THE ECOLOGY OF INVASIONS BY PINUS (PINACEAE) AND HAKEA (PROTEACEAE) SPECIES, WITH SPECIAL EMPHASIS ON PATTERNS, PROCESSES AND CONSEQUENCES OF INVASION IN MOUNTAIN FYNBOS OF THE SOUTHWESTERN CAPE PROVINCE, SOUTH AFRICA

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ABSTRACT

The fire-prone mountain fynbos of the southwestern Cape Province of South Africa has been severely invaded by introduced trees and shrubs. These invasions have transformed fynbos shrublands to dense thickets of trees and shrubs in many parts of the region, thus disrupting various natural ecosystem processes. The ecology of invasions by species of Pinus and Hakea (the most successful genera) was studied using a series of natural experiments in conjunction with autecological studies. The study was divided into main four parts: (i) case studies to elucidate major patterns and processes of invasion; (ii) studies of the life history and population ecology of selected invaders; (iii) studies of the determinants of invasibility; and (iv) assessments of the consequences of invasion and of control programmes.

The invasions were examined at different scales to gain an overall perspective of the phenomenon: a global review of pine invasions revealed that biotic interactions, especially competition from vigorous herbs and grasses, were fundamental in determining the limits of pines. In mountain fynbos, however, pine invasions are overwhelmingly mediated by fire and wind patterns; biotic interactions contribute little to observed patterns. Invasions of serotinous trees and shrubs in mountain fynbos are essentially two-phased. First, isolated colonists establish at great distances from parent populations. The successful invaders have juvenile periods shorter than the average interval between fires. Most adult plants are killed by fire but prolific recruitment results from the accumulated seed store. Dense daughter stands are formed, and progeny from these nascent foci eventually form closed-canopy thickets.

For both pines and hakeas, introduced taxa have shown varying degrees of success as invaders. The most successful taxa in both genera share a suite of life history attributes that facilitate rapid migration and explosive population growth in a fire-prone environment: small seeds, low seed/wing loadings, short juvenile periods, low crop variability, strong to moderate levels of serotiny (seed retention in the canopy) and poor fire-survival as adults. Life history is the most important factor determining the relative success of different taxa. Dissemination by man is also important, especially in the case of pines: those species with the longest residency times and the widest use by man have generally invaded the greatest area. Life history considerations explain the exceptions to this rule.

The perspective gained from the analysis of relative success of different Pinus and Hakea species was used to develop a general risk assessment model for evaluating future introductions. As an additional practical application, a detailed assessment was made of the potential invasiveness of 69 Australian Banksia species.

The study sought to explain why mountain fynbos can support forests of introduced trees (when trees form only a minor component of the native flora), and also how the introduced species are incorporated into fynbos communities. It is suggested that resources (especially moisture) are not fully exploited in fynbos ecosystems (salient features of mountain fynbos are its low height and total biomass/area relative to environmentally analogous areas in other mediterranean-climate regions). The capacity of mountain fynbos to support alien trees appears to be a symptom of this marked imbalance in ecosystem-level resource use. This, and the paucity of vigorous herbs and grasses in the regeneration niche, and inherent features of the dynamics of these communities which include stochastic fluctuations in competitive hierarchies among native components, make mountain fynbos exceptionally vulnerable to invasion by fire-resilient trees and shrubs.

The widespread invasion of introduced trees and shrubs has added a major life form to many mountain fynbos communities. The ecosystem-level changes to the properties of the invaded communities were assessed at biome-, landscape-, community- and plot-scales. Invasions have caused significant reductions in the richness of indigenous plant species at the scale of small quadrats and at the landscape scale. The non-equilibrium status of mountain communities is disrupted by the incorporation of introduced trees and shrubs which establish fire-resilient populations. These invasions alter the properties of the communities and result in new depauperate steady-states. No plant extinctions can yet be directly attributed to invasions, but a cascade of extinctions is likely as dense stands spread and as the time since the establishment of thickets increases. Clearing dense stands can reverse the attrition of species richness. Mechanical control in conjunction with prescribed burning is the only practical option for clearing dense stands. Procedures were developed for reducing the deleterious effects of the exceptionally intense fires that occur when dense stands are controlled in this way.

PREFACE

The eleven chapters of the thesis include nine research papers that have already been published or that have been prepared or submitted for publication in scientific journals. In some cases, the papers have been edited slightly to cut down on repetition in the introduction sections. For this reason, some chapters are not exact copies of the published or submitted papers.

To achieve the major objective of this study (an overall understanding of the patterns, processes and consequences of invasion in mountain fynbos) it has been necessary to collaborate with several other workers in various fields of ecology. For this reason all but one of papers have one or more co-authors. Despite this, the ideas expressed and the concepts developed in this thesis are largely my own. The roles of collaborators are usually masked in dissertations comprising unpublished work. Publications emanating from such dissertations are frequently multi-authored. The benefits to be gained from intensive peer-review in the process of scientific publication while the thesis is taking shape cannot be overemphasized. They have certainly improved this thesis. However, the candidate for the Ph.D. degree must convince examiners that he is capable of independent critical thought. For this reason, I detail my contributions to the published papers included in the thesis.

I was senior author of all the multi-author papers and was principally responsible for formulating research hypotheses, designing the experiment(s), carrying out the bulk of field work and literature studies, for data analysis and for significant parts of interpretation and writing. For chapter 7 my contribution was approximately equal to that of the co-author. Two published reviews are included as Appendices I and II. In both cases, although not the first author, I made substantial contributions at all stages of their formulation i.e. planning, research and writing. These reviews, undertaken in the early stages of the project, formed the basis of much of the subsequent work, and for completeness they are submitted as part of the dissertation. The specific contributions of the co-authors of each paper are given below (see Acknowledgements for details of other assistance).

Chapter 1. General introduction. This was exclusively the work of D.M. Richardson.

Chapter 2. Invasion of mesic mountain fynbos by Pinus radiata. D.M. Richardson planned the investigation, participated in all the field work, analyzed the data and wrote the paper. P.J. Brown assisted substantially in the analysis of aerial photographs and co-ordinated the field work.

Chapter 3. Age structure and regeneration after fire in a self-sown Pinus halepensis forest on the Cape Peninsula, South Africa. This study was the work of D.M. Richardson.

Chapter 4. Aspects of the reproductive ecology of four Australian Hakea species (Proteaceae) in South Africa. D.M. Richardson formulated research questions, planned and conducted all field work, analyzed the data and was responsible for the bulk of interpretation and writing. B.W. Van Wilgen provided assistance with field work and interpretation. D.T. Mitchell determined seed nutrient contents.

Chapter 5. Pine invasions in South African mountain fynbos: life history or extent of cultivation ? D.M. Richardson planned the experiment, supervised and participated in all field work, did all data analysis and was principally responsible for interpretation and writing. R.M. Cowling assisted significantly with theoretical problems, the interpretation of age structures and life history strategies. D.C. Le Maitre assisted with literature studies and the analysis of life history strategies in the genus Pinus.

Chapter 6. Determinants of plant distribution: evidence from pine invasions. D.M. Richardson proposed that the review be undertaken, formulated research questions, undertook the literature study and wrote a first draft of the paper. W.J. Bond assisted with interpretation, introduced several additional questions and improved the manuscript.

Chapter 7. Why is mountain fynbos invasible and which species invade ? This paper was written in "workshop format" by D.M. Richardson and R.M. Cowling. Both authors contributed substantially in all phases of its preparation ie. planning, research and writing.

Chapter 8. Effects of thirty five years of afforestation with Pinus radiata on the composition of mesic mountain fynbos near Stellenbosch. D.M. Richardson planned the study, conducted all the field work, did all the data analysis and wrote most of the paper. B.W. Van Wilgen assisted with interpretation and assisted in the preparation of the paper.

Chapter 9. The effects of fire in felled Hakea sericea and natural fynbos and implications for weed control in mountain catchments. D.M. Richardson planned the experiment, participated in all field work, did all data analysis and wrote the paper. B.W. Van Wilgen assisted with the description of fuel models for the two sites and in the fire behaviour simulation study.

Chapter 10. Reductions in plant species richness under stands of alien trees and shrubs in the fynbos biome. D.M. Richardson planned the study, undertook the literature study, collected most of the original data and did most of the writing. I.A.W. Macdonald provided additional data and assisted with interpretation and writing. G.G. Forsyth assisted with field work.

Chapter 11. General conclusions. This was exclusively the work of D.M. Richardson.

Appendix I. Alien species in terrestrial ecosystems of the fynbos biome. I.A.W. Macdonald and D.M. Richardson contributed approximately equally to this review. Both authors contributed at all stages ie. planning, research and writing.

Appendix II. Processes of invasion by alien plants. F.J. Kruger and D.M. Richardson planned the review, undertook research and wrote the paper, each contributing substantially in all phases. B.W. Van Wilgen added additional information and assisted in the preparation of the final draft.

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Besides the co-authors (who are listed on the first page of each chapter), the following persons deserve special mention for their contributions to this work:

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CHAPTER 1

GENERAL INTRODUCTION

CHAPTER 1: GENERAL INTRODUCTION

This thesis considers several important aspects of plant invasions in mountain fynbos vegetation in the Cape Province of South Africa. Special attention is given to elucidating the patterns, processes and consequences of invasion by species of the genera Pinus (Pinaceae) and Hakea (Proteaceae). The aim of this chapter is to place in a global context the phenomenon of biological invasions, and to introduce very briefly some important concepts. I also examine the salient features of invasions in the fynbos biome and elaborate on the rationale and objectives of the thesis.

1.1. Biological invasions as a global phenomenon

The spread of organisms from sites of introduction in areas remote from their natural ranges is a phenomenon of increasing concern to managers of natural resources. As the human population has grown and the means of intercontinental transport have improved, so the magnitude of transfer of organisms between remote regions has increased. To satisfy his needs for food, shelter and an aesthetically pleasing environment, man has used a select few plants and animals to replace an array of species with less direct value. These introductions have allowed humans to colonize regions where the local resources did not meet their needs. Many introductions have, however, had unexpected and sometimes disastrous environmental and economic impacts due to the alteration they cause to the structure and functioning of natural and semi-natural communities and ecosystems.

Freed from the regulatory effects of their natural enemies, the introduced species often show enhanced fecundity in their new ranges. Provided that the new habitat is suitable for survival and growth of the introduced organism, enhanced fecundity almost invariably results in population growth which may, if dispersal is possible, lead to an increase in the range of the population, i.e. invasion. Biological invasions of this nature have affected almost all communities on earth to some extent.

Although natural communities are, on average, highly resistant to invasion, some organisms have invaded large areas following their introduction by man and now form important, even dominant, parts of the biota of the invaded region. The apparent ease with which some introduced organisms become naturalized and spread in some communities tends to belie the numerous obstacles that an invader must overcome in order to secure membership of a new community (Roughgarden & Diamond 1986; see also Appendix II). Some organisms have been highly successful invaders of communities in one region but have failed completely in others, and this has led to different regions containing different sets of alien species. For example, bulbous plants introduced from southern Africa feature prominently in the naturalized flora of mediterranean-climate Australia (Pate & Dixon 1982). Californian grasslands are today dominated by grasses from the Mediterranean Basin, and few fynbos communities in South Africa are free of self-sown stands of introduced trees and shrubs (Kruger et al. 1988). Charles Elton (1958), in his time-honoured book " The Ecology of Invasions by Animals and Plants", presented a concise review of some well-known invasions. The recent international SCOPE[1] programme on the ecology of biological invasions led to the publication of a number of national synthesis volumes (Groves & Burdon 1986; Macdonald et al. 1986; Mooney & Drake 1986; Kornberg & Williamson 1987) and also a global synthesis of the phenomenon (Drake et al. 1988). I will discuss many concepts from these syntheses in the ensuing chapters.

It is important to realize that invasions induced by the intervention of man are similar in many respects to the migrations of taxa from glacial refugia in the Holocene (or any other natural invasions). The composition of any community is the nett result of recurring invasions, contractions, extinctions and evolutionary processes. Information from both "natural" and "induced" invasions contribute to the understanding of the dynamics of colonization (Mack 1985; Neilson 1987; Richardson, in press). The induced invasions are, however, different in some important ways. Although sporadic long-distance dispersal of organisms by natural means (e.g. seeds adhering to migrating birds or carried by uncommonly strong winds) have probably occurred since the start of life on earth, propagules have never been transported in greater numbers or with such regularity as in the past several hundred years. Even if a few seeds of a herb from the Mediterranean Basin were carried by a migrating swallow to the southern tip of Africa, such are the vicissitudes of any immigrant in a foreign region that the likelihood of a seed thus introduced germinating and then surviving to found a new population is extremely remote.

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[1] Scientific Committee on Problems of the Environment, of the International Council of Scientific Unions.

If there is one golden rule for a successful invasion to be gleaned from the recent syntheses then it must be " Do it in numbers " !; the probability of succeeding as an invader increases exponentially with an increase in "inoculum" intensity. Only with repeated introductions, such as initiated by man, are the dice in the invasion numbers game starting to be loaded in favour of the immigrants.

1.2. Invasions as a management problem

By definition, the introduction of an organism to a community initially increases diversity in that community. The introduced organism may fail to become established in the long-term, in which case the diversity in the community reverts to its initial level. If the colonizer can retain its position in the community, the diversity may remain at a new amplified level for some time. If local conditions allow for reproduction, any resultant propagules will also encounter barriers to membership of the community. The "rules" for entry to the community may or may not have been altered due to the presence of the initial colonizer. Many invaders, once established do alter these rules, thus alleviating conditions for subsequent invaders, both conspecifics and others. For example, in the case of plants, such alterations may take the form of changes to the microclimate in regeneration loci [e.g. Meeuwig & Bassett (1983) and Everett et al. (1986) for pinyon pines] or the attraction of dispersal agents [e.g. Glyphis et al. (1981) for Acacia cyclops]. Frequently, a colonizer may persist at low densities in the community for several generations before significant population growth is accomplished (see Appendix II; II.3.1.). Once population growth occurs, with the accompanying spatial expansion, the invader is inevitably brought into contact with a greater number of resident community members. The outcome of such encounters may be beneficial, neutral or detrimental to both the invader and to each native taxon. The potential results of the sum of all these encounters, in terms of the effect on the structure and functioning of the community, are innumerable. For this reason, the nett effects of introductions and subsequent invasions on community structure and function are so complex that they are virtually unpredictable.

Why do invasions present management problems ? In short, invasions become problematic when they interfere with the activities or interests of humans in some way. The perception of problems resulting from invasions is closely linked to the land ethic in the region under consideration. For example, the spread of pines from plantations into natural communities in Australia, New Zealand and southern Africa is usually considered to reduce the "integrity" of natural communities and this, and the alteration of community functioning that accompanies it, is perceived as a problem (references in chapter 6; see also Richardson, in press). In South America, however, these invasions are sometimes seen in a rather different light, and self-sown pine stands are a welcome supplementary source of fuelwood (E.R. Fuentes, pers. comm. 1989).

Effects of invasions on community structure and function vary considerably in kind and severity among communities. Invasions may influence community processes to the extent that the regional hydrology, and erosion and fire regimes are substantially altered. One of the most common effects of invasions is a reduction or elimination of local biota. The degeneration of the local biota may occur as a result of a number of processes, most commonly through the invader's success in competition for resources with the natives, or through predation. Effects may be direct or indirect. For example, "invasions" by introduced bio-control agents may decimate local populations directly through predation (Moran et al. 1986; Zimmermann et al. 1986). Alternatively, an invader may so alter the structure of the community that reduction of native elements occurs indirectly, as a result of the altered disturbance regime induced by the structural changes. The importance of indirect effects is clearly illustrated in the case of the purposeful alteration of community structure in Californian chaparral. Introduced perennial grasses sown into dense chaparral support fires every two years which is highly unusual in this vegetation. Seed stocks of the native shrubs are depleted by post-fire germination and have insufficient time to be replenished before the next fire, which kills the shrub seedlings before they reach maturity. This series of events, promoted by the invader, has resulted in dramatic changes in community structure (Zedler et al. 1983).

The impacts of plant invasions in the fynbos biome on soil erosion rates, coastal sand movements, hydrology and fire regime, geochemical cycling and species richness of indigenous plant communities are reviewed in Appendix I [see also Breytenbach (1986) and Versfeld & Van Wilgen (1986)].

1.3. The study of invasions: two big questions

Studies of invasions, whether directed at developing effective management strategies or using invasions as natural experiments in biogeography and community ecology, address two fundamental questions:

1.3.1. Which species invade (and why) ?

In order to manage current invasions and to regulate the introduction of new invaders, it is important to determine the life history attributes of species known to be aggressive invaders. Are all species that possess a particular suite of attributes likely to invade a community that has already been invaded by species with these features ?

1.3.2. Which communities are invaded (and why) ?

Some communities are more severely invaded than others. For example, in southern Africa, the fynbos of the southern and western Cape Province, is the most severely invaded of all terrestrial biomes in southern Africa (Macdonald 1984). Invaded communities usually require special management and it is important to ascertain what factors enhance or reduce invasibility of these communities.

1.4. Biological invasions in the fynbos biome

The fynbos biome lies at the southern tip of Africa and includes the Cape Fold Belt Mountains and the coastal lowlands lying to the west and south of these mountains. Relevant physical and biological features of the biome and a detailed account of biological invasions in the region are given in Appendix I. Here, I describe only those aspects that are necessary to place this thesis in perspective.

1.4.1. Which species have invaded?

The most important alien invaders, both in terms of the extent of their infestations and their impacts, are undoubtedly trees and shrubs. However, the biome has been invaded by species from most taxonomic groups, with normally only a few species proving to be important in each of the faunal groups.

1.4.2. What are the characteristics of the invasions?

The invasions by woody plant species have been widespread and have often resulted in dense stands which radically alter biotic and abiotic features of the invaded landscape (Figure 1.1). These species have been able to invade relatively undisturbed ecosystems although the regular occurrence of fire in these ecosystems has tended to favour their spread and proliferation. The impact of these woody plant invasions on the indigenous flora has been marked. Most indigenous plants in the biome appear to be intolerant of shade and decline in vigour or die once overtopped by invading tree species. The invasions of herbaceous species and alien animals have generally been much less successful, with many of the alien species being restricted to sites of human disturbance.

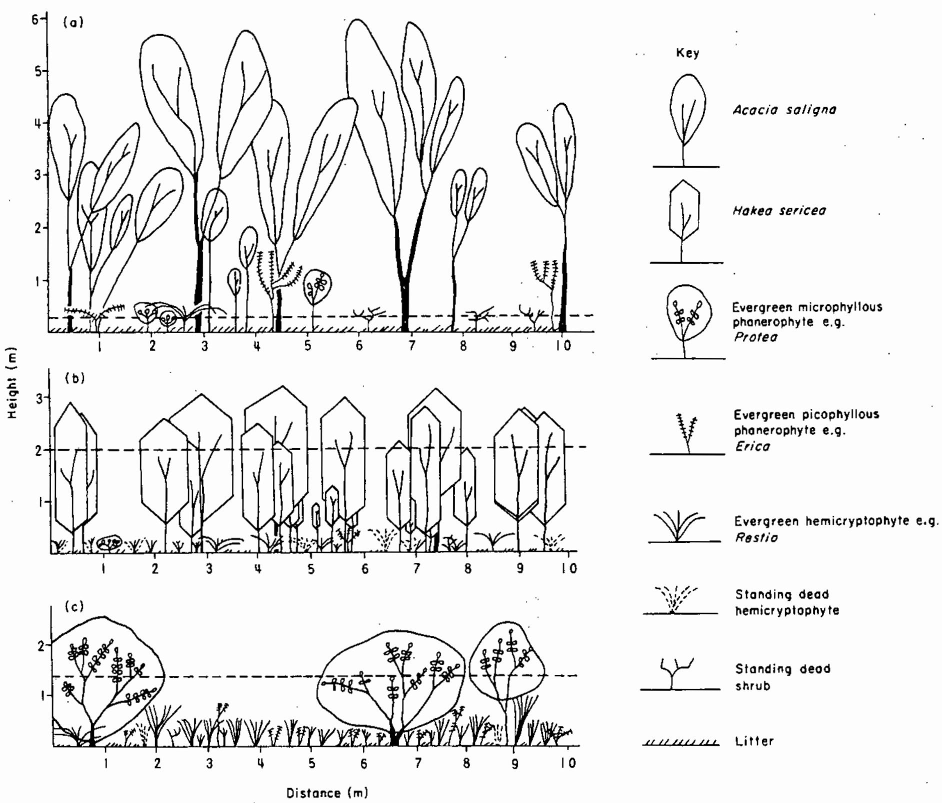

Figure 1.1. Profile diagrams from 1 m transects through three plant communities. (a) Mountain fynbos invaded by Acacia saligna, (b) mountain fynbos invaded by Hakea sericea and (c) uninvaded mountain fynbos (from Van Wilgen & Richardson 1985b).

1.4.3. Do any of these characteristics appear to be unique to the biome?

The dominance of the biome's invasive alien flora by trees and shrubs, at least in terms of the more important species, is possibly one of the features unique to the biome. Another is the large reduction in plant species diversity that follows the invasion of fynbos vegetation by alien woody plants. The apparent high susceptibility of the biome to invasion by species from elsewhere in the subcontinent is possibly also unique. That more alien animal species have been able to establish populations in this biome than elsewhere in the subcontinent might also be unique. However, this could simply be the result of the extensive modification to ecosystems and impoverishment of the fauna that has characterized the biome in recent times.

The apparent occurrence of a 'vacant' tree niche in the biome (Campbell et al. 1979), the alleged occurrence of a 'vacant' fish niche in the biome's rivers (Bruton 1986) and its susceptibility to invasion from elsewhere in the subcontinent all agree with the hypothesis that this small biome is in several ways akin to an island. The high levels of endemism in its indigenous biota strengthen this hypothesis. As in many 'insular' environments throughout the world, alien organisms have wreaked havoc in the fynbos biome and will probably continue to do so.

1.5. Aims, rationale and study methods

1.5.1. Selection of study taxa;

Species of the genera Acacia, Hakea and Pinus have been particularly successful as invaders of mountain fynbos (Macdonald & Jarman 1984; Macdonald & Richardson 1986). The introduced Acacia species have invaded large parts of the biome but only A. longifolia may be considered a major weed in mountain fynbos; the other species have invaded mainly lowland fynbos and riparian habitats (Macdonald et al. 1985). Hakea and Pinus species pose by far the most important weed problems in mountain fynbos (Macdonald & Richardson 1986; Figure 1.2).

Species of both genera were introduced to the Cape more than 150 years ago. Some species of both genera have become important weeds, while others have either failed to invade at all, or invade only small areas. All the invasive species of Pinus and Hakea are from fire-prone environments, and most species of both genera that invade fynbos are serotinous (they maintain seed banks in the canopy). The non-serotinous species have been less successful. The most successful species of Pinus, and all invasive Hakea species have winged seeds that are dispersed by wind. Species of Hakea and Hakea show fundamentally similar patterns of invasion in fynbos: spread has been from multiple, disjunct foci created by numerous introductions and dissemination by man, and from dispersal and repeated establishment of colonizers from founder populations. Different attributes of Pinus and Hakea species make them suitable for different kinds of studies and an overall perspective can be gained by studying salient features of the two taxa.

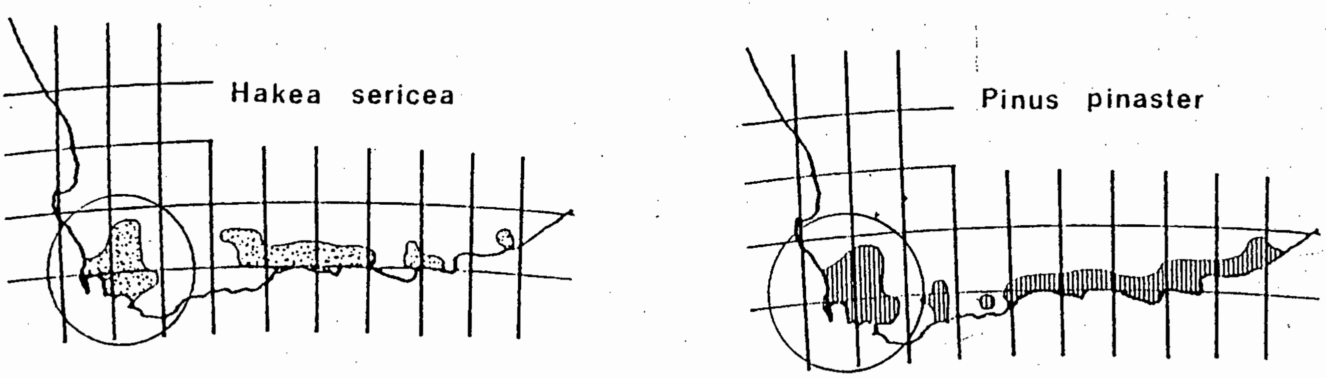

Figure 1.2. The distribution of Hakea sericea (Proteaceae) and Pinus pinaster (Pinaceae) in the fynbos biome of South Africa (after Macdonald et al. 1985). All the field studies reported on in this thesis were conducted in the southwestern Cape (ringed area). See Figure 1.3. for location of study sites.

The two pines that have invaded the largest area in mountain fynbos (Pinus pinaster and P. radiata) also show invasive tendencies on other continents. Indeed, the "weediness" of pine species has been evident throughout the Quaternary and numerous invasions (both within and well outside the natural range of pines) have been documented (Table 1.1.). These provide useful references for evaluating invasions in fynbos. The invasive Hakea species are not major weeds anywhere else in the world, probably because they have limited commercial value, and have therefore not been planted on a large scale in many countries. Hakea sericea has established adventive populations in New Zealand (Burrows et al. 1979:352) and in Portugal (F.M. Catarino, pers. comm. 1987) but is not a major weed in either of these countries.

Table 1.1. *Pinus* species known to be invasive or weedy.

Species	Natural range	Known sites of invasion [numbers refer to sources]
P. albicaulis	Western N America	Wyoming, U.S.A. [1]
P. banksiana	n.eastern N America	Wisconsin, U.S.A. [2,3], New Zealand [4, 5]
P. canariensis	Canary Islands	South Africa [6]
P. caribaea	Caribbean	Caribbean [7]
P. cembra	Central Europe	Austria [8]
P. clausa	s.eastern N. America	U.S.A. (2)
P. contorta	Western N America	U.S.A.: California [9,10,11,12,13,14], Idaho [16] and Wyoming [1]. New Zealand [4,5,17,18,19], Wales [19a]
P. densiflora	Korea / Japan	Japan [20], New Zealand [4]
P. echinata	Southern N America	S.E. U.S.A. [21]
P. edulis	Western N America	Western U.S.A., especially Utah [22, 23,24,25,26]
P. elliottii	s.eastern N America	U.S.A.[2], South Africa [27]
P. flexilis	Western N America	Colorado Front Range, U.S.A. [16, 28]
P. halepensis	Mediterranean Basin	France [29], Israel [30], South Africa [6,31, 32], New Zealand [4,5,33, 34]
P. jeffreyi	Western N America	U.S.A. [2,9]
P. kesiya	South East Asia	South East Asia: Burma, India, Philippines, Vietnam [35]
P. lambertiana	Western N America	U.S.A. [2]
P. lutchuensis	Islands near Japan	Bonin Islands, North-west Pacific [36]
P. massoniana	South East Asia	China [37]
P. merkusii	South East Asia	South East Asia [38,39]
P. monophylla	Western N America	Nevada, U.S.A. [22,25,40,41]
P. monticola	Western N America	Oregon, U.S.A. [2,9,14]
P. muricata	California	Australia [42], New Zealand [4]
P. nigra	Southern Europe	New Zealand [4,5,43], Wales [19a]

continued on next page ....

Table 1.1. (continued). Pinus species known to be invasive or weedy.

Species	Natural range	Known sites of invasion [numbers refer to sources]
P. oocarpa	Mexico	Mexico [7]
P. palustris	s.eastern N America	U.S.A. [2,44]
P. patula	Mexico	South Africa [42,45,46,47,48] New Zealand [4]
P. pinaster	Mediterranean Basin	Australia [49], Chile [50], South Africa [51,52], New Zealand [4,5,33,42]
P. pinea	Mediterranean Basin	South Africa [6,32] New Zealand [4]
P. ponderosa	Western N America	U.S.A.: Colorado [53], S. Dakota [54,55], Nebraska [56], California [57]. Chile [58], New Zealand [4,5,43]
P. pseudostrobus	Mexico	South Africa [48]
P. radiata	California	California, U.S.A. [59], Australia [60,61,62], Argentina [58], New Zealand [4,5], South Africa [6,32,63]
P. resinosa	Eastern N America	Wisconsin, U.S.A.[2,3,67]
P. rigida	eastern N.America	U.S.A. [2]
P. roxburghii	Nepal, Pakistan	Nepal [65], South Africa [27,32]
P. sabiniana	California	U.S.A. [2]
P. serotina	s.eastern N America	U.S.A. [2]
P. strobus	Eastern N America	New England, U.S.A. [66], New Zealand [4]
P. sylvestris	Europe	Central Europe [67], N.E. Europe [68], W. Europe [69,70,71,72,73,74], U.S.A. [2], New Zealand [4,5,74]
P. taeda	s.eastern N America	U.S.A.: N. & S. Carolina, Georgia [66,76,77]; New Zealand [4], South Africa [27]
P. thunbergii	Japan	Japan [20]
P. torreyana	California	New Zealand [4]
P. virginiana	Eastern N. America	U.S.A. [66]
P. wallichiana	S.E. Asia, Afghanistan	Nepal [65]

continued on next page ....

Table 1.1. (continued). Pinus species known to be invasive or weedy.

Sources: 1: Dunwiddie (1977); 2: Holm et al. (1979); 3: Vogl (1970); 4: Sykes (1981); 5: Hunter & Douglas (1984); 6: Macdonald & Jarman (1984); 7: Kemp (1973); 8: Tranquillini (1979); 9: Heath (1967); 10: Debenedetti & Parsons (1979); 11: Ratliff (1995); 12: Helms (1987); 13: Helms & Ratliff (1987); 14: Vale 1981; 15: Vankat & Major (1978); 16: Butler (1986); 17: Wardrop (1964); 18: Benecke (1967); 19: Jamieson (1974) in Hunter & Douglas (1984); 19a: Hodgkin (1984); 20: M. Ohsawa in litt. 1988; 21: Chapman (1944); 22: Woodbury (1974); 23: Aro (1971); 24: Clary (1971); 25: Everett (1986); 26: Seversen (1986); 27: Wells et al. (1986); 28: Veblen (1986); 29: Acherar et al. (1984); 30: Naveh (1973); 31: Richardson (1988); 32: Lister (1959); 33: Esler (1987); 34: Esler & Astridge (1987); 35: Turnbull et al. 1980; 36: Shimuzu & Tabata (1985); 37: Ming (1987); 38: Cooling (1967); 39: Cooling 1968; 40: Blackburn & Tueller (1970); 41: Barney & Frischknecht (1974); 42: Streets (1962); 43: Wills & Begg (1986); 44: Myers (1985); 45: Wormald (1975); 46: Macdonald & Jarman (1985); 47: Kruger et al. (1986); 48: Knight et al. (1987); 49: Brown & Hall (1968); 50: C. Gonzalez in litt. 1988; 51: Kruger (1977); 52: Shaughnessy (1980); 53: Veblen & Lorenz (1986); 54: Thompson & Gartner (1971); 55: Gartner & Thompson (1973); 56: Steinauer & Bragg (1987); 57: Vale (1977); 58: T.T. Veblen in litt. 1988; 59: Forde (1966); 60: Dawson et al. 1979; 61: Burdon & Chilvers (1974); 62: Chilvers & Burdon (1983); 63: Richardson & Brown (1986); 64: Vogl (1967); 65: Ohsawa et al. 1986; 66: Spurr (1964); 67: Holzner (1983); 68: Steijlen & Zackrisson (1987); 69: McVean & Ratcliffe (1962); 70: Watt (1971); 71: Crompton (1972); 72: Duffy et al. (1974); 73: Gimingham & De Smidt (1983); 74: Marrs & Hicks (1986); 75: Bannister (1965); 76: McQuilken (1940); 77: Brender (1974).

Several *Pinus* species are important forestry crops, and the extent of invasion of taxa within the genus appears to correspond roughly to the extent of planting. In contrast, no *Hakea* species are crops of major importance (some have been planted extensively as hedge plants or ornamentals), and there is no correspondence between the magnitude of dissemination and the current status of the taxa as weeds (see chapter 4). Biological control programmes for *Hakea* species show promise for the reduction of the problem. Because of the economic importance of the *Pinus* species for forestry, bio-control options appear very limited and repeated mechanical control is required to curb spread from plantations (Richardson, in press). There is, therefore, an urgent need for detailed information on the factors that control invasion.

1.5.2. Research questions

The five major questions that were addressed in this study are listed below.

1.5.2.1. What are the spatial and temporal characteristics of invasions by trees and shrubs in mountain fynbos ?

1.5.2.2. What are the biological attributes of successful invaders of mountain fynbos ?

1.5.2.3. To what degree is the current extent of invasion in mountain fynbos due to dissemination by man ?

1.5.2.4. What community properties of mountain fynbos permit invasion by introduced trees and shrubs ?

1.5.2.5. What are the impacts of invasions on mountain fynbos plant communities ?

1.5.3. Study methods

The study of invasions by trees and shrubs is complicated to some extent by their long life spans and large size that preclude certain greenhouse studies and various manipulative experiments. These characteristics, however, also have certain advantages for the study of invasions. For example, trees and shrubs are conspicuous and are relatively well studied, especially where they dominate communities or are of economic importance. Invasions by trees and shrubs are frequently well documented or can be reconstructed from historical sources such as the written accounts of pioneer naturalists, maps and photographs. Trees such as pines are easy to age, and this facilitates the determination of population age structure which is important for reconstructing the invasion history and for correlating population responses with environmental factors.

Biological invasions are one of the richest sources of information in community ecology; they present the imaginative investigator with natural experiments on temporal and spatial scales and with scope, realism and generality than can seldom be achieved with laboratory or field experiments (Diamond 1986). Indeed, natural experiments are probably the only practical means to study the long-term consequences of introductions and invasions of long-lived organisms. There are, however, several important limitations of natural experiments in the study of factors underlying species abundances and distributions, the main one being the problem of distinguishing causal from indirect associations (Diamond 1986:16). Despite the limitations, this type of experiment holds great potential for the study of invasions of trees and shrubs, as Kruckeberg (1986:408) explains in the following passage:

"Nearly every floristic province of the world that has felt the hand of man has its share of alien introductions that have spread in ecosystems far beyond their native homes. In all such invasions, we witness only the later stages or end products of an initial introduction. There is scarcely an example of an introduction that has been monitored from its starting time and point-source of its introduction. Such would seem to be the inevitable consequence of accidental introductions: no one presides over the birth of the unplanned population.

The intentional plantings of trees for reforestation purposes, for erosion control, for soil reclamation, etc., can be dated from time zero and planting monitored at intervals to determine the success of the original transplants of seedlings, and their spontaneous progeny, if any. Such instances, while potentially affording the population biologist with ready-made experimental populations, are rarely if at all observed from the demographic standpoint. What exceptional opportunities have been overlooked in plantations of such tree species as Pinus radiata, P. contorta, P. sylvestris, Pseudotsuga menziesii and many others ?".

In this thesis I have used various natural experiments in conjunction with autecological studies to examine the patterns, processes and consequences of invasions by Pinus and Hakea species with special reference to the situation in mountain fynbos. The study may be divided into four parts: i) case studies to elucidate major patterns and processes; ii) studies of life history and population ecology of selected invaders; iii) investigations of the determinants of invasibility; and iv) assessments of the consequences of invasion, and of control programmes. An outline of the approach used in each of these sections is given below.

1.5.3.1. Case studies to elucidate patterns and processes

Two specific invasion events in mountain fynbos were studied. Here, I examined the population dynamics of invasive pines to establish how the invaders interact with environmental conditions. These studies may be read on their own as investigations in plant biogeography and fire ecology, but form the foundation for the studies on the relationship between life history and population ecology (see 1.5.3.2.). Chapter 2 details the spread of Pinus radiata into natural mountain fynbos from a plantation, with special reference to the spatial and temporal dynamics of the invasion and the response (in terms of population structure) of the invader to two important environmental factors in mountain fynbos: fire and wind. In chapter 3, I examined in more detail the population response of P. halepensis to one environmental factor (fire) and attempted to isolate the life history attributes that explain features of the age structure.

1.5.3.2. Studies of the life history and population ecology of selected invaders

These studies examined the interaction between life history and population ecology and addressed the question " What makes a good invader ?". A comparative study of the reproductive ecology of four Hakea species which have shown different degrees of success as invaders in fynbos is described in chapter 4. The allocation of reproductive energy, germinability, the ability to survive fires and to germinate in burnt and unburnt areas, and the nutrient content of seeds were assessed for the four species. The importance of each of these factors was then assessed and related to invasive success. An attempt was then made to define a successful invader. In chapter 5, I assessed the roles of life history attributes and the extent of dissemination by man as determinants of success for invasive pines in mountain fynbos. Using an analysis of life history attributes of 60 Pinus species, an attempt is made to predict which species would be aggressive invaders if introduced.

The question of what makes a good invader in mountain fynbos was also addressed in part of Chapter 7. A risk assessment model was derived from empirical data and theoretical considerations to distinguish between species with low and high probabilities of becoming invaders. An evaluation was also made of the risk of introducing Australian Banksia species.

1.5.3.3. Studies of the target habitat

Two studies addressed the important question " What makes a community invasible ? ". The first of these examined a central question in community ecology: what limits the occurrence of a plant species to a particular site ? This involved a review of the world literature on pine invasions (both expansions in and adjacent to natural ranges, and spread from sites of introduction well outside the contemporary range of pines). The database thus assembled allowed me to explore the relative importance of climatic changes, disturbance, competition (including competition between seedlings and herbaceous plants during early establishment), herbivory, pathogens and other agents that might influence membership of communities by pines. This study (chapter 6) also served to place in the phenomenon of pine invasions in mountain fynbos in a global perspective.

The question of " what makes mountain fynbos vulnerable to invasion by introduced trees and shrubs, and which species invade ? " is addressed in Chapter 7. Data from various sources were used to explore the properties of mountain fynbos community structure and functioning that permit invasion.

1.5.3.4. Assessment of the consequences of invasion, and of control programmes, on features of invaded habitats

The assessment of the effects of invasion on community structure can be undertaken in one of two ways. The first approach involves the comparison of pre- and post-invasion community structure at the same site. Because of the long time intervals involved in the case of tree and shrub invasions, such studies are seldom feasible. An opportunity to conduct such a study was presented in the Biesievlei catchment, where a detailed study of plant communities had been done prior to afforestation with pines. Chapter 8 describes the results of a resurvey of the area, and an assessment of the effects of 35 years of afforestation on fynbos structure and composition. An alternative approach for assessing the effects of invasion (and subsequent weed control measures) is to compare the invaded site with an adjacent site which was not invaded. This approach was used in Chapter 9 to compare the effects of fire in areas where dense stands of Hakea sericea had been felled and in adjacent uninvaded sites. This study also assessed the implications for natural communities of the effects of control of invasive trees and shrubs in mountain fynbos.

Chapter 10 presents a synthesis of published and unpublished data on plant species richness in mountain fynbos with different levels of invasion and different histories of control.

1.5.4. Study sites

All field studies were carried out in the southwestern Cape Province (Figure 1.3). Details of the study sites are given in the different chapters.

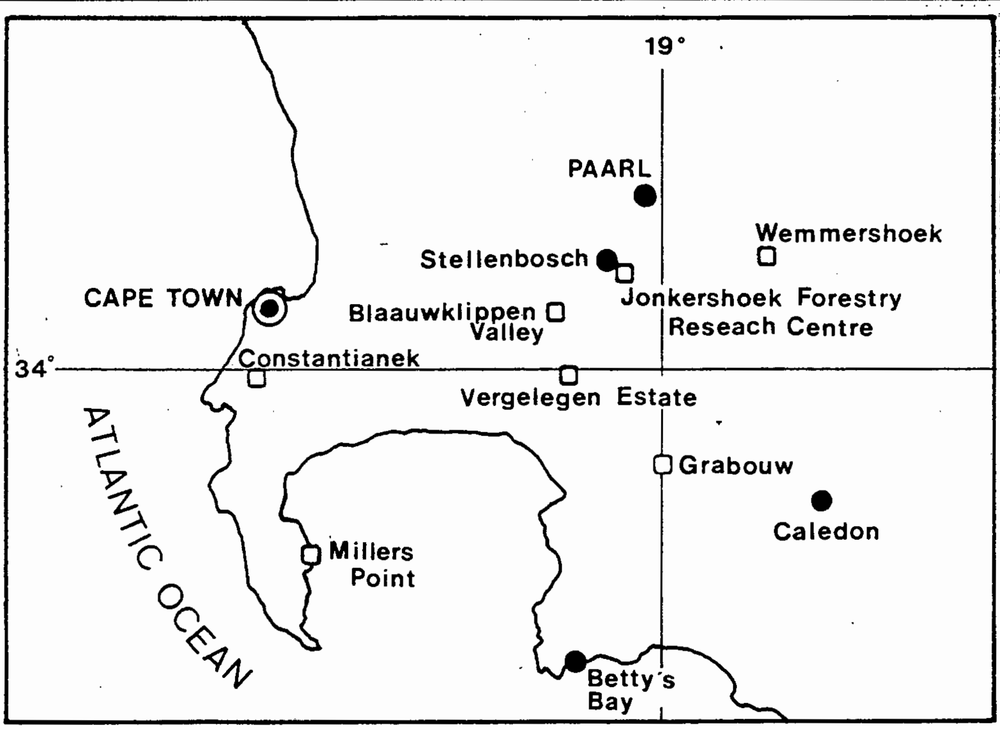

Figure 1.3. The location of field study sites (indicated by hollow blocks) mentioned in this thesis.

PART I

CASE STUDIES TO ELUCIDATE MAJOR PATTERNS AND PROCESSES

CHAPTER 2

INVASION OF MESIC MOUNTAIN FYNBOS BY *PINUS RADIATA*

CHAPTER 2 : INVASION OF MESIC MOUNTAIN FYNBOS BY PINUS RADIATA [1]

2.1. ABSTRACT

Pinus radiata is an important plantation species in South Africa. It also invades Mountain Fynbos in the southern and southwestern Cape Province and is a threat to the conservation of this vegetation type. Knowledge of the invasion process is required to plan effective control. The pattern of invasion was determined by examining aerial photographs and the dynamics of a colonizing population. Invasion commenced almost immediately after the first release of seeds from an adjacent plantation. Initial colonizers established at distances of up to 3 km from the seed source. Populations increased rapidly after a fire and resultant stands were dominated by cohorts that established during the immediate post-fire phase. Where fire had been excluded, population growth was slower, and less dense, uneven-aged stands resulted.

2.2. INTRODUCTION

Pinus radiata D.Don. (Monterey Pine) is native to coastal areas of central California and Guadalupe Island (Critchfield & Little 1966). The species has been planted in many countries on all continents because of its rapid growth and desirable lumber and pulpwood quality. Pinus radiata was introduced to South Africa in about 1865 (Legat 1930), but was little used for afforestation before 1910 (Poynton 1960). In recent years, afforestation has been rapid and by 1984, plantations of this species covered 48 775 ha in the southern and southwestern Cape Province (Unpublished records, Forestry Branch).

In its native and adopted environments, P. radiata is often subject to fire. It does not sprout but seeds freely and regenerates profusely after fire. This is evident both in California (Stebbins 1965, Vogl et al. 1977) and in the Southern Hemisphere where the species has been widely planted (Scott 1960). It has invaded natural vegetation in Australia (Burdon & Chilvers 1977, Chilvers & Burdon 1983) and New Zealand (Bannister 1965, Hunter & Douglas 1984). Pinus radiata has also invaded natural fynbos vegetation in the southern and southwestern Cape Province of South Africa. Self-sown stands of P. radiata occur in 240 of 8 138 (2,95%) 1 km X 1 km grid squares in proclaimed mountain catchment areas in the Western Cape Forestry Region (Combrink 1985). The species is listed as one of the 10 most important woody alien plants in the biome (Macdonald & Jarman 1984). Invasion by alien trees and shrubs is a major problem in the management of mountain fynbos, the

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[1] *Publication status: Richardson, D.M. & Brown, P.J. (1986). Invasion of mesic mountain fynbos by Pinus radiata. South African Journal of Botany 52: 529-536.*

species-rich sclerophyllous vegetation of the Cape coastal mountains (Macdonald & Richardson 1986). Successful alien species from similar fire-prone environments on other continents are adapted to survive fires which usually occur at intervals of 10 to 40 years in mesic mountain fynbos *sensu* Moll *et al*. (1984) (Kruger & Bigalke 1984). In the absence of factors which normally limit fecundity in the native habitat, populations in the adopted habitat often show an excessive increase following fire and dense thickets establish. These radically alter biotic and abiotic features of the invaded landscape (Macdonald & Richardson 1986, Richardson & Van Wilgen 1986).

Three *Pinus* species of the Group *Insignes* (Shaw 1914) (i.e. *P*. *radiata*, *P*. *pinaster* Ait. and *P*. *halepensis* Miller) are important invasive aliens in the fynbos biome (Macdonald & Jarman 1984). Another species, *P*. *patula* Schiede & Deppe, is an important invader of montane grasslands in Natal (Macdonald & Jarman 1985). For only one species has there been any attempt to describe invasion patterns. Kruger (1977) gave a general account of patterns of invasion of fynbos by *P*. *pinaster* but presented no quantitative analysis. In another study, changes over 39 years in the density of self-sown *P*. *pinaster* trees in mountain fynbos near Stellenbosch were documented (Smit & De Kock 1984). Neither of these papers presents a quantitative analysis of invasion patterns or the role of fire in the invasion process. Such information is needed to understand the dynamics of a colonizing population and to plan effective control measures.

In this study we examined the colonization by *P*. *radiata* of mesic mountain fynbos adjoining a plantation. The aims of the study were: 1) to determine how soon after establishment of the plantation invasion of adjacent fynbos commenced; and 2) to determine the rate and pattern of invasion and population growth in relation to disturbance history.

2.3. STUDY AREA

Bosboukloof (33°57′S; 18°56′E) is situated on the south-facing slopes of the Jonkershoek Mountains, 6 km east of Stellenbosch in the southwestern Cape Province, South Africa (Figure 2.1). The area is underlain by granite but stony, sandy soil derived from quartzitic colluvial material covers most of the area (Heth & Donald 1978). Elevation ranges from 240 to 900 m above sea level. Climate is mediterranean, Köppen's humid-mesothermal (type Csb) with a dry summer; the average temperature of the warmest month is below 22°C. Mean rainfall at an altitude of 470 m is 1 800 mm per annum, about 60% of which falls between May and August (Wicht, Meyburgh & Boustead 1969). Winds from the southeast make up the greatest percentage of the total wind run in all months of the year but particularly during summer: 71% and 67% of the total wind run for January and February respectively is from the southeast. Mean maximum daily temperature is also highest during these months (27,5 and 27,3 °C for January and February respectively; five year mean 1976 to 1980, Swartboskloof, Jonkershoek, Unpublished records, Forestry Branch).

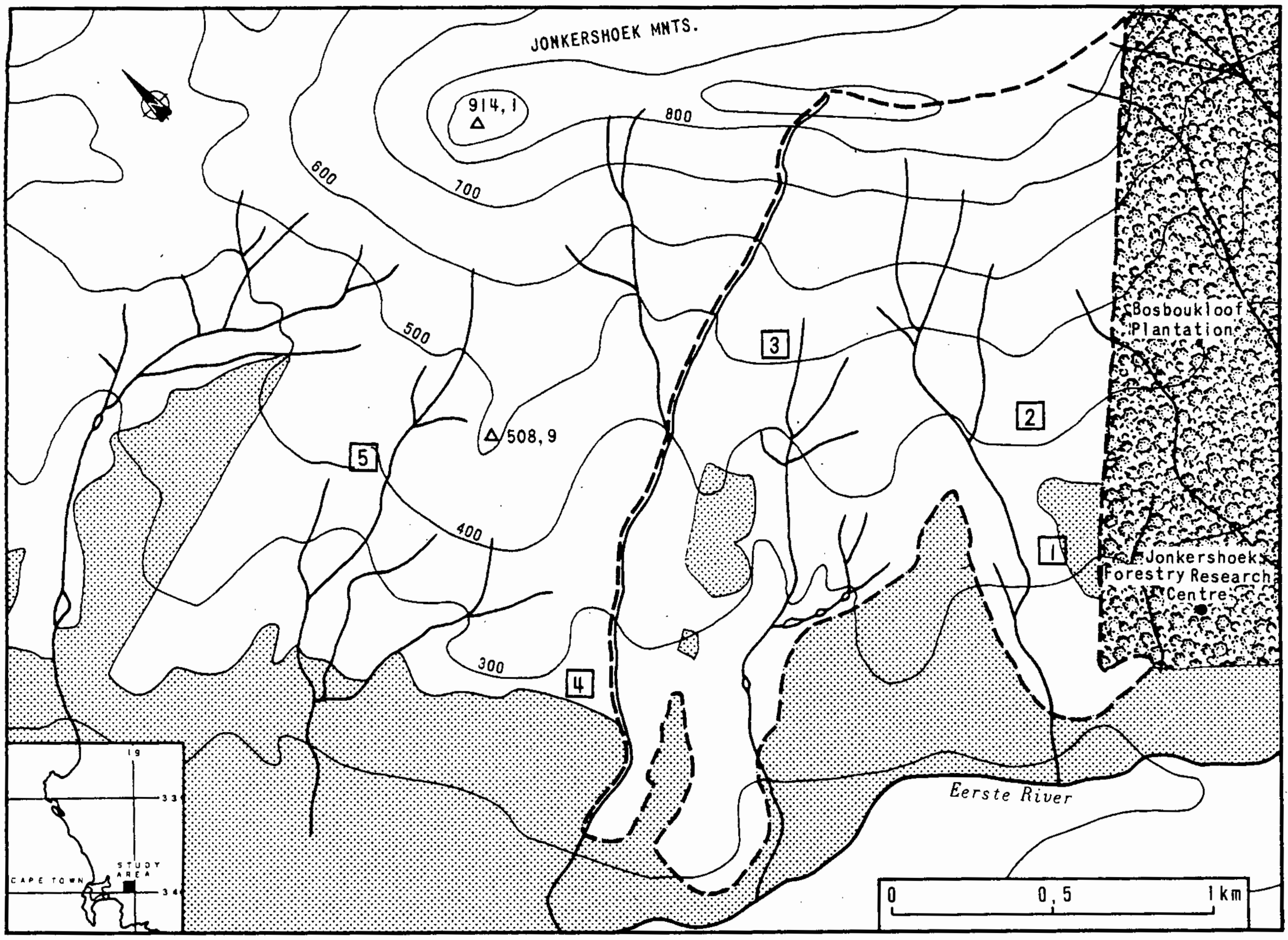

Figure 2.1. Location of the study area. Aerial photographs were used to determine the spread of Pinus radiata in the area enclosed by the dashed line. The positions of five 0.25 ha plots on which the age structure of colonizing populations of P. radiata were studied are shown (1 to 5).

The Bosboukloof catchment was the first of several catchments at Jonkershoek to be afforested with _P. radiata_. Planting took place between 1935 and 1940. Seed used for planting was collected between 1932 and 1937 from plantations at Lebanon (34°12'S; 19°07'E), Elgin (34°07'S; 19°03'E) and Knolvlei (33°25'S; 19°07'E). Afforestation of other catchments to the southeast of Bosboukloof continued until 1963, when 717 ha were covered by _P. radiata_ (unpublished records, Forestry Branch). Except for the replanting of clearfelled stands and the addition of small new areas between established plantations, no new afforestation with _P. radiata_ took place in the Jonkershoek Valley until 1975, when a small plantation was established to the northwest of the study area (unpublished records, Stellenbosch Municipality).

The study area is situated to the northwest of the Bosboukloof plantation (Figure 2.1). The natural vegetation is a tall (4 m) mid-dense to open shrubland (_sensu_ Campbell _et al_ 1981) dominated by _Protea neriifolia_, _Leucadendron salignum_ and _Widdringtonia cupressoides_ and is similar to that of the nearby and physiographically similar Biesievlei (Rycroft 1950, Richardson & Van Wilgen 1986). Examination of aerial photographs taken in 1938 showed no pines in the fynbos on the south-facing slopes of the Jonkershoek mountains to the northwest of Bosboukloof, but forty years later the area was dominated by dense stands of pines (Figure 2.2).

2.4. METHODS

2.4.1. Study of aerial photographs

Aerial photographs taken in 1938, 1953, 1967 and 1977 were used to determine the spread of _P. radiata_ over an area of approximately 237 ha and extending 1 500 m from the edge of the plantation. A grid of 10 mm X 10 mm squares, each being divided into 25 smaller squares was used to provide points of reference. For each pair of photographs, a square representing 1 ha was cut in each of two pieces of white paper and used to demarcate blocks for analysis using a stereoscope (Avery 1978, Liebenberg _et al_ 1978). The positions of the first colonists, taken to be the largest trees evident on the 1953 photograph, were plotted. The density of the trees in each block was categorized for each photograph as shown in Table 2.1.

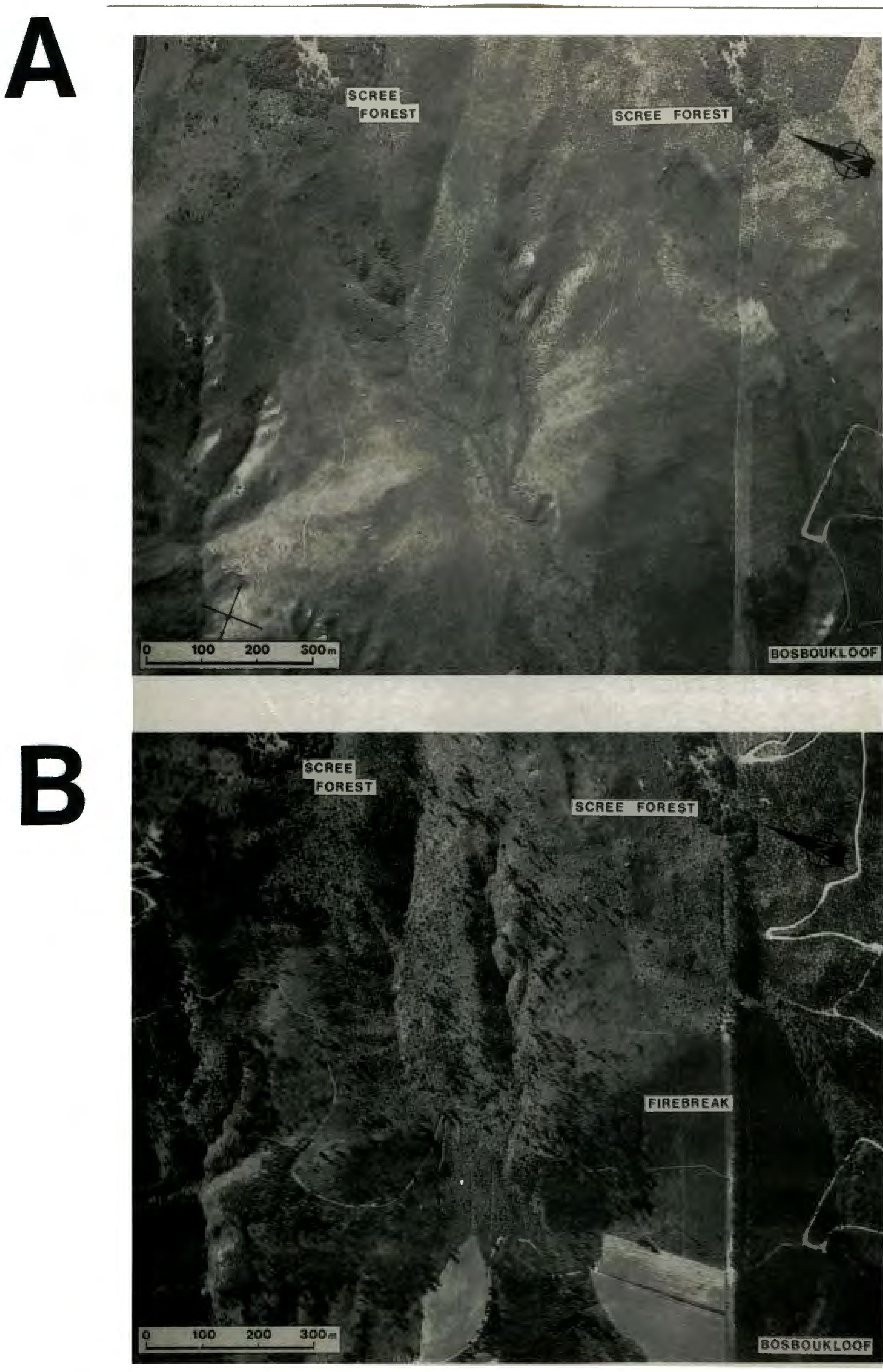

Figure 2.2. Part of the study area in 1938 (A) and in 1981 (B) to show the spread of <u>Pinus</u> species.

Table 2.1. Density of the trees in each block categorized for each photograph.

Code	Density
S = Scattered	1-20 plants / ha
M = Moderate	21-1000 plants / ha
D = Dense	> 1000 plants / ha

Pinus radiata was easily distinguished from P. pinea L. by the shape of the crowns and could be distinguished from P. pinaster and P. halepensis Miller by tone (P. radiata has darker foliage). Areas where P. radiata formed dense mixed stands with P. pinaster and/or P. halepensis were inspected in the field to ascertain the proportional representation of each species. It was not possible to make a more accurate assessment of density in the "moderate" class because young trees were often obscured by older trees of P. radiata or P. pinaster.

2.4.2. Position of first colonizers

Twenty two of the largest trees located in the study area were felled during January 1986. Age was determined in the field by counting growth rings. Their location was plotted on a map and the distance from Bosboukloof measured.

2.4.3. Age structure of the invading population

Five plots (50 x 50 m) were positioned in the invaded vegetation at selected sites at distances of between 150 m and 2 350 m from the seed source. The position of plots is shown in Figure 2.1. Pinus radiata, P. pinaster and P. halepensis trees in each plot were counted. The diameters of all P. radiata trees in each plot were measured at 1,3 m above the ground. In those plots where fewer than 100 P. radiata trees occurred, the diameters of additional P. radiata trees outside the plot were measured to make up a sample of 100. These were selected at random following the method of Catana (1963). In each plot, 25 P. radiata trees were selected subjectively to cover a representative range of diameters. These trees were felled just above ground-level during January 1986 and a disc was taken from the basal section of the trunk. The presence of charred stumps and tree remains was noted, as was any other information relevant to stand history. Discs were oven-dried at 80° C for 72 h and then sanded. Tree age was determined by counting growth rings, and fire history was determined by ageing fire scars.

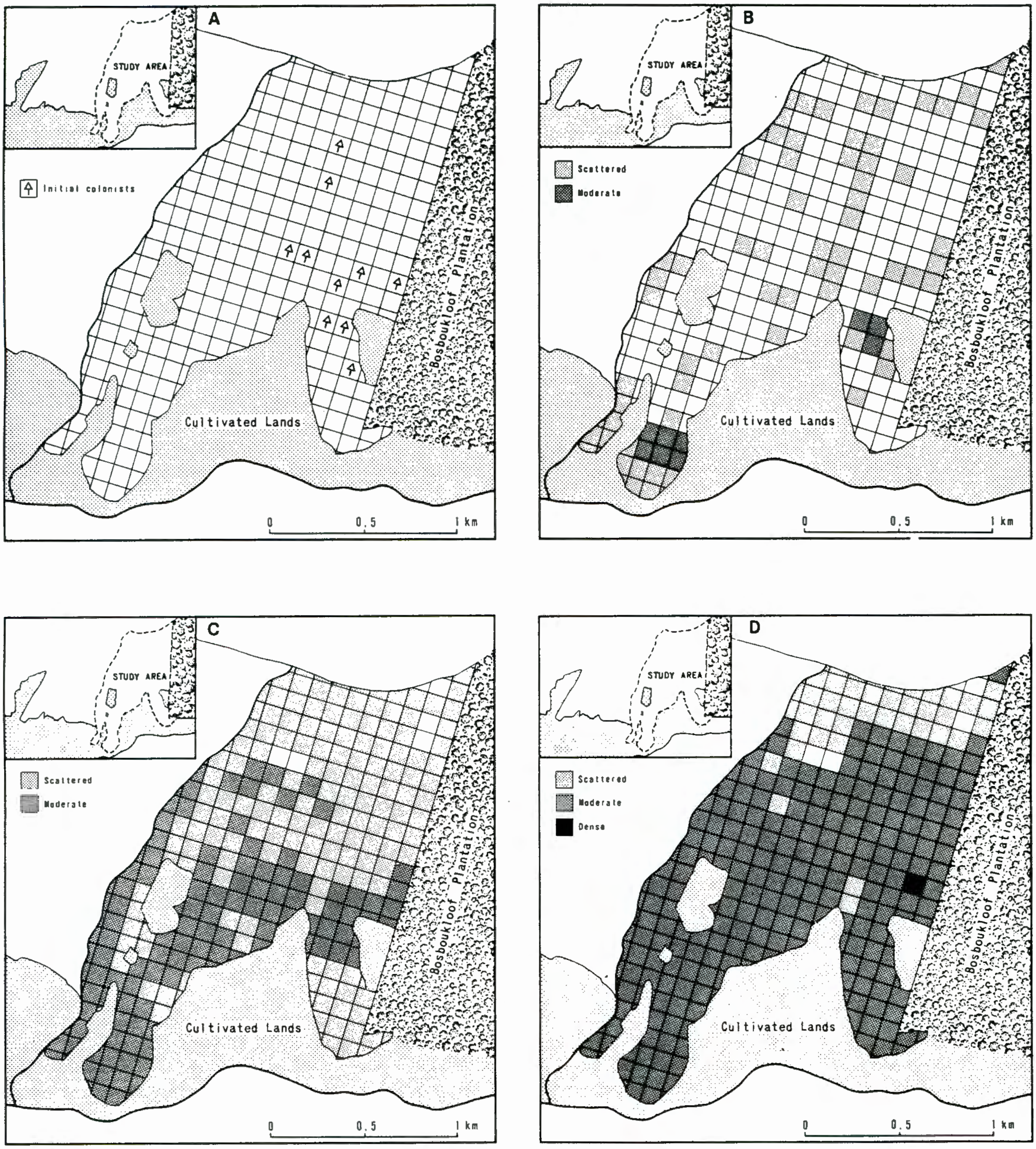

Figure 2.3. The position of initial colonists of <u>Pinus radiata</u> distinguished on the 1953 aerial photograph (A), and the density of <u>P. radiata</u> trees in 1 ha blocks (see text) in 1953 (B), 1967 (C) and 1977 (D).

2.5. RESULTS

2.5.1. Study of aerial photographs

Figure 2.3 shows the position of initial colonizers and the density of invading *P. radiata* trees. By 1953, 18 years after the commencement of afforestation in Bosboukloof, "scattered" stands of *P. radiata* (< 21 plants/ha) were evident in 63 out of 237 (27%) blocks; "moderate" stands (21 - 1 000 plants/ha) occurred in 9 (4%) blocks. Ten blocks contained individuals judged, by comparison with photographs of plantations where the date of planting was known, to be at least six years old. These were located up to 700 m from the edge of the plantation. There were no pines on 69% of blocks. In 1967, 32 years after first plantings, *P. radiata* had invaded all but 5 blocks, and in 93 blocks (39%) more than 21 plants were counted. No blocks contained more than 1 000 plants. In 1977, 42 years after afforestation, all but 4 blocks contained pines. Only 15% of blocks had fewer than 21 plants.

2.5.2. Position of first colonizers

The oldest trees, 37 years old, were found throughout the study area up to 3 200 m from Bosboukloof.

2.5.3. Age structure of the invading population

Age structure histograms for *P. radiata* trees in the five plots are given in Figure 2.4. In plots 2 to 5, age structure was bi- or tri- modal but most trees belong to a cohort aged between 14 and 16 years (Table 2.2). This indicates establishment of the greatest proportion of the population between 1969 and 1971. There is a relatively small coefficient of variation of tree ages about each mode but large variation overall. Analysis of fire scars on large trees in these plots shows that only one fire, dated to 1969, occurred between 1948 and 1986 (Table 2.2). The greatest number of trees established between 1969 and 1971 (Figure 2.4), soon after this fire. Less prolific recruitment in these plots occurred in 1950, 1955 and 1962, but these events are not related to the fire history.

Table 2.2. The density of pines, the age structure of Pinus radiata and the fire history on five 0.25 ha plots at Jonkershoek, Stellenbosch.

Plot	Distance from Bosboukloof (m)	Number of trees/0,25 ha plot			Age structure of *P. radiata* trees			Fire history
		P. radiata	*P. pinaster*	*P. halepensis*	min.	max.	mode	
1	150	46	2	66	12	31	21	No evidence of fire
2	250	34	254	–	13	37	15	Fire in 1969
3	1 050	185	47	–	12	37	14	Fire in 1969
4	1 650	692	–	–	13	37	16	Fire in 1969
5	2 350	46	–	191	13	31	16	Fire in 1969

No fire scars were evident on samples taken from plot 1 and the age structure histogram for this plot differs from the others in that no single cohort dominates the stand (Figure 2.4). The most frequent age in this plot was 21 years (Table 2.2) but all age classes found in the other plots are represented except that no surviving trees established before 1954 and it was only on plot 1 that young saplings were found (estimated age = 2 years). There is a large coefficient of variation overall but also a large coefficient of variation about the mode.

2.6. DISCUSSION

The invasion of fynbos by P. radiata is characterized by a rapid but sparse influx of initial colonizers throughout the study area. This is followed by the slow and erratic establishment of seedlings around these trees in the absence of fire and the recruitment of dense daughter stands following fire. The early colonists are clearly visible on the 1953 aerial photographs and growth ring counts date their arrival to 1948, 13 years after commencement of afforestation. Pinus radiata produces viable seed after 7 years in California (USDA 1974), after about 10 years in Australia (van der Sommen 1986) and after 9 to 12 years in New Zealand (Hunter & Douglas 1984). Cones are first produced after 6 to 7 years at Jonkershoek (personal observation) but ripe cones require 3 to 4 years to be dried out sufficiently to open (Donald 1968). The first seeds were therefore probably released only in 1944, nine years after planting commenced, and four years before the establishment of the oldest surviving trees in the adjacent fynbos. Fielding (1965) has shown that seeds may be retained within the cone for 5 years or more with no loss of viability. Seed fall from P. radiata trees at Jonkershoek varies appreciably from one year to the next (Donald 1968), and it seems feasible that the oldest trees found in this study grew from the first viable seeds released from the Bosboukloof plantation. Establishment of the oldest colonizing trees was aged to 1948. This means that either no seed was released prior to this date or that some seedlings did establish between 1944 and 1948 but did not survive. Fire records for the area (Forestry Branch, unpublished) contain no reference to a large fire during this period and we therefore support the former hypothesis. Donald (1968) has noted that cones may remain closed for up to eight years.

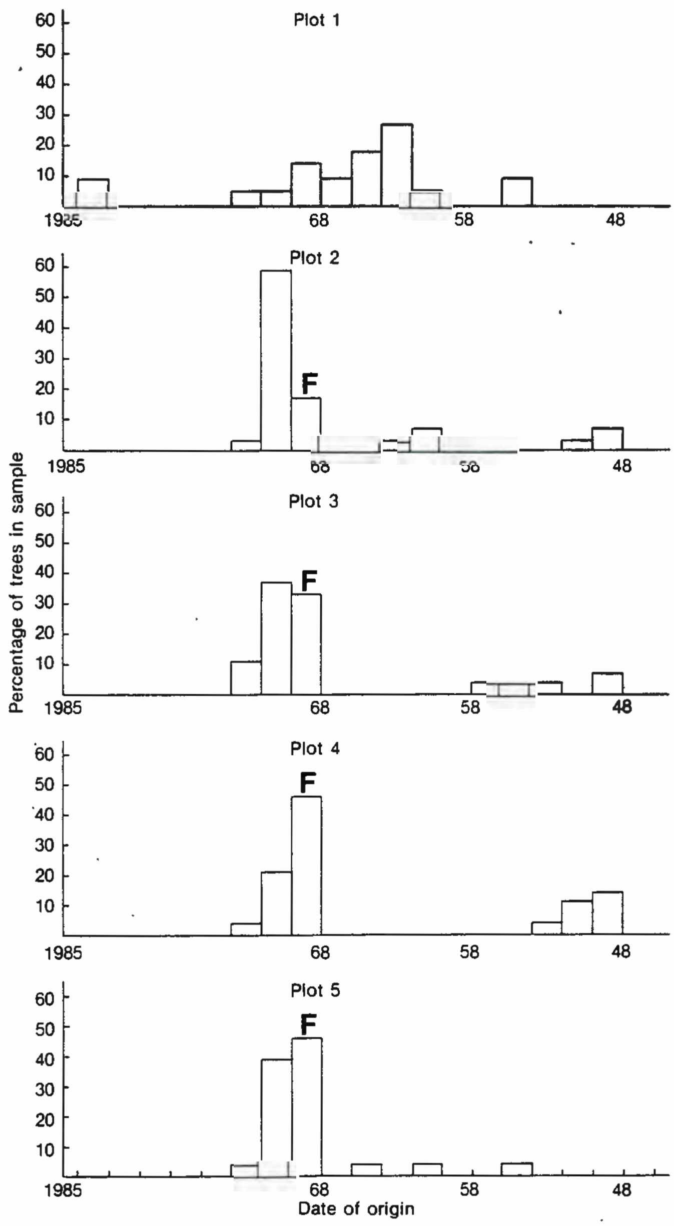

Figure 2.4. Age structure histograms of colonizing Pinus radiata in five 0.25 ha plots. See Table 2.2 for salient features of the plots. F denotes the occurrence of a fire.

