicundus	+	Restio species	+
Grisebachia plumosa	+	Rhus laevigata	+
Ischyrolepis monanthos	+	Salvia africana-caerulea	+
Leucosperm hypophyllo s. canalicula	1	Thamnochortus erectus	+
Passerina vulgaris	+	Thamnochortus species	+
Pelargonium myrrhifolium	+		

=> Relevé number: 24

```
Nr. table in publ.            : H
Cover abundance scale         : Braun/Blanquet (old)
Relev, area (m2)              : 50.00
Altitude (m)                  : 195
Cover tree layer (%)          : 25-50
Lat                           : 333123.44
Long                          : 182959.97
```

Aristea dichotoma	+	Metalasia muricata	1
Aspalathus divaricata	+	Oxalis luteola	+
Aspalathus species	1	Phylica cephalantha	4

Cliffortia falcata	+	Phylica gracilis	+
Ehrharta species	+	Rhus laevigata	+
Erica coarctata	+	Thamnochortus erectus	+
Grisebachia plumosa	+	Thamnochortus species	2
Ischyrolepis monanthos	+	Tribolium uniolae	+
Leucosperm hypophyllo s. canalicula	+	Ursinia species	+
Macrostylis villosa	+		

=> Relevé number: 25

Nr. table in publ.	: I
Cover abundance scale	: Braun/Blanquet (old)
Relev, area (m2)	: 50.00
Altitude (m)	: 195
Cover tree layer (%)	: 50-75
Lat	: 333124.12
Long	: 182900.40

Aristea dichotoma	+	Oxalis polyphylla	+
Asparagus rubicundus	+	Passerina vulgaris	+
Calopsis viminea	+	Phylica cephalantha	3
Cliffortia polygonifolia	+	Phylica stipularis	+
Leucosperm hypophyllo s. canalicula	+	Restio species	3
Macrostylis villosa	+	Rhus laevigata	+
Oxalis luteola	+	Ursinia species	+

=> Relevé number: 26

Nr. table in publ.	: J
Cover abundance scale	: Braun/Blanquet (old)
Relev, area (m2)	: 50.00
Altitude (m)	: 195
Cover tree layer (%)	: 50-75
Lat	: 333139.13
Long	: 182905.06

Cliffortia falcata	+	Passerina vulgaris	+
Cliffortia ruscifolia	+	Pentaschistis species	+
Ehrharta species	+	Phylica abietina	2
Ehrharta villosa	+	Rhus laevigata	2
Metalasia muricata	+	Ursinia species	2
Oxalis versicolor	2		

=> Relevé number: 27

Nr. table in publ.	: N
Cover abundance scale	: Braun/Blanquet (old)
Relev, area (m2)	: 50.00
Altitude (m)	: 195
Lat	: 333156.93
Long	: 182849.05

Aspalathus albens	2	Ruschia species	+
Asparagus capensis	+	Salvia lanceolata	+
Ficinia species	+	Staberoha cernua	2
Leucosperm hypophyllo s. canalicula	+	Staberoha distachyos	1
Oxalis versicolor	+	Thamnochortus species	+
Passerina ericoides	2	Willdenowia sulcata	1
Phylica cephalantha	3	Zygophyllum species	+

=> Relevé number: 28

Nr. table in publ.	: O
Cover abundance scale	: Braun/Blanquet (old)
Relev, area (m2)	: 50.00
Altitude (m)	: 195
Lat	: 333155.66
Long	: 182847.43

Aspalathus albens	2	Rhus laevigata	2
Ischyrolepis monanthos	2	Rumex species	+
Oxalis versicolor	+	Staberoha cernua	2
Passerina vulgaris	2	Staberoha distachyos	1

```
Phylica cephalantha                        4    Struthiola leptantha                    +
Phylica gracilis                           +    Thamnochortus species                  2
```

=> Relevé number: 29

```
Nr. table in publ.              : P
Cover abundance scale           : Braun/Blanquet (old)
Relev, area (m2)                : 50.00
Altitude (m)                    : 195
Lat                             : 333154.14
Long                            : 182846.57
```

```
Aspalathus albens                          2    Phylica cephalantha                    3
Cannomois parviflora                       2    Phylica stipularis                     +
Cliffortia polygonifolia                   +    Restio filiformis                      +
Diosma oppositifolia                       +    Thamnochortus species                  +
Leucosperm hypophyllo s. canalicula        1    Zygophyllum spinosum                   1
Oxalis versicolor                          +
```

=> Relevé number: 30

```
Nr. table in publ.              : Q
Cover abundance scale           : Braun/Blanquet (old)
Relev, area (m2)                : 50.00
Altitude (m)                    : 195
Lat                             : 333152.77
Long                            : 182849.73
```

```
Aspalathus albens                          3    Phylica cephalantha                    2
Asparagus species                          +    Phylica species                        +
Calopsis viminea                           +    Phylica stipularis                     +
Cliffortia falcata                         1    Putterlickia pyracantha                +
Cliffortia polygonifolia                   1    Rhus laevigata                         +
Diosma oppositifolia                       +    Ruschia species                        2
Othonna species                            +    Salvia species                         +
Oxalis versicolor                          +    Zygophyllum spinosum                   2
```

=> Relevé number: 31

```
Nr. table in publ.              : U
Cover abundance scale           : Braun/Blanquet (old)
Relev, area (m2)                : 50.00
Altitude (m)                    : 195
Cover tree layer (%)            : 25-50
Lat                             : 333123.26
Long                            : 182841.54
```

```
Aspalathus divaricata                      1    Phylica cephalantha                    1
Chondropetalum species                     2    Phylica gracilis                       +
Cliffortia falcata                         1    Phylica imberbis                       +
Erica species                              +    Phylica species                        +
Leucosperm hypophyllo s. canalicula        +    Staavia radiata                        +
Metalasia muricata                         2    Struthiola leptantha                   +
Oxalis luteola                             +    Thamnochortus species                  2
Pelargonium oenothera                      +    Tribolium uniolae                      +
```

