Post-fire effects of invasive exotic plants on seed banks, regeneration, soil chemistry and selected soil microbial populations in the Silvermine Nature Reserve, Cape Peninsula, South Africa

By

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Declaration

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

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Abstract

The fires, which occurred during January 2000 on the Southern Cape Peninsula, Cape Province, South Africa, focused attention on the importance of sound, informed management of exotic plant invaders in fynbos, especially at the urban interface. The fires also highlighted the relative lack of knowledge about the combined impacts of fire, exotic plants and the exotic-clearing programme on soil seed banks and regeneration.

This study examines soil borne seed banks, regeneration, soil chemistry and micro biota in different post-fire environments, focusing on three components of exotic plant management: The post-fire effects of standing invasive exotic plants; stacks of slashed exotic plant material which were deliberately burnt and stacks reduced to heat scars by a wildfire.

The primary hypothesis addressed is that post-fire vegetation regeneration patterns, seed bank diversity and seed bank abundance are linked to pre-fire vegetation characteristics and, in particular, to the treatment of exotic plant species. It is also hypothesised that soil microbe population sizes are linked to pre-fire vegetation and soil chemical composition.

Differences in soil seed banks, soil micro biota and vegetation regeneration patterns occur in different post-fire environments. High volumes of (live or dead) woody exotic biomass negatively impact upon post-fire indigenous species diversity and abundance, both above and below-ground. Soil seed banks and above-ground regeneration decline with increasing fire intensity, wildfire burnt stack treatments showing the largest declines followed by wildfire burnt standing exotics, control burnt stacks, wildfire burnt cleared areas and wildfire burnt Mountain Fynbos treatments. Persistent indigenous seed banks are found under some exotic dominated stands. Heat damage, associated with high woody exotic biomass, affects seeds of all species into deep soil layers. Depth of burial is a more important determinant of seed survival during fires than seed size.

Soil microbial populations are variably affected by exotic plants, their management and increases in fire intensity. The most drastic microbial population changes are in post-fire treatments of high exotic plant biomass. Soil chemistry affects microbial population sizes as does seasonal climatic changes.

In this thesis vegetation, seed bank and microbial responses to various exotic plant management practices are shown and management recommendations are made.

Keywords: exotic plants, fire, Fynbos Biome, microbes, post-fire succession, soil seed banks.

Uittreksel

Die Januarie 2000 vure op die Suid Kaapse Skiereiland het fokus gerig op die belangrikheid van goeie, ingeligte bestuur van uitheemse indringerplante in fynbos, veral naby stedelike gebiede.

Die vure het ook 'n relatiewe gebrek aan kennis aangaande die gekombineerde impakte van vuur, uitheemse plantegroei en indringer plant beheer programme op grond saadbanke en die hergroei van plante na 'n vuur aan die lig gebring.

Hierdie projek bestudeer die invloed van vuur op grond saadbanke, hergroei van plante, grond chemie en mikro-organismes. Die klem lê op drie komponente van uitheemse plant bestuur: waar staande uitheemse plante voorkom; waar skoongekapte uitheemse plante in hope gestapel is en gekontraleerd gebrand is en waar soortgelyke hope in 'n onbeplande weghol vuur gebrand is.

Die primêre hipotese is dat plant herstelpatrone, saadbank diversiteit en grootte gekoppel is aan veldtoestande voordat daar gebrand is, en veral aan die bestuur van uitheemse plantspesies. Nog 'n sentrale hipotese is dat die grootte van grond mikrobiale populasies gekoppel is aan veld toestande voor die brand en aan grond chemiese samestelling.

Hierdie studie dui verskille aan in grond saadbanke, mikro-organismes en plant hergroeipatrone onder verskeie toestande na vuur. Die brand van hoë volumes (lewende of dooie) houtagtige uitheemse plant biomassa benadeel inheemse plant spesie diversiteit en getalle (bo en onder die grond oppervlak). Grond saadbanke neem af met vehogings in vuur intensiteit. Die grootste afnames is in wegholvuur gebrande gestapelde uitheemse plantmateriaal gevolg deur wegholvuur gebrande staande uitheemse plante, opsetlik gebrande hope uitheemse plante, gebrande skoongekapte areas en wegholvuur gebrande Berg Fynbos. Ou inheemse saadbanke is gevind onder sommige areas wat voor die vuur oorheers was deur uitheemse plantegroei. Hitteskade, geassosieer met hoë volumes houtagtige uitheemse biomassa, affekteer sade van alle spesies tot diep in die grond. Saad oorlewing tydens brande is meer geaffekteer deur diepte van begrawing in die grond as deur saad grootte.

Grond mikro-organisme populasies is geaffekteer deur uitheemse indringer plante, die bestuur van uitheemse plante en vuur intensiteit. Die grootste veranderinge is waar die biomassa van uitheemse plantegroei baie hoog is. Grond chemiese samestelling en seisoenale veranderinge in weerspatrone affekteer die grootte van mikrobiale bevolkings.

In hierdie tesis word verskille in plantegroei, saad store en grond mikrobes, soos geaffekteer deur uitheemse plant beheer programme uitgewys en voorstelle vir toekomstige bestuur gemaak.

Sleutelwoorde: Fynbos Bioom, grond saad stoor, mikrobes, plant hergroei, uitheemse plante, vuur.

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'Not even a sparrow falls to the ground without the Creator's knowledge'
Matthew 10:29

CHAPTER 1: GENERAL INTRODUCTION AND LITERATURE REVIEW

1.1 Thesis structure

This thesis is divided into four chapters. The first is a general introductory chapter which includes a motivation for the thesis, outline of key questions and a literature review focussing on exotic vegetation and fire in mediterranean ecosystems with particular emphasis on fynbos. The two data chapters were written as independent papers (accounting for some repetition). Chapter two describes the effects of exotic plants and their management on post-fire soil seed banks and above-ground regeneration and is co-authored by C. Cilliers, K. Esler and C. Boucher. Chapter three describes the effects of exotic plants and their management on post-fire soil chemistry and selected soil microorganism populations and is co-authored by C. Cilliers, A. Botha, K. Esler and C. Boucher. The concluding chapter contains a general discussion of the results including a review of hypotheses and predictions outlined in Chapter 1, problems encountered and management implications. A complete reference list and appendices containing additional data are presented at the end of the thesis.

1. 2 Rationale and motivation

In South Africa, exotic plant species pose ecosystem managers with their biggest problem in terms of manpower, money and time spent in their control (Mr. R. Erntzen, Cape Peninsula National Parks pers. comm. 2000). Woody exotic plants have also altered fynbos fire regimes, producing exceptionally intense fires with extreme seed bank and regeneration effects (Cowling and Richardson 1995, Auld and Bradstock 1996, Holmes and Cowling 1997a, Scott *et al.* 2000).

Exotic plant management in the Cape Peninsula National Park's Silvermine Nature Reserve (grid square 3418 AB & AD) (and elsewhere in the Fynbos Biome) currently employs the practice of stacking felled exotic vegetation and leaving these stacks scattered throughout the landscape (Milton and Hall 1981, Ashton 1985, Griffith 1986, Holmes *et al.* 1987b, Macdonald *et al.* 1989, Martens 1994a, Anonymous 1995b, Martens 1997, Euston-Brown 2000, Ms. H. Thompson and Mr. R. Erntzen, Cape Peninsula National Parks pers. comm. 2000, Vlotman and Knight 2000). Stacking has merit in that seeds of serotinous exotic species are concentrated beneath the stacks (they then germinate and could be eliminated by control burning of the stacks at a later stage); access into cleared sites for follow-up eradication is improved and the activities of entrepreneurial wood collectors are concentrated in the vicinity of the stacks (Martens 1997, Ms. H. Thompson pers. comm. 2000). However, it is surmised that accidental fires burn stacks at highly elevated temperatures, potentially altering soil chemistry (which affects soil microbes) and killing soil-stored indigenous and exotic seeds. This results in the formation of so-called heat scars on the landscape (Macdonald *et al.* 1989, Martens 1994b, Martens 1997, Bond *et al.* 1999, Euston-Brown 2000, Scott *et al.* 2000, Vlotman and Knight 2000, Holmes *et al.* 2001). Stacking and deliberate control burning of non-serotinous exotic species also results in mass germination of their seedlings in the vicinity of the stacks (pers. obs. 2001). This results from seed germination cued by heat (Holmes and Richardson 1999), resulting from lower intensity control burns in the stacks.

Holmes and Cowling (1997b) state that "information is needed urgently on what remains in the seed banks of invaded fynbos shrublands and how this translates to restoration potential for these sites" while Holmes and Cowling (1997a) add that: "further studies are required to establish the depth distribution of fynbos seeds in invaded and un-invaded stands". In this study, post-fire depth and seed size distributions of indigenous and exotic seed are examined in various invaded and un-invaded areas. This project also entails a pilot study of the effects of woody exotics and fire on soil borne microbes and chemistry in post-fire sites of increasing exotic plant biomass. Post wildfire and control burning effects of stacking are thus quantified, as well as the effects of wildfire in a standing mature woody exotic stand and in fynbos.

One of the principal management aims of any reserve should be to maintain the diversity of species. The presence of dense stands of exotic trees, the effects of fire in these stands and the damaging effects of certain exotic plant management procedures are clearly incompatible with this objective. It was therefore imperative that the post-fire effects of dense standing exotics and current management practices (viz. the post-fire effects of stacking) be quantified by means of field plot analysis and a nursery germination trial. The findings of this study are extrapolated to assist in the formulation of exotic plant management procedures.

1.3 Research objectives

The principal aim of this study was to investigate seed-banks, regeneration, soil chemistry and microbiology in different post-fire environments within the Silvermine Nature Reserve, focusing on the following components of woody exotic plant management:

- The effects of a fire on a dense stand of invasive exotic plants (compared to an adjacent burnt Mountain Fynbos site) on above-ground vegetation regeneration, below-ground seed banks (chapter 2), soil chemistry and selected microbial populations (chapter 3).

- The effects of packing slashed exotic plant material into stacks and having a subsequent wildfire move through the area, reducing the stacks to heat scars on post-fire vegetation regeneration, seed bank, (chapter 2) soil chemistry and selected soil microbe populations (chapter 3). These effects are compared to adjacent burnt areas, which were cleared of exotics before the fire, but where no stacking took place.

- The post-fire vegetation regeneration effects of similar stacks burnt deliberately in control burns (chapter 2).

The questions addressed here are:

- What are the post-fire impacts (in stands of woody exotic plants in the Silvermine Nature Reserve) on aboveground vegetation regeneration, belowground seed banks, soil chemistry and selected microbial populations where no management or clearing of the exotics has taken place?

- What are the post-fire effects (on aboveground vegetation regeneration, belowground seed banks, soil chemistry and selected microbial populations) of stacking exotic plant material after (a) wildfires and (b) control burn operations (i.e. where management has taken place)?

1.4 Hypotheses and predictions

- The primary hypothesis is that post-fire regeneration patterns, soil borne seed-bank diversity and abundance are linked to pre-fire vegetation and seed characteristics of the component species (chapter 2).

- A second research hypothesis is that certain soil borne microbial population sizes are linked to post-fire soil chemical characteristics and to fire intensity (chapter 3).

Several predictions are made concerning post-fire regeneration and seed bank dynamics.

- It is predicted that in burnt standing exotic sites there would be a high density and abundance of exotic seeds and subsequent high post-fire regeneration. This would be in conjunction with low seed bank abundance, diversity and regeneration of indigenous species. Heat damage in standing burnt exotic stands should be confined to shallow depths; with small seeded (indigenous) species in the upper layers experiencing the greatest negative effects (chapter 2). The rationale is that live serotinous exotic invasive species, such as *Hakea sericea* and *H. suaveolens* release their large canopy-stored seed banks when they are burnt by fire, thereby potentially increasing the post-fire exotic seedling population on germination. The pre-fire paucity of indigenous parent plants (and their stressed state) within standing exotic-dominated stands, should contribute to a low post-fire abundance of indigenous species (Holmes and Cowling 1997a).

- It is predicted that seed distribution in the soil under burnt fynbos (and subsequent regeneration), should be represented by a larger variety and abundance of species than under dense exotic infested stands (chapter 2). The rationale is that cooler fires, (resulting from a lower fuel loading than in exotic stands) should result in less heat damage to all seeds in the soil profile. Coupled with a diversity of pre-fire parent plants, this should result in large numbers of indigenous seeds and better subsequent regeneration within an optimum fire interval regime.

- In exotic stands that have been cleared and stacked prior to wildfire burning, it is predicted that serotinous exotic species would decline in numbers (chapter 2). Those exotic species with soil-stored seed banks would have comparably high levels of abundance. This distribution would, however, be spatially heterogeneous (patchy). The reasoning is that hot fires, resulting from clearing and stacking of the felled woody exotic plants, (very high fuel loads) would kill seedlings of serotinous species. However, soil stored seeds (all species) would only be affected/killed in those patches associated with stacks. It is also predicted that, within stacked areas, heat damage to the soil stored seed bank would be much greater (i.e. to a greater depth) than in the cleared areas adjacent to them (subject to cooler fire temperatures), and to a greater depth than in burnt standing exotics where fuel loads are diffuse (chapter 2). The burnt cleared sites (mechanically cleared of mature exotic stands before burning) should contain much greater numbers of exotic and indigenous seeds throughout the soil profile. Exotic seedlings (and some re-sprouters) should dominate regeneration in the cleared sites (with some fynbos elements present). The rationale underlying the above assumptions is that intense fires resulting from the large biomass of stacked material would have resulted in unnaturally hot burns, killing all but the deepest buried seeds while heat damage in the cleared areas would be negligible (Macdonald *et al.* 1989). Prior to this thesis these assumptions and observations had not yet been formally tested nor had their effects been quantified (in burnt standing exotics; stacks of exotic slash; burnt mechanically cleared areas and in burnt fynbos).

- In mature woody exotic stands that have been cut and stacked prior to control burning it is predicted that there would be large-scale exotic regeneration within the stacked areas (chapter 2). This is due to a concentration of seeds under the stacks and from lower temperatures present during burning of these stacks, (due to cooler winter weather conditions during burning) cueing seed germination (Milton and Hall 1981, Mr. R. Erntzen pers. comm. 2000).

Several predictions are made concerning microbes and soil chemistry.

- It is predicted that soil chemistry alteration would be linked to burn intensity. The hottest burns associated with highest exotic biomass should result in the largest changes in soil chemistry. These soil chemical changes should exhibit some recovery over time with those most affected being the slowest to recover. It is predicted that post-fire microbial activity would be correlated with soil chemistry (chapter 3).

1.5 Literature review: Exotic plants and fire in the Fynbos Biome

1.5.1 Direct effects and competition

The Cape Floristic Region contains between 9000 and 9550 indigenous vascular plant species, almost 69% of which are endemic (Goldblatt and Manning 2000). The Cape Peninsula alone, an area of approximately 4.7 x 10^3 km^2, contains 2250 species, 7.5% of which are endemic (Goldblatt and Manning 2000). Mr. J. Jackelman (Cape Peninsula National Parks pers. comm. 2001) and Low *et al.* (2001b) estimate the total number of species to be still higher (2285 within the Cape Peninsula National Park and 2489 on the Cape Peninsula respectively).

This unique floral diversity and its survival is under increasing threat, due in part to the successful invasion of natural habitats by exotic plant invaders (Wicht 1945, Taylor 1969, Bands 1977, Hall and Boucher 1977, Taylor 1977, Stirton 1978, Kruger and Bigalke 1984, Richardson 1985, Macdonald *et al.* 1986, Macdonald *et al.* 1988, Cowling and Richardson 1995, Trinder-Smith *et al.* 1996, Marais 1998, Holmes and Richardson 1999, Van Wilgen 2000). Currently 141 plant taxa (138 species and three infraspecific taxa) are classified as threatened according to IUCN criteria with at least 39 having become extinct on the Cape Peninsula in the 20th century (Trinder-Smith *et al.* 1996). Furthermore, vegetation surveys indicate that the South African 'Capensis' Region is more severely invaded by woody exotic plants than the other South African biomes (Macdonald 1984). Of the remaining indigenous vegetation on the Cape Peninsula not affected by urbanisation and agriculture in 1996, 10.7% was densely invaded (>25% canopy cover) by exotic plants and another 32.9% was lightly invaded (Richardson *et al.* 1996).

The elimination of populations of indigenous plants is a particularly serious threat in fynbos since many species occur in isolated, small populations (4% of indigenous plants on the Peninsula are endemic and 6% are currently threatened) (Oliver 1977, Kruger 1979, Trinder-Smith *et al.* 1996). The example of *Erica fairii* illustrates this risk. This species was found only in a one-hectare population and was threatened by an infestation of *Pinus pinaster*; fortunately the pines were cleared in time by the Mountain Club of South Africa (Hall and Boucher 1977). Richardson *et al.* (1996) add that it is important that common taxa and widespread habitat types are also protected, since these contain vital reservoirs of genetic diversity.

Various life history traits employed by woody exotic plant invaders contribute to their success in the biome (Van Wilgen *et al*. 1996). These include hard seeded legumes with large soil stored seed banks *(Acacia* spp.) (Milton and Hall 1981, Macdonald *et al.* 1988, Pieterse and Boucher 1997); serotinous canopy stored seeds (*Hakea* spp.) (Fugler 1979b, Richardson *et al*. 1992, Bradstock *et al.* 1994, Holmes and Cowling 1997b); copious seed production (Fugler 1979b, Milton and Hall 1981, Richardson and Van Wilgen 1984, Gill 1985, Pieterse 1986, Pieterse and Cairns 1986, Macdonald *et al.* 1988, Van Wilgen *et al.* 1996); long range seed dispersal (by birds and other animals in the case of *Acacia* spp. and wind in the case of hakeas and some pines) (Kruger and Bigalke 1984, Gill 1985, Macdonald *et al.* 1988, Cronk and Fuller 1995); resistance of adult plants to fires (pines) (Boucher 1984); seed longevity (Cronk and Fuller 1995); high seed temperature tolerance (Jeffery *et al.* 1988); high percentage seed viability (Fugler 1979b, Pieterse 1986, Holmes 1987, Boucher and Mortimer 2000, Fleitmann and Boucher 2001); germination cued to fire (Jones 1963, Bands 1977, Taylor 1977, Boucher 1984, Pieterse and Cairns 1986, Holmes 1987, Richardson *et al.* 1992, Pieterse and Boucher 1997); high growth rates (Hall and Boucher 1977, Milton 1980, Milton and Siegfried 1981, Gill 1985, Rutherford *et al.* 1986, Jeffery *et al.* 1988, Van Wilgen *et al.* 1996); nitrogen fixation (Roux and Warren 1963); possible allelopathy (Jones *et al.* 1963) and lack of natural enemies (Fugler 1979b, Richardson and Van Wilgen 1984, Pieterse and Cairns 1986, Musil and De Witt 1990, Van Wilgen *et al.* 1996, Holmes and Cowling 1997a). *Acacia* spp. are well adapted to the soils of the southwestern Cape which are both sandy and poor in trace elements and their native distributions suggest they can withstand summer drought (Milton 1979). Milton (1979) concluded that pre-adaptation at the genus, sub-genus and species levels, together with a stress tolerant competitive strategy, partly accounts for the invasive success of Australian *Acacia* spp. in the Cape Floristic Region.

Once established, woody exotic plants significantly modify community structure, alter ecosystem processes, reduce local biodiversity and subsequently threaten numerous taxa with extinction (Bands 1977, Oliver 1977, Taylor 1977, Smit 1983, Van Wilgen and Richardson 1985, Macdonald and Richardson 1986, Phillips 1986, Musil and De Witt 1990, Richardson *et al.* 1992, Holmes and Cowling 1997a, Fleitmann and Boucher 2001, Holmes *et al.* 2001, Van Den Berckt 2001). Indigenous taxa are out-competed by the exotics, which increase their dominance after each fire (Bands

1977, Taylor 1977, Van Wilgen and Kruger 1985, Van Wilgen and Richardson 1985, Richardson *et al.* 1989, Holmes and Cowling 1997a, b, Pieterse and Boucher 1997, Holmes and Marais 2000). They replace the diverse indigenous flora with monotonous stands that depress the scientific interest, diversity and beauty of the landscape (Hall and Boucher 1977). They also fragment landscapes and disrupt plant reproductive processes (Cowling and Richardson 1995, Richardson *et al.* 1997). This phenomenon is well illustrated in that seed production of native species under dense acacia stands has been found to be negligible (Holmes and Cowling 1997a). Dense exotic stands reduce structural diversity, increase biomass and subsequently disturb vegetation dynamics, including those affecting soil seed stores (Van Wilgen and Richardson 1985, Versveld and Van Wilgen 1986, Holmes and Cowling 1997a, Van Wilgen *et al.* 1998, Van Den Berckt 2001). Milton and Siegfried (1981) calculated mean above-ground biomass (dry mass) of 10 400 kg/ha in dense mixed *Acacia cyclops* and *A. saligna* stands. This was about three times the biomass of indigenous fynbos vegetation, which seldom realised a biomass of more than 4 000 kg/ha. Their results agree with those of Van Wilgen and Richardson (1985) who recorded 17 840 kg/ha in pristine fynbos, 39 270 kg/ha in hakea invasions and 58 160 kg/ha in acacia stands.

Massive amounts of above-ground plant material in dense exotic infestations result in increased evapotranspiration (Neser and Fugler 1980). This reduces run-off, stream flow and affects the amount of water available to man in infested areas (Kruger 1979, Neser and Fugler 1980, Kruger and Bigalke 1984, Burgers *et al.* 1995, Van Wilgen *et al.* 1996, Richardson *et al.* 1997, Marais 1998, Van Wilgen *et al.* 1998, Holmes and Marais 2000). In 1998 it was estimated that 3 300 million m^3 of water was being used by exotic plants (almost 7 % of the runoff of the country) (Van Wilgen *et al.* 1998). According to Taylor (1977) and Cowling and Richardson (1995), invasion results in huge reductions in the aesthetic, recreational and scientific value of fynbos, which is one of the southwestern Cape's tourism draw cards (Kruger and Bigalke 1984, Marais 1998). Exotic plant invasion also impacts on fire regime, hydrology (Cronk and Fuller 1995, Van Wilgen *et al.* 1996, Van Wilgen *et al.* 1998), nutrient cycling (Richardson *et al.* 1992, 1997) and increases soil erosion in areas dominated by living exotic trees, after burning and especially after clearing followed by burning (Taylor 1977, Richardson and Van Wilgen 1992, Van Wilgen *et al.* 1996, Euston-Brown 2000).

The principal negative impact of woody exotic plants on biodiversity is, however, the out-competing and overtopping of native flora, with the exotics becoming increasingly dominant after each fire (Roux and Middlemiss 1963, Taylor 1977, Milton and Siegfried 1981, Smit 1983, Boucher 1984, Van Wilgen and Richardson 1985, Macdonald *et al.* 1988, Musil 1993, Holmes and Cowling 1997a, b, Pieterse and Boucher 1997). For example, *H. sericea* has been known to form dense, impenetrable thickets of 8 900 to 90 000 plants/ha (Van Wilgen and Richardson 1985, Macdonald and Richardson 1986). Milton and Siegfried (1981) established a mean density of 5 267 stems/ha in self established *Acacia* sp. thickets, Macdonald and Wissel (1991) counted 20 769 *A. saligna* plants/ha and Raitt (1981) counted $15x10^7$ *A. saligna* seedlings/ha regenerating after a fire.

Furthermore, seed densities of up to 47 000 per m^2 (= $47x10^7$ seeds/ha) were recorded under mature acacia stands by Holmes and Cowling (1997a) and $3x10^6$ seedlings/ha nine months after a fire on the Cape Peninsula (Milton and Siegfried 1981).

Macdonald *et al.* (1986) noted that some 425 600 ha in the Fynbos Biome were estimated to be densely infested with thickets comprising mainly exotic *Acacia* species, with an additional 732 000 ha being less densely invaded while Richardson *et al.* (1996) stated that by 1985, an estimated 40% of the Cape Peninsula was already invaded.

1.5.2 Exotic plants, fire intensity, surface and soil temperatures

Higher fuel loads in exotic stands result in much higher intensity burns than would occur in un-invaded fynbos (Martens 1994a, Van Wilgen *et al.* 1996, Holmes and Cowling 1997a, Martens 1997, Holmes and Richardson 1999, Euston-Brown 2000, Van Wilgen 2000, Holmes *et al.* 2001). Fire intensity stimulates seed germination but also determines plants, plant part and seed survival (Manders and Cunliffe 1987). Measured in kW/m, fire intensity is the rate of energy release per unit length of fire front and is the product of the rate of spread, fuel mass combusted and energy content of the fuel (Bond *et al.* 1990). Since energy contents of different plant parts, materials and wood types show little variability (Alexander 1982), energy release may be approximated by the amount of biomass consumed (Euston-Brown 2000, Scott *et al.* 2000).

Fire intensity is variable and is further influenced by vegetation moisture content, vegetation age, season of burn, site topography and weather conditions on the day of the fire (Van Wilgen 1984, Van Wilgen and Van Hensbergen 1992, Van Wilgen *et al.* 1992, Christensen 1994). For example, according to Kruger (1977b), Van Wilgen and Richardson (1982), Van Wilgen and Kruger (1985) above-ground biomass in mature 12 to 20 year old fynbos can vary from approximately 4 000 to 5 000 kg/ha. However Durand (1981), recorded fynbos biomass in the Kogelberg State Forest ranging from 10 430 kg/ha to 13 804 kg/ha while Van Wilgen and Richardson (1985) recorded fynbos biomass as 17 840 kg/ha. Available fuel comprises 50 - 100% of the biomass (Van Wilgen *et al.* 1985) and available data indicates that fynbos fires can vary in intensity from 200 to 21 000 kW/m (Bands 1977, Van Wilgen *et al.* 1985). Van Wilgen and Holmes (1986) predicted the heat per unit area in fynbos fires as 13 344 kJ/m^2 while temperatures of several fynbos fires, studied by Taylor and Kruger (1978), ranged from 149°C to 371°C, with a mode at 316°C. Natural uncontrolled fires however burn in large areas in warm, dry conditions and tend to be of higher intensity (Van Wilgen 1987, Euston-Brown 2000). Van Wilgen and Richardson (1985) however recorded a 50% fuel load increase following *A. saligna* invasion and 60% after *H. sericea* invasion while Versfeld and Van Wilgen (1986) measured a 300% increase in biomass following *Pinus* sp. invasion. Van Wilgen and Richardson (1985) recorded biomass in *Hakea* sp. stands as 39 270 kg/ha and in *Acacia* sp. stands as 58 160 kg/ha while biomass in dense *Acacia* sp. stands amounted to 10 400 kg/ha (compared to 2 000 – 3 000 kg/ha in fynbos) (Milton 1980; Milton and Siegfried 1981). Breytenbach (1989) ascertained that more than 5 910 kJ/m^2 were released by a fire in slashed *H. sericea* sites, compared with 470 to 220 kJ/m^2 in fynbos sites while Holmes (1989), estimated fire intensity for standing *A. cyclops* and found it to be 20 000 to 61 000 kW/m.

Changes in fire intensity, associated with woody exotic plant invasion, changes the heat pulse into the soil (Van Wilgen and Holmes 1986, Van Wilgen 1987, Bond *et al.* 1999). For example, soil temperatures recorded during fynbos fires by Martin (1966) (550°C at the soil surface and 43°C at 0.012 m depth) and De Lange (1992) (means of 500°C at the soil surface, 150°C at 0.0025 m, 57.3°C at 0.01 m and < 50°C at 0.02 m depth) were much lower than those recorded in areas invaded by *A. cyclops* by Van Wilgen and Holmes (1986) (116 – 160°C at 0.01 m and 46 – 71°C at 0.04 m soil depths respectively). Rundel (1983) reported maximum temperatures of about

300°C at the soil surface during fynbos fires and reported 50°C at 0.05 m depths in chaparral fires of similar intensity. Mitchell (1987) concluded that there appears to be negligible temperature changes at depths below 0.01 m in natural fynbos fires. However in related Australian shrubland fires, soil surface temperatures ranged from 90 - 550°C and subsoil temperatures ranged from 50 - 130°C at 0.01 m depth decreasing to 40 - 70°C at 0.05 m depth (Humphreys and Craig 1981).

The extent of soil heating during fire depends on fire intensity and duration, fuel type, structure, moisture, load, packing as well as on soil water content (Renbuss *et al.* 1972, Christensen 1994, Euston-Brown 2000, Scott *et al.* 2000). In general, the direct effects of intense heating are confined to the upper 0.02 to 0.03 m of soil (DeBano *et al.* 1979). However, in areas with extensive fuel accumulation, (eg. stacks of exotic slash) smouldering fires can heat the soil profile to a depth of 0.20 to 0.30 m, resulting in considerable chemical changes and soil sterilisation (Renbuss *et al.* 1972, Rundel 1983, Christensen 1994). For example, Van Wilgen and Holmes (1986) measured soil temperatures under piles of slashed *A. cyclops* exceeding 260°C and 204°C at 0.01 m and 0.04 m below the soil surface respectively and Rundel (1983) reported 500°C soil surface temperatures during the burning of Spruce/Fir slash piles. Roberts (1965) recorded soil temperatures (in fine weather conditions) under a pile of burning (13 to 18 cm diameter) *Eucalyptus* sp. logs in Canberrra. At a soil depth of just over 0.10 m, temperatures remained above 180°C for 21 hours. Peak temperatures ranged from 1 199°C just below the soil surface to 201°C at approximately 0.215 m soil depth. A probe to a depth of 0.38 m showed a temperature of 103°C. Five to eight hours after ignition, temperatures were 968°C at 0.03 m, 593°C at 0.05 m and 168°C at 0.165 m soil depths. Similarly, Renbuss *et al.* (1972), recorded approximate temperatures of 650°C at the soil surface, 350°C at 0.05 m, 250°C at 0.10 m, 150°C at 0.15 m and 100°C at 0.20 m soil depths under piles of burning *Eucalyptus* sp. logs. All depths sustained a temperature of at least 100°C for more than six hours. Likewise, Ketterings *et al.* (2000) measured surface temperatures under piles of slashed indigenous forest vegetation in Sumatra, Indonesia, and recorded temperatures in excess of 600°C. See Table 1.1 for a summary of surface and soil temperatures measured by different authors under diverse treatments during fires.

Temperatures above 120°C are lethal for many seeds of sclerophyllous vegetation (Keeley *et al.* 1985, Musil 1991). Accordingly, Holmes and Cowling (1997a) and

Holmes *et al.* (2001) found that increased fire intensity in exotic stands resulted in the elimination of native seeds and the killing of re-sprouting species still surviving in exotic stands. These fires have also been found to have detrimental effects on soil, increasing water repellency (Scott and Van Wyk 1990, Scott and Van Wyk 1992, Euston-Brown 2000). The realisation that dense stands of exotic invasive trees leads to substantial reductions in stream flow has prompted government initiatives to deal with the problem, and multi-million Rand weed control programmes such as Ukuvuka: Operation Firestop and the Working For Water initiative have been embarked upon (Marais 1998, Van Wilgen *et al.* 1998, Gubb 2000). Current estimates are that it costs 1.3 to 1.5 million Rands per year to clear invasive exotic plants in the catchment of the Swart River near George (Dr. C. Marais, Working for Water, Private bag X4390, Cape Town 8000 pers. comm. 2001) while more than 53 million Rands were invested in clearing invasive exotic spp. in fynbos areas of the Western Cape from October 1995 to March 1997 (Marais 1998). Twelve million Rands are currently spent per anum on clearing operations in the Cape Peninsula National Park (Mr. J. Jackelman pers. comm. 2001). According to Scott *et al.* (2000), the densest and most impenetrable exotic stands are often situated on the urban fringe and around semi-developed areas (particularly on the Cape Peninsula), increasing fire hazard to property. Macdonald *et al.* (1989) noted that in clearing operations, "where branches have been stacked in huge piles, allowed to dry out and then burned, the fires have been of unnaturally high intensity and long duration. This has resulted in the formation of circular patches up to 5 m in diameter of bare soil, often completely devoid of vegetation. Some of these scalded areas are still bare 10 years after they were burned...It is unsure whether these soils will ever regain their original characteristics." Some of the effects of these increases in biomass, fire intensity and heat damage are tested in this study.

Table 1.1 A summary of surface and soil temperatures measured during fires by different authors under various treatments. * indicates no data

Author	Taylor and Kruger (1978)	Martin (1966)	De Lange (1992)	Rundel (1983)	Rundel (1983)	Humphreys and Craig (1981)	Van Wilgen and Holmes (1986)	Van Wilgen and Holmes (1986)	Roberts (1965)	Renbuss *et al.* (1972)	Rundel (1983)	Ketterings *et al.* (2000)
Treatment	fynbos	Grassy Fynbos	fynbos	fynbos	chaparral	Australian shrubland	Standing *A. cyclops*	Stacked *A. cyclops*	Stacked eucalyptus logs	Stacked eucalyptus logs	Spruce / Fir slash piles	Natural forest slash piles
Country	RSA	RSA	RSA	RSA	USA	Australia	RSA	RSA	Australia	Australia	USA	Sumatra
Surface	mode: 316°C	550	500	300	*	90 - 550°C	*	*	1199°C	650°C	500°C	>600°C
0.0025 m	*	*	150°C	*	*	*	*	*	*	*	*	*
0.01 m	*	*	57.3°C	*	*	50 - 130°C	116 – 160°C	260°C	180°C	*	*	*
0.012 m	*	43°C	*	*	*	*	*	*	*	*	*	*
0.02 m	*	*	< 50°C	*	*	*	*	*	*	*	*	*
0.04 m	*	*	*	*	*	*	46 – 71°C	204°C	*	*	*	*
0.05 m	*	*	*	*	50°C	40 - 70°C	*	*	*	350°C	*	*
0.10 m	*	*	*	*	*	*	*	*	*	250°C	*	*
0.15 m	*	*	*	*	*	*	*	*	*	150°C	*	*
0.20 m	*	*	*	*	*	*	*	*	*	100°C	*	*
0.215 m	*	*	*	*	*	*	*	*	201°C	*	*	*
0.38 m	*	*	*	*	*	*	*	*	103°C	*	*	*

1.5.3 Current woody exotic plant management systems

Various biological (Annecke and Neser 1977, Taylor 1977, Fugler 1979b, Kluge and Richardson 1983, Kluge and Siebert 1985, Neser and Kluge 1986, Dennill and Donnelly 1991, Kluge and Neser 1991, Morris 1991, Fleitmann and Boucher 2001, Van den Berckt 2001), chemical (Taylor 1977, Donald and Nel 1989, McVeigh 1990) and mechanical (Fugler 1979b, Kluge and Richardson 1983, Breytenbach 1989, Donald and Nel 1989, Anonymous 1995a, b) control measures have been used in attempts to control woody exotic plants in the Fynbos Biome. Exotic plant management in the Silvermine Nature Reserve plans to make use of the following amended methodologies, also stipulated in the 2001 Silvermine River Action Plan (Anonymous 1995b). These methods are proposed for different management units for different problem species:

- Mature stands of all exotic species should be cleared according to a block management plan. However, the timing of initial clearing operations vary according to the species involved. *P. pinaster, P. pinea* and *H. suaveolens* are best cut one to two years before fire management is applied. This interval serves to allow the release of seed from the protective cones. The slashed material is stacked, encouraging rodents to eat the numerous seeds under a protective canopy (Ashton 1985, Anonymous 2000). A controlled burn is undertaken through a particular area, or block (of dense invasive exotic plants), during late summer to early autumn, usually during the first or second year following clearing and stacking (Anonymous 2000). Any ungerminated, unconsumed seeds released from the parent plants onto the soil surface within the stacks are thus burnt. Similarly, the fire kills immature plants resulting from those seeds released within stacks. It is important for the control of these plants to ensure that a complete, 'clean' burn takes place (Anonymous 2000). Areas that escape the burn should be searched for juveniles and these physically removed. Alternatively, a chemical foliar spray may be used to eradicate re-growth of seedlings (Ashton 1985, Anonymous 2000). Single large trees are felled by chain saw, manual saw or by axe. Ring barking can also be used to kill them (Anonymous 2000).

- Mature *A. mearnsii* and *A. saligna* plants are manually clear-cut and the stumps painted with a 2% solution of Garlon (which is bio-degradable) in diesel oil to kill them (and in so doing, prevent coppicing). They are then dyed either red (e.g. Sudan 3) or blue (e.g. Ecoguard) so that the treated stump is clearly marked. Unwanted manually cut remains of *A. cyclops*, *A. longifolia, A. mearnsii* and *A. saligna* are piled into scattered small stacks (Ashton 1985, Anonymous 2000). Management suggests they be burnt while green under moist, cool conditions, to ensure lowest possible fire temperatures (Anonymous 2000). In recently treated mature stands, follow-up treatment should occur within one year of clearing before treatment survivors flower and produce seed. Appropriate eradication treatment needs to be reapplied where necessary and the area regularly inspected for survivors (Anonymous 2000). Small or juvenile woody exotic plants of all species (up to 2 m tall) can be pulled by hand or using a puller (popper). Juvenile plants may alternatively be cut using a lopper (long-handled secateur-like instrument) and painted. This method is more suitable for light infestations than for dense stands (Anonymous 2000).

- Very dense stands of seedlings are sprayed with a foliar herbicidal spray (e.g. 0.5% Garlon solution) mixed with a wetting agent (e.g. Agripron) and coloured with a dye. Seedlings of the exotic must be less than 2 m tall with few other species in-between. Foliar sprays are generally conducted on wind free days to avoid contamination of non-target plants. Foliar herbicidal sprays are also generally not used within a two-meter wide band on each side of a watercourse to avoid contamination of the water. Here the hand pulling of seedlings is preferable (Anonymous 2000).

- The single most important aspect governing the success of exotic plant control operations, however, is the follow-up work (Fenn 1979, Milton and Hall 1981, Ashton 1985, Pennington 1986, Phillips 1986, Holmes *et al.* 1987 a, b, Macdonald *et al.* 1989, Martens 1994b, Pieterse and Boucher 1997). According to the Silvermine River Action Plan, the sites need to be checked for survivors and new recruits weeded every spring in the appropriate manner (Anonymous 2000).

1.5.4 Literature review of selected exotic plant species

Exotics introduced from Australia in the 19th century include *A. cyclops, A. longifolia* and *A. saligna*. They are widely distributed in the southwestern Cape Province and have already replaced or infested much of the lowland vegetation (Shaughnessy 1980, Musil and De Witt 1990). *H. sericea*, also introduced from Australia in the mid 19th century, spread from limited plantings to occupy 4 800 km^2 or 14% of the Mountain Fynbos. Its current range extends across approximately 1 000 km and incorporates a wide range of climatic regimes (Fugler 1979b, Dyer and Richardson 1992). While *H. sericea* has invaded the largest area, *A. saligna* is considered the greatest threat to fynbos ecosystems (Van Wilgen and Richardson 1985, Cronk and Fuller 1995). Together with *Paraserianthes lophantha*, *P. pinaster*, *Populus canescens, H. gibbosa* and *H. suaveolens*, these are the most important woody exotic plant invaders in the Cape Peninsula National Park's Silvermine Nature Reserve (Ashton 1985, Mr. R. Erntzen pers. comm. 2001, pers. obs. 2000).

1.5.4.1 *Acacia cyclops*

A. cyclops (rooikrans) is an evergreen shrub or shrubby tree (up to 6 m), probably first introduced from southwestern Australia to Baron von Ludwig's garden in the 1830's (Boucher and Stirton 1978c, Cronk and Fuller 1995). The first specific reference to it was in 1857/8 by one McGibbon who catalogued it as being one of a number of exotics growing in the Cape Town Botanic Gardens (Boucher and Stirton 1978c, Shaugnessy 1980).

In subsequent years it was planted for the purposes of sand stabilisation, fodder and shelter belts from Port Nolloth to Port Elizabeth (Roux and Middlemiss 1963, Boucher and Stirton 1978c, Shaugnessy 1980, Cronk and Fuller 1995). As late as 1973, a local Western Cape authority sold 95.1 kg of *A. cyclops* seed for public use (Hall and Boucher 1977). Later *A. cyclops* was to become the most widespread invader plant of Lowland Fynbos (Macdonald and Jarman 1984), the most important exotic in the Cape of Good Hope Nature Reserve (Macdonald *et al.* 1988) and the most widespread on the Cape Peninsula (Richardson *et al.* 1987, 1996). Macdonald and Jarman (1984) list it as the third most important invasive plant in the Cape Floristic Kingdom.

A. cyclops relies on large soil stored seed banks (up to 30 000 seeds m^{-2} canopy cover) for regeneration (Milton and Hall 1981, Holmes *et al.* 1987b, Macdonald *et al.* 1988) and rarely resprouts after felling or burning (Boucher and Stirton 1978c). The high density of the species' soil seed banks makes control difficult and expensive (Macdonald and Richardson 1986). Compounding problems are that seeds are widely dispersed by birds and mammals, such as the striped field mouse (*Rhabdomys pumilio*) and chacma baboon (*Papio ursinus*) (Boucher and Stirton 1978c, Gill 1985, Macdonald *et al.* 1988). *A. cyclops* also readily invades disturbed sites such as roadsides and its spread into established vegetation is especially rapid following fires (Roux and Middlemiss 1963, Boucher and Stirton 1978c, Gill 1985).

1.5.4.2 *Acacia longifolia*

The long-leaved wattle, *A. longifolia* is native to the coastal regions of eastern Australia and is highly invasive in many areas in fynbos and related vegetation types in the southern and southwestern Cape Province (Cronk and Fuller 1995). The earliest records of *A. longifolia* in South Africa date from 1827 and 1835 when one James Bowie planted it in Baron von Ludwig's garden. It was subsequently planted on sand dunes and as an ornamental tree (Boucher and Stirton 1978a, Shaugnessy 1986). It has spread from these initial plantings to become one of the worst threats to Mountain Fynbos vegetation (Cronk and Fuller 1995). According to Macdonald and Jarman (1984), it is the second most important invasive plant in the Cape Floristic Region.

A. longifolia has also invaded Lowland Fynbos, Southern Forest, Eastern Cape Forest and Grassland vegetation types (Boucher and Stirton 1978a). Its invasion success, particularly in Mountain Fynbos, is partly because of its production of large quantities of long-lived seeds, prolific regeneration after fire and the ability to survive on drier mountain slopes and streamsides (Boucher and Stirton 1978a, Milton and Hall 1981, Pieterse and Cairns 1986, Cronk and Fuller 1995). According to Pieterse and Cairns (1986) it is rapidly becoming a greater problem than *H. sericea* in Mountain Fynbos. Once established the long-leaved wattle may grow to a tree 10 m in height while in less optimal conditions it may occur as an erect or low and bushy shrub (Cronk and Fuller 1995).

1.5.4.3 *Acacia saligna*

Commonly known as port jackson, *A. saligna* originates from the southwestern areas of Western Australia (Boucher and Stirton 1978b, Shaugnessy 1980). *A. saligna* was probably introduced to the Cape in about 1833 (first documented occurrence in 1848) and planted to bind drifting sand dunes and as a source of tannin (Boucher and Stirton 1978b, Shaugnessy 1980). According to Shaugnessy (1986) such plantings continued until as late as 1947 when 3 529 ha of *A. cyclops* and *A. saligna* were planted on the Eerste River Plantation. However in 1973, an authority in the Western Cape sold 99.6 kg of *A. saligna* seed for public use along with a warning which stated: "these species are inclined to spread and can, under favourable conditions, become a serious weed" (Hall and Boucher 1977).

From the Cape Flats *A. saligna* has invaded Lowland Fynbos, Mountain Fynbos, Eastern Cape Forest, Southern Forest, Succulent Karoo, Grassland and has spread into the southern margins of the Karoo (Boucher and Stirton 1978b).

A. saligna is a dense shrub or small tree reaching 9 – 10 m in height in South Africa (Boucher and Stirton 1978b, Milton and Siegfried 1981). Eradication is difficult because port jackson plants coppice rapidly after fires or mechanical severing. They also have hard, long-lived seeds that rapidly accumulate to form large soil seed banks (Boucher and Stirton 1978b). According to Cronk and Fuller (1995), one square meter of canopy may produce 10 500 seeds per year while Milton (1980) reported 1200 – 7400 seeds/m^2 in the leaf litter under stands of *A. cyclops*, *A. melanoxylon*, *A. saligna* and *A. longifolia* in the southwestern Cape. Viability of *A. saligna* seed is over 90% and they germinate profusely after fires (which break their dormancy) (Jones 1963, Jeffery *et al.* 1988, Cronk and Fuller 1995). Van Wilgen and Richardson (1985) recorded 9 800 stems/ha resulting from such prolific germination. These are some of the attributes that persuaded Cronk and Fuller (1995) to list *A. saligna* as one of the world's worst woody plant invaders. *A. saligna* is the most serious plant invader in the Fynbos Biome because of its current invasion and it's spreading potential (Van Wilgen and Richardson 1985, Cronk and Fuller 1995).

1.5.4.4 *Hakea sericea*

H. sericea (needlebush or silky hakea) (Proteaceae) from southeastern Australia is a shrub or small tree, 3 – 5 m in height. It has become a weed of major importance in South Africa, particularly in mountainous regions of the southwestern and southern Cape (Fenn 1979, Fugler 1979 a, b, Fugler and Morris 1979, Fugler 1980, 1982, Kluge and Richardson 1983, Van Wilgen and Richardson 1985, Richardson *et al.* 1987, Kluge and Neser 1991). Together with *P. pinaster* it is considered the greatest threat to Mountain Fynbos (Neser and Fugler 1980).

The genus *Hakea* was probably first introduced into the Cape to Baron von Ludwig's Ludwigsburg Gardens in 1833 (Annecke and Neser 1977, Fugler 1980). Fugler (1982) mentions it as one of the first plants used in the attempted stabilisation of sand dunes on the Cape Flats in 1847 (although Shaugnessy (1980) states that its earliest known occurrence dates from 1858). By 1863 *H. sericea* was already present in the Bathurst district where it had started to encroach onto valuable pasture land (Fugler 1979b).

After 1875, "hakea" was widely used as a hedge plant to protect young pine plantations from wild animals (Fugler 1979b, Neser and Fugler 1980, Fugler 1982). It was also used as firewood for the processing of raisins in the Wolseley area (Fugler 1979b, Neser and Fugler 1980). Looking at its current distribution, associated with the occurrence of nutrient poor soils, the foci of plantings were near Cape Town, Stellenbosch, Franshoek and George (Dyer and Richardson 1992).

According to Annecke and Neser (1977), "concern about the alarming density and spread of hakeas on mountain slopes was first recorded in 1838, but many years elapsed before any concerted efforts at controlling these plants was made." Fenn (1979) states that as far back as 1920 the danger of *Hakea* spp. spreading into mountain catchments was realised. However, it took until 1961 before the Minister of Agriculture was finally urged (by the United Municipal Executive) to have the hakea problem examined (Annecke and Neser 1977, Fenn 1979, Fugler 1979b). Following this meeting an Action Committee was appointed to deal with the problem, but they achieved limited success (Fenn 1979). In 1976 the problem was re-addressed and "Operation Hakea" commenced (Fenn 1979). Initial success lead to exaggerated predictions regarding future elimination of hakea in mountain catchments (Fenn 1979, Fugler 1979a). In 1992 self-sown stands still occurred in 30% of quarter degree squares that constitute the Fynbos Biome (Dyer and Richardson 1992).

H. sericea is noted for its adaptations to fire (Fugler 1979b, Kluge and Neser 1991). These adaptations have been important factors in its achievement of remarkable dominance in species-rich vegetation of great conservation importance in South Africa (Cronk and Fuller 1995). Noteworthy adaptations include the fact that it reaches reproductive maturity relatively early, after about two years, and is strongly outbreeding (Dyer and Richardson 1992). It also has large woody serotinous fruit follicles (which accumulate throughout its lifetime) containing two protein rich winged seeds (Fugler 1979b, Kluge and Neser 1991). Lack of specialised pre-dispersal seed predators and prolific seed production ensures a large seed load, which appears to be higher in South Africa than in its native Australia (Fugler 1979b, Cronk and Fuller 1995). Seed production in South Africa is also 16 times greater than that of

H. suaveolens (Richardson *et al.* 1987). In South Africa eight year old plants have been recorded having over 1000 fruits and sixteen year old plants over 10 000 (Fugler 1979b, 1980).

Following the death of the parent plant, often after a fire, the follicles dehisce and release all their seeds (i.e. serotiny) (Fugler 1979b). In South African environments, this may result in densities of up to 7.5 million seeds per hectare in the ash bed following fires (Kluge and Richardson 1983). This gives rise to the dense, impenetrable thickets that make hakea a pest (Fugler 1979b). The winged seeds may also be dispersed by wind over great distances to form satellite foci (Neser and Fugler 1980, Dyer and Richardson 1992, Cronk and Fuller 1995). The rapid germination and growth of a high proportion of the released seeds has also contributed to its success as an invader plant (Richardson and Van Wilgen 1984, Dyer and Richardson 1992). According to Neser and Fugler (1980) and Van Wilgen and Richardson (1985), *H. sericea* invasion results in a fuel load increase of 60% and the low moisture content of the leaves results in more vigorous burns than in un-invaded fynbos.

