THE RELATIONSHIPS BETWEEN FOREST AND MOUNTAIN FYNBOS COMMUNITIES IN THE SOUTHWESTERN CAPE PROVINCE OF SOUTH AFRICA

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Thesis title: **The relationships between forest and mountain fynbos communities in the southwestern Cape Province of South Africa**

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ABSTRACT

Evergreen forests are believed to be restricted to moist sites in the southwestern Cape because of seasonal drought and high fire frequency in adjacent fynbos shrublands. However, soil moisture has not been demonstrated as the controlling factor. Succession to forest has been observed in some areas and not all forest trees in the fynbos are killed in some fires. This thesis determines whether forest and fynbos communities are separated by habitat factors or whether they are different successional stages of the same vegetation type.

The effects of fire on forests, regeneration processes and habitat factors were studied in Swartboskloof, near Stellenbosch. Establishment requirements of forest seedlings were investigated in nearby Assegaiboschkloof. The effects of habitat factors on germination, establishment, growth and competitive abilities of forest and fynbos species were determined in controlled growth experiments.

Established forest stands in Swartboskloof were stable in response to fire. Studies on the relationship between plant size and ability to survive fire showed fire intensity to be the overriding factor. Unlike regeneration in fynbos, regeneration of forest species is not coupled to disturbance. Forests had smaller soil seed banks than nearby fynbos but had the same set of species. Dispersal of forest species seeds into fynbos occurs immediately after fire for wind- and bird-dispersed species. Therefore colonization of fynbos by forest species soon after fire is not limited by seed dispersal.

Evidence of facilitation of forest development was found in mature fynbos. Forest seedlings were associated with tall vegetation, high cover and deep litter layers as well as proximity to perches. Facilitation is enhanced in nuclei of forest species within fynbos communities.

These studies refute the concept of forest and fynbos as distinct vegetation types. The relationships between forest and fynbos are explained on the basis of successional processes. Germination of forest species may occur in post-fire conditions, but establishment is unlikely until habitat amelioration occurs. Soil moisture and nutrients affect the rate of forest development. It is the frequency of fire, in relation to the rate of forest development, which determines the extent of forest development.

SUMMARY

The vegetation of the mountains of the Fynbos Biome in the southwestern Cape Province of South Africa is predominantly fynbos, a fire-prone shrubland vegetation. Patches of evergreen forest tend to occur at low altitudes on southern, coastal mountains and forelands on all substrata. Forests typically occur in sheltered ravines, stream banks and patches of rock scree where the annual precipitation is greater than 650 mm.

This thesis aims to determine the relationships between forest and fynbos vegetation. The principal issue is whether the communities are separated because of habitat factors or whether forest and fynbos communities are different successional stages of the same vegetation type in juxtaposition.

The location of forests in moist habitats is often understood to reflect the climatic amelioration in these zones and the preclusion of forest species in the adjacent vegetation by seasonal drought. However, soil moisture has not yet been demonstrated as the factor controlling the forest-fynbos ecotone. An alternative explanation is that these forests are remnants of previously more extensive forests that have been reduced by too-frequent fires. In contrast to the fire-prone fynbos, forest patches seldom burn. The hypothesis of control by fire is supported by observations of succession to forest after extended fire-free periods in some fynbos areas.

The studies in this thesis comprise an investigation of the forest-fynbos boundary at Swartboskloof in terms of fire, soil seed banks, seed dispersal, post-fire regeneration and habitat factors. Based on these studies, a model of succession of fynbos to forest was developed and processes related to the establishment requirements of forest seedlings (facilitation) and nucleation were investigated in Assegaiboschkloof. These investigations were supported by experiments on the effects of habitat factors on germination and establishment of forest and fynbos species. Experimental studies with varying levels of control were also employed to investigate the effects of soil moisture and soil type on the growth and competitive abilities of forest and fynbos species.

The stability of established forest stands was demonstrated in Swartboskloof by the response to the fire of March 1977. Almost all post-fire regeneration, comprising mainly fynbos and transitional zone species, occurred in burnt areas. The small amount of forest regeneration was almost exclusively in the unburnt areas in the forest. Regeneration of forest species therefore, unlike regeneration in fynbos, is not coupled to disturbance. Population studies on *Cunonia capensis* to determine the relationship between the size of plants and their ability to survive fire showed fire intensity to be the overriding factor.

Forests in Swartboskloof had smaller soil seed banks than nearby fynbos but the species composition of soil seed banks were the same in each vegetation type. In the event of removal of forest plants by fire, therefore, there is likely to be some regeneration from soil-stored seed, including forest precursors. Perches for avian dispersers of forest seeds are not necessarily a fruiting species or a large tree, especially in areas fairly close to the seed source. Dispersal of forest species into fynbos occurs immediately after fire for both wind- and bird-dispersed species. Therefore, colonization of fynbos by forest species soon after fire is not limited by seed dispersal and thus, factors such as germination and establishment requirements must be important in determining community boundaries.

Evidence of facilitation of forest development was found in mature fynbos. Forest seedlings were associated with tall ground layer vegetation, high cover and deep litter layers as well as proximity to perches. Facilitation is enhanced in nuclei of forest species within fynbos communities. Facilitation may involve amelioration of drought stress and in forest nuclei there is enhanced attractiveness to avian dispersers.

Although germination of forest species may occur in post-fire conditions, establishment is unlikely until habitat amelioration occurs. Habitat amelioration may result from the development of fynbos or nuclei of forest species that may have survived the fire. Establishment is enhanced if soil nutrient levels permit rapid growth in the wet winter conditions soon after germination. Soil moisture and nutrients *per se* do not limit forest distribution, but affect the rate of forest development. Most of the Fynbos Biome is bioclimatically suitable for forest. It is the frequency of fire, in relation to the rate of forest development, that determines the extent of forest development.

The studies described in this thesis have refuted the concept of forest and fynbos as two distinct and mutually exclusive vegetation types. Forest species are a late successional (or tolerant) component of the dynamic vegetation of the Fynbos Biome and may potentially predominate, under favourable fire regimes, some areas currently under fynbos communities. The perceived restriction of forest communities to sheltered environments is principally a function of past and present fire regimes. This interpretation of the relationship between forest and fynbos vegetation requires a longer-term view of the time frame over which management objectives are considered. Small changes, in either forest development or forest removal, in a fire cycle may accumulate and magnify over several fire cycles.

Nomenclature: Plant species nomenclature follows that of Bond & Goldblatt (1984).

PREFACE

The introduction and conclusion chapters of this thesis are based on a multi-author book chapter. All other chapters are research papers that have been published or that have been prepared for or submitted for publication in scientific journals. The papers have been edited to achieve uniformity of style and reference lists have been combined to avoid repetition, but are otherwise copies of the published or submitted papers.

The process of publication has enhanced the standards of the work presented here. The peer review system, employed by the journals to which papers have been submitted, has resulted inevitably in an improved product. I have enjoyed and benefited from constructive criticisms of drafts from my colleagues and promoters. Some of the papers involved collaboration and were written with co-authors. I detail my contributions to these papers here for the information of the thesis examiners.

Chapter 1. Introduction. This chapter is based on a book chapter of which PT Manders was senior author. Co-authors were DM Richardson and PH Masson. The basis of the book chapter was a review of the published work presented in this thesis, but included other relevant studies by my co-authors. PT Manders was principally responsible for drawing together the arguments presented in the book chapter and for the literature studies, interpretation and writing. The revision of the book chapter for the thesis was independent of the co-authors.

Chapter 2. Fire and other variables as determinants of forest-fynbos boundaries in the Cape Province. This was exclusively the work of PT Manders.

Chapter 3. Quantifying soil seed banks. A comparison of physical separation and seedling emergence techniques in Cape fynbos and forest vegetation. This was exclusively the work of PT Manders.

Chapter 4. Soil seed banks and post-fire seed deposition across a forest-fynbos ecotone in the Cape Province. This was exclusively the work of PT Manders.

Chapter 5. Colonization of Cape fynbos communities by forest species. This chapter was written by PT Manders as senior author and DM Richardson as co-author. The study was initiated by reciprocal sowings in Swartboskloof and the experiment on the germination requirements of forest and fynbos species carried out previously by PT Manders. DM Richardson and PT Manders deliberated at length on colonization processes, and the study on establishment requirements and nucleation arose from these discussions. After agreeing on hypotheses and sampling strategies, DM Richardson was responsible for the field work related to the nuclei. PT Manders studied the establishment requirements simultaneously and assisted with the study of nuclei on occasion. DM Richardson analyzed the data on nuclei and commented on the draft article after inclusion of the data on nuclei. PT Manders was responsible for all other aspects of the study, including field work, experimentation, data analysis, interpretation and writing.

Chapter 6. Effects of watering regime on growth and competitive ability of nursery-grown Cape fynbos and forest plants. This chapter was written by PT Manders as senior author with RE Smith as co-author. The study was designed as a plant growth study for which PT Manders determined the hypotheses and sampling design. RE Smith provided technical background for the physiological measurements which were incorporated into the growth study, participated in sampling design for these aspects, shared the sampling activities and provided interpretation of the results.

Chapter 7. Effects of artificially established depth to water table gradients and soil type on the growth of Cape fynbos and forest plants. This paper was co-authored with RE Smith on the same basis as Chapter 6.

Chapter 8. Conclusion. This chapter was based on the same book chapter, with the same levels of participation as the introduction. The book chapter was revised for this thesis independent of the co-authors.

Chapter 9. Critique. This was exclusively the work of PT Manders.

ACKNOWLEDGMENTS

This research was funded by the Department of Environment Affairs which does not necessarily concur with the findings or opinions expressed in this thesis. The work was conducted as part of the Conservation Forestry Research Programme of the South African Forestry Research Institute, and latterly as part of the Ecosystem Management Programme of the Division of Forest Science and Technology (Forestek), CSIR. I am most grateful to the Director-General of the Department of Environment Affairs and the Director of Forestek for the funding and for permission to submit this work for thesis purposes.

I thank my supervisors, Richard Cowling, William Bond and Willie Stock for their support and helpful criticism. Several of my colleagues were involved in the project and contributed advice on hypotheses, methods and interpretation of data. In particular I should like to thank Dave Richardson, Brian van Wilgen, David Le Maitre, Fred Kruger and Anthony Duckworth.

I am extremely grateful to Richard Cowling, Dave Richardson, Shirley Cowling, Brian van Wilgen, Willie Stock and David Le Maitre for the efforts they made to review manuscripts for publication. Several referees were particularly constructive and diligent in the review process of publication and I am very grateful to these anonymous contributors to the project.

I was able to rely on several people for assistance during the project and I am very grateful to them. Without their positive attitudes and willingness to work under a variety of situations, this work would not have been completed. Adrian Simmers was a steadfast assistant in almost all the field and support work. Adnaan Abrahams spent the better part of a year assisting in the field and separating seeds from soil. Kevin Higgins, Greg Bailey, Clare Jones and Gerard Mostert helped in the field and in several other ways. Ann Green prepared the figures for publication and for the thesis.

The co-authors of each chapter are listed on the first page of each chapter. I thank all my co-authors, Dave Richardson, Rosemary Smith and Peta Masson for their collaboration and input. I should like to make the following specific acknowledgments, with thanks, for those involved in each of the chapters.

Chapters 1 and 8

- The book chapter on which these chapters are based was reviewed by Bob Scholes and edited by Brian van Wilgen. The revision for this thesis was reviewed by Richard Cowling.

Chapter 2

- Adrian Simmers and Adnaan Abrahams assisted in the field.
- Richard Cowling, Dave Richardson, Brian van Wilgen and two referees provided comment on the manuscript.

Chapter 3

- Shirley Pierce gave advice on methods.
- Adnaan Abrahams assisted with seed extraction and identification.
- Adrian Simmers assisted in the field.
- Dave Richardson, David Le Maitre, Richard Cowling, Shirley Pierce, Brian van Wilgen and particularly constructive referees provided comment on the manuscript.

Chapter 4

- Shirley Pierce gave advice on methods.
- Adnaan Abrahams assisted with seed extraction and identification.
- Adrian Simmers assisted in the field.
- Richard Cowling, Dave Richardson, Shirley Pierce, David Le Maitre and Brian van Wilgen provided comment on the manuscript.

Chapter 5

- The Chief Directorate of Nature and Environmental Conservation of the Cape Provincial Administration gave permission to work in Assegaiboschkloof.
- Adrian Simmers, Clare Jones, Gerard Mostert and Greg Bailey assisted in the field.
- Richard Cowling commented on the text.

Chapter 6

- Kevin Higgins, Adrian Simmers, Gregory Bailey, Gerard Mostert and Clare Jones provided assistance.
- Richard Cowling and Willy Stock commented on the text.

Chapter 7

- Kevin Higgins, Adrian Simmers, Gregory Bailey, Gerard Mostert and Clare Jones provided assistance.
- Richard Cowling, Willy Stock and Dave Richardson commented on the text.

CHAPTER 1

INTRODUCTION

CHAPTER 1: INTRODUCTION

This thesis examines the relationships between forest and mountain fynbos vegetation in the southwestern Cape Province of South Africa. In particular, the studies seek to explain the determinants of forest distribution.

This chapter describes the forests in the southwestern Cape and introduces some of the arguments advanced to explain their distribution. The need to understand the determinants of plant distribution is universal. The studies in this thesis provide interesting comparisons and contrasts with concepts of the mechanisms of vegetation change in other vegetation types, especially other mediterranean-type ecosystems. Some of the current understanding of the development of forests in such areas is presented in this introduction to place the thesis in a global context.

1.1. Forests in the southwestern Cape

The vegetation of the mountains of the Fynbos Biome in the southwestern Cape Province of South Africa is predominantly mountain fynbos. This is a shrubland vegetation, typically including restioid, ericoid and proteoid elements (Taylor 1978). Low to tall microphyllous evergreen forests tend to occur at low altitudes on southern and coastal mountains (Campbell 1985). In this area forests usually occur on granite, shale and sandstone in sheltered ravines, stream banks and patches of rock scree where the annual precipitation is greater than 650 mm (Werger *et al.* 1972; McKenzie *et al.* 1977; Glyphis *et al.* 1978; McKenzie 1978; Kruger 1979; Campbell 1985). Where the forests occur on sandstone-derived soils similar in chemistry to those of fynbos soils, they are usually restricted to sites with year-round moisture (Campbell 1985).

In contrast to the fire-prone fynbos, forest patches seldom burn (Van Wilgen *et al.* 1990). Post-fire development of fynbos is by resprouting or germination of canopy- or soil-stored seed banks (Kruger & Bigalke 1984), whereas almost all forest species resprout after fire (Van der Merwe 1966) without fire-related seedling establishment. Dispersal modes differ in importance between the vegetation types. Over 40 % of forest species are bird-dispersed compared with less than 10 % in the fynbos (Knight 1988). The intermingling of forest and fynbos communities, with apparent maintenance of community integrity, establishes many natural experiments in areas of biological interest such as competition, succession and the ecology of invasions.

There are strong affinities between forests in the southwestern Cape and Afromontane forests, with elements belonging to the Cape and Tongaland-Pondoland phytochoria (Masson & McKenzie 1989). Numbers of species in the forests decrease towards the Cape from the Transvaal system, and from east to west within the Cape (White 1978). This has been associated with climatic differences (McKenzie 1978; Masson & McKenzie 1989). Reduction in species richness could also be associated with island effects as the greater fragmentation of the forests towards the southwestern Cape may affect the effectiveness of seed dispersal (Hanson *et al.* 1990). Forest patches in Swartboskloof have been shown to be representative of forest patches in the south-western Cape with typical species/area relationships and a predominance of Cape and Tongaland-Pondoland elements (Masson & McKenzie 1989).

1.2. Why are there no trees in the fynbos?

The location of forests in moist habitats is often understood to reflect the climatic amelioration in these zones and the preclusion of forest species in the adjacent vegetation by seasonal drought. This tenet originates in the statements that forests have different climatic requirements (Taylor 1978) and that the hot, dry summers preclude the occurrence of tree species (White 1978). To support this statement, White (1978) cites Taylor (1978) and Werger *et al.* (1972), a phytosociological study in Swartboskloof. However, soil moisture has not yet been demonstrated as the factor controlling the forest-fynbos ecotone (Van Daalen 1981; Masson & Moll 1987).

An alternative explanation is that these forests are remnants of previously more extensive forests which have been reduced by too-frequent fires. Destruction of forests by fires is an early observation (Sim 1907;

Wicht 1945; McKenzie 1978). Moll *et al.* (1980) suggested that frequent fires have removed the tree element from fynbos. Succession to forest has been noted in Orange Kloof (mean annual rainfall 1227 mm) near Cape Town after 50 fire-free years (McKenzie *et al.* 1977; Masson & Moll 1987) and was evident in places in the Swartboskloof valley (mean annual rainfall 1475 mm) after 28 fire-free years. These observations indicate that succession to forest may be possible in fynbos areas beyond riparian habitats, at least in those areas with higher rainfall.

The forest-fynbos boundary does not appear to be maintained by limited seed dispersal (Knight 1988). Mammalian herbivory in fynbos is minimal (Bigalke 1979), and is unlikely to affect community boundaries.

When the forest is disturbed or removed, fynbos will occur, and forest may invade fynbos in the absence of frequent disturbance. This suggests that the two communities represent different successional stages of the same vegetation type. The observation that forests occur more readily on soils with higher nutrient content and the relationship with moisture levels (Campbell 1985) suggest that these factors may influence rates of succession, rather than determining absolute limits to forest distribution.

1.3. Historical influences on forests in the southwestern Cape

Forest patches in the southwestern Cape are thought to have expanded and linked up temporarily at repeated times in the Pleistocene, associated with the occurrence of more mesic climates (Deacon 1983). Although there are no reliable records of the extent of the forests prior to european settlement in 1652, a marked decline may be inferred from historical records of utilization and destruction, and from the laws on forest usage promulgated very soon after settlement (Sim 1907; Wicht 1945; Hartwig 1973; Grut 1977). However, there is no evidence that the southwestern Cape has ever had extensive areas of high forest in historical time (Grut 1977; Campbell 1985; Scholtz 1986). Before 1652, the Khoisan, although not copious users of wood, had certainly influenced the fire regime of the vegetation in the Cape for at least 100 000 years (Deacon 1983). Since 1652, exploitation and fire would have been the major factors affecting forests; despite intense utilization, the local forests were not sufficient to provide all the requirements (Grut 1977). Although forests do not burn readily (Van Wilgen *et al.* 1990), fires at short intervals may erode the edges of forest patches, and there are occasional reports of very extensive and destructive fires in forest (Sim 1907; Wicht 1945). Exploitation may have exacerbated the effects of fire; removal of fire-proof forest margins and accumulation of fuel in forests through wasteful extraction could allow fires to penetrate forest patches (Sim 1907; McKenzie 1978).

1.4. How the situation is perceived in other mediterranean-type ecosystems

The mediterranean regions of the world occur on all continents. They are characterised by hot dry summers and cool wet winters, and are dominated by evergreen sclerophyllous shrubs or trees (Specht & Moll 1983).

1.4.1 The Mediterranean Region

The climax vegetation in the Mediterranean Region is a forest of evergreen sclerophyllous trees such as *Quercus ilex* and *Q. calliprinos* (Specht 1969; Naveh & Whittaker 1979). Such species rely almost exclusively on vegetative regeneration after fire and dominate in areas of higher rainfall, better soil and less frequent fires (Naveh 1975; Naveh & Whittaker 1979).

Fire, as in fynbos, is seen as an integral part of Mediterranean ecosystems and their evolution and, together with prolonged agro-pastoral practices, has contributed to the diversity of the Mediterranean landscape (Naveh 1975; Naveh & Whittaker 1979; Naveh 1982). Disturbance by grazing or fire in the Mediterranean systems results in the replacement of forest by low shrubland dominated by *Quercus coccifera* and eventually by grassland or ephemeral therophytes (Specht 1969). These communities may be maintained by disturbance, but development of tree species may occur. Succession in shrub-dominated communities may involve input of wind-dispersed tree seeds (such as *Pinus silvestris* and *Fraxinus excelsior*). Thereafter, modification of microclimates by these trees may facilitate the establishment of vertebrate-dispersed species such as *Fagus sylvatica* (Debussche *et al.* 1980). The succession process also occurs in abandoned cultivated lands and may be enhanced in orchards by the attraction of frugivorous birds to the trees and the establishment of points of nucleation for forest development (Debussche *et al.* 1982). Bird-dispersed species are as significant a proportion of the forests in the Mediterranean region as in the southwestern Cape forests, accounting for 40 % of species in *Quercus ilex* forest (Braun-Blanquet 1936 in Debussche *et al.* 1982).

1.4.2. Californian chaparral

Californian vegetation also has a component which shares many characteristics with forest vegetation in the southwestern Cape. This component comprises obligate resprouting species which establish seedlings in the prolonged absence of fire, suggesting a requirement for long-term changes in site characteristics (Keeley in preparation). Seeds of many of these species are bird-dispersed and do not form a seed bank. In common with southwestern Cape forests and trees in the Mediterranean Region, obligate resprouting species occur on more mesic sites (usually polar-facing slopes) or on nutrient-rich sites (Keeley 1986). Perhaps the critical difference between obligate resprouting species in the chaparral and southwestern Cape forest species is in growth form. Californian obligate resprouting species such as *Heteromeles arbutifolia*, *Quercus dumosa*, *Prunus ilicifolia*, *Rhamnus* spp and *Cercocarpus betuloides* are more shrublike and continue to rejuvenate their canopy by basal resprouts in the absence of fire. They are also resilient to frequent fire (Keeley 1986) in comparison with southwestern Cape forest species.

1.4.3. Southwestern Australia

Trees in south-western Australia are associated with the same features as in the other mediterranean-type ecosystems. *Eucalyptus* and *Casuarina* woodland occur on fertile, well drained soil with high rainfall, and trees are absent or rare in less fertile or drier sites (Specht 1969). Beard (1984) reports the occurrence of *Callitris* communities in fire-free sites, suggesting that the presence of trees is a consequence of succession as in other mediterranean-type ecosystems. However, in kwongan scrub heath older than 25 years, no species changes were detected relative to less mature communities in the same area. Post-fire succession in kwongan is considered to follow the initial floristic composition pattern, with declining species diversity as the vegetation develops (Bell *et al.* 1984).

1.4.4. Chile

Unlike all other mediterranean-type ecosystems, vegetation in the Chilean mediterranean-type climate region is not subjected to natural fires or any other large scale natural disturbance (Mooney & Cody 1977) and shrub recruitment is continuous in time. Clumps of shrubs do form, especially on mesic slopes, in a nucleation process which appears to be arrested by herbivory (Fuentes *et al.* 1984).

1.5. Study sites

The studies on the effects of fire were carried out in the Swartboskloof valley in the Jonkershoek valley (34° 00′ S, 18° 57′ E). The climate is mediterranean (Aschmann 1973); mean annual rainfall is 1620 mm, 58 % of which falls between May and August (Wicht *et al.* 1969). Summers are warm and dry, with droughts (periods in which daily rainfall never exceeds 0.5 mm) of 30 days or longer occurring every 4.2 years (Richardson & Kruger 1990). The floor of the valley is Cape granite and the upper reaches are formed by Peninsula Sandstone of the Table Mountain Group, forming talus slopes or colluvium in places (Söhnge 1988). The mouth of the valley is about 285 m a.s.l. and the ridge around the valley is 1200 m a.s.l. (Werger *et al.* 1972). The vegetation is predominantly mesic mountain fynbos with forest on the stream banks and rock scree slopes (McDonald 1988). Forest communities occupy 28 of the 373 ha of the Swartboskloof catchment (McDonald 1988). Prior knowledge that the catchment was to be burnt provided a unique opportunity for pre- and post-fire observations of the processes controlling forest distribution. The studies included the nature of the forest-fynbos boundary, the effects of fire on populations of forest species and forest structure and environment.

Forest patches in Swartboskloof have been shown to be representative of forest patches in the southwestern Cape with typical species/area relationships and a predominance of Afromontane species, but with considerable Cape and Tongaland-Pondoland elements (Masson & McKenzie 1989).

Swartboskloof was proclaimed a nature reserve in 1933 and protected from fire from then on. Prior to the 1987 fire, however, Swartboskloof was burnt in accidental fires in December 1942 and February 1958 (Werger *et al.* 1972). The distribution of forests in Swartboskloof has remained remarkably stable under this fire regime (Figures 1.1 to 1.3).

Assegaiboschkloof (Figure 1.4) was selected for studies on nucleation and the requirements for establishment of forest species in fynbos. At the time of the study in 1989, Assegaiboschkloof had not been burnt for about 50 years and the establishment of forest species was evident. Assegaiboschkloof is on the same equatorial slope of the Stellenbosch Mountains as Swartboskloof and approximately 4 km to the north-west. No rainfall figures are available, but the catchment is likely to be slightly drier than Swartboskloof as a result of its lower altitude and location closer to the mouth of the Jonkershoek valley (Wicht *et al.* 1969). Drier conditions in Assegaiboschkloof are further suggested by the conspicuous presence of *Dodonea angustifolia*, a species typical of drier slopes (Bond & Goldblatt 1984).

1.6. Practical implications

The degree to which the extent of forest is limited by habitat factors or disturbance regime will influence management (essentially manipulation of the fire regime) of areas containing forests. Two of the reasons for planned burning of fynbos are rejuvenation of the vegetation (avoidance of senescence) and reduction of fire hazard (Kruger & Bigalke 1984; Wilson 1985). The perceived need for rejuvenation follows the perception of a fynbos community as "senescent" once obligate reseeding large shrubs (particularly Proteaceae) have lost regenerative capacity (Bond 1980; Kruger 1984; Kruger & Bigalke 1984). Although the validity of the view that large obligate reseeding Proteaceae are incapable of regeneration

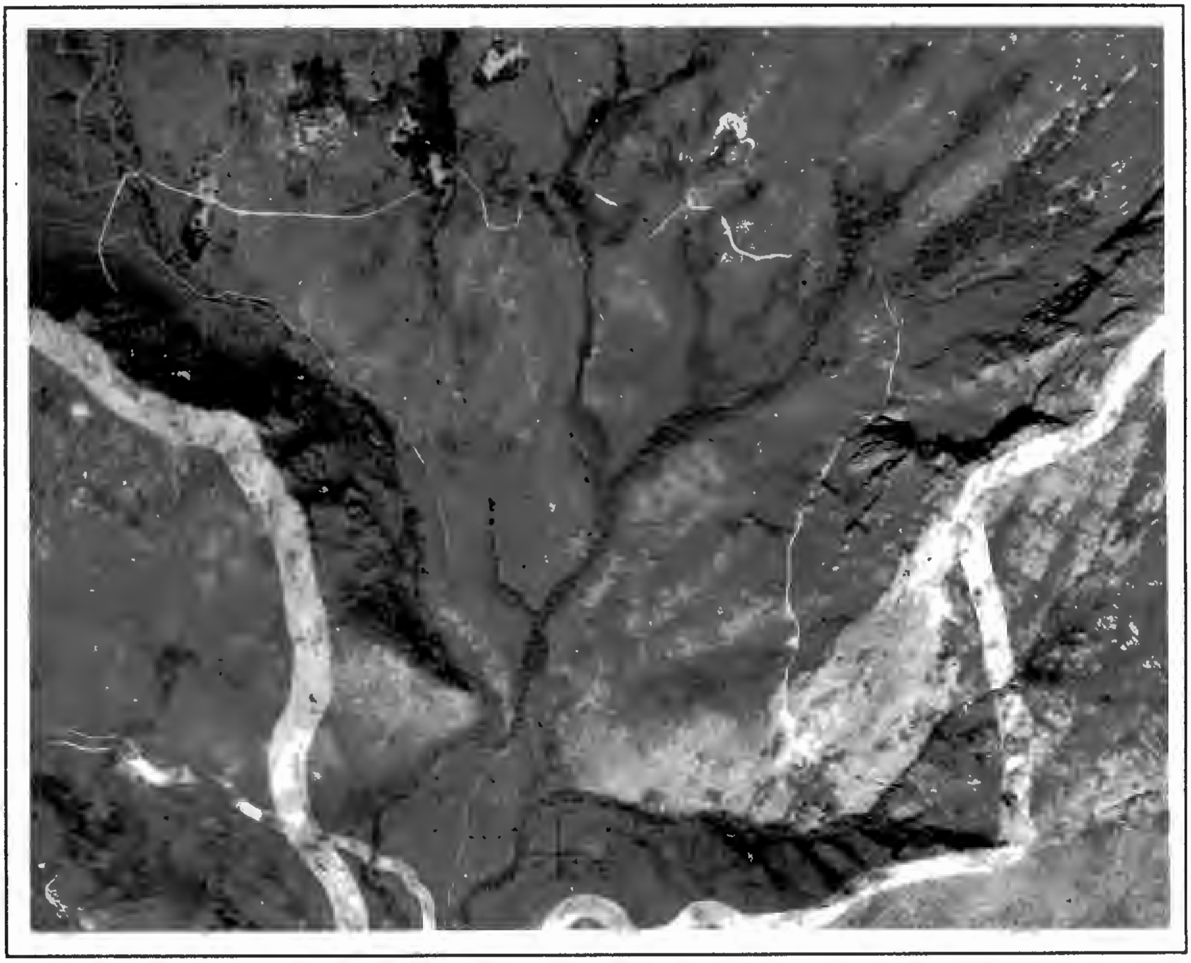

Figure 1.1. Aerial photograph of Swartboskloof taken in 1938, after proclamation of the Swartboskloof Nature Reserve in 1933 and protection from fire since then.

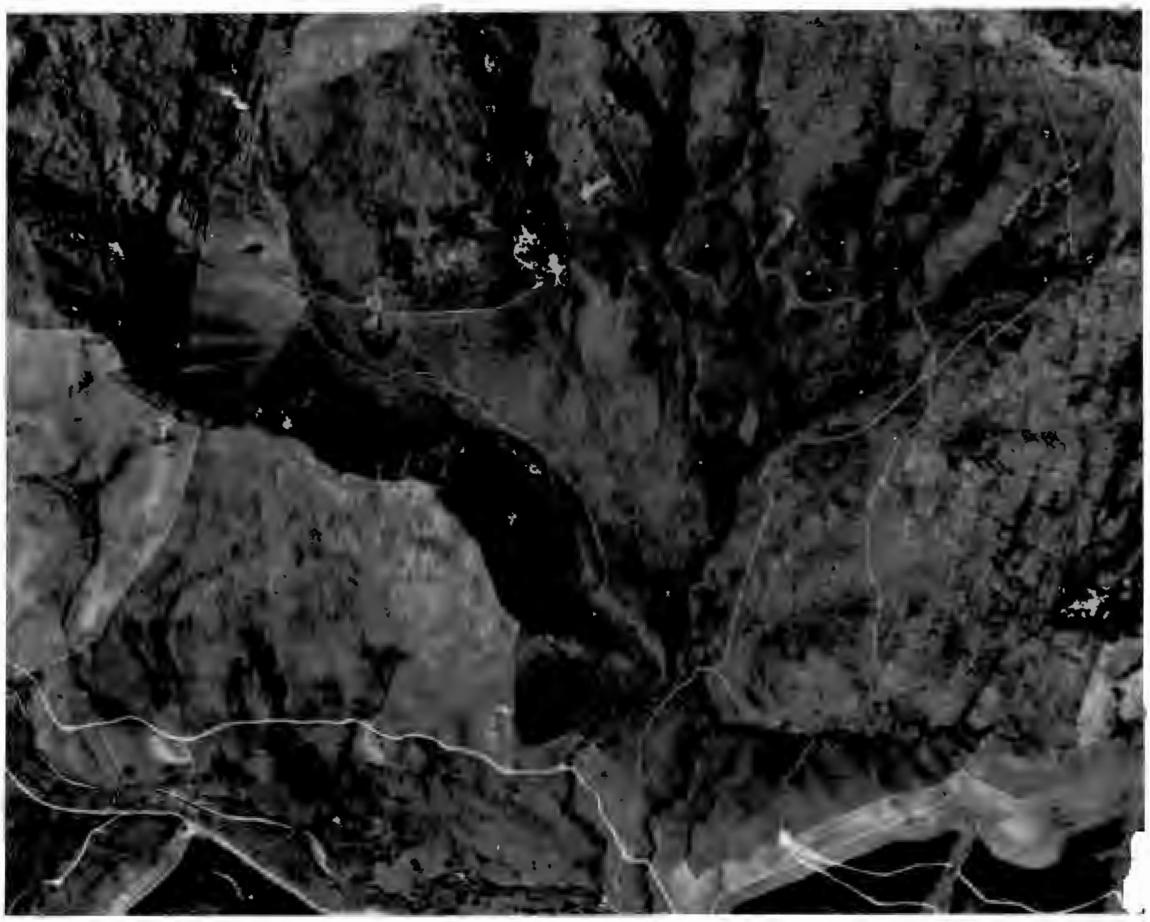

Figure 1.2. Aerial photograph of Swartboskloof taken in 1966. The area had been burnt previously in 1958.

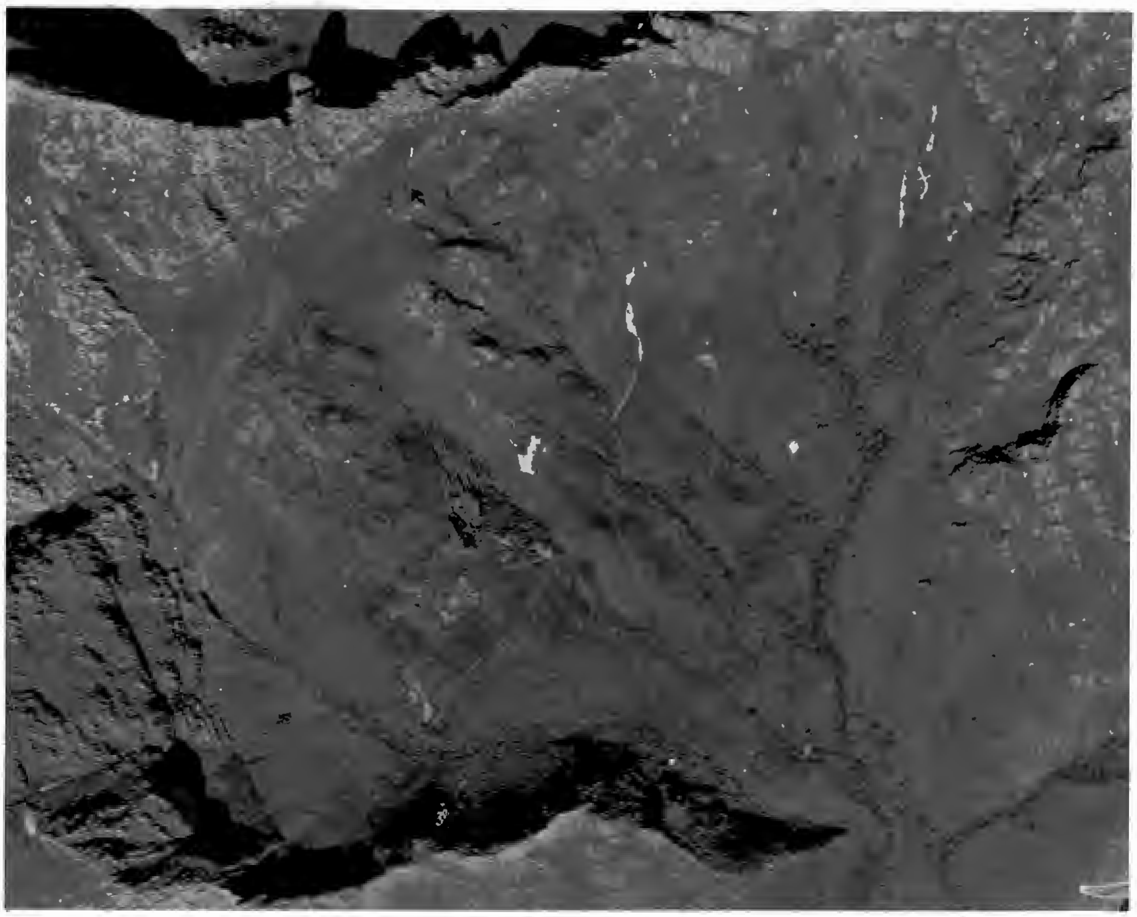

Figure 1.3. Aerial photograph of Swartboskloof taken in 1985. The area had not been burnt since the 1958 fire before Figure 1.2 was taken.

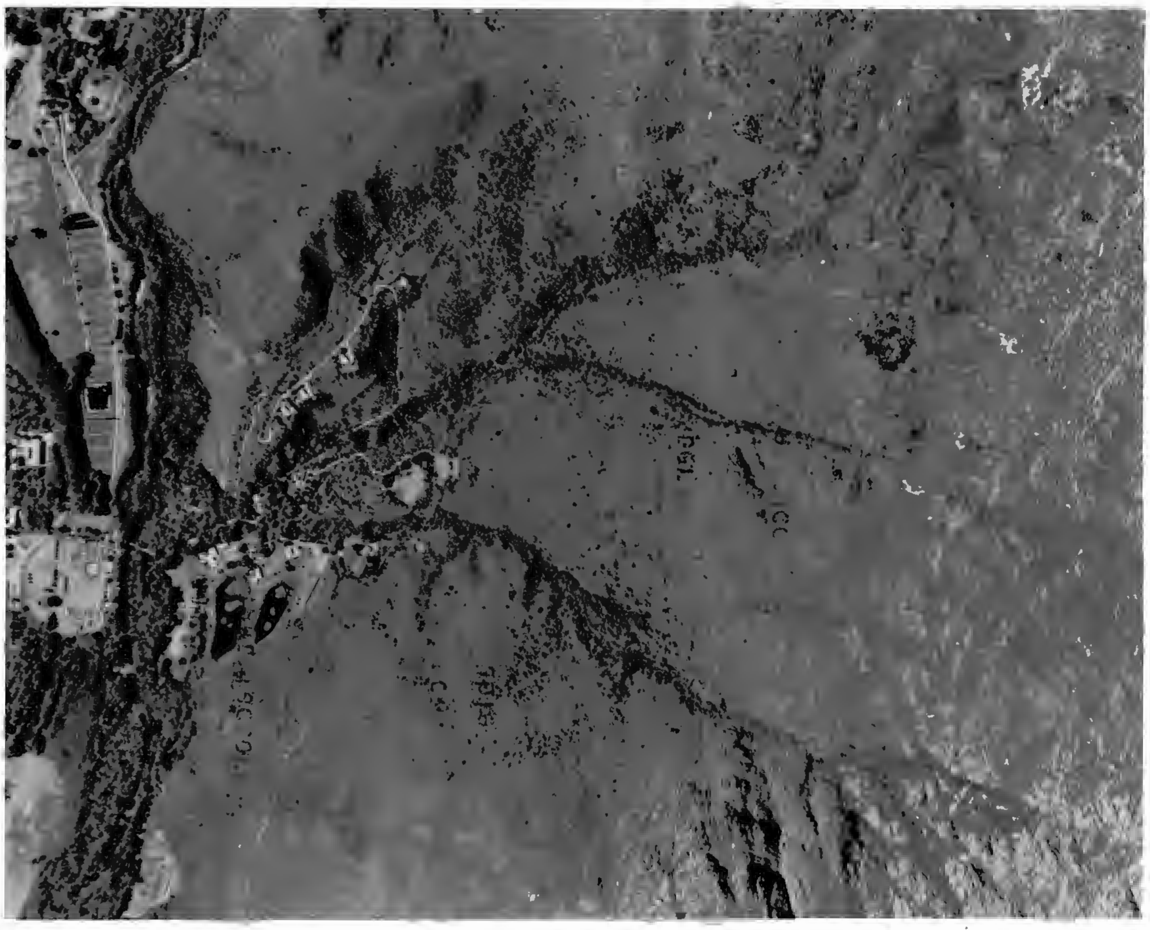

Figure 1.4. Aerial photograph of Assegaiboschkloof taken in 1985. The area had not been burnt for approximately 50 years at the time of the photograph.

without fire has been questioned in itself (Higgins & Manders in preparation), continued succession of the vegetation after the maturity of the slowest-to-mature obligate reseeding shrubs would repudiate the use of the term "senescent". Keeley (1986) expresses similar discomfort at the use of "senescent" and related terms for old stands of chaparral. Is it necessary to burn fynbos for rejuvenation purposes?