=> Relevé number: 32

```
Nr. table in publ.              : V
Cover abundance scale           : Braun/Blanquet (old)
Relev, area (m2)                : 50.00
Altitude (m)                    : 195
Cover tree layer (%)            : 25
Lat                             : 333124.54
Long                            : 182841.05
```

```
Aspalathus divaricata                      +    Pelargonium oenothera                  +
Cliffortia falcata                         +    Phylica cephalantha                    3
Diosma oppositifolia                       2    Phylica stipularis                     1
Grisebachia plumosa                        +    Restio species                         +
Leucosperm hypophyllo s. canalicula        1    Serruria fasciflora                    1
Macrostylis villosa                        +    Thamnochortus species                  +
Oxalis luteola                             +    Zygophyllum spinosum                   +
```

```
Oxalis species                        +
=> Relevé number: 33

Nr. table in publ.         : X
Cover abundance scale      : Braun/Blanquet (old)
Relev, area (m2)           : 50.00
Altitude (m)               : 195
Cover tree layer (%)       : 75-100
Lat                        : 333119.95
Long                       : 182843.97

Phylica species                       +      Rhus laevigata                    +


=> Relevé number: 34

Nr. table in publ.         : W
Cover abundance scale      : Braun/Blanquet (old)
Relev, area (m2)           : 50.00
Altitude (m)               : 195
Cover tree layer (%)       : 75-100
Lat                        : 333119.47
Long                       : 182846.05

Oxalis versicolor                     +      Salvia africana-caerulea          +
Pelargonium triste                    +      Struthiola leptantha              +
Phylica cephalantha                   1      Ursinia species                   +
Rhus species                          +      Zygophyllum spinosum              +


=> Relevé number: 35

Nr. table in publ.         : Y
Cover abundance scale      : Braun/Blanquet (old)
Relev, area (m2)           : 50.00
Altitude (m)               : 195
Cover tree layer (%)       : 75-100
Lat                        : 333120.14
Long                       : 182839.97

Asparagus capensis v. capensis        +      Metalasia muricata                1
Cliffortia falcata                    +      Oxalis luteola                    +
Leucosperm hypophyllo s. canalicula   +      Serruria fasciflora               +


=> Relevé number: 36

Nr. table in publ.         : Z
Cover abundance scale      : Braun/Blanquet (old)
Relev, area (m2)           : 50.00
Altitude (m)               : 195
Cover tree layer (%)       : 75-100
Lat                        : 333123.21
Long                       : 182842.09

Asparagus capensis v. capensis        1      Oxalis luteola                    1
Cliffortia falcata                    +      Phylica ericoides                 +
Diosma species                        +      Phylica species                   1
Metalasia muricata                    +      Serruria fasciflora               +
Othonna species                       +      Ursinia species                   +


=> Relevé number: 37

Nr. table in publ.         : AA
Cover abundance scale      : Braun/Blanquet (old)

Relev, area (m2)           : 50.00
Altitude (m)               : 195
Cover tree layer (%)       : 50-75
Lat                        : 333123.09
Long                       : 182846.07

Cliffortia falcata                    +      Pentaschistis species             +
Cryptadenia grandiflora               +      Salvia species                    +
Metalasia muricata                    +      Staavia radiata                   +
Oxalis luteola                        +      Staberoha distachyos              2
```

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Passerina vulgaris   +   Ursinia species   +
Pelargonium species   +

=> Relevé number: 38

Nr. table in publ.   : AE
Cover abundance scale   : Braun/Blanquet (old)
Relev, area (m2)   : 50.00
Altitude (m)   : 195
Cover tree layer (%)   : 50-75
Lat   : 333123.46
Long   : 182840.54

Agathosma species   +   Oxalis luteola   +
Asparagus capensis v. capensis   +   Phylica cephalantha   2
Chondropetalum nudum   +   Rhus laevigata   +
Cliffortia polygonifolia   +   Salvia species   +
Clutia africana   +   Serruria species   1
Grisebachia plumosa   1   Staavia radiata   +
Leucosperm hypophyllo s. canalicula   +   Staberoha distachyos   +
Metalasia muricata   +   Thamnochortus species   +
Othonna species   +   Zygophyllum spinosum   +

=> Relevé number: 39

Nr. table in publ.   : AN
Cover abundance scale   : Braun/Blanquet (old)
Relev, area (m2)   : 50.00
Altitude (m)   : 195
Cover tree layer (%)   : 50-75
Lat   : 333143.35
Long   : 182834.29

Aspalathus albens   +   Rhus laevigata   +
Asparagus capensis v. capensis   +   Rumex species   +
Erica mammosa   +   Ruschia species   +
Leucadendron species   +   Staberoha cernua   1
Leucosperm hypophyllo s. canalicula   +   Staberoha distachyos   1
Othonna species   +   Thamnochortus sporadicus   1
Oxalis versicolor   +   Zygophyllum species   +
Pelargonium triste   +   Zygophyllum spinosum   +
Phylica cephalantha   1

=> Relevé number: 40

Nr. table in publ.   : AF
Cover abundance scale   : Braun/Blanquet (old)
Relev, area (m2)   : 50.00
Altitude (m)   : 195
Cover tree layer (%)   : 25-50
Lat   : 333115.06
Long   : 182843.11

Cliffortia falcata   +   Phylica cephalantha   2
Diosma oppositifolia   +   Phylica species   +
Erica coarctata   +   Phylica stipularis   +
Grisebachia plumosa   +   Serruria fasciflora   3
Leucadendron species   +   Staberoha cernua   +
Leucosperm hypophyllo s. canalicula   +   Staberoha distachyos   +
Metalasia muricata   +   Thamnochortus erectus   2
Oxalis polyphylla   +   Thamnochortus sporadicus   1
Passerina ericoides   1   Zygophyllum spinosum   +

