STUDIES ON ASPECTS OF THE INTEGRATED CONTROL OF *HAKEA SERICEA* IN THE SOUTH - WESTERN CAPE PROVINCE, SOUTH AFRICA

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ABSTRACT

Invasion by alien woody plants is a major conservation threat in the sclerophyllous shrubland vegetation of the southwestern Cape Province which is known as fynbos. The Australian shrub, Hakea sericea (Proteaceae)is the most serious threat in mountain fynbos catchments. This study comprises four papers and aims to identify and quantify factors controlling the distribution and population dynamics of H. sericea.

The results of a cartographic analysis of the distribution of Hakea spp. in the South-western Cape Province show that the most important physiographic factor characterising infested areas is the presence of quartzite and sandstone substrates of the Table Mountain Series. Other factors examined in this study are annual rainfall, altitude and aspect. The importance of two natural barriers is discussed and predictions are made on the range of potential spread of the species in the Fynbos Biome.

Mechanical control of H. sericea involves the felling of plants and burning 12-18 months later to kill regenerating seedlings. Burning standing infestations is sometimes proposed as an alternative control strategy. An experiment to test the effects of season of seed release in burnt and unburnt fynbos on regeneration

success is described. No significant differences between seasons or between burnt and unburnt veld were detected, but this is ascribed to unusually heavy seed predation on the small plots. Seeds germinated in winter and reproductive success following control operations in large compartments should be greater following felling in autumn. Felling in summer and autumn is most practical due to weather considerations. It seems that reliance on a fairly intense fire to kill seedlings is a better control strategy than manipulation of seedling survival due to season of felling.

H.sericea is reliant on seed for reproduction following fire or felling. The fate of seeds released at three-monthly intervals following felling on four large plots was investigated. After 12 months more than 99% of the seeds had been destroyed by granivores but stands would nonetheless return to pre-felling densities if only 60% of these remaining seeds germinate. Germination on all plots was, however, negligible. Implications for integrated control are discussed.

Large-scale mortality in stands of H.sericea was first reported in 1966. Since then symptoms of infection by the virulent fungus Colletotrichum gloeosporioides have been observed throughout the range of H.sericea in South Africa. The contribution of this gummosis disease to the control of H.sericea has been considered largely opportunistic. A transition matrix model was developed

to quantify and predict the potential of the pathogen for incorporation into the integrated control programme.

82% mortality is predicted after 10 years at the study site. Pathogen-induced mortality occurred mainly between October and January following periods of peak fungus activity during July and August. No regeneration was observed beneath or near infected stands.

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PREAMBLE

This study is presented in the form of four research papers in order to facilitate rapid dissemination of results.
The style and layout differs between papers, depending on the requirements of the Journals for which they have been prepared. There is unavoidably a degree of repetition in the "introduction" and "references" sections.

Botanical nomenclature follows Bond & Goldblatt (1984) for all taxa of the Cape Flora (including naturalised species) with the notable exception of Hakea sericea Schrad. where this name has been retained in preference to H.tenuifolia (Salisb.) Domin. Nomenclature for other Australian taxa follows Specht (1981).

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PART 1.

GENERAL INTRODUCTION

1. Features of the Cape Floristic Region
2. The development of a mountain catchment management policy
3. *Hakea sericea* in Australia
4. *Hakea sericea* in South Africa
5. Aims of this study
6. References

1. FEATURES OF THE CAPE FLORISTIC REGION

The Cape Floristic Region (Goldblatt 1978) occupies an area of c. 90 000 km^2 at the extreme southwest of the African continent. The Region is famous for the richness, diversity and unusual composition of its plant life. There are some 8 504 species of seed plants and 74 species of pteridophytes in the Cape Flora, about 46% of the total for Southern Africa (Bond & Goldblatt 1984). Limits of the Cape Floristic Region were drawn around the major areas of fynbos, the most distinctive vegetation type in the Cape Flora. Although the veld types recognised by Acocks (1953) in his pioneering study of the vegetation of South African do not give a satisfactory description of the different vegetation types in the region, the boundary between the heathland vegetation (Moll & Jarman 1984b) on the mountains of the Cape Folded Belt and that of the semidesert to the interior is readily apparent. The Cape Floristic Region includes the area between this interior border and the south and west coasts (Goldblatt 1978, Bond & Goldblatt 1984).

The northern limit extends from the fynbos on the Nieuwoudtville Escarpement to the Gifberg Massif and the Nardouw-Pakhuis-Cedarberg mountains. The southern inland border runs along the base of the sandstone mountain belt of the Witteberg, Swartberg, Baviaanskloof and the Great Winterhoek Mountains. These ranges form an almost continuous chain which run west to east and terminate

at the Indian Ocean near Port Elizabeth. The Region extends roughly from 31° to 35° S and from 18° to 27° E. Outliers of fynbos vegetation at high altitudes in the Grootrivierberge, Klein Winterhoekberge and Suurberge between Willowmore and Grahamstown are generally excluded from the region (Goldblatt 1978). These have, however, been included in the Fynbos Biome (Moll & Bossi 1983), an area which otherwise closely approximates the geographic area of the Cape Floristic Region.

The climate of the Cape Floristic Region varies from mediterranean in the west with wet winters and relatively dry summers (mostly Köppen (1931) climatic type Cs) to humid temperate in the east with uniform rain throughout the year (Köppen climatic type Cf) (Schulze & McGee 1978). The ranges of folded mountains intercept much of the rain coming from the Atlantic and Indian oceans so that the region is comparatively well watered. Annual rainfall averages 600 to 800 mm but may vary from less than half the lower amount to over four times the higher, depending on slope, aspect and altitude in relation to the rain-bearing winds. Mountain ranges in the region reach an average height of 1 200m but the higher peaks rise above 2 000m. The coastal plain is relatively narrow and the main ranges are separated from one another by long intermountain valleys of which the main ones are the Olifants River Valley in the west, the Breede River Valley in the south western interior and the Little Karoo and Langkloof in the south. The mountains are largely composed of quartzitic rock derived from the erosion resistant Table

Mountain and Witteberg Series of the Cape Geologic System. Soils are coarse-grained, acidic, nutrient poor and infertile. In contrast, the valleys and the coastal plain generally have heavier, richer soils derived from shales of the Malmesbury Series of the Nama System or the Bokkeveld Series of the Cape System. Granites occur locally, especially along the west coast at lower altitudes (Lambrechts 1979). Limestones and calcareous rock are largely restricted to the south coast and support a distinctive assemblage of taxa (Bond & Goldblatt 1984).

The most characteristic vegetation type in the Cape Floristic Region is fynbos. Fynbos may be defined as "evergreen, sclerophyllous shrublands on oligotrophic soils comprising essential Cape Floristic elements, consisting predominantly of either functionally isobilateral picophyllous and/or microphyllous to mesophyllous-leaved shrubs and usually associated with evergreen aphyllous and/or narrow-leaved sclerophyllous hemicrytophytes" (Moll & Jarman 1984a).

Acocks (1953) recognised three categories of fynbos : "coastal macchia", "macchia" and "false macchia". Using landsat MSS imagery, Moll & Bossi 1983 and Moll et al (1984) have produced a refined classification of the vegetation of the Fynbos Biome. The major categories recognised in mapping vegetation of the biome are given in Table 1. Only the Mountain Fynbos will be discussed here. These heathlands occur on sandstone and quartzite mountains of the Cape Folded Belt; from the Cedarberg in the

TABLE 1 : Major fynbos categories recognised in mapping vegetation of the Cape Floral Kingdom (after Moll *et al.* 1984)

Mapped vegetation category	Structural Environmental Descriptions	Biogeographic Affinities	Floral Kingdom Divisions
CAPE FYNBOS SHRUBLANDS			
Mountain Fynbos			
Wet Mountain Fynbos Mesic Mountain Fynbos Dry Mountain Fynbos	Heathlands on sandstone and quartzite mountains		
Grassy Fynbos			
Mesic Grassy Fynbos Dry Grassy Fynbos	Grassy heathlands on sandstone and conglomerates	Cape Communities	Cape Floral Region
Lowland Fynbos			
Sand Plain Fynbos Elim Fynbos Limestone Fynbos			

north west to the Groot Winterhoek mountains near Port Elizabeth. Mesic Mountain Fynbos occupies by far the greatest area of the three sub-divisions and comprises open to closed (40-90% canopy cover) shrublands on seasonally water logged, mesic sites (Moll et al 1984). There is a great diversity of plant communities reflecting the influence of geographic factors and of a complex landscape (Rycroft 1950, Martin 1965, Taylor 1969, Werger et al 1972, Kruger 1974, McKenzie et al. 1977, Boucher 1978, Taylor 1978, Kruger 1979, Bond 1981, Campbell 1983, MacDonald 1983, Van Wilgen & Kruger in prep). Communities are physiognomically characterised by the presence of three elements : ericoid, proteoid and restioid. The ericoid element comprises generally rather low and compact microphyllous shrubs of the genera Erica, Phylica, Aspalathus and other legumes, Rutaceae, Thymelaeaceae, Bruniaceae etc. Proteoid elements are generally taller, more loosely branched sclerophyllous shrubs 1-3 m tall mostly of the Proteaceae. Stout, rather rigidly tufted aphyllous Restionaceae and Cyperaceae comprise the restioid element and are very characteristic of the Cape Flora. Grasses are usually uncommon. General physiognomy varies from a low, more or less dense fine-leaved scrub to a tall closed Protea scrub, or to a mixture of these forms (Taylor 1978, 1981). In many areas, invasion by alien woody weeds has resulted in the replacement of indigenous elements by stands of even-aged trees or shrubs and severe disturbance of natural communities. This poses a most serious conservation threat in the region.

Besides their considerable scientific and aesthetic value, the

natural fynbos communities of catchment areas form the best and most cost-effective catchment cover (Wicht & Kruger 1973). Areas identified as catchments (van der Zel 1981) occupy only 8% of the land surface of South Africa but yield 49% of the country's total water runoff. Almost 19% of the major catchments of Southern Africa fall within the Cape Floristic Region, an area comprising about 4% of the area of the subregion (Bond & Goldblatt 1984).

2. THE DEVELOPMENT OF A MOUNTAIN CATCHMENT MANAGEMENT POLICY

Fire has been a feature of the fynbos environment since at least the late Pliocene to early Pleistocene. Palaeoecological evidence further suggests the deliberate use of fire as early as the middle Pleistocene (Deacon 1983). The role of fire in early land use in the Fynbos Biome has been reviewed by Bands (1977). Cape farmers learnt the practice of veld burning from the Hottentots in the early days. Fire was however condemned as most undesirable from the earliest days of European Settlement in Southern Africa. Strict penalties were proclaimed by the Dutch East India Company for veld burning without special permission. Acts preventing the firing of vegetation that were passed by British authorities after 1806 sought not so much to conserve the veld, but to prevent destruction of crops, buildings and other property. Despite these laws, veld burning continued. The Forest Act of 1913 provided legislation to maintain streamflow by protecting the vegetation of mountain slopes on State land. In 1923 a Drought Investigation Commission expressed the opinion that veld burning was harmful,

especially where the water supply of certain areas was adversely influenced. They proposed that immediate action be taken to safeguard certain catchments by forbidding both burning and grazing in these areas (Bands 1977). Botanists in the early twentieth century condemned fire (Levyns 1924, Marloth 1924, Pillans 1924). In 1934 the government was requested to investigate the cause, and to take steps to counter the drying up of the country's rivers and to generally conserve the country's water resources. Research into various aspects of veld management for the conservation of water, soil and vegetation was initiated. The spread of invasive alien plants in mountain fynbos catchments was recognised as a serious problem and in 1937 the Weeds Act (No 42 of that year) was passed. More than 200 species were declared noxious weeds. In terms of the soil conservation Act of 1946, the Minister of Agriculture could appoint fire protection committees. The first of these committees was appointed in 1949 and within a few years most mountain fynbos areas were subject to some form of protection. In 1948 the Department of Forestry approved limited prescribed burning in the Southern Cape as a measure for protecting plantations and indigenous forests (le Roux 1969). Despite pressure from many foresters for the relaxation of the policy of complete exclusion of fire from mountain fynbos areas, this policy was maintained until the late 1960's.

As preliminary results of research on veld management in fynbos became available, it was evident that fixed rules on conservation

of the entire region were impractical and that separate prescriptions for effective management of the different climatic and vegetation types were required. In a minute addressed to all fire protection committees in fynbos areas in April 1967, the head of the Winter Rainfall Region of the Department of Agricultural Technical Services listed several principles that should serve to guide committees to responsible decisions. These recommendations were based on the findings of an interdepartmental committee convened to investigate the conservation of mountain catchments (Department of Agricultural Technical Services 1961). The total protection from fire of vegetation in low rainfall regions and in certain sections of areas of higher rainfall was advocated. Controlled burning of "foothills and parts of the mountain veld between kloofs, and where no specific or recognised marshes and perennial springs occur" was cautiously recommended. The lack of scientific information to determine optimum season of burn and fire frequency to achieve best results was emphasised. Fires were only to be initiated under conditions where "complete control" could be excercised, and intervals between fires were to be as long as possible until detailed information enabled the specification of fire frequencies. The importance of excluding fire from catchments invaded by Hakea spp. and Pinus pinaster was stressed.

An important development in the evolution of current mountain catchment management policy was the promulgation in 1970 of the Mountain Catchment Areas Act. This Act enabled the Minister

of Forestry to proclaim land, whether publicly or privately owned, as Mountain Catchment on the advice of a technical committee. This further enabled the Minister to serve on any owner of land within a declared catchment, directions with reference to the conservation, use, management and control of such land. The prevention of soil erosion, protection and treatment of natural vegetation and the destruction of vegetation considered undesirable and any other matters considered necessary or expedient for achievement of the objects of the Act are listed.

Spectacular regeneration of Serruria florida ,an endangered species of the Proteaceae (Hall et al 1980), following an accidental fire (Vogts 1982) caused authorities to re-examine the policy of complete protection of vegetation against fire (Boucher 1980). In July 1968 the Department of Forestry carried out the first major prescribed burn for conservation purposes in the fynbos in the Kogelberg State Forest (Boucher & McCann 1975; Kruger & Lamb 1978) and in the middle 1970's introduced regular prescribed burning in mountain fynbos catchment areas (Van Wilgen 1984). In 1976 the catchment management plans for the Western Cape Forestry Region were modified to include a stipulation that all alien woody plants were to be felled prior to burning (Fenn 1980). These plants were mainly Hakea sericea and Pinus pinaster.

3. HAKEA SERICEA IN AUSTRALIA

Hakea sericea , an erect single-stemmed, much branched woody

shrub of the Proteaceae is endemic to south-eastern Australia. The distribution of H.sericea is shown in Figure 1. The climate of the heathland vegetation zone of eastern Australia where H.sericea occurs is characterised by long mild summers (hottest month with mean temperature below 22°C and at best four months above 10°C) and uniform rainfall throughout the year (Koppen climatic type Cfb, Specht 1979). Soils of the heathlands of east and central Australia are derived from sandstone, quartzite and granitic rocks and are inherently low in practically all plant nutrients (Specht 1979). Phosphorus levels appear to be particularly low (Specht 1963, Heddle & Specht 1975) and this appears to be the major controlling factor in the distribution of heathland vegetation in Australia (Specht 1979).