Dispersal is the first stage in the colonization of a new habitat (Kruger *et al* 1986). *Pinus radiata* is well adapted for long-range dispersal. Seeds are released from cones during the hot, dry summer (personal observation) and it is at this time of the year that the strongest winds blow from the southeast. The winged seeds are well adapted for dispersal by wind (Bannister 1965, Van Wilgen & Siegfried 1986); the synchronous occurrence of agents of seed release and long-distance dispersal has added greatly to the invasive potential of *P. radiata* at Jonkershoek. The efficacy of dispersal is demonstrated by the fact that the oldest cohort occurred throughout the study area (up to 3 200 m from Bosboukloof). A further adaptation for long-range colonization is evident. An isolated individual may self-fertilize and perpetuate itself by establishing a colony of seedlings (Bannister 1965). This genetic plasticity allows *P. radiata* to cope satisfactorily with both sedentary and colonizing phases of growth.

Invasion of a new habitat by an alien species is often delayed or precluded due to adverse interactions with the resident biota (Kruger *et al* 1986). In a study of invasion of eucalypt forest in Australia by *P. radiata*, Chilvers & Burdon (1983) found that invasion began only 20 to 21 years after the establishment of local plantations. They suggested that browsing by rabbits may have delayed invasion until these were virtually eliminated by an epidemic of Myxomatosis about four years before invasion commenced. Clearly, colonizing *P. radiata* at Jonkershoek experienced no significant biotic resistance. Debarking of saplings by rodents, probably the most serious and wide-spread animal damage problem in South African forestry plantations (Bigalke 1980), does not cause major problems in the Western Cape Province (Le Roux 1978). Bark-stripping by baboons, *Papio ursinus*, and browzing by ungulates, although serious in parts of the region (Bigalke 1980), have not been a problem at Jonkershoek.

Fire is important in the invasion process; it stimulates the simultaneous release of large quantities of seed from the serotinous cones of *P. radiata*, and creates favourable microsites for germination and establishment. As is the case for *P. radiata* in Australia (van der Sommen 1986) and *P. pinaster* in fynbos (Kruger 1977), establishment is not restricted to the immediate post-fire phase (Figure 2.4). Seeds released at other times may germinate and become established in unburned vegetation. Although the probability of this occurring is smaller than directly after a fire, fynbos is more susceptible to invasion by pines in the absence of fire than grassland (Kruger et al 1986).

The age structures in plots 2 to 5 can be explained by considering the fire history. In plots 2 to 4, individuals of a cohort dated to between 1948 and 1951 were found (Figure 2.4). These trees apparently have served as secondary foci of recruitment, and their offspring make up the greatest part of the population in 1986. There are, however, a number of other age classes represented in these plots. In plot 2, 11% of trees were dated to between 1961 and 1963 and in plot 3, 11% were aged to between 25 and 33 years, indicating establishment between 1953 and 1957. These plots all burned in 1969 and the different numbers of trees aged to between 1953 and 1969 is probably due to variations in fire intensity over the area. The age structure in plot 4 suggests that the fire was most intense here and that all trees younger than 16 years old were killed. The size of the charred remains of 10 trees noted in this plot support this hypothesis. Trees of 7 and 12 years survived the fire in plots 2 and 3 respectively (Figure 2.4), suggesting a less intense fire. The age structure on all plots subjected to fire reflects rapid and prolific recruitment soon after fire.

By 1969, 21 years after establishment of the first colonists, sufficient seed was being produced by the invading pines themselves to permit significant recruitment following fire. This is shown by the large proportion of plants in plots 2,3,4 and 5 that were dated to between 1969 and 1973. Seed from the original source provided a supplementary contribution to recruitment. In plot 1 where there is no evidence of fire, recruitment is irregular and is probably related to the history of disturbance other than fire e.g. windfalls, soil erosion or the opening of gaps due to senescence of the natural vegetation in the absence of fire.

Pinus radiata is considered exceptional among the serotinous pines of California in that fires that produce optimum reproduction are not as often the catastrophic, stand-replacing types that are required by the other species; surface fires in which parent trees survive give best results (Vogl et al. 1977). De Ronde (1982) has shown that fire-induced mortality of P. radiata trees of 22 years and older in South Africa normally occurs only when more than 90% of the crown is scorched. Trees of seven years may survive fire (Figure 2.4) but in general, fires at intervals of less than nine years should eliminate P. radiata trees that have established since the last fire.

Fires at intervals of more than nine years may kill adult plants but recruitment following the release of viable seeds will result in population growth and dispersal to new areas. _Pinus radiata_ in mesic mountain fynbos is a DT species in the Noble & Slatyer (1980) classification of species types. Current catchment management plans stipulate that woody alien plants that retain seeds in fire-resistant structures in the canopy must be felled prior to the execution of prescribed burns which are carried out at intervals of between 12 and 15 years in the mesic mountain fynbos of the southwestern Cape. This practice kills the parent plants and stimulates the release of seeds which, together with any seedlings, are destroyed in the fire.

2.7. CONCLUSION

Pinus radiata has the ability to invade natural communities in the vicinity of plantations. The species is well adapted to local conditions although it is generally considered less aggressive than _P. pinaster_ (Wicht 1945, Scott 1960, Poynton 1979a). For commercial forestry, _P. pinaster_ shows superior performance on the steep, shallow and nutrient poor soils of the region (Grey & Taylor 1983) but this does not necessarily reflect a superior colonizing ability. _Pinus pinaster_ commences seed production earlier than _P. radiata_ (Hunter & Douglas 1984). Seeds of _P. radiata_ are, however, better adapted for long-distance dispersal by wind than are those of _P. pinaster_ (Hunter & Douglas 1984, Van Wilgen & Siegfried 1986). _Pinus pinaster_ was introduced to South Africa 185 years before _P. radiata_ (in 1680; Shaughnessy 1980) and its greater range may simply reflect its wider dissemination by man and the greater time that _P. pinaster_ has had to reach potential sites.

Proliferation of _P. radiata_ following fire results in dense stands that radically alter the structure and composition of natural plant communities (Richardson & Van Wilgen 1986). Long-range dispersal of seeds from plantations adjoining natural areas, particularly proclaimed mountain catchments, will continue to present problems for managers. Systematic control programmes as part of extensive land management are required to contain the spread of the species.

CHAPTER 3

AGE STRUCTURE AND REGENERATION AFTER FIRE IN A SELF-SOWN *PINUS HALEPENSIS* FOREST ON THE CAPE PENINSULA, SOUTH AFRICA

CHAPTER 3 : AGE STRUCTURE AND REGENERATION AFTER FIRE IN A SELF-SOWN PINUS HALEPENSIS FOREST ON THE CAPE PENINSULA, SOUTH AFRICA [1]

3.1. ABSTRACT

Pinus halepensis, introduced into South Africa from the Mediterranean Basin in the mid-nineteenth century, has become an important weed in the fire-prone mountain fynbos of the Cape Province. The age structure in a self-sown stand of P. halepensis at Miller's Point near Simonstown was determined in 1986 from counts of growth rings. The oldest tree at the site was 58 years old but only two of the 657 trees that made up the 1986 stand were present before the last fire in 1972. Nearly 50% of surviving trees established within one year of the last fire and less than 1% of surviving trees established more than four years after the last fire. Seedling regeneration after a fire in part of the stand in March 1986 was prolific and an average of 465 seedlings were counted on six 50 m² plots eight months after the fire. The survival and proliferation of P. halepensis is ascribed to the early attainment of reproductive maturity and the ability of seeds to germinate and establish in the immediate post-fire environment.

3.2. INTRODUCTION

Pinus halepensis Mill. (Aleppo pine) was introduced into South Africa in around 1830 (Shaughnessy 1986). Although not used for large scale afforestation, the species has been planted as an amenity and ornamental tree throughout southern Africa (Poynton 1979a). The species has become naturalized in parts of South Africa (Wells et al. 1986; Macdonald et al. 1987), and is an important invasive plant in the fynbos biome of the southern and southwestern Cape Province (Macdonald & Jarman 1984). It forms dense stands that resemble young Aleppo pine forests of the Mediterranean Region. Self-sown stands of P. halepensis are less widely distributed in the fynbos biome than those of either P. pinaster Ait. or P. radiata D.Don., both of which were planted far more widely for timber (Poynton 1979a). These three species all have persistent serotinous cones, show apparently similar responses to fire, and sometimes occur in mixed stands (Richardson & Brown 1986; Richardson unpublished). Thickets of alien trees and shrubs have radically altered biotic and abiotic features of the fynbos landscape (Macdonald & Richardson 1986) and pose a major problem for natural resource

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[1] *Publication status: Richardson, D.M. (1988). Age structure and regeneration after fire in a self-sown Pinus halepensis forest on the Cape Peninsula, South Africa. South African Journal of Botany 54: 140-144.*

managers (Macdonald et al. 1985).

Recurrent fire at intervals of between 6 and 40 years is a natural feature of mountain fynbos (Kruger & Bigalke 1984). Fire is a major determinant of community composition in mediterranean-type ecosystems (Trabaud 1981) and is an important factor in the ecology of biological invasions of these regions (Kruger et al. 1986; Kruger et al. 1988). An understanding of the relationship between fire and population processes of serotinous alien plants is essential for the formulation of management guidelines for their eradication (Kruger 1977; Richardson & Brown 1986).

This chapter presents data on the population age structure of an unburnt *P. halepensis* stand and post-fire recruitment in a 7-month-old stand. The role of fire in the regeneration of *P. halepensis* in mountain fynbos is discussed and compared to regeneration patterns in the Mediterranean Region.

3.3. STUDY AREA

The study site at Miller's Point (34°01'S; 18°24'E) is situated near Simonstown on the Cape Peninsula, South Africa. The site is located on the exposed east-facing slopes of the Swartkopberge, 30 m from the high-water mark at an altitude of 30 m above sea level. Soils are sandy lithosols weathered from granitic parent material but overlain by sandstone colluvium in places. The natural vegetation (mesic mountain fynbos *sensu* Moll et al. 1984) has been replaced by a dense stand of *P. halepensis* (Figure 3.1). A fire burned through a section of the stand in March 1986. Climate is typically mediterranean, Köppen's (1931) humid-mesothermal (type Csb). Annual rainfall is about 700 mm, most of which falls between May and August.

3.4. METHODS

3.4.1. Population age structure

One 30 x 30 m plot was positioned in an unburnt section of the stand. All *P. halepensis* trees in the plot were felled just above ground-level and a disc was collected from the basal section of each tree (10-50 mm above ground level). Trees were aged by counting the growth rings on discs. In most cases it was possible to age the trees by scraping the cut surface with a sharp blade and counting the rings, using a X 10 lens when necessary. Where the rings were indistinct, discs were sanded and examined with a X 50 dissection microscope. In all cases, the age was recorded only after consensus had been reached by two independent assessors. The presence of charred dead trees was noted.

Figure 3.1. A dense stand of Pinus halepensis 14 years after a fire at Millers Point, Cape Peninsula.

3.4.2. Fire history

The fire history at the site was determined by dating fire scars on the two largest trees in the 30 x 30 m plot. Discs were taken from the basal section of the trunks and sanded. Growth rings and fire scars were well developed and clearly visible.

3.4.3. Fecundity and recruitment

Six 5 x 10 m plots were set out at random in the burnt area. All trees in this part of the stand were killed in the 1986 fire but the charred stems were still standing at the time of the survey. Almost all cones that had not yet opened at the time of the fire were retained on the trees as very few cones were found on the ground. Open cones were consumed by the fire. Dead adults and live seedlings were counted in each plot. Cones were counted on all trees and on the ground in each plot. The relationship between the density of adults and the number of cones per tree and the total number of cones per plot was examined. To determine whether the level of post-fire recruitment was controlled by the size of the seed bank in the canopy in the immediate vicinity, the relationship between the number of seedlings in each 50 m^2 plot and the total number of cones and number of adults in the plot was examined. Regression equations were fitted using the NONLIN procedure of the OXFORD statistical package (Commonwealth Forestry Research Institute, Oxford, England).

3.5. RESULTS

3.5.1. Population age structure

Of the 657 live *P. halepensis* trees in the 30 x 30 m plot in 1986, only two (0.3 %) were older than 14 years (Figure 3.2). These trees were 58 and 49 years old and survived the fire in 1972 when they were 44 and 35 years old respectively. One large tree was killed in the 1972 fire but it was not possible to determine the age of this tree at the time of the fire. More than 50 % of trees in the plot were 14 years old; these trees became established within one year of the fire. More than 70 % of trees became established either in 1972 (the year of the last fire) or in 1973. By 1975 (3 years after the fire), stand density had reached 91 % of the 1986 level. Recruitment of seedlings continued until 1979. No trees surviving in 1986 became established between 1979 and 1985.

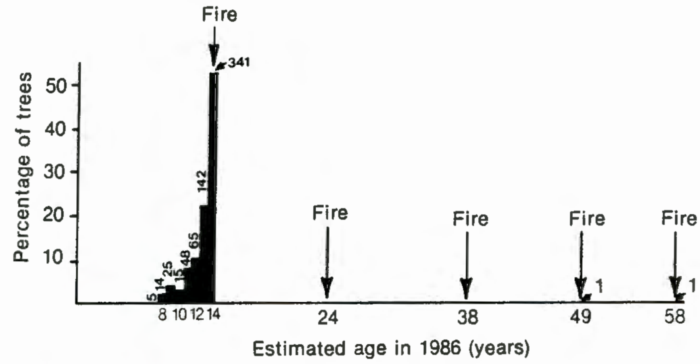

Figure 3.2. Age structure in a stand of Pinus halepensis at Miller's Point. Numbers above bars are the numbers of trees in each age class. THe age structure was determined by counting growth rings on 657 trees. The fire history was determined by ageing fire scars on the oldest trees.

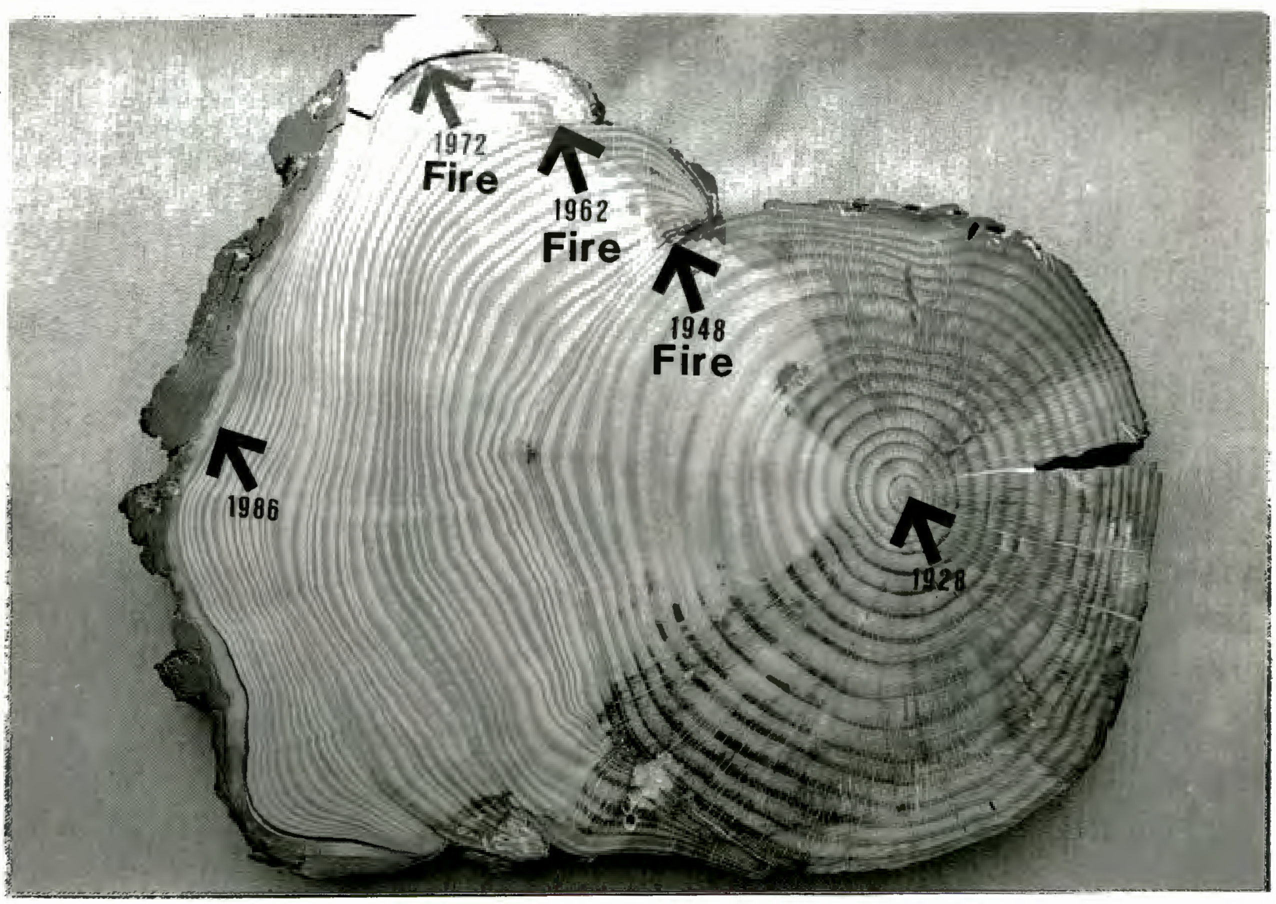

Figure 3.3. A disc from the basal section of a 58-year-old Pinus halepensis tree at Miller's Point on the Cape Peninsula. The tree established in 1928 and survived fires in 1948, 1962 and 1972.

assessing the life history strategies and the role of fire in regeneration. These features are listed and the ecological significance of each is discussed in Table 3.2.

Table 3.1. The distribution of adults, cones and seedlings of Pinus halepensis in six 50 m plots at Millers Point in November 1986, 8 months after a fire. Figures in parentheses are standard errors of the mean.

Plot	Number of dead adults	Total number of cones on dead adults	Mean number of cones/tree	Number of cones on ground	Number of seedlings	Adult: seedling ratio
1	23	649	28,2 (7,2)	4	329	1: 14,3
2	41	628	15,3 (2,2)	1	469	1: 11,4
3	51	872	17,1 (2,6)	38	460	1: 9,0
4	80	636	8,1 (0,8)	10	548	1: 5,9
5	14	440	31,4 (8,7)	4	317	1: 22,6
6	30	444	14,8 (3,0)	14	669	1: 22,3
Mean/ plot	39,8 (9,6)	611,5 (65,2)	19,1 (3,6)	11,8 (5,6)	465,3 (54,5)	1: 14,3 (2,74)
All plots combined	239	3669	15,4 (1,2)	71	2792	1: 11,7

3.6.2. Preadaptation of Pinus halepensis to the fynbos fire regime

The local fire regime, and fire frequency in particular, has been important in structuring the P. halepensis stand at Miller's Point. The approach used in this study does not provide a basis for the reconstruction of year-to-year variations in natality and mortality; it only reveals the current age structure, a bulk account of recruitment and mortality in the interval since colonization of the site. The fire history for the site shows that fires have occurred every 11.6 years on average over the past 58 years. Although it is not possible to express the population growth associated with each fire, it is evident that the prevailing fire regime has permitted the perpetuation of the species. Aleppo pine forests in southern France burn on average every 25 years (Le Houerou 1981) and yet fires at intervals of between 9 and 14 years have not excluded P. halepensis from the Miller's Point site. The juvenile period of P. halepensis in France is at least 10 years (Trabaud & Chanterac 1985) but Nahal (1962 in Acherar et al. 1984) states that fertile seeds are seldom produced before 20 years after a fire. An examination of closed cones on 20-year-old trees near Montpellier in southern France, revealed that 5-year-old cones held viable seeds, indicating a juvenile period of at least 15 years (F.J. Kruger and D.M. Richardson, unpublished data). It is not known when fertile seeds are first produced in South Africa but the prolific

Table 3.2. Features of the age structure of Pinus halepensis at Miller's Point (see Figure 3.2), interpretation of the observed pattern and the significance of the features for P. halepensis as an invasive plant in mountain fynbos.

Features of the age structure histogram	Interpretation	Significance for Pinus halepensis as an invasive plant in mountain fynbos
Only 2 trees are older than 48 years	Survival of fire is rare	Fire survival is not essential for perpetuation and growth of the population
No trees are between 15 and 48 years old	All trees younger than 35 years old were killed in the 1972 fire	Perpetuation of the population is achieved by recruitment of new stands after fire. For this reason, the attainment of reproductive maturity in the interval between fires is important
Over 50% of trees are 14 years old and 91% of trees are between 11 and 14 years old	Fire stimulated seedling recruitment	Fire stimulates rapid population growth by causing the simultaneous release of canopy-stored seeds. Fire also creates favourable conditions for germination and establishment
No trees are younger than 7 years old	No seeds germinated more than 7 years after the fire or seedlings were unable to survive in the 7-year-old stand	Disturbance in the form of fire is required to induce proliferation

seedling recruitment after fire in the 14 year-old stand indicates that maturity is reached before 14 years. Whether one intense fire following a previous fire at an interval less than the juvenile period of P. halepensis would eliminate the species at the site would depend upon: 1) the size of the fire; 2) the distance from the nearest alternative seed source; and 3) the influence of biotic agents that prevent immigrating seeds from germinating or seedlings from becoming established. It appears that the survival and proliferation of P. halepensis at Miller's Point can be ascribed to the early attainment of reproductive maturity and good germination and establishment in the immediate post-fire environment. Fire survival by adults is rare but the contribution of seeds from fecund adults is important for re-establishment following fires at short intervals and also for dispersal to new areas.

3.6.3. Preadaptation to other biotic and abiotic features of the fynbos

Seeds of Pinus halepensis show no adaptation for persistence in the soil for periods longer than the average interval between fires in fynbos (pers.obs.). Reproduction is from seeds which are released from cones that often burst during a fire (Le Houerou 1973; Naveh 1974, 1977). Fire in natural Aleppo pine forests in the Mediterranean Basin usually kills P. halepensis adults, and perpetuation of the population is achieved by the recruitment of new stands after fire (Le Houerou 1973). These stands may be even-aged or nearly even-aged (Le Houerou 1973), or may contain trees of all ages (Trabaud et al. 1985). The stand initiated by the 1972 fire at Miller's Point consists of trees aged between seven and 14 years with only a very small number (0.3 %) older than 14 years. More than 50 % of surviving trees established within one year of the fire. In a study of the colonization of abandoned vineyards in southern France by P. halepensis, Acherar et al. (1984) found that seedlings were intolerant of competition from grasses and suggested that this may limit colonization where grasses are abundant. This probably accounts for the observed differences in age structures of different populations in France; P. halepensis seedlings are excluded from environments that support dense grass swards in the immediate post-fire phase. Kruger et al. (1986) have suggested that one reason for the success of alien trees and shrubs in fynbos is that crowding of the alien seedlings causes little increase in mortality. A high rate of survival for seedlings and weak self-thinning in adults gives rise to dense thickets. The results of this study suggest that fecundity of individual P. halepensis trees in a 14-year-old stand declines with an increase in stand density. This strategy, as an alternative to self-thinning, results in dense stands that displace competitors including conspecific seedlings of late-germinating cohorts. This results in the dominance of cohorts that establish within 2 years of the fire.

The winged seeds of *P. halepensis* weigh 20 mg (Acherar *et al.* 1984) and are lighter than those of *P. pinaster* (57mg) and *P. radiata* (24mg) (Van Wilgen & Siegfried 1986), both of which spread over large areas in the fynbos (Kruger 1977; Richardson & Brown 1986). This implies that the seeds of *P. halepensis* are well adapted for dispersal by wind in fynbos.

3.7. CONCLUSION

This study has provided some information on the relationship between fire and population processes for *P. halepensis* in fynbos. Like *P. pinaster* and *P. radiata*, *P. halepensis* shows rapid population growth after fire in fynbos. The relatively limited extent of invasion by *P. halepensis* is possibly due to the very limited use of this species for afforestation and thus limited availability of seed to initiate invasions. *Pinus halepensis* is, however, widely distributed in the southwestern Cape, and its relatively limited success may indicate that the environment of soil and climate in much of the area invaded by *P. pinaster* is outside the tolerance of this species. *Pinus halepensis* and *P. pinaster* do not occur sympatrically in southern France (L. Trabaud pers. comm.); *P. halepensis* appears to be restricted to calcareous soils with relatively high pH, whereas *P. pinaster* occurs on siliceous soils with low pH (Poynton 1979a). This suggests that *P. halepensis* has limited potential to invade areas with acid, highly leached soils derived from quarzitic parent material. Granite soils, with higher concentrations of nutrients, appear to be more susceptible to invasion by this species.

PART II

LIFE HISTORY AND POPULATION ECOLOGY OF SELECTED INVADERS

CHAPTER 4

ASPECTS OF THE REPRODUCTIVE ECOLOGY OF FOUR AUSTRALIAN HAKEA SPECIES (PROTEACEAE) IN SOUTH AFRICA

CHAPTER 4 : ASPECTS OF THE REPRODUCTIVE ECOLOGY OF FOUR AUSTRALIAN HAKEA SPECIES (PROTEACEAE) IN SOUTH AFRICA [1]

4.1. ABSTRACT

Four shrub species of the Australian Proteaceae (Hakea sericea, H. gibbosa and H. suaveolens and H. salicifolia) were introduced to South African fynbos shrublands between 1840 and 1860. H. sericea is highly invasive, H. gibbosa and H. suaveolens are moderately invasive and H. salicifolia is not invasive. The allocation of reproductive energy, germinability, the ability to survive fires and to germinate in burnt and unburnt areas, and the nutrient content of seeds were assessed for the four species. The information was used to investigate whether the success of H. sericea relative to the other three species could be explained by the superior expression of any trait. The most important trait which separates H. sericea from the other species is its ability to produce a large seed bank in its adopted environment in the absence of seed predators. Seed production in H. sericea shrubs with an above-ground dry mass of 8 kg is four times greater than H. gibbosa and more than 16 times that of H. suaveolens. Although H. salicifolia also produces a large seed bank, its seeds are unable to survive fires due to inadequate insulation by the small follicles. The results are compared to dispersal and seed bank data for indigenous South African Proteaceae, which have low dispersal and suffer high pre-dispersal seed predation. We suggest that potential invasives in the fynbos can be identified as species that have: (i) a potentially high seed production that is limited by specialized predators; (ii) an ability to disperse over long distances; and (iii) are pre-adapted to frequent fires and low soil nutrients. The data also support the current strategy of combatting H. sericea using specialized insect seed predators.

4.2. INTRODUCTION

South African fynbos shrublands occur mainly on nutrient-poor soils and comprise one of the richest floras in the world (Goldblatt 1978). A feature of fynbos shrublands is their high susceptibility to invasion by alien trees and shrubs (Macdonald & Richardson 1986). It is remarkable that invasions of this diverse vegetation type by shrubs from similar environments on other continents occur with little, if any, man-induced change to the environment. Alien trees and shrubs often form dense stands which reduce or eliminate indigenous components (Macdonald & Richardson 1986), reduce surface water resources (Versfeld & Van Wilgen 1986), and increase fire hazard (Van Wilgen & Richardson 1985).

In many areas, fynbos communities dominated by indigenous Proteaceae have been invaded by Australian Proteaceae. The family Proteaceae is concentrated in temperate Australia (about 700 species) and in the Cape Province of South

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[1] Publication status: Richardson, D.M., Van Wilgen, B.W. & Mitchell, D.T. (1987). Aspects of the reproductive ecology of four Australian Hakea species in South Africa. Oecologia 71: 345-354.

Africa (about 350 species). The family is particularly prominent in fire-prone shrublands of the two regions. Proteaceous shrubs are usually the dominant woody plants on the most nutrient-poor soils in both regions (Lamont et al. 1985), but no genera of the Proteaceae are indigenous to both continents.

A large proportion of successful alien plant taxa in the fynbos survive fires by virtue of possessing canopy-stored seed banks, a reproductive syndrome shared with the dominant fynbos Proteaceae (Bond 1985; Lamont et al. 1985).

Four species of evergreen perennial shrubs of the genus Hakea (Proteaceae) were introduced to South Africa from Australia between 1840 and 1860 (Macdonald 1984). Three species, H. sericea Schrad., H. gibbosa (Sm.) Cav., and H. suaveolens R.Br. invade the natural vegetation and have been declared noxious weeds. Although H. sericea was not widely planted, it currently occupies the greatest area of all woody invaders in the fynbos biome (Macdonald & Jarman 1984). Stands of this species occur in 42 % of the 115 quarter-degree squares that constitute the fynbos biome, whereas H. suaveolens and H. gibbosa occur in only 9 and 6 % of squares respectively (Macdonald et al. 1985), despite their wider dissemination by man (Neser 1978 a,b). These three species all form dense thickets that substantially alter vegetation structure. A fourth species, H. salicifolia (Vent.) B.L. Burtt. (syn. H. saligna Knight), has been used extensively as a hedge plant throughout the southwestern Cape but shows no signs of invading natural vegetation.

Fires are an important feature of the fynbos environment and have aided the spread of Hakea species. Three of these species are dependent entirely on seed for regeneration in South Africa but H. salicifolia may also regenerate from stem-bases after fire (S. Neser, pers. comm. 1985). H. sericea, H. gibbosa and H. suaveolens exhibit extreme serotiny in South Africa; all seeds produced during the life of the plant are stored in the woody follicles that open only upon death of the plant. H. salicifolia releases some seed intermittently but retains most seeds in the canopy. Each follicle contains two single-winged seeds (samaras) that are released following death of the parent plant. Seeds are thin-coated and germinate readily after release; there is no viable seed bank in the soil (Richardson 1985).

Several factors have been suggested to contribute to the success of H. sericea in South Africa. These are the ability to produce large numbers of seeds (Neser 1968; Kluge 1983), the high degree of protection afforded to the seeds by the woody follicles (Fugler 1983), high seed longevity in the canopy (Neser 1968), high germinability and rapid germination (Richardson & Van Wilgen 1984), efficient dispersal (Hall 1979) and high nutrient content of seeds (Mitchell & Allsopp 1984). Mooney et al. (1986) have suggested that a valuable approach to the study of the ecological characteristics of successful invaders is a comparison of their traits with those of closely-related non-invasive species.

In this study we investigated aspects of the reproductive ecology of the four Hakea species and related these to the relative success of each species in the fynbos. We determined differences in the allocation of reproductive energy, germinability, the ability to survive fires and to germinate in burnt and unburnt areas and the nutrient content of seeds. This information was used to investigate whether the success of H. sericea relative to the other three species could be explained by the superior expression of any trait. This approach could explain why certain species become invasive, and should also provide information for determining the most appropriate control strategy.

4.3. THE STUDY AREAS

Table 4.1. Salient features of sites at which shrubs of the genus Hakea were harvested for study.

Site	Position	Geology	Mean annual rainfall (mm)	Altitude (m)
Vergelegen Estate	34° 56′ S; 18° 56′ E	Sandstone/granite mixtures	1,200	600
Jonkershoek Valley	33° 57′ S; 18° 54′ E	Sandstone/granite mixtures	1,100	400
Constantianek	34° 14′ S; 18° 28′ E	Sandstone	1,227	200
Millers Point	34° 01′ S; 18° 24′ E	Sandstone/granite mixtures	700	30
Blaauwklippen Valley	34° 59′ S; 18° 52′ E	Granite	1,000	180
Grabouw State Forest	34° 09′ S; 19° 01′ E	Sandstone	650	300
Wemmershoek	33° 53′ S; 19° 02′ E	Sandstone	817	140

Data for H. sericea were collected from populations at the Vergelegen Estate and in the Jonkershoek Valley. Data for H. gibbosa and H. suaveolens were collected from populations at Constantianek and Millers Point respectively. Data for H. salicifolia were collected from localities in the Jonkershoek and Blaauwklippen Valleys, from Grabouw State Forest and from Wemmershoek. Salient features of these sites are given in Table 4.1.

4.4. METHODS

4.4.1. Morphology of follicles and seeds

Fifty follicles with samaras (seed plus wing) of each species were oven-dried at 80^{o}C for 72 hours and then weighed. Samaras (100) were first weighed individually with the wing intact. Wings were then carefully removed and the seed was weighed. The surface area of samaras and of seeds was determined using a leaf area meter. The samara wing loading, defined as W/A, where W is the mean mass (mg) and A is the mean surface area (mm^2) (Green 1980), was calculated for each species.

4.4.2. Longevity of canopy stored seeds

Two classes of follicles (the youngest and the oldest) were harvested from large shrubs of the four species. Follicles were aged by their position on the plant; old follicles were those found closest to the main stem on thick branches while young follicles were those found on the last seasons growing shoots. A 1% aqueous solution of tetrazolium bromide (International Seed Testing Association 1976) was used to test whether the viability of canopy stored seeds declines with age. One hundred seeds (five replicates of 20) of each species were used. A small section (2 mm) of the radicle of dry seeds was removed Seeds were soaked in water for 24 hours and then soaked in the tetrazolium bromide solution for 48 hours. Endosperms were removed from the seed coat and opened to uncover the embryo. Seeds having a completely stained embryo in a completely stained endosperm were considered viable.

4.4.3. Seed release and germination characteristics

The survival of seeds in fire was determined by simulating fires burning in the crowns of the shrubs. One hundred freshly picked, young follicles of each species were suspended on a wire mesh platform in the flames at 0.5 m above a fire for 90 seconds, the normal duration of peak temperatures in fynbos fires (B. W. Van Wilgen, unpublished data). Dry pine cones were used as fuel. The burnt follicles were placed, together with 100 freshly picked but unburnt young follicles of each species, in a dry environment. The number of open follicles was recorded daily for 11 days and then the unopened ones were forced open so that germination experiments could commence. Shade cloth (55 %) was used to simulate the effects of shading by vegetation canopies on germination in unburnt vegetation for comparison with recently burnt (unshaded) sites. The treatments were as follows: (i) follicles burnt with seeds landing in recently burnt areas (unshaded); (ii) follicles burnt with seeds landing in unburnt vegetation (shaded); (iii) follicles unburnt and seeds unshaded and (iv) follicles unburnt and seeds shaded. Data from these experiments were used to test the following null hypotheses: i) Germination values of untreated seeds do not differ for the four species (seeds sown in direct sunlight); ii) Germination values of fire-treated seeds are the same for the four species; iii) The degree of protection against fire afforded by the follicle does not differ for the four species; iv) Heating the follicle does not affect the germination of each of the species individually; iv) Seeds of the four species will germinate equally well in shaded and unshaded sites (this hypothesis was tested for both fire-treated and untreated seeds). One hundred seeds of each species per treatment were planted at a depth of 5 - 10 mm in trays (10 seeds per tray) filled with clean river sand. Trays were watered every three days and were monitored daily for 100 days to record seedling emergence. To take both total germination and the speed of germination into account for comparison between species and treatments, "germination values" were calculated. This composite index is defined as the product of peak value (the maximum quotient derived from the cumulative germination percent on any day divided by the number of days since planting) and the mean daily germination, calculated as the percentage germination at 100 days, divided by the number of days (100) to the end of the test (Czabator 1962).

4.4.4. Fall velocity of samaras

Fall velocity is a good indicator of relative dispersability; seeds that fall slower have the greatest potential for dispersal. The fall velocity was determined by releasing samaras of each species individually from a height of 3.5 m in still air (<0.4 m s^{-1} windspeed) and measuring the descent time.

4.4.5. Seed banks and allocation of reproductive energy

Eighteen H. sericea, 15 H. gibbosa and seven H. suaveolens shrubs were harvested from thickets of approximately equal density, while 13 solitary and unpruned H. salicifolia shrubs were harvested. Shrubs were selected to cover a range of size classes. Follicles (including seeds) were separated in the field and counted. Vegetative parts and follicles were weighed separately using a spring balance. Samples were collected from each shrub, placed in air-tight bottles and oven-dried at 80^{o}C for 72 hours to determine their moisture content. This was used to calculate the oven dry mass of the original material. Regression equations of total above-ground dry mass against the mass of follicles and total above-ground dry mass against number of follicles were fitted using the NONLIN procedure of the OXFORD statistical package (Commonwealth Forestry Research Institute, Oxford, England). In studies on reproductive strategies, dry mass has been used as a measure of energy allocation patterns (Harper & Ogden 1970; Hickman & Pitelka 1975; Evenson 1983; Samson & Werk 1986). This procedure is particularly appropriate in Hakea, where all (except in H. salicifolia) reproductive tissue (follicles and seeds) is retained for the life of the plant. Net reproductive effort, defined as the percentage of the total above - ground dry mass allocated to follicles and seeds was calculated for the four species.

4.4.6. Nitrogen and phosphorus contents of seeds

The wings were removed from the seeds and embryos were dissected from the testas after soaking in distilled water overnight. Each sample was oven-dried at 80^{o}C for 12 hours and consisted of either one seed or 0.1 g ground material (20 mesh). Phosphorus was extracted by means of the digestion method of Jackson (1958) and then assayed by the Murphy & Riley (1962) method. Standard Kjeldahl procedures with selenium catalyst and sodium thiosulphate extracted the total nitrogen and ammonium nitrogen was then determined calorimetrically using the method of Smith (1980).

4.5. RESULTS

4.5.1. Morphology of follicles and seeds

The morphological characteristics of follicles, samaras and seeds are shown in Table 4.2. Significant differences in follicle mass were found between the four species. H. gibbosa has the greatest follicle mass, more than double that of H. sericea and 12 times greater than H. salicifolia. Seeds of all four species bear structures that facilitate dispersal by wind. The lateral extension of the testa to form the wing increases the mass of the structure by between 6.5% (H. sericea) and 15.3 % (H. gibbosa) but increases the surface area by between 259 % (H. suaveolens) and 349 % (H. gibbosa). Examination of structural features of samaras of the four species suggests that samaras of H. suaveolens have the greatest inherent potential for dispersal.

Table 4.2. Structural and morphological characteristics of samaras, seeds and follicles of four Hakea species. Data are mean ± S.E., with number of observations in parentheses. Means with the same superscript letter for each parameter do not differ significantly (Student-Newman-Keuls test; P < 0.05).

	H. sericea	H. suaveolens	H. gibbosa	H. salicifolia
Follicle mass (g)	$5.28^{b}+0.16$ (50)	$3.29^{c}+0.07$ (50)	$12.86^{a}+0.31$ (50)	$1.05^{d}+0.03$ (50)
Samara mass (mg)	$31.67^{b}\pm0.46$ (100)	$13.00^{c}\pm0.29$ (100)	$42.74^{a}\pm1.13$ (100)	$12.55^{c}\pm0.36$ (100)
Follicle: samara mass ratio	$83.52^{c}\pm2.47$ (50)	$131.57^{b}\pm2.70$ (50)	$153.48^{a}\pm4.75$ (50)	$42.77^{d}\pm1.56$ (50)
Seed mass (mg)	$29.66^{b}\pm0.47$ (100)	$12.54^{c}\pm0.24$ (100)	$37.13^{a}\pm1.17$ (100)	$11.59^{c}\pm0.35$ (100)
Samara surface area X 100 (mm^2)	$1.38^{b}\pm0.02$ (100)	$0.88^{c}\pm0.01$ (100)	$2.19^{c}\pm0.02$ (100)	$0.63^{d}\pm0.01$ (100)
Seed surface area X 100 (mm^2)	$0.35^{b}\pm0.01$ (100)	$0.21^{c}\pm0.00$ (100)	$0.51^{a}\pm0.01$ (100)	$0.18^{b}\pm0.01$ (100)
Samara wing loading (mg/100 mm^2)	$23.02^{a}\pm0.42$ (100)	$14.76^{d}\pm0.29$ (100)	$19.47^{c}\pm0.48$ (100)	$20.15^{b}\pm0.54$ (100)

4.5.2. Longevity of canopy stored seeds

No significant differences (P < 0.001) were found between the viability of young and old canopy-stored seeds of Hakea sericea, H. gibbosa and H. suaveolens. The mean viability of young seeds of these three species was 99, 97 and 93 % respectively. The corresponding values for old seeds were 99, 99 and 90 % respectively. In the case of H. salicifolia, young seeds had a mean viability of 97 %, while the corresponding value for old seeds was 0 % . These results indicate that no decline in seed viability with increasing age occurs in any of the species other than H. salicifolia.

4.5.3. Seed release and germination characteristics

Fire-treated follicles of all species opened more rapidly than did untreated ones. All fire-treated follicles of H. sericea and H. gibbosa opened after five and seven days respectively, whereas there was a delay of 2-3 days in the opening of the untreated follicles. After 11 days, 90 % and 73 % of fire-treated follicles of H. salicifolia and H. suaveolens had opened whereas only 48 % of untreated follicles of H. salicifolia had opened at this stage.

No follicles of H. suaveolens opened without heating within 11 days after harvesting.

H. sericea and H. suaveolens showed similar germination patterns for both fire-treated and untreated seeds (Figure 4.1). Germination commenced after 30 days and reached maximum at around 70 days for H. sericea and after 60 days for H. suaveolens. Germination of seeds of H. gibbosa from all treatments, except fire plus shading, commenced at 30 days and reached relatively low maxima only at the end of the test period whereas fire-treated seeds planted in the shade commenced germination only after 50 days (Figure 4.1). No fire-treated seeds of H. salicifolia germinated. Untreated seeds of this species planted in direct sunlight and under shading showed relatively slow germination rates with maximum germination occurring at the end of the test period.

The null hypothesis that the germination value of untreated seeds does not differ for the four species (sown in direct sunlight) is refuted ($P < 0.0001$ in one-way ANOVA). Untreated seeds of H. sericea and H. suaveolens showed significantly greater germination values ($P < 0.0001$) than for H. salicifolia (Table 4.3). This is due to the slow germination rate of seed of H. salicifolia as germination percent after 100 days did not differ significantly for the three species. Germination value for H. gibbosa was significantly lower than for H. salicifolia. Germination values for fire-treated seeds were also not the same for the four species ($P < 0.0005$ in one-way ANOVA). Germination values for H. sericea , H. suaveolens and H. gibbosa were not significantly different but all H. salicifolia seeds were killed by exposure to heat (Table 4.3). Fire treatment significantly reduced germination percent in H. salicifolia, H. sericea and H. suaveolens but had no significant effect on H. gibbosa seeds (Table 4.3).

Shading had no significant effect on germination of seeds from fire-treated and untreated follicles of H. sericea, H. suaveolens and H. salicifolia and from untreated follicles of H. gibbosa (Table 4.4). Shading, however, resulted in a significantly smaller germination value for seeds from fire-treated follicles of H. gibbosa (Table 4.4).

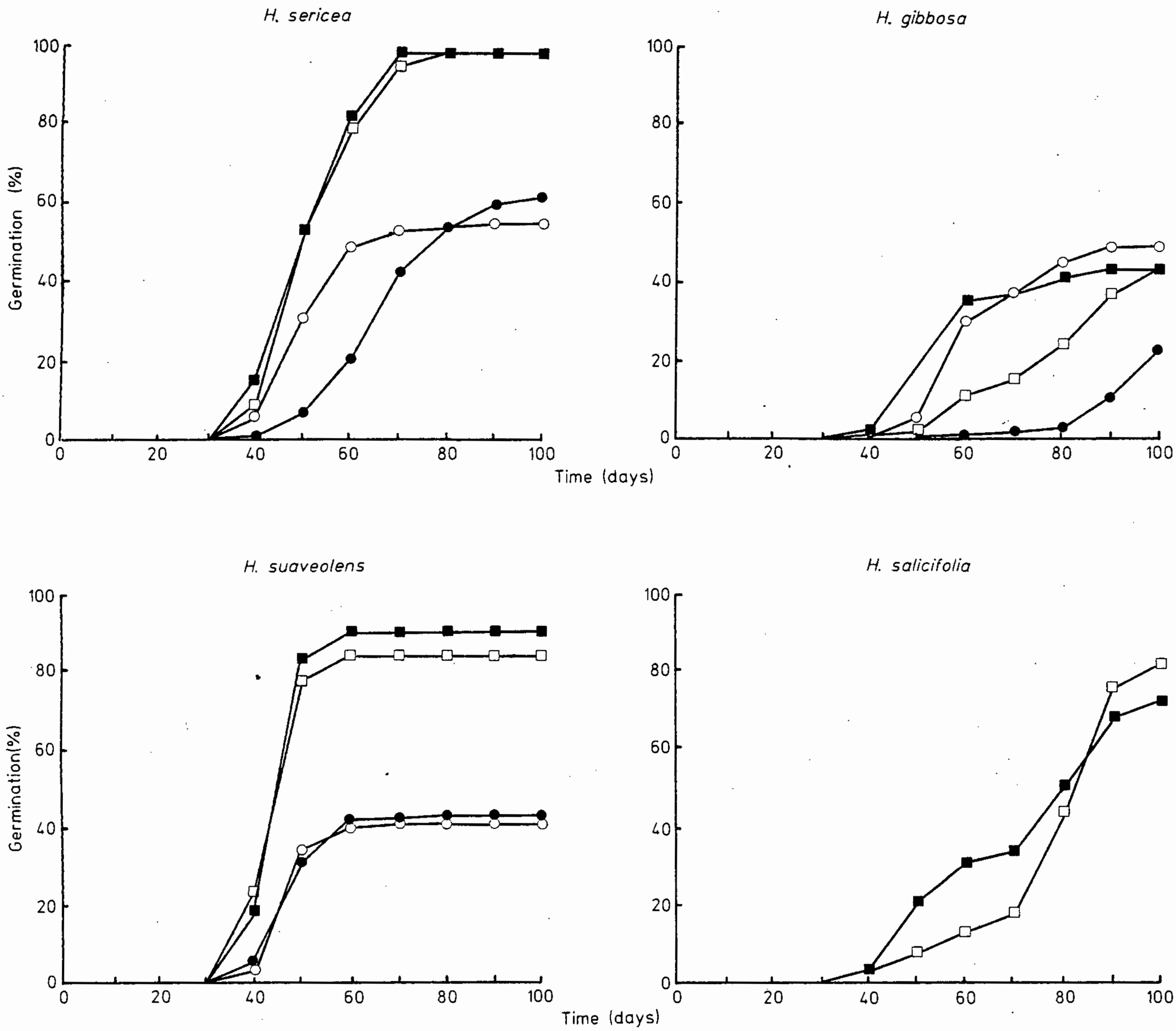

Figure 4.1. Germination patterns of four *__Hakea__* *species. Seeds from fire-treated and untreated follicles were planted in direct sunlight and in 55% shade (see text). Untreated seeds:* □ = *sun,* ■ = *shade. Fire-treated seeds:* ○ = *sun,* ● = *shade.*

Table 4.3. Mean germination values (see text) of seeds of four Hakea species. Fire-treated seeds were taken from follicles exposed to flames for 90 seconds. Seeds were sown in direct sunlight. Data are mean ± S.E. Number of replicates in parentheses. Means with the same superscript letter in each treatment do not differ significantly (Student-Newman-Keuls test; P < 0.05), N.S. denotes not significant.

Species	Mean germination value		t	P
	Fire-treated	Untreated		
H. sericea	$0.61^a \pm 0.15$ (10)	$1.57^a \pm 0.04$ (10)	6.10	<0.0001
H. suaveolens	$0.38^a \pm 0.09$ (9)	$1.55^a \pm 0.14$ (10)	6.98	<0.0001
H. gibbosa	$0.33^a \pm 0.05$ (10)	$0.37^c \pm 0.08$ (10)	0.41	N.S.
H. salicifolia	$0^b \pm 0$ (10)	$0.75^b \pm 0.14$ (10)	5.56	<0.0001

Table 4.4. Germination values (see text) for seeds of four Hakea species 100 days after planting in direct sunlight and in 55% shade. Data are mean ± S.E., with numbers of replicates in parentheses.

Species	Treatment	Germination value		t	P
		Full sunlight	55% shade		
H. sericea	Fire	0.61 ± 0.15 (10)	0.50 ± 0.07 (10)	0.64	N.S.
	Control	1.57 ± 0.03 (10)	1.45 ± 0.05 (10)	1.97	N.S.
H. suaveolens	Fire	0.38 ± 0.09 (9)	0.37 ± 0.05 (10)	0.10	N.S.
	Control	1.55 ± 0.14 (10)	1.46 ± 0.17 (10)	0.42	N.S.
H. gibbosa	Fire	0.33 ± 0.05 (10)	0.07 ± 0.02 (10)	4.84	<0.0005
	Control	0.37 ± 0.08 (10)	0.25 ± 0.07 (10)	1.03	N.S.
H. salicifolia	Fire	0.0 ± 0.0 (10)	0.0 ± 0.0 (10)	–	N.S.
	Control	0.75 ± 0.14 (10)	0.82 ± 0.11 (10)	0.42	N.S.

4.5.4. Fall velocity of samaras

Samaras of the four species rotate when falling and all follow a single helical trajectory (Burrows 1975); the centre of mass of the samara descending in a roughly straight line in still air. The null hypothesis that fall velocities of samaras of the four species do not differ significantly is refuted ($P < 0.0001$ in one-way ANOVA). Samaras of *H. gibbosa* fall more rapidly than those of the other species. Samaras of *H. suaveolens* which have the lowest wing loading (Table 4.2), also have the lowest fall velocity and therefore the greatest potential for dispersal by wind (Table 4.5). All four species, however, have the potential for dispersal over a considerable distance.

Table 4.5. Mean fall velocities (m/s) of samaras of four Hakea species. Samaras were released from 3.5.m under calm conditions (horizontal wind speed < 0.4 m/s). Means with the same superscript letter do not differ significantly (Student-Newman-Keuls test; P < 0.05).

Species	Mean fall velocity (ms^{-1})	Standard error	Sample size
H. gibbosa	1.186^a	0.052	45
H. sericea	1.027^b	0.028	48
H. salicifolia	0.977^b	0.017	74
H. suaveolens	0.871^c	0.018	31

4.5.5. Seed banks and allocation of reproductive energy

Regression equations of total above-ground dry mass against follicle mass and total above-ground dry mass against number of follicles are presented in Appendix 1. Equations of the form $Y = a + bX + cX^2$ provided the best fit in all cases. Both H. sericea and H. gibbosa produce a relatively large mass of follicles and seeds. This is not the case for H. suaveolens and H. salicifolia (Figure 4.2). Figure 4.3 shows the relationship between the number of follicles and the total above-ground dry mass. H. sericea produces a large number of follicles, even at an early stage of development. The number of follicles produced by H. gibbosa is lower despite it producing the same mass of tissue, as follicles are larger (Table 4.2). Conversely, H. salicifolia produces relatively numerous follicles, despite their relatively small contribution to the total above-ground dry mass. H. suaveolens produces few follicles and allocates relatively little energy to this function. The reproductive effort (percentage of above-ground dry mass allocated to follicles and seeds) is shown in Figure 4.4. Differences in reproductive effort between species are significant for all comparisons except H. salicifolia - H. suaveolens as tested by the Mann-Whitney two-tailed U test. Differences between H. gibbosa and the remaining three species and between H. salicifolia and H. suaveolens are significant at $P < 0.001$. Differences between H. sericea and H. salicifolia, and H. sericea and H. suaveolens are significant at $P < 0.05$.

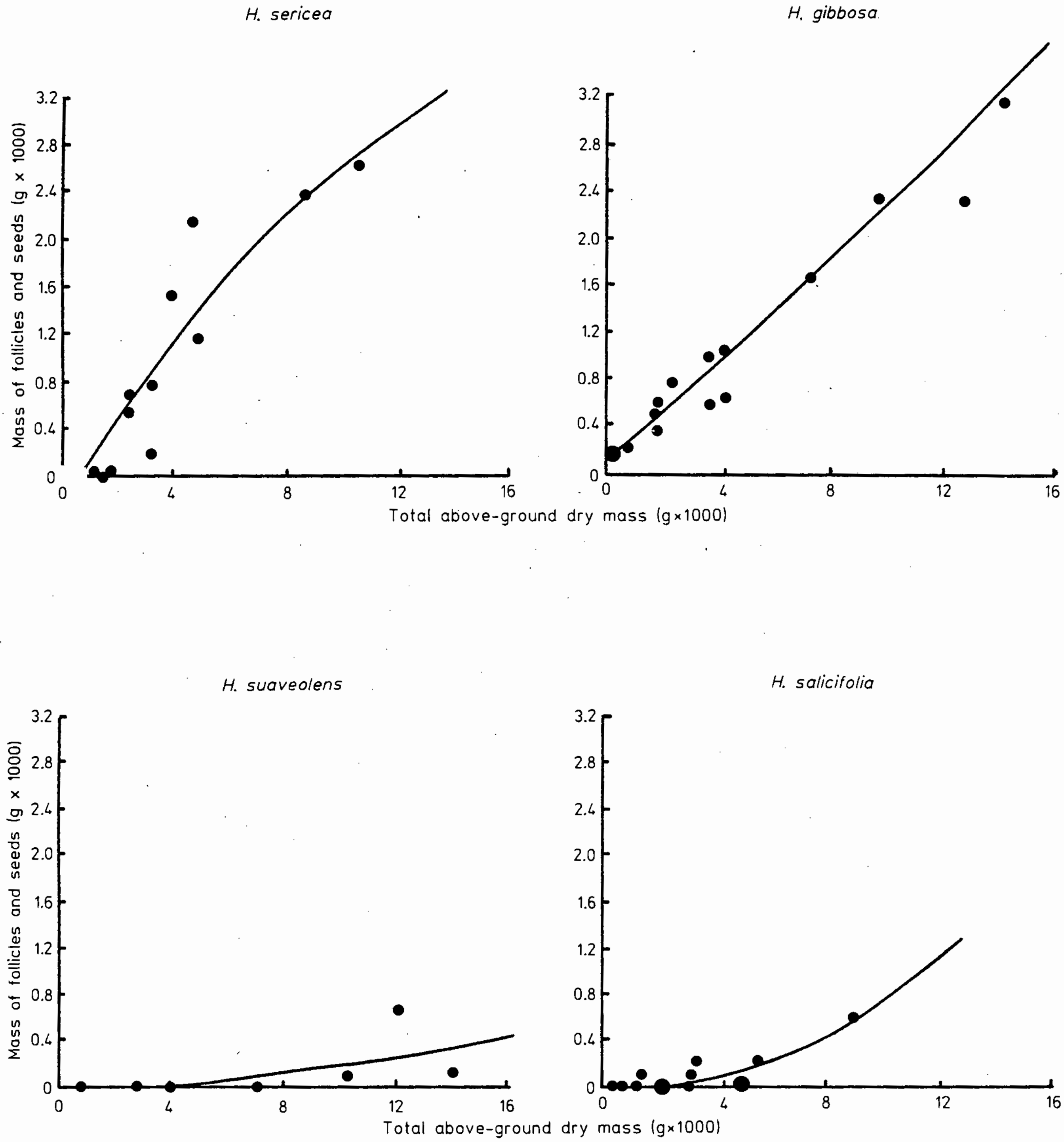

Figure 4.2. The relationship between total above-ground dry mass and the mass of follicles and seeds in shrubs of four Hakea species in the southwestern Cape Province. Large dots represent more than one data point. The equations of the regression lines are given in Appendix 4.1.

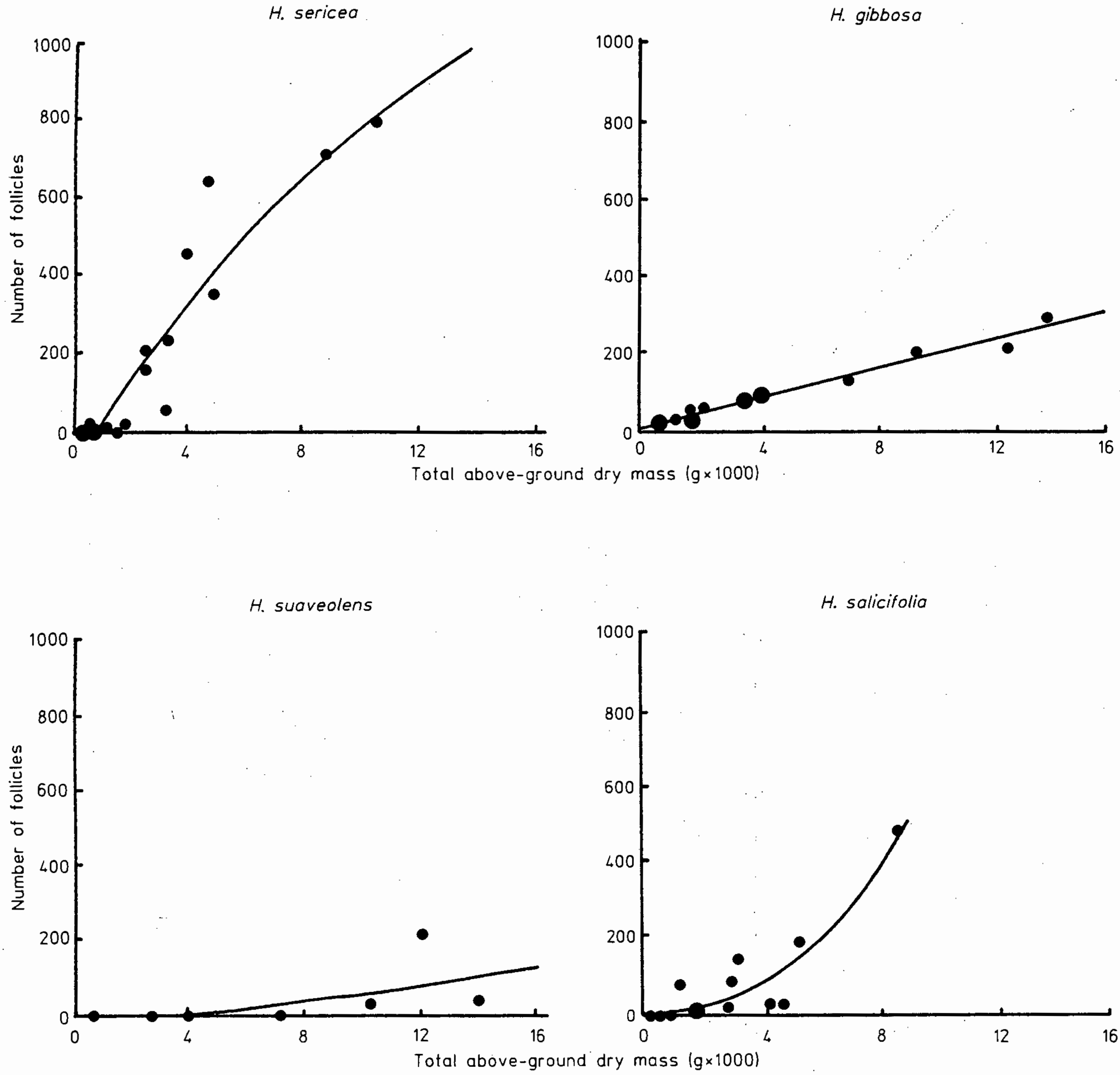

Figure 4.3. The relationship between total above ground dry mass and the number of follicles produced on shrubs of four Hakea species in the southwestern Cape Province. Large dots represent more than one data point. The equations of the regression lines are given in Appendix 4.1.

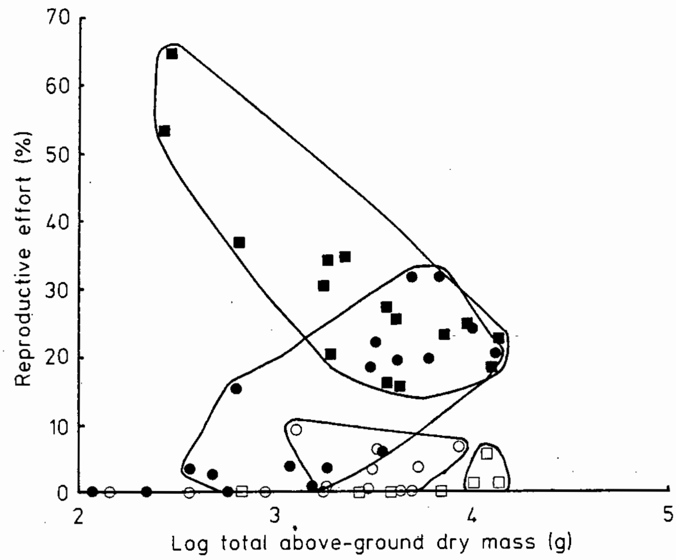

*Figure 4.4. Reproductive effort (ratio of dry weight of reproductive tissue to the total above-ground dry weight * 100) for four Hakea species. Closed curves represent all non-zero points. ● = H. sericea, ■ = H. gibbosa, ○ = H. salicifolia, □ = H. suaveolens.*

4.5.6. Nitrogen and phosphorus content of seeds

There were significant differences between some species in concentrations of both nitrogen and phosphorus in seeds (Table 4.6). Seeds of H. suaveolens and H. salicifolia contained less nitrogen and phosphorus per seed than H. sericea and H. gibbosa (Table 4.6). H. sericea seeds contained the highest concentration of nitrogen. The embryos of all four species contained more than 98 % of total seed phosphorus, although there were significant differences in the phosphorus concentrations of the testae with H. suaveolens having the highest concentration (Table 4.7).

Table 4.6. Nitrogen and phosphorus content of seeds of four species of Hakea. Data are mean ± S.E. Means with the same superscript letter for each parameter do not differ significantly (Student-Newman-Keuls test; P < 0.05)

	Nitrogen		Phosphorus	
	mg seed $^{-1}$	mg g $^{-1}$ dry mass	mg seed $^{-1}$	mg g $^{-1}$ dry mass
Hakea sericea	$2.46^{b} \pm 0.01$	$85.87^{a} \pm 1.21$	$0.32^{b} \pm 0.01$	$10.62^{b} \pm 0.16$
Hakea suaveolens	$0.97^{c} \pm 0.03$	$78.71^{b} \pm 1.59$	$0.18^{c} \pm 0.01$	$14.46^{a} \pm 0.43$
Hakea gibbosa	$3.60^{a} \pm 0.12$	$76.14^{b} \pm 1.73$	$0.63^{a} \pm 0.03$	$11.83^{b} \pm 0.47$
Hakea salicifolia	$1.01^{c} \pm 0.07$	$75.71^{b} \pm 3.90$	$0.16^{c} \pm 0.01$	$11.79^{b} \pm 0.38$
F	220.01	3.98	141.13	18.05
d.f.	3,36	3,36	3,59	3,59
P	0.001	0.05	0.001	0.001

Table 4.7. Phosphorus content of testae and embryos of seed of four Hakea species. Data are mean ± S.E. Means with the same superscript letter for each parameter do not differ significantly (Student-Newman-Keuls test; $P < 0.05$).

	Testa	Embryo	
	mg g^{-1} dry mass	mg $seed^{-1}$	mg g^{-1} dry mass
H. sericea	$0.30^{c} \pm 0.02$	$0.35^{b} \pm 0.01$	$13.90^{b} \pm 0.30$
H. suaveolens	$1.09^{a} \pm 0.08$	$0.18^{c} \pm 0.01$	$16.06^{c} \pm 0.26$
H. gibbosa	$0.19^{c} \pm 0.02$	$0.63^{a} \pm 0.03$	$16.61^{a} \pm 0.49$
H. salicifolia	$0.73^{b} \pm 0.06$	$0.15^{c} \pm 0.01$	$14.64^{b} \pm 0.76$
F	60.33	187.96	9.96
d.f.	3,51	3,55	3,55
P <	0.001	0.001	0.001

4.6. DISCUSSION

The Australian Hakea species in South Africa appear to have two major advantages in reproduction over South African Proteaceae: superior dispersal abilities and much larger seed banks. Bond (1980) found that dispersal of fynbos Proteaceae with canopy-stored seed banks could be limited by minor physical barriers. Manders (1986) reports a maximum dispersal distance of 26 m for Protea laurifolia Thunb., with 95 % of recruitment occurring within 15 m of the parent plant. Myrmecochorous (ant-dispersed) species are even less efficient at dispersal, and Slingsby & Bond (1985) found a maximum dispersal distance of less than 10 m for Leucospermum conocarpodendron (L.) Buek. The winged seeds of Hakea species, on the other hand, facilitate dispersal over several kilometers in some cases. The canopy-stored seed banks of Hakea species in Australia suffer heavy pre-dispersal predation from insects, many of them highly specialized (Neser 1968; Gill & Neser 1984). The development of the woody follicle in Australian Proteaceae is seen primarily as a response to the presence of specialized seed predators (Johnson & Briggs 1963; Neser 1968; Lamont et al. 1985). There is virtually no pre-dispersal predation of Hakea seeds in South Africa (Kluge 1983), and this has led to the production of large quantities of viable seed. Seed production in H. sericea in South Africa is certainly much greater than in Australia (Gill & Neser 1984), but there are no data on the relative fecundity of the other three species on the two continents. The virtual absence of pre-dispersal predation in the alien Hakea species in South Africa is contrasted by heavy insect predation of seeds in indigenous Proteaceae. For example, more than 80 % of seeds of Protea repens (L.) L. are destroyed by insects within two years after flowering

(Coetzee 1984) and almost none remain after four years (Bond 1985).

In order to have been more successful, H. sericea must have displayed superiority in one or more vital trait when compared to the other three Hakea species. In Table 4.8 we compare selected attributes of the reproductive ecology of the four species. Juvenile periods range from two years in H. sericea and H. gibbosa, to four and six years for H. salicifolia and H. suaveolens respectively (Richardson 1985 and unpublished data). Although significant differences in the samara wing loadings were found between the four species, all species nonetheless possess a good ability to disperse by virtue of having a winged seed. Furthermore, while the nutrient concentrations in seeds are high compared to values for indigenous South African Proteaceae (Mitchell & Allsopp 1984), no large differences exist between the four species. The dispersability of individual samaras and the nutrient content of seeds of the four species cannot explain differences in invasive potential.

H. gibbosa shrubs produce relatively few seeds when compared to H. sericea but devote up to 70 % of their resources to reproductive and ancillary organs (Figure 4.4). The very large follicles make up a greater part of the dry mass of small shrubs than in H. sericea (Figure 4.4). The greater protection afforded seeds of H. gibbosa is more than compensated for by the greater number of seeds produced by H. sericea. Slow germination and relatively low germinability of seeds of H. gibbosa and low germination in unburnt sites also limit the success of this species.

The relative lack of success of H. suaveolens as an invader may be explained by the relatively long juvenile period and low seed production. Too little energy is allocated to reproduction. Seed production commences only after 6 years in H. suaveolens and the store of viable seeds in the canopy of large shrubs is smaller than in H. sericea. Seed release following fire is slow and this may lessen its competitive advantage as germination will be correspondingly slower.

Table 4.8. Comparison of selected attributes of the seed biology and ecology of four species of Hakea. The relative values are assigned to the four species on the basis of results of this study.

Attributes	*H. sericea*	*H. gibbosa*	*H. suaveolens*	*H. salicifolia*
Juvenile period	Short	Short	Long	Moderate
Seed production	Very large	Relatively small	Relatively small	Large
Seed longevity in canopy	Long	Long	Long	Moderate?
Reproductive effort[a]	Just enough	Too much	Too little	Too little
Resistance of canopy stored seeds to fire	Resistant	Very resistant	Resistant	Intolerant
Time for follicles to open	Fast	Fast	Slow	Intermediate
Dispersability of individual samaras	Good	Good	Good	Good
Germination on burnt sites	Good	Intermediate	Good	Poor (canopy stored seeds killed)
Germination on unburnt sites	Good	Poor	Good	Poor (canopy stored seeds killed)
Nutrient concentrations in seeds	Relatively high N Normal P	Normal N Normal P	Normal N Relatively high P	Normal N Normal P

[a] Reproductive effort is defined as the ratio of dry mass of follicles and seeds to the total above-ground phytomass

Traits of H. salicifolia that contribute to its failure to invade fynbos are the moderately long juvenile period and the mortality of seeds during fires resulting from too little protection in small follicles. Although not shown in this study, a physiological inability to cope with the fynbos environment has probably contributed to the failure of this species to invade. Although our results show that seed viability declines in very old follicles, there is nonetheless a large seed store on individual shrubs, and the species is probably not held back by low seed numbers.

Our results suggest that the success of H. sericea relative to other alien Hakea species is due largely to the production of relatively large numbers of viable seeds. Fecundity is an important factor influencing not only the maintenance of established populations, but also the range of dispersal. A negative exponential relationship exists between seed numbers and dispersal distance (Harper 1977); such a model reveals that a 20 % increase in seed numbers will increase maximum dispersal distance by 80 %. The potential rate of spread is thus significantly increased by larger seed numbers (Cavers 1983). In order to refute the null hypothesis that the size of seed reserves is irrelevant in determining relative success of congeners, it is first necessary to demonstrate that the amount of seed is a limiting factor in the demography of each species (Macdonald 1984). This is demonstrated by the fact that all three invasive Hakea species form dense thickets, but it is only in H. sericea that colonization of distant areas constitutes a major problem. We ascribe the limited areal expansion of H. gibbosa and H. suaveolens populations to low seed numbers. Control measures aimed at reducing the seed bank using specialized insect seed predators (Neser 1968; Kluge 1983; Neser & Kluge 1985) should provide the most effective means of combatting H. sericea.

Careful studies of the life history attributes of other species in their native habitats may reveal potential invaders of the fynbos. From the study of Hakea sericea, it appears that such species would: 1) have a potentially high seed production that is limited by specialized predators; 2) have an innate ability to disperse over long-distances; and 3) be pre-adapted to frequent fires and low soil nutrients.

Appendix 4.1. Exponential curves of the form $Y = A + bX + cX^2$ describing the relationships between total above-ground dry mass, and the mass and number of follicles on shrubs of four Hakea species. The curves are depicted in Figures 4.2 and 4.3.

Total dry mass in g (X) vs follicle mass in g (Y)

Species	A	B	C	n	r^2
H. sericea	−225.11	0.370	-8.318×10^{-6}	18	0.877
H. suaveolens	−52.328	0.017	8.251×10^{-7}	7	0.343
H. gibbosa	121.168	0.205	1.677×10^{-6}	15	0.954
H. salicifolia	37.501	−0.025	9.923×10^{-6}	13	0.810

Total dry mass in g (X) vs number of follicles (Y)

Species	A	B	C	n	r^2
H. sericea	−68.120	0.112	-2.518×10^{-6}	18	0.877
H. suaveolens	−16.543	0.005	2.617×10^{-7}	7	0.343
H. gibbosa	12.042	0.019	-4.018×10^{-8}	15	0.981
H. salicifolia	26.899	−0.021	8.149×10^{-6}	13	0.853

CHAPTER 5

PINE INVASIONS IN SOUTH AFRICAN MOUNTAIN FYNBOS : LIFE HISTORY OR EXTENT OF CULTIVATION ?