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Braun-Blanquet table

```
Cassytha ciliolata        2 2.  . |.  .  .  . |.  .  . |.  .  . |. |. |.  .  . |.  .  |.  .  .  . |.  .  |.  .  .  . |.  .  |.  .  .
Serruria species          2.  .  3|.  .  .  . |.  .  . |.  .  . |. |. |.  .  . |.  .  |.  .  .  . |.  .  |.  .  .  . |.  .  |.  .  .
Thalassodend species      2.  .  . |.  .  .  . |.  .  . |.  .  . |. |. |.  .  . |.  .  |.  .  .  . |.  .  |.  .  .  . |.  .  |.  .  .
Ursinia anthemoides       2.  .  . |.  .  .  . |.  .  . |.  .  . |. |. |.  .  . |.  .  |.  .  .  . |.  .  |.  .  .  . |.  .  |.  .  .
Berzelia abrotanoides      . 2.  . |.  .  .  . |.  .  . |.  .  . |. |. |.  .  . |.  .  |.  .  .  . |.  .  |.  .  .  . |.  .  |.  .  .
Crassula setulosa          . 2.  . |.  .  .  . |.  .  . |.  .  . |. |. |.  .  . |.  .  |.  .  .  . |.  .  |.  .  .  . |.  .  |.  .  .
Diosma aspalathoides       . 2.  . |.  .  .  . |.  .  . |.  .  . |. |. |.  .  . |.  .  |.  .  .  . |.  .  |.  .  .  . |.  .  |.  .  .
Ficinia deusta             . 2.  . |.  .  .  . |.  .  . |.  .  . |. |. |.  .  . |.  .  |.  .  .  . |.  .  |.  .  .  . |.  .  |.  .  .
Heliophila species         . 2.  . |.  .  .  . |.  .  . |.  .  . |. |. |.  .  . |.  .  |.  .  .  . |.  .  |.  .  .  . |.  .  |.  .  .
Macros villos s. minor    .  . 2.  |.  .  .  . |.  .  . |.  .  . |. |. |.  .  . |.  .  |.  .  .  . |.  .  |.  .  .  . |.  .  |.  .  .
Agathosma species         .  .  . 2|.  .  .  . |.  .  . |.  .  . |. |. |.  .  . |.  .  |.  .  .  . |.  .  |.  .  .  . |.  .  |.  .  .
Euchaetis scabricosta      . 2.  . |.  2.  . |.  .  . |.  .  . |. |. |.  .  . |.  .  |.  .  .  . |.  .  |.  .  .  . |.  .  |.  .  .
Cryptadenia grandiflor    2.  .  . |.  .  .  . |.  .  . |.  .  . |. |. |.  .  . |.  .  |.  .  .  . |.  .  |.  .  .  . |.  .  |.  .  2
Pelargonium oenothera     .  . 2.  |.  .  .  . |.  .  . |.  .  . |. |. |.  .  . |.  .  |.  .  .  . |.  .  |. 2.  . |.  .  |.  .  .
Metalasia muraltiifoli    .  .  . 2|.  .  .  . |.  .  . |.  .  . |. |. |.  .  . |.  .  |.  .  .  . |.  .  |.  .  2| .  .  .  |.  .  .
Pentaschistis species     2.  .  . |.  .  .  . |.  .  . |. |. |.  .  . |.  .  .  . |.  .  |.  .  .  . |.  .  |.  .  .  . |. 2 2
Thamnochortus erectus     .  .  .  . | 2.  .  . |.  .  . |.  .  . | 3| .  2.  . |.  7.  6| .  3| .  6.  | 6.  | 2.  .  . |.  .  .  . |.  .  .