Forest species and forest communities are less likely to burn than fynbos species and communities (Van Wilgen *et al.* 1990). Therefore allowing forest species to become more dominant in some areas may go some way to achieving the management aim of reducing fire hazard.

PART 1

FIRE AND THE STABILITY OF FOREST-FYNBOS BOUNDARIES

CHAPTER 2

THE EFFECTS OF FIRE AND OTHER VARIABLES AS DETERMINANTS OF FOREST-FYNBOS BOUNDARIES IN SWARTBOSKLOOF, STELLENBOSCH, CAPE PROVINCE.

CHAPTER 2: THE EFFECTS OF FIRE AND OTHER VARIABLES AS DETERMINANTS OF FOREST-FYNBOS BOUNDARIES IN SWARTBOSKLOOF, STELLENBOSCH, CAPE PROVINCE.[1]

2.1. Abstract

Forests in the southwestern Cape are restricted to sheltered stream banks and patches of rock scree owing to protection from recurrent fire and the more favourable soil moisture conditions in these habitats. The effects of a prescribed burn on 17 March 1987 on the forest-fynbos boundaries in the Swartboskloof catchment are described. No evidence of erosion of the forest edge was recorded, although this could be ascribed to the low intensity of the fire. Soil properties, primarily pH and aluminium and available phosphorus levels, differed markedly between forest and fynbos. It is argued, however, that this is a result, not a cause of vegetation change. Light extinction levels and soil moisture availability after the fire were lower in the fynbos than in the forest, and are considered to preclude incursions of forest species into fynbos of a low post-fire age.

2.2. Introduction

The predominant vegetation in the Fynbos Biome of the southwestern Cape Province of South Africa is mountain fynbos (Campbell 1985). Forests occur in sheltered ravines, stream banks and patches of rock scree on all substrates where the annual precipitation is greater than 650 mm (Werger *et al.* 1972; McKenzie *et al.* 1977; Kruger 1979). Two hypotheses, based on soil moisture and fire, are advanced to account for the restricted distribution of forests. The first hypothesis relates to higher soil moisture in forested habitats and preclusion of forest species in adjacent vegetation by seasonal drought (White 1978). Similar arguments are used to explain the world-wide phenomenon of gallery forests where vegetation along watercourses differs in species composition from adjacent communities (Miller & Johnson 1986). Southwestern Cape forest sites are usually wetter than adjoining areas, but soil moisture has not

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[1] Publication status: Manders, P.T. 1990. Fire and other variables as determinants of forest/fynbos boundaries in the Cape Province. *Journal of Vegetation Science* 1: 481-490.

yet been shown to control the forest-fynbos ecotone (Van Daalen 1981; Masson & Moll 1987).

The second hypothesis is that the forests are remnants, reduced by climatic change or too frequent fires (McKenzie *et al.* 1977; Campbell *et al.* 1979; Moll *et al.* 1980). Succession to forest has been noted in Orange Kloof (mean annual rainfall 1227 mm) near Cape Town after 50 fire-free years (Masson & Moll 1987) and was evident in the Swartboskloof valley (mean annual rainfall 1475 mm) after 28 fire-free years. Therefore succession to forest may be possible in areas beyond riparian habitats, at least those with higher rainfall.

Optimum fire regimes for the promotion of forest may be inferred from the effects of fire on forest margins and on individuals of forest species which have established away from the forest. This study took advantage of prior knowledge that the Swartboskloof catchment was to be burnt, to make observations on the effects of fire on forest margins and individual plants in the vicinity of the forest margin. Various aspects of the habitat were quantified as a preliminary indication of changes in ecosystem processes across the boundary.

2.3. Study area

The study area is in the Swartboskloof valley, about 373 hectares in extent, in the Jonkershoek valley near Stellenbosch, Cape Province. The mouth of this fan-shaped valley is about 285 m a.s.l., and the highest peak in the ridge surrounding the valley is 1200 m a.s.l. The predominant vegetation is mesic mountain fynbos with forest communities along the streams and on the rock scree slopes (McDonald 1988). The climate is mediterranean (Aschmann 1973); the mean annual rainfall is 1620 mm, 58 % of which falls between May and August (Wicht *et al.* 1969). Summers are warm and dry, with 30 day or longer droughts (periods in which daily rainfall never exceeds 0.5 mm) occurring every 4.2 years (Kruger *et al.* 1988). The three major streams in the valley are perennial. Cape granite forms the lower floor of the valley. The upper reaches are formed by Peninsula Sandstone of the Table Mountain Group forming talus slopes or colluvium in places (Söhnge 1988).

Swartboskloof was proclaimed a nature reserve in 1933 and protected from fire. Accidental fires burnt the entire catchment in December 1942 and February 1958 (Werger *et al.* 1972).

Studies were carried out at three sites in the valley. The main study site (site A) was at an altitude of 425 m, situated on the main stream. The riparian forest here has been classified as *Rapanea melanophloeos* - *Cunonia capensis* high forest with a *Rhus angustifolia* - *Ischyrolepis sieberi* tall closed shrubland fynbos community adjacent to it (McDonald 1988). The forest was dominated by *Cunonia capensis* and *Ilex mitis* trees, and the fynbos by the shrubs *Protea neriifolia* with *P. repens*, *P. nitida* and *Cliffortia ruscifolia*. There was a transitional zone between the two vegetation types, with *Cliffortia cuneata*, *Rhus angustifolia* and *Halleria elliptica* shrubs predominant. The soils were derived from a mixed granite and sandstone talus scree.

Site B was situated further up the valley, on an ephemeral tributary of the Swartboskloof stream at an altitude of 595 m. The forest was not well developed, and there were forest-free gaps on the tributary below the site. Several large *Cunonia capensis* trees dominated the forest area, and the adjacent vegetation was dominated by *Protea neriifolia*. The forest was classified the same as that of site A, and the fynbos was classified as *Rhus angustifolia* - *Ischyrolepis gaudichaudianus* high closed shrubland (McDonald 1988). There was no transitional zone. The soils were derived from granite (Söhnge 1988).

Site C was situated on the edge of a scree forest in the centre of the valley at an altitude of 565 m. The site was approximately 100 m from the nearest stream which is ephemeral. Dominant species in the sparse scree forest (*Diospyros glabra* - *Rapanea melanophloeos* tall forest, McDonald 1988) were *Olinea ventosa*, *Maytenus acuminata*, *Olea europaea* ssp *africana* and *Podocarpus elongatus*. The scree was formed by a sandstone boulder scree and the fynbos vegetation, dominated by *Protea repens* and *P. neriifolia*, adjacent to the scree forest was on a sandstone talus slope (Söhnge 1988). The fynbos vegetation was classified as *Nebelia palacea* - *Erica sphaeroidea* high closed shrubland (McDonald 1988).

Swartboskloof was burnt in a prescribed burn on 17 and 18 March 1987. The fire was not very intense in the vicinity of site A owing to the mild weather, the damp evening and because the fire was burning downhill, and parts of the site did not burn. The unburnt patches in site A were ignited on 19 March and all the fynbos and transitional zone vegetation was burnt. The fire was also burning downhill, but with moderate intensity, when it passed through site B. The fire burnt uphill through site C and was very intense there. The forest did not burn, apart from scorching of the canopy, in any of the sites.

2.4. Methods

2.4.1. Plant cover

Five transects, each 20 m long and 2 m wide, were set out at site A, perpendicular to the boundary and extending from within the forest to within the fynbos community. The transects were separated by 3 to 20 m. The boundary and each 1 m x 1 m block in the transect were permanently marked. Similar transects of 2 m wide were located at sites B and C. Two transects were set out 5 m apart at site C. Three transects, 5 to 10 m apart were established at site B, but were shorter owing to the abruptness of the boundary and the steepness of the terrain. Two of these transects were 12 m long and the third 10 m long.

Pre-fire cover and population enumerations were carried out during January 1987. Data were collected for each 1 m^2 plot within the transects. Cover and height were estimated for each species present, including those not rooted in the plot. The height, diameter at 100 mm above the ground, and cover was recorded for all individuals of tree and shrub species rooted in the plot and each individual was marked. Those species which sucker profusely and do not have recognizable individuals (such as *Rhus tomentosus* and *Halleria elliptica*) were not included in the population enumeration. Observations on whether each plot had burnt were made on 25 March 1987. Full re-enumerations were carried out in March 1988, allowing sufficient time for resprouting, and germination and establishment of re-seeding plants.

All species recorded on the transects were categorized, according to consensus of five colleagues acquainted with the vegetation, as typical of the forest, fynbos or transitional zones. Each 1 m^2 plot on the transects was classified before and after the fire as forest or fynbos, according to which type contributed the greater cover. Plots where the cover of forest and fynbos species totalled less than 50 %, or where forest and fynbos cover were equal, were classified as transitional. Median positions of each class of plot along the transects (position 1 within the forest) were calculated for each site before and after the fire.

2.4.2. Populations

Movement of the forest-fynbos boundary was also determined by comparing pre- and post-fire distributions of tree and shrub species. Post-fire populations comprised new seedlings and surviving resprouts. The distance along the transect of individuals was taken as the midpoint of the plot on which the individual occurred.

The relationships between individual plant size, fire intensity and distance away from the forest edge were investigated using a chi-square frequency analyss on the most numerous species, *Cunonia capensis*, at site A. The fire intensity at each plant was judged on 25 March 1987, and plants were classed as not affected, scorched (leaves killed but intact) or burnt (at least the leaves burnt off). Distances along the transect were taken as the midpoint of the plot in which the individual occurred.

2.4.3. Photosynthetically-active radiation

Pre- and post-fire photosynthetically-active radiation intensity measurements were taken on 24 February and 23 March respectively. Ten point readings were taken with a quantum sensor every 2 m on the southern side of each transect, with the sensor placed vertically at ground level. Readings were taken between 11h00 and 13h30 on both occasions, and full radiation light readings were taken above the canopy twice in each transect. Extinction rates were calculated as the percentage of full radiation prevented from reaching the ground.

The vegetation in each 2 m section was classified according to the classification of the pair of plots in the section, as forest or fynbos (if both were classified as such) or as transitional. Differences in light extinction between the three vegetation classes, the effects of the fire on light extinction and differences between means were investigated using the GLM procedure for analysis of variance with the SNK (Student-Newman-Keuls) option (SAS Institute Inc. 1985a).

2.4.4. Soil

Soil samples were taken at 2 m intervals from the A horizon adjacent to the transects before the fire. Samples were air-dried and sieved to 2 mm prior to analysis. The vegetation type at each sampling point was classified and the analyses performed in a similar manner as in the light extinction study.

The seasonal availability of water along the transects was determined by sampling the top 5 cm of soil at 2 m intervals adjacent to each transect. Pre-fire samples were taken on 13 February and post-fire samples were taken on 27 March 1987 and monthly thereafter until 2 May 1988. Samples were sealed in plastic bags and analyzed for gravimetric water content.

Soil depth was measured after the fire at site A only as the slope at site B was too steep and meaningful measurements were not possible on the rock scree at site C. Depths were estimated by driving a steel stake to a maximum of 75 cm into the soil at three random points at 2 m intervals adjacent to each transect.

2.5. Results

2.5.1. Plant cover

The median post-fire positions of 1 m^2 plots classified as forest in site A moved three metres towards the fynbos ends of the transects from the pre-fire median, and the median position of the plots classified as fynbos moved two metres towards the forest ends of the transects (Table 2.1). No other significant differences between pre-fire and post-fire median positions of vegetation types were observed.

Table 2.1. Median positions of plots, classified according to vegetation type, along transects across the forest-fynbos boundary before and after fire in Swartboskloof. * = $P < 0.01$, median test (Zar 1974). Numbers of plots in each observation are given in brackets.

Site	Vegetation type	Median plot position (m)		
		Pre-fire	Post-fire	
A	Forest	5.0 (80)	8.0 (95)	*
	Transitional	9.0 (15)	13.0 (50)	
	Fynbos	15.0 (105)	13.0 (55)	*
B	Forest	4.0 (46)	5.0 (44)	
	Transitional	9.0 (3)	9.0 (7)	
	Fynbos	10.0 (19)	9.0 (17)	
C	Forest	4.5 (32)	5.5 (38)	
	Transitional	13.5 (6)	8.0 (2)	
	Fynbos	15.0 (42)	15.0 (40)	

2.5.2. Populations

The positions along the transects of post-fire seedling populations at site A differ from those of adult populations for some fynbos and transitional zone species which tended to move towards the forest ends of the transects (Table 2.2). *Cunonia capensis* individuals in the forest or on the edge of the forest were not affected by the fire or were scorched only (Table 2.3a). The survival of individuals was not independent of the initial effect of the fire (Table 2.3b). All burnt individuals died (effect contribution to chi-square = 17.6), but mortality did occur in those individuals which were not affected by the fire. Testing for association between initial effect, size of plant and survival produced a non-zero Mantel-Haenszel statistic, indicating a relationship between size and survival at some level of initial effect. Because no burnt plants survived, this could be meaningful for scorched plants only, and within this category there was greater mortality amongst the smaller plants (Table 2.3c).

Table 2.2. Positions along transects through the forest-fynbos boundary of pre-fire adult and juvenile tree and shrub individuals and post-fire seedlings and resprouts. * = $P < 0.05$ and ** = $P < 0.01$, median test (Zar 1974). Numbers of individuals in each observation are given in brackets.

Site	Species	Type	Pre-fire median position	Post-fire median position	
A	*Cunonia capensis*	Forest	6.5 (60)	7.5 (37)	
	Kiggelaria africana	Forest	3.5 (21)	3.5 (60)	
	Olea europaea	Forest	5.5 (14)	4.5 (9)	
	Podalyria calyptrata	Trans.	15.0 (22)	6.5 (60)	*
	Cliffortia cuneata	Fynbos	15.5 (64)	12.5 (365)	**
	Cliffortia ruscifolia	Fynbos	14.5 (45)	15.5 (41)	
	Phyllica pubescens	Fynbos	16.0 (12)	12.5 (464)	*
	Protea neriifolia	Fynbos	14.5 (35)	14.5 (90)	
B	*Kiggelaria africana*	Forest	3.5 (21)	3.5 (57)	
	Podalyria calyptrata	Trans.	2.0 (10)	7.5 (34)	
	Cliffortia cuneata	Fynbos	3.5 (5)	9.5 (35)	*
	Protea neriifolia	Fynbos	10.5 (11)	8.5 (27)	*
C	*Olea europaea*	Forest	7.5 (16)	4.5 (25)	
	Protea repens	Fynbos	17.5 (10)	17.0 (2)	
	Protea neriifolia	Fynbos	17.5 (5)	18.5 (13)	

Table 2.3. Frequencies of *Cunonia capensis* individuals in various categories showing a) the initial effects of fire at different distances along transects through the forest-fynbos boundary (chi-square = 78.4, $P < 0.001$), and survival and mortality in categories of b) the initial effect of fire on the plants (chi-square = 23.3, $P < 0.001$) and c) plant size (chi-square = 6.1, $P < 0.05$).

a)

Distance from forest end of the transect (m)	Initial effect of fire		
	Burnt	Scorched	No effect
0 - 8	1	8	51
5 - 8	11	29	0
> 8	3	4	0

b)

Outcome	Initial effect of fire		
	Burnt	Scorched	No effect
Survive	0	22	36
Die	15	19	15

c)

Outcome	Initial plant height		
	< 100 cm	100-200 cm	> 200 cm
Survive	6	8	8
Die	12	5	2

After the fire, almost all seedlings of fynbos and transitional zone species occurred in burnt plots (Table 2.4). When the species were grouped according to their vegetation type, the relationship between type and plot condition was significant at $P < 0.001$ for sites A and B (chi-square = 1305 and 152 respectively), and at $P < 0.001$ in a Fisher's exact test for site C.

Table 2.4. Numbers of seedlings on burnt and unburnt 1 m^2 plots after fire on transects through the forest-fynbos boundary.

Site	Species	Type	Regeneration	
			Burnt plots	Unburnt plots
A	*Cunonia capensis*	Forest	0	12
	Kiggelaria africana	Forest	8	36
	Aspalathus spicata	Trans.	631	2
	Podalyria calyptrata	Trans.	148	0
	Cliffortia cuneata	Fynbos	360	4
	Cliffortia ruscifolia	Fynbos	41	0
	Phyllica pubescens	Fynbos	462	2
	Protea neriifolia	Fynbos	90	0
B	*Cunonia capensis*	Forest	0	52
	Kiggelaria africana	Forest	6	39
	Podalyria calyptrata	Trans.	24	3
	Phyllica pubescens	Fynbos	78	6
	Cliffortia cuneata	Fynbos	26	9
	Protea neriifolia	Fynbos	17	10
C	*Olea europaea*	Forest	4	8
	Cliffortia cuneata	Fynbos	19	0
	Protea neriifolia	Fynbos	13	0

2.5.3. Photosynthetically-active radiation

The fire reduced the light extinction in all vegetation types at site A (Table 2.5). A similar pattern occurred at site B, but was less distinct owing to variance resulting from the abrupt boundary between forest and fynbos, and lower numbers of observations. Similar problems in pattern identification occurred in the scree forest at site C. Readings in the forest had high variance owing to the open nature of the forest on the scree. The fire did have a significant effect, however, on light extinction in the vegetation (transitional and fynbos) which burnt at this site.

Table 2.5. Extinction of photosynthetically-active radiation in the three vegetation types at sites A, B and C before and after fire. Means with the same letter superscript do not differ between vegetation types at a site at $P < 0.05$ (Student-Newman-Keuls test). * and ** denote differences between pre-fire and all post-fire observations in a vegetation type at $P < 0.05$ and $P < 0.01$ respectively. § denotes differences between burnt and unburnt post-fire observations at $P < 0.05$.

Site	Vegetation type	n	Photosynthetically-active radiation extinction (%)			
			Pre-fire	Post-fire		
				All	Burnt	Unburnt
A	Forest	170	95.8^{a}	86.8^{a**}	77.4^{a}	$90.7^{\S}$
	Transitional	80	77.7^{b}	50.4^{b**}	50.4^{b}	---
	Fynbos	250	64.2^{c}	50.5^{b**}	50.5^{b}	---
B	Forest	30	90.5^{a}	82.6^{a*}	83.9^{a}	81.7
	Transitional	30	72.9^{b}	84.6^{a}	84.6^{a}	---
	Fynbos	30	77.0^{b}	62.7^{b}	62.7^{b}	---
C	Forest	70	83.7^{a}	81.8^{a}	---	81.8
	Transitional	20	85.4^{a}	48.6^{b**}	48.6^{a}	---
	Fynbos	110	60.9^{b}	11.2^{c**}	11.2^{b}	---

2.5.4. Soil

Soils in the forest at site A were of a finer texture, less acidic, and were consistently richer in nutrients than the other vegetation types (Table 2.6). Aluminium levels were lower than in the fynbos, and very much lower than in the transitional zone. Trends at site B were not as clear, owing to fewer sampling points, shorter transects, less developed forest vegetation, and the more abrupt change from forest to fynbos than at site A (Table 2.7). Available phosphorus levels in the forest were significantly higher than in the other vegetation types.

Table 2.6. Characteristics of soils sampled in the three vegetation types at site A. * = $P < 0.05$, ** = $P < 0.01$ and *** = $P < 0.001$ (ANOVA). Means with the same letter superscript do not differ between vegetation types at $P < 0.05$ (Student-Newman-Keuls multiple range test).

Soil property	Vegetation type			
	Forest	Transitional	Fynbos	
	(n = 19)	(n = 11)	(n = 25)	
Coarse sand (0.5-2.0 mm) (%)	4.4^a	5.0^a	5.3^a	*
Fine sand (0.053-0.5 mm) (%)	41.2^a	49.6^b	48.5^b	***
Silt & clay (<0.053 mm) (%)	54.7^a	45.5^b	46.4^b	***
pH (water)	4.62^a	3.86^b	3.99^b	***
Organic carbon (%)	7.3^a	4.4^b	4.3^b	**
Total nitrogen (%)	0.3^a	0.2^b	0.2^b	*
Bray No 2 phosphorus (ppm)	12.8^a	6.8^b	6.0^b	***
Aluminium (ppm)	44.7^a	136.9^b	88.7^c	***
Potassium (ppm)	72.6^a	41.1^b	39.3^b	***
Calcium (ppm)	807.4^a	211.5^b	225.1^b	***
Magnesium (ppm)	270.3^a	67.2^b	88.7^b	***
Sodium (ppm)	34.3^a	19.8^b	21.6^b	**

Surface soil moisture was consistently higher in the sampling positions within the forest in site A (Figure 2.1). In the first summer after the fire the soil in the transitional and fynbos zones was particularly dry from December to March, whereas in the forest soils the moisture content dropped to similar levels in March only. A similar pattern was observed in site B.

Table 2.7. Characteristics of soils sampled in the three vegetation types at site B. * = $P < 0.05$ (ANOVA). Means with the same letter superscript do not differ between vegetation types at $P < 0.05$ (Student-Newman-Keuls multiple range test).

Soil property	Vegetation type			
	Forest (n = 10)	Transitional (n = 3)	Fynbos (n = 5)	
Coarse sand (0.5-2.0 mm) (%)	26.2^{a}	17.0^{a}	17.6^{a}	*
Fine sand (0.053-0.5 mm) (%)	43.6^{a}	39.4^{a}	35.6^{a}	*
Silt & clay (<0.053 mm) (%)	30.1^{a}	44.0^{b}	46.6^{b}	*
pH (water)	4.62^{a}	4.66^{a}	4.41^{a}	
Organic carbon (%)	7.1^{a}	7.3^{a}	8.4^{a}	
Total nitrogen (%)	0.3^{a}	0.3^{a}	0.3^{a}	
Bray No 2 phosphorus (ppm)	17.2^{a}	12.8^{b}	12.57^{b}	*
Aluminium (ppm)	89.1^{a}	75.0^{a}	124.6^{a}	
Potassium (ppm)	107.0^{a}	88.8^{a}	73.4^{a}	
Calcium (ppm)	285.4^{a}	175.8^{a}	131.4^{a}	
Magnesium (ppm)	168.4^{a}	117.4^{a}	53.8^{a}	
Sodium (ppm)	54.2^{a}	42.4^{a}	44.4^{a}	

The median soil depth of the five samples of three points each at the forest end of the site A transects was 65 cm, at all other sampling points the median depth was greater than 75 cm. There was no relationship between vegetation type at the sampling point and soil depth.

2.6. Discussion

It is not possible to generalize too far from this study as only three sites in one fire were studied. There is great spatial variability in a fire, however, even over a few meters, governed by fuel distribution and type (Hobbs & Atkins 1988). This gives some support for the acceptance of transects and even plots within transects as independent samples.

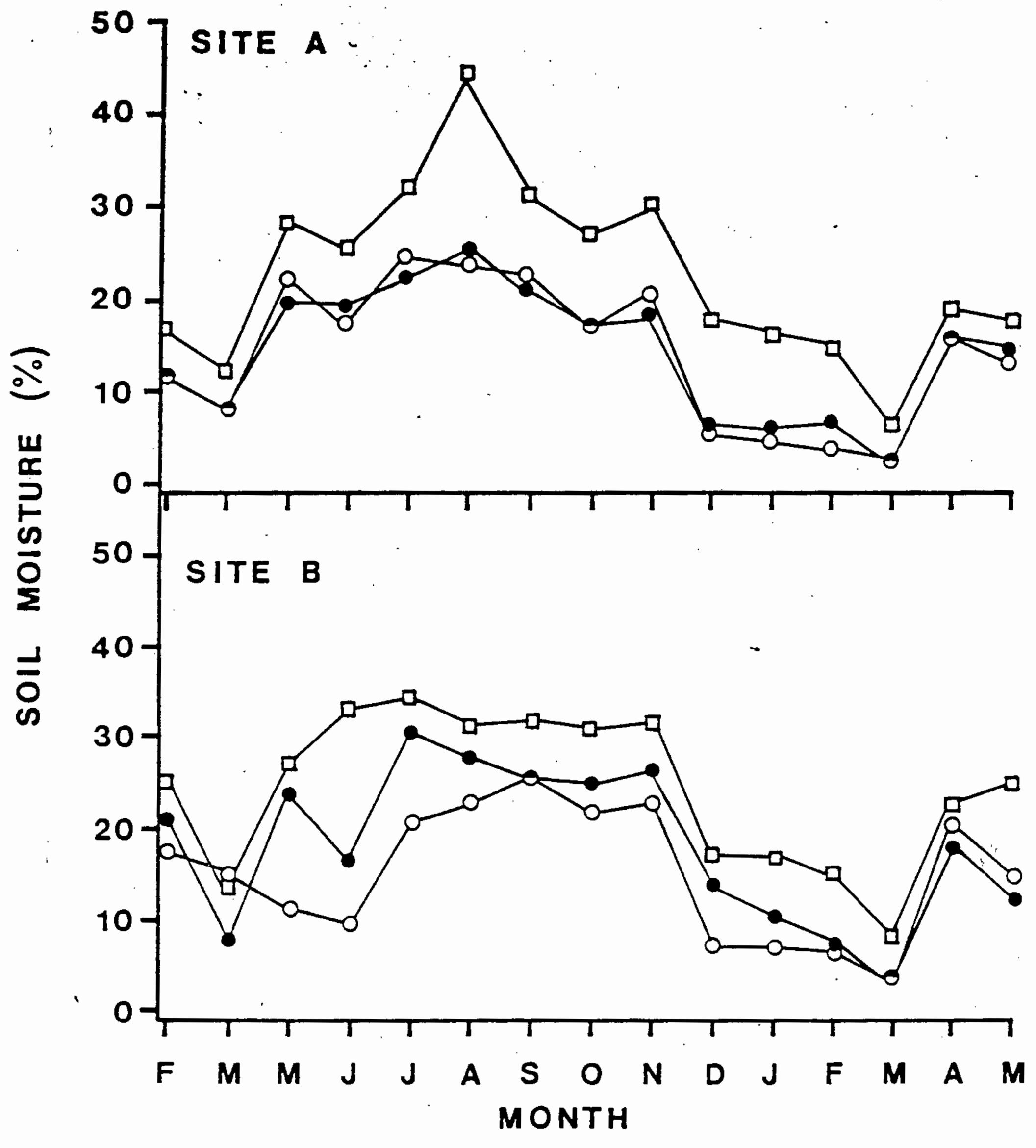

Figure 2.1. Pre-fire and monthly post-fire surface soil moisture in each of the three vegetation types, at sites A and B (□-□ = forest, ● -● = transitional zone, ○-○= fynbos).

Frequent reference is made to erosion of forest edges in fire (McKenzie *et al.* 1977; Campbell *et al.* 1979; Moll *et al.* 1980), yet no evidence was produced in this study to support this argument. Although it could be argued that the fire was not very intense at sites A and B, no erosion was noted at site C either, despite the high intensity of the fire there. In the main study site (A), however, there was an apparent extension of the other vegetation types into the transitional zone after the fire. The outward extension of the forest is caused by the early ascendancy and dominance in cover of resprouting forest species which had been relatively insignificant components on the plots before the fire. The apparent extension of fynbos towards the forest was a result of the often numerous seedlings of fynbos species which occurred in what had been the transitional zone. There is evidence, therefore, that the transitional zone was disrupted by the fire, and this may influence the effect of a further fire on the transitional zone and the forest, if it occurs while the transitional zone is in an altered condition. The increased number of plots classified as transitional after the fire reflects the number of plots with low cover and the numerous *Aspalathus spicata* seedlings which appeared in places after the fire.

Aerial photographs dating back to 1936 indicate that the extent of forests in Swartboskloof has remained very stable for over 50 years, during which time 2 fires occurred, at intervals far greater than the range of 9 to 15 years recommended for fynbos management (Kruger & Bigalke 1984). These observations and the minor effects of fire in the present study indicate that it may be the fire regime (specifically frequency, intensity and season of burn) which is likely to affect the extent of forests, rather than individual fires.

It would seem logical for survival of a resprouting forest species in fire to increase as the plant matures, or at least for there to be a critical lower size limit. This was not supported in the study of *Cunonia capensis*, where the apparent intensity of the fire at each plant determined the survival, and survival was correlated positively with plant size in partially damaged plants only. If this holds true for other forest species, it means that growth rates of forest species may not be used realistically to determine minimum fire-free intervals required for the promotion of forests.

The effects of processes in the maintenance of distinct communities were demonstrated. The pattern of seedling regeneration in burnt and unburnt portions of the transects reflects differential germination and establishment requirements related to habitat and the effects of disturbance. Differences in the light extinction recorded between communities before the fire could contribute to the maintenance of distinct communities. This applies mainly to prevention of fynbos development in forest through excessive shading. Forest development, however, is possible with increased shading in old fynbos vegetation. Removal of the fynbos canopy during fire will remove the facilitative influence of the shading.

Campbell (1985) and Campbell & Werger (1988) predict that high tree cover is associated with relatively nutrient-rich soils with high moisture availability. Nutrient levels and soil properties, especially pH, aluminium content and phosphorus content, do differ greatly between the vegetation types at site A. Forest soils, unlike the other vegetation types, have a pH higher than 4.5, below which aluminium toxicity is often apparent (Smith 1974 p. 172). Similar differences have been reported from the southern Cape (Lambrechts 1986).

The magnitude and trend of differences between the soils of forest and fynbos vegetation are site-specific, as demonstrated in this study and in comparisons with the results of Cowling (1984), van Daalen (1984), Lambrechts (1986) and Masson & Moll (1987), but differences do occur in each instance. The present study differed from these earlier studies in that the forest and fynbos samples were taken from within a few meters of each other. This indicates strongly that the differences are not related to differences in parent material, but result from different nutrient cycling processes within each community. This has been suggested earlier by the conclusion of Lambrechts (1986) that "under similar soil, terrain and climate conditions forest communities will maintain a higher nutrient status in the soils, especially in the surface horizons, compared with fynbos communities". The influence of changing species composition during succession to forest on soil properties has been noted elsewhere (Ellis & Graley 1987). Once different soil chemistry has been brought about by vegetation changes, such differences may affect the establishment abilities of species, thus maintaining the distinctness of the developing community.

Fire is the major perturbation to the cycling of nutrients in fynbos (Groves 1983), but forests do not burn each time the adjacent fynbos burns. One possible consequence is that phosphorus, which is deposited immediately after a fire in the ash and is often lost in surface run-off of ash particles (Rundel 1983), may be washed into unburnt riparian forest communities. Such a mechanism could explain some of the differences in nutrient status between communities.

The difference in seasonal patterns of soil moisture availability in forest and fynbos in this study is confirmed by observations of Kruger *et al.* (1988). They found that soil water potentials at a depth of 300 mm in a riparian zone in Swartboskloof did not reach -0.1 MPa in two summers. On a hillslope, however, soil water potentials at 300 mm were frequently more negative than -0.1 MPa. Such differences may preclude the invasion of forest species into fynbos, especially after fire when increased radiation reaching the ground will exacerbate the drier surface soil conditions.

The development of forest in fynbos areas would appear to be a stochastic process which makes it difficult to extrapolate the results of this study to other fires in other areas, but the processes involved should prove similar in most cases. There is no establishment of fynbos species in forest, but forest species may enter fynbos. The fynbos community, on the other hand, is favoured at the expense of forest communities by high frequency or severe fires as postulated by Campbell *et al.* (1979) and Moll *et al.* (1980). Recorded reductions in the distribution of forests since european settlement in the southwestern Cape would indicate, therefore, that there has been a change in the fire regime.

CHAPTER 3

QUANTIFYING SOIL SEED BANKS: A COMPARISON OF PHYSICAL SEPARATION AND SEEDLING EMERGENCE TECHNIQUES IN CAPE FYNBOS AND FOREST VEGETATION

CHAPTER 3: QUANTIFYING SOIL SEED BANKS: A COMPARISON OF PHYSICAL SEPARATION AND SEEDLING EMERGENCE TECHNIQUES IN CAPE FYNBOS AND FOREST VEGETATION.[1]

3.1. Abstract

Two techniques, physical separation and seedling emergence, were used to estimate soil seed banks in three plant communities in Swartboskloof, near Stellenbosch, Cape Province. Physical separation produced higher seed numbers (including non-viable seeds) than seedling emergence. The seedling emergence technique under-estimates seed banks of those species for which appropriate germination stimuli are not provided. For example large, hard-coated seeds which were found easily by physical separation achieved low percentage germination. However, seedling emergence revealed the presence of many small seeds which escaped detection in the physical separation. Adopting the greater estimate from either technique for each species gives a more complete array of species and seed numbers present. Although these figures are not reliable estimates of viable seed density, they provide a means for comparison among sites.

3.2. Introduction

A complete evaluation of the seed composition of soils is difficult, and the results may be biased by the evaluation technique employed (Roberts 1981). The two commonly used techniques are physical separation (after sieving or flotation) and placing soil under conditions suitable for germination and seedling emergence (Roberts 1981).

Estimates derived by physical separation are usually higher than those derived by seedling emergence (Roberts 1981; Vlahos & Bell 1986), as the seed bank includes non-viable seeds. This may be countered by testing the seeds for viability, for example by breaking the seeds to check for the presence of endosperm (Kramer & Johnson 1987), or using the tetrazolium test (Roberts 1981). Results of viability tests may be influenced by the

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time taken to search all soil samples, and may be impractical for large numbers of seeds. With the exception of legume seeds, viability of soil-stored seeds is often low, but varies greatly among species, with the test used to determine viability, and with the criteria used to determine whether a detected seed is recorded as a full seed (Roberts 1981).

The seedling emergence technique usually under-estimates the numbers of viable seeds present as the conditions for germination may not be optimal for all species. Some studies have attempted to provide a range of conditions (for example Pratt *et al.* 1984) or disturbance by stirring (for example Kramer & Johnson 1987) to maximize seedling emergence. Such measures, however, are unlikely to provide the full range of germination cues required by all the seed types present, especially those sampled from under a diverse flora. Species requiring specialized germination cues may be poorly represented in the seedling counts.

Seedling emergence and physical separation have been used in a single soil seed bank study (Naka & Yoda 1984) and physical separation has been used to evaluate the reliability of seedling emergence studies in submerged seed banks of prairie wetlands (Poiani & Johnson 1988). I used seedling emergence and physical separation to investigate soil seed banks across boundaries between riparian forest and fynbos (the fire-prone sclerophyllous shrubland of the south-western Cape) communities to determine the rôle of soil seed banks in the boundary dynamics. Both techniques were used to derive a better estimate of the presence of seeds than would be provided by either technique alone. This provided the opportunity for a comparison of the techniques in such an application. I did not attempt viability tests because of the large numbers of seeds involved and the wide diversity of seed types. Furthermore, many seeds may have lost viability between extraction from the soil and identification (up to 10 months). Committing seeds to tests with stains would have precluded identification of those seeds. Assessing viability by germination would underestimate viability in those seeds with unknown germination cues and would also prevent identification of those seeds which did not germinate.

3.3. Methods

One hundred and five soil samples were taken from the Swartboskloof valley in the Jonkershoek valley near Stellenbosch, Cape Province. The predominant vegetation is mesic mountain fynbos with forest communities along the streams and on the rock scree slopes (McDonald 1988). Samples were taken from 30 cm x 30 cm plots in fynbos, forest and transitional communities in February and March 1987. Plot boundaries were marked and the litter removed and bagged. The plot was then excavated in successive layers to 5 10 and 15 cm, with each layer forming a subsample. The surrounding litter and loose soil were moved away from the plot as it was excavated to minimize contamination of the subsamples. Many of the lower subsamples had reduced volumes owing to the presence of rocks.

Each subsample was halved by mass and one half was spread over 2 cm of damp acid-washed sand in a black plastic seedling tray (22 cm x 15 cm). One tray provided sufficient space for most subsamples following removal of the larger stones, but if the soil formed a layer exceeding 2 cm, additional trays were used. The trays were placed in a germination stand enclosed by 60 % shade cloth and with a fibreglass roof. Watering was done by an automatic sprinkler system, with the duration of irrigation varied, according to the season, in order to maintain dampness. Six trays containing damp acid-washed sand only were placed in the germination stand to determine whether seeds may be blown into the stand. Seedling emergence was recorded at least once weekly for the rest of 1987. No seedlings emerged after September 1987. Five individuals of each species were transplanted to pots for later identification by matching them with herbarium material.

The other half of each subsample was searched after being air dried and sieved through a series of sieves of decreasing mesh size to separate particles of similar size as an aid in searching. Particles smaller than 0.8 mm diameter were not searched.

Seeds were collected from a range of mature plants in Swartboskloof during the period of the study and used to identify seeds found in the soil. Seeds were classified into categories of hard (apparently typical of soil-stored seeds) or soft (apparently atypical of soil-stored seeds), or zoochorous (principally bird dispersed) in which apparent coat texture may not be related to properties of storage in soil and germination of hard-coated seeds may be stimulated by passage through the disperser's gut. Seeds of species which germinated but were not identified were classed as type unknown. Seeds of each species were classed in size categories of 1 = < 1 mm, 2 = 1 - 2 mm, 3 = 2 - 4 mm and 4 = > 4 mm diameter. Seed sizes of species found only in the seedling emergence technique were determined from field samples, herbarium records, or estimated from the seed size of similar species.

I used chi-square analysis to determine the efficacy of each technique in detecting the presence of different-sized seeds. This analysis was carried out on size classes 2 to 4, as seeds in category 1 may have passed through the 0.8 mm mesh and would not have been included in the soil searched for seed. I also used chi-square frequency analyses to determine the relationships between species and seeds found by each technique, soil depth layer and seed type (excluding those for which the seed type was unknown).

3.4. Results

Twenty-nine species, of which 21 were identified to at least the genus level, were found in the subsamples searched for seed (Table 3.1). The total of seeds found was 2227, averaging 76.8 per species. Seedling emergence from subsamples produced 41 species which were identified to at least the genus level. A further 15 species were noted as small seedlings, but none survived to the stage where positive identifications could be made. A total of 1557 seedlings emerged, averaging 27.8 per species. Only eleven of the positively identified species were found by both techniques. No seeds germinated in the control seedling trays of sterile sand placed in the germination stand.

Table 3.1. Numbers of seeds of species in all soil samples collected in Swartboskloof determined by physical separation (excluding size class 1) and seedling emergence techniques. Seed types: H = hard, S = soft, Z = zoochorous (bird dispersed) and U = unknown. Seed size categories are; 1 = < 1 mm, 2 = 1 - 2 mm, 3 = 2 - 4 mm and 4 = > 4 mm. Categories marked with asterisks are estimates.

Species	Growth form	Seed type	Seed size	Technique	
				Separation	Emergence
Arctotis semipapposa	Herb	S	2*	0	6
Argyrolobium lanceolata	Herb	H	2	65	24
Aspalathus cf *nivea*	Shrub	H	3	56	27
Aspalathus cf *spicata*	Shrub	H	3	49	0
Brachylaena neriifolia	Shrub	S	3	8	0
Cassytha ciliolata	Epiphyte	Z	3	75	39
Centella eriantha	Herb	S	3	0	44
Cliffortia cuneata	Shrub	H	4	359	21
Cliffortia polygonifolia	Low shrub	H	3*	0	2
Cliffortia ruscifolia	Shrub	H	3	111	18
Conyza scabrida	Herb	S	2*	0	132
Cotula turbinata	Herb	S	1*	-	1
Crassula fascicularis	Herb	S	1*	-	4
Crassula umbellata	Herb	S	1	-	1
Cunonia capensis	Tree	S	2	0	5
Diospyros glabra	Shrub	Z	4	19	0
Diosma hirsuta	Low shrub	H	3	0	1
Erica sphaeroidea	Low shrub	S	1	-	370
Gnidia sp	Herb	S	1*	-	10
Halleria lucida	Tree	Z	2	0	75
Hypochoeris radicata	Herb	S	1	-	9
Ilex mitis	Tree	Z	3	5	9
Indigofera sp	Low shrub	H	3	3	0
Indigofera cytisoides	Low shrub	H	3	15	11
Kiggelaria africana	Tree	Z	3	29	4
Metalasia muricata	Low shrub	S	2	0	95
Olea europaea ssp *africana*	Tree	Z	4	335	1
Olinea ventosa	Tree	Z	4	88	0
Othonna quinquedentata	Herb	S	3	0	10
Pelargonium myrrhifolium	Herb	S	3	0	3
Pelargonium tabulare	Herb	S	4	0	4
Pelargonium sp	Herb	S	2*	0	77
Pentaschistis sp	Graminoid	S	3	0	34
Peucedanum sp	Herb	S	1	-	7
Phylica pubescens	Shrub	H	4	168	75
Podalyria calyptrata	Tree	H	4	62	10
Protea neriifolia	Shrub	S	4	670	0

Table 3.1. Continued.