Fire is an integral part of the Australian heathland ecosystem and the adaptive responses of vascular plant species to fire have been widely studied (see Gill 1981 for a review). In the genus Hakea, woody follicles are produced which open upon desiccation of the parent branch which usually occurs upon death of the plant.

For effective storage of seed between fires an adequate protective mechanism is essential (Gill 1981). Within the genus Hakea there appears to be a clear correlation between the extent of reliance on seed for regeneration and the thickness of the woody follicle. Species with relatively small follicles (e.g. H. propinqua , a species of dry scrub in East and Central Australia) rely almost entirely on vegetative regeneration while a continuum

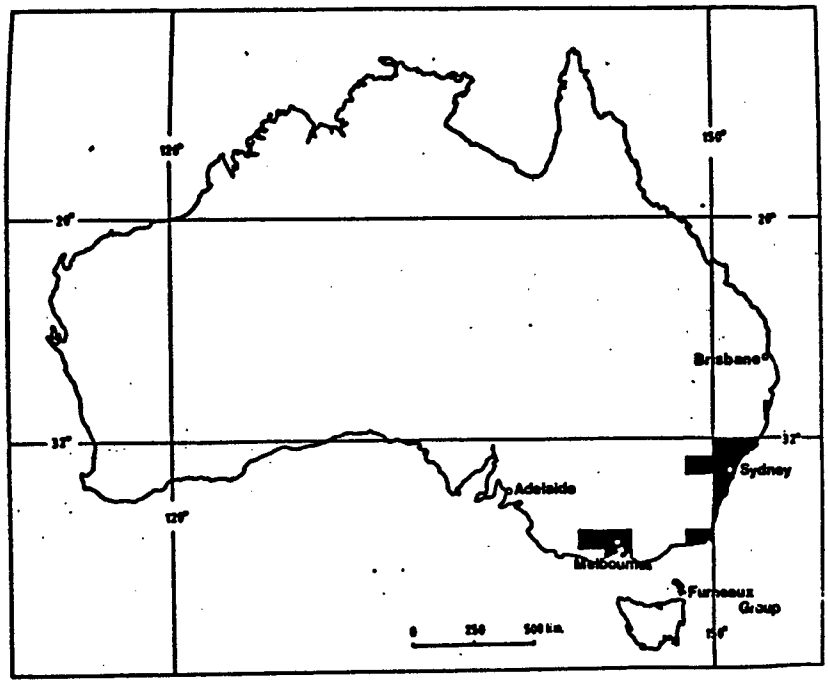

FIGURE 1. The distribution of *Hakea sericea* in Australia (Fugler 1979).

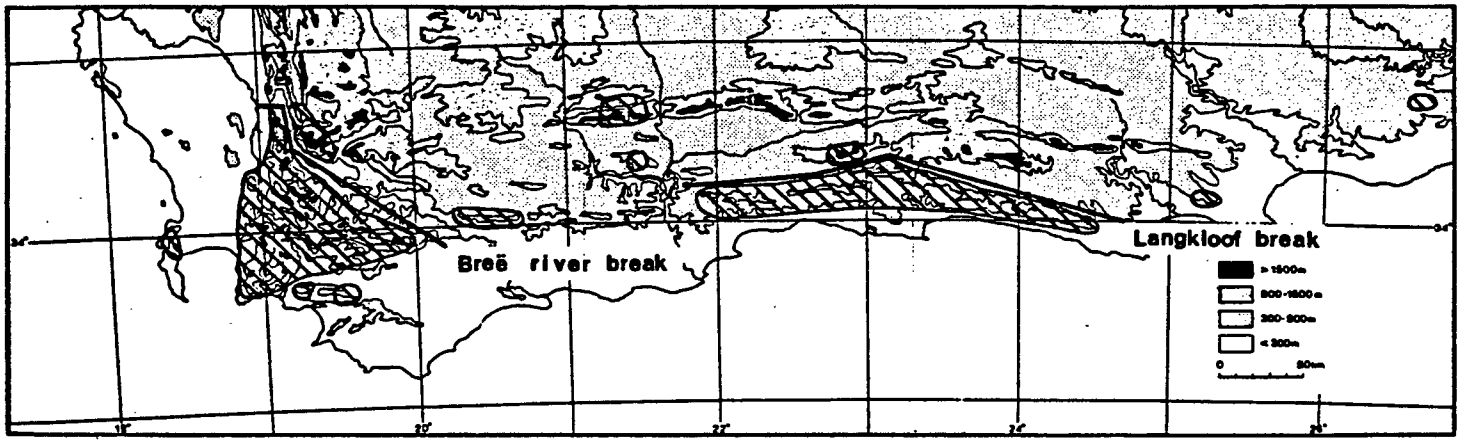

FIGURE 2. The approximate distribution of *Hakea sericea* in South Africa (Fugler 1979). For discussion of the relevance of the Breë River and Langkloof breaks see Paper 1.

of increasing reliance on seed for propagation with increasing thickness of the follicle is evident (S. Neser, personal communication). Within H.sericea there is great variation in fruit size. The smallest follicles are borne on plants of a root-regenerating ecotype in the Australian Capital Territory (Gill & Neser 1984).

Fruit production in Australia begins at c. 4-6 years (Gill & Neser 1984). In the formative stages, when follicles are moist and relatively soft, insect and fungal attack results in mortality of a proportion of the young fruits. Neser (1968) reports that in a study of natural enemies of H. sericea, H. gibbosa and H. suaveolens, plants were found to be attacked by a wide range of insects. In some species displaying the trait of storing protected seed in the canopy (e.g. Banksia ornata), heat is required for the dehiscence of most follicles, suggesting that the trait is adaptive to the occurrence of fire alone. In Hakea spp., however, seed is shed without the application of heat and it could be hypothesised that the storage phenomenon is one related to drought, fire or any other agency of shoot death.

4. HAKEA SERICEA IN SOUTH AFRICA

Invasion by alien plants is a major conservation threat in the fynbos. Sixteen out of 23 terrestrial plant species listed by Hall & Boucher (1977) as alien weeds are trees or shrubs that rely on seed for regeneration. In the mountain fynbos, the major alien plant infestations comprise three Hakea species, and in

particular H.sericea.

H. sericea was introduced to the Cape during the late 1830's. It was used as a hedge plant, a sand-binder and was utilised as a source of firewood in the processing of raisins in the Wolseley area (Neser & Fugler 1978). Although some information is available on the planting of this species in the vicinity of Cape Town (Shaughnessy 1980) and around Knysna (unpublished records, Directorate of Forestry), there is little known of the spread of the species in mountain fynbos areas. As early as c. 1863 it is reported that farmers in the Bathurst district between Grahamstown and Port Alfred discussed the potential of the species to spread (Phillips 1938). In 1914, J.S. Henkel, Conservator of Forests in the Midland Conservancy, wrote: "From observations and enquiries made I feel that hakea is spreading in this conservancy and will if not checked become a serious pest. In the circumstances I would suggest that the plant be proclaimed a noxious weed". He urged that all sales of Hakea spp. from government nurseries be stopped. The latter measure was agreed to by the Chief Conservator of Forests (unpublished records, Directorate of Forestry) but it was not until 1937 that H. sericea was declared a noxious weed throughout South Africa.The Weeds Act (No. 42 of 1937) provided legislation to compel land owners to eradicate declared noxious weeds on their land. In the case of H. sericea and other species invading mountain fynbos often in inaccessable areas, the Act contributed very little to stop the spread. H. sericea comes from a fire-prone

environment in Australia, similar in many respects to the fynbos region and is well adapted to survive fires. Because it was introduced in the form of seed, it was freed from the limiting effects of pre-dispersal seed predation. The lack of a definite catchment management policy, and the general attitude against the use of controlled fire as a management tool, facilitated the spread of the species through nearly all the major coastal ranges of the south-western, southern and south-eastern Cape. When wildfires occurred in areas infested with H. sericea, profuse regeneration resulted and dense impenetrable thickets of even-aged plants that smothered the indigenous vegetation became a feature of many mountain fynbos catchments. The approximate distribution range of H.sericea in South Africa is shown in Figure 2.

There are several records of experiments conducted to compare the cost efficiency of various control methods (unpublished records, Directorate of Forestry). Measures that were tested in an experiment undertaken by the District Forest Officer at George in 1939 included a) slashing scattered hakea and subsequent burning of the area and b) hoeing, heaping and burning. The first method was considered only for areas adjoining plantations as other areas were completely protected against fire. The latter method proved successful but the practical and financial implications were unfavourable.

Several records exist of experiments to test various herbicides for use on H. sericea (Schutte 1953, Jooste 1967, Theron 1976, 1978, 1979, unpublished records; Directorate of Forestry). Because of the needle-like leaves of H. sericea, higher than

normal dosages of herbicide were required to kill the plant. When plants are killed by herbicide application, follicles open and seeds are released to be dispersed by wind over large distances. Herbicides have thus made no significant contribution towards the control of H. sericea.

A biological control programme was initiated by the Department of Agricultural Technical Services in the early 1960's. In 1962, D. Webb, an entomologist of this Department, visited Australia to explore the possibilities of biological control of Hakea spp. in South Africa. The host-specificity of insects attacking Hakea spp. in Australia was studied by Neser(1968) and two species, the hakea fruit weevil, Erytenna consputa Pascoe and the hakea seed moth Carposina autologa Meyrick were brought to South Africa during 1970 for the establishment of colonies under quarantine conditions. The first field release of these insects was made in 1972. Large-scale introductions of E. consputa were undertaken from 1975-1980 and by 1984 some 7 500 weevils had been introduced (Kluge 1983, 1984). E. consputa is well established in 80 protected release sites from Wolseley in the west to Grahamstown in the east. At a study site at Goudini near Worcester, where 20 weevils were released in 1975, up to 85% of annual seed production was being destroyed after six years (Kluge 1983). The hakea seed moth, C. autologa, establishes poorly and only one colony is still surviving. No further work on this species is envisaged in the near future (R.L. Kluge, personal communication). A third insect, the hakea leaf weevil, Cydmaea binotata Lea, has also

been introduced (Kluge & Richardson 1983).

Biological control using seed-attacking insects only will not remove the existing infestations but it has the potential, by limiting the reproductive capacity of the plant, to reduce the risk of re-infestation and spread and possibly reduce the density of subsequent generations of the weed (Neser & Kluge 1984).

The most important development for the immediate control of H. sericea has been the active eradication policy adopted by the Directorate of Forestry (Fenn 1980). With the acceptance of the role of fire in mountain fynbos, and the initiation of regular prescribed burning, proclaimed catchments were divided into management units (compartments), usually 800-1 500 ha in extent. These compartments are burnt about once every 15 years. All alien woody vegetation is felled before burning. The accumulated seeds of H.sericea are released. A large proportion of seeds are consumed by rodents and birds but some germinate. Nine to 12 months after the felling operation the compartment is burnt. Seedlings are killed before they have produced any seed. Biennial follow-up operations are carried out and surviving plants are uprooted. To date some 140 000 ha of mountain catchments in the Southern Cape, Western Cape and Tsitsikamma Forestry Regions have been cleared in this manner and it is predicted that, at the present rate of progress, most of the areas for which the Directorate of Forestry is responsible will have been cleared within the next 10-15 years. This, in terms of a recent amendment to the Mountain Catchment Act includes hakea on private

land up to 5 km around any declared catchment area (Kluge & Richardson 1983).

Large scale mortality of H.sericea has been reported throughout the distribution range of the species in South Africa. The causal organism has been identified as a strain of the fungal pathogen Colletotrichum gloeosporioides (Morris 1982 a,b). Active human dispersal of spore suspensions of the fungus have been undertaken (Morris 1983). Large scale trials have, however, been discontinued as symptoms of infection are already evident in all stands of H.sericea (M.J.Morris, personal communication, Siebert 1984).

Despite the encouraging results achieved in the initial stages of the biological control programme, mechanical control will remain the most important short-term control measure in the foreseeable future.

5. AIMS OF THIS STUDY

The Directorate of Forestry is responsible for the control of H.sericea within State Forests and in declared mountain catchment areas and may, according to a recent ammendment to the Mountain Catchment Areas Act, clear H.sericea on land within 5 km of declared mountain catchments.

This study aims to identify and quantify factors controlling the distribution and population dynamics of the species, with a view to improving it's integrated control in mountain fynbos areas.

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PART 2.

PAPER 1: A CARTOGRAPHIC ANALYSIS OF PHYSIOGRAPHIC FACTORS INFLUENCING THE DISTRIBUTION OF *HAKEA* SPP. IN THE SOUTH WESTERN CAPE

D.M.RICHARDSON

SYNOPSIS

Results of a cartographic analysis of the distribution of Hakea spp. in the South-Western Cape Province show that the most important physiographic factor characterising infested areas is the presence of quartzite and sandstone substrates of the Table Mountain Series. Other factors examined are the annual rainfall, altitude and aspect. The importance of two natural barriers is examined and predictions are made on the range of potential spread of the weed.

INTRODUCTION

Hakea sericea, H.gibbosa and H.suaveolens were proclaimed noxious weeds in South Africa in terms of proclamations 161/1938 and 171/1940 (Stirton 1978).

H.sericea presents the most serious problem and has infested nearly all major coastal mountain ranges of the Cape Province (Fugler 1982). The history and autecology of this species in South Africa are discussed by various authors (Phillips 1938, Neser 1968, Neser & Fugler 1978, Fugler 1979 & 1982 and Shaughnessy 1980).

It has been suggested that the potential range of spread of H.sericea "corresponds roughly to the areas of Mountain Fynbos and to sandstone and granite areas that receive their rainfall in winter or throughout the year" (Neser & Fugler 1978). In

the present study, hakea distribution (no distinction is made between the three species) in the Western Cape is examined in terms of several physiographic factors.

Distribution studies (Fugler 1979) have revealed that some important areas still remain uninfested by H.sericea. He lists the Cedarberg, parts of the Langeberg and the area north of the Langkloof. Of particular interest are two natural barriers: the Bree River Valley and Langkloof breaks, which it has been proposed, should be used to prevent the spread of hakea to areas to the north.

The object of this study is to determine which factors characterise the areas invaded by Hakea spp. and, in the light of this information, to make predictions on the range of potential spread.

METHODS

In 1977 the Directorate of Forestry completed the mapping of hakea-infested areas in the Western Cape Forestry region. With the aid of aerial photographs and 1:50000 topocadastral maps an area of 960000 ha was covered. All hakea-infested areas encountered were sketched as accurately as possible onto maps at a scale of 1:50000 (Fenn 1980). A number of these maps were randomly selected for detailed analysis. A list of the maps used is given in Table 1.

An overlay of 1 km grid squares was used to randomly select 10 points per quarter degree square. One quarter degree square covers an area of approximately 670 square kilometers.