1.5.4.5 *Hakea suaveolens*

According to Shaugnessy (1980), the first known occurrence of sweet hakea, or *H. suaveolens* in South Africa is from 1850. *H. suaveolens* is an erect shrub or small tree, which may branch at ground level in open situations (Neser 1980). It originates from isolated coastal granite outcrops in southwestern Australia and the nearby Recherche Archipelago (Fugler 1979b, Neser 1980, Fugler 1982). Sweet hakea was probably one of the Australian exotics used in the attempted stabilisation of a major area of drift sand (known at the time as White Sands) on the Cape Peninsula (Fugler 1982).

After 1855, sweet hakea and an abundance of other exotic species were distributed to the public by the Cape Town Botanical Gardens and by private nurseries contributing to their spread (Shaugnessy 1986). Later, during 1904-1908, the conservator of forests for the Transvaal distributed about a half a million seedlings annually, including various *Pinus* species and *H. suaveolens* (Wells *et al.* 1986).

There is some disparity regarding the time it takes for *H. suaveolens* to produce its first fruit, but it has been shown to take longer than six years (Fugler and Morris 1979, Fugler 1979b, 1982). The seeds contained in the fruit are typically released on a large scale only after fires (Cronk and Fuller 1995). The time taken to produce fruit limits its rate of spread, but it poses a serious threat to fynbos in those areas where it has become well established (Neser 1980, Cronk and Fuller 1995). Fugler (1979b), Fugler and Morris (1979), Fugler (1982) and Neser (1980) consider it less of a problem than *H. gibbosa* or *H. sericea.*

Fugler (1979b, 1982) stated that: "in 1977 Annecke and Neser, at the Second National Weeds Conference, called for the total eradication of *H. suaveolens*. Distribution and phenological studies indicate that this would be a relatively simple task at the present time". He also stated that: "This plant could easily be eradicated in the near future by felling the plants and stacking them into piles. The piles would have to be inspected only three years later for seedlings which may have grown". Unfortunately this "easily controllable" exotic has not been successfully eradicated and still poses serious threats to indigenous vegetation and ecosystem functioning in fynbos for example in the Silvermine Nature Reserve (pers. obs. 2000).

1.5.4.6 *Pinus pinaster*

Cluster or maritime pine is native to the Mediterranean Region of Europe, from the Adriatic in the east to the Adriatic seaboard of France, through the Iberian Peninsula, on some Mediterranean islands and in parts of North Africa (Kruger 1980, Cronk and Fuller 1995). It occurs naturally on acid aeolian sands, podzols and skeletal lithosols. Similar soils characterise mountainous habitats in the Fynbos Biome, where it is a serious invader (Kruger 1977a, Taylor 1977, Day 1983).

Shaugnessy (1980) determined that *P. pinaster* was introduced to Cape Town at some time between 1685 – 1693 under the name *P. sylvestris* and that by 1810 *P. pinea* and *P. pinaster* were conspicuous features of the Cape Town landscape. The French Huguenots also introduced the tree to South Africa when they established a plantation at Genadendal in 1825 (Kruger 1980). In 1857 the Uitvlugt Plantation (formerly known as White Sands) on the Cape Flats became an experimental forestry area and the success of *P. pinaster* at this site lead to widespread planting on Table Mountain (Shaugnessy 1986). Forestry officials justified this afforestation in terms of timber production, improved water supply, aesthetics and fire control (Shaugnessy 1986). According to J.S. Lister, the forester in charge in the 1880's: "the bleak and naked appearance" of Table Mountain in its natural state was a "subject of daily comment." Likewise in the 1890's, D.E. Hutchins saw the afforestation of Devil's Peak as a way to "cover the bare and stony slopes" which were "a reproach and eyesore to Cape Town" (Shaugnessy 1986). Human intervention thus played a central role in the establishment and spread of this important invasive tree (Taylor 1977, Shaugnessy 1986).

P. pinaster (which may grow to 40 m in height), is currently widely cultivated as a commercial forestry tree, and its powers of escape from these plantings is notorious (Hall and Boucher 1977). It is listed by Cronk and Fuller (1995) as "a serious or widespread invader affecting important natural or semi-natural habitats" (i.e. species-rich vegetation, nature reserves and areas containing rare or endemic species). This is certainly the case in Mountain and Lowland Fynbos where it grows on acid, leached soils often surviving fynbos fires of relatively low intensity (Kruger 1977, Boucher 1984, Cronk and Fuller 1995).

P. pinaster does not have the capacity to resprout after fires when stands are killed, but seedling reproduction following fires is prolific aiding in the spread of this exotic (Kruger 1977, Boucher 1984). According to Kruger (1977), a variable proportion of its cones remain closed for months or years after ripening (i.e. are serotinous), but most seed is shed in autumn or winter. However according to Dr. C. Boucher (pers. comm. 2000), *P. pinaster* is not serotinous in South Africa, shedding all its seeds two years after ripening. Its faster growth rate and longer life span than native flora, along with a short primary growth period, aids its invasibility (Kruger 1977, Cronk and Fuller 1995). Spread in the biome occurs mainly through wind dispersal of seeds although chacma baboons (*Papio ursinis*) and exotic grey squirrels (*Sciuris carolinensis*) also play a role (Kruger 1980). Trees bear seed from about their sixth year, germination of seeds being especially rapid following fires forming dense stands within a few generations (Kruger 1980, Boucher 1984).

1.6 Literature review: soil microbiology and chemistry in fynbos and other Mediterranean-type ecosystems

1.6.1 The effects of fire on soil chemistry

Mediterranean type ecosystem nutrient cycles are dominated by fire, as large nutrient stores, especially of nitrogen are often lost during fires through volatilisation (Rundel 1983, A. Milewski, Percy Fitzpatrick Institute of African Ornithology, University of Cape Town pers. comm. 2001). These losses may be especially important in fynbos, which is a nitrogen-limited system (Bollen 1959, Stock 1985, A. Milewski pers. comm. 2001). Fire can also cause severe (short-term) nitrogen (N) losses from grassland, chaparral, and temperate and boreal forest ecosystems (Grogan *et al.* 2000). Where fire stimulates nitrification, (often the case in Mediterranean climate ecosystems); nitrogen losses may be greater than expected based on fuel consumption alone (Christensen 1994). Conversely, fires may increase mineralisation of nitrogen and release basic cations tied up in live woody material (and in litter resistant to decomposition), temporarily increasing soil cation amounts and so increasing soil pH (Cass *et al.* 1984). Fire-caused changes in the nature and distribution of organic matter might also alter soil physical properties, the extent of soil organic mineral loss (and concomitant decrease in CEC) varying in direct proportion to soil temperature (DeBano *et al.* 1979, Christensen 1994). Post-fire changes in soil resulting from microbial or higher plant response contribute to the complexity of soil responses. For example biological nitrogen fixation may balance losses of N caused by fire (Cass *et al.* 1984), at least in natural ecosystems. These and other conflicting effects of fire and soil microbiology on soil chemistry (in Mediterranean and other ecosystems) are discussed below.

Fires usually result in net ecosystem nutrient loss in the following ways: oxidation of liquid compounds to gaseous forms (gasification); vaporization of solid compounds; convection of ash particles in fire-generated winds; leaching of ions in solution and accelerated soil erosion following fires (Christensen 1994). Gasification may account for significant losses of nitrogen and sulphur, moderate losses of phosphorus and minor losses of other elements. Vaporization and convection may cause considerable losses of phosphorus, potassium, calcium, sulphur, chlorine, nitrogen and magnesium (Rundel *et al.* 1983, Cass *et al.* 1984, Christensen 1994). Post-fire nutrient losses due to leaching and erosion usually increase with increased slope and factors regulating overland water flow, for example while surface erosion may remove elements closely tied to organic matter, extensive erosion removes the entire nutrient spectrum (Cass *et al.* 1984, Christensen 1994). Cation leaching losses also depend on precipitation, vegetation, soil texture and the availability of mobile anions (some of which are essential plant nutrients) (Alexander 1977, Cass *et al.* 1984). Fire induced chemical changes can also increase or decrease element susceptibility to leaching loss (Cass *et al.* 1984, Van Wyk *et al.* 1992). These chemical changes may influence soil microbiology, affecting further changes. For example, post-fire soil nitrogen may be altered by soil heating and subsequent microbial activity to the highly available NH_4+ and NO_3- forms (Dunn *et al.* 1979, Pietikainen and Fritze 1995). Leaching may result in significant losses of N, P, Mg, S, Ca and modest amounts of C and/or K (Alexander 1977). The relative importance of each nutrient loss mechanism fluctuates for each nutrient as a result of variations in fire intensity, soil, topography, and climatic patterns, however few estimates of nutrient loss exist from Mediterranean type ecosystems (Christensen 1994).

Fire may also cause increases in mobility and availability of a variety of nutrients, despite overall loss of nutrient capital (Christensen 1994). Post-fire nutrient increases take place in the following ways: direct mineral addition in ash; decreased plant uptake; altered patterns of nutrient adsorption and immobilization, increased microbial activity/decomposition and changes in oxidation-reduction transformations. Post-fire increases in nutrient availability, fluxes and recovery rates are however often spatially heterogeneous and variable (resulting from slope and aspect variations, varying vegetation characteristics, fuel loads, ash deposition patterns, fire intensity, climate and soil) (Cass *et al.* 1984, Christensen 1994). Increases in nutrient availability are also usually relatively short lived, usually one or two growing cycles long (Christensen 1994). Given potential burning affected nutrient fluxes, information is lacking with respect to post-fire patterns of nutrient recovery (Christensen 1994). For example the period needed for nitrogen fixation to replace volatised N in fynbos ecosystems is unknown, as is the rate of weathering of soil and bedrock (Van Wyk *et al.* 1992). Both of these factors could potentially lead to balanced nutrient budgets showing fire to have no long-term effect on the nutrient capital in (invader-free) fynbos ecosystems (Van Wyk *et al.* 1992).

It can be concluded that fires result in a variety of nutrient fluxes and recovery patterns, some of which are illustrated by the following papers. Volatilisation resulted in losses of Ca, K, Mg and N from phrygana and fynbos, however phosphorous levels remained constant in phrygana and dropped in fynbos (Arianoutsou and Margaris 1981, Van Wyk *et al.* 1992). No immediate changes occurred in total post-fire phosphorous in Sand Plain Lowland Fynbos (however reductions occurred during winter) while resin-extractable phosphorous increased after fire, re-attaining study pre-fire levels within four months (Brown and Mitchell 1986). Nine months after burning in Mediterranean pine forest soils, soil conductivity, nitrates, exchangeable NH_4^+, available P and K increased while C (total organic, extractable and water-soluble) humic acids, carbohydrates (total and water-soluble) were lower than those of unburnt soils (Hernandez *et al.* 1997). Similarly, fire increased surface pH, Ca, available P and Mn and nutrient content in Mountain Fynbos, other chemicals only showing increases for up to six months (Durand 1981, Musil and Midgley 1990). While balanced fire-induced nutrient losses, gains and fluxes may lead to balanced nutrient budgets in natural (fynbos) ecosystems (Van Wyk *et al.* 1992), exotic plant invasion, altered fire regimes and post-fire microbial activity may upset this equilibrium (Musil and Midgley 1990).

In unburnt *Acacia* invaded sites, soil CEC, Ca, Mg, K, total N, Mn, B and Zn concentrations were higher and resistance lower than in unburnt Lowland Fynbos and Strandveld ecosystems (Musil and Midgley 1990, Witkowski 1991) while in burnt *A. saligna* stands, higher soil N, Ca, Mg, K, Mn and B and lower Fe concentrations were measured than in burnt fynbos habitats (Musil 1993). *Acacia* sp. invasion thus poses nutrient enrichment threats, possibly rendering fynbos soils unsuitable for indigenous plant species (Milton 1980, Jackelman 1986), although this could be a reflection of habitat selection differences by woody exotics (Dr. C. Boucher, Botany Department, University of Stellenbosch pers. comm. 2001). A study of the effects of an unburnt stand of mixed exotic trees (*Acacia*, *Hakea* and *Pinus* spp.), burnt standing exotics, stacks of wildfire burnt slash and soil microbial influences on nutrient chemistry (of originally a pristine Mountain Fynbos habitat) will aid in the elucidation of post-fire nutrient fluxes and recovery rates in disturbed environments.

1.6.2 The ecological importance of soil microorganisms (bacteria, actinomycetes and fungi)

1.6.2.1 Ecological roles played by soil microorganisms

Most soil microorganisms (including bacteria, actinomycetes and fungi) are present in surface soil, declining rapidly with depth and in their absence many, if not all, soil biochemical reactions will come to a standstill (Tan 1994). Soil microorganisms play vital roles in many physiological processes and are crucial to a number of biochemical reactions essential to plant survival (Tan 1994, Paul and Clark 1996, Botha and Wolfaardt 2000). Insoluble organic materials and nutrients are changed (by fungi and bacteria) into soluble plant available forms, thus rendering "potential fertility available" (Lawrence 1956, Bollen 1959, Botha and Wolfaardt 2000). Of the most important arenas of microbial decomposition and mineralisation are carbon and nitrogen cycling (Tan 1994, Volk 1994). Some microbes are agents in production of ammonia and nitrates from protein material while others utilize atmospheric nitrogen, organizing it into compounds which ultimately become incorporated with humus, so adding to the limiting supply of soil nitrogen (Bollen 1959). Microbial production of CO_2 (which, with water, forms carbonic acid) and production of other acids (such as nitric and sulphuric) is responsible for gradual liberation of available food from insoluble soil minerals (Bollen 1959). Microbes are also central to the cycling of sulphur and phosphorous (Clark 1979). Plant utilizable sulphate is microbially transformed from elemental sulphur and sulphides (Bollen 1959). Paul and Clark (1996) describe these cycles (and their importance to higher plants) and expound on the roles of soil microorganisms in transformations of iron, manganese and mercury.

Higher plants and soil microorganisms grow in close relationship and are dependant on each other in many ways, for example large numbers of bacteria and fungi utilize plant and animal residues as food and actively transform them to humus and available plant nutrients (Bollen 1959). Every kind of soil microorganism causes chemical transformations, which in turn affects the development of all other organisms (including higher plants), develops soil and maintains its fertility (Bollen 1959). Given the ecological importance of soil microorganisms (bacteria, actinomycetes and fungi) it is imperative that effects of environmental disturbance (such as exotic plant invasion and fire) on their populations are quantified.

1.6.2.2 The ecological roles of soil bacteria

Bacteria (the smallest and most numerous soil organisms comprising more than 400 genera and an estimated 10^4 species) take part in most organic transactions of importance to soil fertility (and growth of higher plants) and are responsible for a number of enzymatic reactions including nitrogen fixation, ammonification and nitrification (Lawrence 1956, Clark 1979, Tan 1994, Paul and Clark 1996).

Other important ecological roles include hydrolysis of starch, sugars, alcohols, organic acids, amino acids, aldoses and many other organic compounds; oxidation of hydrogen, methane and other compounds; reduction of sulphates; synthesis of active organic compounds (including biotics, antibiotics and toxins); putrification of proteins (forming NH_3, H_2S and other compounds) and degradation of humic acids and pesticides/pollutants (Botha and Wolfaardt 2000). Some soil bacteria are destructive phytopathogens while still others form biotic substances (including vitamins B1, B2 and auxins) and various amino acids (Lawrence 1956, Krasil'nikov 1958, Paul and Clark 1996).

Quantification of the ecological effects of increases in fire intensity (associated with elevated exotic plant biomass) on soil bacterial populations is especially important, given not only their importance in ecosystem functioning, but also the susceptibility of nitrate-forming bacteria to heat (Lawrence 1956).

1.6.2.3 The ecological roles of actinomycetes

According to their structure and growth, actinomycetes are higher organisms than bacteria (Krasil'nikov 1958). They are heterotrophic feeders; some strains are able to decompose cellulose, proteins, lipids, starch, inulin, chitin, pectin, keratin, complex aromatics and humic acids (Krasil'nikov 1958, Alexander 1977). Other strains synthesise toxic metabolites, releasing antibiotics which have the capacity to, in culture at least, inhibit growth or cause elimination of populations of bacteria, yeast and various fungi (Krasil'nikov 1958, Alexander 1977). In addition to antibiotic production, many species of *Streptomyces* liberate extracellular enzymes, which are also possibly important in maintenance of soil microbial equilibria (Krasil'nikov 1958).

While their activities in soil transformations are not clearly defined, the significance of this group in soil appears to be their capacity to degrade a variety of organic molecules (including some herbicides and pesticides) (Krasil'nikov 1958, Paul and Clark 1996); form humus; produce several amino acids (which may serve as supplementary nutrients) and cause plant disease (Krasil'nikov 1958). These important biological functions, some quite different from those of bacteria, justify the study of the post-fire effects of invasive exotic plants, their management and fire on soil actinomycete populations.

1.6.2.4 The ecological roles of soil fungi

There are possibly in excess of 100 000 fungal species on earth including many saprophytic groups (such as lipomycetaceous and basidiomycetaceous yeasts, hymenomycetaceous and mucoralean fungi) which contribute to nutrient cycling and various biological processes in the soil mantle (Cooke 1979, Tan 1994, Paul and Clark 1996). Saprophytic fungi, with non-actinomycetous and actinomycetous bacteria, also decompose organic residue (cellulose, chitin, pectin and keratin) in soils, breaking it down into simpler forms, which then become available to plants (Cooke 1979, Tan 1994, Paul and Clark 1996, Botha & Wolfaardt 2000). Some lipomycetaceous and basidiomycetaceous soil yeasts oxidize sugar to pyruvate and then to CO_2 and H_2O. Basidiomycetes, hymenomycetaceous fungi and mucorales are important agents of wood rotting, destroying both lignin and cellulose, many being facultatively parasitic (Cooke and Rayner 1984, Paul and Clark 1996). Hymenomycetaceous fungi are especially important in mycorrhizal associations and in their ability to decompose hemicelluloses while mucorales are active in animal excreta decomposition (Alexander 1977, Cooke and Rayner 1984, Paul and Clark 1996). Some ascomycetes and basidiomycetes form symbiotic and others parasitic relationships with algae, insects and higher plants and (as phytopathogens) some cause enormous crop losses while some zygomycetes are predatory, actively trapping and consuming nematodes (Paul and Clark 1996).

Since they have no obvious economic value, saprotrophic fungi have received very little attention from mycologists in the past and consequently many of their impacts in fynbos ecosystems remain unknown (Botha and Wolfaardt 2000). However the various ecosystem functions played by many divergent groups of fungi and their large biomass in soil (far exceeding that of bacteria and actinomycetes) (Van Reenen 1992) more than justify exploration of ecosystem disturbance effects on population sizes.

1.6.3 Fire effects on soil microbiology

The effects of fire on soil microbiology and decomposition in Mediterranean and other ecosystems appear variable (Wright and Bollen 1961, Martin 1966, Renbuss *et al.* 1972, Dunn *et al.* 1979, Arianoutsou-Faraggitaki and Margaris 1982, Cass *et al.* 1984, Van Reenen 1992, Van Reenen *et al.* 1992, Fritze *et al.* 1993, Christensen 1994, Pietikainen and Fritze 1995, Dumontet *et al.* 1996, Pattinson *et al.* 1999, Jensen *et al.* 2001) even though microbes begin dying as soil temperatures rise above 30°C and as soil water content drops below -2MPa (Stock 1985). Mediterranean Regions are comparable with respect to soil microbes and chemistry since some are characterised not only by climatic similarity but also by strongly leached nutrient-poor soils, especially N (Bollen 1959, Day 1983, Groves *et al.* 1983, Stock 1985).

Microbes affect N availability by uptake of organic nitrogen from the soil. The rate of uptake is a function of population growth, which in turn is affected by soil water content and temperature (Stock 1985). The relative rate of microbial nitrogen uptake is however low, adding to this microbes and plant roots compete for different forms of nitrogen, (the C/N relationship determining if roots or microbes get the available nitrogen) (Stock 1985). Availability of N, P and S is determined by biotic (microbial) factors in Mediterranean ecosystems, whereas that of other macro and micronutrients is largely controlled by geochemical release (Groves *et al.* 1983). Biotic and geochemical nutrient releases are seasonally variable processes, water and temperature being limiting factors (Clark 1979, Groves *et al.* 1983). Seasonal activities of soil microorganisms and the significance or effects of N-fixation by free-living microorganisms in Mediterranean ecosystems have however been understudied (Rundel *et al.* 1983, De Koker 1994).

Although the effects of fire on soil microbiology in Mediterranean and other ecosystems appear variable, some trends (not without exception) related to fire intensity are apparent. In "natural" Mediterranean type ecosystems of relatively low vegetative biomass, burning does not appear to affect microbial biomass and populations, observed differences being both minor and transient (Martin 1966, Arianoutsou-Faraggitaki and Margaris 1982, Van Reenen 1992, Pattinson *et al.* 1999). In contrast Christensen (1994) stated that (in Mediterranean environments): "except where fires have been especially intense, microbial activity and decomposition are generally higher in burned areas, resulting in higher rates of mineralisation and transformations such as nitrification." Where vegetation biomass (and/or fire intensity is high), especially in areas of exceptional fuel loading (slash and log pile burning), microbial populations are generally negatively impacted and show varying recovery times (Wright and Bollen 1961, Dunn *et al.* 1979, Fritze *et al.* 1993, Pietikainen and Fritze 1995, Dumontet *et al.* 1996, Hernandez *et al.* 1997, Jensen *et al.* 2001). In certain circumstances however, quite the opposite occurs and microbial populations are benefited by post-fire conditions (Renbuss *et al.* 1972). During intense laboratory burning of chaparral soils most fungi and bacteria were killed, while less were killed in moderate burns, especially where the soil was moist (Dunn *et al.* 1979). Similarly, nine months after fire in Mediterranean pine forest soils, burnt soils contained a less abundant and active microbial biomass than unburnt soils while one year after fire, prescribed burning of coniferous forests (north-eastern Finland) had severely affected soil fungi (Pietikainen and Fritze 1995, Hernandez *et al.* 1997). The effects of burning areas of high live vegetation biomass may be lasting, for example eleven years after fire, microbial biomass was lower in burnt pine forest soil (from a dunal Mediterranean environment in southern Italy) than in a neighbouring unburned site (Dumontet *et al.* 1996). Although soil burnt in Douglas fir slash fires of exceedingly high intensity (akin to wildfire burning of exotic slash in fynbos ecosystems) was initially sterilised, rapid recolonisation of actinomycetes and fungi occurred fourteen months after burning. This prompted Wright and Bollen

(1961) to conclude that "hard-burned soil" acquires a complex micro flora about a year after burning and in the second year begins to exhibit a population characteristic of unburned soil. Inconsistently, burning plots with "doubled plant biomass" in a woodland savannah led to reduced microbial biomass in topsoil a year after burning while it took microbial biomass and activity at least 10 years to recover after prescribed burning of spruce slash in southern Finland (Fritze *et al.* 1993, Jensen *et al.* 2001). Opposing trends were observed in microbial populations of an "ash bed" soil, (produced by burning a pile of eucalyptus logs on the soil surface in Australia). Bacterial populations expanded rapidly to higher than pre-fire levels while actinomycetes and fungi populated the soil at slower rates. After about a year microbial species and population sizes had reverted to "normal", however, the initial fungal and bacterial recolonisers contained many species not present in the control soil (Renbuss *et al.* 1972). In summary, burning areas of high vegetation biomass results in enduring changes in soil microbial populations, biomass and activity while burning natural vegetation of low biomass results in minor transient changes.

In addition to variations resulting from fire and habitat differences, post-fire microbial populations exhibit wide monthly/seasonal fluctuations, (which are also inconsistent), complicating interpretation of population recovery (Bollen 1959, Wright and Bollen 1961, Visser 1990, Van Reenen *et al.* 1992, Volk 1994, Samson *et al.* 2000). For example, widely fluctuating microbial populations were largest in winter and smallest in summer under Douglas-fir slash piles while microbial biomass was greatest in autumn and spring in Mountain Fynbos (Wright and Bollen 1961, Visser 1990, Van Reenen *et al.* 1992). In Temperate Grasslands however, microbial activity slows to a near standstill during the cold winter months while higher temperatures benefit microbial growth, Tropical Grasslands having much higher levels of activity year-round (Volk 1994). In summary, environmental conditions including temperature, rainfall, soil moisture content and soil structure influence post-fire activity and distribution of soil microbes, albeit variably (Bollen 1959, Visser 1990, Volk 1994). Stock (1985) however maintains that soil fungi are insensitive to changes in soil water content and can operate at potentials below -5Mpa. The four microbial assays carried out in the present study (between November 2000 and September 2001) will thus aid in the interpretation of post-fire recovery patterns (chapter 3).

To conclude, while information about effects of burning on soil microbial populations is fragmentary and variable (Cass *et al.* 1984), the present study will add to the knowledge base by elucidating post-fire patterns of microbial (fungal, bacterial and actinomycete) recovery in Mountain Fynbos, habitats with high exotic plant biomass, habitats cleared of exotics and areas of exceptional fuel loading (stacks of exotic slash). These post-fire recovery patterns are compared to seasonal population fluctuations in unburnt Mountain Fynbos and standing exotic plant dominated habitats. All observed microbial population growth patterns are correlated to environmental variables (soil minerals, texture and fire intensity) in order to establish factors determining microbial distribution and population growth. At the same time possible post-fire microbial effects on soil mineralogy in various vegetation types are investigated in the Silvermine Nature Reserve.

1.7 Study Area

1.7.1 Study site locality and sample plot layout within sites

Silvermine Nature Reserve (mapping grid-square 3418AB14) – situated on the South Peninsula Mountain Chain, close to the suburb of Noordhoek, Cape Town, South Africa – was the study site for this project. The study site and sample plot localities are illustrated in Figure 1.1. Examples of the treatments are depicted in Figure 1.2 while the field plot design is illustrated in Figures 1.3 and 1.4. Main plots in the burnt standing exotic treatment were randomly selected approximately twenty paces apart across the slope. Main field plots in the burnt fynbos treatments were selected randomly while wildfire and control burnt stacks were arbitrarily chosen. Burnt cleared area plots were located within five meters of each wildfire burnt stack.

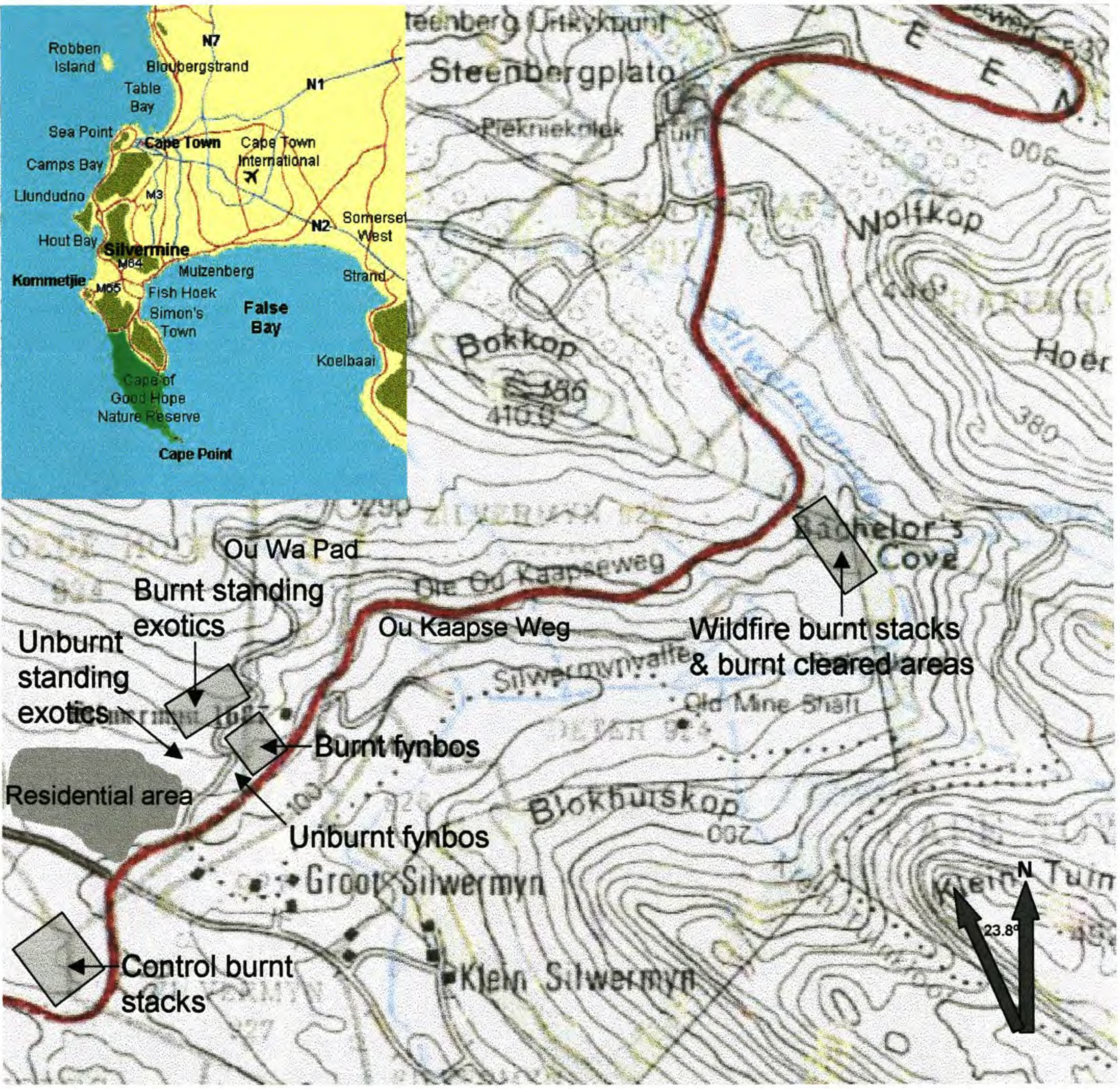


Figure 1.1 Field plot locality map indicating locality of control burnt stack plots, wildfire burnt stack plots, burnt cleared area plots, burnt standing exotic plots, burnt fynbos plots, unburnt fynbos and unburnt standing exotics. Adapted from South Africa 1:50 000 sheet 3418 AB & AD. Kaapse Skiereiland. Fifth Edition. 1983.
Map inset adapted from WWW.sunsetbeach.co.za/Cape_Town_information/Cape_Town.area.map.htm

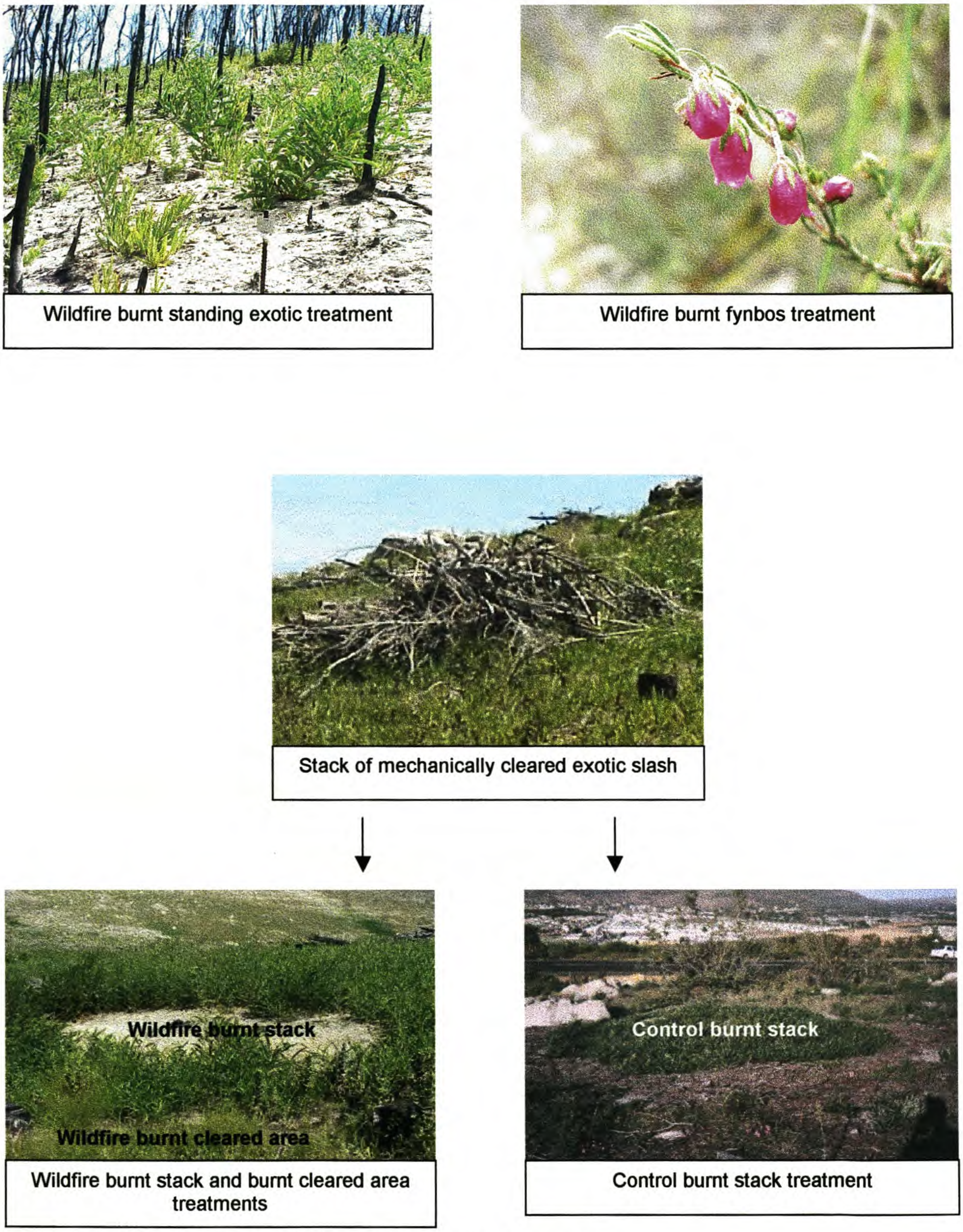


Figure 1.2 Examples of the treatments investigated in this study

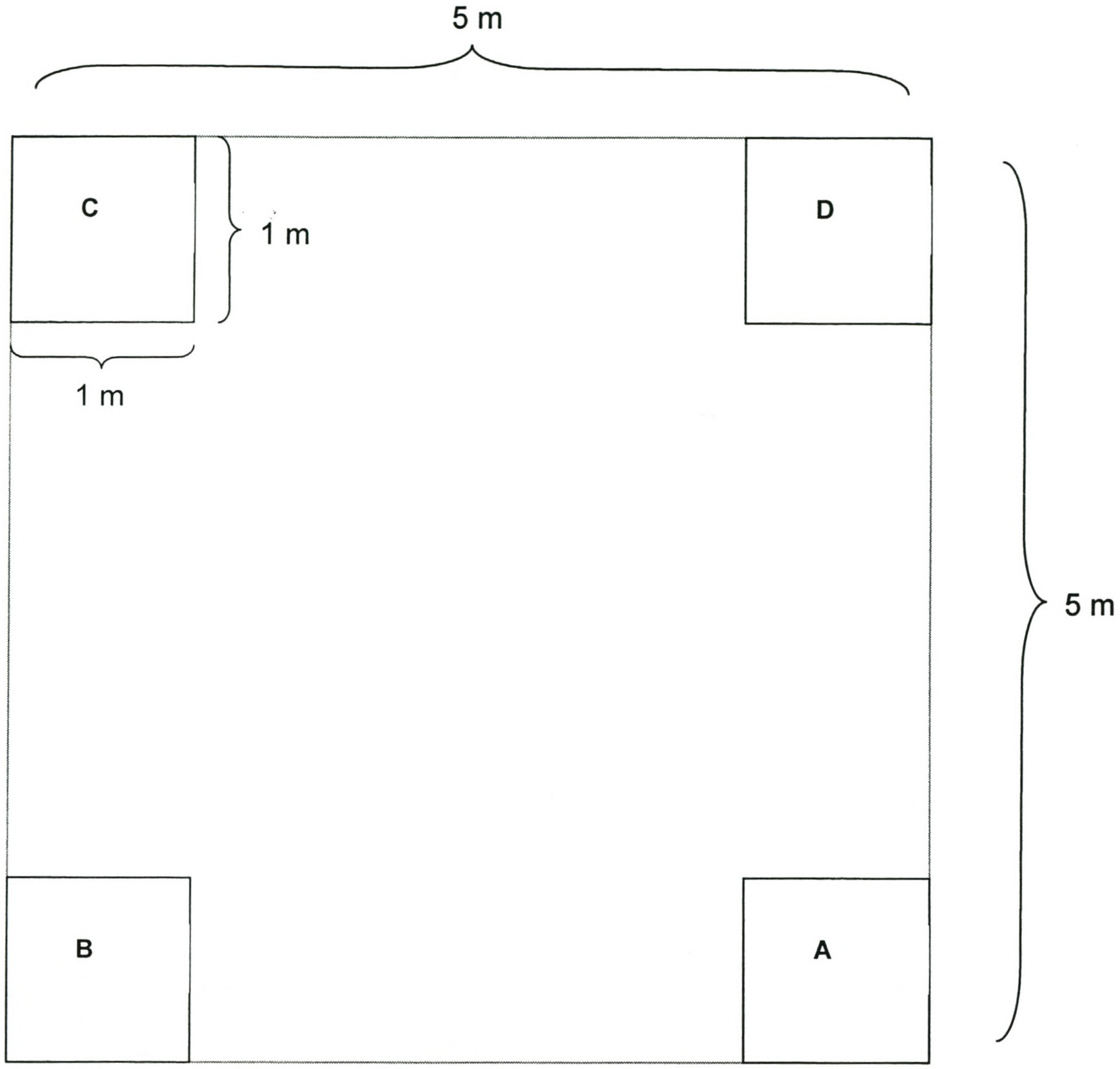


Figure 1.3 Field plot design for burnt fynbos and burnt standing exotic habitats. Regenerating plant counts were made in each of the 1x1 m corner plots (chapter 2). Five similar 5x5 m plots were laid out in each of these post-fire habitats. Soil was sampled from just outside the main plots for the nursery germination trial and microbial assays (chapter 3)

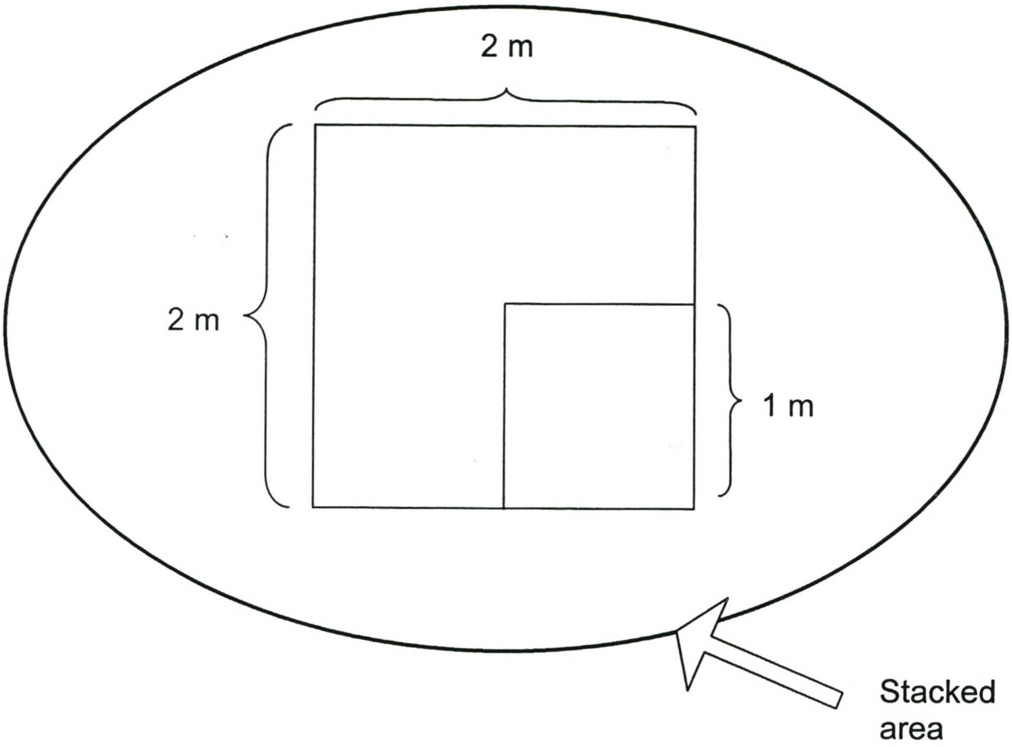


Figure 1.4 Field plot design for wildfire and control burnt stacks and burnt cleared areas. Regenerating plant counts were made in each of the 1x1 m plots (chapter 2). Five similar plots were laid out in each of these post-fire habitats. Soil was sampled from just outside the 2x2 m plots for the nursery germination trial and microbial assays (chapter 3)

1.7.2 Historical background of the Silvermine Nature Reserve (pre- and post-European)

Fynbos landscapes have been inhabited since the Early Stone Age (over 600 000 years ago), evidenced by the scattered occurrence of artefacts dating from this time (Deacon 1983, Avery *et al.* 1995). The more widespread occurrence of Middle and Later Stone Age artefacts indicate a progressively greater spread of human habitation (and influence) and that the area was favourable for human habitation (Deacon 1983, Avery *et al.* 1995). These people were, however, limited to areas where food resources, such as game and especially geophytes, were plentiful (Anonymous 1995a). According to Durand (1981) and Deacon (1983), even low density populations would have caused a considerable increment in the number of fires above the number expected under the prevailing natural regime. However, several authors are of the opinion that Middle Stone Age people were not significant agents of ecological change (Deacon 1983, Groves *et al.* 1983, Hall 1984, Avery *et al.* 1995).

More numerous distinctive archaeological finds have been made in the Biome dating from the Holocene (10 000 years ago). These and other evidence suggest that the San lived at this time as organised groups of hunter-gatherers and used fire to encourage the growth of geophytes (Deacon 1983, Anonymous 1995a). Two thousand years ago the Namaqua group of Khoikhoi pastoralists spread into the Cape and displaced the San, introducing the effects of fixed settlements, livestock grazing and exotic cultigens (Deacon 1983, Groves *et al.* 1983; Anonymous 1995a, Anonymous 2000). These peoples, due to their widespread distribution, mobility and control of fire, were able to effect considerable modifications to their environment (Deacon 1983). According to Hall (1984), use of fire in the South African sub region may have started in the Early Stone Age but was not widely employed until the succeeding Middle Stone Age. Deacon (1983) concludes that the vegetation of the Fynbos Region has been subject to some form of fire management for at least the past 100 000 years. It must however be considered that the natural fire regime would have differed significantly under glacial and interglacial periods, as a result of climatically induced vegetation changes (Deacon 1983). The Silvermine catchment has been inhabited since pre-European times, for at least the past 16 000 years (Anonymous 1995a). This history is evidenced by archaeological discoveries made in the Skildergatskop archaeological site (Peer's Cave), most notably the skeleton of the famous "Fish Hoek Man" (Greenland 1966, 1973). These early inhabitants would have had a notable effect on fire regimes (and fire occurrences) in the valley (Anonymous 2000).

The major anthropomorphic influences in the Silvermine Valley however escalated in post-European times (Avery *et al.* 1995). Colonial settlement here commenced in 1652 and a mere 61 years after the arrival of Jan van Riebeeck at the Cape, Khoikhoi society had collapsed (Anonymous 1995a). On 22 November 1699, a Niclaas Oortmans was first granted a licence to shoot hartebeest, eland and rhinoceros in the present day Silvermine Nature Reserve. These animals all subsequently disappeared from this terrain (Anonymous 1995a). The Silvermine Valley was further impacted during the 1680s by short-lived, ill-fated attempts to mine silver from the mountain slopes. Remains of the mining legacy include the mouth of an audit tunnel on the western slope of the Silvermine Valley and some buildings hidden behind a dense grove of *P. canescens* upstream of Silvermine Homestead (Anonymous 1995a, Anonymous 2000).

Later European influences on the Biome (and on Silvermine) included artificial dune stabilisation, using aggressive invasive Australian *Acacia* spp, urbanisation (the towns of Fish Hoek and Noordhoek border Silvermine Nature Reserve), afforestation and the construction of roads such as "Ou Kaapse Weg". The Reserve was further impacted in 1889 by dam construction in the upper reaches of the Silvermine River to provide drinking water to the Kalk Bay / Muizenberg Municipal Districts (Anonymous 1995a, Anonymous 2000).

In 1902 the Silvermine Forest Reserve was proclaimed in the upper catchment. It was a 472 ha extension to the Tokai Forest Reserve. By 1905 part of this area was planted with the exotic forest trees *Pinus canariensis* and *P. pinaster.* Similar plantings apparently also took place on the Steenberg Plateau. These plantations were, however, soon abandoned by the Forestry Department, but the municipality continued afforestation in the upper catchment until the 1960's with *Eucalyptus* spp., *P. pinaster* and *P. pinea*. Commercial management of these plantations was also later abandoned (Ashton 1985, Anonymous 1995a). Large areas of these old plantations were burnt in the fires of January 2000 and have subsequently been cleared (pers. obs. 2000). The current distribution of exotic vegetation at Silvermine is related to the history of deliberate plantings of these species (especially

A. mearnsii; *A. melanoxylon*; *A. saligna* and *P. pinaster*) by various authorities (Ashton 1985).

While sporadic efforts were made on Table Mountain in the late 1930s, exotic plant management only received real attention after 1950 when the Cape Town City Council embarked on a policy of exotic plant removal on Table Mountain and in Silvermine. After the proclamation of Silvermine Nature Reserve in 1965 (Mr. J. Jackelman pers. comm. 2001), the Parks and Forest Branch formulated control measures to be incorporated into operational planning programmes (Ashton 1985). The fell and burn method was developed during the 1970's (Combrink 1985) and was subsequently incorporated into the overall management plan for the conservation of mountain catchment areas (Kluge and Neser 1991). These clearing actions and the treatment of species have also had profound influence on the Reserve, its habitats and vegetation (pers. obs. 2000, 2001, Scott *et al.* 2000).

Evidence of past agricultural activity in the catchment is also apparent along the course of the Silvermine River. Terracing of the lower mid-reaches of the valley above and below the Silvermine Homestead is clearly evident, as are diversion weirs that would have been used to impound water for farming activities (Anonymous 1995a, Anonymous 2000). The history of the Fish Hoek area, including the Silvermine River, has been documented elsewhere (Greenland 1966, Burman 1977, Cobern 1983).

1.7.3 Topography

Silvermine Nature Reserve is located on the South Peninsula Mountain Chain (Ashton 1985). It extends from the Muizenberg Mountains and Trappieskop in the east (immediately above Boyes Drive), to Noordhoek Peak in the west. "Ou Kaapse Weg" cuts its way through the Reserve, effectively dividing it into two regions, one to the east and the other to the west. The western area rises from Steenberg Plateau to Noordhoek Peak, the summit of which is 754 m above sea level. The Muizenberg and Kalk Bay Mountains are situated in the larger half of the reserve, to the east of "Ou Kaapse Weg". The reserve is currently 2158.68 ha in extent (Anonymous 1995a, Anonymous 2000).

1.7.4 Geology and Soils

The upper reaches of the catchment (Silvermine Nature Reserve) consist primarily of quartzitic sandstones of the Table Mountain Group (Peninsula Formation) which overlay shales of the Malmesbury Group. The highly leached thin white sandy lithosols, common to fynbos mountain landscapes, are acidic, skeletal and weakly developed (Taylor 1977, Kruger 1979, Heydorn and Grindley 1982). Deep, moist and organically rich, coarse colluvial sands occur in the high altitude marshlands at the source of the river in the mountains above the Silvermine Dam (Anonymous 2000). The lower slopes, (where the sample plots are located) have colluvial accumulations of sandstone debris with rocks and finer material that are intermixed. Additionally, fine wind-blown (aeolian) sands have been blown up the valley from the lower-lying sand dunes and have become mixed with the colluvial deposits (Anonymous 1995a, Anonymous 2000, pers. obs. 2000). This has resulted in the formation of a deep mixed soil, for the most part more than 0.50 m deep within the study site (Anonymous 1995a).

The low-lying Tertiary to Recent sand dunes in the Fish Hoek - Noordhoek Gap are rich in carbonates originating from weathered seashells. This material is relatively unstable and sensitive to disturbance (Heydorn and Grindley 1982, Anonymous 2000). Organically rich and sandy materials are found in the lower valley (Anonymous 2000).

1.7.5 Vegetation communities/assemblages

Silvermine Nature Reserve supports at least 979 known species (and a further 203 species that are either expected to occur within the Reserve or whose identity has not yet been confirmed (Kesting 1994). The Reserve has also been identified as a floral “hot-spot” of species diversity on the Cape Peninsula (Trinder-Smith 1995). Silvermine, like most fynbos floras, has a high number of species, but a moderate number of genera and families, leading to a high species-to-genus ratio (Anonymous 1995a, Goldblatt and Manning 2000).