Species	Growth form	Seed type	Seed size	Technique	
				Separation	Emergence
Protea repens	Shrub	S	4	7	0
Protasparagus rubicundus	Herb	Z	3	2	0
Psoralea pinnata	Shrub	H	3	6	0
Rhus angustifolia	Shrub	Z	4	26	0
Rhus sp	Shrub	Z	4	0	3
Rubus rigidus	Low shrub	Z	2	0	31
Scirpus sp	Herb	S	1*	-	16
Selago spuria	Herb	S	2	0	17
Solanum nigrum	Herb	Z	2	0	28
Stoebe sp	Low shrub	S	1*	-	62
Sutera sp	Herb	S	1*	-	1
Tetraria sp	Graminoid	S	3*	0	14
Zaluzianskya benthamiana	Herb	S	1*	-	14
Zantedeschia aethiopica	Herb	Z	4	0	1
sp 1		H	3	19	0
sp 2 Restioid		H	2	9	0
sp 3		S	2	1	0
sp 4		S	3	2	0
sp 5		S	2	8	0
sp 6 Graminoid		S	3	2	0
sp 7 Fabaceae		H	3	27	0
sp 8 Restioid		H	2	1	0
sp 9		U		0	7
sp 10		U		0	10
sp 11		U		0	11
sp 12		U		0	3
sp 13 Asteraceae		S		0	66
sp 14 Asteraceae		S		0	3
sp 15		U		0	27
sp 16		U		0	16
sp 17		U		0	73
sp 18		U		0	8
sp 19		U		0	8
sp 20		U		0	5
sp 21		U		0	1
sp 22		U		0	1
sp 23		U		0	2

Physical separation was more successful for large seeds than small seeds, whereas the seedling emergence demonstrated the presence of many small seeds (Table 3.2). There was a relationship between the technique of seed bank estimation and the numbers of species and seeds found in each seed type (Table 3.3). More soft-seeded species and greater numbers of soft seeds germinated than expected, while more hard-seeded species and larger numbers of hard seeds than expected were found by physical separation. There was no relationship between technique and occurrence of species in soil layers, but the techniques differed in the estimation of the numbers of seeds in different soil layers (Table 3.4). Seedling emergence produced fewer seeds than expected from the litter layer and physical separation produced more seeds than expected from the litter layer.

Table 3.2. Numbers of seeds found by physical separation and seedling emergence techniques in all samples in size categories 2 to 4 (see Table 1) Numbers in brackets show cell contributions to chi-square. Chi-square = 1414, significant at $P < 0.0001$

Technique	Seed size			
	2	3	4	Totals
Separation	84 (268)	409 (457)	1734 (1351)	2227
Emergence	490 (724)	216 (14)	115 (294)	821
Totals	574	625	1849	3048

Table 3.3. Numbers of a) species and b) seeds found by physical separation and seedling emergence techniques in all samples in categories of seed types: H = hard, S = soft, Z = zoochorous. Numbers in brackets show cell contributions to chi-square. Chi-square values and levels of significance are given in square brackets below each table.

a)

Technique	Seed type			
	H	S	Z	Totals
Separation	14 (2.4)	7 (2.7)	8 (0.2)	29
Emergence	9 (1.6)	25 (1.8)	9 (0.1)	43
Totals	23	32	17	72

[$\chi^2 = 8.86$, $P < 0.01$]

b)

Technique	Seed type			
	H	S	Z	Totals
Separation	950 (87)	698 (118)	579 (23)	2227
Emergence	189 (140)	1005 (190)	191 (37)	1385
Totals	1139	1703	770	3612

[$\chi^2 = 595$, $P < 0.001$]

Table 3.4. Numbers of a) species and b) seeds found by physical separation and seedling emergence techniques in all samples in each soil layer. Numbers in brackets show cell contributions to chi-square. Chi-square values and levels of significance are given in square brackets below each table.

a)

Technique	Soil layer				
	Litter	0-5 cm	5-10 cm	10-15 cm	Totals
Separation	18 (.16)	26 (.03)	21 (.12)	18 (.05)	83
Emergence	29 (.08)	51 (.01)	44 (.06)	31 (.03)	155
Totals	47	77	65	49	238

[$\chi^2 = 0.55$, NS]

b)

Technique	Soil layer				
	Litter	0-5 cm	5-10 cm	10-15 cm	Totals
Separation	1261 (237)	658 (61)	186 (65)	122 (19)	2227
Emergence	133 (338)	859 (88)	381 (94)	184 (27)	1557
Totals	1394	1517	567	306	3784

[$\chi^2 = 930$, $P < 0.001$]

3.5. Discussion

This study supports the general trend of finding more seeds by physical separation than by seedling emergence (Roberts 1981; Vlahos & Bell 1986). This study revealed, however, that there is tremendous variation in the relative efficacy of the techniques among species and seed types. Each technique has limitations with regard to accuracy in assessing the composition of soil seed banks, and both are very time-consuming. The seedling emergence technique is less time-consuming than physical separation, and seedlings are usually easier to identify than seeds. Physical separation may provide data immediately, but is work-intensive and in this study it took longer than the seedling emergence technique owing to the large volumes of soil searched. Large seeds are more likely to be found by physical separation than small seeds, therefore this procedure alone will not provide a satisfactory estimate of seed banks for the entire flora in vegetation, such as fynbos, with many small-seeded species. Poiani & Johnson (1988) concluded that seedling emergence studies of submerged soil seed banks should be supported by physical separation to estimate numbers of seeds with unusual germination requirements. In another study (Kramer & Johnson 1987), the two techniques of seed extraction have been used in succession; the soil was searched and seeds broken to check for the presence of endosperm, and then the soil was spread out in a greenhouse to germinate the remaining seeds. Although this was a remarkably thorough investigation, several factors still could influence the accuracy of the results; for example did seeds lose viability in storage, initial wet sieving or searching processes? Although the soil was stirred to maximize germination, it is possible that some viable seeds remained dormant.

I conclude that realistic estimates of viable seed densities can be obtained only by physical extraction, followed by a reliable viability test. This is not possible for all species, however, and an acceptable accuracy is possible for selected (large-seeded) species only, and not for surveys of the entire seed flora. Estimates from any technique should be used to gauge the relative abundance of species, and not as accurate values of densities (Thompson 1986). In the present study more information can be revealed by combining the results from both techniques and adopting the greater estimate of the two techniques, than by relying on one technique alone. The value of such information does not lie in its estimation of viable seed stores, but in allowing comparison among sites or identification of changes with time.

CHAPTER 4

SOIL SEED BANKS AND POST-FIRE SEED DEPOSITION ACROSS A FOREST-FYNBOS ECOTONE IN SWARTBOSKLOOF, CAPE PROVINCE, SOUTH AFRICA

CHAPTER 4: SOIL SEED BANKS AND POST-FIRE SEED DEPOSITION ACROSS A FOREST-FYNBOS ECOTONE IN SWARTBOSKLOOF, CAPE PROVINCE, SOUTH AFRICA.[1]

4.1. Abstract

The relative sizes and composition of soil seed banks, the influence of fire and the post-fire deposition of seeds were investigated in a riparian forest and adjacent fynbos and transitional vegetation in Swartboskloof. Brief complementary studies of soil seed banks were conducted in poorly-developed forest and scree forest soils.

Numbers of species in each vegetation type were very similar, but there were fewer seeds in riparian forest soil than in the transitional and fynbos zones. These patterns were not repeated in poorly-developed forest and scree forest. No effects of fire on soil seed banks were detected. Forest soil had relatively large numbers of seeds stored at 10 to 15 cm deep, many zoochorous and few myrmecochorous seeds.

Anemochorous and ornithochorous seeds of forest species formed a major component of seed deposition within the transitional and fynbos zones in the first year after fire. The numbers of anemochorous forest seeds in the fynbos declined with distance from the forest edge. The deposition of ornithochorous forest seeds was less closely related to distance from the source, and was not exclusively associated with the presence of tall or fruit-bearing shrubs.

Regeneration after canopy-destroying disturbance in the forest is likely to emanate from the soil seed banks of pioneer species which now or previously occurred on forest margins. Seed availability does not appear to limit colonization of fynbos by forest species soon after fire.

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[1] Publication status: Manders, P.T. 1990. Soil seed banks and post-fire seed deposition across a forest-fynbos ecotone in the Cape Province. *Journal of Vegetation Science* 1: 491-498.

4.2. Introduction

In contrast to the fire-adapted fynbos (shrubland) vegetation dominating the south-western Cape Province, the small patches of forest in the region seldom burn. Forest communities are very distinct, and although forest precursors may colonize fynbos communities, no fynbos species occur in forest communities. The forest patches usually occur in sheltered ravines, stream banks and on patches of rock scree (Werger *et al*. 1972; Glyphis *et al*. 1978; McKenzie 1978; Kruger 1979). Restriction of forests to sheltered habitats is explained by the preclusion of forest species from the adjacent vegetation by seasonal drought (for example White 1978), or as the result of protection from too-frequent fires in the surrounding fynbos (McKenzie *et al*. 1977; Campbell *et al*. 1979; Moll *et al*. 1980).

Post-fire regeneration in the fynbos is by resprouting or from canopy- or soil-stored seedbanks (Kruger & Bigalke 1984), whereas almost all species in the forests usually resprout after fire. However, the adult plants in forest patches are sometimes killed in high intensity fires and there is a dearth of information on pyric succession in forests in the Cape (Kruger 1984). Since no forest species store seeds in the canopy for post-fire release, post-fire regeneration after destruction of the canopy must come from soil-stored seed banks or rely on colonization processes. Forest species may establish in fynbos vegetation, especially where soil moisture and nutrients are high (Campbell 1985) and usually late in the succession of fynbos (Kruger 1984). The presence of viable forest seeds in fynbos soils would indicate whether the process of colonization of fynbos adjacent to forest involves some storage of seeds in the soil, perhaps until suitable germination conditions occur.

Vegetation types, such as forest, with low frequencies of disturbance are unlikely to have extensive soil seed banks (Thompson 1978), particularly where the vegetation is not likely to be destroyed in the lifetime of its seeds (Young *et al*. 1987). Differences in reproductive modes and different degrees of reliance on soil seed banks, as determined by different selection pressures in the communities, will be reflected in the seed banks.

Canopy-stored seed banks were not considered in this study. Some fynbos species - particularly the large shrubs of the Proteaceae - accumulate seed reserves in the canopy of the plant, and these are released on the death of the adult plant - usually in fire. As such, these seeds are considered disturbance-related seed dispersal. Forest seeds form part, albeit transiently, of the soil seed bank.

Between disturbances, recruitment of forest species in the area adjacent to the forest (the transitional zone) and in fynbos areas is likely to be more from the seed rain than from the seed bank. For succession to proceed in the transitional and fynbos zones, therefore, there must be an allochthonous component in the seed rain (i.e. seeds that are produced in the forest and dispersed into these zones). Debate on colonization of fynbos by forest includes a facilitative effect (*sensu* Connell and Slatyer 1977) in which ornithochorous forest seed dispersal into the fynbos depends on the development of perches in the fynbos; such as fully-developed shrubs or fruit-bearing shrubs (Masson & Moll 1987; Knight 1988). This implied constraint would not, however, apply to anemochorous seeds.

I sampled soil seed banks before and after fire in a riparian forest and the adjacent fynbos and transitional zones in Swartboskloof near Stellenbosch to determine the distinctness of soil seed banks, the effect of fire and the nature of the components of the seed bank. Brief studies were made of soil seed banks in and next to a poorly-developed forest and a scree forest for comparison. The deposition of seed in and adjacent to the riparian forest was monitored for a year after the surrounding fynbos had been burnt to determine the nature of the seed rain in each community and whether there was an allochthonous component in the fynbos. I compared the patterns of dispersal of anemochorous and ornithochorous seeds to determine the effects different seed sources may have on rates of colonization.

4.3. Study area

The study area was in the Swartboskloof catchment in the Jonkershoek valley near Stellenbosch, Cape Province. The predominant vegetation was mesic mountain fynbos with forest communities along the streams and on the rock scree slopes (McDonald 1988). Details of the study sites are included in Manders (1990a).

Studies were carried out at three sites in the valley. The well-developed riparian forest at the main study site (A) was dominated by *Cunonia capensis* and *Ilex mitis* trees, and the fynbos by the tall shrubs *Protea neriifolia* with *P. repens*, *P. nitida* and *Cliffortia ruscifolia*. There was a transitional zone with shrubs of *Cliffortia cuneata*, *Rhus angustifolia* and *Halleria elliptica* predominant. The soils were derived from a mixed granite and sandstone talus scree (Söhnge 1988).

At site B the forest was not well developed and there was no transitional zone. Several large *Cunonia capensis* trees dominated the forest area, and the adjacent vegetation was dominated by *Protea neriifolia*. The soils were derived from granite (Söhnge 1988).

Site C was situated on the edge of a forest on a rocky scree slope. Dominant species in the sparse scree forest were *Olinia ventosa*, *Maytenus acuminata*, *Olea europaea* ssp *africana* and *Podocarpus elongatus*. The scree was formed by sandstone boulders with no surface soil and the adjacent fynbos vegetation, dominated by *Protea repens* and *P. neriifolia*, was on a sandstone talus slope (Söhnge 1988).

The vegetation communities are described fully in McDonald (1988). Swartboskloof was burnt in a prescribed burn on 17 and 18 March 1987. The forest did not burn, apart from scorching of the canopy, in any of the sites.

4.4. Methods

Fifteen pre-fire (February 1987) and ten post-fire (March 1987) soil samples were collected from each vegetation type (forest, transitional and fynbos) in site A. Five pre-fire and five post-fire soil samples were collected from each of the forest and the fynbos at site B. Only five post-fire soil samples were collected from each of the forest and the fynbos at site C. Sampling intensity was at a level similar to recent work on soil seed banks where 5 to 10 similar- or smaller-sized samples were used per site (Hill & Stevens 1981; Roach 1983; Mallik *et al*. 1984; Young *et al*. 1987).

A stretch of approximately 30 m of the boundary between the vegetation types was sampled at site A. The transitional zone samples were taken from up to 5 m from the edge of the forest canopy and the fynbos samples were taken 10 to 27 m from the forest canopy. At site B the distances were shorter owing to the steeper slope, and the fynbos samples were taken between 5 and 10 m from the forest edge. At site C the fynbos samples were taken 15 to 20 m from the forest canopy. Samples at sites B and C were spaced 1 to 2 m apart in each vegetation type.

Each sample was taken from a 30 cm x 30 cm plot. The boundaries of the plot were marked and the litter removed and bagged. The plot was then excavated successively to 5, 10 and 15 cm, and the subsamples from each layer were bagged separately. Many of the subsamples in the lower layers had reduced volumes because of the presence of stones. This factor was not corrected for.

Each subsample was halved on the basis of its mass and one half was physically searched for seeds. Seeds were identified from ripe seeds collected from plants in Swartboskloof during the study. The seed content of the other half was determined by spreading the soil in seedling trays and observing seedling emergence. Details of the methods are presented in Manders (1990b). Seedlings were identified by comparison with herbarium material. Where possible the dispersal mode of each seed species found was noted. Categories of dispersal mode used were: zoochory (mainly bird dispersed), anemochory (winged or plumed seeds), myrmecochory (ant dispersed), gravity (no apparent mechanism of dispersal), and unknown (mainly for germinated seedlings which could not be identified).

Manders (1990b) has compared the two techniques of seed bank evaluation used in this study and concluded that the greater of the two estimates for each species provides the most information on the array of species present. All analyses, unless stated otherwise, are based on the greater of the estimates for each species in each sample stratum. These figures are not accurate estimates of viable seed densities, but provide a basis for comparison between sites.

Ordinations of the samples at each site, based on the species and seed numbers present, were carried out to determine the degree to which the seed bank communities in each vegetation type are distinguishable, and the effects of fire on this. The ordination technique used was multidimensional scaling (Schiffman *et al*. 1981). A matrix of Euclidean distances was generated and input to the ALSCAL procedure of SAS (SAS Inst. Inc. 1985a). The Euclidean model was selected in the procedure, and a metric analysis with classical regression techniques was used (Young & Lewyckyj 1986).

Post-fire seed rain was sampled in 35 traps situated in each vegetation type at site A, in the same areas sampled for soil seed banks. The transitional zone samples were taken from up to 5 m from the edge of the forest canopy and the fynbos samples were taken 10 to 27 m from the forest canopy. Seed traps comprised plastic plant pots with an internal upper diameter of 196 mm, giving a catchment area of 0.03 m^2. The drainage holes in the base of each pot were covered with 1 mm nylon mesh to permit drainage while preventing seed loss. The traps were set out in each vegetation type at the beginning of April, after the canopy-stored seeds had been released from fynbos shrubs killed in the fire. Seeds were removed and counted monthly until June 1988, and identified by comparison with seeds collected from plants in Swartboskloof during the study. Intact berries of *Ilex mitis* (containing an average of 5.2 seeds each) which occurred mainly below the parent trees were considered apart from the bird dispersed seeds.

4.5. Results

Similar numbers of species occurred in each vegetation type at site A before and after the fire (Table 4.1). Seed densities, however, were higher in the transitional and fynbos zones than in the forest at both samplings. Species and seed densities at site B did not differ between vegetation types. Post-fire species and seed densities were not significantly different from the pre-fire densities at either site A or B, even when only the estimates from the seedling emergence technique were used. In the post-fire observations at site C, both species and seed densities in the forest were higher than in the fynbos.

The two-dimensional scaling of the sample similarities for the three sites (Figure 4.1) shows there are very few samples unique to one vegetation type, especially at site A where the transitional zone was also sampled. The most separation between the samples was found at site C. These models were not improved meaningfully by adding a third dimension. The patterns of association found by multi-dimensional scaling are explained by examination of the seed banks in each vegetation type, grouped according to the vegetation type associated with the parent plant (Figure 4.2). There is little conformity between vegetation type and seed banks.

Table 4.1. Numbers of a) species and b) seeds per soil sample in each vegetation type before and after fire at sites A and B, and after the fire at site C. Differences between two means were assessed with the Mann-Whitney *U* test, and between more than two means with the Kruskal-Wallis *H* test. NS = $P > 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

a)

SITE	VEGETATION	SAMPLING TIME				
		PRE-FIRE		POST-FIRE		
		Mean	*n*	Mean	*n*	
A	Forest	7.87	15	8.80	10	NS
A	Transitional	8.93	15	11.40	10	NS
A	Fynbos	9.13	15	8.80	10	NS
		NS		NS		
B	Forest	7.80	5	8.60	5	NS
B	Fynbos	7.00	5	8.80	5	NS
		NS		NS		
C	Forest	--		6.80	5	
C	Fynbos	--		2.60	5	
				**		

b)

SITE	VEGETATION	SAMPLING TIME				
		PRE-FIRE		POST-FIRE		
		Mean	*n*	Mean	*n*	
A	Forest	13.9	15	19.6	10	NS
A	Transitional	35.1	15	47.7	10	NS
A	Fynbos	34.7	15	36.7	10	NS
		***		**		
B	Forest	19.6	5	19.6	5	NS
B	Fynbos	16.4	5	24.0	5	NS
		NS		NS		
C	Forest	--		79.6	5	
C	Fynbos	--		3.2	5	
				***		

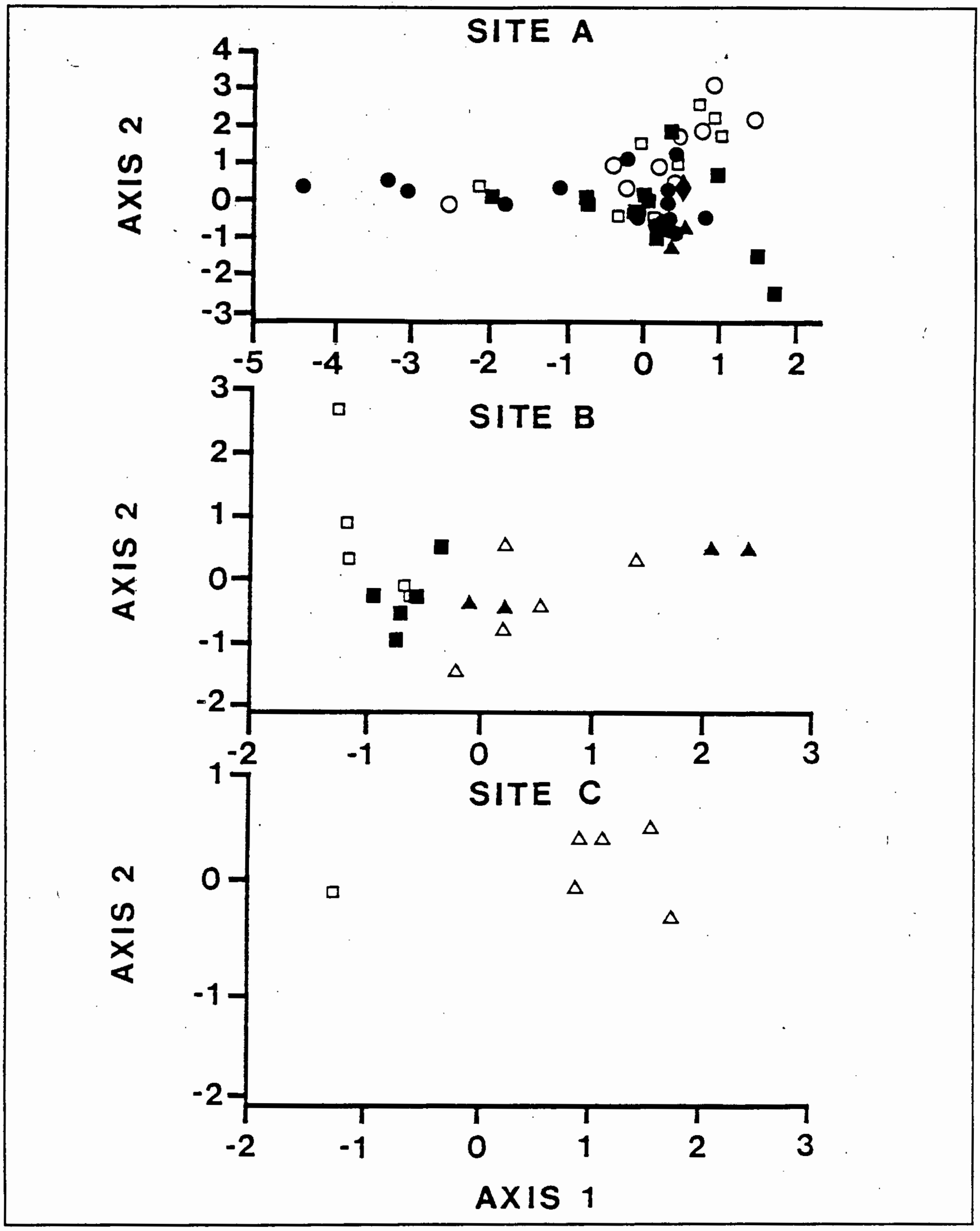

Figure 4.1. Two-dimensional scaling of the soil seed bank samples at three sites in Swartboskloof. △ = forest, ○ = transitional, □ = fynbos. Solid symbols show pre-fire observations, empty symbols show post-fire observations. The five observations in the fynbos at site C are superimposed.

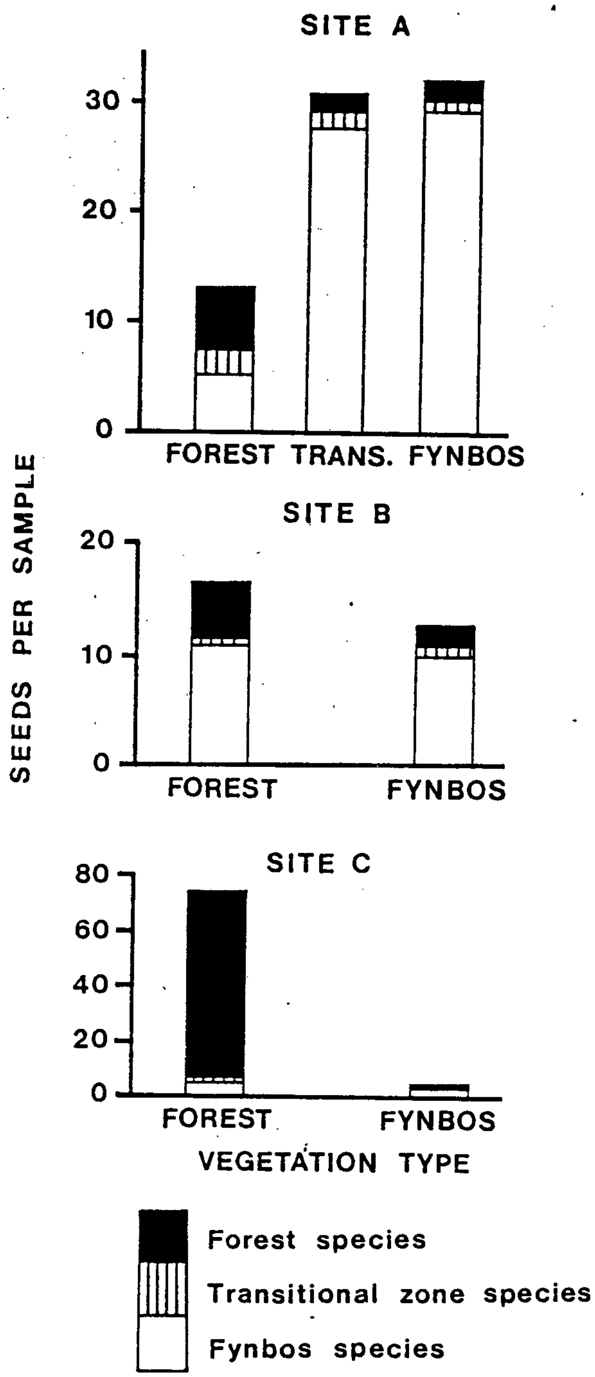

Figure 4.2. Numbers of seeds of forest, transitional and fynbos species in soils under each vegetation type at three sites in Swartboskloof.

Numbers of species in soil layers at site A were independent of vegetation type, but the numbers of seeds in each soil layer differed between vegetation type (Table 4.2). The relationship was largely accounted for by large numbers of seeds in the 10 to 15 cm layer in the forest. There was no relationship between vegetation type and numbers of species in different dispersal modes in soil seed banks at site A. The relationship between vegetation type and numbers of seeds in different dispersal modes (Table 4.3) was due to many zoochorous and few myrmecochorous seeds in the forest soil, many gravity dispersed seeds in the transitional zone and many myrmecochorous seeds in the fynbos. The forest also had many seeds with no known dispersal mode.

Table 4.2. Contingency table of numbers of seeds in soil layers in each vegetation type at site A. Numbers in round brackets show cell contributions to chi-square.

VEGETATION	SOIL LAYER				
	Litter	0 - 5 cm	5 - 10 cm	10 - 15 cm	TOTALS
Forest	44 (18)	138 (15)	121 (16)	101 (69)	404
Transitional	161 (2)	504 (16)	164 (2)	58 (17)	887
Fynbos	261 (16)	451 (1)	195 (1)	97 (2)	1004
TOTALS	466	1093	480	256	2295

[$\chi^2 = 176$, $P < 0.0001$]

The numbers of species of seeds deposited in the transitional and fynbos zones increases with time after the fire (Figure 4.3), reflecting the seed release phenology of the species in the area and the maturation of species which regenerated after the fire. The numbers of seeds are dominated by very few species (Figure 4.4). Even in the fynbos the seed rain in the post-fire environment is dominated by seeds from the forest species *Ilex mitis*.

Table 4.3. Contingency table of numbers of seeds in dispersal modes in vegetation types at site A. Numbers in round brackets show cell contributions to chi-square. Z = zoochory, A = anemochory, M = myrmecochory, G = gravity dispersed, U = dispersal mode unknown.

VEGETATION	DISPERSAL MODE					
	Z	A	M	G	U	TOTALS
Forest	124 (87)	86 (13)	5 (45)	97 (4)	92 (33)	404
Transitional	78 (25)	309 (1)	116 (3)	383 (28)	118 (1)	1004
Fynbos	109 (1)	324 (8)	187 (39)	187 (19)	80 (9)	887
TOTALS	311	719	308	667	290	2295

[χ^2 = 314, $P < 0.0001$]

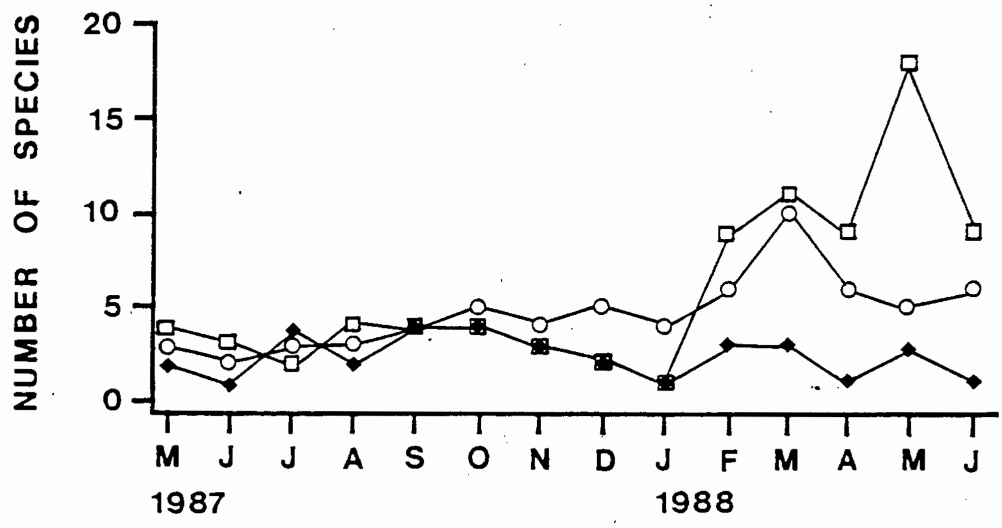

Figure 4.3. Numbers of species of seeds deposited monthly in seed traps in all vegetation types. ◆-◆ = forest, ○-○ = transitional, □-□ = fynbos.

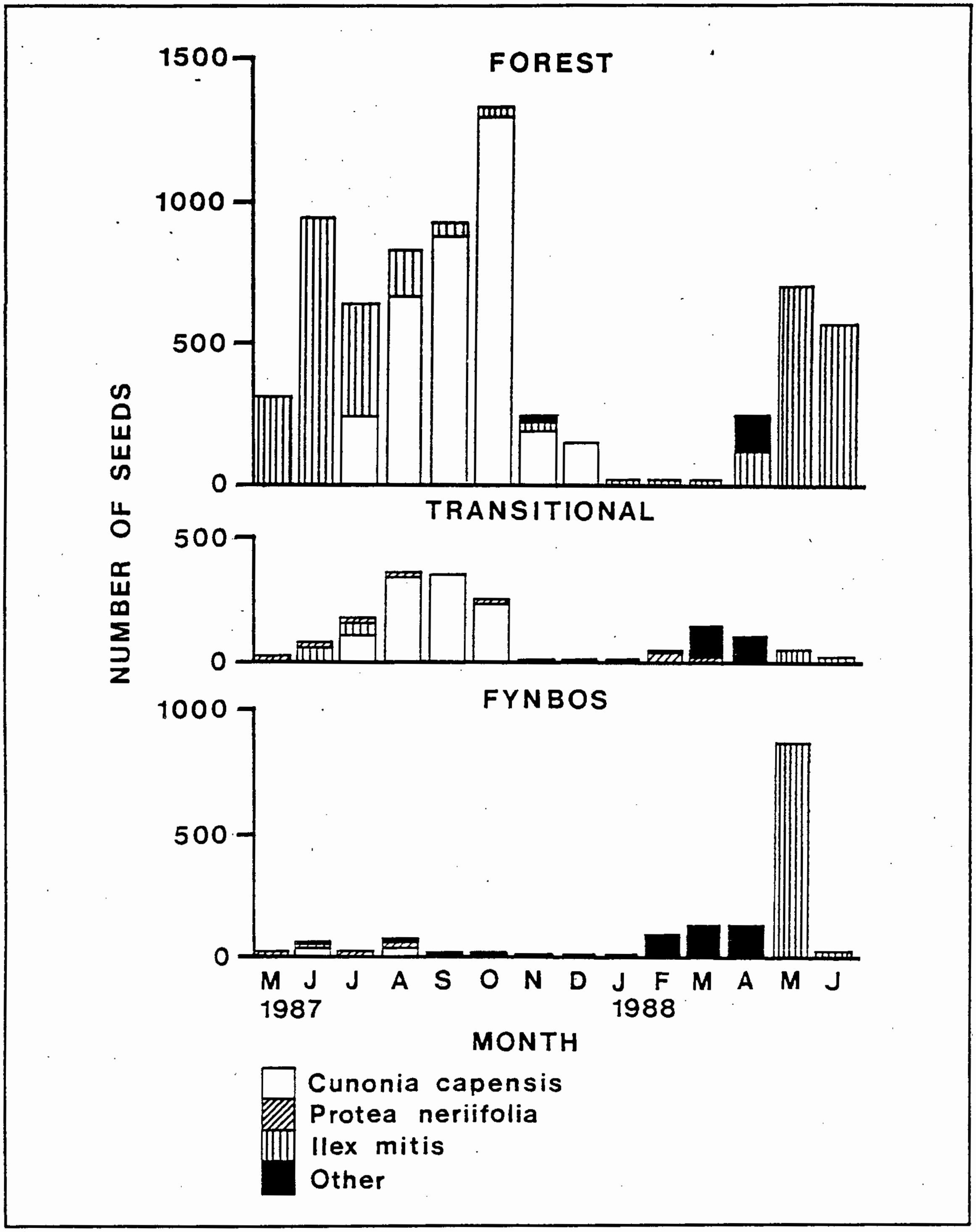

Figure 4.4. Numbers of seeds of tree and shrub species collected monthly in seed traps in each vegetation type.

Table 4.4. Mean numbers of seeds per trap and variance to mean ratios of selected tree and shrub species collected from May 1987 to June 1988 from 35 seed traps in each vegetation type. *Ilex mitis* berries are entire fruits which have dropped from the parent tree. Dispersal modes: O = ornithochory, A = anemochory, G = gravity.

SPECIES	DISPERSAL MODE	VEGETATION TYPE					
		FOREST		TRANSITIONAL		FYNBOS	
		MEAN	VAR/MEAN	MEAN	VAR/MEAN	MEAN	VAR/MEAN
Cunonia capensis	A	97.3	53.0	31.6	35.5	0.9	2.5
Protea neriifolia	A	--	--	3.9	5.4	3.2	4.4
Maytenus oleoides	O	0.5	1.2	2.6	20.2	0.4	4.4
Ilex mitis	O	81.8	61.6	5.7	33.8	25.8	508.3
Ilex mitis (berries)	G	9.9	12.4	0.03	1.0	0.06	2.0

The deposition of ornithochorous *Ilex mitis* seeds in the traps in the fynbos is highly clumped compared with the anemochorous species, but this is less apparent in the forest and transitional zones (Table 4.4). The nature of the dispersal from the forest and from the fynbos is reflected in the relationship between the numbers of seeds and distance from the forest edge. The abundance of *Cunonia capensis* declines exponentially with distance from the source, whereas the distribution of *Ilex mitis* is more episodic (Figure 4.5). The distribution pattern for *Maytenus oleoides* is masked by two trees of this species which occurred in the fynbos at the site. The distribution of *Protea neriifolia* seeds, with multiple sources in the fynbos, is given for comparison. Spearman rank correlation coefficients between seed numbers and distance from the forest were; -0.786 for *Cunonia capensis* (n = 46, $P < 0.001$), -0.013 for *Protea neriifolia* (n = 50, not significant), 0.189 for *Ilex mitis* (n = 42, not significant) and -0.011 for *Maytenus oleoides* (n = 21, not significant).

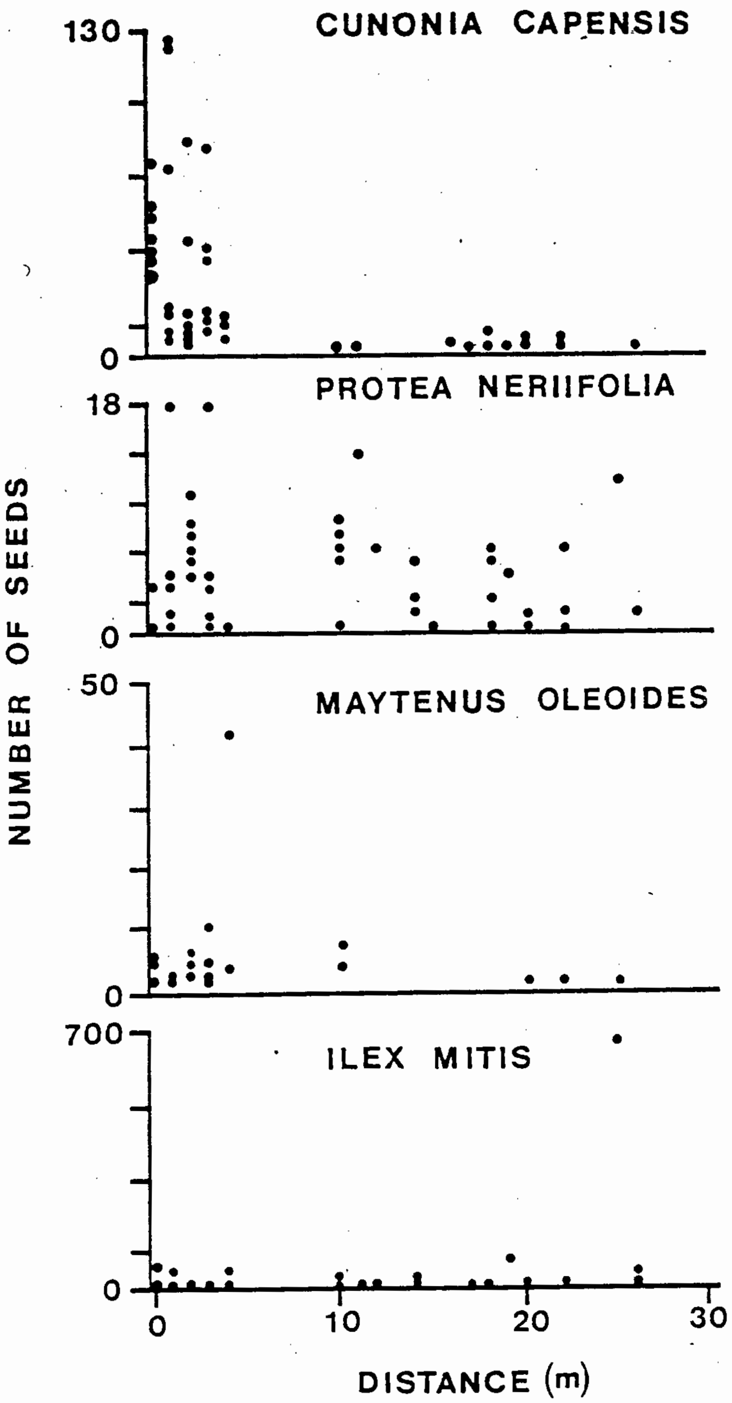

Figure 4.5. Numbers of seeds of selected tree and shrub species collected in seed traps in the transitional and fynbos vegetation at different distances from the edge of the forest canopy. Note that vertical axis scales differ.