At each point the following information was recorded:

TABLE 1 : List of 1:50 000 topographical maps used in the survey. Maps marked with an asterisk were selected for a more detailed analysis (See Text)

Map Title	Number
Baardskeerdersbos	3 419 DA and DC
Bain's Kloof*	3 319 CA
Barrydale	3 320 DC
Caledon*	3 419 AB
Cape Town	3 318 CD
Ceres	3 319 AD
Franschhoek*	3 319 CC
Grabouw*	3 419 AA
Greyton	3 419 BA
Hangklip	3 418 BD
Hermanus*	3 419 AC
Jongensklip	3 419 BC
Paarl	3 318 DB
Riviersonderend	3 419 BB
Scheepsrus	3 320 CD
Simonstown	3 418 AB and AD
Somerset West	3 418 BB
Stanford*	3 419 AD
Stellenbosch	3 318 DD
Stormsvlei	3 420 AA
Tulbach	3 319 AC
Villiersdorp*	3 319 CD
Worcester*	3 319 CB

TABLE 2 : Symbols used to denote geological types

Symbol	Explanation	Series	System/Formation
C1	Quartzite, Shale, tillite	Table Mountain	Cape System
C2	Shale, sandstone	Bokkeveld	Cape System
C3	Quartzite, shale	Witteberg	Cape System
N	Quartzite, arkose, limestone, shale, phyllite, tillite, lava, tuff		Nama System
AG9	Granite, syenitic rocks, quartz porphyry	Cape Granite	
U/C	Unconsolidated superficial deposits		Tertiary to Quaternary
K1	Conglomerate, greywacke, shale		Klipheuwel
C.P.G.	Coarse porphyritic granite	Cape Granite	Instrusive rocks older than Klipheuwel formation but younger than Malmesbury formation
R.T.G.	River terrace gravel		Quaternary
MA1	Massive subgreywacke	holgat	Malmesbury
E.G.	Equigranular granite	Cape Granite	Instrusive rocks older than Klipheuwel formation but younger than Malmesbury formation

* Grid reference to nearest 5 seconds
* Presence/absence of Hakea spp.
* Altitude (m)
* Aspect (degrees) : taken at right angles to the contour
* Geology (determined by reference to the 1:125000 geological maps). Symbols used to denote geological types are explained in Table 2.
* Mean annual rainfall (mm/a) (determined by reference to the 1:125000 isohyetal maps - based on the period 1921 to 1960).

Points were divided into two categories for analysis, namely "all points" (all random points examined) and "positive strikes" (points at which hakea was encountered). Because of the preponderance of positive strikes on quartzite, shale and tillite substrates (C1), positive strikes on a random sample of eight maps were subjected to a more detailed analysis by referring to the 1:250000 geological survey maps in conjunction with aerial photographs. Maps selected for this purpose are marked with an asterisk in Table 1. Positive strikes on C1 substrates were then divided into the following categories:

a) Quartzite and sandstone with thin bands of shale and conglomerate (C1Q2).

b) As in a) but with sporadic basal conglomerate (C1Q1).

c) Shale, frequently micaceous, with thin bands of sandstone (C1S2).

d) Tillite, grit and conglomerate (C1G).

The two breaks distinguished by Fugler (1979) were carefully plotted on to the 1:25000 geological maps and a transectional analysis was made of the geological types.

RESULTS

Geology

The results of the analysis of geological types in relation to "all points" and "positive strikes" are summarised in Table 3 and a graphical representation appears in Figure 1.

While in the entire survey, quartzite, shale and tillite substrates of the Table Mountain series (C1) made up only 36.7% of the total, 77,2% of positive strikes had C1 as substrate. An analysis of the associations between hakea occurence and geological substrates is presented in Table 4.

A positive association (significant at the 0,001 level) was found to exist between Hakea distribution and the occurrence of C1 substrates.

Further detailed analysis of "positive strikes" on C1 substrates revealed that most Hakea infestations are encountered on soils derived from quartzite and sandstone with thin bands of shale and conglomerate, occasionally with basal conglomerate (types C1Q2 and C1Q1).

Negative associations were found to exist between Hakea distribution

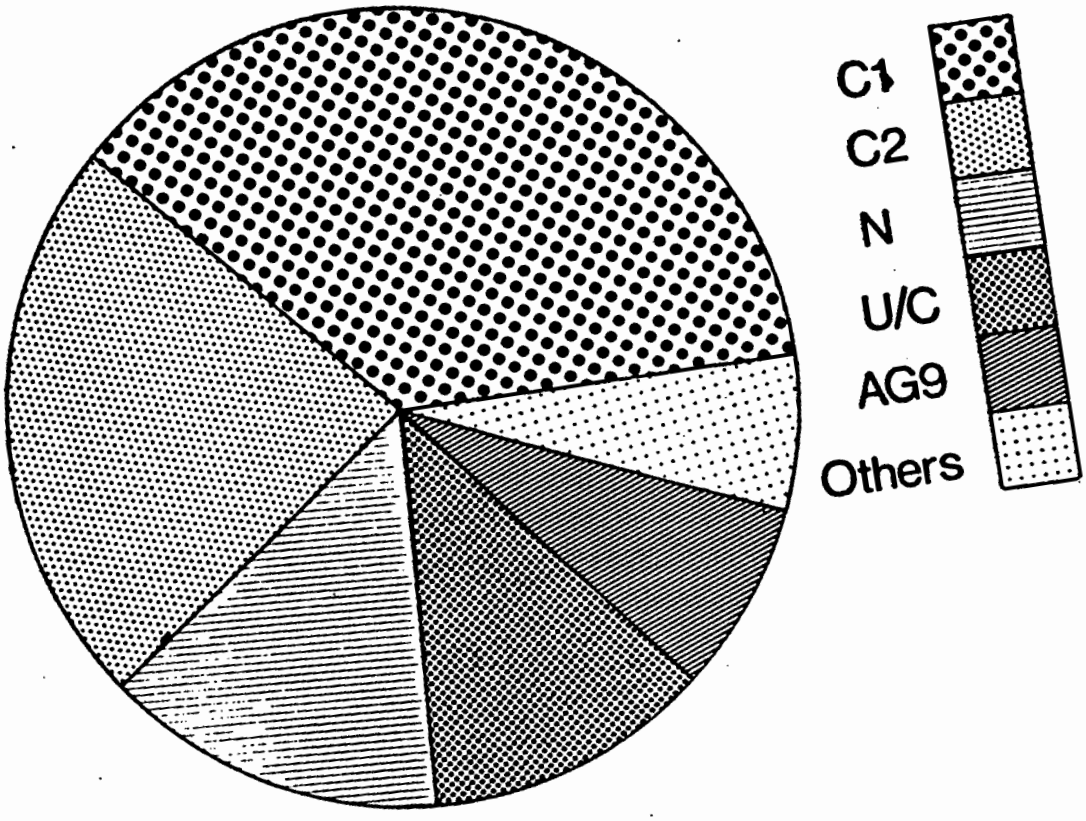
TABLE 3 : The distribution of geological types determined by a sample of random points. Positive strikes indicate the presence of Hakea spp.

Geological type	All points	Positive strikes	Positive strikes as % of all points
C1	83	44	53,3
C2	52	1	1,9
N	32	1	3,1
U/C	27	1	3,7
AG9	18	7	38,9
C3	10	2	20,0
K1	1	0	0,0
C.P.G.	1	0	0,0
MA1	1	0	0,0
EG	1	0	0,0

TABLE 4 : Statistical relationship (chi-square) and nature of association between geological substrate and Hakea occurrence

Geological type	Chi-square value	Significance	Nature of association
C1	53,730 4	***	Positive
C2	20,555 3	***	Negative
N	10,780 1	**	Negative
U/C	8,647 5	**	Negative
AG9	1,347 5	N/S	-
C3	0536 8	N/S	-
K1	3,013 4	N/S	-
C.P.G.	3,013 4	N/S	-
MA1	3,013 4	N/S	-
EG	3,013 4	N/S	-

Footnote: Level of significance: *** = 0,001
** = 0,01
* = 0,05
N/S not significant



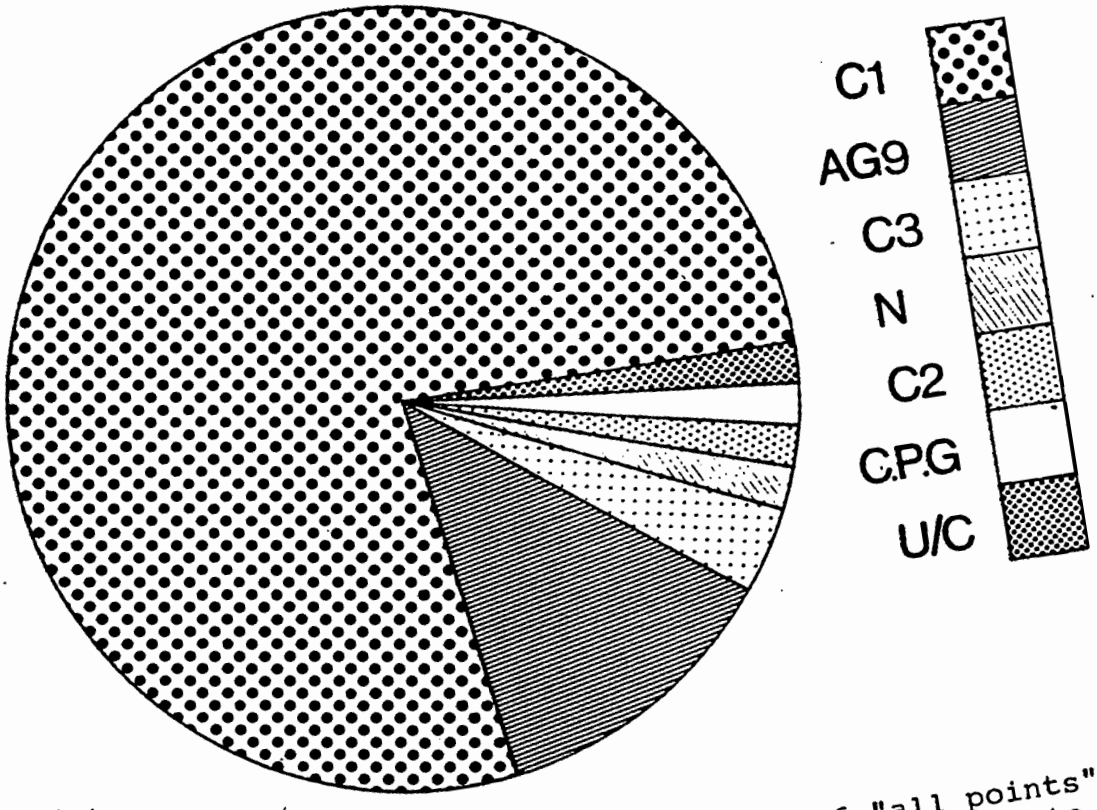


FIGURE 1. Pie diagram of geological types of "all points" an
"positive strikes". Positive strikes indicate the
presence of *Hakea* spp.

and the occurrence of C2, N and U/C substrates (significant at the 0,001 level for the first-mentioned and at the 0,01 level for the remaining two).

No significant association was found between Hakea distribution and the occurrence of other substrates.

Rainfall

The results of an analysis of mean annual rainfall (mm) in relation to "provide strikes" and "all points" are summarised in Table 5.

A regression of "positive strikes" as a percentage of "all points" (Y) against rainfall per annum in mm X 100(X) gave y = -1,884 + 0,037X (r = 0,786; n = 226).

Altitude

The results of an analysis of altitude (m) in relation to "positive strikes" and "all points" are summarised in Table 6. A regression of "positive strikes" as a percentage of "all points" (Y) against the altitude class midpoints (m) (X) gave y = 0,801 + 0,064X (r = 0,822; n = 226).

Aspect

Results of the analysis of aspect (degrees) in relation to "positive strikes" and "all points" are summarised in Table 7. The distribution of Hakea spp. appears to be independent of aspect.

DISCUSSION

TABLE 5 : The distribution of mean annual rainfall classes determined by a sample of random points. Positive strikes indicate the presence of Hakea spp.

Rainfall (mm/a)	All points	Positive strikes	Positive strikes as % of all points
0 - 200	2	0	0,0
201 - 400	35	2	5,7
401 - 600	78	5	6,4
601 - 800	46	15	32,6
801 - 1 000	29	15	51,7
1 001 - 1 200	14	6	42,9
1 201 - 1 400	2	1	50,0
1 401 - 1 600	8	5	62,5
1 601 - 1 800	0	0	-
1 801 - 2 000	4	4	100,0
2 001 - 2 200	0	0	-
2 201 - 2 400	6	3	50,0
2 401 - 2 600	0	0	-
2 601 - 2 800	0	0	-
2 801 - 3 000	2	1	50,0

TABLE 6 : The distribution of altitude classes determined by a sample of random points. Positive strikes indicate the presence of Hakea spp.

Altitude class (m)	All points	Positive strikes	Positive strikes as % of all points
0 - 100	27	1	3,7
101 - 200	47	3	6,4
201 - 300	40	6	15,0
301 - 400	30	8	26,7
401 - 500	22	12	54,5
501 - 600	11	1	9,1
601 - 700	14	4	28,6
701 - 800	13	7	53,8
801 - 900	4	2	50,0
901 - 1 000	9	7	77,8
1 001 - 1 100	2	1	50,0
1 101 - 1 200	1	0	0,0
1 201 - 1 300	3	3	100,0
1 301 - 1 400	2	1	50,0
1 401 - 1 500	1	1	100,0

It is useful, in the light of this information, to examine the two breaks as defined by Fugler (1979). The Bree River break runs from the vicinity of Robertson north-westwards, along the wine-producing valley of the Bree River to Worcester and on to Tulbagh and Gouda via Goudiniweg and Wolseley.

Geological types occurring along the break are, in order of importance, unconsolidated, superficial deposits (U/C); quartzite, arkose, limestone, shale, phyllite, tillite, lava and tuff of the Nama system (N); conglomerate, greywacke and shale of the Klipheuwel Formation (K1); shale and sandstone of the Bokkeveld series (C2); conglomerate, sandstone, shale and limestone of the lower series (Cr1); and quartzite and shale of the Witteberg Series (C3).

The importance of this break in halting the spread of Hakea from the Du Toitsberge and Riviersonderend ranges in the south to favourable substrates of the Hex River, Skurweberg and Cedarberg ranges to the north is clear.

The Langkloof break consists of a narrow band of shale and sandstone (C2) and stretches from St Francis Bay westwards to Volmoed in the vicinity of Oudtshoorn. Land use along this line is chiefly agricultural, with the important Langkloof apple producing region being centred in the area. The fact that the geological type along almost the entire break is shale and sandstone (C2), shown to be strongly negatively associated with Hakea occurrence, suggests that this natural break is indeed important in preventing the spread of Hakea from the Outeniqua and Tsitsikamma mountains

in the south to the Kammanassie and Kouga mountains to the north. The area to the north of the break should be closely examined and all Hakea eradicated as soon as possible.