In common with other southwestern flora of the Cape Floristic Region, Silvermine Nature Reserve has a high concentration of species in taxa such as *Erica*, *Aspalathus*, *Thesium*, *Gladiolus*, *Pelargonium*, *Helichrysum* and *Nemesia* (Kruger 1979, Anonymous 1995a, pers. obs. 2000). This species concentration is correlated mainly with the mountainous sandstone areas, although the sandy flats, river and drainage lines contribute to habitat diversity and associated floral variety. One hundred and thirty-three rare and endangered plant species have been identified in the Silvermine Nature Reserve (Kesting 1994, Anonymous 2000). A large portion of these species occur in four Mesic Mountain Fynbos communities, including complex Upland Mixed Fynbos, which occurs on well-drained skeletal soils which overly bedrock. This is the most extensive community type and it occurs throughout the Silvermine Nature Reserve. Dominant species include *Erica baccans, Erica hirtiflora* and *Erica lutea* (Anonymous 1995a).

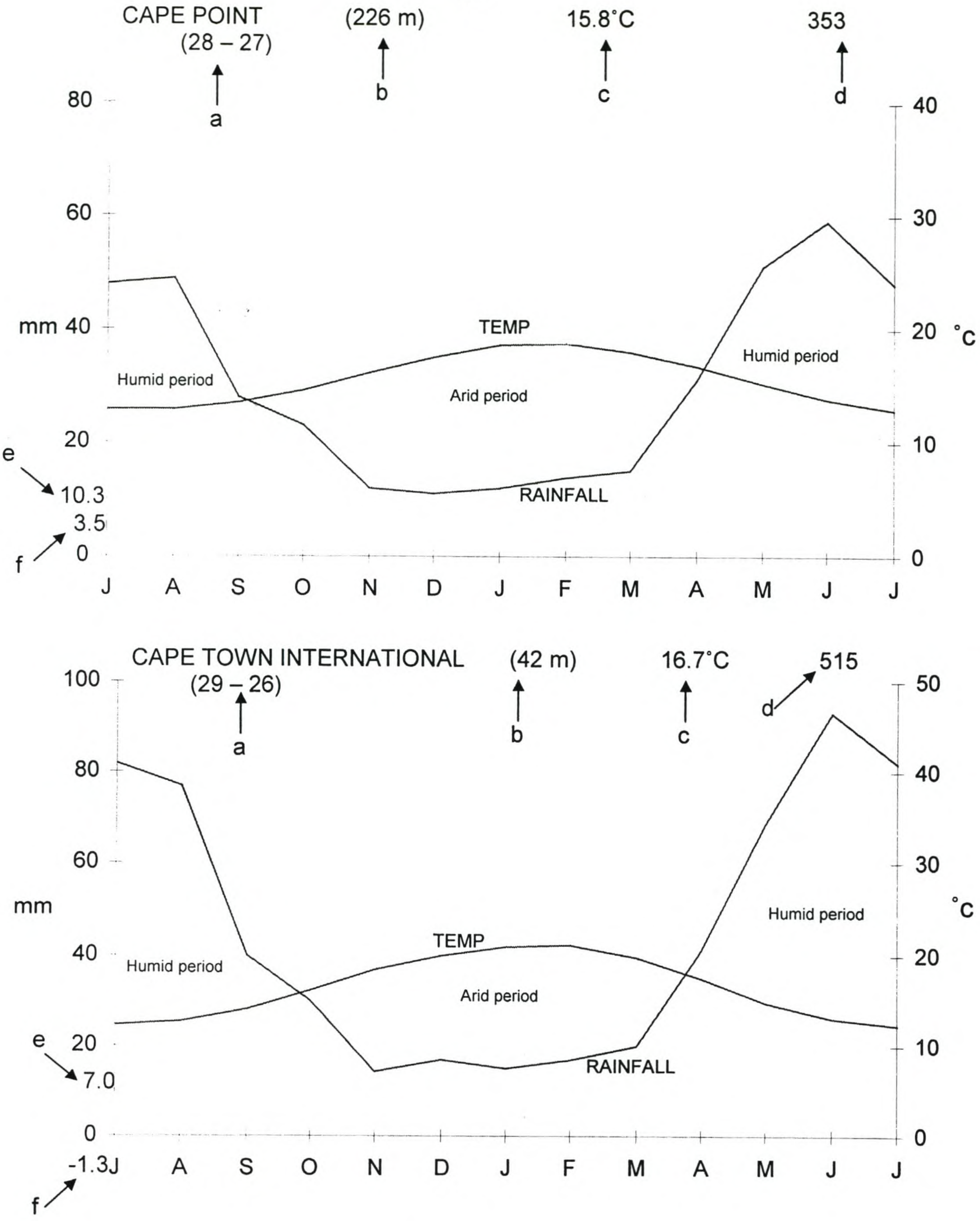
The sites studied in the present project are located on the lower sandy slopes and are typified by *Leucospermum conocarpodendron, Mimetes fimbriifolius* and *Protea lepidocarpodendron*. Sandstone outcrops and yellow iron-rich soils characterise this community. This community is extremely variable and complex partly due to topographic variation over its extent. It comprises many sub-communities and associations. The community at the study site is quite mesic and occurs on an eastern slope. It is also diverse, containing several strata. The richness of this community is illustrated by its containing 30 species (including one exotic plant, *P. pinaster*) in a single 5 x 10 m plot surveyed (during 2000) in unburnt five year old veld occurring immediately adjacent to the burnt fynbos site (Appendix A). The fynbos community examined was previously invaded (medium density) by various exotic *Hakea*, *Acacia* and *Pinus* species (Ashton 1985). These invasives had, however, been largely cleared from this area before the fire of January 2000.

In other large areas the fynbos community has been severely invaded by woody exotic plants. Adjacent to the "pristine" Mountain Fynbos sites, above "die Ou Wapad", are tracts of dense woody exotic plant infestations dominated by *A. cyclops*, *A. longifolia*, *A. saligna, H. sericea*, *H. suaveolens* and *P. pinaster*, most of which burnt in January 2000 (pers. obs. 2000). The invaded study site below "Ou Kaapse Weg" (where the wildfire burnt stacks occur, Figure 1.1) was dominated by *A. cyclops*, *A. longifolia*, *A. saligna* and *P. pinaster*, most of which burnt in the January

2000 wildfire. Additional woody exotic plants present in the reserve include *A. mearnsii*, *A. melanoxylon*, *Eucalyptus diversicolor, H. gibbosa*, *Leptospermum laevigatum*, *P. lophantha* and *P. pinea*. Herbaceous exotics occurring in fynbos and woody exotic plant dominated sites include *Anagallis arvensis* var. *caerulea*, *Fumaria muralis* and a number of other species (Anonymous 1995a and pers. obs. 2000). Introduced grasses and forbs, although present, are not considered to pose any threat to native species or ecosystem function within the Cape Peninsula National Park (Macdonald *et al.* 1988). This assumption should also hold true for the Silvermine Nature Reserve.

1.7.6 Climate

The Silvermine Nature Reserve is situated in the Winter Rainfall Region of the Cape and has a Mediterranean type climate characterised by hot, dry summers and cool, wet winters (Taylor 1977, Kruger 1979). Rainfall is mainly cyclic and orographic, highest falls typically occur during June to August, with February usually being the driest month of the year. Rainfall in the upper catchment (400 – 530 m above sea level) is approximately 1300 mm/a while the lower slopes (100 – 250 m above sea level) are much drier, with the mean for Fish Hoek approximately 630 mm/a. The study sites have southeasterly aspects and are located at altitudes of approximately 200 m above sea level and it is therefore surmised that the mean annual rainfall for the sample plots lies between these limits. Prevailing winds are from the south and southeast during the summer, producing orographic mists above 300 m altitude. Northwesterly frontal winds characterise and dominate rainfall patterns during winter. Estimated mean monthly summer temperatures in the Silvermine Valley vary from 18°C (on the plateau) to 23°C on the lower slopes. Corresponding mean monthly winter temperatures lie between 7°C and 12°C (Anonymous 1995a, Anonymous 2000). The climate of the Silvermine Valley is further described by klima diagrams of the two closest weather stations, situated at Cape Point and Cape Town International Airport (Figure 1.5).



LEGEND

a Number of years of observation (the first = temperature, the second = precipitation)
b Altitude
c Mean annual temperature in °C
d Mean annual sum-total of precipitation in mm
e Mean daily minimum of coldest month
f Absolute minimum

Figure 1.5 Klima diagrams for Cape Point and Cape Town International Airport weather stations. Data courtesy of the S A WEATHER SERVICES

1.7.7 Weather conditions prior to, during the fire and during the study period

Hot, dry weather conditions, which preceded the fire (16 – 20 January 2000) during 1999 and January 2000, contributed to a particularly high fire danger (Figures 1.6 – 1.11, Tables 1.2 and 1.3). During the fire, high temperatures and wind speeds exacerbated this danger (Tables 1.4 and 1.5) (Scott *et al.* 2000). The extreme weather conditions experienced during the fires, in combination with high fuel loads, contributed to fires of high intensity during January 2000 (Euston-Brown 2000, Scott *et al.* 2000). The year 2000 was also a relatively hot, dry year – a factor which could have had some bearing on post-fire regeneration and microbial establishment (Figures 1.6 – 1.11, Tables 1.2 and 1.3). The year 2001, when microbial assays were done, was however cooler and wetter than 2000 (Figures 1.6 – 1.11, Tables 1.2 and 1.3). All climatic data were supplied by courtesy of the S A WEATHER SERVICES. Email: info1@weathersa.co.za

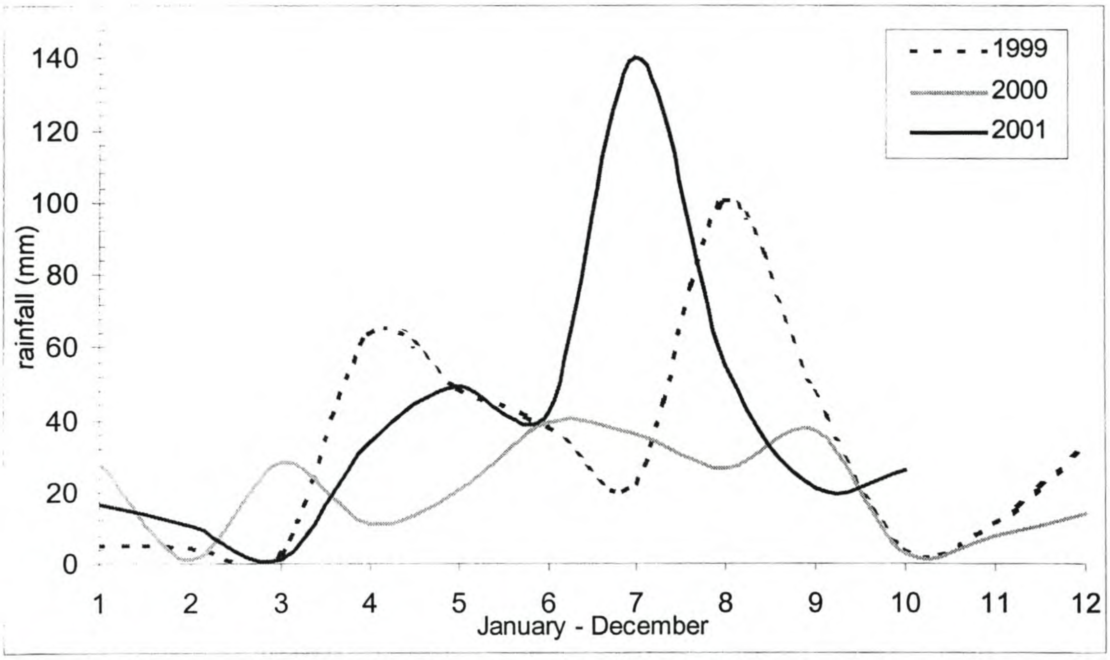


Figure 1.6 Monthly rainfall (mm) for Cape Point Weather Station

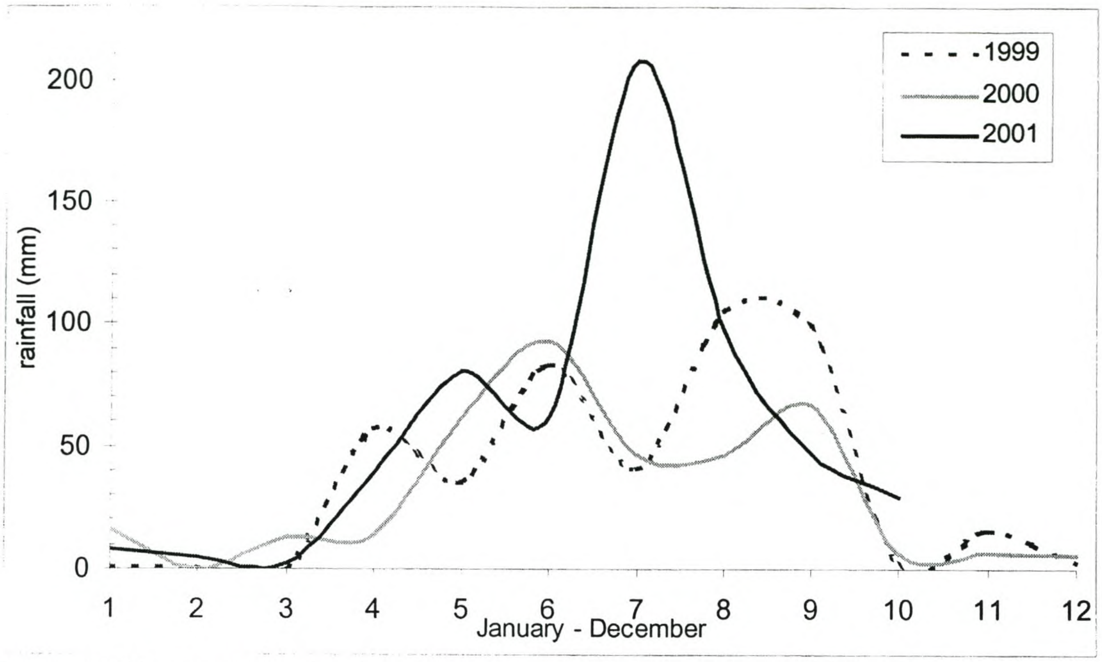


Figure 1.7 Monthly rainfall (mm) for Cape Town International Airport Weather Station

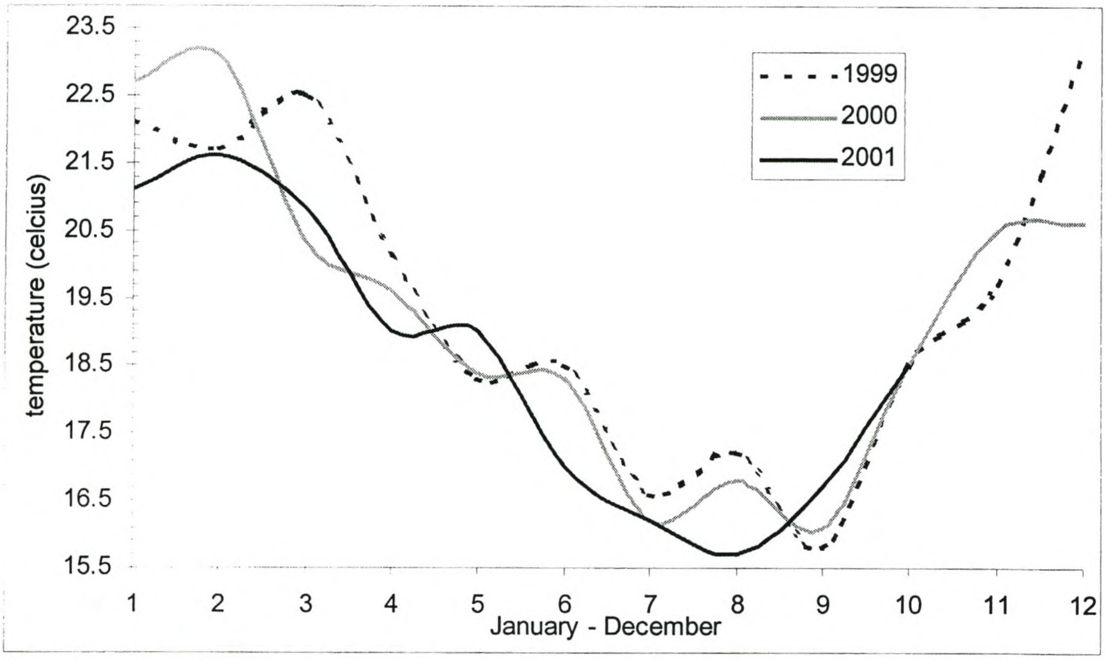


Figure 1.8 Maximum average temperatures (°C) for Cape Point Weather Station

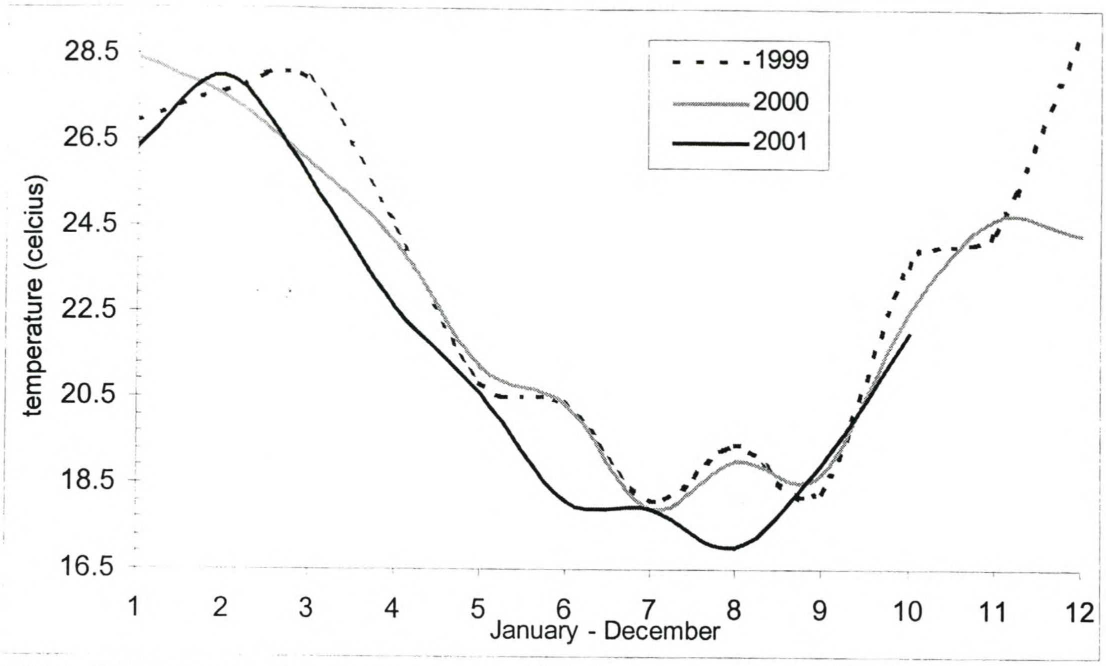


Figure 1.9 Maximum average temperatures (°C) at Cape Town International Airport

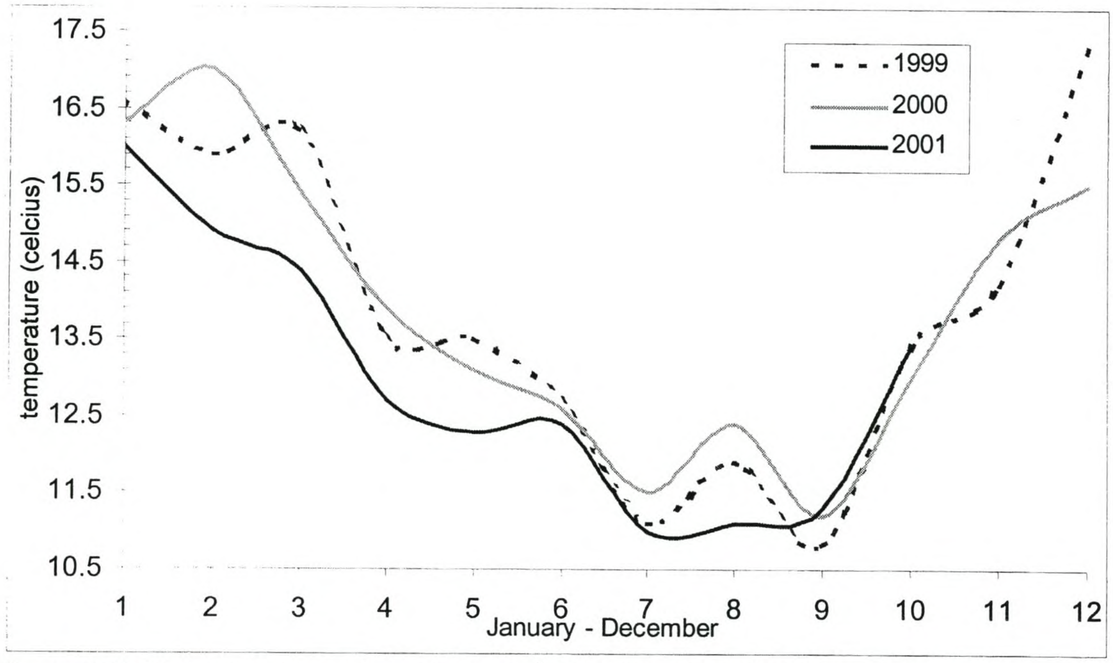


Figure 1.10 Minimum average temperatures (°C) for Cape Point Weather Station

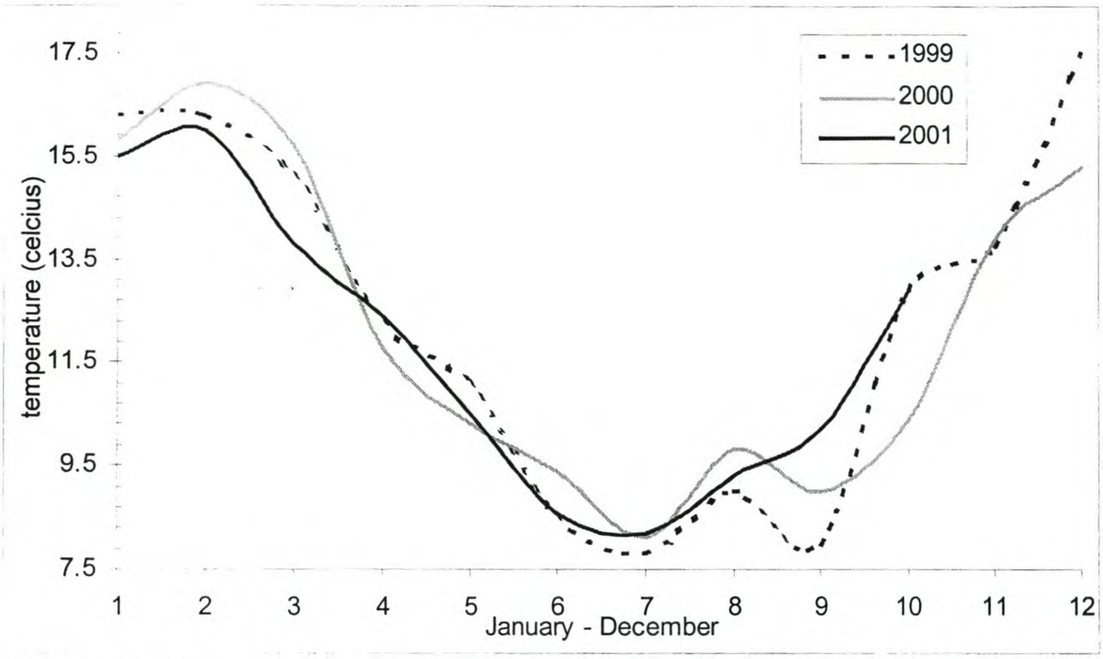


Figure 1.11 Minimum average temperatures (°C) at Cape Town International Airport

Table 1.2 Daily average maximum temperatures (°C) for Cape Town International Airport Weather Station. Columns denote number of days in the year above or below a set temperature. Ave = Forty year mean. 2001 values are from Jan – Aug

DAYS	>=40°	>=35°	>=30°	>=25°	>=20°	>=15°	<=10°
1998	0	4	29	112	230	357	0
1999	0	4	44	142	245	353	0
2000	1	4	30	122	248	355	1
2001	0	1	17	58	86	87	0
AVE	0	1.9	22.6	100	229.2	348.7	0

Table 1.3 Daily average maximum temperatures (°C) for Cape Point Weather Station. Columns denote number of days in the year above or below a set temperature. Ave = Forty year mean. 2001 values are from Jan – Aug

DAYS	>=25°	>=20°	<=15°	<=10°	<=5°	<=0°	<=-5°
1998	0	1	259	124	36	0	0
1999	0	5	247	108	14	0	0
2000	0	0	264	114	18	0	0
2001	0	0	34	2	0	0	0
AVE	0	1.3	275.6	127.9	32.4	0.4	0

Table 1.4 Daily weather conditions during the fire in 2001 at Cape Point Weather Station

Date	Max Temp (°C)	Min Temp (°C)	Wind Direction	Wind Speed (Km/h)
16-Jan	21.1	25	SE	72-90
17-Jan	no data	no data	E	72-108
18-Jan	29.2	24	ESE	54-90
19-Jan	38.4	13	ENE	18-36
20-Jan	33.1	11	E	18-36

Table 1.5 Daily weather conditions during the fire in 2001 at Cape Town International Airport Weather Station

Date	Max Temp (°C)	Min Temp (°C)	Average Temp (°C)	Rel. Humidity	Wind Direction	Wind Speed (Km/h)
16-Jan	32.5	16.6	24.6	43	SSE	18-36
17-Jan	33.7	18.1	25.9	46.5	WSW	0-36
18-Jan	34.9	14.4	24.7	51.5	S	0-36
19-Jan	41.3	14.3	27.8	46.5	S	0- 18
20-Jan	32.2	17.6	24.9	59	NNW	0-36

1.7.8 Fire, vegetation and fire severity in the various sites

At the time of the January 2000 fires in Silvermine Nature Reserve, the soil, live and stacked vegetation would have been especially dry because of the particularly low rainfall and higher than average temperatures in the months preceding the fires (Figures 1.6 – 1.11, Tables 1.2 and 1.3). As a result, the fire risk was extreme and the potential for soil heating and damage during the fires, which occurred during extreme weather conditions (Tables 1.4 and 1.5), was at its greatest (Scott *et al.* 2000). Various parameters indicative of soil heating were subsequently measured by Euston-Brown (2000) in the Silvermine Nature Reserve. Euston-Brown (2000) and Scott *et al.* (2000) concluded that dense areas of woody exotic plant infestation were burned in exceptionally high intensity fires. Scott *et al.* (2000) recorded flame lengths of 2 – 4 m in fynbos, 4 – 6 m in hakea and acacia invaded sites and up to 10 m in *Pinus* sp. stands. From these observations and rate of spread of the fire front, fire intensities of 10 000 to 40 000 kW/m were estimated (Scott *et al.* 2000). Both these authors also noted that stacks of exotic slash formed hot spots during the fires due to high volumes of concentrated and closely packed dry fuels. Shortly after the fire the positions of these stacks were clearly visible as white ash spots, plainly indicating localised points of severe soil heating (pers. obs. 2000).

Euston-Brown (2000) devised a Fire Severity Index based on various parameters measured in post-fire field plots. One of these parameters, which showed a high degree of correlation with fire intensity, was the basal diameter of charred stumps. The rationale was that in a severe fire, most flammable plant material is completely consumed while in a less severe burn, this flammable material is incompletely consumed. Using this method, Euston-Brown's (2000) study concluded that fire severity was greater in exotic vegetation and in areas where cleared exotics were stacked than in un-invaded fynbos.

This method was adopted with slight modifications in the present study. In this study the number of charred stumps (< and > 50 cm height) were counted in 2 cm diameter classes in February 2000. These counts were done in five 2 m^2 burnt standing exotic and five 2 m^2 burnt fynbos field plots respectively (Tables 1.6 and 1.7). Counts were not done in wildfire burnt stack (heat scar) plots nor in the burnt cleared areas surrounding heat scars. The rationale for omitting counts in these treatment types was because there were no charred stumps present within the heat scars. Stump counts in the burnt cleared areas would have been misleading since biomass in these areas had been slashed, removed and piled into stacks. The burnt fynbos sites contained an additional component, namely burnt hemicryptophytic (hereafter tussock) remains which were completely absent in the burnt standing exotic sites (Table 1.8). Figures 1.12 and 1.13 show a greater proportion of smaller woody stump diameter size classes in the burnt fynbos plots when compared to the burnt standing exotic plots. This indicates higher fire severities in burnt standing exotics.

Table 1.6 Mean number ± standard error of charred stumps (<50 cm height) per 2m^2 field plot (n = 5) in 2 cm diameter classes

	< 2	**2 - 3.9**	**4 - 5.9**	**6 - 7.9**	**8 - 9.9**	**10 - 11.9**	**16 - 17.9**
Exotic	231.60±35.10	36.00±6.58	13.80±2.35	4.80±1.80	3.20±2.22	0.60±0.49	0.20±0.20
Fynbos	446.40±120.65	14.60±4.39	4.00±1.00	0.40±0.24	0.00±0.00	0.00±0.00	0.00±0.00

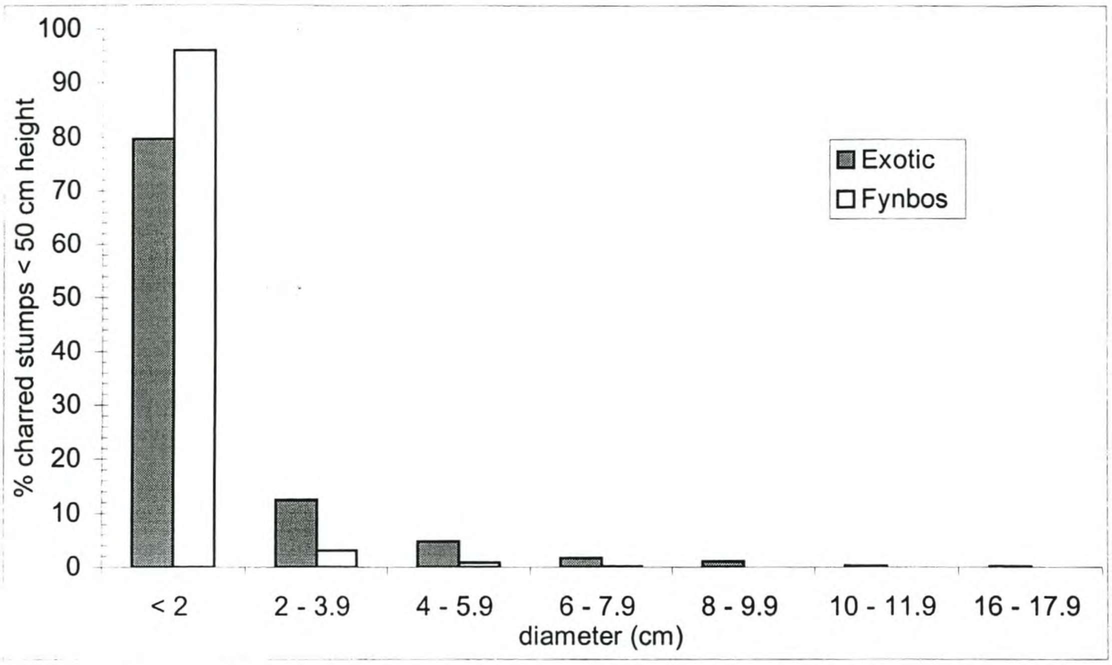


Figure 1.12 Proportion of charred stumps (%) (<50 cm height) in burnt fynbos and burnt standing exotic sites in 2 cm diameter classes. Field plots were 2m^2 and n = 5 at each site

Table 1.7 Number of charred stumps (>50 cm height) per 2m^2 field plot in 2 cm diameter classes (n = 5)

	<2	**2 – 3.9**	**4 - 5.9**	**6 - 7.9**	**8 - 9. 9**	**10 - 11.9**	**12 - 13.9**	**14 - 15.9**
Exotic	0.00±0.00	0.60±0.40	0.80±0.37	2.20±1.11	1.00±0.45	0.40±0.40	0.60±0.24	0.00±0.00
Fynbos	31.40±13.06	14.60±5.43	2.80±1.50	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00

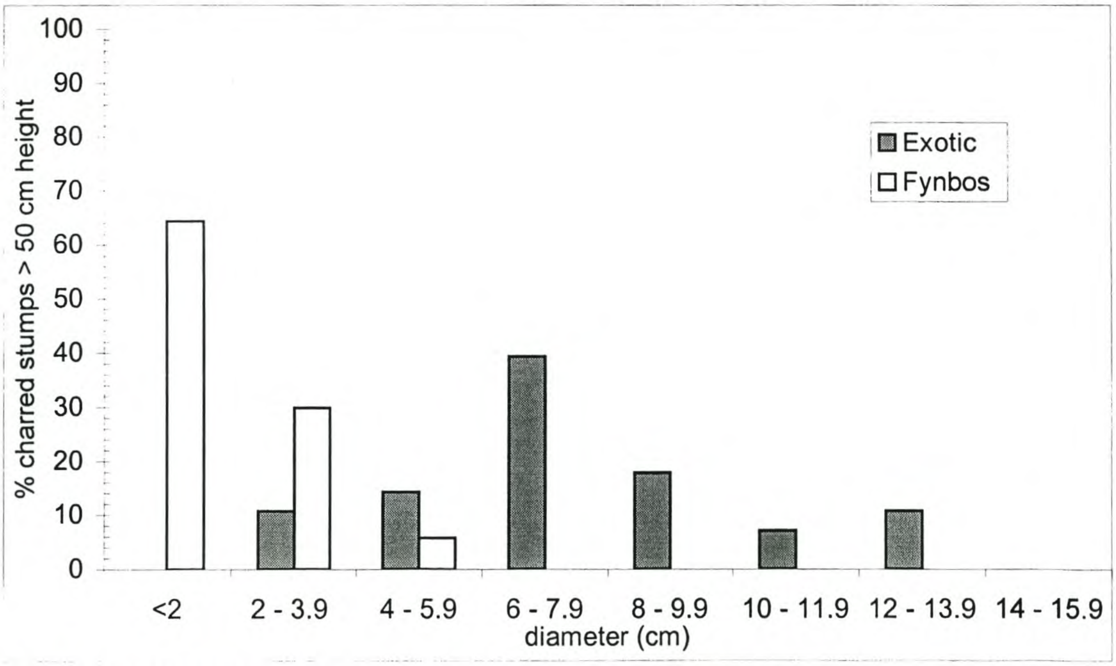


Figure 1.13 Proportion of charred stumps (%) (>50 cm height) in burnt fynbos and burnt standing exotic sites in 2 cm diameter classes. Field plots were 2m^2 and n = 5 at each site

Table 1.8 Number of charred tussock remains in five $2m^2$ fynbos field plots in 2 cm diameter classes

	0 - 2	2 - 3.9	4 - 5.9	6 - 7.9	8 - 9.9	10 - 11.9	12 - 13.9	14 - 15.9	Total
Plot 1	0	12	24	17	2	1	0	0	56
Plot 2	0	6	13	2	4	0	0	0	25
Plot 3	29	78	25	11	3	1	0	1	148
Plot 4	0	1	0	1	1	1	1	0	5
Plot 5	1	18	39	14	5	3	1	0	81

Following these counts, Euston-Brown's (2000) fire severity index (E.B.F.S.I) was adapted to include subjective assessments of pre-fire climatic conditions, weather conditions during the fire, pre-fire fuel loads and packing along a sliding scale of increasing influence. Charred stump diameter distributions are also included in the index; distributions indicating greater proportions of smaller stump sizes indicative of lower intensity fires (i.e. lower values along the sliding scale) and vice versa. Extremely hot fires (such as those associated with wildfire burnt stacks), which result in the combustion of all flammable plant material, irrespective of diameter; are assigned the highest value in this category. Control burnt stacks are also assigned high values in this category since elevated fuel loads and fuel packing arrangement result in lengthy burns consuming all stumps (pers. obs. 2001). Burnt cleared areas are assigned a medium-high value in this category, the reasoning being that their close proximity to stacks (burning at very high intensities) would probably have increased surrounding temperatures.

The adapted fire severity index (A.F.S.I) is illustrated in Table 1.9 and the associated indices and categories for the studied treatments in Table 1.10. From the calculated indices, field observations and literature sources (Euston-Brown 2000, Scott *et al.* 2000) it could be inferred that fire severity would have increased from burnt fynbos –► burnt cleared areas –► control burnt stacks –► burnt standing exotics –► wildfire burnt stacks in that order. These inferences and the A.F.S.I also concur with Durand's (1981) "soil heating severity index" which concluded that physical damage to the soil is strongly linked to woody exotic plant invasions. His index was 5.5 for un-invaded sites, 8.3 at sites with light infestations, and 12.1 at sites that were heavily invaded.

Table 1.9 Calculation of the Adapted Fire Severity Index (A.F.S.I.) and comparison with Euston-Brown's (2000) fire severity index (E.B.F.S.I)

Parameters	Subjective weighting of parameters influencing fire intensity						
	Low	**Med-low**	**Medium**	**Med-high**	**High**	**Very High**	**Exceptional**
Pre-fire climate	0	0	0	1	2	3	4
Fire weather	0	0	1	2	3	4	5
Fuel load & packing	3	4	5	6	7	8	11
Burnt stump diameter	0	1	2	3	4	5	6
TOTAL	3	5	8	12	16	20	26
A.F.S.I.	**0 - 1.5**	**1.6 - 2.5**	**2.6 - 4**	**4.1 – 6**	**6.1 - 8**	**8.1 - 10**	**10.1 - 13**
E.B.F.S.I	**0 - 4**		**4.1 - 8**		**8.1 - 12**		

Table 1.10 A.F.S.I. indices and categories for the sites studied

Parameters	Sites/Treatments						
	Unburnt fynbos	**Unburnt exotics**	**Burnt fynbos**	**Burnt cleared areas**	**Control burnt stacks**	**Burnt standing exotics**	**Wildfire burnt stacks**
Pre-fire climate	N/A	N/A	4	4	1	4	4
Fire weather	N/A	N/A	5	5	1	5	5
Fuel load & packing	N/A	N/A	4	3	11	8	11
Burnt stump diameter	N/A	N/A	1	3	3	5	6
TOTAL	0	0	14	15	16	22	26
A.F.S.I. Index	**0**	**0**	**7**	**7.5**	**8**	**11**	**13**
A.F.S.I. Category	**0**	**0**	**High**	**High**	**High**	**Very High**	**Exception**

1.8 Conclusion and incentive for this project

While there is no hope of eliminating pest plants completely (Taylor 1977), we must strive towards a "permanent balance between friends and foes", maintained by management; hence the importance of research in this field. As Prof. Wicht wrote in 1945: " The people of South Africa would be disgraced if they did not make a supreme effort to prevent the total loss of the extraordinally rich and beautiful Cape vegetation, which at the same time is an invaluable protective groundcover ". It is hoped that this project will contribute towards an improved understanding of the effects of woody exotic plants and their management on fynbos ecosystems and result in better protection of our natural heritage.

CHAPTER 2

Some effects of invasive exotic plants and fire on soil seed banks and regeneration in the Silvermine Nature Reserve, Cape Peninsula, South Africa

2.1 ABSTRACT

This study examines exotic and indigenous soil seed banks and above-ground regeneration in different post-fire environments following the extensive January 2000 wildfires on the Cape Peninsula, South Africa. The effects of wildfire burning of standing exotic plants and stacks of mechanically cleared exotic plant material on post-fire seed banks and vegetation recovery are investigated. These are compared to wildfire burning of fynbos and to the cleared areas surrounding wildfire burnt stacks. The effects of stacking and control burning of exotic slash under cool weather conditions are also reported.

Differences in soil seed banks and regeneration occurred in the various post-fire environments studied. Seed banks and regeneration are linked to pre-fire vegetation characteristics, fire intensity and in particular, to the management of exotic plants. High volumes of (standing or stacked) woody exotic plant biomass impact negatively upon post wildfire seed banks and recruitment. Heat damage, associated with high woody exotic biomass, affects seeds to a soil depth of at least 0.15 m. In contrast, control burning of stacks results in large scale localised germination of exotic seeds. Persistent indigenous seed banks are found in the burnt cleared areas surrounding stacks of exotic slash burnt in wildfires.

Keywords: Fire, Fynbos Biome, management, regeneration, soil seed banks, woody invasive exotics.

2.2 INTRODUCTION

Mediterranean climate region floras of the world have been recognised as needing special conservation action (Macdonald *et al.* 1988). Two of the major characteristics of the Cape Flora, its high levels of endemism and species diversity (regional and local) afford it especially high conservation significance (Oliver 1977, Taylor 1977, Goldblatt 1978, Kruger 1979, Oliver *et al.* 1983, Pierce 1984, Cowling *et al.* 1992, 1996, Simmons and Cowling 1996, Goldblatt and Manning 2000, Low *et al.* 2001a). However European colonisation, settled agriculture and the introduction of a variety of exotic plants had led to the transformation of at least 68% of lowland and about 10% of montane ecosystems by 1984 (Moll and Bossi 1984). The invasion of the species-rich fynbos flora by exotic vegetation poses a serious threat to the long-term survival of the remaining natural vegetation (Bands 1977, Oliver 1977, Hall and Boucher 1977, Stirton 1978, Richardson and Van Wilgen 1986, Trinder-Smith *et al.* 1996, Marais 1998, Holmes and Richardson 1999). This threat of exotic woody invasives is also considered unique to fynbos amongst Mediterranean-type climate regions of the world (Macdonald *et al.* 1988).

Invasion by woody exotic plants is by far the most extensive disturbance on Cape Peninsula National Parks land (Wood *et al.* 1994, Richardson *et al.* 1996), affecting about 45% of the area (Holmes and Richardson 1999). Elevated fuel loads in dense stands of exotic plants (Kruger 1979, Milton 1980, Milton and Siegfried 1981, Van Wilgen and Richardson 1985, Scott and Van Wyk 1992, Scott *et al.* 2000) cause much higher intensity burns than take place in uninvaded fynbos (Van Wilgen and Holmes 1986, Breytenbach 1989, Holmes 1989, Scott and Van Wyk 1990, Scott and Van Wyk 1992, Holmes and Richardson 1999, Scott *et al.* 2000) (chapter 1, tables 1.9 and 1.10). The variability of fynbos fire intensities may be critical for the maintenance of its overall diversity (Christensen 1994, Holmes and Richardson 1999). However high intensity burns in exotic stands have damaging effects on the soil (Musil and Midgley 1990, Scott and Van Wyk 1990, Martens 1997, Euston-Brown 2000), on indigenous soil-stored seed banks (Holmes *et al.* 1987a, b, Holmes and Cowling 1997a, Holmes and Richardson 1999, Holmes *et al.* 2001) and on re-sprouting species persisting in exotic stands (Richardson and Van Wilgen 1986, Holmes and Cowling 1997a, Holmes and Richardson 1999).

Prescribed burning has been a standard fynbos management policy since the early 1970's (Bands 1977, Mitchell 1987). This practice has been justified by fuel load reduction for wildfire control, maintenance of maximum water yields in mountain catchments, conservation of the diverse indigenous flora and eradication of invasive plants (Bands 1977, Mitchell 1987). Current management of fynbos still consists largely of controlling and applying fire, and of controlling invasions of woody weed species (Anonymous 1995b, Van Wilgen and Richardson 1995). Felled woody exotic vegetation in the Silvermine Nature Reserve is currently stacked or piled after mechanical clearance. These stacks are left scattered throughout the landscape and subjected to a control burn under cool weather conditions a year or two later (Ashton 1985, Ms. H. Thompson and Mr. R. Erntzen, Cape Peninsula National Parks, pers. comm. 2000). This practice however temporarily increases the localised fire risk in that a larger proportion of the fuel load is dead and cured (Scott *et al.* 2000). Also, if cleared exotic vegetation is cut down and stacked the resultant potential for high soil temperatures developing during fires is increased (Holmes and Richardson 1999, Euston-Brown 2000, Scott *et al.* 2000). This is evident when wildfires burn the stacks at highly elevated temperatures, killing indigenous and exotic seeds, rootstocks, bulbs and other propagules and resulting in ash spots or heat scars on the landscape (Griffith 1986, Breytenbach 1989, Macdonald *et al.* 1989, Martens 1997, Bond *et al.* 1999, Euston-Brown 2000, Scott *et al.* 2000, Vlotman and Knight 2000).

Species with soil stored seed banks are especially important in contributing to community richness and diversity (Wisheu and Keddy 1991, Holmes and Cowling 1997a, Holmes 2001, Holmes *et al.* 2001) and form the dominant plant cover in many uninvaded Mountain Fynbos areas (Kruger 1979). Intermittent fire kills many fynbos species, which then regenerate largely from soil-stored seed banks, although serotiny is common among overstorey dominants (Kruger 1984, Kruger and Bigalke 1984, Pierce 1987, Holmes and Cowling 1997a). For example, most members of the larger fynbos genera: *Erica*, *Agathosma*, *Phylica*, *Muraltia*, *Aspalathus* and *Cliffortia*, are obligate post-fire seeders with soil-stored seed banks (Pierce 1987). Ignoring annual species, soil stored seed banks may contain 24% to 42% of the species present in mature fynbos vegetation (Le Maitre and Midgley 1992). Regeneration from soil seed banks is also the only mode among annuals and is prominent in short-lived forbs and shrubs (Holmes and Cowling 1997a). Fynbos shrublands are thus largely dependant on soil seed banks for recruitment after fire (Le Maitre and Midgley 1992).

In the two January 2000 fires that burnt extensive areas in the Cape Peninsula, South Africa, fireline intensities were extremely high and are estimated to have reached 10 000 to 40 000 kW/m (Scott *et al.* 2000). The extreme intensities were the result of well-cured fuels (resulting from hot, dry conditions which lasted from October 1999 until the fire), extreme weather conditions experienced during the fires (hot, dry and windy) and large fuel volumes (Scott *et al.* 2000) (Chapter 1, Figures 1.6 – 1.11, Tables 1.2 – 1.5). Prior to the fire, less than 10% of the total burned area (approximately 8 700 ha) was uninvaded, roughly 64% was moderately invaded (< 25% cover) and 37% heavily invaded by woody exotic plants (> 25% cover) (Scott *et al.* 2000). Woody exotic plant infestation thus increased fuel loads over most areas burnt in the January 2000 fire. Those areas with dense woody exotic vegetation had exceptionally high fuel loads and were subjected to the fires of highest intensity (Euston-Brown 2000, Scott *et al.* 2000). Of the total burned area, 26% had been subjected to clearing activity in the two years prior to the fire (Scott *et al.* 2000). In these cleared areas, slashed stacked exotic vegetation subsequently formed heat scars (Scott *et al.* 2000).

Several studies have documented significant reductions in fynbos vegetation under exotic trees and shrubs (Richardson and Van Wilgen 1986, Holmes 1989, Richardson *et al.* 1989, Holmes and Cowling 1997b) and effects of fire in dense stands of exotic plants on fynbos regeneration (Musil 1993, Holmes and Cowling 1997a, Holmes and Marais 2000). Canopy stored seed banks have also been investigated in detail in fynbos (Le Maitre 1987a, b) while soil seed banks and post-fire vegetation recovery have been described in other Mediterranean (and heathland) vegetation types (Levyns 1935, Keeley 1977, Mallik *et al.* 1984, Meney *et al.* 1994, Moreno and Oechel 1994, Zammit and Zedler 1988, 1994, Edwards and Whelan 1995, Williams and Clarke 1997, Segura *et al.* 1998). In contrast, relatively little information is available on fynbos soil seed banks (Pierce 1987, Manders 1990b, Kilian 1991, Musil 1991, Pierce and Cowling 1991) or responses of fynbos to different fire intensities (Bond *et al.* 1990). Griffith (1986), Holmes *et al.* (1987b) and Holmes (1989) investigated the effects of different clearing treatments on the seed-bank dynamics of *Acacia cyclops* and *A. saligna*, including the effects of control burning stacks of slash. However, the effects of an intense wildfire on soil seed banks and regeneration in burnt standing exotics; stacks of exotic slash; burnt mechanically cleared areas (surrounding stacks); burnt fynbos and the effects of control burning of exotic slash stacks under cool weather conditions have not been formally quantified.

2.3 MATERIALS AND METHODS

During February 2000, field plots were selected in the following areas: wildfire burnt standing exotics; wildfire burnt fynbos; wildfire burnt stacked exotics (heat scars) and the burnt cleared areas which surround stacks (Chapter 1, Figure 1.1). This was done in order to monitor regeneration patterns and to infer viable seed-bank and propagule sizes (Roberts 1981). Experimental design between the sites differed in the following ways. Five 5 x 5 m plots were randomly selected in burnt fynbos and in burnt standing exotic vegetation above Ou Kaapse Weg with four 1 x 1 m sub-plots situated at the corners of each 5 x 5 m plot. Five wildfire burnt stacks were selected below Ou Kaapse Weg with a single 2 x 2 m plot centered in each of them. A 1 x 1 m plot in was selected in the southeastern corner of each 2 x 2 m plot. Five 2 x 2 m plots were also selected in the burnt cleared areas between wildfire burnt stacks with similarly selected 1 x 1 m plots in each of them (Chapter 1, Figures 1.3 and 1.4).