The occurrence of seeds in seed traps in the forest (Table 4.5) was related to the species of tree directly above the trap. Seeds of the two predominant species, ***Cunonia capensis*** and ***Ilex mitis***, in the forest were concentrated under trees of the same species. The occurrence of seeds in the traps in the transitional and fynbos zones were also related to the type of perch above the trap. There were no seeds of ornithochorous *Ilex mitis* and ***Maytenus oleoides*** in the open in the transitional zone, but more than expected occurred in traps under branches (Table 4.6). In the fynbos the relationship was largely due to the large numbers of anemochorous ***C. capensis*** in the open and many ornithochorous *I. mitis* under branches of dead shrubs (Table 4.7). In May 1988, 675 *I. mitis* seeds were collected from one trap in the fynbos, situated under a single dead branch of ***Protea neriifolia***.

Table 4.5. Contingency table of the numbers of seeds of species recovered from seed traps in the forest from May 1987 to June 1988, indicating the relationship between the species of seeds deposited and the dominant species above each trap (perch species). *Ilex mitis* berries are entire fruits which have dropped from the parent tree. $\chi^2 = 1899$, $P < 0.001$. Numbers in round brackets show cell contributions to chi-square.

PERCH TYPE	*n*	SEED SPECIES				
		Cunonia capensis	*Ilex mitis* (berries)	*Ilex mitis*	*Maytenus oleoides*	TOTALS
Brabejum stellatifolium	11	844 (0)	55 (10)	706 (0)	5 (0)	1610
Cunonia capensis	8	1619 (535)	14 (68)	151 (499)	4 (0)	1788
Ilex mitis	14	812 (366)	281 (90)	1958 (309)	8 (0)	3059
Maytenus acuminata	2	227 (9)	8 (6)	128 (5)	1 (0)	364
	TOTALS	3502	358	2943	18	6821

Table 4.6. Contingency table of the numbers of seeds of species recovered from seed traps in the transitional zone from May 1987 to June 1988, indicating the relationship between the species of seeds deposited and the dominant species above each trap (perch species). $\chi^2 = 82.4$, $P < 0.001$. Numbers in round brackets show cell contributions to chi-square.

PERCH TYPE	*n*	SEED SPECIES				
		Protea neriifolia	*Cunonia capensis*	*Ilex mitis*	*Maytenus oleoides*	TOTALS
Forest precursor	12	92 (2)	628 (0)	112 (0)	40 (2)	872
Dead branch	18	35 (2)	314 (4)	89 (10)	50 (16)	488
Open	5	11 (1)	164 (11)	0 (23)	0 (10)	175
	TOTALS	138	1106	201	90	1535

Table 4.7. Contingency table of the numbers of seeds of species recovered from seed traps in the fynbos from May 1987 to June 1988, indicating the relationship between the species of seeds deposited and the dominant species above each trap (perch species). $\chi^2 = 308$, $P < 0.001$. Numbers in round brackets show cell contributions to chi-square.

PERCH TYPE	*n*	SEED SPECIES			
		Protea neriifolia	*Cunonia capensis*	*Ilex mitis*	TOTALS
Forest precursor	23	26 (59)	1 (0)	33 (2)	60
Dead branch	10	70 (10)	15 (7)	860 (3)	945
Open	2	17 (31)	17 (172)	11 (20)	45
	TOTALS	113	33	904	1050

4.6. Discussion

The clumping of species' seeds in soil seed banks was similar to that found by Thompson (1986) from which he recommended a minimum of 50 samples. Samples in Thompson's (1986) study were 7 cm x 7 cm, compared with 30 cm x 30 cm in this study, and he conceded that increasing sample size can improve the reliability of estimation. The sampling intensity in this study (25 samples per vegetation type at site A) is considered adequate, especially as it aims to compare between vegetation types, rather than estimate viable seed densities.

Thompson (1978) predicted that seed banks will decrease with increasing successional age and with decreasing disturbance intensity. This was seen in the lower seed banks in the riparian forest which does not burn at the same frequency as the fynbos and transitional areas. The lack of pattern at site B is ascribed to the short distances between vegetation types, and the reversal of the trend in the scree forest at site C was because the samples were collected from where litter had accumulated in depressions between rock surfaces.

Typically, pioneer and forest margin species are more common than forest climax species in soil seed bank, but do not germinate beneath the undisturbed canopy (Whitmore 1983; Hopkins & Graham 1983; 1984; Putz & Appanah 1987). Seeds suitable for lengthy soil storage are likely to remain intact when buried at depth, whereas more transient components are likely to occur in the upper soil layers. There was a large component of seeds stored at depth in forest soil. These were mainly hard seeds of the Fabaceae which have dispersed into the forest and which may contribute to regeneration after fires severe enough to kill forest trees. The low soil seed banks of local climax species (predominantly *Ilex mitis* and *Cunonia capensis)* may be explained by the rapidly germinating, short lived seeds, as noted for many species in Australian lowland tropical forests (Hopkins & Graham 1983).

No evidence of stimulation or depletion of fynbos or transitional zone soil seed banks was discerned in this study, as the hard-seeded species were found easily and germinated readily in pre- and post-fire samples. Soil seed banks have hitherto received little attention in the fynbos, but could play a rôle in post-fire succession. Fires vary in extent, intensity, frequency and duration, producing a range of selection pressures on reproductive strategies, including soil stored seeds (Vlahos & Bell 1986; Bell *et al*. 1987). This may contribute to the species richness of the south-western Cape by contributing a further dimension (response to fire) to the range of transient regeneration niches (*sensu* Cowling 1987).

Processes related to seed dispersal and soil storage differed in importance between the fynbos and the well-developed forest at site A. Myrmecochory is not well represented in the forest, whereas zoochory is far more important in the forest than in the fynbos. Although such differences may contribute to the maintenance of distinct communities, no absolute exclusion of species was detected. The lack of distinction between soil seed banks of the communities indicates that seed dispersal crosses community boundaries and that factors such as the requirements for germination and establishment are important in the maintenance of distinct communities.

Seed dispersal of forest trees is not related to fire. Vegetation adjacent to the forest had a considerable input of allochthonous seeds from the forest species. Most importantly, this occurs immediately after disturbance for both anemochorous and ornithochorous species. Colonization of fynbos by forest species soon after fire, therefore, is not limited by seed dispersal.

The regeneration of later successional species in a community of earlier successional species is strongly related to the distance from the seed source (McClanahan 1986). This was evident for the anemochorous *Cunonia capensis* which usually establishes near the forest edge, but may establish remotely from the seed source, as noted elsewhere for anemochorous species (Read & Hill 1983). The deposition of ornithochorous *Ilex mitis* was less uniform and had little relation to distance from the source at the scale measured in this study. This pattern conforms to the predictions of McClanahan & Wolfe (1987) that the availability of perches affects ornithochorous seed occurrence more than distance from the source. Most bird species in the forest are visitors in response to abundant fruits or are opportunistic feeders, and there is frequent movement of birds between forest and fynbos (Richardson & Fraser in press). Therefore, frequent dispersal of ornithochorous seeds beyond the forest is probable. The general decline in seed numbers away from the source (especially in relation to the numbers deposited within the forest) is probably related to the decreasing activity of bird dispersers with distance from the source (Holthuijzen & Sharik 1985).

Previous studies (Masson & Moll 1987; Knight 1988; Janzen 1988) suggest that forest species established away from the forest attract bird dispersers and result in increased densities of ornithochorous seeds in their vicinity. Complexity of perches affects bird abundance and diversity, and consequently the degree of seed deposition (McClanahan & Wolfe 1987). This study demonstrated, however, that one or two dead branches can serve as a perch, and effective perches need not be a fruiting species or a large complex tree, especially in areas fairly close to the seed source.

If colonization of fynbos by forest species soon after disturbance is not limited by the dispersal of forest seeds into the fynbos, there are two explanations for the current understanding of succession to forest in fynbos (*sensu* Kruger 1984). The first possibility is that forest precursors escape notice during early stages of fynbos succession because of their small size and slow growth. Alternatively, colonization by forest species is limited by requirements for processes (such as germination or seedling establishment) which occur later in the life cycle than seed dispersal. Then the facilitation model of succession (Connell & Slatyer 1977) applies to fynbos succession to forest, but involves more than the provision of perches. Facilitative effects could include direct facilitation in the provision of shading or litter, or the release of inhibitory factors such as competition by early successional herbaceous species.

PART 2

SUCCESSION

CHAPTER 5

COLONIZATION OF CAPE FYNBOS COMMUNITIES BY FOREST SPECIES

CHAPTER 5: COLONIZATION OF CAPE FYNBOS COMMUNITIES BY FOREST SPECIES.[1]

5.1. Abstract

Forest and mountain fynbos communities intermingle the southwestern Cape, but are quite distinct in terms of species composition and community processes. Fires occur frequently in fynbos communities, but seldom in the forest communities which are usually restricted to sheltered ravines or stream banks. Forest species establish in fynbos between fires, and may predominate eventually in exceptional circumstances. We proposed a conceptual model for the development of forest in fynbos and examined processes in the model related to nucleation and the establishment of forest species. Germination and establishment requirements of forest and fynbos species were examined to determine causes of community distinctness.

Nuclei of forest species dominated by fruiting species had more seedlings of forest species and more species than nuclei dominated by non-fruiting species. Reciprocal sowings showed that forest and fynbos species have similar germination requirements, but the seedlings establish in their appropriate communities only. Germination studies demonstrated that soil moisture is not the only factor limiting establishment of forest species, and that enhanced soil nutrient levels, litter and a canopy of vegetation influence seedling survival even in wet conditions. Field studies, to characterize the habitats in fynbos vegetation in which forest seedlings are able to become established, showed forest seedlings to be associated with a tall herb layer and vegetation cover greater than 50 %. Seedlings were invariably under or within 1 m of a perch, which could be a fruiting forest species or a fynbos shrub.

Recruitment of fynbos species is coupled with disturbance whereas recruitment of forest species in fynbos is associated with nucleation, habitat amelioration and occurs in the absence of fires. The lack of

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coupling of recruitment of forest species with disturbance results in the exclusion of forest from most areas of the fire-prone Fynbos Biome.

5.2. Introduction

Boundaries between vegetation types are influenced by many biotic and abiotic factors, particularly those affecting movement of propagules across the boundary and those determining whether the propagules survive and establish. Boundaries shift if populations of immigrant species develop and convert one vegetation type to the other. Colonization involving vertebrate seed dispersal is characterized by the formation of nuclei of one vegetation type within the other (Janzen 1988). We examine the factors determining community boundaries in the mountain fynbos (shrubland) of the southwestern Cape Province, where patches of forest occur, usually in sheltered ravines or stream banks. The two intermingling vegetation types are quite distinct with respect to species composition and community processes. Fires occur frequently in fynbos communities, but forests rarely burn. Fynbos species rarely occur in forest communities, but forest species are capable of colonizing fynbos communities in some areas, usually after prolonged absence of fire (Kruger 1984; Manders 1990a). Colonization by forest species may eventually change the nature of the community from fynbos into forest (Masson & Moll 1987). This process of forest development is more rapid where soil moisture and nutrient levels are higher (Campbell 1985).

The dispersal of seeds of forest species (the first phase in establishment) into the fynbos has been documented for anemochorous and ornithochorous seeds (Knight 1988; Manders 1990c). Anemochorous forest seeds, such as those of *Cunonia capensis* and *Brachylaena neriifolia*, are deposited uniformly (not under perches) with decreasing density away from the source (Manders 1990c). The timing of anemochorous seed dispersal is not related to disturbance by fire as the source plants are not killed by fire and movement into the fynbos does not depend on the development of perches or the avifauna community. Given the uniform occurrence of suitable sites for establishment, colonization by anemochorous species is likely to be in the form of a uniform wave from the edge of the forest (see for example Read & Hill 1983).

The seeds of 40 % of forest species are dispersed by vertebrates, mainly birds, whereas less than 10 % of fynbos species are vertebrate dispersed (Knight 1988). The dispersal of ornithochorous seeds into fynbos is considered to be dependent on the presence of perches for the avian dispersers (Knight 1988). The abundance of seed deposited from perches is related to the complexity and size of the perch (McClanahan & Wolfe 1987), with an overall decrease in deposition of ornithochorous seeds with distance from the forest edge, related to the decreasing activity of avian dispersers (Holthuijzen & Sharik 1985). Previous studies in the fynbos have indicated that complexity and height of perches are not critical, especially near the forest margin (Manders 1990c). This may be because common avian dispersers such as the olive thrush (*Turdus olivaceus*) and Cape robin (*Cossypha caffra*) frequent undergrowth, rather than tall perches, and have small home ranges. In this manner, the colonization pattern of ornithochorous species will have a component of wave-like development from the forest edge. Other avian dispersers, such as rameron pigeons (*Columba arquatrix*), are attracted to distinct perches only, especially forest species such as *Maytenus oleoides*, in the fynbos. Large fynbos shrubs may provide perches for birds which are not obligate frugivores such as the southern boubou (*Laniarius ferrugineus*) and the fiscal flycatcher (*Sigelus silens*). Establishment of forest individuals under remote perches leads to nuclei of forest development (Janzen 1988) and succession proceeds through nucleation and the eventual coalescence of the nuclei (Yarranton & Morrison 1974)

Given the arrival of seed, the factor inhibiting the establishment of forest species in the fynbos is believed to be the inability of forest seedlings to survive summer water deficits (White 1978). Biotic factors, especially competition from vigorous herbs and grasses in the regeneration niche (Richardson & Cowling In press) and mammalian herbivory (Bigalke 1979) are notably weak in the fynbos.

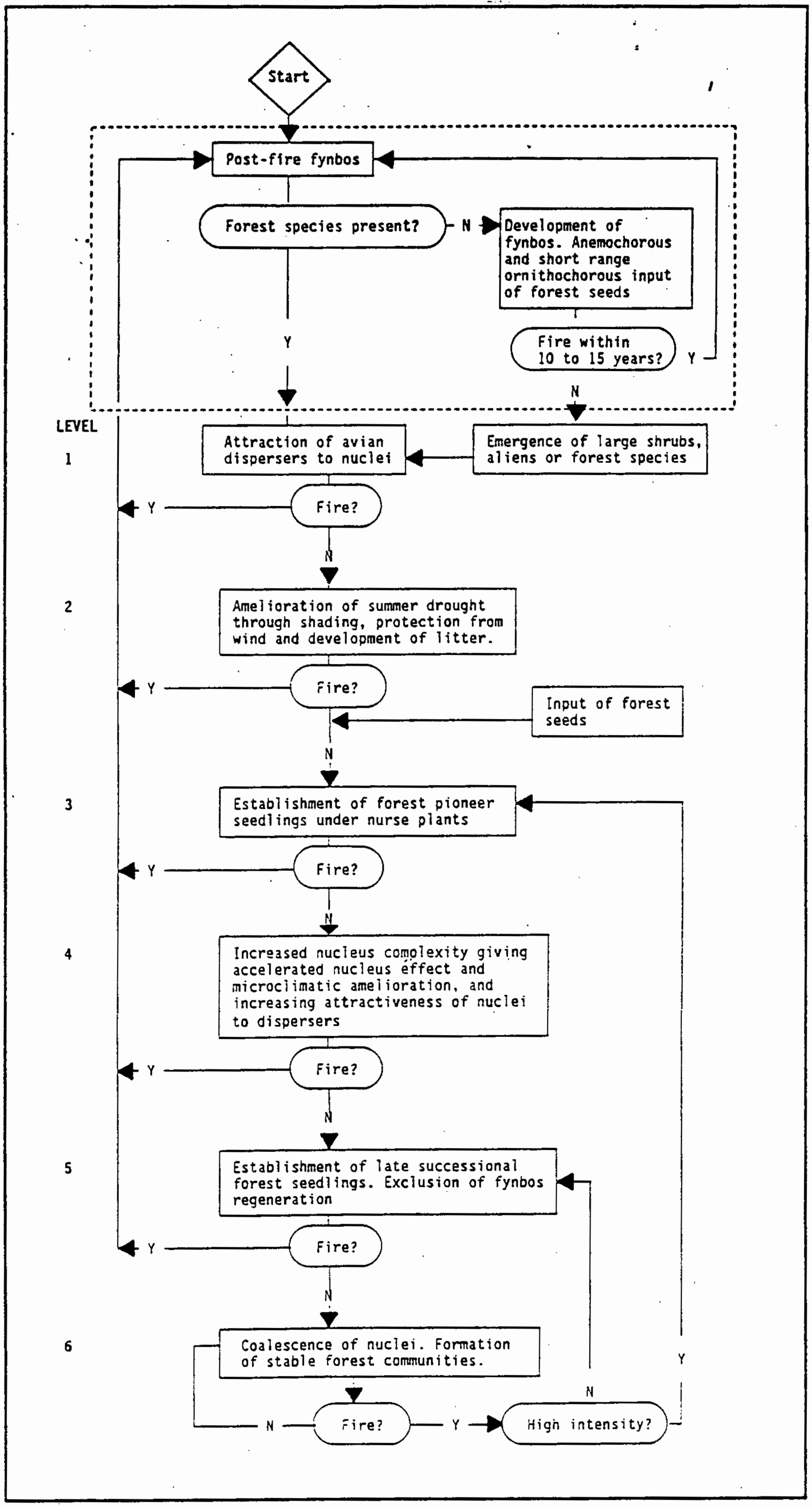

Figure 5.1 A conceptual model of the development of forest species within fynbos communities. The model assumes the availability of forest seeds. Post-fire age increases as the model proceeds from the start situation.

We propose that the development of forest in a fynbos area follows the conceptual model in Figure 5.1. According to this model the successional mechanism involved in the development of forest in fynbos is facilitation (*sensu* Connell & Slatyer 1977). We suggest that this involves the increased attractiveness of the area to avian dispersers and the amelioration of the inhibitory effects of seasonal water deficits as the vegetation develops. Although some forest species such as *Maytenus oleoides* usually survive fire and provide permanent perches, we suggest that the overall attractiveness of the vegetation to avian dispersers is related to the growth of fynbos shrubs. Factors ameliorating summer drought probably include the mulching effects of litter, 'nurse plants' (protection from radiation and wind) or decreased competition for water owing to reduced herbaceous cover. Growth and maturation of forest species at a perch site provide positive feed-back by adding to the complexity of the perch and to the attractiveness to avian dispersers. The community may eventually reach a state where the predominance of forest species reduces the effects of fire and the forest community becomes stable.

The processes preceding level 1, the stability of communities in level 6 and the input of forest seeds in the model in Figure 5.1 have been verified (Knight 1988; Van Wilgen *et al*. 1990; Manders 1990a; 1990c). This study was aimed at identifying those processes involved in the establishment of forest and fynbos species which maintain forest community distinctness, and at identifying important processes in the colonization of fynbos. The attractiveness of nuclei to avian dispersers (level 1) and the effects of nursery trees on forest seedling establishment (level 3) were determined by studying the composition of forest nuclei in a mature fynbos community. Levels 2, 4 and 5 of the model involved climatic amelioration, establishment requirements of forest species and the preclusion of fynbos establishment in forest communities. These processes were investigated in reciprocal sowings, experimental germination studies and characterization of the habitat of forest seedlings in the mature fynbos community.

5.3. Study sites

Forest nuclei and forest seedling habitats were studied in 50 year-old fynbos in Assegaiboschkloof (33° 59′ S 18° 55′ E) and reciprocal sowings were conducted in forest and newly-burnt fynbos in Swartboskloof (34° 00′S 18° 57′E). These catchments are secondary valleys in the Jonkershoek Valley near Stellenbosch, Cape Province.

The vegetation of both valleys is predominantly mesic mountain fynbos with forest communities along the streams and on the rock scree slopes. The climate is mediterranean (Aschmann 1973); mean annual rainfall at Swartboskloof is 1620 mm, 58 % of which falls between May and August (Wicht *et al.* 1969). Summers are warm and dry, with droughts (periods in which daily rainfall never exceeds 0.5 mm) of 30 days or longer occurring every 4.2 years (Richardson & Kruger 1990). Assegaiboschkloof is on the same equatorial slope of the Stellenbosch mountains as Swartboskloof and approximately 4 km to the north-west. No rainfall figures are available, but the catchment is likely to be slightly drier than Swartboskloof as a result of its lower altitude and location closer to the mouth of the Jonkershoek valley (Wicht *et al.* 1969). Drier conditions in Assegaiboschkloof are further suggested by the conspicuous presence of *Dodonea angustifolia*, a species typical of dry rocky slopes (Bond & Goldblatt 1984) and which is not present in Swartboskloof. Cape granite forms the lower floor of the valleys. The upper reaches are formed by Peninsula Sandstone of the Table Mountain Group resting on the granite, and forming surface deposits of talus slopes or colluvium in places (Söhnge 1988).

5.4. Methods

5.4.1. Forest nuclei

Eighty-one nuclei or plants considered to be potential nuclei were surveyed in 10 ha of Assegaiboschkloof. Diameters of the nuclei were measured, and the number and size (basal diameter and height) of the predominant plants and all individuals of forest species were noted. Species such as *Rhus tomentosa*, *R. angustifolia* and *Myrsine africana* which produce numerous ramets were not considered as individuals and were not included in the analysis. Nuclei were classified according to whether they were dominated by species with fleshy fruit likely to attract avian seed dispersers or by species without fleshy fruit such as fynbos shrubs or alien trees such as pines.

Relationships between nucleus size and numbers of forest seedlings and species were interpreted by spline interpolation of the plotted data. The cubic spline minimizes a linear combination of the sum of squares of the residuals of fit and the integral of the square of the second derivative (SAS Inst. Inc. 1985b).

5.4.2. Reciprocal sowings

Seeds of *Protea neriifolia, Protea repens, Protea nitida* and *Kiggelaria africana* were planted in forest (unburnt), fynbos and a transitional zone (both burnt sites) the day after the Swartboskloof catchment was burnt on 17 March 1987. A grid of ten rows of ten pegs at 1 m centres was set out in each site, and three seeds of each species were planted approximately 5 mm deep near each peg. Seedlings were counted monthly until May 1988. Thirteen replicates of 24 seeds of each species were planted in seedling trays in a daily-watered germination stand at the same time as the field sowings to determine potential germination. Germination was recorded twice a week until the end of October 1987, at which time there had been no germination for over 30 days.

5.4.3. Germination studies

The effects of soil moisture, soil type, shading and litter on the establishment were determined by cultivation of forest and fynbos species in seedling boxes measuring 290 by 300 mm and 100 mm deep at the Jonkershoek Forestry Research Centre. Each species was grown in fynbos soil, forest soil and forest soil with litter. The forest soil was collected from a forest site in the Jonkershoek valley and the fynbos soil was collected from the Franschhoek Valley 15 km away (Table 5.1). Replicates with forest soil and litter had approximately 20 mm of litter, comprising mainly *Cunonia capensis* leaves collected from a forest floor in the Jonkershoek valley, placed on top of the soil. The litter was held in place by four strands of string. Each soil type was represented in the open and under the shade of a *Harpephyllum caffrum* tree to simulate a forest canopy, and in each position one set of replicates was watered three times a week and the other set was dependent on rainfall. Light extinction under the *Harpephyllum caffrum* was 93.9 % (SEM = 0.60) based on 510 point readings with a quantum sensor. There were five boxes of fifty seeds in each combination of treatments for each species. Comparisons between treatments were based on means of the five replicates. Seeds were sown when the ripe seeds were available; *Protea neriifolia, Protea repens, Protea nitida* and *Kiggelaria africana*, were sown on 5 April 1989, *Ilex mitis* on 2 May 1989, and *Cunonia capensis* on 15 May 1989. Seedlings were counted and deaths were noted weekly.

Table 5.1. Properties and nutrient contents of forest and fynbos soils on which forest and fynbos species were grown. Standard errors of the means are given in brackets. n = 4 for all variables. NS, *, ** and *** denote no significant difference between means and significant differences between means at $P < 0.05$, 0.01 and 0.001 respectively (Mann-Whitney U test).

Soil property		Forest	Fynbos	
Texture:	Cg (%)	33.8 (0.8)	34.8 (1.9)	NS
	Mg (%)	15.0 (4.0)	27.2 (5.4)	NS
	Fg (%)	11.0 (1.7)	16.8 (2.6)	NS
	VFg (%)	2.8 (0.6)	4.8 (0.8)	NS
	CSi (%)	18.5 (2.6)	11.2 (6.6)	NS
	FSi (%)	12.8 (2.3)	3.8 (0.6)	*
	Clay (%)	6.2 (1.1)	1.5 (0.5)	*
pH		5.4 (0.1)	5.8 (0.1)	*
Organic carbon (%)		7.5 (1.4)	0.8 (0.2)	*
Total nitrogen (μg/g)		1763.0 (240.7)	89.0 (21.8)	**
Bray No 2 phosphorus (μg/g)		11.3 (3.6)	14.3 (2.4)	NS
Aluminium (μg/g)		0.4 (0.1)	0.0 (0.0)	NS
Potassium (μg/g)		67.0 (10.5)	8.5 (1.2)	*
Calcium (μg/g)		150.2 (24.8)	46.8 (8.5)	*
Magnesium (μg/g)		33.8 (3.0)	2.8 (0.5)	**
Sodium (μg/g)		56.5 (3.8)	14.8 (3.0)	***

5.4.4. Habitat characterization

The characterization of forest seedling habitat in Assegaiboschkloof was based on observations in four 4 m wide transects extending 100 m from the edges of riparian forests on the two streams in the valley to approximately the centre of the fynbos area between them. The habitat of each forest seedling found in the transects was characterized. Litter depth was measured next to each seedling and the canopy cover of the area of the seedling and the space for 10 cm around it was estimated visually. The height of the herbaceous layer surrounding the seedling was measured. The distance from each seedling to the nearest likely perch tree or shrub was measured and the type (non-fruiting alien, fynbos shrub or fruiting species) and the height of the shrub were noted. The distance from the forest edge was recorded for each seedling. Points were located randomly within the transects and the same data, and whether a forest seedling was present, were recorded for each point. Relationships between habitat and the occurrence of seedlings were determined by chi-square tests of independence.

5.5. Results

5.5.1. Forest nuclei

Eight forest species, identifiable as individual plants, were found in the nuclei (Figure 5.2). Some species were comparatively rare (eg. *Maytenus oleoides, M. acuminata* and *Olinea ventosa*) and some existed as juveniles only (eg. *Hartogiella schinoides*). *Olea europaea* ssp. *africana* was the most abundant species in the nuclei. There were only small individuals of *Rapanea melanophloeos, Kiggelaria africana* and the alien *Pittosporum undulatum*; these appeared to be more recent colonizers. No anemochorous forest species occurred in the nuclei. There was no relation between distance from the forest edge and size or species diversity of nuclei.

The number of forest seedlings (plants less than 1 m tall) was related to the size of the nucleus (Figure 5.3). In nuclei dominated by non-fruiting species (type B nuclei) this relationship was linear, but there

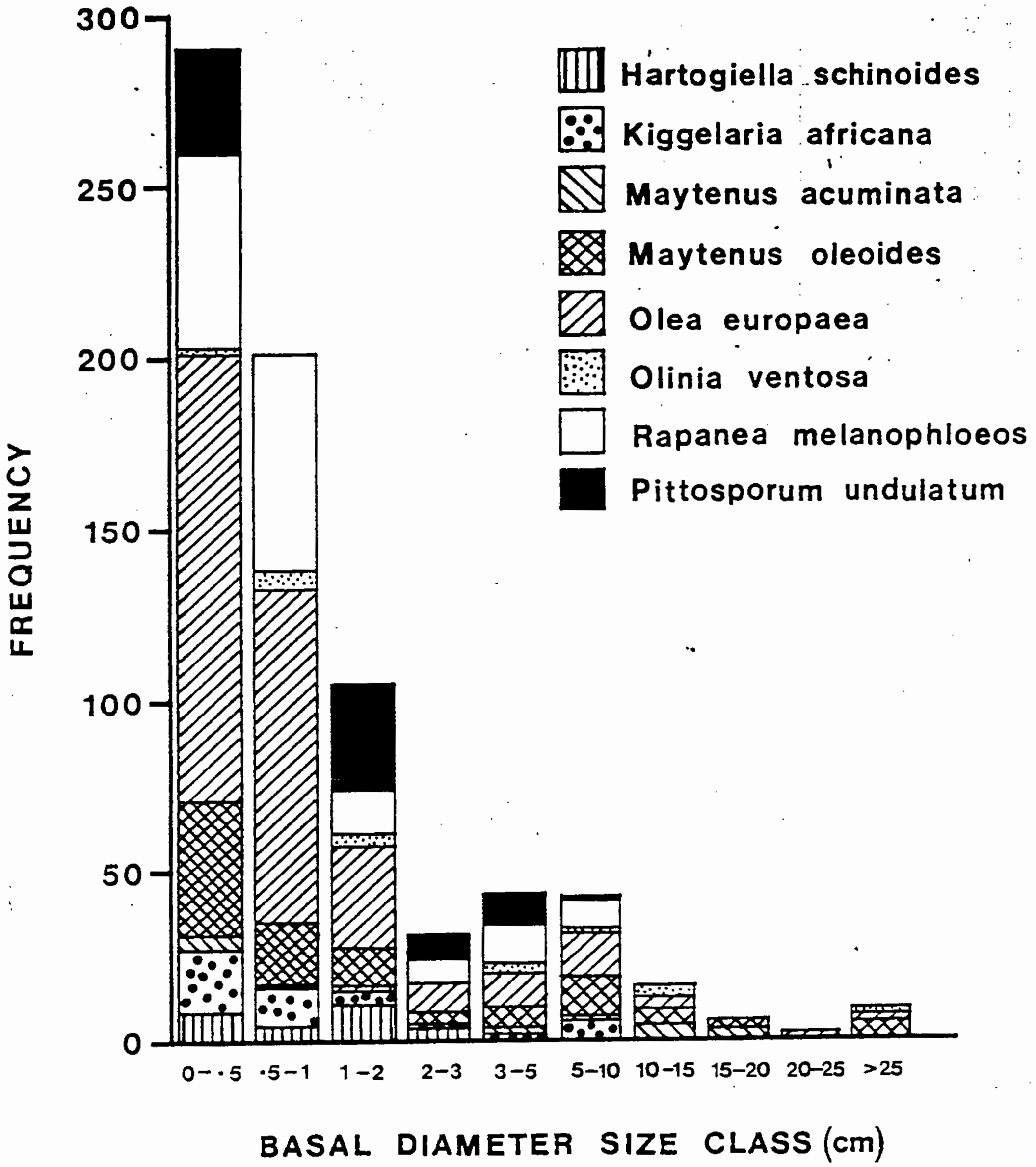

Figure 5.2. Numbers of forest species in 81 forest nuclei in Assegaiboschkloof in basal diameter size classes.

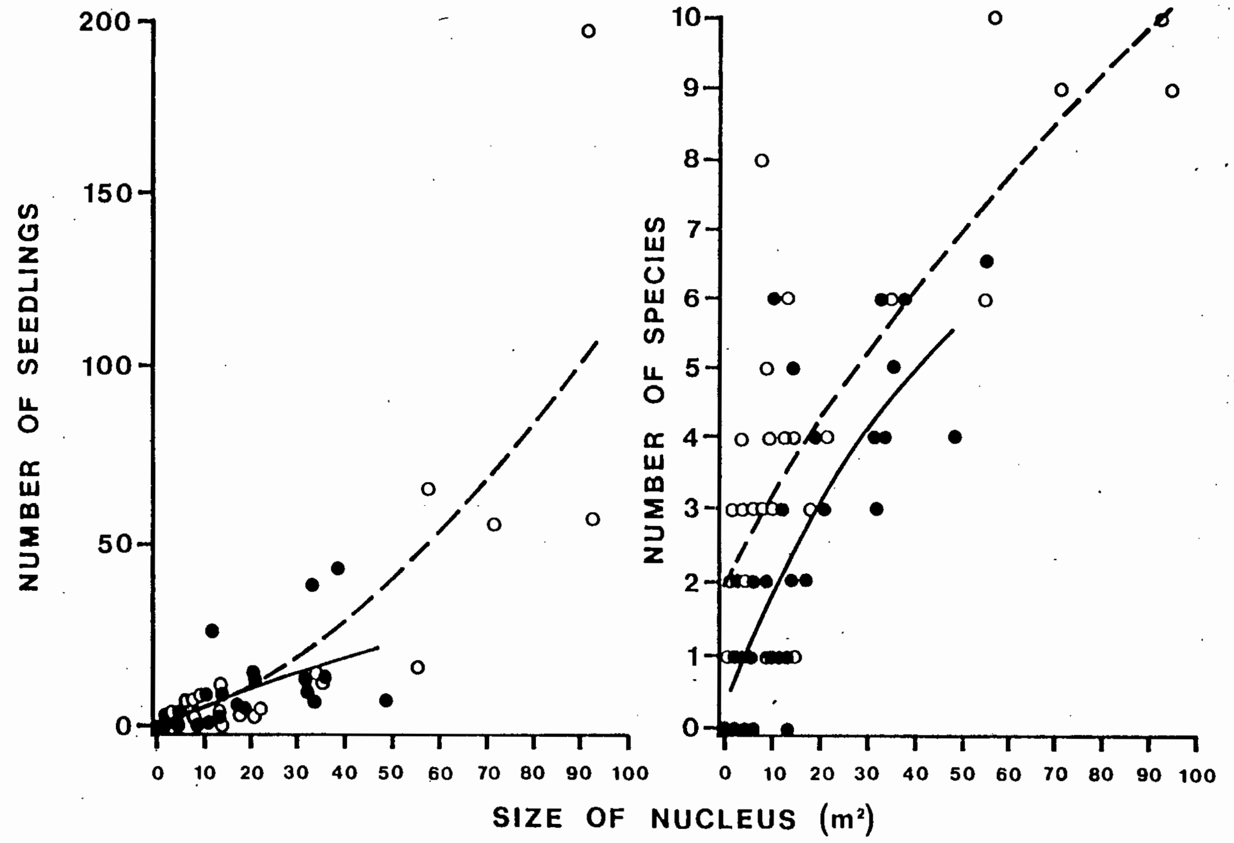

Figure 5.3. Seedlings of forest species and number of forest species per nucleus in Assegaiboschkloof in relation to nucleus size, for type A nuclei dominated by fleshy-fruited species (empty circles and dashed lines) and type B nuclei dominated by species without fleshy fruits (filled circles and continuous lines). The lines were fitted by spline interpolation.

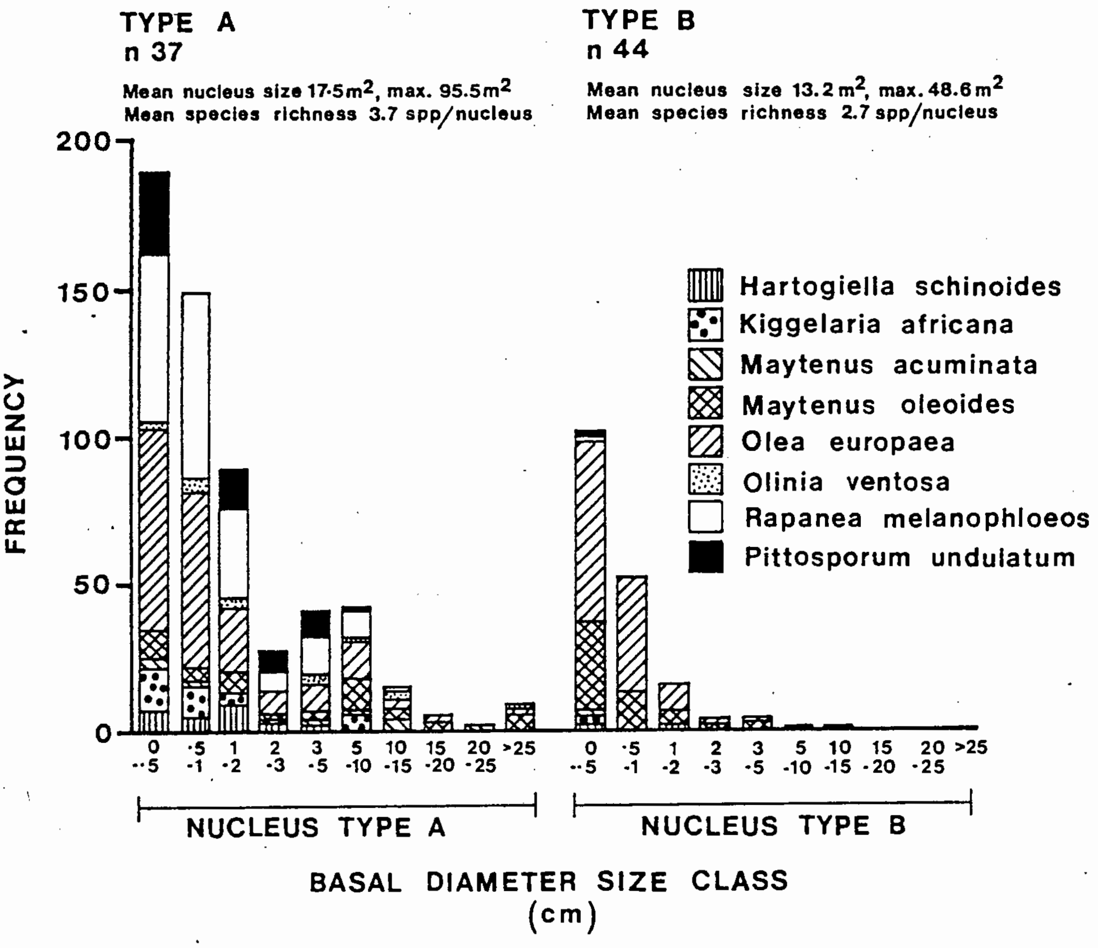

Figure 5.4. Numbers of forest species in 81 forest nuclei in Assegaiboschkloof in basal diameter size classes, for nuclei dominated by species with fleshy fruits (type A) and those dominated by species without fleshy fruits (type B).

was an indication of a non-linear response in the nuclei dominated by fruiting species (type A nuclei). Type B nuclei contained fewer forest species than type A nuclei, but the rate of increase in species richness with nucleus size was similar. The size class distribution of forest individuals differed between the two types of nuclei (Figure 5.4). Juveniles (plants with basal diameters of less than 1 cm) of the more recent colonizers (*Rapanea melanophloeos*, *Kiggelaria africana* and *Pittosporum undulatum*) occurred almost exclusively in type A nuclei whereas *Olea europaea* ssp. *africana* was common in type B nuclei (significant at $P < 0.0001$; chi-square = 140).

5.5.2. Reciprocal sowings

Germination in the germination stand of *Protea neriifolia* (84.6%, SEM = 1.4), *Protea repens* (35.2, SEM = 4.8), *Protea nitida* (51.6 SEM = 4.6) and *Kiggelaria africana* (31.8 SEM = 2.5) varied considerably. The same trends in viability occurred in the reciprocal sowings in the field. All fynbos species germinated readily in the forest but died rapidly, whereas the *Kiggelaria africana* seeds germinated more slowly and the seedlings persisted (Figure 5.5). Fynbos species took longer to germinate in the fynbos site than in the forest, but survival was high. Although some *Kiggelaria africana* seeds germinated in the fynbos, there was no survival after the summer. *Kiggelaria africana* and the *Protea* species established successfully in the transitional zone, but at slightly lower levels than in their respective vegetation types.