Two important gaps are evident in the break and the spread of Hakea in these areas should be prevented at all costs. The first is along the Krom River from Assegaaibos, south-eastwards for a distance of 20 km, and the second from Louterwater to the north of Nature's Valley, north-westwards to Misgund, a distance of approximately 13 km.

Extrapolation of the observed associations between geological types and Hakea occurrence requires caution for two reasons.

Firstly, the study of the distribution of any (weed) species requires cognizance of the fact that the non-occurrence of the species under consideration at a given site does not necessarily mean that it is unable to exist there (Shaughnessy 1980).

Secondly, areas under Table Mountain series soils are generally mountainous, inhospitable regions unsuitable for cultivation or urbanisation. Hakea has therefore been largely unhindered in its spread. Any Hakea encroaching on land with economic potential would receive much more urgent attention.

The analysis of rainfall and altitude data must be considered in conjunction with the geological data.

The "positive strike": "all points" ratio is positively correlated with both rainfall and altitude.

It should be realised that the high mountainous areas (largely C1 and AG9) receive the highest rainfall and that the positive correlation that exists between Hakea occurrence and rainfall

is probably due to the presence of favourable sandstones and quartzite substrates rather than to the higher rainfall *per se*. The results do show, however, that *Hakea* occurs over a wide range of annual rainfall regions (200 to over 3 000 mm). With an increase in altitude and a corresponding increase in rainfall and the probability of encountering the favourable substrates mentioned above, an increase in the probability of scoring a positive strike is evident.

Again, despite the strong relationship between altitude and the "positive strike": "all points" ratio, it is clear that *Hakea* is found over a wide range of altitude classes (from 0 to over 1 500 m above sea level).

CONCLUSION

The major factor limiting the distribution on *Hakea* spp. in the South-Western Cape appears to be the presence of shale-bearing and unconsolidated substrates (*C2*, *N* and *U/C*) surrounding the areas under quartzite and sandstone of the Table Mountain Series. *Hakea* spp. coming from a roughly similar, low nutrient, fire-prone mediterranean type region in South Eastern Australia are best adapted to the low nutrient soils derived from quartzite and sandstone substrates. Both altitude and rainfall are closely related to geological type and therefore also show positive correlations with *Hakea* occurrence. *Hakea* distribution appears to be independent of aspect.

The importance of the two natural breaks defined by Fugler (1979)

is emphasised. The Skurweberg, Kouebokkeveld and Cedarberg ranges to the north of the Bree River break and the Kammanassie and Kouga ranges beyond the Langkloof break appear to possess all the characteristics necessary for invasion by Hakea spp. The reason for the absence of Hakea spp. in these ranges appears to be historical rather than ecological.

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PART 3.

PAPER 2: FACTORS AFFECTING THE REGENERATION SUCCESS OF HAKEA SERICEA

D.M.RICHARDSON & B.W.VAN WILGEN

SYNOPSIS

Hakea sericea is an aggressive woody invader of fynbos communities. Clearing operations aimed at the control of this weed are conducted in mountain catchment areas. This paper describes an experiment to test the effects of season of seed release in burnt and unburnt fynbos. No significant differences between seasons or between burnt and unburnt veld were detected, but this is ascribed to unusually heavy predation on the small plots. Seeds germinated in winter and differences in reproductive success following control operations in large areas should be similar to patterns observed for indigenous serotinous Proteaceae after fire. While more data from actual control operations are necessary, it seems that reliance on a fairly intense fire to kill seedlings is a better control strategy than manipulation of seedling survival due to season of felling.

INTRODUCTION

Hakea sericea, an Australian member of the Proteaceae, was introduced to South Africa in the early nineteenth century (Fugler 1979). It has invaded nearly all the major coastal mountain ranges of the Cape Province (Neser & Fugler 1978). The infestations are largely restricted to quartzite and sandstone substrates of the Table Mountain Series (Richardson 1984). H.sericea succeeds

as a weed because of its prolific seed production and the lack of predispersal seed predation by insects. Evidence on weedy shrub recruitment (Louda 1983) suggests that significant seed losses are caused by insect feeding, and that exclusion of flower- and seed-feeding insects leads to increased maturation and release of viable seed. Bond (in prep) has found that in many indigenous Proteaceae with canopy stored seed (serotiny), the contribution of seeds of more than two years old towards the total viable seed reserve is small. This suggests a significant loss of viable seed due to predation by insects. H.sericea in South Africa, by comparison, retains almost all of the seeds produced during its lifetime in a viable state. The seeds are borne in heat-resistant woody follicles and are released only when the parent plant dies.

Properly managed fynbos is the most cost-effective cover for conserving the water resources of the Cape mountains (Wicht & Kruger 1973). The conversion from low plant communities (fynbos) to closed hakea shrubland results in a decline in streamflow (J.M.Bosch personal communication). Invasion of natural vegetation by alien species is also incompatable with nature conservation, and for these reasons H.sericea infestations should be cleared.

The Directorate of Forestry began clearing invasive alien plants within proclaimed mountain catchments in the Western Cape Forestry region in 1976 (Fenn 1980). Prescribed burning is carried out at intervals of 12-15 years in mountain catchments to reduce

fire hazard, control woody weeds and to rejuvenate the vegetation. Prior to each burn all woody invasive plants are felled. Felled H.sericea plants are left on the ground and the accumulated seed load is released within a week. Dispersal of the winged seed is reduced because adult plants are not upright. Some of the seeds suffer predation and most of the remainder germinate. The area is burnt 12 to 18 months after clearing and the remaining seed and immature seedlings are killed. Such operations with regular follow-up measures result in the virtual eradication of H.sericea but a variable degree of success has been noted.

It is necessary to determine whether season of seed release after felling can influence subsequent regeneration of H.sericea and therefore the degree of success achieved in control operations. Bond (1984) has shown that season of seed release in indigenous serotinous Proteaceae influences subsequent regeneration because of differences in the time that seeds are exposed to predation before germination. H.sericea seed also suffers predation, and observations on small plots (one ha) show that up to 99% of released seeds can be consumed by granivores (Richardson, unpublished data). The seeds of indigenous Protea species germinate in winter (Deall & Brown 1981). Seed release in spring therefore results in poor regeneration, while seed release in autumn results in good regeneration as seeds are not exposed to predation for a long period (Bond 1984). If germination patterns are similar in H.sericea and indigenous Protea species, then it would be theoretically possible to influence reproductive success through

season of felling.

Burning H.sericea infestations standing is sometimes proposed as an alternative control strategy. While this method is much cheaper than felling, it is usually ineffective and seed release after the fire results in profuse regeneration of the weed. It would nonetheless be of interest to determine the effects of fire season on the regeneration of standing H.sericea so that the effects of unplanned fires in hakea infestations could be predicted. This study was therefore designed to test the following null hypotheses: a) season of felling has no effect on the subsequent regeneration of H.sericea; and b) germination is equally effective on recently burnt and unburnt sites.

STUDY AREA

The study took place in the Zachariashoek Experimental Catchments on La Motte State Forest (33° 49' S, 19° 02' E). The experiment was laid out in a firebreak adjacent to the southern side of the Zachariashoek subcatchment at an altitude of 520 m.

The vegetation of the catchment has been described by Van Wilgen & Kruger (in prep.). The plant community of the study area consists of mid-dense or open graminoid shrublands (vide Campbell et al. 1981).

The climate of the area is typical of the mountains of the winter rainfall zone. Annual rainfall in nearby Kasteelkloof varies between 930 and 2300mm with a mean over eight years of 1458mm

(Van Wilgen & Kruger 1981). Rainfall records for the duration of the study are presented in Figure 1.

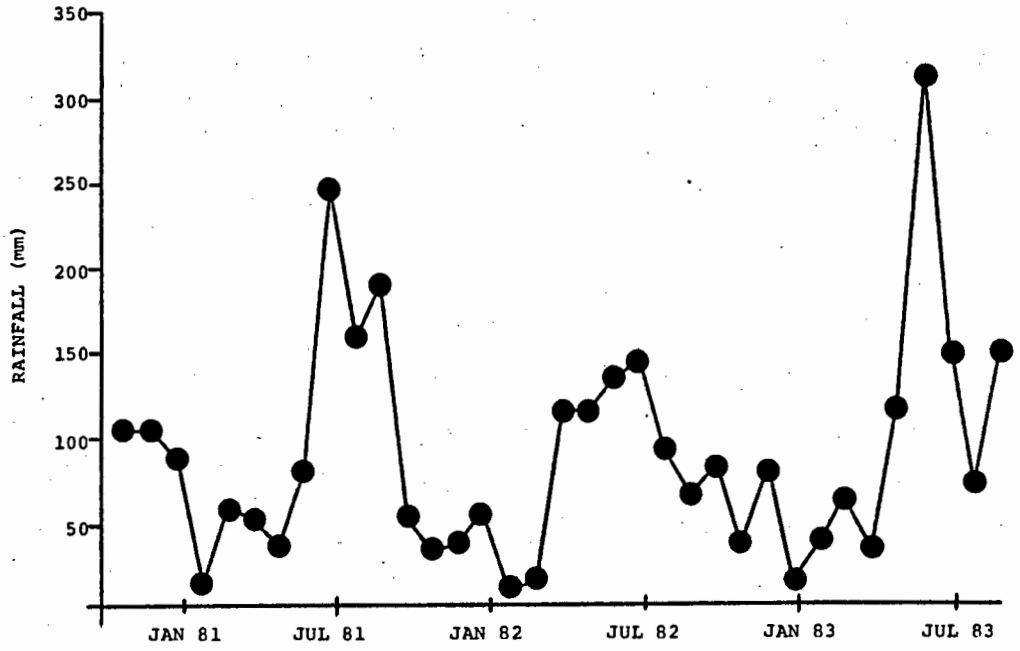

FIGURE 1 : Rainfall (mm) for the duration of the study. Zachariashoek upper raingauge (1).

Sandstones of the Table Mountain Group predominate (Van Wilgen & Kruger 1981). Soils are shallow (from 30 to 70 cm), apedal and sandy. Soil forms include Mispah,Glenrosa, Clovelley and Constantia (MacVicar et al. 1977).

METHODS

Experimental design

Sixty plots, each 5x10m, were paired and grouped into five blocks

of six pairs each (a two by six factorial in a split-block layout). Paired plots within each block were selected at random. The layout of blocks and plot pairs is shown in Figure 2. Treatments consisted of sowing H.sericea seed every two months from November 1980 to September 1981. One plot in each pair was burnt a few days prior to sowing.

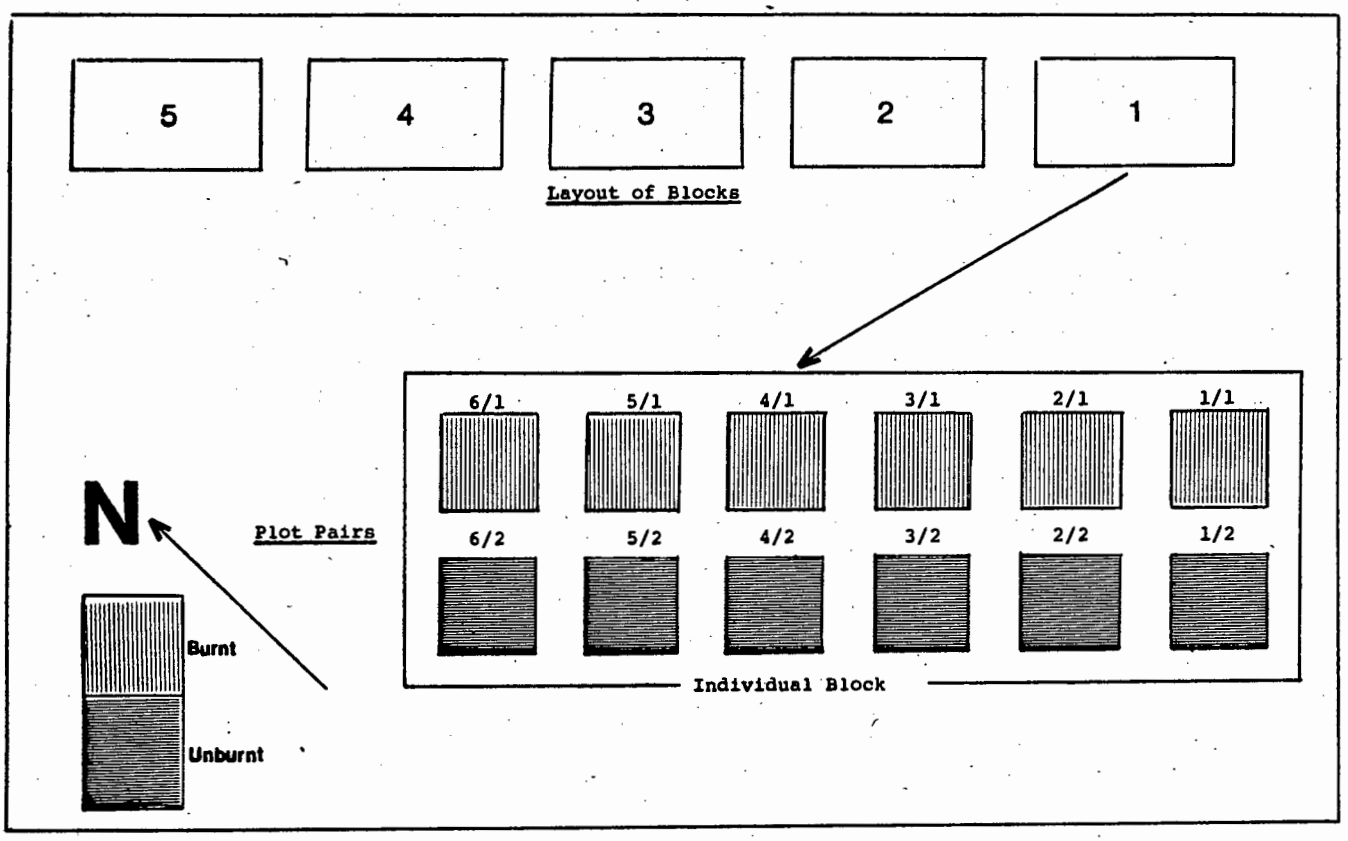

FIGURE 2 : The layout of blocks and plot pairs
(A two by six factorial in split-block layout)

Seed collection and sowing

Seed was collected from Stellenboschberg in the Jonkershoek valley three weeks prior to each sowing. The fruits were opened by drying in the sun. The seed was stored in a cool dry environment until sowing. Seed was sown in five burnt and corresponding

unburnt plots. Eight hundred seeds were sown in each plot. A portable grid was used to facilitate even sowing throughout the plot. The seeds were lightly pressed into the ground.

Seed germination test

A trial to determine the viability of the seed was conducted. Three hundred seeds collected on Stellenboschberg were sown in a mixture of vermiculite and sawdust (six trays of 50 seeds).

Enumeration of plots

Plots were inspected at two-monthly intervals from January 1981 to September 1983. The total number of live seedlings present in each plot was recorded.The presence of flowers was noted at each observation.

