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Impacts of alien clearing on post-fire biodiversity and erosion

By WENDY FODEN
Supervisor: Professor W.J. Bond
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Abstract

The 'cut and burn' strategy currently used in the Western Cape for clearing alien infestations is reported to have negative impacts on fynbos biodiversity and on soil erosion. I hypothesized that high intensity fires would cause increased soil erosion and that this was due, in part to changes in soil water repellency. I also hypothesized that where alien fuel loads were large, high intensity fires would cause a large degree of soil heating resulting in (a) mortality of shallow-buried seeds and (b) higher mortality of small seeds. These hypotheses were tested experimentally, and effects at the community level were tested by post-burn observation. Soil erosion after 55 days was strongly related to fire intensity, although no significant changes in soil water repellency occurred following fire. At the experiment site (Franschhoek) pre-fire fuel loads were correlated with fire intensity. Fire intensities were greater where fuel was positioned 45-65cm above the ground than where it was on the ground. Both small and large seeds were planted at different depths before the experiment fire. Post-fire seedling emergence of planted seeds was observed for 5 months following the fire. Small seeds failed to germinate and no significant relationships were found between large-seeded germination and either fire intensity or planting depth. This may have been due to the moderating effects of high soil moisture contents on soil heating during the fire. At the Franschhoek experiment site naturally occurring seeds and resprouters were negatively affected by high fire intensities while no significant relationships between these variables were found at the Villiersdorp site. Suggested reasons for this apparent contradiction include differences between sites in duration of invasion and topography. Alien-invaded sites differed from uninvaded sites in seedling abundance and resprouter cover, but not in species richness. Areas in which aliens were unfelled at the time of the fire had significantly greater post-fire seedling species richness, seedling abundance and resprouting than felled areas. Contradictions between the findings of this and other studies highlight that the complicated phenomenon of fire intensity and the variables affecting it are, as yet, not well understood. Conclusions should be treated as tentative. Management implications of the study are discussed.

Contents

Introduction

Dense stands of the Australian shrub, *Hakea sericea* Schrad. (Proteaceae) and the tree *Pinus pinaster* (Pinaceae) occupy approximately 1 130 km^2 or 4% of the total area of mountain fynbos in the southern and south western Cape (Richardson and Van Wilgen 1986). These aliens present a major threat to biodiversity of indigenous plants and other biota (Holmes and Cowling 1997). This is due to both the direct effects of competition for space, water, nutrients and light and the indirect effects of altering ecosystem properties such as flammability (Van Wilgen et al. 1994).

The weed control programme of the Department of Environmental Affairs (Forestry branch) as well as community-orientated projects such as the "Working for Water" project, operating in the Cape, use the 'slash and burn' strategy to remove aliens. Aliens are felled and left *in situ* for about 18 months, during which cones and follicles open, releasing seeds. The winged seeds are released close to the ground and are thus not carried far by wind, and felled adults provide shelter for seed predators. The felled area is burnt after the few remaining seeds have germinated and seedlings are killed. *H. sericea* and *P. pinaster* rely entirely on seed for regeneration and thus these control measures are usually successful. The 'cut and burn' strategy succeeds due to the close succession of felling and fire (Van Wilgen 1994; Richardson and Van Wilgen 1986).

Although the success of the 'slash and burn' method of alien clearing helps to improve biodiversity and rehabilitate invaded areas, there have been several suggestions that the method has some adverse effects. The heavy alien fuel loads, concentrated near the soil surface result in uncharacteristically intense fires (Richardson and Van Wilgen 1986; Breytenbach 1986, Van Wilgen et al. 1994; Whelan 1995; Holmes and Cowling 1997; Grant 1997). This may lead to the elimination of remnant natural vegetation by killing subterranean rootstocks and the seeds of native species resident in the soil, thereby reducing fynbos species richness (Richardson and Van Wilgen 1986). It may also result in severe soil erosion (Van Wilgen et al. 1994; Scott and Van Wyk 1992, 1995).

1990, 1993

Fire intensity is a difficult phenomenon to measure or study and little is known of its physical nature or of how it is affected by site and climatic variables. Although most studies on the effect of fire on ecosystem components make reference to fire intensity, they lack accurate descriptions of the physical characteristics of the fires (Moreno and Oechel 1991; Whelan 1995). This makes comparisons of the effects of these fires very difficult. The most commonly used measure of fire intensity is Byram's (1959 in Bond and Van Wilgen 1996) fire-line intensity equation. Although maximum temperatures reached are often presented in publications, they are not easily related to ecological effects (Bond and Van Wilgen 1996). The experimental methods of this study make use of two indirect methods of estimating fire intensity, namely cans from which water is evaporated during the fire (Bradstock and Auld 1995) and minimum remaining branch diameters after the fire (Moreno and Oechel 1989). These provide relevant assays of above-ground fire intensity (Whelan 1995). Through the accurate measurement of pre-fire fuel, climatic conditions, fire intensity and ecological changes following the fire, this study aims to contribute to the very small number of studies of fire intensity in fynbos to which managers can refer, to help them determine burning policies.

Investigations have been conducted into the direct effects of aliens on fynbos through competition (e.g. Holmes and Cowling 1997) as well as into the indirect effects of increased fire intensity on fynbos composition (e.g. Richardson and Van Wilgen 1986, B). These studies help to determine the ultimate effects of alien invasion. But it is only through experimental studies that the *processes* producing these results become apparent. As a successful method of removing aliens, the 'slash and burn' strategy must continue to be implemented. A thorough understanding of how and why this adversely effects fynbos is vital if a management strategy to minimise these impacts is to be found.

The ultimate determinant of fire intensity is the amount of energy stored in the fuel (Whelan 1995). However, few fires actually consume all above-ground biomass, and “available fuel” represents only a fraction of the total biomass in an area. For example, a *Eucalyptus* forest had an estimated biomass of 265 $t.ha^{-1}$ of which only 4.7% was available to be consumed by fire (Walker 1981 in Grant 1997), however, in another Australian study, 43.5% of total biomass was available fuel (Ward and Koch 1996 in Grant 1997). The proportion of total biomass consumed during fires is determined by inherent fuel properties such as aeration, flammability and fuel height distribution, as well as climate-related factors such as wind speed and fuel moisture contents (Bond and Van Wilgen 1996).

No previous experimental studies have been conducted to determine what percentage of total felled *P. pinaster* and *H. sericea* biomass will combust and thereby constitute "available fuel" under climatic conditions common in the South Western Cape. This study aims to determine how fuel flammability, height distribution and hence aeration will affect fire intensity. In conjunction with fuel moisture contents and climatic conditions at the time of burning a knowledge of extent of fuel combustion will allow for more accurate prediction of fire intensity in alien-felled areas. This will help managers to allocate their manpower and resources efficiently during fires.

Consequences of increased fire intensities

Erosion and soil water repellency

Several studies suggest that increased fire intensity, particularly after alien clearing, causes increased soil erosion (Scott and Van Wyk 1992, 1995; Bond and Van Wilgen 1996). This is thought to be due to changes in the physical nature of the soils. One such change is the induction of water repellency. Water repellency is an abnormality in soils caused by the coating of soil particles with particular organic substances which decrease the soil's affinity for water (DeBano et al. 1967 in Scott and Van Wyk 1990; Whelan 1995). It has been suggested that these substances are aliphatic hydrocarbons which originate from plant litter (DeBano et al. 1970) and that, when heated, they become polarised and form strong bonds with soil particles. There is a direct relationship between the degree of soil heating and the development of soil water repellency (Scott and Van Wyk 1995). Pine litter contains relatively large amounts of repellency-inducing compounds (Scott and Van Wyk 1995) making soils in pine-invaded particularly vulnerable to water repellency.

Water repellency of surface soils prevents water infiltration and/or percolation and this results in increased overland flow (DeBano 1971 in Scott and Van Wyk 1995) and ultimately to increased soil erosion (Swanson 1981 in Whelan 1995). This has been clearly shown in experiments by Campbell et al. (1977) in Ponderosa pine forest (Arizona) and by Osborne et al. (1964 in Whelan 1995). Subsurface soils may become repellent during intense fires when hydrophobic compounds are vaporised and then condense in lower soil layers. Although surface soils are then wettable and water may infiltrate the soil, percolation is impeded in repellent areas. Repellent layers are seldom continuous over large areas and are often broken by root channels and rocks (Scott and Van Wyk 1995), but if water entry rate through non-repellent areas is less than rainfall intensity, saturation overland flow will eventually result (Scott and Van Wyk 1995).

This study aims to test whether increased fire intensity causes greater soil erosion and to find out the role of the induction of water repellency in causing erosion. It was hypothesised, firstly, that soil subjected to intense heat would have greater total repellency and secondly, that repellency in the upper soil layers would decrease following an intense fire while repellency in lower layers would increase. There was expected to be little change in repellency after low intensity burns.

Post-fire germination of soil-stored seeds and resprouting

High soil temperatures are important with regard to the death or survival of soil-stored seed (Beadle 1940). The heat produced by fire provides a germination cue for many species but threshold intensities exist above which mortality results (Bradstock et al. 1992, Richardson and Van Wilgen 1986). A gradient of decreasing soil temperatures with increased soil depth arises during a fire. Extending this, the following hypotheses are proposed:

1) During intense fires, seeds near the soil surface will be killed (figure 1a).

2) Of the seeds which survive in the deeper soil layers, only those with sufficient nutrient reserves i.e. large seeds will reach the surface and germinate (figure 1b).

Ultimately, this is expected to cause a change in community structure and a decrease in biodiversity as only species with large, deeply-buried seeds will survive.