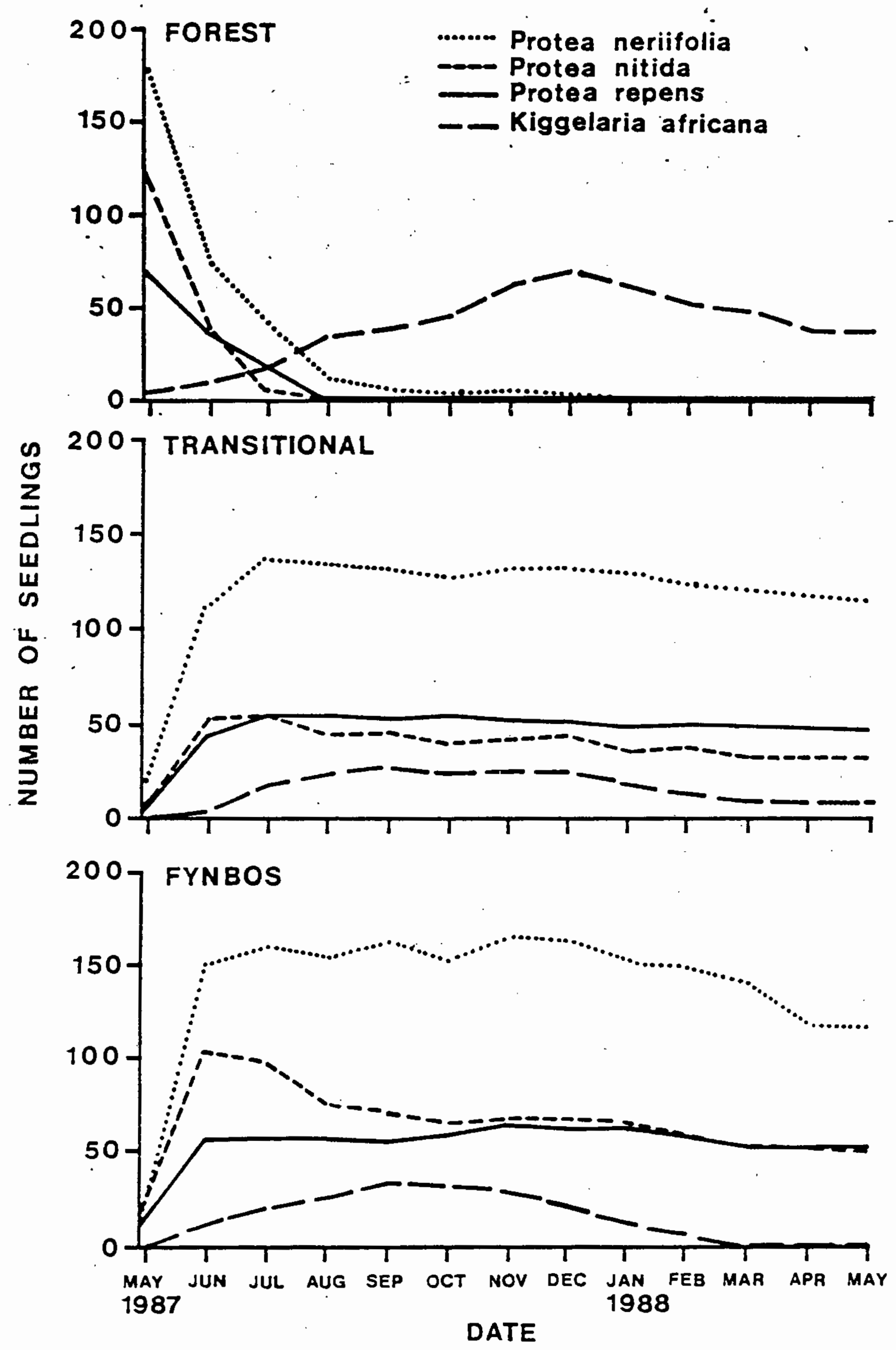

Figure 5.5. Numbers of seedlings of fynbos species (*Protea neriifolia*, *P. repens* and *P. nitida*) and a forest species (*Kiggelaria africana*) after sowing in forest, transitional and fynbos areas in Swartboskloof after fire in March 1987.

5.5.3. Germination studies

Fynbos species germinated in seedling boxes in the open in all soil types (Figure 5.6). There was some survival of seedlings in boxes with no additional watering, but survival was lower than in the watered boxes. Germination of fynbos species in the shaded position was similar to the open position but survival was very low. Although some forest seeds did germinate in the unshaded boxes, there was no survival in the dry treatment and only *Kiggelaria africana* showed any appreciable survival in the watered treatment, and then only in the forest soil with litter. In the shaded position the forest species had better survival than in the open and established far better in the forest soil with litter than in the bare forest and fynbos soils.In the shaded position the forest species had better survival than in the open and established far better in the forest soil with litter than in the bare forest and fynbos soils.

5.5.4. Habitat characterization

Forest seedlings were associated with a tall herb layer, projected plant cover in excess of 50 % and a well developed litter layer (Table 5.2). Most seedlings occurred under or within 1 m of the canopy of a perch. Perches were not necessarily fruit-bearing species, and many forest seedlings were found under fynbos shrubs. Perch height was important and fruiting species lower than 1.5 m, such as *Rhus tomentosa*, *R.angustifolia* and *Diospyros glabra*, supported relatively few seedlings (Table 5.3). There was no relationship between seedling occurrence and distance from the forest edge.

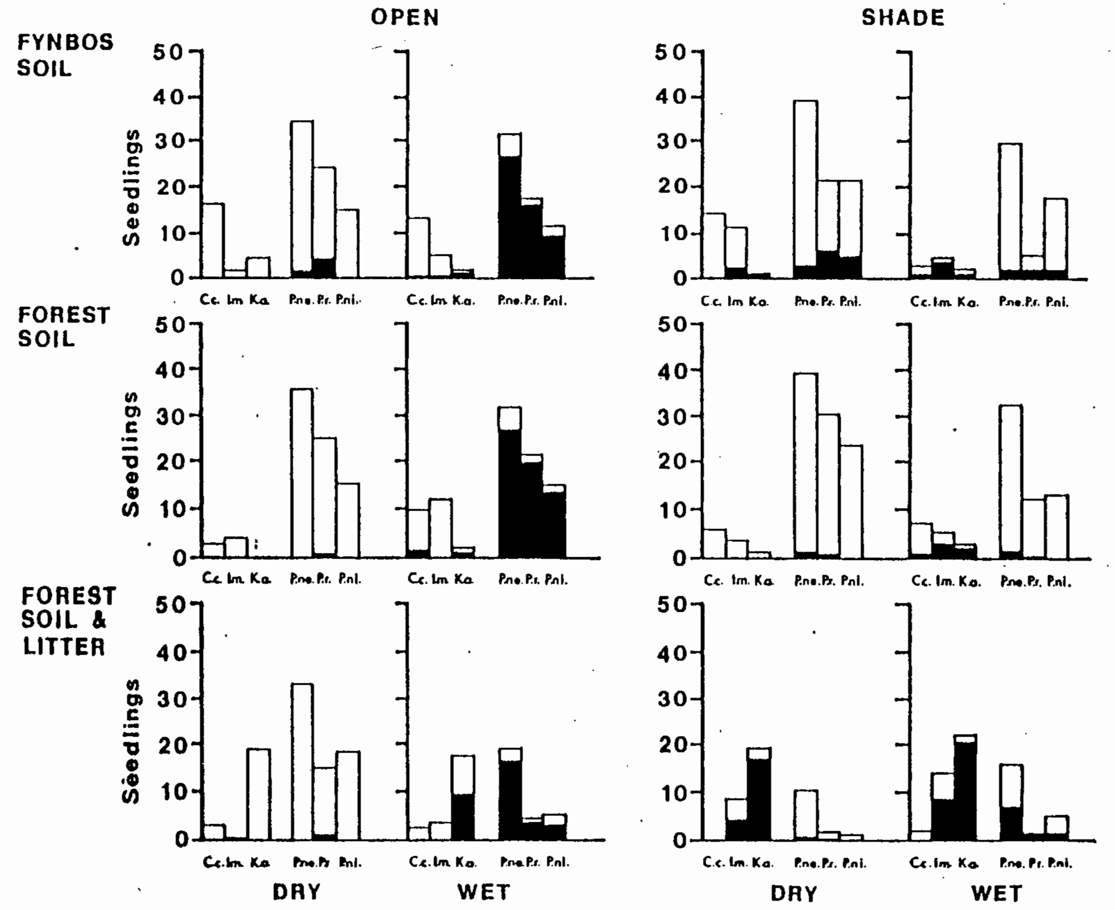

Figure 5.6. Numbers of seeds germinating (open bars) and surviving after a summer (closed bars) from 50 seeds sown in a seedling box (mean of five boxes) in the open and in the shade with different soil types and moisture regimes. C.c. = *Cunonia capensis*, I.m. = *Ilex mitis* and K.a. = *Kiggelaria africana*. Fynbos species: P.ne. = *Protea neriifolia*, P.r. = *Protea repens* and P.ni. = *Protea nitida*.

Table 5.2. The relationship between a) height of herb layer, b) vegetation cover and c) litter depth and the occurrence of seedlings of forest species and points without seedlings in Assegaiboschkloof. Chi-square values and levels of significance are given in square brackets below each table. Numbers in round brackets show cell contributions to chi-square. Signs indicate whether a cell is over- (+) or under-represented (-).

a) Herb layer

Herb layer height (cm)	Seedlings	Points without seedlings
0	0 (1.6) -	7 (0.5) +
1 - 10	2 (0.1) +	5 (0.0) -
11 - 50	11 (2.4) -	64 (0.7) +
51 - 100	39 (1.0) -	156 (0.3) +
> 100	62 (4.4) +	141 (1.3) -

[χ^2 = 12.5, $P < 0.05$]

b) Vegetation cover

Vegetation cover (%)	Seedlings	Points without seedlings
0	0 (1.6) -	7 (0.5) +
1 - 50	39 (3.1) -	182 (1.0) +
51 - 100	75 (3.4) +	184 (1.0) -

[χ^2 = 10.7, $P < 0.005$]

c) Litter depth

Litter depth (cm)	Seedlings	Points without seedlings
0	4 (9.1) -	65 (2.8) +
0 - 1	16 (3.8) -	95 (1.2) +
1 - 2	39 (0.2) +	115 (0.1) -
2 - 3	34 (2.5) +	77 (0.8) -
> 3	21 (12.7) +	21 (3.9) -

[χ^2 = 37.1, $P < 0.0001$]

Table 5.3. The relationship between a) distance to the nearest perch and b) type of perch and the occurrence of seedlings of forest species and points without seedlings in Assegaiboschkloof. Chi-square values and levels of significance are given in square brackets below each table. Numbers in round brackets show cell contributions to chi-square. Signs indicate whether a cell is over- (+) or under-represented (-).

a) Perch distance

Perch distance (m)	Seedlings	Points without seedlings
0	83 (22.0) +	130 (6.7) -
0 - 1	17 (13.6) -	156 (4.2) +
1 - 2	8 (4.5) -	63 (1.4) +
2 - 3	5 (0.0) -	17 (0.0) +
> 3	1 (0.4) -	7 (0.1) +

[$\chi^2 = 52.9$, $P < 0.0001$]

b) Perch type

Perch type	Seedlings within 1 m of a perch	Points without seedlings
Open	14 (3.9) -	87 (1.2) +
Non-fruiting alien	4 (2.1) -	31 (0.6) +
Fynbos shrub	21 (4.0) +	37 (1.2) -
Fruiting perch < 1.5 m	18 (0.8) -	77 (0.2) +
Fruiting perch > 1.5 m	57 (2.4) +	141 (0.7) -

[$\chi^2 = 17.5$, $P < 0.01$]

5.6. Discussion

Forest development in fynbos has been observed before (Kruger 1984; Masson & Moll 1987), but the process of forest development has not been studied. The reverse 'J' shaped curve of the combined populations of forest species and the addition of species to the smaller size classes in the nuclei provide evidence of the continuous colonization of the fynbos in Assegaiboschkloof by forest species. It was possible to classify forest species in nuclei as colonizers or persisters. Colonizing species (*Olea europaea* ssp. *africana*, *Rapanea melanophloeos* and *Kiggelaria africana*) were present as abundant juveniles only, whereas persistent species (***Maytenus oleoides, M.*** acuminata and *Olinea ventosa*) were present as large plants (survivors of previous fires) and low numbers of seedlings.

Olea europaea ssp. *africana* grows in a variety of habitats and is regarded as drought-resistant (Coates-Palgrave 1983). The predominance of this species, and the absence of juveniles of other colonizing species, in nuclei dominated by non-fruiting species indicates less amelioration within these often smaller, slower-developing nuclei. There are, however, a few seedlings of the other species in these nuclei, suggesting that, with development and fire exclusion, conditions approach those of nuclei dominated by fruiting forest species.

All forest species in the nuclei at Assegaiboschkloof were ornithochorous. The relationship between seedling number and nucleus size suggests that there is a true nucleus effect, and that factors such as change in habitat, and the frequency of visits and length of stay of avian seed dispersers influence and are influenced by the size of the nucleus. The absence of a relationship between distance from the forest edge and nucleus complexity could imply that the distances involved (up to 200 m) were too short to have any effect, or that the pattern was obscured by other nuclei acting as sources of seeds.

Some of the processes important in the establishment of forest and fynbos species were identified in the reciprocal sowings and the cultivation of species in seedling boxes. The quality of light (high far red and low red) under a forest canopy has an inhibiting effect on the germination of pioneer species and those dependent on canopy gaps for regeneration (Whitmore 1983). Both these studies, however, demonstrated that forest and fynbos species have similar germination requirements, but differ in establishment requirements. Fynbos species were able to establish in exposed (post-fire) situations whereas forest species established under closed canopy conditions. The mortality of the fynbos species in the boxes exceeds that in the field trial and is ascribed to prevention of rapid development of deep roots in these species (Manders & Smith in preparation b) in the boxes. Establishment of forest species is not dependent on high soil moisture availability alone, and litter, shade and high quality forest soil were required to achieve maximum establishment. Colonization of fynbos by forest depends on development of similar conditions in the fynbos - identified as fynbos senescence and litter development by Masson & Moll (1987). This dependence was confirmed in the characterization of the habitat of forest seedlings in the fynbos in Assegaiboschkloof, but does not necessarily involve the senescence of the fynbos vegetation.

Having demonstrated the process of colonization, involving facilitation and nucleation, we attempt to place the evidence from this study into perspective in terms of the conceptual model in Figure 5.1. The final level of the model, of coalescence and formation of stable forest communities, remains undetermined, but is a critical phase determining the eventual outcome of the successional process. The largest nucleus in the 50 year old fynbos in Assegaiboschkloof is 95 m^2. The likelihood of fire in this area soon is very high (given the current fire regime of 10 to 20 years over much of the fynbos biome) and the size of this nucleus will be reduced to an extent depending on the intensity of the fire. Coalescence of nuclei and eventual predominance of forest species seem unlikely under this scenario. We attempt to place some relative time scales for forest development in various soil nutrient and moisture conditions (Figure 5.7). The relative time scales would be further influenced by the presence of perches in the initial stages. Forest predominance under the current fire regime, with these rates of development, is realistically probable in prime habitat conditions (high soil nutrients and moisture) only. With extended fire-free intervals, however, forest development is possible in other areas, and if the forest patch has time to develop sufficiently between fires, or if the fires are not too intense, then forests may predominate in what is currently dominated by fynbos species. Currently, therefore, fire is the major factor limiting forest expansion and preventing the establishment of a stable forest community.

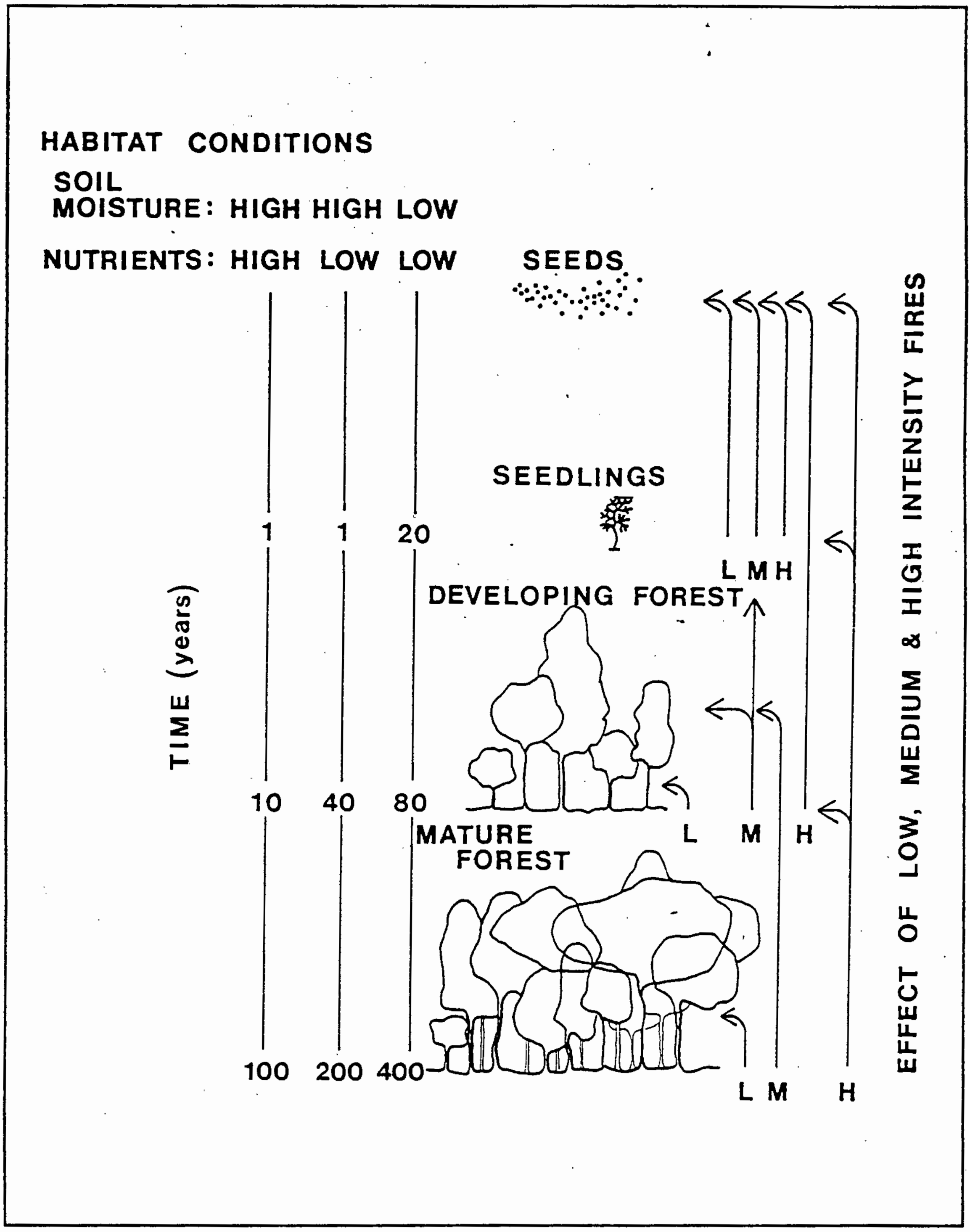

Figure 5.7. A conceptual model of the development of forest in fynbos and the effects of fire on forest development. The rate of growth of forest is determined by the habitat, primarily water and nutrient availability. There is an acceleration of forest development with positive feedback due to habitat amendment and attraction of greater numbers of ornithochorous seeds. As forests develop, they become progressively less vulnerable to the effects of fire (Knight 1988).

In most fynbos areas forest species form a transient component, which develops between fires and is eliminated in each fire. This transience is in contrast to alien tree species, notably pines, which have recruitment episodes coupled with disturbance by fire and which have established self-perpetuating populations in fynbos areas (Richardson and Cowling, in press). The reason for the absence of indigenous trees in the fynbos, therefore, is not the high frequency of fire *per se* (*sensu* Moll *et al.* 1980), but rather that the recruitment of the indigenous tree flora is not coupled to disturbance by fire. The lack of coupling with disturbance may be traced back to the origins of the forest species in the relatively disturbance-free Afromontane or Tongaland-Pondoland centres of endemism.

PART 3

EFFECTS OF SOIL MOISTURE AND SOIL NUTRIENTS

CHAPTER 6

THE EFFECTS OF WATERING REGIME ON GROWTH AND COMPETITIVE ACTIVITY OF NURSERY-GROWN CAPE FYNBOS AND FOREST PLANTS

CHAPTER 6: EFFECTS OF WATERING REGIME ON GROWTH AND COMPETITIVE ABILITY OF NURSERY-GROWN CAPE FYNBOS AND FOREST PLANTS.[1]

6.1. Abstract

Indigenous forests in the south-western Cape are restricted to sheltered habitats. Two forest species, (*Cunonia capensis* L. and the pioneer *Kiggelaria africana* L.) and three fynbos species (*Protea neriifolia* R. Br., *P. nitida* Miller and *P. repens* (L.) L.) were individually cultivated under three levels of water availability to determine the influence of this factor on forest distribution. The alien invasive *Acacia longifolia* (Andrews) Willd. was included to ascertain the basis of its invasive ability. A diallel experiment with all combinations of pairs of *C. capensis*, *K. africana*, *P. neriifolia* and *P. nitida* was carried out under the same treatments to investigate competitive abilities.

Growth of all species under individual cultivation improved with increased water availability. Morphological indicators of water stress (leaf size and specific leaf area) did not follow predicted patterns and diurnal measurements of conductance did not differentiate between forest and fynbos species. *C. capensis* and *A. longifolia* showed high levels of mortality in the dry watering regime, but *K. africana* persisted in this treatment.

The diallel experiment showed *K. africana* to be a superior competitor at all levels of water availability. *C. capensis* was an inferior competitor, especially in the dry treatment. *P. nitida* was an inferior competitor with high water availability, but watering regime had little effect on the competitive abilities of *P. neriifolia*.

Forest development in xeric habitats may be precluded by the inability of forest species to establish in normal summer drought conditions. Once established under wet conditions, however, pioneer species such as *K. africana* may persist and develop.

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[1] Publication Status: Manders, P.T. & Smith, R.E. The effects of watering regime on growth and competitive ability of nursery-grown Cape fynbos and forest plants. Submitted to *S. Afr. J. Bot.*

6.2. Introduction

Indigenous forests have a patchy distribution amongst the predominant fynbos (shrubland) vegetation in the mountains of the south-western Cape (Campbell 1985). Forests are usually restricted to sheltered habitats such as streambanks, ravines or rock screes (White 1978). Restriction to these habitats is thought to be either a consequence of protection from fire, which occurs more frequently in the more flammable fynbos (Moll *et al.* 1980), or because of the greater soil moisture availability in such habitats. Forest development does occur between fires in fynbos vegetation in less protected areas (Kruger 1984; Masson & Moll 1987), especially where soil moisture or nutrient levels are higher than normal fynbos levels (Campbell 1985).

The exclusion of forest species in more open areas is thought to result from the failure of forest species seedlings to survive seasonal water deficits (White 1978). Greater and more prolonged seasonal water deficits have been measured in a fynbos habitat than in a nearby riparian habitat, but no differences in stomatal behaviour or water use efficiency were detected between adult riparian species in the riparian habitat and adult hillslope species in the xeric habitat (Richardson & Kruger 1990). However, it is very difficult to test in the field the ability of forest species to establish in dry habitats, as established individuals of forest species growing in such habitats have survived the period of greatest vulnerability to drought. Ideally, such tests should be carried out on freshly-germinated seedlings. It is also very difficult to determine what sources of soil moisture are available to individual plants in the field, some of which may have very deep roots.

The object of this study was to determine the different responses of forest and fynbos plants to levels of soil moisture during and after the establishment phase to develop an understanding of the factors limiting the establishment of forest species in fynbos. Individual plants were cultivated in separate containers, where soil moisture could be controlled, to overcome the problems with field investigations. This excluded competitive effects and did not allow plants to evade moisture stress by developing deep root systems. *Protea neriifolia* R. Br., *P.*

nitida Miller and *P. repens* (L.) L. were used as representatives of large sclerophyllous fynbos shrub species, closest in size and morphology to forest species, and *Cunonia capensis* L. and the pioneer species *Kiggelaria africana* L. were used as representatives of evergreen forest tree species. The Australian shrub *Acacia longifolia* (Andrews) Willd., which invades mountain fynbos and riparian areas (Macdonald & Richardson 1986), was included in an attempt to explain its invasive ability.

Plant mass at harvesting was used as the measure of the sum of each plant's physiological activity throughout its life. However, some measures of transpiration were made to allow comparisons with earlier field studies (Richardson & Kruger 1990). A selection of variables, including specific leaf areas and allometric root / shoot relationships, were measured to determine their potential for use in the field as measures of the water stress under which a plant has developed. Competitive abilities of *P. neriifolia, P. nitida, K. africana* and *C. capensis* were measured using a diallel experiment (Harper 1977: 267).

6.3. Methods

Plants were cultivated in black plastic nursery bags measuring 300 mm high and 170 mm diameter when full. The bags were filled with silt from a weir in the Jonkershoek valley. Analyses of the soil, using standard laboratory techniques, were performed by the Saasveld Forestry Research Centre near George (Table 6.1).

Seeds of *P. neriifolia, P. nitida* and *P. repens* were collected from the Jonkershoek valley during March 1987. *Acacia longifolia* seeds were supplied by Mr PJ Pieterse of Plant Protection Research Institute, Stellenbosch. Seeds were sown in seedling trays during June and seedlings were transplanted into the bags on 29 July 1987. Seedlings of *C. capensis* and *K. africana* were collected from the field and transplanted on the same day. Ten seedlings from each species were harvested during

Table 6.1. Properties of the soil used for individual and diallel cultivation of plants in plastic nursery bags under different watering regimes.

Soil property	Value (S.E.)
Coarse sand (0.5-2.0 mm) (%)	43.5 (4.7)
Fine sand (0.053-0.5 mm) (%)	43.0 (4.7)
Silt & clay (<0.053 mm) (%)	15.8 (1.2)
pH (H_2O)	5.68 (0.15)
Organic carbon (%)	4.01 (1.39)
Total nitrogen (μg/g)	1102.5 (224.3)
Bray No 2 phosphorus (μg/g)	14.9 (2.5)
Aluminium (μg/g)	0.2 (0.2)
Potassium (μg/g)	37.0 (9.5)
Calcium (μg/g)	141.8 (9.3)
Magnesium (μg/g)	28.8 (2.0)
Sodium (μg/g)	40.0 (7.7)

transplantation to compare initial sizes. The experiment was carried out in a greenhouse to prevent rain from affecting the soil moisture.

One plant of each species was cultivated per bag with ten replicates of each species in each of three watering regimes; wet, medium and dry. Plants in the wet regime were watered to saturation three times a week and those in the medium and dry treatments were watered with 200 ml per bag twice and once a week respectively. The amount given to each bag in the medium and dry treatments was increased to 500 ml during the hot, dry period of 25 January to 1 April 1988. Plant mortality was noted weekly.

All bags were weeded and pesticides were used to control herbivory by *Acraea horta* L. (Subfamily Acraeinae) butterfly larvae and red spider (Order Acari, Family Tetranychidae), both of which affect *K. africana* in particular.

The plants were harvested in December 1988. Plants were divided into roots, stem and leaves before drying to constant mass at 70 °C. Leaf area and fresh mass of twenty leaves per plant were measured to determine the specific leaf area (SLA) from the relationship;

$$SLA = \frac{\text{leaf surface area (dm}^2\text{)}}{\text{leaf fresh mass (g)}}$$

The relationship between leaf fresh mass and leaf area was used to determine total leaf area from the total fresh mass of the leaves on each plant.

The effects of species and watering regime on total plant mass, height, total leaf area, leaf size and specific leaf area were determined by two-way analysis of variance. Significant interactions between species and treatment were identified in all variables measured. Therefore an overall statement for each factor would have little meaning (Sokal & Rohlf 1968: 315). For this reason, and because confidence intervals are often more useful than significance tests for multiple comparisons (SAS Institute Inc. 1985a: 471), comparisons between species and treatments were based on 95 % confidence intervals about the means. The allometric relationships between root and shoot development ($R = bS^K$, where R = root mass, S = shoot mass and K is the allometric constant) were determined by principal axis correlation analysis of the logarithmic relationship

$$\log_{10}R = \log_{10}b + K\log_{10}S,$$

based on a matrix of covariance. Values of K greater than unity indicate rootiness and values less than one indicate shootiness (Hunt 1978).

Stomatal conductances and ambient relative humidity and temperature were measured, with a null-balance diffusion porometer (MCS 301 Null Balance Porometer, MC Systems, Plumstead, Cape Province) designed to take measurements on whole leaves, on all the species in the dry and wet watering regimes. The principle of the null-balance porometer is described fully by Beardsell *et al.* (1972). Measurements were repeated on two leaves in similar positions on each of two plants per species for each watering regime at hourly intervals from pre-dawn until dusk on 28 November 1988 - a clear, still, warm day. The plants in the dry watering regime had last been watered a week prior to the conductance measurements, while those in the wet regime had been saturated three days before the measurements. The leaf areas of the sample leaves were determined at the end of the diurnal run. Transpiration rates (Tr) per unit leaf area (g/cm2*s) were approximated from the equation:

$$Tr = F/LA * (pc-pa)$$

where F (cm^3/s) is the flow rate within the porometer, LA is the leaf area (cm^2), pc (g/cm^3) is the water vapour density in the cuvette and pa (g/cm^3) is the water vapour density of the dry airstream entering the cuvette (2% relative humidity) (Li-Cor Products Manual 1981). Total water transpired per unit leaf area ($mmol/m^2$) per day was derived by summing the areas under the straight lines connecting consecutive pairs of observations.

Competitive abilities were measured in a diallel experiment (Harper 1977). Two individuals of *P. neriifolia, P. nitida, K. africana* or *C. capensis* were planted in each bag, to produce all possible pairwise combinations. The same nursery bags and soil were used as for the individual cultivation. Ten replicates of each combination were grown under wet, medium and dry watering regimes, with the same treatments, planting and harvesting times as in the individual cultivation. On harvesting, root systems were washed clean, and the plants in each bag were separated and dried to constant mass at 70 °C.

Analysis of plant growth followed the method of Wilson & Keddy (1986), based on the mass accumulation of individual plants. The relative increase in plant mass (RIP) per plant of species i grown with species j was calculated as

$$RIP_{ij} = (HDM_{ij} - SDM_i)/(HDM_{ii} - SDM_i),$$

where HDM_{ij} is the dry mass of the plant at harvesting, SDM_i is the mean starting dry mass of species i, and HDM_{ii} is the mean dry mass at harvesting of plants in species i when grown with a conspecific neighbour. Plants which died were not included in the growth analysis. A plant with an RIP, when grown with a plant of another species, greater or less than 1 indicates better or poorer growth respectively in the presence of the neighbour than with a conspecific neighbour. Differences between target scores (the mean RIP of each species grown with all species of neighbours) and neighbour scores (the mean RIP of all target species with which a particular neighbour species was grown) within each treatment were based on two-way analysis of variance. Competitive superiority is indicated by high target scores and low neighbour scores. A similar analysis was performed on the relative survival of plants in each of the combinations.

6.4. Results

6.4.1. Individual cultivation

Initial plant sizes varied considerably between species (Table 6.2). This factor was not included in analyses of the final harvest of individually cultivated plants, however, as final plant sizes were several orders of magnitude greater than the original sizes and the initial pattern of size differences disappeared quickly.

Table 6.2. Initial sizes of seedlings used in the individual cultivation and diallel experiments. Ten seedlings were sampled in each species.

SPECIES	PLANT HEIGHT (mm) (S.E.)	ROOT DEPTH (mm) (S.E.)	TOTAL DRY MASS (mg) (S.E.)
Protea neriifolia	16.0 (0.6)	49.1 (2.3)	21.6 (1.3)
Protea nitida	24.1 (7.3)	49.3 (4.7)	100.0 (34.0)
Protea repens	9.3 (1.0)	66.7 (2.2)	25.8 (1.4)
Kiggelaria africana	35.3 (1.7)	117.7 (9.3)	34.9 (3.1)
Cunonia capensis	25.3 (2.7)	46.5 (6.4)	27.0 (14.0)
Acacia longifolia	22.0 (1.6)	56.8 (3.7)	8.8 (0.7)

Watering regime and species, and the interactions between these factors had significant effects on all variables in the growth analyses (Table 6.3). All species, except *P. nitida*, in the medium watering regime had greater biomasses than in the dry watering regime (Figure 6.1). In the wet watering regime, all species had greater biomass than in the dry, but not consistently greater than in the medium regime. There was no pattern of different responses between forest and fynbos species within treatments. Height growth (Figure 6.1) showed a very similar pattern to biomass accumulation, but identified the extreme vigour of *K. africana*, comparable to that of *Acacia longifolia*, in the medium regime.

Table 6.3. F values of two-way analysis of variance between treatment (watering regimes) and species for variables measured in growth analyses of forest and fynbos species, and the exotic weed *Acacia longifolia*. All F values are significant at $P < 0.0001$.

Variable	Treatment	Species	Treatment x Species
Total plant mass	154.3	41.7	20.6
Plant height	113.8	67.4	12.1
Total leaf area	117.4	39.5	12.4
Leaf size	176.6	287.8	34.2
Specific leaf area	14.6	334.1	7.8

Total leaf areas of all species except *P. nitida* in the dry treatment were very similar to each other and exhibited similar increases in the medium treatment (Figure 6.2). The total leaf areas of fynbos species (except *P. nitida)* and *Acacia longifolia* showed greater positive response to enhanced water availability than the forest species. Responses in individual leaf size varied between species (Figure 6.2). Although the sizes of *C. capensis* and *K. africana* leaves were greater in the medium treatment than in the dry treatment, there was a slight decrease in the wet treatment compared with the medium treatment. *P. neriifolia*, *P. nitida* and *P. repens* showed consistent increases in leaf size with enhanced water availability, but the increase in leaf size in *P. repens* was trivial compared with the massive increase in total leaf area (Figure 6.2), which results from the production of greater leaf numbers. Although leaves of *Acacia longifolia* were largest in the wet treatment, there was no trend of reduction in size with decreased water availability. Specific leaf areas did not vary consistently with watering regime (Figure 6.2). The slope of the principal axes correlating log root mass and log shoot

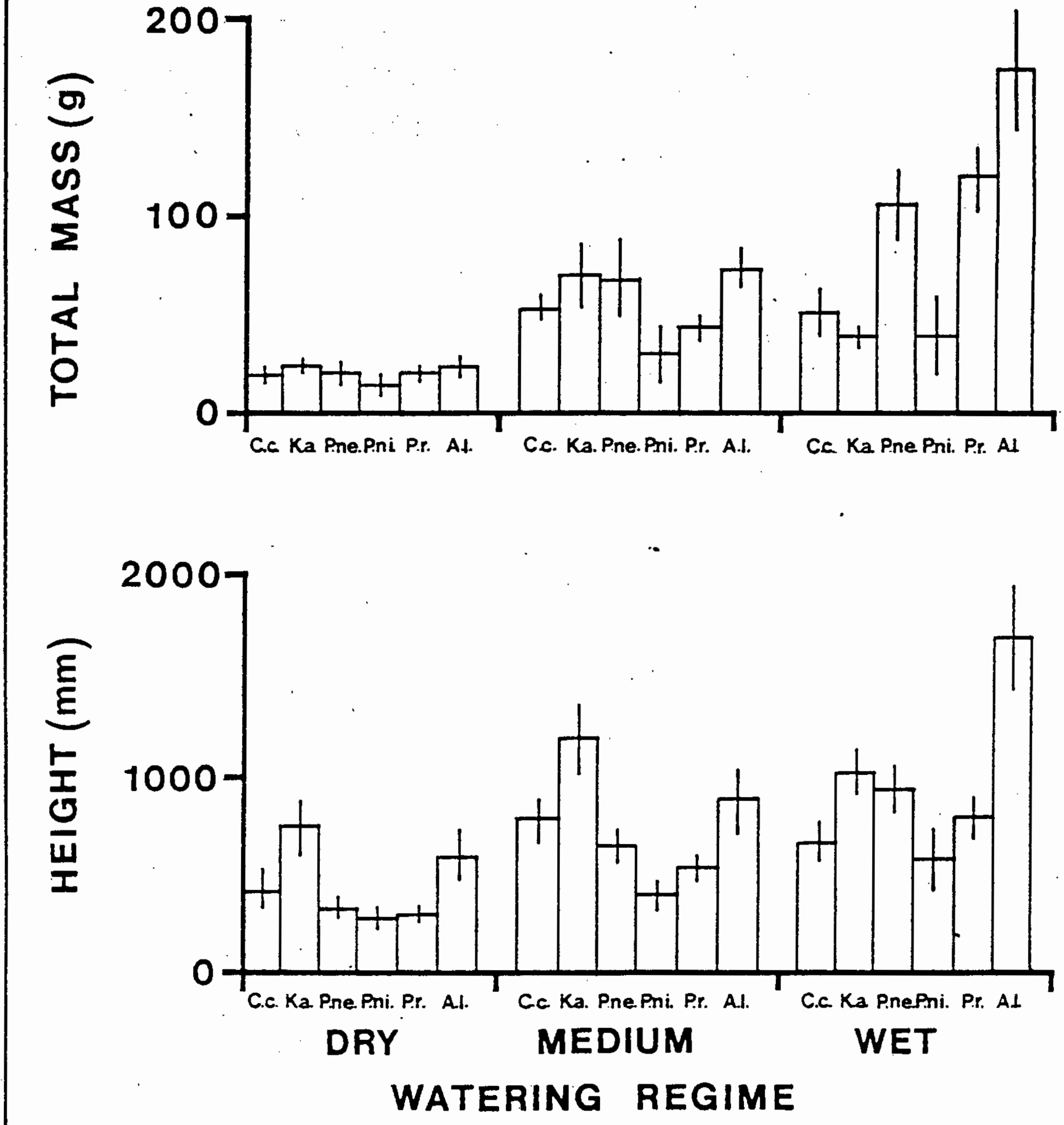

Figure 6.1. Total mass and height of forest and fynbos plants and an invasive alien cultivated from seedlings in July 1987 to December 1988 under three watering regimes. C.c. = *Cunonia capensis*, K.a. = *Kiggelaria africana*, P.ne.= *Protea neriifolia*, P.ni. = *Protea nitida*, P.r. = *Protea repens* and A.l. = *Acacia longifolia*. 95 % confidence limits about the means are represented by vertical lines.