RESULTS

Seed germination test

Germination of seeds sown in vermiculite and sawdust began within one month after sowing and at 60 days after sowing 100% germination was recorded.

Regeneration patterns in the field

Regeneration patterns in the burnt veld are depicted in Figures 3 and 4 for seeds sown in January 1981 and July 1981 respectively. Seeds sown in November 1980 and March 1981 showed a similar

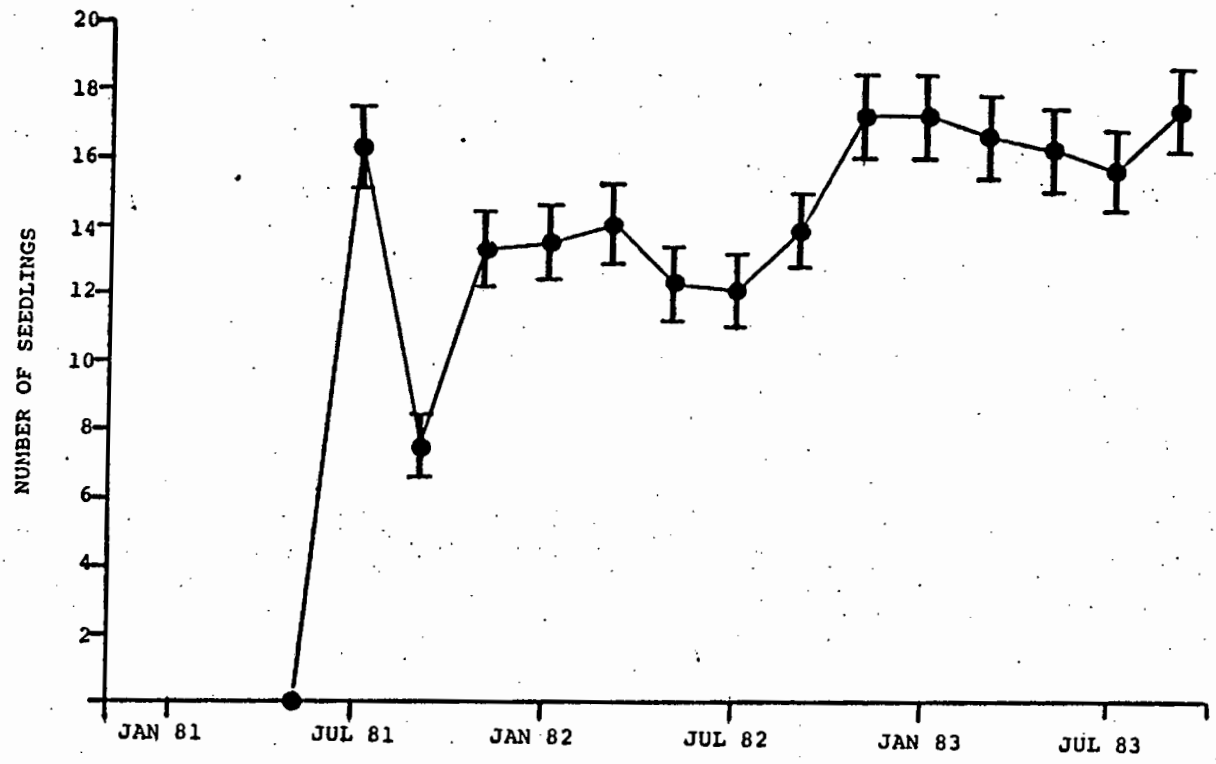

FIGURE 3 : Germination pattern for seed sown in January 1981 in burnt veld. Similar patterns were observed for seed sown in November 1980 and March 1981. Vertical bars represent standard deviations of the mean. (n = 5)

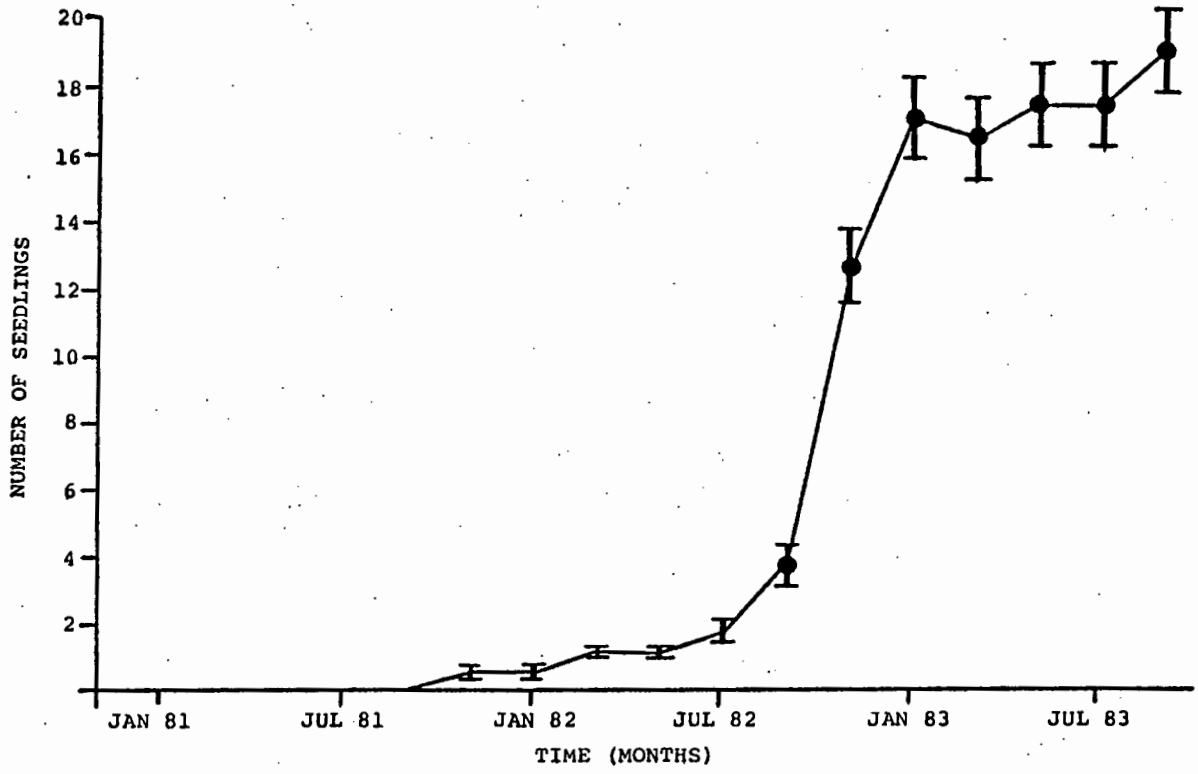

FIGURE 4 : Germination patterns for seed sown in July 1981 in burnt veld. Similar patterns were observed for seed sown in May and September 1981. Vertical bars represent standard deviations of the mean. (n= 5)

response to those sown in January 1981. The pattern of response illustrated in Figure 4 adequately describes the response of seeds sown in May and September 1981. The total number of live seedlings remaining in the plots is plotted against the date of each two-monthly observation. In the case of the unburnt plots, location of seedlings proved most difficult in the early stages. Comparable curves for unburnt plots have not been constructed as data collected prior to March 1982 are inaccurate.

TABLE 1 : ANOVA table for the 2 x 6 factorial in split-block lay-out.

Source of variation	S.S.	D.F.	M.S.	F
Total	3145,92			
Blocks	329,42	4		
Factor A (Season of sowing)	510,66	5	102,13	2,67 N.S.
Blocks X A	765,83	20	38,29	
		29		
Factor B (Burning)	40,33	1	40,33	1,39 N.S.
Blocks X B	116,17	4	29,04	
		5		
A B Interaction	788,42	5	157,66	5,30***
Error	595,08	20	29,75	

***A B Interaction significant at 0,005 level

An analysis of variance (Table 1) for live seedling numbers after two winters revealed no significant differences for the six sowing dates or between burnt and unburnt veld. The hypotheses that season of seed release has no effect on subsequent regeneration and that germination success does not differ between burnt and unburnt veld are accepted. A significant difference ($P<0.005$) was however found for the interaction between the two factors.

Treatment means are presented in Table 2.

TABLE 2 : Mean number of H. sericea seedlings surviving in plots after two winters following sowing at two-monthly intervals in burnt and unburnt veld.

	Sowing Date					
	Nov. 1980	Jan. 1981	March 1981	May 1981	July 1981	September 1981
Burnt	23,0	14,0	18,4	11,0	19,2	10,4
Unburnt	11,4	8,8	6,8	10,8	18,6	10,6

Germination and flowering of H.sericea seedlings

Observations on the development of H.sericea seedlings in the burnt veld are summarised in Figure 5. The time between sowing and the onset of germination and flowering is plotted for the six sowing dates. Fruit development was not monitored.

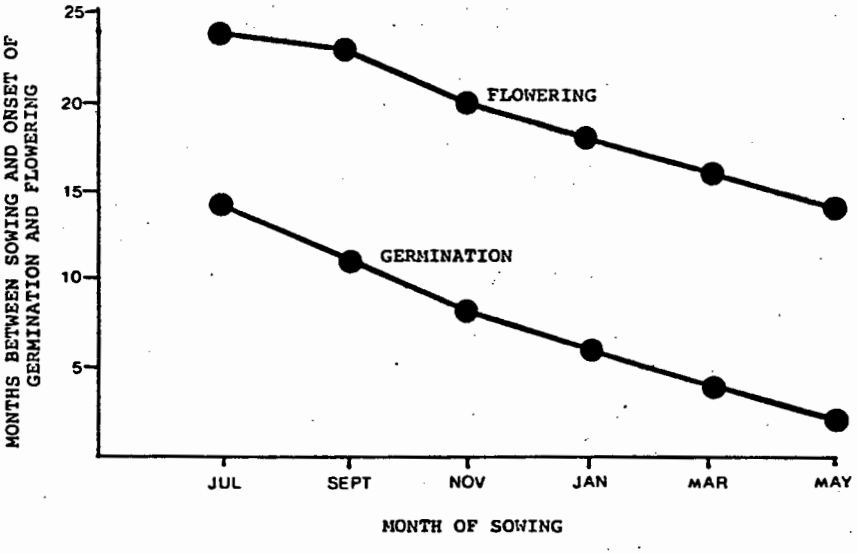

FIGURE 5: Time elapsed between sowing dates and the onset of germination and flowering.

DISCUSSION

Germination patterns

Seeds sown between November 1980 and March 1981 show a distinct germination peak between May and July 1981 (two to six months after sowing). Seed sown between May and September 1981 germinated mainly between September and November 1982 (12 to 16 months after sowing).The differences in total seedling numbers after two winters are not significant in the analysis of variance (Table 1). Thus while we have shown that seasonal germination patterns are similar in indigenous Proteaceae and H.sericea, we were unable to detect any differences in germination success similar to those shown for indigenous Proteaceae by Bond et al. (1984) and Van Wilgen & Viviers (1984). This is an unexpected result but it can be explained by weaknesses in the experimental design. The burnt plots where sowing was carried out were small. The adjacent unburnt vegetation would provide cover for diurnal rodents and these , together with nocturnal rodents and birds, would deplete the seed store to an unnatural degree. Secondly, the sowing density in the experiment was low (16 seeds/m^2), compared with about 200 seeds/m^2 in moderately dense H.sericea stands (Richardson unpublished data). The numerous seeds released in large burnt areas (over 500 ha) would probably not suffer predation from diurnal rodents deprived of cover, as these rodents usually disappear immediately after burns (G.J.Breytenbach pers. comm.) This would result in greater germination success in

large burnt areas when compared to small plots.

The failure to detect differences between burnt and unburnt veld can also be attributed to the nature of the experimental design. The "unburnt" treatment comprised sowing seed in a firebreak of low plant biomass (estimated at below 250 g/m^2). Mature fynbos stands usually support a plant biomass of between 1000 and 3500 g/m^2 (Van Wilgen 1982,1984 a). Factors affecting germination, such as available moisture, light, competition and rodent densities would therefore be vastly different in a firebreak when compared to mature fynbos. Differences in germination success between burnt and unburnt fynbos could therefore not be detected as the unburnt plots were more representative of burnt areas (low biomass) than of mature fynbos stands.
We are unable to explain the significant interaction between season of sowing and burning.

Management implications

Certain intuitive implications for the management of weed populations can be drawn from results of this study. Peak germination of H.sericea seeds takes place in mid-winter (for seeds sown between November and March) . Felling in winter and spring when the cue for germination has passed will expose seeds to maximum predation before germination occurs .This would appear to be the best time to conduct felling operations. The time between seed release and the attainment of reproductive maturity (Figure 4) is maximised. This generalisation does not apply to all areas

of the fynbos biome however. For example, Leucadendron xanthoconus showed no response to season of burn at Lebanon near Grabouw (Kruger 1972). This is probably due to quick germination after burning. Van Wilgen (1984 b) shows that seasonal fluctuations in the climate of the fynbos biome are far less marked along the southern coastal areas (Langeberg and Outeniqua ranges). Season of felling may have little effect on the germination of H.sericea in these areas as germination takes place soon after seed release in any season.

A problem faced by managers in the south-western Cape is that weather conditions suitable for clearing operations are rare in winter and spring. Clearing operations should therefore be undertaken between spring and autumn (September to March) and the area burnt in the following autumn (March to April).This is the best time to burn inland fynbos (Bond et al 1984, Van Wilgen & Viviers 1984) and a fairly intense fire should ensure that the seedlings are killed. This study has concentrated on examining the effects of season of fire and felling and has ignored the element of fire intensity. Prescribed burns are timed to result in "safe" fires; such fires are often of low intensity and many small H.sericea seedlings survive. Fires should be sufficiently intense to achieve adequate control. The ability to select conditions which will result in the desired fire intensity would be an advantage. This is possible using systems based on Rothermel's (1972) fire model (Van Wilgen et al. in press) and managers should be encouraged to make use of these aids. Reliance on the fire to kill seedlings would

seem to be a better weed control strategy than manipulation of seedling survival due to season of felling. Where dense infestations are cleared, the massive fuel load can result in exceptionally intense fires with heat concentrated near the soil surface. The effect of such fires on fynbos recovery is not known and warrants investigation.

It is encouraging to note that the hakea fruit weevil, Erytenna consputa Pascoe, an introduced biological control agent, has destroyed more than 80% of the annual fruit production of H.sericea at a study site near Worcester (Kluge 1983). The weevil is now well established in 80 protected release sites throughout the distribution range of H.sericea in South Africa (Kluge & Richardson 1983). This means that seed loads could be reduced from around 100-200 to 20-40 seeds/m^2 in regenerating stands. This is close to the density used in this experiment. Although the seed used in this experiment was 100% viable, germination and survival in the field was very low ($\bar{X}$=1,7%), due to predation by rodents and birds. Once the dense infestations have been cleared, biological control should limit seed production of plants of subsequent generations. This, combined with the heavy mortality of seeds prior to germination such as we have observed, should significantly reduce the invasive potential of this weed. Future research should concentrate on documenting the degree of success achieved in actual management operations and deducing the reasons for this, rather than on the plot experiment approach (with all its inherent difficulties) that was adopted here.