Counts were made of the following regenerating guilds in all field plots: woody exotic reseeders; woody exotic resprouters; indigenous reseeders; woody indigenous resprouters; herbaceous indigenous resprouters; resprouting hemicryptophytes (hereafter tussocks) and geophytes. Morpho-species diversity of each guild was also recorded in each 1 x 1 m plot (morpho species are plant taxa recorded as being distinct based on morphological differences observed in field). Counts were conducted in the burnt standing exotic and burnt Mountain Fynbos vegetation types in February, March, April, May, June and September 2000 and in January 2001. Counts in wildfire burnt stacks (heat scars) and the burnt cleared areas were conducted in April and September 2000 and again in January 2001. In April 2001, additional field plots were selected where an *A. saligna* stand had been mechanically cleared and the slash stacked. These stacks had been deliberately control-burnt under cool weather conditions in June 2000. Five control burnt stacks were randomly selected with a single 2 x 2 m plot centered in each of them. Counts of individuals and morpho-species were made in May 2001. Locations and layout of all field plots are illustrated in Chapter 1, Figures 1.1, 1.3 and 1.4.

The following sampling and seedling emergence techniques were used to infer post-fire soil seed bank sizes. During March 2000, soil was collected from burnt fynbos; burnt standing exotic; wildfire burnt stacks and burnt cleared area sites. Four blocks of soil were removed using a garden spade immediately outside each 5 x 5 m plot (burnt standing exotic & burnt fynbos habitats) to avoid disturbance within the monitoring plot (Roberts 1981). Each sample was made up of three sub-samples collected from 0.00 –0.02 m, 0.02 – 0.05 m and 0.05 – 0.15 m below the surface. The four samples taken from outside each 5 x 5 m plot were then bulked into their respective depth classes and mixed.

One soil sample (made up of three sub-samples from same soil depths) was collected from the centre of each of five wildfire burnt stacks (heat scars) while five similar samples were collected from the burnt cleared area. The heat scar sub-samples were then bulked into their respective depth classes and mixed. The same procedure was followed for samples collected from burnt cleared areas.

Each bulked depth sample was then sifted into four particle size classes (8 - 2 mm; 2 mm – 1000 µm; 1000 µm – 425 µm and < 425 µm) in order to investigate the size distribution of seeds within the soil profile. After sifting, measured volumes of soil (arising from each site, depth and size class combination) were planted out in flat seedling trays (57 x 127 mm) on a layer of "fynbos soil mix", obtained from the National Botanical Institute, Kirstenbosch. Four additional control trays containing only "fynbos soil mix" were prepared. All the trays were stored dry at ambient temperatures until the onset of the rainy season (June 2000) at the study area (approximately 2 ½ months) (De Villiers *et al.* 1993).

The trays were then transferred to a glasshouse at the Stellenbosch University Botanical Gardens. The glasshouse has ventilated sides, which enables diurnal temperature fluctuation, a necessary germination cue in some taxa (Roberts 1981, Brits 1986, Pierce and Cowling 1991, Pierce and Moll 1994). The ventilated sides also ensure air movement, essential for optimal germination (Mr. D. Kotze, Stellenbosch University Botanical Gardens, pers. comm. 2000). A micro jet system was used to irrigate the trays from June 2000 to June 2001. The trays were also shifted intermittently in an attempt to homogenise growing conditions. Emergent seedlings were counted on 2 June 2000; 20 June 2000; 26 July 2000; 1 September 2000; 18 October 2000; 18 January 2001 and during May 2001. All new seedlings counted on these dates were marked with coloured pins/toothpicks. Upon flowering, seedlings were removed for identification and most duplicates were removed on 18 October 2000 to provide remaining plants with additional growing space.

Standard errors of the means were calculated using Microsoft Excel while Dendrograms and Multi-dimensional Scaling Analyses were done using the Cluster, MDS and Conplot applications of the software program Primer (Clarke and Warwick 1994). Cluster analysis is a technique whereby a series of samples (in this case field plots) are compared simultaneously with all other samples according to many attributes, (in this case abundance of regenerating individuals in various guilds). The first result is a similarity matrix (dendrogram) which shows the degree of association between all possible pair-wise combinations (of plots in this case). Examination of the dendrogram indicates homogeneity within clustered plots and great distinction between some clusters (Knight 1979). Multidimensional scaling is another way of looking at the same similarity matrix, now plotting the samples (field plots) in a two dimensional graph. This graph (MDS) depicts relationships within individual clusters and between clusters. The technique shows trends of gradual change between treatments (as affected by pre-fire vegetation characteristics, management and fire intensity in this case) (Knight 1979).

2.4 RESULTS

FIELD COUNTS

In field abundance and diversity (m^{-2}) of all seven regeneration guilds differed in response to invasion, clearing, stacking and associated fire temperatures. Total counts of indigenous propagules were highest in burnt fynbos plots, control burnt stacks, burnt cleared areas, burnt standing exotics and wildfire burnt stacks in that order (Tables 2.1 and 2.2). Conversely, counts of woody exotic seedlings were highest in control burnt stacks, burnt standing exotics, burnt cleared areas, burnt fynbos plots and wildfire burnt stacks in that order (Tables 2.1 and 2.2). Morpho-species diversity counts resulted in similar trends (Table 2.3). One year after the fire indigenous species diversity in the burnt cleared areas (11.80/m^2) approximated that of un-invaded burnt fynbos (12.30/m^2). Indigenous morpho-species diversity at this stage was 3.90/m^2 in control burnt stacks, 1.68/m^2 in burnt standing exotics and the lowest in heat scars, viz: 0.80/m^2 (Table 2.3).

Multidimensional scalings (MDS's) and dendrograms (Bray-Curtis similarities) clearly reflected change in post-fire communities associated with pre-fire vegetation/fuel load characteristics and increasing fire intensity. The clearest MDS's and dendrograms were from 2 x 2 m field plots in September 2000 and January 2001 (Figures 2.1 – 2.4). Most guilds reached maximum abundance levels by September 2000 while some peaked in January 2001 (Tables 2.1 and 2.2, Appendix B and D). January 2001 was also the month when regenerating propagules in the control burnt areas were enumerated. September 2000 and January 2001 data are thus presented in here in MDS, dendrogram and tabular form. Complete monthly counts are presented in Appendix B while additional MDS's and dendrograms are depicted in Appendix C. Indigenous/exotic seedling and propagule ratios in the various habitats are depicted graphically in Appendix D.

Table 2.1 Mean abundance of regenerating individuals per m^2 in post-fire sites in September 2000. Figures in parenthesis indicate standard errors of the means (n=5)

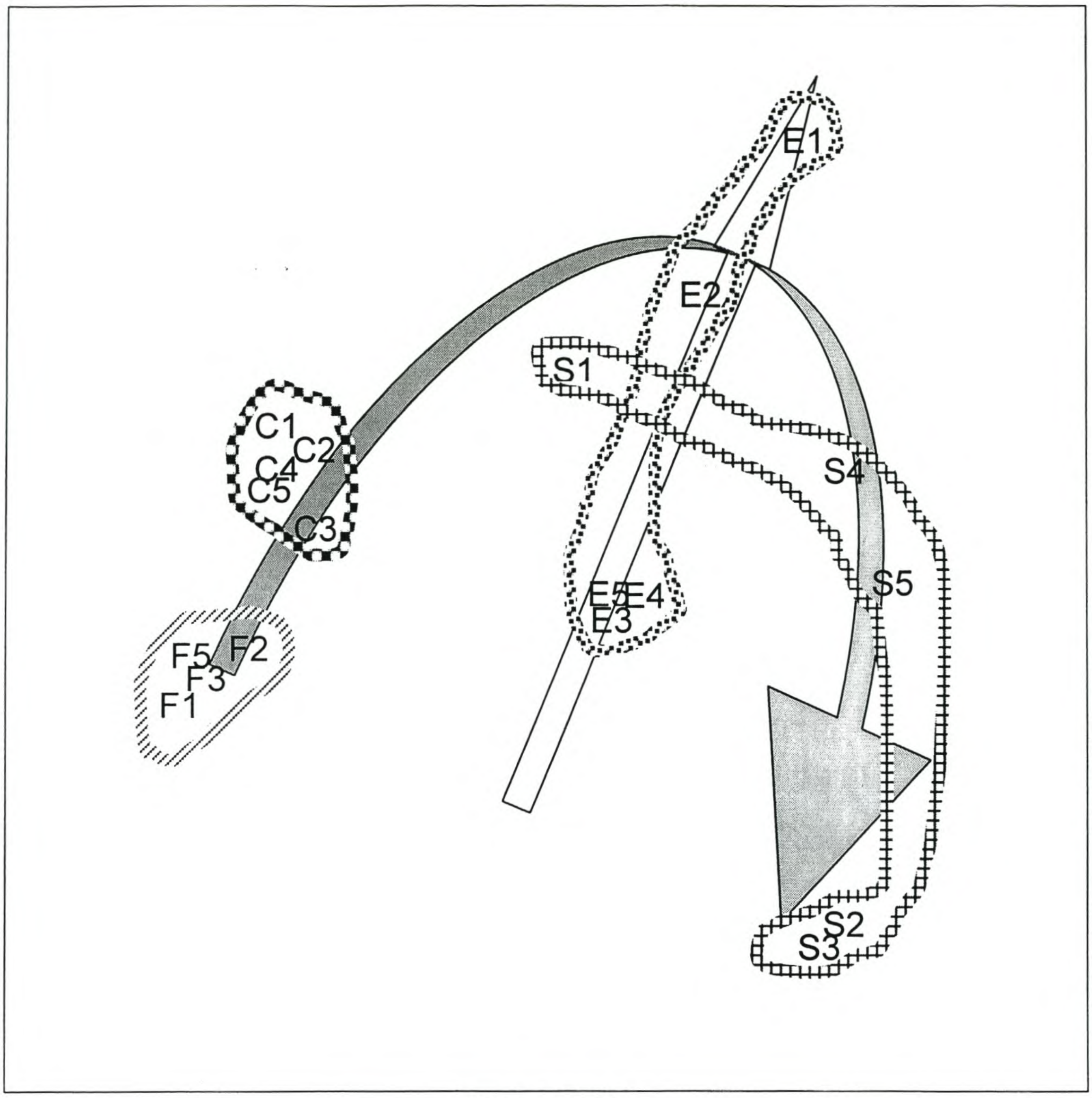
Regeneration guild	Number of propagules per treatment			
	Wildfire burnt fynbos	Wildfire burnt standing exotic	Wildfire burnt cleared	Wildfire burnt stacks
Indigenous Seedlings	131.61 (17.78)	2.75 (1.44)	84.25 (14.58)	1.65 (0.47)
Exotic Seedlings	2.28 (0.87)	35.25 (8.11)	46.95 (13.25)	1.90 (1.59)
Exotic Resprouters	0	0	1.05 (0.37)	0
Tussocks	38.11 (8.07)	0	25.8 (6.97)	0.05 (0.05)
Geophytes	36.61 (10.71)	0	8.15 (3.53)	0.15 (0.10)
Herbaceous Resprouters	6.11 (1.63)	0.15 (0.08)	1.50 (1.50)	0.15 (0.10)
Woody Resprouters	1.78 (0.92)	0.15 (0.08)	0.25 (0.19)	0
Total propagules	216.50 (39.98)	38.40 (9.71)	167.95 (40.39)	3.90 (2.31)

Table 2.2 Mean abundance of regenerating individuals per m^2 in post-fire sites in January 2001. Figures in parenthesis indicate standard errors of the means (n=5)

Regeneration guild	Number of propagules per treatment				
	Wildfire burnt fynbos	Wildfire burnt standing exotic	Wildfire burnt cleared	Wildfire burnt stacks	Control burnt stacks
Indigenous Seedlings	37.25 (5.63)	4.45 (1.31)	58.70 (10.23)	1.35 (0.69)	86.85 (14.60)
Exotic Seedlings	2.20 (0.89)	31.60 (8.34)	23.10 (2.59)	1.55 (0.96)	504.3 (56.14)
Exotic Resprouters	0	0	0.30 (0.15)	0	0
Tussocks	33.90 (9.17)	0	19.40 (3.60)	0	0
Geophytes	3.95 (3.28)	0	0.80 (0.30)	0	0
Herbaceous Resprouters	6.60 (1.44)	0.15 (0.08)	0	0.05 (0.05)	0
Woody Resprouters	1.35 (0.63)	0.15 (0.08)	0.05 (0.05)	0	0
Total propagules	85.25 (21.04)	36.35 (9.81)	102.35 (16.92)	2.95 (1.70)	591.15 (70.74)

Table 2.3 Mean species richness per m^2 in post-fire sites in September 2000 and January 2001. Figures in parenthesis indicate standard errors of the means (n=5)

Regeneration guild	Species richness per treatment						
	Wildfire burnt fynbos	Wildfire burnt standing Exotic	Wildfire burnt fynbos	Wildfire burnt Standing Exotic	Wildfire burnt cleared	Wildfire burnt stacks	Control burnt stacks
	Sep-00	Sep-00	Jan-01	Jan-01	Jan-01	Jan-01	Jan-01
Indigenous Seedlings	12.06 (0.55)	1.05 (0.29)	7.55 (0.55)	1.37 (0.17)	9.25 (0.50)	0.75	3.90
Exotic Seedlings	0.61 (0.14)	1.95 (0.17)	0.80 (0.12)	1.79 (0.16)	1.15 (0.08)	0.40 (0.15)	1.00 (0.00)
Exotic Resprouters	0	0	0	0	0.20 (0.09)	0	0
Tussocks	2.83 (0.36)	0	2.80 (0.34)	0	2.10 (0.23)	0	0
Geophytes	3.56 (0.41)	0	0.55 (0.19)	0	0.40 (0.11)	0	0
Herbaceous Resprouters	0.94 (0.10)	0.15 (0.08)	0.90 (0.07)	0.16 (0.08)	0	0.05	0
Woody Resprouters	0.56 (0.19)	0.15 (0.08)	0.5 (0.15)	0.16 (0.08)	0.05 (0.05)	0	0
Indigenous richness	19.95	1.35	12.30	1.68	11.80	0.80	3.90
Total richness	20.56	3.30	13.10	3.47	13.15	1.20	4.90



Stress = 0.09

Figure 2.1 Multidimensional scaling diagram (Clarke and Warwick 1994) indicating differences in regeneration of above-ground vegetation in 2 x 2 m field plots in September 2000, 8 months after an extensive wildfire on the Cape Peninsula

F = wildfire burnt fynbos; C = wildfire burnt cleared areas
E = wildfire burnt standing exotics; S = wildfire burnt stacks
Grey arrow = increasing fire intensity
White arrow = increasing number of exotic propagules
Numbers indicate replicates

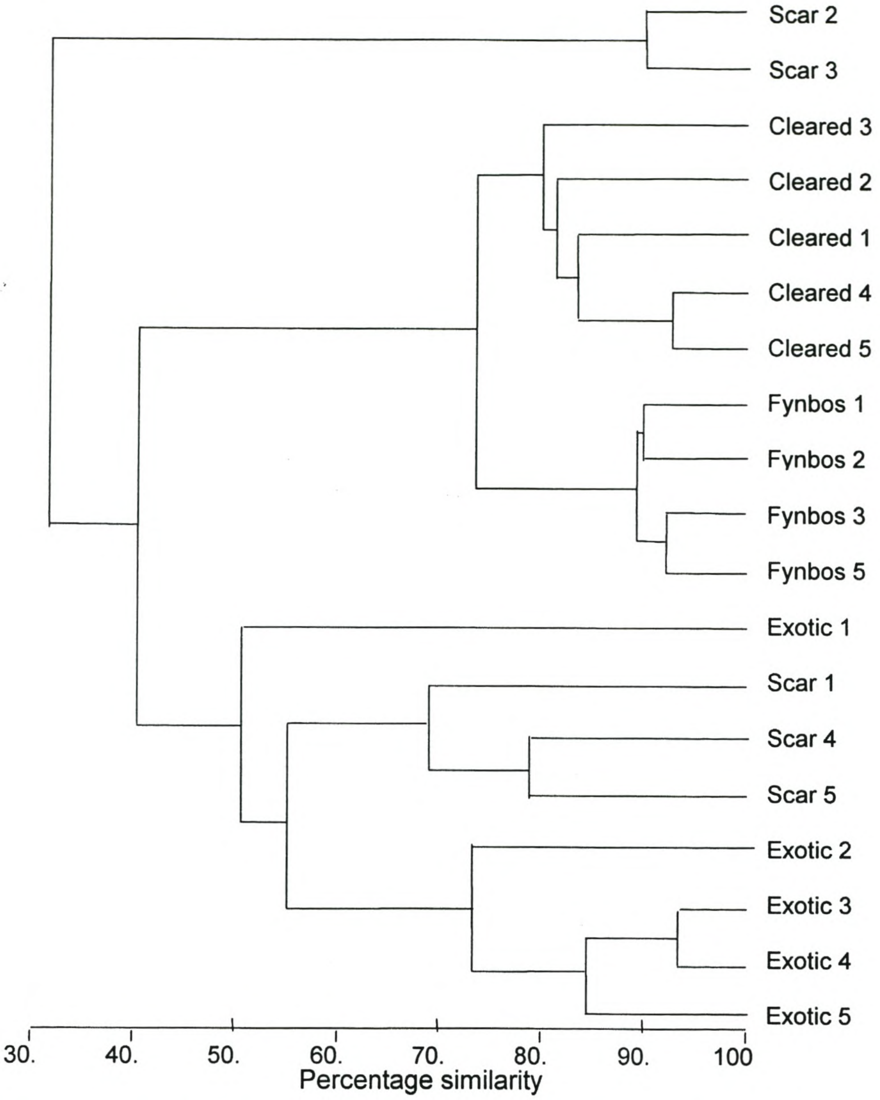
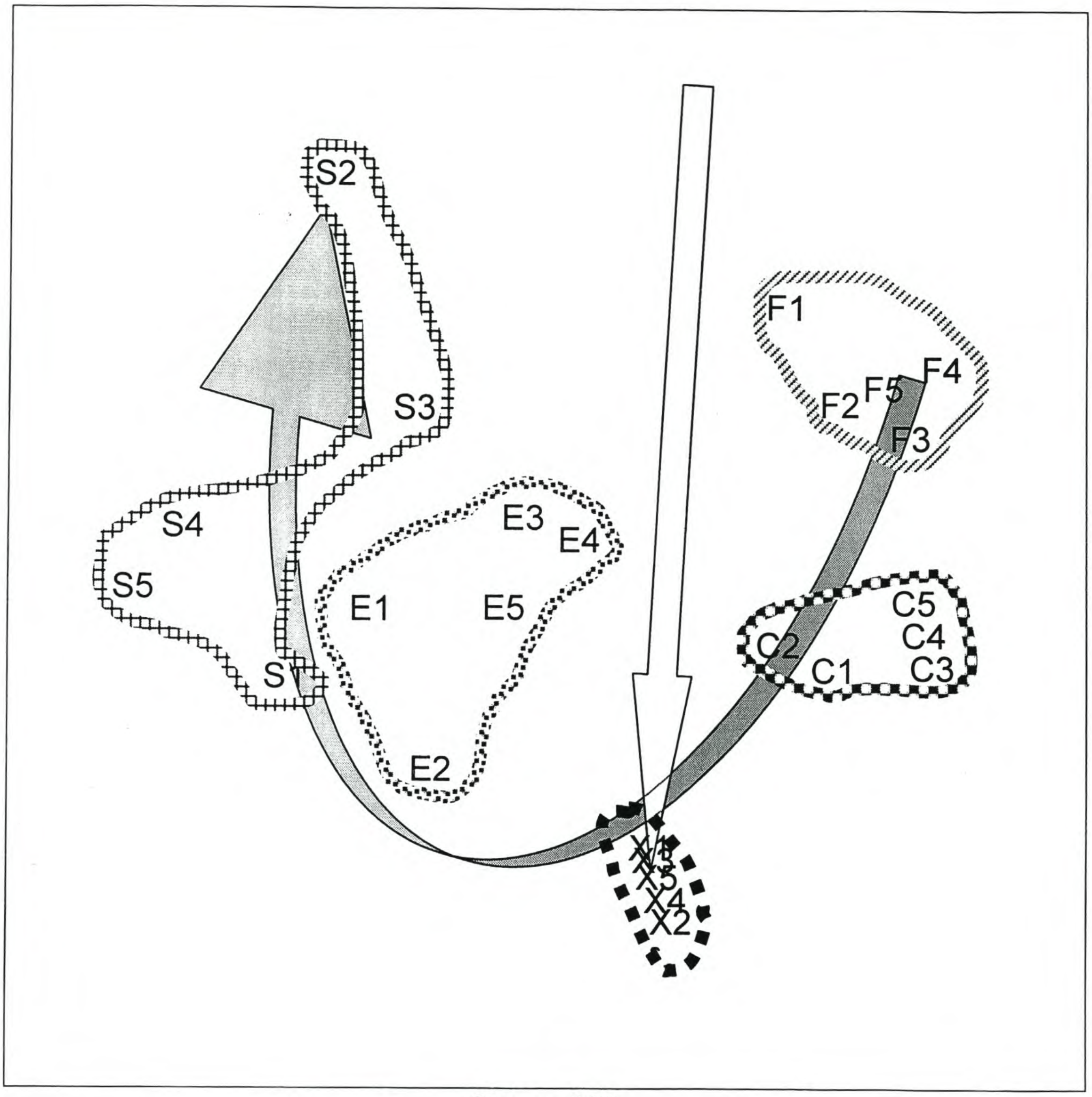


Figure 2.2 Dendrogram depicting Bray-Curtis Similarities between 2 x 2 m post wildfire field plots in September 2000 (Clarke and Warwick 1994)

Fynbos = wildfire burnt fynbos; Cleared = wildfire burnt cleared areas
Exotic = wildfire burnt standing exotics; Scar = wildfire burnt stacks
Numbers indicate replicates



Stress = 0.08

Figure 2.3 Multidimensional scaling diagram (Clarke and Warwick 1994) indicating differences in regeneration of above-ground vegetation in 2 x 2 m field plots in January 2001, 12 months after an extensive wildfire on the Cape Peninsula

F = wildfire burnt fynbos; C = wildfire burnt cleared areas
E = wildfire burnt standing exotics; S = wildfire burnt stacks
X = control burnt stacks
Grey arrow = increasing fire intensity
White arrow = increasing number of exotic propagules
Numbers indicate replicates

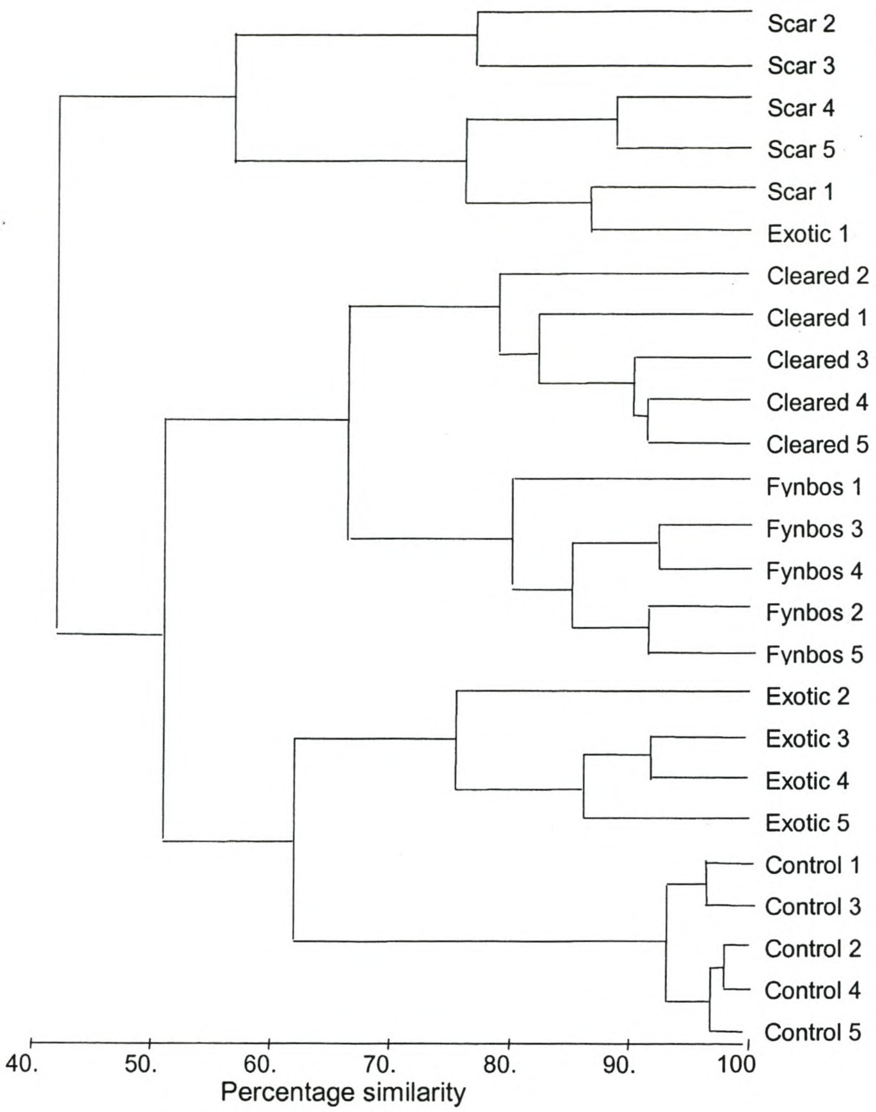


Figure 2.4 Dendrogram depicting Bray-Curtis Similarities between 2 x 2 m post wildfire field plots in January 2001 (Clarke and Warwick 1994)

Fynbos = wildfire burnt fynbos; Cleared = wildfire burnt cleared areas
Exotic = wildfire burnt standing exotics; Scar = wildfire burnt stacks
Control = control burnt stacks
Numbers indicate replicates

NURSERY GERMINATION TRIAL

The nursery germination trial also exhibited differences in soil seed bank abundance and diversity in response to invasion, clearing, stacking and associated fire temperatures. While the mean total amounts of indigenous seedlings (+- standard errors) was similar in soil from the fynbos (22.74 ± 3.29) and cleared areas (26.76 ± 10.60), native seed germination was considerably lower in soil from the burnt standing exotics (2.92 ± 0.67) and wildfire burnt stacks (1.11 ± 0.85) (Figure 2.5). Few woody exotic seedlings germinated in the trial but fewer germinated in burnt fynbos (0.14 ± 0.14), wildfire burnt stack (0.83 ± 0.83) and burnt standing exotic soils (2.02 ± 0.82) than in burnt cleared area soils (2.50 ± 1.79) in that order (Figure 2.5). One fynbos sample was an outlier (0.05 - 0.15 m depth and 2 mm – 1000 µm size) containing approximately 1595 seedlings per litre of soil, most of which were an unidentified *Erica* species. Results and discussions hereafter exclude this outlier.

In burnt fynbos soils, most indigenous (including *Erica hirtiflora*, *Metalasia muricata* and *Diascia elongata*) and a single *A. saligna* seedling germinated from 0.02 – 0.05 m soil depth (Table 2.4). The majority of indigenous seedlings in fynbos soils also regenerated from 2 mm – 1000 µm and 1000 – 425 µm particle size classes (Table 2.5 and 2.6). Similar patterns were evident in burnt cleared area soils where the majority of indigenous seedlings (including *Erepsia anceps* and *Pelargonium chamaedryfolium*) germinated from 0.05 – 0.15 m depth while four *A. cyclops* seedlings germinated from 0.02 – 0.05 m soil depth (Table 2.4). The majority of indigenous seedlings were also counted from 2 mm – 1000 µm and 1000 – 425 µm particle size classes in the burnt cleared area trays (Table 2.5). Appreciable germination also occurred in soils from 0.02 – 0.05 m depth (1000 – 2 µm and 425 – 1000 µm particle size) in these areas (Table 2.6). In soils from under burnt standing exotics, the majority of exotic seedlings germinated from 0.02 – 0.05 m depth while most indigenous seedlings (including *Erica phylicifolia*) germinated from the deepest (0.05 – 0.15 m) soil layers, many being small-seeded species (Tables 2.5 and 2.6). The exotic seeds were also larger (Table 2.5). Very few seedlings germinated from the wildfire burnt stack soils irrespective of particle size or depth of burial (Tables 2.4, 2.5 and 2.6). One *A. cyclops* seedling germinated from 0.02 – 0.05 m soil depth, two *Lobelia* sp. and two *Lepidium pinnatum* plants germinated from 0.00 – 0.02 m soil depth (Table 2.4). A total of 43 species were recorded in the fynbos soils, 20 in burnt standing exotic soils, 15 in burnt cleared area soils and four in heat scar soils

soils, 20 in burnt standing exotic soils, 15 in burnt cleared area soils and four in heat scar soils (Appendix E). Complete lists of species in seedling trays and their abundances are presented in Appendix E.

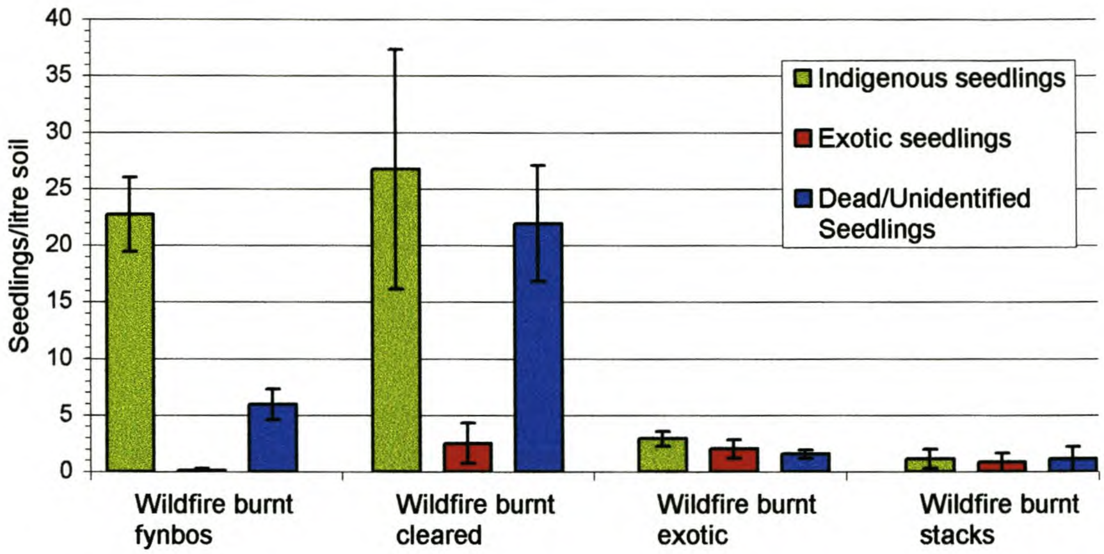


Figure 2.5 Total numbers of indigenous, exotic and dead/unidentified seedlings regenerating per litre of soil from different post-fire sites. Error bars indicate standard errors of the means

Table 2.4 Depth distribution of seedlings/litre of soil from different post-fire treatments. Figures in parentheses indicate standard errors of the means

Treatments	Soil depth	Indigenous seedlings	Exotic seedlings	Dead/Unidentified seedlings
Wildfire burnt fynbos	0.00-0.02 m	20.03 (5.15)	0	3.39 (1.17)
	0.02-0.05 m	34.31 (7.15)	0.40 (0.40)	10.41 (3.73)
	0.05-0.15 m	13.40 (3.24)	0	3.95 (1.33)
Wildfire burnt exotic	0.00-0.02 m	1.47 (0.74)	0.67 (0.67)	0.35 (0.26)
	0.02-0.05 m	1.24 (0.56)	4.20 (1.99)	1.99 (0.68)
	0.05-0.15 m	6.04 (1.60)	1.20 (1.20)	2.38 (0.79)
Wildfire burnt cleared	0.00-0.02 m	7.78 (3.33)	2.50 (2.50)	14.44 (1.76)
	0.02-0.05 m	18.89 (7.78)	5.00 (5.00)	27.78 (10.12)
	0.05-0.15 m	53.61 (28.02)	0	23.61 (12.40)
Wildfire burnt stacks	0.00-0.02 m	3.33 (2.357)	0	3.33 (3.33)
	0.02-0.05 m	0	2.50 (2.50)	0
	0.05-0.15 m	0	0	0

Table 2.5 Size distribution of seedlings/litre of soil from different post-fire treatments. Figures in parentheses indicate standard errors of the means

Treatments	Seed size	Indigenous seedlings	Exotic seedlings	Dead/Unidentified seedlings
Wildfire burnt fynbos	2-8 mm	6.99 (1.98)	0.53 (0.53)	6.67 (2.91)
	2mm-1000 µm	37.40 (8.22)	0	7.94 (3.67)
	1000-425 µm	36.89 (6.73)	0	7.3 (3.20)
	<425 µm	10.63 (3.33)	0	2.00 (0.92)
Wildfire burnt standing exotic	2-8 mm	2.55 (1.00)	5.42 (2.48)	2.13 (0.95)
	2mm-1000 µm	2.43 (1.00)	2.67 (1.93)	1.49 (0.68)
	1000-425 µm	3.70 (1.53)	0	1.67 (0.89)
	<425 µm	3.00 (1.80)	0	1.00 (0.35)
Wildfire burnt cleared	2-8 mm	0	10.00 (5.77)	5.55 (2.94)
	2mm-1000 µm	41.48 (23.28)	0	13.33 (4.44)
	1000-425 µm	52.22 (32.45)	0	38.89 (11.28)
	<425 µm	13.33 (0)	0	30.00 (8.82)
Wildfire burnt exotic stacks	2-8 mm	3.33 (3.33)	3.33 (3.33)	0
	2mm-1000 µm	0	0	4.44 (4.44)
	1000-425 µm	0	0	0
	<425 µm	0	0	0

Table 2.6 Total seedlings per litre of soil from different post-fire sites and from specific depth/size class combinations. Figures in parentheses indicate standard errors of the means

Soil depth	Seed size	Treatments			
		Wildfire burnt fynbos	Wildfire burnt exotic	Wildfire burnt cleared	Wildfire burnt stacks
0.00-0.02 m	2-8 mm	8.71 (4.22)	1.78 (1.78)	0	10.00
0.00-0.02 m	1000-2 mm	29.07 (8.20)	3.60 (2.23)	4.44	0
0.00-0.02 m	425-1000 µm	35.13 (16.01)	0.50 (0.50)	13.33	3.33
0.00-0.02 m	<425 µm	7.20 (3.38)	0	13.33	0
0.02-0.05 m	2-8 mm	7.47 (3.31)	1.78 (1.78)	0	0
0.02-0.05 m	1000-2 mm	56.00 (19.71)	1.20 (1.20)	35.56	0
0.02-0.05 m	425-1000 µm	53.13 (8.58)	1.20 (0.80)	26.67	0
0.02-0.05 m	<425 µm	20.63 (8.07)	0.80 (0.80)	13.33	0
0.05-0.15 m	2-8 mm	4.80 (3.20)	4.09 (1.79)	0	0
0.05-0.15 m	1000-2 mm	24.58 (9.37)	2.49 (1.62)	84.44	0
0.05-0.15 m	425-1000 µm	22.40 (5.11)	9.40 (3.39)	116.67	0
0.05-0.15 m	<425 µm	4.07 (1.13)	8.20 (4.82)	13.33	0

2.5 DISCUSSION

FIELD COUNTS

Post-fire field counts of regenerating guilds undertaken during 2000 and 2001 showed that invasion by woody exotic plants, whether under burnt standing exotics, burnt cleared areas or under burnt stacked materials, affected regeneration of indigenous and exotic propagules. Exotic woody plant invasions, their management and resultant increased fire intensities affect the total number of regenerating individuals and species diversity.

While there was no perceived advantage gained by exotic seedlings over indigenous propagules in terms of speed of establishment, their faster growth rates enabled them to eventually dominate the burnt cleared areas (Hall and Boucher 1977, Milton 1980, Milton and Siegfried 1981, Gill 1985, Rutherford *et al.* 1986, Jeffery *et al.* 1988, Van Wilgen *et al.* 1996, pers. obs. 2001). The paucity of indigenous propagules (as a result of high fire intensity) in the burnt standing exotic areas resulted in the post-fire dominance by a mixture of woody exotic species (*A. cyclops*, *A. longifolia*, *A. saligna*, *Hakea sericea* and *H. suaveolens*). The composition of the burnt standing exotic community had also shifted from a hakea – pine dominated one to a more evenly mixed exotic community as a result of the fire. Exotic seeds in this site were either better adapted to higher fire intensities than their indigenous counterparts (Jeffery *et al.* 1988), or large pre-fire seed stores and high percentage viability resulted in their post-fire dominance (Richardson and Van Wilgen 1984, Holmes 1987, Manders 1990a, Holmes and Cowling 1997a, Boucher and Mortimer 2000, Fleitmann and Boucher 2001). Indigenous seeds, which escaped the fire in these areas, may also have been too deeply buried and seed sizes too small for in-field germination, confirming Bond *et al.*'s (1999) findings. Control burning of stacks under cool weather conditions produced the expected result, viz. large-scale regeneration of woody leguminous exotic plants (Mr. R. Erntzen, pers. comm. 2000). Counts of regenerating seedling densities/m^2 in control burnt stack sites would probably result in a reasonable determination of total exotic soil seed bank size (since fewer are destroyed in these lower intensity burns). While effective in removing exotic biomass after felling, the resulting propagules have to be pulled or sprayed within a year of burning before plants mature and produce more seed (Anonymous 2000). Stacking does not lead to a concentration of seeds of non-serotinous species and surrounding unburnt areas thus retain their large ungerminated soil-borne exotic seed store, (which could potentially germinate following succeeding fires) (Holmes and Cowling 1997a, Boucher and Mortimer 2000). Interestingly, winter burning of exotic slash piles resulted in good recruitment of indigenous reseeder species in contrast to suggestions made by Holmes and Richardson (1999).

Multidimensional scalings and dendrograms of the various post-fire conditions (as determined by propagule abundance) describe influences of pre-fire vegetation characteristics, management and associated fire intensity on subsequent regeneration. They show fire intensity to be a clear determinant of post-fire community structure. The images show that heat scarred areas (under wildfire burnt stacks) are the most affected by increasing fire intensity followed by burnt standing exotics, control burnt stacks, burnt cleared areas and burnt fynbos in that order.

An encouraging result of the field analyses was that indigenous species diversity in burnt cleared areas approximated that of the burnt fynbos after one year. This is indicative of a viable, persistent store of indigenous propagules under dense stands of woody exotic plants. These findings agree with Holmes and Cowling (1997a, b), Holmes and Richardson (1999), Holmes (2001) and Holmes *et al.* (2001) who described persistent indigenous soil seed banks in exotic plant dominated Mountain Fynbos communities. In this study however, buried indigenous propagules were largely destroyed by exceedingly hot fires in dense stands of living exotics and completely eliminated where stacks of exotic slash were burnt by wildfires. The latent indigenous soil seed bank potential may therefore only be realised if exotic biomass is removed from the area before hot summer burns occur.

NURSERY GERMINATION TRIAL

Results of the nursery germination trial supported in-field findings; total counts showing parallel trends in terms of numbers of individuals per litre of soil and to a lesser extent, species diversity. Total seed tray counts of indigenous seedlings decreased along a scale of increasing fire intensity. Burnt fynbos soils exhibited the highest total counts of indigenous seedlings, supporting the findings of Manders (1990b) and Kilian (1991) who found no significant reductions in indigenous soil borne seed banks after burning fynbos. Burnt cleared area soils had a strong indigenous component, burnt standing exotic soils showed much diminished numbers and soils under stacks of wildfire burnt exotics exhibited almost no soil-stored seed banks.

The depth distribution of regenerating indigenous seedlings showed that in areas dominated by pre-fire stands of exotic plants, surface layers show depauperate amounts of seeds when compared to burnt Mountain Fynbos. This may be a result of diminished seed rain from parent plants (probably the case in burnt cleared areas) or a consequence of seed bank destruction by highly elevated burn intensities (evidently the reason in burnt standing exotics) (Holmes *et al.* 1997a). Holmes (2001) concurred, finding depauperate surface layers and deeply buried relictual indigenous seed banks in invaded stands in Mountain Fynbos. The distribution in wildfire burnt stack soils shows virtual elimination of all seeds, indigenous and exotic, to depths exceeding 0.15 m. Similarly, Milton and Hall (1981), Griffith (1986), Holmes *et al.* (1987b), Holmes (1989), Martens (1997) and Vlotman and Knight (2000) note much reduced exotic seed banks under stacks of wildfire burnt slash in fynbos habitats. At two out of three sites surveyed by Holmes *et al.* (1987), elimination of exotic seed banks was complete. The depth distribution of post-fire soil seed banks is therefore an important determinant of ensuing community composition.

Trends indicate that exotic legume seeds may be better able to survive higher fire intensities than their indigenous counterparts (Jeffery *et al.* 1988). Maximum germination of exotic seedlings was from shallower soil depths in burnt standing exotic and burnt cleared area seed trays, a possible explanation being that improved fire survival is linked to larger seed size of exotic legume species. In contrast, size-class distribution patterns of indigenous seedlings in burnt standing exotic seed trays suggested no influence of seed size on survival while distributions in burnt cleared area soils were "normal" (akin to the distribution in fynbos seed trays), except for elimination of the largest seed-size component (elimination of this component possibly being a stochastic effect of small sample size or a result of indigenous pre-fire parent plant paucity and suppression by woody exotics (Holmes and Cowling 1997a). Too few seeds survived in wildfire burnt stack soils to draw any valid statistical conclusions pertaining to size effects barring the fact that one of five surviving seeds was a large seeded exotic, *A. cyclops* (it is also possible that the indigenous constituent (two *Lobelia* and two *Lepidium* plants) was ruderal).

These findings do not support the findings of Musil and De Witt (1990) who established that seed size is an important determinant of post-fire regeneration in Sand Plain Lowland Fynbos. While seed size in Mountain Fynbos may have some importance in determining fire survival in indigenous species, fynbos plants possibly rely more on the production of large numbers of small seeds to escape fire.

As was the case in field, the germination trial showed that wildfire burnt stacked areas are the worst affected by fire followed by burnt standing exotics, burnt cleared areas and burnt fynbos habitats.

FUTURE WOODY EXOTIC PLANT MANAGEMENT

The January 2000 fires on the Cape Peninsula demonstrated an inability to control wildfires under extreme conditions. Large areas of exotic and cleared vegetation remain vulnerable, therefore planning without expecting runaway fires is unacceptable (Euston-Brown 2001). Considering the observed destructive effects of stacking and associated scarring, amendments should be made to current management practices or alternatives sought. Amendments and alternatives could include control burning dense live stands of woody exotics (Breytenbach 1989, Holmes 1989, Holmes *et al.* 2001) during cooler weather conditions, then doing follow-up weeding after one year, checking for survivors every six months after that for at least 10 years (Macdonald and Jarman 1984, Combrink 1985, Holmes 1989, Dr. C. Boucher pers. comm. 2001). Weeding in these areas could be done using a novel implement known as a "popper", which facilitates easier pulling of larger plants (Dr. C. Boucher pers. comm. 2001). While labour saving, the popper method has its drawbacks. If the soil is hard or rocky the plants may break off, this results in them resprouting later, additionally, soil disturbance may result when plants and roots are pulled (Dr. C. Boucher pers. comm. 2001). This disturbed environment may then form a niche for exotic plant recruitment. Martens (1994a) however considers pulling as the most selective and environmentally friendly method, although *Pinus* species should be cut at the base of the stem with secateurs (Martens 1997). In summary, the popper method should only effectively be used for juvenile plants in sandy areas exhibiting low levels of invasion.

A chemical defoliation agent may also be applied to adult plants in order to reduce biomass prior to burning the area. Alternatively, the chemically treated area may be left unburnt for a longer period while new areas are cleared, allowing indigenous plants to re-establish without cueing mass germination of exotic seedlings (Dr. C. Boucher pers. comm. 2001). Problems associated with chemical treatments include overlooking of individuals in rocky areas, incomplete wetting, spraying of non-target plants and unsightly dead plants (Anonymous 1995b, Anonymous 2000, Zavaleta *et al.* 2001). The effects of spraying treatments on indigenous plants and their seed-banks are also unknown. Spraying treatments do however have a number of advantages over cutting methods. Most notably, fewer disturbances occur to the surrounding soil and vegetation and, should a wildfire occur, the standing leafless plants tend to generate cooler fires, particularly at the soil surface (Dr. C. Boucher, pers. comm. 2001, Anonymous 2000). This is less destructive to soil flora and fauna resulting in more rapid recovery, the surface cover is also more complete and less erodable (Anonymous 2000).

Pieterse *et al.* (1997) and A. Milewski (pers. comm. 2001) suggest mechanical clearing, slash removal, chipping, composting the debris and using the mulch in restoration projects (in arid areas). Care must however be taken that harvesting is not undertaken when ripe seeds are present on the plants which would result in further spread of the exotics (Pieterse *et al.* 1997). There are also doubts as to the effectivity of composting in terms of exotic seed elimination. Anything short of 100% mortality would aid in spreading these weeds (Holmes *et al.* 1987a, Dr. C. Boucher pers. comm. 2001). Perhaps a better alternative would be to chemically kill large individuals and to hand-pull small plants leaving them *in situ* (Mr. A. Brown, Ukuvuka: Operation Firestop, pers. comm 2001). Hand pulling of small/young plants would also disturb the soil and could bring some buried exotic seeds to the surface. Following these procedures, Mr. A. Brown (pers. comm. 2001) recommended burning the treated area in relatively cool weather conditions and stressed the importance of re-pulling or spraying of post-fire regenerating seedlings regularly, as did Holmes *et al.* (1987a). Tillage of scarred areas after burning has also been suggested to bring buried seeds to the surface (Dr. P. Holmes, Cape Ecological Services, 23 Dreyersdal Road, Bergfliet, pers. comm. 2001), however the results showed elimination of the seed bank to at least 0.15 m depth. Effective tillage to such depths may prove difficult and prohibitively labour-intensive as well as destructive to living indigenous flora. A method eliminating scarring or limiting the extent thereof may prove to be a better option.

Mr. D. Euston-Brown (PO Box 44066, Scarborough, 7975, pers. comm. 2001) suggested an adaptation of the current stacking procedure, which may serve to limit environmental damage. The suggestion is to identify an area of minimal environmental significance or importance, such as a road or firebreak, drag the mechanically cleared slash there and concentrate burning (during cool weather conditions) at such a site. In the absence of a nearby road or firebreak, a site should be chosen with the least botanical, aesthetic or other significance and burning should be concentrated there in order to minimise the area affected. While more labour-intensive, this method will result in less scarring to smaller areas and achievement of better veld restoration.

2.6 CONCLUSIONS

This paper showed that post-fire regeneration patterns, soil borne seed-bank diversity and abundance are linked to pre-fire vegetation and seed characteristics of the component species. The field study and nursery germination trial have also shown the pre wildfire destructive effects of stacking exotic slash. The current reasons for stacking have to be weighed against the costs incurred to the environment, not only in terms of biodiversity, but also in terms of aesthetic value. If the ultimate goal of exotic plant management/eradication programmes is to restore the veld to its original state, then the current management practice of stacking is clearly incompatible with this ideal.

CHAPTER 3

A pilot study of the effects of invasive exotic plants, fire and soil chemistry on selected soil microorganism populations in the Silvermine Nature Reserve, Cape Peninsula, South Africa

3.1 Abstract

This study examines soil chemical and microbial population changes in different sites following the extensive wildfires in 2000 on the Cape Peninsula. The effects of standing exotic plants and stacks of mechanically cleared exotic plant material on post-fire populations and their recovery are investigated. These are compared to burnt fynbos and the burnt cleared areas which surround wildfire burnt stacks. Microbial populations and chemical changes are also monitored in unburnt Mountain Fynbos and dense unburnt stands of invasive exotic plants.

Differences in soil chemistry and microbial populations occurred in the various post-fire environments studied while marked seasonal changes were also apparent. Microbial populations are linked to pre-fire vegetation characteristics, fire intensity, to the management of exotic plants, soil chemical changes and seasonal influences but are variable in their responses. High volumes of (standing or stacked) woody exotic plant biomass have the most drastic impacts on post wildfire microbial populations, especially during summer. During winter however, microbial populations are determined by soil nutrients and texture.

Keywords: Fire, Mountain Fynbos, management, microbiology, soil chemistry, invasive exotic plants.

3.2 Introduction

Fire is considered to be the chief perturbation in many Mediterranean type ecosystems and is important for the combustion and mineralisation of slowly decomposing litter (Groves 1983, Mitchell 1983, Van Wilgen *et al.* 1996). Decomposition as a biological mineralisation process operating between fires may also be extremely significant (Rundel 1983). Soil borne microorganisms play major roles in the decomposition and mineralisation of organic compounds and in transformations of inorganic nutrients in ecosystems (Alexander 1977, Botha and Wolfaardt 2000). The important biotic interactions that occur between the soil, microorganisms and plants are, however, complex (Groves 1983). For example, available phosphorous content in fynbos soils have been shown to be extremely low, and thus its microbial release from organic complexes is of vital importance for the maintenance of ecosystem productivity between fires (Mitchell 1983).