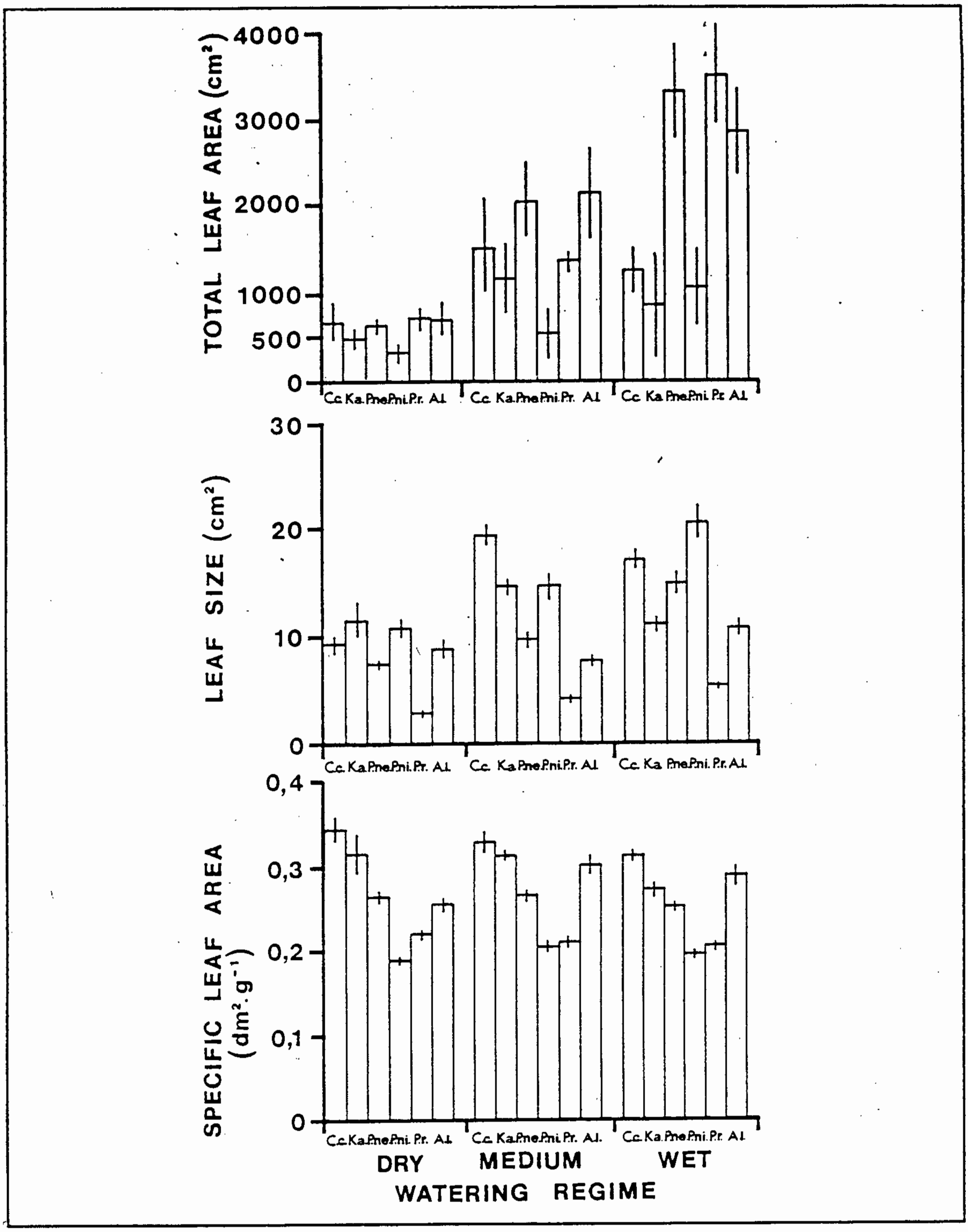

Figure 6.2. Total leaf area, leaf size and specific leaf area of forest and fynbos plants and an invasive alien cultivated from seedlings in July 1987 to December 1988 under three watering regimes. C.c. = *Cunonia capensis*, K.a. = *Kiggelaria africana*, P.ne. = *Protea neriifolia*, P.ni. = *Protea nitida*, P.r. = *Protea repens* and A.l. = *Acacia longifolia*. 95 % confidence limits about the means are represented by vertical lines.

mass of individually cultivated plants did not show any clear trend (Table 6.4).

Table 6.4. Slopes (K) of principal axes describing the allometric relationship between root and shoot mass ($\log_{10}R = \log_{10}b + K\log_{10}S$) for all plants in each species and within dry, medium and wet watering regimes. Figures in brackets show the proportion of variance explained by the eigenvalue of the covariance matrix of the first principal axis.

Species	Treatment			
	All	Dry	Medium	Wet
Cunonia capensis	1.13 (0.93)		1.04* (0.91)	1.01 (0.97)
Kiggelaria africana	0.72 (0.93)	0.88 (0.60)	0.74 (0.78)	0.72 (0.85)
Protea neriifolia	0.91 (0.94)	2.05 (0.92)	2.05 (0.90)	1.61 (0.93)
Protea nitida	0.96 (0.94)	1.23 (0.96)	0.70 (0.96)	0.94 (0.98)
Protea repens	0.84 (0.97)	2.99 (0.81)	3.43 (0.85)	1.52 (0.84)
Acacia longifolia	1.46 (0.95)		1.04* (0.93)	16.30 (0.91)

* Figures include plants grown under dry and medium watering regimes.

No plants died in the wet and medium watering regimes except for some *C. capensis* in the medium treatment. All deaths in the dry treatment occurred within the first 20 weeks of the experiment. Greatest mortality occurred within *C. capensis* and *Acacia longifolia*. There was no mortality in *K. africana* and very little amongst the fynbos species (Figure 6.3).

Stomatal conductances (median values of four leaves per species per hour) were similar for all the species in dry watering regime (Figure 6.4). All species responded positively to the wet regime (with the exception of *P. repens* and *A. longifolia)*, at least doubling their conductances with the increased water availability. There was no differentiation between conductances of forest and fynbos species. No species exhibited midday stomatal closure in either of the water regimes.

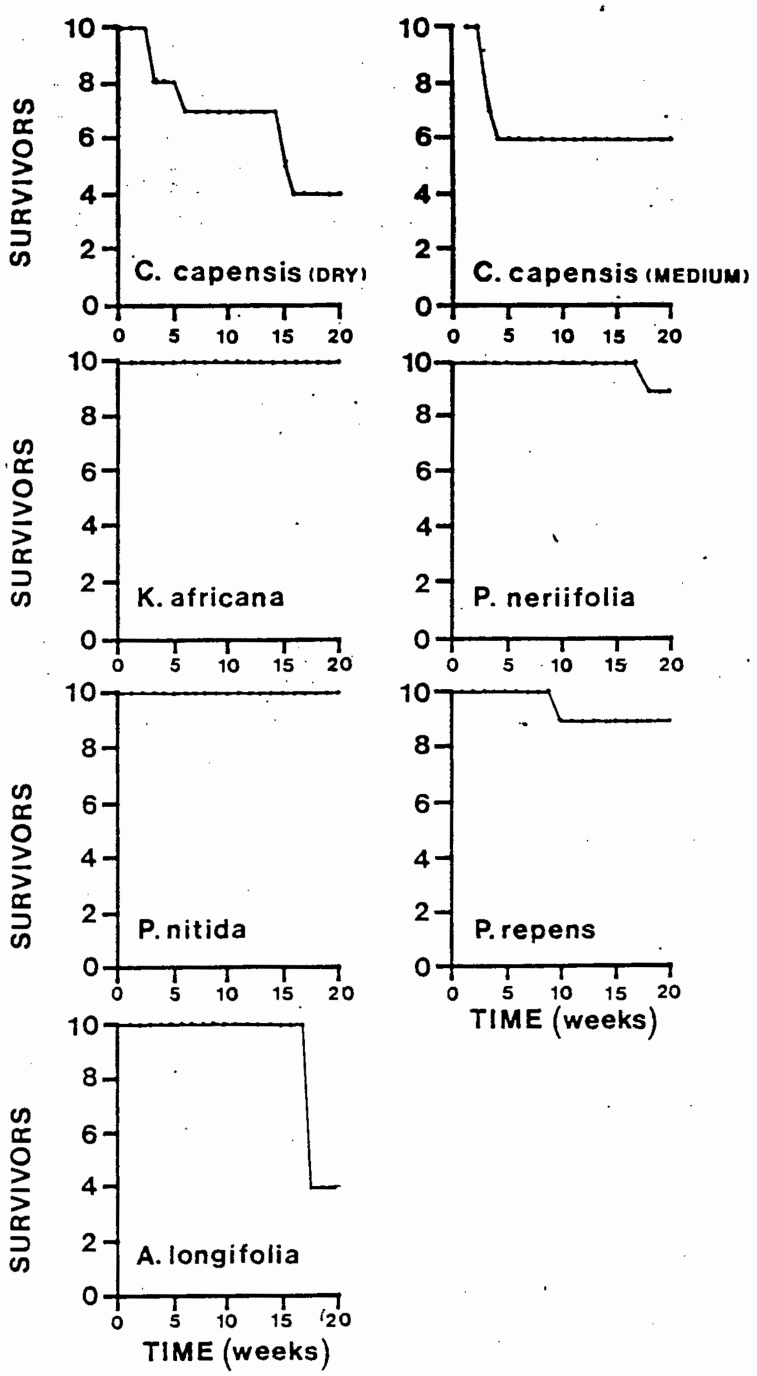

Figure 6.3. Numbers of individually cultivated forest and fynbos plants and an invasive alien surviving during the first 20 weeks of cultivation under a dry watering regime (see text) and numbers of *Cunonia capensis* surviving during the first 20 weeks of cultivation under a medium watering regime (see text). Cultivation began on 30 July 1987.

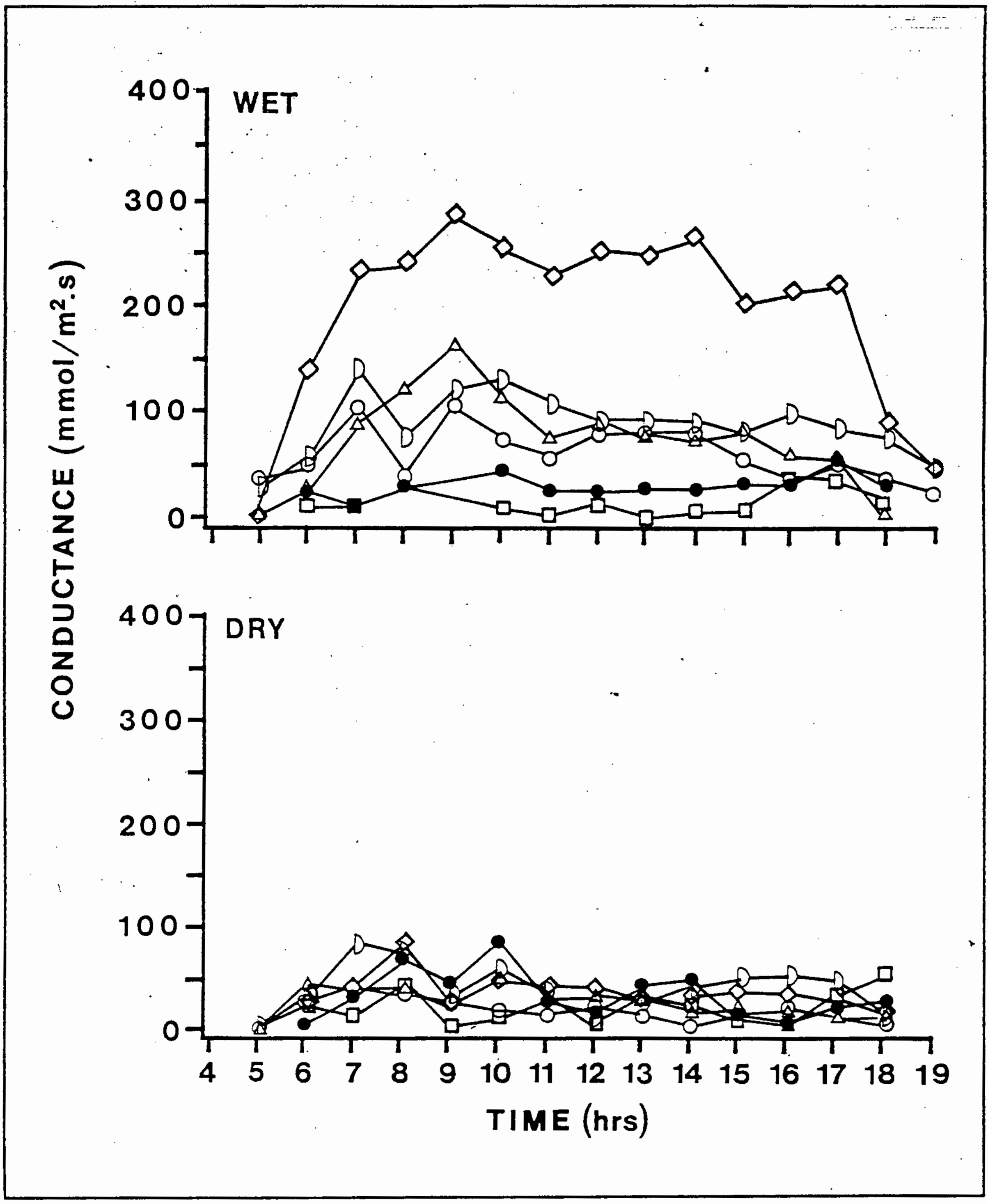

Figure 6.4. Diurnal conductance rates of all species individually cultivated in the dry and wet watering regimes (see text). Values represent the median of four leaves per species. ○ = *Cunonia* capensis, □ = *Kiggelaria africana*, △ = *Protea neriifolia*, ◇ = *Protea* nitida, D = *Protea repens* and ● = *Acacia longifolia*.

6.4.2. Diallel

Analysis of variance showed significant effects for both target and neighbour scores, with no significant interactions, in all watering treatments (Table 6.5). Significant differences between target scores and between neighbour scores occurred within each treatment (Table 6.6). Relative competitive abilities are shown in Figure 6.5. Species in the upper left quadrant (high target and low neighbour scores) are superior competitors, those in the lower right quadrant (low target and high neighbour scores) are inferior competitors. *K. africana* was a superior competitor at all levels of water availability, whereas *C. capensis* was a consistently inferior competitor, but tended to greater competitive ability with increased water availability. The competitive abilities of *P. neriifolia* were little influenced by water availability. *P. nitida* was never a strong competitor, and lost competitive ability as the water levels increased. No species showed evidence of mutual suppression or mutual stimulation (lower left and upper right quadrants of Figure 6.5 respectively).

Target survival is the survival of a species when grown with all other species, and reflects the ability of a species to persist rather than competitive ability. This variable showed very similar trends to the target score in the mass analysis (Table 6.7). Neighbour survival is the survival of other species in the presence of the target species, reflecting the competitive ability of the target species. This variable ranked the species differently to the neighbour scores in the mass analysis. *K. africana* in the dry treatment is associated with low survival of neighbours of other species. This identifies the species as a stronger competitor (Figure 6.6) than indicated by the mass analysis (Figure 6.5). Similarly, *P. nitida* in the dry and medium treatments, while maintaining the pattern of decreasing competitive ability with increasing water supply, is identified as a stronger competitor than shown by the mass analysis. Analysis of survival confirmed the lack of effect of water availability on *P. neriifolia* and the competitive inferiority of *C. capensis* (improving with increased water availability) indicated by analysis of mass increment.

Table 6.5. Two-factor analysis of variance of the diallel competition experiment under dry, medium and wet watering regimes (see text). Target and neighbour scores are given in Table 6.6.

Dry watering regime

Source	df	ss	ms	*F*	*P*
Factorial model	14	23.2	1.6	6.89	0.0001
Error	118	28.4	0.2		
Total	132	51.6			
Target scores	3	2.8		3.94	0.0102
Neighbour scores	3	17.3		24.03	0.0001
Interaction	8	3.0		1.58	0.1383

Medium watering regime

Source	df	ss	ms	*F*	*P*
Factorial model	15	25.1	1.7	6.48	0.0001
Error	160	41.3	0.3		
Total	175	66.4			
Target scores	3	13.4		17.24	0.0001
Neighbour scores	3	8.0		10.32	0.0001
Interaction	9	3.8		1.62	0.1134

Wet watering regime

Source	df	ss	ms	*F*	*P*
Factorial model	15	16.6	1.1	5.63	0.0001
Error	164	32.1	0.2		
Total	179	48.7			
Target scores	3	7.8		13.26	0.0001
Neighbour scores	3	7.8		13.28	0.0001
Interaction	9	1.0		0.54	0.8421

Table 6.6. Relative increases in dry mass of four plant species grown in all pairwise combinations from July 1987 to December 1988 under a dry, medium and wet watering regimes (see text). Target score is the mean dry mass increase of each species grown with all species of neighbours. Neighbour score is the mean dry mass increase of all target species with which a particular neighbour species was grown. Target and neighbour scores are weighted by the numbers of plants within each combination. Target and neighbour scores not significantly different from one another (Student-Newman-Keuls multiple range test, $P < 0.05$) are denoted by common superscripts. P.ne. = *Protea neriifolia*, P.ni. = *Protea nitida*, K.a. = *Kiggelaria africana*, C.c. = *Cunonia capensis*.

Dry watering regime

Target species	Neighbour species				Target scores
	P.ne.	P.ni.	K.a.	C.c.	
P.ne.	1.00	0.56	1.22	1.72	1.21^{a}
P.ni.	1.04	1.00	0.71	2.08	1.12^{a}
K.a.	0.92	1.31	1.00	1.91	1.24^{a}
C.c.	0.27	0.00	0.34	1.00	0.54^{b}
Neighbour scores	0.95^{b}	1.06^{b}	0.94^{b}	1.83^{a}	

Medium watering regime

Target species	Neighbour species				Target scores
	P.ne.	P.ni.	K.a.	C.c.	
P.ne.	1.00	1.08	0.76	0.78	0.92^{b}
P.ni.	0.77	1.00	0.58	0.88	0.85^{b}
K.a.	1.65	1.55	1.00	2.02	1.44^{a}
C.c.	0.84	0.60	0.40	1.00	0.75^{b}
Neighbour scores	1.06^{a}	1.12^{a}	0.76^{b}	1.18^{a}	

Table 6.6 Continued.

Wet watering regime

Target species	Neighbour species				Target scores
	P.ne.	P.ni.	K.a.	C.c.	
P.ne.	1.00	1.40	0.92	1.21	1.11^{ab}
P.ni.	0.56	1.00	0.41	0.71	0.72^{c}
K.a.	1.38	1.44	1.00	1.53	1.28^{a}
C.c.	0.94	1.28	0.56	1.00	0.93^{b}
Neighbour scores	0.98^{bc}	1.25^{a}	0.79^{c}	1.12^{ab}	

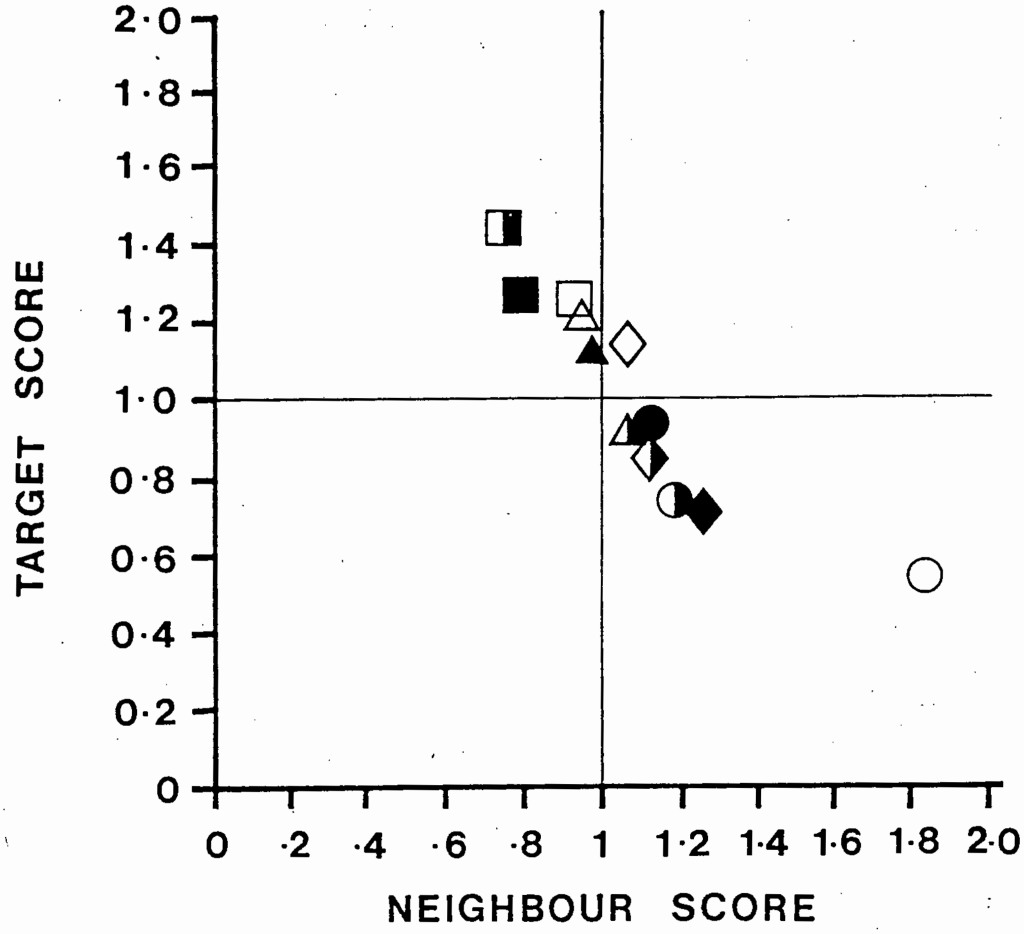

Figure 6.5. Relationships between target scores and neighbour scores determined by the diallel experiment. ○ = *Cunonia capensis,* □ = *Kiggelaria africana,* △ = *Protea neriifolia* and ◇ = *Protea nitida.* Empty, half filled and filled symbols represent dry, medium and wet treatments respectively. Observations with high target scores and low neighbour scores represent strong competitive abilities and observations with low target scores and high neighbour scores represent low competitive abilities.

Table 6.7. Survival of four plant species grown in all pairwise combinations from July 1987 to December 1988 under a dry, medium and wet watering regimes (see text). Numbers show survivors from the initial 10 plants of each species in each combination (20 when grown with the same species). Target score is the total survival of each species grown with all species of neighbours excluding itself. Neighbour score is the total survival of all target species (excluding itself) with which a particular neighbour species was grown. Species abbreviations as in Table 6.6.

Dry watering regime

Target species	Neighbour species				Target survival
	P.ne.	P.ni.	K.a.	C.c.	
P.ne.	16	3	8	10	21
P.ni.	8	20	10	7	25
K.a.	9	10	18	10	29
C.c.	2	0	2	2	4
Neighbour survival	19	13	20	27	

Medium watering regime

Target species	Neighbour species				Target survival
	P.ne.	P.ni.	K.a.	C.c.	
P.ne.	18	9	10	9	28
P.ni.	10	20	10	9	29
K.a.	10	10	20	10	30
C.c.	8	3	9	11	20
Neighbour survival	28	22	29	28	

Table 6.7 Continued.

Wet watering regime

Target	Neighbour species				Target
species	P.ne.	P.ni.	K.a.	C.c.	survival
P.ne.	20	10	10	10	30
P.ni.	10	16	8	8	26
K.a.	10	10	19	10	30
C.c.	10	7	9	6	26
Neighbour survival	30	27	27	28	

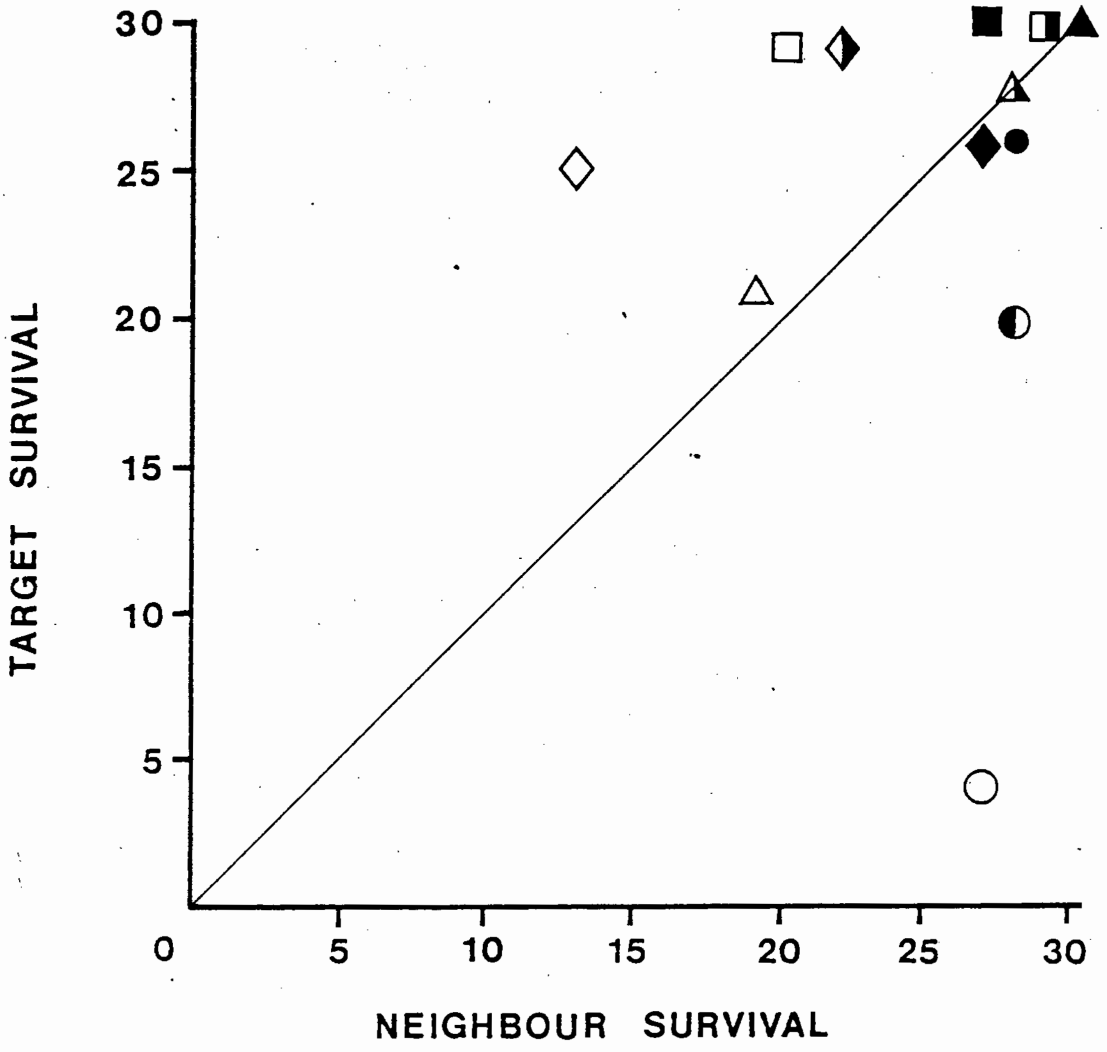

Figure 6.6. Relationships between target survival and neighbour survival determined by the diallel experiment. ○ = *Cunonia capensis*, □ = *Kiggelaria africana*, △ = *Protea neriifolia* and ◇ = *Protea nitida*. Empty, half filled and filled symbols represent dry, medium and wet treatments respectively. Symbols above and below the line of equality represent competitive superiority and inferiority respectively. The degree of superiority or inferiority is denoted by the perpendicular distance from the line of equality.

6.5. Discussion

There is no practical method for precise control of soil moisture in numerous small containers, and the watering regimes applied in these experiments were entirely subjective. The dry regime was determined by the minimum quantity of water which appeared necessary for reasonable seedling survival, and the wet regime provided an excess of water. Although such treatments are not directly applicable to field situations, the wet treatment was equivalent to a riparian situation. The lower mass accumulation of plants in the medium and dry treatments compared with the wet treatment suggests that an objective range of conditions existed among which comparative studies are possible.

Development of forest is influenced by soil nutrient levels as well as soil moisture availability (Campbell 1985). The soil used in this experiment is not too dissimilar to soils of forest and fynbos sites near Stellenbosch (Manders 1990a), and the high nitrogen and phosphorus levels, slight acidity and low aluminium levels, would not discriminate against forest species.

Biomass accumulation of all species in this experiment responded positively to increased water availability. Studies on the growth of individually cultivated species could not discriminate between forest and fynbos species.

No method was found to assess the moisture stress experienced by plants in field situations. Leaves which develop under dry conditions tend to be smaller and more divided, and have a smaller SLA (Larcher 1983). This pattern was not noted in this study and this variable has little potential for use in field studies.

Plant mortality provided the truest explanation for the different establishment abilities of forest and fynbos species. Under conditions of water stress *C. capensis* is not as hardy as fynbos species. *K. africana*, however, has an ability to colonize fynbos areas (Kruger 1984), and this ability was reflected in the survival of all plants of this species in the dry treatment.

The growth experiment explains much of the invasive properties of *Acacia longifolia*. The species had high mortality in the dry treatment, but showed a massive response in biomass accumulation and root development to greater water availability. Such behaviour may explain why the species invades riparian and fynbos areas in mountains, but only wet areas in low-lying areas (Macdonald & Richardson 1986), which have lower rainfall than mountain areas (Campbell 1985).

Diurnal measurements of transpiration, as in the field studies of Richardson & Kruger (1990), failed to differentiate between forest and fynbos species or the invasive *Acacia longifolia* in any of the treatments. Such measurements, whether in the field or under experimental conditions, are made on surviving plants; i.e those which have established. Physiological measurements are usually over relatively instantaneous time intervals, and differences during such periods may be minimal. Biomass accumulation (and survival rates in extreme cases) sum minor differences in physiological activity over the life of the plant, and provide better measures of the ability to establish and competition.

Diallel experiments, whether involving one or several individuals of each species per container, do not include the effects of initial densities and may not reflect behaviour in multispecies mixtures. Caution is also required in the interpretation of RIP values in diallel experiments. Exploitation of a different array of resources may be reflected as apparent competitive superiority. Apparent competitive inferiority, however, may only be attributed to interspecific competition (Wilson & Keddy 1986). The low survival of neighbour species in the dry treatment in the presence of *K. africana* and *P. nitida* indicates that these species may out-compete neighbours for a resource and persist, without enhanced biomass accumulation. The ability of a species to persist in certain conditions may be more important, if habitat amelioration is likely at a later stage, than its initial competitive superiority. Addition of the survival analysis to the mass analysis of the diallel experiment not only confirmed the general pattern of relative competitive abilities, but also enhanced the interpretation of the experiment. The competitive superiority of *P. nitida* compared with *P. neriifolia* in dry conditions and the loss of this ability in wet conditions are consistent with these species' distribution ranges.

P. nitida is associated with dry mountain ranges, whereas *P. neriifolia* is found on southern slopes of moister coastal ranges, only occurring on northern slopes in high rainfall areas (Rourke 1980). The lack of response of *P. neriifolia* to water availability also fits existing knowledge. This species is well recognized in the horticultural industry for its tolerance of different conditions (Vogts 1982). Such confirmation lends credibility to other patterns demonstrated by the diallel experiment, despite the shortcomings of the design discussed above.

The restriction of forest vegetation to riparian and scree habitats is related to the enhanced water availability in these environments. Fynbos species were shown to be superior competitors in xeric habitats. Forest development in xeric habitats may well be precluded by the inability of climax forest species to establish in normal summer drought conditions. Once established however, seedlings of forest pioneers such as *K. africana* can persist in relatively xeric environments. Therefore, given occasional establishment of forest seedlings under favourable circumstances, progressive development of forests away from typical habitats may be expected in the absence of disturbance. To some extent, fynbos species were shown to be inferior competitors in mesic environments. This may prevent invasion of mesic environments by such species and could explain the observed stability of forests in mesic habitats.

CHAPTER 7

EFFECTS OF ARTIFICIALLY ESTABLISHED DEPTH TO WATER TABLE GRADIENTS AND SOIL TYPE ON THE GROWTH OF CAPE FYNBOS AND FOREST PLANTS

CHAPTER 7: EFFECTS OF ARTIFICIALLY ESTABLISHED DEPTH TO WATER TABLE GRADIENTS AND SOIL TYPE ON THE GROWTH OF CAPE FYNBOS AND FOREST PLANTS.[1]

7.1. Abstract

Different responses of forest and fynbos species to water table depth may restrict forests to moist, sheltered habitats in the fynbos region of the Cape. *Cunonia capensis* L. (a mature forest species) and *Kiggelaria africana* L. (forest precursor) and fynbos shrub species *Protea neriifolia* R. Br. and *P. nitida* Miller were cultivated in two sloping troughs, one with fynbos soil and one with forest soil. Fynbos species grew at all depths to water table in the fynbos trough, but *K. africana* grew very poorly and *C. capensis* died in dry situations. Growth of all species, especially the forest species, was greater in the forest soil than in the fynbos soil.

Protea species had taproots reaching to the water table with little development of lateral roots, even where water was plentiful. Forest species had well developed roots in the forest trough, but not in the fynbos trough. Predawn leaf xylem potentials of forest species were similar to fynbos species in both troughs and did not fall below -1.5 MPa.

This study supports the hypothesis that forests are limited to sheltered habitats by dry conditions in exposed habitats. The enhanced development of forest in areas with greater soil moisture availability and more nutrients is related to the establishment requirements of the species. Forest precursors are more able to persist in less optimal conditions than mature forest species.

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[1] Publication status: Manders, P.T. & Smith, R.E. The effects of artificially established depth to water table gradients and soil type on the growth of Cape fynbos and forest plants. Submitted to *S. Afr. J. Bot.*

7.2. Introduction

Gallery forests, where vegetation along watercourses differs in species composition from adjacent communities, are a world-wide phenomenon (Miller & Johnson 1986). The mountain fynbos (shrubland) vegetation of the south-western Cape includes small patches of forest, usually restricted to sheltered habitats such as streambanks, ravines or rock screes (White 1978; Campbell 1985). The environment of the forests is often very obviously different to that of the fynbos. Plant form and litter accumulation in the forests are different to fynbos, there is often abundant soil moisture, and the forests do not usually burn when the adjacent fire-prone fynbos burns (Van Wilgen *et al.* 1990). Two explanations; protection from fire (Moll *et al.* 1980) and greater soil moisture availability (White 1978), based on these obvious differences, are advanced to account for the restricted distribution of forests. However, forest development does occur between fires in fynbos vegetation (Kruger 1984; Masson & Moll 1987), especially where soil moisture or nutrient levels are higher (Campbell 1985).

Vigour and density of forest precursor seedlings have been observed to decline with distance from streambank forest (Kruger 1984). Such observations suggest that the exclusion of forest species in more open areas results from the failure of forest species seedlings to survive seasonal water deficits (White 1978). Greater summer soil water deficits have been demonstrated in hillslope habitats, where soil water potentials at depths of 900 mm frequently dropped below -0.1 MPa, than in riparian habitats where potentials remained above -0.1 MPa (Richardson & Kruger 1990).

Differences between the abilities of forest and fynbos species to survive soil moisture deficits may result from differing efficacies in conservation of water after uptake by the roots, or differing patterns of root development affecting access to soil water. Manders & Smith (in preparation a) studied nursery-grown forest and fynbos plants in limited containers at different levels of water availability and found fynbos species to be inferior competitors in mesic conditions and forest species to be inferior competitors in xeric conditions. Such experiments, however, while testing the effects of water availability and indicating which plants conserve water, exclude the effects of rooting behaviour. This study sought to complement the previous studies by cultivation of the same species in a situation where root development could play a rôle, even though the effects of water availability *per se* might be obscured. We examined the growth and root development of forest and fynbos species on an artificially established gradient of depth to water table. The effects of such gradients will be affected by the capacity of the soil to draw up or retain water, and the nutrient status of the soil may affect forest and fynbos species differently. Therefore the experiment was conducted simultaneously in a fynbos-type soil and in a forest-type soil. The species used in the study were the sclerophyllous fynbos shrub species *Protea neriifolia* R. Br. and *P. nitida* Miller, and the orthophyllous evergreen forest tree species *Kiggelaria africana* (L.) (forest precursor) and *Cunonia capensis* (L.) (a mature forest species).

7.3. Materials and methods

Two troughs were constructed from galvanized steel plating, following the design of Mueller-Dombois (1964). Each trough measured 4.5 m long and 1.25 m wide, 1.0 m tall at the lower end and 2.5 m tall at the taller end. The troughs were open at the bottom and each stood in a galvanized tray filled with water 0.3 m deep. The trays were 60 cm longer and wider than the troughs to permit water circulation. The sides of the trough were supported on 10 mm spacers and a 50 mm layer of 20 mm stones was spread in the bottom of each trough to permit even distribution of water under the soil in the trough. Water was passed continuously through the trays to prevent stagnation. Troughs and trays were painted with bitumen to prevent leakage. The troughs were in a greenhouse to exclude rainfall.

One trough was filled with a forest soil collected from a road cutting through a riparian forest site in the Jonkershoek valley near Stellenbosch. The other trough was filled with a fynbos soil from the Berg River valley near Franschhoek. Soil analyses, using standard laboratory techniques, were carried out by the Saasveld Forestry Research Centre near George.

Seeds of *Protea neriifolia* and *P. nitida* were collected from the Jonkershoek valley during March 1987. Seeds were sown in seedling trays during June and seedlings were transplanted into the troughs on 29 July 1987. Seedlings of *Cunonia capensis* and *Kiggelaria africana* were collected from the field on 29 July 1987 and transplanted into the troughs. Ten seedlings from each species were harvested during transplantation to compare initial sizes.

Ten evenly-spaced rows of eight plants were planted across each trough. Each row comprised two sequences in the order *Protea neriifolia*, *Kiggelaria africana*, *P. nitida* and *Cunonia capensis*. The species starting the sequence in each row was staggered along the trough. Both trough surfaces were watered periodically by sprinkler until the end of 1987, and dead plants were replaced to ensure that the experiment began with a full complement of plants. The only water supply after 4 January 1988 was from the artificially established water table.

Water contents of the soils in the troughs were estimated with a neutron probe (Campbell Pacific Nuclear Corporation Hydroprobe Model 503). Measurements were taken at various depths in four access tubes which had been installed at even spacing centrally along each trough at the time of filling. A mean of five neutron probe readings taken over 1 minute intervals was derived for each depth in each tube on 18 February 1988, 6 July 1988 and shortly before harvesting on 27 November 1988. The neutron probe counts were calibrated for each soil type in galvanized steel drums of 1.5 m diameter with a centrally placed access tube. The soils were saturated and five neutron probe counts were taken at a depth of 30 cm. These counts were corrected for background counts and converted to ratios of full counts in water. Three soil samples, equally spaced around the drum were removed from the same depth at 50 cm from the tube, and volumetric water contents were determined gravimetrically, correcting for bulk density of the soil. The procedure was repeated as the soils dried.

The troughs were kept free of weeds. Pesticides were used to control herbivory by *Acraea horta* L. (Subfamily Acraeinae) butterfly larvae and red spider, both of which affect *Kiggelaria africana* in particular.

Xylem pressure potentials, as a relative indicator of plant water stress, were measured using a Scholander pressure chamber as described by Ritchie & Hinckley (1975). Two leaves on each of the two plants per species in each row were measured in each of the troughs. The period of measurement was between 22h30 on 29 November and 04h00 (before dawn) on the 30 November.

The lower end of each trough was removed in January 1989 and the soil was washed out of the troughs. Plants were removed intact, heights and overall root length were recorded and plants were divided into roots, stem and leaves before drying to constant mass at 70 °C. Lateral root development was described by an expression of root mass per unit root length. Fresh leaf mass and area of twenty leaves per plant were determined before drying to determine the specific leaf area (SLA) from the relationship;

$$\text{SLA} = \frac{\text{leaf surface area (dm}^2\text{)}}{\text{leaf fresh mass (g)}}$$

The relationship between leaf fresh mass and leaf area was used to determine total leaf area from the total fresh mass of the leaves on each plant.

Positions along each trough were defined as; 1 = the lower four rows, 2 = rows 5 and 6 and 3 = the upper four rows, to provide replications for comparisons between plants at different positions. The effects of species and position in the trough on total plant mass, height, total leaf area, leaf size and specific leaf area, and root length and root mass per unit root length were determined for each trough by two-way analysis of variance. Significant interactions between species and position were identified in some of the variables measured. An overall statement for each factor would have little meaning for these variables (Sokal & Rohlf 1968: 315) and significance tests for multiple comparisons are often difficult to interpret (SAS Institute Inc. 1985a: 471). Therefore comparisons between species and treatments were based on 95 % confidence intervals about the means. The allometric relationships between root and shoot development ($R = bS^K$, where R = root mass, S = shoot mass and K is the allometric constant) were determined by principal axis correlation analysis of the logarithmic relationship

$$\log_{10}R = \log_{10}b + K\log_{10}S,$$

based on a matrix of covariance. Values of K greater than unity indicate rootiness and values less than 1 indicate shootiness (Hunt 1978).