Grisebachia plumosa       2.  2 3| .  2.  . |.  .  . |.  .  . | 3| .  .  3 2| .  .  | .  3.  | 2 2| 2.  .  . |.  .  .  . |.  .  .
Willdenowia species        . 2.  . |.  .  .  . |.  .  . |. |. |.  .  . |.  .  2.  | .  . |.  .  .  . |.  3| .  .  .  . |.  .  |.  .  .
Cliffortia polygonifol    .  .  . 2| .  .  .  . |.  2.  . |.  .  . |.  .  .  . |. |.  | 2 2 2| 2.  . |.  .  .  . |.  .  |.  .  .
Phylica stipularis         . 2 3.  |.  .  .  . | 2 2 2| 3.  . |. |.  .  .  . |.  .  2 2| 6.  | .  .  2| .  2| .  .  .  . |.  .  .
Willdenowia sulcata       2 2.  . | 6 6 3.  |.  .  . |. 3.  | .  | .  .  .  . |.  .  .  . | 6 6| .  .  .  . | .  | .  .  .  . |.  .  |.  .  .
Restio species            2 2 2.  | .  2.  2| .  .  . |.  .  . |. | .  2.  . |.  .  .  . | .  | 6.  7| .  .  | .  .  .  . |.  .  |.  .  .
Chondropetalum nudum      3 2.  2| .  .  .  . |.  .  . |.  .  . |. |. |.  .  . |.  .  3.  | .  . |.  .  .  . |.  .  |.  .  .  . |.  .  |.  .  .
Ischyrolepis monanthos    2 2.  . |.  .  .  . |.  .  . | 6.  .  | 6| .  2 6.  | 3.  2.  | .  .  | .  |.  .  2| 2.  .  . |.  .  .
Othonna species           .  .  . 2| 2 2 2.  | 2.  2| .  .  2| 2| .  .  .  . |.  .  |.  .  | 2 2.  | 2 2| .  .  .  2| .  .  |.  .  .
Zygophyllum species       2 2.  . |.  .  .  . |. |.  .  | .  2 2| .  |.  .  .  . |.  .  | .  | .  2.  | 2.  |.  .  .  . |.  .  .
Staberoha cernua          2.  .  . |.  .  3.  | 3.  . | 2 6 3| .  |.  .  6.  | .  .  2| .  2| .  .  .  . |.  .  .  . |.  .  .
Oxalis species            .  . 2.  |.  .  .  . | 2.  . |.  .  . | 2| .  .  .  . |.  .  . |.  .  .  . |.  .  |.  .  .  . |.  .  |.  .  .
Erica mammosa             2.  .  . |.  .  .  . |.  .  | .  2| 2| .  .  .  . |.  .  | .  |.  .  | .  .  .  . |.  .  | .  |.  .  .
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Aspalathus albens        2. . .  | 6. .  8| . 6 7| 6 6 2| . | 2. 6. |. . . . |. . |. . . |. . |. . |. . . |. . |. . |. . . |. . .
Zygophyllum spinosum   . 2 2 2|. 2 2 2| 2 3 6| 2. 2|. |. . . 2|. . . 2|. . |. . |. . |. . . |. . |. . |. . 2 2|. . . |. . .
Diosma oppositifolia     3 3 6. |. . . . |. 2 2|. . . | 2|. . . . |. . 2 2|. . |. . |. . . |. . |. . |. . . |. . . |. . .
Serruria fasciflora      . 2 3. | 2 3 6. |. . . |. . . |. |. . . . |. 6 2 7|. . |. 3. |. . |. . |. . 2 2|. . . |. . .
Phylica cephalantha    6 6 7 6| 6 7 7 6| 6 7 6| 6 7 3| 2| 3 3 8 3| 6 6 8 6| 7. | 3 7 7| 3 6| 8 3. . |. . . |. 6. .
Rhus laevigata          2. . 2| 2. 2. |. . 2|. . 2| 6| 3. . . | 2 2. . | 7. |. . 2| 2 2|. . . . |. . |. 6.