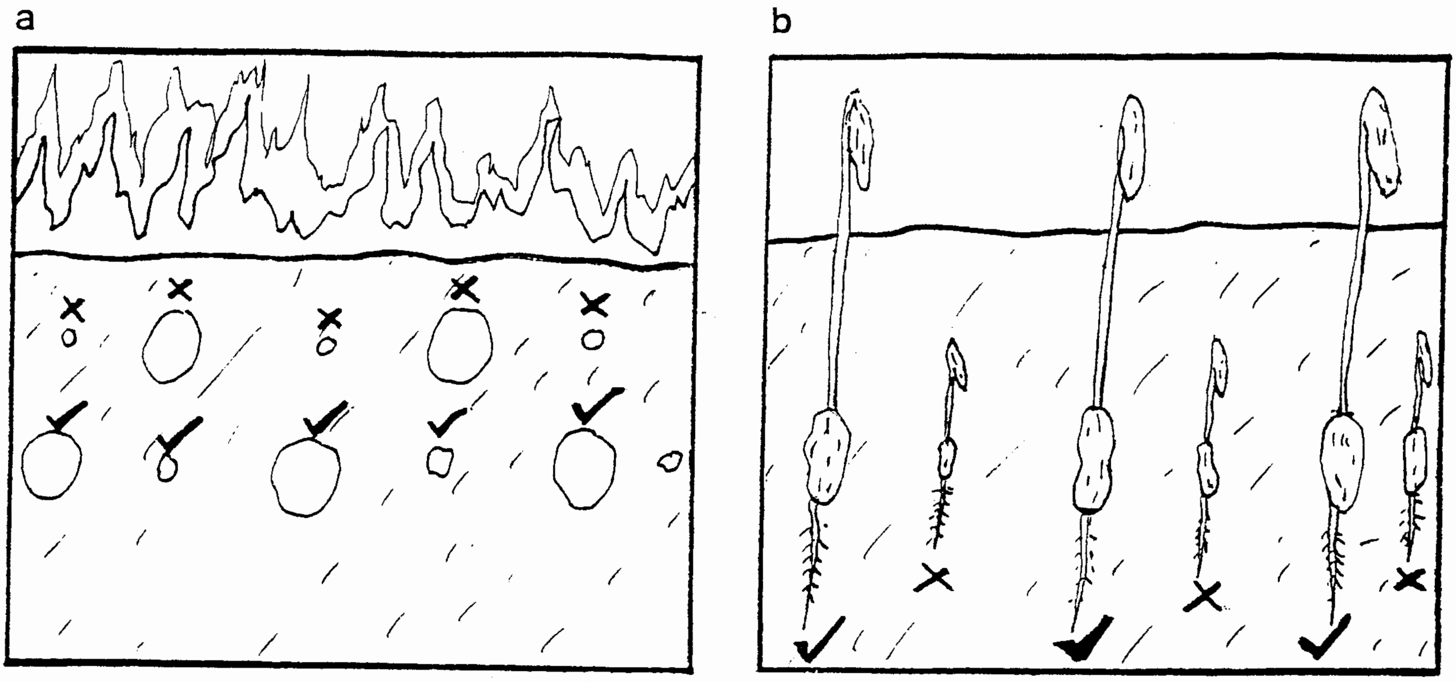


Figure 1: Diagram illustrating the hypothesised processes occurring in soils during intense fires. (a) During intense fires, seeds near the soil surface are killed. (b) Of the seeds which survive in the deeper soil layers, only those with sufficient nutrient reserves i.e. large seeds will reach the surface and germinate. (Ticks indicate survival and croosses indicate mortality.)

I conducted an experiment to test the above hypotheses and, in order to see if there were effects at the community level, I also observed post-fire germination of naturally-occurring seeds at the experiment site. In December 1997 a wildfire swept through an alien-invaded valley that had been partially felled. This site provided a further opportunity for an observational study on the effects of high fire intensity as a result of high alien fuel loads on natural seed germination. For both sites, I hypothesised that in intensely burned areas, number of seedlings and species richness would be reduced due to the loss of shallow-buried and small-seeded plants.

An important factor affecting the heating of soils during fires is soil moisture content. Higher soil moisture contents decrease the heating effect because, firstly, dry soils have a lower heat capacity and lower conductivity (Hillel 1980 in Scott and Van Wyk 1992). Secondly, above 100°C energy is used to vaporize water and thus in wet soils, less energy remains to heat the soil. Soil moisture effects were determined experimentally and the Villiersdorp wild-fire also provided an ideal opportunity to examine the effects of soil moisture on seed germination. As the north-facing slope is generally far drier than the southern aspect it was expected that soil temperatures during the fire would have been greater on the north-facing slope, thereby causing greater seed mortality. This study aims to assess manipulating soil moisture as a potential management technique to reduce fire intensity.

A long-standing debate exists over whether or not aliens should be felled before being burnt. Living plants would have higher soil moisture contents, thereby reducing fire intensity and secondly, fuel would burn above the ground, reducing soil heating which normally results due to conduction from burning fuel. I aimed to determine whether burning standing aliens is more advantageous for post-fire biodiversity than burning felled aliens.

Resprouters are defined as plants possessing an underground lignotuber from which new coppicing shoots are produced after fire (Schutte et al. 1995). There is an unusually high percentage of resprouting species in the fynbos biome, with a decrease in proportion of resprouters in the genera *Cyclopia*, *Liparia* and *Podalyria* from west to east and an increase in the tribe *Proteaceae* (Schutte et al. 1995). Moreno and Oechel (1991) found that the Californian chaparral resprouter *Adenostoma fasciculatum* showed increased mortality with increasing fire intensity. Similar results were found for *Quercus coccifera* in the garrigue of southern France and *Calluna vulgaris* in Scottish heather (Moreno and Oechel 1991). Richardson and Van Wilgen (1986) found that at a burnt, alien-invaded site, resprouter contribution to plant cover was particularly small. This study investigates the nature of the relationship between fire intensity and resprouter survival.

In this study I set out, firstly, to document fire intensity in an experimental burn under known fuel and weather conditions. Secondly, I aimed to determine the effects of fire intensity on soil erosion, and thirdly, I attempted to determine the biodiversity consequences of variable fire intensity for seedling emergence and resprouter survival.

Materials and methods

Part I: Seed germination experiment, Franschhoek

The study site

An experimental study was conducted to determine how variation in fire intensity due to variable alien fuel loads affects seedling emergence. The study was conducted in a 2.5 ha pine plantation in the Franschhoek mountains of the South-Western Cape, South Africa (33° 10’ E; 33 ° 57’ S) (figure 2). Aerial photographs showed that *Pinus pinaster* had been growing at the site for approximately 47 years. The site also contained numerous individuals of *Hakea sericea* and *Acacia mearnsii*. Several months prior to the start of the study all the trees were felled and logs and large amounts of litter were distributed unevenly around the site. Based on a visual assessment of fuel loads, ten 2X2m high fuel plots and ten 2X2m low fuel plots were selected (see plate 1 (a) and (b)). Plot corners were marked using metal stakes.

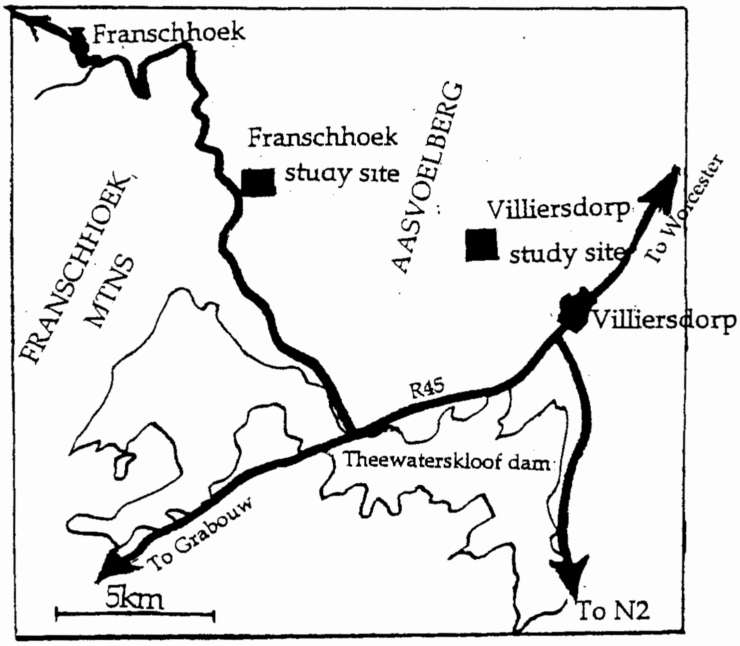


Figure 2: Map showing the locations of the Franshhoek and Villiersdorp study sites.

Plate 1: Photographs showing an example of (a) a low fuel plot and (b) a high fuel plot at the Franschoek study site.

Quadrats (25X25cm) were established at the centres of each of the 20 plots. All fuel with diameters less than 25mm were removed from these quadrats and divided into 3 size classes: small fuel (<6mm); medium fuel (6-25mm) and ground fuel including leaf litter and decomposing organic matter. The fuel in each size class was placed in a bag and weighed using a spring balance. In order to record the height distribution of fuel, a meter-rule was then inserted vertically into fuel piles. The number of times fuel from the small and medium size classes touched a selected edge of the meter-rule as well as the height above the ground at which the contact occurred was recorded.

Seed germination experiment

To accurately determine depth and size-related effects of fire intensity on seeds an experiment was conducted in which seeds of known sizes were planted at known depths before the fire. Quadrats (1x1m) were established for seed planting in the centre of each of the plots. The following plant species were selected for use in the seed germination experiment due to their stimulation by heat, seed size, reports of good seed viability, their successful use in a previous study of a similar nature (Maze, unpublished) and seed availability: *Acacia saligna* (large-seeded), *Virgilia oroboides* (large-seeded), *Dorotheanthus bellidiformis* (small-seeded)and *Lobelia valida* (small-seeded). Seeds were planted in 4 rows, 25cm apart and at 5 sites, 20cm apart in each of these rows (figure 3). Planting depths alternated from 2cm and 5 cm between rows. Rows planted with shallow-buried seeds were marked with white pebbles at either end and rows with deep-planted seeds were marked with small heaps of white river-sand. Rows were orientated parallel to the slope in order to avoid slope effects on germination.

The planting process involved inserting a cherry-borer (2cm diameter) into mineral soil to a depth of either 2cm or 5cm as required. Soil remained inside the borer when it was removed, leaving a cylindrical hole of known depth into which seeds were inserted. The following combination of seeds was used: 2X *Acacia saligna*; 2X *Virgilia oroboides*; approx. 6X *Dorotheanthus bellidiformis* and approximately 12X *Lobelia valida*. During the planting process wind proved to be a problem as the small seeds were often blown away during insertion into the holes. This problem was solved by precounting all seeds into drinking straws which had been sealed at one end. Seeds were poured into the holes. The cherry-borer was then reinserted into the hole, and the soil remaining inside it was pushed back into the hole. Fuel was then replaced in a manner similar to before planting.

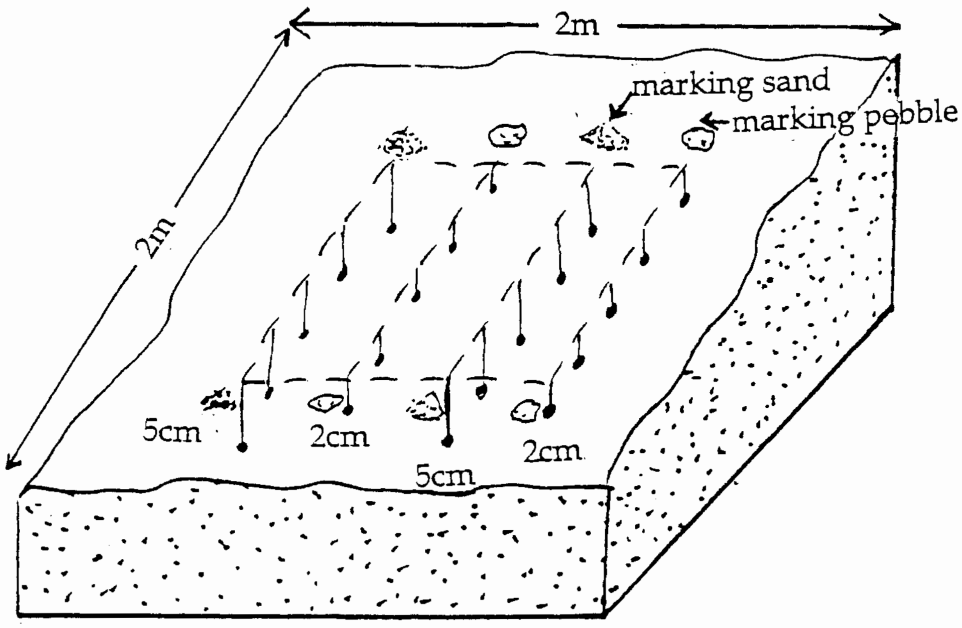


Figure 3: Diagram showing the layout of quadrats and planting positions within plots at the Franchhoek site.