ACKNOWLEDGEMENTS

Mr S.R.Fugler initiated the experiment and was responsible for enumeration of the plots in the early stages. The technical assistance of staff of the Jonkershoek Forestry Research Centre and in particular Mr G.G.Forsyth is acknowleged with thanks. Mr I.A.W. Macdonald, Dr R.L.Kluge and Mr W.J.Bond provided useful comment and Prof. A. van Laar assisted with aspects of data analysis.

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PART 4.

PAPER 3: SEED DYNAMICS FOLLOWING FELLING OF *HAKEA SERICEA* AND IMPLICATIONS FOR THE INTEGRATED CONTROL OF THIS WEED

D.M.RICHARDSON

SYNOPSIS

Hakea sericea, an invasive woody shrub in the fynbos, is normally entirely reliant on seed for reproduction following fire or felling. In this study, the fate of seeds released at three-monthly intervals in large plots was investigated. Most seed released after death of the plants falls straight to the ground and felling reduces dispersal over large distances by wind. After 12 months less than 1% of seed had escaped granivory, but stands would nonetheless return to pre-felling densities if only 60% of these remaining seeds germinate. A study of seed longevity and factors affecting germination is required to predict germination success in order to achieve optimum control.

INTRODUCTION

Hakea sericea, a woody shrub of Australian origin, is an aggressive invader of mountain fynbos ecosystems in South Africa (Neser & Fugler 1978). Mechanical control of this weed in proclaimed mountain catchments is undertaken by the Directorate of Forestry. The control involves felling the plants and then burning 12 to 18 months later.

H.sericea relies on its large reserve of viable seed for proliferation. The large seed store accumulates due to the lack of pre-dispersal predation by insects. The seeds are borne in woody heat resistant follicles and are released upon death

of the parent plant. Gill (1981) has suggested that for some species the simultaneous release of canopy-stored seed may be analagous to mast fruiting and be a means of escaping seed predators. Bond (in prep) has provided evidence to support this hypothesis for indigenous fynbos Proteaceae with canopy-stored seed reserves. H.sericea, from a similar fire-prone environment in southeastern Australia, shows similar fire-survival adaptations (Neser 1968).

Insect seed predation (together with the lack of growth promoters such as cytokinins) in fynbos Proteaceae result in a typically low percentage germination (Van Staden & Brown 1977, Van Staden 1978 a&b). The absence of specific insect enemies of H.sericea has contributed to the accumulation of large reserves of seed which are 100% viable (Richardson & Van Wilgen 1984). As in the case of indigenous Proteaceae (Bond 1984), no soil-stored seed reserves accumulate between fires.

The introduction from Australia and successful establishment of several host-specific insect enemies of H.sericea has significantly lessened its invasive potential (Kluge 1984). As a result, the need for active containment and follow-up measures after formal initial control programmes will be reduced and may eventually be unnecessary. The Directorate of Forestry is however still faced with the problem of large, densely infested areas. Mechanical control will remain the most important control measure until the large infestations have been cleared. Plants severed below the lowest growing shoot display no vegetative regrowth. H.sericea is therefore normally entirely reliant on seed for re-estab-

lishment following effective felling operations or fire. A thorough knowledge of the seed biology and the dynamics of the seed bank in the immediate post-release phase will assist in optimizing control. In this study seed loads in moderately dense stands of H.sericea were determined to provide baseline data for use in further studies on the integrated control of the species. The fate of seeds released from felled plants in large (100 X 100m) plots at different times of the year was examined.

METHODS

Studies were conducted on four 100x100m plots in a moderately dense H.sericea stand on the Vergelegen Estate near Somerset West. The physiography of the study area is described by Richardson & Manders (in press). The density of H.sericea shrubs on the four plots ranged from 0,48 to 0,90 plants/m^2.

All H.sericea shrubs on respective plots were felled at the following times: October 1982 (plot 1), January 1983 (plot 3), April 1983 (plot 2) and July 1983 (plot 4). The seed load on each plot was estimated by counting the number of mature healthy follicles on 15 randomly selected shrubs harvested from each plot. The basal diameter of each of these shrubs was measured. The relationship between these two variables was investigated by fitting linear, exponential, logarithmic and power curves to the data for each plot. For all plots, an exponential curve yielded the highest coefficient of determination (r^2). The slopes

of the four curves were compared by means of an analysis of covariance. The differences in regression relationships among three of the four curves were not significant. For plot 4 the low coefficient of determination (Table 1) indicated that relatively little variation in log number of follicles is explained by the linearised relationship to basal diameter. Similarily low r^2 values were obtained for all other curve forms fitted to data from this plot. Data for the other three plots were pooled and used to fit a common curve.

The number of seeds (number of follicles X 2) per shrub on each plot was estimated as follows: The basal diameters of 200 randomly selected shrubs were measured within that plot and the expected number of seeds/shrub was estimated by using the exponential equation for the pooled data. A mean number of seeds per shrub was estimated from these values. Prior to felling the number of H.sericea shrubs were counted on two 10 X 50m transects sited at random in the plot. This, together with the estimated mean seed load per shrub, was used to estimate total seed load for the plot.

Plots were enumerated twelve months after felling. Each plot was divided into four sub-plots of equal size. Preliminary surveys showed that seeds were located almost exclusively under felled shrubs. Only 1-2 seeds/m^2 occurred between shrubs compared to more than 500 seeds/m^2 under felled shrubs. A grid (50 X 50m) was laid out in the centre of each plot, with five lines 10m apart in both directions. The proportion of each line in the grid that passed over felled shrubs was used to estimate the

area of each plot covered by prostrate H.sericea shrubs.
Twenty five random litter samples were taken from beneath felled H.sericea shrubs in each sub-plot. A metal ring (area=0.0573 m^2) was used to demarcate sampling sites. The litter and a thin soil layer (c. 2cm) were collected. The samples were then oven-dried and sorted. All H.sericea seeds were recovered and divided into "full seeds" and "empty seeds". The former were defined as those having a firm, undamaged endosperm.

RESULTS

Exponential curve equations for predicting the number of follicles from the basal diameter in the four plots and for the combined data of plots 1,2 and 3 are shown in Table 1. Data for the estimation of seed loads for the four plots are presented in Table 2. Data from the seed samples collected 12 months following the felling operation are presented in Table 3. The initial estimates of seed load (Table 2) are adjusted in Table 3 to estimate seed load per unit area for the whole plot by multiplying by the proportion of the total area in which the seed is concentrated. In this way figures comparable to those in Table 2 are obtained. This assumes that no seeds occur on areas between felled shrubs.
If the means for the four plots in Tables 2 and 3 are compared, it is evident that for three of the plots, the estimates of seed load using regressions are within 50% of the seed load as estimated by sampling litter 12 months after felling. (The

TABLE 1 : Exponential curve equations for predicting the number of follicles from the basal diameter of Hakea sericea shrubs on four 1ha plots at Vergelegen, Somerset West

Plot	Date of Felling	Exponential curve Equation	Coefficient of determination (r^2)
1	October 1982	$y = 4,33\ e^{0,06x}$	0,94
2	April 1983	$y = 1,52\ e^{0,09x}$	0,81
3	January 1983	$y = 4,57\ e^{0,07x}$	0,83
4	July 1983	$y = 5,54\ e^{0,05x}$	0,42
Pooled data for plots 1,2 and 3	-	$y = 3,04\ e^{0,07x}$	0,82

TABLE 2 : Estimation of seed load in moderately dense stands of Hakea sericea at Vergelegen, Somerset West (See Text)

Plot	Estimated mean number of seeds per shrub	Estimated number of H. sericea shrubs/ha	Estimated number of seeds/m^2 for plot
1	152,33	5910	90,03
2	316,52	4825	152,72
3	99,43	5560	55,28
4	194,21	9000	174,79

TABLE 3 : Estimation of the soil seed store of H. sericea 12 months after seed release. Seed was collected beneath felled shrubs and the data adjusted to estimate seed load for the plot (See Text)

Plot	Total number of seeds/m^2 under felled shrubs	Percentage of plot covered by felled H. sericea shrubs	Estimated number of seeds/m^2 for plot	Number of full seeds/m^2	Estimated number of full seeds/m^2 for plots
1	331,14	28,17	93,29	0,70	0,20
2	747,17	30,13	225,14	7,34	2,21
3	664,21	38,44	255,32	0,87	0,34
4	370,44	39,48	146,24	2,62	1,03

method underestimated seed load by 3,6% and 47,4% for plots 1 and 2 and overestimated seed load by 16,3% for plot 4.) Discrepancies of this order should be expected as neither of the two methods estimate seed loads accurately. For plot 3, the estimate of soil stored seed was 362% greater that the estimate for the canopy stored seed.

It is clear that most of the seed released after felling falls straight to the ground and is not dispersed over large distances by wind. The spread of seed to adjacent areas is considerably reduced. Of the seed collected 12 months after felling, only between 0,13 and 0,98% remained whole (Table 3).

DISCUSSION

Examination of seed remains suggests that rodents were responsible for seed destruction (S.A.Botha, pers.comm.). No small mammal trapping was undertaken at the site but striped field mice (Rhabdomys pumilio) were frequently observed beneath felled shrubs. Diurnal rodents are afforded shelter from predators by felled shrubs and other vegetation and consume large quantities of seed (personal observation). This is in contrast to the situation in burnt veld where diurnal rodents are deprived of cover and the seeds therefore suffer less predation (cf Richardson & Van Wilgen 1984).

Sommerville (1977) found no significant difference in germination success between H.sericea seeds incubated after one and after 14 weeks of desiccation (25°C at an unspecified constant humidity).

No data are available on longevity of seed beyond this period. No dormancy strategy has been reported for H.sericea and it is generally assumed that germination takes place as soon as favourable micro- and macro-climatic conditions are realised. Richardson & Van Wilgen (1984) found that peak germination occured between May and June for seeds sown in burnt veld between November and March (2-7 months after sowing). Seeds sown between September and November showed no distinct germination peak but some germination took place between September and November of the following year (12 to 16 months later). This suggests that fresh seeds rely on a winter germination cue.

Although germination was negligible on all plots 12 months after felling in this study, this is not the case in all areas (personal observation). Estimates in Table 3 show that an average of 0,945 full seeds/m^2 remain 12 months after the felling. If 60% of these seeds survive to germinate, the number of plants in the ensuing generation will be the same as the previous generation despite heavy predation. The reason for the failure of seeds to germinate in this study remains unanswered but it is obvious that a sound knowledge of these factors would enhance our ability to conduct successful control operations. Further work on this aspect is identified as a research priority.

Laboratory trials (Van Staden 1978 b) and field studies (Bond 1980) have shown that for several species of serotinous Protea, seed is short lived after release from the cone. H.sericea, with similarily thin-walled seed, probably displays similar early seed mortality in the absence of conditions suitable for

germination. H.sericea seed is well adapted to germinate in post-fire fynbos environments, but may not survive for long under felled stands. Thus a determination of seed longevity is also a priority for research aimed at optimising control.

Fires through areas where dense H.sericea infestations have been cleared can produce intense heat near the surface due to the concentration of fuel in this stratum (personal observation). Such intense fires result in oxidisation of organic material of the surface soil horizons, drastically modify physical properties and often lead to accelerated erosion (Kruger & Bigalke 1984). Adverse effects on the structure of indigenous vegetation following such a fire are also evident (Richardson in prep).
Once seed longevity and the factors controlling germination are known, it may be possible to leave dense felled infestations for longer periods before burning to allow for decomposition of the fuel loads, thus minimising the impact of the control burns on the ecosystem.

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PART 5.

PAPER 4: PREDICTING PATHOGEN-INDUCED MORTALITY IN *HAKEA SERICEA* (PROTEACEAE), AN AGGRESSIVE ALIEN PLANT INVADER IN SOUTH AFRICA

D.M.RICHARDSON & P.T.MANDERS

SUMMARY

The woody shrub Hakea sericea is an aggressive invader of natural vegetation in South Africa. Large-scale die-back in H.sericea is attributed to a form of the fungus Colletotrichum gloeosporioides.

The progression of symptoms of the disease were monitored over 21 months. Results were used to construct a transition matrix model to predict further progression of the disease. 82% mortality is predicted after 10 years. Pathogen induced seed release occurred mainly between October and January. No regeneration was observed beneath or near infected stands of H.sericea. The model will be useful to managers when identifying priority areas for weed control operations.

INTRODUCTION

The problem

Hakea sericea Schrad. (= H.tenuifolia (Salisb.) Domin) (Proteaceae) was introduced to South Africa from Australia in the 1830's as a hedge plant (Neser & Fugler, 1978). Since then it has invaded nearly all the major mountain ranges of the south-western, southern and south-eastern Cape Province (Fugler, 1982). It is typically an erect single-stemmed, much-branched shrub 2-3m

high. In thickets, however, it may grow into a slender, more or less unbranched tree up to 5 m in height. In places it forms a dense, impenetrable cover which threatens the indigenous fynbos vegetation. Fynbos is characteristic of a large part of the Cape Floristic Region (Goldblatt, 1978) and includes types described by Acocks (1953) as macchia, false macchia and coastal macchia. Fynbos is floristically rich and unique and is thus of considerable ecological importance. Invasion by woody weeds is a major conservation threat in this vegetation type (Kruger,1981).

H.sericea is particularly well adapted to survive the periodic fires which are a feature of the fynbos environment (Neser, 1968). The lack of specialised pre-dispersal seed predators ensures a large seed load (Kluge,1983). The winged seed is retained in woody heat-resistant follicles and is released only on death of the parent plant or branch (serotiny sensu Le Maitre, 1985). Standing plants killed by fire liberate seed within a few days. The seeds may then be dispersed by wind over great distances. The copious seed production and serotinous habit ensure prolific regeneration following fires.

The control of H.sericea

Mechanical control combined with burning is undertaken by government agencies as a conservation measure and has been largely successful in controlling H.sericea (Fenn, 1980). The method involves the felling of plants and burning 9 - 12 months later when the surviving

seeds have germinated (a large proportion of seeds are consumed by granivores) but before the seedlings have produced seed. Seed is released nearer the ground after felling and dispersal by wind over large distances is less likely. This method is extremely expensive and control programmes are generally reduced during periods of budgetary restraint. The additional fuel load of dead H.sericea plants in areas where control measures have been carried out can result in exceptionally intense fires which may have a detrimental effect on the recovery of fynbos elements.

Several highly specific natural insect enemies of H.sericea have been introduced from Australia (Neser & Annecke, 1973). Biological control should, in the long term, lessen the risk of re-infestation by reducing seed loads (Neser, 1968; Kluge, 1983).