Salvia species          . . . 2|. 2. . | 2. 2|. . . |. |. . . . |. . . . |. . |. . |. . |. . 2 2|. . . . |. . |. . 2
Leucos hypoph s. canal 2 3 3 2| 2. . 6| 2 3. |. 2 2|. |. 3. . |. 2. 2|. . |. . 2|. . | 2 2 2. |. . |. . .
Staberoha distachyos    . . . 2|. 3 3. |. 3. . | 3 3 3| 3|. . 3. |. . . 2|. . |. . |. . |. . . |. . |. . |. . 6
Struthiola leptantha     2 2. . |. . . 2|. . . |. . . |. | 2. 2 2|. . . . |. . |. . |. . | 3. |. 2. |. . |. . .
Thamnochortus species 3. 2 2|. . . . |. 2. | 2 2. |. | 6 2 6. |. . . . |. . |. 2| 3. . |. . | 6 6. . |. . |. . .
Staavia radiata          2 2. 2|. . . . |. . . |. . . |. |. . . . |. . . . |. . |. . |. . |. 2. . |. . |. . 2
Aspara capens v. capen . . . 2| 2. 2. |. . . |. . . | 2|. |. . . . |. . . . |. . |. . |. . |. . 2 3| 2. . |. . .
Cliffortia falcata       . . 2. | 2 2. . |. 2. 3|. . . | 2|. . . . |. . 2|. . |. 2. |. . | 2 3 2 2|. . . | 2 2 2
Oxalis luteola          . . 2 2|. . . . |. . . |. . . |. |. . . . |. 2. . | 2. |. 2 2| 2 2| 2 2 2 3|. . . |. . 2
Aspalathus divaricata    . . 2. |. . . |. . . |. . . | 2|. . . . |. . . . |. . |. . |. 3| 2 3. . |. . . |. . .
Clutia africana         . . . 2|. . . |. . . |. . . |. |. . . . |. . . . |. . |. . |. 2|. . . . |. 2. |. . .
Passerina vulgaris      2. . . | 2 2. . |. . . |. . . |. |. 2 6. | 2 3 3. | 3. |. 2 2|. . |. . . | 2 2. | 2 2 2
Acrosanthes teretifoli   . . . . | 2. . . |. . . |. . . |. |. . . . |. . . . |. . |. . |. . |. . . . |. . |. . .
Thamnochortus obtusus . . . . | 2. . . |. . . |. . . |. |. . . . |. . . . |. . |. . |. . |. . . . |. . |. . .
Aspalathus microphylla  . . . . |. . 2. |. . . |. . . |. |. . . . |. . . . |. . |. . |. . |. . . . |. . |. . .
Isolepis marginata       . . . . |. . 2| . . . |. . . |. |. . . . |. . . . |. . |. . |. . |. . . . |. . |. . .
Oxalis polyph v. alba    . . . . |. . 2|. . . |. . . |. |. . . . |. . . . |. . |. . |. . |. . . . |. . |. . .
Calopsis viminea        . . . |. 2. . | 2. 2| 2. . |. |. . . . | 2. 2. | 2 2. . | 2|. 3|. . . . |. . |. . .
Ficinia species          . . . |. 2. . |. . . |. 2. |. |. . . . |. . . . |. . | 2|. . . . |. . |. . .
Thamnochortu sporadicu . . . . |. 6. 3|. . . |. . 3|. |. . . . | 3. . 3|. . |. . |. . . . |. . |. . .
Clutia polifolia         . . . . |. . 2. |. . . |. . . |. |. . . . |. . . . |. 2. . |. . . . |. . |. . .
Pelargonium triste      . . . . |. . 2. |. . . | 2|. |. . . 2|. . . . |. . |. 2. |. . . . |. . |. . .