CHAPTER 5 : PINE INVASIONS IN SOUTH AFRICAN MOUNTAIN FYNBOS : LIFE HISTORY OR EXTENT OF CULTIVATION ? [1]

5.1. ABSTRACT

Many Pinus species have been introduced to the southwestern Cape Province of South Africa. Some species have invaded fire-prone mountain fynbos shrublands and three species have become major weeds. Pine invasions were studied at a mountain fynbos site to determine the roles of cultivation (including residency time and the magnitude of afforestation) and life history strategies in determining the relative success of seven Pinus species as invaders. We examined the distribution of invading trees, the age structures of self-sown stands in relation to historical factors (time since introduction, proximity of plantations, disturbance history) and salient life history attributes. Despite having markedly different histories of introduction and dissemination in the region, P. halepensis, P. pinaster and P. radiata all formed dense stands with similar age structures over large areas. Pinus pinea also showed moderate invasion, but stands were clumped around old parent trees. Pinus canariensis, P. elliottii and P. taeda did not invade mountain fynbos. Pinus pinaster which has the longest residency (nearly 300 years) and the greatest extent of dissemination by man has also invaded the greatest area. However, P. pinea which was introduced soon after P. pinaster, has invaded only relatively small areas both because of its limited cultivation and because its large seeds require specialized dispersal agents. Pinus radiata has only recently emerged as a major weed, in parallel with its increasing importance as a plantation species. Pinus halepensis, with long residency but very limited dissemination by man, has invaded a greater area than would be predicted from the "population size/time" hypothesis. We conclude that invasive potential increases substantially with an increase in population size and time since introduction but that the most successful Pinus species possess a suite of attributes that have permitted proliferation and spread.

We collated data for 60 Pinus taxa on six life history attributes fundamental for persistence, recruitment and proliferation in mountain fynbos (juvenile period, fire tolerance, seed crop variability, degree of serotiny, seed mass and seed wing loading index). This matrix was ordinated using correspondence analysis to show the range of life history strategies in the genus. The most successful invaders in mountain fynbos are fire-resilient species characterized by small seed size, low seed wing loadings, short juvenile periods, moderate to high degrees of serotiny and poor fire-tolerance as adults. Other species with these attributes, especially from mediterranean-climate regions in North America and the Mediterranean Basin, would be high-risk introductions.

5.2. INTRODUCTION

Most communities on earth have been invaded by introduced species, some of which have caused severe disruptions of natural ecological processes. Management of invaded habitats should involve both the control of current

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invaders, and the screening of new introductions. What factors (if any) can be used to predict whether a species will proliferate or become extinct when introduced to a new environment ? There is irrefutable evidence that introductions of species from regions with environmental conditions similar to those of the target site are more likely to succeed than those from markedly dissimilar regions (Baker 1986). However, species differ considerably in their adaptability to new habitats, and the invasive potential of an introduced species (its performance in response to physical, biological and historical constraints) can seldom be predicted by bioclimatic analysis alone (Booth et al. 1988). Assuming that the introduced species is physiologically capable of growth and reproduction in a new environment, two hypotheses may be advanced to explain its relative success.

The "population size/time hypothesis" states that there is a population size threshold, and once this is exceeded the population is bound to colonize irrespective of life history. However, if the existence of the initial population is guaranteed for a long time relative to the reproductive lifespan of the species, colonization may occur irrespective of the initial size of that population (Richter-Dyn & Goel 1972). The population size/time hypothesis incorporates a number of demographic and genetic considerations such as minimum viable population size (Gilpin & Soulé 1986), infection pressure and founder effect (Salisbury 1961; Baker 1986), which may individually determine the success of an invader. In all cases, however, two major determinants of success are the size of the initial population (or inoculum) and the time that this population (and its progeny) has been conserved. Increased population size increases the likelihood of that population surviving demographic accidents (Pimm et al. 1988) and reduces the potentially deleterious effects of genetic depauperization through inbreeding (Ledig 1986). In general, genotypic variation increases with time since introduction (Nei et al. 1975), thus improving the chances for colonization (Kruger et al. 1986). Also, if conditions for spread occur episodically and infrequently then the likelihood of colonization will improve with an increase in time since introduction (Kruger et al. 1986). The "life history hypothesis" argues that invasive potential is dependent on the life history of the species in relation to the biotic and abiotic features of the target environment (e.g. Crawley 1987a).

Invasions from plantings of introduced conifers provide exceptional, but overlooked, natural experiments in population biology (Kruckeberg 1986). Plantings can be dated to time zero, and the extent of invasion provides an index of population growth. In this chapter we evaluate the above-mentioned hypotheses with respect to the relative success as invaders of several Pinus species (Pinaceae) [1] in the fire-prone mountain fynbos shrublands of the southwestern Cape Province of South Africa.

The fynbos biome is exceptional among mediterranean-climate regions of the world in that introduced trees and shrubs, rather than herbs, have been remarkably successful, and are the most important life forms in the invasive flora (Macdonald & Richardson 1986; Kruger et al. 1988). Invasive trees and shrubs often dominate fynbos landscapes (Figure 5.1) (e.g. Richardson and Brown 1986), suppressing or eliminating natural elements (Richardson et al. 1989), and causing severe disruption of natural ecological processes (Macdonald & Richardson 1986).

Of the hundreds of species of trees and shrubs that have been introduced to the fynbos biome, few have spread from cultivation, and fewer than twenty species may be classified as major weeds (Macdonald & Jarman 1984). Most species that have become important weeds have been cultivated, and it has been argued that their spread can be attributed, at least partially, to the establishment by man of multiple seed sources which have served as foci of spread (Shaughnessy 1980; Kruger et al. 1986). This appears to be the case for the five species of Pinus that invade mountain fynbos in the biome, where the extent of invasion (Macdonald et al. 1985) is roughly correlated with the extent of cultivation (Shaughnessy 1980; Macdonald 1984; Kruger et al. 1986). Many Pinus species have been introduced to South Africa (Poynton 1979a), and at least 23 species were distributed from the three principal forest nurseries in the Cape Province (Tokai, Kluitjieskraal and Concordia) in the years 1881 - 1902 (unpublished records, Forestry and Environmental Conservation Branch). The two most important forestry plantation species in the Cape Province, Pinus pinaster and P. radiata are both major weeds in mountain fynbos (Kruger 1977; Macdonald & Jarman 1984; Richardson & Brown 1986). Three other Pinus species are also known to invade mountain fynbos: P. canariensis, P. halepensis and P. pinea (Macdonald & Jarman 1984; Richardson 1988). Another four species, P. elliottii, P. patula, P. roxburghii and P. taeda are classified as 'problem

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[1] Nomenclature for the genus Pinus follows Critchfield & Little (1966).

plants' in South Africa (Wells et al. 1986), but have never been recorded as weeds in the fynbos biome.

Species in the genus Pinus show a wide array of reproductive and demographic traits (Yeaton 1978; Strauss & Ledig 1885; McCune 1988). For example, pinyon pines (P. edulis and P. monophylla) produce few, relatively large vertebrate-dispersed seeds and have long juvenile periods (20-30 years) whereas species such as P. banksiana and P. contorta produce numerous, small, wind-dispersed seeds and have short juvenile periods (c. 4 years) (McCune 1988). This diversity is reflected in the Pinus species which have been introduced to the Cape.

Figure 5.1. Pinus pinaster invading mountain fynbos at Jonkershoek. Note the dense stand of pines in mid-background.

Are there traits that can explain the relative invasive success of different Pinus species in mountain fynbos ? For example, do species with a juvenile period longer than the median fire interval fail to invade ? Similarly, are those species that maintain large canopy-stored seed banks (serotiny) more likely to invade than species with spontaneous seed release (Lamont *et al*. in press) ? In this chapter we assess the invasive success of seven *Pinus* species introduced to a mountain fynbos site in terms of selected life history traits and cultivation history. In addition, we present an analysis (based on a literature study of selected life history attributes) of a representative sample of taxa in the genus *Pinus* to: a) determine the relationships within the genus of the successful invaders in the fynbos; and b) compile a biological profile of "the good invader", and thus predict what other species could be successful invaders.

5.3. THE STUDY AREA

The Jonkershoek Valley (33°57'5; 18°55'E) is near Stellenbosch in the southwestern Cape Province of South Africa. We chose this area because: a) it was one of the first in South Africa to be settled by Europeans (about 300 years B.P.); b) it has been inhabited continuously since the first settlement; c) at least seven *Pinus* species have been planted in the area; and d) there is no evidence of significant utilization of self-sown pines or of weed control operations outside cultivated areas.

The valley is enclosed on three sides by mountains formed mainly from sandstones of the Table Mountain Group. The north-facing slopes (Stellenbosch Mountain) are underlain by sandstones, or sandstone-granite mixtures whereas the south-facing slopes (Jonkershoek Mountains) are underlain by granite. Soils are acid and highly leached. The climate is mediterranean, Köppen's humid-mesothermal (type Csb) with a dry summer; the average temperature of the warmest month is below 22°C. Mean rainfall at an altitude of 470 m is 1800 mm per annum, about 60% of which falls between May and August (Wicht *et al*. 1969). The natural vegetation is mesic mountain fynbos (Moll *et al*. 1984), and consists mainly of a tall (2 - 3 m) mid-dense to open shrubland (*sensu* Campbell *et al*. 1981) dominated by sclerophyllous, broad-leaved shrubs such as *Protea neriifolia*, *P. nitida* and *P. repens* (Proteaceae). This conforms to the Jonkershoek type of Campbell's (1985) mesic proteoid fynbos subseries. Indigenous trees are uncommon in the vegetation except in riparian zones. Fires occur at intervals of between 5 and 40 years but fire-free intervals seldom exceed 20 years, (unpublished records, Jonkershoek Forestry Research Centre).

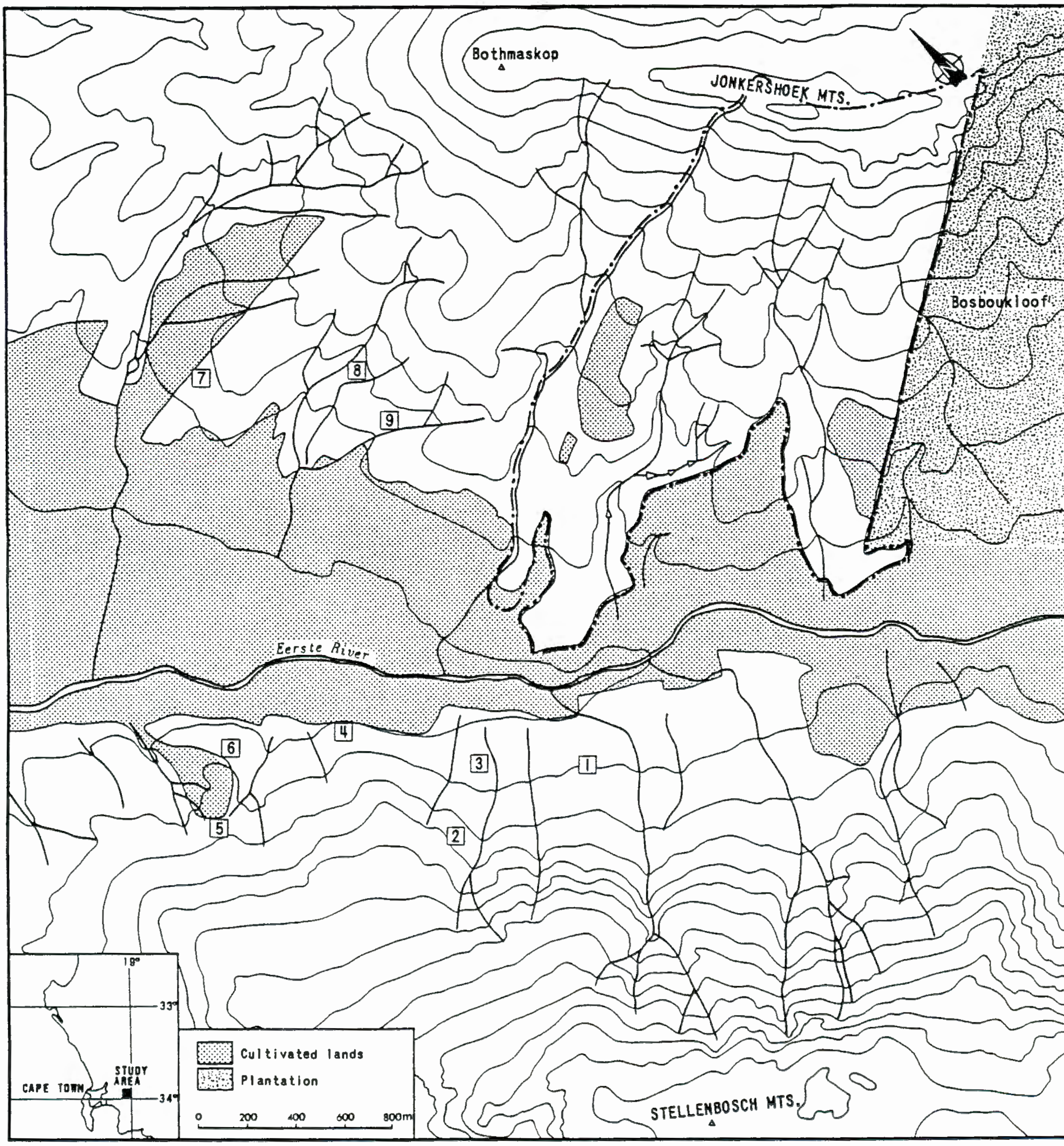

Figure 5.2. Location of the study area in the Jonkershoek Valley, southwestern Cape Province. The positions of the nine sites selected for the study of the age structure of invasive pines are shown. The stippled line (--*-*) shows where a separate study was carried out on the spread of <u>Pinus</u> <u>radiata</u> (Richardson & Brown 1986).*

5.4. METHODS

5.4.1. Cultivation history

The history of land use and cultivation of *Pinus* species in the study area was determined from published and unpublished records, including maps and aerial photographs.

5.4.2. Species composition, density and age structure of self-sown pine stands

The study area was surveyed to determine the relative abundance, dispersion and habitat preferences of self-sown pine stands. Nine sites were selected in the Jonkershoek Valley to give a representative sample of densities and ages of the different species (Figure 5.2). No sites were located in the area studied by Richardson & Brown (1986) (Figure 5.2) because this area had burnt in a wildfire in 1987. All sites were situated outside areas where regular weed control operations and prescribed burns are carried out, and were in close proximity to human habitation and/or cultivated lands.

At each site a 30m X 30m plot was positioned at random within the stand. All pines in the plots were felled and identified during December 1986. A disc was taken from the basal section of each tree and aged by counting growth rings. Ageing was usually done in the field by scraping the cut surface with a sharp blade and counting growth rings, using a X 10 lens when necessary. Where rings were indistinct or when discs showed fire scars, discs were collected, oven-dried and sanded before examination (Arno & Sneck 1977). Tree age was recorded after consensus of two independent observers, but occasional errors of ± 1-2 years are considered likely (Arno & Sneck 1977). Age structure histograms were constructed for each species found at each site.

5.4.3 Fire history

The fire history at each site was inferred from fire scars (Arno & Sneck 1977), and checked with the fire records at the Jonkershoek Forestry Research Centre.

5.4.4. Life history attributes

A matrix of life history attributes for the seven Pinus species was constructed from data collected in the field at Jonkershoek, and from the literature. The age of first reproduction was determined for P. halepensis, P. pinaster and P. radiata. Free-standing trees with one or more cohorts of fully-developed cones were selected at random in the area. Cones were aged by noting their size, position on the tree, colour and amount of weathering. To determine whether cones of different age classes contained viable seed, a sample of seed was collected from each cone age class of each species (5 replicates of 25 seeds for each). Seeds were stratified for 45 days at 3°C and germinated in petri dishes. The age at which viable seed was first produced was then determined by calculating the date of attainment of maturity of the oldest cohort of cones that contained viable seed. Cones of Pinus pinea are not retained on the tree after maturity, and the juvenile period of this species could not be determined using the method described above. Estimates of the juvenile periods for P. pinea and for P. canariensis, P. elliottii and P. taeda were obtained from the literature.

Seed dispersal characteristics of P. canariensis, P. elliottii, P. halepensis and P. taeda were determined by weighing 50 intact samaras (seed plus wing), measuring the surface area of each samara, and calculating the samara wing loading, defined as W/A, where W is the mass (mg) and A is the surface area (mm^2) (Green 1980). Comparable data for P. pinaster, P. pinea and P. radiata were available from an earlier study in the same area (Van Wilgen & Siegfried 1986).

The dynamics of the canopy-stored seed banks were studied for the three serotinous species (P. halepensis, P. pinaster and P. radiata). Cones of all ages (except immature conelets of 50 mm or less in length) were collected from 5-10 randomly selected trees of each species with three or more cohorts of cones during February and April 1988. Only isolated trees were sampled to exclude density-dependent effects. Cones were divided into age classes by assessing the colour, amount of weathering and position of cones relative to terminal branches. The cones in each age class were counted. Conelets that were less than 1 year old at the time of sampling were placed in age class 0 (and were not collected), those that were between one and two years old in age class 1, and so on (McMaster & Zedler 1981). The percentage of open scales on each mature cone was estimated. Samples of 10-30 cones were collected at random from each age class on each tree. Cones were heated at 50°C for 24 hours to stimulate opening. Cones were then broken open and all seeds extracted. All seeds were bisected, and those containing firm white endosperms were considered full. By calculating the mean number of full seeds per cone in each age class for each tree of known age, it was possible to estimate: 1) the total number of full seeds held in the canopy of trees of different ages; 2) the contribution of seeds in cones of each age class to the total store of viable seeds in the canopy.

5.4.5. Life history traits related to regeneration in the genus Pinus

We extracted from the literature data on life history attributes considered fundamental for an invasive pine in mountain fynbos (Table 5.1). These attributes all relate to recruitment and spread in a nutrient-poor environment subject to intense fires at intervals seldom exceeding 15 years (Kruger & Bigalke 1984).

In order to determine and interpret the relationships between taxa and traits, we subjected the species X trait matrix to correspondence analysis (Greenacre 1984; Underhill & Peisach 1985). We standardized the matrix by dividing each value by its corresponding column mean so that each character was equally weighted and the analysis was not distorted by the different scales of the character values used (Underhill & Peisach 1985). The correspondence analysis was implemented using the algorithms provided by Underhill & Peisach (1985), SAS IML (SAS Institute Inc. 1985a) for the matrix manipulations and SAS GRAPH (SAS Institute Inc. 1985b) for the plots.

5.5 RESULTS

5.5.1. Cultivation history

Organized farming in the Jonkershoek Valley commenced in 1692 (Visagie 1979) and vineyards now cover most of the lower slopes (Figure 5.2). Pinus pinaster and P. pinea were the first pines established in the region (Table 5.2). Seeds of P. pinaster were actively dispersed by forest rangers in many parts of the fynbos biome in the 18th and 19th centuries in an effort to increase the tree cover in the shrubland vegetation (Woods 1950). Pinus pinaster was the principal commercial forest tree in the southwestern Cape until about 1910 at which time P. radiata gained importance (Poynton 1960). No other Pinus species have been used extensively for afforestation in the southwestern Cape (Poynton 1979a).

Large-scale afforestation in the Jonkershoek Valley started in 1935, and by 1963, 717 ha had been planted to Pinus radiata. Small areas (< 15 ha in total) were also planted to P. canariensis, P. elliottii and P. taeda (unpublished plantation records). Small plantations of P. halepensis (<5 ha in total) are visible on aerial photographs taken in 1938. P. pinaster and P. pinea were also planted on a small scale on farms for shade and windbreaks. There is no evidence of planting of other Pinus species in the valley.

5.5.2. Species composition, density and age structure of self-sown pine stands

Pinus pinaster was the most abundant and widespread of the Pinus species (Table 5.2). Pinus halepensis and P. radiata were equally abundant but whereas the former species was widespread, the latter was confined to slopes downwind of a plantation of that species. Pinus pinea was considerably less abundant and was aggregated in small stands around original plantings. Of the remaining species, only P. canariensis occurred in the study area where it was recorded as isolated individuals confined to wet sites.

Only one of the nine sample sites was free of P. pinaster. Pinus halepensis and P. pinea trees were found in four and two of the nine stands respectively and only one P. radiata tree was recorded in the course of the study. No P. canariensis, P. elliottii or P. taeda trees were encountered in the plots. Several scattered individuals (<10 in total) of P. canariensis were found in the Jonkershoek Valley, mainly close to perennial streams. Pinus pinaster was the dominant species in six of the plots, P. halepensis in two, and one plot was dominated by P. pinea. Pinus pinaster and P. halepensis occurred in very dense stands (> 1800 trees/ha), but in the densest P. pinea stand in the area (plot 4), only 40 trees were found (444 trees/ha) (Table 5.3). The oldest trees of each species found in this study were : 70 years (P. pinea in plot 4), 48 years (P. pinaster in plot 9) and 37 years (P. halepensis in plot 7) (Table 5.3).

Table 5.1. Attributes selected for an analysis of life history strategies in the genus <u>*Pinus*</u> *with particular emphasis on survival and proliferation in a nutrient-poor environment subject to intense fires at intervals seldom exceeding 15 years.*

Attribute	Importance for success as an invader in mountain fynbos shrublands
Juvenile period [1] (years)	A short juvenile period is essential to build up seed reserves between fires (Swain 1978). Juvenile period is inversely related to plant growth rate (Harper & White, 1974; Loehle 1988) which is an important factor determining competitive ability. Species with short juvenile periods typically have high growth rates as seedlings (Strauss & Ledig 1985).
Fire tolerance index [2]	Thick bark enhances survival of ground fires, at least for adult trees (Loehle, 1988; McCune, 1988) enabling them to persist as seed sources (Richardson 1988).
Seed crop variability 3	The longer the interval between good seed crops, the greater the probability of local extinction following a fire in a poor seed year (Waller 1979; Bergeron & Gagnon 1987).
Degree of serotiny [4]	The accumulation of canopy seed banks is an advantage in fire-prone environments as it maximizes post-fire recruitment (Lamont <u>et al</u>. in press).
Seed mass (mg) [5]	Large seeds provide greater reserves for seedlings, which become more independent of the physical environment (Canham & Marks 1985) thus provide them with a competitive advantage (Crawley 1986). Large pine seeds are more susceptible to predation than small pine seeds (references in Yeaton 1978). Production of smaller seeds means an increased range of dispersal for wind dispersed species (Siggins 1933).
Seed wing loading index 6	Abiotic dispersal is generally an advantage for an invading species, unless suitable dispersal agents are present in the new habitat (Baker 1986; Groves 1986). The typically high summer (fire season) wind velocities in the Western Cape (see Richardson & Brown 1986) facilitate dispersal of anemochorous species. No indigenous birds disperse large non-fleshy seeds in mountain fynbos (Richardson and Fraser in press), unlike the situation in the Northern Hemisphere (e.g. Lanner 1982).

Table 5.1. (continued) Attributes selected for an analysis of life history strategies in the genus Pinus with particular emphasis on survival and proliferation in a nutrient-poor environment subject to intense fires at intervals seldom exceeding 15 years.

Notes:

1: We used the minimum juvenile periods given by Krugman & Jenkinson (1974) except for the following species (sources in parentheses): P. cembra (Perrin 1954), P. cembroides, P. contorta var. contorta (McCune 1988), P. densiflora (Nakagoshi et al. 1982), P. monticola (Loehle 1988), P. pinaster (this study), P. rigida (Ledig & Little 1979) and P. roxburghii (Troup 1921).

2: Derived from descriptions in Sudworth (1908), Den Ouden & Boom (1965) and Dallimore & Jackson (1966): 0=thin bark, 1=thin bark in juveniles but thicker in adults, 2=thick bark.

3: Mean intervals between good seed crops are from Krugman & Jenkinson (1974), except for the following species (sources in parentheses): P. aristata (taken as equivalent to P. balfouriana cf. McCune 1988), P. ayacahuite (Poynton 1979a), P. caribaea (USDA 1948), P. cembra, P. pinaster and P. pinea (Perrin 1954). P. armandii was given the mean value of ecologically similar species from a preliminary analysis of the data and their position on axis 1 (Figure 5.4), P. roxburghii and P. wallichiana (Singh & Singh 1987).

4: 1=seed release at maturity; 2=intermittent seed release; 3=mass seed release only after fire. Principal sources: Shaw (1914), Loock (1950), Dallimore & Jackson (1966) and Krugman & Jenkinson (1974).

5: Principal source: Krugman & Jenkinson (1974), except for P. ayacahuite (South African Forestry Research Institute seed store), P. brutia (Strauss & Ledig 1985 syn. P. eldarica), P. roxburghii and P. wallichiana (Troup 1921)

6: SWLI = (seed mass)/(seed length + wing length) in mg/mm. Primary source: Dallimore & Jackson (1966), also Sudworth (1908), Sargeant (1921) and Loock (1950).

TABLE 5.2 The extent of cultivation and invasion of seven introduced *Pinus* species in the Jonkershoek Valley

Species	Approximate date of introduction[1]	Distance from (km), and area (ha) of, nearest planting	Relative cover (%) of self-sown pines	Dispersion of self-sown trees	Habitat
P. pinaster	1680	None[2]	50	Widespread	All
P. halepensis	1830	2km; 5 ha	20	Widespread	All
P. radiata	1865	0 (Southern 20 boundary of study area); 717 ha	20	Restricted to slopes downwind from afforestation	All
P. pinea	1750	None	8	Aggregated around original plantings near human settlements	All
P. canarienses	1878	7km; 10 ha	<1	Isolated trees widespread in study area	Streamsides and seepages
P. elliottii	1916	7km; c. 1 ha	0	None	-
P. taeda	1880	7km; c. 2 ha	0	None	-

Notes:

1: Data from Poynton (1979)

2: There is no evidence that *Pinus pinaster* has used for afforestation in the valley. However, large plantations of this species exist in the Franschhoek Valley, approximately 10 km from the study area.

The age distribution of P. pinaster trees differed between plots (Figure 5.3). In four plots (1,2,3 and 8), age distribution showed well-defined peaks, which clearly show the influence of a disturbance such as fire. For plots 1, 2 and 3 there was evidence of fire in the years with such recruitment peaks (Table 5.4). There was, however, no direct evidence of a fire in plot 8 corresponding to the recruitment peak in 1972. In some plots, recruitment peaks were less well-defined (plots 5, 7 and 9) or stands were multi-aged (plot 6; Figure 5.3). The stand in plot 6 consisted mainly of trees older than 25 years which formed a closed canopy. There was evidence of fires in 1974 and 1975 in sections of the stand (Table 5.4), but neither fire caused significant mortality or induced recruitment (cf Figure 5.3).

In the P. pinaster stands with well-defined peaks, a large proportion of the trees that survived to 1986, established within a short period. In all cases the difference in age between the first and third quartile is less than or equal to 2 years, indicating rapid recruitment following a major disturbance. In the case of plots 1, 2 and 3, at least 50 % of trees established within one year of the last recruitment peak (1974/5). In plot 8, 50 % of P. pinaster trees established within two years of the recruitment peak in 1971.

The age structures of P. halepensis trees in plots 2 and 7 suggest the influence of a major disturbance resulting in recruitment peaks during 1975/6; this is confirmed by the fire record (Table 5.4). Pinus pinea stands were multi-aged, but the stand in plot 4 showed at least two cohorts, one with a modal age of 69 years and the other of between 25 and 35 years (Figure 5.3; Table 5.4). There was no direct evidence of a fire at this site.

Only plot 2 contained enough trees of more than one species (>20) to permit a meaningful comparison of the age structures at the same site. At this site, the age structure distributions for P. halepensis and P. pinaster were very similar (Table 5.3; Figure 5.3); $Z=-0.6025$ $P = 0.5469$ in a nonparametric median test (PROC NPAR1WAY in SAS; SAS Institute Inc. 1985c). Stands of both species consist of more than one cohort, with the younger cohort comprising well over 80% of trees. For both species, over 85% of trees in the plot were 11 years old or less and became established after the last fire in 1976. The age structure histograms reveal that 15 year old P. pinaster trees survived the 1976 fire whereas the youngest P. halepensis tree to survive the same fire was 23 years old (Figure 5.3; Table 5.4).

Table 5.3. Descriptive statistics of the age structure of invasive pines in the Jonkershoek Valley, Stellenbosch. Figures in parentheses are standard deviations from the mean.

Plot	Species	Number of trees	Mean age	Median age	Mode age	Minimum age	Maximum age
1	P. pinaster	173	10.6(2.8)	10	11	7	29
2	P. halepensis	167	9.6(2.9)	9	10	6	34
	P. pinaster	41	10.8(5.4)	9	8	7	31
3	P. pinaster	140	10.3(4.0)	10	10	7	32
4	P. halepensis	2	9.0(2.8)	9	7/11	7	11
	P. pinea	40	29.4(8.3)	26.5	26	14	69
5	P. pinaster	39	16.7(8.5)	11	10	8	33
	P. pinea	8	28.9(14.0)	25.5	24	10	59
6	P. pinaster	62	31.5(6.6)	32	30	16	47
7	P. halepensis	105	11.2(3.4)	10	10	7	36
	P. pinaster	8	17.9(14.4)	24.5	8	8	41
8	P. pinaster	120	17.1(7.4)	14	14	9	47
9	P. pinaster	36	11.1(7.3)	9	9	5	40

Table 5.4. Fire histories at the nine plots selected for the study of the age structure of invasive pines in the Jonkershoek Valley (Figure 5.2). Fire histories were determined by ageing fire scars, and by reference to unpublished fire reports and aerial photographs. Discrepancies of 1-2 years between the two sources are attributed to errors in dating fire scars (McBride 1983).

Plot	Fire scars	Dates of fires (from fire reports and aerial photographs)
1	1976 (2), 1978, 1979	1955 and 1976
2	No clear fire scars but scorched bark on all old trees	1955 and 1976
3	No fire scars	1955 and 1976
4	No fire scars	No evidence of fire
5	1974 (2)	February 1975
6	1974	February 1975
7	No fire scars	No evidence of fire
8	No fire scars	December 1969
9	1967	December 1969

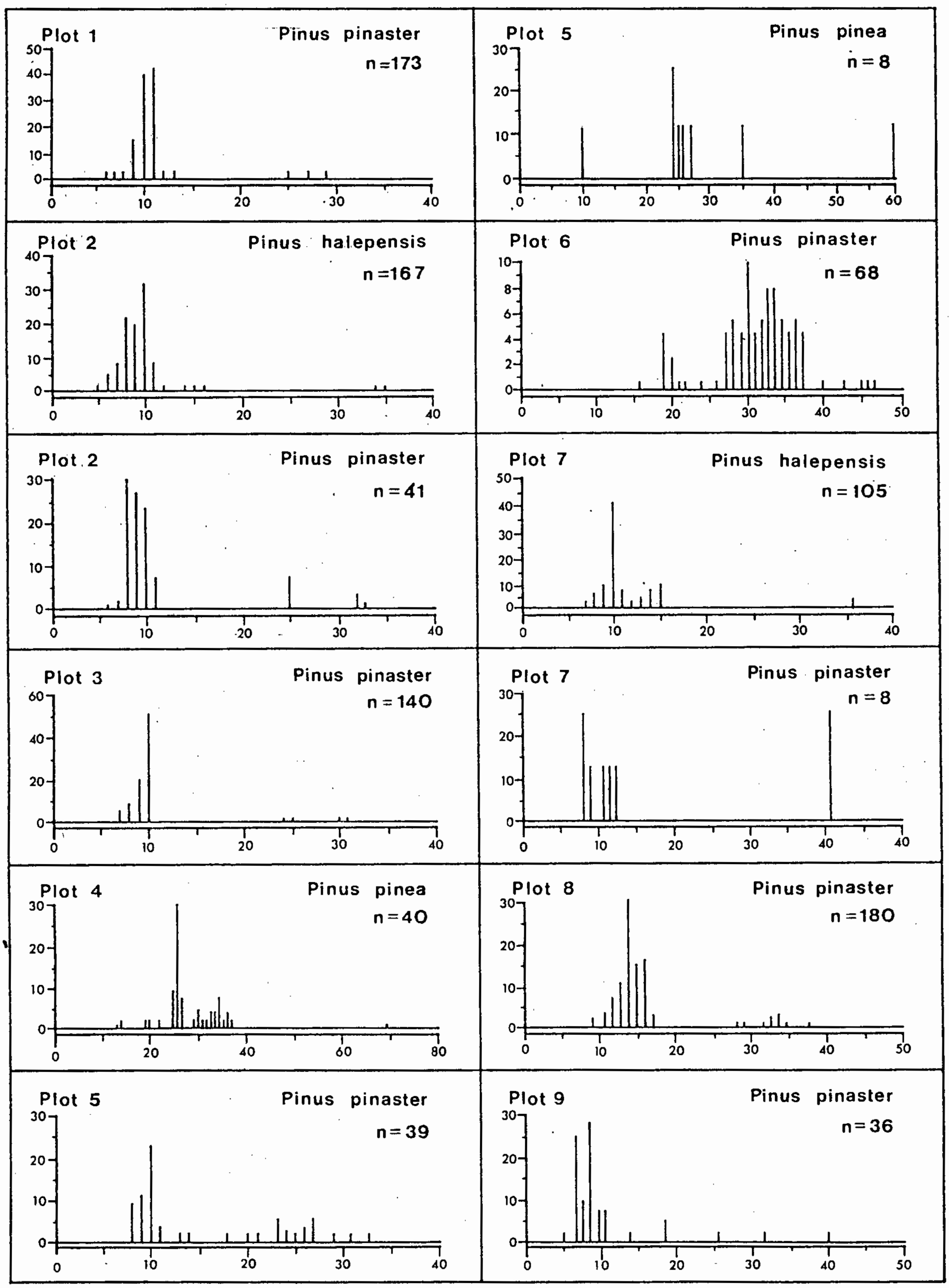

Figure 5.3. Age structure histograms for stands of invasive pines in the Jonkershoek Valley, southwestern Cape Province.

For all species on all plots (except P. pinaster on plot 7, where only 8 trees were found), the median tree age was very close to the modal tree age (Table 5.3). This is characteristic of populations that are reliant on disturbances for recruitment and where overlapping of generations is uncommon. Differences between the mean tree age and the modal tree age were smaller for P. halepensis than for the other two species. Some recruitment of P. halepensis, P. pinaster and P. pinea occurred between fires.

Table 5.5. Juvenile periods and seed attributes of seven Pinus species planted in the Jonkershoek Valley. Data for seed dimensions of P. pinaster, P. pinea and P. radiata are from Van Wilgen and Siegfried (1986).

Species	Juvenile period (years)	Seed fresh mass (mg)	Samara wing loading ($mg/100\ mm^2$)
P. canariensis	15	120.1	40.2
P. elliottii	8	21.6	17.2
P. halepensis	12	24.4	14.2
P. pinaster	6	56.8	26.8
P. pinea	15	710.2	513.8
P. radiata	8	24.4	20.5
P. taeda	7	22.2	16.5

5.5.3. Life history attributes

Juvenile periods for the seven species range from 6 to 15 years (Table 5.5). There was a positive correlation between juvenile period and seed mass (Spearman's rank $r = 0.53$) although the relationship was not significant ($P = 0.18$). Seeds of P. pinea were between six times (P. canariensis) and 33 times (P. elliottii) heavier than those of the other species. Corresponding values for samara wing loading were 13 and 36.

For the three species for which seed banks were quantified (P. halepensis, P. pinaster and P. radiata), cones of age class 2 were the youngest to contain viable seeds (Table 5.6). There was considerable variation in the size of the canopy-stored seed banks (full seeds) within species (Table 5.6), and there was no clear age-fecundity relationship. Within the age class 14 to 18 years, P. halepensis and P. radiata trees were consistently more fecund than those of P. pinaster (Table 5.6). For all species there was a significant relationship between cone age and both total and full seed numbers (Table 5.7). Pinus halepensis and P. radiata showed similar levels of serotiny; the mean number of full seeds/cone in cones of age class 4 was 29% and 28% of the mean for cones of age class 1 for the two species respectively. Cones of P. pinaster held less than 5% of full seeds for 3 years, and only 7% for two years (Table 5.7). Cone scales of P. pinaster cones open soon after maturity; more than 50% of cones in age class 2 were 100% open.

5.5.4. Life history traits related to regeneration in the genus Pinus

Reliable data on the selected life history traits were located for 60 Pinus taxa (c. 60% of the genus), covering all the adaptive modes evident in the genus (McCune 1988)(Appendix 5.1). In the ordination by correspondence analysis, the taxa are separated along axis 1 by seed mass and the seed wing loading index, and along axis 2 by the degree of serotiny, juvenile period, seed crop variability and fire tolerance (Figure 5.4). All the species planted in the Jonkershoek Valley except P. pinea lie to the right of the origin on axis 1 (i.e. they have relatively small seeds and low seed wing loading index). Pinus halepensis, P. pinaster and P. radiata are closely associated (group D) and have intermediate juvenile periods, low crop variability, poor fire tolerance and relatively strong serotiny (see Appendix 5.1). Pinus canariensis, P. elliottii and P. taeda (group C) have relatively long juvenile periods, good fire tolerance, variable seed crops and no retention of seeds in the canopy. Pinus pinea has large seeds and a high seed wing loading index and is associated with its ecological analogues, the pinyon pines (especially P. quadrifolia, P. cembroides) in group A.

5.6. DISCUSSION

In evaluating the population size/time hypothesis for introduced pines in mountain fynbos, we would argue that colonization success would depend on the

Table 5.6. Estimated number of full seeds in the canopies of three Pinus species at Jonkershoek (see text). Seeds in cones of age class 1 contain no viable seeds, and none of the sampled trees held more than 3 cohorts of cones. Numbers in parentheses are the number of cones in that age class.

Species	Tree age (years)	Seed age class 2	Seed age class 3	Seed age class 4	Total no. full seeds
P. halepensis	14	324 (4)	146 (2)	265 (5)	735 (11)
	14	133 (11)	120 (24)	2 (13)	255 (48)
	15	5773 (131)	585 (111)	- (0)	6358 (242)
	17	2788 (41)	1329 (23)	293 (26)	4410 (90)
	17	3890 (53)	1748 (38)	29 (12)	5667 (103)
P. pinaster	11	342 (4)	88 (6)	15 (1)	445 (11)
	17	87 (3)	53 (1)	75 (3)	215 (7)
	17	222 (14)	4 (5)	0 (1)	226 (20)
	18	0 (2)	2 (4)	- (0)	2 (6)
P. radiata	15	2202 (27)	937 (11)	- (0)	3139 (38)
	17	2354 (24)	1763 (13)	153 (4)	4270 (41)
	17	7469 (70)	1129 (37)	- (0)	8598 (10)
	18	1979 (21)	634 (10)	- (0)	2613 (31)

Table 5.7. The number of seeds in cones of different age classes of three Pinus species at Jonkershoek. The upper row for each species gives the mean total number of seeds per cone (including empty seeds) in the different age classes. The lower row gives the average number of full seeds (see text). Note that cones in age class 1 contain no viable seeds. Means for the same seed category with the same superscript letter for each species do not differ significantly (Student-Newman-Keuls test; P < 0.05). The numbers in parentheses are the sample sizes. The numbers in square brackets indicate the level of significance in the general linear model relating the number of full seeds per cone to age class for each species (SAS Institute Inc. 1985c).

	Cone age class			
Species :	**1**	**2**	**3**	**4**
P. halepensis	105.52 ^{a}	82.90 ^{a}	52.46 ^{a}	29.06 ^{a}
[0.0045]	39.33 ^{a}	44.72 ^{a}	28.36 ^{a}	11.26 ^{a}
	(21)	(39)	(84)	(31)
P. pinaster	152.50 ^{a}	34.53 ^{b}	10.53 ^{b}	8.00 ^{b}
[0.0001]	123.33 ^{a}	28.84 ^{b}	8.80 ^{b}	5.80 ^{b}
	(6)	(19)	(15)	(5)
P. radiata	108.63 ^{a}	100.40 ^{a}	94.50 ^{a}	43.75 ^{b}
[0.0001]	91.74 ^{a}	78.17 ^{a}	76.78 ^{a}	25.38 ^{b}
	(12)	(94)	(55)	(8)

extent of cultivation (and other forms of intentional dispersal leading to increased population sizes) and residency time in the area. Alternatively, colonization potential would be determined by life histories that would permit proliferation in the mountain fynbos environment which is characterized by high-intensity fires at intervals of 10 to 20 years. Below, we evaluate these hypotheses for the seven Pinus species at Jonkershoek.

In terms of the population size/time hypothesis, we would expect Pinus pinaster to have invaded the greatest area at Jonkershoek, and indeed this was the case (Table 5.2). However, despite the long residency of P. pinea in the study area, it has only invaded on a limited scale. Pinus halepensis and P. radiata have similar residency times but only the latter is used for extensive afforestation. Despite this, the total areas invaded by the two species are similar although P. radiata individuals are confined to regions immediately downwind of plantations. As predicted by this hypothesis, the remaining species have not invaded the study area to any extent.

What life history traits should a pine have in order to invade mountain fynbos? Firstly, a successful invader would have a juvenile period of less than about eight years in order to ensure adequate seed production between fires (see Kruger & Bigalke 1984). Species which produce large seed crops should be more invasive than species with a low reproductive output. Relative to spontaneous seed release, serotiny (canopy storage of overlapping seed crops) maximizes seed available for the next generation, provided fires occur at intervals less than the life span of the Pinus species (Lamont et al., in press). Since mountain fynbos fires occur at intervals far less than the potential life spans of all the introduced pines, serotiny must be seen as a trait enhancing the invasiveness of these species. High seed dispersibility would enhance colonization and hence invasive success (Van Wilgen & Siegfried 1986; Richardson et al. 1987). Finally, for those species without complete serotiny, the ability to establish and reach reproductive maturity between fires would also promote invasibility.

In terms of these life history traits, we would expect P. radiata to be the most invasive species. This is because it has a short juvenile period (Table 5.5), the highest fecundity (Table 5.6), is the most serotinous (Table 5.7), has highly dispersible seeds (Table 5.5) and is capable of inter-fire recruitment (Richardson & Brown 1986). The age structure in P. pinaster stands (Figure 5.3) is similar to that in self-sown stands of P. radiata (Richardson & Brown 1986), but the former species should be a less aggressive invader since it has lower seed production (Table 5.6) and is only weakly serotinous (Table 5.7). However, its shorter juvenile period (6 vs 8 years) would make it more resilient to shorter fire rotations. Pinus halepensis also has traits similar to P. radiata except that the former species reaches maturity only after 14 years, compared to the 8 years of P. radiata. These two species show approximately equal fecundities (Table 5.6), canopy seed retention (Table 5.7) and seed dimensions (Table 5.5). Pinus pinea has a relatively long juvenile period and very large seeds that are released at maturity and are poorly dispersed by wind. For all three attributes, this species is markedly different to the other invasive pines. The fact that P. pinea has invaded at all suggests that at least the first two attributes have been reasonably successful. The large seeds of P. pinea are dispersed in the study area by the introduced squirrel Sciurus carolinensis (Millar 1980). It is likely that this species would have failed to invade mountain fynbos had it not been for the establishment of this opportunistic mutualism.

Both the "population size/time" and the life history explanations contribute to the relative success of the introduced pines as invaders in mountain fynbos. Pinus halepensis, P. pinaster and P. radiata all have life histories compatible with invasive success in fynbos as they have all evolved in environments with similar selective forces (i.e. mediterranean-type climate, nutrient-poor soils and regular fires). These species all show invasive tendencies on other continents. Pinus halepensis is a weedy species in its natural range e.g. in southern France where it invades abandoned fields (Acherar et al. 1984) and in Israel, where it readily invades exposed and nutrient-poor sites and is considered to be a "a pioneer plant with low ecological requirements and broad tolerances" (Naveh 1973). It also invades rangelands on South Island, New Zealand (Sykes 1981; Hunter & Douglas 1984). Paleobotanical sources also point to the weediness of this species which became prominent in the Mediterranean Region only in the late Holocene as a result of colonization of anthropogenically disturbed sites (Huntley & Birks 1983; Delcourt & Delcourt 1987). Pinus pinaster also colonized most of its contemporary range following human disturbance (Huntley & Birks 1983; Delcourt & Delcourt 1987) and has invaded rangelands adjacent to plantations on South Island, New Zealand (Sykes 1981; Hunter & Douglas 1984) and Chile (C. Gonzalez, pers. comm. 1986). Although the natural range of P. radiata covers only 8400 ha, Forde (1966) mentions the ability of P. radiata to colonize abandoned agricultural land and take advantage of disturbances in California. This characteristic has enabled P. radiata to invade a variety of habitats in all regions where it has been planted e.g. in Chile (C. Donoso, E. Fuentes, C. Gonzalez and T.T. Veblen, in litt. 1988), the Bariloche area of Argentina (T.T. Veblen in litt. 1988), Australia (Dawson et al. 1979; Burdon & Chilvers 1974; Chilvers & Burdon 1979) and New Zealand (Sykes 1981; Hunter & Douglas 1984; Wills & Begg 1986).

The three species mentioned above are all well adapted for both rapid migration and explosive population increases. We ascribe the greater success of P. pinaster , relative to P. halepensis and P. radiata, to its longer residency time (Table 5.1) and extent of cultivation. Pinus halepensis has achieved significant importance as a weed in mountain fynbos (Macdonald & Jarman 1984; Richardson 1988), despite its insignificance as a commercial forestry tree (Poynton 1979a). This species was observed to be spreading in the Caledon district as early as 1855, only 25 years after its introduction (Lister 1959:63). Pinus radiata has only recently succeeded P. pinaster as the major forestry tree in the Western Cape and we predict that this species will increase in importance as a weed.

As for the other pines of the Mediterranean Basin, there is evidence that P. pinea became prominent in the region only in the late Holocene, probably as a result of colonization of anthropogenically disturbed sites (Huntley & Birks 1983; Delcourt & Delcourt 1987). This species has escaped from cultivation on the Canterbury Plains, New Zealand (Sykes 1981). Pinus pinea has a long residency time in the Cape but massive invasion and spread appear to be severely hampered by life history constraints, especially its large seeds that require dispersal by animals. The establishment of a new mutualism between this species and the introduced squirrel has permitted limited invasion. Self-sown stands of P. pinea are always aggregated close to stands of another introduced tree Quercus robur, which is the principal source of food for the squirrels (Millar 1980), but which does not invade mountain fynbos (D.M. Richardson pers. obs.).

Pine invasions have resulted in severe disruption of natural ecological processes in mountain fynbos and control operations aimed at eliminating pines from natural communities are expensive. For this reason it is important to be able to predict which other species would invade if introduced and used for afforestation. Can the life history hypothesis be developed and generalized to allow predictions to be made on which other Pinus species would succeed as invaders if introduced and cultivated ? The genus may be divided into five ecological groups based on the ordination of six life history attributes (Figure 5.4; Appendix 5.1). The species that have achieved significant spread in mountain fynbos, P. halepensis, P. pinaster and P. radiata, are closely associated (group D) in terms of seed crop variability, seed mass, degree of serotiny, dispersal features and fire tolerance. Our groups D and E correspond to McCune's (1988) "fire-resilient" group for North American pines; the two groups are separated mainly by more intense serotiny in group E. These "fire-resilient" pines have a high potential for colonization and explosive reproduction in fire-prone environments (Yeaton 1978; McCune 1988) and we suggest that species in these groups are the most likely potential invaders of mountain fynbos. Several species in groups D and E that have not yet achieved weed status in mountain fynbos have already been introduced to the Cape. Some of these species (e.g. P. patula) have failed in experimental plantings due to unpredictable interactions with local biota, whereas other species (e.g. P. serotina) have shown considerable potential (Table 5.8). Most of these species have short residency times and small populations in the Western Cape, and we predict increased levels of invasion as these increase.

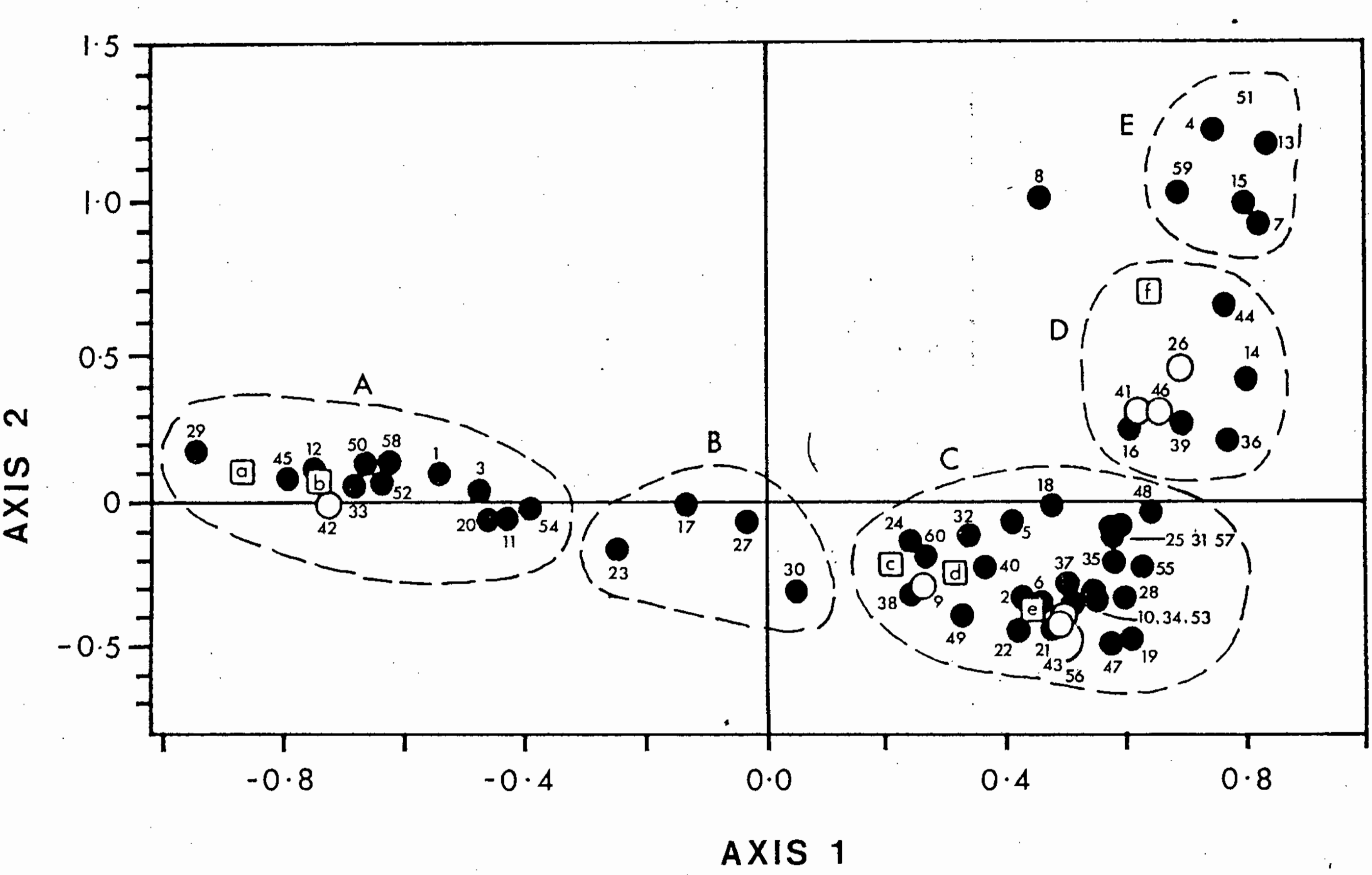

Figure 5.4. Plot of the first two axes from a correspondence analysis of a matrix of life history attributes of 60 Pinus taxa. Axes 1 and 2 account for 57% and 20% of the inertia respectively. Hollow dots indicate the positions of the seven Pinus species planted at Jonkershoek (see text). Other taxa are indicated by solid dots. Numbers correspond to taxa in Appendix 5.1. Life history attributes (blocks) are: a=seed wing loading index; b=seed mass; c=age at maturity; d=seed crop variability; e=fire-tolerance index; f=degree of serotiny.

In general, "fire-resilient" pines introduced from mediterranean-climate regions such as California (P. radiata) and the Mediterranean Basin (P. halepensis, P. pinaster) have been most successful both as forestry trees and as invaders. We conclude that introductions of new taxa from these regions are most likely to yield new invaders. Many taxa in group C (Figure 5.4) display "weedy" characteristics in other parts of the world (Richardson & Bond, submitted), but most of these species are unsuited to the mountain fynbos environment and are unlikely to become important invaders.

Table 5.8. The extent of cultivation, performance and potential invasiveness of fire-resilient Pinus species (groups D and E in Figure 5.4) that have not yet achieved weed status in mountain fynbos.

Species	Ecological group (Figure 5.4)	Extent of cultivation in Western Cape [1]	Index of planting success [2]	Potential invasiveness [3]
P. attenuata	E	1	1	1
P. banksiana	E	1	1	1 [4]
P. brutia	E	1	2	2
P. clausa	E	1 [5]	1	1
P. contorta var. latifolia	E	0	-	2
P. serotina	E	2 [6]	2	2
P. virginiana	E	0 [7]	-	1
P. contorta var. contorta	D	0/1	-	2
P. contorta var. murrayana	D	0/1	-	1
P. muricata	D	1	2/3	2
P. patula	D	1	0	0 [8]
P. pungens	D	0	-	1

Notes:

1: 0=not introduced to Western Cape; 1=experimental plantings only; 2=small areas afforested (e.g. woodlots, windbreaks); 3=limited commercial afforestation; 4=major commercial afforestation (Data from Poynton 1979a)

2: Index of success as a commercial forestry species in the Western Cape: 0=total failure; 1=survival but no commercial potential; 2=limited commercial potential; 3=good commercial potential (Data from Poynton 1979a)

3: The index of potential as a weed was derived from assessments of experimental plantings and the potential importance of the species as a commercial plantation tree (data from Poynton 1979a): 0=negligible; 1=moderate; 2=good; 3=outstanding

4: P. banksiana is "so lacking in vigour under local conditions (in southern Africa) as to be of no practical value" (Poynton 1979a).

5: P. clausa was only introduced to South Africa in 1969 (Poynton 1979a).

6: P. serotina was only introduced to South Africa in 1958 (Poynton 1979a).

7: P. virginiana was only introduced to South Africa in 1958 (Poynton 1979a).

8: P. patula is "not well adapted to the uniform and winter rainfall areas" (Poynton 1979a).

Appendix 5.1. Selected life history attributes of 60 Pinus taxa. See Table 5.2 for details of attributes. Ecological groups are shown in Figure 5.4.

	Pinus Species	Age at maturity (yrs)	Fire tolerance index	Seed crop variability	Degree of serotiny	Seed mass (mg)	Seed wing loading index	Ecological group
1	albicaulis	20	0	4.0	1.0	174.0	165.1	A
2	aristata	20	1	5.5	1.0	25.0	13.9	C
3	armandii	20	0	5.0	1.0	283.0	117.3	A
4	attenuata	5	0	1.0	3.0	18.0	4.7	E
5	ayacahuite	5	1	1.5	1.0	40.0	8.6	C
6	balfouriana	20	1	5.5	1.0	27.0	8.0	C
7	banksiana	3	0	3.5	2.5	3.0	1.8	E
8	brutia	7	0	1.0	3.0	49.9	16.7	-
9	canariensis	15	2	3.5	1.0	108.0	21.3	C
10	caribaea	12	1	5.5	1.0	15.0	2.6	C
11	cembra	20	1	4.5	1.0	227.0	178.7	A
12	cembroides	15	0	6.5	1.0	412.0	259.5	A
13	clausa	5	0	1.5	3.0	6.0	2.4	E
14	contorta var. contorta	4	1	1.0	2.0	3.0	2.1	D
15	contorta var. latifolia	5	0	2.5	2.5	5.0	3.4	E
16	contorta var. murrayana	6	0	2.5	1.0	3.9	2.5	D
17	coulteri	8	2	4.5	2.0	324.0	68.2	B
18	densiflora	20	0	2.0	1.0	9.0	4.0	C
19	echinata	5	2	6.5	1.0	10.0	5.7	C
20	edulis	25	1	3.5	1.0	300.0	161.8	A
21	elliottii	8	2	3.0	1.0	34.0	11.4	C
22	engelmanii	28	2	3.5	1.0	45.0	13.3	C
23	flexilis	20	2	3.0	1.0	180.0	142.7	B
24	gerardiana	28	0	3.5	1.0	45.0	19.7	C
25	glabra	10	1	1.0	1.0	10.0	4.8	C
26	halepensis	15	1	1.0	3.0	16.0	5.0	D
27	jeffreyi	8	1	3.0	1.0	123.0	41.7	B
28	kesiya	5	2	1.0	1.0	17.0	8.0	C
29	koraiensis	15	0	4.0	1.0	553.0	345.6	A
30	lambertiana	40	2	4.0	1.0	216.0	48.5	B

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Appendix 5.1. (continued) Selected life history attributes of 60 Pinus taxa. See Table 5.2 for details of attributes. Ecological groups are shown in Figure 5.4.

	Pinus Species	Age at maturity (yrs)	Fire toler-ance index	Seed crop varia-bility	Degree of serotiny	Seed mass (mg)	Seed wing loading index	Ecol-ogical group
31	leiophylla	28	1	3.5	2.0	11.0	5.3	C
32	merkusii	10	1	1.5	1.0	42.0	15.0	C
33	monophylla	20	1	1.5	1.0	378.0	212.6	A
34	monticola	10	1	5.0	1.0	17.0	3.9	C
35	mugo	15	1	1.0	1.0	7.0	4.0	C
36	muricata	5	2	2.5	3.0	10.0	3.5	D
37	nigra	15	1	3.5	1.0	17.0	7.6	C
38	palustris	20	1	6.0	1.0	93.0	18.3	C
39	patula	10	1	1.0	2.0	9.0	4.3	D
40	peuce	12	1	3.5	1.0	41.0	15.5	C
41	pinaster	6	2	1.0	2.5	45.0	11.2	D
42	pinea	15	2	6.0	1.0	256.0	340.2	A
43	ponderosa	15	2	3.5	1.0	38.0	10.7	C
44	pungens	5	1	1.0	3.0	14.0	5.1	D
45	quadrifolia	15	1	3.0	1.0	472.0	295.0	A
46	radiata	5	2	1.0	3.0	34.0	10.7	D
47	resinosa	20	2	5.0	1.0	9.0	4.5	C
48	rigida	8	1	6.5	2.0	10.2	4.0	C
49	roxhurghii	25	2	4.5	1.0	81.0	22.5	C
50	sabiniana	10	2	3.0	2.0	282.0	216.8	A
51	serotina	4	0	1.0	3.0	8.0	2.8	E
52	sibirica	25	0	5.5	1.0	252.0	261.1	A
53	strobiformis	15	1	3.5	1.0	225.0	127.5	C
54	strobus	5	1	6.5	1.0	17.0	5.4	A
55	sylvestris	5	1	3.5	1.0	6.0	3.6	C
56	taeda	5	1	8.0	1.0	25.0	7.9	C
57	thunbergiana	6	1	1.0	1.0	13.0	5.1	C
58	torreyana	12	2	1.0	2.0	674.0	189.5	A
59	virginiana	5	0	1.0	2.0	9.0	6.1	E
60	wallichiana	15	1	2.5	1.0	60.0	18.9	C

PART III

THE DETERMINANTS OF INVASIBILITY

CHAPTER 6

DETERMINANTS OF PLANT DISTRIBUTION : EVIDENCE FROM PINE INVASIONS

CHAPTER 6: DETERMINANTS OF PLANT DISTRIBUTION: EVIDENCE FROM PINE INVASIONS [1]

6.1. ABSTRACT

The question of what limits the occurrence of a plant species to a particular site was addressed by considering 53 instances where the distribution of pines (Pinus species; Pinaceae) has changed in the last century. We considered both expansions of pines in and adjacent to their natural ranges and spread from sites of introduction well outside the contemporary range of pines. We first considered the null model (with respect to climate or biological interactions as determinants of invasion) i.e. that invasion requires simply that a species is present in sufficient numbers, with sufficient propagules over sufficient time to invade. We then explored the relative importance of climatic changes, disturbance, competition (including competition between seedlings and herbaceous plants during early establishment), herbivory, pathogens and other agents that might influence membership of communities by pines.

Determinants of invasibility often interact in a complex fashion but the following generalizations apply: i) Pine invasions are most prevalent where there is limited competition in the regeneration niche; ii) Invasions occur more easily where the dominant growth form in the target habitat is most different to that of pines viz. in grasslands; iii) The disturbance regime in the receiving habitats is important and interacts directly and indirectly with the "inherent invasibility" to determine the outcome of an introduction; iv) life history attributes such as seed size influence the effect of biotic and abiotic factors on invasibility; v) Contemporary practices such as deforestation and increased grazing pressure and those leading to accelerated erosion, modified fire regimes and climate amelioration essentially duplicate ice-age stresses and disturbances that shaped plant communities in the Holocene. The fundamental role of biotic factors (either direct or indirect) in regulating the distribution of pines is discussed with reference to aspects of land husbandry including the management of biological invasions.

6.2. INTRODUCTION

Studies of existing plant community patterns provide relatively weak correlative evidence for the agents that control plant distribution. Field and greenhouse experiments are a valuable adjunct to studies of pattern but seldom tell us whether a factor such as competition is sufficiently intensive and extensive to account for observed distributions. Studies of changes in distribution patterns provide a largely neglected source of evidence for determinants of community structure (but see Mack 1985 for plants and Moulton & Pimm 1986a, 1986b for birds). Here we address the question of what limits the occurrence of a species to a particular site by considering what kinds of events lead to a change in distribution.

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Plant invasions offer several advantages for studying the nature of ecological limits. Firstly, they usually occur over large areas, far larger than the typical field experiment. Secondly, "transplant" experiments are common in some groups, such as conifers, and have been made on a very large scale. Where invasive species have been exposed to a completely novel biota, one can determine whether the absence of a co-adapted fauna and flora significantly alters the "rules" governing invasion. Thirdly, invasions are often well documented, especially where the invading species are economically significant.

Invasions are particularly useful for studying determinants of tree distribution. Trees, because of their long lifespans, are the least well studied with respect to the causes underlying population ranges with the least recourse to field experiments and the heaviest dependence on inference from pattern analysis (e.g. Yeaton 1983; Hubbell & Foster 1986). We focus only on range expansions since the study of retreats is complicated by the time lags inherent in plants with long life spans. For example, trees may persist long after conditions suitable for establishment of their seedlings have changed (Wright 1968; LaMarche 1973; Ford 1982 p. 149; Davis 1986).

We surveyed a large number of studies of invasions to answer the general question: what determines the distributional limits of plants? By analyzing those cases where the distribution limits change, one should get an indication of the sensitivity of different factors that determine species presence. To simplify our task we have considered the dynamics of invasion only in a closely related group of plants, the genus _Pinus_ [1], which share a similar growth form. Trees in general and pines in particular are conspicuous, and are therefore well-studied invaders.

We first consider a neutral model (with respect to climate or biological interactions as determinants of invasion) i.e. that invasion requires simply that a species is present in sufficient numbers, with sufficient propagules over sufficient time to invade (Salisbury 1961; Baker 1986; Kruger _et al_. 1986). We then explore the relative importance of climate, disturbance, competition (including competition between seedlings and herbaceous plants

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[1] Nomenclature for the genus _Pinus_ follows Duffield (1952).

during early establishment), herbivory, pathogens and other agents that might influence the boundaries of pine populations. Disturbance has long been cited as a major "cause" of invasions but the term conceals a number of distinct effects (Mooney & Godron 1983; Crawley 1986; Orians 1986). We attempt to separate direct effects of disturbance on pines related to life history attributes from indirect effects on other species, especially potential competitors, which may interact with pines.

The rate at which a population spreads clearly depends on biogeographic factors such as the availability of propagules and the rate of propagule immigration (Crawley 1987a). In this study, however, we are concerned primarily with the processes that occur after the immigration of propagules. We do not address in detail the question of what life history attributes of pines make them good invaders (but see Govindaraju 1984; Straus & Ledig 1985; McCune 1988).

6.2.1. Characteristics of Pinus

The genus Pinus consists of about 105 species with a great ecological diversity (e.g. Yeaton 1978; McCune 1988) that occupy a wide range of habitats, from the arid plateaus of western North America to the tropical lowlands of the Caribbean (Mirov 1967). Some species have played major pioneering roles in revegetating the deglaciated continents of the Northern Hemisphere in the past 10000 years (e.g. Huntley & Birks 1983; Critchfield 1985; Delcourt & Delcourt 1987). The mechanisms that have enabled these pines to expand their ranges, colonizing a variety of habitats, persist in the taxa today and the distributions of many species appear to be unstable, expanding and contracting with changing environmental conditions (Mirov 1967; Vale 1982; Huntley & Birks 1983; Betancourt 1987; Delcourt & Delcourt 1987). The present distribution of pines (Critchfield & Little 1966), together with recent reconstructions of invasions (migrations) of different taxa since the late Holocene (e.g. Davis 1981; Huntley & Birks 1983; Delcourt & Delcourt 1987) provide many clues on the relative invasibility of different habitats (Neilson 1987).

Pines generally occupy marginal habitats. Although they are capable of vigorous growth in more favourable situations, they are thought to be excluded from these because their seedlings are light demanding and are usually suppressed by more vigorous species (Huntley & Birks 1983; Delcourt & Delcourt 1987). In many parts of the world, pines have increased their ranges since colonization by man. For example, the late-Holocene "pine-rise" in Europe, particularly in Spain, southern France and Greece has been attributed to invasion of man-disturbed habitats (Huntley & Birks 1983; Delcourt & Delcourt 1987). In some regions, modern range expansions by pines cause major problems, such as suppression of pasture grasses (e.g Dwyer & Pieper 1967; Aro 1971; Clary 1971; Gartner & Thompson 1973; Barney & Frischknecht 1974; DeBenedetti & Parsons 1976; Severson 1986; Everett 1987). Thus, despite the widespread fragmentation of large pine forests in the last few hundred years by land clearance and the introduction of pathogens, pines continue to dominate landscapes in many parts of the Northern Hemisphere (Mirov 1967).

Because of the widespread dominance of pines and the economic importance of many species, pine dynamics (including invasions) have been well studied in many parts of the world (e.g. McQuilken 1940; Bormann 1953; Kowal 1966; Heath 1967; Blackburn & Tueller 1970; Naveh 1973; Spring et al. 1974; Dunwiddie 1977; Vale 1977, 1978; Vankat & Major 1978; Turnbull et al. 1980; Vale 1981a; Acherar et al. 1984; Butler 1986; Ming 1987; Yeaton et al. 1987). In addition, there are many "transplant experiments" in the form of commercial plantations both near natural distribution ranges and completely outside the natural range of pines. In many cases the introduced pines have invaded natural communities in the new habitat, sometimes becoming vigorous and dominant constituents of the local flora. A few of these invasions have been documented (Bannister 1965; Burdon & Chilvers 1974; Sanson 1978; Dawson et al. 1979; Chilvers & Burdon 1983; Hunter & Douglas 1984; Shimizu & Tabata 1985; Richardson & Brown 1986). This allows us to explore the question of whether invasibility is inversely associated with the degree to which a biota is "co-adapted". Pines provide the added interest of being conifers, so that observation of the conditions under which they expand may provide information on the continuing mystery of gymnosperm persistence in a world dominated by angiosperms (Regal 1977; Bond 1989).

6.3. METHODS

To obtain a sample of cases where pine invasions have been studied in different parts of the world, we made a thorough search of the ecological and forestry literature for studies of the dynamics of pine forests. A computer search was made in January 1988 using the "BIOSIS Previews Database" which contains all papers summarized in Biological Abstracts since 1969. In addition, we scrutinized numerous technical and popular books on ecology, forestry, geography and range management, and the following journals: American Naturalist, Botanical Review, Ecology, Ecological Abstracts, Ecological Monographs, Forestry Abstracts, Great Basin Naturalist, Journal of Biogeography, Journal of Ecology, Journal of Forestry, Journal of Range Management, New Phytologist, Oecologia, Quaternary Research, Tall Timbers Fire Ecology Conference Proceedings and Vegetatio. Correspondence and personal communication with authorities from all parts of the world (see Acknowledgments) and our own observations yielded additional information.

A number of criteria were used in the selection of cases for inclusion in the analysis. Firstly, we selected only those papers that described either a shift of the forest boundary (i.e. invasion of adjacent communities) or a marked increase in the density of pines in communities that were previously dominated by other taxa. Secondly, we excluded those papers that either contained no attempt to explain the invasion, or presented insufficient information to allow us to assess the role of the various factors. For example, Spring et al. (1974) provide a detailed account of the population ecology of Pinus taeda invading old fields in South Carolina, USA, but make no attempt to explain the invasion other than quoting a series of hypotheses. Some papers presented accounts of invasion by more than one species. In such cases, the invasion by each species was considered separately. Where more than one study has addressed the invasion of a species at one locality, the studies were considered together. In some parts of the world (e.g. Eastern and Western U.S.A.) there have been numerous studies of pine invasions, and we selected only a representative sample for analysis (generally the most recent studies because these usually cite earlier work). Far fewer studies have been carried out in other parts of the world, and many of these give incomplete accounts.

For each of the selected studies of pine invasion, we noted:
1) the locality (degrees latitude);
2) altitude (m. above mean sea level);
3) the type of vegetation invaded:
   a) bare soil (including surfaces exposed by volcanic activity, landslides etc, and heavily eroded slopes);

b) disturbed sites (vegetation type not specified);

c) old fields (abandoned cultivated fields including areas remaining after shifting cultivation);

d) grassland

e) mixed brush and grass (including open scrubland are prairie);

f) shrubland;

g) forest;

4) the level and type of disturbance that initiated or halted invasion (both natural disturbances such as climatic changes, volcanic eruptions, landslides and fire, and man-induced disturbances or alterations to local disturbance regimes e.g. land clearing, shifting cultivation, fire suppression, increased fire frequency, changes in grazing pressure etc);

5) any interactions with local or introduced biota other than man (e.g. dispersal, predation, herbivory, disease etc).

To establish the relationship between the magnitude of competition in the regeneration niche and the invasibility of communities, we studied the literature on the requirements for site preparation in commercial forestry in the Southern Hemisphere.