Die-back in H.sericea

Large-scale mortality in H.sericea stands was first noted in 1966 (S.Neser and R.L.Kluge, personal communication). The causal organism was identified as a form of Colletotrichum gloeosporioides (Penz.) Sacc., a virulent fungal pathogen (Morris, 1982a). Subsequently symptoms of this gummosis disease have been observed throughout the range of H.sericea in South Africa (Morris, 1982a,b). The characteristic symptoms of the disease are stem and branch cankers exuding quantities of gum. These cankers girdle the stem, killing the host plant. The girdling often occurs near ground level but some individual branches are also girdled and

break off. Shoot tips of mature plants may be infected and die back progressively. Growing points of seedlings are attacked resulting in necrosis extending down the stem and killing the plant (Morris, 1982a).

Active human dispersal of spore suspensions of C.gloeosporioides was tested (Morris, 1983). Large scale tests have been discontinued as the pathogen was found to spread adequately unaided (M.J.Morris, personal communication). The contribution of this disease to the control of H.sericea has been considered largely opportunistic (Kluge & Richardson, 1983). No attempt has yet been made to quantify or predict the potential of the pathogen for incorporation into an integrated control programme. This paper deals with the development of a transition matrix model to predict the mortality of H.sericea through infection by C.gloeosporioides.

Transition matrix models have been used extensively for tree population dynamics (Usher 1966, 1969; Hartshorn, 1975; Enright & Ogden, 1979; Enright, 1982). They have also been employed for the dynamics of other plant forms (Bierzychudek, 1982) and plant parts (Maillette, 1982). Caswell (1982a,b) has used transition matrices to describe the dynamics of populations with complex life cycles. The model should be of use in planning H.sericea control programmes.

STUDY AREA

The Vergelegen Estate (34° 02'S ,18° 56'E) is situated on the

western (sea-facing) slopes of the Hottentots-Holland mountain range near the town of Somerset West in the south-western Cape Province. Altitudes range from 375 to 1590m. The lower slopes on which the study sites are located are underlain by sandstones and sandstone-granite mixtures. Climate is typically mediterranean and is characterised by warm dry summers and cool wet winters. Mean annual rainfall is about 1200 mm. No detailed climate data are available for the study site. The shrub Hakea sericea forms a continuous and impenetrable cover smothering the indigenous sclerophyllous vegetation which was originally a 2-3 m tall open shrubland comprising tall (2m) shrubs of the families Proteaceae (Protea neriifolia dominant), Ericaceae (Erica spp.) and Bruniaceae (Brunia nodiflora). The understorey (which survives to some degree below the H.sericea canopy) contains smaller shrubs of the Asteraceae (Stoebe spp. and Metalasia muricata) with a significant restiod (Restionaceae and Cyperaceae) component. Nomenclature follows Bond & Goldblatt (1984).

METHODS

Monitoring of infection states

Four plots were sited on the lower slopes at elevations ranging from 400 to 450m, to represent the various physical and vegetation conditions evident. A summary of plot characteristics appears in Table 1. Within each plot, a one metre wide path was cleared. One hundred randomly selected live Hakea sericea shrubs within 1 m of the path were tagged. The shrubs were examined at 3-monthly

intervals from April 1982 to January 1984 except during the 6-month period January - July 1983 when no observation was made. Symbols used to denote observation times are explained in Table 2. Each shrub was assigned a code number according to the degree of infection as follows: 1= dead leaf tips only; 2= cankers on branches but not on the main stem; 3= cankers and/or gum exudation on the main stem; 4= plant dead (all follicles open). No uninfected shrubs were found.

Table 1. Summary of plot characteristics

Plot	Density (*H. sericea* plants/m²)	Mean height of *H. sericea* (14 July 1982) (m)	Slope (degrees)
A	5,24	1,45	15
B	1,27	1,49	0
C	4,73	1,38	30
D	4,56	0,96	26

Table 2. Symbols used to denote observation times

Symbol	Observation
T_0	April 1982
T_1	July 1982
T_2	October 1982
T_3	January 1983
T_4	July 1983
T_5	September 1983
T_6	January 1984

Development of the transition probabilty matrix

In order to predict the fate of infected stands, the fungal infection on each shrub was considered as a unit in a population. The

fact that all plants in the sample were infected precluded the use of an epidemic model (*sensu* Hoppensteadt, 1974) which aims to predict the ultimate size of an epidemic. The intention to predict the fate of specific stands of *H.sericea* precluded the use of standard regression techniques or population growth models. These methods do not allow for the effects of the initial distribution of stages (in this case the development stages of the infection) on the development of the population.

The transition matrix model used here is based on the Leslie matrix model (Leslie, 1945, 1948) but differs from the standard application (Williamson, 1972; Jeffers, 1978) in that there are no fertility rates involved and therefore no contribution to the first class. The dominant eigenvalue and eigenvector therefore have no meaning, as for all cases λ will equal 1 (there is no increase in numbers and the stable age structure is achieved when all the sampled states of infection progress to the last state of infection). The model proposed is therefore not a model of population growth, but rather a model to predict the development of a population of degrees of infection, based on the intial distribution of categories and is limited by the maximum number of host plants available.

CONSTRUCTION OF THE TRANSITION PROBABILITY MATRIX

The observed distribution of infection states at the initial observation and the subsequent progression of tagged plants

through infection states were used to fit a transition matrix model. It was necessary to test the stationarity of transition probabilities over the chosen intervals for the four plots and also between plots (Bishop, Fienberg & Holland, 1975). For this purpose, transition count matrices were constructed to display the change in infection state of individuals over the given intervals. As infection state progression appears to be strongly seasonal, it was considered necessary to examine transitions over 3, 6 and 12 month intervals. Only those 3-month transitions for which observational data were available were examined. (No observation was made between January and July 1983.) As insufficient data were available to test two discrete 12 month intervals, it was necessary to include a 6 month overlap. Cursory examination of the 3 month transition count matrices reveals that infection progression is largely concentrated over the period July to October. As the two compared 12 month intervals have unique periods of such maximum infection progression, the comparison is deemed valid.

Transition count matrices for 3, 6 and 12 month periods for plots A, B, C and D are presented in Figures 1, 2 and 3 respectively. Figures in the transition count matrices represent the number of plants staying in infection states (column headings indicate initial infection states) and progressing to other infection states in the interval (row headings indicate final infection states). Column and row totals represent the number of plants in each infection state at the begining and at the end of the interval respectively. The total number of individuals

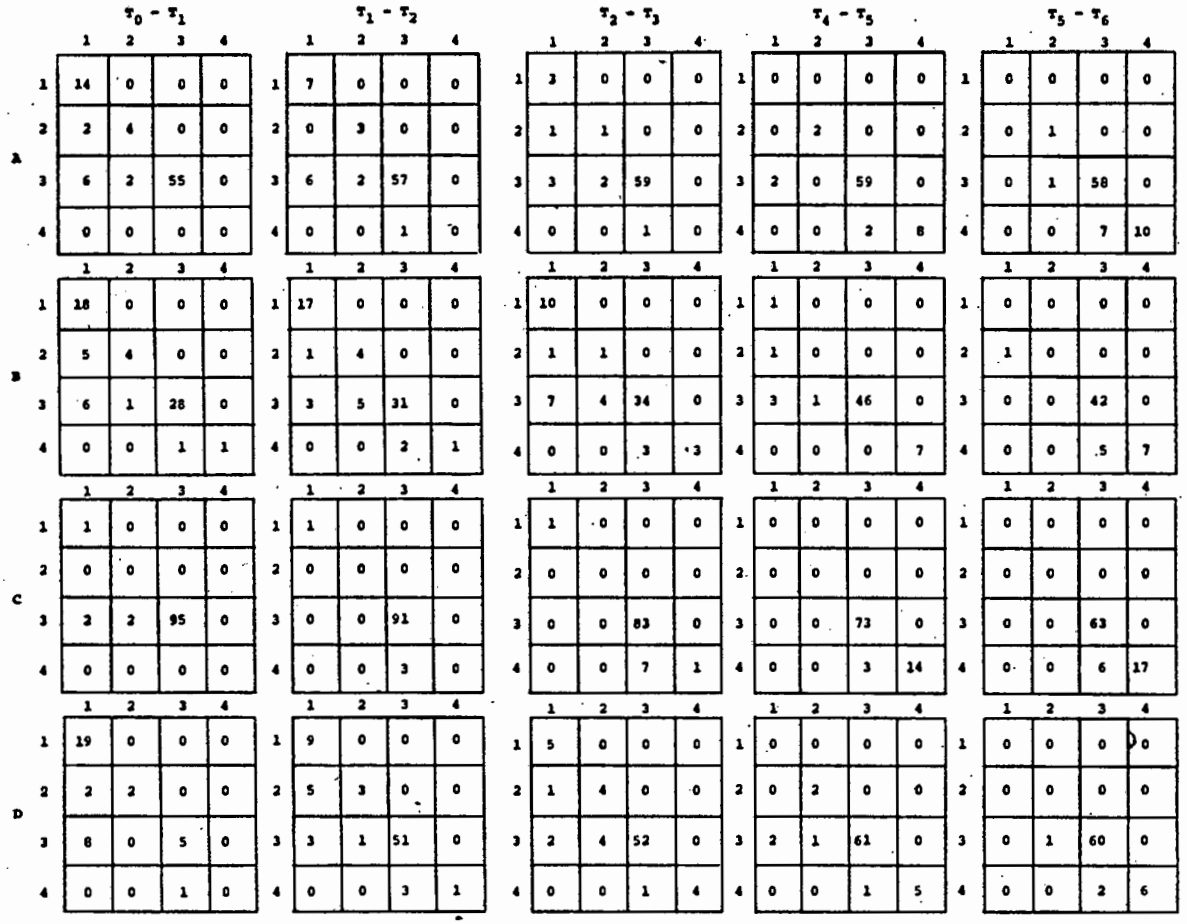


Figure 1. Transition count matrices for 3-month transitions for the 4 plots. For explanation of symbols used to denote observation times see Table 2

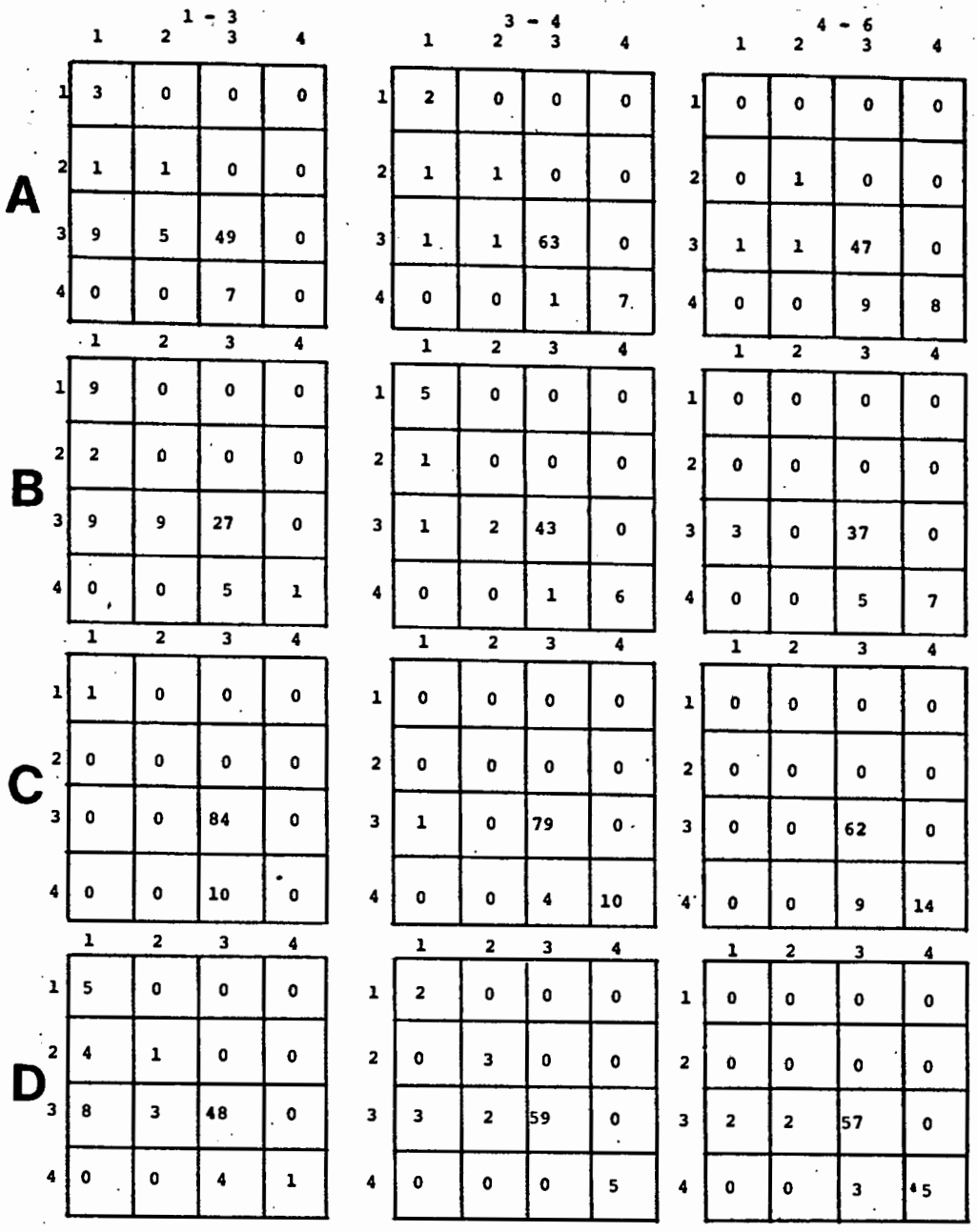
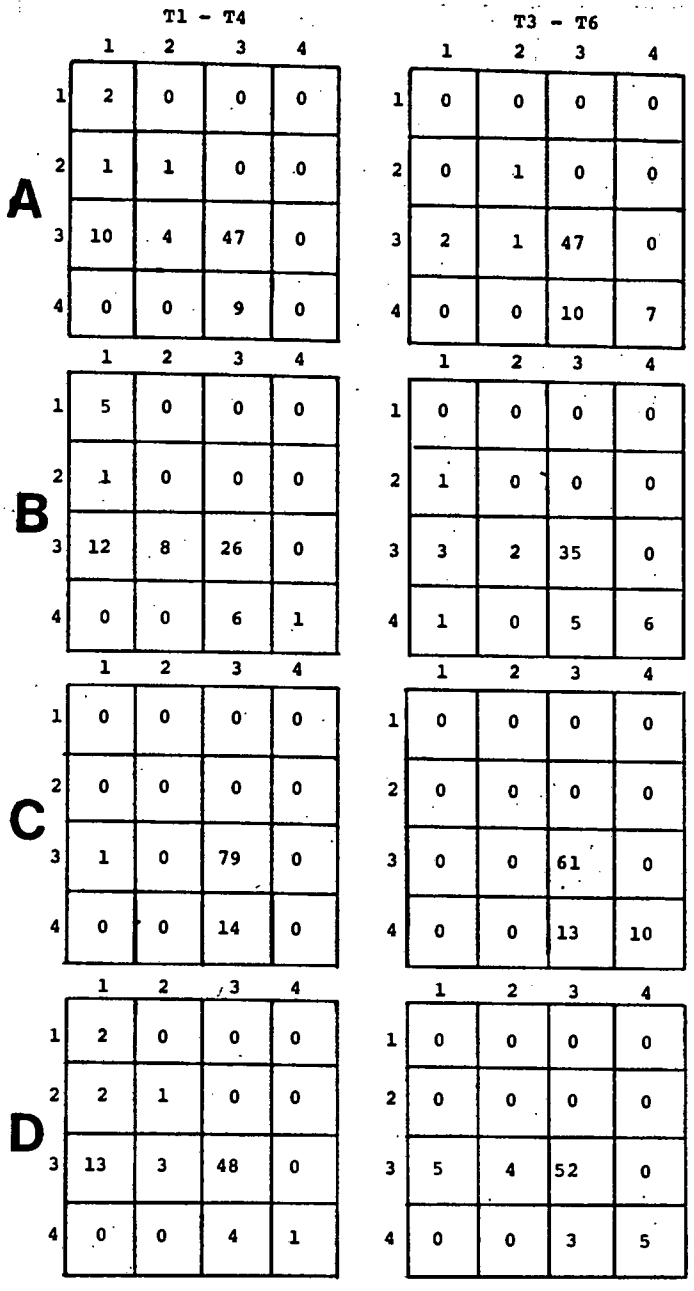