Cannomois parviflora    . . . . |. . 3. | 3 6. |. . . |. |. . . . |. . . . |. . |. . |. . . . |. . |. . .
Salvia africana-cae     . . . |. . . 2|. . . |. . |. | 2. 2|. . . . |. . |. . |. . . . |. . |. . .
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Aristea dichotoma   . . . . | 2 2 2 2| . . . | . . . | . | . . . . | . . . . | . . | . . | . . 2| . 2| 2. . . . | . . . | . . .
Leucadendron species   . . . . | . . . . | 2. . | . . 2| . | . . . . | . . 2| . . | . . . | 2 2| . . . . | . 2. | . . .
Oxalis versicolor   . . . . | . . 2. | 2 2 2| 2 2 2| 2| 2. 2 2| 2. . . | 2. | 2 2. | 2 2| . . . . | . . . | 6 6.
Phylica species   . . . . | . 2 2. | . . 2| . . . | . | . . . . | . . 2| . . | . . . | . . | 2. 3| . . 2| . . .
Restio filiformis   . . . . | . . . . | . 2. | . . . | . | . . . . | . . . | . . | . . . | . . | . . . . | . . . | . . .
Cliffortia polita   . . . . | . . . . | . . 3| . . . | . | . . . . | . . . | . . | . . . | . . | . . . . | . . . | . . .
Putterlickia pyracanth . . . . | . . . . | . . 2| . . . | . | . . . . | . . . | . . | . . . | . . | . . . . | . . . | . . .
Asparagus species   . . . . | . . . . | . . 2| . . . | . | . . . . | . . . | . . | . . . | . 2| . . . . | . . . | . . .
Ruschia species   . . . . | . . . . | . . 6| 2 2 2| 2| . . . . | . . . | . . | . . . | 2 2| . . . . | . . . | . . .
Anthospermum species   . . . . | . . . . | 2. . | . . . | . | 2 2. . | . . . | . . | . . . | . . | . . . . | . . . | . . .
Griseb plumos s. ecili . . . . | . . . . | 2. . | . . . | . | . 2. . | . . . | . . | . . . | . . | . . . . | . . . | . .
Ursinia species   . . . . | . . . . | 2. . | . . . | 2| . . . 2| . . . | . . | 2. 2| . . | 2. . 2| . . . | . 6 2
Tribolium uniolae   . . . . | . . . . | 2. . | . . . | . | . . . . | . . . 2. | . . | . . . | 2 2. . | 2. . | . . .
Eriospermum species   . . . | . . . . | . . . | 2. . | . | . . . . | . . . | . . | . . . | . . | . . . . | . . . | . . .
Helichrysum indicum   . . . | . . . . | . . . | 2. . | . | . . . . | . . . | . . | . . . | . . | . . . . | . . . | . . .
Passerina filiformis   . . . | . . . . | . . . | 2. . | . | . . . . | . . . | . . | . . . | . . | . . . . | . . . | . . .
Willdenowia arescens   . . . | . . . . | . . . | 3. . | . | . . . . | . . . | . . | . . . | . . | . . . . | . . . | . . .
Aspalathus capensis   . . . | . . . . | . . . | . 2. | . | . . . . | . . . | . . | . . . | . . | . . . . | . . . | . . .