7.4. Results

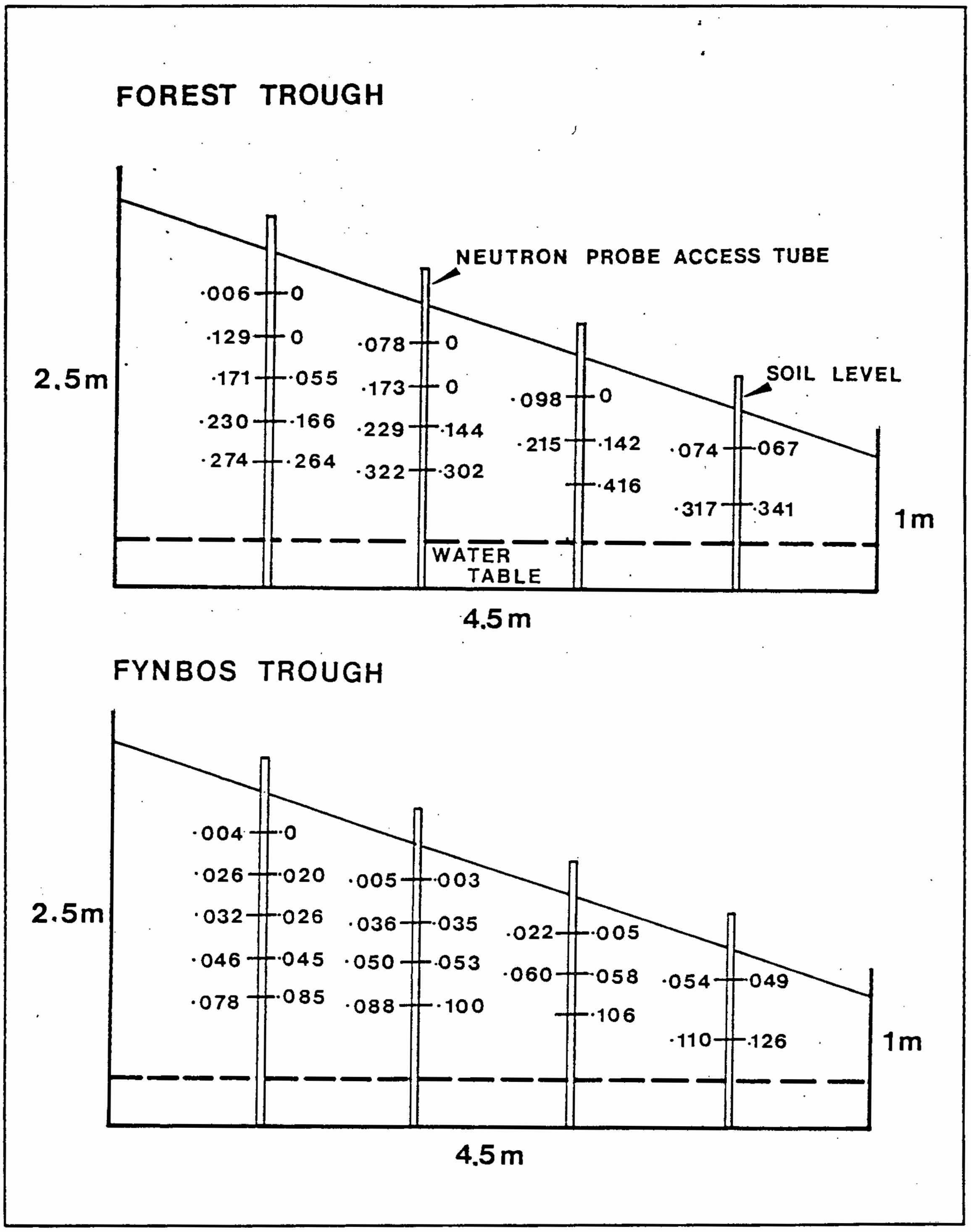
Seedling sizes at time of transplanting into the troughs were reasonably similar (Table 7.1). Since plants were generally several orders of magnitude larger than their initial sizes when harvested, variables were not adjusted for differences in initial size.

Table 7.1. Sizes of seedlings when transplanted into the troughs. Ten seedlings were sampled in each species.

SPECIES	PLANT HEIGHT (mm) (S.E.)	ROOT LENGTH (mm) (S.E.)	TOTAL DRY MASS (mg) (S.E.)
Protea neriifolia	16.0 (0.6)	49.1 (2.3)	21.6 (1.3)
Protea nitida	24.1 (7.3)	49.3 (4.7)	100.0 (34.0)
Kiggelaria africana	35.3 (1.7)	117.7 (9.3)	34.9 (3.1)
Cunonia capensis	25.3 (2.7)	46.5 (6.4)	27.0 (14.0)

The soils in the troughs differed in their capacity to absorb water from the water table (Figure 7.1). The forest soil at the deep end of the trough was drier near the surface than the fynbos soil in the corresponding situation. At depths of 75 cm and deeper, however, the forest soil held considerably more water than fynbos soil owing to the finer particle size and higher organic carbon content in the forest soil (Table 7.2).

The forest soil had a greater total nitrogen and cation content than the fynbos soil (Table 7.2). Plant mass and height were greater on the forest soil than on the fynbos soil. Plant mass in both soil types, root length in the fynbos soil trough and total leaf area in the forest soil trough did not vary with position in the trough, but differed between species.


FOREST TROUGH

FYNBOS TROUGH

Figure 7.1. Soil moisture content at various depths in troughs of forest and fynbos soils with gradients of depth to water table. Numbers to the left and right of each neutron probe access tube show the volumetric water content ($cm^3.cm^{-3}$) in July and November 1988 respectively.

Table 7.2. Properties and nutrient contents of forest and fynbos soils on which forest and fynbos species were cultivated on artificially-established gradients of depth to water table. Standard errors of the means are given in brackets. *n* = 4 for all variables. NS, *, ** and *** denote no significant difference between means and significant differences between means at $P < 0.05$, 0.01 and 0.001 respectively (Mann-Whitney *U* test).

Soil property		Forest trough	Fynbos trough	
Texture:	Cg (%)	33.8 (0.8)	34.8 (1.9)	NS
	Mg (%)	15.0 (4.0)	27.2 (5.4)	NS
	Fg (%)	11.0 (1.7)	16.8 (2.6)	NS
	VFg (%)	2.8 (0.6)	4.8 (0.8)	NS
	CSi (%)	18.5 (2.6)	11.2 (6.6)	NS
	FSi (%)	12.8 (2.3)	3.8 (0.6)	*
	Clay (%)	6.2 (1.1)	1.5 (0.5)	*
pH (H_2O)		5.4 (0.1)	5.8 (0.1)	*
Organic carbon (%)		7.5 (1.4)	0.8 (0.2)	*
Total nitrogen (μg/g)		1763.0 (240.7)	89.0 (21.8)	**
Bray No 2 phosphorus (μg/g)		11.3 (3.6)	14.3 (2.4)	NS
Aluminium (μg/g)		0.4 (0.1)	0.0 (0.0)	NS
Potassium (μg/g)		67.0 (10.5)	8.5 (1.2)	*
Calcium (μg/g)		150.2 (24.8)	46.8 (8.5)	*
Magnesium (μg/g)		33.8 (3.0)	2.8 (0.5)	**
Sodium (μg/g)		56.5 (3.8)	14.8 (3.0)	***

In general, the effects of species were stronger than the effects of position (Table 7.3). In the forest soil *Kiggelaria africana* dominated in all positions. *Cunonia capensis*, close to the water table at the bottom end and in the middle of the forest trough also grew better than the fynbos species, but was smaller at the top end of the trough (Figure 7.2). Forest species persisted to some extent in the top end of the fynbos trough, but the mass of these plants was negligible and further mortality, especially in *Cunonia capensis*, seemed likely at the time of harvesting (Table 7.4). Growth of fynbos species on the fynbos soil also declined at the top end of the trough, but there was little mortality and those plants which remained appeared to be established by the time of harvesting. *Kiggelaria africana* in the forest trough showed no mortality, and mortality of *Cunonia capensis* was very much lower, even at the top end of the trough, than in the fynbos trough. A few individuals of the fynbos species died in the forest trough, in a pattern not obviously related to the gradient of depth to water table.

Table 7.3. F values of two-way analysis of variance between position along the gradient and species cultivated along artificially-established gradients of depth to water table on fynbos and forest soils. ***, ** and * denote significance at $P < 0.0001$, 0.01 and 0.05 respectively.

Trough	Variable	Position	Species	Position x Species
Forest	Total plant mass	2.5 NS	54.7***	1.5 NS
	Plant height	10.1**	143.2***	1.6 NS
	Total leaf area	1.3 NS	20.9***	0.6 NS
	Leaf size	11.2***	76.8***	14.5***
	Specific leaf area	8.1**	205.0***	11.7***
	Root length	10.5***	73.2***	1.4 NS
	Root mass/length	10.6***	28.3***	2.9*
Fynbos	Total plant mass	3.0 NS	12.5***	1.7 NS
	Plant height	4.1*	13.0***	2.1 NS
	Total leaf area	4.2*	12.6***	2.4*
	Leaf size	15.6***	203.4***	13.1***
	Specific leaf area	18.9***	522.5***	42.3***
	Root length	0.3 NS	12.1***	0.5 NS
	Root mass/length	10.3**	10.0***	2.8*

Total leaf area per plant (Figure 7.3) showed a very similar pattern of differences between species, positions and soil types to that shown by plant mass. *Cunonia capensis* leaves in the forest trough and *C. capensis*, *Kiggelaria africana* and *Protea neriifolia* in the fynbos trough followed the expected pattern and were smaller in the upper positions than in

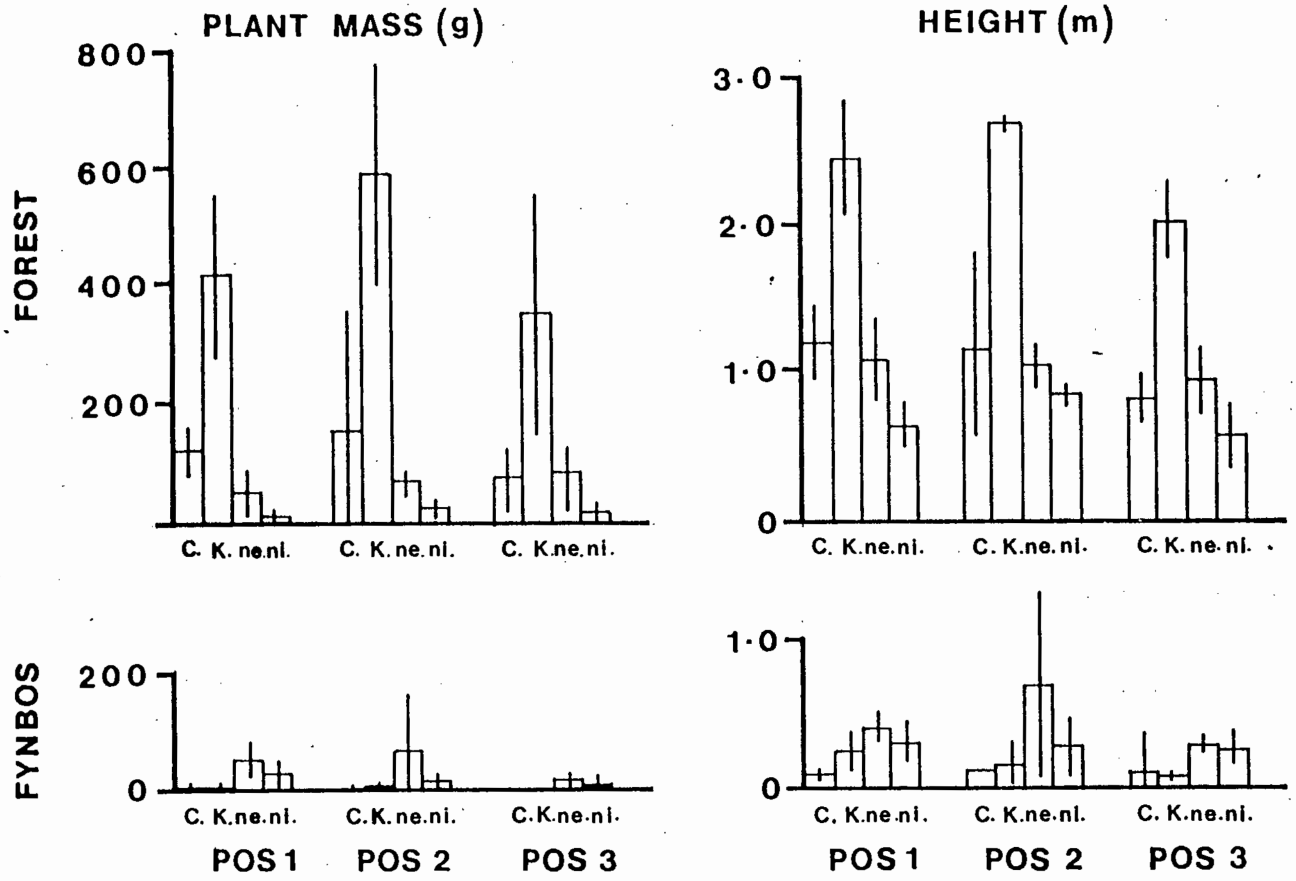


Figure 7.2. Total plant mass and height of forest and fynbos plants cultivated from seedlings in July 1987 to January 1989 on two troughs, one with forest soil and one with fynbos soil, with gradients of depth to water table. C = *Cunonia capensis*, K = *Kiggelaria africana*, ne = *Protea neriifolia* and ni = *Protea nitida*. Position 1 = rows 1-4 (nearest the water table), position 2 = rows 5-6, and position 3 = rows 7-10 (furthest from the water table). 95 % confidence limits about the means are represented by vertical lines.

Table 7.4. Survival of plants in each species cultivated along artificially-established gradients of depth to water table on fynbos and forest soils.Position 1 (nearest the water table) = rows 1-4, n=8; position 2 = rows 5-6, n=4 and position 3 (furthest from the water table) = rows 7-10, n=8.

Trough	Species	Survival (%)		
		Pos. 1	Pos. 2	Pos. 3
Forest soil	*Cunonia capensis*	100	75	88
	Kiggelaria africana	100	100	100
	Protea neriifolia	75	100	100
	Protea nitida	100	100	88
Fynbos soil	*Cunonia capensis*	75	50	25
	Kiggelaria africana	100	75	62
	Protea neriifolia	100	100	100
	Protea nitida	100	100	100

position 1. The other species in each trough, however, showed no or even the opposite trend. Leaves which develop under dry conditions tend to be smaller and more divided, and have a smaller SLA (Larcher 1983) but no such pattern occurred in any species in the forest trough, and the opposite trend was shown by all species in the fynbos trough.

Root development differed between species (Figure 7.4). In the trough of forest soil *Kiggelaria africana* had considerable lateral root extension and the roots grew down to the water table. *Cunonia capensis* also had many secondary roots, but these were shorter and finer, and those in the upper rows did not extend to the water table. Both Protea species had relatively very little lateral root development, but had a single main root which usually reached the water table before dividing to a limited extent. Overall root length confirms these patterns and the relationship between root mass and root length demonstrates the differences in lateral root development (Figure 7.5). The roots of the Protea species in the fynbos trough were very similar to those in the forest trough and usually extended to the water table, whereas the forest species had very poorly developed roots.

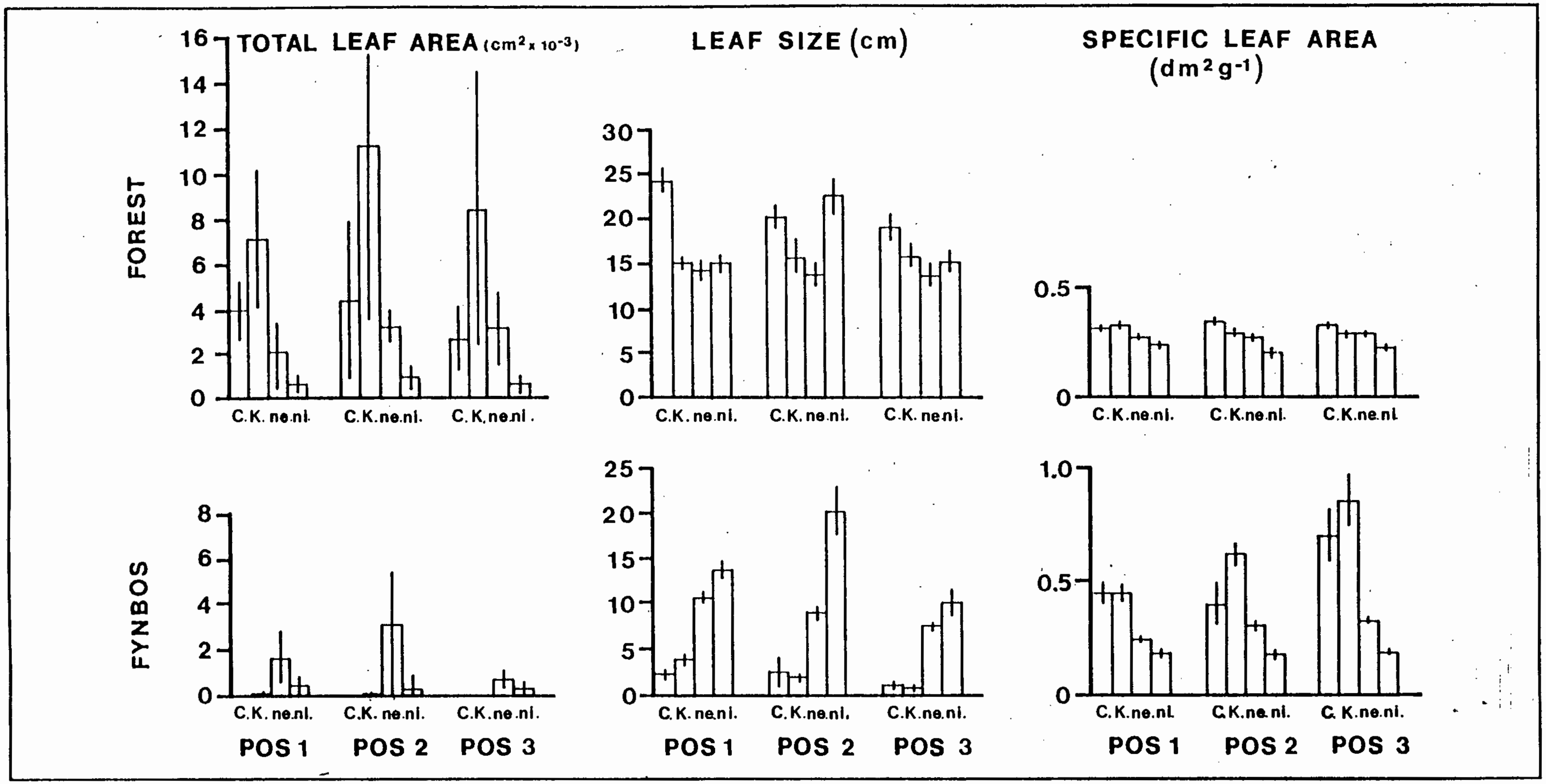


Figure 7.3. Total leaf area per plant, mean leaf size and specific leaf area of forest and fynbos plants cultivated from seedlings in July 1987 to January 1989 on two troughs, one with forest soil and one with fynbos soil, with gradients of depth to water table. C = *Cunonia capensis*, K = *Kiggelaria africana*, ne = *Protea neriifolia* and ni = *Protea nitida*. Position 1 = rows 1-4 (nearest the water table), position 2 = rows 5-6, and position 3 = rows 7-10 (furthest from the water table). 95 % confidence limits about the means are represented by vertical lines.

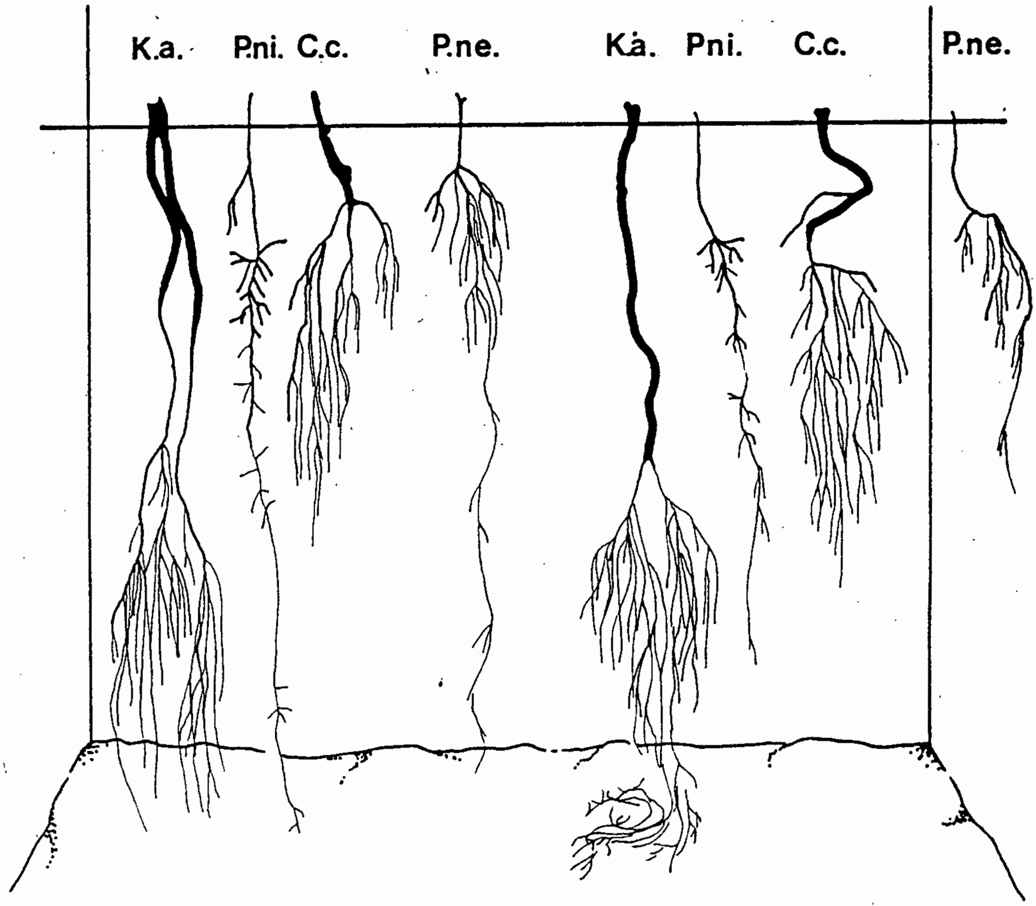


Figure 7.4. Root development of forest and fynbos species in the row on the forest soil furthest from the water table. Plant stems are connected to a wire at the original soil level to facilitate excavation. The ground level is the level of the permanent water table. K.a = *Kiggelaria africana*, P. ni. = *Protea nitida*, C.c. = *Cunonia capensis*, and P.ne. = *Protea neriifolia*.

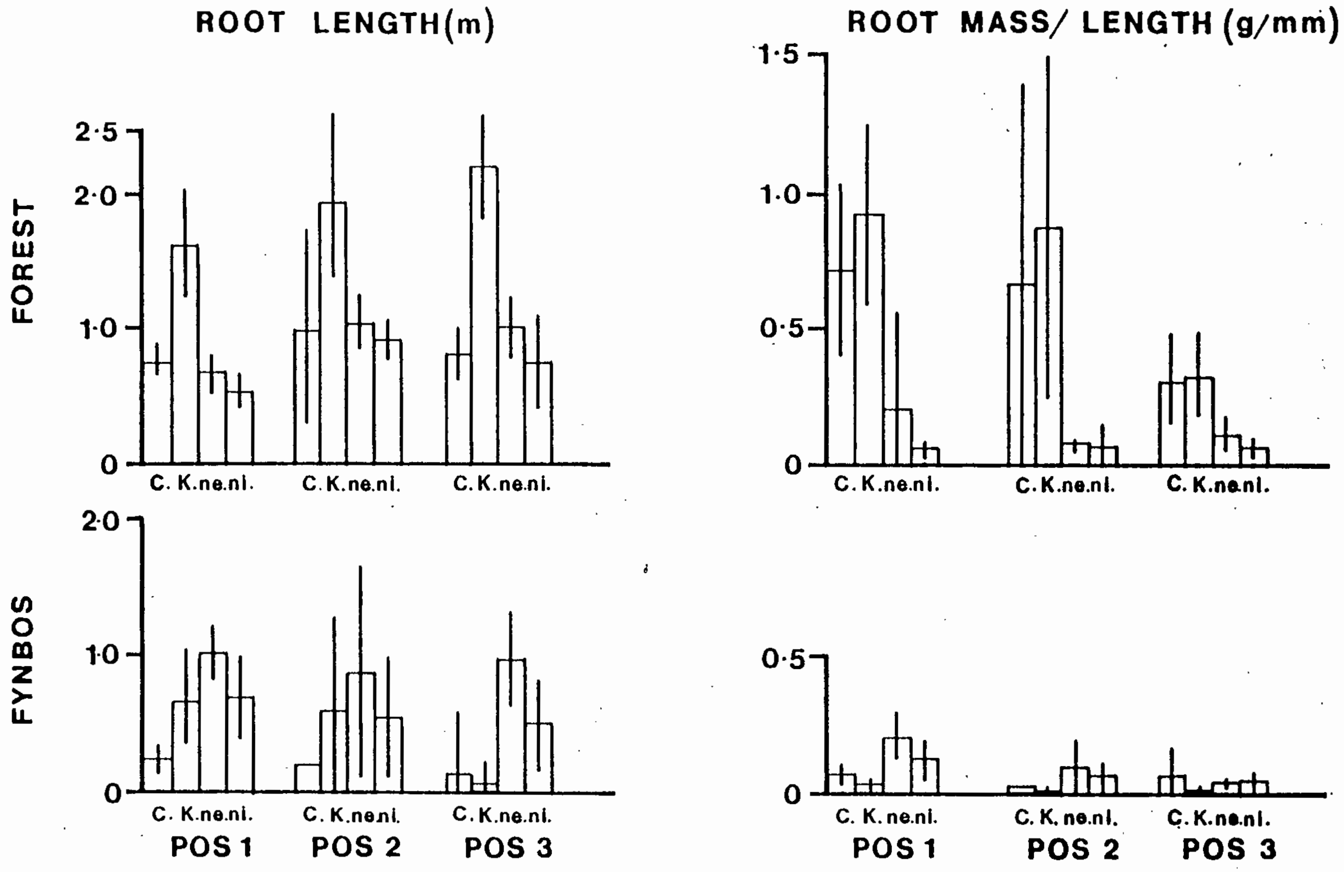


Figure 7.5. Root length and the root mass per unit root length (a measure of lateral root development) of forest and fynbos plants cultivated from seedlings in July 1987 to January 1989 on two troughs, one with forest soil and one with fynbos soil, with gradients of depth to water table. C = *Cunonia capensis*, K = *Kiggelaria africana*, ne = *Protea neriifolia* and ni = *Protea nitida*. Position 1 = rows 1-4 (nearest the water table), position 2 = rows 5-6, and position 3 = rows 7-10 (furthest from the water table). 95 % confidence limits about the means are represented by vertical lines.

The relationship between root and shoot development of plants in the forest trough differed between the plants in the lower rows and those in the upper rows, with all species tending to less shootiness in the upper rows. All species in all positions, however, had a very strong tendency to shootiness (Table 7.5). There was no pattern in the relationship between shoot and root development of forest species in the fynbos trough, probably as a result of their erratic growth. There was no clear pattern for fynbos species in this trough, but some of the plants had very strong root development.

Table 7.5. Slopes (K) of principal axes describing the allometric relationship between root and shoot mass ($\log_{10}R = \log_{10}b + K\log_{10}S$) for plants in each species in the lower four rows (those nearest the water table) and the upper four rows in two troughs with gradients of depth to water table and different soil types. Figures in brackets show the proportion of variance explained by the eigenvalue of the covariance matrix of the first principal axis.

Trough	Species	Position	
		Rows 1-4	Rows 7-10
Forest soil	*Cunonia capensis*	0.08 (0.87)	0.32 (0.99)
	Kiggelaria africana	0.09 (0.95)	0.13 (0.98)
	Protea neriifolia	0.18 (0.94)	0.39 (0.96)
	Protea nitida	0.20 (0.97)	0.38 (0.99)
Fynbos soil	*Cunonia capensis*	0.32 (0.87)	0.32 (0.99)
	Kiggelaria africana	2.98 (0.98)	0.88 (0.60)
	Protea neriifolia	0.13 (0.77)	2.05 (0.92)
	Protea nitida	1.61 (0.99)	1.23 (0.96)

There was no evidence of water stress for any of the species in the forest trough (Figure 7.6) although in the deeper soils, the forest species had slightly higher (more negative) water potentials than the fynbos species. Water potentials of all species in the fynbos trough were low and

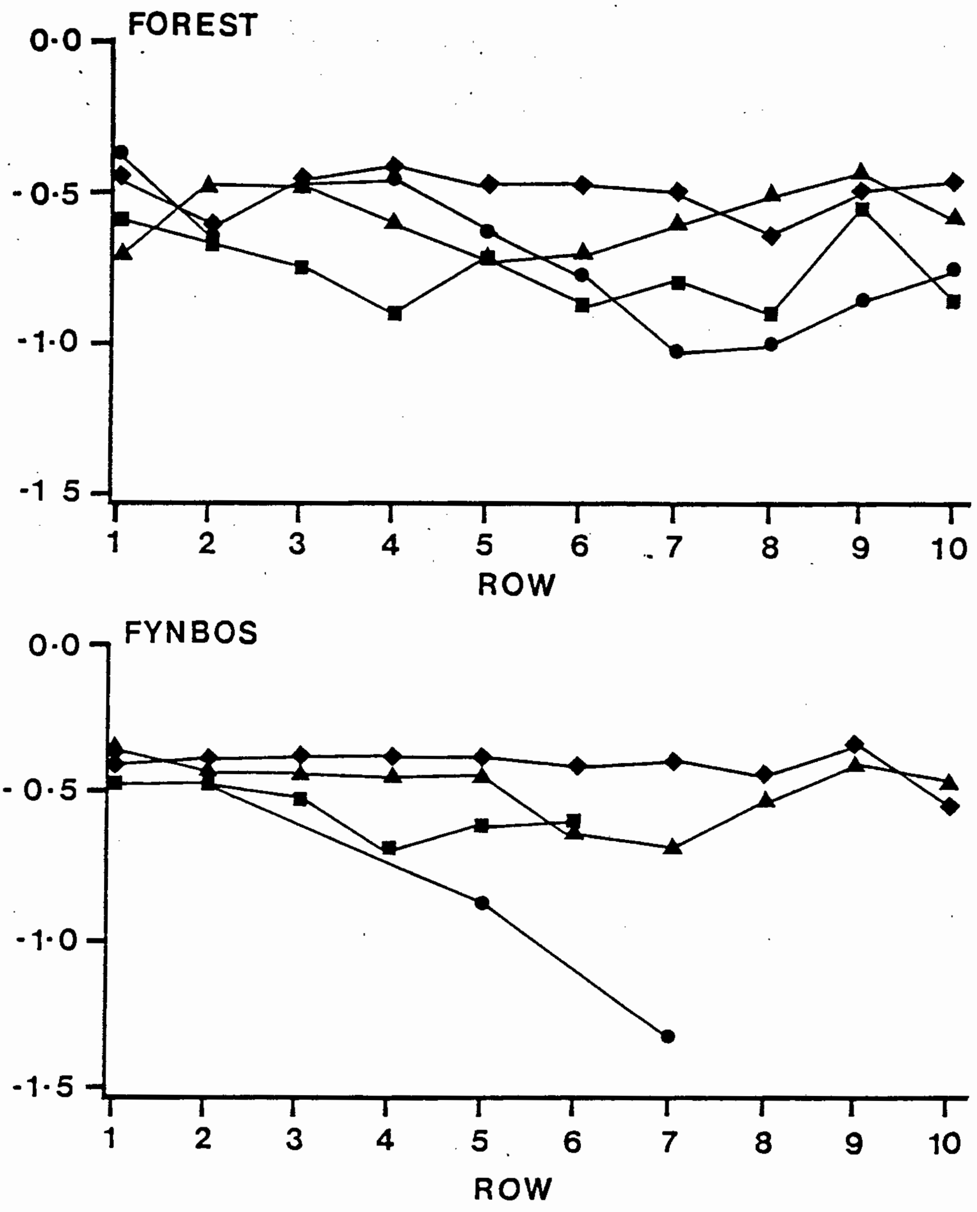


Figure 7.6. Pre-dawn leaf xylem pressure potentials of forest and fynbos species cultivated in two troughs, one with forest soil and one with fynbos soil, with gradients of depth to water table. Row 1 is closest to the water table and row 10 furthest from the water table. ● = *Cunonia capensis*, = *Kiggelaria africana*, ▲ = *Protea neriifolia* and ◆ = *Protea nitida*.

differences were almost negligible between the fynbos and forest species. Forest species which survived in the upper rows of the fynbos trough had higher, although not excessive, water potentials (up to -1.35 MPa).

7.5. Discussion

Both forest and fynbos species responded positively to the greater nutrient availability in the forest soil. The response of the forest species, however, was far greater than that of the fynbos species. The smaller particle sizes and greater carbon content of the forest soil resulted in superior water conduction and retention than in the fynbos soil. Similar differences between the water contents of a sand and a loamy sand on artificially-established gradients of depth to water table have been noted by Mueller-Dombois & Sims (1966). Although the forest soil was drier near the surface than the fynbos soil, the enhanced growth permitted greater or more rapid root development, resulting in utilization of the greater water availability in the deeper soil than found in the fynbos soil.

The rooting behaviour of a species is related to the habitat in which each usually occurs and may influence its ability to exploit different habitats. *Cunonia capensis* is usually found in or close to riparian habitats and did not show changes in root development in response to soil moisture conditions. *Kiggelaria africana* is sometimes found away from riparian areas (Kruger 1984). Although this species grew very well close to the water table, it developed longer roots with less lateral development where the soil moisture was deeper, without reduction in plant mass. The root development of the fynbos species in this study was similar to field studies where Proteaceae had tap roots up to 3.5 m deep, with lateral roots concentrated in the upper soil (Higgins *et al.* 1987). Fynbos species showed no response in root development, such as enhanced lateral root development, which would enable them to take full advantage of abundant water supplies.

Attempts to gauge the effects of water supply through the measurement of variables such as leaf size and specific leaf area proved fruitless. This failure indicates that there is compensation for the lower water supply (probably stomatal closure and slower growth) which are not expressed in terms of plant form.

Differential root development between plants in different situations may also contribute to the lack of plant moisture stress indicated by pre-dawn leaf xylem water potentials. Although the Fynbos Biome is described as having a summer moisture deficit, plant moisture stress as indicated by xylem pressure potentials has not been detected during the dry summer (Miller *et al.* 1983). Similarly Richardson & Kruger (1990) were unable to detect differences between riparian and hillslope species during summer. The pre-dawn leaf xylem pressure potentials measured on Protea species in this experiment were within the range for proteoid species measured over summer in high and low rainfall areas by Miller *et al.* (1983) and on a hillslope by Richardson & Kruger (1990). The potentials of the Proteas in the troughs, however, are greater (more negative) than those measured for proteoids after winter rain (Von Willert *et al.* 1989), suggesting that the gradients in the trough approached the levels of water availability experienced by plants in the field during summer, and that those plants furthest from the water table did experience some stress.

A complementary study conducted on the species in this experiment (Manders & Smith in preparation a) indicated that fynbos species are inferior competitors in mesic environments, possibly explaining the exclusion of fynbos species from forest communities. Some evidence - a tendency to less growth and some mortality in the most mesic positions in the trough of forest soil - was found in this experiment to confirm this observation. This lack of competitive ability in mesic environments may result from low plasticity of the roots in response to abundant water supplies.

The assertion by Campbell (1985) that development of forests in the Fynbos Biome, in areas other than riparian or scree habitats, will be enhanced by high nutrient levels and water availability is supported by this study. This experiment approximated a field situation in which seedlings germinate in autumn, become established during winter, and then are subjected to a summer drought. High nutrient levels may contribute to forest seedling survival by enabling rapid root growth in the wet winter soon after germination. Seedlings with well-developed root systems stand more chance of surviving the following summer drought than poorly-developed seedlings on nutrient-poor soils. At the same time the study demonstrated that forest species, particularly those regarded as forest precursors, are at least able to persist under very xeric conditions. Plants which manage to persist through the first few summer droughts may be able to develop when larger, or take advantage of any habitat amelioration in later stages of succession. Therefore forest communities could develop in many fynbos areas in the absence of fire.

PART 4

CONCLUSION AND CRITIQUE

CHAPTER 8

CONCLUSION

CHAPTER 8: CONCLUSION

Previously, forest communities in the southwestern Cape have been considered to have different edaphic and climatic requirements to fynbos communities (Taylor 1978; White 1978; Campbell 1985). This thesis considers whether forest and fynbos communities are different successional stages of the same vegetation type in juxtaposition. The thesis proposes that the relations between forest and fynbos follow the conceptual model of succession in Figure 8.1. Several of the stages and transitions of the model have been described in other vegetation types. Regeneration of rainforest on clearfelled land, for example, involves the introduction of wind- and bird-dispersed seeds, and amelioration of microclimate (Read & Hill 1983). Woody plant encroachment in grasslands has been described as a process of nucleation (Archer 1989), and invasion of sagebrush by pinyon and juniper has been ascribed to protection from fire (Blackburn & Tueller 1970). The model assumes that disturbance by fire is part of the cycle, and that processes exist whereby the system is re-set after the disturbance. In the absence of fire the model predicts that a semi-stable forest community will be established eventually, but that shrublands may predominate under a regime of frequent disturbance.

Such an interpretation of vegetation development has particular theoretical and practical implications for disturbance-driven systems such as those in mediterranean-climate regions. The process of vegetation development may be held at different levels by different disturbance regimes, leading ultimately to different paths of landscape development (Naveh 1982). Nevertheless, apparently stable shrublands may revert to forest if disturbance regimes are altered, as noted in the Mediterranean Basin (Specht, 1969; Debussche *et al.* 1980).

There are essential assumptions in the model; mature forests are stable under normal fire regimes but developing forest is susceptible to disturbance, forest development is re-initiated after disturbance and development of forest components in fynbos is governed by facilitation.

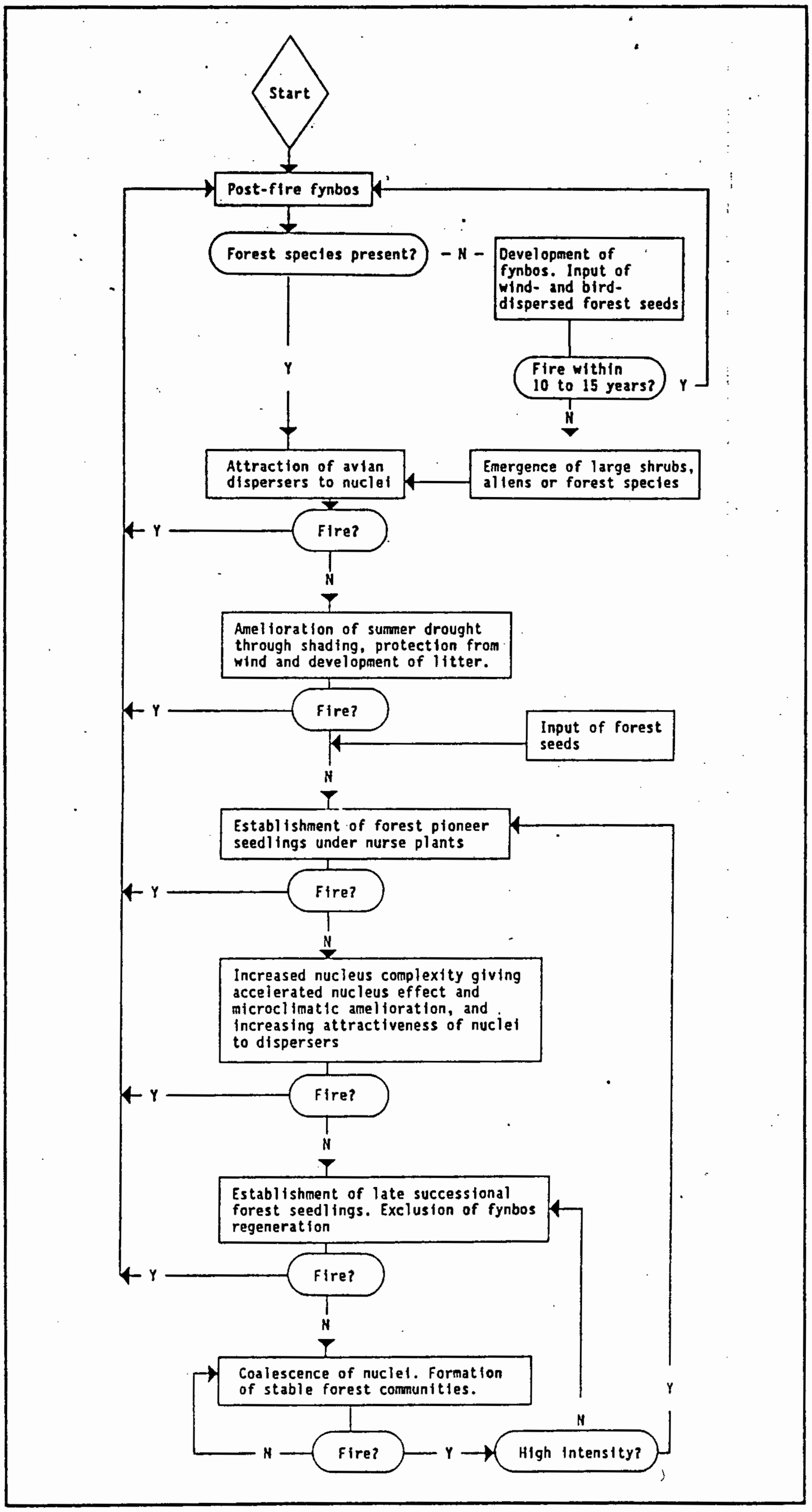


Figure 8.1 A conceptual model of the development of forest species within fynbos communities. The model assumes the availability of forest seeds. Post-fire age increases as the model proceeds from the start situation.