Soil water repellency before the fire was measured by collecting approximately 28 ml of soil in a container from both the soil surface and from a depth of 4cm. Four millilitres of water were then pippetted onto the surface of the sample. The time taken for all the water to drain below the soil surface was recorded. This process was repeated for each of the 20 plots both before and after the fire. The results were analyzed using Wilcoxin's test for matched pairs.

Burning conditions

Site and climatic conditions influence fire intensity and accurate recordings of these factors are therefore necessary if results from this study are to be compared with other studies. Shortly before burning began, approximately 45g of soil was collected from each plot and sealed in polythene bags. Samples of the 3 fuel types were also collected and placed in sealed polythene bags. These samples were later transported to the lab. and weighed. Samples were dried by placing them in an oven at 104 °C for 2 days. They were then reweighed and moisture contents calculated.

The site was burned in the afternoon on the 8th of April 1997, approximately 2 weeks after the first seeds had been planted. During the fire, regular measurements were made of wind-speed, humidity and air temperature.

Shortly before the burn, 340ml cans were placed at the centre of each plot and filled with water. A control can was also filled and placed away from the fire, so that evaporation due to the sun could be factored out from fire effects. Immediately after the fire the amount of water remaining in each of the cans was measured using a measuring cylinder. Details of fire damage to each can were also recorded.

The fire's rate of spread was estimated for several plots by recording the time taken for flames to move along the ground between the metal stakes marking the corners of the plots which were 2m apart. Flame height was also estimated at several times.

Fire intensity and fuel load data were tested for normality of distribution and homogeneity of variance using Kolmogorov-Smirnov and Hartley's tests. Spearman's rank order correlation coefficients were calculated for the relationships between fire intensity, as indicated by water loss from cans during the fire, and the mass of fuel in each size class as well as total fuel mass. Six of the plots contained similar total fuel masses (1500-1600g) although fire intensity measures differed markedly between them. Height distributions of the fuel from these plots were compared.

Measurements after the fire

Recordings of germination of planted seeds were made 66, 117 and 155 days after the burn. For each plot, number and position of each seedling was recorded. Once counted, the seedlings were cut off from their bases so that they would not be recounted during later observations. In order to monitor fire effects at the community level, during the second and third observations, the numbers of naturally occurring seedling species and individuals were also recorded. During the third observation, the numbers of resprouting individuals were recorded.

Data were found to be nonparametric using Kolmogorov-Smirnov and Hartley's tests. The number of shallow and deep-buried seeds that germinated in each plot were correlated with water lost from cans and soil moisture content for each plot using Spearman's Rank order correlation coefficients. Differences in germination of seeds from different planting depths and fuel conditions were analyzed using Kruskall-Wallis 1-way ANOVA.

Part II: Erosion experiment and post-fire community observations, Villiersdorp nature reserve

The study site

A large valley in the Villiersdorp nature reserve (33 ° 15' E; 33 ° 58' S) was subject to severe invasion by *Pinus pinaster* and *Hakea sericea* (see figure 2). The aliens were in their first fire cycle (approximately 12 years old). Alien clearing operations had begun and were only partially completed by March (1997) when a wild-fire swept through the valley.

Erosion experiment

In late April (the beginning of the wet season), 14 sites were selected in the Villiersdorp valley . Sediment traps ("walls", approximately 1m wide and 30-50cm high, perpendicular to the slope) were constructed on slopes of similar inclination (mean=27^{0}) using logs, rocks and shadecloth. The amount of sediment caught in each trap was estimated by inserting a stick into the ground just above each "wall" at the time when the sediment traps were built and marking the level of the ground on it. The fire intensity at each site was measured retrospectively using minimum remaining branch diameters (Moreno & Oechel 1989). Recordings of slope aspect and inclination, soil colour and fire damage to rocks and termitaria were also made at each site.

The erosion experiment was terminated towards the end of the wet season, 88 days after the sediment traps had been erected. Sediment heights were marked on the inserted sticks and the sticks were removed from the ground. The distance between insertion depth markings at the start and termination of the study were recorded to give an indication of sediment deposition in each trap. Data were non-normal according to Kolmogorov-Smirnov and Hartley's tests and Spearman's rank order correlation coefficient was calculated to test the strength of the relationship.

Observations of seedling emergence and resprouting

Post-fire observations of germination and resprouting were conducted to monitor fire intensity effects at the community level. In thirty-seven 3x0.5m plots, the incidence of seedling species (excluding serotinous species) was recorded. In four 0.5x0.25m squares within these plots the total numbers of germinating seedlings (excluding serotinous species) were recorded and mean values were then calculated as number of seedlings per $0.125m^2$. Percentage cover of resprouters was calculated by estimating interception of a 3m tape measure with living resprouter plant matter. The number of logs and stumps of *Pinus* and *Hakea* within a 5m semi-circle above the dam wall were recorded to give an indication of the degree of infestation of the area before the fire. Details of rock and termitaria shattering were also recorded for each plot.

Near the edge of the areas where the aliens had not been felled before the fire, 8 pairs of matched standing and felled sites were selected. Measurement of germination and resprouters was carried out as described above.

Data were tested for normality of distribution and homogeneity of variances using Kolmogorov-Smirnov and Hartley's tests and were found to be nonparametric. Differences in number of seedlings, number of seedling species, percentage resprouting and minimum remaining diameter between alien invaded vs. uninvaded sites and north-facing vs. south-facing slope sites were tested for significance using the Mann-Whitney U-test. To determine the effects of fire intensity on germination and resprouting, Spearman's rank order correlation coefficients were calculated for the relationships between minimum remaining diameters and species numbers, seedling number and percentage resprouter covers. Wilcoxin's test for matched pairs was used to test for significant differences between standing vs. felled sites.

Results

Part I: Seed germination experiment, Franschhoek

Burning conditions

Fuel loads

Mean fuel masses of each of the three size classes for both high fuel and low fuel plots are presented in table 1.

Table 1: Means and standard deviations (SD) of fuel of different size classes from high fuel (n=10) and low fuel (n=10) plots (g.m^{-2}) at the Franschhoek study site.

	small fuel (g.m^{-2}) (<6mm diameter)	medium fuel (g.m^{-2}) (6mm-25mm)	ground fuel (g.m^{-2})	TOTAL fuel (g.m^{-2})
HIGH FUEL	543.05	298.05	240.05	1405.05
SD	238.57	139.04	158.24	315.53
LOW FUEL	243.05	141.25	228.05	920.05
SD	118.91	141.76	132.92	292.42

Climatic conditions

Air temperature at the time that the fire began was approximately 26°C. At 11 a.m., shortly before burning began the wind speed was 2.59 km.hour^{-1}. During the early afternoon when backburning of the site began, wind speed had dropped to 2.46 $km.hour^{-1}$ and by the time all plots had been burned (15:00h) wind speed was 0.86 $km.hour^{-1}$. Mean wind speed during the burn was 1.11 $km.hour^{-1}$ (n=4). Humidity ranged from 70 to 85%.

Fuel moisture contents at the time of the burn (shown in table 2) were high due to recent rains. Mean soil moisture content of soil at a depth of 0-5cm was also high (0.274 $g_{water}.g_{dry\ soil}^{-1}$ (n=20; S.D.=13.69)).

Table 2: Mean moisture contents of fuel from the Franschhoek study site at the time of the fire.

Fuel class	Mean moisture content ($g_{water}.g_{dry\ fuel}^{-1}$)	n	Standard Deviation
fine fuel (<6mm diameter)	9.75	2	0.44
medium-fuel (6-25mm diameter)	12.03	3	0.46
ground fuel	51.29	2	2.29
TOTAL FUEL	24.36	7	18.927

Fire intensity

Flame heights ranged from 0.75-2.4m on the upper parts of the slope and from 2-3m lower down the slope. Rate of spread was approximately 2m per minute. Mean water losses from high fuel and low fuel plots were 255.9ml (n=10; S.D.=51.46) and 128.4ml (n=10; S.D.=79.27) respectively.

The relationships between fuel masses and fire intensity, as quantified by water loss from the cans, are shown in figure 4. Data distribution and homogeneity of variances were tested using Kolmogorov-Smirnov and Hartley's tests in Statistica. All data sets were found to be non-parametric. Spearman's rank order correlation coefficients describing the relationships between fuel classes and fire intensity are: R=0.624 (fine fuel); R=0.641 (medium fuel); R= 0.698 (ground fuel) and R= 0.656 (total fuel). All of these coefficients are significant ($p<0.05$).

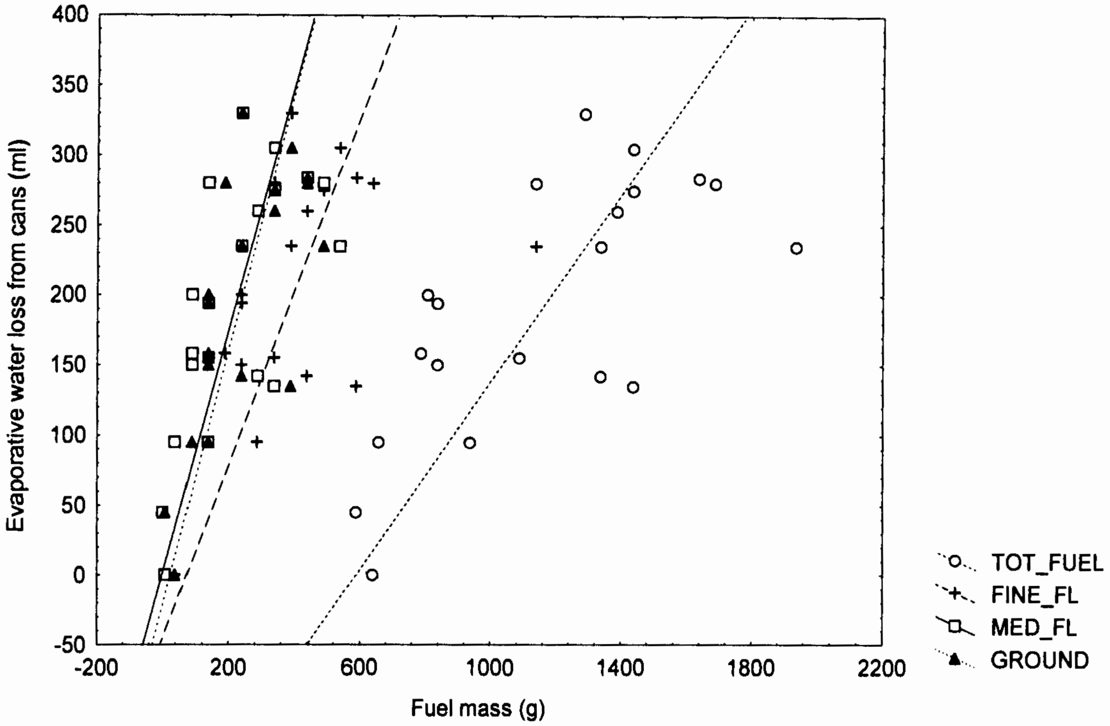


Figure 4: Graph showing the relationships between fire intensity (indicated by evaporative loss of water during the fire (ml)), and fine fuel (<6mm diameter) (R=0.624; $p<0.05$); medium-sized fuel (6-25mm) (R=0.641; $p<0.05$); ground fuel (R=0.698; $p<0.05$) and total fuel masses (R=0.656; $p<0.05$) ($g.m^{-2}$) at the Franschhoek study site. Correlations were calculated using Spearman's test.