Figure 2. Transition count matrices for 6-month transitions for the 4 plots. For explanation of symbols used to denote observation times See Table 2



A	1	2	3	4
1	2	0	0	0
2	1	1	0	0
3	10	4	47	0
4	0	0	9	0

A	1	2	3	4
1	0	0	0	0
2	0	1	0	0
3	2	1	47	0
4	0	0	10	7

B	1	2	3	4
1	5	0	0	0
2	1	0	0	0
3	12	8	26	0
4	0	0	6	1

B	1	2	3	4
1	0	0	0	0
2	1	0	0	0
3	3	2	35	0
4	1	0	5	6

C	1	2	3	4
1	0	0	0	0
2	0	0	0	0
3	1	0	79	0
4	0	0	14	0

C	1	2	3	4
1	0	0	0	0
2	0	0	0	0
3	0	0	61	0
4	0	0	13	10

D	1	2	3	4
1	2	0	0	0
2	2	1	0	0
3	13	3	48	0
4	0	0	4	1

D	1	2	3	4
1	0	0	0	0
2	0	0	0	0
3	5	4	52	0
4	0	0	3	5

Figure 3. Transition count matrices for 12-month transitions for the 4 plots. For explanation of symbols used to denote observation times see Table 2

in each plot shows a decline with time as several tags were lost.

Stationarity was tested by means of chi-square analysis (Zar, 1974). The null hypothesis in each case is that given the state at the start of a transition, the state at the end of the transition is independent of the location of that transition in the temporal continuum representing the entire observation period of 21 months.

Initially the following categories of change in infection state over the given intervals were considered: (a) No change, and (b) promotion from an infection state (j) to an infection state (j+i) where j = 1,2,3 and i = 1,2,3 for j = 1, i = 1,2 for j = 2 and i = 1 for j = 3. The latter category represents the total number of individuals that showed an increase in infection severity during the interval. Comparisons for 3, 6 and 12 month transitions are presented in Table 3. For all chosen intervals, the null hypothesis was rejected. Due to the small number of plants remaining in classes 1 and 2 at the end of the 21 month observation period (between 0 and 1,8 % for the former and between 0 and 2,6% of the population in each plot for the latter), it was not possible to test the stationarity of transitions for these classes individually. As individuals occupying class 3 make up the greatest part of the population, it is appropriate to compare transition from this class over the different intervals (Table 4). Stationary probabilities are evident only for the 12 month intervals.

Differences between <u>plots</u> were tested over the intervals T_1-T_4

Table 3. Comparison of 3, 6 and 12 - month transitions to test whether infection state advancement is independent of the temporal location of the transition over the 21 month observation period

Transitions	Degrees of Freedom	χ^2
(3-monthly intervals) April - July 1982, July - October 1982, October 1982 - January 1983, July - August 1983, August 1983 - January 1984	5	10,350
(6-monthly intervals) July 1982 - January 1983, January - July 1983, July 1983 - January 1984	2	35,851
(12-monthly intervals) July 1982 - July 1983, January 1983 - January 1984	1	5,9185

Table 4. Comparison of 3, 6 and 12 - month transitions to test whether advancement from infection state 3 is independent of the temporal location of the transition over the 21 month observation period

Transitions	Degrees of Freedom	χ^2
(3-monthly intervals) April - July 1982, July - October 1982, October 1982 - January 1983, July to August 1983, August 1983 - January 1984	5	21,044
(6-monthly intervals) July 1982 - January 1983, January - July 1983, July 1983 - January 1984	2	16,952
(12-monthly intervals) July 1982 - July 1983, January 1983 - January 1984	1	0,01890

and T_3-T_6 by comparing transitions from class 3 by means of chi-square analysis (Table 5).

Table 5. Comparison of transitions from class 3 for the 4 plots over intervals $T_1 - T_4$ and $T_3 - T_6$

Plots	Degrees of Freedom	χ^2
A, B, C and D*	3	2,574
A, B, C and D≠	3	4,855
A, B and C*	2	0,2202
A, B and C≠	2	0,5725

* Transition $T_1 - T_4$

≠ Transition $T_3 - T_6$

For both intervals, deviations from the expected values for plot D provided the greatest contribution to the chi-square value and resulted in rejection of the null hypotheses at the 50 and 75% confidence limits respectively. Removal of plot D from the contingency table resulted in the null hypotheses being accepted. Data from 12 monthly transitions over intervals T_1-T_4 and T_3-T_6 in plots A, B and C were therefore used to construct the matrix of transition probabilities ($M_{i,j}$) for incorporation into the model.

The diagonal coefficients of the transition probability matrix (where i=j) are the proportions of individuals remaining in state j over the interval. The subdiagonal coefficients where i= j+1 ($M_{2,1}$; $M_{3,2}$; $M_{4,3}$) are the annual proportions of individuals moving up one state. Similarly, coefficients in

the second subdiagonal where i= j+2 ($M_{3,1}$; $M_{4,2}$) are the annual proportions of individuals moving up two stages. The third subdiagonal coefficient where i =j+3 ($M_{4,1}$) is the annual proportion of individuals moving up three states. The coefficient $M_{4,4}$ is equal to one as death of the host plant is the final stage. As no individuals regressed a state between observations, all other coefficients are zero. The combined transition count matrix for intervals T_1-T_4 and T_3-T_6, the derived transition probability matrix and the initial infection state structure at T_0 are shown in Figure 4.

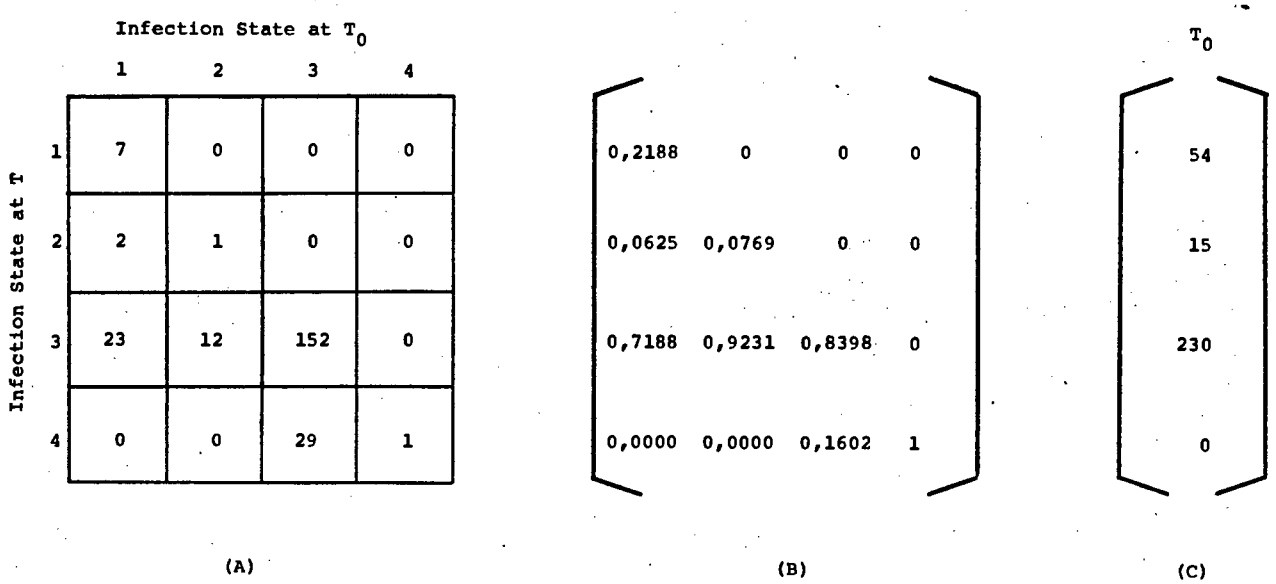


Figure 4. The combined transition count matrix for intervals T_1 - T_4 and T_3 - T_6 (A), the derived probability matrix (B) (See text) and the initial infection state structure at T_0 (C)

Entries in the transition probability matrix were derived by taking each entry of the transition count matrix as a proportion of the total of the entries in that column. In the model, the progression of the population of infection states through each

unit of time (one year) was estimated by premultiplying the population structure at the begining of the period by the transition probability matrix.

Table 6 shows the predicted distribution of infection states for 10 years.

Table 6. The predicted distribution of infection states for 10 years. Figures represent the percentage of the population in each infection state

	Infection State			
Year	1	2	3	4
0	18	5	77	0
1	3	1	84	12
2	0	0	75	25
3	0	0	62	38
4	0	0	52	48
5	0	0	44	56
6	0	0	37	63
7	0	0	31	69
8	0	0	26	74
9	0	0	22	78
10	0	0	18	82

DISCUSSION

Infection state progression

Elements of the transition probability matrix were derived from data from 12 month transitions as both 3 and 6 month transitions were found to contain non-stationary transition probabilities. Data from three of the four study plots were found to yield transition probabilities that did not differ significantly from one another. As observations were carried out for nearly two years, it is

considered that confidence can be expressed in the predictions for at least 10 years. Although 18% of the population remains alive at the end of the predicted 10 year period, these plants are all severely infected (infection state 3) and may be presumed to have a high proportion of dead branches. Although no data are available on the effects of climatic fluctuations and fire on the development of the disease, it is considered that the model described here will be of value in planning control operations.

The parameters in the transition matrix are ideally estimated using maximum likelihood. In future work, data should be collected over a number of discrete 12 month periods. All the parameters could then be estimated simultaneously using maximum likelihood. A vector of (estimated) initial proportions would then be multiplied by the matrix of transition probabilities to give the estimated distribution of infection states at T_o + 12 months, T_o + 24 months etc. These proportions would then be used to calculate the likelihood for the observed data at T_o, T_o + 12 months etc.

A factor contributing to the success of Hakea sericea as a weed in South Africa is its serotinous habit which leads to massive and simultaneous release of canopy-stored seed after fire or felling. A significant proportion of seed is consumed by granivores following seed release when sparse infestations or small patches of dense H.sericea are cleared (D.M.Richardson, unpublished data). When large areas are cleared, granivore satiation (cf Bond, 1984) occurs and a large quantity of seed remains to

germinate.

Seed is short-lived and the prolonged absence of conditions conducive to germination can lead to substantial seed loss and failure of the population to re-establish itself. It has been demonstrated (G.J.Breytenbach, unpublished data) that the rodent fauna in dense H.sericea thickets is at least as rich, both in numbers and in species as nearby uninfested areas.

Progression of H.sericea plants to infection state 4 and the subsequent release of seed is largely confined to the period October to January (T_2-T_3 and T_5-T_6 in Figure 1). Peak germination of H.sericea seed occurs in May/June (Richardson & van Wilgen, 1984). Seeds released from October to January are steadily depleted by rodents for 4 to 7 months before germination. No seedlings were observed beneath the canopy and it is concluded that the sporadic seed release induced by Colletotrichum gloeosporioides considerably reduces the eficacy of the serotinous strategy. A study to determine the effect of the level of seed release on germination would provide data necessary to enable the prediction of levels at which granivore satiation would occur. This would facilitate the development of a model to predict the fate of seeds released at different rates.

Practical applications

Mechanical control of H.sericea is expensive, time-consuming and possibily detrimental to fynbos regeneration. The infection states of a given H.sericea population may be determined simply and rapidly enabling the fate of the stand to be determined

using the transition matrix model.

It is proposed that an estimate of the seed release intensity required to achieve significant recruitment should be used in conjunction with this model. This will facilitate prediction of the stage at which a population of H.sericea will cease to maintain its numbers through seed regeneration. For certain stands, therefore, felling before burning may be unnecessary. Alternatively, delaying a proposed fire for a year or two may allow the seed crop to decline to below a critical level. The transition probability matrix derived from the data presented here may not be applicable to all stands of H.sericea. At the study site all plants showed signs of infection, which may not be the case in all areas. It may therefore be necessary to collect data in different areas to formulate a standardised transition probability matrix, or to define areas in which different matrices are applicable.

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PART 6.

GENERAL CONCLUSIONS

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The analysis of physiographic factors characterising areas infested with Hakea spp. (Paper 1) should be seen as a preliminary investigation of biogeographic features of the species in South Africa. Detailed analysis of bioclimatic, geological and habitat features in the natural range of H.sericea in Australia and the interpolation of results to South African conditions should provide a valuable insight on the potential range of the species. There is an opportunity to develop more effective management strategies by combining work on the characteristics of invasive species with that on the characteristics of invaded ecosystems (Ferrar and Kruger 1983).

Much of the research effort on alien invasive species in South Africa has been directed towards those vascular plants of economic importance in the agricultural sector. H.sericea in South Africa is confined to mountain fynbos, natural or semi-natural areas of low economic value (despite their importance as mountain catchments). For this reason, extensive control measures must be effectively integrated with veld management practices. Fire is the most important management tool in fynbos and a thorough knowledge of the relationship between fire and the ecology of the species is essential for effective control. To date some 140 000 ha of mountain catchments in the fynbos biome have been cleared of H.sericea and it is predicted that, given the current rate of progress, most areas for which the Directorate of Forestry is responsible will have been cleared within 10-15 years (Kluge

and Richardson 1983). In this study, aspects of the reproductive ecology of the species were examined and recommendations made on ways to improve the efficiency of control measures (Papers 2 and 3).

Accurate scientific monitoring of control operations should be initiated so that comparisons can be made between different methods. The lack of such data made it necessary to a adopt a plot experiment approach in these studies which caused certain difficulties (see Paper 2).

The mechanical control programme will remain the most important control measure until the large, dense infestations have been cleared. The contribution of biological control by means of introduced insects and an indigenous fungus will increase in importance as the emphasis shifts from one of systematic, large scale clearing to one of containment.

Detailed guidelines for managers on optimum use of integrated measures are required.

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