Salvia lanceolata   . . . | . . . . | . . . | . 2. | . | . . . . | . . . | . . | . . . | . . | . . . . | . . . | . . .
Rumex species   . . . | . . . . | . . . | . . 2| . | 2. 2. | . . . . | . . | . 2. | . . | . . . . | . . . | . . .
Passerina ericoides   . . . | . . . . | . . . | . 6. | . | . . . . | . . 3| . . | . . . | . . | . . . . | . . . | . . .
Rhus laevig v. laevig . . . . | . . . . | . . . | 6. . | . | . 2 6. | . . . . | . . | . . . | 2. . . | 2 2 2| . . .
Diosma species   . . . | . . . . | . . . | . . . | 2| . . . . | . . . | . . | . . . | . . | 2| . . . | . . .
Microloma sagittatum   . . . | . . . . | . . . | . . . | . | 2. . . | . . . | . . | . . . | . . | . . . . | . . . | . . .
Thesium virgatum   . . . | . . . . | . . . | . . . | . | 2. . . | . . . | . . | . . . | . . | . . . . | . . . | . . .
Pelargonium myrrhifoli . . . | . . . . | . . . | . . . | . | . 2. . | . . . | . . | . . . | . . | . . . . | . . . | . . .
Rhus species   . . . | . . . . | . . . | . . . | . | . . 2| . . . . | . . | 2. | . . | . . . . | . . . | . . .
Asparagus rubicundus   . . . | . . . . | . . . | . . . | . | . 2. . | . . . | . . | . . 2| . . | . . . . | . . . | . . .
Phylica gracilis   . . . | . . . . | . . . | . . . | . | . 2. | . . . . | . . | . . . | 2 2. . | . . . | . . .
Aspalathus attenuata   . . . | . . . . | . . . | . . . | . | . . . . | 2. | . . | . . . | . . | . . . . | . . . | . . .

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Prismatocarpus species  . . . | . . . . | . . . | . . . | . . . | . | . . . . | . . 2. | . . | . . . | . . | . . . . | . . . | . . .
Asparagus capensis      . . . | . . . . | . . . | . . . | . . | . | . . . . | 2 2. . . | . . | . . . . | 2. | . . . | . . . | . . .
Oxalis polyphylla        . . . | . . . . | . . . | . . . | . . | . . . . | 2 2. 2| . 2| . 2 2| . . | . . . . | . . . |
Poa species              . . . | . . . | . . . | . . . | . . . | 2. . . | . | . | . | . | . | . |
Thamnochortu punctatus  . . . | . . | . . . | . . . | . . . | 2 7. . | . . | 3 6. | 6. | . . . . | . . . | . . .
Metalasia muricata       . . . | . . . | . . . | . . | . | . . . | . . 2 2| . 3| . . . | . . | 3 6 3. | . . . | 2 2 2
Ehrharta villosa         . . . | . . . | . . . | . | . | . . . | . . 2. | . . | . . . | . 2| . . . . | . . | 2 2.
Erica coarctata          . . . | . . . | . . . | . . | . | . . . | . . 2| . . | . . | . . . | 2. . . | . . | . . .