Fire and fire temperatures influence the nutrient status of the soil in fynbos (Rundel 1983, Brown and Mitchell 1986, Van Reenen *et al.* 1992) and in a variety of other ecosystems (DeBano *et al.* 1979, Arianoutsou and Margaris 1981, Christensen 1994, Pietikainen and Fritze 1994, Dumontet *et al.* 1996, Hernandez *et al.* 1997, Grogan *et al.* 2000, Jensen *et al.* 2001). High temperatures increase volatilisation from the canopy and litter and reduce fluxes to the soil compartments (Rundel 1983). This may influence post-fire microbial populations, their development and activity (Brown and Mitchell 1986). However, Van Reenen *et al.* (1992) found no long-term effects of fynbos fires on soil microbial respiration, fungal, actinomycete and bacterial biomass.

Elevated fuel loads in dense stands of invasive woody exotic plants (Kruger 1979) cause much higher intensity burns than would normally take place in uninvaded fynbos (Scott and Van Wyk 1990, Euston-Brown 2000, Van Wilgen 2000). For example, Breytenbach (1989) measured more than 5 910 kJ/m^2 in a burn in a slashed *Hakea sericea* site. In contrast, fynbos sites released only 470 to 220 kJ/m^2 when burnt. Fire line intensity in a stand of *Acacia cyclops* was estimated by Holmes (1989) who found it to be in the region of 20 000 – 61 000 kW/m while temperatures measured by Martin (1966) in Grassy Fynbos included a brief maximum of 550°C at the soil surface and less than 43°C at 0.012 m depth. In stacks of exotic slash however, smouldering fires could heat the soil profile to a depth of 0.20 to 0.30 m, resulting in considerable chemical changes, soil damage and sterilisation (Renbuss *et al.* 1972, Holmes 1989, Christensen 1994). Van Wilgen and Holmes (1986) measured soil temperatures exceeding 200°C at 0.04 m depth under piles of felled *A. cyclops.* Roberts (1965) recorded soil temperatures under a pile of burning eucalyptus logs which exceeded 180°C at a depth of just over 0.10 m. Similarly, Renbuss *et al.* (1972), recorded approximate temperatures of 650°C at the soil surface, 350°C at 0.05 m, 250°C at 0.10 m, 150°C at 0.15 m and 100°C at 0.20 m soil depths under piles of burning eucalyptus logs.

Burn intensities in the January 2000 fires (which burnt Mountain Fynbos in the Silvermine Nature Reserve, Cape Peninsula, South Africa) were extremely high because of large volumes of well-cured fuels; hot, dry conditions before and during the fire and high wind speeds (Euston-Brown 2000, Scott *et al.* 2000). Fire line intensities were estimated to have reached 10 000 to 40 000 kW/m (Scott *et al.* 2000). Those areas overrun with dense woody exotic vegetation had exceptionally high fuel loads and were consequently subjected to the hottest fires (Scott *et al.* 2000). Current fynbos management consists largely of controlling and applying fire, and combating invasions of woody weed species (Van Wilgen and Richardson 1985). About a quarter of the total area burned on the Cape Peninsula was cleared mechanically of woody exotic plants in the two years before the fire (Scott *et al.* 2000). In these areas, the cleared vegetation was pulled into stacks. During the fire these stacks burnt at highly elevated temperatures (because of high concentrations of dead dry fuel), and they consequently formed so-called heat scars on the landscape (Breytenbach 1989, Macdonald *et al.* 1989, Euston-Brown 2000, Scott *et al.* 2000).

Some studies have documented the effects of fire on soil microorganisms and their activities in the soil of kwongan in Australia (Pattinson *et al.* 1999); chaparral in California (Dunn *et al.* 1979, 1985); Jack Pines in Minnesota (Ahlgren 1974); Douglas Fir in Oregon (Wright and Bollen 1961), prairie in Manhattan (Ajwa *et al.* 1999) and phrygana in Greece (Arianoutsou-Faraggitaki and Margaris 1982) while Van Reenen *et al.* (1992) tested this association in fynbos. No study has yet investigated possible links between fire, soil chemistry and soil micro-organisms in burnt standing exotic, stacked exotics, burnt mechanically cleared areas (surrounding scars) and in burnt fynbos. This study examines some of the post-fire effects of exotic vegetation and management on selected soil microorganism populations.

3.3 Materials and Methods

On 1/11/2000 (Summer) 10 months after the fire, soil samples were collected in the following habitat types: burnt standing exotic; burnt fynbos; unburnt fynbos; unburnt standing exotic; burnt stacks and the burnt cleared areas which surround stacks. An auger (0.075 m diameter) was used to sample soil to a depth of 0.10 m. The samples included any surface organic material (or humus), which may have been present. Five independent samples (of approximately 0.001767 m^3) were taken from each habitat and bulked. Similar sampling was repeated on 15/3/2001 (Autumn), 4/7/2001 (Winter) and 7/9/2001 (Spring) to assess seasonal changes.

Bemlab^{BK} (AECI building W21, De Beers Street, Somerset West 7130), using the following methods, conducted soil chemical and physical analyses. Particle size distribution was determined using the hydrometer method of Van der Watt (1966). Exchangeable cations (Ca, Mg, K and Na) were determined in a 1M ammonium acetate extract (Doll and Lucas 1973). The trace elements of manganese, copper and zinc were determined in a di-ammonium EDTA extract (Beyers and Coetzer 1971) and a hot water extract was used for boron (Anonymous 1974). Total nitrogen was determined by digestion in a LECO FP-528 nitrogen analyser, while organic carbon was determined with the Walkley-Black method (Nelson and Sommers 1982). Total organic matter was then calculated by multiplying organic carbon content by 1.72 (Baldock and Skjemstad 1999). Ammonium and nitrate were determined in a 1M KCl extract (Bremner 1965). pH was determined in 1M KCl (McClean 1982). Cation Exchange Capacity (CEC) was determined at pH 7 by saturation with 0.2 M ammonium acetate. Ammonium was displaced with K_2SO_4 and determined by Kjeldahl distillation (Peech 1965).

Selected soil microbial populations in the bulked samples were enumerated, using standard plate count methods (Samson *et al.* 2000). The dilution plate technique was used in combination with a series of selective and non-selective isolation media. Total bacterial and actinomycete counts were obtained using tryptone soy agar (TSA) and sodium caseinate agar respectively. Malt extract agar with streptomycin sulphate (MEA) is a relatively non-selective fungal isolation medium and was used to enumerate a wide diversity of fungi in the soil, while thymine-mineral-vitamin medium (TMV) was used to enumerate lipomycetaceous and basidiomycetaceous soil yeasts (hereafter referred to as soil yeasts). Hymenomycetacous fungi were enumerated using a benomyl-dichloran-streptomycin medium (BDS-medium) (Worrall 1991). Mucor isolation medium A was used to enumerate the mucoralean fungi. Compositions of the various media are presented in Appendix F.

After inoculation, cultures prepared from all of the above mentioned media were incubated for 7 days at 22°C before the microorganisms on the plates were enumerated as colony forming units (cfu). All experiments were conducted in triplicate.

Euston-Brown's (2000) Fire Severity Index was adapted to include subjective assessments of pre-fire climatic conditions, weather conditions during the fire, pre-fire fuel loads and packing along a sliding scale of increasing influence (Chapter 1, Tables 1.9 and 1.10). Calculated values obtained from this Adapted Fire Severity Index (A.F.S.I) were included as abiotic environmental variables in the analyses.

Maximum Harmonic (weighted Spearman) correlations (r_w) of the distributions of fungi and bacteria with sets of environmental variables were calculated using the BIOENV application of the software program PRIMER (Clarke and Warwick 1994). When viewing the results it must be considered that environmental variable sets portrayed in Tables 3.1 – 3.6 are a consequence of optimal selection by the BIOENV procedure and result from repeated runs of the analysis. Repeated analyses were necessitated because the application can only cope with a maximum of 10 000 combinations. Repetition does, however result in the possibility of type 1 errors, furthermore the ranks are not mutually independent variables and are based on a large number of strongly interdependent similarity calculations. It is therefore erroneous to refer r_w to standard statistical tables to assess significance. This does not however compromise the use of r_w as an "index of agreement" between matrices since any variables featuring arbitrarily or marginally in one run would be unlikely to do so in further repetitions. In conclusion the use of BIOENV is that of an exploratory rather than an inferential statistical tool. Its use is to rank various variable combinations and to compare these clusters against each other in order to produce an optimal cluster of abiotic variables "best explaining" patterns in measured biotic data (Clarke and Warwick 1994).

3.4 RESULTS

SOIL CHEMICAL CHANGES

Differences in soil chemical status were observed between natural and transformed Mountain Fynbos habitats and between seasons. Only the most important and obvious changes are summarised here.

Soil pH (KCl) dropped markedly while CEC rose in the period from November 2000 to March 2001, in the absence of large rainfall events (Figures 3.1 and 3.2). The drop in pH in March 2001 corresponded with a sharp rise in NO_3 and NH_4 levels (Figures 3.3 and 3.4). Potassium, measured in mg/kg and cmol/kg, remained relatively constant in unburnt fynbos and burnt cleared areas but fluctuated in all the other treatments (Figure 3.5). In November 2000 and March 2001, K levels were higher in burnt fynbos, burnt standing exotics and burnt stacked areas than in unburnt fynbos, unburnt standing exotics and burnt cleared areas respectively (Figure 3.5). Phosphorous levels (mg/kg) were consistently higher in burnt than unburnt areas, except in September 2001, unburnt and burnt fynbos had similar levels and burnt stack sites had low levels (Figure 3.6). The changing amounts of phosphorous in the soil showed some correlation with plate counts of mucoralean fungi in November 2000; soil yeasts in March 2001; MEA and with total bacteria (TSA) in September 2001. Magnesium % in the soil samples gradually increased from November 2000 to September 2001 (Figure 3.7). Tables showing all the chemical and textural analyses are depicted in Appendix G.

SOIL FUNGI

Populations of lipomycetaceous and basidiomycetaceous (soil) yeasts (as enumerated on TMV medium) showed clear differences between sites in the November 2000 and March 2001 assays (Figure 3.8). These distributions showed maximum correlation with soil texture and fire intensity in November, this however changed to maximum correlation with a set of macronutrients and fire intensity by March (Table 3.1). By July 2001 soil yeast populations had shown growth (particularly in the unburnt standing exotic area) however burnt sites still had lower counts, except for burnt stacked areas where counts were higher than for burnt cleared areas. Maximum correlation was with soil texture; Mg %; Na % and soil pH.

By September 2001, populations of soil yeasts were similar except for unburnt fynbos, which exhibited larger population sizes. Maximum correlation in this assay again was with soil texture, Mg (cmol/kg) and Na (cmol/kg).

While counts of mucoralean fungi in November 2000 showed differences between burnt and unburnt areas (Figure 3.9), maximum correlation was not with fire intensity, but with soil texture and the macronutrients P and K (mg/kg) (Table 3.2). The distribution in Autumn (March 2001) was correlated with a different set of nutrients viz. Na (cmol/kg); Ca (cmol/kg); NO_3 (N) as well as resistance (ohms); fine sand %; stone % and fire intensity. While populations had increased by July 2001, the counts showed poor correlation with environmental variables measured. Populations were unstable in September 2001 with large increases in burnt standing exotic areas and a total collapse in burnt stacked sites. Environmental variables showing maximum correlation with these counts were soil texture, H (cmol/kg), Ca (cmol/kg) and fire intensity.

In November 2000, some hymenomycetaceous fungal populations showed reduced population sizes (Figure 3.10). Observed trends indicated reductions in burnt standing exotics and in burnt stack populations, however there were no observed differences between burnt fynbos, unburnt fynbos and burnt cleared area samples. The environmental variables "best explaining" this distribution included soil texture and Mg % (Table 3.3). Nutritional variables became more important by March 2001 when counts were best correlated with T-value (cmol/kg), Ca (cmol/kg) as well as stone % and coarse sand %. All the post-fire habitats also had higher counts in March than unburnt habitats, those habitats subjected to the most severe burns, burnt standing exotics and wildfire burnt stacks having the highest counts. Differences between the means (in July 2001), although essentially negated by large standard errors, are "best explained" by soil Mg %, medium sand %, Ph (KCl) and NO_3 (N). September 2001 was marked by the disappearance of all traces of hymenomycetes in the heat scar samples, the other habitats having similar population sizes. This pattern is "best explained" by differences in H (cmol/kg), stone and clay % between the studied habitats.

Populations of total fungi (as enumerated on MEA medium) in November 2000 were higher in soils under burnt stacks than in the burnt cleared areas (Figure 3.11). By March 2001 however, total populations of fungi were similar across all the treatments. In July 2001, burnt standing exotics had the highest populations of total fungi while in September 2001, unburnt and burnt standing exotic habitats had the highest totals. Only in September was the distribution of total fungi (MEA) adequately "explained" by strong correlation with environmental variables measured viz. clay %, stone %, fine sand %, resistance (ohms), P (mg/kg) and N % (Table 3.4).

SOIL ACTINOMYCETES AND BACTERIA

Actinomycete counts on Sodium Caseinate agar in November 2000 were highest in burnt and unburnt fynbos habitats and higher in burnt exotics and burnt stacked soils than unburnt exotics and burnt cleared areas respectively (Figure 3.12). Actinomycete populations at this stage showed maximum correlation with a combination of soil texture and nutrients: CEC; resistance and Na (cmol/kg). By March 2001, the actinomycete counts in unburnt fynbos had shown larger increases in population size than in any of the other areas. This distribution was maximally correlated with soil texture (silt, medium sand, coarse sand and stone) and not to the soil nutrients measured. By July all areas (except for unburnt fynbos) had shown large population size increases (coinciding with the advent of cool, wet winter weather), the largest increases being in non-fynbos areas. There was however poor correlation between distributions patterns in this assay and the measured environmental variables. By September 2001 all populations had declined, burnt fynbos soils retaining the highest actinomycete counts. This distribution showed maximum correlation with H (cmol/kg); Ca (cmol/kg); C %; clay % and T-value (cmol/kg) (Table 3.5).

Total bacterial counts (on TSA medium) in November 2000 revealed little difference between the sites, only the wildfire burnt stacks and the burnt cleared areas surrounding them differed, stack counts being higher than cleared area counts (Figure 3.13). The distribution of total bacteria in this assay showed some correlation with Na %, H (cmol/kg) and soil texture. Unburnt fynbos exhibited by far the highest total bacterial counts in March 2001 and the distribution's maximum correlation with environmental variables was again with soil texture, H (cmol/kg) but now included CEC. In July 2001 showed a complete turnaround with wildfire burnt stack soils having by far the highest counts of bacteria on TSA medium. Nonetheless, the environmental variables "best explaining" the observed distribution were clay %; Mg%; C % and Ca (cmol/kg). In September 2001 showed large variation in total now included CEC. In July 2001 showed a complete turnaround with wildfire burnt stack soils having by far the highest counts of bacteria on TSA medium. Nonetheless, the environmental variables "best explaining" the observed distribution were clay %; Mg%; C % and Ca (cmol/kg). In September 2001 showed large variation in total bacterial counts but total plate counts from stacked area soils were now the lowest. The environmental variables showing maximum correlation with this distribution of means were stone % and P (mg/kg) (Table 3.6).

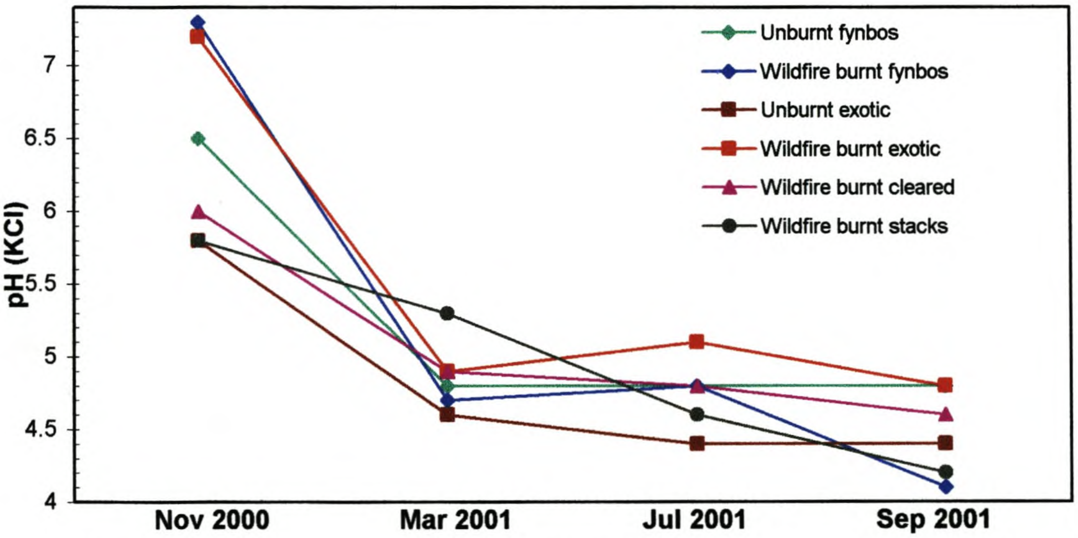


Figure 3.1 Seasonal change in soil pH (KCl) in various natural and transformed Mountain Fynbos habitats

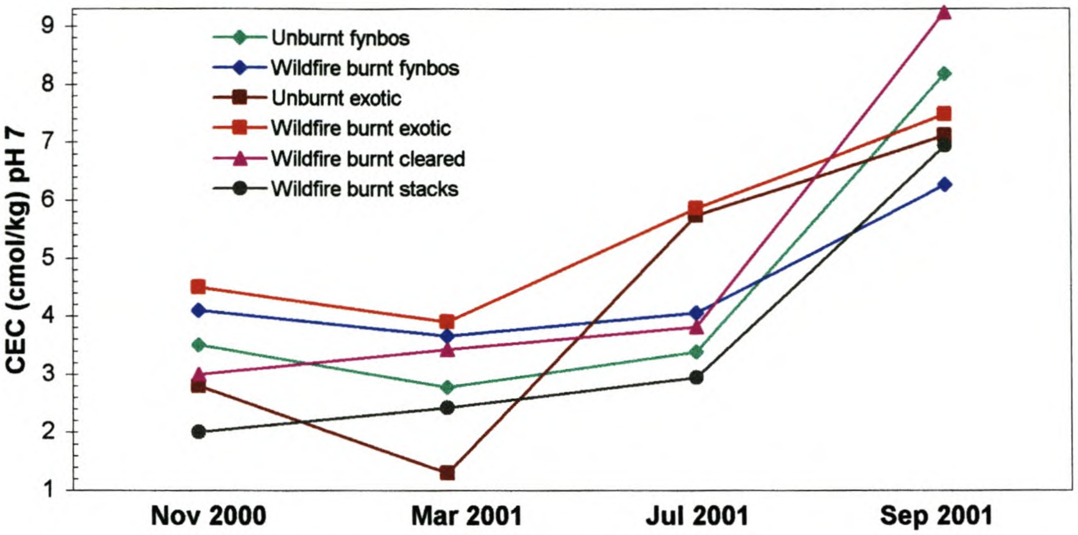


Figure 3.2 Seasonal change in soil cation exchange capacity (CEC) in various natural and transformed Mountain Fynbos habitats

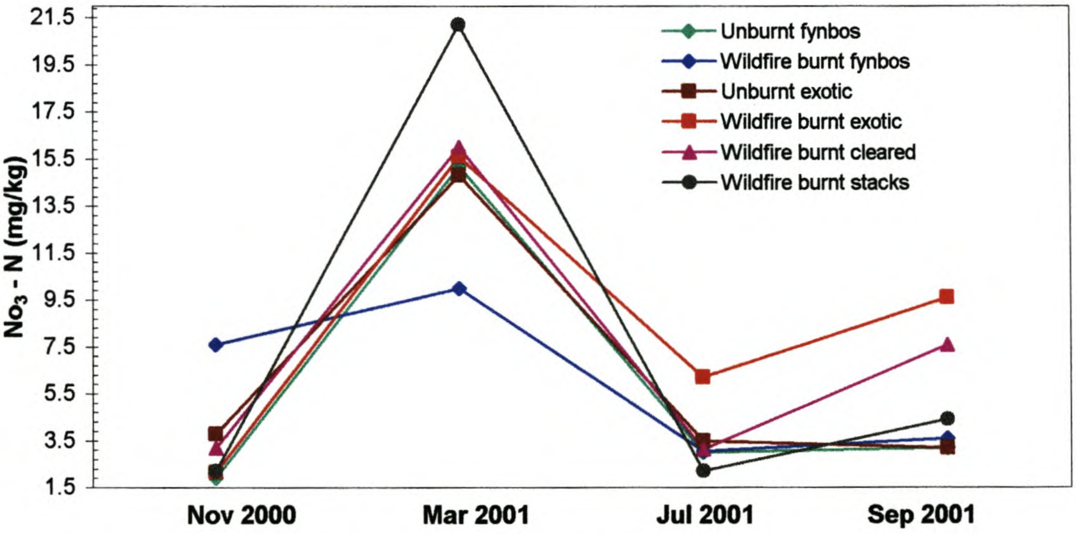


Figure 3.3 Seasonal change in soil NO_3 (N) in various natural and transformed Mountain Fynbos habitats

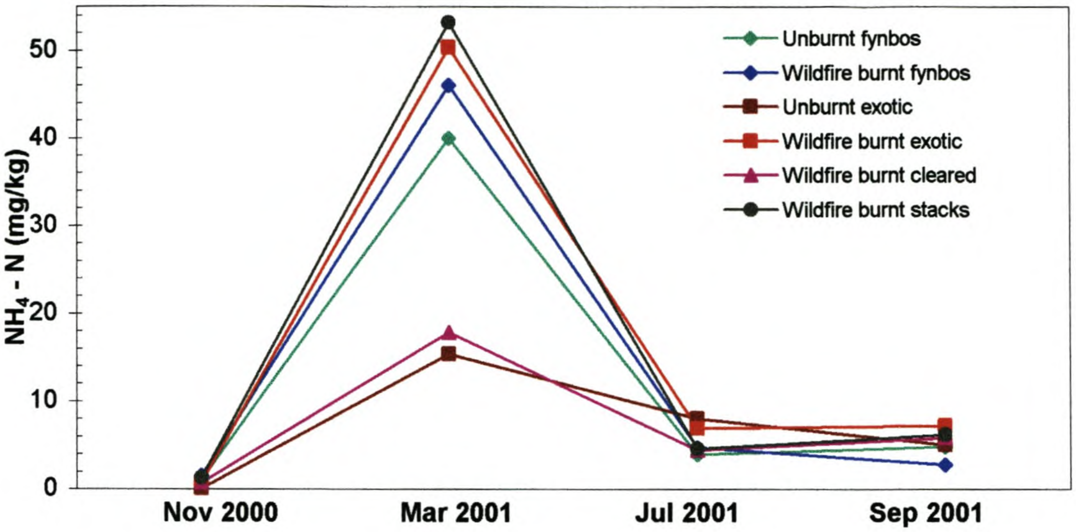


Figure 3.4 Seasonal change in soil NH_4 (N) in various natural and transformed Mountain Fynbos habitats

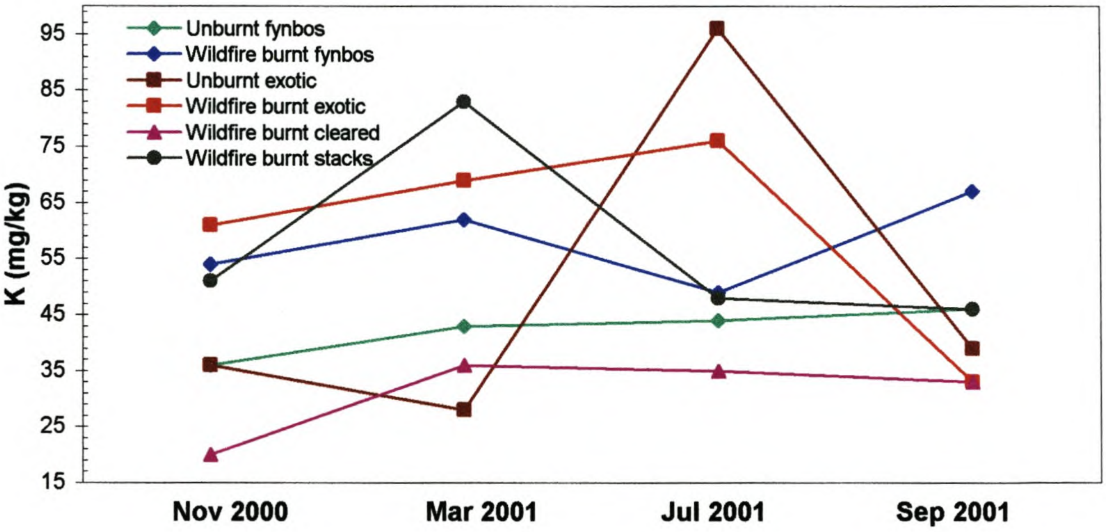


Figure 3.5 Seasonal change in soil K (mg/kg) in various natural and transformed Mountain Fynbos habitats

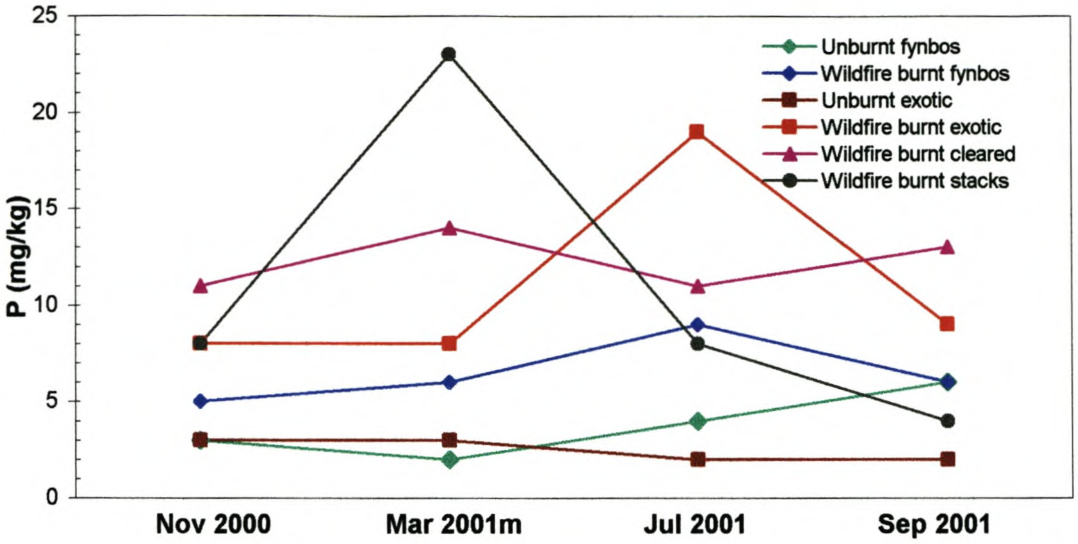


Figure 3.6 Seasonal change in soil P (mg/kg) in various natural and transformed Mountain Fynbos habitats

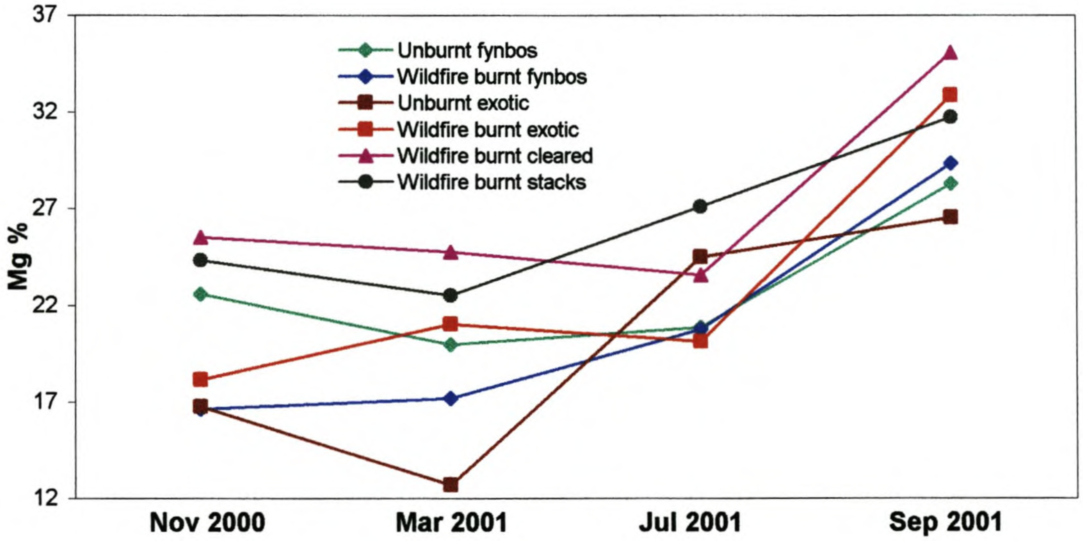


Figure 3.7 Seasonal change in soil Mg % in various natural and transformed Mountain Fynbos habitats

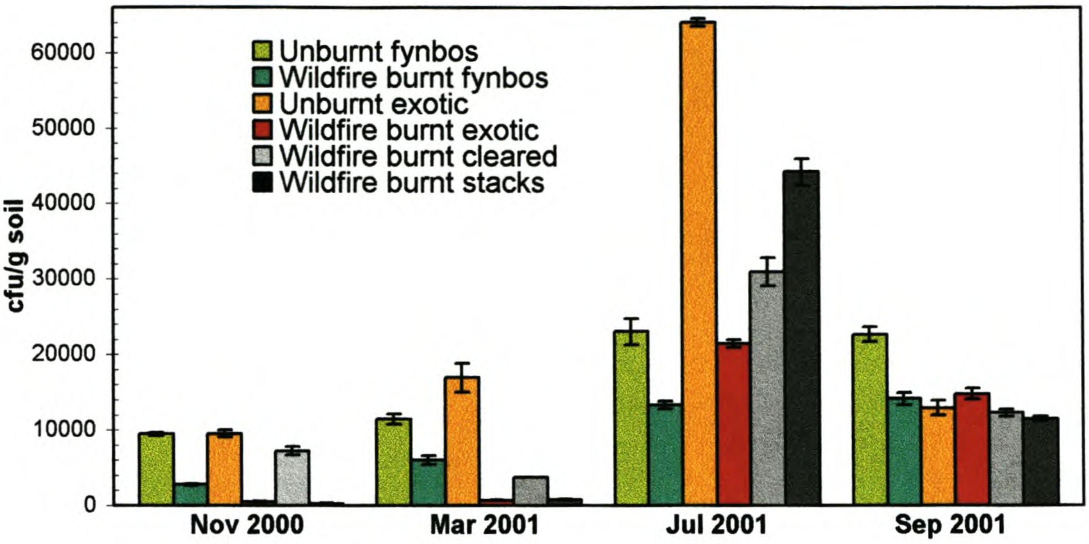


Figure 3.8 Seasonal changes in combined population sizes of soil lipomycetaceous and basidomycetaceous yeasts.
Error bars indicate standard errors of the means

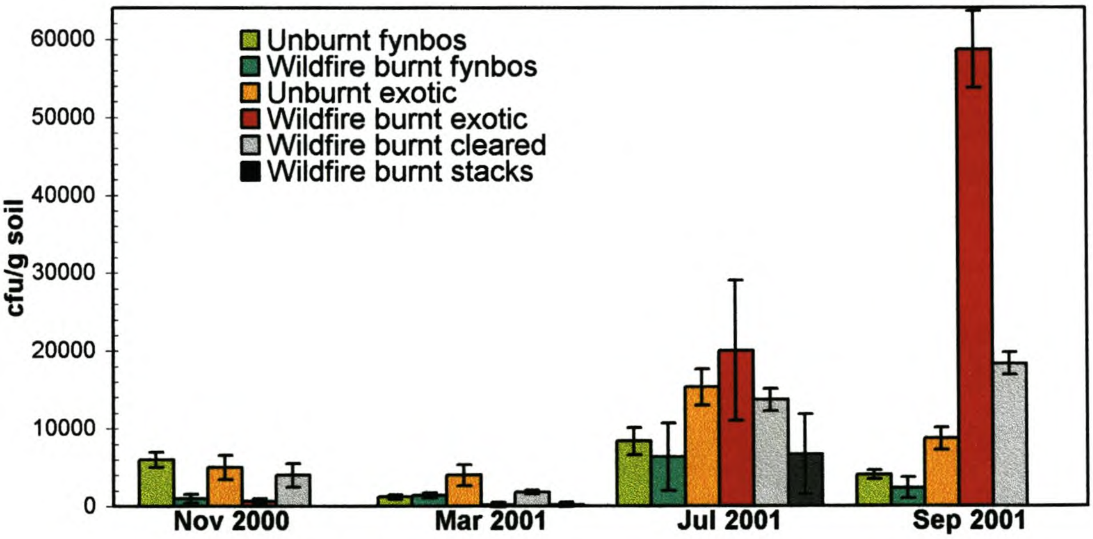


Figure 3.9 Seasonal changes in population sizes of soil mucoralean fungi. Error bars indicate standard errors of the means

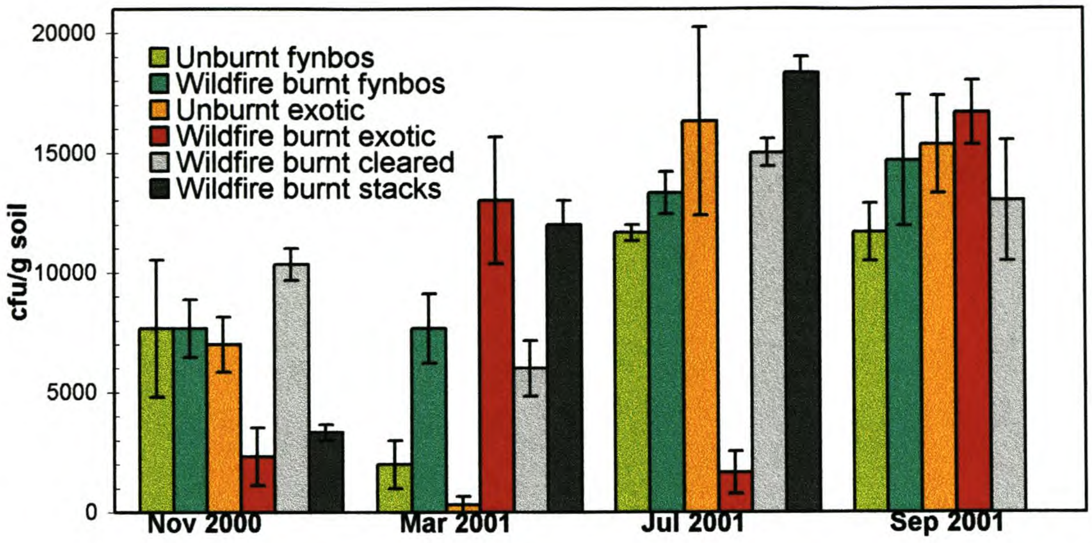


Figure 3.10 Seasonal changes in population sizes of soil hymenomycetaceous fungi. Error bars indicate standard errors of the means

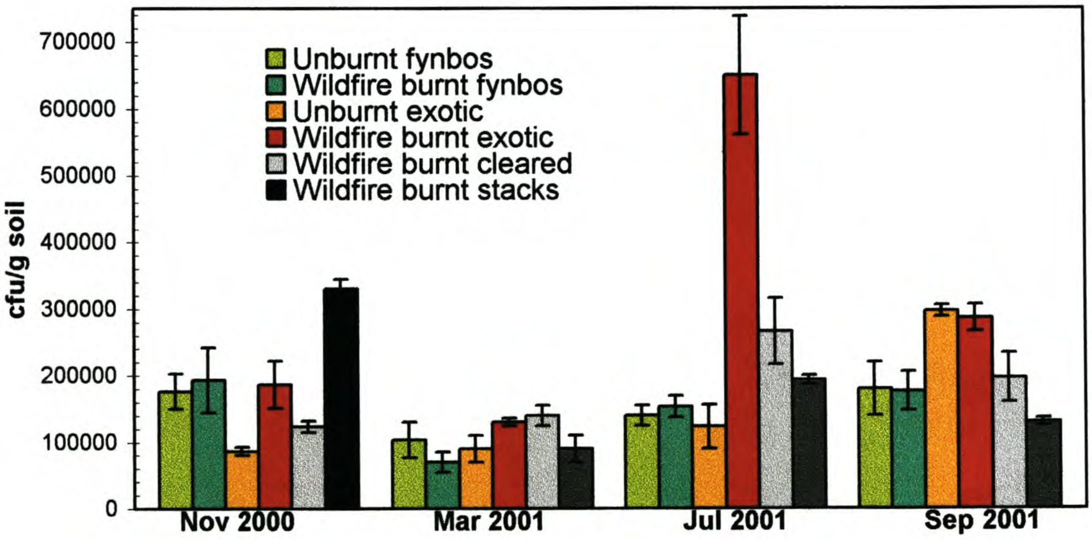


Figure 3.11 Seasonal changes in the populations of total soil fungi (MEA medium). Error bars indicate standard errors of the means

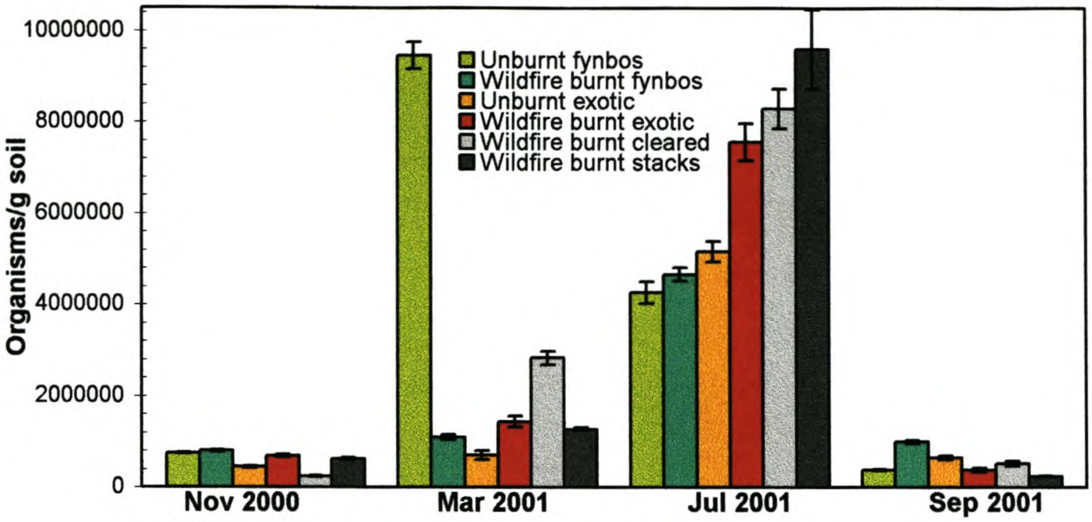


Figure 3.12 Seasonal changes in population sizes of soil actinomycetes. Error bars indicate standard errors of the means

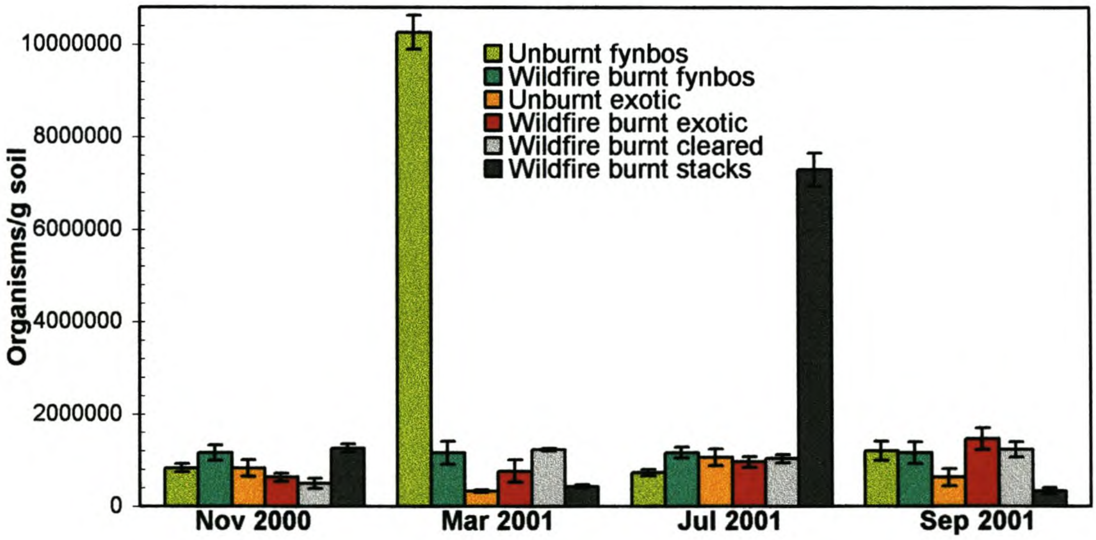


Figure 3.13 Seasonal changes in population sizes of total soil bacteria (TSA). Error bars indicate standard errors of the means

Table 3.1 Sets of environmental variables showing maximum correlation (r_w) with the distributions of lipomycetaceous and basidiomycetaceous yeasts in each of four assays

Assay 1 **Summer 2000**	**Assay 2** **Autumn 2001**	**Assay 3** **Winter 2001**	**Assay 4** **Spring 2001**
Silt %	Stone %	Silt %	Coarse sand %
Fine sand %	P (mg/kg) *log (x)*	Mg %	Mg (cmol/kg) *log (x)*
	K (mg/kg) *log (x)*	Clay %	Clay %
	Na (cmol/kg) *log (x)*	Na %	Na (cmol/kg) *log (x)*
	NO_3 (N) *log (x)*	pH (KCl) *log (x)*	Medium sand %
Fire intensity	Fire intensity		
r_w : 0.812	r_w : 0.872	r_w : 0.798	r_w : 0.834

Table 3.2 Sets of environmental variables showing maximum correlation (r_w) with the distributions of mucoralean fungi in each of four assays

Assay 1 **Summer 2000**	**Assay 2** **Autumn 2001**	**Assay 3** **Winter 2001**	**Assay 4** **Spring 2001**
Clay %	Fine sand %	Fine sand %	Coarse sand %
Silt %	Resistance *log (x)*	Resistance *log (x)*	H (cmol/kg) *log (x)*
Fine sand %	Stone %	Medium sand %	Stone %
P (mg/kg) *log (x)*	Na (cmol/kg) *log (x)*	Mg (cmol/kg) log *(x)*	
K (mg/kg) *log (x)*	Ca (cmol/kg) *log (x)*	NH_4 (N) *log (x)*	Ca (cmol/kg) *log (x)*
	NO_3 (N) *log (x)*	CEC *log (x)*	
	Fire intensity		Fire intensity
r_w : 0.927	r_w : 0.877	r_w : 0.555	r_w : 0.868

Table 3.3 Sets of environmental variables showing maximum correlation (r_w) with the distributions of hymenomycetaceous fungi in each of four assays

Assay 1 **Summer 2000**	**Assay 2** **Autumn 2001**	**Assay 3** **Winter 2001**	**Assay 4** **Spring 2001**
Mg %	T (cmol/kg) *log (x)*	Mg %	H (cmol/kg) *log (x)*
Clay %	Stone %	Medium sand %	Clay %
Silt %	Ca (cmol/kg) *log (x)*	Ph (KCl)	Stone %
Coarse Sand %	Coarse sand %	NO_3 (N) *log (x)*	
r_w : 0.783	r_w : 0.989	r_w : 0.836	r_w : 0.883

Table 3.4 Sets of environmental variables showing maximum correlation (r_w) with the distributions of total fungi in each of four assays

Assay 1 Summer 2000	**Assay 2 Autumn 2001**	**Assay 3 Winter 2001**	**Assay 4 Spring 2001**
Fine sand % Resistance *log (x)* Stone % K (mg/kg) *log (x)* C %	Clay % Silt % H (cmol/kg) *log (x)* NO_3 (N) *log (x)*	Fine sand % N % Fire intensity NO_3 (N) *log (x)*	Clay % Resistance *log (x)* Stone % Fine sand % P (mg/kg) *log (x)* N %
r_w : 0.662	r_w : 0.560	r_w : 0.771	r_w : 0.856

Table 3.5 Sets of environmental variables showing maximum correlation (r_w) with the distributions of actinomycetes in each of four assays

Assay 1 Summer 2000	**Assay 2 Autumn 2001**	**Assay 3 Winter 2001**	**Assay 4 Spring 2001**
Clay % Silt % Resistance *log (x)* Stone % Na (cmol/kg) *log (x)* CEC *log (x)*	Medium sand % Silt % Coarse sand % Stone %	Mg % K (cmol/kg) *log (x)* Ca (cmol/kg) *log (x)* NO_3 (N) *log (x)* Fire intensity	H (cmol/kg) *log (x)* Clay % Ca (cmol/kg) *log (x)* C % T (cmol/kg) *log (x)*
r_w : 0.826	r_w : 0.939	r_w : 0.329	r_w : 0.803

Table 3.6 Sets of environmental variables showing maximum correlation (r_w) with the distributions of total bacteria in each of four assays

Assay 1 Summer 2000	**Assay 2 Autumn 2001**	**Assay 3 Winter 2001**	**Assay 4 Spring 2001**
Na % Fine sand % Medium sand % H (cmol/kg)	Silt % Stone % Medium sand % H (cmol/kg) *log (x)* Coarse sand % CEC *log (x)*	Mg % Clay % Ca (cmol/kg) *log (x)* C %	P (mg/kg) *log (x)* Stone %
r_w : 0.734	r_w : 0.847	r_w : 0.828	r_w : 0.800

3.5 DISCUSSION

SOIL CHEMICAL CHANGES

Reasons for the observed soil chemical changes are speculative, viz: the pH drop in autumn 2001 corresponded with a sharp rise in NO_3 and NH_4 levels, a possible result of the activities of nitrifying and denitrifying bacteria. The rises in NO_3 and NH_4 levels also corresponded with increased population sizes of actinomycetes and total bacteria. Trends indicated possible influences of burning, plant cover, biomass and associated fire intensity on the levels of potassium in the soil during summer and autumn. In these assays (November 2000 and March 2001) wildfire burnt stacks, burnt standing exotics and burnt fynbos treatments exhibited higher levels than unburnt treatments, wildfire burnt stacks also had higher potassium levels than the immediately adjacent burnt cleared areas. Potassium was also one of the environmental determinants of the distribution of soil yeasts in autumn. With the advent of winter however (July 2001), the influence of burning, plant cover, biomass and fire intensity on K levels was no longer apparent. Winter was also the time of maximum fungal growth, and K showed no correlation with fungi or bacteria during this period.

SOIL FUNGI

Correlation of soil yeast populations with environmental variables indicate prolonged effects of fire and fire intensity (at least 13.5 months) while macronutrient availability during autumn is an important determinant of soil yeast population sizes. Some recovery of soil yeast populations coincided with the onset of cooler winter weather and increased rainfall (July 2001). Macronutrients, fire and fire intensity were no longer important, (due perhaps to the relief of summer drought) while texture, Mg and N were winter determinants. Evidently Autumn is the period where macronutrients are most important and the effects of fire on soil yeast population size seemingly disappears with periods of prolonged rainfall/low temperatures.

The observed mucoralean fungal distribution in November 2000 suggests an influence of fire and fire intensity, however standard errors are large, somewhat negating the significance of this assumption. Rapid growth rates of mucoralean fungi may explain the importance of macronutrient foodstuffs at an earlier time than for soil yeasts (maximum correlation during November was not with fire intensity but with soil texture, P and K). Although total population sizes were still small in March 2001, the counts (large standard errors aside) suggest an influence of fire intensity on Mucor population sizes, burnt standing exotics and burnt stacked exotics exhibiting smaller totals than unburnt standing exotics and burnt cleared areas respectively. Macronutrient foodstuffs (coupled with resistance, soil texture and fire intensity) were however still the key determinants of mucoralean population size. No significant population size differences were measured in July 2001 (due to prohibitively large standard errors of the means); there were also no strong correlations with the environmental variables measured. Populations had however grown, coinciding with the advent of cooler, wetter conditions. Reasons for the large increases observed in burnt standing exotic areas in September 2001 are speculative. It is possible that species turnover had occurred and that a specific group/species had benefited from the post-fire conditions prevalent in the burnt standing exotic area. Conversely the species due to colonise the burnt stacked (heat scarred) areas had all but disappeared, perhaps a relictual effect of superheating. In summary, indications are that early summer is the time when macronutrients are important and the effects of fire on mucoralean fungi population size seemingly disappeared with periods of prolonged rainfall/low temperatures. Population sizes also exhibit large fluctuations, possibly indicative of a more easily diffused group with associated patchy dispersal patterns (Ingold 1953).

Hymenomycetaceous fungal distributions in November 2000 suggested reduced population sizes in areas subjected to intense burning (standing and stacked exotics), conversely the March 2001 pattern (which was highly correlated with soil texture, T-value and Ca) suggested a negative association with fire and fire intensity. Hymenomycetes are however highly mobile, easily dispersed organisms and it is therefore possible that the observed patterns are indicative of patchy dispersal patterns (Ingold 1953). This may also explain the observed collapse in hymenomycetaceous fungal populations in burnt standing exotics in July 2001 while there were increases in other areas (coincident with the advent of winter). Alternatively, this collapse and the disappearance of hymenomycetes in the burnt stack samples in September 2001 may be a relictual effect of superheating, eliminating a group due to colonise the scars at that time. Differences in environmental variable sets (showing maximum correlation with fungal populations within the study period) may also indicate a succession of different species or groups of species. Except for the elimination of hymenomycetaceous and basidiomycetaceous fungi in heat scars in September, exotic plants and fire seem to have little effect on total populations of hymenomycetaceous fungi in soil.