8.1. Fire and the stability of forest boundaries

Forest canopies have higher moisture contents, sparser crowns, are more separated from the litter layer than fynbos canopies and are therefore less likely to burn than shrublands. Consequently forest communities seldom burn unless fire intensities are very high (Van Wilgen *et al.* 1990). When forest canopies are scorched or forests are burnt, regeneration is by resprouting (Van der Merwe 1966) and the community survives more or less intact. The stability of established forest stands in Swartboskloof is demonstrated by aerial photograph records (Chapter 1) and the response to the fire of March 1977 (Chapter 2). Given an equal fire intensity, the size of a forest nucleus or stream bank forest will determine the effect of the fire. As forests develop and nuclei coalesce, higher intensity fires are required to remove the forest, and there will be a greater probability of the forest remaining intact or being partly damaged only.

Fire intensity, rather than plant size, appears to be the factor controlling the mortality of forest plants in the transition zones between forest and fynbos or within the fynbos. Studies on *Cunonia capensis* in Swartboskloof showed that survival of partly damaged plants was related to plant size, but that fire intensity was the overriding factor. No *Cunonia capensis* which had been burnt (all leaves burnt off in the fire) resprouted after the fire (Chapter 2).

Trees in forest patches are sometimes killed in high intensity fires. Since no forest species store seeds in the canopy for post-fire release, post-fire regeneration after destruction of the canopy must come from soil-stored seed banks or rely on colonization from distant sources. Forests in Swartboskloof had smaller soil seed banks than nearby fynbos (Chapters 3 & 4). Similar numbers of species occurred in each vegetation type, but seed densities were higher in the transitional and fynbos zones than in the forest. This follows predictions that vegetation types with low frequencies of disturbance are unlikely to have extensive soil seed banks (Thompson 1978), particularly where the vegetation is not likely to be destroyed in the lifetime of its seeds (Young *et al.* 1987). There was no evidence of any effect of the fire on the numbers of species and seeds present. The seed banks in each vegetation type, especially in the forest, contained many seeds from the other vegetation types, suggesting that a transitional or fynbos community will develop after destruction of the forest canopy. Many of the non-forest seeds in the forest were hard seeds of typical transitional zone species of the Fabaceae, stored deep in the soil, which would contribute to the community after a very intense fire. In the event of removal of forest plants by fire, therefore, the system is likely to be re-initiated by soil-stored seed.

There were some differences in processes related to seed dispersal and soil storage between the fynbos and forest soil seed banks (Chapter 4). Seeds dispersed by ants are not well represented in the forest, whereas bird dispersal is far more important in the forest than in the fynbos. Although such differences may contribute to the maintenance of distinct communities, no species were excluded from the seed banks of any of the vegetation types. Therefore factors such as germination and establishment requirements, and not the limits to seed dispersal, are important in determining community boundaries.

8.2. Limits to the development of forest species in fynbos.

8.2.1. Seed dispersal

The movement of seeds between vegetation types was suggested in the study of soil seed banks (Chapter 4). The seeds of 40 % of forest species are dispersed by vertebrates, mostly birds rather than mammals, in contrast with less than 10 % of fynbos species which are vertebrate dispersed. Wind dispersal is the next most prevalent mode, with 32 % of forest species' seeds dispersed in this manner (Knight 1988). The avifauna of Swartboskloof contains nine species that regularly eat and disperse seeds of forest tree species (Richardson & Fraser in press). Most of the species forage in both forest and fynbos, moving frequently between vegetation types.

Dispersal of forest seeds by birds into fynbos areas is considered to be dependent on the development of perches such as fully-developed shrubs or fruit-bearing shrubs in the fynbos (Masson & Moll 1987; Knight 1988).

The degree of seed deposition below a perch is governed by its features such as height, size and complexity and the fruit it bears (McClanahan & Wolfe 1987). In the studies in Chapter 4, the occurrence of seeds in the traps in the transitional and fynbos zones was related to the type of perch above the trap. Surprisingly, however, branches of dead shrubs appear to act as perches and effective perches are not necessarily a fruiting species or a large tree, especially in areas fairly close to the seed source. More distinct perches are likely to attract avian dispersers further from the forest. This study showed that dispersal of forest species into fynbos occurs immediately after fire for both wind- and bird-dispersed species. Therefore colonization of fynbos by forest species soon after fire is not limited by seed dispersal and forest development may be re-initiated by the input of seeds after removal from an area.

8.2.2. Germination requirements

Seeds of all communities at site A in Swartboskloof occur in the seed banks of the other communities, and seed dispersal crosses community boundaries (Chapter 4). Yet almost all post-fire regeneration on the transects occurred in burnt sub-plots. Most regeneration comprised fynbos and transitional zone species. The small amount of forest regeneration which occurred in the first year after the fire was almost exclusively in the unburnt sub-plots in the forest (Chapter 2).

The differences in regeneration patterns may be related to different germination requirements of the species in each vegetation type. Regeneration of fynbos and transitional zone species is closely coupled to disturbance (*sensu* Grubb 1988). Germination and establishment requirements may be related directly to fire (in provision of germination cues, seed release cues or decreased competition) or indirectly via the habitat (soil moisture, cover or litter accumulation). Germination cues for soil stored seeds may include increased diurnal fluctuations in soil temperature as a result of the removal of the canopy (Thompson *et al.* 1977).

Reciprocal sowings showed, however, that germination of the species studied is more or less equally successful in all vegetation types, but establishment differs between vegetation types (Chapter 5). Establishment of seedlings of forest species is not dependent on high soil moisture availability alone. Conditions of forest soil (i.e. of higher nutrient status than the fynbos soil), litter and added water in the open were not sufficient to achieve survival as high as non-watered seedling boxes with forest soil and litter under the canopy of a tree. Similarly, forest seedlings under the tree required forest soil and litter as well as added water to achieve maximum survival (Chapter 5).

8.2.3. Facilitation

If the development of forest in fynbos between fires is not limited by seed dispersal or germination requirements, but by differential abilities of seedlings to survive in the open, there must be some factors which permit such development in some places on some occasions. The study in Assegaiboschkloof sought to identify features characterizing the habitat of forest seedlings which have developed in fynbos, and whether these are related to the development of the fynbos vegetation (Chapter 5). Habitat features may be related to amelioration of drought stress, including the mulching effects of litter, nurse plants, protection from radiation and wind, and reduced competition for water owing to reduced herbaceous cover. Forest seedlings were associated with tall ground layer vegetation, projected plant cover in excess of 50 % and a well developed litter layer. The importance of perches in forest development was demonstrated by the paucity of seedlings in the open relative to numbers under perches. Perches were not necessarily fruit-bearing species, and many forest seedlings were found under fynbos shrubs. Perch height was important, and fruiting species less than 1.5 m tall, such as *Rhus tomentosa*, *R. angustifolia* and *Diospyros glabra*, supported relatively few seedlings.

In Chapter 5 it is proposed that the groups of forest species which are often present in fynbos act as nuclei of forest development (*sensu* Yarranton & Morrison 1974). Forest regeneration is enhanced in such nuclei and the development of forest communities involves their coalescence (Janzen 1988). Studies in Assegaiboschkloof indicated the presence of nucleation processes in that species richness was related to nucleus size and type. This suggests that the development of perches, maturing fynbos vegetation and nurse plants facilitate the development of forest species in fynbos.

8.3 Factors influencing forest development

Having established the processes involved in the development of forest, The thesis examines those factors (soil nutrients and soil moisture) which may influence the operation of the processes. In many other vegetation types herbivory is a determinant factor, interacting with other factors in the dynamics of community boundaries (for example Blackburn & Tueller 1970; Davis & Mooney 1985). There is no evidence, however, of any significant influence of herbivores on the dynamic balance of forest and fynbos vegetation.

8.3.1. The rôle of nutrients in forest development

The availability of soil nutrients is a major factor affecting distribution of vegetation in mediterranean-type ecosystems (Specht & Moll 1983). Campbell (1985) and Campbell & Werger (1988) predict that high tree cover in the Fynbos Biome is associated with relatively nutrient-rich soils with high moisture availability. The prediction that forests occur on soils richer in nutrients than nearby fynbos has been supported by several studies, but the magnitude and trend of differences between the soils of forest and fynbos vegetation are very site-specific (Cowling 1984; Van Daalen 1984; Lambrechts 1986; Masson & Moll 1987).

Soils in the forest in Swartboskloof were of a finer texture, less acidic, and were consistently richer in nutrients than the other vegetation types. Aluminium levels were lower than in the fynbos, and very much lower than in the transitional zone (Chapter 2). Similar differences, with higher levels of available phosphorus and lower levels of aluminium in the forest than in the fynbos (although inorganic levels of phosphorus were similar) have been reported from the southern Cape (Lambrechts 1986). The Swartboskloof study differed from earlier studies in that the forest and fynbos samples were taken from within a few meters of each other. This indicates strongly that the differences in soil features at this scale are not related to differences in parent material, but are a result of different nutrient cycling processes operating within each community. It has been suggested that "under similar soil, terrain and climate conditions forest communities will maintain a higher nutrient status in the soils, especially in the surface horizons, compared with fynbos communities" (Lambrechts 1986). Therefore, nucleation may include facilitation through enhanced nutrient status under groups of forest species. The influence of changing species composition during to succession to forest on soil properties has been noted elsewhere (Ellis & Graley 1987). Once different soil chemistry has been brought about by vegetation changes, such differences may affect the establishment abilities of species, thus maintaining the identity of the developing community.

8.3.2. The rôle of soil moisture in forest development.

Forests in the south-western Cape are considered to comprise mesophytic species, confined to sheltered or riparian habitats by the water stress experienced by these species in adjacent fynbos areas (White 1978). In particular, the restriction is considered to reflect intolerance of summer moisture deficits associated with the summer drought of the mediterranean-type climate. Despite the mediterranean rainfall regime, Swartboskloof receives 12.4 % (200 mm) of its annual rainfall during the driest months of December through March (Wicht *et al*. 1969) and soil water potentials are not excessive, even on hillslopes (Richardson & Kruger 1990). Surface soil (the top 5 cm) moisture content, however, was shown to be higher in the forest than the fynbos during summer (Chapter 2).

In general, fynbos in areas with precipitation greater than 650 mm per year cannot be regarded as a drought-stressed vegetation (Miller *et al*. 1983). Adults of mesophytic species in riparian habitats and xerophytic species in hillside habitats exhibit very similar stomatal behaviour, net photosynthesis and water use efficiencies, and do not reflect any selective influence of contrasting soil moisture regimes (Richardson & Kruger 1990). The absence of differences in water stress between adult riparian and hillslope plants, and that only surface soils in fynbos dry out more than forest soils, suggest that discrimination between forest and fynbos species in non-riparian areas are limited to the establishment phase. Soil moisture deficits in fynbos soil surfaces would be heightened after fire, due to increased radiation and wind activity resulting from lost vegetation cover. These effects would be greatest in surface soils in which seedlings are rooted. Therefore, the facilitative effects of vegetation cover noted in Assegaiboschkloof may involve amelioration of drought stress. Observations that the vigour and density of forest precursor seedlings decline with distance from stream bank forest (Kruger 1984) confirm that the effects are on seedlings.

Studies on the effects of soil moisture on establishment of forest and fynbos species in individual containers demonstrated that the forest precursor *Kiggelaria africana* is very persistent in dry conditions and a superior competitor at all levels of water availability (Chapter 6). In a more natural situation, *Kiggelaria africana*, although more successful than the mature forest species *Cunonia capensis*, was less successful than fynbos species in a nutrient-poor soil on an artificial gradient to the water table. On a similar gradient in a better soil, forest species, especially *Kiggelaria africana*, were more successful.

Once established under wet winter conditions, forest species, especially precursor species, may persist and develop. The greatest importance of soil nutrients in affecting forest distribution may be in enhancing early development of forest seedlings. Rapid early development may ensure that root systems are sufficiently developed to allow persistence as surface soils dry during the first summer after germination. Rapid early growth may also promote the development of fire tolerance - if tolerance is related to plant size.

Plants which manage to persist through the first few summer droughts may be able to take advantage of any habitat amelioration in later stages of succession. *Kiggelaria africana*, for example, shows greater ability to persist and is better able to colonize relatively dry fynbos areas than *Cunonia capensis*.

Soil moisture and nutrients *per se* do not limit forest distribution, but affect the rate of forest development. The proposed model of forest development (Figure 8.1) includes time increments, but does not include a time scale as there is tremendous variation in rates of forest development. Forests appear stable in Swartboskloof (Figures 1.1, 1.2 & 1.3) with two fires over a similar period, although there was evidence of developing forest species in the fynbos in 1986 after 28 fire-free years (Chapter 2). Baviaanskloof, between Swartboskloof and Assegaiboschkloof in the Jonkershoek valley, has definite development of forest after 50 fire-free years (Figures 8.2, 8.3 & 8.4). Orange Kloof near Cape Town has granitic soils and high rainfall and there is substantial evidence of development to forest in a similar fire-free period (Masson & Moll 1987). In contrast, Assegaiboschkloof which is near to but slightly drier than Swartboskloof and Baviaanskloof, had only isolated nuclei of forest development after 50 or more fire-free years (Figure 1.4). Van Daalen (1981) found no evidence of forest regeneration on fynbos "islands" in evergreen forest on the southern Cape, despite the absence of fire for up to 70 years, which lead him to conclude that fynbos is not seral to forest. Clearly, most of the Fynbos Biome is bioclimatically suitable for forest. It is the frequency of fire, in relation to the rate of forest development, which determines the extent of forest development.

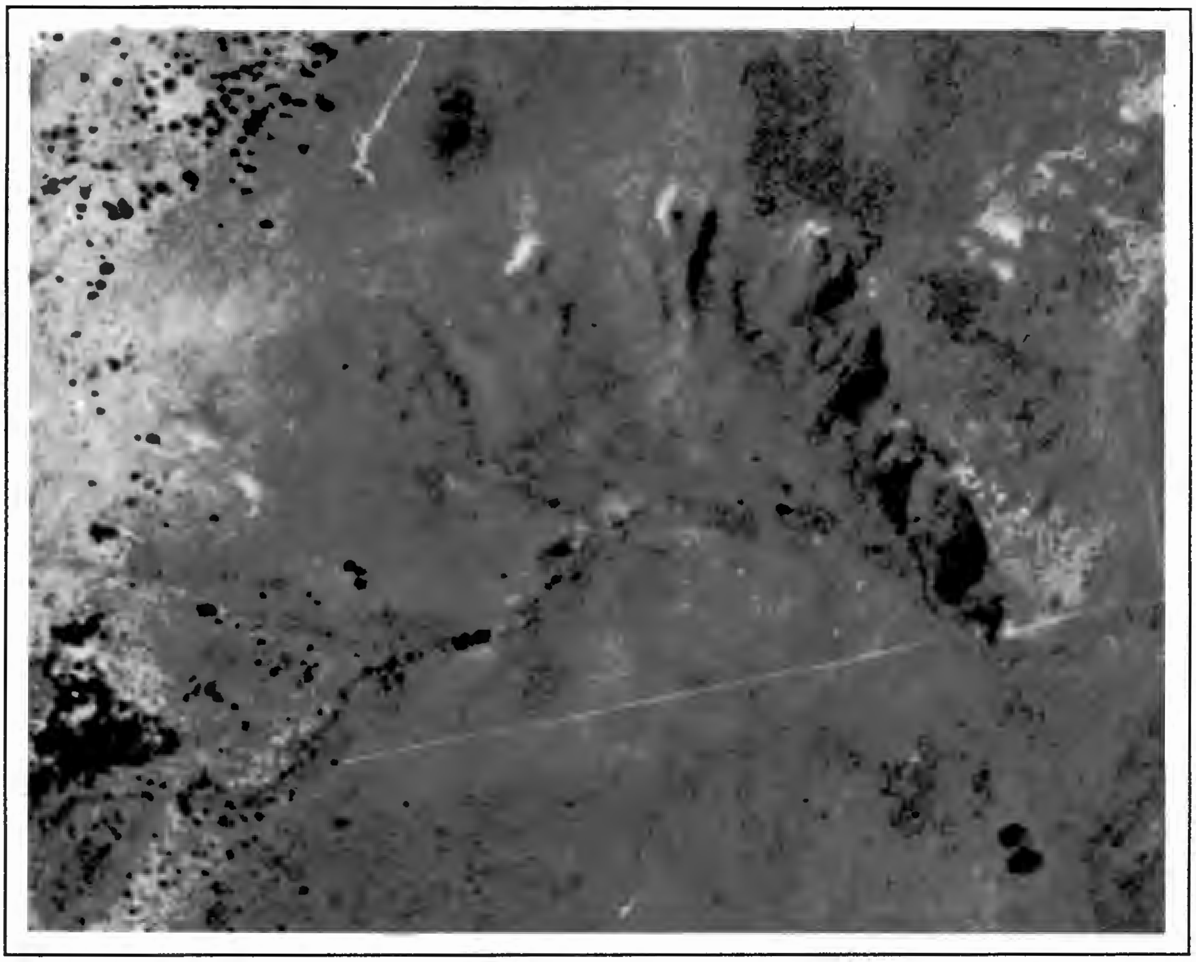


Figure 8.2. Aerial photograph of Baviaanskloof taken in 1938. Note the discontinuous stream bank vegetation and the very few trees on the slope above the stream.

Figure 8.3. Aerial photograph of Baviaanskloof taken in 1966. The area had not been burnt since the 1938 photograph in Figure 8.1. Note the almost continuous stream bank vegetation and the emergence of several trees on the slope above the stream.

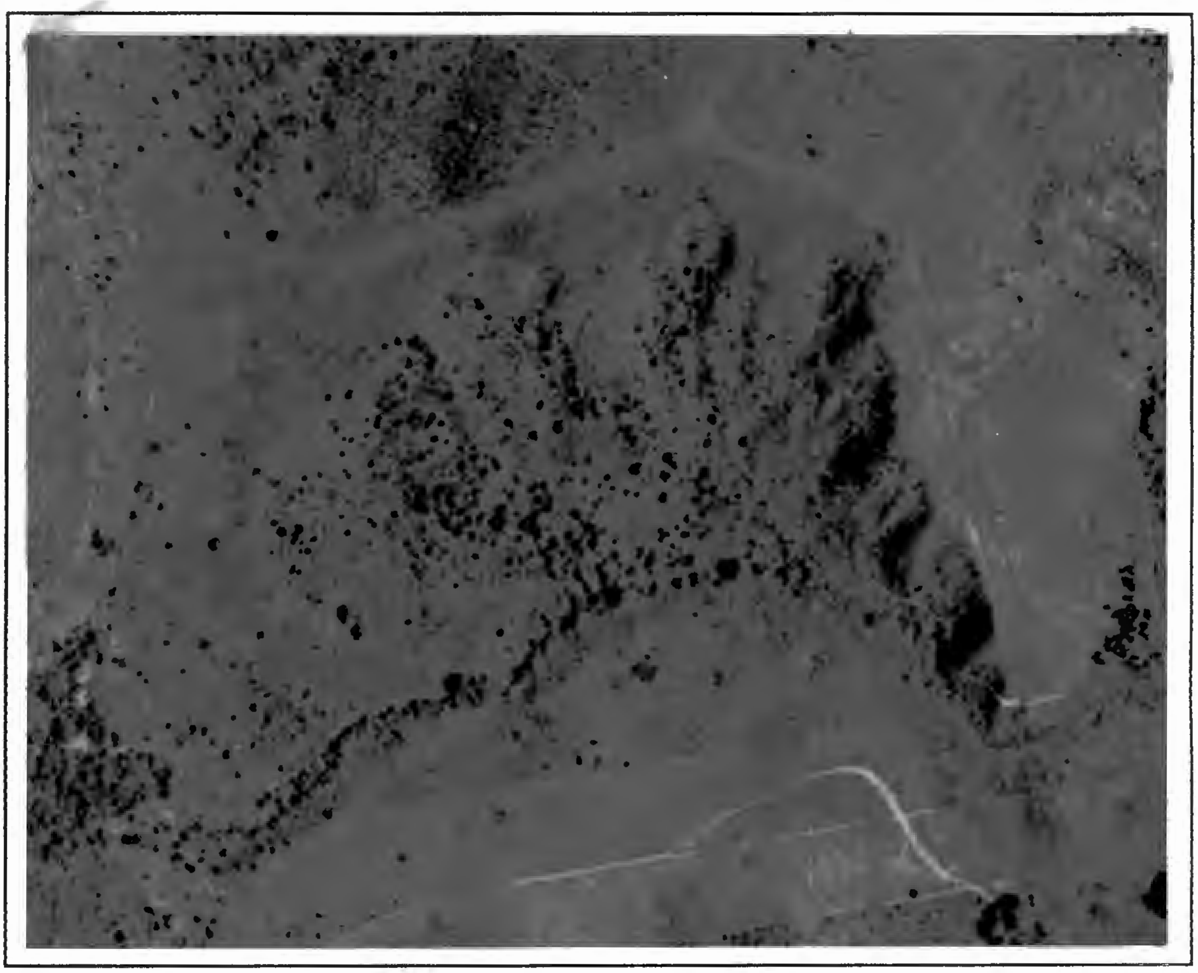


Figure 8.4. Aerial photograph of Baviaanskloof taken in 1985. The area had not been burnt since the 1938 photograph in Figure 8.1. Note the continuous stream bank vegetation and the numerous trees on the slope above the stream.

8.4. Fynbos succession

The distribution of forest and fynbos, the development of forest species in fynbos and the occasional conversion of fynbos to forest can be explained on the basis of successional processes in the model in Figure 8.1. The lack of forest development in young fynbos (Kruger 1984) is not determined by seed availability as seed banks and dispersal cross community boundaries. Forest seed dispersal by wind is not influenced by fire in the adjacent fynbos, and bird-dispersed seeds are introduced soon after fire. Germination of forest species may occur in post-fire conditions, but establishment is unlikely until habitat amelioration through the development of the fynbos or nuclei of forest species that may have survived the fire.

Gill & Groves (1981) considered fynbos to follow the initial floristic composition (IFC) model of succession (*sensu* Egler 1954; Connell & Slatyer 1977), but this model fails if forest species are introduced later. The studies reviewed in this chapter support the application of a facilitation model (Connell & Slatyer 1977) in which changes in the community are autogenic (i.e. driven by forces within the community). Evidence for this is provided by the enhanced forest seedling establishment in sheltered areas - under either fynbos vegetation or forest nuclei.

Recently a reductionist approach has been applied to forest succession (see Finegan 1984) in which the facilitation hypothesis is rejected and autogenic forces are seen as neutral or inhibiting factors rather than the driving force in succession. It could be argued that the alleviation of the constraints on the establishment of forest species, through the provision of shading or litter, represents a release from inhibitory factors and supports the reductionist approach. Furthermore, the reductionist concept of tolerance (the ability of a plant to survive in the presence of high densities of other species) applies to forest species colonizing mature fynbos. Succession of fynbos to forest involves interdependent mechanisms, best understood by a synthetic approach of general and reductionist models (*sensu* Finegan 1984).

The studies in this thesis also argue strongly for the concept of succession being the consequence of the different life cycles of the species involved (Gómez-Pompa & Vázquez-Yanes 1981). This explanation allows for the predominance of fynbos shrublands under a disturbance regime, although forest may be predicted in the absence of disturbance.

The studies described in this thesis have refuted the concept of forest and fynbos as two distinct and mutually exclusive vegetation types. Forest species are a late successional (or tolerant) component of the dynamic vegetation of the Fynbos Biome and may potentially predominate some areas currently under fynbos communities. The application of the term "senescent" to fynbos after the maturation of the slowest-to-mature obligate reseeding shrubs has been invalidated by the demonstration of continued succession after this stage. The use of this term contributes to the perception of an ecological barrier between forest and fynbos. The perceived restriction of forest communities to sheltered environments is principally a function of past and present fire regimes. The distinctness of the forest communities results from the exclusion of fynbos species from forests because of the inferior competitive abilities of fynbos species in these environments.

8.5. Practical implications

The concept of a tree element being part of the system, but which is often absent from the system is accepted in southwestern Australia (Specht 1969) and the Mediterranean Basin (Naveh 1975). Phillips (1931) suggested that fynbos is seral to forest in the southern Cape, but this has not been validated (Van Daalen 1981), and fynbos regeneration after fire was considered cyclical (Kruger & Bigalke 1984). There were no useful generalizations about patterns of vegetation replacement in the absence of fire (Kruger 1983). However, simulated responses of coastal sage communities to different fire intervals show irreversible changes in site composition which magnify over time (Malanson 1983). Therefore, while succession in mediterranean-climate regions may appear cyclical in two or three cycles, much longer studies and computer simulations are necessary to determine the long-term trends of change under the influence of repeated disturbance (Westman 1986). The major practical implication, therefore, is the recognition of the time frame over which management objectives may be considered.

The aim of this thesis is not to campaign for the encouragement of forest development in every mountain fynbos community. However, allowing forest development extends management options and may prove a biologically sound and cost-effective management strategy in appropriate areas. Forest communities are more stable than fynbos communities and occupy space on a permanent basis in ecological time. In fynbos communities, competition for space in a lottery process at each disturbance enhances diversity by allowing more species to coexist. Therefore, shorter fire cycles than those favourable for forest development may be required to maintain biotic diversity - if this is a management objective.

Invasions of the fynbos by alien trees and shrubs are usually in response to a disturbance, and usually establish in the disturbed area in a discrete episode (Richardson & Cowling in press). In contrast, invasions of fynbos by indigenous trees are related to low frequencies of disturbance. This may allow for some manipulation of vegetation through the fire regime. High frequencies of fire aimed at the control of biomass and fuel accumulation may promote invasions by aliens, whereas low fire frequencies may result in a less flammable indigenous community with a greater forest component.

The model in Figure 8.1 identifies processes which are susceptible to disruption by aliens. Alien trees in fynbos create new perches (Richardson & Van Wilgen 1986) and may initiate nucleation of forest elements. However, utilization of alien fruits by avian dispersers may diminish dispersal of indigenous seeds (Knight 1988) and alien birds may modify dispersal patterns. Therefore the impact of alien invasions may enhance or inhibit forest development, depending on which process is limiting at a site.

The ability of species to migrate slowly across a landscape and the dynamic constitution of plant communities will need to be incorporated in management plans (Grubb & Hopkins 1986). Recognition of the process of nucleation will enable managers to incorporate the management (initiation, growth and coalescence) of nuclei into landscape management (Janzen 1988). In mediterranean-climate areas, recovery after disturbance which involves migration is usually very slow. Consequently, where it is necessary to rehabilitate, it may be necessary to introduce propagules artificially (Grubb & Hopkins 1986).

CHAPTER 9

CRITIQUE

CHAPTER 9: CRITIQUE

9.1. Advances in the understanding of the relationships between forest and fynbos vegetation

The model of forest development in fynbos (Figure 8.1) is the first attempt to conceptualise the complete series of processes involved in forest development in an attempt to determine the limiting processes. The early studies (Chapters 2, 3 & 4) eliminated soil seed banks, seed dispersal and germination requirements as the limiting factors - at least in areas where there is forest in the vicinity. Studies on the requirements of establishment identified the regeneration niche, which develops through a process of facilitation, as the limiting factor (Chapter 5). The explanation of the limits to forest development on this basis, rather than by habitat *per se*, is an advance in the conceptualization of forest development.

Fire, soil moisture and nutrient availability have been recognised as the determinants of forest distribution. The conceptual model, with information derived from studies on soil moisture and nutrients (Chapters 6 & 7) relates these determinants to each other. Recognition of forest species as components of the fynbos identifies disturbance by fire as the mechanism which maintains the predominance of fynbos shrubland vegetation, despite the potential of the forest species to dominate eventually. Establishment of forest species is enhanced with favourable soil nutrient and moisture levels. These levels, therefore, determine the rate of succession, rather than determining the distribution of forest directly. On a smaller scale, nutrient levels are shown to be influenced by vegetation development rather than *vice versa*.

The greater the development of forest species between fires, the greater the ability of forest nuclei or patches to persist through the next fire. Fires are inevitable before forest domination of the fynbos vegetation in all but the most prime areas. The interplay between rates of forest development, fire frequency and the effects of fire intensity on the survival of forest components indicates a long-term transition between the vegetation types, rather than the previous concept of cyclical succession between fires. This suggests that a longer-term view of vegetation development over several fire cycles should be considered when determining the potential of an area and the end products of management.

9.2. Referees' comments

The chapters in the thesis have been submitted for publication (see Preface). Those which have been published have benefited from referees' comments. The review process also identified the weaknesses in some of the chapters. General comments on value and acceptability are repeated here and specific criticisms are reported and discussed.

9.2.1. Chapter 1: Introduction and Chapter 8: Conclusion.

These chapters rely heavily on a book chapter submitted for publication in a volume of Ecological Studies entitled "Swartboskloof - Fire in a Mountain Fynbos Ecosystem" to be published by Springer-Verlag. The book chapter was reviewed by one referee who commented "this chapter is thorough, with few errors of interpretation, and warrants publication." Apart from an eloquent and urgent plea for reduction of text and detail ("This chapter could be half as long and twice as interesting. The quality of the work deserves it."), the reviewer made some minor points on structure and style.

9.2.2. Chapter 2: Fire and other variables as determinants of forest-fynbos boundaries in the Cape Province.

This chapter was published in the *Journal of Vegetation Science* after minor revision. The first referee found the paper "an interesting contribution worthy of publishing in JVS" but requested reduction of the text, omission of some figures and more careful comments on the results. This referee considered transects, subplots or sampling points within each of the three sites as non-independent samples and that the paper was an example of pseudo-replication. This criticism is accepted, but an argument was inserted in the revised discussion that the great spatial variability in fire intensity provides some support for the acceptance of transects and even subplots and sampling points as independent samples.

The second referee stated "This is an interesting and worthwhile paper, well researched and presented. It makes a substantial contribution to fire ecology, as well as to the understanding of the rôle of fire in controlling the forest-fynbos boundary in Cape Province" and requested minor revisions to clarify some points.

9.2.3. Chapter 3: Quantifying soil seed banks: A comparison of physical separation and seedling emergence techniques in Cape fynbos and forest vegetation.

This chapter was published in the *South African Journal of Ecology* and was reviewed by two referees. Both referees found the paper interesting and asked for minor revisions. The first referee felt that the importance of the estimations of fynbos soil-stored seed banks had been underestimated, and that this should have been developed further, in the studies as well as in the paper. The second referee recommended that the importance of the comparison between methods should be emphasized.

9.2.4. Chapter 4: Soil seed banks and post-fire seed deposition across a forest-fynbos ecotone in the Cape Province.

Chapter 4 was submitted to the *Journal of Vegetation Science* as two papers, one dealing with the soil seed banks and the other with post-fire seed deposition. The papers met with varying appreciation. Two referees found the seed bank paper worthy of publication, but asked for condensation, combination with the seed deposition paper and removal of "overgeneralization from limited results". A third referee was critical of the seed bank paper in that sample sizes were small and there were conflicting patterns between sites. This referee found "the contribution of dubious value" and recommended major revision, rejection or combination with the seed deposition paper.

The paper on seed deposition was reviewed more favourably. One referee found that the paper "is well presented and covers an interesting topic" but recommended combination with the soil seed bank paper. The second referee recommended more major revisions, principally condensation of the text, matching text to results and combination of the two papers.

9.2.5. Chapter 5: Colonization of Cape fynbos communities by forest species.

This chapter was accepted for publication with minor revisions by *Forest Ecology and Management*. The reviewer found the paper "interesting and well written" and requested more detailed description of some methods and the statistical procedure.

9.2.6. Chapter 6: Effects of watering regime on growth and competitive ability of nursery-grown Cape fynbos and forest plants.

Chapter 6 was not accepted for publication by *Oecologia*. The first referee questioned the applicability of the watering regimes to natural situations; "While the paper provides some interesting comparisons between fynbos and forest species native to the south west Cape....., the value of the data in interpreting field behaviour is highly questionable and I doubt the value of the study for readers of *Oecologia*." The referee questioned the value of the conductance data as even plants in the wet treatment showed signs of water deficits and the data were specific to the day of measurement and did not correspond with dry matter accumulation and leaf areas.

The second referee considered that the stated problem did not agree with the information and that the data had been over-interpreted. The paper was criticised for

- addressing only part of the water relations of plants, and ignoring others such as rooting depth and morphology,
- the method of conductance measurement and calculation of transpiration,
- dismissing the effects of initial differences in seedling size,
- several points related to loose interpretations of results, particularly that trends were not uniform within the groups of forest and fynbos species.

The paper was revised where the comments could be accommodated, especially regarding interpretation of the results, and submitted to the *South African Journal of Botany*. A caveat was inserted to accept the watering regimes on a comparative basis as there was no feasible method of controlling moisture levels in multiple containers. Arguments for dismissing the initial differences in seedling size were strengthened on the basis that trends were reversed in the final results.

The reviewers' emphasis on the ecophysiological studies is perhaps regrettable. The studies were intended as growth studies, with conductance measurements included for comparison with field measurements. Indeed, the poor relationship between overall growth and single ecophysiological measurements emphasized the need for care in the interpretation of field studies. The inadequacies involved in using a null-balance porometer for measurement of conductance are recognised, but this equipment is accepted locally. The assumptions made in calculation of transpiration from these conductance figures, although accepted locally, are not necessarily valid and these results were omitted from the revision. No comments have been received from *South African Journal of Botany* yet.

9.2.7. Chapter 7: Effects of artificially established depth to water table gradients and soil type on the growth of Cape fynbos and forest plants.

This chapter was submitted to *Functional Ecology*, but found unacceptable. The first referee found the paper confusing, largely because the results did not justify the conclusions, and that the study "amounted to no more than a prototype". The second referee found the paper "too limited in its scope to provide much new information other than a purely descriptive account of a not wholly unexpected situation".

The first referee's confusion appears to result from some loose statements in the introduction and conclusion and from the inadequate discussion on the effects of nutrient differences. The comments from both referees that the study did not test limits of forest development adequately are accepted. On its own the study did not have as much value as it did in combination with the cultivation of plants in containers, dealt with in the previous paper. Both of these methods have limitations and the simultaneous studies were designed to complement each other. It may be argued, therefore, that the papers should have been combined. This had been considered earlier, but the single paper was thought to be too complex.

The parochial interest of this and the previous paper is acknowledged. The title of this paper was amended to include the differences in the soils and the text was amended to accommodate the comments on the definition of the scope of the study and the interpretation of the results. The paper has been submitted to the *South African Journal of Botany*, but no comments have been received yet.

9.3. Suggestions for future research

Although there has been interest in the relationship between forest and fynbos vegetation for some time, there has been little advancement in the understanding of this relationship. The model of forest development (Figure 8.1) presented in this thesis is simplistic and non-definitive. Not all pathways of development to forest are necessarily described by the model and there is no quantification of the time scale or habitat conditions. However, it is hoped that future studies will be based on tests of this or some similar model. Then such research would be directed more towards increasing understanding of the processes involved, rather than describing the *status quo*.

The model, as it stands, begs several questions:

- How does fire intensity affect individuals of forest species, forest nuclei and forest patches?
- What are the effects of different soil nutrient levels on the rates of forest development?
- How do these rates vary between areas with different rainfall or soil moisture levels?
- If there is a relationship between the size of individuals and their fire tolerance, then how soil nutrient and moisture levels affect the achievement of fire tolerance in different species?

The philosophy behind answering these questions should take cognisance of the long-term nature of community change rather than a cyclical process. Because of the long-term nature, it would be instructive to attempt the measurement of forest development from historical series of aerial photographs of areas with different soil nutrients, rainfalls of soil moisture levels and with known fire histories. The history of such records is limited, however, and there is a need to assess the effects of fire history, site factors and fire intensity on forest elements in field studies.

Opportunities such as the Swartboskloof fire, where the timing of the fire is known well in advance, seldom occur. Therefore future studies are likely to be in recently-burnt areas without the opportunity of pre-fire observations. In such studies it is impossible to determine how many forest individuals have been destroyed completely, and it may prove difficult to gauge the pre-fire size of nuclei. However, fire intensity is determined by weather (humidity, temperature and wind speed), topography and fuel characteristics. The amount of fuel present is partly a function of the time since the previous disturbance. This information may be determined after the event and it should be possible to derive some estimate, at least, of fire intensity. Variables such as the change in size of forest nuclei and mortality of recognisable forest individuals of different sizes should be explained as a function of the previous fire history (at least the duration of the previous interval between disturbances), as well as site factors and fire intensity to allow for the long-term nature of community change.

Controlled experiments to determine the effects of soil nutrient and moisture levels on growth rates of forest species would add great value to post-fire studies, especially as the determination of pre-fire soil nutrient and moisture levels may be problematic. It may be fairly easy to decide on a few forest species (for example the most common pioneer species) and to establish an array of nutrient levels which are applicable to field situations. Setting soil moisture levels, however, is difficult in multiple containers. Therefore, rather than cultivation of individual plants, several plants should be cultivated per container, and each container should exceed 1 m^2 so that soil moisture can be measured with a neutron probe. Then watering regimes could aim to maintain a range of soil moisture levels and allow comparisons between levels which are applicable to field situations. If the logistics of large containers are excessive, smaller containers, with a series of nylon blocks in each, could be used.

The establishment phase is critical in the development of forest species in fynbos areas. Different forest species appear to act as pioneers in different areas (*Cunonia capensis* on forest edges in Swartboskloof, *Kiggelaria africana* and *Hartogiella schinoides* in Langrivier, Jonkershoek, and *Olea europaea* ssp *africana* in Orange Kloof and Assegaiboschkloof). Such differences may be explained by the different establishment requirements of the species and the conditions at each site. Cultivation of a range of forest species from seed may demonstrate meaningful differences in seedling growth patterns. Such differences have been detected in pines and used to explain differences in abilities to withstand competition (Strauss & Ledig 1985). One of the most important features of seedling growth is root development. The study of the growth of forest and fynbos species in large troughs identified major differences in rooting behaviour. It seems that this is a critical feature of seedling development which may discriminate between species which are able to colonise areas subject to summer water deficits and those restricted to mature forests.

Knowledge of the pioneering abilities of different species should enable some predictive understanding of situations where forest elements are present in fynbos. From the species present it should be possible to determine the level and the potential of forest development in more meaningful terms than total frequency or total cover of forest species.

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