6.4. RESULTS AND DISCUSSION

Of the 53 cases of pine invasions that were selected, 40 were from the Northern Hemisphere and 31 were located in North America (see Appendix 6.1.). In the Southern Hemisphere, the only studies that contained sufficient information were those from Australia, New Zealand and South Africa. Data from various sources were collated to suggest likely causes of colonization behaviour in Chile ([47][1]). The selected studies represent invasions of 23 species (c. 22% of the genus) and include typical fugitive species (subgenus Diploxylon; Duffield 1952) with small seeds and short juvenile periods (e.g. P. banksiana and P. contorta) and species usually associated with later seral stages i.e. species of the subgenus Haploxylon (Duffield 1952) with large seeds and longer juvenile periods such as P. edulis, P. monophylla, P. lambertiana and P. pinea.

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[1] Numbers in square brackets refer to the studies cited in Appendix 6.1.

6.4.1. Invasions - the neutral model

The simplest model for predicting range extension (invasion) requires only that a species is present in sufficient numbers, with sufficient propagules and over sufficient time to invade. Taken to extremes, this model suggests that all species will invade new communities and that biotic and abiotic stresses can be ignored when formulating predictions of invasion. Though early studies suggested that population sizes as small as 20 individuals were adequate to avoid a random walk to extinction (e.g. Mc Arthur & Wilson 1967), more recent studies suggest that the minimum population size needed to persist and therefore invade an area depends strongly on the environmental variance in population growth rates (Goodman 1987; Roughgarden 1986). In terms of pines for example, high year to year variation in conditions suitable for seedlings would reduce the likelihood of range extension.

Because pines have been widely used for afforestation in the southern hemisphere where they do not naturally occur, invasiveness in these areas can be related to the areal extent of plantations (ie the size of founder populations) and to the time of introduction of a species into a region (Macdonald 1984; Kruger *et al*. 1986; Richardson & Brown 1986). Available evidence is difficult to compile but appears to support the null model, at least in southern Africa, since the *Pinus* species showing the greatest extent of invasion are those species with the widest cultivation and the greatest extent of dissemination by man (e.g. Kruger *et al*. 1986; Richardson & Brown 1986). Long "residency" is also associated with the area invaded (Kruger *et al*. 1986) though there are some striking exceptions. *Pinus pinea*, for example, was one of the first pines introduced to the Cape (Shaughnessy 1980) but, with its dependence on nut-hoarding dispersers, has hardly spread from long-established plantings (Kruger *et al*. 1986).

6.4.2. Abiotic causes of pine invasions

6.4.2.1. Climate

Climate and soils have traditionally been thought to be the primary controls on plant distribution and the main determinants of vegetation types of the world (e.g. Woodward 1987). It follows that changes in climate should lead to changes in plant distribution. This assumption underlies most paleoecological studies. For example the northward expansion of pines in Europe during the late-glacial has been attributed to climatic amelioration (Huntley & Birks 1983).

Some (but not all) modern pine invasions have also been attributed directly or indirectly to climatic change. Nearly a quarter of our studies cite climatic change as a possible factor in pine invasion ([4], [5], [8], [14], [30], [3], [44]). The most intensively studied examples are fluctuations in tree lines. There is evidence of broadly synchronous tree-line advances and retreats during the past several thousand years at many places in the northern hemisphere (references in La Marche 1973, Tranquillini 1979). These correlate closely with changes in temperature (La Marche 1973). Expansion of pinyon pines into arid areas has also been linked to climatic change. The range of <u>P. edulis</u> and <u>P. monophylla</u> spread in western North America coinciding with increased temperature and rainfall between 1850 and 1940 (West <u>et al</u>. 1975).

Climate fluctuations may also influence regeneration and invasion at a local scale. Invasion of <u>P. radiata</u> into eucalypt forests in Australia ceased during a prolonged drought (Chilvers & Burdon 1983, p.243) while invasion of subalpine meadows in Yosemite National Park was found to coincide with dry conditions ([3]).

Though invasions may correlate with climatic change the causes of the invasions are often obscure. Does climate act directly on the distribution of a plant species or indirectly through some biological agent such as a pathogen or competitor ? If the latter, then a change in the biota could alter the magnitude and direction of the climatic response. There are few examples of direct effects of climate on changes in pine distribution. Again tree lines provide the best examples. Low temperatures and short growing seasons directly prevent reproduction at timber line (e.g. Tranquillini 1979). Climate has also been invoked as a reason for the failure of <u>P. caribaea</u> to invade subtropical areas of southern Africa though it grows well in plantations (Kruger <u>et al</u>. 1986). The species fails to reproduce adequately in the light and temperature conditions prevailing in the local climate (Poynton 1979a). Curiously, the "primitive" wind pollination system of pines does not seem to be strongly influenced by climate and there are no reports of seed crop failures due to pollination occurring under inappropriate weather conditions.

In one study, pine invasion into subalpine meadows in Yosemite National Park occurred under dry conditions ([3]). The invasion was attributed to the failure of free-flowing water during snow-melt to wash away pine seeds falling in the meadow before they germinated [3].

In most cases, invasions correlating with climatic fluctuation are thought to be caused by climate acting indirectly on biological interactions. For example, a frequently-cited hypothesis for invasion of mesic montane grasslands is that invasion is limited by the relative vigour of tree seedlings versus the meadow vegetation. During dry periods, for example, meadow grasses may be reduced in vigour and at these times tree seedlings experience less competition and therefore enjoy enhanced survival. The evidence for this is tenuous although invasion in subalpine meadows is sometimes more marked on dry sites than on wet ones (e.g. [4], [8]). In more arid environments the converse may apply with invasion linked to wet periods when the tree seedlings have a longer growing season. In grassland and mixed grass and brush in East Central Nevada, pines invade the densest grass swards only in wet years ([32]). Similarly, McKee and Knutson (1987) report the episodic establishment of _P. ponderosa_ seedlings in a disjunct stand only during moist periods.

Climate may also influence pathogen activity thereby limiting distributions. Kruger _et al_. (1986) suggest that _Pinus radiata_ is prevented from spreading into the northern parts of South Africa by hailstorms. Hail damage provides entry points for the needle disease, _Sphaeropsis sapinea_. _P. radiata_ is invasive in the southern and south-western parts of the continent where hailstorms are rare.

6.4.2.2. _Physical disturbance_

Invasions are usually preceded by disturbance (Elton 1958; Fox & Fox 1986). Some form of change to the historical disturbance regime is implicated in all of the studies of pine invasions. In 53% of the 54 studies, fire _per se_ was cited as a disturbance in the invaded habitat. In fynbos shrublands in South Africa, fire appears to be the only disturbance required to initiate pine invasions ([19], [37], [38], [44]). Fire stimulates the release of seeds from serotinous cones, and provides suitable conditions for seedling establishment and growth. In 12 of the studies (23%) fire <u>suppression</u> was noted explicitly as a factor that contributed to invasion. This factor was most important in grassland ([4], [5], [9], [41], [49], [52]) and in mixed brush and grass ([31], [32], [40]) at high latitudes (36^o to 44^o) and high altitudes (usually above 2000 m). Fire was only invoked as an explanation for invasion in areas adjacent to natural ranges in North America, where the dictum of absolute protection from fire has probably had the most marked effect on plant communities (e.g. Vale 1982).

Other physical disturbances that were found to influence the invasibility of communities were natural events such as volcanic eruptions ([10], [19], [24], [25], [31]) and flooding ([3]), and a variety of man-induced disturbances such as logging and fuel wood cutting ([11], [18], [21], [22], [25], [26], [37], [45], [49], [50], [51], [53]) and mining or construction activities ([39]. Frequently, a number of natural or man-induced disturbances have acted in concert to initiate invasions by stimulating seed release, creating suitable conditions for seedling growth, and by eliminating dominant and vigorous plants that would compete with pine seedlings for resources.

6.4.2.2.1. How does disturbance influence invasion?

Two major effects of disturbance may be distinguished. First, disturbance may interact with the life history of an organism to exclude it or make its presence possible. Noble & Slatyer (1980) have classified those attributes of organisms most sensitive to disturbance frequency. These include the means of surviving disturbance, age at first reproduction and longevity. For example, if fires are suppressed, pine seedlings may grow large enough to be fire resistant and bear seed permitting their invasion. We classify this effect of disturbance as abiotic and due to change in the disturbance regime. Only four studies explicitly relate invasion to the effects of disturbance on life history attributes ([22], [33], [39], [40]). All of these are in grasslands and attribute exclusion of pines to the frequent fires which kill any tree seedlings.

Disturbance may also lead to a reduction of biotic pressures including competition and herbivory, and thus influence the invasibility of communities indirectly. Invasion due to such causes are more appropriately classified as due to biotic interactions. Such studies are far more commonly cited than direct effects of disturbance and are discussed further below.

6.4.3. Biotic causes of pine invasions

6.4.3.1. Invasions and the "limiting similarity" hypothesis:

Several recent papers have discussed (usually critically) the view that plant coexistence is predicated by niche similarity (Shmida & Ellner 1984; Auerbach & Shmida 1987; Silvertown & Law 1987). There have been a few attempts to apply such ideas to explain coexistence of plants in the field (e.g. Werner & Platt 1976; Yeaton 1983). The limiting similarity argument suggests that since competition is strongest between species with the most similar niches, invasions should occur most readily in vegetation with the least abundance of comparable growth forms (Mac Arthur 1972). Thus, in the case of pines, treeless vegetation should be most invasible, followed by shrublands, open woodlands and lastly forest.

Of the seven categories of vegetation (including bare soil) that were invaded by pines, grasslands appear to be particularly susceptible to invasion; 28 of the studies (53%) documented invasion of grassland communities. Invasions of bare soil (23%) and old fields (11%) are also well represented in the selected studies. Mixed brush and grass (9%), shrubland (8%) and forest (8%) communities appear to be more resistant to invasion. These results lend support to the limiting similarity hypothesis; in most cases, invasion of grassland communities proceeds with less severe disturbance in grasslands than in mixed brush and grass, shrubland, and forest communities. In the case of invasions of pines into forests, it appears that severe disturbance is required to permit invasion (see [20],[21] and [44]). An exception is the invasion of indigenous forests on the Bonin Islands in the Pacific by _P. luchuensis_ ([25]), where invasion appears to have proceeded without initial disturbance to the forest. In this case it was concluded that the pine succeeded in invading because the local forest contained no species of similar growth form (Shimizu & Tabata 1985). In Vietnam, _P. kesiya_ establishes itself within untouched broadleaved forest in small pockets where a drier microclimate provides favourable conditions (Cooling 1967). Invasion of native eucalypt forests in Australia by _P. radiata_ is also most severe on dry sites with poor shallow soils. Forests of the "wet sclerophyll" type are resistant to invasion (Chilvers & Burdon 1983 p. 244).

One variation of the "limiting similarity" argument predicts that species-rich communities should better resist invasion by outside species than species poor communities (Elton 1958). Recently Moulton & Pimm (1986b) have found support for this hypothesis in the introduced avifauna of Hawaii. According to this hypothesis, pine invasions into species-rich communities should be the exception. There is too little information on species richness of the invaded communities to test this prediction for the pine studies. However we note that Cape fynbos shrublands in South Africa are extremely rich in plant species but are particularly susceptible to invasion by pines (Kruger et al. 1988).

6.4.3.2. Competition in the regeneration niche:

Several authors have pointed out that plants compete for the same essential resources and that the outcome of competition is highly asymmetric and depends primarily on relative size (e.g. Sebens 1982; Goldberg & Werner 1983). Since even the tallest tree starts life as a seedling and passes through very different environments in its ontogeny, competition with widely disparate growth forms may ultimately exclude a species from a site (Goldberg 1985; Goldberg & Werner 1983; Grubb 1977). If competition acts primarily through juvenile mortality, one would predict that invasions are most likely to occur where there is some change in composition or reduction in the density or growth rate of vegetation interacting with pines in their regeneration niche. The most competitive growth forms during establishment are likely to be those least like pines - that is fast growing herbs or shrubs with deciduous rather than evergreen foliage and the capacity for rapidly spreading and utilizing ephemerally available resources. Grass is known to compete intensely with pine seedlings, especially for moisture (Pearson 1942; Brown & Hall 1968; Larson & Schubert 1969; Madany & West 1983; Elliott & White 1987).

If stresses during establishment are significant in limiting plant distributions then the habitats most easily invaded by pines ought to be those with the least competitive conditions during seedling establishment i.e. cold, high or nutrient poor sites which the pines can nevertheless tolerate (Bond 1989; Board 1988, p. 254). Natural or man-induced disturbances, according to this hypothesis, are important in initiating invasions by changing the degree of openness of a community to invasion through reduction of competitive pressure at the seedling stage.

One prediction of this hypothesis is that invasions would be rare at low latitudes or altitudes since the climate would favour rapid herbaceous growth. The magnitude of disturbance required to initiate or sustain invasions should vary inversely with the vigour of angiosperm growth in regeneration gaps and should thus increase with a decrease in latitude. Examination of the latitudinal distribution of the selected studies, and the degree of disturbance implicated in the invasion at each site, appears to support these predictions (Figure 6.1).

Severe disturbances resulting in total or near-total elimination of biomass may initiate invasions at any latitude (providing that an adequate source of seeds exists). Invasions in tropical and near-tropical regions are always preceded by relatively severe disturbances. This is demonstrated by the invasions of <u>P. kesiya</u> ([20] to [23]), <u>P. massoniana</u> ([26]), <u>P. merkusii</u> ([27]) and <u>P. roxburghii</u> ([49]) in South East Asia. In these regions, pines invade areas abandoned after shifting cultivation or other natural or man-induced disturbances that have caused significant reductions in plant cover. Here, vigorous grasslands and areas where trees such as <u>Quercus</u>, <u>Castanopsis</u> and <u>Podocarpus</u> spp. persist are able to resist invasion ([21]). Other invasions at relatively low latitudes, such as <u>P. patula</u> invading montane grassland in South Africa ([33]) are also governed by man-induced changes in disturbance regimes, such as fire suppression. An exception among low-latitude studies is that of <u>P. luchuensis</u> on the Bonin Islands [25] where invasion apparently occurred without significant disturbance (Shimizu & Tabata 1985).

Areas between 30 and 35 degrees latitude require intermediate levels of disturbance to permit invasion (Figure 6.1). Examples of invasions in these latitudes are the spread of Pinyon pines in western North America ([11], [12] and [28]) and the observed colonization behaviour of species such as <u>P. halepensis</u> ([16], [17], [18]), <u>P. pinaster</u> ([34] and [35]) and <u>P. radiata</u> ([43] to [47]) in mediterranean-climate regions. Anthropogenic disturbances such as grazing and changes in fire frequency are usually implicated in these invasions. At latitudes higher than 36 degrees, pines colonize areas denuded by natural disturbances (such as avalanches, erosion, landslides, volcanoes) and areas (especially subalpine meadows) where factors such as increased grazing pressure, fire suppression, forest clearance, abandonment of cultivated land (and frequently a combination of these) have reduced the cover of grasses or the vigour of other competing angiosperms (Figure 6.1). Only seven Pinus species have natural ranges that extend well north of 46 degrees (Critchfield & Little 1966), and we could find no detailed studies of contemporary range fluctuations in these latitudes. The recent expansion of P. sylvestris in north-east Europe, which resulted from colonization of poor, sandy soils following abandoning of cultivation (Huntley & Birks 1983) suggests that pine invasions at these latitudes is also preceded by alterations to natural disturbance regimes.

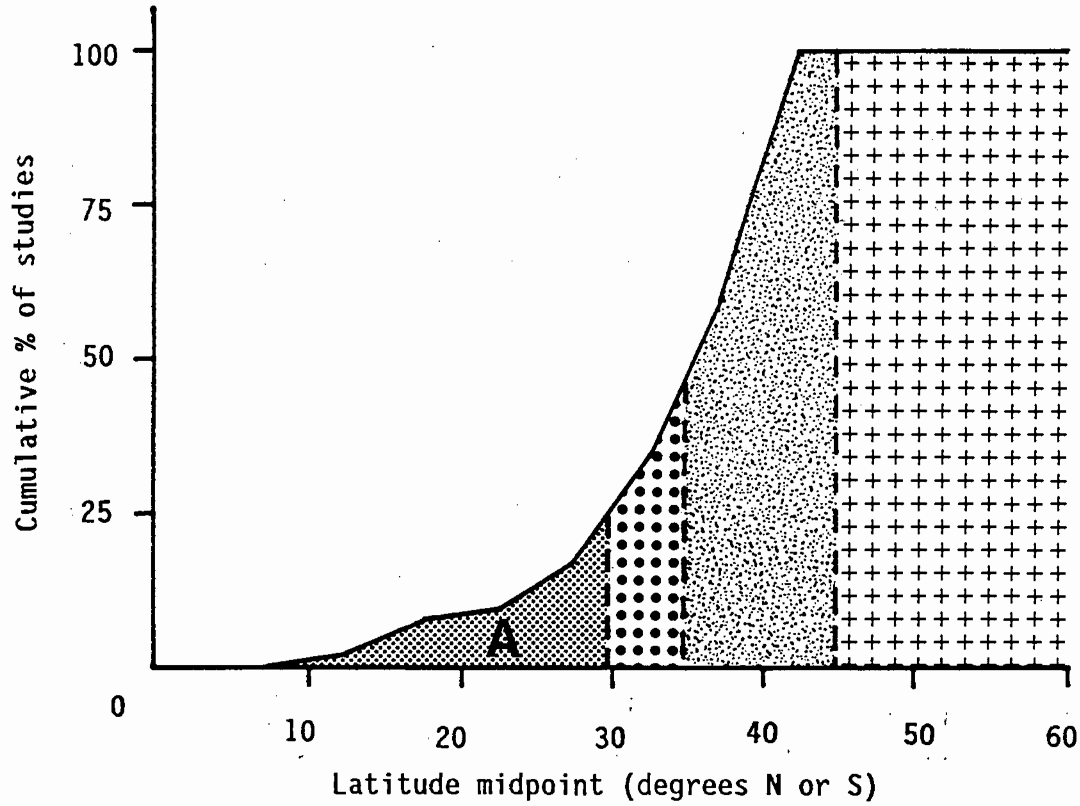

Figure 6.1. The latitudinal distribution of pine invasions (criteria for the selection of studies are given in the text). High latitude habitats are more open to invasion by pines because these habitats tend to be less productive. Disturbance interacts with "inherent invasibility" to determine the openness of a community to invasion by pines. Severe disturbances may initiate invasions at any latitude but invasions at low latitudes (A) are invariably preceded by severe disturbance (see text).

In virtually all cases, whether the invasions occurred in areas adjoining the natural range of the species, or in areas far removed from it, invasion was initiated by a factor that reduced the plant cover. Even fire suppression leads to reduced competition when grass swards degrade to a moribund state (Vogl 1967; 1970). In most of the cases that we surveyed, the release from competition with local grasses and other herbs in the regeneration niche was clearly implicated in pine invasions. The influence of the composition and density of grass cover on pine seedling establishment was perhaps best demonstrated for P. ponderosa in the Black Hills of South Dakota, U.S.A. ([39]). At this site, annual grasses such as western wheatgrass (Agropyron smithii) and blue grama (Bouteloua gracilis) grow in the cool season, and compete directly with pine seedlings. Invasion of P. ponderosa was most pronounced where these vigorous species were absent (Thompson & Gartner 1971). Similarly, in western North Dakota, Potter & Green (1964) found that P. ponderosa seedling establishment was most often successful in grass communities where the highly competitive species Andropogon scoparius and Calamovilfa longifolia were poorly represented. This correlative evidence supports the results of earlier manipulative experiments of Pearson (1942), which showed that P. ponderosa seedlings grew well after removal of grass on sites where they had failed previously. There is also evidence that competition from grasses in improved grasslands on South Island, New Zealand prevents invasion by P. contorta ([7]). Marked differences were evident between seedling survival rates in the improved grasslands and those with less vigorous species (Benecke 1967).

6.4.3.3. Site preparation for commercial afforestation:

Competition with herbs prevents natural regeneration of forest trees (e.g. Novikov 1987), even in localities where planted seedlings can survive without herb control (e.g. Brown & Carvell 1962). We have suggested that the role of competition in the regeneration niche should vary considerably between biomes. The most intense effect should be observed in conditions most favorable for rapid herbaceous growth - well lit, well watered and nutrient rich sites (see Moral 1983). Site preparation is often practiced in commercial afforestation. To control competition from grasses, sites are pitted, ripped, cultivated or treated with herbicides (in progressively more intense treatment; Donald 1984). The intensity of site preparation should vary in different regions depending on the capacity of a site to support vigorous herbaceous growth. This is demonstrated by the different levels of site preparation required to establish pine plantations in natural vegetation in southern Africa. In Cape fynbos shrublands on nutrient-poor soils, little clearing is required to establish pines (Zahn & Neetling 1929; Donald 1971, 1986). In contrast, site preparation is important for establishing pines in the grassland biome, but the intensity of preparation required varies between regions; the most intensive treatment is needed in the vigorous lower latitude montane grasslands of the northern Transvaal (Donald 1971, 1986). There is also considerable variation within regions. Grassland sites at low altitudes require more intensive site preparation than those at higher elevations (Donald 1984). The degree of disturbance required to permit or accelerate invasions would be expected to vary among the biomes, just as the site preparation techniques required in forestry vary (Kruger et al. 1986). This appears to be the case in southern Africa where invasion proceeds with little or no disturbance in the fynbos, but requires major disturbance in grasslands (Kruger et al. 1986).

6.4.3.4. Grazing and competition in the regeneration niche:

There is evidence that diverse forms of disturbance including grazing of competitive grasses, fire, trampling, landslide or volcanic ash, windthrow and climatic change have influenced invasibility. These disturbances all have direct effects (see above), but may also act indirectly to modify the invasibility of communities.

Changes in grazing pressure are commonly cited as disturbances facilitating invasion. The changes may initiate, sustain or halt invasions, depending on the regime. Grazing is often cited as one of a suite of disturbance factors that have interacted to influence invasibility. Livestock grazing - fire regime interactions are often complex (see e.g. Madany & West 1983; Ratliff 1985), and in many of the cases that we studied, we were unable to assess the relative importance of single factors. However, at least the following patterns are discernible in the selected studies: the introduction of grazing at moderate to heavy intensities was frequently found to coincide with the initiation of invasions (e.g. [1], [5], [6], [11], [12], [23], [28], [29], [30], [37], [38], [39], [40], [41], [42], [45] and [46]). These cases are most prevalent in mesic subalpine meadows (e.g. [1], [5], [6]), and in grasslands (e.g. [11], [28], [40]) and mixed grass and brush (e.g. [29], [30], [38]) in more arid regions. Where abandoned fields are invaded by pines (e.g. [45]), grazing may also facilitate invasion. In all these cases, it appears that grazing reduces the cover of vigorous grasses and thus competition with pine seedlings. Evidence that invasions are also halted by the removal of herbivores (e.g. [1], [6]) lends additional support to this hypothesis. Areas subjected to heavy grazing may remain susceptible to invasion long after grazing pressure has been greatly reduced or eliminated (e.g. [9], [37], [45]).

6.4.3.5. Herbivory, pathogens and other biotic agents:

Herbivores also, of course, prevent range extensions directly through trampling or consumption of seedlings and thus prevent invasion. Similarly, release from herbivore pressure or pathogens may lead to range expansions. Prevention of invasion through trampling of seedlings was cited in a number of studies (e.g [1], [2], [4], [6], [7], [8], [9], [15], [16], [22] and [46]). In such cases the initiation of invasions or accelerated invasions coincided with cessation of grazing or reduction in grazing pressure (e.g. [1], [2], [4], [6], [8], [9], [14] and [32]). Trampling may, however, benefit the establishment of invading species, as it may aid in the "planting" of seeds (e.g. [9] and [29]); seedbeds are formed as the dense vegetation is broken by hoofs. Browsing of pine seedlings by grazing livestock ([2], [7], [16], [46]), local small herbivores ([47]) or introduced rabbits ([44] and Duffy et al. 1974) may prevent invasions. In Sequoia National Park the removal of invading pines by park managers has caused surface disturbance that has created favourable conditions for immediate recolonization (DeBenedetti & Parsons 1976).

6.5. CONCLUSIONS

We have examined a large number of studies of pine invasions in an attempt to obtain a global perspective of the determinants of pine invasions. The approach is a combination of a "natural snapshot experiment" and a "natural trajectory experiment" (Diamond 1986). We have aimed to achieve the latter i.e. to reconstruct the trajectory leading to invasion. In several cases it was difficult to isolate the causes of pine invasions at a particular site as these invasions appeared to be contingent on several interacting agents. Though the intricacies of special cases may foil attempts at generalization, we propose a hierarchical model of factors controlling pine invasions.

6.5.1. Pine invasions and the determinants of plant distributions

The studies reviewed above lend some support to all the hypotheses that were tested. Climate has been shown to be an important regulator of pine distribution. The environmental stresses created by drought and temperature factors appear to exercise primary control on invasibility at xeric and high elevation sites respectively, but play a smaller role in determining invasibility at intermediate locations. Many species are, however, not in equilibrium with climate. Their ranges are limited instead by the availability of propagules and the ability of seedlings to survive interactions with the resident biota in adjacent communities. These interactions define another gradient that must be superimposed on the gradient of abiotic stresses determined by climate.

Some biotic and abiotic factors control invasibility in a nonmonotonic way. For example, increasing grazing pressure enhances invasibility up to a critical level by reducing plant cover and thus enhancing the survival of pine seedlings. Above a threshold, grazing animals limit invasibility by trampling seedlings. Thus, when gradients of climate and various disturbances are superimposed, a model to describe invasions is more complex and may need to allow for discontinuities in part of the response surface. For example, Jameson (1987) has proposed a cusp catastrophe model to represent pinyon-juniper invasion patterns due to climatic shifts and the effects of fire and grazing. In this model, invasion under mesic conditions proceeds without jumps whereas the transition from grassland to woodland under xeric conditions requires additional "force", and typically follows a catastrophic course.

Despite the often complex interactions of the determinants of invasibility, the following points emerge: i) Pine invasions are most prevalent where there is limited competition in the regeneration niche; ii) Invasions occur more easily where the dominant growth form is most different to that of pines viz. in grasslands; iii) The disturbance regime in the receiving community is especially important both because it effects the intensity of interactions during establishment but also because of direct effects on the invading species and its life history attributes - a habitat can be made more invasible by altering the disturbance regime.

We have shown that biotic interactions, especially between plant competitors, limit coexistence and are fundamental in determining the invasibility of communities for pines. Could the patterns described above be applied to other genera ? The biotic interactions involved are likely to be different for different taxa. For pines, competition in the regeneration niche appears to be the primary regulating mechanism. Several features of pines make them particularly good colonizers and thus contribute to the inordinate resilience of the genus : i) many species are drought-tolerant and can survive on nutrient-poor sites (e.g. Govindaraju 1984; Board 1988); ii) seeds and pollen are exceptionally well dispersed and most do not require co-adapted agents (e.g. Givnish 1980; Ledig 1986; Levin 1988); iii) isolated pioneers can give rise to colonies by selfing (e.g. Bannister 1965). All these factors suggest that pines are adapted to both rapid migration and explosive population increases (see Bennett 1983), and are thus an exceptionally good taxon to use in a study of the biotic and abiotic determinants of invasibility. Biotic interactions are thus probably **more** important in regulating distribution in pines than in taxa where demographic or genetic considerations may be of overriding importance.

6.5.2. Implications

The influence of biotic factors on plant distribution is often indirect. Climate fluctuations and changes in disturbance regimes influence productivity and thus invasibility. Contemporary practices such as deforestation and increased grazing pressure and those leading to accelerated erosion, modified fire regimes and climate amelioration essentially duplicate ice-age stresses and disturbances that shaped plant communities in the Holocene. In this sense, man is acting as a "para-glacial" agent (Fairbridge 1976).

The potential to change the distributional limits of pines by direct or indirect manipulation of biotic factors has practical value in land management. Besides the benefits of site preparation in commercial forestry that are detailed above, biotic factors influence recruitment dynamics and thus control membership of communities. For example, heavy grazing following years of good seed production of P. ponderosa has been proposed as a means of increasing seedling recruitment (Pearson 1942; Ellison 1960). The results also have important implications for the management of biological invasions. In virtually every community on earth, disturbance regimes are being altered through the influence of man. This will lead to the increased vulnerability of communities to invasion by a select group of organisms that are colonizing habitats from which they may have been ousted by superior competitors in the past. Some pines are important forestry trees and are planted in many parts of the world. In parts of the Southern Hemisphere, pines have already invaded the plant communities adjacent to plantations, often resulting in severe disruption to natural processes. Whether the invasions illustrate recolonization of sites from which pines were eliminated by man, or victorious encounters with a novel biota, the ability to predict the probability of invaders succeeding in a given habitat, given the features of that habitat, will be most useful. The inordinate success of invasive pines in the fynbos shrublands of the Cape Province of South Africa (Kruger et al. 1988) and the failure of introduced pines to invade natural communities in Europe and North America (Orians 1986 p. 135) are enigmas that could be explained by considering relevant properties of the target environments.

Appendix 6.1. Summaries of case studies. Entries for each study are: 1) Pinus species involved, the locality and selected environmental features of the invaded area; 2) The vegetation type invaded; 3) The environmental disturbances cited in the study; 4) Whether release from competition is explicitly or implicitly cited as a factor facilitating invasion; and 5) Information on the role of different biotic and abiotic factors in initiating, sustaining or halting invasion.

1	2	3	4	5
[1]: Pinus albicaulis; Wind River Mountains, western Wyoming, U.S.A.; 42.5°N; Altitude: 3036m; Ann. rain.: 1400mm;	grassland (subalpine meadows)	Grazing	Yes	Intensive grazing reduced the density of the meadow vegetation sufficiently to permit pine seedling establishment but most seedlings were trampled or browsed by cattle. Reduction in grazing intensity resulted in accelerated invasion, probably due to reduced browsing damage and trampling. Total cessation of grazing resulted in an increase in density of meadow vegetation and this halted invasion (Dunwiddie 1977).
[2]: Pinus banksiana; South Island, New Zealand; c. 42°S;	grassland	grazing, browsing (rabbits)	Yes	Grazing reduces competition from grasses. Heavy grazing also prevents invasion when pine seedlings are eaten or destroyed by trampling (Hunter & Douglas 1984).
[3]: Pinus contorta; Yosemite National Park, California; 38°N; Altitude: 2100m;	grassland	Grazing, flooding	?	Encroachment of pine seedlings into meadows was limited by lack of seedling survival, rather than by adequate seed supply or seed predation. Free-flowing water that covers parts of the meadow during snow-melt washes away seeds before they germinate; invasion therefore occurs under dry conditions (Helms 1987; Helms & Ratliff 1987).
[4]: Pinus contorta; Yosemite National Park, California, U.S.A.; 38°N; Altitude: 2720m;	grassland, bare soil	Fire suppression, grazing	Yes	Invasion began shortly after sheep were removed from the area suggesting that the trees could not survive trampling and foraging of the flocks, but were favoured by the conditions created by the animals. The meadows recovered so slowly from this disturbance that they continue to be susceptible to new tree invasion. Invasions of alpine meadows above the tree line seem to be related to climate change and not grazing pressure. Invasions were concentrated on dry sites on upland meadows; wet meadows were often, but not always free of invasive trees (Vale 1987).
[5]: Pinus contorta; Dana Meadows, Yosemite National Park, California, U.S.A.; 38°N;	grassland	Fire suppression, grazing	Yes	Heavy grazing created conditions conducive to invasion, but climate change may also be implicated (Vale 1981b).

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[6]: Pinus contorta; Wind River Mountains, western Wyoming, U.S.A.; 42.5°N; Altitude: 3036m; Ann. rain.: 1400mm;	grassland (subalpine meadows)	Grazing	Yes	Intensive grazing reduced the density of the meadow vegetation sufficiently to permit pine seedling establishment but most seedlings were trampled or browsed by cattle. Reduction in grazing intensity resulted in accelerated invasion, probably due to reduced browsing damage and trampling. Total cessation of grazing resulted in an increase in density of meadow vegetation and this halted invasion (Dunwiddie 1977).
[7]: Pinus contorta; South Island, New Zealand; c. 43°S;	grassland	Grazing, browsing (rabbits), fire	Yes	Competition from grasses in improved grasslands appears to prevent pine invasions. On unimproved and ungrazed grassland, seedling survival rates were high (Benecke 1967). Where there is heavy grazing pressure, seedlings are browsed or trampled by cattle and sheep and this may prevent invasion in some cases (Benecke 1967; Hunter & Douglas 1984).
[8]: Pinus contorta; Central Lemhi Mountains, Idaho, U.S.A.; 44.5°N; Altitude: 2400m; Ann. rain.: 4250mm;	grassland (subalpine meadows)	Grazing, fire	Yes	Cessation of grazing by sheep probably initiated invasion by reducing the grass component. Fire suppression and climate factors are probably also implicated; invasions were attributed to dry conditions between 1920 and 1940 (Butler 1986).
[9]: Pinus contorta ssp. murrayana; Sequoia National Park, California, 36°N;	grassland	Fire suppression, grazing	Yes	Heavy grazing by sheep prior to 1900 resulted in modification of edaphic, vegetative, and physical properties of meadows (and an overall decrease in herbaceous cover). Invasion of the meadows by P. contorta, however, only commenced after elimination of heavy grazing, suggesting that the presence of the sheep prevented regeneration through trampling and/or browsing of seedlings. (DeBenedetti & Parsons 1976; Vankat & Major 1978).
[10]: Pinus contorta var. murrayana; Lassen Volcanic National Park, California, U.S.A.; 40.5°N; Altitude: 2000m;	Bare soil	Volcano	Yes	The elimination of competing vegetation by volcanic activity facilitated the establishment of pine seedlings (Heath 1967).

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[11]: Pinus edulis; Gilia National Forest, New Mexico, U.S.A.; 33°N; Altitude: 1940m; Ann. rain.: 393mm;	grassland	grazing, fire, fuelwood cutting, land clearance	Yes	Heavy grazing by horses, mules and cattle reduced competition from herbaceous growth and thus enhanced survival of pine seedlings (Severson 1986). New seedlings are more prevalent beneath tree canopies. Armentrout & Pieper (1988) showed that the cover of grasses and forbs decreases with an increase in tree cover in south-central New Mexico. The concentration of perch sites for birds is probably implicated, but the improved microclimate and reduced competition may explain the prevalence of seedlings beneath canopies of established trees (Armentrout & Pieper 1988).
[12]: Pinus edulis; Arizona, Colorado, Nevada, New Mexico, Utah, U.S.A.; 34°N; Altitude: 3050m; Ann. rain.: 305mm;	grassland	grazing, fire suppression	Yes	Heavy grazing of pinyon-juniper ranges has been accompanied by an increase in the density and extant of tree stands. This is probably due to the removal of competing grasses and thus enhanced survival of pine seedlings (Aro 1971).
[13]: Pinus flexilis; Colorado Front Range, Colorado, U.S.A.; 40°N; Altitude: 3170m;	not specified (grassland ?)	Fire	Yes	Fire reduces competition in the regeneration niche (Veblen 1986).
[14]: Pinus flexilis; Central Lemhi Mountains, Idaho, U.S.A.; 44.5°N; Altitude: 2400m; Ann. rain.: 4250mm;	grassland (subalpine meadows)	grazing, fire	Yes	Cessation of grazing by sheep probably initiated invasion by reducing grass component. Fire suppression climate factors are probably also implicated; invasions were attributed to dry conditions between 1920 and 1940 (Butler 1986).
[15]: Pinus halepensis; South Island, New Zealand; c. 44°S;	grassland	grazing, Fire, browsing (rabbits)	Yes	Browsing of seedlings by cattle limits invasion in places (Hunter & Douglas 1984).
[16]: Pinus halepensis; Mount Carmel, Israel; 33°N;	shrubland	grazing, fire, browsing	Yes	Fire, grazing, browsing all influence post-fire recovery; browsing of seedlings prevents regeneration in places (Naveh 1973).
[17]: Pinus halepensis; Cape Peninsula, South Africa; 34°S; Altitude: 30m;Ann. rain.: 700mm;	shrubland	Fire	Yes (only fire)	The prolific regeneration of P. halepensis in the fynbos was ascribed to the creation of seedbed conditions by fire, and the poor representation of vigorous grasses and herbs in the post-fire environment (Richardson 1988). There is no evidence that disturbances such as grazing have enhanced invasion (D. M. Richardson, pers. obs.).
[18]: Pinus halepensis; Montpellier, southern France; 43°N; Altitude: 900m;	old fields	Forest clearing, cultivation	Yes	The lack of competition from grasses in the old fields is cited as the main factor permitting invasion (Acherar et al. 1984).

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[19] Pinus jeffreyi; Lassen Volcanic National Park, California, U.S.A.; 40.5^{o}N; Altitude: 2000m;	Bare soil	Volcano	Yes	The elimination of competing vegetation by volcanic activity facilitated the establishment of pine seedlings (Heath 1967).
[20]: Pinus kesiya; Burma; c. 20^{o}N;	forest	Shifting cultivation	Yes	Shifting cultivation has resulted in a reduction in plant cover and thus in competition in the regeneration niche (Allsop 1949 in Turnbull et al. 1980).
[21]: Pinus kesiya; Vietnam; c. 12^{o}N;	Forest (disturbed), bare soil	Fire, forest clearing, shifting cultivation,	Yes	1) Seeds are released at a time when local annual herbs are dormant; seeds fall on exposed ground; 2) Fire provides seedbed conditions; 3) Shifting cultivation; P. kesiya occupies "virtually all sites except man-made grasslands and the moister inaccessible sites such as ravines and protected situations at high altitudes where Quercus, Castanopsis, Podocarpus and other species persist". Fires kill seedlings of 5 years old or less (Turnbull et al. 1980).
[22]: Pinus kesiya; Philippines; c. 17^{o}N;	bare soil, forest (clearings and disturbed areas)	Fire, forest clearing,	Yes	Destruction of herb layer and pine litter by fire and man reduces competition with pine seedlings and allows invasion. Grazing prevents pine regeneration, especially at low altitudes; Regular burning and grazing is detrimental to pine regeneration. Fires kill young trees especially at low elevations (Turnbull et al. 1980).
[23]: Pinus kesiya; India; 25^{o}N; Altitude: 1876m; Ann. rain. 1750mm;	bare soil, scrubland	Fire, grazing, shifting cultivation	Yes	Burning, shifting cultivation and grazing by cattle, goats and sheep have resulted in destruction of the climax forest and creation of conditions suitable for colonization by P. kesiya (Turnbull et al. 1980).
[24]: Pinus lambertiana; Lassen Volcanic National Park, California, U.S.A.; 40.5^{o}N; Altitude: 2000m;	Bare soil	volcano	Yes	The elimination of competing vegetation by volcanic activity facilitated the establishment of pine seedlings (Heath 1967).
[25]: Pinus lutchuensis; Chichijima Island, Bonin Islands, North-West Pacific; 27^{o}N;	old fields, forest, disturbed sites, bare soil	Forest clearing, volcano	Yes	The invasion of areas denuded by forest clearance, road construction and volcanic activity can be explained by the lack of competition from grasses and herbs in these sites. However, the invasion of undisturbed forest cannot be explained by release from competition (Shimizu & Tabata 1985).

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[26]: <u>Pinus massoniana</u>; Mount Jinyun, Sishuan, China; 29°N; Altitude: 650m;	Bare soil	Forest clearing	Yes	Destruction of original evergreen broad-leaved forest reduces competition and permits the establishment of <u>P. massoniana</u> (Ming 1987).
[27]: <u>Pinus merkusii</u>; South East Asia;	bare soil, disturbed sites, old fields	shifting cultivation, fire, grazing	Yes	Shifting cultivation, involving clearing of forests and regular burning, reduces the plant cover. Where fire is excluded for sufficiently long periods, abandoned fields are invaded by hardwood species which eventually exclude <u>P. merkusii</u> (Cooling 1967; Cooling 1968).
[28]: <u>Pinus monophylla</u>; Arizona, Colorado, Nevada, New Mexico, Utah, U.S.A.; c. 34°N; Altitude: 3050m; Ann. rain.: 305mm;	grassland	grazing, fire	Yes	Heavy grazing of pinyon-juniper ranges has been accompanied by an increase in the density and extent of tree stands. This is probably due to the removal of competing grasses and thus enhanced survival of pine seedlings (Aro 1971).
[29]: <u>Pinus monophylla</u>; Wasatch National Forest, West Central Utah, U.S.A.; 37.5°N; Altitude: 2070m; Ann. rain.: 325mm;	mixed brush and grass	grazing, fire suppression	Yes	Heavy grazing reduces the vigour and cover of perennial grasses and thus enhances conditions for establishment of invading trees. Trampling may benefit establishment of invading species, as it may aid in "planting" the seeds (Barney & Frischknecht 1974).
[30]: <u>Pinus monophylla</u>; East Central Nevada, U.S.A.; c. 39.5°N; Altitude: 2130m; Ann. rain.: 500mm;	grassland, mixed grass and brush	grazing, fire suppression	Yes	Grazing reduces grass cover and thus competition with establishing pine seedlings. Climatic change is apparently also implicated; in wet years, pines invaded even the most dense grass stands (Blackburn & Tueller 1970).
[31]: <u>Pinus monticola</u>; Lassen Volcanic National Park, California, U.S.A.; 40.5°N; Altitude: 2000m;	bare soil	volcano	Yes	The elimination of competing vegetation by volcanic activity facilitated the establishment of pine seedlings (Heath 1967).
[32]: <u>Pinus monticola</u>; Cascade Mountains, Oregon, U.S.A.; 43°N; Altitude: 1365m;	grassland	Fire, grazing	Yes	Cessation of sheep grazing coincides with the initiation of invasions, but fire suppression, and the sequence of dry conditions (which reduced the vigour of herbaceous plants) followed by a wet period may have contributed to the conditions which favoured the unstable ecotones (Vale 1981a).
[33]: <u>Pinus patula</u>; Drakensberg, Natal, South Africa; 28°N; Altitude: 1890m; Ann. rain.: 1380mm;	grassland	Fire, frost terracettes	Yes	<u>P. patula</u> is prevented from invading vigorous grasslands by competition from grass swards. Those seedlings that do establish are killed by fire which occurs at intervals of about 2 years. Invasion is restricted to areas protected from fire (where the grass sward becomes moribund) or to areas where erosion or other natural processes have exposed the soil and where the reduced fuel loads afford pine seedlings protection from fire (Kruger <u>et al</u>. 1986; D.M. Richardson, unpublished).

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[34]: Pinus pinaster; Abel Tasman National Park, New Zealand; 41°N;	mixed brush and grass	Fire, grazing	Yes	Poor seedling success in closed canopy scrubland and forest community (Sanson 1978; Hunter & Douglas 1984).
[35]: Pinus pinaster; Southwestern Cape, South Africa; c. 34°S; Altitude: 0 - 1000 +m; Ann. rain.: 700-2000mm;	shrubland	Fire	Yes	P. pinaster invades montane shrublands with no apparent disturbance to the habitat other than the fires that occur at intervals of between 6 and 40 years. Recruitment occurs mainly during the immediate post-fire phase because of the abundant supply of seeds and suitable microsite conditions. Seedlings are, however, regularly encountered in mature communities (Kruger 1977; D. M. Richardson, unpublished data).
[36]: Pinus pinea; Southwestern Cape Province, South Africa; c. 34°N; Altitude: 300m; Ann. rain.: 700-2000mm;	shrubland	Fire	Yes (only fire)	P. pinea has invaded fire-prone mountain fynbos. The large seeds are dispersed by the introduced squirrel, Sciurus carolinensis, and self-sown stands are restricted to areas where these animals are present (D. M. Richardson, unpublished data).
[37]: Pinus ponderosa; Boulder County, Colorado, U.S.A.; 40°N; Altitude: 2600m; Ann. rain.: 551mm;	grassland	Fire, wind damage, insect attack, logging, mining	Yes	Overgrazing by cattle in the late 19th century exposed bare mineral soil. Continued invasion of grasslands that have not been heavily grazed for several decades suggests that additional factors are also important (Marr 1961; Veblen & Lorenz 1986).
[38]: Pinus ponderosa; Warner Mountains, California, U.S.A.; 41.5°N; Ann. rain.: 550mm;	mixed brush and grass	fire suppression, grazing	Yes	Fire suppression and grazing have reduced the cover of herbaceous plants, and thus competition with pine seedlings (Vale 1977).
[39]: Pinus ponderosa; Black Hills, South Dakota, U.S.A.; 44°N; Altitude: 1000m; Ann. rain.: 450mm;	grassland	grazing, mining, fire, fire suppression, logging	Yes	The western wheatgrass, blue grama and associated species grow in the cool season, and compete directly with pine seedlings for moisture and nutrients. Invasion was much more pronounced where these species were absent. Grazing reduced grass density and thus competition with pine seedlings. Pine invasion occurred only on shallow, course-textured soils and not on adjacent finer--textured soils occupied by western wheatgrass Agropyron smithii. Controlled burning kills pine seedlings (Thompson & Gartner 1971; Biswell 1972; Gartner & Thompson 1972).
[40]: Pinus ponderosa; Sandhills Prairie, Nebraska, U.S.A.; 43°N; Ann. rain.: 5100mm;	grassland	fire suppression, grazing	Yes	Pines were originally restricted to canyon walls by recurrent prairie fires and competition of seedlings with grass. The decrease in fire frequency after settlement and the decrease in grass cover due to grazing promoted successful pine establishment in the sandhills prairie (Steinauer & Bragg 1987).

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[41]: Pinus ponderosa; Zion National Park, Utah, U.S.A.; 37 ^{o}N; Altitude c. 2000m;	grassland	fire suppression, grazing	Yes	Major differences were found between the vegetation structure in two otherwise similar areas in the Zion National Park. One area had been grazed heavily by livestock in the late 19th and early 20th centuries. The grazing caused a reduction of the herbaceous groundlayer and permitted the establishment of the (less palatable) pine seedlings (Madany & West 1983).
[42]: Pinus ponderosa; Otago, New Zealand; c. 45^{o}S; Altitude: 275-790m; Ann. rain.: c. 500mm;	grassland	grazing, browsing (rabbits), fire	Yes	Grazing reduced vegetation cover and has apparently encouraged the establishment of pine seedlings (Wills & Begg 1986; see also Hunter & Douglas 1984).
[43]: Pinus radiata; Stellenbosch, Cape Province, South Africa; 34^{o}S; Altitude: 350m; Ann. rain.: 1800mm;	shrubland	Fire	Yes (only fire)	The only disturbance required for invasion of mountain fynbos by P. radiata is fire. Fire causes the release of seeds from serotinous cones and prepares microsite conditions suitable for germination and establishment. Grazing pressure in invaded areas is negligible, and there appear to be no other biotic barriers to invasion. The poor representation of grasses or other vigorous herbs in the vegetation means that there is little competition for resources in the regeneration niche (-Richardson & Brown 1986; D.M. Richardson, unpublished).
[44]: Pinus radiata; Eastern Australia; 35^{o}S; Altitude: 650m;	forest (Disturbed eucalypt forest)	Fire, browsing (rabbits)	Yes	The invaded eucalypt forests were disturbed in many ways prior to invasion; e.g. through partial clearing to improve grass production, by frequent burning and overgrazing. Browsing by rabbits appears to have prevented invasion prior to their virtual elimination (Dawson et al. 1979; Chilvers & Burdon 1983).
[45]: Pinus radiata; Monterey, California, U.S.A.; 36.5^{o}N; Altitude: 100m; Ann. rain.: 424mm;	old fields	land clearance, grazing, fire, logging	Yes	Grazing and other disturbances have reduced the cover of grasses (Forde 1966).
[46]: Pinus radiata; South Island, New Zealand; c. 44^{o}S; Altitude: <700m;	grassland	grazing, browsing (rabbits), fire	Yes	Invasion has been restricted to unimproved grasslands which are often overgrazed. It has been suggested that the plant cover in these unimproved grasslands provides a "low competition nurse crop favouring seedling success". Competition with vigorous grasses in improved grasslands markedly reduces seedling success. Grazing cattle also browse seedlings (Hunter & Douglas 1984).

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[47]: Pinus radiata; southern Chile; c. 45°S	disturbed sites (not natural vegetation)	Fire	?	Activities of small herbivores have prevented the establishment of transplants of P. radiata in Chile (Fuentes & Etchegary 1983), and this may explain the inability of this species to invade significantly (Kruger et al. in press; C. Donoso, pers. comm.; E. Fuentes, pers. comm.; C. Gonzalez, pers. comm.; T.T. Veblen, pers. comm.).
[48]: Pinus resinosa; Wisconsin, U.S.A.; c. 44°N;	grassland	Fire suppression,	Yes	Fire suppression led to moribund grass swards and reduction in competition (Vogl 1967; Vogl 1970).
[49]: Pinus roxburghii; Eastern Nepal; 27°N;	bare soil	forest clearing, shifting cultivation, fire	Yes	This species colonizes sites where the plant cover has been reduced (Ohsawa et al. 1986).
[50]: Pinus strobus; Eastern U.S.A.; c. 43°N;	old fields	forest clearing, cultivation,	Yes	Release from competition from grasses enables pines to establish (Spurr 1964).
[51]: Pinus strobus; Oswegatchie Plains, New York, U.S.A.; 44°N; Ann. rain.: 1054mm;	grassland	logging, wind damage, insect attack, fire, browsing, tree cutting (beavers)	Yes	The invasion of the grasslands appears to have resulted from the complex interactions of many disturbance factors (Bonkoungou et al. 1983).
[52]: Pinus strobus; Wisconsin, U.S.A.; 44°N;	grassland	Fire suppression	Yes	Fire suppression led to moribund grass swards and reduction in competition (Vogl 1967; Vogl 1970).
[53]: Pinus virginiana; Eastern U.S.A; c. 43°N;	old fields	forest clearing, cultivation	Yes	Release from competition following abandonment of cultivated fields (Spurr 1964).

CHAPTER 7 : WHY IS MOUNTAIN FYNBOS INVASIBLE AND WHICH SPECIES INVADE ? [1]

7.1. ABSTRACT

In order to manage invaded ecosystems it is necessary to understand the determinants of invasibility of component communities. In practical terms, a manager must know why a particular community is invasible, how the invader gains entry to the community, and also what type of species will invade. Comparative studies of community patterns have yielded a number of broad generalizations of the determinants of invasibility. These may be divided into three main categories: those relating to the role disturbance in initiating and sustaining invasions, those that correlate invasibility with species richness, and those that detail the role of extrinsic factors in determining the outcome of introductions. It is shown that these broad generalization contribute little to understanding the mechanisms of plant invasions in South African mountain fynbos. This chapter examines why the mountain fynbos environment can support dense stands of invasive trees and shrubs and also how the invaders are incorporated into the natural communities.

The vulnerability of mountain fynbos to plant invasions is unrelated to the species richness of the invaded community. A unique feature of mountain fynbos is its low steady-state biomass relative to analogous areas for a wide range of resource levels. Provided that introduced trees and shrubs can overcome establishment barriers, there are sufficient resources for the transformation of fynbos plant communities into tall shrub and forest formations. The ready incorporation of introduced species into fynbos communities can be explained by the stochastic fire-induced changes in community structure, which result in large spatial and temporal fluctuations in population sizes of component species and therefore competitive hierarchies. These fires are part of the natural disturbance regime and there is no evidence that invasion in mountain fynbos is dependent on a man-induced alteration of this regime. Invasions in mountain fynbos are influenced markedly by extrinsic factors (e.g. large-scale afforestation and man-assisted dissemination of pines, the geographic location of the Cape and its cultural history etc.).

A biological profile of a successful invader of mountain fynbos was compiled using both theoretical and empirical analyses. The most successful invaders are trees and shrubs introduced from other mediterranean-climate regions and that have small seeds, low seed wing loadings, short juvenile periods, moderate to high degrees of serotiny and poor fire-tolerance as adults. A risk assessment model for screening new introductions is proposed and used to evaluate the relative risk of invasibility for future introductions of Australian Banksia species.

7.2. INTRODUCTION

Few communities on earth have escaped the damaging effects of invasive alien organisms (Drake et al. 1988). The apparent ease with which some organisms invade some communities tends to belie the numerous obstacles that an introduced species must overcome in order to invade (Roughgarden & Diamond

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[1] *Richardson, D.M. & Cowling, R.M. Why is mountain fynbos invasible and which species invade ? To be published.*

1986; Kruger et al. 1986). The successful invaders in any community are, however, invariably few in number relative to the total set of introduced organisms (Elton 1958; Groves & Burdon 1986; Macdonald et al. 1986; Mooney & Drake 1986; Drake et al. 1988). Which communities are invasible and what species invade ? In addressing these questions one is forced to address fundamental questions regarding the determinants of community structure. This kind of information also provides the insight that is required to manage and control invasive organisms. Despite the attractiveness of gaining such an understanding, recent reviews (e.g Ehrlich 1986; Simberloff 1986; Crawley 1987b) have emphasized the difficulty of gaining insights with regard to both questions.

South African mountain fynbos (Taylor 1978; Kruger 1979; Campbell 1985) has been severely invaded by introduced trees and shrubs (Macdonald & Richardson 1986). In this chapter we examine this phenomenon by addressing two fundamental questions: what makes fynbos communities invasible, and what type of species invade ? To answer the first question, we examine resource utilization and aspects of the structure and dynamics of fynbos communities that render them prone to invasion. To determine what type of plants invade, we examine the life history attributes of species that have already become major weeds and generate a biological profile of a successful invader. Our analysis is mainly confined to a discussion of invasive trees and shrubs with canopy-stored seed; this guild (largely species of *Hakea* and *Pinus*) has been remarkably successful in mountain fynbos (Macdonald & Richardson 1986). We also extend the model and make predictions regarding the potential invasiveness of south-western Australian *Banksia* species which have not yet been introduced on a large scale. Before addressing these questions, we will review briefly the potential determinants of invasibility in terrestrial plant communities.

7.2.1. Determinants of invasibility

Is it possible to predict, from a study of community properties, the potential of a community to accept additional members ? Several recent papers have addressed this question at a regional or global scale. Two important issues are examined in most of these contributions: the role of disturbance in initiating and sustaining invasions, and the relationship between species richness of a community and its vulnerability to invasion. The role of extrinsic factors that influence the invader's ability to gain access to the community has also received some attention.

Communities differ substantially in their response to different factors (e.g. Hobbs 1988), but in almost all cases where invasions have been studied, the disturbance regime has been found to be an important determinant of invasibility. There is strong evidence in support of an "intermediate disturbance hypothesis" which argues that moderate levels of disturbance would allow invasion of a community by the widest range of species and thus maintains the highest species richness (e.g. Grime 1973; Abele 1976; Connell 1978; Hubbell 1979; Peet et al. 1983; Baker 1986; Crawley 1987a,b; Richardson & Bond, submitted). Exclosure experiments in grazed grasslands (e.g. Grime 1973) probably provide the best evidence for this phenomenon. In these cases, enhanced invasibility (due to reduced competition for resources resulting from selective grazing) may result in increased species diversity, provided there is a source of potential immigrants. Clearly, disturbance may free otherwise unavailable resources which could be utilized by a potential invader. Hobbs (1988) has, however, emphasized that disturbance will enhance invasibility only if it increases the availability of a limiting resource; not all disturbances do this. Nevertheless, most syntheses evoke a very general "disturbance / resource" explanation as a major "cause" of invasions (e.g. Elton 1958; Harper 1965; Baker 1986; Crawley 1987b; Fox & Fox 1986; Orians 1986; Rejmanek 1988). Invasions do proceed more easily in sites subjected to ecosystem-level disturbances (e.g. Baker 1986; Crawley 1987b; Pimm 1986 p.318; Richardson & Bond, submitted). Communities subject to recurrent disturbances are also generally more prone to invasion (Myers 1983; Fox & Fox 1986; Orians 1986 p.133), and those subject to catastrophic disturbances are the most prone to invasion (Fox & Fox 1986; Rejmanek 1988).

A second major generalization concerning invasibility is that the richer in species a community, the less open it is to invasion, presumably since resource niches are more fully occupied in species-rich communities (Elton 1958; Fox & Fox 1986; Moulton & Pimm 1986a,b). This generalization assumes that competition determines the structure of niche-differentiated communities, and conforms with the notion that more complex communities are more stable (review in Pimm 1986). This was derived mainly from studies on oceanic islands, where communities are often "unsaturated" because of their isolation from regions with similar biota (MacArthur & Wilson 1967; Elton 1958; Moulton

& Pimm 1986a,b). For many communities, however, especially those dominated by sessile organisms (e.g. plants), species richness is a poor reflection of the diversity of resource niches (Grubb 1977; Agren & Fagerstrom 1984; Yodzis 1986). Indeed, species richness may be unrelated to resource availability and species-rich plant communities need not be less invasible than species-poor ones.

Factors extrinsic to either the community or the invader are often important determinants of invasibility and sometimes override all other factors. For example, areas close to large sources of potential immigrants are most severely invaded (Crawley 1987b). Historical factors such as the cultural ties between regions are often important determinants of the composition of invasive biotas (Kruger et al. 1988) and must be considered when evaluating the relative success of different organisms in invasive biotas of different parts of the world.

The formulation of the generalizations discussed above has to some extent improved our comprehension of the determinants of invasibility at a global scale. Besides providing some empirical support for Elton's (1958) pioneering hypotheses, these syntheses have also served to emphasize the complexity of the determinants of invasibility due to the intermingling of intrinsic and extrinsic factors. For example, Richardson & Bond (submitted) have shown in a global review of pine invasions that the susceptibility of a community to invasion is usually the product of its "inherent susceptibility" (which for pines can be predicted from latitude and elevation) and the cumulative effects of various extrinsic factors that may, individually, act to enhance or diminish invasibility. The foregoing generalizations have mostly been gleaned from comparative studies of community patterns. As Pimm (1986) has pointed out, these are unsure ways of understanding what factors affect community persistence. In this chapter we have attempted to achieve an understanding of the mechanisms underlying plant invasions in mountain fynbos by examining why the fynbos environment can support dense stands of invasive trees and shrubs, and also how the invaders gain entry to the fynbos communities.

Table 7.1. A summary of frequently-cited explanations for the severe invasion of fynbos by introduced trees and shrubs.

PROPERTIES OF THE INVADER:

Life history attributes

- Enhanced seed production in the absence of natural limiting factors (Neser 1968; Kluge 1983; Gill & Neser 1984) together with high germinability and rapid germination (Richardson & Van Wilgen 1984) results in abnormally high recruitment (Richardson et al. 1987).
- Enhanced seed production, together with good inherent dispersability of individual seeds, results in exceptional dispersal which has permitted proliferation and spread (Middlemiss 1963; Kruger 1977; Hall 1979; Richardson et al. 1987).
- greater longevity (Kruger 1977), and better fire-survival (Kruger 1977; Fugler 1983)

Resource utilization

- Invaders show earlier shoot growth (Sommerville 1981), faster height growth (Richardson 1985; Rutherford et al. 1986), than the seed-regenerating shrubs that dominate most fynbos communities.
- Invaders are better adapted to certain trace-element deficiencies (Schutte 1960).
- Invaders have nutrient-rich seeds which lead to enhanced germination and survival in the nutrient-poor fynbos soil (Mitchell & Allsop 1984).
- The nitrogen-fixing ability of some species (e.g. Acacia spp.) has given them a competitive advantage (Roux & Warren 1963).

PROPERTIES OF THE RECEIVING ENVIRONMENT :

- The increased dispersion and size of transformed habitats means that most points within the fynbos biome are within "plant dispersal distance" of invasives (Hall 1979).
- Altered fire regimes (Kruger 1979), herbivore communities (Skead 1980), insect communities [(Skaife (undated); Slingsby & Bond (1982)] and sediment erosion and deposition patterns [(Moll & Campbell (1976); Shaughnessy (1980); Brownlie (1982)] have favoured the invasives.
- The elimination of indigenous large mammals from the fynbos biome (without replacement by introduced mammals) has allowed introduced species to regenerate (Macdonald 1984).
- Invaders replace native species whose regenerative and maintenance capacities have been reduced through environment changes i.e. fynbos is in a state of bio-climatic compression and the indigenous flora are not in equilibrium with the present environment (Cone 1973).
- The "vacant tree niche" hypothesis: trees that can cope with the fynbos environment (low nutrient status, summer drought, periodic fires) have failed to evolve in the biome, and this niche has been filled by introduced trees (Campbell et al. 1979).

7.3. PLANT INVASIONS IN MOUNTAIN FYNBOS: WHY AND HOW ?

7.3.1. Invasions by trees and shrubs

Fynbos is sometimes considered to be remarkably susceptible to invasion by introduced plants when compared to other vegetation types (e.g. Taylor 1977; Kruger 1981). Macdonald (1984) has, however, argued that whereas the fynbos biome is more severely invaded than other southern African biomes, available data do not support the view that the fynbos is inherently more invasible. Certainly, the fynbos biome does not contain a disproportional number of major weeds. The few major weeds (sensu Baker 1986) (only about ten species of trees or shrubs: see Appendix 7.1) have, however, invaded large areas of mountain fynbos and, in many cases, have severely disrupted natural ecosystem processes (Macdonald & Richardson 1986).

The dominance of trees and shrubs, and the absence of herbs and grasses in the invasive flora of mountain fynbos (Kruger et al. 1988) is unusual when compared with those of other southern Africa biomes (Macdonald et al. 1986) or with other mediterranean-climate regions (cf. Groves 1986b; Mooney et al. 1986; Kruger et al. 1988). Historical and cultural differences which have influenced the history of introductions to mediterranean-climate regions, make the evaluation of the anomalous success of invasive trees in the Cape difficult (Kruger et al. 1988). Trees such as pines were introduced earlier and in greater numbers to the Cape (see Shaughnessy 1980, 1986) than to other mediterranean-climate regions (cf. Groves 1986a,b; Mooney et al. 1986) and this may explain, at least partially, their inordinate success as invaders (Kruger et al. 1988). Many other hypotheses have been put forward to explain the remarkable success of introduced trees and shrubs as invaders in fynbos (Table 7.1). Although we accept some elements of these hypotheses, most are untestable and none provide a comprehensive explanation of the phenomenon. To achieve a meaningful understanding of the processes involved in the invasion of mountain fynbos communities we examine patterns of resource utilization and the spatial and temporal dynamics of communities.

7.3.2. Why is mountain fynbos invasible ?

Fynbos plant communities differ in some important characteristics when compared with communities in other mediterranean-climate regions. One of the most remarkable features of fynbos vegetation is its low height (Milewski 1981; Cowling & Campbell 1980). This is perhaps best demonstrated by comparing vegetation formations in the Cape with those in environmentally equivalent regions of Western Australia. Generally, Australian formations are an order of magnitude taller than the Cape for matched sites (Figure 7.1). For example, proteoid fynbos in the Cape (Campbell 1985) is the predominant formation over a wide rainfall range on sand. Corresponding formations in Australia range from structurally-similar scrub-heath at lower rainfalls (c. 450 mm/yr) to woodlands and forests up to 18 times taller than fynbos at higher rainfalls. What is striking is the predominance of trees in West Australia where rainfall exceeds about 600 mm on sands and granites. Trees are entirely lacking from the Cape except for the trees in closed forests on the wettest sites on granites (Campbell et al. 1979; McKenzie et al. 1977). There is no conclusive evidence that the Cape, and mountain fynbos in particular, supported taller vegetation composed of trees during the last glacial - interglacial cycle (Scholtz 1986). Fynbos communities are also characterized by much lower biomass than other mediterranean-climate regions for matched sites. The above-ground biomass in mature (but not senescent) mountain fynbos shrublands range from 15000 to 51000 kg/ha (Kruger 1977; Van Wilgen 1982; Van Wilgen et al. 1985). This is lower than in most structurally-similar communities in the other regions (cf. Ehleringer & Mooney 1983) which have richer soils but lower rainfall, and an order of magnitude less than areas within other mediterranean-climate regions with similar rainfall (Ehleringer & Mooney 1983). Most mountain fynbos areas receive more than 800 mm of rainfall per year. Equivalent habitats in the other regions support forest with much higher biomass. For example, above-ground biomass in dense pine forests in mediterranean-climate France with an annual rainfall of around 1100 mm is up to two orders of magnitude greater than that of fynbos communities in parts of the Cape with an equivalent annual rainfall (cf. L. Trabaud unpublished; Van Wilgen et al. 1985). Similarly, in lower rainfall (<800 mm/yr) regions [e.g. dry heaths in Australia (Specht 1969), Ceanothus chaparral in California (Gray 1982) and Chilean matorral (Kummerow et al. (1981)] above-ground biomass of fynbos communities is markedly lower (cf. Kruger 1977; Rutherford 1978; Van Wilgen et al. 1985).

Annual biomass increments of between 1000 and 4000 kg/ha in the first few years after fire in fynbos (Kruger 1977) approximate or slightly exceed those

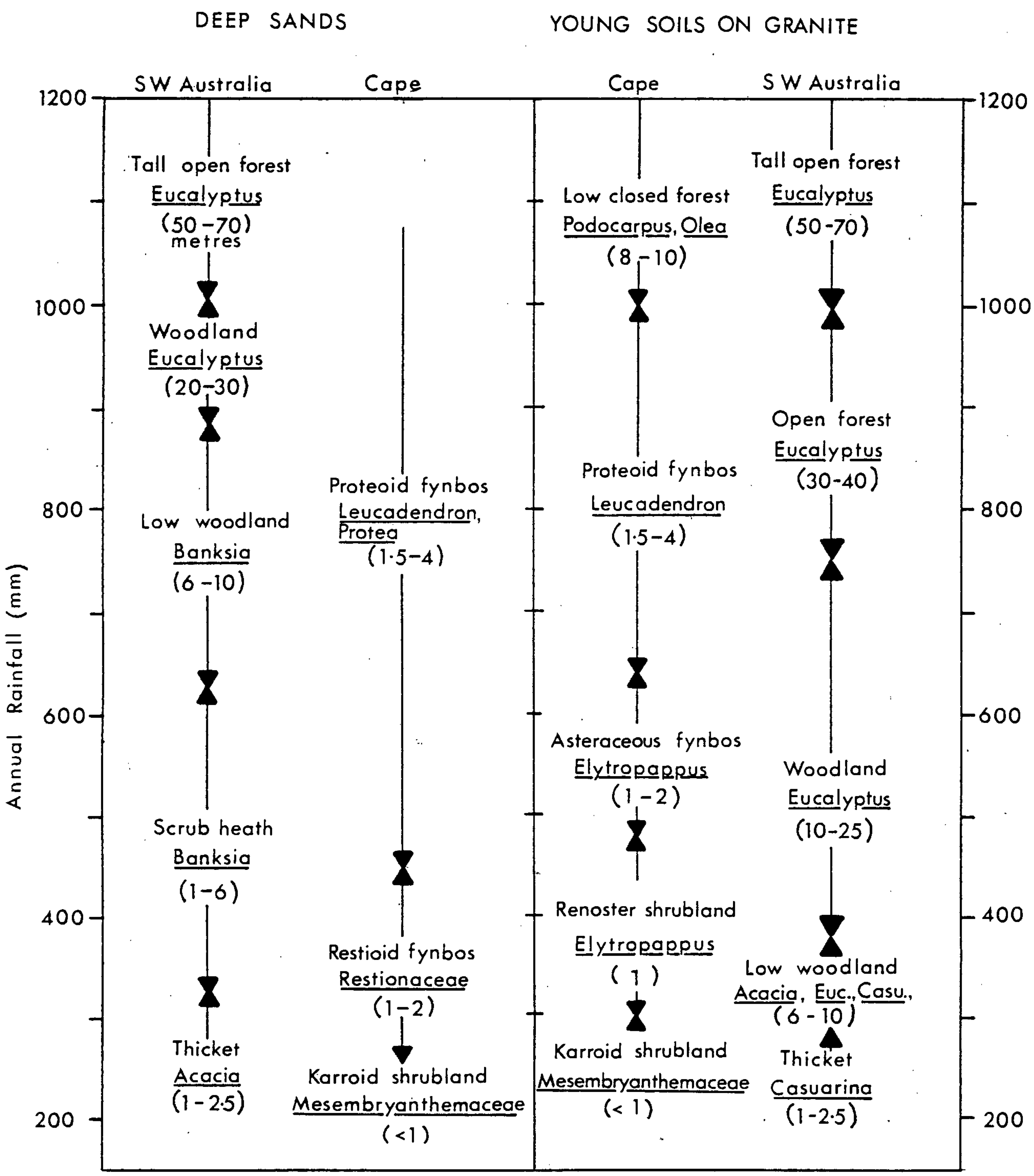


Figure 7.1. A comparison of structural formations on two substrata and across a rainfall gradient for lowland (0-300 m) sites in mediterranean south-western Australia and the Cape, South Africa. Adapted from Beard (1976; 1981; 1983; 1984), Moll *et al.* *(1984) and Campbell (1985).*

in chaparral, garrigue, heath and malee-broombush communities (Long et al. 1967; Specht 1969; Specht 1981; Ehleringer & Mooney 1983). Fynbos shrubs have leaves with similar photosynthetic capacities to leaves from evergreen shrubs in other mediterranean-climate regions (Mooney et al. 1983) but are apparently constrained by the need to survive fire and to exploit the brief period after fire. The fynbos shrubs appear to lack the capacity (either as individuals or as a community) to optimize resource use later in stand development. Invasion of mountain fynbos by Acacia saligna, A. longifolia and Hakea sericea can double or treble the total above-ground plant biomass (Milton & Siegfried 1981; Van Wilgen & Richardson 1985) and the biomass in self-sown pine forests can be up to five times that of the pre-invasion fynbos (Versfeld & Van Wilgen 1986). Even as seedlings, introduced trees and shrubs show more rapid growth than those of indigenous fynbos shrubs. For example, seven years after a fire in mountain fynbos near Somerset West the mean height of the dominant indigenous shrub Protea repens was 0.75 m whereas the introduced species Pinus pinaster (1.75 m), P. radiata (2.05 m) and Hakea sericea (1.78 m) were much taller (Richardson 1985c and unpublished data).