Environmental variables were only strongly correlated with counts of total fungi (on MEA medium) in September 2001, when a combination of soil texture and nutrients were determinants. A possible explanation is that the environmental variables measured did not include those parameters most important in determining total fungal populations. Alternatively, the studied group (total fungi on MEA) could have been prohibitively diverse, clouding establishment of environmental determinants. Observed trends (large standard errors of the means aside) indicated that the highest total fungal counts were always from non-fynbos sites, burnt non-fynbos areas having higher counts until spring 2001 (September). It is therefore possible that total fungal populations on (MEA medium) are benefited by the presence of exotic vegetation and by the burning thereof.

SOIL ACTINOMYCETES AND BACTERIA

The distribution of actinomycetes in November 2000 indicates that burning benefits populations at this stage. It may also be inferred that higher intensity burns are more beneficial for actinomycetes since populations were significantly higher in heat scars than in the burnt cleared areas immediately adjacent to them. Larger, albeit variable, population sizes in March 2001 denote that actinomycetes are able to reproduce and grow during hot, dry summer months. All areas (except for unburnt fynbos) had shown further increases in population size by July 2001. It is possible that the actinomycetes which showed such rapid population increases in unburnt fynbos soils by March 2001 and which then dropped by July were different species than those present in the other areas and had completed their life cycles earlier. An alternative hypothesis is that coinciding increases in population sizes of predatory soil amoebae are accountable for decreases in actinomycetes in some areas (Alexander 1977, Paul and Clark 1996). It was also apparent in July that burnt non-fynbos areas had the highest counts, (counts in burnt fynbos, unburnt fynbos and unburnt standing exotics being similar and lower) and that a combination of exotic plant invasion and burning benefits actinomycete population size in winter. While actinomycete counts across the different areas sampled were highly variable they all reacted to the advent of winter conditions. It is therefore probable that different species are dominant in the different indigenous and exotic plant-dominated sites and that they show variable responses to seasons, burning and to soil environmental variables.

While clear patterns in the distributions of total bacteria (on TSA) were not apparent, a similar pattern to actinomycete populations was obtained in March 2001, a possible manifestation of these counts. This pattern and the elevated levels in burnt stacked (heat-scarred) areas in June 2001 could possibly be explained by a different species or group of species benefiting from the post-fire environmental conditions present in unburnt fynbos and heat-scarred areas respectively. However it must be taken into account that no one medium is nutritionally adequate for all the species present and the observed counts therefore only represent fractions of the total. The errors in sampling and sample preparation are frequently far greater than the inherent variations and a single rootlet or particle of plant debris may be sufficient to change counts ten or a hundred fold (Alexander 1977). The observed decreases in total bacterial counts in unburnt fynbos and heat scarred areas in July and September 2001 may however also have been a result of increased amoeboid activity utilising flushes of bacterial growth (Alexander 1977, Paul and Clark 1996). In conclusion, indications are that habitat modification (resulting from exotic plant invasion and burning) on total bacterial counts variably influences different species or groups of species, benefiting some and detrimenting others. This may serve to explain the large variation between samples and between seasons.

3.6 CONCLUSIONS

This pilot study showed that woody exotic plants; fire; fire intensity; season; soil texture and chemical characteristics together determine fungi and bacterial populations in the upper 0.10 m of the soil profile. Current management of exotic plant infestations have also been shown to have influence on some microbial populations. Supplementary investigations are warranted on particular species or taxa within the studied groups as well as on protozoa (supported by soil chemical and molecular analyses) to further elucidate environmental effects of exotic plants, fire and their management, which will then aid in informed management decision-making.

CHAPTER 4

General Conclusions

4.1 Introduction

The findings and the recommendations made in this thesis can be applied to management of woody exotic plants (within the Silvermine Nature Reserve and elsewhere in the Fynbos Biome) in an effort to achieve the goal of optimal veld restoration. The methods used in this study may be implemented (incorporating the recommended improvements mentioned below) to investigate the effects of different treatments/management practices on soil seed banks, vegetation regeneration, soil chemistry and microbiology in fynbos and in Mediterranean type ecosystems around the world.

This chapter contains a review of the predictions outlined in chapter 1 (section 1.4), a summary of problems and shortcomings of this study, recommendations for future study and implications for future management of woody exotic plants within the Fynbos Biome.

4.2 Realisation of research predictions and objectives

4.2.1 Post-fire seed bank and regeneration study

- The principal aim of this study was to investigate seed-banks and regeneration in different post-fire environments within the Silvermine Nature Reserve, focusing on the following components of woody exotic plant management: The effects of a fire on a dense stand of invasive exotic plants (compared to an adjacent burnt Mountain Fynbos site). The effects of packing slashed exotic plant material into stacks and having a subsequent wildfire move through the area (compared to adjacent burnt areas, which were cleared of exotics before the fire, but where no stacking took place). The third component investigated included the post-fire regeneration effects of similar stacks burnt deliberately in control burns during cool winter weather conditions. The success of this study is evidenced by the realisation of the original research predictions and objectives mentioned in Chapter 1 (described below).

- The prediction that the burnt standing exotic sites would exhibit high in-field densities of exotic seedling regeneration and low seed bank abundance, diversity and *in situ* regeneration of indigenous species was realised. High exotic plant seed densities were however not adequately reflected in the nursery trial (a possible artefact of patchy in-field seed distribution or inadequate sample size) and, in contrast to the original prediction that heat damage in standing burnt exotic sites would be confined to shallow depths, indigenous species were only present in reduced numbers at the 0.05 – 0.15 m depth interval in the soil profile, indicating significant heat damage to a depth of at least 0.05 m. The presence of these deeply buried indigenous seeds concur with findings made by Holmes and Cowling (1997a, b), Holmes and Richardson (1999), Holmes (2001) and Holmes *et al.* (2001) who described persistent indigenous soil seed banks in exotic plant dominated Mountain Fynbos communities. However, the depth of burial of the indigenous seeds along with the fact that many indigenous species are small seeded, prohibited successful in-field germination (Bond *et al.* 1999).

- The prediction that soil seed banks under burnt fynbos (and subsequent regeneration), should be represented by a larger variety and abundance of species than under dense exotic infested stands was realised, supporting the findings of Kilian (1991) and Manders (1990b) who found no significant reductions in indigenous soil borne seed banks after burning fynbos. Similarly Holmes *et al.* (1987a, b), Holmes and Cowling (1997a), Holmes and Richardson (1999) and Holmes *et al.* (2001) observed reductions in indigenous soil seed banks following fires in dense stands of woody exotic plants.

- As expected, soil stored seeds of all species were affected/killed in those patches associated with wildfire burnt stacks (heat scars) confirming the observations/statements made by Griffith (1986), Breytenbach (1989), Macdonald *et al.* (1989), Martens (1997), Bond *et al.* (1999), Euston-Brown 2000, Scott *et al.* (2000) and Vlotman and Knight (2000) that stacking of exotic slash results in elimination of soil-stored propagules following wildfires. Heat damage was also to a greater depth (elimination of practically all seeds to at least 0.15 m) than in the burnt cleared and burnt standing exotic treatments.

- The prediction that burnt cleared sites should contain greater exotic and indigenous seed numbers and that exotic seedlings should dominate regeneration in the cleared sites was met. The strong indigenous component (evident in the field and in the nursery) showed that these areas must not be considered as having high development but rather high restoration potential (Van Wilgen *et al.* 1996, Gubb 2000), providing exotic biomass is removed prior to wildfires. Again, the presence of the indigenous component confirms observations made by Holmes and Cowling (1997a, b), Holmes and Richardson (1999), Holmes (2001) and Holmes *et al.* (2001) of persistent fynbos propagules surviving in dense exotic stands. The post-fire dominance of exotic plants observed in these areas may be attributed to copious seed production by parent plants (Fugler 1979b, Milton and Hall 1981, Richardson and Van Wilgen 1984, Gill 1985, Pieterse 1986, Pieterse and Cairns 1988, Macdonald *et al.* 1988, Van Wilgen *et al.* 1996), resultant large soil stored seed banks (Milton and Hall 1981, Macdonald *et al.* 1988, Pieterse and Boucher 1997) and high growth rates (Hall and Boucher 1977, Milton 1980, Milton and Siegfried 1981, Gill 1985, Rutherford *et al.* 1986, Jeffery *et al.* 1988, Van Wilgen *et al.* 1996, pers. obs. 2000, 2001).

- The prediction that stacked and cleared areas would result in a decline in serotinous exotic species while exotic species with soil seed banks would be numerous in cleared areas was also met, however it later became clear that the pre-fire exotic community composition in this area was dominated by Australian *Acacia* spp. (with soil stored seed banks) (Ms. H. Thomson, Cape Peninsula National Parks, pers. comm. 2001). Species with soil-stored seed banks were numerous in the burnt cleared areas because stacking does not lead to a concentration of seeds of non-serotinous species. These areas thus retained their large soil-borne exotic seed stores, which germinated following the January 2000 wildfire.

- In accordance with predictions it is evident that large-scale exotic seedling regeneration results from clearing and control burning of exotic slash under cool weather conditions. These results confirmed that seeds of woody exotic species are cued to germinate by fire (Jones 1963, Bands 1977, Taylor 1977, Pieterse and Cairns 1986, Holmes 1987, Richardson *et al.* 1992, Pieterse and Boucher 1997). However, in contrast to suggestions made by Holmes and Richardson (1999), winter burning of slash piles resulted in good recruitment of indigenous reseeder species.

- In conclusion, woody exotic plants affect post-fire seed banks and regeneration along a scale of increasing biomass and associated fire intensity. Current management (mechanical clearing and stacking) induced the most drastic changes which included the virtual elimination of indigenous and exotic soil seed banks and other propagules.

4.2.2 Microbes and chemistry study

The goal of this investigation was to assess links between soil microbial population sizes, exotic plants, their management, fire intensity and post-fire soil chemical and physical characteristics.

- While it was predicted that soil chemistry alteration would be correlated to burn intensity (chapter 1, section 1.4), only phosphorous and potassium showed appreciable changes related to fire intensity, their levels being higher in the more severely burnt sites. This contrasts with Rundel *et al.* (1983), Cass *et al.* (1984), Christensen (1994) who stated that vaporization and convection during fires may cause considerable losses of phosphorus; potassium; calcium; sulphur; chlorine; nitrogen and magnesium. The increased levels of P and K observed in this study corresponded with findings made by Hernandez *et al.* (1997), Durand (1981) and Musil and Midgley (1990) in Mediterranean pine forest and fynbos soils respectively while Musil (1993) also found higher levels of K in soils derived from burnt *A. saligna* stands than in burnt fynbos soils. It must be considered that this study commenced in November 2000 after a particularly dry winter (Chapter 1, figures 1.6 and 1.7) and soil chemistry could thus have been influenced by climate, soil microbial activity and other factors affecting nutrient flux. Observed post-fire changes in cation exchange capacity, pH, NH_4 and NO_3 levels were also attributed to seasonal and/or soil microbial influences. These observations concur with Bollen (1959), who stated that some microbes are agents in production of ammonia and nitrates from protein material while others utilize atmospheric nitrogen, organizing it into compounds which ultimately become incorporated with humus, so adding to the limiting supply of soil nitrogen.

- While it was predicted that soil chemical changes should exhibit some recovery over time with those most affected being the slowest to recover (chapter 1, section 1.4), only phosphorous levels showed some apparent recovery in fynbos habitats.

- Predicted post-fire correlations of microbial activity with soil chemistry were investigated using the output generated by the BIOENV application of the software program PRIMER (Clarke and Warwick 1994). Maximum correlations were shown between a variety of soil nutrients, soil texture and microbial population sizes over four assays from November 2000 to September 2001. During this time large seasonal changes in microbial populations were observed, these included large population expansions with the onset of cold, winter weather.

In conclusion this study showed considerable effects of (and correlations between) woody exotic plants, fire intensity, post-fire soil chemical and physical characteristics on soil microbial population sizes. Current management of exotic plant infestations was also shown to have influence on some microbial populations. These changes potentially affect changes in soil chemical composition, decomposition and nutrient cycling, all of which may influence plant establishment and growth.

4.3 Methods used in the research studies

4.3.1 Regeneration study

While field counts of regenerating propagules in the various sites were at times tedious and time consuming, they resulted in reasonably accurate determinations of post-fire propagule abundance and morpho-species diversity. Temporal field counts of a variety of growth forms allowed determination of the post-fire succession interval associated with maximum species abundance and diversity (September 2000). Counts in this interval were then compared across sites allowing accurate resolution of differences associated with environmental disturbance and management.

Difficulties were encountered in the field, including problems in assigning affinities (guilds) to regenerating propagules. It was often difficult to determine in the field whether a plant was a reseeder or a resprouter. For example to the untrained eye, the perennial, *Ficinia oligantha* and the annual, *Isolepsis incomptula* are similar and difficult to tell apart in the field. Individuals of the former rely on resprouting and reseeding for regeneration while the latter is an exclusive reseeder (pers. obs. 2000, 2001). Similar problems were encountered in decisions involving guild affinity (reseeder or resprouter) of grass species. Delimitation of individual grass and herbaceous resprouting plants was also troublesome, however for the purposes of this study, functional units were counted as individuals. These in field "identification" problems were resolved by repeated checking, ensuring accuracy of the final counts. Similar methods were also effective in determining "field germination and establishment" of *Calluna-Arctostaphylos* heath in northeastern Scotland (Mallik *et al.* 1984) and fynbos in the Grahamstown Nature Reserve (Martin 1966).

4.3.2 Seed bank study

While the nursery germination trial showed good results, it was not without problems including: seedling mortality prior to identification (Malone 1967), consumption of *Protea lepidocarpodendron* seedlings by snails and removal of some labels by the public. The seedling trays also took up a substantial amount of glasshouse space (Roberts 1981, Gross 1990, Ter Heerdt *et al.* 1996). Due to the limited glasshouse space only four control trays were prepared which proved insufficient for identification of regenerating weedy seedlings in this way. This limitation necessitated the identification of ruderal species regenerating in all the seed trays and their exclusion from subsequent analyses. A considerable amount of weed seeds germinated during the trial since the "fynbos soil mix" (on which measured volumes of soil from the various sites were planted out), was not sterile as originally thought. Another problem encountered was that some (indigenous and exotic) species took a long time before flowering while some had not flowered by the end of the trial (November 2001), complicating their identification (Ter Heerdt *et al.* 1996). Other problems associated with nursery germination trials include a potential under-estimation of the number of viable propagules in soil due to dormancy and variable greenhouse conditions (Roberts 1981, Manders 1990a, Brown 1992, De Villiers *et al.* 1993). In contrast to this assumption, Pierce and Cowling's (1991) study showed no significant difference between estimates (of post-fire fynbos seed banks) using emergence and physical extraction methods. Samples in this project were from post-fire areas, negating the need for a dormancy breaking treatment such as a smoke water application, while the glasshouse had ventilated sides enabling diurnal temperature fluctuation and air movement, necessary germination cues in some taxa (Brits 1986, Pierce and Moll 1994, Dr. C. Boucher, Botany Department, University of

Stellenbosch, pers. comm. 2000, Mr. D. Kotze, Stellenbosch University Botanical Gardens, pers. comm. 2000).

The following physical seed extraction methods were attempted in this study: Small (5 - 25 ml) sub-samples were taken from each sieved soil depth/size class combination and manually searched for seeds under a stereomicroscope (Manders 1990a, Kilian 1991). A flotation method (similar to that used by Malone 1967 and Benoit *et al.* 1989) of physical seed extraction was also attempted with similar sub-samples. Both methods were abandoned because they proved impractical, excessively time-consuming and labour intensive (Gross 1990, Manders 1990a, Brown 1992, De Villiers *et al.* 1993, Ter Heerdt *et al.* 1996). The flotation method was also impeded by exceedingly fine soil texture and high organic contents, which caused entire samples to float. Further problems were encountered when the floating matter was decanted as most stuck to the inside of the glass container. Extraction methods also overestimate seed banks as many seeds are not viable and small volumes of soil searched curtail accuracy (Gross 1990, Brown 1992). For example Kilian (1991) used direct seed counts and germination techniques to investigate seed and seedling ecology of two co-occurring ericoid fynbos shrub species and found only 35% viability in *Phylica ericoides* and 50% in *Passerina paleacea.* Labour and time needed for physical extraction methods are potentially further increased by viability tests while seed identification is problematic (especially between species with similar seed characteristics) requiring a large seed library (Roberts 1981, Gross 1990, Manders 1990a, Brown 1992, De Villiers *et al.* 1993). Moreover, available viability tests are unsuccessful in fynbos seed banks due to the small nature of many seeds (De Villiers *et al.* 1993). In conclusion, physical extraction methods are unsatisfactory for the enumeration of fynbos seed banks that contain many small-seeded species (which are easily overlooked) (Gross 1990, Manders 1990a).

The lower labour requirements and relative ease of the emergence method was a key reason for its implementation (a physical method may have been better suited to a single species study requiring larger sample numbers), moreover a higher amount of smaller seeded species (common in fynbos) are detected than in extraction methods (Manders 1990a, Brown 1992, De Villiers *et al.* 1993). Method selection was primarily based on the project goal (Manders 1990a, Brown 1992) that aimed to investigate relative abundance (and not absolute densities) between treatments as a function of exotic plant invasion, fire and management (Manders 1990a).

In conclusion, the methods (field regeneration and nursery germination trial) used for the most part adequately depicted post-fire differences in exotic and indigenous seed-banks in the various habitats (in terms of abundance, species diversity, depth of burial and seed size). Ratios of seedling abundance and diversity in the nursery germination trial and the field were similar, confirming the success of the nursery germination trial.

4.3.3 Microbes and soil chemistry study

Methods employed in the gathering of soil samples were neither tedious nor labour intensive (relative to the seed bank and regeneration study) even though sampling was done during heavy downpours in July and September 2001. Bemlab used standard soil chemical analyses and Ms. S. Cornelissen and Mr. K. du Plessis (Microbiology Department, Stellenbosch University) used standard plate count methods to conduct microbial population counts.

A problem inherent to microbial assays is that plate counts are the most reliable enumeration method available. Plate counts are based on the rationale that where there is a spore an organism will result. This premise is not always accurate, partly due to vast numbers of spores produced. Fungal counts are thus at best viewed as estimates of potential population size. Alternative methods however seldom result in accurate microbial population size estimations of (Ms. S. Cornelissen pers. comm. 2001).

4.4 Recommendations for future seed bank and regeneration studies

Post-eradication monitoring is extremely valuable since it allows managers to document positive outcomes of eradication successes while providing the opportunity to learn from mistakes (Zavaleta *et al.* 2001). The choice of sound methods in these projects will serve to maximise learning opportunities. Some recommendations are provided here.

Since physical seed extraction methods proved to be unsatisfactory in this study and in fynbos ecosystems in general (Gross 1990, Manders 1990a), future studies should include paired nursery germination and *in situ* regeneration trials. Future studies may also include a wider range of treatments, for example after post-fire chemical applications to regenerating exotic seedlings. Further studies should include the seasonal effects of burning on indigenous seedling recruitment since winter burning of exotic slash piles resulted in good germination of native species in this study (contrasting with Holmes and Richardson 1999). More work is also needed on the effects of seed size on fire survival and post-fire establishment. It may also be useful to compare indigenous and exotic seed banks and regeneration across environmental gradients including soil type, slope, aspect and climate. Sites used in the current study may be re-sampled to determine seed bank and regeneration effects of succeeding management or fires. Prospective studies may include more detailed work on phenology and changes in species composition/succession *in situ* as affected by exotic plants and their management.

In the future, soil samples used in nursery germination trials should be planted out on acid washed sand to reduce contamination (Manders 1990a) while sufficient nursery space must be provided for control trays. Field sampling design is important and maximum size of plots should not exceed 1 m^2. Larger plots are impractical if the total number of regenerating propagules are to be accurately counted. Boucher and Mortimer (2000) suggest that future studies of soil borne seed banks of exotic *Acacia* spp. should be carried out to depths of at least 1 m where physically possible. Methods used in the present study combined with these recommendations should result in studies that will contribute maximally to the understanding of seed bank ecology of exotic and native species.

4.5 Recommendations for further microbial and chemical studies

Supplementary investigations should be done in fynbos and other biomes on soil microbial populations (supported by soil chemical and molecular analyses). These should be done seasonally, in various indigenous and exotic plant dominated habitats (with and without the influence of fire) over periods longer than one year in order to tease out seasonal and post-fire effects. Similar methods may be used for more extensive studies because of their relative ease of execution and expeditious nature. These and studies on particular microbial species/taxa (and protozoa) may further elucidate ecological effects of exotic plants, fire and their management resulting in better understanding of fynbos ecosystem functioning and informed management decision-making.

4.6 Management implications of this study

As knowledge about effective eradication methods accumulates, attention should turn to combining such methods with broader ecological principles to form cost-effective removal strategies that accomplish overall restoration goals (Zavaleta *et al.* 2001). If restoration of pristine Mountain Fynbos is the goal, then the current management practice of stacking slashed exotic plant material is clearly incompatible with this ideal. This study has shown that highly elevated temperatures in stacks of exotic slash destroy soil seed banks (and other propagules) and impact on soil chemistry and microbiology.

Considering the findings made in this thesis, future management of exotic plant invaded sites in the Silvermine Nature Reserve (and elsewhere in the Fynbos Biome) may continue to use the methods outlined in the 2001 Silvermine River Action Plan (summarised in Chapter 1, section 1.5.3) with the following amendments and suggestions.

- Due to the danger of wildfire, slashed exotic plant material should **not** be stacked and left *in situ*.

The following options may be considered regarding disposal/use of the slash.

  - Slash removal should be included in invasive clearing contracts (Dr. C. Boucher pers. comm 2001).
  - After removal from the site, the slash may be sold as firewood or made into charcoal, mulch or compost (Pieterse *et al.* 1997, A. Milewski, Percy Fitzpatrick Institute of African Ornithology, University of Cape Town pers. comm. 2001).

In areas where this is impractical, the following alternatives are recommended.

- The current stacking procedure could be adapted to limit environmental damage by:
    - Identification of a site of minimum environmental or aesthetic significance, (preferably on a road, firebreak or old scar) and burning slash during cool weather conditions at such a site (Mr. D. Euston-Brown, PO Box 44066, Scarborough, 7975, pers. comm 2001) .
    - Concentration of slash at a minimum number of points in order to minimise the area affected. While more labour-intensive and expensive, this method will result in less scarring to smaller areas and achievement of better veld restoration (Mr. D. Euston-Brown pers. comm 2001).

- Alternatively, live stands of woody exotics may be control burnt under cool weather conditions (Breytenbach 1989, Holmes 1989, Holmes *et al.* 2001).
    - Follow up weeding should be done within after one year, checking for survivors every six months after that for at least 10 years (Combrink 1985, Macdonald and Jarman 1984, Holmes 1989). The frequency of weeding may however be curtailed by costs necessitating a longer clearing cycle (Dr. C. Marais, Working for Water, Private bag X4390, Cape Town 8000 pers. comm. 2001.)
    - Regenerating seedlings may be pulled or sprayed, depending on ecological sensitivity of the site.
    - A "popper" may be used for weeding of low-density invasions of juvenile plants in sandy areas (Dr. C. Boucher pers. comm. 2001).
    - *A. saligna* sites should not be re-burnt for an extended period (of at least 14 – 16 years) allowing relictual fynbos species to recover and reinstate their own seed stores (Dr. C. Boucher pers. comm. 2001)
    - Hakea and pine invasions may be re-burnt within 24 months and six years respectively, effectively controlling heat sensitive seedlings (Kruger and Bigalke 1984).

- An important consideration (if burning treatments are to be applied) is that *H. sericea* seedlings are sensitive to season of burning with more being killed if burning occurs soon after flowering (Brown and Whelan 1999).

- A chemical defoliation agent may also be applied to adult plants in low-density sites prior to further management controls. Australian *Hakea* and *Pinus* spp. are resistant to chemical control (Kluge and Richardson 1983, Martens 1997) but post-control burning techniques are successful controls with these species (Dr. C. Boucher pers. comm. 2001).

- The optimal strategy for a 'typical' western Cape *A. saligna* thicket, if the area has to be burned after initial mechanical clearing, is a foliar arbocide application (in combination with mechanical clearing) to the post-fire regeneration, followed in subsequent years by repeated mattocking operations (Macdonald and Wissel 1991).

- Non-burning treatments are an option following removal of slash from the area, especially in the case of *A. cyclops* and along rivers (Homes 1989, Dr. C. Boucher pers. comm. 2001). *A. cyclops* shows a decline in seed banks following removal of parent plants (Holmes 1989). This would also give indigenous species a chance to reinstate their seed stores.

- Clearing operations should first concentrate on recently invaded areas since they have the highest potential for complete restoration (Holmes and Cowling 1997b).

- All clearing actions should include inoculation of exotic regrowth with biocontrol agents, which have been shown to be effective in the suppression and death of adult plants (Van den Berckt 2001) and in reducing seed production (Annecke and Neser 1977, Neser and Kluge 1986, Dennill and Donnelly 1991). Care must however be taken to always include a seed predator since it has been shown that *Uromycladium tepperianum*, while highly effective in the killing of adult *A. saligna* plants (Fleitmann and Boucher 2001, Van den Berckt 2001) increases the soil seed bank of this species after inoculation (Fleitmann and Boucher 2001).

Eradication alone may not allow (Mountain Fynbos) ecosystems to recover, because some invaders change the nature of the habitat so as to render it unsuitable for native species (Zavaleta *et al.* 2001). Owing to the short dispersal distances of most fynbos species, natural re-colonisation of large degraded areas by seed is likely to take several fire cycles (Holmes and Richardson 1999).

- For these reasons, some restoration work may be applicable (Holmes and Cowling 1997b, Holmes and Richardson 1999).
- After mechanical clearing, a smoke water treatment or other stimulation may be applied to the soil surface, to stimulate the germination of fynbos seeds and result in better veld restoration (De Lange and Boucher 1990, Brown 1993).
- Restoration work is necessary on old scars (even though many occur in a mixed fynbos/exotic matrix and are < 50m in diameter) since they may otherwise persist for more than ten years (Macdonald *et al.* 1989, Holmes and Richardson 1999), potentially impacting on erosion (wind and water) and decreasing local species diversity.

4.7 Conclusion

The primary hypothesis that post-fire regeneration patterns, soil borne seed-bank diversity and abundance are linked to pre-fire vegetation and seed characteristics of the component species is supported by the findings outlined in this study. Pre-fire increases in biomass following exotic plant invasion and the management thereof (stacking) are determinants of fire intensity. This study has shown that increasing fire intensity is a principal determinant of post-fire community structure and that current exotic plant management (which causes localised increases in fire intensity by wildfire burning slash piles) is unsound.

The second research hypothesis that certain soil borne microbial population sizes are linked to post-fire soil chemical characteristics and to fire intensity is also accepted. Here the picture is less clear, however the results did show varying effects of fire and post-fire soil chemical conditions on the selected microbial populations studied. Fire was shown to be a determinant of microorganism population size, especially during summer. In general nutrients were important, particularly during autumn while cooler, wetter winter weather was associated with increased microbial population sizes. This study showed the importance of seasonal monitoring of microorganisms when searching for determinants of population sizes because of the large fluctuations observed and the associated variability in environmental determinants.

The results shown and recommendations made in this study, if correctly applied, will result in improved understanding and management of woody exotic plant invasions and hopefully serve to promote future research in this complex field.

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Appendix A. Species recorded in two 5 x 10 m Braun-Blanquet plots (Werger 1974) during March 2000, one in unburnt fynbos and one in an exotic plant dominated site. Inclusion of the O category expands the effective size to 15 x 7 m. Nomenclature follows Goldblatt and Manning (2000)

Unburnt fynbos plot	**BB value**
Caryophyllaceae	O
Cliffortia sp.	2b
Cymbopogon sp.	+
Danthonia sp.	O
Diosma sp.	O
Diospyros glabra (L.) De Winter	+
Elegia racemosa (Poir.) Pers.	O
Erepsia sp.	R
*Erica viscaria*L.	2a
Erica imbricata L.	+
Erica plukenetii L.	O
Erica sp.	+
Erica sp.	R
Ficinia sp.	R
Hellmuthia sp.	R
Leucadendron salignum P.J. Bergius	O
Leucospermum conocarpodendron (L.) H. Buek.	1
Mastersiella digitata (Thunb.) Gilg-Ben	4
Passerina vulgaris Thoday	R
Pinus pinaster Ait.	+
Phylica sp.	+
Trichocephalus stipularis (L.)	+
Polygalaceae	O
Protea lepidocarpodendron (L.) L.	+
Protea repens (L.) L.	2b
Restio *sp.*	+
Serruria cf. *villosa* (Lam.) R. Br.	R
Staavia radiata (L.) Dahl	+
cf. *Struthiola*	R
Tetraria sp.	+
Thamnochortus sp.	+

Unburnt exotic plant dominated plot	**BB value**
Acacia cyclops A. Cunn. ex G. Don	+
Acacia longifolia (Andrews) Willd.	1
Acacia saligna (Labill.) H.L. Wendl.	+
Anthospermum aethiopicum L.	+
Aristea sp.	R
Osyris compressa (P.J. Bergius)	R
Erica ericoides (L.) E.G.H. Oliv.	+
Hakea suaveolens R. Br.	2
Leptospermum laevigatum (Gaertn) F. Muell.	+
Pinus pinaster Ait.	4
Rhus tomentosa L.	R

Legend

R Rare plants or single individuals.
+ Present but not abundant, cover < 1%.
1 Numerous, but covering less than 1 % of the quadrat area, or not so abundant but covering 1 – 5% of the quadrat area.
2 Very numerous, covering < 5% of the quadrat area, or covering 5 – 25% of the quadrat area, independent of abundance.
2a Covering between 5 and 12% of the quadrat area, independent of abundance.
2b Covering between 13 and 25 % of the quadrat area, independent of abundance.
4 Covering 50 – 75 % of the quadrat area, independent of abundance.
O Those plants falling just outside the 5 x 10 m plot.

Appendix B. Total field counts of regenerating propagules in 1 x 1 and 2 x 2 m field plots from February 2000 to January 2001.

Table B.1 Mean abundance of regenerating propagules in burnt standing exotic field plots per m^2 from February 2000 to January 2001

	Feb-00	Mar-00	Apr-00	May-00	Jun-00	Sep-00	Jan-01
Indigenous seedlings	0	0	0	0	0.35 (0.15)	2.75 (1.43)	4.45 (1.31)
Exotic seedlings	0	0	0.50 (0.25)	1.05 (0.76)	3.45 (1.67)	35.25 (8.11)	31.60 (8.33)
Exotic resprouters	0	0	0	0	0	0	0
Tussocks	0	0	0	0	0	0	0
Geophytes	0	0	0	0	0.05 (0.05)	0	0
Herbaceous resprouters	0	0	0.15 (0.08)	0.10 (0.07)	0.10 (0.07)	0.15 (0.08)	0.15 (0.08)
Ind. woody resprouters	0.10 (0.07)	0.10 (0.07)	0.10 (0.07)	0.15 (0.08)	0.15 (0.08)	0.15 (0.08)	0.15 (0.08)
Total abundance	0.10 (0.07)	0.10 (0.07)	0.75 (0.40)	1.30 (0.91)	4.10 (2.02)	38.3 (9.70)	36.35 (9.80)

Table B.2 Mean abundance of regenerating propagules in burnt fynbos field plots per m^2 from Feb 2000 to Jan 2001

	Feb-00	Mar-00	Apr-00	May-00	Jun-00	Sep-00	Jan-01
Indigenous seedlings	0.70 (0.42)	2.50 (2.08)	1.75 (0.80)	7.90 (3.30)	25.94 (7.89)	131.61 (17.78)	37.25 (5.63)
Exotic seedlings	0	0.05 (0.05)	0.25 (0.20)	0.25 (0.20)	0.81 (0.42)	2.28 (0.87)	2.20 (0.89)
Exotic resprouters	0	0	0	0	0	0	0
Tussocks	4.10 (2.37)	2.45 (0.79)	8.05 (6.25)	4.05 (2.16)	5.25 (2.83)	38.11 (8.07)	33.90 (9.17)
Geophytes	0.15 (0.11)	1.20 (0.56)	2.65 (0.84)	9.55 (4.91)	26.25 (13.40)	36.61(10.72)	3.95 (3.28)
Herbaceous resprouters	2.35 (0.74)	4.35 (1.20)	4.35 (0.95)	4.55 (0.94)	5.25 (1.14)	6.11 (1.63)	6.60 (1.44)
Ind. woody resprouters	0.10 (0.07)	0.55 (0.20)	0.70 (0.24)	1.40 (0.62)	1.75 (0.76)	1.78 (0.92)	1.35 (0.63)
Total abundance	7.40 (3.71)	11.10 (4.88)	17.75 (9.28)	27.70 (12.13)	65.25 (26.44)	216.50 (39.99)	85.25 (21.04)

Table B.3 Mean species richness/m^2 of regenerating propagules in burnt fynbos field plots from February 2000 to January 2001

	Feb-00	Mar-00	Apr-00	May-00	Jun-00	Sep-00	Jan-01
Indigenous seedlings	0.20 (0.09)	0.10 (0.07)	0.50 (0.15)	3.40 (0.99)	2.69 (0.34)	12.06 (0.55)	7.55 (0.55)
Exotic seedlings	0	0.05 (0.05)	0.10 (0.70)	0.10 (0.70)	0.31 (0.12)	0.61 (0.14)	0.80 (0.12)
Exotic resprouters	0	0	0	0	0	0	0
Tussocks	0.50 (0.14)	0.40 (0.11)	0.20 (0.09)	0.35 (0.11)	0.56 (0.16)	2.83 (0.36)	2.80 (0.34)
Geophytes	0.10 (0.07)	0.50 (0.14)	0.95 (0.21)	1.70 (0.26)	2.75 (0.37)	3.56 (0.41)	0.55 (0.19)
Herbaceous resprouters	0.50 (0.12)	0.80 (0.09)	0.90 (0.07)	0.90 (0.07)	0.88 (0.09)	0.94 (0.10)	0.90 (0.07)
Ind. woody resprouters	0.10 (0.07)	0.40 (0.13)	0.40 (0.11)	0.65 (0.21)	0.75 (0.25)	0.56 (0.19)	0.50 (0.15)
Total species richness	1.40 (0.49)	2.25 (0.59)	3.05 (1.33)	7.10 (2.34)	7.94 (1.33)	20.56 (1.75)	13.10 (1.42)

Table B.4 Mean species richness/m^2 of regenerating propagules in burnt standing exotic field plots from February 2000 to January 2001

	Feb-00	Mar-00	Apr-00	May-00	Jun-00	Sep-00	Jan-01
Indigenous seedlings	0	0	0	0	0.30 (0.13)	1.05 (0.29)	1.37 (0.17)
Exotic seedlings	0	0	0.20 (0.09)	0.30 (0.15)	0.70 (0.21)	1.95 (0.17)	1.79 (0.16)
Exotic resprouters	0	0	0	0	0	0	0
Tussocks	0	0	0	0	0	0	0
Geophytes	0	0	0	0	0.05 (0.05)	0	0
Herbaceous resprouters	0	0	0.15 (0.08)	0.10 (0.07)	0.10 (0.07)	0.15 (0.08)	0.16 (0.08)
Ind. woody resprouters	0.10 (0.07)	0.10 (0.07)	0.10 (0.07)	0.15 (0.08)	0.15 (0.08)	0.15 (0.08)	0.16 (0.08)
Total species richness	0.10 (0.07)	0.10 (0.07)	0.45 (0.24)	0.55 (0.30)	1.30 (0.54)	3.30 (0.62)	3.48 (0.49)

Table B.5 Mean abundance of regenerating propagules in $2m^2$ burnt cleared area and wildfire burnt stack field plots from April 2000 to January 2001.

Burnt cleared	Apr-00	Sep-00	Jan-01
Indigenous seedlings	9.00 (3.54)	337.00 (58.34)	234.40 (71.17)
Exotic seedlings	12.40 (2.16)	187.80 (52.98)	88.20 (12.48)
Exotic resprouters	4.20 (1.46)	4.20 (1.46)	4.20 (1.46)
Tussocks	6.00 (2.51)	103.20 (27.88)	77.60 (28.20)
Geophytes	6.00 (3.70)	32.60 (14.13)	3.20 (1.24)
Ind. herbaceous resprouters	6.00 (6.00)	6.00 (6.00)	6.00 (6.00)
Ind. woody resprouters	0.60 (0.25)	1.00 (0.78)	0.20 (0.20)
Total abundance	44.20 (19.62)	671.80 (161.57)	413.80 (120.75)
Wildfire burnt stacks	Apr-00	Sep-00	Jan-01
Indigenous Seedlings	0.40 (0.40)	6.60 (1.19)	5.40 (2.32)
Exotic seedlings	0	7.60 (6.34)	6.20 (4.28)
Exotic resprouters	0	0	0
Tussocks	0	0.20 (0.20)	0
Geophytes	0	0.60 (0.40)	0.60 (0.40)
Ind. herbaceous resprouters	0.60 (0.40)	0.60 (0.40)	0
Ind. woody resprouters	0.60 (0.40)	0.60 (0.40)	0
Total abundance	1.60 (1.60)	16.20 (8.93)	12.20 (7.00)

Appendix C. Additional MDS's and dendrograms in 1 x 1 and 2 x 2 m field plots during 2000 and 2001 indicating differences in above-ground vegetation regeneration between treatments

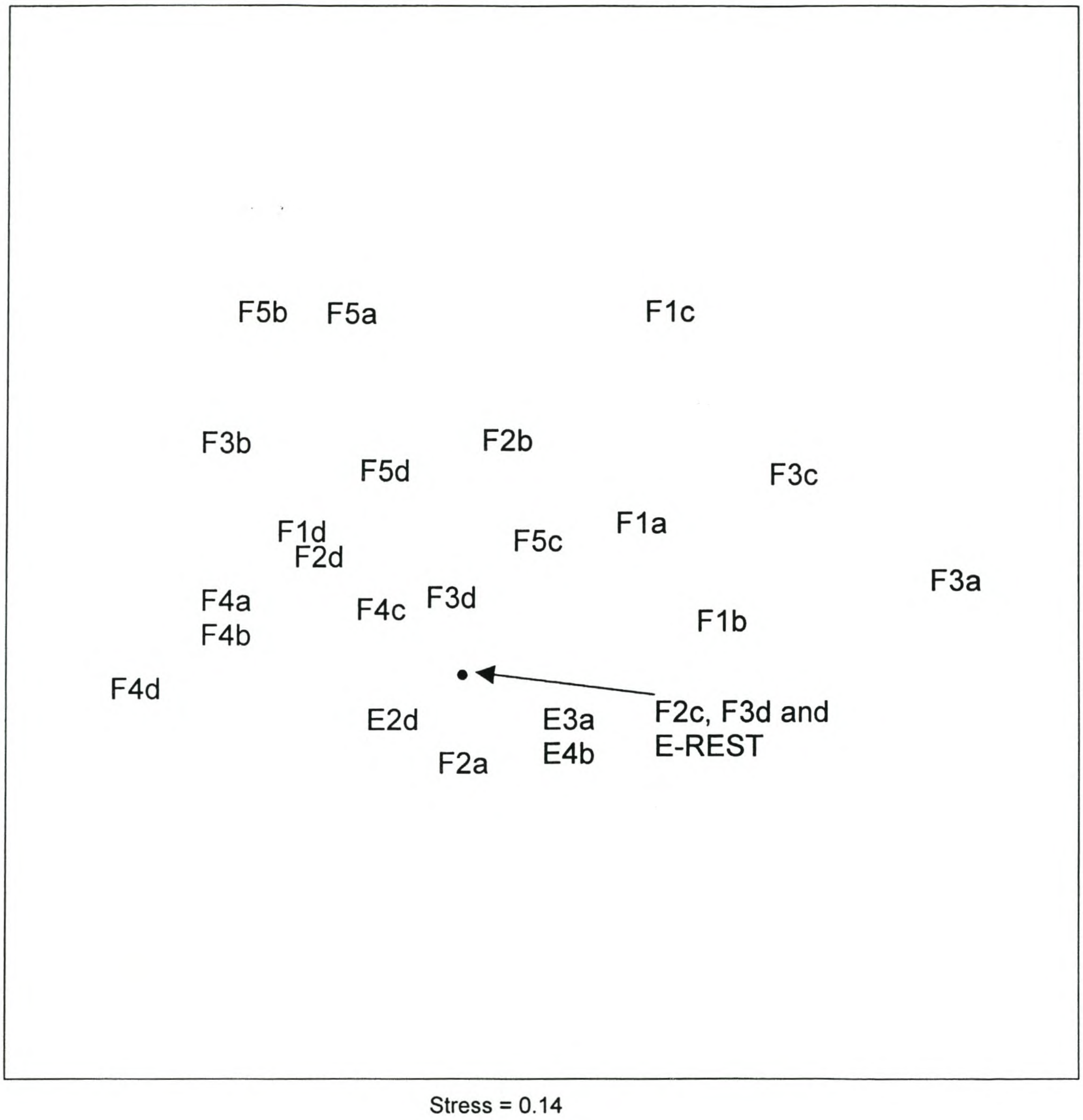


Figure C.1 Multidimensional scaling diagram (Clarke and Warwick 1994) indicating differences in regeneration of above-ground vegetation in 1 x 1 m field plots in February 2000, 1 month after an extensive wildfire on the Cape Peninsula

E = wildfire burnt standing exotics; F = wildfire burnt fynbos
Numbers indicate replicates; a – d = 1 x 1 m sub-plots
E-REST = all other wildfire burnt standing exotic plots

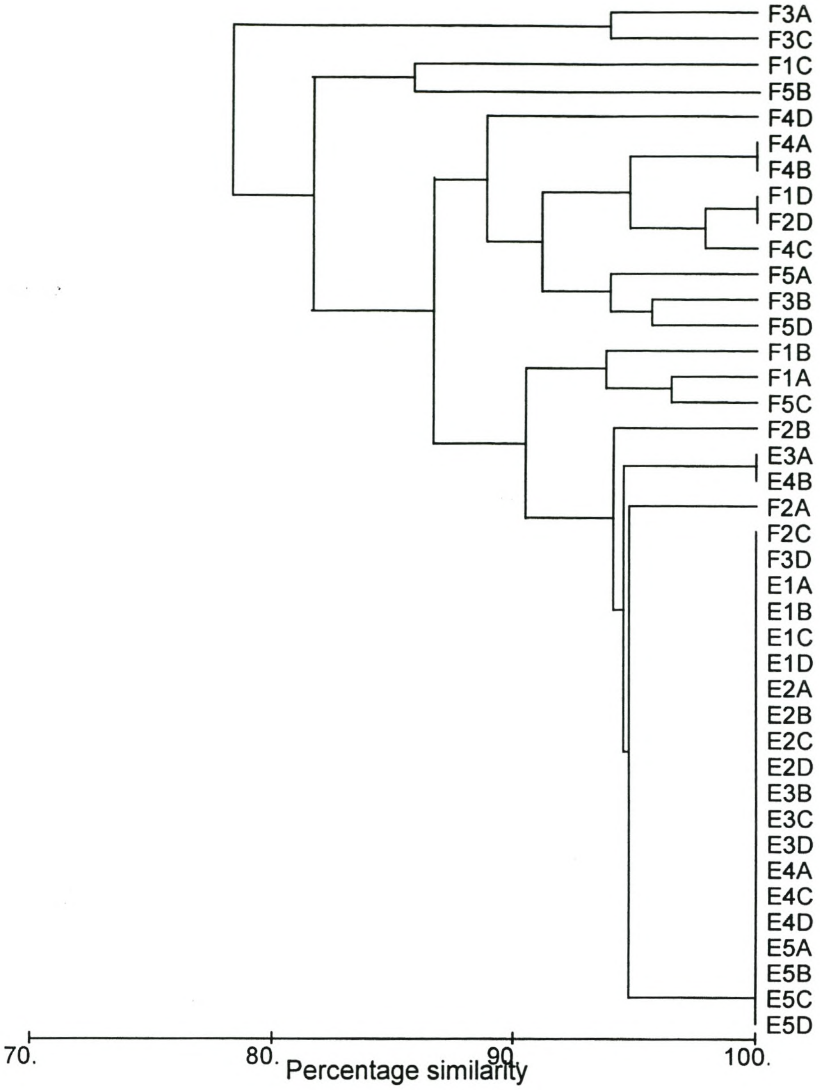
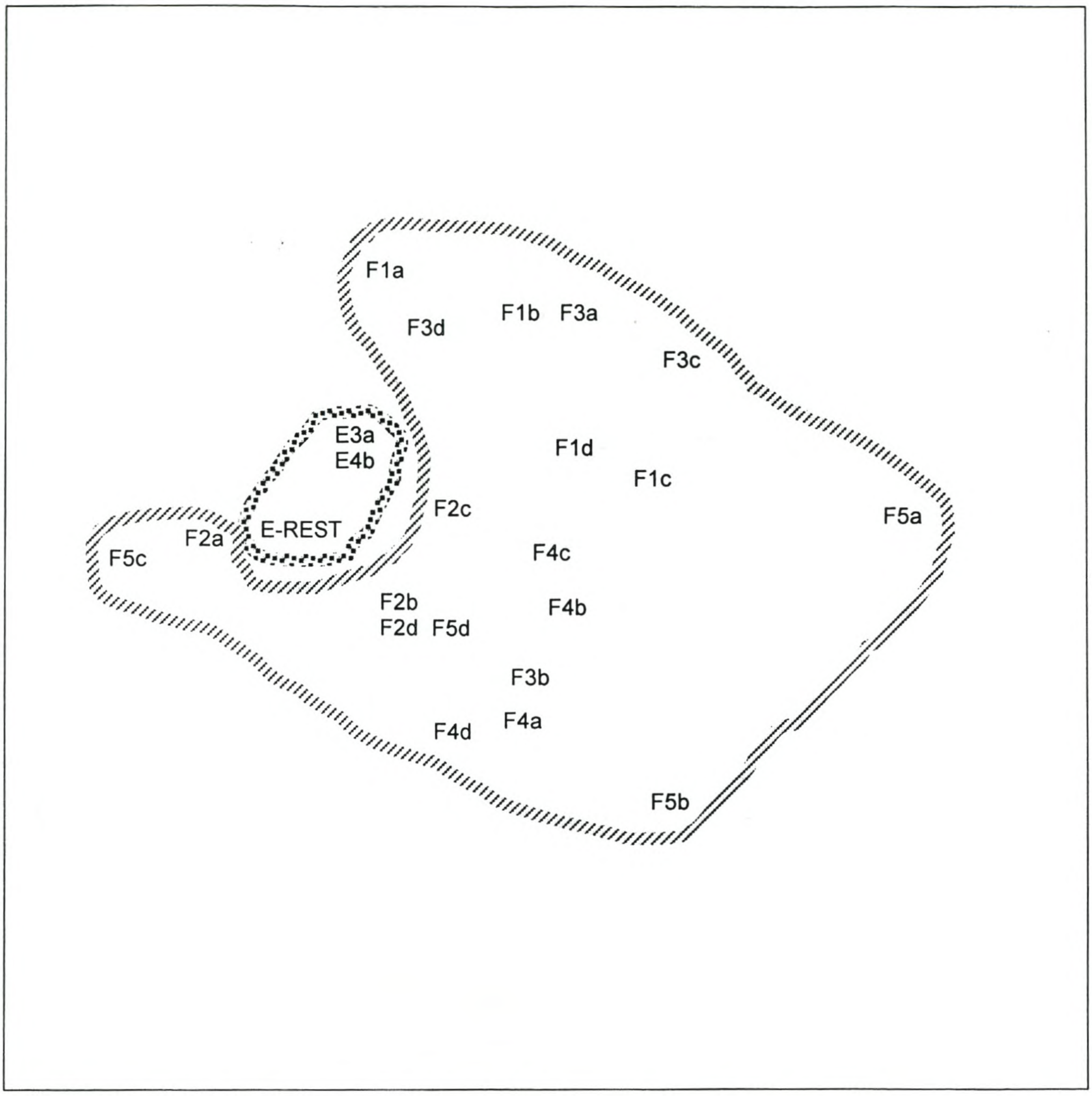


Figure C.2 Dendrogram depicting Bray-Curtis Similarities between 1 x 1 m post wildfire field plots in February 2000 (Clarke and Warwick 1994)

Fynbos = wildfire burnt fynbos
Exotic = wildfire burnt standing exotics
Numbers indicate replicates; A – D = 1 x 1 m sub - plots



Stress = 0.13

Figure C.3 Multidimensional scaling diagram (Clarke and Warwick 1994) indicating differences in regeneration of above-ground vegetation in 1 x 1 m field plots in March 2000, 2 months after an extensive wildfire on the Cape Peninsula