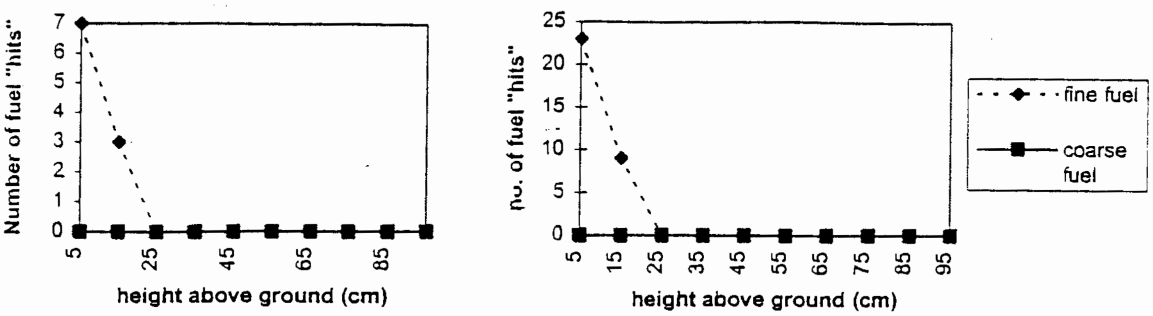
Plots of the height distribution of fuel in 6 plots of similar total fuel masses (1500-1600g) are shown in figures 5(a-f). These graphs show that fire intensity at the soil surface varies with the distribution, and not only the amount of fuel. Maximum intensities were reached when fuel (coarse and/or fine) was distributed most evenly from ground level to approximately 55cm above the soil surface.

Backburning effects on fire intensity

Flame heights for the back-burn plots were smaller than for front-burn sites, ranging from 0.75-2.4m as opposed to a range of 2-3m for front-burn plots. Figure 6 shows water loss from cans at backburned sites in relation to front-burn sites. There appears to be no difference in fire intensity measured in this way between back-burned and front-burned sites.

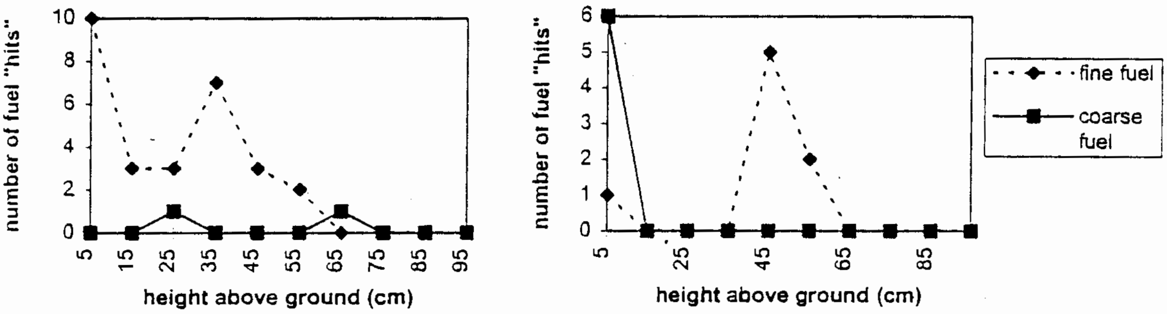
(a) 135ml evaporated from can

(b) 142ml evaporated from can



(c) 235ml evaporated from can

(d) 260ml evaporated from can



(e) 275ml evaporated from can

(f) 305ml evaporated from can

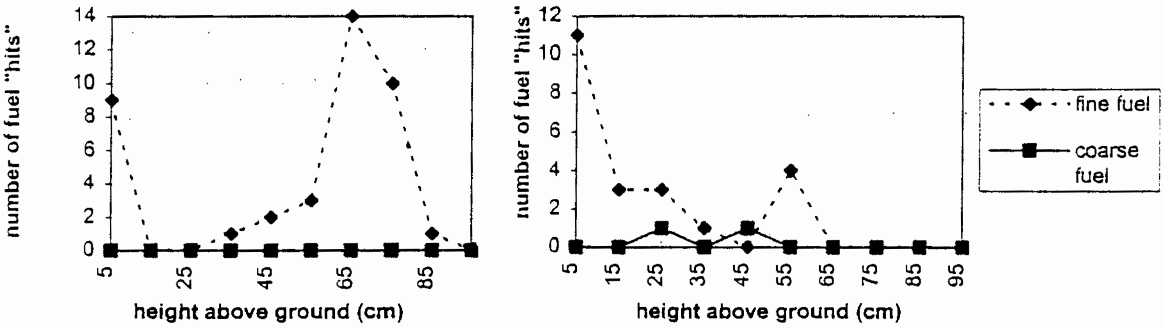


Figure 5: Graphs showing the number of times fuel contact (a "hit") was made between the edge of a verticle meter rule and pieces of fine (>6mm diameter) and coarse (6mm-25mm diameter) fuel, and the heights at which these "hits" occurred. Plots shown all had total fuel loads in the range 1500-1600g at the Franschhoek study site. Fire intensities at each plot, as indicated by the amounts of water evaporated from cans (ml), are shown above graphs and increase from (a) to (f).

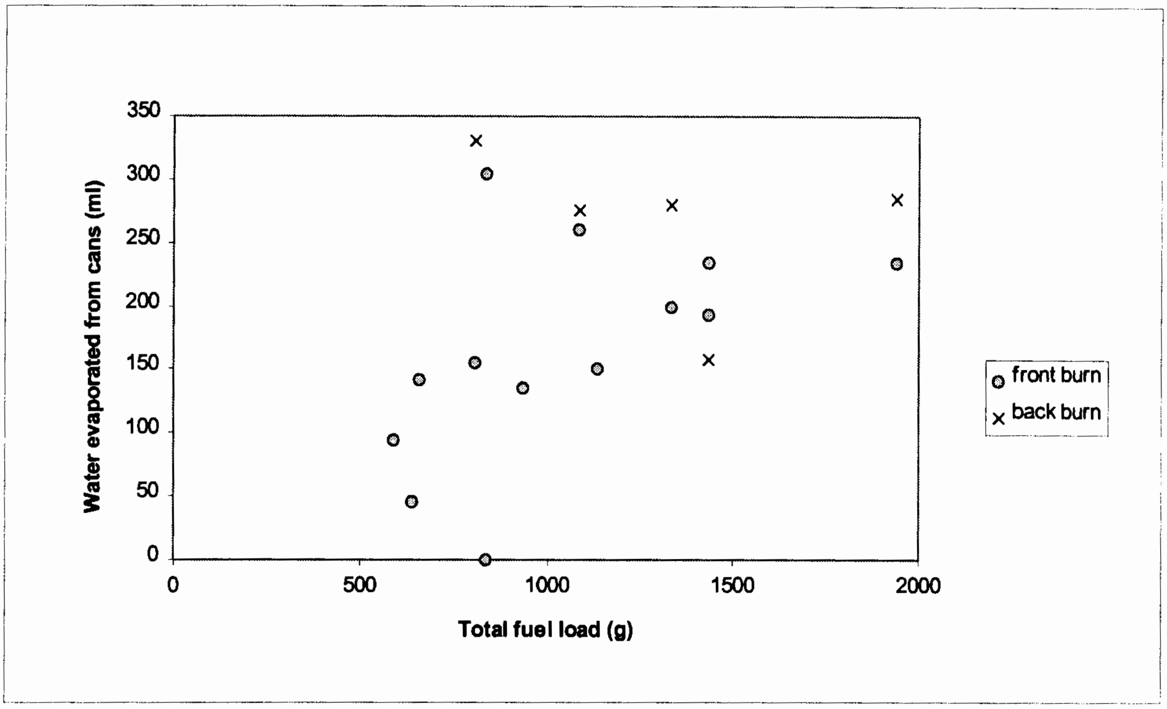


Figure 6: Graph comparing the relationship between fire intensity (indicated by the amount of water evaporated from cans(ml)) and total fuel load (<25mm diameter) for back-burned and front-burned plots at the Franschhoek study site.

Soil water repellency

In order to determine how fire affects soil water repellency of the soil, measurements of repellency were made both before and after the fire. Table 3 shows the mean water repellency for high and low fuel plots before and after the fire. Total water repellency in 0cm and 4cm soil layers did not increase after the fire as they were expected to in the high fuel plots. There was a trend towards decreased repellency after the fire in 0cm soil in high fuel plots and to a lesser extent in low fuel plots as expected. At 4cm, repellency increased in high fuel plots and to a lesser extent in low fuel plots as expected. However, Wilcoxin's test showed that these changes were not significant (high fuel plots changes for 0cm and 4cm soil layers were ($Z=1.325$; $p>0.05$) and ($z=0.255$; $p>0.05$) respectively; low fuel plot changes for 0cm and 4cm soil layers were ($Z=1.070$; $p>0.05$) and ($Z=1.172$; $p>0.05$) respectively).

Table 3: Mean water penetration times (n=10) and standard deviations (in parentheses) for different soil depths in high fuel and low fuel plots at the Franschhoek study site.

	Depth (cm)	**Mean water penetration time BEFORE FIRE (seconds)**	**Mean water penetration time AFTER FIRE (seconds)**	**Percentage change**
High fuel plots	0	13.42	9.24	-31.15
		(7.31)	(7.91)	(-8.21)
	4	25.31	29.68	+88.60
		(14.02)	(21.91)	(+56.27)
TOTAL	(0cm + 4cm)	38.73	38.92	+0.49
Low fuel plots	0	15.20	14.38	-14.38
		(9.78)	(18.25)	(+86.6)
	4	21.13	33.05	+56.41
		(12.97)	(20.97)	(-61.68)
TOTAL	(0cm + 4cm)	36.33	47.43	-30.55

Germination of planted seeds

Of the small seeds planted, only 5 individuals of *Dorotheanthus* germinated. Three of these were from low fuel plots and two were from high fuel plots and all five were from shallow-planted seeds. It is expected that this large-scale failure of seed germination is due to low seed viability.

A total of 362 of the 1600 large seeds that were planted germinated. Figure 6 shows the number of germinating seedlings of each species for the different conditions. The distribution of data was analyzed using the Kolmogorov-Smirnov test and was found to be non-normal. The Kruskall-Wallis test of 1-way ANOVA showed that differences between high and low fuel plots in both shallow-planted and deep-planted seeds were not significant (χ^2=1.978 and 1.818 respectively; $p>0.05$). The difference between shallow-planted and deep-planted seed germination was also found to be non-significant for both low fuel and high fuel plots (χ^2=3.200 and 0.000 respectively; $p>0.05$).