What are the implications of the low resource use in fynbos for invasibility ? Clearly fynbos lies below the steady-state biomass predicted from precipitation (see Miller 1981 p.382). The low biomass in fynbos communities cannot be attributed to the nutrient-poor soils; Australian soils are poorer than those of the Cape [Di Castri (1981 p.22); Milewski & Cowling (1985); Lamont et al. (1985)]. It appears that resources, particularly moisture, are not fully exploited in fynbos ecosystems. The insular nature of the biome has probably prevented migrations of preadapted trees from other regions. The evolution of fynbos plant communities has been a gradual in situ process, rather than a migration event (Deacon 1983), and for some reason fynbos taxa have not adapted to exploit fully the available resources.

Plant invasions in the fynbos have resulted in an increase in biomass so as to push the fynbos communities closer to the steady-state biomass predicted for the resource (precipitation) level (Figure 7.2). This process is readily achieved by the incorporation into fynbos of invasive trees and shrubs. In the mediterranean-climate regions of Australia and California plant invasions have not resulted in a large increases in steady-state biomass (cf. Groves 1986a,b; Mooney et al. 1986). We argue that in these regions the biomass of the natural communities approximates the steady-state biomass. For this reason, plant invasions in these regions usually involve the replacement of resident species by similar life forms or guilds [e.g. geophytes in Western Australian heath (kwongan) and Mediterranean grasses in chaparral].

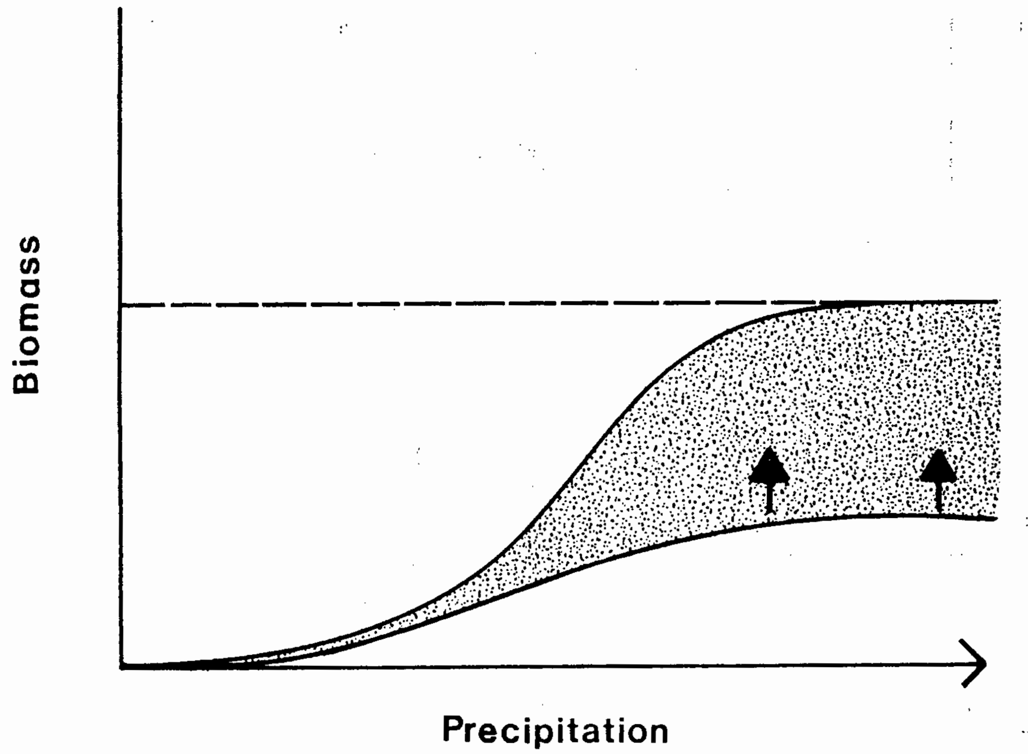


Figure 7.2. Hypothetical relationship between precipitation and above-ground plant biomass in terrestrial ecosystems. The upper curve defines the steady-state biomass (sensu Miller 1981) of biomass for any given rainfall. The lower curve defines the biomass / rainfall relationship for mountain fynbos. The shaded area represents the biomass that can still be incorporated into mountain fynbos communities through replacement of indigenous by introduced plants at different precipitation levels.

Another factor that appears to have permitted invasion of fynbos by trees and shrubs from other mediterranean-climate regions is the relatively mild moisture stress during summer which may alleviate seedling mortality. For example, California generally shows a distinct seasonal drought and plant xylem pressure potentials below -6.0 MPa are common (Poole et al. 1981; Davis & Mooney 1986; Hart & Radosevich 1987; Oechel 1988). A distinct seasonal drought is also common in mediterranean-climate Chile (Poole et al. 1981). In mountain fynbos xylem pressure potentials seldom fall below -2.0 MPa for deep-rooted proteoid shrubs and -4.0 for shallow-rooted ericoid and restioid species (Miller et al. 1983; Miller 1985; Van der Heyden & Lewis in press; Richardson & Kruger, submitted; R.E. Smith, unpublished data). In general, soil moisture in mountain fynbos areas appears to be recharged rapidly following relatively light rainfall events (Richardson & Kruger, submitted).

Another feature of fynbos community structure (at least in the Western Cape), which is shared with other mediterranean-climate regions, is the poor representation in the field layer of vigorous and productive C_4 grasses (Vogel et al. 1978; Cowling 1983). These fast-growing species can potentially out-compete woody plants, especially the relatively slow growing gymnosperms such as pines, in the regeneration phase (references in Richardson & Bond, submitted). Many C_4 grasslands could, like mountain fynbos, support woody vegetation with a much higher biomass. Unlike mountain fynbos, however, the incorporation of these woody species is often prevented by the competitive strength of the grasses (Bond 1989).

We have identified reasons why mountain fynbos can support communities of plants with much greater resource use efficiency than that exhibited by the natural communities. There remain, however, fundamental barriers for the incorporation of these alien organisms into fynbos communities.

7.3.3. How is mountain fynbos invaded ?

We believe that the process of invasion in mountain fynbos can be explained by examining the dynamics of fynbos communities in relation to fire. There has been much comment on the floristic complexity of fynbos communities, particularly in the southwestern part of the biome (e.g. Taylor 1978; Kruger 1979; Campbell 1985). At the landscape level it is possible to recognize broadly-defined structural and floristic formations that are predictably related to environmental factors (e.g. Taylor 1969; Boucher 1972; Cowling 1984; Campbell 1985; Cowling et al. 1988; McDonald 1988). At the level of the community (or more specifically the phytosociologically-defined association) the characterization of fynbos vegetation becomes intractable. Both Taylor (1969) and Boucher (1972), who have conducted detailed phytosociological studies in large areas (c. 8000 ha and 24000 ha respectively) of fynbos in the southwestern Cape, bemoan the high within-community floristic variation and associated difficulties in defining lower level phytosociological units. Witness the large number of general and infrequent species (equivalent to noise) in Boucher's (1972) and Van Wilgen & Kruger's (1985) phytosociological tables.

Cowling (1987) has argued that much of the floristic complexity of fynbos vegetation could result from differential post-fire recruitment of co-existing species. Thus, each fire [(or parts of the same fire; Hobbs & Atkins (1988)] could be unique in its effects on recruitment levels as determined by pre-fire factors (e.g. sizes of seed banks), the fire itself (e.g. heat pulse for breaking seed dormancy or releasing seed), and post-fire conditions (e.g. drought-induced seedling mortality or predator dynamics). The result could be that over a number of fire cycles each species would encounter at least one set of conditions favourable for recruitment: competitive hierarchies would fluctuate with the changing relative abundances of species and co-existence would be maintained. This model incorporates elements of Chesson & Warner's (1981) lottery model with a storage effect (Warner & Chesson 1985).

At present, all the evidence for post-fire variation in recruitment of fynbos species comes from non-sprouting, serotinous, overstorey Proteaceae (Protea and Leucadendron spp.) (Bond et al. 1985; Van Wilgen & Viviers 1985; Le Maitre 1988; Cowling & Gxaba in prep.). Post-fire recruitment of this guild is highly variable. Cowling & Gxaba (in prep.) have demonstrated high spatial variation of Leucadendron laureolum recruitment after a single summer fire. They concluded that this species shows "drifting clouds of species abundance", the location, shape and density of the clouds varying after each fire. Moreover, dense stands of this species reduce significantly the understorey species richness (see also Campbell & van der Muelen 1980; Esler & Cowling 1989). Thus, a vagile and marauding population of an overstorey species imposes on the landscape a dynamic array of habitats which promotes community-wide floristic patchiness (Cowling & Gxaba in prep.). Many of these overstorey proteoids are capable of forming dense thickets (or being driven to local extinction) in a wide range of communities, phytosociologically defined by the understorey flora. Examples in the southwestern Cape fynbos are Leucadendron laureolum (Taylor 1969; Boucher 1972; Cowling & Gxaba in prep.), Protea repens (Boucher 1972) and P. neriifolia (McDonald 1988).

Mountain fynbos communities with their high proportion of, and dominance by, non-sprouting species (Kruger & Bigalke 1984) can show large fire-induced changes in population sizes of component species. In Yodzis's (1986) terms, the communities show a high degree of founder control where community structure is essentially a relict of the original colonization event (fire). Founder control would be most evident in the small-leaved understorey shrub component which includes numerous structurally (and possibly functionally) similar species which could be regarded as trophically equivalent (sensu Shmida & Ellner 1984, see Cowling 1987). Amongst these species, inter- and intra-specific competition would be broadly similar, resulting in no dominance interactions (cf. Yodzis 1986). Dominance control is introduced by the overstorey component which is capable of suppressing or even eliminating understorey species.

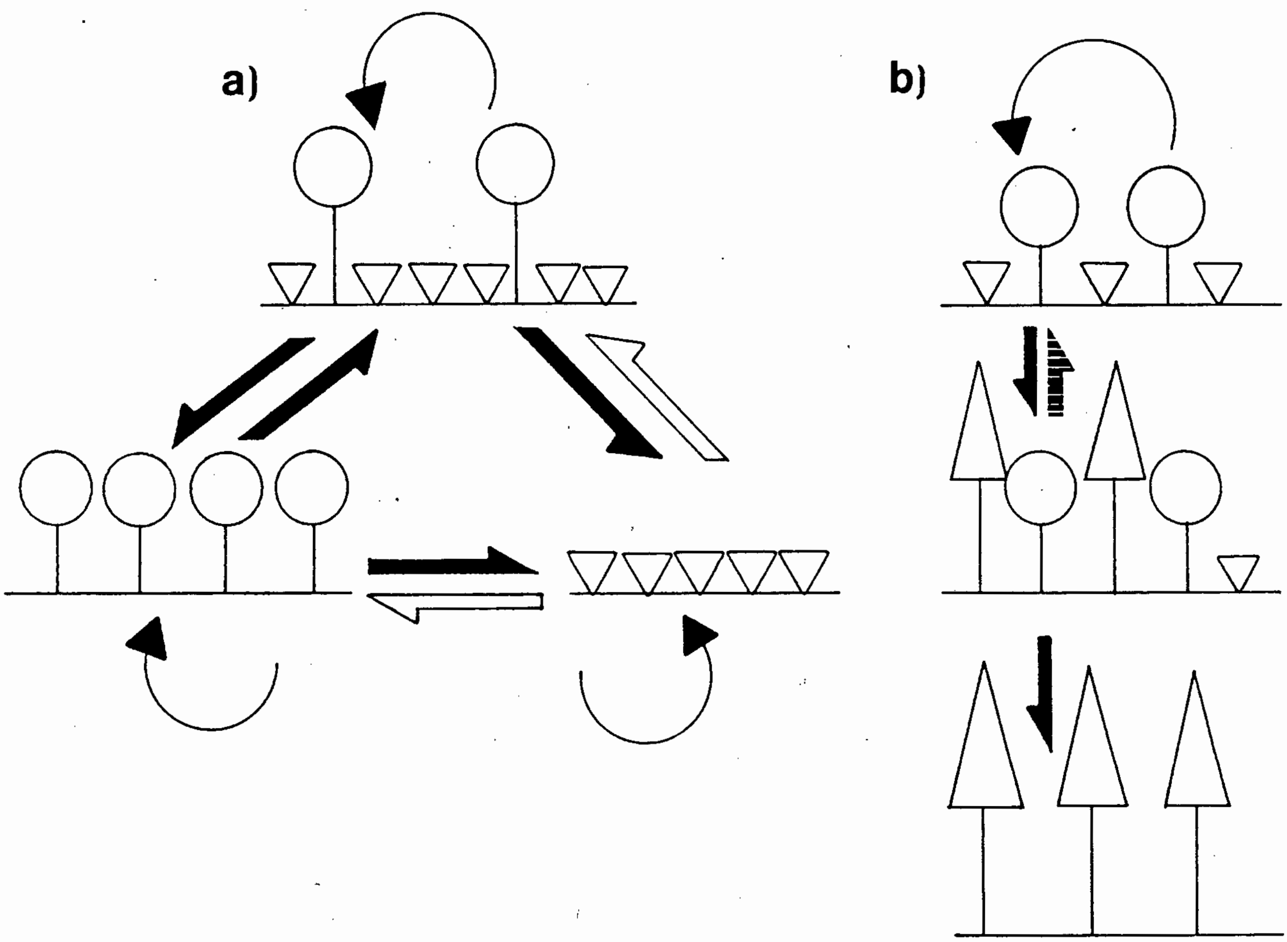


Figure 7.3. Schematic representation of fire-induced changes in the structure of mountain fynbos shrublands: a) in the absence of invasive pines (note cyclical replacement processes); b) invaded by pines. The overstorey shrub is a non-sprouting serotinous proteoid. Solid arrows indicate change in the absence of (re)invasion of components; unshaded arrows indicate change requiring (re)invasion of components; dashed arrow indicates where change (removal of pines) can be affected by man.

What are the implications of this non-equilibrium model of fynbos species population dynamics for invasion by introduced species ? The fire-induced variation in the floristic structure of fynbos communities implies that local extinction of community components and invasion (or re-invasion) is a normal and regular process. We argue that mountain fynbos communities, which are vulnerable to invasion and suppression by indigenous species, are readily invaded by introduced species, particularly if the latter exert strong dominance interactions. The effect of the aliens on reducing species richness (Cowling et al. 1976; Richardson et al. 1989) and on other aspects of community structure and functioning (Breytenbach 1986; Macdonald & Richardson 1986; Richardson & Van Wilgen 1986; Versfeld & Van Wilgen 1986) would persist if they are not prone to fire-induced local extinction. The aliens initially behave much like the indigenous shrubs but, because the former are well buffered against fire-induced population crashes (because of their short juvenile periods and massive reserves of viable seeds), the non-equilibrium status of natural communities is disrupted, resulting in new depauperate steady-states (Figure 7.3).

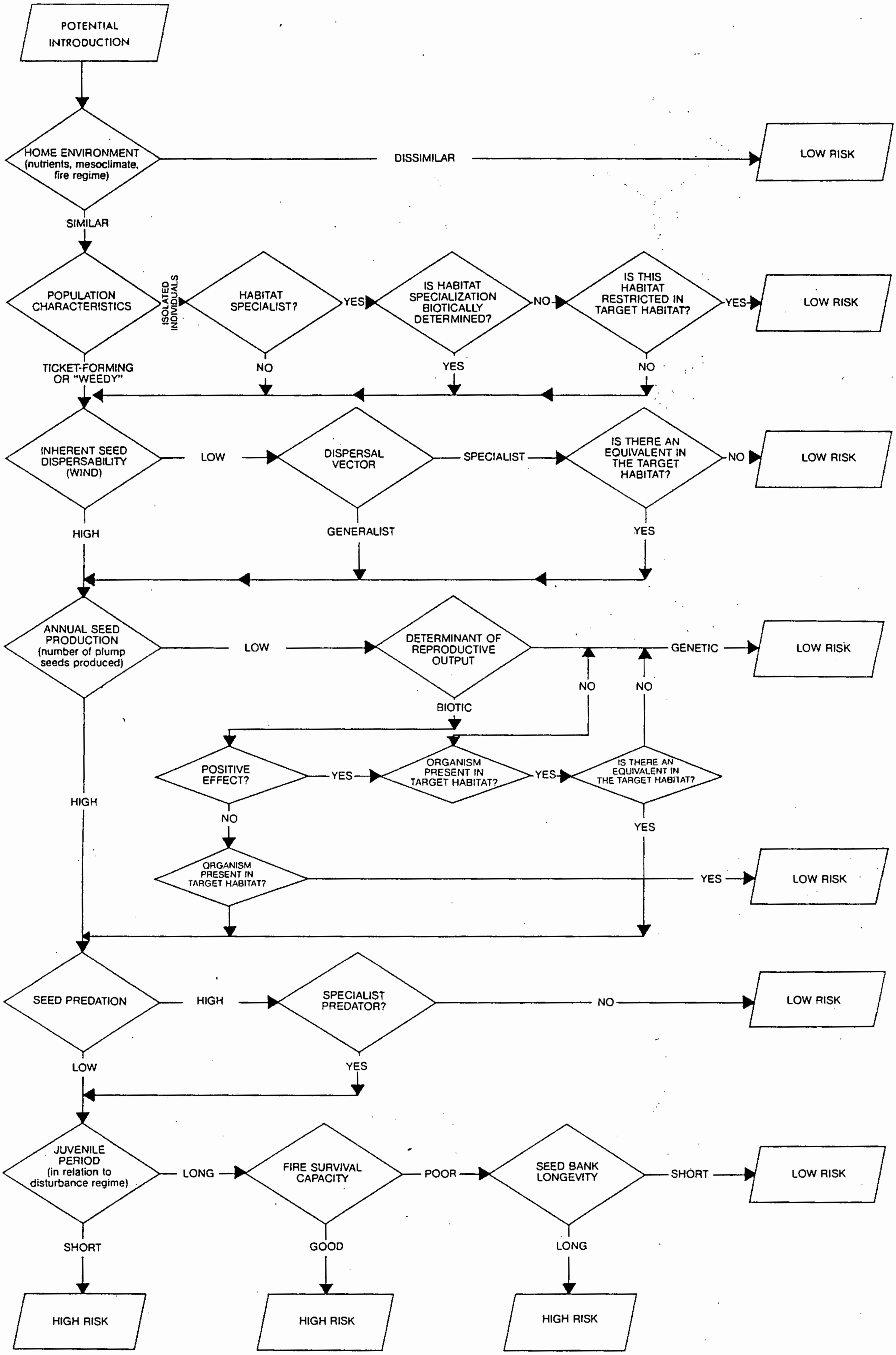
7.4. WHICH SPECIES INVADE ?

7.4.1. Describing a good invader

A major question of both applied and theoretical importance, is "which species will invade ?". Several authors, most notably entomologists, have argued that this question is almost impossible to answer (Ehrlich 1986; Simberloff 1986; Crawley 1987b). However, while accepting that biological invasions are highly idiosyncratic, we believe that attempts must be made to generalize and predict. This is especially crucial for mountain fynbos where there will be a sustained need for the introduction of trees and shrubs for forestry and horticulture. Many of the species are likely to come from environmentally analogous regions.

A profile of a successful invader in a particular environment can be developed a priori from theoretical considerations and a posteriori from empirical data (Baker & Stebbins 1965; Baker 1986; Bazzaz 1986). From a theoretical point of view, a good potential invader must be physiologically capable of growth and reproduction in the target environment and must possess life history attributes which permit population growth under the prevailing disturbance regime (Kruger et al. 1986). Empirical data for the biological characterization of successful invaders comes from natural experiments involving numerous introductions over long periods. Using both approaches, we have compiled a flow diagram to distinguish between species with low and high probabilities of becoming invaders in mountain fynbos (Figure 7.4). The chart

Figure 7.4. Proposed protocol of risk assessment for determining the likelihood of an introduced species invading mountain fynbos. The flow diagram distinguishes between low risk and high risk species [those with low and high probabilities of becoming major weeds (sensu Baker 1986; Kruger et al. 1986)] in mountain fynbos. Note that high risk introductions may possess either a short juvenile period or a good capacity for surviving fires or long seed bank longevity (or a combination of these attributes).


POTENTIAL INTRODUCTION
HOME ENVIRONMENT (nutrients, mesoclimate, fire regime)
DISSIMILAR
LOW RISK
SIMILAR
POPULATION CHARACTERISTICS
ISOLATED INDIVIDUALS
HABITAT SPECIALIST?
YES
IS HABITAT SPECIALIZATION BIOTICALLY DETERMINED?
NO
IS THIS HABITAT RESTRICTED IN TARGET HABITAT?
YES
LOW RISK
TICKET-FORMING OR "WEEDY"
NO
YES
NO
INHERENT SEED DISPERSABILITY (WIND)
LOW
DISPERSAL VECTOR
SPECIALIST
IS THERE AN EQUIVALENT IN THE TARGET HABITAT?
NO
LOW RISK
HIGH
GENERALIST
YES
ANNUAL SEED PRODUCTION (number of plump seeds produced)
LOW
DETERMINANT OF REPRODUCTIVE OUTPUT
GENETIC
LOW RISK
NO
NO
BIOTIC
POSITIVE EFFECT?
YES
ORGANISM PRESENT IN TARGET HABITAT?
YES
IS THERE AN EQUIVALENT IN THE TARGET HABITAT?
HIGH
NO
YES
ORGANISM PRESENT IN TARGET HABITAT?
YES
LOW RISK
SEED PREDATION
HIGH
SPECIALIST PREDATOR?
NO
LOW RISK
LOW
YES
JUVENILE PERIOD (in relation to disturbance regime)
LONG
FIRE SURVIVAL CAPACITY
POOR
SEED BANK LONGEVITY
SHORT
LOW RISK
SHORT
GOOD
LONG
HIGH RISK
HIGH RISK
HIGH RISK

defines a research protocol for screening potential introductions.

What attributes would we expect a successful invader of mountain fynbos to have ? The disturbance regime in mountain fynbos is overwhelmingly characterized by intense fires at intervals of 10 to 30 years (Kruger & Bigalke 1984) Invasive species must have life history attributes which can cope with this fire regime. Firstly, a successful invader would have a juvenile period of less than about eight years in order to ensure adequate seed production between fires (see Kruger & Bigalke 1984). Species which produce large seed crops should be more invasive than species with a low reproductive output. Relative to spontaneous seed release, serotiny (canopy storage of overlapping seed crops) maximizes seed available for the next generation, provided fires occur at intervals less than the life span of the species (Lamont et al., in press). Since mountain fynbos fires occur at intervals far less than the potential life spans of all trees and shrubs, serotiny must be seen as a trait enhancing the invasiveness of these species. High seed dispersability would enhance colonization and hence invasive success (Van Wilgen and Siegfried 1986; Richardson et al. 1987). Finally, for those species without complete serotiny, the ability to establish and reach reproductive maturity between fires would also promote invasibility.

In the next section we describe the characteristics of invasive trees and shrubs in mountain fynbos. We evaluate the relative success as invaders of different species of Hakea and Pinus using the risk assessment model (Figure 7.4) as a framework for our discussion.

7.4.2. Those that have made it: pines and hakeas

Taxa of the genera Hakea (Proteaceae) and Pinus (Pinaceae) have been particularly successful as weeds in mountain fynbos (Appendix 7.1). Several genera of both taxa have been introduced, some of which have become major weeds while others have shown moderate invasion or have not invaded at all. Are there general rules that govern the expression of invasive success ?

In the case of Hakea, four species (H. sericea, H. gibbosa and H. suaveolens and H. salicifolia) were introduced to the Cape between 1840 and 1860. Hakea sericea is highly invasive, H. gibbosa and H. suaveolens are moderately invasive and H. salicifolia does not invade mountain fynbos. The major weed,

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The dominance of trees and shrubs, and the absence of herbs and grasses in the invasive flora of mountain fynbos (Kruger et al. 1988) is unusual when compared with those of other southern Africa biomes (Macdonald et al. 1986) or with other mediterranean-climate regions (cf. Groves 1986b; Mooney et al. 1986; Kruger et al. 1988). Historical and cultural differences which have influenced the history of introductions to mediterranean-climate regions, make the evaluation of the anomalous success of invasive trees in the Cape difficult (Kruger et al. 1988). Trees such as pines were introduced earlier and in greater numbers to the Cape (see Shaughnessy 1980, 1986) than to other mediterranean-climate regions (cf. Groves 1986a,b; Mooney et al. 1986) and this may explain, at least partially, their inordinate success as invaders (Kruger et al. 1988). Many other hypotheses have been put forward to explain the remarkable success of introduced trees and shrubs as invaders in fynbos (Table 7.1). Although we accept some elements of these hypotheses, most are untestable and none provide a comprehensive explanation of the phenomenon. To achieve a meaningful understanding of the processes involved in the invasion of mountain fynbos communities we examine patterns of resource utilization and the spatial and temporal dynamics of communities.

7.3.2. Why is mountain fynbos invasible ?

Fynbos plant communities differ in some important characteristics when compared with communities in other mediterranean-climate regions. One of the most remarkable features of fynbos vegetation is its low height (Milewski 1981; Cowling & Campbell 1980). This is perhaps best demonstrated by comparing vegetation formations in the Cape with those in environmentally equivalent regions of Western Australia. Generally, Australian formations are an order of magnitude taller than the Cape for matched sites (Figure 7.1). For example, proteoid fynbos in the Cape (Campbell 1985) is the predominant formation over a wide rainfall range on sand. Corresponding formations in Australia range from structurally-similar scrub-heath at lower rainfalls (c. 450 mm/yr) to woodlands and forests up to 18 times taller than fynbos at higher rainfalls. What is striking is the predominance of trees in West Australia where rainfall exceeds about 600 mm on sands and granites. Trees are entirely lacking from the Cape except for the trees in closed forests on the wettest sites on granites (Campbell _et al_. 1979; McKenzie _et al_. 1977). There is no conclusive evidence that the Cape, and mountain fynbos in particular, supported taller vegetation composed of trees during the last glacial - interglacial cycle (Scholtz 1986). Fynbos communities are also characterized by much lower biomass than other mediterranean-climate regions for matched sites. The above-ground biomass in mature (but not senescent) mountain fynbos shrublands range from 15000 to 51000 kg/ha (Kruger 1977; Van Wilgen 1982; Van Wilgen _et al_. 1985). This is lower than in most structurally-similar communities in the other regions (_cf_. Ehleringer & Mooney 1983) which have richer soils but lower rainfall, and an order of magnitude less than areas within other mediterranean-climate regions with similar rainfall (Ehleringer & Mooney 1983). Most mountain fynbos areas receive more than 800 mm of rainfall per year. Equivalent habitats in the other regions support forest with much higher biomass. For example, above-ground biomass in dense pine forests in mediterranean-climate France with an annual rainfall of around 1100 mm is up to two orders of magnitude greater than that of fynbos communities in parts of the Cape with an equivalent annual rainfall (_cf_. L. Trabaud unpublished; Van Wilgen _et al_. 1985). Similarly, in lower rainfall (<800 mm/yr) regions [e.g. dry heaths in Australia (Specht 1969), _Ceanothus_ chaparral in California (Gray 1982) and Chilean matorral (Kummerow _et al_. (1981)] above-ground biomass of fynbos communities is markedly lower (_cf_. Kruger 1977; Rutherford 1978; Van Wilgen _et al_. 1985).

Annual biomass increments of between 1000 and 4000 kg/ha in the first few years after fire in fynbos (Kruger 1977) approximate or slightly exceed those

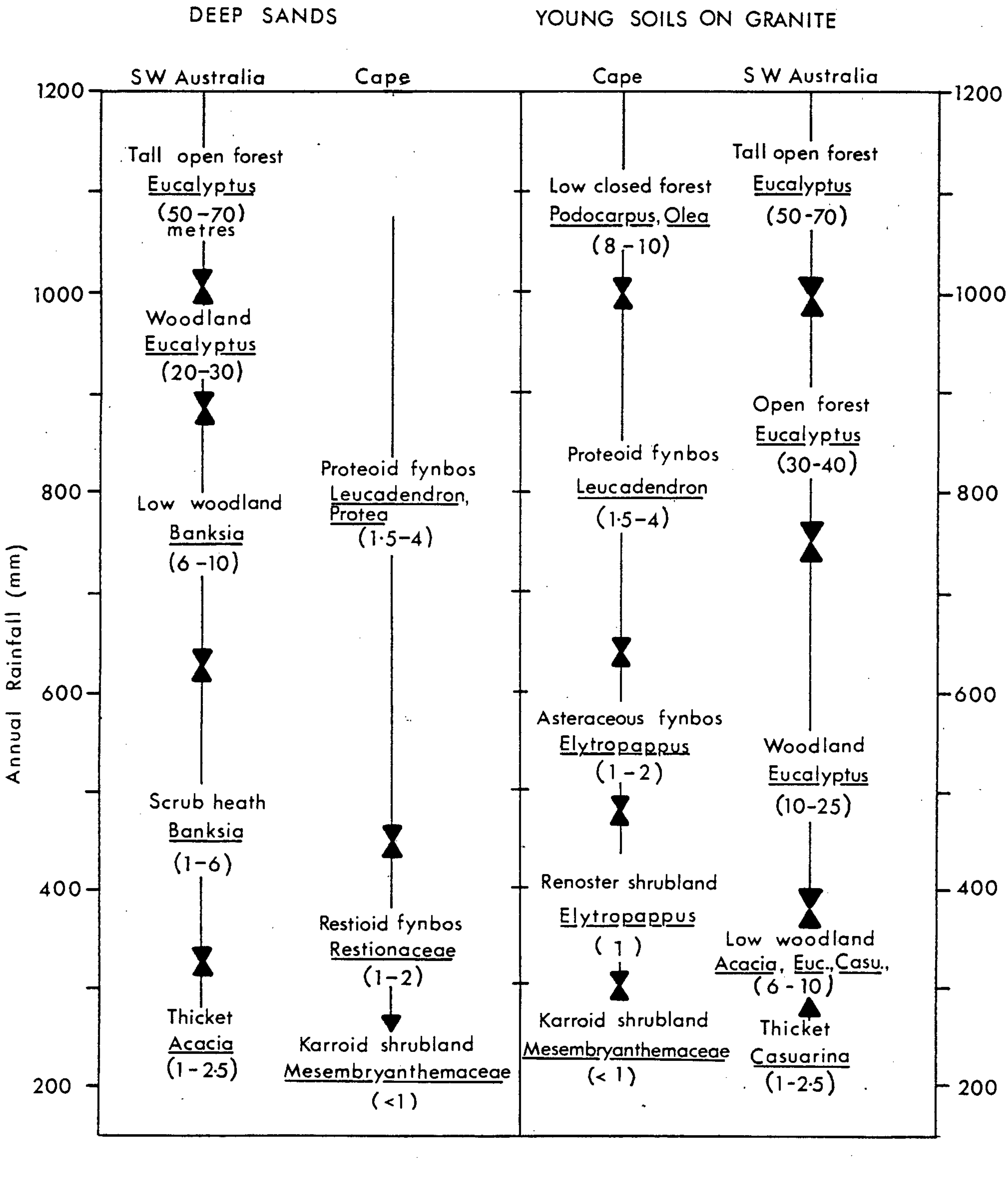


Figure 7.1. A comparison of structural formations on two substrata and across a rainfall gradient for lowland (0-300 m) sites in mediterranean south-western Australia and the Cape, South Africa. Adapted from Beard (1976; 1981; 1983; 1984), Moll et al. (1984) and Campbell (1985).

in chaparral, garrigue, heath and malee-broombush communities (Long _et al_. 1967; Specht 1969; Specht 1981; Ehleringer & Mooney 1983). Fynbos shrubs have leaves with similar photosynthetic capacities to leaves from evergreen shrubs in other mediterranean-climate regions (Mooney _et al_. 1983) but are apparently constrained by the need to survive fire and to exploit the brief period after fire. The fynbos shrubs appear to lack the capacity (either as individuals or as a community) to optimize resource use later in stand development. Invasion of mountain fynbos by _Acacia saligna_, _A. longifolia_ and _Hakea sericea_ can double or treble the total above-ground plant biomass (Milton & Siegfried 1981; Van Wilgen & Richardson 1985) and the biomass in self-sown pine forests can be up to five times that of the pre-invasion fynbos (Versfeld & Van Wilgen 1986). Even as seedlings, introduced trees and shrubs show more rapid growth than those of indigenous fynbos shrubs. For example, seven years after a fire in mountain fynbos near Somerset West the mean height of the dominant indigenous shrub _Protea repens_ was 0.75 m whereas the introduced species _Pinus pinaster_ (1.75 m), _P. radiata_ (2.05 m) and _Hakea sericea_ (1.78 m) were much taller (Richardson 1985c and unpublished data).

What are the implications of the low resource use in fynbos for invasibility ? Clearly fynbos lies below the steady-state biomass predicted from precipitation (see Miller 1981 p.382). The low biomass in fynbos communities cannot be attributed to the nutrient-poor soils; Australian soils are poorer than those of the Cape [Di Castri (1981 p.22); Milewski & Cowling (1985); Lamont _et al_. (1985)]. It appears that resources, particularly moisture, are not fully exploited in fynbos ecosystems. The insular nature of the biome has probably prevented migrations of preadapted trees from other regions. The evolution of fynbos plant communities has been a gradual _in situ_ process, rather than a migration event (Deacon 1983), and for some reason fynbos taxa have not adapted to exploit fully the available resources.

Plant invasions in the fynbos have resulted in an increase in biomass so as to push the fynbos communities closer to the steady-state biomass predicted for the resource (precipitation) level (Figure 7.2). This process is readily achieved by the incorporation into fynbos of invasive trees and shrubs. In the mediterranean-climate regions of Australia and California plant invasions have not resulted in a large increases in steady-state biomass (_cf_. Groves 1986a,b; Mooney _et al_. 1986). We argue that in these regions the biomass of the natural communities approximates the steady-state biomass. For this reason, plant invasions in these regions usually involve the replacement of resident species by similar life forms or guilds [e.g. geophytes in Western Australian heath (kwongan) and Mediterranean grasses in chaparral].

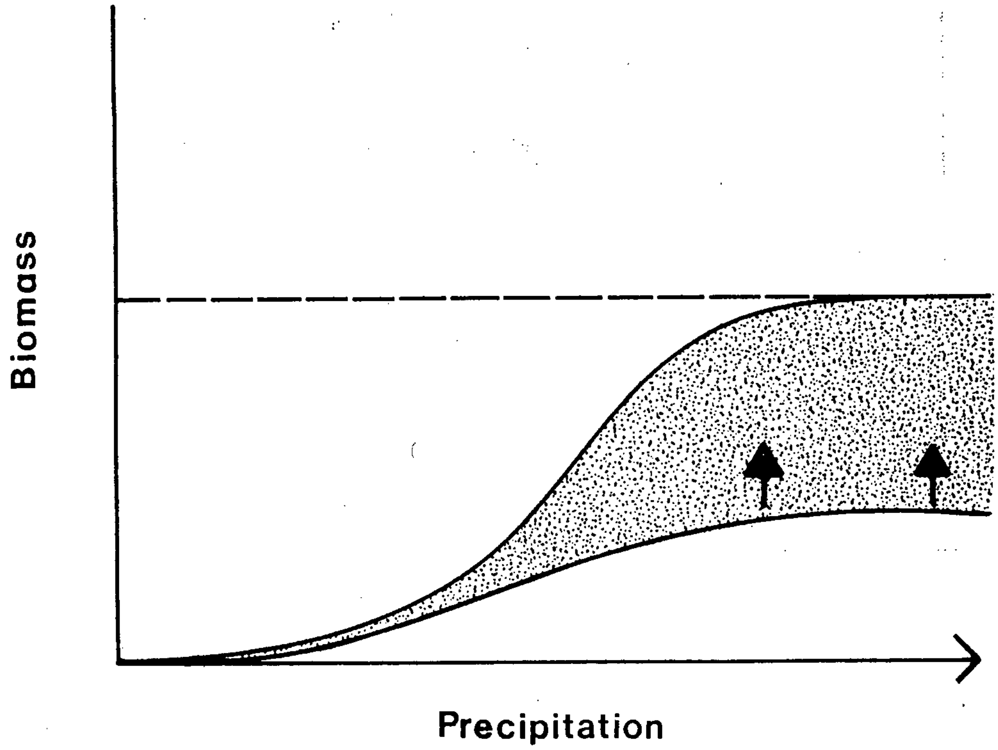


Figure 7.2. Hypothetical relationship between precipitation and above-ground plant biomass in terrestrial ecosystems. The upper curve defines the steady-state biomass (sensu Miller 1981) of biomass for any given rainfall. The lower curve defines the biomass / rainfall relationship for mountain fynbos. The shaded area represents the biomass that can still be incorporated into mountain fynbos communities through replacement of indigenous by introduced plants at different precipitation levels.

Another factor that appears to have permitted invasion of fynbos by trees and shrubs from other mediterranean-climate regions is the relatively mild moisture stress during summer which may alleviate seedling mortality. For example, California generally shows a distinct seasonal drought and plant xylem pressure potentials below -6.0 MPa are common (Poole et al. 1981; Davis & Mooney 1986; Hart & Radosevich 1987; Oechel 1988). A distinct seasonal drought is also common in mediterranean-climate Chile (Poole et al. 1981). In mountain fynbos xylem pressure potentials seldom fall below -2.0 MPa for deep-rooted proteoid shrubs and -4.0 for shallow-rooted ericoid and restioid species (Miller et al. 1983; Miller 1985; Van der Heyden & Lewis in press; Richardson & Kruger, submitted; R.E. Smith, unpublished data). In general, soil moisture in mountain fynbos areas appears to be recharged rapidly following relatively light rainfall events (Richardson & Kruger, submitted).

Another feature of fynbos community structure (at least in the Western Cape), which is shared with other mediterranean-climate regions, is the poor representation in the field layer of vigorous and productive C_4 grasses (Vogel et al. 1978; Cowling 1983). These fast-growing species can potentially outcompete woody plants, especially the relatively slow growing gymnosperms such as pines, in the regeneration phase (references in Richardson & Bond, submitted). Many C_4 grasslands could, like mountain fynbos, support woody vegetation with a much higher biomass. Unlike mountain fynbos, however, the incorporation of these woody species is often prevented by the competitive strength of the grasses (Bond 1989).

We have identified reasons why mountain fynbos can support communities of plants with much greater resource use efficiency than that exhibited by the natural communities. There remain, however, fundamental barriers for the incorporation of these alien organisms into fynbos communities.

7.3.3. How is mountain fynbos invaded ?

We believe that the process of invasion in mountain fynbos can be explained by examining the dynamics of fynbos communities in relation to fire. There has been much comment on the floristic complexity of fynbos communities, particularly in the southwestern part of the biome (e.g. Taylor 1978; Kruger 1979; Campbell 1985). At the landscape level it is possible to recognize broadly-defined structural and floristic formations that are predictably related to environmental factors (e.g. Taylor 1969; Boucher 1972; Cowling 1984; Campbell 1985; Cowling et al. 1988; McDonald 1988). At the level of the community (or more specifically the phytosociologically-defined association) the characterization of fynbos vegetation becomes intractable. Both Taylor (1969) and Boucher (1972), who have conducted detailed phytosociological studies in large areas (c. 8000 ha and 24000 ha respectively) of fynbos in the southwestern Cape, bemoan the high within-community floristic variation and associated difficulties in defining lower level phytosociological units. Witness the large number of general and infrequent species (equivalent to noise) in Boucher's (1972) and Van Wilgen & Kruger's (1985) phytosociological tables.

Cowling (1987) has argued that much of the floristic complexity of fynbos vegetation could result from differential post-fire recruitment of co-existing species. Thus, each fire [(or parts of the same fire; Hobbs & Atkins (1988)] could be unique in its effects on recruitment levels as determined by pre-fire factors (e.g. sizes of seed banks), the fire itself (e.g. heat pulse for breaking seed dormancy or releasing seed), and post-fire conditions (e.g. drought-induced seedling mortality or predator dynamics). The result could be that over a number of fire cycles each species would encounter at least one set of conditions favourable for recruitment: competitive hierarchies would fluctuate with the changing relative abundances of species and co-existence would be maintained. This model incorporates elements of Chesson & Warner's (1981) lottery model with a storage effect (Warner & Chesson 1985).

At present, all the evidence for post-fire variation in recruitment of fynbos species comes from non-sprouting, serotinous, overstorey Proteaceae (Protea and Leucadendron spp.) (Bond et al. 1985; Van Wilgen & Viviers 1985; Le Maitre 1988; Cowling & Gxaba in prep.). Post-fire recruitment of this guild is highly variable. Cowling & Gxaba (in prep.) have demonstrated high spatial variation of Leucadendron laureolum recruitment after a single summer fire. They concluded that this species shows "drifting clouds of species abundance", the location, shape and density of the clouds varying after each fire. Moreover, dense stands of this species reduce significantly the understorey species richness (see also Campbell & van der Muelen 1980; Esler & Cowling 1989). Thus, a vagile and marauding population of an overstorey species imposes on the landscape a dynamic array of habitats which promotes community-wide floristic patchiness (Cowling & Gxaba in prep.). Many of these overstorey proteoids are capable of forming dense thickets (or being driven to local extinction) in a wide range of communities, phytosociologically defined by the understorey flora. Examples in the southwestern Cape fynbos are Leucadendron laureolum (Taylor 1969; Boucher 1972; Cowling & Gxaba in prep.), Protea repens (Boucher 1972) and P. neriifolia (McDonald 1988).

Mountain fynbos communities with their high proportion of, and dominance by, non-sprouting species (Kruger & Bigalke 1984) can show large fire-induced changes in population sizes of component species. In Yodzis's (1986) terms, the communities show a high degree of founder control where community structure is essentially a relict of the original colonization event (fire). Founder control would be most evident in the small-leaved understorey shrub component which includes numerous structurally (and possibly functionally) similar species which could be regarded as trophically equivalent (sensu Shmida & Ellner 1984, see Cowling 1987). Amongst these species, inter- and intra-specific competition would be broadly similar, resulting in no dominance interactions (cf. Yodzis 1986). Dominance control is introduced by the overstorey component which is capable of suppressing or even eliminating understorey species.

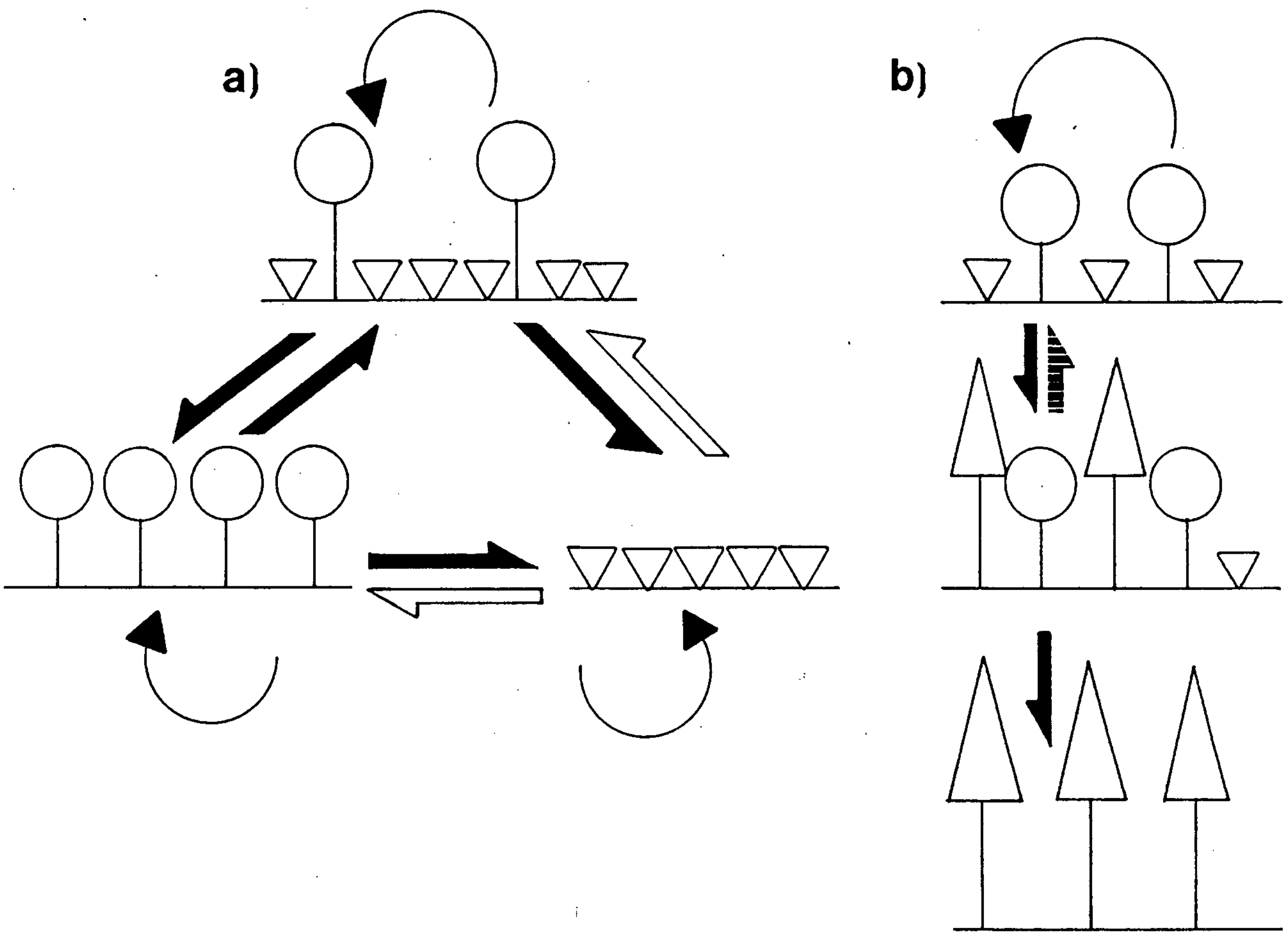


Figure 7.3. Schematic representation of fire-induced changes in the structure of mountain fynbos shrublands: a) in the absence of invasive pines (note cyclical replacement processes); b) invaded by pines. The overstorey shrub is a non-sprouting serotinous proteoid. Solid arrows indicate change in the absence of (re)invasion of components; unshaded arrows indicate change requiring (re)invasion of components; dashed arrow indicates where change (removal of pines) can be affected by man.

What are the implications of this non-equilibrium model of fynbos species population dynamics for invasion by introduced species ? The fire-induced variation in the floristic structure of fynbos communities implies that local extinction of community components and invasion (or re-invasion) is a normal and regular process. We argue that mountain fynbos communities, which are vulnerable to invasion and suppression by indigenous species, are readily invaded by introduced species, particularly if the latter exert strong dominance interactions. The effect of the aliens on reducing species richness (Cowling et al. 1976; Richardson et al. 1989) and on other aspects of community structure and functioning (Breytenbach 1986; Macdonald & Richardson 1986; Richardson & Van Wilgen 1986; Versfeld & Van Wilgen 1986) would persist if they are not prone to fire-induced local extinction. The aliens initially behave much like the indigenous shrubs but, because the former are well buffered against fire-induced population crashes (because of their short juvenile periods and massive reserves of viable seeds), the non-equilibrium status of natural communities is disrupted, resulting in new depauperate steady-states (Figure 7.3).

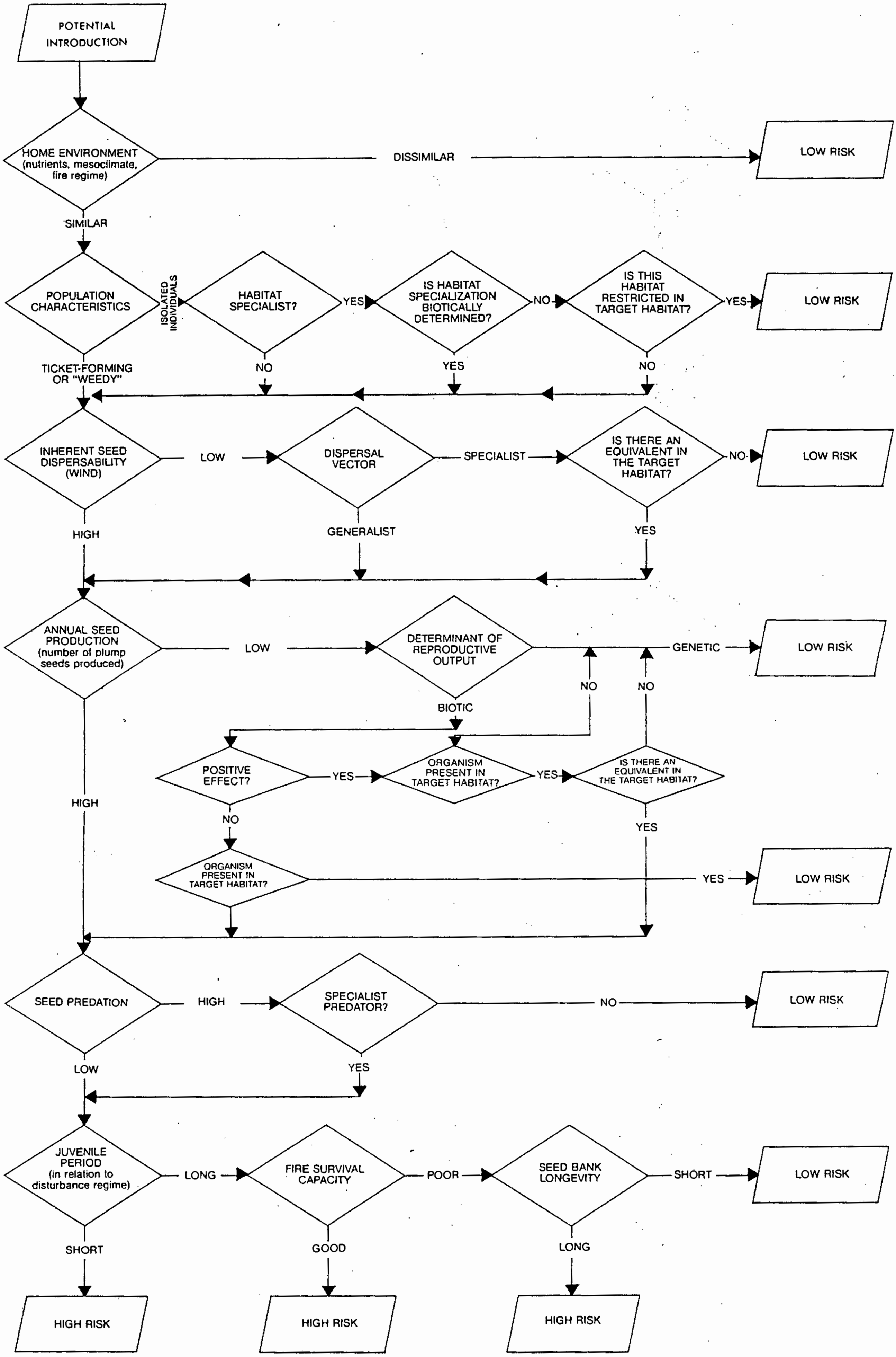
7.4. WHICH SPECIES INVADE ?

7.4.1. Describing a good invader

A major question of both applied and theoretical importance, is "which species will invade ?". Several authors, most notably entomologists, have argued that this question is almost impossible to answer (Ehrlich 1986; Simberloff 1986; Crawley 1987b). However, while accepting that biological invasions are highly idiosyncratic, we believe that attempts must be made to generalize and predict. This is especially crucial for mountain fynbos where there will be a sustained need for the introduction of trees and shrubs for forestry and horticulture. Many of the species are likely to come from environmentally analogous regions.

A profile of a successful invader in a particular environment can be developed a priori from theoretical considerations and a posteriori from empirical data (Baker & Stebbins 1965; Baker 1986; Bazzaz 1986). From a theoretical point of view, a good potential invader must be physiologically capable of growth and reproduction in the target environment and must possess life history attributes which permit population growth under the prevailing disturbance regime (Kruger et al. 1986). Empirical data for the biological characterization of successful invaders comes from natural experiments involving numerous introductions over long periods. Using both approaches, we have compiled a flow diagram to distinguish between species with low and high probabilities of becoming invaders in mountain fynbos (Figure 7.4). The chart

Figure 7.4. Proposed protocol of risk assessment for determining the likelihood of an introduced species invading mountain fynbos. The flow diagram distinguishes between low risk and high risk species [those with low and high probabilities of becoming major weeds (sensu Baker 1986; Kruger et al. 1986)] in mountain fynbos. Note that high risk introductions may possess either a short juvenile period or a good capacity for surviving fires or long seed bank longevity (or a combination of these attributes).



POTENTIAL INTRODUCTION
HOME ENVIRONMENT (nutrients, mesoclimate, fire regime)
DISSIMILAR
LOW RISK
SIMILAR
POPULATION CHARACTERISTICS
ISOLATED INDIVIDUALS
HABITAT SPECIALIST?
YES
IS HABITAT SPECIALIZATION BIOTICALLY DETERMINED?
NO
IS THIS HABITAT RESTRICTED IN TARGET HABITAT?
YES
LOW RISK
TICKET-FORMING OR "WEEDY"
NO
YES
NO
INHERENT SEED DISPERSABILITY (WIND)
LOW
DISPERSAL VECTOR
SPECIALIST
IS THERE AN EQUIVALENT IN THE TARGET HABITAT?
NO
LOW RISK
HIGH
GENERALIST
YES
ANNUAL SEED PRODUCTION (number of plump seeds produced)
LOW
DETERMINANT OF REPRODUCTIVE OUTPUT
GENETIC
LOW RISK
NO
NO
BIOTIC
POSITIVE EFFECT?
YES
ORGANISM PRESENT IN TARGET HABITAT?
YES
IS THERE AN EQUIVALENT IN THE TARGET HABITAT?
HIGH
NO
YES
ORGANISM PRESENT IN TARGET HABITAT?
YES
LOW RISK
SEED PREDATION
HIGH
SPECIALIST PREDATOR?
NO
LOW RISK
LOW
YES
JUVENILE PERIOD (in relation to disturbance regime)
LONG
FIRE SURVIVAL CAPACITY
POOR
SEED BANK LONGEVITY
SHORT
LOW RISK
SHORT
GOOD
LONG
HIGH RISK
HIGH RISK
HIGH RISK

defines a research protocol for screening potential introductions.

What attributes would we expect a successful invader of mountain fynbos to have ? The disturbance regime in mountain fynbos is overwhelmingly characterized by intense fires at intervals of 10 to 30 years (Kruger & Bigalke 1984) Invasive species must have life history attributes which can cope with this fire regime. Firstly, a successful invader would have a juvenile period of less than about eight years in order to ensure adequate seed production between fires (see Kruger & Bigalke 1984). Species which produce large seed crops should be more invasive than species with a low reproductive output. Relative to spontaneous seed release, serotiny (canopy storage of overlapping seed crops) maximizes seed available for the next generation, provided fires occur at intervals less than the life span of the species (Lamont _et al_., in press). Since mountain fynbos fires occur at intervals far less than the potential life spans of all trees and shrubs, serotiny must be seen as a trait enhancing the invasiveness of these species. High seed dispersability would enhance colonization and hence invasive success (Van Wilgen and Siegfried 1986; Richardson _et al_. 1987). Finally, for those species without complete serotiny, the ability to establish and reach reproductive maturity _between_ fires would also promote invasibility.

In the next section we describe the characteristics of invasive trees and shrubs in mountain fynbos. We evaluate the relative success as invaders of different species of _Hakea_ and _Pinus_ using the risk assessment model (Figure 7.4) as a framework for our discussion.

7.4.2. Those that have made it: pines and hakeas

Taxa of the genera _Hakea_ (Proteaceae) and _Pinus_ (Pinaceae) have been particularly successful as weeds in mountain fynbos (Appendix 7.1). Several genera of both taxa have been introduced, some of which have become major weeds while others have shown moderate invasion or have not invaded at all. Are there general rules that govern the expression of invasive success ?

In the case of _Hakea_, four species (_H. sericea_, _H. gibbosa_ and _H. suaveolens_ and _H. salicifolia_) were introduced to the Cape between 1840 and 1860. _Hakea sericea_ is highly invasive, _H. gibbosa_ and _H. suaveolens_ are moderately invasive and _H. salicifolia_ does not invade mountain fynbos. The major weed,

H. sericea, does differ from the other species in some important characteristics, notably in its relatively high seed production, short juvenile period and good ability to persist in an environment subjected to intense crown fires (Table 7.2).

Table 7.2. A comparison of available data on life history attributes of four introduced Hakea species. The order follows the flow chart in Figure 7.4. Sources of data are referenced in Richardson et al. (1987).

* Of the four species, only H. salicifolia appears to lack the necessary preadaptation to the mountain fynbos environment. However, because of the very limited information available on the ecology of this species in its natural range, we do not at this stage exclude this species as a potential HIGH RISK introduction.
* None of the species are inherently weedy in their native habitats but we consider this to be biotically determined (through seed predation). Hakea sericea has, however, established adventive populations in New Zealand.
* All four species have seeds that are well adapted for long-distance dispersal by wind.
* The relative annual seed production of the four species in Australia is unknown. In the Cape H. salicifolia and H. sericea are much more fecund than the other two species.
* All four species have host specific pre-dispersal seed predators. Pre-dispersal seed predation is generally low and generalist predators have a very small influence on the seed bank.
* Hakea gibbosa and H. sericea have short juvenile periods (2 years) compared to H. salicifolia and H. suaveolens (c. 6 years).
* All species are fire-sensitive in that seedlings and adults are killed by fire. Hakea salicifolia differs markedly from the other three species in its capacity to persist in an environment subject to intense crown fires; The relatively small follicles provide insufficient insulation of seeds.
* All species are serotinous but H. salicifolia much less so than the other three species. For the other three species, a large proportion of the seeds accumulated in the canopy are held in a viable condition for at least the average inter-fire period in mountain fynbos.

Many Pinus species have been introduced to the Cape. Most species have become naturalized but three species (P. pinaster, P. radiata and P. halepensis) readily invade mountain fynbos. The major invasive pines are all from environmentally similar regions and all show weedy behaviour in other parts of the world (inside and outside their natural ranges). These species, with several others, form a distinguishable group within the genus Pinus and may be described as fire-resilient pines with small seeds, low seed wing loadings, short juvenile periods, moderate to high degrees of serotiny and poor fire-tolerance as adults (Richardson et al., submitted). Species of Hakea and Pinus with canopy-stored seed (serotiny) are prominent among successful invasive plants in mountain fynbos (Appendix 7.1). In these species fire stimulates the release of seeds onto the nutrient-rich and competition-free ash bed which provides a good environment for germination and establishment (Bond 1985; Lamont et al. in press). Seedling recruitment of these species is mainly in the immediate post-fire phase, and leads to the formation of even-aged thickets (Kruger 1977; Richardson & Brown 1986; Richardson 1988; Richardson et al., submitted). Sporadic inter-fire recruitment does occur [e.g. Kruger (1977); Richardson & Brown (1986); Richardson et al. (submitted) for Pinus spp.] and this contributes to spread and population growth through the establishment of new satellite seed banks. For most species, juvenile periods (the time between germination and the production of viable seeds) is less than 7 years. This facilitates the establishment of new seed sources between fires, which seldom occur at intervals of less than 8 years. As would be predicted, those species with longer juvenile periods, such as Pinus halepensis, are not widespread; persistence is achieved either through fire survival, which is rare, or through rapid immigration of seeds following local extinction (Richardson 1988). The serotinous invaders have winged seeds that are easily dispersed over several kilometres by wind (Kruger 1977; Richardson & Brown 1986; Van Wilgen & Siegfried 1986).

The perception of what makes a successful invader in mountain fynbos that emerges from the empirical analysis of past introductions corroborates the theoretical considerations presented above. We can, thus, identify characteristics that are associated with invasive success within the guild of serotinous trees and shrubs from mediterranean-climate regions. For some taxa risk assessment based on life history attributes is relatively straightforward. For example, we consider any Pinus species with the attributes described above to be high risk introductions. We would reason that all previous introductions of pines that possess this set of attributes (and that have enjoyed sufficient initial dissemination by man) have led to major invasions, and that further introductions of this type of species would also have a high probability of invading. Some of the species assigned high risk status would probably fail to achieve major weed status (sensu Baker 1986); we would attribute this to population responses and interactions in the target habitat which are difficult to quantify and impossible to predict (see Richardson et al., submitted). We would be relatively confident to assign low risk status to non-serotinous pines with large seeds, high seed/wing loadings, long juvenile periods and moderate to good fire tolerance as adults. We would expect that some low risk taxa would invade moderately due to unpredictable interactions; such has been the case for P. pinea which has established an opportunistic mutualism with another introduced species, the squirrel Sciurus carolinensis (Richardson et al., submitted). We would, however, be relatively confident of excluding potential major weeds among pines in the screening process. But pines are perhaps a special case; the biology and ecology of many species have been well studied, largely because of the economic importance of the genus. Few other genera of trees and shrubs have been studied this well. The thorough evaluation of decisions in the flow diagram (Figure 7.4) requires a good data base of biological and ecological information, ideally for a representative sample of taxa in the genus containing the species to be screened.

A rigorous evaluation of the risk assessment model requires independent data on the biological attributes of species and their invasive success. A genus with several potential invaders of mountain fynbos that has been relatively well studied is Banksia (Proteaceae). Only recently have a few species been introduced on a limited scale, so it is not possible to assess invasive success at this stage. However, we can evaluate the relative risk of invasibility for future introductions.

7.4.3. Banksias as potential invaders

Sixty of the 75 described species of Banksia (Proteaceae) are endemic to south-western Australia (Taylor & Hopper 1988) where they are often the dominant plants in fire-prone scrub-heath and woodland on nutrient poor soils (Beard 1984). The environments in which they grow share many features with mountain fynbos (nutrient-poor soils, winter rainfall, fire regime) (Milewski 1979; Lamont et al. 1985; Milewski & Cowling 1985). Many banksias have economic value as cut flowers (Burgman & Hopper 1982). Some of these have been introduced to the Cape (Appendix 7.2) and the scope and extent of these introductions are likely to increase due the proximity of the Cape to European markets (B. Gibson, pers. comm.). Banksias have been planted in orchards in mountain fynbos in the last decade (pers. obs.) but there is as yet no evidence of invasions.

We believe that many banksias possess life history attributes which make them high risk introductions in mountain fynbos. For example, as in Pinus and

Hakea, many banksias are highly serotinous and maintain large canopy-stored seed banks (Lamont et al. 1985; Cowling et al. 1989). Furthermore, the seeds of banksias are stored in massive, heat-resistant cones, and even the most intense fires do not result in seed death (Enright & Lamont 1989a). Seed predators are highly specialized and almost no predation occurs after follicle ripening (Scott 1982), with the result that much of the canopy-stored seed crop is maintained intact. Finally, in many banksias seeds are retained in the cones after fires until the onset of cool, wet (winter) conditions which are optimal for germination and establishment (Cowling & Lamont 1985a). Thus, post-dispersal seed predation is minimized irrespective of the season of burn (cf. Bond 1984; Cowling & Lamont 1987).

In order to assess the invasive potential of banksias, we collated life history data for 67 south-western Australian taxa (species, subspecies, varieties and ecotypes). For each taxon we noted the juvenile period, number of viable seeds per mature (c. 15 years old) plant, degree of serotiny, seed area, wing area, maximum height and regeneration mode (Appendix 7.2). With the exception of seeds/plant, data for the attributes were derived from published sources (see Appendix 7.2 for references). Published data on seeds/plant were available for 11 taxa only (Cowling et al. 1989). For the remaining taxa we made rough estimates of the viable seed loads on the basis of published data on fruits/cone and degree of serotiny, and estimates of cones/plant. All attributes were scored on an ordinal scale (see Appendix 7.2) and the data were subjected to correspondence analysis using the algorithms provided by Underhill and Peisach (1985). The regeneration mode (sprouter / non-sprouter) was not used in the correspondence analysis but was indicated for each taxon on the ordination diagram.

In the ordination, the taxa are separated along axis 1 mainly by seeds/plant, seed area, wing area and maximum height, and along axis 2 mainly by juvenile period (Figure 7.5). Degree of serotiny was not well expressed on either axis. Taxa in the bottom right hand corner of the ordination are tall serotinous shrubs with many, small (and presumably well-dispersed) seeds per plant. They also have short juvenile periods and are all killed by fire (Appendix 7.2). These taxa have many traits which would allow them to invade mountain fynbos (cf. Figure 7.4). Included in this group are many thicket-forming species which maintain very large viable seed banks [e.g. B. burdettii (Lamont & Barker 1988); B. hookeriana (Enright & Lamont 1989b); B. leptophylla

(Cowling et al. 1987)].

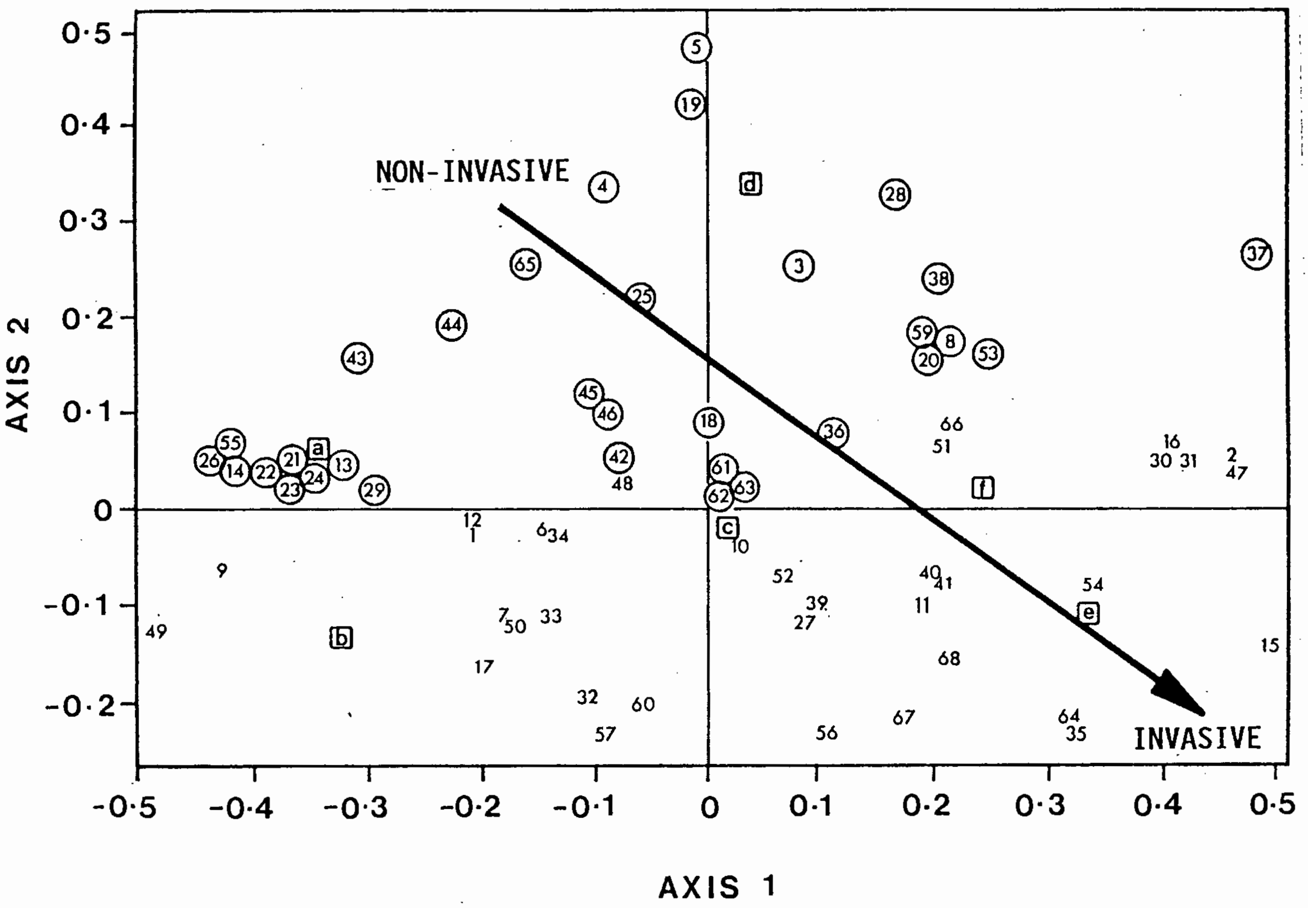


Figure 7.5. Plot of the first two axes from a correspondence analysis of a matrix of life history attributes of 69 Banksia taxa. Axes 1 and 2 account for 54% and 21% of the inertia respectively. Numbers correspond to taxa in Appendix 7.2. (p. 140). Encircled numbers indicate species which sprout from either lignotubers or epicormic buds. Life history attributes (blocks) are: a = seed area; b = wing area; c = degree of serotiny; d = juvenile period; e = viable seeds/plant; f = maximum height. The arrow reflects a likely gradient of increasing invasive potential in mountain fynbos.

Low sprouting shrubs with few, large seeds per plant, and long juvenile periods are clustered in the top left hand corner of the ordination diagram. These species are unlikely to become invasive in mountain fynbos (cf. Figure 7.4). This group includes the shrubby forms of the widespread species, B. menziesii and B. attenuata (Cowling et al. 1987; Enright & Lamont 1989b). Also in this group are B. elegans, which produces less than 1 seed per plant on average (Lamont & Barrett 1988), and B. tricuspis and has a juvenile period of over 20 years (Lamont & Van Leeuwen 1988).

Taxa occupying intermediate positions in the ordination diagram are presumably intermediate in terms of their invasive potential. For instance, species in the top right hand corner include weakly serotinous trees and shrubs with moderate to large seed crops and long juvenile periods. Those in the bottom left hand corner are mostly non-sprouting, serotinous dwarf to low shrubs with small crops and short juvenile periods. Of interest is the absence of species in the top left hand corner. This region would be characterized by dwarf to low shrubs with long juvenile periods and small seed crops. Clearly, this combination of life history attributes is not feasible for banksias in the southwestern Australian scrub-heath environment.

Our analysis has indicated a group of southwestern Australian banksias which could, if introduced and cultivated, become invaders in mountain fynbos. There are no empirical tests of our predictions but such experiments, if not tightly controlled, could bring about disruptions to mountain fynbos ecosystems in a way similar to Hakea invasions (Van Wilgen & Richardson 1985b; Breytenbach 1986; Macdonald & Richardson 1986; Versfeld & Van Wilgen 1986).