E =wildfire burnt standing exotics; F = wildfire burnt fynbos
Numbers indicate replicates; a – d = 1 x 1 m sub-plots
E-REST = all other wildfire burnt standing exotic plots

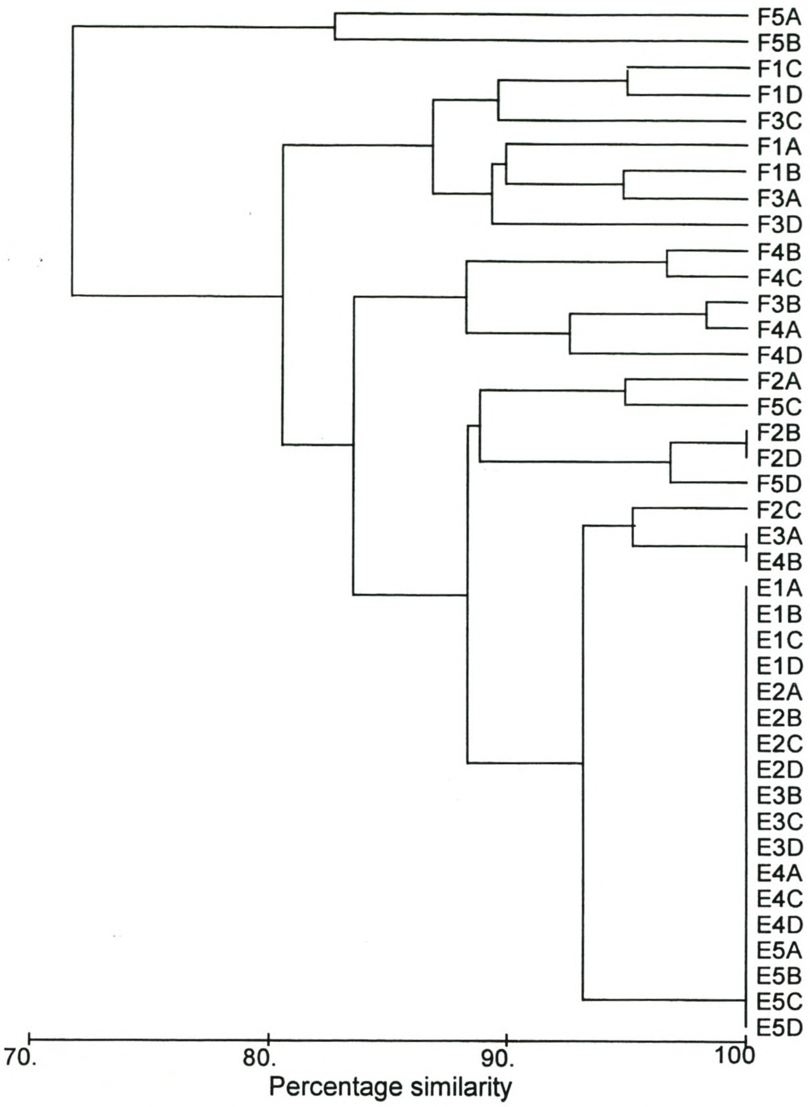


Figure C.4 Dendrogram depicting Bray-Curtis Similarities between 1 x 1 m post wildfire field plots in March 2000 (Clarke and Warwick 1994)

F = wildfire burnt fynbos
E = wildfire burnt standing exotics
Numbers indicate replicates; A – D = 1 x 1 m sub - plots

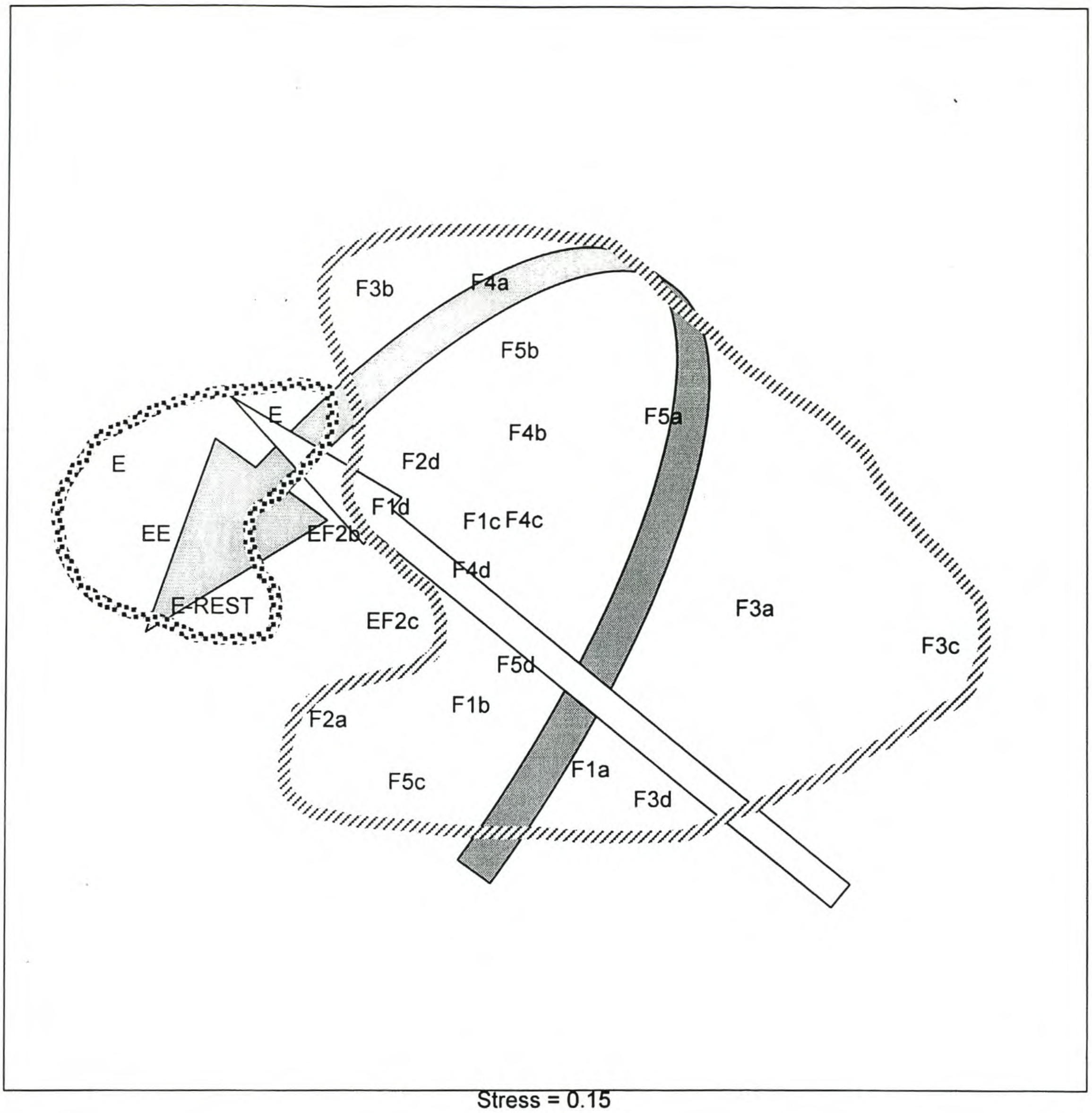


Figure C.5 Multidimensional scaling diagram (Clarke and Warwick 1994) indicating differences in regeneration of above-ground vegetation in 1 x 1 m field plots in April 2000, 3 months after an extensive wildfire on the Cape Peninsula

F = wildfire burnt fynbos; E = wildfire burnt standing exotics
Numbers indicate replicates; a – d = 1 x 1 m sub-plots
E-REST = all other wildfire burnt standing exotic plots
Grey arrow = increasing fire intensity
White arrow = increasing number of exotic propagules

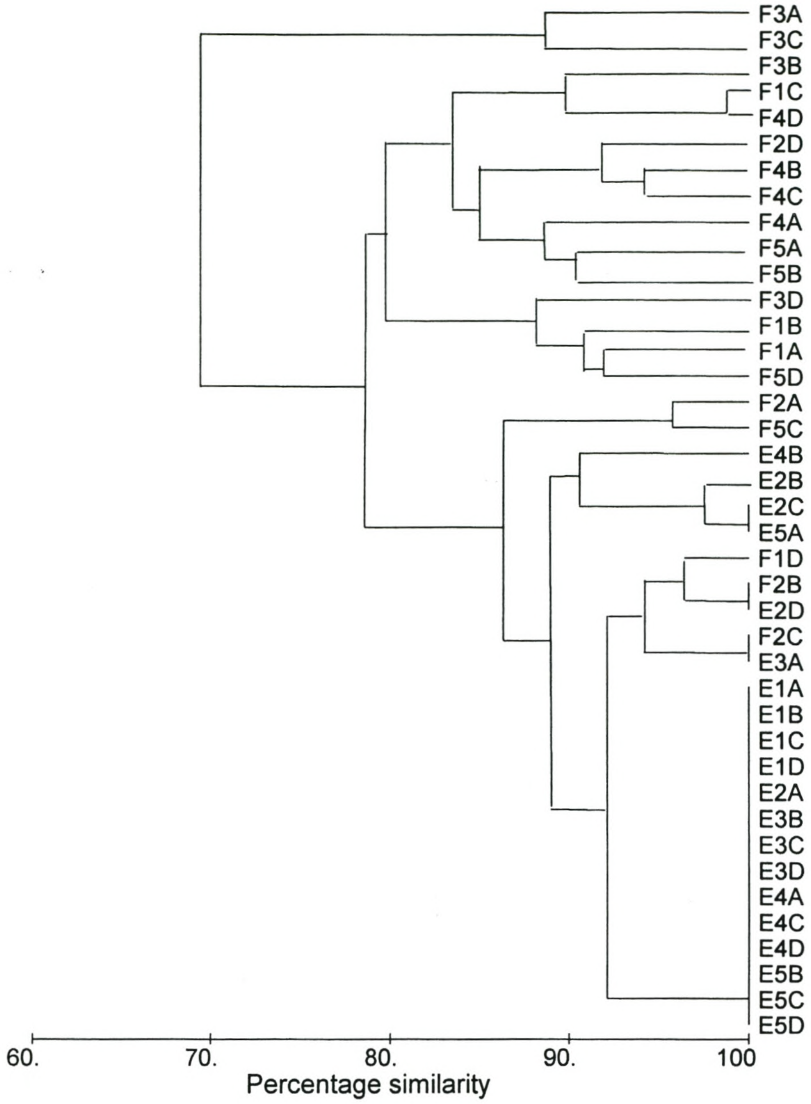
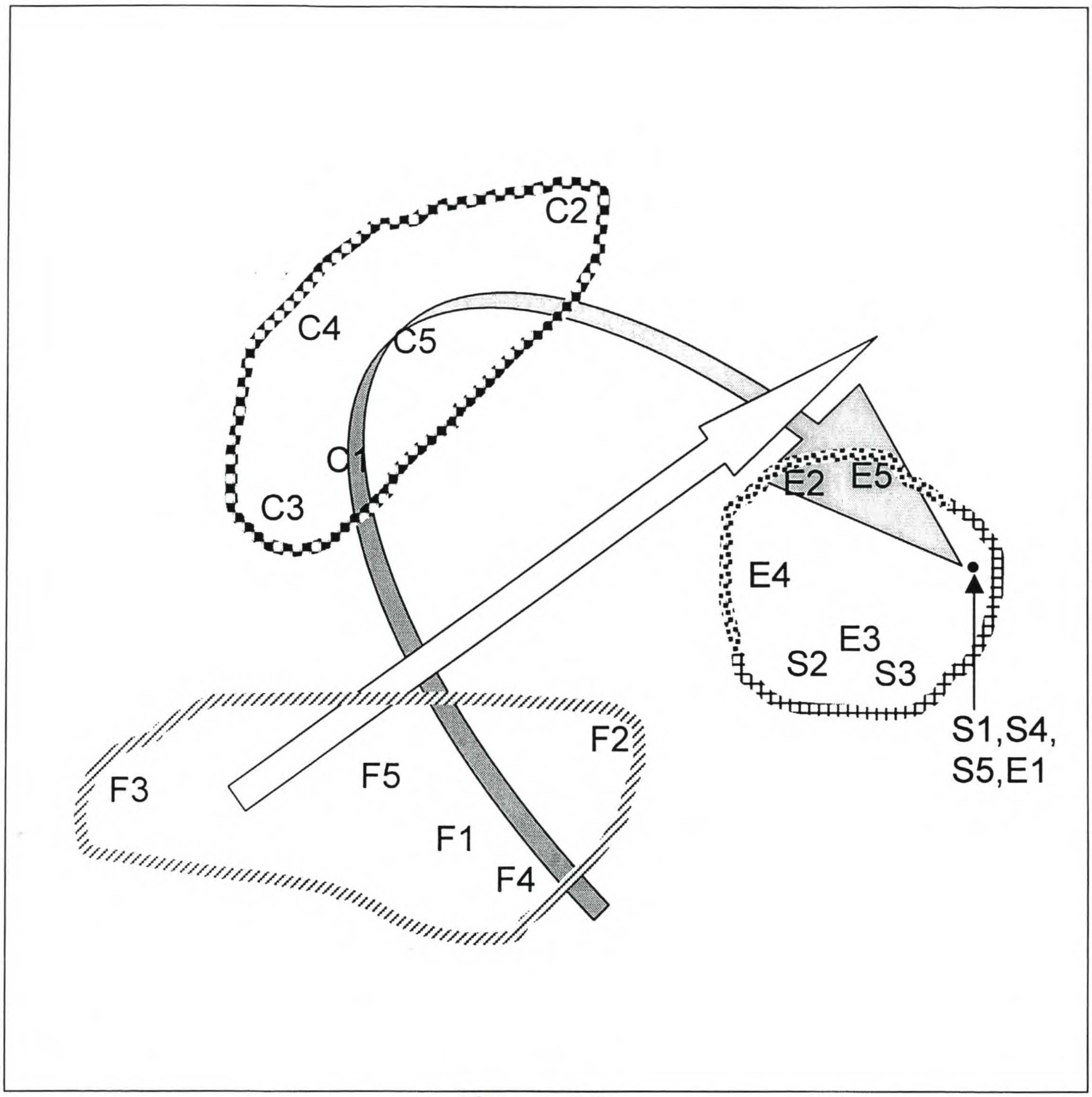


Figure C.6 Dendrogram depicting Bray-Curtis Similarities between 1 x 1 m post wildfire field plots in April 2000 (Clarke and Warwick 1994)

F = wildfire burnt fynbos
E = wildfire burnt standing exotics
Numbers indicate replicates; A – D = 1 x 1 m sub - plots



Stress = 0.09

Figure C.7 Multidimensional scaling diagram (Clarke and Warwick 1994) indicating differences in regeneration of above-ground vegetation in 2 x 2 m field plots in April 2000, 3 months after an extensive wildfire on the Cape Peninsula

F = wildfire burnt fynbos; C = wildfire burnt cleared areas
E = wildfire burnt standing exotics
S = wildfire burnt stacks; Numbers indicate replicates
E-REST = all other wildfire burnt standing exotic plots
Grey arrow = increasing fire intensity
White arrow = increasing number of exotic propagules

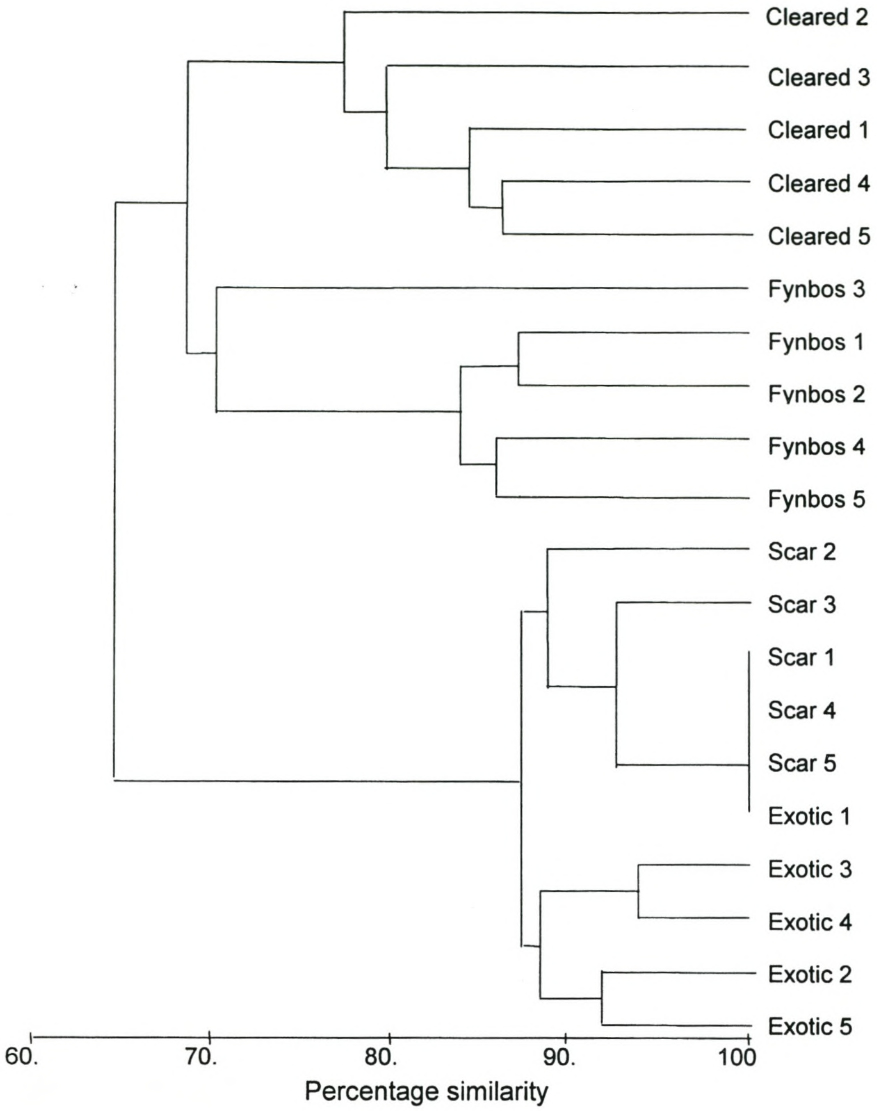


Figure C.8 Dendrogram depicting Bray-Curtis Similarities between 2 x 2 m post wildfire field plots in April 2000 (Clarke and Warwick 1994)

Fynbos = wildfire burnt fynbos; Cleared = wildfire burnt cleared
Exotic = wildfire burnt standing exotics; Scar = wildfire burnt stacks
Numbers indicate replicates; A – D = 1 x 1 m sub - plots

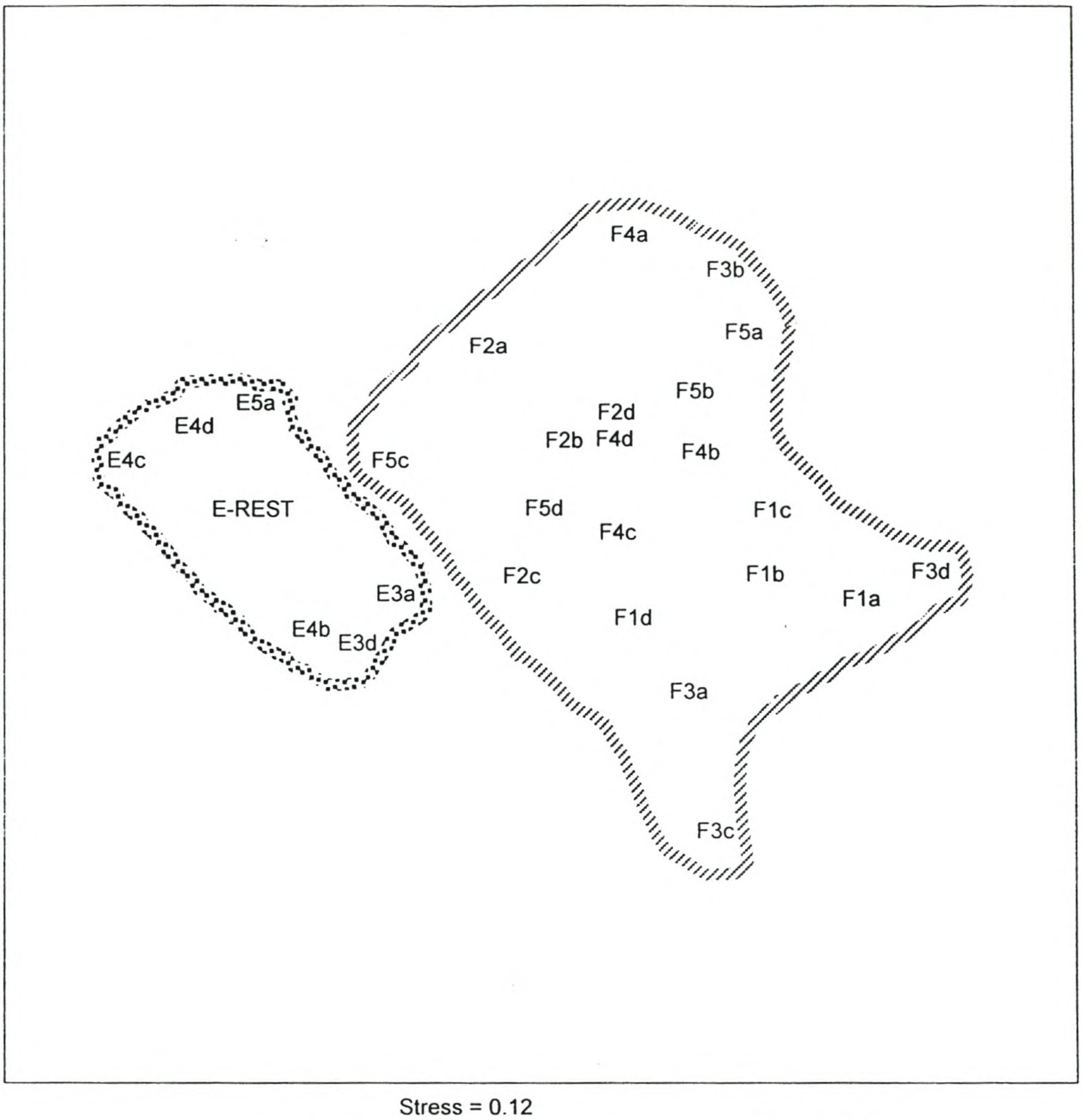


Figure C.9 Multidimensional scaling diagram (Clarke and Warwick 1994) indicating differences in regeneration of above-ground vegetation in 1 x 1 m field plots in May 2000, 4 months after an extensive wildfire on the Cape Peninsula

F = wildfire burnt fynbos
E = wildfire burnt standing exotics
Numbers indicate replicates; a – d = 1 x 1 m sub - plots
E-REST = all other wildfire burnt standing exotic plots

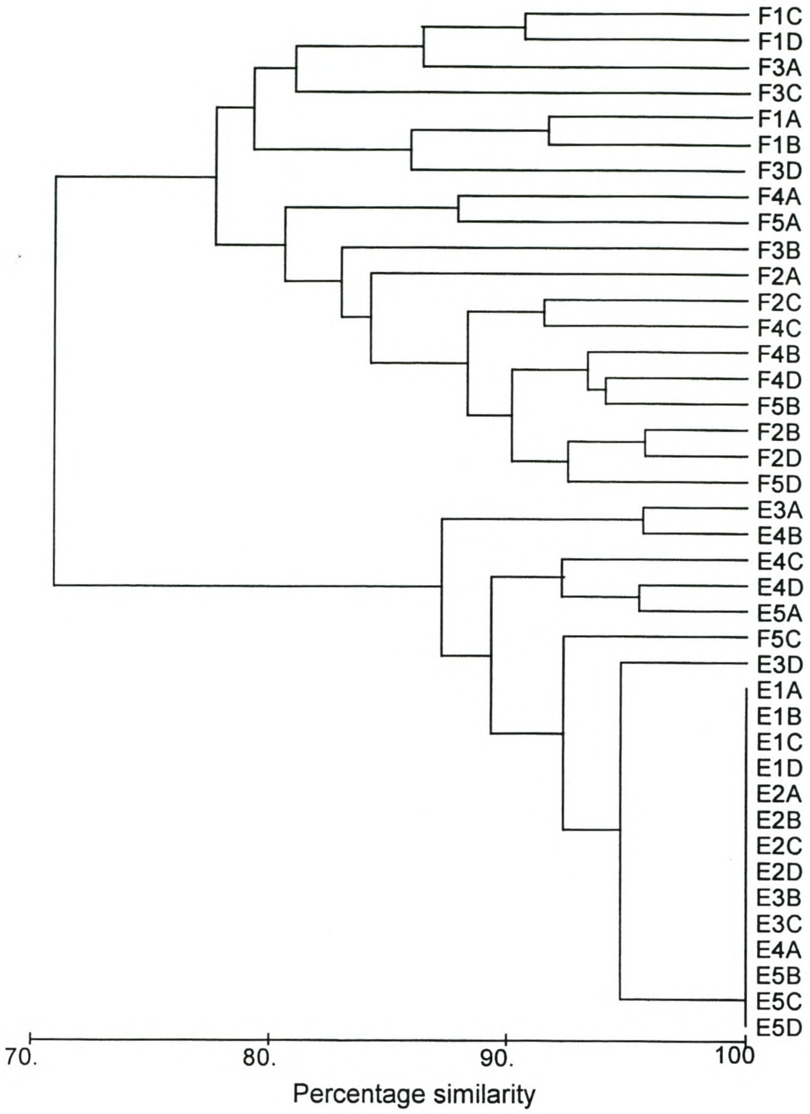


Figure C.10 Dendrogram depicting Bray-Curtis Similarities between 1 x 1 m post wildfire field plots in May 2000 (Clarke and Warwick 1994)

F = wildfire burnt fynbos
E = wildfire burnt standing exotics
Numbers indicate replicates; A – D = 1 x 1 m sub - plots

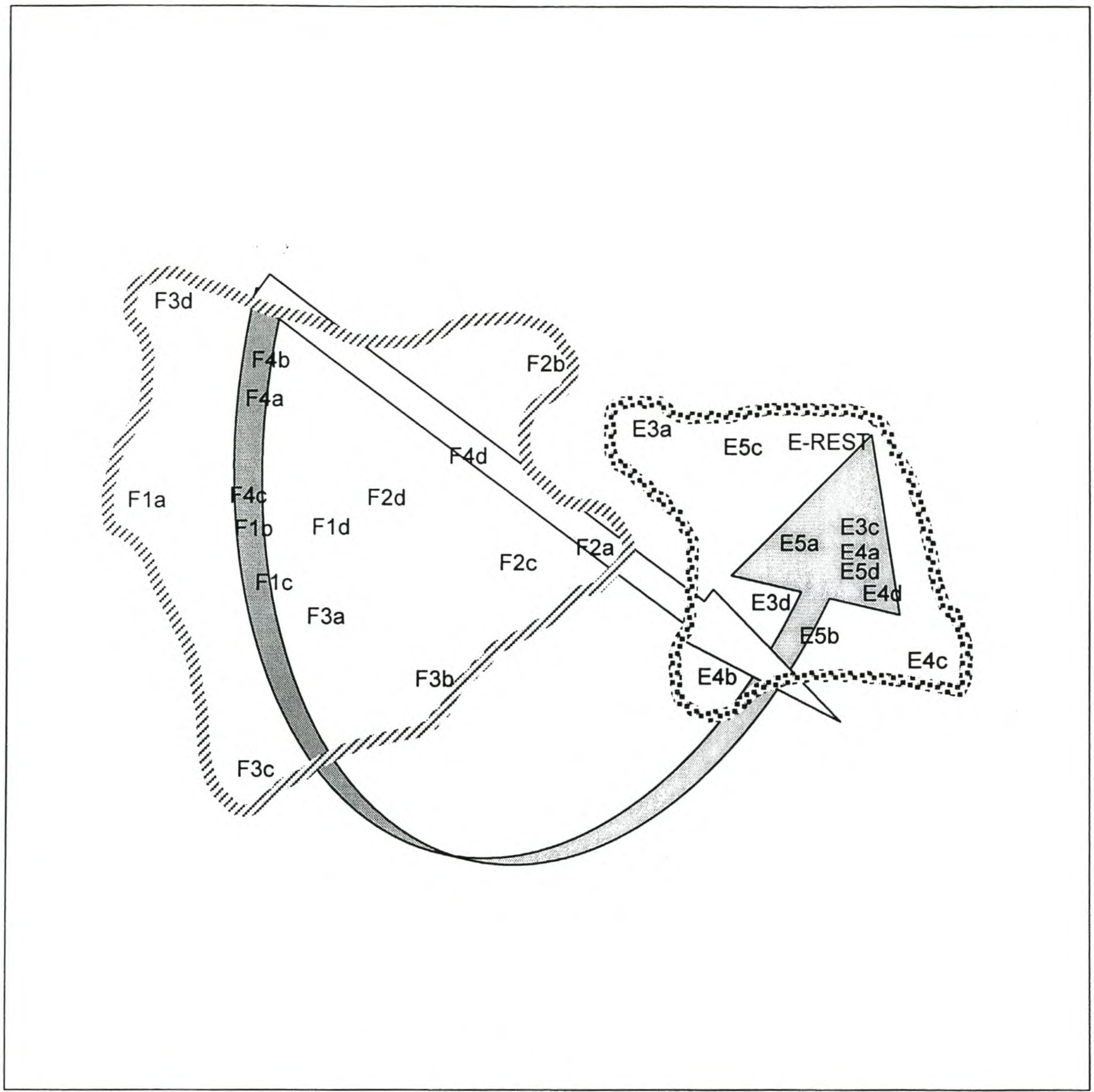


Figure C.11 Multidimensional scaling diagram (Clarke and Warwick 1994) indicating differences in regeneration of above-ground vegetation in 1 x 1 m field plots in June 2000, 5 months after an extensive wildfire on the Cape Peninsula

F = wildfire burnt fynbos
E = wildfire burnt standing exotics
Numbers indicate replicates; a – d = 1 x 1 m sub-plots
E-REST = all other wildfire burnt standing exotic plots

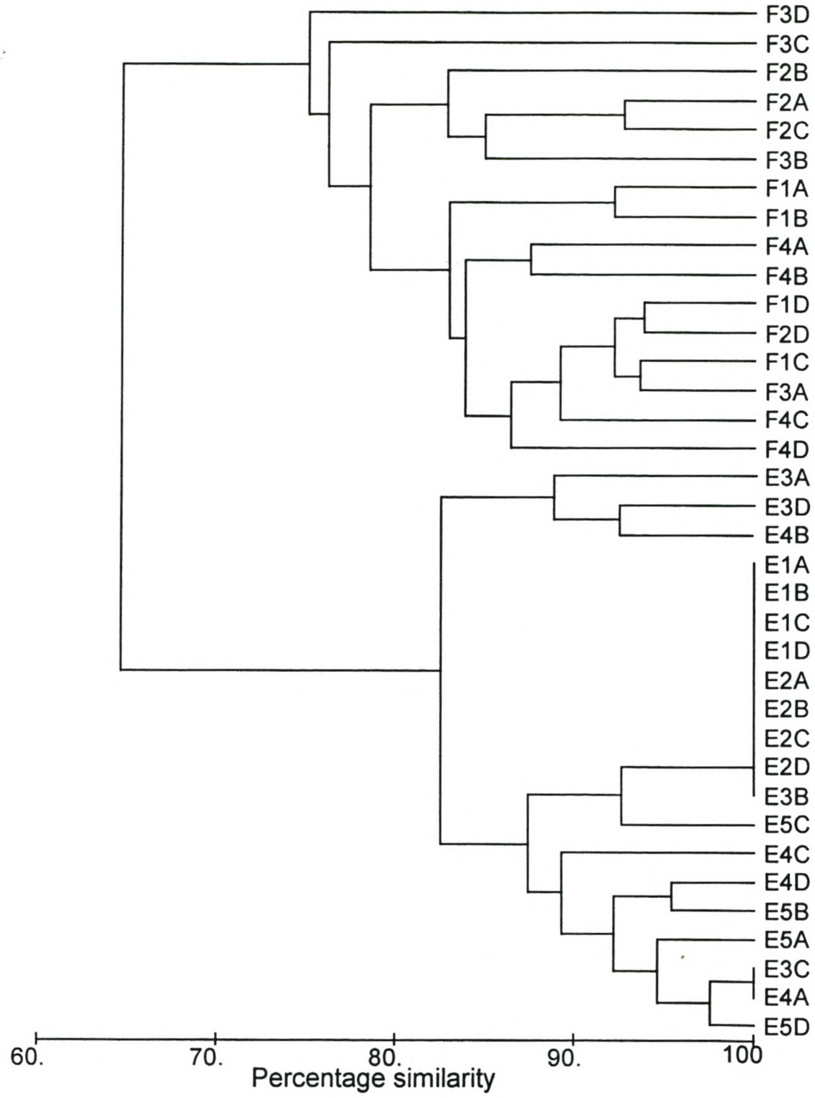


Figure C.12 Dendrogram depicting Bray-Curtis Similarities between 1 x 1 m post wildfire field plots in June 2000 (Clarke and Warwick 1994)

F = wildfire burnt fynbos
E = wildfire burnt standing exotics
Numbers indicate replicates; A – D = 1 x 1 m sub - plots

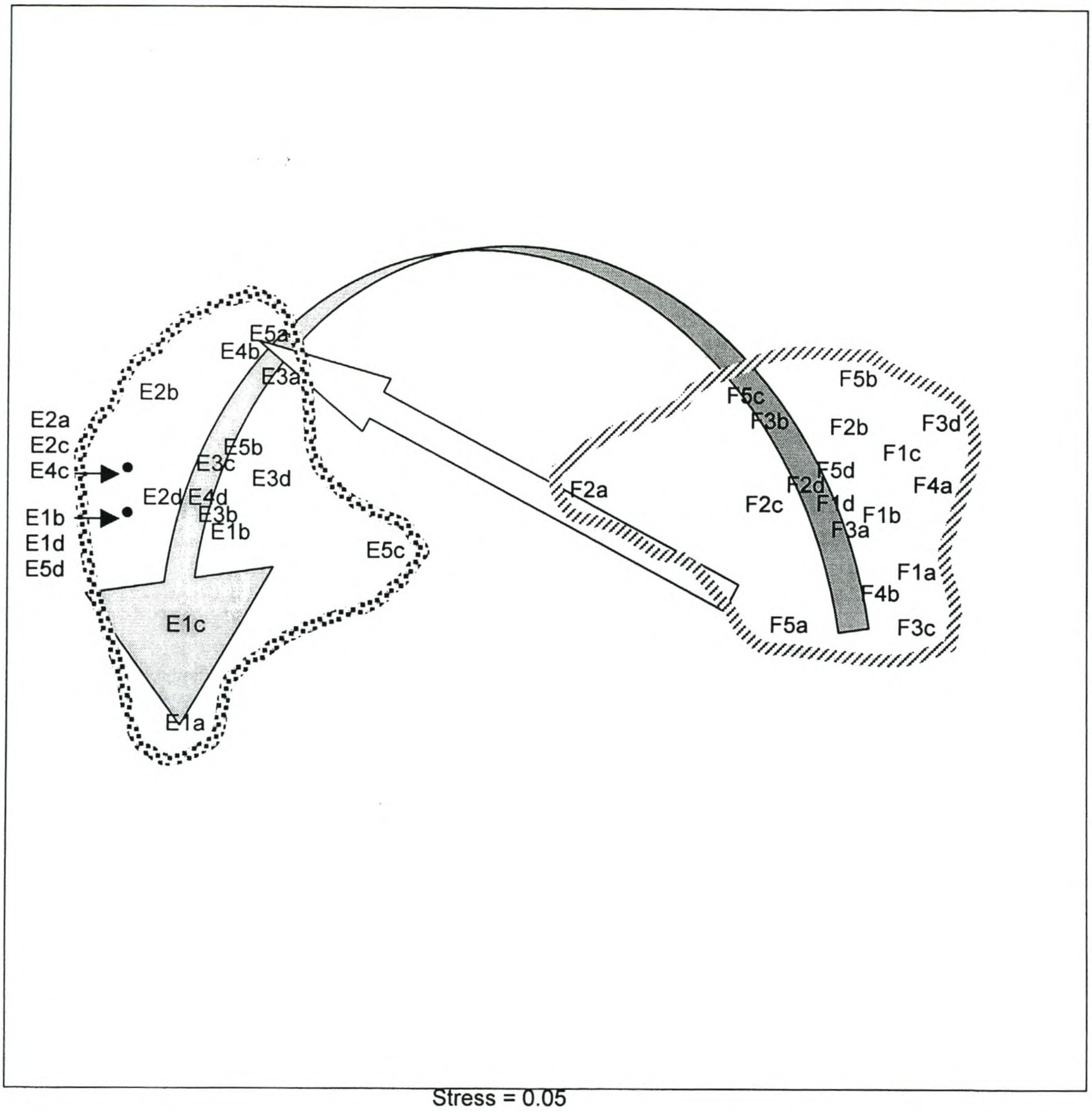


Figure C.13 Multidimensional scaling diagram (Clarke and Warwick 1994) indicating differences in regeneration of above-ground vegetation in 1 x 1 m field plots in September 2000, 8 months after an extensive wildfire on the Cape Peninsula

F = wildfire burnt fynbos
E = wildfire burnt standing exotics
Numbers indicate replicates; a – d = 1 x 1 m sub-plots

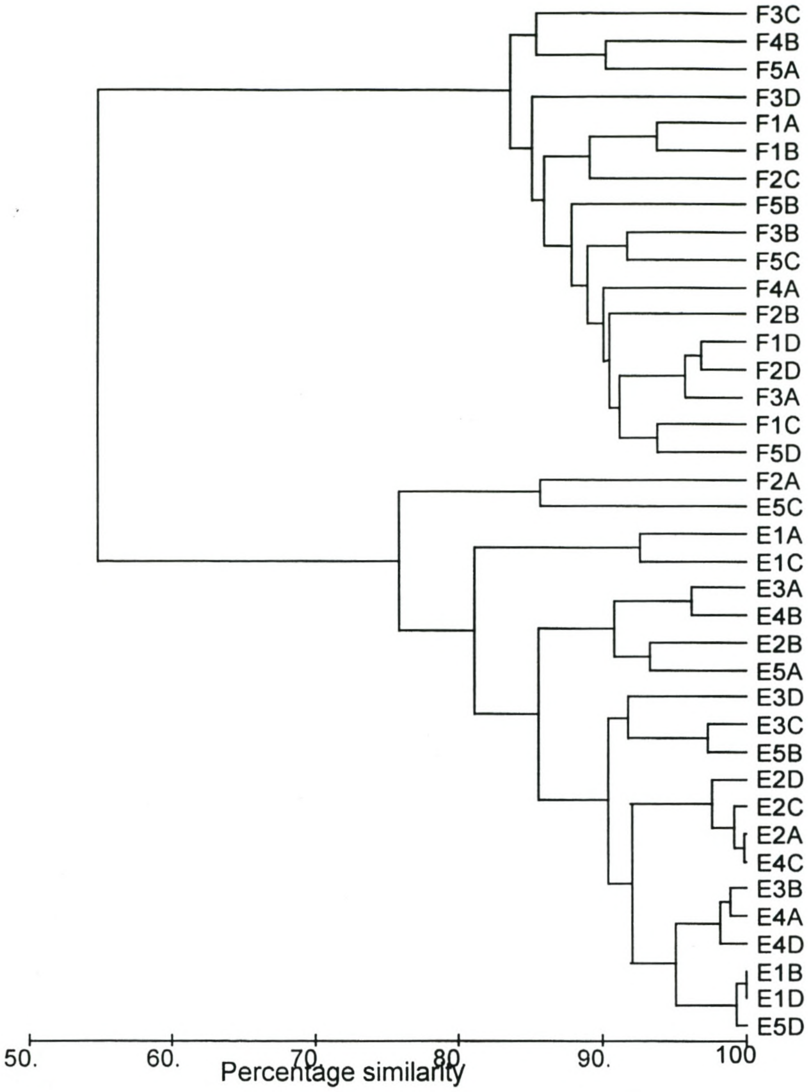


Figure C.14 Dendrogram depicting Bray-Curtis Similarities between 2 x 2 m post wildfire field plots in September 2000 (Clarke and Warwick 1994)

F = wildfire burnt fynbos
E = wildfire burnt standing exotics
Numbers indicate replicates; A – D = 1 x 1 m sub - plots

Appendix D. Additional field results

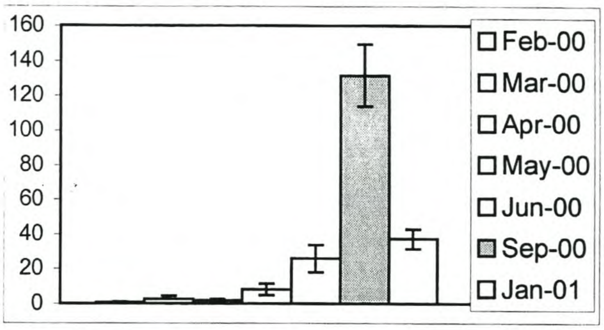


Figure D.1 Monthly counts of indigenous seedlings per m^2 in burnt fynbos plots.
Error bars = standard errors of the means
Y axis = number of individuals. X axis = months.

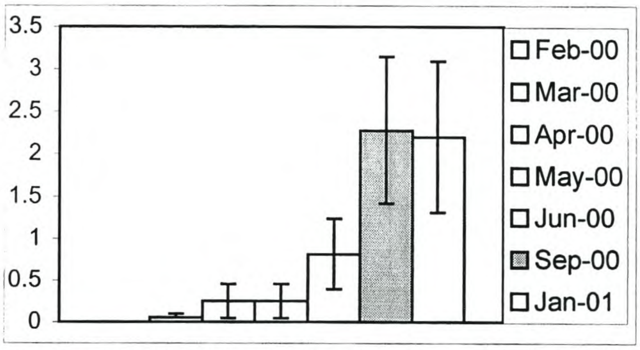


Figure D.2 Monthly counts of exotic seedlings per m^2 in burnt fynbos plots.
Error bars = standard errors of the means.
Y axis = number of individuals. X axis = months

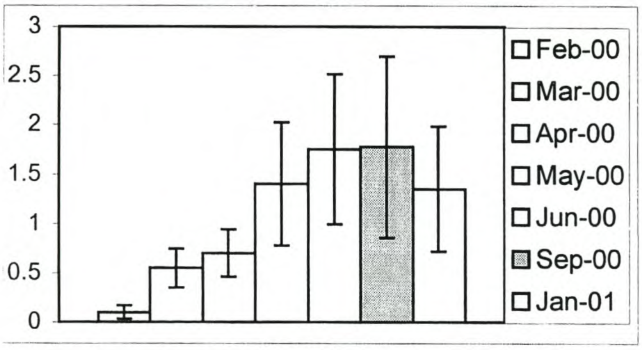


Figure D.3 Monthly counts of indigenous woody resprouters per m^2 in burnt fynbos plots.
Error bars = standard errors of the means.
Y axis = number of individuals. X axis = months

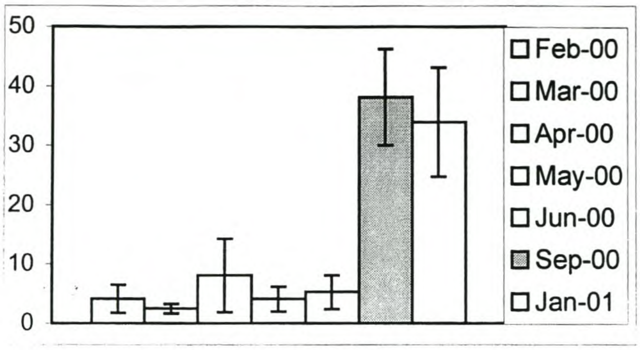


Figure D.4 Monthly counts of tussocks (hemicryptophytes) per m^2 in burnt fynbos plots.
Error bars = standard errors of the means.
Y axis = number of individuals. X axis = months

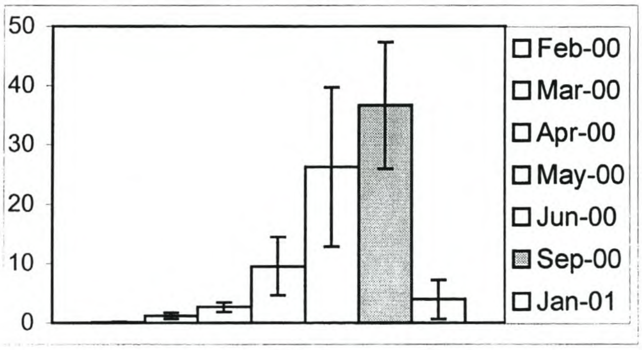


Figure D.5 Monthly counts of geophytes per m^2 in burnt fynbos plots.
Error bars = standard errors of the means.
Y axis = number of individuals. X axis = months.

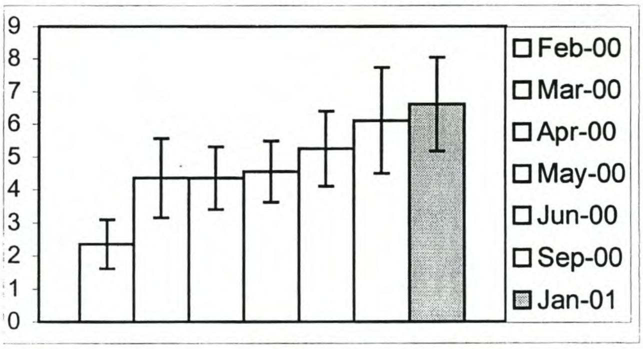


Figure D.6 Monthly counts of indigenous herbaceous resprouters per m^2 in burnt fynbos plots.
Error bars = standard errors of the means.
Y axis = number of individuals. X axis = months

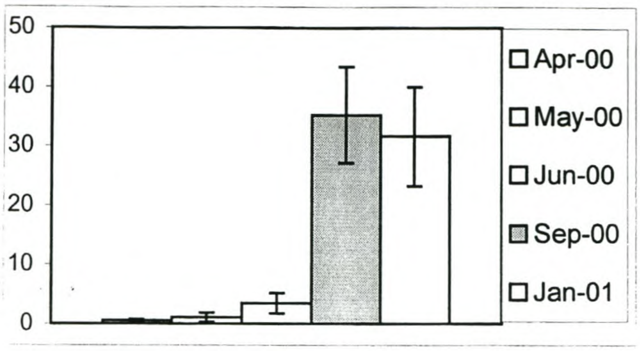


Figure D.7 Monthly counts of exotic seedlings per m^2 in burnt standing exotic plots.
Error bars = standard errors of the means.
Y axis = number of individuals. X axis = months

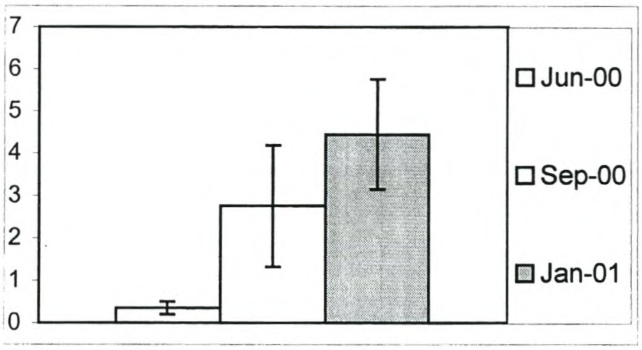


Figure D.8 Monthly counts of indigenous seedlings per m^2 in burnt standing exotic plots.
Error bars = standard errors of the means.
Y axis = number of individuals. X axis = months.