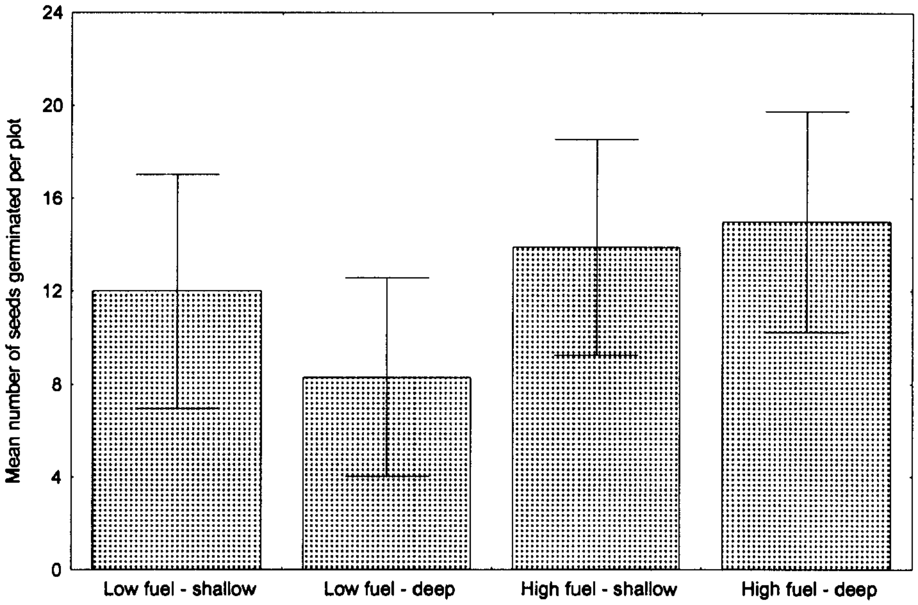


Figure 7: Graph showing means and standard deviations of seed germination per plot under combinations of high fuel, low fuel, shallow-planted and deep-planted conditions at the Franschhoek study site. Kruskall-Wallis 1-way ANOVA showed that there was no significant difference between any of the conditions ($p<0.05$).

The relationships between fire intensity and both shallow and deep germination are shown in figure 8. Data distribution was tested for normality and homogeneity of variances using Kolmogorov-Smirnov and Hartley's tests and were found to be non-normal. Spearman's rank order correlation coefficients were used to test the strength of these relationships. The relationship between fire intensity and shallow-buried seed germination was found to be nonsignificant ($R = -0.125$; $p>0.05$) as was the relationship between fire intensity and deep-planted seed germination ($R= 0.254$; $p>0.05$). There was, however, a slight trend of decreased germination at higher intensities amongst shallow-planted seeds and a trend of increasing germination at higher intensities in the deep-planted seeds.

The relationships between soil moisture content at the time of the fire and the number of germinated shallow-planted and deep-planted seeds are shown in figure 9. Kolmogorov-Smirnov and Hartley's tests on the data showed that it was non-normal (Statistica). The relationships between soil moisture and seed germination were quantified by Spearman's rank order correlation coefficients and it was found that soil moisture content was not significantly correlated to either shallow-planted seed germination (R= -0.259; p>0.05) or deep-planted seed germination (R= 0.105; p >0.05).

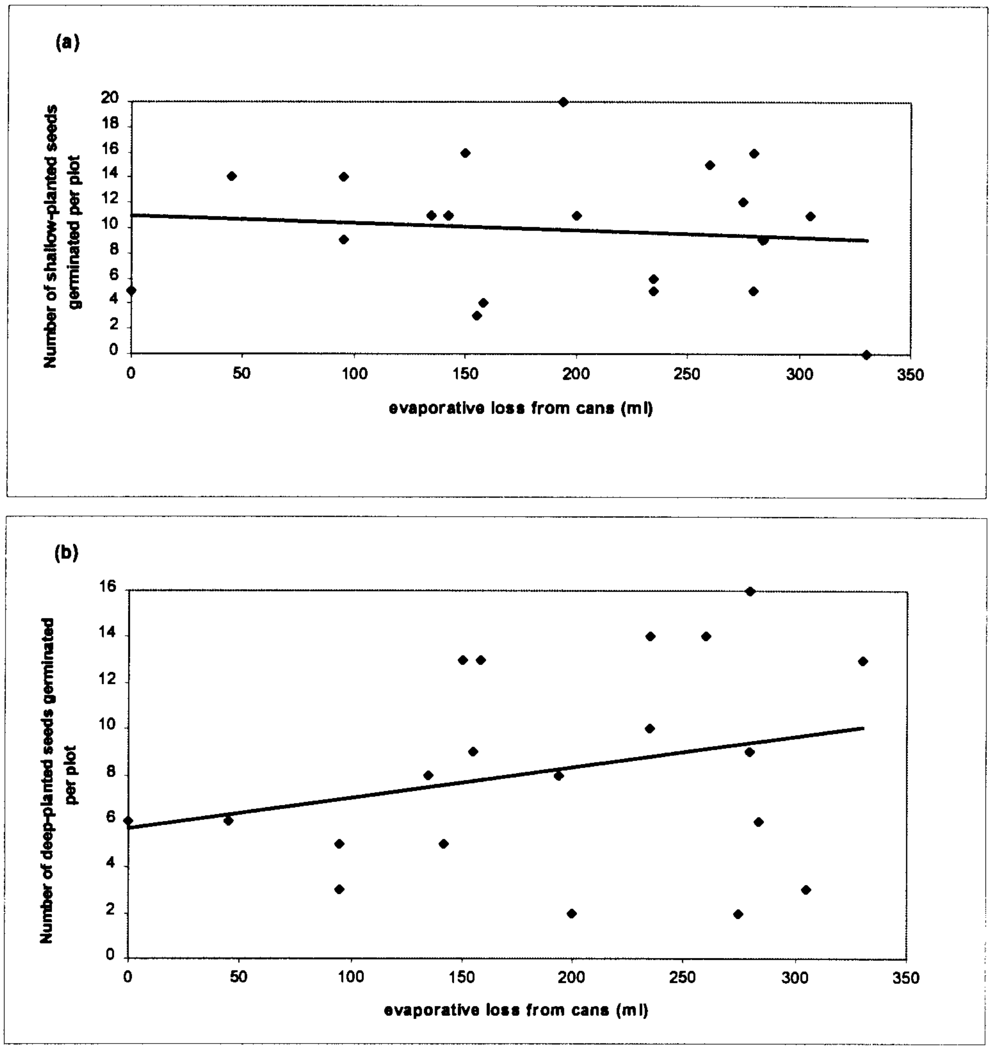


Figure 8: Graphs showing the relationships between fire intensity, as indicated by evaporative loss of water during the fire (ml) and (a) number of shallow-planted seeds (Spearman; R=-0.125; p>0.05) and (b) number of deep-planted seeds which germinated per plot (Spearman; R=0.254; p>0.05) at the Franschhoek study site.

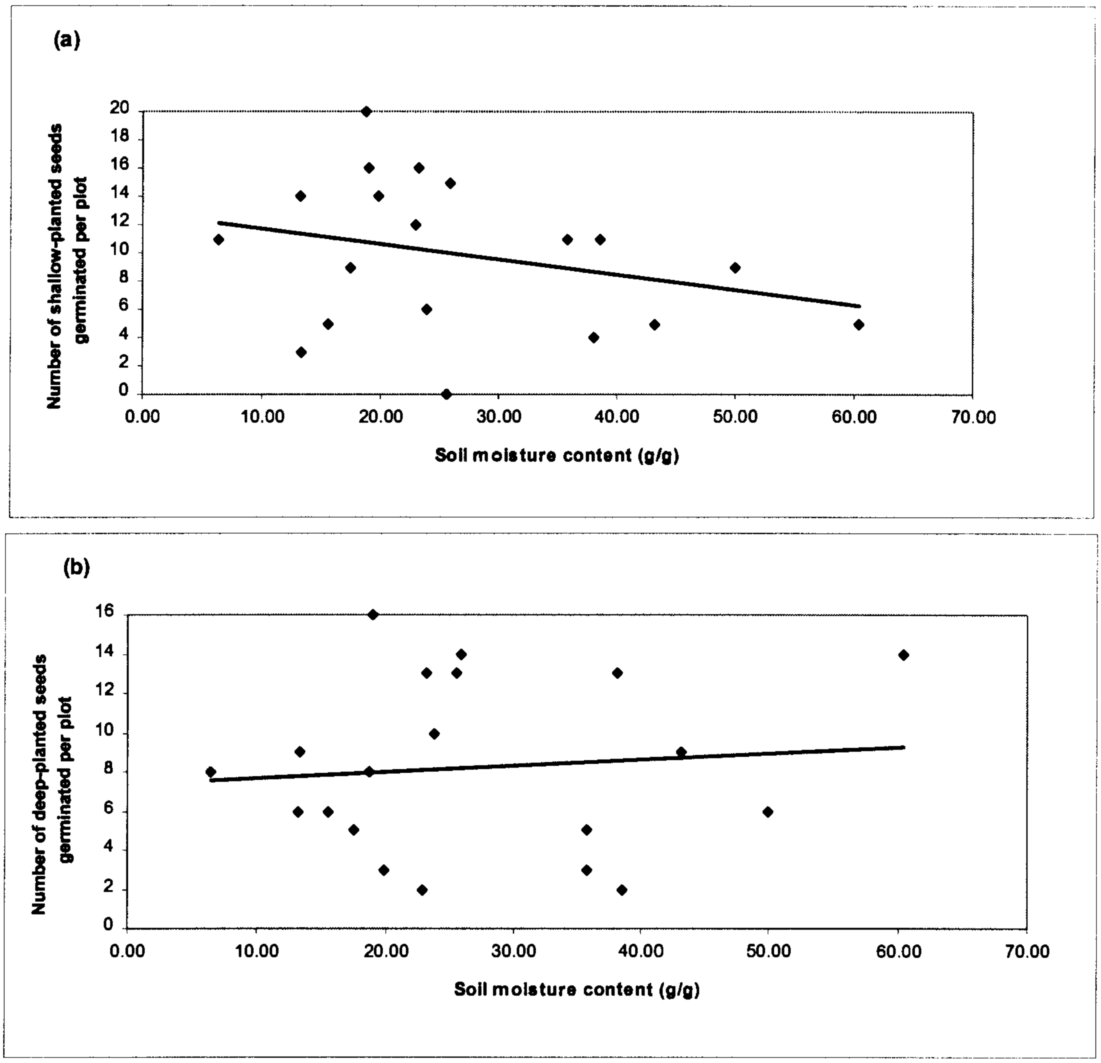


Figure 9: Graph showing the relationships between soil moisture content ($g_{water}.g_{drysoil}^{-1}$) and (a) number of shallow-planted seeds (Spearman; R=-0.259; p>0.05) and (b) number of deep-planted seeds germinated per plot (Spearman; R=0.105; p>0.05) at the Franschhoek study site.