Anthos galioi s. galio   . . . | . . . | . . . | . . . | . . . | . . . | 2. | . . | . . . | . . . | . . . | . . .
Zygophyllum sessilifol   . . . | . . . | . . . | . . . | . . . | . . . | 2| . . . | . . | . . . . | . . . | . . .
Muraltia species         . . . | . . . | . . . | . . . | . . . | . . | . 2. | . . | . . | . . . | . . . | . . .
Aspalathus species       . . . | . . . | . . . | . . . | . . . | . . | 3. . | . . | 3. . . | . . . | . . .
Macrostylis villosa      . . . | . . . | . . . | . . . | . . . | . . | 2| . . | 2. . . | . . . | . . .
Othonna filicaulis       . . . | . . . | . . . | . . . | . . . | . . | 2. | . . . | . . . | . . .
Cliffortia drepanoides   . . . | . . . | . . . | . . . | . . . | . . | 2| . . . | . . . | . . .
Stoebe bruniades         . . . | . . . | . . . | . . . | . . . | . . | 2| . . . | . . . | . . .
Chondropetalum species  . . . | . . . | . . . | . . . | . . . | . | 6. . | . . | . . . | . . .
Erica species            . . . | . . . | . . . | . . . | . . . | . | 2. . | . . | . . . | . . .
Phylica imberbis         . . . | . . . | . . . | . . . | . . . | . | 2. . | . . | . . . | . . .
Phylica ericoides        . . . | . . . | . . . | . . . | . . . | . . | 2| . . | . . .
Ehrharta species         . . . | . . . | . . . | . . . | . . . | . | 2. . | . 2. | . 2.
Clutia species           . . . | . . . | . . . | . . . | . . . | . . | 2. . |
Cliffo ruscif x theodo   . . . | . . . | . . . | . | . | . . . | . . | 2 2.
Phylica abietina         . . . | . . . | . . | . | . | . . . | . . | 6.
Pelargonium species      . . . | . . . | . . . | . . . | . . . | . . . | . . 2
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Appendix C
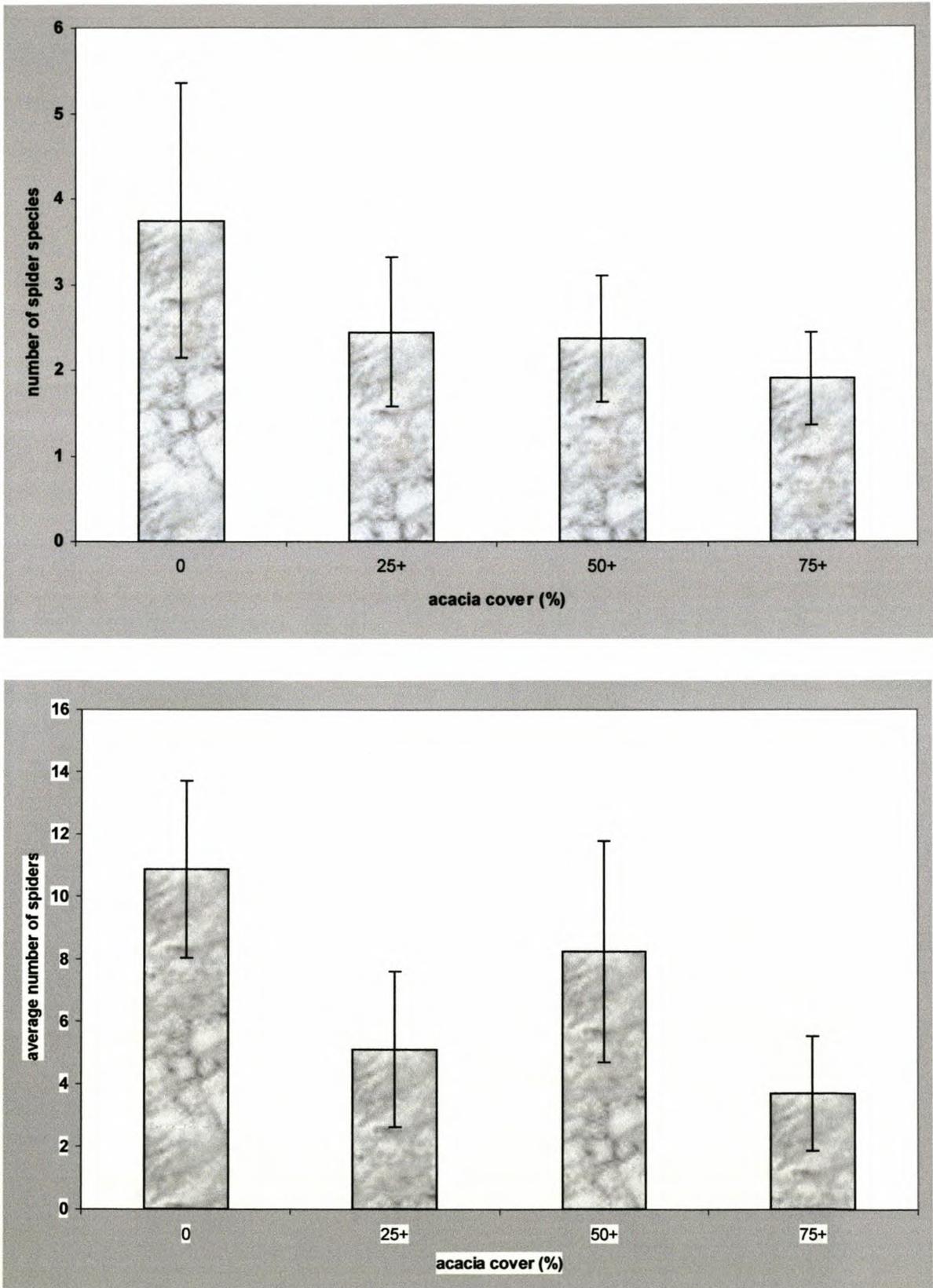
Fig 1: Average number of trapped spider species (top) and average number of individual spiders (bottom), in Coastal Fynbos with a varying degree of *A. saligna* infestation.
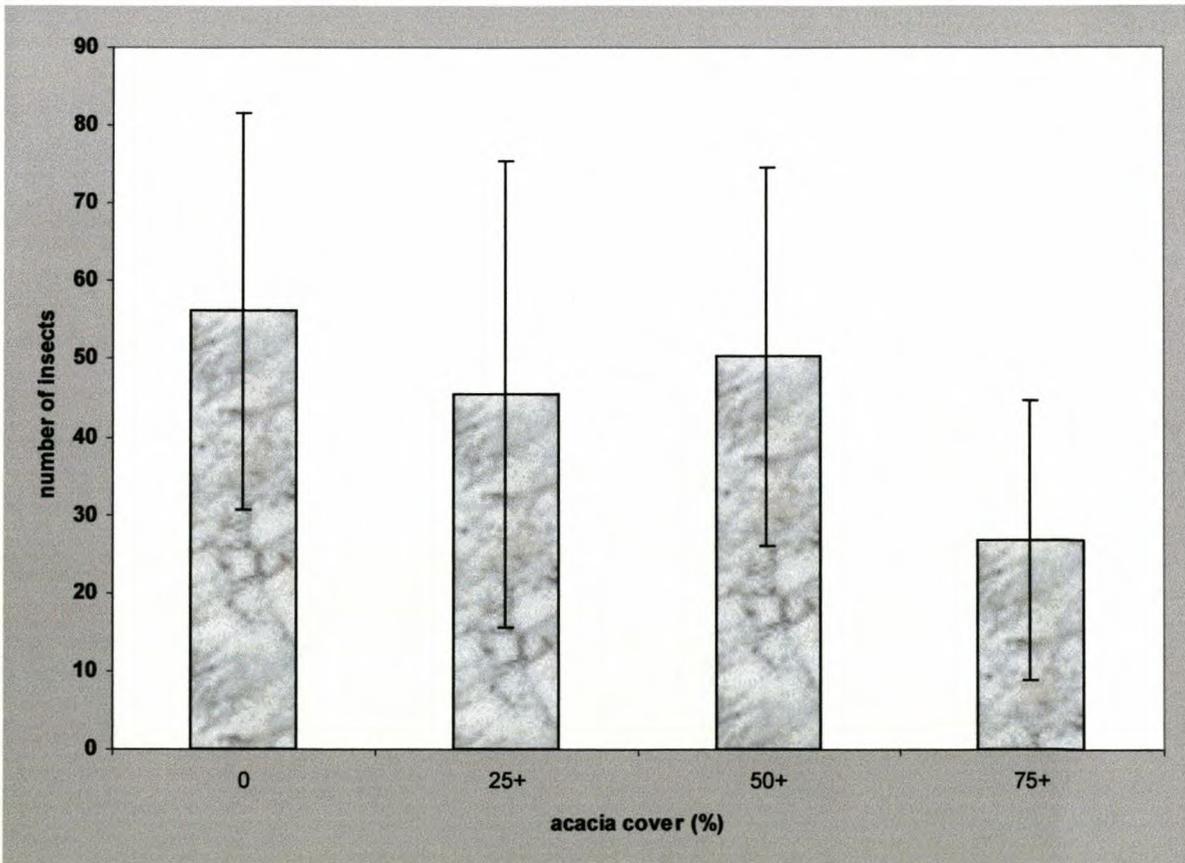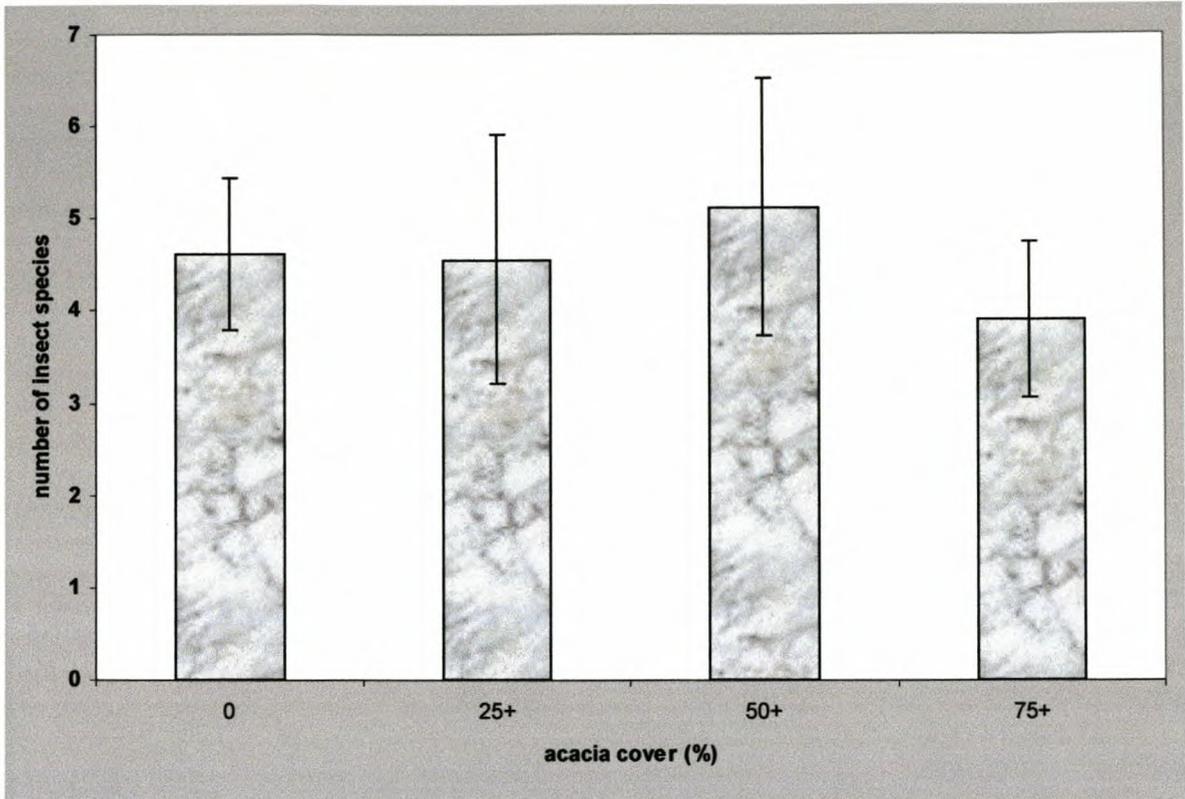
Fig 2: Average number of trapped insect species (top) and average number of individual insects (bottom), in Coastal Fynbos with a varying degree of *A. saligna* infestation.
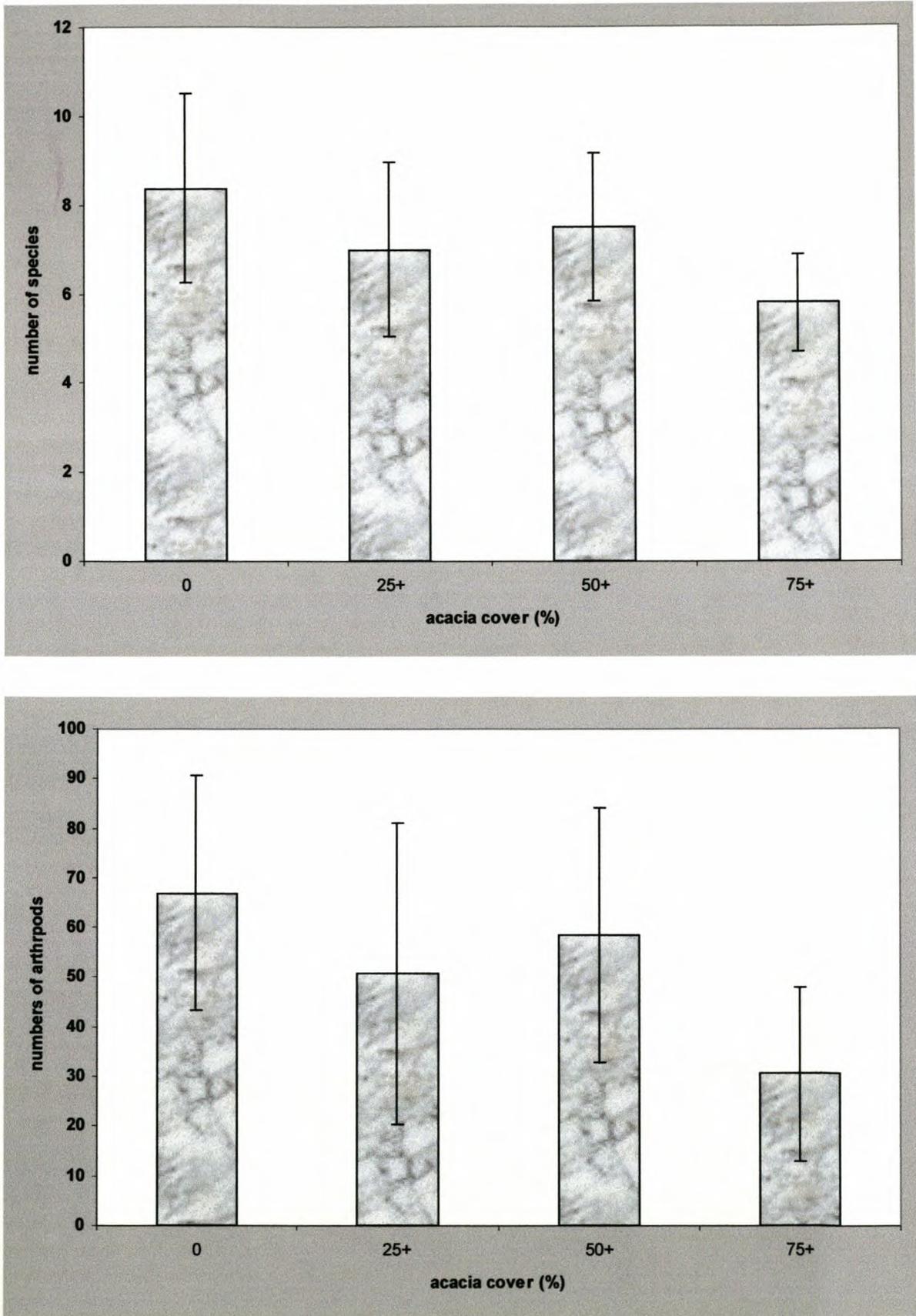
Fig 3: Average number of trapped arthropod species (top) and average number of individual arthropods (bottom), in Coastal Fynbos with a varying degree of *A. saligna* infestation.