7.5. CONCLUSIONS

In this chapter we have attempted to achieve an understanding of plant invasions in mountain fynbos by examining why the environment can support dense stands of invasive trees and shrubs, and also how the invaders gain entry to natural plant communities. Our analysis both refutes and corroborates global generalizations regarding biological invasions. For example, the vulnerability of mountain fynbos to plant invasions is unrelated to species richness of the invaded community. Rather, it is probably a function of the dynamics of mountain fynbos where recurrent fire results in large spatial and temporal fluctuations in population sizes of component species. These stochastic fire-induced changes in community structure explain the ready incorporation of selected new (both indigenous and introduced) species into fynbos communities. However, these fires are part of the natural disturbance regime: there is no evidence that invasion in mountain fynbos is dependent on a man-induced alteration of this regime. Consistent with most other cases, invasions in mountain fynbos are influenced markedly by extrinsic factors (e.g. large-scale afforestation and man-assisted dissemination of pines, the geographic location of the Cape and its cultural history etc.).

A unique feature of mountain fynbos is its low steady-state biomass relative to analogous areas for a wide range of resource levels. Provided that introduced trees and shrubs can overcome establishment barriers, there are sufficient resources for the transformation of fynbos shrublands into tall shrub and forest formations. We believe that this profound imbalance in ecosystem-level resources, which is probably a function of historical events, explains these dramatic and unique transformations.

Through both theoretical and empirical analysis we have generated a biological profile of a successful invader. We have also developed a risk assessment model for screening new introductions. This model has the potential to identify with reasonably confidence those species with low invasive potential. Predicting which of the high risk species will become major weeds is more problematic. The success or failure of biological invasions may be determined by idiosyncratic events which sometimes confound predictions. For example, we note that some banksias that we have identified as high risk introductions (B. burdettii, B. coccinea and B. hookeriana) are readily infected by the pathogenic fungus Phytophthora cinnamomi in the Cape (Von Broembsen 1984b: Von Broembsen & Brits 1985). This may conceivably have a marked influence on invasive success. Nonetheless, we believe that an attempt at risk assessment, based on biological data of the potential introduction and an understanding of the structure of the target community is worthwhile. We hope that our contribution to the problem of biological invasions may go some way towards countering the pessimism expressed by Crawley (1987b) when he stated " What little we do know tends to suggest that we will never be able to predict which of a set of invaders is likely to establish, and which, having established, is likely to become the most abundant" (see also Simberloff 1986). Much of this pessimism can be attributed to attempts to generalize across taxonomic groups and geographic regions. Comparisons across systems have served their purpose but cannot provide the insight required to manage individual systems. We have shown that an analysis of invasive plants in mountain fynbos provides a reasonably coherent synthesis.

Appendix 7.1 Major invasive plants in fynbos, listed in order of importance (ranked according to current magnitude of invasion, extent of potential habitat and potential rate of spread; Macdonald & Jarman 1984). Species marked with asterisks regularly invade mountain fynbos. (the status in the whole fynbos biome may be different): (*) = occasionally invades, but usually confined to other vegetation types in the biome; * = forms dense stands over small areas; ** = a major weed. Numbers in round brackets indicate the source of data: 1 = P.J. Pieterse (unpublished data); 2 = Richardson et al (submitted); 3 = Richardson et al (1987); 4 = Johnson (1978); 5 = D.M. Richardson (unpublished data).

Species	Origin	Life form	Juvenile period (years)	Fresh seed mass (mg)	Seed storage strategy[1]	Dispersal agent[2]	Fire tolerance (adults)[3]	Sprouting ability[4]
Acacia saligna*	Australia	Tree/Shrub	3(1)	16.4(1)	S	Wa	0	2
Acacia longifolia**	Australia	Tree/Shrub	3(1)	10.8(1)	S	Wa/B	0	0
Acacia cyclops*	Australia	Tree/Shrub	3(1)	35.0(1)	S	B/Wa	0	1
Pinus pinaster**	Mediterranean Basin	Tree	6(2)	45.0(2)	C1	Wi	1	0
Leptospermum laevigatum*	Australia	Tree/Shrub	5(4)	0.3(5)	C1	Wa/Wi	0	0
Hakea sericea**	Australia	Tree/Shrub	2(3)	29.7(3)	C2	Wi	0	0
Pinus radiata**	California	Tree	5(2)	34.0(2)	C2	Wi	1	0
Pinus halependis*	Mediterranean Basin	Tree	15(2)	16.0(2)	C2	Wi	1	0
Paraserianthus lophantha	Australia	Tree	3(1)	82.0(1)	S	Wa	0	0
Acacia melanoxylon	Australia	Tree	3(1)	16.7(1)	S	Wa	0	2
Acacia mearnsii	Australia	Tree	3(1)	12.8(1)	S	Wa	0	2
Hakea gibbosa	Australia	Tree/Shrub	2(3)	37.1(3)	C2	Wi	0	0

Notes: [1] S = Soil-stored; C1 = canopy-stored (weakly serotinous); C2 = canopy-stored (strongly serotinous).

[2] B = birds; Wa = water; Wi = Wind.

[3] 0 = poor (thin bark); 1 = moderate; 2 = good (adult plants often survivce fires).

[4] 0 = does not sprout; 1 = occasionally sprouts, but sprouting does not ensure persistence after fire; 2 = good sprouting ability.

Appendix 7.2. Selected life history attributes of 69 Western Australian Banksia taxa. Juvenile period: 1 = < 5 yrs, 2 = 5-10 yrs, 3 = > 10 yrs; Viable seeds per plant: 1 = < 50, 2 = 50-500, 3 = > 500; Serotiny: 1 = non-serotinous, 2 = weakly, 3 = strongly serotinous. Seed and wing areas were obtained by measuring scaled drawings in George (1987). For the correspondence analysis, data on seed and wing areas were divided into four categories corresponding to the quartiles. Maximum plant height was categorized as follows: <= 1.0 m, 1-5 m and > 5m. Data were collated from: George (1981); Cowling & Lamont (1985b); Cowling et al. (1987); George (1987); Lamont & Barker (1988); Lamont & Barrett (1988); Lamont & Van Leeuwen (1988); Enright & Lamont (1989b); Stock et al. (1989) and the unpublished data and personal observations of S. Connell, R.M. Cowling and B.B. Lamont. Taxa marked with asterisks have already been introduced to the Cape (A. Brink, pers. comm.).

	Banksia Taxon	Juv. period	seeds/ plant	sero- tiny	seed area (mm^2)	wing area (mm^2)	max ht (m)	regen. mode
1	aculeata	2	2	3	125	959	2.0	1
2	ashbyi *	2	3	3	20	84	8.0	1
	attenuata							
3	tree	3	2	2	73	181	10.0	3
4	shrub	3	1	3	73	181	2.0	2
5	audax	3	1	3	45	87	1.0	2
6	baueri	2	2	3	62	346	2.0	1
7	baxteri *	1	2	3	125	268	4.0	1
8	benthamiana	2	2	3	31	104	4.0	2
9	blechnifolia	1	1	3	120	270	0.5	1
10	brownii	2	3	3	78	223	4.0	1
11	burdettii	1	3	3	51	116	4.0	1
12	caleyi	2	2	3	104	892	2.0	1
13	candolleana	2	1	3	115	859	1.3	2
14	chamaephyton	2	1	3	208	494	0.5	2
15	coccinea *	1	3	3	15	38	8.0	1
16	cuneata	2	3	3	14	70	5.0	1
17	dryandroides	1	2	3	54	206	1.0	1
18	elderiana	2	2	3	58	197	3.0	2
19	elegans	3	1	3	74	119	4.0	2
20	epica	2	2	3	41	116	2.0	1
	gardneri							
21	var. brevidentata	2	1	3	99	457	0.2	2
22	var. gardneri	2	1	3	99	457	0.2	2
23	var. hiemalis	2	1	3	99	457	0.2	2
24	goodii	2	1	3	95	383	0.2	2
25	grandis *	3	2	1	104	218	10.0	3
26	grossa	2	1	3	101	485	1.0	2
27	hookeriana *	1	2	3	50	132	3.0	1
28	ilicifolia	3	2	2	53	104	10.0	3
29	incana	2	1	3	45	318	0.7	2
	laevigata							
30	ssp. fuscolutea	2	3	3	15	92	3.5	1
31	ssp. laevigata	2	3	3	15	92	3.5	1

continued on next page ....

Appendix 7.2 (continued).

	Banksia Taxon	Juv. period	seeds/ plant	sero-tiny	seed area (mm^2)	wing area (mm^2)	max ht (m)	regen. mode
32	lanata	1	2	3	40	237	1.0	1
33	laricina	1	1	3	30	237	1.7	1
34	lemanniana	2	2	3	66	741	5.0	1
	leptophylla							
35	var. leptophylla	1	3	3	26	181	2.0	1
36	lindleyana	2	2	3	50	133	3.0	2
37	littoralis	3	3	1	18	58	12.0	3
38	lullfitzii	3	2	3	28	136	1.5	2
39	media	2	3	3	44	308	10.0	1
	meisneri							
40	var. ascendens	2	3	3	18	208	2.0	1
41	var. meisneri	2	3	3	18	208	2.0	1
	menziesii							
42	tree	2	2	2	117	223	10.0	3
43	shrub *	2	1	1	117	223	3.0	2
44	micrantha	2	1	3	92	177	0.6	2
	nutans							
45	var. cernuella	2	2	3	60	191	1.0	1
46	var. nutans	2	2	3	60	191	1.0	1
47	occidentalis	2	3	3	6	27	7.0	1
48	oreophila	2	2	3	52	253	3.0	1
49	petiolaris	1	1	3	163	275	0.4	1
50	pilostylis *	1	2	3	109	263	4.0	1
51	praemorsa	2	2	3	29	143	4.0	1
52	prionotes *	1	2	2	51	124	10.1	1
53	pulchella	2	2	3	24	58	1.0	1
54	quercifolia	1	2	3	11	86	3.0	1
55	repens	2	1	3	171	398	0.4	2
56	scabrella	1	3	3	39	235	2.0	1
57	sceptrum	1	2	3	46	353	5.0	1
58	seminuda	2	2	1	38	28	25.0	1
59	solandri	2	2	3	37	111	4.0	1
60	speciosa *	1	3	3	106	586	8.0	1
	sphaerocarpa							
61	var. caesia	2	2	3	39	200	2.0	2
62	var. dolichostyla	2	2	3	39	200	2.0	2
63	var. sphaerocarpa	2	2	3	39	200	2.0	2
64	telmatiaea	1	3	3	18	153	2.0	1
65	tricuspis	3	1	3	79	238	4.0	3
66	verticillata	2	2	2	16	182	5.0	1
67	victoriae	1	3	3	43	246	7.0	1
	violacea							
68	non-sprouting	1	2	3	18	158	1.5	1
69	lignotuberous	2	1	3	18	158	1.5	2

PART IV

THE CONSEQUENCES OF INVASION AND CONTROL PROGRAMMES

CHAPTER 8

EFFECTS OF THIRTY FIVE YEARS OF AFFORESTATION WITH *PINUS RADIATA* ON THE COMPOSITION OF MESIC MOUNTAIN FYNBOS NEAR STELLENBOSCH

CHAPTER 8 : EFFECTS OF THIRTY FIVE YEARS OF AFFORESTATION WITH PINUS RADIATA ON THE COMPOSITION OF MESIC MOUNTAIN FYNBOS NEAR STELLENBOSCH [1]

8.1. ABSTRACT

The fynbos vegetation of Biesievlei, Jonkershoek, was surveyed and described in 1945. In 1948 the catchment was afforested with Pinus radiata. This chapter presents results of a reassessment of the vegetation in 1984 using the same methods that were used in 1945. Afforestation has reduced the cover of the vegetation (excluding P. radiata) from 75 % to 20 %. The total number of species was reduced by 43 % from 298 to 126. At least 190 species found in 1945 were not found in 1984, and at least 18 species were added to the list. The mean plant density was reduced from 260 to 78 plants/m^2. Only stream bank vegetation, comprising mainly large-leaved sprouting shrubs, persists in a relatively unmodified state. Away from the stream, annuals, geophytes and hemicryptophytes were dominant. Dominant species in the pre-afforestation flora were not resilient to afforestation. Serotinous Proteaceae, woody small-leaved sprouting and myrmecochorous shrubs and large-leaved sprouting shrubs have been virtually eliminated. Certain groups may re-establish after clearfelling, but others, notably various groups of shrubs may have been permanently eliminated. The implications for weed control in conservation areas are discussed.

8.2. INTRODUCTION

The Jonkershoek Forest Influences Research Station, as it was then known, was established in 1935, chiefly to investigate the effects of afforestation on streamflow. Biesievlei is one of seven experimental catchments that were afforested for this purpose. A study of the fynbos vegetation of Biesievlei was undertaken in October-November 1945 (Rycroft 1950). This study was the first to analyze sclerophyllous fynbos vegetation using quantitative methods. Its main purpose was to develop methods for sampling vegetation in the fynbos but the results provide a unique opportunity to assess the effects of afforestation on the composition of the indigenous vegetation. Invasion by alien trees and shrubs is a major threat to the conservation of fynbos. Seagrief (1950), Cowling et al. (1976) and Milton (1976) have described fynbos plant communities under pine plantations or infestations near Grahamstown, on Table Mountain and at Jonkershoek respectively but no quantitative information is available on the effects of afforestation on the floristics and structure of indigenous vegetation. This study was aimed at quantifying the effects of 35 years of suppression by a closed-canopy stand of Pinus radiata. This may be used to represent the effects of severe invasion by alien trees and, by

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[1] *Publication status: Richardson, D.M. & Van Wilgen, B.W. (1986). Effects of thirty five years of afforestation with Pinus radiata on the composition of mesic mountain fynbos near Stellenbosch. South African Journal of Botany 52: 309-315.*

assessing the effects of such "invasions", certain hypotheses on the effects of weed-clearing operations can be proposed.

8.3. THE STUDY AREA

The Jonkershoek Valley (33°57′S; 18°55′E) is situated to the south-east of Stellenbosch in the southwestern Cape Province, South Africa (Figure 8.1). It is surrounded on three sides by mountains formed predominantly from sandstones of the Table Mountain Group. The Biesievlei Catchment, 27 ha. in extent, lies on the south-facing slopes of the valley. The area is underlain by Cape Granite with a small band of Malmesbury Shale in the upper catchment. The soil of the upper slopes is a grey-brown loam on partly decomposed shale while at the lower elevations, grey heavy loam soils on yellow clay predominate (Rycroft 1950). Elevation ranges from 290 m at the stream-recording weir to 580 m at the highest point. The mean aspect and slope of the catchment (each measured at 200 random points) are 226° and 19° respectively (Rycroft 1950). The upper portion of the catchment has steep rounded ridges separated by steep-sided gullies; the average slope of this portion is 26°. The lower portion flattens out below 355 m to a gentle slope of about 9° (Rycroft 1950).

The climate of the area is mediterranean Köppen's (1931) humid- mesothermal type Csb) with a dry summer and the average temperature of the warmest month below 22°C. The mean annual rainfall is 1427 mm, of which about 63 % falls between May and August (unpublished records, Forestry Branch).

Rycroft (1950) described the natural vegetation of the area and distinguished 13 communities. Dominant species included _Protea burchellii_, _P. neriifolia_ (listed as _P. lepidocarpodendron_ by Rycroft (1950)), _Leucadendron salignum_ (Proteaceae), _Anthospermum aethiopicum_ (Rubiaceae), _Rhus angustifolia_ (Anacardiaceae), _Cliffortia cuneata_ (Rosaceae), and _Widdringtonia cupressoides_ (Cupressaceae). Nomenclature in this chapter follows Bond & Goldblatt (1984). Families with 15 or more species (number of species in brackets) were: Asteraceae (59), Fabaceae (36), Iridaceae (31), Poaceae (24), Cyperaceae (17), Oxalidaceae (17) and Proteaceae (15). Ten species of Restionaceae and nine of Ericaceae were present. The vegetation of upper Biesievlei was last burnt approximately 19 years before afforestation (Van Wyk 1977). Vegetation in the lower part of the catchment was burnt in a wildfire in 1942 (unpublished records, Forestry Branch). In 1947 the vegetation around individual planting sites was slashed but not burnt. Almost the whole catchment (98 %) was afforested with P. radiata in 1948. Areas not afforested were steep cliffs where planting was not possible. Trees were planted at 1200 stems ha^{-1}. Thinnings to 740, 494, 320 and 158 stems ha^{-1} were carried out in 1959, 1964, 1971 and 1976 respectively. Trees were pruned to 7 m in 1962. The catchment was clearfelled in 1985.

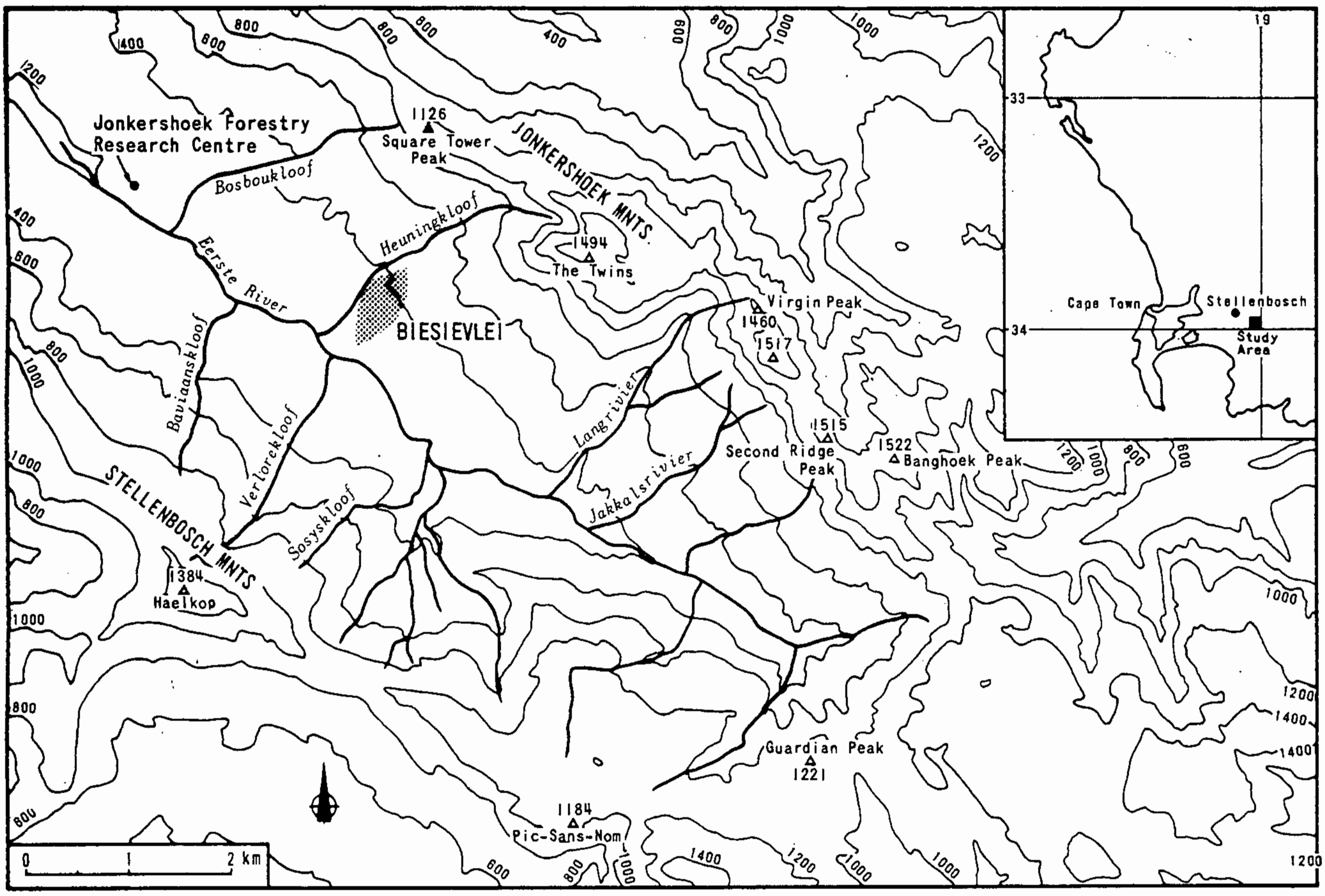

Figure 8.1. The Jonkershoek Valley near Stellenbosch showing the position of Biesievlei.

8.4. METHODS

In the 1945 survey, 200 quadrats of 0.1 m^2 each (0.40 X 0.25 m) were located at random in the catchment. Species were listed on each quadrat. Individual plants rooted in the quadrats were counted on each quadrat to estimate density. Total plant cover and the cover of all Poaceae; Restionaceae and Cyperaceae; geophytes; and the species Anthospermum aethiopicum and Leucadendron salignum was estimated on each plot. Each species was assigned to a life form (after Raunkiaer 1934) and the cover of each life form on each plot was determined. The life forms were stem succulents, epiphytes, megaphanerophytes and mesophanerophytes, microphanerophytes, nanophanerophytes, chamaephytes, hemicryptophytes, geophytes, helophytes and hydrophytes, and therophytes. The proportion of the flora in each life form was then determined.

In November 1984, 39 years after the initial study, the vegetation was re-surveyed. Two hundred quadrats were positioned at random in the area. Seven of these fell outside the catchment boundaries and were excluded. A portable steel frame was used to demarcate the remaining 193 quadrats. Data were collected in such a way as to be directly comparable to Rycroft's (1950) survey. In addition, we also estimated the cover of individual species in each quadrat. Specimens which could not be identified in the field were collected, and these were identified by matching them with herbarium specimens at Jonkershoek. Specimens that could not be identified (very small individuals or seedlings with no flowers or fruit) were given serial numbers so that an accurate assessment of the number of species present was made.

As Rycroft (1950) did not give cover values for individual species, direct comparison of dominant components of the vegetation was not possible. In order to compare the dominant components of the vegetation in 1945 and 1984, lists of the most important species encountered in the two surveys were compiled. Rycroft (1950) described 13 vegetation communities based on his survey. From these accounts, we listed all those species described by Rycroft variously as abundant, characteristic, chief, common, conspicuous, dominant, frequent, principal, prominent or well represented. We will use the term dominant to describe these species in further discussion. For the 1984 survey, an importance value (<u>sensu</u> Mueller-Dombois & Ellenberg 1974) was calculated for each species as the sum of relative density, relative frequency and relative cover. Relative density was defined as the number of individuals of the species in all quadrats expressed as a percentage of the total number of individuals of all species. Relative frequency was defined as the frequency of the species (the number of quadrats in which it occurred divided by the total number of quadrats) expressed as a percentage of the sum total of frequency values for all species. Relative cover was defined as the sum of all cover estimates for the species in all quadrats expressed as a percentage of the sum total of cover values for all species. Species in both lists were assigned to reproductive and growth form guilds (see Table 8.5) in order to compare the proportional distribution of the dominant flora in such guilds.

8.5. RESULTS

8.5.1. Plant canopy cover

Cover values for the vegetation categories recorded from both surveys are given in Table 8.1. The total cover of species excluding Pinus radiata has been reduced from 74.7 to 19.7 % following afforestation. The cover of each category of plants has been reduced markedly except for geophytes. Rycroft (1950) did not give standard deviations for the mean values which prevents statistical treatment of the data.

Table 8.1. Percentage plant cover for categories of vegetation in two surveys in the Biesievlei Catchment in 1945 and 1984.

	Mean cover (%)	
Vegetation component	1945	1984
All plants	74,7	19,7
Poaceae	12,3	2,3
Cyperaceae and Restionaceae	17,9	1,6
Geophytes	6,6	4,4
Anthospermum aethiopicum	2,9	0,1
Leucadendron salignum	1,2	0,1

8.5.2. Plant density

Plant density as estimated from the two surveys is compared in Figure 8.2, which reflects a marked decline in the number of plants per quadrat. The mean plant density has declined by 70 % from 260 plants/m^2 in 1945 to 78 plants/m^2 in 1984. Only one quadrat (0.5% of the total) contained no plants in the 1945 survey whereas 37 quadrats (19.2% of the total) were empty in 1984. The maximum plant densities recorded in 1945 and 1984 were 1390 and 700 plants/m^2 respectively.

8.5.3. Species diversity and turnover

The change in the number of species per quadrat shown in Figure 8.3 reflects a reduction in alpha diversity due to afforestation. The mean number of species per quadrat declined from 8.5 in 1945 to 2.1 in 1984. The total number of species encountered in the catchment was 298 in 1945 and only 126 in 1984. We were unable to identify 54 specimens from the 1984 sample due to the nature of the material. Of our sample of 126 species, 54 were common to Rycroft's list, 18 were not found in 1945 and 54 could not be identified to species level. This means that at least 64 % of species (190 species) recorded by Rycroft (1950) were not found in 1984. This figure is potentially as high as 82 %, which would be the case if our 54 unidentified specimens are all species not found by Rycroft. Similarly, between 18 and 71 species were added to the list. Afforestation thus results in the elimination of a very large proportion of the species. Some species survive in reduced numbers despite afforestation. Some species not found in pristine fynbos appear after afforestation. Many of these are small herbaceous plants or cosmopolitan weeds. Alien woody plants found in Biesievlei in 1984, although not recorded on the quadrats, were Acacia melanoxylon, Hakea sericea, Pittosporum undulatum and Solanum mauritianum.

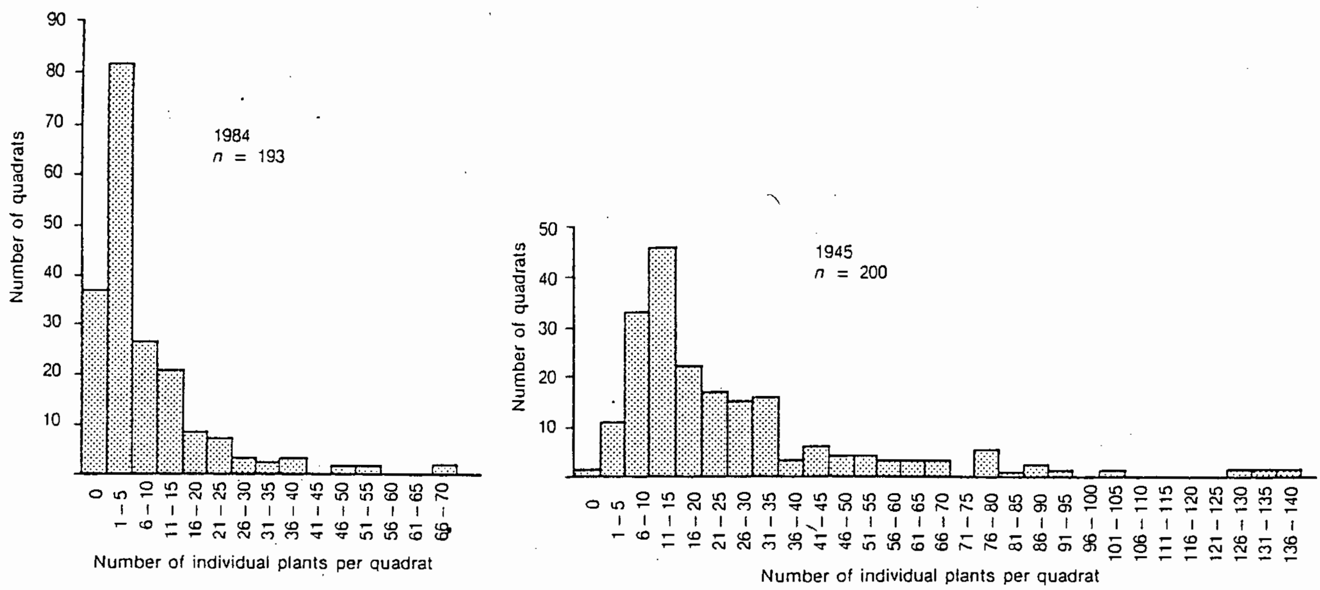

Figure 8.2. Comparison of plant density (plants per 0.1 m^2 quadrat) in two surveys in Biesievlei in 1945 and 1984.

8.5.4. Species dominance

Examination of Rycroft's (1950) community descriptions revealed 73 dominant species. These are listed in Table 8.2 under the corresponding reproductive

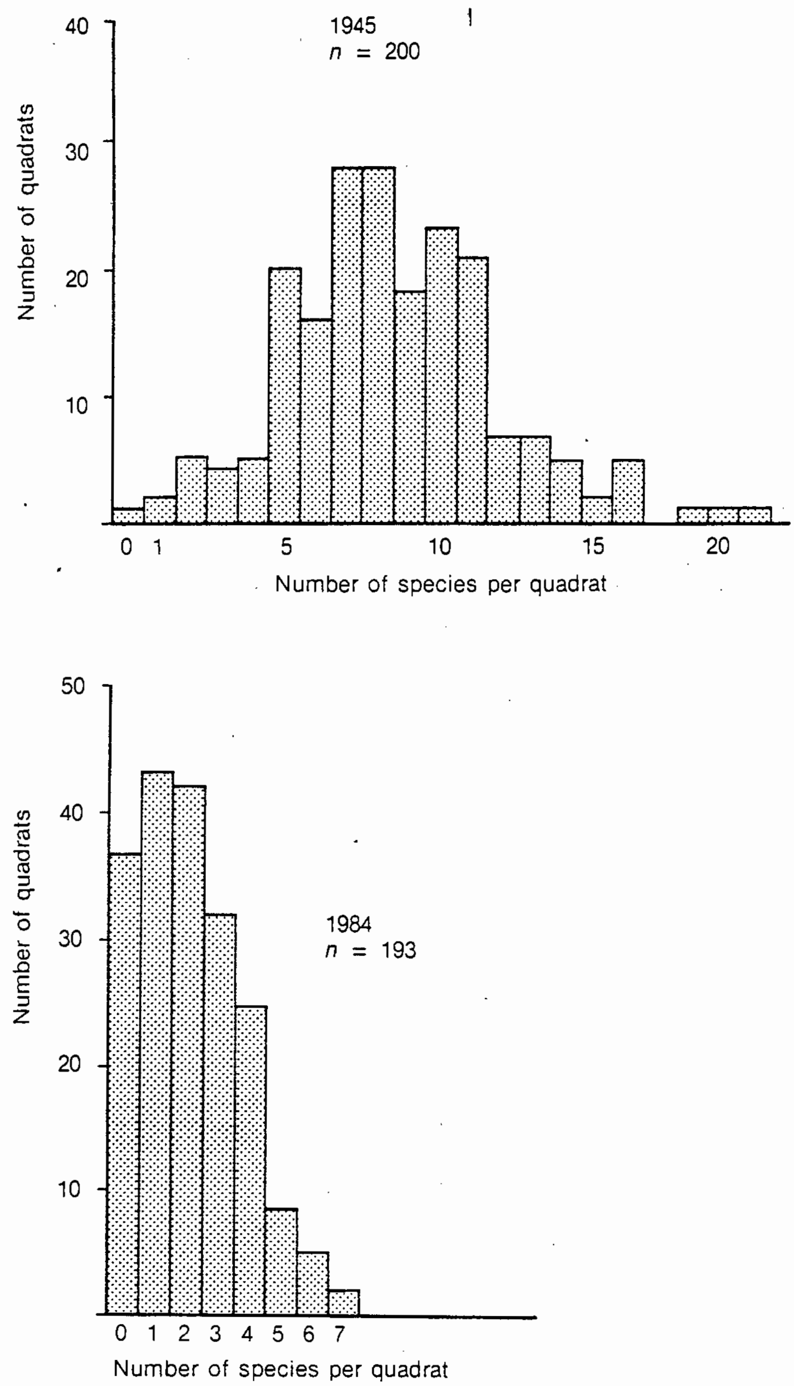

Figure 8.3. Comparison of the number of species per quadrat (0.1 m^2) in two surveys in Biesievlei in 1945 and 1984.

Table 8.2. Seventy-three dominant species from Rycroft's (1950) description of the plant communities of Biesievlei in 1945 (see text for criteria used to select species).

Herbaceous plants

Annuals: *Sebaea aurea*

Geophytes: *Corymbium glabrum, C. villosum, Micranthus alopecuroides, Protasparagus rubicundus*

Non-seasonal hemicrytophytes: *Bobartia indica, Cannamois virgata, Carpha capitellata, Ficinia filiformis, F. indica, Hypodischus albo-aristatus, Ischyrolepis subverticellata, Restio filiformis, Tetraria bromoides, T. burmanii, Zantedeschia aethiopica.*

Seasonal hemicrytophytes: *Berkheya armata, Dryopteris bergiana, Ehrharta longifolia, Pennisetum macrourum, Pentaschistis curvifolia, Pentaschistis* sp., *Plagiochloa uniolae, Pteridium aquilinum, Themeda triandra.*

Other herbs: *Cassytha ciliolata, Gunnera perpensa, Senecio pinifolius*

Woody small-leaved plants (⩽ leptophyllous)

Sprouters: *Brunia nodiflora, Diosma hirsuta, Helichrysum teretifolium, Montinia caryophyllacea, Muraltia heisteria, Phylica spicata, Struthiola myrsinites, Widdringtonia cupressoides*

Reseeders:
- Ericaceae: *Erica coccinea, E. imbricata*
- Myrmecochorous: *Anthospermum aethiopicum, Cullumia ciliaris, C. setosa, Indigofera cytisoides, Psoralea aphylla*
- Wind dispersed: *Helichrysum odoratissimum, Oedera* sp., *Senecio subcanescens, Stoebe plumosa*

Woody large-leaved plants (⩾ nanophyllous)

Sprouters:
- Bird dispersed: *Halleria elliptica, Ilex mitis, Maytenus oleoides, Olea europaea* ssp. *africana*
- Other: *Brabejum stellatifolium, Cunonia capensis, Freylinia lanceolata, Leonotus leonurus, Leucadendron salignum, Metrosideros angustifolia, Otholobium fruticans, O. obliquum, Podalyria calyptrata, Protea nitida, Rhus angustifolia, Rhus tomentosum, Salvia africana-caerulea*

Reseeders:
- Serotinous: *Leucadendron rubrum, Protea burchellii, P. neriifolia*
- Myrmecochorous: *Bolusafra bituminosa* (?), *Cliffortia cuneata, C. pterocarpa*
- Wind dispersed: *Othonna quinquidentata*
- Bird dispersed: *Chrysanthemoides monilifera*

Succulents

Erepsia anceps

Table 8.3. The thirty most important species in the Biesievlei Catchment in 1984. Importance was defined as the sum of relative frequency and relative cover (see text). For explanation of guild codes see Table 8.5.

Species	Reproductive and growth form guild	Frequency (%)	Mean density (plants m^{-2})	Mean (%) cover	Importance value
Oxalis lanata	GEO	25,4	13,4	1,5	37,0
Briza maxima	ANN	12,4	16,8	1,7	35,8
Oxalis purpurea	GEO	13,0	13,4	2,0	32,6
Hypochoeris radicata	ANN	21,8	4,9	0,9	21,1
Brabejum stellatifolium	LLSO	4,7	0,7	2,6	15,2
Halleria elliptica	LLSB	8,3	1,7	1,2	11,8
Rubus rigidus	LLSB	5,7	0,7	0,7	7,0
Berkheya armata	GEO	4,7	0,5	0,8	6,7
Pteridium aquilinum	SHE	3,1	1,2	0,7	6,2
Stoebe cinerea	SLW	1,0	0,1	0,9	4,7
Rhus angustifolia	LLSO	2,6	0,3	0,6	4,5
Oxalis bifida	GEO	3,1	1,8	0,1	4,4
Oxalis incarnata	GEO	0,5	2,3	0,2	4,3
Maytenus oleoides	LLSB	1,0	0,1	0,8	4,1
Grass sp.	SHE	2,6	1,7	0,2	4,0
Protasparagus rubicundus	GEO	2,1	0,2	0,5	3,7
Ehrharta bulbosa	SHE	2,1	1,5	0,1	3,4
Myrsiphyllum scandens	GEO	3,1	0,5	0,3	3,3
Senecio sp.	ANN	2,1	1,2	0,1	3,1
Tetraria bromoides	SHE	1,6	0,5	0,4	3,0
Rhus tomentosa	LLSO	2,1	0,3	0,2	2,5
Plectostachys polifolia	SLW	1,6	0,3	0,2	2,2
Pellaea pteroides	SHE	2,1	0,3	0,2	2,1
Tetraria cuspidata	NHE	1,0	0,2	0,3	2,0
Tetraria involucrata	NHE	1,0	0,1	0,3	2,0
Erica hispidula	SLE	1,0	0,1	0,3	1,8
Ischyrolepis gaudichaudianus	NHE	2,1	0,4	0,1	1,8
Olea europaea ssp. *africana*	LLSB	1,6	0,2	0,0	1,8
Tetraria sp.	NHE	0,5	0,1	0,3	1,7
Cliffortia cuneata	LLM	2,1	0,2	0,1	1,6

and growth form guilds. The 30 most important species in 1984 and the corresponding frequency, density and cover values are given in Table 8.3. Of Rycroft's 13 original communities, only the stream bank community persists 39 years after afforestation. The remainder of the understorey vegetation consists of a sparse cover dominated by a few species (mainly Oxalis spp., Briza maxima, Hypochoeris radicata and Halleria elliptica) (Table 8.3).

8.5.5. Life form spectra

Rycroft gave life form data for Biesievlei as the number of species in a given life form expressed as a percentage of the total number of species present. Comparative figures for the two surveys are given in Table 8.4. Chamaephytes have been markedly reduced by afforestation while the proportion of hemicryptophytes has increased. Other life forms have remained at much the same proportion of the flora. The increase in mega- and mesophanerophytes and reduction in microphanerophytes can be attributed to differences in interpretation when assigning species to life forms. For example, we classified the species Brabejum stellatifolium, Kiggelaria africana, Maytenus oleoides and Olea europaea as mega- or mesophanerophytes. These species were all present in 1945 which can only mean that they were called microphanerophytes by Rycroft (1950).

Table 8.4. Plant life form distribution in Biesievlei in two surveys expressed as a percentage of the flora. The figure in brackets for the 1984 survey is the mean cover of the life form calculated from 193 quadrats.

Life form	1945	1984	
Epiphytes	0,3	0	(0)
Mega- and mesophanerophytes	0	3,2	(3,9)
Microphanerophytes	6,4	3,2	(1,0)
Nanophanerophytes	23,5	24,8	(4,6)
Chamaephytes	23,2	5,6	(0,4)
Hemicryptophytes	14,1	38,4	(4,9)
Geophytes	22,1	22,4	(4,4)
Hydro- and helophytes	2,3	1,6	(0,2)
Therophytes	8,1	0,8	(1,7)
Total number of species	298	126	

8.5.6. Reproductive and growth form guilds

The proportion of the dominant flora in terms of reproductive and growth form guilds for the two surveys is compared in Table 8.5. Dominant species in 1984 are mainly herbaceous plants (63 %) and woody, large-leaved shrubs (23 %). Annuals, geophytes and hemicryptophytes are dominant away from the stream bank whereas large-leaved sprouting shrubs form the dominant guild in the riparian zone. Small-leaved sprouting shrubs and large-leaved shrubs (especially those that regenerate from canopy-stored seeds) have been greatly reduced or eliminated (Table 8.5). There is also a noticeable increase in the relative proportion of bird dispersed, large leaved sprouters.

Table 8.5. Reproductive and growth form guilds of the dominant species of Biesievlei in 1945 (see Table 8.2) and 1984 (see Table 8.3).

		1948		1984	
Life form	Reproductive and growth form guilds	Number of dominant species	% of the dominant flora	Number of dominant species	% of the dominant flora
Herbaceous plants					
Annuals	ANN	1	1	3	10
Geophytes	GEO	4	5	7	23
Non-seasonal hemicryptophytes	NE	10	14	4	13
Seasonal hemicryptophytes	SHE	9	12	5	17
Other Herbs	HER	3	4	0	0
Woody, small-leaved (⩽ leptophyllous)					
Sprouters	SLS	8	11	0	0
Seeders					
Ericaceae	SLE	2	3	1	3
Myrmecochorous	SLM	5	7	0	0
Wind dispersed	SLW	4	6	2	7
Woody, large-leaved (⩾ nanophyllous)					
Sprouters					
Bird dispersed	LLSB	4	6	4	13
Other	LLSO	13	18	3	10
Seeders					
Serotinous	LLC	3	4	0	0
Myrmecochorous	LLM	4	6	1	3
Wind dispersed	LLW	1	1	0	0
Bird dispersed	LLB	1	1	0	0
Succulents	SUC	1	1	0	0
Total		73		30	

8.6. DISCUSSION

8.6.1. The validity of the basis of comparison

This study aimed to repeat the work of Rycroft (1950) and the data were collected in exactly the same way as was done in that pioneering study. The science of vegetation ecology has advanced considerably since then. If our aim had been to describe the vegetation, we would have taken such advances into account. For example, much larger plots would have been used and the classification of species into life forms (as done by Rycroft) could have been done along more meaningful lines, such as we have attempted to do with the dominant species (Table 8.5). However, such differences in methodology would have prevented direct comparisons. Through direct comparison we have been able to quantify changes in cover, density and in broad life form composition.

We also listed cover by species on each plot and have used this to compile a list of the dominant flora (Table 8.3). We have compared this to the subjectively determined list of dominants in 1945. Such a comparison must be seen as coarse and the results indicative of broad trends rather than an exact account of changes in composition of dominant species. Given the magnitude of changes that have occurred, we feel that such a comparison is both valid and useful.

8.6.2. Effects of afforestation on vegetation

Afforestation has caused a clear reduction in the number of species present, and in the cover and density of remaining species in Biesievlei. Afforestation has also changed the relative importance of various reproductive and growth form guilds in the remaining vegetation. The most important families in the impoverished flora are Oxalidaceae, Poaceae and Asteraceae whereas Proteaceae, Rosaceae and Cyperaceae were found to be most important in terms of cover in an undisturbed fynbos community at Jonkershoek (Van Wilgen 1981). A tall closed shrubland with a rich assemblage of species has become a very sparse understorey with relatively few species under the closed pine canopy. Similar patterns of vegetation change are evident under severe infestations of pines and other species such as Hakea sericea and Acacia saligna (Van Wilgen & Richardson 1985a; Macdonald & Richardson 1986). Populations of many species have crashed in response to afforestation and the resultant "stable state" consists of pines, relictual fynbos populations, cosmopolitan weeds and other fugitive herbaceous plants. Serotinous non-sprouters (Protea spp.), woody small-leaved sprouters and woody small-leaved myrmechochorous species have been eliminated. The number of dominant sprouting shrub species has been reduced from 21 to 3 (Table 8.5). Herbaceous plants have become dominant by default as other species have been eliminated. This does not necessarily imply that they have become more abundant. Of the species listed as dominant in 1984 (Table 8.3), only the small, deep-rooted forb Hypochoeris radicata is a new species. Only large-leaved shrubs of the stream bank community have persisted in significant numbers. Natural communities on permanently moist sites on Table Mountain showed similar resistance to modification following invasion by pines (Cowling et al. 1976). These authors found that the Osmitopsis asteriscoides - Berzelia lanuginosa community was "not severely affected" by invasion. The stream bank above the 335 m contour in Biesievlei was not fringed by tall woody plants prior to afforestation (Rycroft 1950), but seedlings of Kiggelaria africana and the alien weed Solanum mauritianum have become established in this zone. The pines have provided perching sites for frugivorous birds and thus new foci for the deposition of seed.

8.6.3. Disturbance and stress as ecological factors in afforested habitats

Disturbances are defined as " mechanisms which limit the plant biomass by causing its partial or total destruction" (Grime 1979). Uninvaded mountain fynbos habitats are subject to disturbance in the form of fires at intervals of 10 to 40 years. Dominant species in habitats subject to disturbance are generally resilient under a particular disturbance regime. Stress factors are defined as phenomena which " restrict photosynthetic production, such as shortages of light, water, and mineral nutrients " (Grime 1979). Dominant species in disturbed habitats are able to withstand low levels of stress. An unnatural increase in the intensity of stress (such as that caused by afforestation) could, however, be expected to eliminate many elements of the flora (Grime 1979). Afforestation with pines has increased stress in a number of ways. Pines are more effective users of available resources; they grow faster and reach a much greater size than the indigenous plants. Litter fall from pines causes considerable suppression of the understorey vegetation. Litter fall in a 35 year-old P. radiata stand at Jonkershoek was estimated at 372 g/m^2/annum (Versfeld 1981). Litterfall in coastal fynbos amounts to between 72 and 84 g/m^2/annum in 9 year old vegetation (Mitchell et al. 1986), while at Jonkershoek the figure is 217 g/m^2/annum in 22 year old vegetation (F.J. Kruger & A.J. Lamb unpublished data). Vapour from decomposing P. radiata litter inhibits growth of certain species (Lill & Mc Wha 1976). Shading will further affect photosynthesis and germination of understorey plants. The relative contribution of each of these stress factors to the suppression of elements of the natural vegetation is not known but the combination of factors has undoubtedly caused the demise of several groups of species. Invaded habitats can be seen as analogous to afforested sites. Invaded habitats are subject to increased stress which, if the invasions are severe enough, will eliminate many elements of the previously dominant flora.

The reproductive output of the community has been clearly reduced in proportion to the reduction in density and cover of the vegetation. The following question then arises: which species will be able to regenerate following a disturbance such as clearfelling or fire ? Examining the response of reproductive and growth form guilds to stress may answer this. Geophytes were the only group away from streams apparently not affected by the increased stress (Table 8.4). Woody, large-leaved serotinous re-seeders such as Protea species have no viable strategy to survive such stress and may be permanently eliminated. Seeds of these species have a low dispersal efficiency and do not persist in the soil (Bond 1980). Sprouting shrubs may also be permanently eliminated as seed production is not usually vital to the survival of sprouters, and no large seed banks can be expected to remain. Myrmecochorous shrubs, although severely reduced in the above-ground flora, may re-establish from soil-stored seed banks. Wind dispersed species may recolonize from outside the area. Other species survive in certain habitats. This may be due to the inherent tolerance of these species to stress or to ameliorating factors that reduce the magnitude of stress. Woody large-leaved sprouting shrubs persist near streams where moisture is abundant and where P. radiata grows least well (Grey & Taylor 1983).

8.6.4. Implications for conservation in invaded habitats

The results of this study can be useful for assessing priorities for weed clearing in the fynbos. Afforestation has created a new community with properties and attributes entirely different from the pre-afforestation fynbos which was resilient in relation to the disturbance regime (fires) under which most of its component species evolved. Following disturbance (clearing and/or fire) in heavily invaded sites, the altered community probably cannot return to its pre-invasion state. This means that the vegetation has been stressed to a point where it is no longer resilient to the disturbance regime under which its dominant components have evolved. This can be tested following clearfelling in Biesievlei by monitoring succession on larger, permanent plots.

Two important points arise with regard to the practical implications of this study. Firstly, dense closed-canopy infestations of pines or other large trees and shrubs will alter the composition of fynbos in such a way that clearing alone will probably not restore the original flora. Shrubby elements of the flora will be eliminated. In the future it may be necessary to repair such impoverished ecosystems ("restoration ecology" sensu Diamond 1985). Secondly, infestations which are currently sparse should not be left to become dense (and thus cause the natural vegetation to become stressed) before clearing. Priority should be given to the clearing of sparse or moderate infestations as restoration of the areas will be difficult should weed populations become dense.

Given that dense, closed-canopy infestations have already radically altered the composition of the vegetation, and that clearing will not restore the natural vegetation, should such infestations be cleared? Dense infestations have a number of disadvantages besides causing drastic changes in community structure and species diversity. Surface water resources and the scientific, aesthetic and recreational value are reduced, and fire hazard is increased (Kruger 1981, Van Wilgen & Richardson 1985a). We suggest that these areas be cleared of dense infestations, but that this work should proceed at a lower priority than the clearing of sparse or moderate infestations to allow for restoration. Restoration in these areas must concentrate on the re-establishment of shrubby species.

CHAPTER 9

THE EFFECTS OF FIRE IN FELLED *HAKEA SERICEA* AND NATURAL FYNBOS AND IMPLICATIONS FOR WEED CONTROL IN MOUNTAIN CATCHMENTS

CHAPTER 9 : THE EFFECTS OF FIRE IN FELLED HAKEA SERICEA AND NATURAL FYNBOS AND IMPLICATIONS FOR WEED CONTROL IN MOUNTAIN CATCHMENTS [1]

9.1. ABSTRACT

Dense stands of the alien shrub Hakea sericea were felled and later burned accidentally under severe weather conditions. The recovery of the natural vegetation was monitored for 19 months on 12 permanent plots. Cover increased slowly to 13% and 42 species were recorded. Data were collected at a similar but uninvaded site burnt in the same fire. Mean cover on 12 plots at this site 19 months after the fire was 34% and the total number of species was 95. Sprouters were adversely affected at the invaded site, where species regenerating from seed stored in the soil predominated. Sprouters were dominant at the uninvaded site. Fire behaviour was simulated using Rothermel's fire model. Simulated fire intensity at the invaded site was particularly high (79 700 kW/m). Managers should attempt to burn felled hakea under conditions that will lead to less intense fires to reduce the adverse effects caused by high fuel loads. Fire behaviour prediction models should prove useful in this regard. Alternative control strategies for dense stands should also be investigated.

9.2. INTRODUCTION

Dense stands of the Australian shrub Hakea sericea Schrad. (Proteaceae) and the tree Pinus pinaster (Pinaceae) cover approximately 1 130 km^2 or 4% of the total area of mountain fynbos in southern and southwestern Cape Province of South Africa (Macdonald et al. 1985). The invasion of fynbos by alien trees and shrubs is a major threat to the conservation of this vegetation type (Macdonald & Richardson 1986). Fire is an important management tool in mountain fynbos and forms an important part of the integrated programme for the control of alien woody plants. Control of H. sericea (hakea) involves felling the shrubs, leaving them in situ where the canopy-stored seeds are released, and then burning the area once the seeds have germinated to kill the seedlings. Felling operations are scheduled so that prescribed burns can be carried out in late summer or early autumn at intervals of between 12 and 15 years. Hakea sericea relies entirely on seed for regeneration and these control measures are usually successful.

Stands of hakea that had been felled as part of the weed control programme of the Department of Environment Affairs (Forestry Branch) were burned during one of the worst wildfires on record for the Western Cape Forestry Region. This

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[1] *Publication status: Richardson, D.M. & Van Wilgen, B.W. (1986). The effects of fire in felled Hakea sericea and natural fynbos and implications for weed control in mountain catchments. South African Forestry Journal 139: 4-14.*

fire burnt through 37 000 ha in the Du Toits Kloof, Franschhoek, Villiersdorp and Rawsonville mountains and traversed the study area on 23 January 1984. The stands that occurred in the Wemmershoek area (33° 51′S; 19° 10′E) were particularly dense. Hakea plants were felled between April and June 1983 (Figure 9.1). The intention was to burn the area in April 1984, but it was burned in the wildfire described above. The combination of the very heavy fuel load concentrated near the soil surface and the warm (28°C), dry (30% relative humidity) and windy (20 km/hr) weather conditions during the fire (Van Wilgen 1985) resulted in a very intense fire.

Figure 9.1. Felled Hakea sericea shrubs at the invaded site two months after felling and two months before the fire. Estimated fuel load is 7180 g/m and the fuel bed depth is 0.85 m.

In this chapter we present data on the recovery of fynbos vegetation after the fire at a site with felled hakea at Wemmershoek and compare the species composition and plant cover at this site with that at a nearby site not invaded by hakea, but burned in the same fire. We describe the probable fire behaviour using Rothermel's (1972) fire model and compare predicted fire behaviour parameters at this site with those predicted for uninvaded fynbos and for thickets of standing hakea. These data will be useful in explaining the observed effects and this approach can be used to assess the effects of changes to the fuel-bed that will result from various control options.

9.3. METHODS

9.3.1. Vegetation composition

Six permanently marked quadrats (2 m x 2 m) were positioned along each of two lines located at random in the area affected by the fire in felled hakea. Plots were first enumerated 37 days after the fire and at intervals of between two and three months thereafter until 29 August 1985 (584 days after the fire). The species occurring on each plot, the projected canopy cover of each species and the total plant cover on the plot were recorded. Cover values were assigned by ocular estimation and consensus of two observers. Twelve quadrats were positioned at random at a nearby and physiographically similar site not invaded by hakea but also burned in the fire of 23 January 1984. We refer to the first site as the invaded site and the second as the uninvaded site. The uninvaded site was enumerated once only; on 4 September 1985 (590 days after the fire). The mean number of species and the mean total plant cover were plotted against time for the invaded site. The number of species and total plant cover values from the invaded site at 584 days were compared with those for the uninvaded site at 590 days to assess the combined effects of invasion and fire on the composition of fynbos vegetation.

Species were divided into "species types" using vital attributes that describe the method of arrival or persistence of the population of that species at the site during and after the fire and the ability of the species to establish and grow to maturity in the developing community (Noble & Slatyer 1980). Three species types that are exclusively propagule-based, one that is vegetatively based, and one that shows a combination of mechanisms were distinguished among the species encountered at the two sites. All species found at both sites are able to establish and grow at a site immediately after the fire but show minimal recruitment in later stages of succession ("intolerant" species in the Noble and Slatyer (1980) classification). Species types were therefore distinguished according to the method of persistence and arrival at the site. The five species types that were distinguished are explained in Table 9.1. The contribution of each species type to the plant cover in each of the twelve plots at the two sites was calculated. Analysis of variance was used to test whether there were significant differences in the total plant cover and the cover of each of the five species types between the two sites.

Table 9.1. Species types distinguished among species at two sites c. 590 days after a fire (after Noble & Slatyer 1980).

Species type	Explanation
DI	Propagules are dispersed over an area large enough for them to be available for recruitment at the site at any time.
SI	Propagules are available at all life stages extending beyond the death of the mature individual until the local extinction of the seed pool. This pattern is typical of species with seeds capable of maintaining viability in the soil for periods which may be substantially longer than the life span of the individuals.
CI	Species that retain a short-lived seed pool which can survive and germinate immediately after a fire. The seed pool is so short-lived that there is effectively no survival beyond the adult stage.
ΣI	Species that possess two mechanisms for persistence. An example is Hypodiscus argenteus (Restionaceae) which has the ability to sprout from a subterranean rootstock but may also reproduce from propagules that are buried in the soil by ants.
UI	Species which have the ability to sprout from aerial buds or subterranean rootstocks or bulbs after a fire and remain reproductively mature in the immediate post-fire phase.

9.3.2. Fire behaviour

Fire behaviour was simulated using Rothermel's (1972) fire model and fuel models (descriptors of the fuel properties of the vegetation) for the various fuel complexes considered. Van Wilgen & Richardson (1985a) described fuel models for simulating fire behaviour in uninvaded fynbos and in fynbos invaded by hakea. The fynbos fuel model (Van Wilgen & Richardson 1985a) was used to simulate the likely fire behaviour at the uninvaded site. A modified hakea fuel model was used as a basis for simulating fire behaviour in standing hakea. The stands at Wemmershoek were much older than those described by Van Wilgen & Richardson (1985a), and estimates from photographic records suggest that the aerial plant biomass was at least double at Wemmershoek. Fuel loads for the hakea component were doubled to account for this. In order to simulate fire behaviour in felled hakea (the invaded site), live shrub fuel loads were transferred to dead fuel and the fuel bed depth (estimated from photographs) was decreased accordingly. The three fuel models are quantified in Table 9.2. Environmental conditions prevailing during the fire of 23 January 1984 (Table 9.3) were used to estimate fire behaviour. Weather conditions at the nearby Zachariashoek weather station (33° 49′S; 19° 02′E) were used to simulate fuel moistures in the United States National Fire Danger Rating System (Deeming et al. 1978). Fuel modelling and fire behaviour predictions were done using the BEHAVE system (Burgan & Rothermel 1984). Predictions of fire behaviour from these fuel models for less severe weather conditions were then obtained using the BEHAVE system, to determine optimal conditions for prescribed burning.

Table 9.2. Fuel models used in simulating fire behaviour in uninvaded fynbos, fynbos dominated by Hakea sericea and in areas where H. sericea shrubs have been felled.

Fuel model	Fuel load (g/m^2)					Surface area to volume ratio (m^2/m^3)					Heat content (J/g)	Fuel bed depth (m)	Extinction moisture (%)
	Dead fuel			Live herbs	Live shrubs	Dead fuel			Live herbs	Live shrubs			
	< 6 mm	6–25 mm	26–75 mm			< 6 mm	6–25 mm	26–75 mm					
Uninvaded fynbos	400	95	12	500	224	7 215	357	98	5 900	4 920	20 000	1,4	34
Standing hakea	800	80	20	130	2 400	8 000	357	98	5 900	8 450	18 500	2,1	34
Felled hakea	3 200	2 000	1 850	130	0	8 450	357	98	5 900	0	18 500	0,85	34

Table 9.3. Conditions of fuel moisture, wind and slope used in simulating fire behaviour. Fuel moisture was estimated using weather conditions during the wildfire as inputs for the United States Fire Danger Rating System (Deeming et al. 1978).

Parameter		Condition
Dead fuel (<6 mm) moisture	(%)	5
Dead fuel (6–25 mm) moisture	(%)	6
Dead fuel (26–75 mm) moisture	(%)	10
Herbaceous fuel moisture	(%)	83
Shrub fuel moisture	(%)	100
Windspeed	(km/h)	20
Slope	(%)	0

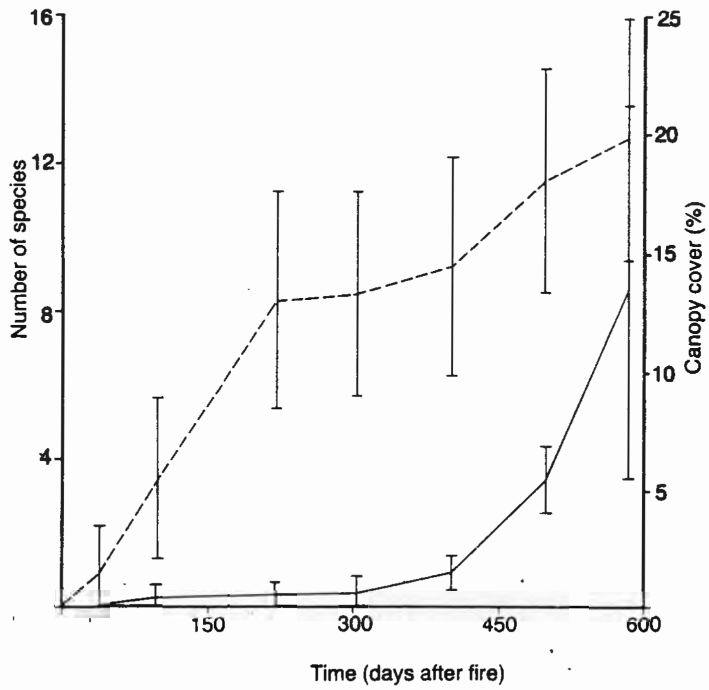

Figure 9.2. The increase in the mean number of species per plot (dashed line) and mean percentage canopy cover (solid line) on 12 plots following a fire in felled hakea at the invaded site. Bars are standard deviations from the mean.

9.4. RESULTS

9.4.1. Vegetation composition

Plant cover was negligible for more than a year following the fire at the invaded site, and the mean number of species per plot gradually increased to 12.8 at 584 days after fire (Figure 9.2). The invaded site was characterized by significantly fewer species per plot (mean = 12.8; S.D. = 3.4) and a significantly sparser total plant cover (mean = 13.4; S.D. = 7.9) than was the case at the uninvaded site where the corresponding values were 32.0 species (S.D. = 4.1) and 33.6% (S.D. = 9.5) respectively ($P < 0.001$ for both). The total number of species on the quadrats in the invaded area at the last enumeration was 42 compared with 95 at the uninvaded site. The highly significant difference in total cover between the two sites is mainly attributed to the greatly reduced contribution of species types **UI** (species that sprout and remain reproductively mature after a fire) but also to the diminished proportional representation of species types **Σ**.I (species that sprout but that also reproduce by means of seeds) and **DI** (species with well dispersed propagules) at the invaded site (Table 9.4). Species belonging to type **UI** are dominant in terms of cover (42%) at the uninvaded site but comprise only 15% of the cover at the invaded site (Figure 9.3). At the invaded site, the greatest proportion of the total plant cover was made up of species belonging to species type **SI** (62%), plants that rely on soil-stored seed for regeneration. Species belonging to this type make up only 31% of the cover at the uninvaded site (Figure 9.3) but the actual cover values for this type at the two sites do not differ significantly (Table 9.4). A list of all species encountered in the surveys and their corresponding species types is given in Appendix 9.1.

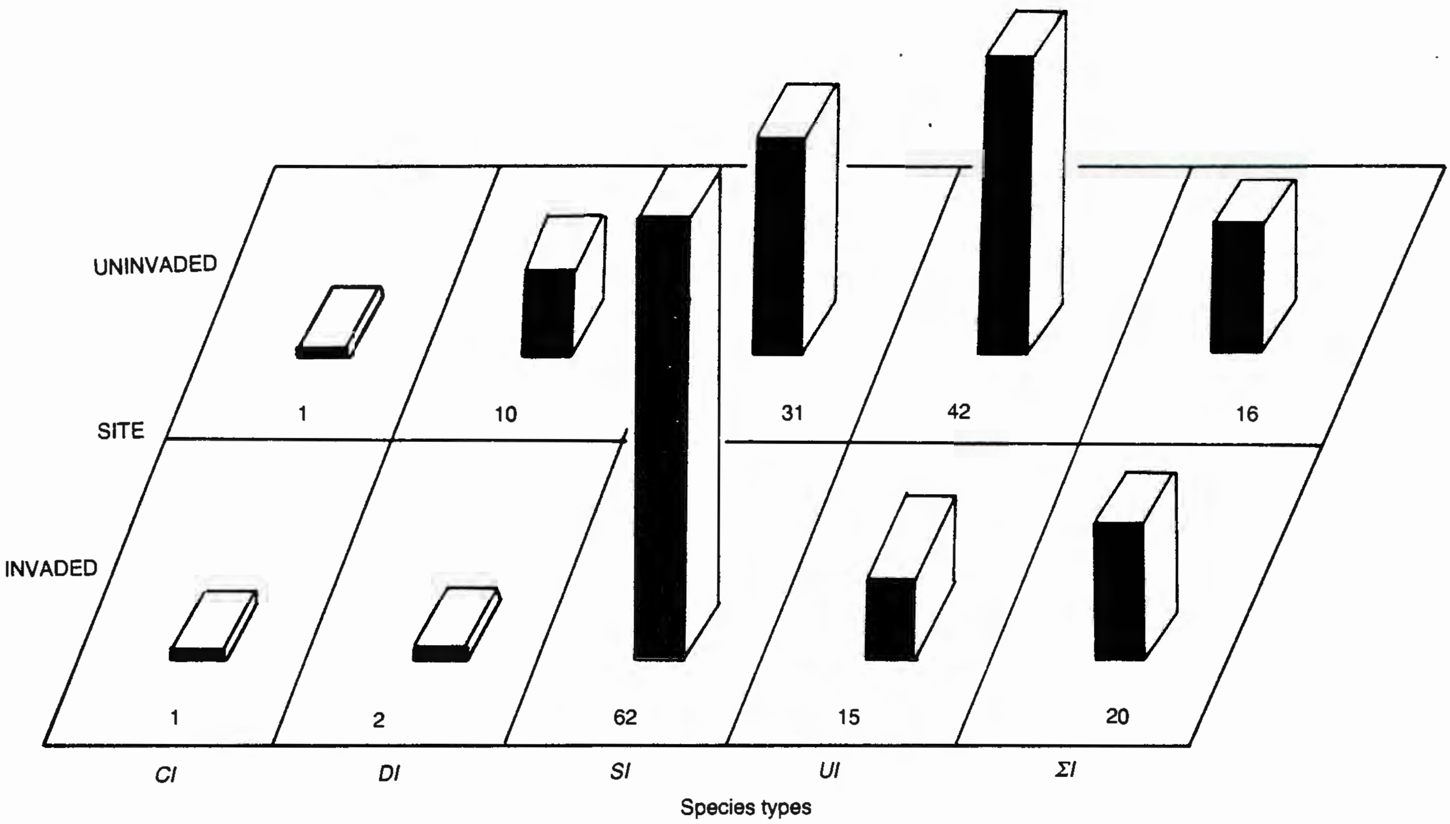

Figure 9.3. The relative contribution of five species types (Table 9.1) to the total canopy cover at two sites 19 months after a fire. The invaded site was covered with felled hakea shrubs prior to the fire. The vegetation at the uninvaded site was mature fynbos. Figures at the base of blocks are the percentage contribution to the total canopy cover at each site.

Table 9.4. Mean percentage cover of five species types (see Table 9.1) 19 months after a fire . Means were calculated from the sum of cover values of the species in each species type.

Species type	Cover value		*F*	*P*
	Uninvaded site	Invaded site		
UI	14,6	2,0	16,48	<0,001
ΣI	5,6	2,8	6,07	<0,05
SI	10,6	8,4	0,59	N.S.
DI	3,3	0,3	8,76	<0,05
CI	0,2	0,1	1,05	N.S.
Total	34,3	13,6	31,83	<0,001

9.4.2. Fire behaviour

Simulated fire behaviour parameters for the conditions in Table 9.3 are shown in Table 9.5. The predicted rate of fire spread in felled hakea was about 1.1 times the predicted value for uninvaded fynbos. Three measures of fire intensity were simulated. Reaction intensity, measured in $kJ/m^2/s$ describes the rate of energy release per unit area in the active combustion zone. Total heat release, measured in kJ/m^2, is simply a reflection of the total fuel consumed. Fireline intensity was defined by Byram (1959) as I = H w r where I is the fireline intensity (kJ/m/s or kW/m), H is the heat yield of the fuel (kJ/g), w is the weight of available fuel (g/m) and r is the rate of fire spread (m/s). The predicted heat per unit area was 2.5 times greater in felled hakea than in fynbos, which reflects the weighting by fuel load in the fuel models (Table 9.2). Predicted reaction intensity and fireline intensity were 3.3 and 2.8 times greater respectively for felled hakea than for fynbos. The predicted intensity values for the uninvaded fynbos site are relatively high when compared with published values of fire behaviour in fynbos (Bands 1977; Van Wilgen et al 1985), indicating the severity of the conditions during the fire. Predicted fire behaviour in a hypothetical stand of standing hakea indicates that a fire would have been less severe had the shrubs been left standing rather than felled. Another factor, not simulated by Rothermel's model, which contributes to biological effects is the increased penetration of heat into the soil where increased fuel loads are concentrated near the ground. For example, Van Wilgen & Holmes (1986) found that soil temperatures exceeded 200°C at 40mm below the soil surface under piles of felled Acacia cyclops but that soil temperatures ranged from 49 to 70°C or more at the same depth below standing A. cyclops stands. Some measure of the fuel load and its proximity to the ground may provide better predictions of biological effects than above ground measures of fire intensity.

Table 9.5. Predicted fire behaviour parameters for three fuel models. The environmental conditions are given in Table 9.3.

Fuel model	Rate of spread (m/s)	Total heat release (kJ/m^2)	Fireline intensity (kW/m)	Reaction intensity ($kJ/m^2/s$)	Flame length (m)
Uninvaded fynbos	2,11	13 338	28 120	1 105	8,63
Standing hakea	1,07	9 785	10 470	1 071	5,49
Felled hakea	2,40	33 241	79 711	3 593	13,93

9.5. DISCUSSION

9.5.1. Vegetation composition

The recovery of the vegetation at the invaded site was particularly poor. Cover usually returns to about 40% within the first year after a fire in fynbos (Van Wilgen 1981; Kruger & Bigalke 1984; Richardson et al. 1984), but was less than 0.4% at the invaded site. The number of species was also much lower at the invaded site when compared with the uninvaded site. Of particular significance is the relatively small contribution of sprouting species to the plant cover 19 months after the fire at the invaded site. Although no data are available on the pre-fire plant composition at this site, observations at other invaded areas (D. M. Richardson, unpublished data) have shown that indigenous plant cover beneath a 6 m tall, closed-canopy stand of hakea usually varies between 10 and 25%. Of this indigenous plant cover, between 70 and 94% consists of species that have the ability to sprout. Species types SI and CI (those that rely on seed stored in the soil and in the canopy respectively for regeneration) are rare or absent under these conditions but form the dominant plant cover in many uninvaded mountain fynbos areas (Kruger 1979). Any sprouters that may have been present before the fire at the invaded site, were probably killed by the fire of above-average intensity.

Post-fire succession in uninvaded fynbos is characterized by rapid expansion of the cover of graminoid and restioid plants (Table 9.4). It has, however, been shown (D.C. Le Maitre, unpublished data) that the ratio of pre- to post-fire net growth ($g/m^2/yr$) of the restioid component in undisturbed fynbos decreases with increasing fire intensity. In other words, more hemi-cryptophytes are killed as fire intensity increases. These results are in agreement with our observations. The rapid increase in cover of the graminoid and restioid plants after fires is important in stabilizing the site. This was emphasized at the invaded site at Wemmershoek where very heavy rains fell during the week of 14-20 May 1984, 112 days after the fire. At this stage, the average plant cover at the invaded site was less than 0,5% and serious soil erosion occurred. The intense fire probably killed the axillary buds of the sprouting species that should, had the fire been less intense, have recovered to around 20% cover after 112 days despite the pre-fire suppression by the closed-canopy stand of hakea, thus preventing serious erosion.

Nineteen months after the fire, 62% of the plant cover at the invaded site was made up of species reliant on soil-stored seed for survival. Many of these species have seeds that are buried by ants at a depth of 4-7 cm below the soil surface (Bond & Slingsby 1983). These seeds are less susceptible to mortality due to the heating of the surface layers of the soil than are seeds that are not myrmecochorous (dispersed by ants). Only species with this type of seed are able to survive extremely intense fires in reasonable numbers.