Germination of naturally occurring seeds and resprouting

The relationships between fire intensity and species number, number of individual seedlings and number of resprouter individuals are shown in figures 10 (a-c). Mean number of species per plot ($1m^{-2}$) was 4.8 (SD=2.95) and mean number of individuals per plot was 27.05 (SD=44.35). Mean resprouter cover was 12.3% (SD=22.21). Using Kolmogorov-Smirnov and Hartley's tests, data was found to be non-normal. Spearman's rank order correlation analysis showed that there were significant negative correaltions between fire intensity and number of species per plot (R=-

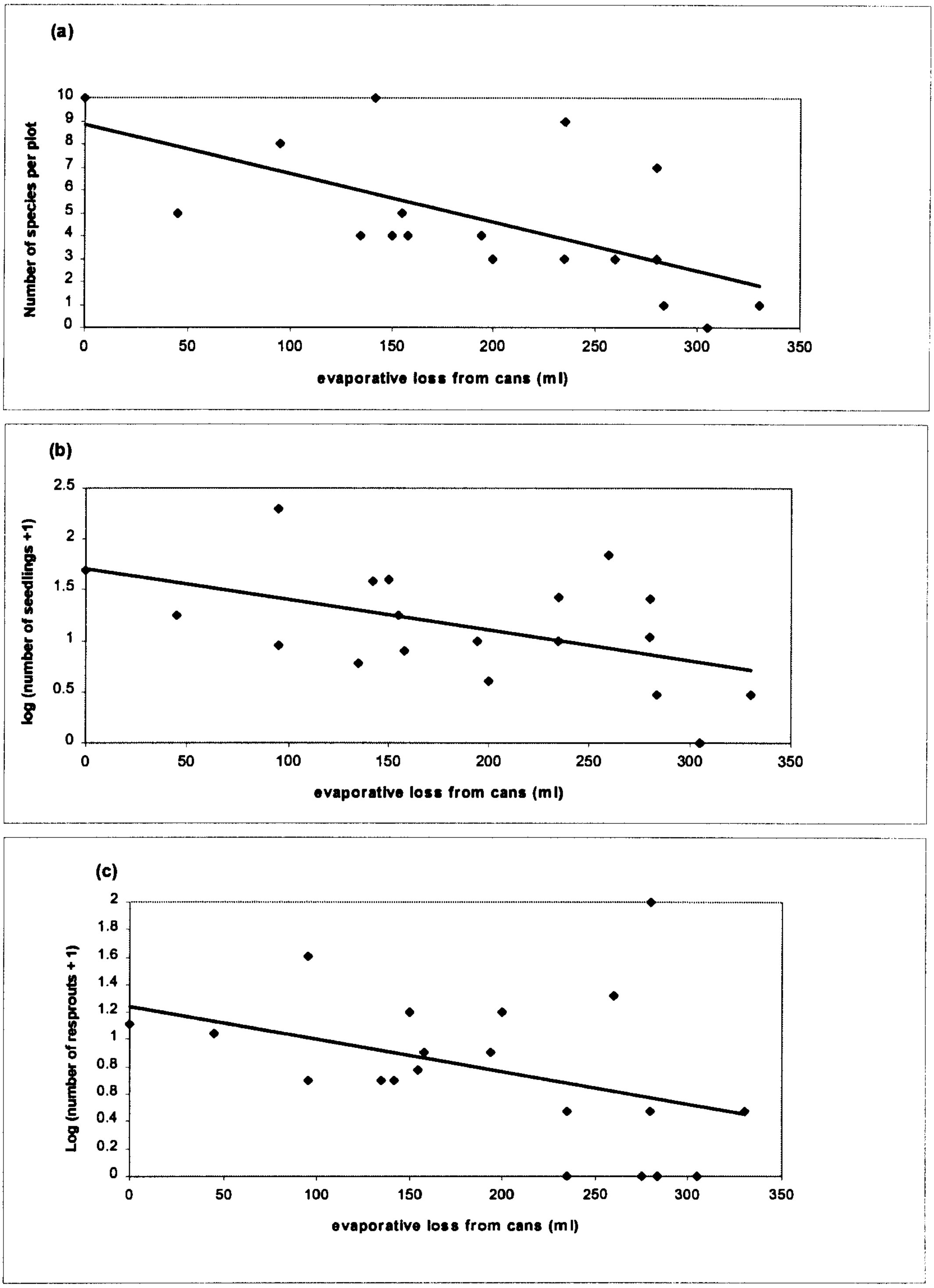


Figure 10: Graphs showing the relationships between fire intensity, as indicated by evaporative loss from cans (ml) and (a) number of species (Spearman; R=-0.741; $p<0.05$), (b) number of seedling individuals (Spearman; R=-0.485; $p<0.05$)and (c) number of resprouter individuals per plot (Spearman; R=-0.463; $p<0.05$) at the Franschhoek study site.

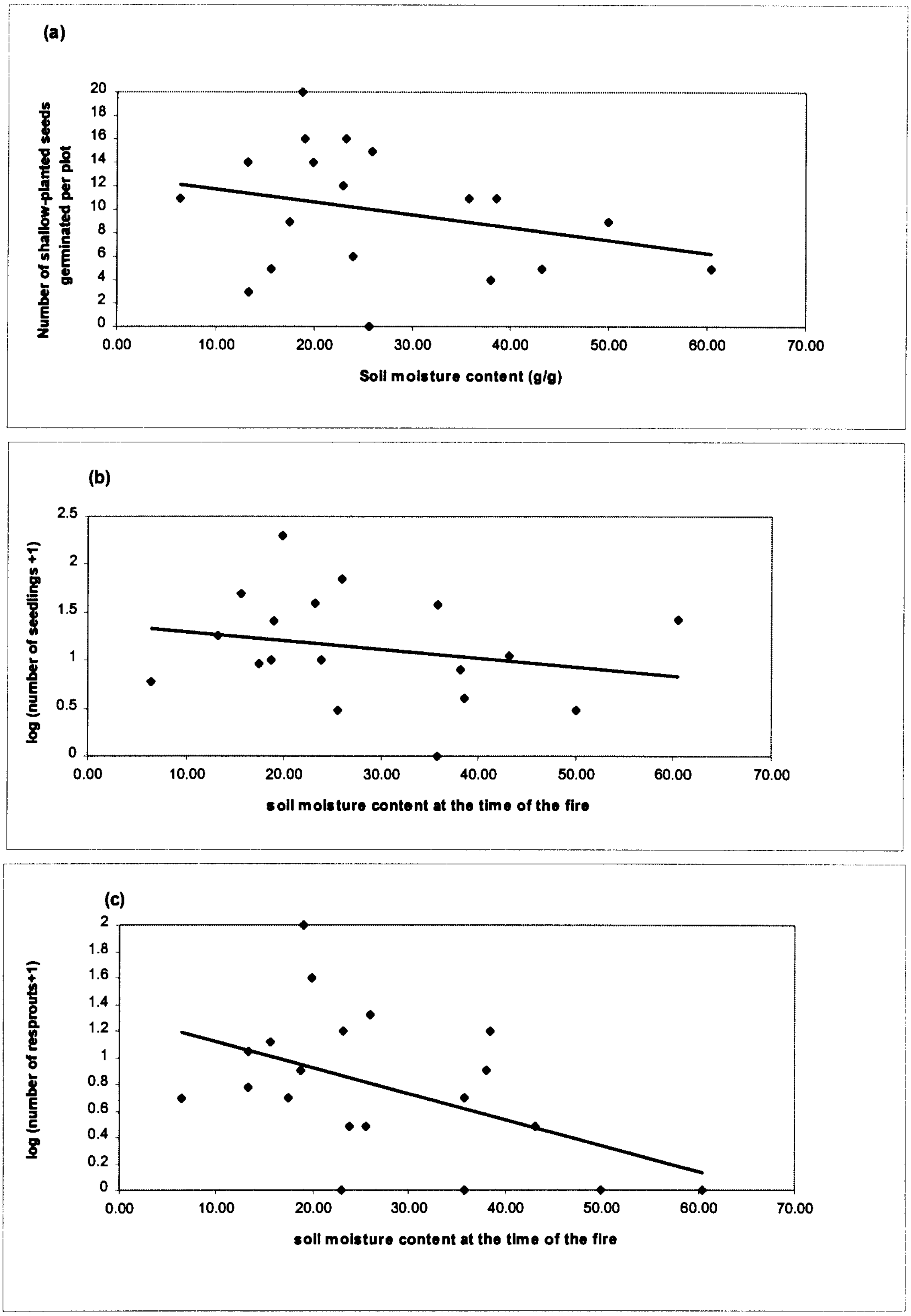


Figure 11: Graphs showing the relationships between soil moisture content (gwater.gdry soil-1) and (a) number of species (Spearman; R=-0.210; p>0.05), (b) number of seedling individuals (Spearman; R=-0.197; p>0.05) and (c) number of resprouter individuals per plot (Spearman; R=-0.375; p>0.05) at the Franschhoek study site.

0.741; $p<0.05$), log (number of individuals +1) (R= - 0.485; $p<0.05$) and log (number of resprouters +1) (R= -0.463; $p<0.05$). There was found to be no significant correlation between numbers of species and numbers of individuals (R= 0.064; $p>0.05$).

Soil moisture contents at the time of the fire were not found to be significantly correlated to species number (R= -0.210; $p>0.05$), log (number of seedlings +1) (R= -0.197; $p>0.05$)) and log (number of resprouters +1) (R=-0.375; $p>0.05$) (figure 11).

Part II: Erosion experiment and post-fire community observations, Villiersdorp

Erosion experiment

A large difference was found between the amount of sediment collected in traps in high and low intensity burn areas (plate 2). A strong positive relationship was observed between fire intensity, as indicated by the minimum remaining diameters, and sediment depths behind the walls of each of the sediment traps (n=12) (figure 12). Data distribution necessitated the use of a non-parametric statistical test and Spearman's rank order correlation coefficient describing the relationship was R=0.739 ($p<0.01$).

Post-fire seedling germination and resprouting

Invaded vs. uninvaded sites

The distribution of data was found to be non-normal using the Kolmogorov-Smirnov test for normality. The results of the Mann-Whitney U-test for significant difference (table 4) show that invaded sites had significantly larger minimum remaining diameters, numbers of stumps and logs and a significantly smaller number of individuals and percentage resprouter cover. Species richness was not significantly different between the two sites.

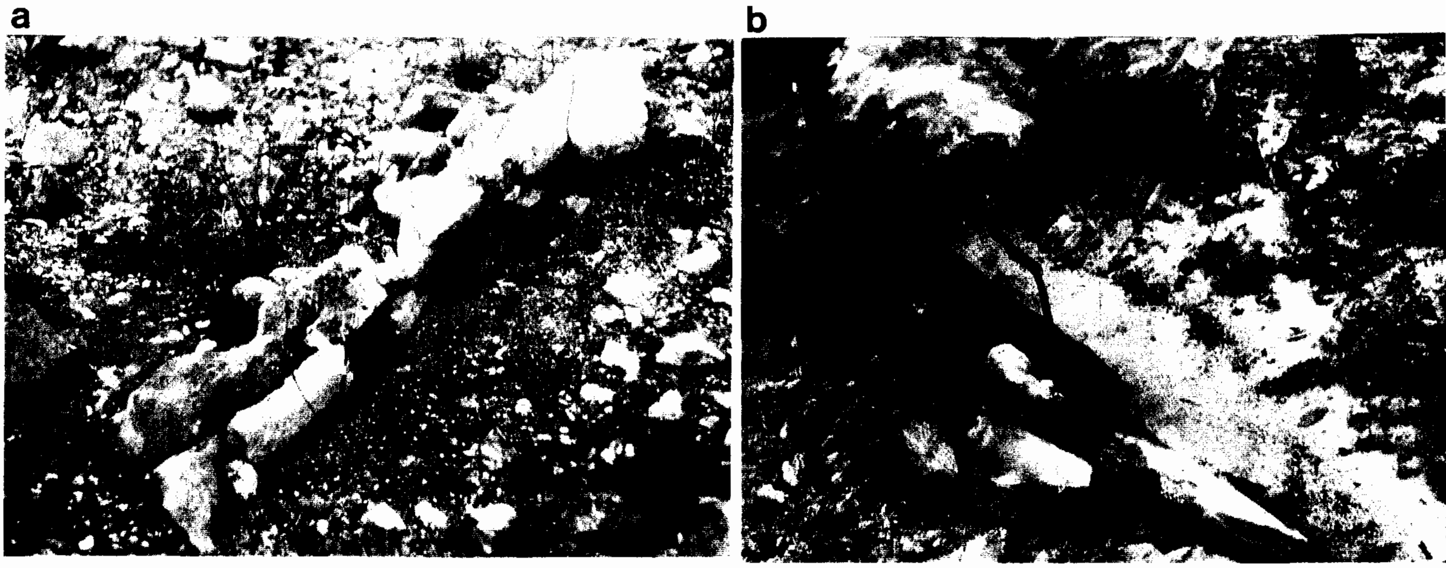


Plate 2: Photographs showing examples of sediment traps in (a) low intensity burn areas and (b) high intensity burn areas after 35 days, at the Villiersdorp site.