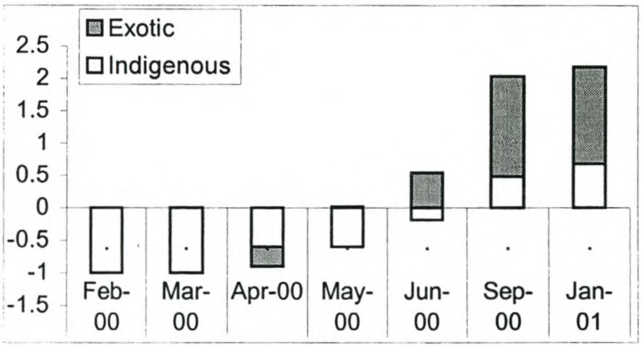


Figure D.9 Log$_{10}$ Exotic/Indigenous propagules/m^2 in burnt standing exotic plots

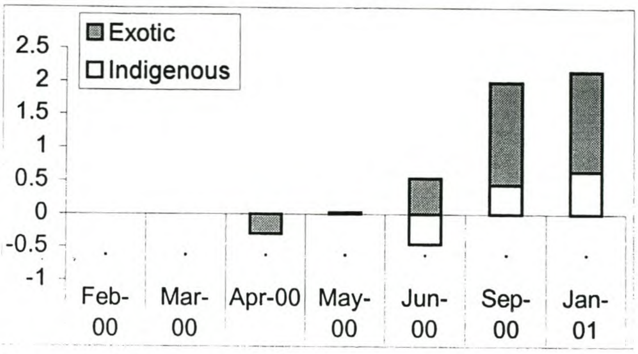


Figure D.10 Log$_{10}$ Exotic/indigenous seedlings/m^2 in burnt standing exotic plots

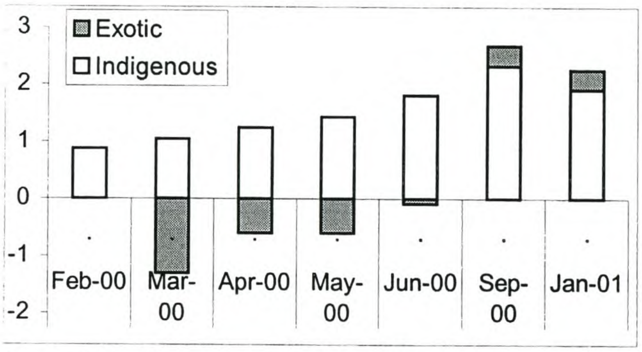


Figure D.11 Log$_{10}$ Exotic/Indigenous propagules/m^2 in burnt fynbos plots

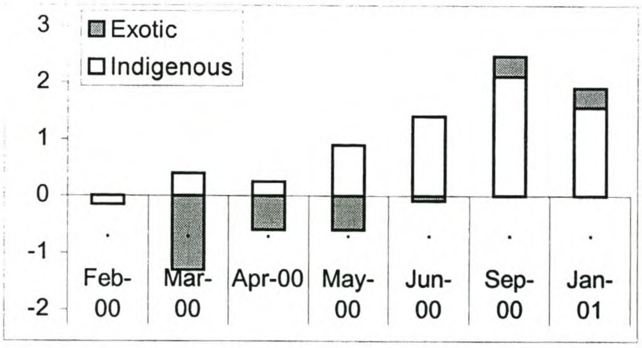


Figure D.12 Log$_{10}$ Exotic/Indigenous seedlings/m^2 in burnt fynbos plots

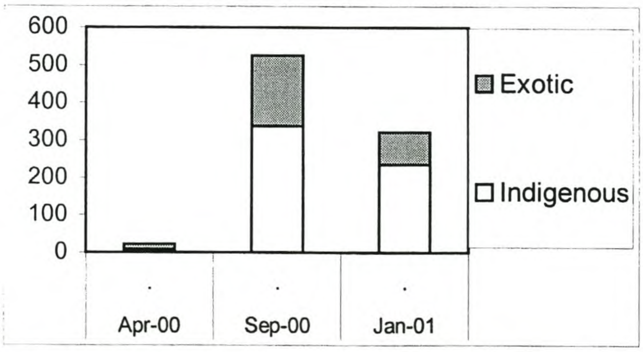


Figure D.13 Exotic/Indigenous seedling ratio in 2 x 2 m burnt cleared area plots

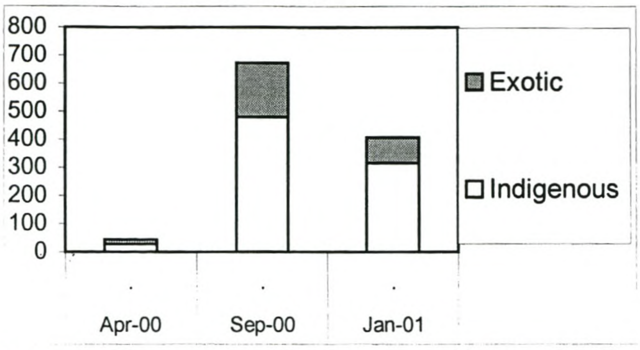


Figure D.14 Exotic/Indigenous propagule ratio in 2 x 2 m burnt cleared area plots

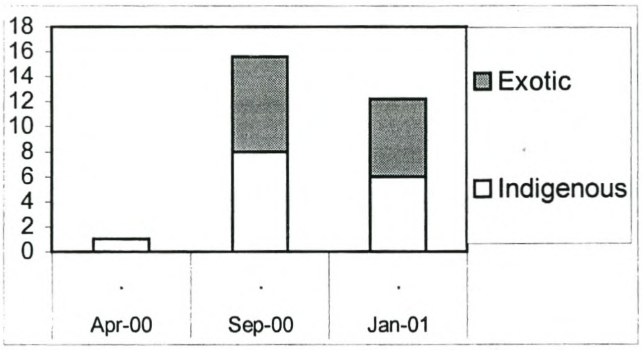


Figure D.15 Exotic/Indigenous propagule ratio in 2 x 2 m wildfire burnt stack plots

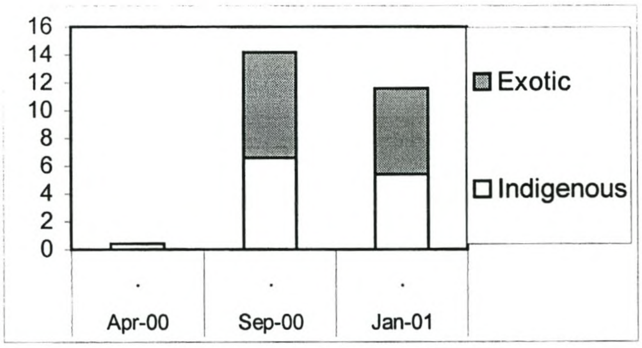


Figure D.16 Exotic/Indigenous seedling ratio in 2 x 2 m wildfire burnt stack plots

Appendix E. List of seedling species identified in the nursery germination trial. Nomenclature follows Goldblatt and Manning (2000)

Table E.1 Total list of species identified in the nursery germination trial. Presence in a treatment is denoted by *

Plant name	Specimen number	Wildfire burnt fynbos	Wildfire burnt standing exotics	Wildfire burnt cleared	Wildfire burnt stacks
Isolepsis incomptula Nees	1	*	*	*	
Isolepsis prolifer R.Br.	2	*			
Crassula natans var. *natans* Thunb.	3	*		*	
Wahlenbergia exilis A.DC.	4	*			
Lepidium pinnatum var. *natans* Thunb.	5				*
Phyllopodium cordatum (Thunb.) Hillard	6	*		*	
Crassula umbellata Thunb.	7	*			
Crassula thunbergiana Schult. Subsp. *thunbergiana*	8	*			
Cerastium capense Sond.	9	*	*		
Lepidium sp.	10	*			
Polycarpon tetraphyllum L.f	11	*	*		
Wahlenbergia cernua (Thunb.) A.DC.	12	*			
Polygonum aviculare L.	13		*		
Pseudognaphalium undulatum (L.) Hillard & B.L. Burtt	14	*			
Erepsia anceps (Haw.) Schwantes	15	*		*	
Roella ciliata L.	16	*			
Pelargonium chamaedryfolium Jacq.	17	*		*	
Helichrysum indicum (L.) Grierson	18	*	*		
Lobelia anceps L.f.	20	*	*		*
Lobelia erinus L.	21		*		*
cf. *Carex*	22	*			
Agrostis lachnantha Nees	23	*	*		
Pentachistis pallida (Thunb.)	24	*			
Wahlenbergia capensis L. A.DC.	25	*			
Ehrharta calycina J.E.Sm.	26	*		*	
Lobelia pinifolia L.	27	*		*	
Berzelia lanuginosa (L.) Brongn.	28	*	*		
cf. *Ehrharta* no. 1	29	*			
cf. *Cliffortia*	30	*			
Diascia elongata Benth.	31	*			
Passerina vulgaris Thoday	32	*		*	
Hemimeris racemosa (Houtt.) Merrill	33	*			
Ficinia ramosissima Kunth	34	*			
Ficinia oligantha (Steud.) J. Raynal	35	*	*	*	
Helichrysum moeserianum Thell.	36	*			
Selago sp.	37	*			
Holothrix sp.	38	*			
Nemesia affinis Benth.	39	*			
cf. *Stoebe*	40	*			
cf. *Ehrharta* no. 2	41	*			
Chrysanthemoides monilifera (L.) Norl.	42	*			

Acacia longifolia (Andrews.) Willd.	43	*	*		
Erica sp.	44	*			
Erica hirtiflora Curtis	45	*		*	
cf. Campanulaceae	46	*			
cf. *Anthospermum aethiopicum* L.	47	*			
Metalasia muricata (L.) D. Don	48	*		*	
Crassula capensis (L.) Baill.	49	*			
cf. *Pentaschistis*	50	*	*	*	
Protea lepidocarpodendron (L.) L.	51	*			
cf. *Senecio rigidis* L.	52	*	*		
Tetraria compar (L.) Lestib.	53	*			
cf. *Centella asiatica* (L.) Urban	54	*		*	
cf. *Serruria*	55	*			
cf. *Cymbopogon*	56		*		
cf. *Aspalathus* no. 1	57		*		
cf. *Aspalathus* no. 2	58		*		
cf. *Elegia*	59		*		
Acacia cyclops A. Cunn. ex G. Don	60		*	*	*
Unidentified	61		*	*	
Erica phylicifolia Salisb.	62		*		

Table E.2 List of species, their abundance and soil volume in each wildfire burnt fynbos seedling tray

PLOT	DEPTH	SIZE	SPECIES	n	Soil vol.
Fynbos1	0-0.02m	8-2mm	*Polycarpon tetraphyllum* L.f.	1	125
			Berzelia lanuginosa (L.) Brongn.	1	
Fynbos1	0-0.02m	2mm-1000µm	cf. *Ehrharta* no. 1	1	125
			cf. *Passerina vulgaris* Thoday	1	
			cf. *Cliffortia*	1	
			Cerastium capense Sond.	1	
			Diascia elongata Benth.	3	
Fynbos1	0-0.02m	1000-425µm	*Hemimeris racemosa* (Houtt.) Merrill	5	500
			Pelargonium chamaedryfolium Jacq.	3	
			Isolepsis incomptula Nees	12	
			cf. *Ehrharta* no. 1	6	
			cf. *Ficinia ramosissima* Kunth	8	
			Ficinia oligantha (Steud.) J. Raynal	4	
			cf. *Helichrysum moeserianum* Thell.	1	
			Selago sp.	1	
			Cerastium capense Sond.	3	
			Diascia elongata Benth.	3	
			Phyllopodium cordatum (Thunb.) Hillard	3	
Fynbos1	0-0.02m	<425µm	*Polycarpon tetraphyllum* L.f	1	500
			Holothrix sp.	1	
			Phyllopodium cordatum (Thunb.) Hillard	5	
			Cerastium capense Sond.	1	
			Hemimeris racemosa (Houtt.) Merrill	2	
Fynbos1	0.02-0.05m	8-2mm	*Nemesia affinis* Benth.	1	125
			Hemimeris racemosa (Houtt.) Merrill	1	

Fynbos1	0.02-0.05m	2mm-1000µm	*Diascia elongata* Benth.	1	225
			Phyllopodium cordatum (Thunb.) Hillard	1	
			Hemimeris racemosa (Houtt.) Merrill	7	
			Ficinia oligantha (Steud.) J. Raynal	2	
			Ehrharta calycina J.E.Sm.	1	
			cf. *Stoebe*	1	
			Isolepsis incomptula Nees	1	
			Pelargonium chamaedryfolium Jacq.	7	
Fynbos1	0.02-0.05m	1000-425µm	cf. *Ehrharta* no. 1	1	500
			Polycarpon tetraphyllum L.f	1	
			Hemimeris racemosa (Houtt.) Merrill	12	
			Phyllopodium cordatum (Thunb.) Hillard	4	
			Isolepsis incomptula Nees	17	
			Crassula umbellata Thunb.	1	
			Cerastium capense Sond.	3	
			Pseudognaphalium undulatum (L.) Hillard & B.L. Burtt	1	
Fynbos1	0.02-0.05m	<425µm	*Phyllopodium cordatum* (Thunb.) Hillard	17	500
			Holothrix sp.	2	
			Hemimeris racemosa (Houtt.) Merrill	2	
			cf. *Helichrysum moeserianum* Thell.	1	
			Helichrysum indicum (L.) Grierson	3	
			cf. *Ehrharta* no. 2	1	
			Crassula thunbergiana Schult. Subsp. *thunbergiana*	1	
			Cerastium capense Sond.	3	
			Wahlenbergia exilis A.DC.	2	
			Erepsia anceps (Haw.) Schwantes	1	
Fynbos1	0.05-0.15m	8-2mm	*Crassula natans* var. *natans* Thunb.	1	125
Fynbos1	0.05-0.15m	2mm-1000µm	*Passerina vulgaris* Thoday	10	225
			Diascia elongata Benth.	1	
Fynbos1	0.05-0.15m	1000-425µm	*Phyllopodium cordatum* (Thunb.) Hillard	2	500
			Nemesia affinis Benth.	1	
			Isolepsis incomptula Nees	5	
Fynbos1	0.05-0.15m	<425µm	cf. *Helichrysum moeserianum* Thell.	1	500
			Holothrix sp.	1	
			Phyllopodium cordatum (Thunb.) Hillard	2	
Fynbos2	0-0.02m	8-2mm	No species recorded	0	125
Fynbos2	0-0.02m	2mm-1000µm	*Chrysanthemoides monilifera* (L.) Norl.	1	125
			Berzelia lanuginosa (L.) Brongn.	1	

Fynbos2	0-0.02m	1000-425µm	*Roella ciliata* L.	1	500
			Holothrix sp.	2	
			Wahlenbergia capensis (L.) A.DC.	1	
			Wahlenbergia cernua (Thunb.) A.DC.	1	
Fynbos2	0-0.02m	<425µm	*Phyllopodium cordatum* (Thunb.) Hillard	2	500
			Wahlenbergia exilis A.DC.	1	
			Pentachistis pallida (Thunb.)	1	
Fynbos2	0.02-0.05m	8-2mm	Acacia longifolia (Andrews.) Willd.	1	125
			Isolepsis incomptula Nees	1	
Fynbos2	0.02-0.05m	2mm-1000µm	*Erica* sp.	20	225
			Pelargonium chamaedryfolium Jacq.	1	
			Berzelia lanuginosa (L.) Brongn.	1	
			Passerina vulgaris Thoday	1	
Fynbos2	0.02-0.05m	1000-425µm	*Lobelia anceps* L.f	2	500
			Erica sp.	5	
			Erepsia anceps (Haw.) Schwantes	1	
			cf. *Stoebe*	1	
			Erica hirtiflora Curtis	1	
			Isolepsis incomptula Nees	6	
			Holothrix sp.	1	
			Phyllopodium cordatum (Thunb.) Hillard	1	
Fynbos2	0.02-0.05m	<425µm	*Phyllopodium cordatum* (Thunb.) Hillard	5	500
			cf. *Carex*	1	
			Isolepsis prolifer R.Br.	1	
			Holothrix sp.	1	
Fynbos2	0.05-0.15m	8-2mm	No species recorded	0	125
Fynbos2	0.05-0.15m	2mm-1000µm	*Erica* sp.	295	225
			Berzelia lanuginosa (L.) Brongn.	1	
			Passerina vulgaris Thoday	3	
			cf. Campanulaceae	3	
			Hemimeris racemosa (Houtt.) Merrill	1	
Fynbos2	0.05-0.15m	1000-425µm	*Erica* sp.	1	500
			Lobelia anceps L.f.	2	
			Pentachistis pallida (Thunb.)	1	
			Isolepsis incomptula Nees	2	
			Diascia elongata Benth.	1	
Fynbos2	0.05-0.15m	<425µm	*Phyllopodium cordatum* (Thunb.) Hillard	1	500
Fynbos3	0-0.02m	8-2mm	No species recorded	0	125
Fynbos3	0-0.02m	2mm-1000µm	*Polycarpon tetraphyllum* L.F.	1	150
			Berzelia lanuginosa (L.) Brongn.	3	
Fynbos3	0-0.02m	1000-425µm	cf. *Anthospermum aethiopicum* L.	1	500
			Metalasia muricata (L.) D. Don	2	
			cf. *Stoebe*	2	
			Ficinia oligantha (Steud.) J. Raynal	1	
			Isolepsis incomptula Nees	2	

Fynbos3	0-0.02m	<425µm	*Erica hirtiflora* Curtis *Hemimeris racemosa* (Houtt.) Merrill *Berzelia lanuginosa* (L.) Brongn. *Wahlenbergia exilis* A.DC.	1 1 1 1	500
Fynbos3	0.02-0.05m	8-2mm	No species recorded	0	125
Fynbos3	0.02-0.05m	2mm-1000µm	*Erica hirtiflora* Curtis *Isolepsis incomptula* Nees	1 1	225
Fynbos3	0.02-0.05m	1000-425µm	*Isolepsis incomptula* Nees *Phyllopodium cordatum* (Thunb.) Hillard *Erica hirtiflora* Curtis *Holothrix* sp. *Helichrysum indicum* (L.) Grierson	8 2 1 1 1	500
Fynbos3	0.02-0.05m	<425µm	*Helichrysum indicum* (L.) Grierson *Erica hirtiflora* Curtis	2 1	500
Fynbos3	0.05-0.15m	8-2mm	*Crassula capensis* (L.) Baill. cf. *Pentaschistis*	1 1	125
Fynbos3	0.05-0.15m	2mm-1000µm	*Polycarpon tetraphyllum* L.f. *Berzelia lanuginosa* (L.) Brongn.	2 1	225
Fynbos3	0.05-0.15m	1000-425µm	*Isolepsis incomptula* Nees cf. *Helichrysum moeserianum* Thell. cf. *Anthospermum aethiopicum* L. *Erica hirtiflora* Curtis *Lobelia pinifolia* L.	7 2 1 1 2	500
Fynbos3	0.05-0.15m	<425µm	*Isolepsis incomptula* Nees	1	500
Fynbos4	0-0.02m	8-2mm	*Protea lepidocarpodendron* (L.) L.	5	225
Fynbos4	0-0.02m	2mm-1000µm	*Berzelia lanuginosa* (L.) Brongn.	2	150
Fynbos4	0-0.02m	1000-425µm	*Erica hirtiflora* Curtis *Berzelia lanuginosa* (L.) Brongn. cf. *Stoebe* cf. *Anthospermum aethiopicum* L. *Pentachistis pallida* (Thunb.) *Wahlenbergia capensis* L. A.DC. *Isolepsis incomptula* Nees *Agrostis lachnantha* Nees	1 1 1 1 1 1 3 1	400
Fynbos4	0-0.02m	<425µm	No species recorded	0	400
Fynbos4	0.02-0.05m	8-2mm	*Agrostis lachnantha* Nees	1	225
Fynbos4	0.02-0.05m	2mm-1000µm	*Erica hirtiflora* Curtis *Ficinia oligantha* (Steud.) J. Raynal *Pelargonium chamaedryfolium* Jacq.	2 1 3	225
Fynbos4	0.02-0.05m	1000-425µm	cf. *Stoebe* *Erica hirtiflora* Curtis cf. *Senecio rigidis* L. *Tetraria compar* (L.) Lestib. *Isolepsis incomptula* Nees *Wahlenbergia capensis* L. A.DC.	3 1 1 1 14 2	400

Fynbos4	0.02-0.05m	<425µm	cf. *Stoebe* *Erica hirtiflora* Curtis	1 4	400
Fynbos4	0.05-0.15m	8-2mm	No species recorded	0	125
Fynbos4	0.05-0.15m	2mm-1000µm	*Passerina vulgaris* Thoday *Holothrix* sp.	1 1	200
Fynbos4	0.05-0.15m	1000-425µm	*Metalasia muricata* (L.) D. Don cf. *Centella asiatica* (L.) Urban cf. *Serruria* *Isolepsis incomptula* Nees	1 1 1 1	400
Fynbos4	0.05-0.15m	<425µm	cf. *Centella asiatica* (L.) Urban *Erica hirtiflora* Curtis	1 1	400
Fynbos5	0-0.02m	8-2mm	*Agrostis lachnantha* Nees	1	75
Fynbos5	0-0.02m	2mm-1000µm	cf. *Stoebe* *Berzelia lanuginosa* (L.) Brongn. *Ficinia oligantha* (Steud.) J. Raynal *Pentachistis pallida* (Thunb.) *Hemimeris racemosa* (Houtt.) Merrill *Ehrharta calycina* J.E.Sm. *Lepidium* sp.	2 1 1 1 1 1 1	200
Fynbos5	0-0.02m	1000-425µm	*Isolepsis incomptula* Nees *Hemimeris racemosa* (Houtt.) Merrill *Wahlenbergia cernua* (Thunb.) A.DC.	3 2 1	300
Fynbos5	0-0.02m	<425µm	No species recorded	0	300
Fynbos5	0.02-0.05m	8-2mm	No species recorded	0	75
Fynbos5	0.02-0.05m	2mm-1000µm	cf. *Stoebe* *Ehrharta calycina* J.E.Sm. *Diascia elongata* Benth. *Isolepsis incomptula* Nees *Pelargonium chamaedryfolium* Jacq.	1 1 1 5 1	225
Fynbos5	0.02-0.05m	1000-425µm	cf. *Stoebe* *Isolepsis incomptula* Nees *Pentachistis pallida* (Thunb.)	5 14 1	300
Fynbos5	0.02-0.05m	<425µm	*Phyllopodium cordatum* (Thunb.) Hillard *Helichrysum indicum* (L.) Grierson *Pseudognaphalium undulatum* (L.) Hillard & B.L.Burtt	2 1 2	300
Fynbos5	0.05-0.15m	8-2mm	No species recorded	0	125
Fynbos5	0.05-0.15m	2mm-1000µm	*Passerina vulgaris* Thoday *Pelargonium chamaedryfolium* Jacq..	6 1	200
Fynbos5	0.05-0.15m	1000-425µm	*Helichrysum indicum* (L.) Grierson *Isolepsis incomptula* Nees *Holothrix* sp.	1 9 2	300
Fynbos5	0.05-0.15m	<425µm	*Pseudognaphalium undulatum* (L.) Hillard & B.L. Burtt	1	300

Table E.3 List of species, their abundance and soil volume in each wildfire burnt standing exotic seedling tray

PLOT	DEPTH	SIZE	SPECIES	n	Soil vol.
Exotic1	0-0.02m	8-2mm	cf. *Elegia*	2	225
Exotic1	0-0.02m	2mm-1000µm	No species recorded	0	225
Exotic1	0-0.02m	1000-425µm	No species recorded	0	500
Exotic1	0-0.02m	<425µm	No species recorded	0	500
Exotic1	0.02-0.05m	8-2mm	cf. *Pentaschistis*	1	225
			cf. *Cymbopogon*	1	
Exotic1	0.02-0.05m	2mm-1000µm	cf. *Pentaschistis*	2	500
			cf. *Cymbopogon*	1	
Exotic1	0.02-0.05m	1000-425µm	*Lobelia anceps* L.f.	2	500
Exotic1	0.02-0.05m	<425µm	No species recorded	0	500
Exotic1	0.05-0.15m	8-2mm	cf. *Cymbopogon*	1	225
Exotic1	0.05-0.15m	2mm-1000µm	cf. *Aspalathus* no. 1	1	500
			cf. *Aspalathus* no. 2	1	
			cf. *Cymbopogon*	2	
Exotic1	0.05-0.15m	1000-425µm	*Isolepsis incomtula* Nees	2	500
			cf. *Pentaschistis*	2	
			Lobelia anceps L.f.	7	
Exotic1	0.05-0.15m	<425µm	cf. *Pentaschistis*	4	500
			Ficinia oligantha (Steud.) J.Raynal	1	
Exotic2	0-0.02m	8-2mm	*Acacia cyclops* A. Cunn. ex G. Don	2	150
Exotic2	0-0.02m	2mm-1000µm	No species recorded	0	225
Exotic2	0-0.02m	1000-425µm	*Polycarpon tetraphyllum* L.f.	1	500
Exotic2	0-0.02m	<425µm	No species recorded	0	500
Exotic2	0.02-0.05m	8-2mm	*Acacia longifolia* (Andrews.) Willd.	3	150
Exotic2	0.02-0.05m	2mm-1000µm	*Polycarpon tetraphyllum* L.f.	1	225
			Acacia longifolia (Andrews.) Willd.	3	
Exotic2	0.02-0.05m	1000-425µm	cf. *Senecio rigidus* L.	1	500
Exotic2	0.02-0.05m	<425µm	*Lobelia erinus* L.	2	500
Exotic2	0.05-0.15m	8-2mm	*Lobelia erinus* L.	1	125
			Acacia longifolia (Andrews.) Willd.	1	
Exotic2	0.05-0.15m	2mm-1000µm	No species recorded	0	200
Exotic2	0.05-0.15m	1000-425µm	*Lobelia erinus* L.	4	500
			Lobelia anceps L.f.	1	
Exotic2	0.05-0.15m	<425µm	*Isolepsis incomptula* Nees	3	500
			Lobelia erinus L.	6	
			Lobelia anceps L.f.	1	
			Unidentified	1	
Exotic3	0-0.02m	8-2mm	No species recorded	0	125
Exotic3	0-0.02m	2mm-1000µm	*Cerastium capense* Sond.	1	200
			cf. *Elegia*	1	
Exotic3	0-0.02m	1000-425µm	No species recorded	0	400
Exotic3	0-0.02m	<425µm	No species recorded	0	400
Exotic3	0.02-0.05m	8-2mm	*Acacia longifolia* (Andrews.) Willd.	3	125
Exotic3	0.02-0.05m	2mm-1000µm	cf. *Elegia*	1	225
			Acacia longifolia (Andrews.) Willd.	6	
Exotic3	0.02-0.05m	1000-425µm	No species recorded	0	400
Exotic3	0.02-0.05m	<425µm	No species recorded	0	400

Exotic3	0.05-0.15m	8-2mm	*Acacia longifolia* (Andrews.) Willd.	3	125
Exotic3	0.05-0.15m	2mm-1000µm	No species recorded	0	225
Exotic3	0.05-0.15m	1000-425µm	*Lobelia anceps* L.f. *Isolepsis incomptula* Nees *Erica phylicifolia* Salisb.	1 2 1	400
Exotic3	0.05-0.15m	<425µm	*Isolepsis incomptula* Nees *Lobelia erinus* L.	1 1	400
Exotic4	0-0.02m	8-2mm	No species recorded	0	125
Exotic4	0-0.02m	2mm-1000µm	No species recorded	0	225
Exotic4	0-0.02m	1000-425µm	*Helichrysum indicum* (L.) Grierson	1	400
Exotic4	0-0.02m	<425µm	No species recorded	0	400
Exotic4	0.02-0.05m	8-2mm	No species recorded	0	125
Exotic4	0.02-0.05m	2mm-1000µm	No species recorded	0	225
Exotic4	0.02-0.05m	1000-425µm	No species recorded	0	400
Exotic4	0.02-0.05m	<425µm	No species recorded	0	400
Exotic4	0.05-0.15m	8-2mm	*Berzelia lanuginosa* (L.) Brongn.	1	125
Exotic4	0.05-0.15m	2mm-1000µm	cf. *Elegia*	1	225
Exotic4	0.05-0.15m	1000-425µm	*Agrostis lachnantha* Nees *Isolepsis incomptula* Nees	1 1	400
Exotic4	0.05-0.15m	<425µm	No species recorded	0	400
Exotic5	0-0.02m	8-2mm	No species recorded	0	50
Exotic5	0-0.02m	2mm-1000µm	*Polygonum aviculare* L.	1	125
Exotic5	0-0.02m	1000-425µm	No species recorded	0	200
Exotic5	0-0.02m	<425µm	No species recorded	0	300
Exotic5	0.02-0.05m	8-2mm	No species recorded	0	125
Exotic5	0.02-0.05m	2mm-1000µm	No species recorded	0	175
Exotic5	0.02-0.05m	1000-425µm	No species recorded	0	300
Exotic5	0.02-0.05m	<425µm	No species recorded	0	400
Exotic5	0.05-0.15m	8-2mm	No species recorded	0	150
Exotic5	0.05-0.15m	2mm-1000µm	No species recorded	0	225
Exotic5	0.05-0.15m	1000-425µm	*Helichrysum indicum* (L.) Grierson	1	400
Exotic5	0.05-0.15m	<425µm	No species recorded	0	400

Table E.4 List of species, their abundance and soil volume in each wildfire burnt stack seedling tray

PLOT	DEPTH	SIZE	SPECIES	n	Soil vol.
Scar	0-0.02m	8-2mm	*Lobelia erinus* L.	1	100
Scar	0-0.02m	2mm-1000µm	*Lepidium pinnatum* var. *natans* Thunb.	2	150
Scar	0-0.02m	1000-425µm	*Lobelia anceps* L.f.	1	300
Scar	0-0.02m	<425µm	No species recorded	0	300
Scar	0.02-0.05m	8-2mm	*Acacia cyclops* A. Cunn. ex G. Don	1	100
Scar	0.02-0.05m	2mm-1000µm	No species recorded	0	225
Scar	0.02-0.05m	1000-425µm	No species recorded	0	300
Scar	0.02-0.05m	<425µm	No species recorded	0	300
Scar	0.05-0.15m	8-2mm	No species recorded	0	100
Scar	0.05-0.15m	2mm-1000µm	No species recorded	0	225
Scar	0.05-0.15m	1000-425µm	No species recorded	0	300
Scar	0.05-0.15m	<425µm	No species recorded	0	300

Table E.5 List of species, their abundance and soil volume in each wildfire burnt cleared area seedling tray

PLOT	DEPTH	SIZE	SPECIES	n	Soil vol.
Cleared	0-0.02m	8-2mm	*Acacia cyclops* A. Cunn. ex G. Don	1	100
Cleared	0-0.02m	2mm-1000µm	*Phyllopodium cordatum* (Thunb.) Hillard	1	225
Cleared	0-0.02m	1000-425µm	*Isolepsis incomptula* Nees	1	300
			Pelargonium chamaedryfolium Jacq.	1	
			Erepsia anceps (Haw.) Schwantes	1	
			Erica hirtiflora Curtis	1	
Cleared	0-0.02m	<425µm	*Phyllopodium cordatum* (Thunb.) Hillard 3	3	300
			Crassula natans var. *natans* Thunb.	1	
Cleared	0.02-0.05m	8-2mm	*Acacia cyclops* A. Cunn. ex G. Don	3	150
Cleared	0.02-0.05m	2mm-1000µm	*Ficinia oligantha* (Steud.) J.Raynal	2	225
			Passerina vulgaris Thoday	6	
Cleared	0.02-0.05m	1000-425µm	*Isolepsis incomptula* Nees	4	300
			Metalasia muricata (L.) D. Don	3	
			Erica hirtiflora Curtis	1	
Cleared	0.02-0.05m	<425µm	*Crassula natans* var. *natans* Thunb.	1	300
			cf. *Centella asiatica* (L.) Urban	1	
			Erica hirtiflora Curtis	1	
			Phyllopodium cordatum (Thunb.) Hillard	1	
Cleared	0.05-0.15m	8-2mm	No species recorded	0	100
Cleared	0.05-0.15m	2mm-1000µm	*Isolepsis incomptula* Nees	11	225
			Crassula natans var. *natans* Thunb.	1	
			Passerina vulgaris Thoday	5	
			Ehrharta calycina J.E.Sm.	1	
			cf. *Pentaschistis*	1	
Cleared	0.05-0.15m	1000-425µm	*Isolepsis incomtula* Nees	32	300
			Unidentified	1	
			Crassula natans var. *natans* Thunb.	2	
			Lobelia pinifolia L.	1	
Cleared	0.05-0.15m	<425µm	Unidentified	1	300
			cf. *Centella asiatica* (L.) Urban	1	
			Crassula natans var. *natans* Thunb.	2	
			Phyllopodium cordatum (Thunb.) Hillard	1	

Appendix F. Composition of media used in microbial assays

Table F.1 The composition of the media used to enumerate bacterial numbers

Components	Tryptone soy agar (TSA)	Sodium caseinate agar
Pancreatic digest of casein	15.0 g	
Pancreatic digest of soybean meal	5.0 g	
Sodium caseinate		0.2 g
NaCl	5.0 g	
K_2HPO_4		0.5 g
$MgSO_4$		0.2 g
$FeCl_3$		0.01 g
Agar	15.0 g	15.0 g
Distilled water	1000.0 ml	1000.0 ml
pH	7.3	6.7

Table F.2 The composition of malt extract agar containing streptomycin sulphate (MEAs)

Components	Quantity
Malt extract	20 g
Streptomycin sulphate	0.5 g
Agar	20.0 g
Distilled water	1000.0 ml

Table F.3 Composition of thymine-mineral-vitamin medium (TMV) adapted from Mothibeli (1996)

Components	Quantity
Glucose	5.00 g
KH_2PO_4	1.00 g
$MgSO_4 \cdot 7H_2O$	0.10 g
NaCl	0.10 g
$CaCl_2$	0.10 g
Thymine	0.10 g
Chloramphenicol	0.20 g
[1]Trace element solution	1.00 ml
[2]Vitamin solution	5.00 ml
Cycloheximide	200.00 μg
Agar	10.00 g
Distilled water	1000.00 ml
PH	5.2

[1]See F.4, [2]See F.5

Table F.4 Components of the trace element solution. (Van der Walt 1992)

Components	Quantity
H_3BO_3	0.50 g
$CuSO_4 \cdot 5H_2O$	0.04 g
KI	0.10 g
$FeCl_3 \cdot 6H_2O$	0.20 g
$MnSO_4 \cdot H_2O$	0.40 g
$Na_2MoO_4 \cdot H_2O$	0.20 g
$ZnSO_4 \cdot 7H_2O$	0.40 g
NaCl	1.00 g
$CoSO_4$	0.10 g
$CaCl_2$	0.10 g
$AlK(SO_4)_2 \cdot 12H_2O$	0.01 g
Distilled water	1000.00 ml

Table F.5 Composition of Vitamin solution (Van der Walt and Yarrow 1984)

Components	Quantity
Biotine	0.2 mg
Calcium pentothenate	40.0 mg
Folic acid	0.2 mg
Inositol	200.0 mg
ρ- aminobenzoic acid	20.0 mg
Pyridoxine hydrochloride	40.0 mg
Riboflavin	20.0 mg
Thiamine	100.0 mg
Distilled water	1000.0 ml

Table F.6 Composition of BDS-medium. (Worrall 1991)

Components	Quantity
Malt extract (g)	15
Benomyl (mg)	2
Streptomycin sulphate (mg)	100
[1]Dichloran (mg)	2
Phenol (mg)	50
Agar (g)	15
Distilled H_2O (ml)	1000

[1] 2,6-dichloro-4-nitroaniline

Table F.7 The composition of *Mucor* isolation medium A (Muc A). (Strauss *et al*. 2000)

Components	Quantity
Starch	10.00 g
NH_4Cl	1.00 g
KH_2PO_4	1.00 g
$MgSO_4 \cdot 7H_2O$	0.50 g
Yeast extract	0.50 g
$FeSO_4 \cdot 7H_2O$	10.00 mg
$ZnSO_4 \cdot 7H_2O$	10.00 mg
$MnSO_4 \cdot H_2O$	0.80 mg
$CuSO_4 \cdot 5H_2O$	0.05 mg
Chloramphenicol	0.20 g
[1]Benomyl	0.02 g
Agar	16.00 g
Distilled water	1000.00 ml
PH	5.5

[1] Aldrich catalogue no. 38,158-6

Appendix G. Soil chemical and textural analyses

Table G.1 Soil chemical and textural analyses of six treatment types in November 2000 (assay one).

	Unburnt fynbos	Unburnt exotic	Wildfire burnt cleared	Wildfire burnt fynbos	Wildfire burnt exotic	Wildfire burnt stacks
Na %	4.19	3.37	2.36	18.64	2.61	4.83
Na (cmol/kg)	0.16	0.13	0.1	1.34	0.19	0.14
K %	2.44	2.38	1.16	1.91	2.1	4.55
K (mg/kg)	36	36	20	54	61	51
K (cmol/kg)	0.09	0.09	0.05	0.14	0.16	0.13
Ca %	70.8	46.3	48.73	62.82	77.14	42.64
Ca (cmol/kg)	2.68	1.8	2.1	4.5	5.72	1.23
Mg %	22.58	16.76	25.51	16.64	18.14	24.33
Mg (cmol/kg)	0.85	0.65	1.1	1.19	1.35	0.7
T (cmol/kg)	3.78	3.88	4.32	7.17	7.42	2.88
pH (KCl)	6.5	5.8	6	7.3	7.2	5.8
Resistance	1920	1790	3330	350	1080	1470
H (cmol/kg)	0	1.21	0.96	0	0	0.68
P (mg/kg)	3	3	11	5	8	8
N %	0.092	0.102	0.061	0.106	0.199	0.059
C %	2	1.65	1.55	2.02	2.4	1.14
NO_3 (N)	1.9	3.8	3.2	7.6	2.15	2.2
NH_4 (N)	1.17	0.07	0.73	1.52	0.8	1.3
CEC	3.5	2.8	3	4.1	4.5	2
Clay %	0.6	2.5	3.7	4.9	2.2	1.4
Silt %	2.3	4.4	2	3.9	3.1	3.9
Fine sand %	23.2	25.9	28.2	21	20	22.1
Medium sand %	62.6	54.1	50.6	52.9	57.1	56.3
Coarse sand %	11.3	13.1	15.5	17.3	17.6	16.3
Stone %	1	2	0	1	1	0

Table G.2 Soil chemical and textural analyses of six treatment types in March 2001 (assay two).

	Unburnt fynbos	Unburnt exotic	Wildfire burnt cleared	Wildfire burnt fynbos	Wildfire burnt exotic	Wildfire burnt stacks
Na %	4.46	7.64	2.9	3.32	5.06	4.5
Na (cmol/kg)	0.17	0.11	0.14	0.15	0.26	0.18
K %	2.89	4.9	1.95	3.54	3.48	5.17
K (mg/kg)	43	28	36	62	69	83
K (cmol/kg)	0.11	0.07	0.09	0.16	0.18	0.21
Ca %	48.8	21.91	50.18	43.74	47.25	52.16
Ca (cmol/kg)	1.84	0.32	2.38	1.94	2.39	2.13
Mg %	19.96	12.7	24.76	17.18	21.04	22.52
Mg (cmol/kg)	0.75	0.19	1.18	0.76	1.06	0.92
T (cmol/kg)	3.77	1.48	4.75	4.44	5.05	4.09
PH (KCl)	4.8	4.6	4.9	4.7	4.9	5.3
Resistance	1740	1670	1670	1630	1440	1090
H (cmol/kg)	0.9	0.78	0.96	1.43	1.17	0.64
P (mg/kg)	2	3	14	6	8	23
N %	0.093	0.043	0.107	0.128	0.12	0.107
C %	1.66	0.73	1.69	1.69	2.17	1.54
NO_3 (N)	15.2	14.8	16	10	15.6	21.2
NH_4 (N)	40	15.4	17.9	46	50.3	53.2
CEC	2.78	1.3	3.43	3.66	3.9	2.42
Clay %	0.6	2.5	3.7	4.9	2.2	1.4
Silt %	2.3	4.4	2	3.9	3.1	3.9
Fine sand %	23.2	25.9	28.2	21	20	22.1
Med sand %	62.6	54.1	50.6	52.9	57.1	56.3
Coarse sand %	11.3	13.1	15.5	17.3	17.6	16.3
Stone %	2	1	1	1	0	0

Table G.3 Soil chemical and textural analyses of six treatment types in July 2001 (assay three).

	Unburnt fynbos	Unburnt exotic	Wildfire burnt cleared	Wildfire burnt fynbos	Wildfire burnt exotic	Wildfire burnt stacks
Na %	3.48	10.09	2.88	3.1	3.41	3.97
Na (cmol/kg)	0.15	0.6	0.12	0.14	0.2	0.11
K %	2.66	4.13	2.1	2.88	3.25	4.5
K (mg/kg)	44	96	35	49	76	48
K (cmol/kg)	0.11	0.25	0.09	0.13	0.19	0.12
Ca %	52.63	32.58	49.96	49.16	51.98	37.17
Ca (cmol/kg)	2.22	1.94	2.12	2.16	3.09	1.02
Mg %	20.85	24.51	23.59	20.77	20.14	27.11
Mg (cmol/kg)	0.88	1.46	1	0.91	1.2	0.75
T (cmol/kg)	4.22	5.96	4.24	4.4	5.94	2.75
PH (KCl)	4.8	4.4	4.8	4.8	5.1	4.6
Resistance	3040	910	1740	2200	1300	2300
H (cmol/kg)	0.86	1.71	0.91	1.06	1.26	0.75
P (mg/kg)	4	2	11	9	19	8
N %	0.08	0.149	0.103	0.125	0.198	0.08
C %	1.46	2.79	2	2.11	2.68	1.43
NO_3 (N)	3	3.48	3.12	3.04	6.2	2.2
NH_4 (N)	3.96	8	4.44	4.76	6.92	4.6
CEC	3.38	5.73	3.81	4.06	5.86	2.94
Clay %	0.6	2.5	3.7	4.9	2.2	1.4
Silt %	2.3	4.4	2	3.9	3.1	3.9
Fine sand %	23.2	25.9	28.2	21	20	22.1
Med sand %	62.6	54.1	50.6	52.9	57.1	56.3
Coarse sand %	11.3	13.1	15.5	17.3	17.6	16.3
Stone %	7	9	2	1	2	1

Table G.4 Soil chemical and textural analyses of six treatment types in September 2001 (assay four).

	Unburnt fynbos	Unburnt exotic	Wildfire burnt cleared	Wildfire burnt fynbos	Wildfire burnt exotic	Wildfire burnt stacks
Na %	2.46	3.06	2.97	4.37	2.77	4.96
Na (cmol/kg)	0.12	0.12	0.15	0.13	0.16	0.19
K %	2.35	2.56	1.72	5.65	1.52	2.98
K (mg/kg)	46	39	33	67	33	46
K (cmol/kg)	0.12	0.1	0.09	0.17	0.09	0.12
Ca %	44.86	41.88	38.81	27.18	44.9	25.55
Ca (cmol/kg)	2.24	1.63	1.92	0.82	2.53	1
Mg %	28.29	26.56	35.07	29.37	32.88	31.74
Mg (cmol/kg)	1.41	1.03	1.73	0.89	1.85	1.24
T (cmol/kg)	4.99	3.89	4.94	3.02	5.63	3.91
PH (KCl)	4.8	4.4	4.6	4.1	4.8	4.2
Resistance	4360	4310	1900	2490	2650	2060
H (cmol/kg)	1.1	1.01	1.06	1.01	1.01	1.36
P (mg/kg)	6	2	13	6	9	4
N %	0.092	0.087	0.057	0.028	0.13	0.074
C %	1.6	1.4	1.87	1.06	2.02	2.64
NO_3 (N)	3.2	3.2	7.6	3.6	9.6	4.4
NH_4 (N)	4.8	5	5.8	2.76	7.24	6.2
CEC	8.17	7.12	9.23	6.26	7.48	6.94
Clay %	0.6	2.5	3.7	4.9	2.2	1.4
Silt %	2.3	4.4	2	3.9	3.1	3.9
Fine sand %	23.2	25.9	28.2	21	20	22.1
Med sand %	62.6	54.1	50.6	52.9	57.1	56.3
Coarse sand %	11.3	13.1	15.5	17.3	17.6	16.3
Stone %	2	4	2	2	4	26

Appendix H. Incidental field observations

During the course of the study, several field observations were made (relating to floristics and associated faunal activity) in the habitats studied and in adjoining areas. These are summarised here.

It took less than a month before various plants and animals started appearing in the burnt habitats. On 3 February 2000, a Cicadidae larval exoskeleton (cicada), *Chrematogaster* sp. (cocktail ants) and Oniscomorpha (pill millipedes) were noted in the burnt standing exotic habitat while a member of the Aeshnidae (a dragonfly) was spotted in the burnt fynbos habitat. *Asparagus* sp. plants were recorded resprouting in the burnt standing exotic habitat, (longest stems 570 mm in length) while *Haemanthus* sp. and *Watsonia borbonica* were recorded resprouting in the burnt fynbos.

Just over a month after the fire, on 23 February 2000, bees and cicadas were heard while *Sylvicapra grimmia* (Common Duiker) spoor was abundant amongst the burnt standing exotics. The first bird recorded, a *Cisticola fulvicapilla* (Neddicky), made its appearance in burnt fynbos while Acrididae and Pyrgomorphidae (grasshoppers), Sarcophagidae (flesh flies), ants, spiders, cocoons and Colletidae (solitary bees) were also noted in this habitat type. A few weeks later, on 9 March, some *Asteraceae* sp. were flowering, scattered *Asparagus* sp. plants were fruiting and *Haemanthus* sp. flowers were recorded dying. The next species to flower were *Erica cerinthoides*, *Watsonia borbonica* and the annual *Pelargonium chamaedryfolium* (all recorded on 31 March in the burnt cleared areas surrounding the heat scars and in the burnt fynbos habitat types). On 16 April, a *Psammophylax rhombeatus* (Rhombic Skaapsteker) was surprised in the burnt cleared area. *Dyra clytus* (Cape Autumn Widow butterflies) were also evident while *Falco tinnunculus* (Rock Kestrels) and *Corvus albicollis* (Whitenecked Ravens) were seen circling overhead.

By 13 June, *Asparagus* sp. had already started dropping their fruit and many fynbos species were flowering. Associated insect and arachnid activity was abundant in the burnt fynbos sites with solitary bees, Chrysomelidae (beetles) and Thysanoptera (thrips) occurring in *Oxalis* sp. flowers and *Caerostris* sp. (bark spiders) perched on burnt *Leucadendron* sp. plants. Unfortunately, signs of sheet and gully erosion were becoming evident in the burnt standing exotic habitat type. Drainage lines in the burnt fynbos habitat were soon filled with sand, washed down from the higher burnt standing exotic area. This sand was filled with exotic acacia seeds, and they soon germinated, grew prolifically and threatened to overrun the drainage lines. Fortunately the seedlings were cleared by hand pulling by July 2001.

In September 2000, a *Haliaeetus vocifer* (African Fish Eagle) was seen overhead while *Nectarinia famosa* (Malachite Sunbirds) and *Prinia hypoxantha* (Spotted Prinias) were prominent in the recovering burnt fynbos. January 2001 was marked by the occasional *Buteo buteo* (Steppe Buzzard) cruising overhead and by an abundance of grasshoppers and *Trichostetha fasicularis* (protea beetles) in the burnt fynbos habitat. On 10 January a member of the Tettigoniidae (Armoured Ground Cricket) was found in the same habitat and later a pair of *Aquila verreauxii* (Black Eagles) flew by. On 28 February 2001, a *Circaetus cinereus* (Brown Snake Eagle) a vagrant from the north and north east of the subcontinent, visited the Silvermine Valley (Maclean 1993). The largest satyrine butterfly, *Aereopetes tulbaghia* (Table Mountain Beauty) was recorded during March. This butterfly is an important pollinator of *Disa uniflora* and has been recorded feeding on *Disa cornuta* as well as on *Kniphofia*, *Nerine*, *Haemanthus*, *Antholyza*, and *Aloe* species (Williams 1994).

In May an *Accipiter tachiro* (African Goshawk) put in an appearance and in July, Spotted Prinias, Malachite Sunbirds and *Promerops cafer* (Cape Sugarbirds), were spotted in the patch of unburnt fynbos immediately adjacent to the studied burnt fynbos habitat. The following mushrooms were recorded during May in the study sites: *Lactarius deliciosus*; *Laccaria laccata*; *Russula capensis*; *Schizophyllum commune*; *Pycnoporus* sp. and *Coprinus comatus* while a *Sphenoaecus afer* (Grassbird) was spotted in unburnt fynbos. Of interest was the fact that numerous *L. laccata* fruiting bodies were found in three out of five wildfire burnt stacks (heat scars). There is a wide scope for the future study of insects, spiders, reptiles, mammals, birds and mushrooms in post-fire indigenous and transformed habitats in Mountain Fynbos.

Appendix I. List of plant species mentioned in the text. Nomenclature follows Goldblatt and Manning (2000)

Acacia cyclops A. Cunn. ex G. Don
Acacia longifolia (Andrews.) Willd.
Acacia mearnsii De Wild.
Acacia melanoxylon R. Br.
Acacia saligna (Labill.) H.L. Wendl.
Anagallis arvensis var. *caerulea* L.
Diascia elongata Benth.
Disa cornuta (L.) Sw.
Disa uniflora Bergius
Erepsia anceps (Haw.) Schwantes
Erica baccans L.
Erica cerinthoides L.
Erica fairii Bolus
Erica hirtiflora Curtis
Erica lutea P.S. Bergius
Erica phylicifolia Salisb.
Eucalyptus diversicolor Bonpl.
Ficinia oligantha (Steud.) J.Raynal
Fumaria muralis Sond. ex Koch
Hakea gibbosa (Sm.) Cav.
Hakea sericea Schrad.
Hakea suaveolens R. Br.
Isolepsis incomptula Nees
Lepidium pinnatum var. *natans* Thunb.
Leptospermum laevigatum (Gaertn.) F. Muell.
Leucospermum conocarpodendron (L.) H. Buek.
Metalasia muricata (L.) D. Don
Mimetes fimbriifolius Salisb. ex Knight
Paraserianthes lophantha (Willd.) I. Nielsen
Passerina paleacea Wikstr.
Pelargonium chamaedryfolium Jacq.
Pinus canariensis Sweet ex K. Spreng
Pinus pinaster Ait.
Pinus pinea L.
Populus canescens (Ait.) J.E. Sm.
Protea lepidocarpodendron (L.) L.
Phylica ericoides L.
Watsonia borbonica (Pourr.) Goldblatt