9.5.2. Fire intensity

Figure 9.4 shows the effects of dead fuel moisture on predicted fire intensity using the felled hakea and fynbos fuel models, assuming a 10 km/hr wind and with other conditions as in Table 9.3. The predicted fireline intensity in fynbos with 5% dead fuel moisture is about 7 000 kW/m· Prescribed burns in felled hakea should be aimed at achieving fire intensities of about the same magnitude. The same fireline intensity can be obtained by burning felled hakea at around 17% dead fuel moisture. Alexander (1982) has stated that fireline intensity is the most valid characteristic of a fire's impact on above-ground vegetation. None of the outputs of Rothermel's fire model are very satisfactory for measuring the impact of a fire on below-ground vegetation though (R. E. Burgan, pers. comm. 1985). Measures of heat penetration

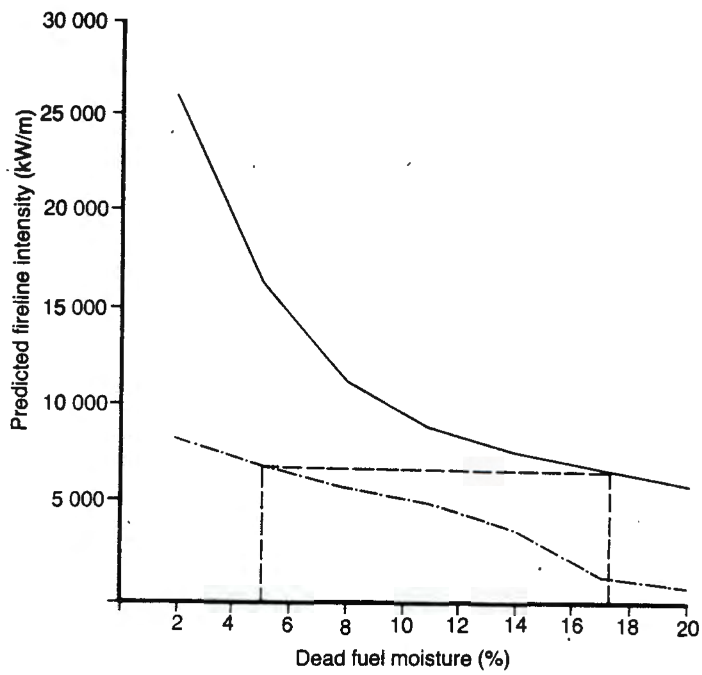

Figure 9.4. The effect of dead fuel moisture content on predicted fireline intensity. Conditions are as in Table 9.3, except that the wind speed was assumed to be 10 km/h. The upper curve (——) is for the felled hakea fuel model, and the lower curve (—·—) is for the fynbos fuel model (Table 9.2). The dashed line (- - -) indicates the moisture contents required to achieve similar fireline intensities for the two fuel models.

into the soil would be more satisfactory. Lowering the fireline intensity is achieved largely by lowering the rate of spread but this does not necessarily lower the other types of intensity. For example, the predicted heat per unit area and reaction intensity for felled hakea with 17% dead fuel moisture are 25 484 kJ/m^2 and 2 754 kJ/m^2/s, both double that for fynbos (13 344 kJ/m^2 and 2 754 kJ/m2/s) with 5% dead fuel moisture, despite the similar fireline intensities. Secondly, residual burning of the heavy fuel load after the flaming front has passed (which is not accounted for in the above measures of intensity) will also have a considerable impact on below-ground vegetation, and it seems unlikely that these variables could be lowered significantly by burning under conditions of higher fuel moisture.

It is sometimes suggested that stands of hakea should be burnt standing. This will lead to far less severe fires (Table 9.5) and less drastic effects on the remaining vegetation and on physical features of the soil. There are, however, a number of problems associated with this approach. In very dense stands, even under suitable weather conditions, fires sometimes do not spread through the crowns of hakea shrubs. This has been attributed to the very high packing density of particles in the fuel bed (Van Wilgen & Richardson 1985a). Secondly, follow-up operations required to eradicate resultant seedlings will be hampered by the standing dead shrubs, possibly making such operations prohibitively expensive. Dispersal of seeds is more efficient from standing shrubs than from felled ones and more seeds will disperse to new sites. The option of burning standing hakea plants and then eradicating seedlings appears to be feasible in some cases but detailed cost-benefit analysis data are lacking.

The practice of felling and burning should not present problems in sparse or moderate stands (where shrubs are scattered so that a relatively large area remains unaffected by the increased fuel load). The management of dense stands such as those at Wemmershoek, will however require careful planning. We suggest that in stands where the felling of shrubs would leave at least 25% of the area free of reclining shrubs, burns should be conducted to achieve low fireline intensity. Rothermel's fire model should be used to predict optimal burning conditions so as to minimize the deleterious effects of burning on the recovery of natural vegetation. These operations should be carefully monitored to assess their impact. Only in very dense stands (those where the reclining shrubs cover more than 75% of the area) should alternative measures be sought. Under these conditions, it may be necessary to kill standing shrubs so as to facilitate the spread of fire through the canopy. Methods have been developed for the aerial application of spore suspensions of the fungus *Colletotrichum gloeosporioides* (Penz.) Sacc. to stands of hakea (Morris 1983). This virulent pathogen causes die-back and mortality of shrubs and has shown potential for incorporation into the integrated control programme (Richardson & Manders 1985). Successful inoculation and the spread of symptoms will result in a greater proportion of dead material in the canopy and will facilitate the spread of fire. Fire in standing shrubs will in turn have less impact on the below-ground vegetation.

Despite the apparent disastrous effects of the fire in felled hakea, there is evidence from elsewhere that a remarkable degree of recovery of fynbos can occur. For example, Van Wilgen and Kruger's (1981) report on the effects of fire in the nearby Zachariashoek catchments shows that, although shrub life forms were reduced, a relatively healthy cover of fynbos exists today despite clearing and burning of hakea stands similar to those at Wemmershoek. Thus, although care should be taken to reduce the effects of clearing and burning operations as far as possible, we do not believe that clearing should in any way be postponed pending the results of further research into clearing methods. Careful monitoring of the recovery of vegetation following clearing and burning using the above methods will indicate whether recovery can be improved. If deleterious effects are sufficiently reduced by reducing fireline intensity alone then the application of fire behaviour prediction techniques will be useful.

Appendix 9.1 Plant species found on 12 plots at each of the two sites 19 months after a fire with their corresponding "species types" after Noble & Slatyer (1980) (Table 9.1). Species marked with '' and '+' were found at the uninvaded and the invaded site respectively (see text). Botanical nomenclature follows Bond & Goldblatt (1984).*

Poaceae			
Cymbopogon marginatus	UI	*	
Themeda triandra	UI	*	
Merxmuellera rufa	UI	*	+
Merxmuellera stricta	UI	*	
Pentaschistis	UI	*	
Plagiochloa uniolae	UI	*	
Poaceae sp. #1	UI	*	
Poaceae sp. #2	UI	*	
Poaceae sp. #3	UI	*	+
Poaceae sp. #4	UI	*	
Cyperaceae			
Ficinia deusta	ΣI	*	+
Ficinia filiformis	UI	*	+
Ficinia levynsae	ΣI	*	
Ficinia sp.	UI	*	
Tetraria capillacea	UI	*	
Tetraria ustulata	UI	*	
Tetraria sp. #1	UI	*	
Tetraria sp. #2	UI		+
Tetraria sp. #3	ΣI		+
Restionaceae			
Ischyrolepis capensis	UI	*	
Ischyrolepis curviramus	UI	*	
I. gaudichaudiana	UI	*	
Restio filiformis	UI	*	
Restionaceae sp. (seedling)	ΣI	*	+
Restionaceae sp. (sprouter)	UI	*	
Elegia sp.	UI	*	
Hypodiscus argenteus	ΣI	*	
Liliaceae			
Trachyandra hirsuta	UI	*	
Caesia contorta	ΣI		+
Eriospermum sp.	UI	*	
Albuca canadensis	UI	*	+
Asparagus compactus	UI	*	
Liliaceae sp. #1	UI	*	
Liliaceae sp. #2	UI	*	
Liliaceae sp. #3	UI		+
Haemodoraceae			
Dilatris ixioides	UI	*	
Wachendorfia paniculata	UI	*	
Iridaceae			
Bobartia indica	UI		+
Geissorhiza confusa	UI	*	
Babiana sp.	UI		+
Anapalina sp.	UI		+
Iridaceae sp.	UI	*	
Proteaceae			
Serruria fasciflora	ΣI		+
Protea laurifolia	CI	*	
Leucadendron sp.	CI		+
Hakea sericea (alien)	DI	*	
Santalaceae			
Thesium sp. #1	SI		+
Thesium sp. #2	SI	*	
Thesium sp. #3	SI	*	

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Appendix 9.1. (continued) Plant species found on 12 plots at each of the two sites 19 months after a fire with their corresponding "species types" after Noble & Slatyer (1980) (Table 9.1). Species marked with '' and '+' were found at the uninvaded and the invaded site respectively (see text). Botanical nomenclature follows Bond & Goldblatt (1984).*

Aizoaceae			
Acrosanthes teretifolia	SI		+
Mesembryanthemaceae			
Erepsia anceps	SI	*	
Lauraceae			
Cassytha ciliolata	DI	*	
Crassulaceae			
Crassula fascicularis	SI	*	
Montiniaceae			
Montinia caryophyllaceae	UI	*	+
Rosaceae			
Cliffortia ruscifolia	SI	*	+
Fabaceae			
Acacia longifolia(alien)	SI		+
Rafnia capensis (L.)	SI		+
Aspalathus divaricata	SI	*	
Aspalathus juniperina	SI	*	+
Aspalathus linearis	UI	*	+
Aspalathus sp.	UI		+
Indigofera sp. cf. I. dillwynioides	SI	*	
Gentianaceae			
Sebaea exacoides	SI	*	
Geraniaceae			
Pelargonium triste	UI	*	
Pelargonium sp. #1	UI	*	
Pelargonium sp. #2	UI	*	
Pelargonium sp. #3	UI	*	
Oxalidaceae			
Oxalis strigosa	UI		+
Oxalis sp. #1	UI		+
Oxalis sp. #2	UI	*	
Oxalis sp. #3	UI		+
Polygalaceae			
Muraltia thunbergii	SI		+
Rutaceae			
Diosma hirsuta	SI	*	
Euphorbiaceae			
Clutia alaternoides	UI	*	
Euphorbia genistoides	SI	*	
Anacardiacae			
Rhus rosmarinifolia	UI	*	+
Sapindaceae			
Dodonaea viscosa var. angustifolia	UI	*	
Rhamnaceae			
Phylica callosa	SI	*	
Sterculiaceae			
Hermannia angularis	SI	*	

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Appendix 9.1. (continued) Plant species found on 12 plots at each of the two sites 19 months after a fire with their corresponding "species types" after Noble & Slatyer (1980) (Table 9.1). Species marked with '' and '+' were found at the uninvaded and the invaded site respectively (see text). Botanical nomenclature follows Bond & Goldblatt (1984).*

Thymelaeaceae			
Gnidia anomala	SI		+
Struthiola ciliata	SI		+
Umbelliferae			
Centella glabrata	UI	*	+
Lichtensteinia trifida	SI	*	+
Ericaceae			
Erica sp. (seedling)	SI	*	
Boraginaceae			
Lobostemon glaucophyllus	UI	*	
Selaginaceae			
Selago spuria	SI	*	
Rubiaceae			
Anthospermum aethiopicum	SI	*	
Anthospermum ciliare	SI	*	
Campanulaceae			
Roella ciliata	SI	*	+
Prismatocarpus fruticosus	SI	*	
Wahlenbergia exilis	SI	*	
Lobeliaceae			
Cyphia volubilis	UI	*	+
Lobelia coronopifolia	UI	*	+
Asteraceae			
Corymbium glabrum	UI	*	+
Corymbium villosum	UI	*	
Helichrysum sp.	?	*	
Stoebe incana	DI		+
Stoebe plumosa	DI	*	
Stoebe sp. #1	DI	*	
Stoebe sp. #2	DI	*	
Stoebe sp. #3	DI	*	
Elytropappus glandulosus	SI	*	
Metalasia muricata	DI	*	
Senecio sp.	SI		+
Euryops abrotanifolius	SI	*	
Ursinia crithmoides	SI	*	
Haplocarpha lanata	UI	*	
Gazania serrata	UI	*	
Berkheya armata	UI	*	
Asteraceae sp.	UI	*	
Other			
Geophyte #1	UI	*	
Geophyte #2	UI	*	
Geophyte #3	UI	*	
Geophyte #4	UI	*	
Geophyte #5	UI	*	
Seedling #1	SI	*	
Seedling #2	SI		+
Seedling #3	SI		+
Seedling #4	SI		+
Shrub	UI	*	

CHAPTER 10

REDUCTIONS IN PLANT SPECIES RICHNESS UNDER STANDS OF ALIEN TREES AND SHRUBS IN THE FYNBOS BIOME

CHAPTER 10: REDUCTIONS IN PLANT SPECIES RICHNESS UNDER STANDS OF ALIEN TREES AND SHRUBS IN THE FYNBOS BIOME [1]

10.1. ABSTRACT

The reduction of species richness of indigenous plants is one of the major problems associated with the presence of dense stands of invasive alien trees and shrubs in the Fynbos Biome of the Cape Province, South Africa. A synthesis was made of published and unpublished data on plant species richness in fynbos with different levels of invasion and different histories of control. Linear regressions of species richness on the log of quadrat size were significant for both uninvaded fynbos and fynbos under dense stands of alien trees and shrubs. The slopes of the regression equations did not differ significantly between invaded and uninvaded sites, but elevations were significantly different, indicating a marked reduction in richness of indigenous plant species in invaded areas. The linear regression of species richness on quadrat size for cleared areas was not significant, but quadrats at most cleared sites showed species richness values intermediate to those of uninvaded fynbos and dense stands of aliens. Reductions in species richness at the scale of the sample quadrats used in this study (4 - 256 m^2) occur once the canopy cover of aliens exceeds about 50 % and there is evidence of reduced species richness with increased time of suppression. For this reason, stands should be cleared before canopy closure is achieved.

10.2. INTRODUCTION

Fynbos is the most characteristic vegetation type in the Cape Floristic Region (Goldblatt 1978). This unique vegetation type occurs on the Cape Fold Belt mountains and the adjacent coastal strip in the southern and southwestern Cape Province of South Africa. The high species richness and levels of endemism in the indigenous flora of the fynbos make it a resource worthy of high conservation status (Goldblatt 1978).

A modern feature of the fynbos biome is the widespread occurrence of dense stands of alien trees and shrubs (Macdonald & Richardson 1986). The widespread invasion by introduced trees and shrubs is unique to the fynbos biome amongst the mediterranean-type climate regions of the world (Macdonald et al. 1988). The marked reduction in native plant species diversity concomitant with plant invasions is also apparently unique to the fynbos biome (Macdonald et al. 1988, in press). Several studies have shown that a high proportion of the indigenous species currently threatened with extinction are affected by stands of invasive alien trees and shrubs (Hall et al. 1980; Hall

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[1] *Publication status: Richardson, D.M., Macdonald, I.A.W. & Forsyth, G.G. (1989). Reductions in plant species richness under stands of alien trees and shrubs in the Fynbos Biome. South African Forestry Journal 149: 1-8.*

& Ashton 1983; Hall & Veldhuis 1985). There have also been several studies of the effects of invasion or afforestation on the structure and composition of vegetation in the fynbos biome (Seagrief 1950; Cowling et al. 1976, Milton 1976; Jacot Guillarmod 1980; Richardson & Van Wilgen 1986a). Macdonald & Richardson (1986) presented a preliminary assessment of the phenomenon of reduction in species richness following invasion. The potential reduction in species richness that could occur if stands of aliens are not cleared needs to be quantified to justify the control operations which are extremely expensive (Macdonald et al. 1985). In addition, the possibility that further loss of species could occur where control measures damage the natural vegetation and soil (Richardson & Van Wilgen 1986b; Holmes et al. 1987) needs to be assessed.

10.3. METHODS

We extracted from the literature all the data on plant species richness in the fynbos biome that could be related to known densities or cover of alien trees and shrubs, or to definite histories of alien plant control. In all cases, only indigenous plant species were included in the assessment of species richness.

In addition, a number of 4 m^2 quadrats (2 m x 2 m) were located randomly within 13 sites chosen to represent various alien plant densities or control histories. Quadrats of this size give a good measure of alpha diversity in fynbos, relatively free of the effects of habitat patchiness (Wicht 1948; Bond 1983; Kruger 1987). These surveys were carried out between 1983 and 1987 and in each case only one survey was made. All plants visible on the plots at the time of the survey were listed. The density of alien plants at a site was estimated either as the average number of plants per ha or as the percentage canopy cover of all alien trees and shrubs. For the estimation of alien plant density or cover, circular quadrats of 5 m radius centered on each of the species richness quadrats were used.

Sites with more than 25% canopy cover of alien tree species were classed as 'dense', and sites with a canopy cover of between 1 and 25% were termed 'lightly invaded'. Sites where alien cover was negligible (less than 1%), were considered 'uninvaded'. Where the density of alien trees was assessed as numbers of plants per hectare, the equivalent classes vary between species depending on their stature and therefore the relative contribution of single trees or shrubs to the canopy cover. Stands of Acacia species having densities in excess of 5 000 plants per hectare were classed as 'heavily invaded' (derived from Milton & Siegfried 1981). For Pinus species, mature stands with densities greater than 400 plants per hectare were classed as 'dense'. For Hakea sericea, stands with densities in excess of 2 000 plants per hectare were called 'dense'.

We have included data from eight sites in plantations of alien species that are known to be invasive within the fynbos biome (Macdonald et al. 1985) and from 14 self-sown stands. In five cases the origin of the stand was unknown. The use of data from both types of alien stands is considered valid as the self-sown stands often become indistinguishable from dense plantations and are therefore considered to have the same effects on the indigenous flora (see Richardson & Van Wilgen (1986a) for the justification of this assumption). In some areas (e.g. Table Mountain Nature Reserve) the distinction between plantations and self-sown stands is unclear (Behrens 1985). It is not considered likely that indigenous species were eliminated from 4 m^2 areas within a plantation at the time of planting, as site preparation for commercial afforestation in the fynbos biome requires only slight disturbance to the indigenous vegetation (Donald 1986). In the cited studies from within plantations, species richness was measured in quadrats varying in size from 16 to 256 m^2. We consider it highly unlikely that species richness as measured at these scales will have been significantly affected by plantation management.

The data from all dense stands were compared with those from uninvaded fynbos and with those from cleared stands. Regression equations of mean species richness against the log of quadrat size were fitted using the REG procedure of SAS (SAS Institute Inc. 1985c). In all cases linear equations provided the best fit (highest F values and r^2).

10.4. RESULTS

10.4.1. Overall reductions in species richness under alien tree stands

The linear regressions of mean species richness on the log of quadrat size for uninvaded and densely invaded sites (Figure 10.1) were significant ($F=31.25$, $P < 0.0001$ for uninvaded fynbos, and $F=20.39$, $P=0.0015$ for 'dense' alien stands). The slopes of these regressions are not significantly different ($t=2.129$; $P < 0.05$), but elevations are significantly different ($t=3.565$; $P < 0.005$) (Zar 1984). For 4 m^2 plots, the mean species richness at uninvaded sites is nearly three times higher than at invaded sites (uninvaded : mean = 21.2; SE = 1.9; n=9; 'dense' : mean = 7.8; SE = 3.0; n = 3).

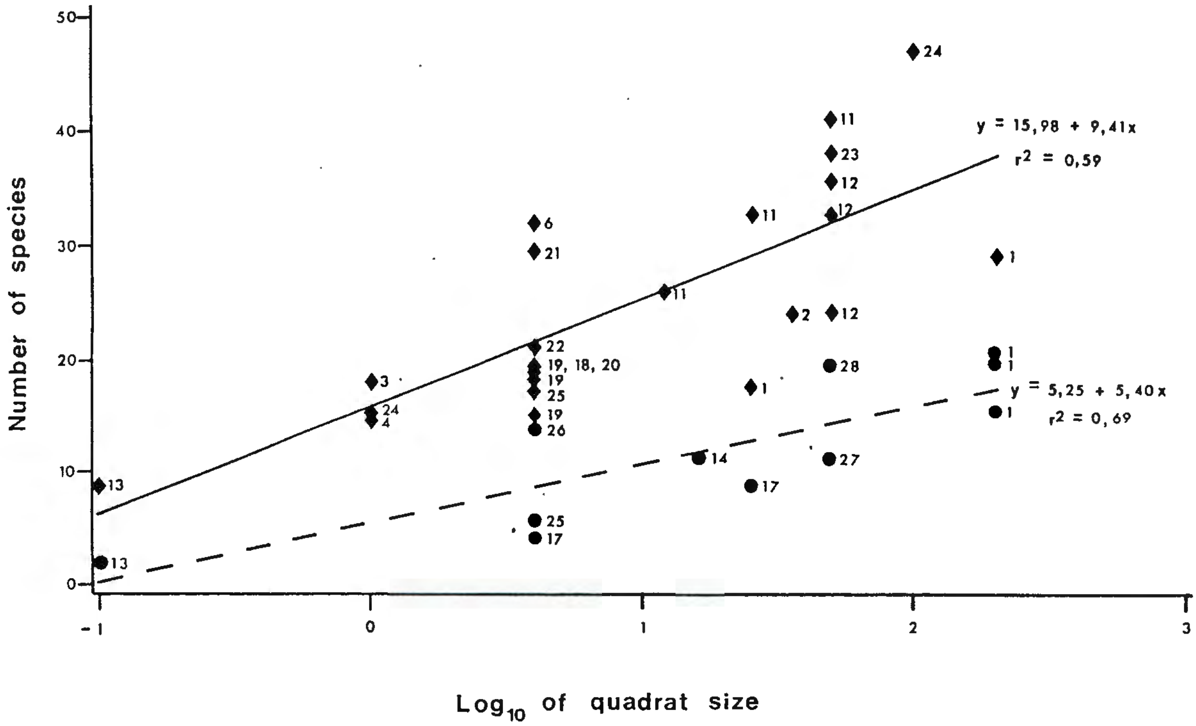

Figure 10.1. The relationships between the size of sample quadrats and the mean richness of indigenous plant species for uninvaded and invaded sites in the Fynbos Biome. '♦' = uninvaded sites; '●' = 'dense' alien stands. Numbers refer to sites in Appendix 10.1.

10.4.2. Changes in species richness with increasing alien tree cover

The trend of progressive reduction in indigenous species richness with increase in alien plant canopy cover is shown for stands of Pinus pinaster on Table Mountain (Figure 10.2).

10.4.3. Paired comparisons of uninvaded and invaded sites

In several cases, data from uninvaded and invaded fynbos were available for the same area. These allow for a more detailed investigation of changes resulting from alien plant invasions.

On Table Mountain, where the mean species richness measured in 1975 in 25 m^2

quadrats was 17.6 species in uninvaded fynbos (site 1 in Appendix 10.1), the corresponding figure for quadrats (200 m^2) located in dense Pinus pinaster stands was only 15.4 (Cowling et al. 1976). At Kylemore (site 25 in Appendix 10.1), the average number of species in 4 m^2 quadrats in uninvaded fynbos was 17.2. In an adjacent stand of Acacia melanoxylon and Hakea sericea, species richness had been reduced to an average of 5.4. Similarly, in uninvaded fynbos at Biesievlei (site 13 in Appendix 10.1), the mean species richness in 0.1 m^2 quadrats was 8.5 whereas 35 years after afforestation with Pinus radiata, the mean number of indigenous species per quadrat was only 1.8 (Richardson & Van Wilgen 1986a).

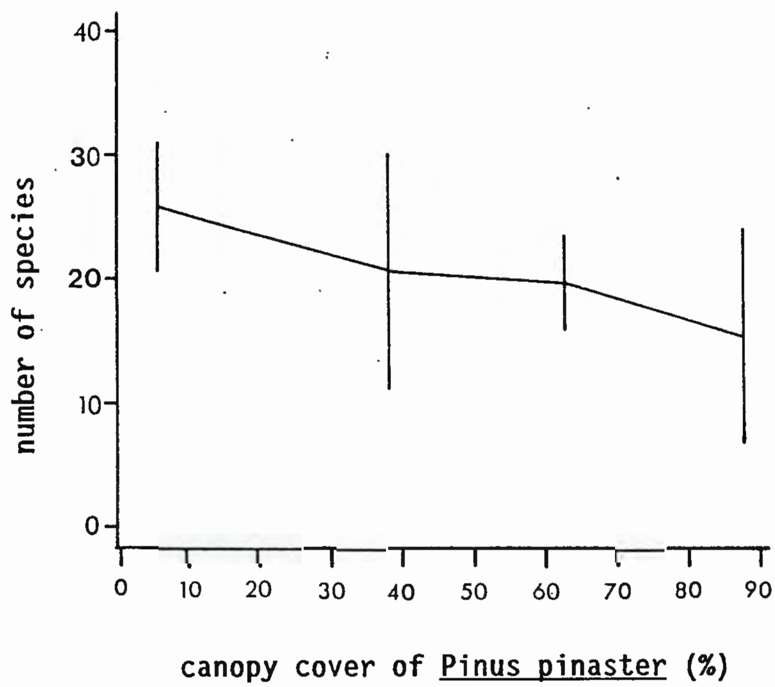

Figure 10.2. The progressive reduction in indigenous species richness in 10 m X 20 m quadrats with increase in cover of Pinus pinaster on Table Mountain (calculated from Cowling et al., 1976). Mean species richness is plotted against midpoints of canopy cover classes. Bars are standard deviations from the mean.

10.4.4. Paired comparisons of cleared and uninvaded sites

Two years after the clearing of a 56 year-old Pinus radiata plantation at Algeria in the Cederberg State Forest (site 18 in Appendix 10.1), the mean number of species in 4 m^2 quadrats was 13.8. In an adjacent area free of aliens, the mean number of species was 19.3. Species richness in the two areas was significantly different ($t = 3.477$; $P < 0.005$).

The results of several studies on Table Mountain (sites 1 to 4 in Appendix 10.1) show that the mean number of species in uninvaded fynbos is greater than in areas recently cleared of _Pinus pinaster_: Species richness measured in uninvaded fynbos in the late 1920's and early 1930's (Adamson 1931) ranged from 11 to 18 species per quadrat where quadrat size varied from 1 to 4 m^2. In 1976, Cowling _et al_. (1976) obtained a mean of 17.6 species in 25 m^2 quadrats, and, in 1985, Behrens (1985) obtained a mean of 24 species/quadrat in 36 m^2 quadrats. In 1985, where _Pinus pinaster_ plantations had been felled 6 months prior to the enumeration, mean species richness in 25 m^2 quadrats was only 7.5 whereas plantations felled more than 1 year prior to the enumeration and recently burned held 8.8 species. A lightly invaded area, felled and burned two to three years prior to the enumeration was the only site with species richness values equivalent to those of uninvaded fynbos (mean = 20.4 species per 25 m^2 quadrat).

The apparent high similarity between species numbers in large plots (256 m^2) in cleared and uninvaded sites at the Muizenberg site (Holmes _et al_. 1987; site 16 in Appendix 10.1) is considered to be an artefact due to the extremely low species richness in the uninvaded area. This number (30) is much lower than has been obtained for plots in this size range elsewhere in the fynbos (Bond 1983), and is possibly a consequence of the abnormally long period of protection from fire in the sampled stand. Adamson (1931) shows that species diversity at the scale of 1 - 4 m^2 declines from 2 years post-fire to the "near-climax" condition (site 2 in Appendix 10.1). At Jonkershoek (site 12 in Appendix 10.1), Van Wilgen (1981) using larger plots (50 m^2) showed that mean species richness was lower at 21 years post-fire than either at 4 or 37 years post-fire. The stand sampled at Muizenberg was estimated to be 25 years post-fire (Holmes _et al_. 1987). It is also known that the uninvaded plot at this site was on steeper ground with shallower soils than were the cleared plots (P.M. Holmes, pers. comm. 1988).

10.4.5. Paired comparisons of a cleared and an invaded site

A dense stand of _Acacia saligna_ at Muizenberg (Site 17 in Appendix 10.1) in 1984 had a mean species richness of 4.3 in 4 m^2 quadrats. An immediately adjacent area which had previously held the same infestation and which had been felled, burned and sprayed with a non-selective herbicide ("Gramoxone" / paraquat) one year previously (site 16 in Appendix 10.1) had a mean of 9.8

species per 4 m^2 quadrat. Species richness was significantly higher in the cleared area ($t = 2.418$; $P < 0.05$). At the same site, 25 m^2 quadrats in the dense Acacia saligna stand had a mean of 8.9 species (P.M. Holmes and E.R. Ashton, unpublished data). In adjacent areas that had been cleared using the same treatment regime between 2 and 8 years previously, the mean species richness in 25 m^2 quadrats ranged from 12.0 to 18.5 (Dallas 1986).

10.4.6. Unpaired comparisons of cleared with invaded and uninvaded sites

There was no significant relationship between species richness and the log of quadrat size in areas where alien trees and shrubs had been cleared ($F=1.27$; N.S. in linear regression model; Figure 10.3). The lack of a clear relationship probably reflects the different degrees of disturbance due to suppression by the presence of the stand, and also the different effects of various clearing methods on the indigenous plants. In general, sites which had been cleared were richer in species than were heavily invaded sites, but poorer than uninvaded fynbos (Figure 10.3). For 4 m^2 plots, the mean species richness at cleared sites was 14.2 ^{ab} (SE = 2.3; n = 9). Comparable mean species richness figures for uninvaded sites and 'dense' stands are 21.2 ^{a} (SE = 1.9; n = 9) and 7.8 ^{b} (SE = 3.0; n = 3) respectively. The null hypothesis that species richness does not differ significantly among the categories is refuted [$F = 6.22$ $P < 0.01$ in one-way ANOVA; means with the same superscript letter do not differ significantly (Student-Newman-Keuls test $P < 0.05$)]. Species richness at cleared sites which had not been very heavily invaded (e.g. sites 7 and 8 in Appendix 10.1) approximated that of uninvaded fynbos (Figure 10.3). Where heavily invaded sites had been cleared, species richness was sometimes even lower than that of heavily invaded sites (e.g. sites 2 and 9; Figure 10.3).

10.5. DISCUSSION

Invasion of fynbos by alien trees and shrubs results in a significant reduction in the richness of indigenous plant species at the scale of quadrats used in this study. Plant invasions have caused local extinctions of many plant species. The impact of invasive plants on natural fynbos communities has been very severe when considered at this scale. Indeed, no other plant communities anywhere in the world have been so markedly changed by introduced plants as have fynbos communities (cf. Pimm 1986).

How have these effects influenced species richness at the landscape scale ? In the whole fynbos biome, the current level of invasion by alien plants has resulted in a maximum of 26 extinctions (Hall & Veldhuis 1985). None of the extinctions can be attributed exclusively to the influence of alien plants. On the Cape Peninsula (471 km^2), where most rare plant species are threatened by stands of alien trees and shrubs, only five species (out of a total of 2256; 0.22 %) have become extinct since the introduction and spread of the alien species (Hall & Ashton 1983).

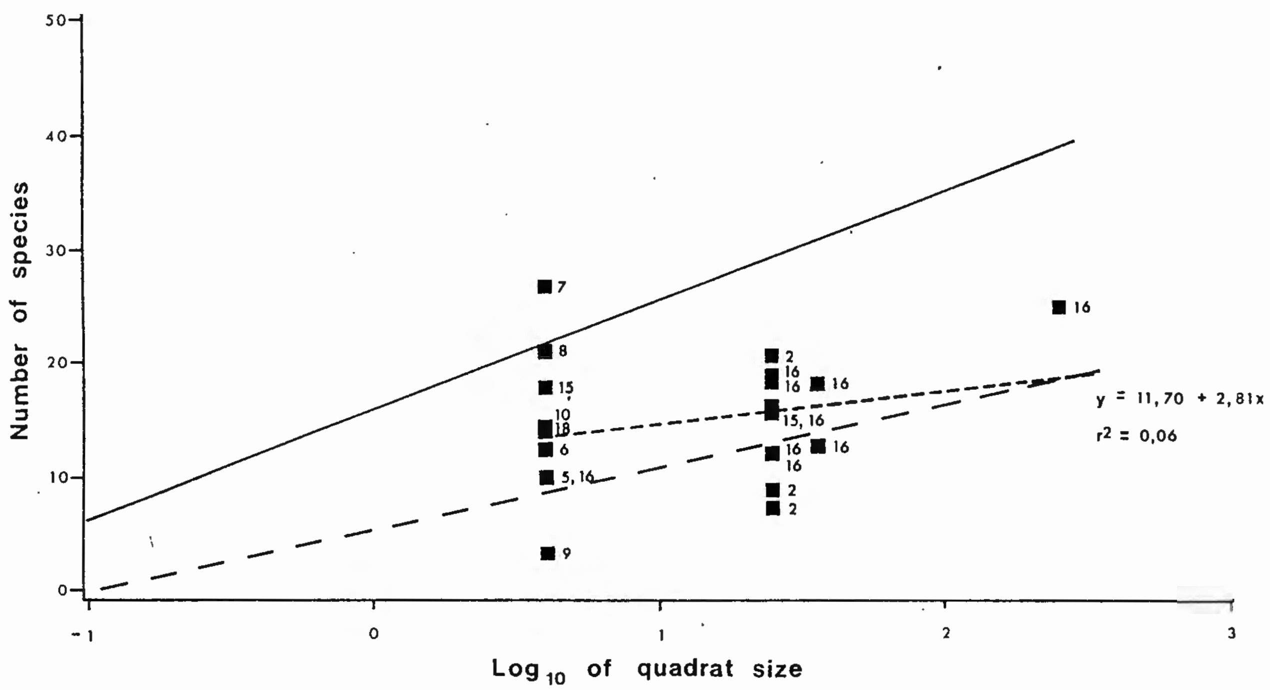

Figure 10.3. The mean number of indigenous plant species at sites cleared of alien vegetation plotted against the log of quadrat size, as compared with the regressions of this relationship for uninvaded and densely invaded sites. '——' = uninvaded fynbos; '— —' = 'dense' alien stands; '- - - -' = cleared sites. Numbers refer to sites in Appendix 10.1.

We have not assessed the vulnerability of particular species or life forms to elimination following canopy closure. In a study of the changes in vegetation composition and structure following afforestation with Pinus radiata, Richardson & Van Wilgen (1986a) showed that shrubs, usually the dominant life form in fynbos communities, were particularly vulnerable to elimination. Geophytes and other herbaceous elements are less noticeably influenced, and may even increase in abundance (Richardson & Van Wilgen 1986a). These generalizations appear to apply equally in self-sown stands of alien trees.

Insufficient data are available for an assessment of possible differential effects of various alien species on the indigenous flora. However, the data presented in this chapter indicate that dense stands of *Acacia* species, *Hakea sericea* and *Pinus* species all bring about significant reductions in the richness of indigenous species.

The decline in species richness with an increase in alien plant cover (Figure 10.2) was also noted under stands of *Acacia cyclops* at the Cape of Good Hope Nature Reserve (Turpey 1986). For this reason, stands should be cleared before canopy closure is attained. It appears that clearing stands of alien trees and shrubs can reverse the attrition of indigenous species richness (Figure 10.3). Areas cleared of dense stands recover more slowly than do those cleared of light infestations. Indications from studies carried out in widely different areas with different soil types and following invasion by both *Acacia saligna* and *Pinus* species indicate that even where dense stands have been present for long periods (15 to 40 years), unaided recovery of the fynbos following clearing does occur (e.g. site 16 in Appendix 10.1). Where stands are very old, recovery is slower (e.g. site 6 in Appendix 10.1). Further studies are required to elucidate the relative resilience of different fynbos communities. Critical issues that require attention are: the rate of depletion of indigenous seeds under dense stands of aliens, and the role of dispersal in the recolonization of cleared sites by indigenous species.

Appendix 10.1. Indigenous vascular plant species richness in uninvaded fynbos vegetation, in areas invaded by alien woody plants and in areas recently cleared of aliens.

Locality, site number and study number	Vegetation type (after Moll et al 1984) and condition	Size of sample areas (m2)	No. of species in uninvaded vegetation min-mean-max (n)	Alien species and invasion level (sph = stems per hectare)	No. of species in invaded vegetation min-mean-max (n)
Table Mountain Nature Area	Mesic Mountain Fynbos	25	13-17, 6-28 (13)	Pinus spp.	
33° 55'S; 18° 21'E		200	-	1% cover	10-29, 1-39 (8)
(1)		200		1 - 25% cover	18-25, 7-38 (8)
		200		25- 50% cover	11-20, 6-38 (5)
		200		50- 75% cover	10-19, 7-35 (17)
		200		75-100% cover	2-15, 4-19 (5)
Table Mountain (Back Table)	Mesic Mountain Fynbos	36	18-24, 0-36 (5)	Pinus pinaster	
(2)			-	Plantations	
		25		- felled 6 mths	7- 7, 5- 8 (2)
				- felled 16-20 mths	
		25		& burned 2 mths	5- 8, 8-16 (6)
				Infestation	
				- felled 36 mths	
		25		& burned 31 mths	15-20, 4-26 (5)
Table Mountain (North Slope)	Mesic Mountain Fynbos on			no aliens	-
(3)	Sandstone				
	2 years since burn	1	mean = 18 (50)		
	longer since burn	variable	mean = 16 (25)		
	'near climax'	1 to 4	mean = 11 (50)		
Table Mountain (West Slope)	Mesic Mountain Fynbos on			no aliens	-
(4)	Granite				
	recent burn	1	mean = 15 (25)		
	'near climax'	variable	mean = 14 (50)		
		1 to 4			
Table Mountain (Plateau)	Mesic Mountain Fynbos on			no aliens	-
(4)	Sandstone	"	mean = 14 (25)		
Devil's Peak	Mountain Fynbos	4		Pinus radiata plantation,	
33° 57'S; 18° 26'E				established 1894, cleared,	
(5)				burned March 1982, sam-	
				pled December 1983	7- 9, 8-12 (5)
Wemmershoek	Mesic Mountain Fynbos	4	27-32, 1-40 (12)	Hakea sericea (100%	
33° 51'S; 19° 10'E				cover), felled May 1983	
(6)				burned January 1984	
				sampled August 1985	6-12, 6-20 (12)

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Locality, site number and study number	Vegetation type (after Moll et al 1984) and condition	Size of sample areas (m2)	No. of species in uninvaded vegetation min-mean-max (n)	Alien species and invasion level (sph = stems per hectare)	No. of species in invaded vegetation min-mean-max (n)
Wemmershoek 33° 48'S; 19° 05'E (7)	Mesic Mountain Fynbos	4	-	Hakea sericea (550 sph) felled December 1981, burned April 1982, sampled August 1983	13-26, 6-37 (8)
Baken Kop, La Motte State Forest (8)	Mesic Mountain Fynbos	4	-	Pinus pinaster infestation (760 sph) felled 1981, burned May 1982, sampled August 1983	8-20, 8-29 (6)
La Motte State Forest 33° 55'S; 19° 02'E (9)	Mesic Mountain Fynbos	4	-	Pinus pinaster infestation (324 sph) felled 1982, sampled 1983	1- 3, 2- 5 (5)
La Motte State Forest 33° 55'S; 19° 02'E (10)	Mesic Mountain Fynbos	4	-	Pinus pinaster infestation (74 sph) felled 1982, sampled 1983	10-14, 0-19 (4)
Zachariashoek Catchment 34° 40'S; 19° 02'E (11)	Mesic Mountain Fynbos	12 25 50	4-26, 0-52 (119) 6-33, 0-66 (119) 7-41, 0-86 (119)	no aliens	-
Jonkershoek State Forest 34° 00'S; 18° 57'E (12)	Mesic Mountain Fynbos 37 years since burn 21 years since burn 4 years since burn	 50 50 50	 21-32, 6-54 (40) 13-24, 2-35 (10) 19-35, 8-45 (50)	no aliens	-
Biesievlei, Jonkershoek 33° 57'S; 18° 55'E (13)	Mesic Mountain Fynbos	0,1	0- 8, 5-20 (200)	Pinus radiata plantation, planted 1948, sampled 1984	0- 2, 1- 7 (193) mean = 1,8 excluding aliens
Bosboukloof, Jonkershoek 33° 56'S; 18° 57'E (14)	Mesic Mountain Fynbos	16	-	Pinus radiata plantation, planted 1938, sampled 1976	0-11, 1-15 (126)
Helderberg, Jonkershoek 34° 00'S; 18° 54'E (15)	Mesic Mountain Fynbos	4	-	Hakea sericea (3000 sph) felled, burned October 1981, sampled October 1983	11-17, 5-24 (10)

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Appendix 10.1 Continued

Locality, site number and study number	Vegetation type (after Moll et al 1984) and condition	Size of sample areas (m2)	No. of species in uninvaded vegetation min-mean-max (n)	Alien species and invasion level (sph = stems per hectare)	No. of species in invaded vegetation min-mean-max (n)
Muizenberg 34° 04'S; 18° 27'E	Mesic Mountain Fynbos		-	Acacia saligna (9800 sph) felled, burned herbicide applied (Gramoxone)	
(16 - study 1)	1984	4		1 year since felled	3- 9, 8-22 (8)
(16 - study 2)	1985	25		2 years since felled	15-15, 5-16 (2)
	1986	36		3 years since felled	10-12, 5-15 (2)
	1985	25		3 years since felled	3-12, 0-18 (7)
	1986	36		4 years since felled	15-18, 0-21 (2)
	1985	25		5 years since felled	13-15, 7-18 (4)
	1986	25		6 years since felled	15-18, 0-21 (2)
	1985	25		7 years since felled	16-18, 5-21 (2)
	1986	25		8 years since felled	10-12, 0-14 (2)
	1986	256		3-8 years since felled	23-24, 7-27 (4)
Muizenberg 34° 04'S; 18° 27'E	Mesic Mountain Fynbos		-	Acacia saligna 25 to 50 year old stand, (9000 sph)	
(17 - study 1)		4			3- 4, 3- 6 (4)
(17 - study 2)		25			4- 8, 9-13 (9)
Algeria, Cederberg State Forest 32° 21'S; 19° 02'E (18)	Mesic Mountain Fynbos	4	17-19, 3-24 (6)	Pinus radiata plantation, planted 1925, clearfelled 1981, sampled November 1983	10-13, 0-19 (10)
Cederberg State Forest 32° 20'S; 19° 03'E (19)	Mesic Mountain Fynbos				
	14 years since burn	4	14-18, 3-25 (50)	no aliens	-
	18-20 years since burn	4	9-15, 0-23 (50)	no aliens	-
	21 years since burn	4	11-19, 6-28 (50)	no aliens	-
Kogelberg State Forest 34° 16'S; 19° 00'E	Mesic Mountain Fynbos				
(20)	20 years since burn	4	14-19, 2-26 (140)	no aliens	-
(21)	1, 5-4 years since burn	4	23-29, 3-36 (140)	no aliens	-
Du Toits Kloof, Hawequas State Forest 33° 42'S; 19° 04'E (22)	Mesic Mountain Fynbos	4	18-21, 0-26 (7)	no aliens	-

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Appendix 10.1 Continued

Locality, site number and study number	Vegetation type (after Moll *et al* 1984) and condition	Size of sample areas (m2)	No. of species in uninvaded vegetation min-mean-max (n)	Alien species and invasion level (sph = stems per hectare)	No. of species in invaded vegetation min-mean-max (n)
Cape of Good Hope Nature Reserve 34° 15'S; 18° 25'E (23)	Coastal Mountain Fynbos	50	5-38, 2-83 (100)	no aliens	-
Mean of 20 sites in southern Cape (24)	Mesic Mountain Fynbos	1 100	10-15, 4-27 (100) 26-47, 1-68 (20)	no aliens	-
Kylemore 33° 55'S; 18° 58'E (25)	Mesic Mountain Fynbos	4	12-17, 2-22 (5)	Mixed *Acacia melanoxylon* and *Hakea sericea* (100% cover)	4- 5, 4- 9 (5)
De Bordje 33° 55'S; 18° 58'E (26)	Mesic Mountain Fynbos	4	-	*Hakea sericea* 9-year old stand (15 700 sph) 30% cover	10-13, 8-20 (5)
Bergsig, Jonkershoek 33° 57'S; 18° 55'E (27)	Mesic Mountain Fynbos	50	-	*Pinus radiata* 17-year old, self-sown stand (2 770 sph, 100% cover)	5-11, 2-15 (5)
Stellenboschberg, Jonkershoek 33° 57'S; 18° 54'E (28)	Mesic Mountain Fynbos	50	-	*Pinus pinaster* self-sown stand (100% cover)	12-19, 6-23 (5)

Source:

(1) Cowling *et al* (1976)
(2) Behrens (1985)
(3 & 4) Adamson (1931)
(5) D M Richardson & G G Forsyth (unpublished data)
(6) Richardson & van Wilgen (1986b)
(7, 8, 9 & 10) D M Richardson & G G Forsyth (unpublished data)
(11) Van Wilgen & Kruger (1985)
(12) Van Wilgen (1981)
(13) Richardson & van Wilgen (1986a)
(14) Milton (1976)
(15, 16 study 1 & 17 study 1) D M Richardson & G G Forsyth (unpublished data)
(16 study 2) Dallas (1986)
(17 study 2) P M Holmes & E R Ashton (unpublished data)
(18) D M Richardson & B W van Wilgen (unpublished data)
(19, 20 & 21) D C le maitre (unpublished data)
(22) D M Richardson & G G Forsyth (unpublished data)
(23) Taylor (1984)
(24) Bond (1983)
(25, 26, 27 & 28) D M Richardson & G G Forsyth (unpublished data)

CHAPTER 11

GENERAL CONCLUSIONS

CHAPTER 11: GENERAL CONCLUSIONS

This study examined the ecology of invasions by pines (Pinus spp.) and hakeas (Hakea spp.) in the mountain fynbos of the southwestern Cape Province of South Africa. A series of natural experiments and autecological studies (Chapters 2 to 10) were used to address the following questions (see p. 12):

1. What are the spatial and temporal characteristics of invasions by trees and shrubs in mountain fynbos ?
2. What are the biological attributes of successful invaders of mountain fynbos ?
3. To what degree is the current extent of invasion in mountain fynbos due to dissemination by man ?
4. What community properties of mountain fynbos permit invasion by introduced trees and shrubs ?
5. What are the impacts of invasions on mountain fynbos plant communities ?

The results of the investigations and experiments conducted during this study are presented in this thesis in four main parts (p. 13):

I. Case studies to elucidate major patterns and processes;
II. Studies of life history and population ecology of selected invaders;
III. Investigations of the determinants of invasibility;
IV. Assessments of the consequences of invasion, and of control programmes.

This chapter presents a synopsis of the major results of the studies with reference to the five questions listed above. The practical and theoretical implications of the major findings are outlined.

11.1. What are the spatial and temporal characteristics of invasions by trees and shrubs in mountain fynbos ?

This question was addressed principally in Part I but also in Part II of this thesis. Invasion events were studied to determine the spatial and temporal characteristics of invasions by four Pinus species in mountain fynbos. Chapter 2 documented the spread of Pinus radiata from a plantation and examined the response (in terms of population structure) of the invader to important environmental factors. The invasion was reconstructed using sequential aerial photographs and inference from the age structures of self-sown stands at five localities in a 6 km^2 study area. The initiation of invasion coincided with the first release of seeds from the plantation. Pinus radiata is serotinous but releases some seed each year, notably during summer when the high temperatures cause cones to open. Strong south-east winds are a feature of the western Cape summers, and the synchronous occurrence of the agents of seed release (high temperatures) and seed dispersal (strong winds) ensures the efficient dissemination of seeds to initiate invasions.

Pine invasions in mountain fynbos are essentially two-phased (Figure 2.3. p. 23). Invasion commences with the establishment of isolated colonists downwind of seed sources. Seedlings grow rapidly and attain reproductive maturity in less than the mean inter-fire interval. Exponential population growth from these foci is mediated by fires which usually kills pines but stimulates the mass release of canopy-stored seeds and creates suitable micro-habitats for germination. The recruitment of dense, even-aged, daughter stands around the initial colonists eventually results in the formation of dense stands. The transformation of mountain fynbos shrublands to closed-canopy pine forest over large areas can occur over two fire cycles (c. 30 years) (Figures 2.2 and 2.3).

A detailed study of the age structure and regeneration dynamics of a Pinus halepensis stand on the Cape Peninsula emphasized the fundamental role of fire in pine invasions in mountain fynbos (Chapter 3). Correlation of features of the age structure of P. halepensis with the fire history revealed that: (i) fire-survival is not essential for perpetuation and growth of populations, but the contribution of seeds from fecund adults that do survive fires is important for re-establishment following fires at short intervals and also for dispersal to new areas; and (ii) perpetuation of pine populations is usually achieved by the recruitment of new stands after fire, and for this reason the attainment of reproductive maturity in the interval between fires is important.

The spatial and temporal characteristics of invasions are similar for most invasive species of Pinus and Hakea in mountain fynbos. Differences in observed patterns of invasions for these taxa are largely explained by considering the role of various life history attributes in population growth (Chapter 5). Serotinous pines (P. halepensis, P. pinaster and P. radiata) show very similar population responses to fire. The mass release of winged seeds of these species after fire results in the recruitment of dense daughter stands around the parent trees, but also recruitment of scattered progeny at great distances from the parent. All these species show the typical two-phased invasion pattern that was detailed for P. radiata in Chapter 2. Pinus pinea, which has large seeds which are not stored in canopy, also recruits dense daughter stands after fire but does not recruit distant progeny. For this reason, the spread of this species has been relatively slow.

The two-phase pattern of spread described for serotinous pines can account for the current distribution of Pinus pinaster and Hakea sericea (Figure 1.2). These species conform with Baker's (1986) definition of "major weeds" - they have pre-adaptations that enabled plants to thrive more or less in variety of habitats, and their populations contain plants with "general purpose genotypes" that can build populations immediately (see also II.2.2. p. 219).

Populations comprising multiple foci (such as pine plantations and self-sown stands scattered throughout the fynbos biome) and that have the potential for continual establishment of new foci (see above) are difficult to regulate. Moody & Mack (1988) have simulated the spatial growth of invading plant populations with these attributes, and also the relative success of different control options in reducing spread. Their study emphasized the importance of the satellite foci for population growth; effectiveness of control measures was greatly increased by destroying even 30% of the satellites. These findings, together with the results presented in this thesis, suggest that operations aimed at controlling the spread of pines and hakeas in mountain fynbos should be focussed on the satellite foci - those trees that establish far from plantations or dense stands. Biological control, using seed-attacking insects, can contribute to this by reducing seed banks and thus the maximum potential dispersal distance (see p. 56; also Kluge 1983) - fewer satellite foci will establish and these will be closer to the seed source. This option has already been applied with very promising results in the case of Hakea sericea (Kluge 1983; Kluge & Richardson 1983; Neser & Kluge 1985). No seed-attacking insects have been introduced for the biological control of pines, and forestry authorities are reluctant to sanction such introductions (Richardson, in press). As the total area of pine plantations (and therefore the total pine seed bank) increases, satellite foci will establish in more remote areas and some of these will proliferate to form dense stands. The eradication of these isolated foci in the rugged terrain of the Cape mountains is extremely difficult to co-ordinate (the logistics of location and follow-up phases of control are baffling). For this reason, there is little hope of controlling invasive pines in mountain fynbos in the long-term without using biological control. There is an urgent need for a pragmatic review of the perceived conflict of interests that surrounds the question of biological control of pines.

11.2. What are the biological attributes of successful invaders of mountain fynbos ?

This question was addressed in parts II and III of the thesis. The relative importance of different life history attributes for invasion in mountain fynbos was studied by comparing the attributes of successful invaders with those of less successful congeners in the genera *Hakea* and *Pinus*. The most successful taxa in both genera possess a suite of life history attributes that include relatively small seed size, low seed/wing loadings, short juvenile periods, moderate to high degrees of serotiny and poor fire-tolerance as adults (Chapters 4 and 5). For these two genera, empirical information has supported the theoretical notion that a successful invader must be physiologically capable of growth and reproduction in the target environment and must possess life history attributes which permit population growth under the prevailing disturbance regime. This suggests that invasive potential can be predicted from a study of life history and a knowledge of the disturbance regime. One way that this knowledge can be used is to define the suite of attributes that has been successful for invasion by a taxon and then predict what other closely related taxa would invade if introduced. An analysis was made of life history strategies of a representative sample of *Pinus* taxa, including those introduced to mountain fynbos. A number of ecological groups were thus defined. The most successful invaders were grouped together on the basis of life history strategies (group D in Figure 5.4. p. 82), thus providing good evidence that life history is an integral mediator in invasions. This analysis also provides an objective framework for assessing future introductions of pines. Taxa closely allied to those that have invaded in terms of life history strategies will have a good chance of also becoming invaders. Those differing substantially in terms of life history strategies from proven successful invaders are less likely to become major weeds. This analysis ignores the role of biotic interactions in the target habitat in determining invasiveness. Pinus pinea differs substantially in life history to the "good invader" prototype defined for mountain fynbos, and yet this species has achieved a measure of success - through the establishment of an opportunistic mutualism with an introduced squirrel (Chapter 5). Interactions such as this introduce an unavoidable element of stochasticity to these predictions, but do not detract from the overall utility of the approach.

The perspective gained from the studies on Pinus and Hakea was used for two additional practical applications. Firstly, a general risk assessment model, based largely on life history attributes, was compiled to facilitate the objective evaluation of future introductions (Figure 7.4. p. 129). Secondly, an analysis was made of the potential of Western Australian Banksia species to become invaders. Using selected attributes that were important for explaining the relative success of pines and hakeas as invaders, and other theoretical considerations, a likely risk gradient was defined for banksias (Figure 7.5. p. 136). Tall serotinous shrubs that produce large numbers of small seeds and that have short juvenile periods have the greatest probability of invading mountain fynbos.

Several authors, and most notably entomologists, have expressed scepticism concerning the ability of ecologists to predict what introduced species will become invaders (e.g. Ehrlich 1986; Simberloff 1986; Crawley 1987b). I readily concede that there is no such thing as "the perfect invader" and that unforeseeable interactions can confound even the most astute predictions. However, I believe that the scepticism expressed by these authors can be attributed largely to their attempts to make extremely broad, global predictions. The studies presented in this thesis have demonstrated that, for introduced species in mountain fynbos, the possession of certain life history traits by an introduced species virtually guarantees a measure of success as an invader. Not all of these invaders will become major weeds (sensu Baker 1986).

11.3. To what degree is the current extent of invasion in mountain fynbos due to dissemination by man ?

This question was addressed in part II of the thesis. A study was made to determine the relative importance of life history and cultivation (including residency time and the magnitude of dissemination by man) in regulating the current extent of invasions by different pines. There is conclusive evidence that the extent of invasion is positively correlated with population size and time since introduction (see also II.3.1. p. 222), although there are exceptions. Pinus pinaster, which has the longest residency (nearly 300 years) and has enjoyed the greatest dissemination by man, has also invaded the greatest area. Most other pines in mountain fynbos have adventive ranges roughly proportional to their residency time and extent of cultivation and dissemination (Chapter 5). However, the most successful invaders also possess a suite of attributes that have permitted proliferation and spread. Pinus pinea, which is not adapted for long-distance dispersal and rapid population growth, has invaded a smaller area than would be predicted from its long residency and relatively widespread dissemination by man. Man-aided dissemination appears to have been relatively unimportant in determining the relative extent of invasion for four introduced Hakea species (4.2. p. 41; I.3.2. p. 199; Table II.3. p. 225).

It was concluded that the life history is primarily important in determining invasiveness, but that dissemination by man must also be taken into account when explaining the success of past invasions. This factor should also be borne in mind when screening potential introductions: a major crop plant will have an advantage over a non-crop plant if they have similar life history attributes.

11.4. What community properties of mountain fynbos permit invasion by introduced trees and shrubs ?

This question was addressed in part II of the thesis. A global review of pine invasions was undertaken to determine what factors limit the distribution of these trees in different parts of the world (Chapter 6). This study provided a valuable perspective of pine invasions in mountain fynbos. Determinants of invasibility interact in a complex fashion but, in general: i) Pine invasions are most prevalent where there is limited competition in the regeneration niche; ii) Invasions occur more easily where the dominant growth form in the target habitat is most different to that of pines viz. in grasslands; iii) The disturbance regime in the receiving habitats is important and interacts directly and indirectly with the "inherent invasibility" to determine the outcome of an introduction; iv) life history attributes such as seed size influence the effect of biotic and abiotic factors on invasibility; v)

Contemporary practices such as deforestation and increased grazing pressure and those leading to accelerated erosion, modified fire regimes and climate amelioration essentially duplicate ice-age stresses and disturbances that shaped plant communities in the Holocene. These findings emphasized the fundamental role of biotic factors (either direct or indirect) in regulating the distribution of pines in virtually every case that was examined - <u>except in the fynbos</u> ! In mountain fynbos, the dynamics of pine invasions are overwhelmingly governed by fire (Chapters 2, 3 and 5); biotic interactions, and especially competition of vigorous herbs and grasses in the regeneration niche (which are often overriding factors in other parts of the world - see 6.4.3.2. p.98 and Appendix 6.1) are apparently of negligible importance in mountain fynbos. I know of no other system where the spatial and temporal characteristics of pine invasions can be explained adequately by considering only the fire regime and wind patterns. Also, pine invasions in mountain fynbos are unique in that they can proceed with no disturbance other than the naturally-occurring fires. The perspective gained from this review shows that mountain fynbos is extraordinarily "open" to invasions by pines, and points to a "lack of structure" (<u>sensu</u> Roughgarden & Diamond 1986 p. 336) which has profound implications for explaining many features of these communities.

The determinants of invasibility of mountain fynbos were examined in more detail in Chapter 7 by considering <u>why</u> this area can support introduced trees (when these are so rare in the natural flora), and also <u>how</u> the aliens are incorporated into these communities. A feature of mountain fynbos is its low steady-state biomass relative to mediterranean-climate regions on other continents (see 7.3.2. p. 120). It is suggested that resources (especially moisture) are not fully exploited in fynbos ecosystems (see p. 123), and that the capacity of mountain fynbos to support alien trees is a symptom of this marked imbalance in ecosystem-level resource use. But this alone cannot explain the inordinate vulnerability of mountain fynbos to invasion by trees and shrubs. For example, many C_4 grasslands can also support woody vegetation (e.g. reviews in Everett 1987). Unlike mountain fynbos, however, the incorporation of these woody species is often prevented by the competitive strength of the resident biota (see p. 125). The ready incorporation of introduced trees into mountain fynbos communities can be explained by stochastic, fire-induced changes in community structure caused by large spatial and temporal fluctuations in population sizes of component species (see Figure 7.3. p. 127).

11.5. What are the impacts of invasions on mountain fynbos plant communities ?

This question was addressed principally in part IV of the thesis, but also in part III. The widespread invasion of introduced trees such as pines has added a major life form to many mountain fynbos communities. As would be expected (Vitousek 1986), these invasions have resulted in drastic ecosystem-level changes to the properties of the invaded communities. The non-equilibrium status of mountain communities is disrupted by the incorporation of introduced trees and shrubs which establish fire-resilient populations (Figure 7.3. p. 127). These invasions alter the properties of the communities and result in new depauperate steady-states (Chapters 8, 9 and 10). Invasions have caused significant reductions in the richness of indigenous plant species at the scale of small quadrats (Chapters 8, 9 and 10; Figure 10.1. p. 176) and at the landscape scale (Chapter 8). In this respect, the impacts of plant invasions in mountain fynbos have been exceptionally severe (cf. Vitousek 1986 for North America, and Crawley 1987b p. 441 for Britain). As is the case in Britain (Crawley 1987b), no plant extinctions can yet be directly attributed to invasions (Chapter 10). However, many endemic plant species in the fynbos biome are currently threatened with extinction due to the effects of invasions by trees and shrubs and extinctions are inevitable. Indeed, there is likely to be a cascade of extinctions in the next few decades as more communities are disrupted by invasions, and as the time since the establishment of thickets of these species increases (with concomitant attrition of seed banks of suppressed endemic species).

Clearing of dense stands of pines and hakeas can reverse the attrition of indigenous species richness to some extent (Figure 10.3. p. 180), but recovery in old stands is poor. Control measures that utilize fire in conjunction with mechanical means sometimes cause more harm to the natural communities than the combined effects of invasion. These deleterious effects can be reduced by using the fire behaviour modelling approach detailed in Chapter 9. Additional research is required to determine the rate of depletion of indigenous seeds and the potential of indigenous species to recolonize cleared sites. Methods for restoring severely degraded sites should be developed.

11.6. General comments on the contribution of this study to the international literature on biological invasions

This study has added significantly to the understanding of the processes of invasion, especially in the fynbos biome of South Africa, but has also contributed new information that should be of value for studies of invasions in other parts of the world. It is hoped that the approach followed in this thesis may define a protocol for investigating the patterns, processes and consequences of invasions in other systems. The examination of invasions in mountain fynbos at different scales has proved valuable in gaining an overall perspective. For example, a global review of pine invasions gave a new insight on the dynamics of invasive pines in the fynbos, and aided in the interpretation of landscape- and community-scale patterns. The value of comparative studies involving introduced congeners, some successful and some not, and studies involving the same species under contrasting conditions has been demonstrated.

The study has shown that plant invasions in mountain fynbos are understandable in terms of community properties and dynamics. Also, it has been possible to construct a biological profile of a successful invader that is supported by empirical evidence. Both findings are major developments in the study of biological invasions, and counter the rather pessimistic scenarios that emerged from recent regional and global syntheses. The concept of risk assessment has been developed; this has immediate practical application in the screening of potential introductions for horticulture and forestry in southern Africa and elsewhere.

APPENDIX I

ALIEN SPECIES IN TERRESTRIAL ECOSYSTEMS OF THE FYNBOS BIOME

APPENDIX I: ALIEN SPECIES IN TERRESTRIAL ECOSYSTEMS OF THE FYNBOS BIOME [1]

I.1. INTRODUCTION

In this chapter we review alien invasions of the fynbos biome and address the following questions: (a) which species have invaded? (b) what are the characteristics of the invasions? and (c) do any of these characteristics appear to be unique to the biome? An outline of the salient features of the environment of the fynbos, the biotic communities which constitute it, and the history of human activities in the biome serve as background to the review.

I.1.1. Geographic extent

The fynbos biome is defined by Moll & Bossi (1984) and is here taken to include all the Mountain Renosterveld (Acocks 1975). As such, it occupies 77 172 km^2. The biome lies at the southern tip of Africa and includes the Cape Fold Belt Mountains and the coastal lowlands lying to the west and south of these mountains. The biome has a latitudinal range from 31^{o}S on the west coast to 34^o 50$'$S at Cape Agulhas to 33^o 15$'$S near Grahamstown in the east. The longitudinal range is from 17^o 51$'$E to nearly 27^{o}E near Grahamstown. Various outlier patches occur in the mountains of the Karoo and further north in Transkei and Natal but their extent is small and their identity as true fynbos communities is disputed (Kruger 1979).

I.1.2. Geology and soils

The predominant geological features are the quartz arenites of the Table Mountain and Witteberg Groups of the Cape Supergroup which form the main mountain and ridge crests. Shales of the Malmesbury Series of the Nama System and Bokkeveld Series of the Cape System form outcrops on the valley floors and coastal lowlands. Extensive areas of Quaternary and Tertiary sands are found along the southern and western coasts. Soils derived from sandstone rock types are predominantly acid and poor in nutrients. Those derived from shales

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are relatively fertile and often saline. Granites occur locally, especially along the west coast at lower altitudes (Lambrechts 1979) and limestones and calcareous rock are largely restricted to the south coast.

I.1.3. Climate

The biome has climatic gradients from west to east, south to north, coast to interior and also a pronounced altitudinal gradient (Campbell 1983). These gradients, superimposed on the mountainous topography, give rise to a mosaic of spatially diverse climates (Fuggle & Ashton 1979). In the west, the lower mountain slopes experience a true Mediterranean-type climate with cold, wet winters and dry, hot summers (Köppen's climatic type Cs); summer drought is less severe on the upper peaks (Campbell 1983). Further east, rain falls throughout the year, with maxima in spring and autumn (Köppen's climatic type Cf; Fuggle & Ashton 1979). The biome is comparatively well watered and 19% of the major catchments of southern Africa fall within the biome (van der Zel 1981), an area comprising only about four per cent of the area of the subregion (Goldblatt 1978). Persistent high speed winds are an important factor in most fynbos ecosystems (Taylor 1984; Van Wilgen & Kruger 1985).

I.1.4. Fire regime

Possibly the most important aspect of the climate is that, in combination with the low-nutrient soils, it gives rise to patterns of plant production and combustibility that favour a fire regime of high intensity fires at intervals varying from 10-40 years depending on site conditions and sources of ignition (Kruger & Bigalke 1984). This fire regime is the single factor that most clearly differentiates the fynbos biome from the adjacent biomes. Fynbos plant species have characteristic adaptations that enable them to survive these periodic high-intensity fires (e.g. serotiny, myrmecochory and the ability to resprout).

I.1.5. Biogeography

The combination of topography, geology and climate has given rise to environments that are ecologically unique in southern Africa, so much so that the area has been classified as a separate floral kingdom, distinct from the rest of Africa (Goldblatt 1978). The flora of the biome is renowned for its high alpha, gamma and delta species diversities (Kruger & Taylor 1979; Bond 1983). There is a high degree of endemism in several taxonomic groups: the flora (Goldblatt 1978); archaic invertebrates (Stuckenberg 1962); terrestrial molluscs (Van Bruggen 1978); Coleoptera (Endrödy-Younga 1978); Lepidoptera (Cottrell 1978); amphibia (J.C. Poynton 1960) and fishes (Bowmaker et al. 1978). This reflects the antiquity and quasi-insular nature of the fynbos biome. Although a distinct biotic zone is recognized for the mammalian fauna (Rautenbach 1978), the species richness and endemism in this and other higher vertebrate classes does not parallel that of the flora (Bigalke 1978; Siegfried & Crowe 1983).

I.1.6. Vegetation and fauna

The vegetation of the biome is usually characterized by the presence of proteoid shrubs which form an upper storey of highly variable density. Ericoid shrubs and restioid hemicryptophytes together usually form the understorey. In mid-high sparse to tall mid-dense shrublands (Campbell et al. 1981), woody shrubs make up the greatest part of the above-ground living phytomass but the contribution of this component is very variable (van Wilgen 1984). Trees are generally restricted to ravines and riparian habitats and seldom dominate the landscape. Towards the east, grasses become more important in the understorey. Populations of the dominant plant species are generally even-aged with recruitment occurring directly post-fire (Kruger 1979). Plants are often protected by secondary chemicals and the level of herbivory is generally low except for the period directly after fire.

In general, the lowland environment comprises a few different plant communities, usually covering relatively large areas (Siegfried & Crowe 1983) whereas in the montane environment, a much greater variety of communities, often widely dispersed, occur as relatively small entities over the landscape. The great diversity of plant communities in this zone reflects the influence of geographic factors and of a complex landscape.

Populations of small mammalian granivores are of the same order as in other biomes (Cody et al. 1983), but avian granivores are scarce except in some instances after fire when they take advantage of serotinous seed releases. Avian communities are generally sparse. Nectarivores, feeding mainly on nectar of Proteaceae and Ericaceae and the associated insect fauna, and small insectivores are the most important guilds represented (Siegfried & Crowe 1983). Low bird density in the biome is ascribed to the low insect density (Siegfried 1969).

I.2. PATTERNS OF LAND USE AND DISTURBANCE

I.2.1. Overall impacts of man

Man has been present in the fynbos biome for at least 600 000 years and the implications of the activities of prehistoric man for alien invasions have been extensively reviewed (Deacon 1986). The impacts on the biome of the burning, hunting and stock grazing of these peoples, although profound, have probably been smaller than those arising from man's activities since European colonization. Within 330 years, settled agriculture and the cultivation of a wide variety of alien plants has led to the complete transformation of at least 68% of the 28 508 km^2 of lowland ecosystems (Moll & Bossi 1984).

Transformation of the montane ecosystem has been less extensive, only 10% of the 42 064 km^2 occurring in the main block having been transformed by 1981 (Moll & Bossi 1984), and 10 823 km^2 (or 26%) currently being protected in State Forests or as proclaimed Mountain Catchment Areas (NAKOR 1984).

I.2.2. Simplification of faunal communities

Indigenous large mammals have been virtually eliminated throughout the biome (Skead 1980) and domestic livestock now graze much of the remaining areas of natural vegetation on the lowlands. Large mammalian predators (Stuart et al. 1985) and a few of the large avian predators (Boshoff et al. 1983) have been eliminated or reduced in numbers within the biome.

I.2.3. Alteration of fire regimes

One of the man's main impacts throughout the biome, as it relates to alien invasions, has been the alteration of the natural fire regime (Macdonald 1984). We suggest the main changes have been: (a) increased fire frequency; (b) altered seasonal incidence (Van Wilgen & Richardson 1985a) and (c) reduced fire size. Lower mean fire intensities would have resulted from (a) and (b). As in the pre-colonial era, the altered fire regime is virtually the only direct human impact on large tracts of the montane environment. Intensive grazing of recently burnt veld of domestic stock has, in places, led to severe degradation of natural communities (Wicht 1945). The degree of which fire regimes have been altered is greatest around urban areas (Kruger & Bigalke 1984) where alien organisms are also most prolific.

I.2.4. Afforestation with alien trees

One of the first actions of the European colonists was the planting of alien tree species (e.g. Krüger 1966) and afforestation was strongly advocated by authorities in the Cape of Good Hope in the late nineteenth and early twentieth century (Shaughnessy 1980, 1986). Trees were planted for fuel and timber, to stabilize driftsands and for aesthetic reasons. Afforestation in the biome was on a limited scale up to the time of the First World War. It reached a peak in the period between the First and Second World Wars and again after the Second World War. Mainly *Pinus radiata*, *P. pinaster*, *P. canariensis* and *Eucalyptus* species were planted for commercial use. *Acacia cyclops* and *A. saligna* were planted widely for driftsand reclamation and by 1938, 102 km^2 of lowland fynbos had been thus treated (King 1943).

I.3. HISTORY OF INTRODUCED SPECIES

I.3.1. The role of prehistoric man

The early Khoi and San inhabitants of the area apparently introduced few species, if any, and not even commensals such as the house rat *Rattus rattus* and domestic cat *Felis catus* (Skead 1980; Deacon 1986). The introduction of alien species began with European settlement in 1652, although there is a putative record of *Rattus rattus* from Robben Island in 1614 (Skead 1980).