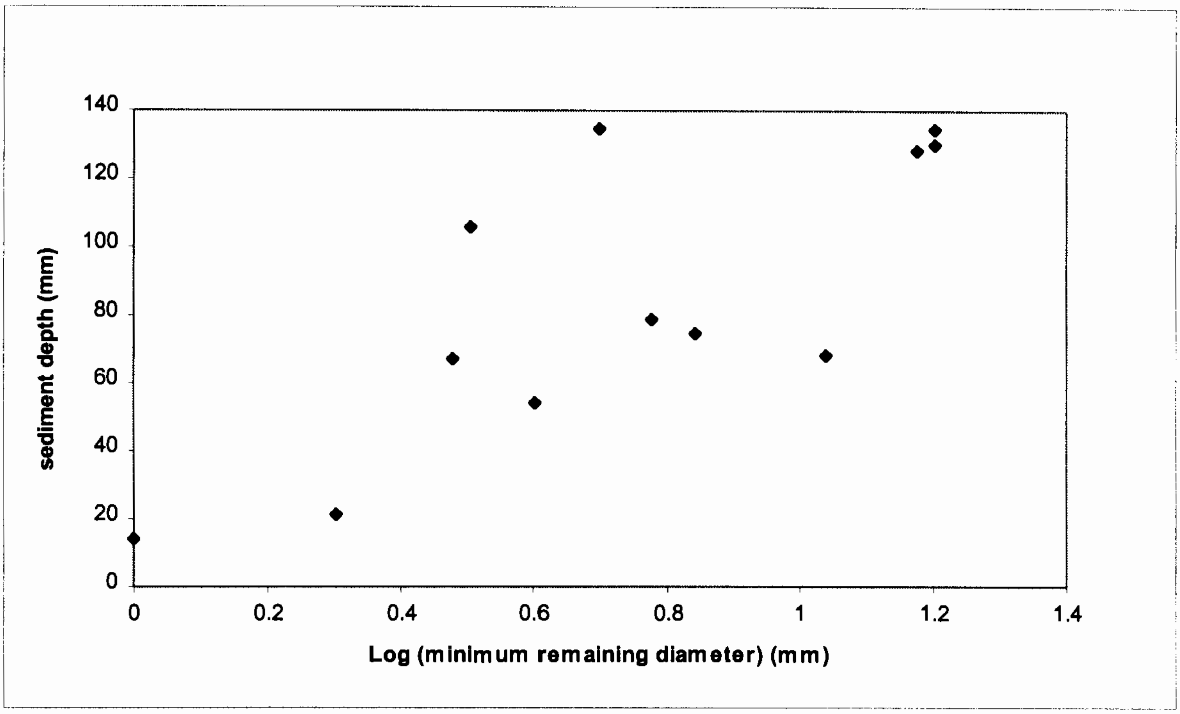


Figure 12: Graph showing the relationship between minimum remaining branch diameters (mm) and the log of sediment depth in sediment traps (mm) at the Villiersdorp study site (Spearman; $R=0.739$; $p<0.01$).

Table 4: The results of the Mann-Whitney U-test conducted to analyze differences between invaded and uninvaded sites at the Villiersdorp study site. Factors analyzed were minimum remaining branch diameters, numbers of alien stumps and logs, numbers of species and individuals of seedlings regenerating in transects and the percentage of the plots covered by resprouters.

	UNINVADED means		INVADED means		Z	Significance ($p<0.05$)
Minimum remaining diameter (mm)	1.55	n=8 SD=0.51	7.01	n=29 SD=4.64	-4.062	Significant
Number of stumps	1.43	n=7 SD=1.81	35.30	n=27 SD=21.23	-4.028	Significant
Number of logs	0.86	n=7 SD=1.21	6.07	n=28 SD=65.28	-2.995	Significant
Number of species (per $1.5m^2$)	11.75	n=8 SD=2.38	12.62	n=29 SD=3.45	-0.817	Not significant
Number of individuals (per $0.125\ m^2$)	28.16	n=8 SD=13.06	10.99	n=29 SD=8.98	3.672	Significant
Percentage resprouters	8.38	n=7 SD=4.44	1.69	n=28 SD=3.34	3.701	Significant

Fire intensity effects

Figure 13 shows the relationships between fire intensity as indicated by the minimum remaining branch diameter, and numbers of species, individuals and percentages of resprouter cover. Spearman's Rank order correlation analyses show that there were no significant correlations between fire intensity and either number of species ($R=0.161$; $p>0.05$), number of individuals ($R=0.032$; $p>0.05$) and percentage resprouter cover ($R=-0.361$; $p>0.05$). There was found to be a significant correlation between species numbers and individual numbers (Spearman; $R=0.564$; $p<0.01$).

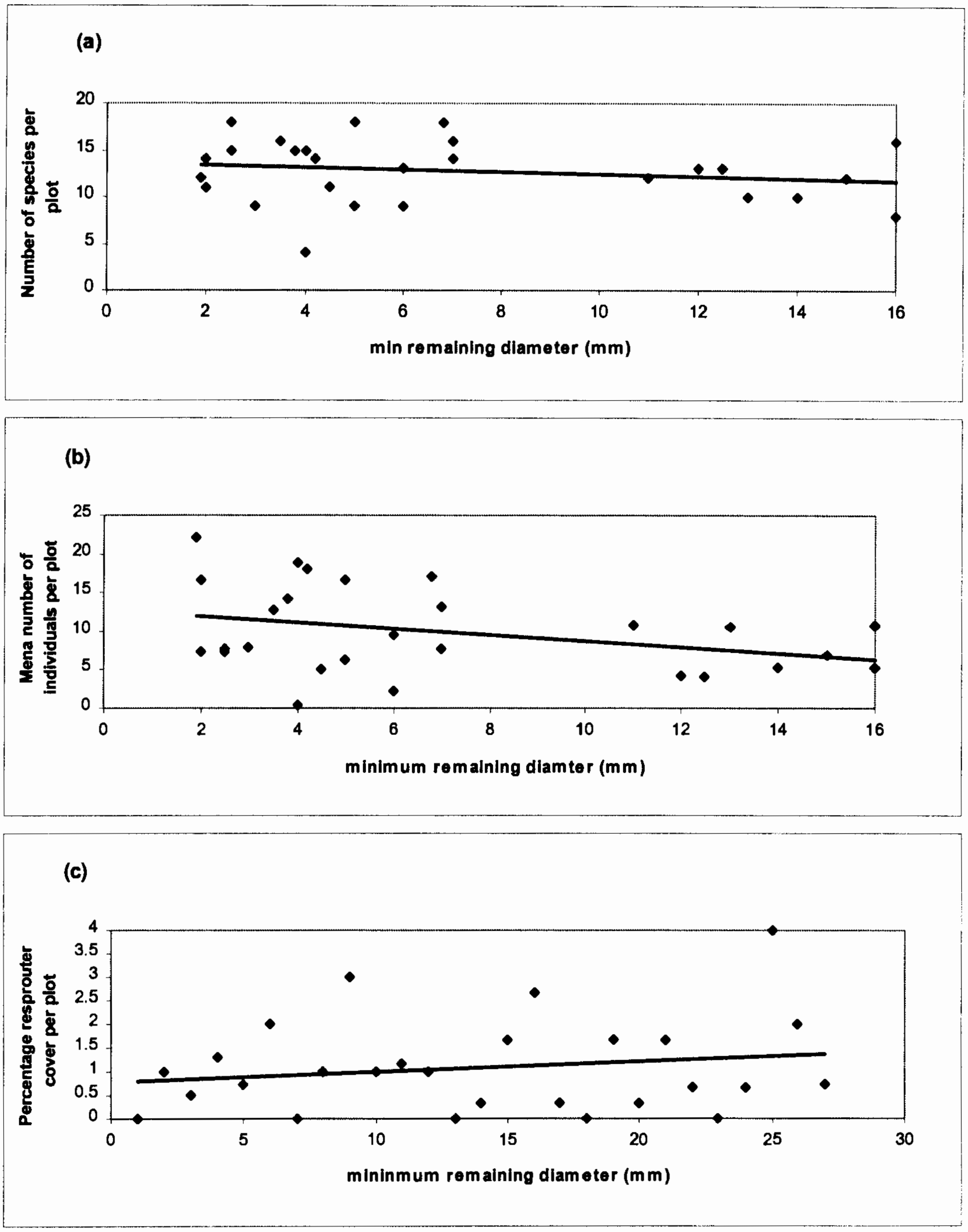


Figure 12: Graphs showing the relationships between fire intensity, as indicated by minimum remaining branch diameters (mm) and (a) numbers of species (R=0.161; p>0.05) (b) numbers of individuals (R=0.032; p>0.05) and (c) percentage resprouter cover (R=-0.361; p>0.05) per plot at the Villiersdorp study site.

North-facing vs. South-facing slopes

The results of Mann-Whitney U-tests (shown in table 5) indicate that there were no significant differences in fire intensity, number of species, number of individuals or percentage resprouter cover between north-facing and south-facing slopes.

Table 5: The results of Mann-Whitney U-tests conducted to analyze differences between north-facing and south-facing slopes at the Villiersdorp study site. Factors analyzed were minimum remaining diameters, numbers of species and individuals of seedlings regenerating in transects and the percentage of the plots covered by resprouters.

	NORTH-FACING means		SOUTH-FACING means		Z	Significance ($p<0.05$)
Minimum remaining diameter (mm)	7.66	n=14 SD=5.27	9.20	n=7 SD= 4.18	-0.597	Not significant
Number of species (per $1.5m^2$)	10.86	n=14 SD=3.72	12.71	n=7 1.80	-1.425	Not significant
Number of individuals (per $0.125\ m^2$)	9.52	n=14 SD=11.49	9.11	n=7 6.35	-0.336	Not significant
Percentage resprouters	4.35	n=12 SD=6.61	1.20	n=7 SD=1.38	0.421	Not significant

Felled vs. standing aliens

The results of Wilcoxin's test for significant difference between matched pairs, as shown in table 6, indicate that fires in felled areas were more intense (had significantly larger minimum remaining diameters) and that there are significant differences in minimum remaining diameter, number of species, number of individuals and percentage resprouter cover between felled and unfelled sites.