I.3.2. Plant introductions

Shaughnessy (1980, 1986) has documented the history of the more important invasive alien trees and shrubs in the Cape Town area. Most were intentionally introduced for shade, timber and sand-binding over the period 1830 to 1900, although *Pinus pinaster* was introduced as early as 1680. Many of the species that have spread were extensively propagated and cultivated throughout the biome (Shaughnessy 1980; Stirton 1978). Notable exceptions are Hakea sericea and Sesbania punicea where the extent of the invasions are disproportionately greater than the extent of their cultivation (Kruger et al. 1986).

I.3.3. Faunal introductions

Most vertebrate introductions have been intentional. Examples are the grey squirrel *Sciurus carolinensis* (Millar 1980), European Starling *Sturnus vulgaris* and Chaffinch *Fringilla coelebs* (Siegfried 1962). However, in cases such as the Himalayan Tahr *Hemitragus jemlahicus* and *Felis catus*, the species have established from individuals which escaped from captivity (Siegfried 1962). Still other introductions have been inadvertent. The slow worm *Ramphotyphlops braminus*, for example, was possibly introduced to the Kirstenbosch Botanical Gardens with potted plants (McLachlan 1978). By contrast almost all invertebrate introductions have been unintentional. These include the numerous alien molluscs, the termite *Cryptotermes brevis*, the ant *Iridomyrmex humilis* and the wasp *Vespula germanica* which are thought to have been introduced in cargo or in ships' ballast (Skaife 1955; van Bruggen 1964; Whitehead & Prins 1975; Coaton 1981).

I.3.4. Introductions from elsewhere in southern Africa

Several southern African species have been introduced into the biome and have established free-living populations here, e.g. the Helmeted Guineafowl *Numida meleagris* (Skead 1962), the gecko *Pachydactylus bibroni* (Siegfried 1962), several species of trees and shrubs (Moll & Scott 1981; de Villiers & McDowell 1982) and grasses (Adamson & Salter 1950). Within southern Africa, the fynbos biome seems to be uniquely susceptible to invasion by species from elsewhere in the subcontinent. Possibly this is a reflection of the quasi-insular nature of the biome, a situation mirrored by the mesic south-west of Australia which is also being invaded by intracontinental aliens (Macdonald 1985a,b).

I.4. PATTERNS OF INVASION BY SOME SUCCESSFUL ALIEN SPECIES

Figure I.1 shows patterns of invasion by four alien organisms in the fynbos biome and serves to illustrate differences in patterns and rates of spread of plants, molluscs, birds and mammals.

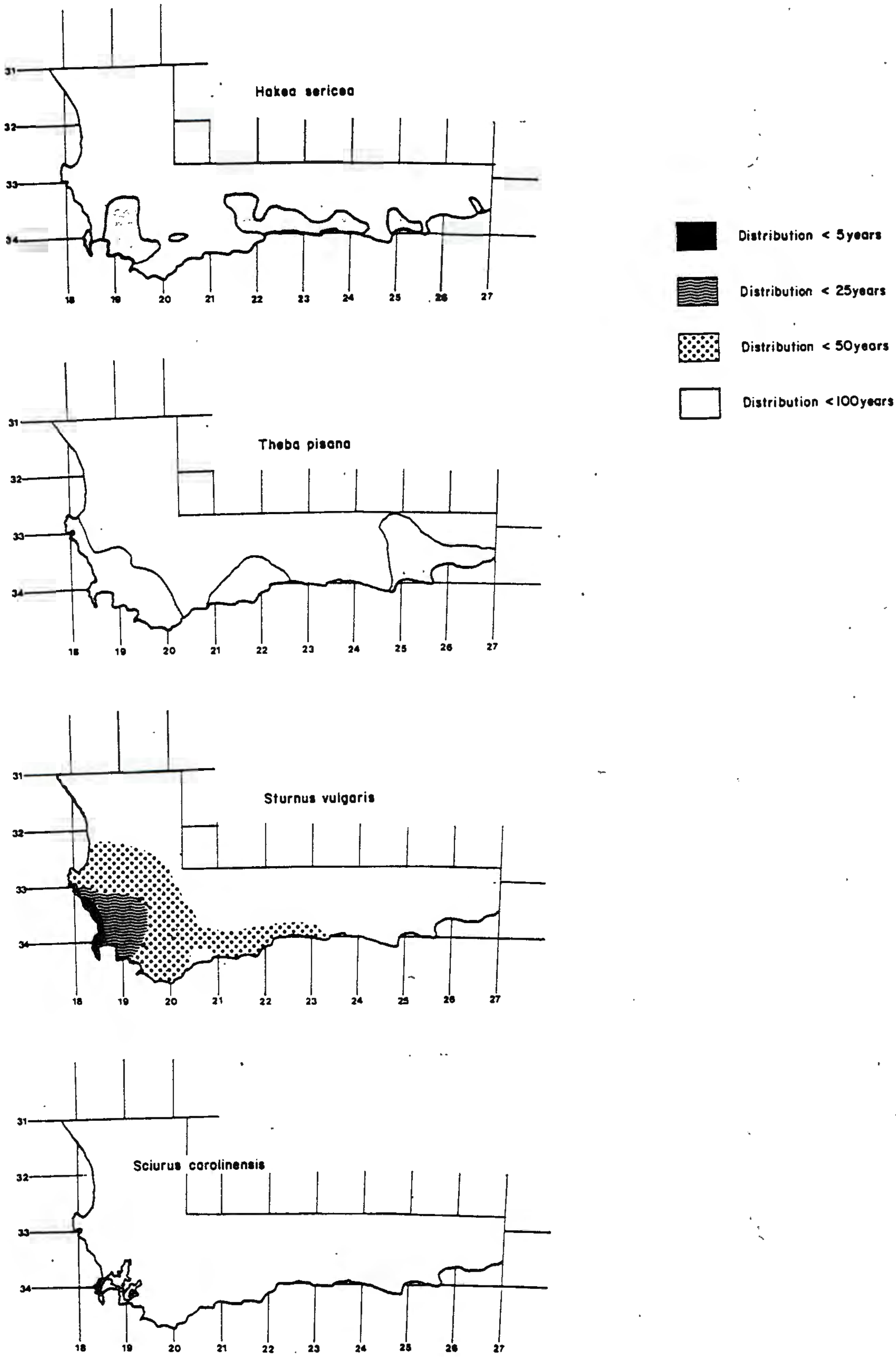

Figure II.1. Distribution of some successful alien invaders of the fynbos biome.

Hakea sericea has spread to occupy most mountain veld around Cape Town, Franschhoek and George. Spread was rapid in all directions and was not significantly aided by human dissemination, in marked contrast to most of the other important woody plant species (Shaughnessy 1986). Invasion by the snail Theba pisana, after its introduction to ports was facilitated by artificial dispersal by rail, road or ship tough natural dispersal over short distances is apparently also implicated (Van Bruggen 1964). The starling Sturnus vulgaris, introduced in 1899, spread along a front in all directions from Cape Town to occupy the entire biome within 70 years of introduction. Spread was most rapid eastwards, where the availability of alien trees and man-made structures for roosting and nesting facilitated rapid colonization (Winterbottom & Liversidge 1954). The squirrel Sciurus carolinensis spread rapidly to occupy all potential habitat around Cape Town but further spread in the biome was prevented by the absence of suitable habitat. The slow increase in this species range has apparently been facilitated by the increase and maturation of stands of its favoured alien tree species (Millar 1980).

I.5. THE NATURE OF THE INVASIONS

I.5.1. Invasions of Mountain Fynbos by trees and shrubs

The most important alien invaders of the biome are numerous tree and shrub species, most of which have spread from cultivation and now cover small portions of the biome entirely. Coastal mountain ranges throughout the biome are invaded by Hakea sericea, Pinus pinaster and Acacia longifolia which form dense impenetrable thickets. Hakea sericea, introduced to the biome in around 1830 and planted on a very limited scale around Cape Town, Franschhoek and George, spread rapidly eastwards from Cape Town and Franschhoek and in all direction from George to cover almost 4 800 km^2 or 14% of the area of Mountain Fynbos about 130 years after its introduction (Kluge & Richardson 1983; Macdonald 1984). The present distribution of this species is positively associated with the occurrence of soils derived from quartzite and sandstone and its spread eastwards from Cape Town and northwards from George has ben restricted to some extent by barriers of unsuitable nutrient-rich substrates (Fugler 1979; Richardson 1984). Typical stands of this species consist of three to four metres tall shrubs at a density of around 9 000 stems per ha ten years after a fire (Van Wilgen & Richardson 1985b). The other major invader of Mountain Fynbos, P. pinaster has been found to be the most widely dispersed species in the Cape Peninsula mountains where it was present in 82% of 98 circular quadrats (10,5 ha) systematically located throughout the northern Peninsula mountains (Hall 1961). The spread of P. pinaster on Stellenboschberg has been analyzed from successive aerial surveys (Smit & De Kock 1984). The area covered by "dense infestations" (more than 50 plants km^{-2}) increased from four per cent in 1938 to 36% in 1977. The most recent estimate of the area invaded by Hakea and Pinus species throughout the biome is 7 592 km^2 (Macdonald et al. 1985a).

Hakea sericea and P. pinaster have the following factors in common which may have contributed to their success: both are dispersed by wind; both have winged seed which are held in heat-resistant serotinous cones and which are often released after fire has killed the parent plants. However, the degree of serotiny is much higher in H. sericea than in P. pinaster (see chapters 4 and 6).

Acacia longifolia is a comparatively recent arrival in most Mountain Fynbos areas. However, it has recently shown rapid increases in both its distribution and density (McLachlan et al. 1980; Taylor et al. 1985) and is currently ranked the second most important alien plant invader in the biome (Macdonald & Jarman 1984). Its seeds are spread both by birds and water and it often forms dense thickets following fire, alien clearing operations or soil disturbance (McLachlan et al. 1980; Pieterse 1984; Macdonald & Richardson unpublished).

I.5.2. Invasions of lowland areas and riparian communities by trees and shrubs

In contrast to the situation in Mountain Fynbos, Acacia cyclops and A. saligna are the most important species in the Strandveld and Coastal Fynbos. A survey of the western lowlands between the Berg River and False Bay revealed that by 1971, 17% of the remaining area of natural vegetation was invaded by alien woody plants (Boucher 1981). The seeds of the most important woody plant invaders of the lowlands are dispersed by birds and mammals (Middlemiss 1963; Knight and Macdonald 1985), man and water (Macdonald & Jarman 1984; Macdonald et al. 1985a). Studies of sequential air photos have shown that certain Acacia species invade most rapidly along watercourses. The direction and rate of spread suggest that seed dispersal in water is the major cause of these patterns (Brownlie 1982). Possibly as a consequence of the efficacy of waterborne seed dispersal, riparian habitats throughout the biome are heavily invaded by numerous species, eg. *A. longifolia*, *A. saligna*, *A. mearnsii*, *Paraserianthes* (=*Albizia*) *lophantha* and *Sesbania punicea* (Macdonald & Jarman 1984). A helicopter survey of the lowlands in the western Cape showed that *Sesbania punicea* was present in 64% of the 532 km of river course surveyed (Bruwer 1983). *Acacia* and other thicket-forming alien woody plant species in the biome were estimated to have invaded some 8 962 km^2 in 1984 (Macdonald *et al.* 1985a). The extent of invasion by herbaceous alien plants has not been studied.

I.5.3. Vertebrate invasions

Of the vertebrate invaders, only the starling *Sturnus vulgaris* and the house sparrow *Passer domesticus* have spread throughout the biome. *Fringilla coelebs* is confined to the Cape Peninsula and is declining in numbers (Cape Bird Club 1979). Of the introduced mammals only the Himalayan Tahr *Hemitragus jemlahicus* has been able to invade unmodified fynbos ecosystems and even it has not spread from Table Mountain because of intensive shooting since the early 1970's and because there are not corridors to other suitable habitats. The house mouse *Mus musculus* and *Rattus rattus* both have extensive ranges in the biome but are thought to occur mainly in areas of human habitation especially in drier areas (Smithers 1983). However, instances are known where both species have invaded areas of indigenous fynbos vegetation (Macdonald, Powrie & Siegfried 1986). The brown rat *R. norvegicus* is mainly restricted to ports and coastal towns (Smithers 1983) but has been recorded invading semi-natural areas within the biome (Middlemiss 1975; Stuart 1976). The squirrel, *Sciurus carolinensis*, introduced to Cape Town in 1900, rapidly became naturalized but is entirely dependent on introduced tree species (*Pinus* species and *Quercus robur*) and has not invaded natural ecosystems (Millar 1980).

I.5.4. Invertebrate invasions

A possibly important alien invertebrate that has invaded natural communities in the biome is the Argentine ant *Iridomyrmex humilis* (Skaife 1955; Donnelly 1983). The extent of invasion by this species is, however, related to the extent of disturbance in the form of roads and human habitation (De Kock 1984). Iridomyrmex humilis was found at 42% of 83 sites sampled within the fynbos between the Cederberg and the De Hoop Nature Reserve during 1983/84 (De Kock 1984). Theba pisana and Helix adspersa are the two most widely distributed alien molluscs in the biome, although at least 17 terrestrial species are known from the Cape Peninsula alone (Van Bruggen 1964). Theba pisana, first noted in the biome in 1881, is now found along most of the coastal strip south of St Helena Bay and has extended its range on the lowlands inland around Cape Town and Port Elizabeth (Van Bruggen 1964)

I.5.5. The case of Phytophthora cinnamomi

The pathogenic root fungus Phytophthora cinnamomi was thought to have been introduced to the biome and was considered to pose a considerable threat to its flora (Knox-Davies 1975). More recently, analyses of the current distribution of P. cinnamomi in the river systems of the biome (Von Broembsen 1984a), its host range (Von Broembsen 1984b) and the patterns of mortality in indigenous vegetation (Von Broembsen & Kruger 1985) have led to the conclusion that the species is indigenous. However, the possibility that one of the two genetic strains of the species present in the biome is alien requires further investigation.

I.6. ECOLOGICAL IMPACTS

I.6.1. Effects of woody plants on soil erosion rates

The only known impacts of invasive alien organisms on ecosystem processes in the fynbos biome are those of woody plant species. Soil erosion and deposition are considered to be severely affected in several ways. River bank erosion has been accelerated following the invasion of riparian vegetation by species such as Acacia mearnsii, A. longifolia, A. saligna, Sesbania punicea and Pinus pinaster. These species establish in and grow up through the indigenous vegetation which is well adapted to the flash floods that occur in most fynbos catchments. The alien trees, however, are not able to withstand these floods and are ripped out, often dislodging mats of indigenous vegetation such as those of Prionium serratum (Beyers 1959; Heydorn & Tinley 1980; Macdonald unpublished). The exposed mineral soil is then subjected to accelerated erosion.

Soil erosion is also considered to be accelerated under dense stands of certain woody alien species such as Pinus species which characteristically have a very sparse ground cover (Cowling et al. 1976; Jacot Guillarmod 1980). However, other writers consider the establishment of alien woody plants to have decreased erosion rates, both of water erosion, as on Table Mountain (Lückhoff 1951), and of wind erosion, as on the Cape Flats (Wicht 1945). Following the clearing of long-established infestations of these species, particularly where the plants are felled, allowed to dry out and then burned, soil erosion is often accelerated on steep slopes (Cowling et al. 1976; Richardson & Van Wilgen 1986a).

I.6.2. Effects of woody plants on coastal sand movements

Alien trees and shrubs have had a marked effect on the movement of coastal dune sands, thus altering sediment dynamics. The species mainly responsible for this are the Australian wattles Acacia cyclops and A. saligna. These have been extensively planted by the state forestry authorities to stabilize areas of windblown sand (Walsh 1968; Shaughnessy 1980, 1986). Although some of this area was caused by man-induced changes in the vegetal cover (King 1943), recent research has shown that there are naturally occurring unvegetated dunes within the biome (McLachlan et al. 1982; Lord et al. 1985; Lubke & Avis 1985). Where the dunes that have been stabilized form part of a headland bypass dunefield, the reduction in sand movement can have profound effects on the distribution and extent of sandy beaches in the vicinity (Heydorn & Tinley 1980; Lord et al. 1985; Lubke 1985). The ability of alien plants to establish and grow more successfully than indigenous plants on coastal sand dunes has been observed in southern and eastern Australia and has been recorded as having had profound effects on coastal sediment dynamics in these areas as well (Heyligers 1985; Sauer 1985).

I.6.3. Effects of woody plants on hydrology and fire regime

Although it is widely contended that dense stands of alien woody plants reduce the flow of water from fynbos catchments (e.g. Jacot Guillarmod 1980) there are no data available on this point. Extrapolation from plantations of alien tree species indicates that this reduction does occur (Van Wyk 1977; Bosch & Hewlett 1982).

Fuel loads are greater in dense stands of aliens than in fynbos but fires are generally more easily ignited in fynbos where there is an abundance of fine material in the herbaceous layer. Only under extreme weather conditions is fire intensity much higher in invaded areas. Fires under these conditions are more difficult to contain and are potentially more damaging to ecosystems than fires in indigenous vegetation (Van Wilgen & Richardson 1985b).

I.6.4. Effects of woody plants on geochemical cycling

Dense infestations of alien Acacia species affect geochemical cycling. Acacia cyclops has been shown to fix nitrogen (Roux & Warren 1963) and soil nitrogen levels have been shown to be increased by an order of magnitude following dune stabilization with this species (McLachlan et al. 1982). Carbon cycling is also radically changed with above-ground biomass and mean litterfall rates being approximately three times higher in thickets of A. cyclops and A. saligna than in indigenous fynbos vegetation (Milton 1981; Milton & Siegfried 1981). Soil organic matter content under a thicket of A. cyclops has been found to be twice that under indigenous dune thicket on the Alexandria dunefield east of Port Elizabeth (McLachlan et al. 1982).

Milton (1981) has calculated from litterfall data and information on the chemical composition of alien and indigenous plants, that annual inputs of nitrogen and phosphorus to the soil under a dense thicket of Acacia would be about nine times greater than those under indigenous fynbos vegetation. Subsequent investigations of soil phosphorus levels in Strandveld have shown that both total and available phosphorus are approximately 50% greater under Acacia thickets than under fynbos (E. Witkowski and D.T. Mitchell unpublished). No work has yet been conducted on the relative rates of mineral cycling in alien and indigenous communities. Because fynbos plants are generally adapted to conditions of low soil nutrients the eutrophication of fynbos soils possibly has important implications for the survival or re-establishment of indigenous species on invaded sites. In the comparable heathlands of South Australia, Heddle & Specht (1975) showed that three years' application of phosphate fertilizer resulted in the elimination or reduction in density of several indigenous species and their replacement by a range of herbaceous alien plants as measured twenty years after the fertilization.

I.6.5. <u>Effects of woody plants on species richness of indigenous plant communities</u>

Impacts on community properties have been more extensively documented the have those on ecosystem properties. Once again it is the impacts of alien woody plants that are best known. Plant species richness has been shown to be reduced in communities dominated by alien plants relative to uninvaded indigenous communities (Figure II.2). This reduction in species richness has been best documented in a 'before and after' study of the fynbos in an area planted to <u>Pinus radiata</u> (Richardson & Van Wilgen 1986b). The alien trees were planted in small pits in the fynbos with minimal disturbance to the indigenous vegetation. After 35 years the mean number of species per 0,1 m^2 quadrat was 2,1 (1,8 if alien species were excluded) compared with 8,5 prior to planting. The cover of the indigenous vegetation had decreased from 74 to 19% and plant density from 260 to 78 plants m^{-2}. Different life forms showed varying degrees of resistance to suppression by alien plants. Proteaceous shrubs with canopy-stored seeds and limited dispersal capabilities were particularly susceptible (Richardson & van Wilgen 1986b).

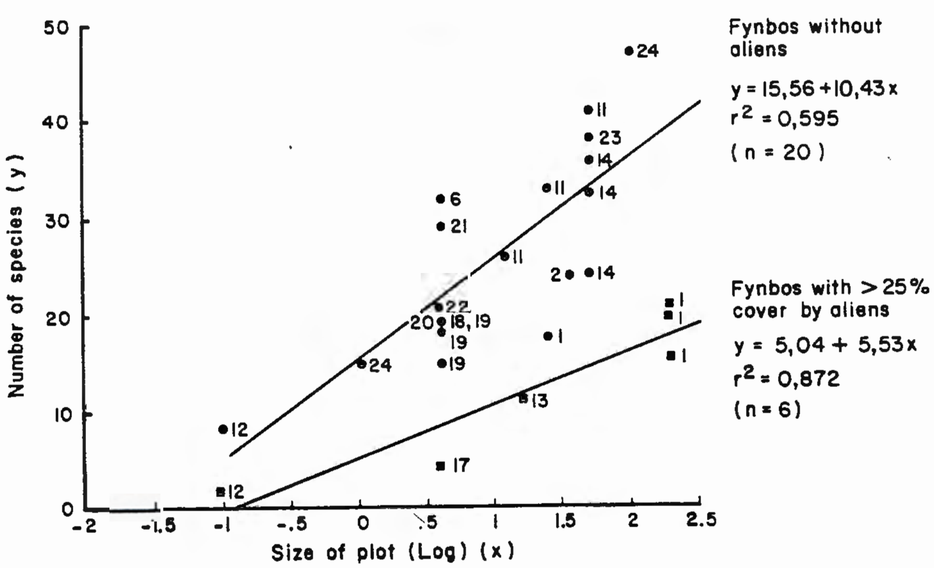

Figure I.2. The relationship between the number of indigenous vascular plant species and plot size in fynbos areas densely infested (■) by alien woody plants and in uninfested areas (●). Each number indicates a different site. Numbers refer to study sites (see Richardson <u>et al</u>. 1989).

All the studies where paired estimates had been made of indigenous plant diversity, density or cover show these parameters to be reduced by dense or moderately dense infestations of alien plants (Cowling et al. 1976; Behrens 1985). The poor development of understorey vegetation in dense stands of alien trees is similar to that shown in indigenous forest vegetation in the south-western Cape (Bester 1976). Allelopathy, documented for Pittosporum undulatum in Australia (Gleadow 1982), has become evident where this species has invaded scrub and forest patches in parts of the biome (Richardson & Brink 1985).

Measures applied to control invasive trees and shrubs sometimes reduce the rate of recovery of indigenous elements relative to recovery following normal disturbance. Burning of slashed H. sericea shrubs under severe weather conditions has resulted in very intense fires which kill subterranean rootstocks and seeds on or in the soil (Richardson & Van Wilgen 1986a). Following the felling of an infestation, with or without subsequent burning, species richness is still depressed. Species richness has not been monitored in the long term so that it is not known if it ever returns to pre-infestation levels and, if it does, how long it take to do so. In eastern Cape grassy fynbos is has been shown that, six years after the eradication of a 15 to 20-year old multi-species alien infestation (primarily Pinus species), the fynbos had regenerated sufficiently for a fire to be followed by normal post-fire regeneration of the vegetation (Jacot Guillarmod 1980, 1983; Richardson et al. 1984). This agrees with the unsubstantiated assertion of Lückhoff (1951) that if Pinus pinaster infestations up to 20 years old are removed, recovery of the fynbos is still possible.

If infestations are not removed there is little doubt that local populations of at least certain indigenous species will become extinct. An analysis of a sample of 70 plant species in the south-western Cape which were evidently threatened with extinction showed that 33 were affected thus by invasive alien woody plants (Hall et al. 1980). Similarly, of the 58 threatened plant species occurring on the Cape Peninsula, 31 are jeopardized by alien woody plants (Hall & Ashton 1983). As the extent of the remaining areas of natural vegetation decreases and alien plant invasions increase, more indigenous species will become endangered. Several authors have predicted the almost total disappearance of the fynbos flora if the spread of alien plants is not checked (Wicht 1945; Taylor 1977).

I.6.6. Effects of woody plants on the indigenous fauna

The impacts of alien woody plants on the fauna of the biome have also been considerable. Thickets of Acacia cyclops and A. saligna have been shown to have a depauperate avifauna (total species number 86 with 37 occurring on five per cent or more of the bird lists made in this habitat) compared to the coastal fynbos they had replaced (total = 146 with 56 occurring on five per cent or more of lists) (Winterbottom 1970). The avifauna shows a reduced percentage of insectivores and an increase in granivores. The species that decrease most in frequency of occurrence in these thickets are those dependent on the smaller ericoid and graminoid plants within the indigenous vegetation e.g. Karoo Robin Erythropygia coryphaeus, Grassbird Sphenoeacus afer, Greybacked Cisticola Cisticola subruficapilla and Lesser Doublecollared Sunbird Nectarinia chalybea. Of the 14 species most frequently recorded in these thickets 10 are generalist species that are also amongst the 154 species most frequently recorded in gardens e.g. Cape Turtle Dove Streptopelia capicola, Laughing Dove S. senegalensis, Fiscal Shrike Lanius collaris and Cape Sparrow Passer melanurus (Winterbottom 1970). The alien woody plants are not merely having local effects on the avifauna; studies have shown that at least two species, the Hadeda Ibis Bostrychia hagedash and Pied Barbet Lybius leucomelas, which are dependent on trees for roosting and nesting, have invaded the biome at least partly in response to the spread of alien trees (Macdonald 1986; Macdonald, Richardson & Powrie 1986). Historical analysis of the avifauna of terrestrial habitats in the south-western portion of the biome indicates that 36 species have invaded the area as a result of alien vegetation. A further 27 species have markedly expanded their ranges within the biome. Thus 63 of the current total avifauna of 224 species (28%) have been favoured by these alien plants (Macdonald et al. 1985b).

Small mammal communities are reduced in species richness in some instances. In the Alexandria dune field, pure stands of Acacia cyclops were found to have only a single species of rodent, the four-striped fieldmouse Rhabdomys pumilio, while five species were recorded on adjacent littoral dunes having an indigenous plant cover (McLachlan et al. 1982). Biomass of R. pumilio in mixed thickets of A. cyclops and A. saligna on the Cape Flats has been estimated at 2,5-9,4 km^{-ha} (David 1980). This is approximately five to 10 times higher than the total rodent biomass in fynbos (David 1981). Its diet in the alien thicket was primarily Acacia seed (Shelton 1975). On the other hand, in Hakea sericea stands of varying density (1%, 35% and 95% of canopy cover) communities of indigenous small mammals, birds and arthropods were found to be similarly rich, both in species and in numbers (Breytenbach 1986). The effects of these faunal communities on their indigenous food plants were, however, much greater in the densely infested stand to the extent that recruitment of these plants following a fire could be jeopardized.

I.6.7. Impacts of other alien groups

Ecological impacts have not been investigated for herbaceous alien plants which, within this biome, are generally restricted to modified ecosystems, such as along railway lines (Raitt 1983), or are present only briefly following fire in areas of natural vegetation.

The browsing and trampling of Hemitragus jemlahicus is considered to have given rise to a reduction in plant cover and a concomitant increase in soil erosion (Lloyd 1975).

Iridomyrmex humilis displaces indigenous ant species (Skaife 1955; Donnelly 1983; De Kock 1984). The implications of this for the regeneration of the many myrmecochorus indigenous plant species has been stressed by Bond and Slingsby (1984). Such displacement has changed the pattern and reduced the abundance of seedling recruitment in Mimetes cucullatus, for example (Bond & Slingsby 1984).

I.7. HISTORY OF CONTROL

I.7.1. The evolution of control programmes

Invasive trees and shrubs have long been a cause of concern in the biome. Phillips (1938) reported that farmers in the Bathurst district first met to discuss the spread of Hakea sericea in about 1863. Shaughnessy (1980) defines three phases of opinion by authorities concerning alien trees around Cape Town between 1884 and 1936: i) a determination to achieve total cover of trees (1884-1905); ii) defined plantations plus areas of abandoned plantations beyond which a policy of laissez faire applied (1906-1935); iii) areas beyond demarcated plantations were to be actively cleared of pines (1936 onwards). This is an accurate reflection of developments in the fynbos biome as a whole.

I.7.2. The control of Hakea and Pinus species in Mountain Fynbos areas

In the case of Hakea species and Pinus pinaster, the Weeds Act of 1937 did little to stop their spread. The lack of a definite mountain catchment management policy, together with the general opposition to the use of controlled burning as a management tool, made the attainment of control objectives impossible. A biological control programme for *H. sericea* was initiated in 1962, resulting in the release of two species of host-specific seed-attacking insects (Neser & Annecke 1973; Moran *et al*. 1986; Neser & Kluge 1986). The other important development in the control of *H. sericea* and other alien plants in mountain land has been the initiation of an active control policy by the Forestry Branch (Fenn 1980). With the initiation of regular prescribed burning in the late 1970's, proclaimed catchments were divided into management units. Each unit was to be burned at approximately 15-year intervals. All woody alien plants are felled prior to a burn and the area is burned about 18 months later to kill seedlings (Kruger 1977; Fugler 1983). This programme has been very successful and of the 7 592 km^2 once infested by *Hakea* and *Pinus* species, 1 579 km^2 (21%) had been successfully cleared by the end of 1984 (Macdonald *et al*. 1985a). Assuming that the current rate of progress is maintained, most areas for which the Forestry Branch is responsible will have been cleared by around 1995 (Kluge & Richardson 1983).

The relatively recent emergence of the hard-seeded *Acacia* species and *Paraserianthes* (=*Albizia*) *lophantha* is important invaders of Mountain Fynbos is complicating control programmes. Prolific regeneration of these species after fire is now having to be treated with arboricides which is both expensive, often ineffective, and potentially damaging to indigenous plant regeneration (Macdonald *et al*. 1985a).

I.7.3. The control of woody aliens in the lowlands

Acacia saligna and *A. cyclops*, the most important aliens in lowland vegetation of the biome, were, until very recently, widely planted for driftsand reclamation and a variety of other purposes. The use of these species has been strongly discouraged by the Forestry Branch since 1980 and official management instructions currently stipulate that indigenous species should be used for reclamation. In contrast to the montane environments of the biome, where some control is exercised over land use in proclaimed catchments, most land invaded by A. saligna and A. cyclops falls outside the area of jurisdiction of the Forestry Branch. Control of these species is carried out by a number of smaller organizations, municipalities and volunteer groups. In total it is estimated that of the 8 962 km^2 infested by alien plants other than Hakea and Pinus species, i.e. mainly Acacia species, only 870 km^2 (10%) had been successfully cleared by 1984 (Macdonald et al. 1985a). The ability of several of these species to coppice after felling and the density and longevity of the soil-stored seed bank makes control of these species difficult and expensive (Milton & Hall 1981; Macdonald et al. 1985a). The control of these species, particularly on privately owned farm land, poses one of the most significant challenges to fynbos conservation.

I.7.4. The control of herbaceous alien plants

The large-scale control of herbaceous alien plant invaders in areas of natural vegetation has not yet been undertaken within the biome. The only exceptions have been the subshrub Hypericum perforatum and the grass Stipa trichotoma, both of which are confined mainly to areas of modified vegetation within the biome. The former has been the subject of a successful biocontrol programme (Kluge & Gordon 1983) while the latter is being controlled manually in at least one of the small areas currently known to be infested (Hall & Bulley 1980). Both these species are being controlled primarily on account of their potential threat to agriculture.

I.7.5. The control of alien fauna

The control of alien animals has not yet been accorded a high priority. Early attempts to limit the spread of Sciurus carolinensis through the application of a bounty system were abandoned as being futile (Millar 1980). The control of Hemitragus jemlahicus on Table Mountain is possibly the only example of the control of an alien animal for nature conservation reasons in the biome. The population density has been reduced to and kept at low levels through a programme of shooting initiated in the early 1970's and no increase in distribution range has been observed since then (Lloyd 1975). Research is being conducted on the ant Iridomyrmex humilis, to define the extent of its distribution, to analyze its effects and explore methods of control;

recommendations have been made for limiting its further spread into fynbos areas (Macdonald & Jarman 1984; De Kock 1984). Until the ecological impacts of faunal aliens such as Theba pisana and Vespula germanica have been investigated, no rational basis exists for evaluating the importance of controlling these species.

I.7.6. Control priorities within the biome

The obvious impacts of alien woody plants has led to their control being accorded overriding significance in the management of natural and semi-natural vegetation throughout the fynbos biome. This situation will not change unless major progress is made in the control techniques available for these species. In this respect, the biological control for the Australian Acacia species should be given the highest priority.

I.8. CONCLUSIONS

No attempt is made to draw conclusions regarding the assertion that the fynbos biome is especially susceptible to alien plant invasions, as this matter is dealt with in detail elsewhere (Macdonald 1984; Macdonald, Powrie & Siegfried 1986). Instead conclusions will be made on the three questions posed at the start of this review.

I.8.1. Which species have invaded?

The most important alien invaders, both in terms of the extent of their infestations and their impacts, are undoubtedly trees and shrubs. However, the biome has been invaded by species from most taxonomic groups, with normally only a few species proving to be important in each of the faunal groups.

I.8.2. What are the characteristics of the invasions?

The invasions by woody plant species have been widespread and have often resulted in dense stands which radically alter biotic and abiotic features of the invaded landscape. These species have been able to invade relatively undisturbed ecosystems and the regular occurrence of fire in these ecosystems has tended to favour their spread and proliferation.

The impact of these woody plant invasions on the indigenous flora has been marked. Most indigenous plants in the biome appear to be intolerant of shade and decline in vigour or die once overtopped by invading tree species.

The invasions of herbaceous species and alien animals have generally been much less successful, with many of the alien species being restricted to sites of human disturbance.

I.8.3. What appears to be unique about alien invasions of the fynbos?

The dominance of the biome's invasive alien flora by trees and shrubs, at least in terms of the more important species, is possibly one of the features unique to the biome. Another is the large reduction in plant species diversity that follows the invasion of fynbos vegetation by alien woody plants.

The apparent high susceptibility of the biome to invasion by species from elsewhere in the subcontinent is also possibly unique. That more alien animal species have been able to establish populations in this biome than elsewhere in the subcontinent might also be unique (see Macdonald, Powrie & Siegfried 1986). However, this could simply be the result of the extensive modification to ecosystems and impoverishment of the fauna that has characterized the biome in recent times.

The apparent occurrence of a 'vacant' tree niche in the biome (Campbell et al. 1979), the alleged occurrence of a 'vacant' fish niche in the biome's rivers (Bruton 1986) and its susceptibility to invasion from elsewhere in the subcontinent all agree with the hypothesis that this small biome is in several ways akin to an island. The high levels of endemism in its indigenous biota strengthen this hypothesis. As in many 'insular' environments throughout the world, alien organisms have wreaked havoc in the fynbos biome and will continue to do so until effectively controlled.

APPENDIX II

PROCESSES OF INVASION BY ALIEN PLANTS

APPENDIX II: PROCESSES OF INVASION BY ALIEN PLANTS [1]

II.1. INTRODUCTION

A model to describe the process of colonization or invasion of a new habitat by a species has three principal elements (Roughgarden & Diamond 1986). Firstly, the colonizing species must overcome the barriers to dispersal between its native habitat and the new; secondly, on arrival it must withstand the rigours of the new habitat, and thirdly, if the habitat allows growth and reproduction, then the colonizer must survive the adverse interactions with resident species which are competitors, inhibitors, or predators, or establish new mutualistic relations (Figure II.1). Such a model may conveniently be applied at two scales: the that of intercontinental transfer, and then to the subsequent processes involved in the spread within a region.

In this chapter we examine the information on introduced plant species that are invasive in South Africa to find general explanations for their invasions. Few studies have been aimed directly at explaining the invasions so that it is often possible only to derive tentative hypotheses from the results reported. Because of this we often resort to the forestry literature, since many tree species have been introduced to South Africa and their introduction to and propagation in uncultivated land has been studied experimentally.

II.2. ENTRY OF PLANT SPECIES TO SOUTH AFRICA

II.2.1. Introductions

By definition, introduced species are those translocated by man. Species of the coastal littoral and adjacent habitats may arrive without the aid of man but no problematic species have dispersed to South Africa this way. There is evidently a steady arrival of exotic pollens on Marion Island, for example, but no seeds have been detected in this drift (Scott & Van Zinderen Bakker

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[1] *Publication status: Kruger, F.J., Richardson, D.M. & Van Wilgen, B.W. (1986). Processes of invasion by alien plants. In : Macdonald, I.A.W., Kruger, F.J. & Ferrar, A.A. (eds), The ecology and control of biological invasions in southern Africa, pp. 145-155, Oxford University Press, Cape Town.*

1985).

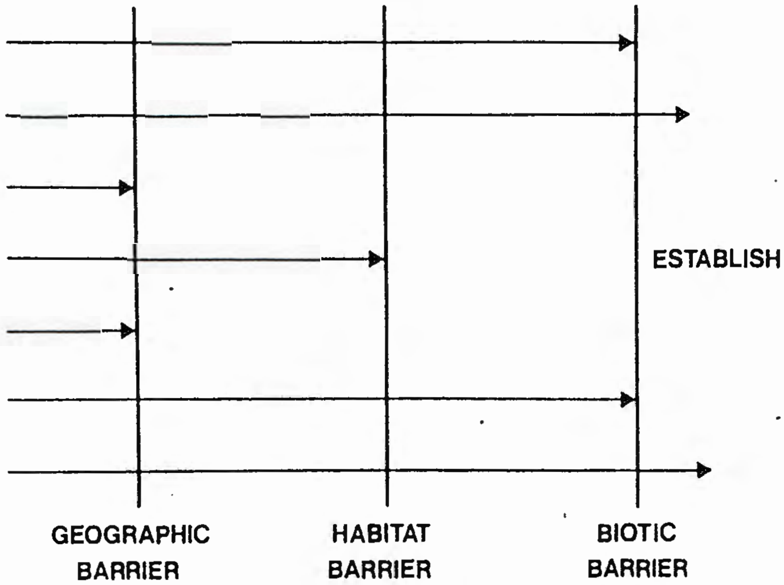

Figure II.1. A model to describe the processes involved in the invasion of a new habitat by an alien species. The geographic barrier must be overcome by dispersal. The habitat barrier requires preadaptation to the conditions of the new environment or a genetic adjustment to it. The biotic barrier includes the forces of predation, herbivory, competition and interference which must be overcome in the new community, or the new mutualistic relationships which must develop.

Of the invasive species introduced by man, many have been inadvertent introductions. Baker (1986) lists four modes of such introductions, to which we may add one for South Africa, i.e. introduction of Nicotiana glauca with hay for horses (Tarr & Loutit 1985) (Table II.1). Modes of entry of alien invasive plants to South Africa are discussed by Wells et al. (1986). Because species which are inadvertently introduced are seldom, if ever, propagated, there may be many such introductions which have failed to survive.

Species intentionally introduced would have been propagated deliberately and this would tend to favour a proportionately higher rate of success in establishment. At least 400 alien species of trees and shrubs are successfully cultivated in South Africa or are naturalized (Poynton 1984) and this is about 40% of the native tree and shrub flora (De Winter et al. 1978). Among herbs, domesticated varieties are used more often than in the case of alien trees and shrubs, especially among ornamentals and crop plants. Because domesticated varieties of ornamentals have been selected for garden conditions and not for competitive ability, and are often sterile or nearly so (Baker

1986), they are seldom invasive. In South Africa, the relative rarity of invaders among introduced pasture plants is striking (Wells et al. 1986). Thus, the frequency of invasive species may be higher among the woody species than among the herbaceous. In South Africa, the need to introduce woody plants to a landscape relatively devoid of trees (e.g. Shaughnessy 1986) would have motivated the importation of more such trees and shrubs than was the case in other regions of the world.

Table II.1. Modes of entry of alien plants to a new continent (Baker 1986), with some examples of species introduced to South Africa.

Mode of entry	Example
Inadvertent introductions	
by ballast in ships	
by impure seed imports	*Hypericum perforatum* (Gordon 1978)
by adhesion to domesticated animals	*Medicago* spp. (Deacon 1986)
in soil surrounding the roots of nursery stock	
in fodder for horses	*Nicotiana glauca* (Tarr and Loutit 1985), *Stipa trichotoma* (Stirton 1978)
Deliberate introduction as	
forage plants	*Prosopis* spp. (Stirton 1978)
fibre plants	-
medicinal plants	-
ornaments	*Sesbania punicea*, *Opuntia aurantiaca* (Stirton 1978)
erosion controls	*Acacia cyclops*, *A. saligna* (for stabilization of driftsands, Stirton 1978)
forest plantation	*Pinus* spp. (Poynton 1979a), *Eucalyptus* spp. (Poynton 1979b), *Acacia meansii*, *A. melanoxylon* (Stirton 1978)

II.2.2. Preadaptation to the new habitat

Those who introduced species have often attempted to match the climates and substrata of the source regions with those of the target region in South Africa, and then selected appropriate species from such matched source regions (King 1938). Many introduced species were therefore preadapted to the new environment and some at least should have spread from cultivation. What is interesting is why all introduced species have not spread. Although bioclimatic matching may aid successful introductions, it does not necessarily result in invasive spread. Pinus caribaea achieves vigorous growth on the Zululand coast, but does not invade because the local climate does not allow adequate reproduction (Poynton 1979a). The many species of Eucalyptus introduced to South Africa were selected to match the new habitats. Over 170 species have been introduced to South Africa over the past two centuries (Poynton 1979b, 1984), but few rank high on any list of species invasive in unmodified habitats (Henderson & Musil 1984; Macdonald and Jarman 1984, 1985), though about 25% of the species introduced tend to spread (Poynton 1984) and they are often problem weeds in forest plantations (Le Roux 1980). The reproductive biology and early growth of Eucalyptus species seem to make them poor competitors in the natural environments of South Africa (see below).

Baker (1972; 1974; 1986) draws the distinction between major weeds, whose habitat requirements are general, and minor weeds, with special habitat requirements and distributional ranges which are actually and potentially limited. Poynton (1984) has summarized the data on cultivated trees and shrubs in South Africa and has divided the country into 48 silvicultural zones on the basis of climate, with relative aridity, seasonality of rainfall, and severity of frost being the most important factors. He has classified the performance of each species in each zone, as well as their tendency to invade the surrounding habitat. Among the 300 or so species of Acacia, Eucalyptus and Pinus introduced into South Africa there is great variation among species in the number of silvicultural zones to which each is suited (Poynton 1984; see below). Among those which are invasive this ranges from about six to 36 of the 48 zones. There is a poor correlation between the number of zones to which species are suited and the number in which they are classified as invasive (r^2 = 0.177, P = 0.189). Some species with wide habitat tolerances invade widely whereas others, with similar histories and tolerances, invade only in a few regions. Acacia dealbata, for example, is suited to about half the zones and is recorded as invading in all of these. By contrast, Acacia melanoxylon, which has about the same ecological amplitude, is recorded as an invasive only in half of its zones i.e. the humid ones. Acacia podalyriifolia invades in all the 18 zones to which it is suited but A. cultriformis, a species suited to the same zones and used for similar horticultural purposes, is recorded as invasive in only two. Clearly, some introduced species in South Africa may be classified as major weeds in Baker's definition, and others as minor weeds. Pinus pinaster and P. radiata are able to invade habitats within the winter- and all-year-rainfall regions of South Africa which vary widely in rainfall and soil conditions (e.g. Kruger 1977). These are major weeds. Among minor weeds in the same region one may count Pittosporum undulatum, whose distribution is severely limited by microclimatic conditions required for establishment (Gleadow 1982; Richardson & Brink 1985).

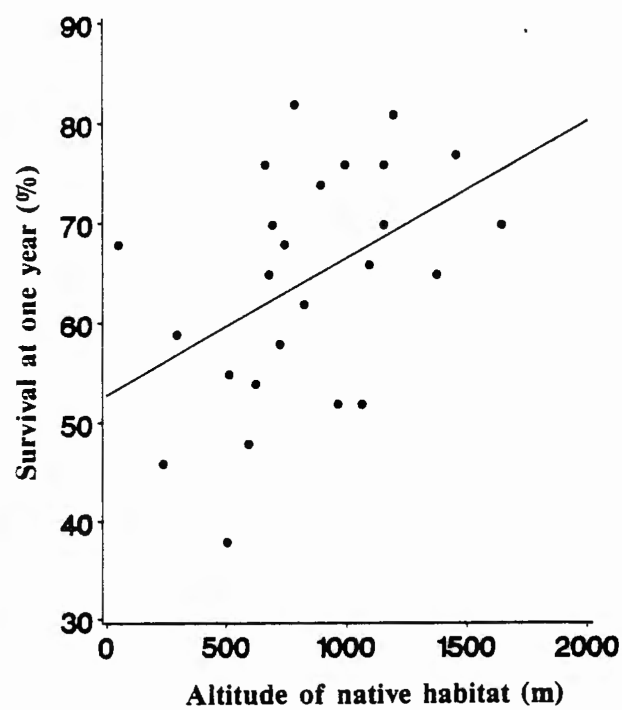

Figure II.2. Variation in the survival of frost by Eucalyptus viminalis at one year after planting at Jessievale, Eastern Transvaal. Survival was significantly related to altitude of native provenance (r=0.53). Data from Darrow (1984).

The genotype of P. pinaster that has invaded most of the area concerned is the "Franschhoek" form, introduced in the seventeenth century (Kruger 1977). There is marked racial variation in P. pinaster and provenance trials have shown which have the most desirable characteristics (Rycroft & Wicht 1948). The preferred form, from Portuguese provenances, apparently produces less cones and therefore less seed under South African conditions than the others (Rycroft & Wicht 1948). It remains to be seen whether this genotype will have general capabilities for invasion after its widespread introduction subsequent to 1948.

Intraspecific variation in tolerance of habitat factors may determine whether the introduced genotype will establish or which habitats within a bioclimatic region will be invaded. Frosts in the highveld grasslands of South Africa exclude most species of trees. Introduced species of frost-hardy Eucalyptus vary in their tolerance, both between and within species (Darrow 1984). In Eucalyptus viminalis, for example, there is pronounced variation among populations of different provenances in their survival of frost (Darrow 1984) and this is evidently related to native microclimatic conditions (Figure II.2). Eucalyptus viminalis is a slow invader of grassland habitats (Poynton 1984). The habitat invaded locally would depend on which genotype had been introduced, at least in relation to frost. The overall degree of invasion would depend on the variety of genotypes selected for introduction. In the past, selection of varieties may not have been optimal in this respect, but formal programmes of provenance trials in forestry, for example, will ensure progressively better matching of genotypes and environment.

II.2.3. Preadaptation to the biota and communities

Invasive weeds are often plants which have evolved in long association with man in the source region, often the Mediterranean Basin (Baker 1986). Few of the grasses which have succeeded in overwhelming communities elsewhere (e.g. Mack 1986), and which often include the forms which Baker referred to, have penetrated substantially into native South African pastures. In these habitats we have seen invasions by plant forms not normally classified as weeds, i.e. trees and shrubs, although there are some exceptions such as Stipa trichotoma in the grasslands and Bromus japonicus in the winter-rainfall karoo. Macdonald (1985a) has drawn the contrast between the situation in South Africa and that in Australia, for example, where most invasive plants are herbs. He suggested that this was because the abundant African herbivores impaired the vigour of introduced herbs to the point that any advantage over equivalent native species was lost.

The role of such biotic factors in determining whether and introduced species invades successfully has received little attention. Many alien species of timber trees suffer severe pressure from native mammals (Bigalke 1980). Certain species and even races are often preferred, and these may be excluded from further propagation as a result. This is illustrated by the case of *Pinus oocarpa*, a potentially productive Central American timber tree. Trials have shown markedly different rates of casualty among plants of different provenances, with damage caused mainly by bushpigs *Potamochoerus porcus* and, to a lesser extent, baboons *Papio ursinus* (e.g. Steyn 1980). Termites are known to have prevented the successful establishment of *Eucalyptus* species in plantations in tropical regions prior to the advent of chemical pesticides (Poynton 1979b). It is thus likely that the establishment of some introduced species in South Africa has been prevented or at least delayed by the effects of the native biota.

II.3. INVASION OF NEW HABITAT BY THE ESTABLISHED ALIEN

II.3.1. Evolution of invasions after introduction

Introduced species sometimes persist in small colonies, often in cultivation, for several generations before invasion is noticed. One explanation offered for this is the so-called "infection pressure" (Salisbury 1961; Baker 1986). The hypothesis is that an introduced species would have to reproduce sufficient generations locally for the population to reach a condition which allows spread from the point of introduction. Baker (1986) speculated that this could be connected to the founder effect, in that a population arising from one or a few initial seeds would require time before sufficient genotypic variation could evolve to permit colonization of variable habitats. Alternatively, the effect could be purely demographic, time being needed for populations to pass through the initial phase of exponential growth to the stage where observers would begin to notice problematic invasions. It could also be ecological, in that some change in the environment is needed before the species' requirements for spread are met. Finally, it might also be that the conditions required for spread occur episodically and infrequently.

An analysis of the information on species of *Acacia*, *Eucalyptus* and *Pinus* in Poynton (1984) together with the data on dates of introduction taken from seed-stock records and other sources, (e.g. Shaughnessy 1986) allows a test of the hypothesis of infection pressure. About 309 species in these genera have been introduced, mainly in the period from 1850 to 1950 (Table II.2). The data indicate that about 57 of these have become invasive to a greater or lesser extent. A weighted regression analysis of the percentage of invasive species on period of introduction is highly significant (r^2 = 0.835, F =15.1, P = 0.0301) with a negative coefficient, indicating a real increase in the incidence of invasion with time since introduction. Most of the invasive species are among the large number of plants introduced between 1850 and 1900. This provides support for the hypothesis of infection pressure and could presage more problems in future once the large numbers of species introduced since 1900 have passed through this hypothetical stage of initial adjustment. Macdonald (1984) could find only limited evidence that the extent of invasion was related to time since introduction of a plant species to South Africa, so that although the inception of an invasion by a given species may sometimes depend on the passage of time, the subsequent rate of spread may be less dependent on time.

Table II.2. Summary of information on introduction of species of Acacia, Eucalyptus and Pinus to South Africa, from Poynton (1979a,b, 1984) and unpublished records of the Seed Section, South African Forestry Research Institute, Pretoria.

	Interval, year					
	<1700	1701-1800	1801-1850	1951-1900	1901-1950	1951 +
Total number of species introduced	3	0	6	126	132	42
Number of invasive	2	0	5	38	12	0

Where an invasion is delayed this may involve a lag in the establishment of a required mutualistic interaction. The most obvious of these is when animals feed on fruit and disperse the seed. Richardson & Brink (1985) have inferred from the absence of early reports of *Pittosporum undulatum* invaders that the species began to spread only several decades after the initial introduction. This may have been because there was a lag before native birds switched to the new kind of fruit, after which spread became more marked (Richardson pers. obs.). Similar dispersal mutualisms have evolved in *Acacia cyclops*, *A. saligna* and *A. longifolia* now dispersed by the Black Korhaan, *Eupodotis afra* (Knight & Macdonald 1985) and the Redwinged Starling *Onychognathus moria*

(Richardson pers. obs.) as well as in Solanum mauritianum (see below).

There is as yet no evidence for genetic change in invasive plants introduced to South Africa. Gill (1978) has suggested that the hard-seededness evident in invasive populations of Acacia cyclops may have ben strongly selected for in South Africa from an Australian stock with a very low frequency of hard-seededness (Christensen in Gill 1981). Soft-seeded strains, it is argued, would have been initially eliminated before invasion began.

Evidence that delayed invasion could be the result of infrequent occurrence of episodically suitable conditions has been adduced for Prosopis in the Karoo and southern Kalahari by Macdonald (1985b). Species of Prosopis had been introduced to the region concerned over a lengthy period from about 1910. Rapid invasion and growing concern about it were noticed in the late 1970's. Macdonald suggested that this was at least partly owing to the run of high-rainfall years beginning around 1974; for example, dense infestations became established on riparian sites on river courses which had flowed in those years but not in human memory before then.

In other cases, no initial adjustment was apparently necessary. Analyses of historical aerial photographs and the plantation history of Jonkershoek and inference of past population dynamics from the age structure of stands of Pinus radiata invading fynbos show that invasion began about years after first planting of the species in the area. This was just sufficient time for the parent trees to begin seed production (Richardson & Brown 1986).

II.3.2. Dispersal

II.3.2.1. Dissemination by people

Cultivation and dissemination of introduced species by human are often implicated in the invasion process and it is frequently difficult to isolate the effect of these from that of unaided dispersal (Shaughnessy 1986). Seventeen of the 20 most important invasive aliens in the fynbos biome (Macdonald & Jarman 1984) have been actively propagated, many from as early as the mid-nineteenth century (Richardson unpublished). Even so, the majority of species that were widely planted have failed to become naturalized or invade habitats only in the immediate vicinity of plantations (Table II.3).

For example, Eucalyptus globulus was sold in greater numbers than any other

Table II.3. List of alien tree species of which 100 000 individuals or more were sold from or supplied by the four principal forestry nurseries in the fynbos biome (Tokai, Kluitjieskraal, Concordia, George) during the period 1881 - 1902 (Richardson unpublished) and the ranking of extent of invasion of the biome (Macdonald & Jarman 1984). Large quantities of seed of Acacia saligna were supplied for driftsand stabilization.

	Plants sold 1891-1902		Extent of invasion (rank according to Macdonald and Jarman 1984)
	Rank	Number	
Eucalyptus globulus	1	757 569	-
Leptospermum laevigatum	2	594 648	8
Hakea suaveolens	3	571 905	14
Pinus pinaster	4	515 735	4
Acacia mearnsii	5	251 359	6
Eucalyptus diversicolor	6	238 452	14
Pinus radiata	7	198 933	7
Eucalyptus camaldulensis	8	195 348	-
Cupressus macrocarpa	9	160 541	-
Eucalyptus gummifera	10	143 216	-
Eucalyptus robusta	11	115 402	-
Acacia saligna	12	104 323	2
Eucalyptus cornuta	13	103 040	-
Quercus robur	14	101 899	14

species from five nurseries in the Cape between 1891 and 1902 but is has not succeeded in invading the natural vegetation in the fynbos biome, or at most invades very slowly (Taylor et al. 1985). Very few Hakea sericea plants were supplied from the five principal forest nurseries in the biome over the period 1891-1902 (Richardson unpublished), although the species had been introduced by 1850 (Neser & Fugler 1978). The species was planted on a limited scale and at isolated places, yet Hakea sericea is estimated to occupy the greatest area of all woody alien plants in the fynbos biome (Macdonald & Jarman 1984; see also Shaughnessy 1986).

II.3.2.2. Modes of dispersal

Successful alien plants in the different biomes are characterized by different modes of dispersal. Dispersal by animals is of cardinal importance in the forest, karoo and desert biomes and important in the savanna biome. Birds are the principal agents except in the karoo and desert where mammals rank most important. In grasslands and fynbos dispersal is mainly by wind though sometimes by animals, mainly birds (Richardson 1985a). Within the fynbos biome bird dispersal is important in Strandveld but relatively unimportant in Coastal Fynbos, Renosterveld and Mountain Fynbos (Knight 1985). Abiotic dispersal is most important in Mountain Fynbos and in Coastal Fynbos. The nutrient-deficient soils of these ecosystems preclude species with fleshy fruits (Milewski & Bond 1982). Wind is important in mountain areas where the short stature of the grassland and fynbos allows for unimpeded dispersal of winged seed over great distances. Riverine habitats in all biomes host a suite of alien plants that are dispersed in soil and water (Richardson 1985a).

II.3.2.3. Dispersal distances

The importance of quantitative differences between species in their dispersal ability is readily illustrated by way of example. Van Wilgen & Siegfried (1986) have made a comparative analysis of invasive pines. *Pinus pinaster* and *P. pinea* occupy similar habitats in Mediterranean Europe, sometimes occurring parapatrically. Abundant, apparently suitable, habitat is available to both in the south-western Cape, and both have been present since the seventeenth century (Shaughnessy 1986). Yet *P. pinea* is an invader of little consequence (e.g. Taylor *et al*. 1985); its seeds are large (0.6 g) and have relatively small wings, with ratio of total mass to wing surface area ("samara wing loading") of 4.6 mg mm^{-2}. Recruitment of young trees is confined to the immediate vicinity of parent trees. *Pinus pinaster* and *P. radiata* share similar seed characters, and contrast with *P. pinea*. Seeds have masses of 0.0485 and 0.0195 respectively, and "samara wing loadings" of 0.25 and 0.19 g mm^{-2}. Dispersal distances for these species in excess of one kilometre are common (Richardson & Brown 1986).

Studies of dispersal of seed by wind are often quoted to show how few seeds are dispersed over distances greater than a few times the height of the parent tree (Harper 1977). Whereas it is true that the majority of seed fall close to the parent plant, the few carried in turbulent air are crucial in colonization of new habitat. Such seed must initiate a two-phase invasion, involving the initial establishment of isolated individuals and the subsequent recruitment of dense daughter populations, that is so often observed in hakea and pine species (e.g. Richardson & Brown 1986).

Despite the frequent observation of involvement of animals, especially birds, in the dispersal of introduced plants in South Africa there have been no studies undertaken to determine what distances and rates of dispersal are involved. Glyphis et al. (1981) have examined patterns of dispersal by birds of Acacia cyclops but did not go beyond demonstrating the strong correlation of plant recruitment with perch sites so often reported for such case.

II.3.3. Habitat factors

As noted previously, it is difficult to discriminate between the effects of human activity and other historical factors on the one hand and the role of ecological interactions on the other in determining the patterns and rates of invasions by introduced plants. Poynton (1984) records an average of about 51 species of introduced Acacia, Eucalyptus and Pinus in each of the 12 humid silvicultural zones of South Africa and 48 for the 12 subhumid zones, the difference not being statistically significant. On average about 20 species are recorded as invasive in the former case, and about 10 in the latter. The highest incidence of invasive species, 41 out of 53 introduced, was found in zone As3, ie the humid summer-rainfall zone with moderately severe frosts. This is a complex transitional forestry zone with many species of trees used in scattered forestry projects and farm woodlots, so that the high incidence of invasives may be owing to cultural rather than ecological factors. In the arid and semi-arid zones a mere handful of species are recorded as invasive, but far fewer have been introduced.

The distribution of an invasive species within the biogeographic region to which it is preadapted is limited by habitat factors other than climate. For example, an analysis of the distribution of Hakea sericea and congeneric invaders in the south-western Cape showed that the most important factor characterizing invaded areas is the presence of soils derived from quartzite and sandstone. Occurrence of Hakea species was negatively associated with shales and unconsolidated substrata (Richardson 1984).

Factors determining susceptibility of habitats to invasion have received more critical attention for Cereus peruvianus which is invading bushveld of the central Transvaal (Taylor & Walker 1984). Here, the invading cactus is confined to habitats with heavy soils and trees dominated by native species of Acacia, and does not occur on adjacent sites with leached sandy soil and broad-leaved trees. Distribution of the weed was related to availability of perch-sites for bird vectors and to conditions required for seedling establishment. Seedlings became established only in areas which have fine-textured soils and a high density of trees, which in turn related to the seasonal duration of available soil moisture in the surface horizon. This combination of factors effectively confined the invasion to acacia savanna, and excluded the cactus from the mixed savanna of oligotrophic sands. Within the acacia habitat, trees and understorey grasses interact to determine soil moisture status and hence cactus establishment.

Habitat factors may sometimes interact with biotic factors to limit distribution. Pinus radiata, for example, is susceptible to infection by the needle disease, Sphaeropsis sapinea (= Diplodia pinea) (Poynton 1979a). Infection of hail-damaged needles often occurs during the warm humid period following hail storms. This effectively prevents the species from invading the summer-rainfall regions of South Africa where such storms are common. Fire is a regular phenomenon in fynbos, grassland and savanna ecosystems of South Africa. The role of the fire regime in limiting invasions has been little studied and it is usually considered to be a disturbance factor enabling invasion (e.g. Macdonald 1984). Clearly fire or a particular fire regime excludes certain potential invaders. Species of Acacia and Pinus which have a youth period of four years or more and are unable in the juvenile stage to sprout after fire are excluded under normal circumstances from grasslands in which fire recurs at intervals of about two years. Fire may also directly exclude species. Of four species of Hakea introduced to the south-western Cape from Australia, one, H. salicifolia, does not spread despite having being planted extensively in hedges in diverse forest, fynbos and grassland habitats. It may be excluded from grassland and fynbos because its seeds do not survive normal fire temperatures. The small follicles do not provide sufficient insulation against the heat of crown fires. The other three Hake species have large follicles which provide effective protection (Richardson et al. 1987).

II.3.4. Biotic factors

Herbivores may determine the kinds of introduced species which may succeed in invading a particular habitat and hence the extent of invasion by any given species. Macdonald (1983, 1984, 1985a) has drawn attention to this in South Africa, pointing to the role of the black rhinoceros Diceros bicornis in eliminating plants of Acacia mearnsii from the river banks in the Umfolozi Game Reserve and of elephants Loxodonta africana doing the same for Opuntia ficus-indica in the Addo Elephant National Park. Effects of this kind must vary considerably with the identities, abundances, and foraging preferences of the available herbivores. There is as yet no evidence for control by native herbivores or other consumers of the distribution of introduced plant species analogous to that of introduced biological control agents on Opuntia species reported by Zimmerman et al. (1986).

Richardson (1985b) has quantified losses of Hakea sericea seed after the mass release when the parent stand is killed amounting to 99-99.9% of the 55-174 seed m^{-2} available. This loss was ascribed to rodents, but even such heavy predation has not prevented invasion, most likely because the rodents, even when abundant, do not find the last seeds.

There is tentative evidence that competition and interference between native and the alien invasive plant species may also determine the rate of invasion by some aliens, if not all. Turning once more to examples from forestry, we find that several actual or potential invaders are extremely sensitive to competition from a vigorous grass sward. Eucalyptus species, planted extensively in grassland ecosystems, are intolerant of competition from indigenous grasses even if the grassland has been burnt (Schonau & Stubbings 1983; Schonau 1984) and intensive site preparation is necessary to ensure successful establishment. Pits prepared in otherwise undisturbed grassland are seldom sufficient to ensure adequate survival and growth of transplants. Ploughing to a depth of at least 100 mm to kill grasses is needed to ensure successful establishment of Acacia mearnsii (Stubbings & Schonau 1983). Effects of competition with the grass sward have also been invoked as a factor limiting proliferation in Cereus peruvianus (Taylor & Walker 1984).

The role of competition at the establishment phase evidently varies between South African biomes as indicated by a survey of forestry establishment problems by Donald (1971). He found that fynbos in general requires little clearing to reduce competition for pines. In contrast, site preparation is important for establishing pines in grassland, but the intensity of preparation required varies for the different regions; the most intensive treatment is needed in the north-eastern Mountain Sourveld of the northern Transvaal (Acocks 1975). Therefore the degree of disturbance required to permit or accelerate invasions would be expected to vary among the biomes, just as the site preparation techniques required in forestry vary.
There are numerous examples where dispersal and sometimes germination is dependent on the action of native or naturalized frugivores. The invasion of species with fleshy fruit (e.g. Cereus peruvianus, Solanum mauritianum, Pittosporum undulatum) or with funicles Acacia cyclops) follows a typical pattern. Establishment of second-generation individuals is generally restricted to the area around bushes or trees that bear fruit attractive to birds or around elevated perching sites (Glyphis et al. (1981; Taylor & Walker 1984; Richardson & Brink 1985).

The bush clumps which arise serve as foci for further bird activity and thus for further seed deposition. The size and complexity of these clumps increase with age and with the number of native and alien plants species involved. Solanum mauritianum in Natal, ten years ago confined to access roads and plantation edges, now often forms a complete understorey in wattle and pine plantations (Richardson unpublished). This is due to the fact that the Rameron Pigeon Columba arquatrix is exploiting a new and expanding ecological niche (Oatley 1984), though dispersal by other bird species (I.A.W. Macdonald pers. comm. 1986) and the common duiker, Sylvicapra grimmia, is also implicated (T. Allan-Rowlandson pers. comm. 1986). Native animals may determine invasion in ways other than through dispersal of seed. The structure of native habitats may be markedly affected by activities of native ungulates and this has been invoked as a factor favouring the penetration of forest margins by Chromolaena odorata once browsing by nyala Tragelaphus angasii has opened the canopy (Macdonald & Jarman 1985).

The abundant evident invasion of certain South African landscapes tends to belie the significance of biotic factors that act against invasion. The underlying factor permitting the invasions is some deviation from or disturbance to normal community functions. For example, changes in the fire regime in grassland may be one such disturbance, allowing invasion of moribund vegetation by pines and acacias. Another example is Pinus patula which is unable to invade vigorous Themeda triandra grasslands but does establish in forest margins, and in sparse grass swards induced by shallow soil and excessive burning and grazing (F.R. Smith pers. comm. 1986). Acacia species tend to become established along streams and on other sites where erosion, shading or other factors tend to debilitate the grass sward.

II.4. DEMOGRAPHIC FACTORS INVOLVED IN THE PROCESS OF INVASION BY PLANTS

An alien invasive plant becomes a problem because populations spread and grow from the initial introduction to the extent that these cause some direct or indirect cost to society. This involves population changes arising from the more favourable birth and death rates in the successful invader, relative to the native species.

II.4.1. Seed crop sizes

Large seed crops in an invasive alien are often contrasted with low fecundity of native populations of the same species and this difference is then invoked as being the reason for its invasion (e.g. Neser & Kluge 1986). However, the importance of the quantity of seed or other propagules produced over its lifespan or maintained in its seed bank by an invasive plant is not clear. Gill & Neser (1984), for example, confirm larger seed crops for Hakea sericea in South Africa than in Australia but found not difference for Acacia cyclops. Taylor & Walker (1984) found for Cereus peruvianus that the ratio of seedlings to seed produced per parent plant was in the order of 1:10 000, about the same as for cacti in their native habitats. They concluded that a high fecundity was of lesser importance than the influence of soil moisture regime on seedling establishment.

Richardson *et al.* (1987) have compared seed production in four species of Hakea in the south-western Cape. Of three species that have been declared noxious weeds in South Africa, only H. sericea is a widespread problem. Hakea gibbosa and H. suaveolens are rapid invaders only in isolated areas, despite widespread propagation following their introduction in the mid-nineteenth century. This discrepancy in invasive ability between congeners with similar, canopy-stored and wind-dispersed seeds has been attributed to differences in seed numbers produced by the three species (Richardson et al. 1987). For example, average seed loads on a shrub with a dry mass of 14 kg range from about 100 on H. suaveolens to about 500 on H. gibbosa and 2 000 on H. sericea. Such differences are not necessarily important in the maintenance of established populations, where factors governing relative survival rate of seedlings become more important than absolute seed numbers (Harper 1977). They are important in expanding populations, for two reasons. First, the range of dispersal is affected. The relationship between seed density and dispersal distance may be expressed as a negative exponential function. Such a model reveals that with an increase in seed number of around 20%, maximum distance of dispersal increases by around 80% (Harper 1977). Dispersal over a great distance is a relatively rare event but the probability of it occurring increases exponentially with an increase in seed numbers. The potential rate of spread is thus significantly affected by seed numbers. This would have been an important factor in facilitating the relatively rapid invasion by H. sericea of its present range and no doubt also of Chromolaena odorata (Liggit 1983). Second, high fecundities may be assumed to be an essential part of rapid recruitment of subpopulations from colonizing individuals at the leading edge of an invasion front. High fecundity, if coupled with high recruitment, is also important for outcrossing colonizing species because rapidly expanding populations regain genetic diversity relatively quickly (Barrett & Richardson 1986). The greater the number of seeds, the greater the chance that a successful new genotype will be added to the population and, with qualifications, the greater the number of genotypes accruing to the population (Templeton & Levin 1979; Cavers 1983). These aspects have not yet been studied in the species which invade South African ecosystems.

II.4.2. Growth to maturity

The age at which a plant first reaches reproductive maturity has relevance principally to disturbance regime, as noted above for fire regime. Invasive aliens enjoy no special advantage in this respect. Species such as Pinus pinaster (Kruger 1977), Hakea sericea and Chromolaena odorata mature early, at ages between two and six years. However, native species are equally precocious for example in _Protea_ (Kruger & Bigalke 1984). Nevertheless, late attainment of reproductive age will often preclude invasion by an introduced species. The low fecundity in _Hakea suaveolens_ results from a long youth period. _Eucalyptus nitens_, favoured for afforestation on the eastern Transvaal highveld, seeds for the first time at about 15 - 16 years (Darrow 1984). Since it is grown on a rotation shorter than this it is likely to invade slowly, if at all.

II.4.3. Survival and mortality

The hallmark of many successful invaders lies perhaps in the fact that crowding of seedling populations causes little increase in mortality. Taylor & Walker (1984) found for _Cereus peruvianus_, for example, that population density and recruitment rate were positively correlated: "there is no negative feedback on new seedling establishment", and populations increased rapidly to very high density, in excess of 20 000 stems ha^{-2}. The same phenomenon may be found in _Hakea sericea_, _Pinus pinaster_ and _Chromolaena odorata_ (Richardson unpublished). Mortality in adult populations is also often marked by weak self-thinning; instead, individuals in crowded populations are smaller than normal (K von Gadow pers. comm. 1986). Such invasive species rapidly displace competitors. It may be that species with these characteristics can invade natural communities with less need for initial disturbance than do invaders with variable mortality at the seedling stage, such as _Acacia_ (see Milton 1981) and _Eucalyptus_ species.

II.5. CONCLUSIONS

The relatively limited degree of understanding of the processes involved in the invasion of South African ecosystems by introduced plants prevents any useful generalization at this stage. Comparative studies involving introduced congeners, one successful and one not, could provide the quickest means to making progress with the problem, as would studies involving the same species under contrasting conditions.

If the history of introduction and invasion is anything to go by then many problems lie ahead. An understanding based on much more thorough studies of the processes involved will be needed to predict and manage invaders of the future. Dispersal is crucial. The dynamic relationships between dissemination and animal vectors appear to be complex. South African biomes are distinguished from each other by invaders with different syndromes. It is not clear whether these patterns are determined by habitat or whether the interactions between species will change with time and shift the pattern, presenting new problems with weed control.

There is sufficient evidence that, even for major weeds, clearly quantifiable and hence predictable relationships between habitat factors and invasion may be obtained. Determining these relationships could provide an important tool in evaluating introduced plants in terms of potential spread.

The patterns of success and failure among introduced plants point clearly to the governing role of biotic interactions, disruption of which is often needed before invasion begins. However, there is at least tentative evidence that in some biomes and with certain introduced species the conditions for invasion exist without undue disturbance. Speculation about the relative roles of fire, competition between plants, and herbivory and predation, in permitting or preventing invasion must be addressed experimentally if management of the habitat is to be effectively adjusted to counter biological invasions.

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