Table 6: The results of Wilcoxin's test for significant difference between matched felled and unfelled sites. Factors analyzed were minimum remaining branch diameters, numbers of species and individuals and the percentage of the plots covered by resprouters.

	FELLED means (n=8)		STANDING means (n=8)		Z	Significance ($p<0.05$)
Minimum remaining diameter (mm)	7.63	SD=4.77	3.98	SD=1.48	3.41	Significant
Number of species (per $1.5m^2$)	12.50	SD=2.72	15.63	SD=1.60	3.52	Significant
Number of individuals (per $0.125m^2$)	7.84	SD=3.09	15.22	SD=3.79	3.52	Significant
Percentage resprouters	0.87	SD=0.82	1.19	SD=1.04	1.87	Significant

Discussion

Fuel loads and fire intensity

Results indicate that total biomass (<25mm diameter) is a good predictor of fire intensity and that most of the fuel in this category is consumed by the fire. Ground fuel, medium-sized fuel and fine fuel are also valid indicators of fire intensity. These results are similar to those of Stinson and Wright (1969 in Whelan 1995), Beadle (1940) and Hobbs (1981 in Hobbs and Gimingham 1984).

It is important to note, however, that these fuel mass-fire intensity relationships may change if climatic conditions differ. In cooler, damper conditions more of the large fuel components would be unavailable for fire consumption, while in drier, hotter conditions a far larger percentage of the total fuel biomass becomes available. Fuel moisture content plays an important role in determining fire intensity (Bond and Van Wilgen 1996, Richardson and Van Wilgen 1986). Fire rate of spread, as influenced by wind speed during the burn, also has an effect on fire intensity (Hobbs and Gimingham 1984). The effects of wind on fire intensity are, however, contradictory. While higher wind speeds were reported to have a cooling effect by Hobbs and Gimingham (1984), Sparling and Smith (1966) and Smith and James (1978, in Hobbs and Gimingham 1984), increased fire intensities have been reported by Daubenmire (1968) and Whittaker (1961 in Hobbs and Gimingham 1984).

Fuel height distribution appears to play a large role in determining fire intensity at the soil surface. Intensity when fuel is concentrated close to the ground (approximately 5cm) is less than half as great as when a similar mass of fuel is situated above the ground (45-65cm above the soil surface). There appears to be a trend of increasing fire intensity with increased height of the upper fuel layers. However some threshold height must be reached, above which surface intensity begins to decline.

A possible reason for the greater fire intensity when fuel is elevated is that, while ground fuel is compacted, fuel higher in the profile is better mixed with air and more oxygen is therefore available during combustion. This fuel may combust more completely, thereby increasing energy output (Whelan 1995). Secondly, convective heat from the burning ground fuel would preheat and dry higher fuel making it more combustible. And thirdly, ground fuel moisture contents were exceptionally high (51.3%; SD= 2.287). This would greatly retard combustion and thereby cause ground fuel to become an insulating layer between the fire and the soil.

The use of water-filled cans to measure fire intensity appears to have been successful. The can size was ideal as the range of water loss was wide, though even where the fire was most intense, not all water was evaporated and thus no information was lost. It must be noted, however, that the can method of measuring fire intensity may not provide an accurate representation of soil exposure to heat under a situation where large logs remain smouldering for long periods after the fire. In such a case, little heat would be radiated, and there would thus be little heating of the can, even though a large amount of heat would be transmitted to the soil by conduction.

Soil erosion and water repellency

The significant increase in soil erosion after intense burns is in agreement with the findings of Scott and Van Wyk (1990, 1992), Richardson and Van Wilgen (1986), Cowling et al (1976 in Macdonald and Richardson 1986), Lindley et al. 1988 and Swanson (1981 in Whelan 1995). They indicate that in mountainous, rocky areas, fires after alien-clearing have a significant negative impact on the post-fire environment due to soil erosion. Management efforts therefore need to be directed towards minimising soil erosion. These are discussed later.

Total soil water repellency did not change after the fire in the high fuel treatment indicating no further induction of repellency due to higher fire intensity. There was, as hypothesised, a trend of decreased repellency at 2cm depth and increased repellency at 5 cm after the fire, but these changes were not significant. A possible reason for the lack of significant change in repellency is the high soil water content at the time of the fire. Scott and Van Wyk (1992) reported a large reduction in heating and thus in the potential for repellency induction at soil moisture content of 13.8% (mean gravimetric wetness). This is approximately half as wet as soils at the experiment site at the time of the fire (mean gravimetric wetness = 27.4%). Another complicating factor is that soils at the site had a very variable, but generally high clay content. Clay soils have higher moisture contents than other soil types in the area are thus less susceptible to water repellency (DeBano et al. 1970).

Another possible extraneous variable is the soil moisture content at times of sampling. As repellent soils gain moisture they become more repellent (DeBano et al. 1967, Gilmour 1968 in Scott and Van Wyk 1992). The post-fire repellency measurements were taken after heavy rains and this may thus have reduced the time taken for water to penetrate the soil. The spatial distribution of water in an area is also likely to have been heterogeneous (Beadle 1940). It therefore appears that the method of quantifying soil water repellency that was used in this study is not suitable for field measurement. Many of the above-mentioned problems could have been alleviated if soil conditions were standardised in a laboratory situation and with increased replication.

Since repellency and erosion measurements were conducted at different sites and after fires under different conditions, it is difficult to make inferences between the two. This study is unable to quantify the extent of the role that repellency plays in affecting post-fire soil erosivity. It does, however, suggest that factors aside from soil water repellency have contributed to a large extent to soil erosion. Fires remove litter and may consume organic matter in the upper 2-15mm of soil (Scott and Van Wyk 1990). This decreases soil water-holding capacity, increasing over-land flow and hence soil loss (Whelan 1995). This may be exacerbated by decreased transpiration (Lindley 1988). Fire may also burn roots which previously held soil together (Swanson 1981 in Whelan 1995) and may break down aggregates (Scott and Van Wyk 1992). The lack of vegetation after fire is directly related to soil erosion (Bond and Van Wilgen 1996) and may cause increased wind at the soil surface which will further increase erosion. A decrease in ground cover results in increased splash erosion (Whelan 1995) and a reduction in resistance to surface flow.

Seed germination experiment

The failure of the majority of small seeds to germinate under any fuel and moisture conditions and from either of the planting depths is likely to be due to low viability of the planted seeds. This study has therefore not succeeded in testing the second part of the proposed hypothesis (i.e. that small seeds would suffer greater mortality than large seeds in intense fires). The experimental study does test the validity of the first part of the hypothesis (i.e. that hotter fires kill seeds near to the surface). Results show that fire intensity has had no significant effects on large seed germination under experimental conditions.

It is difficult to interpret germination responses to fire intensity without data on the maximum temperatures reached at 2cm and 5cm soil depths and heating durations. Table 8 shows the findings of various studies on soil temperatures for different ecosystems and fuel types. There appears to be large variation in soil temperatures with depth, under different fuel loads and climatic conditions and in different ecosystems. Coupling maximum temperatures for heavy-fuel plots with threshold temperatures for large seed germination and mortality sheds some light on this problem.

Table 8: A summary of the maximum soil temperatures recorded during fires in various studies and different ecosystems. Authors and further details of the fires are given below the table.

	Maximum soil temperatures (°C)					
Soil depth (cm)	**0**	**2**	**4**	**5**	**7**	**10**
1. Bushland, SE Australia	>150	45	35	30	27	20
2. Mallee-shrublands, Australia	>150	43	37	35	34	33
3. Grass paramo, Equador	383	33				
4. Dense woodland, Jarrah (spring)	120	<45				
(autumn)	245	120	66	66	<45	
5. Pine forest, S-E U.S.A.	>110	75				
6. Chaparral, California	360	150	45	10	<10	
7. Slash fuels in forest	220	115	65	50	35	20
8. Eucalyptus forest, E. Austr. (Natural fire)	>250	110	100	85		
(Pile of logs completely burnt)	>250	>250	>250	250	230	140

1. Bradstock and Auld (1995). Head fire during strong wind.

2. Bradstock et al. (1992). Temperatures given indicate the means from 11 experimental fires with *Acacia*, *Eucalyptus* and *Triodia* fuels.

3. Ramsay and Oxley (1996).

4. Grant (1997). Spring fires took place when soil moisture content was high.

5. Heyward (1938 in Whelan 1995). Very high fuel loads in long-leaf pine forest.

6. DeBano et al. (1977 in Whelan 1995).

7. Neal et al. (1965 in Whelan 1995). Heavy slash fuels after logging in forest.

8. Beadle (1940). In the natural fire mostly undergrowth was burned. A Large timber pile was completely burned in a fire lasting 8 hours.

Jeffreys et al. (1988) found that *Acacia saligna* seed dormancy was significantly increased relative to unheated controls from temperatures of 60 °C for 5 or more minutes and 80 °C for 1 or more minutes. Mortality thresholds for *Acacia saligna* occurred at 100 °C for 60 or more minutes and 150 °C for greater than 5 minutes. *Virgilia oroboides* germination was only stimulated at 80 °C for 30 and 60 minutes. Comparing these temperatures with the range of expected maximum soil temperatures suggests that soil temperatures in high fuel plots at the Franshhoek site could have approached or surpassed the lethal temperatures for the large seeds. However, at the time of the fire, the soil moisture content was extremely high and this is likely to have decreased soil temperatures, particularly in the upper soil layers (Whelan 1995, Beadle 1940). Soil temperatures may therefore not have been in the proximity of the seed mortality threshold.

The proposal that high soil moisture contents are responsible for decreasing seed mortality is supported, firstly, by the fact that deep-seeded germination increases with increased fire intensity (figure 7(b)). This indicates that where fire was less intense, seeds did not receive sufficient heat to stimulate germination. Soil temperatures were probably closer to the threshold of germination than of mortality. Secondly, shallow-seeded germination decreases slightly with increased fire intensity (figure 7(a)), indicating that, although the relationship is not significant, some seeds may have been killed due to high temperatures near the surface. Large spatial heterogeneity in soil moisture (Beadle 1940) may also weaken the relationship between fire intensity and germination by decreasing the precision of trends. This means that the proposed hypothesis is not necessarily incorrect, but that this study has not succeeded in testing it during a fire under dry soil conditions in which the lethal effects of fire intensity would be most apparent.

Although high soil moisture contents reduce soil temperature, where intensities are high, seeds become subject to the action of hot water and steam and this has been suggested to have a negative effect on seeds (Beadle 1940; Whelan 1995). In theory, the hard seed coats of *Acacia saligna* and *Virgilia oroboides* are impermeable to water and would thus be unaffected by any level of soil moisture. However, Beadle (1940) found that the percentage germination of hard-coated seeds decreased with time of boiling. Boiling for five minutes reduced germination from

98% to 63%, while boiling for 70 minutes decreased germination to 3%. Results from the Franshhoek experiment suggest that germination of shallow seeds is negatively (though not significantly) related to soil moisture. This could indicate that moist heat has adversely affected seeds. The stronger (though still not significant) relationship between soil moisture and naturally-occurring seed germination supports this. Deep-seeded germination shows no relationship with soil moisture and this may be because there was insufficient heat to vaporise water at this depth.

Germination of naturally occurring seeds and resprouting

Significant differences between minimum remaining diameters and the number of remaining logs and stumps in the invaded and uninvaded sites confirm that fuel load differences have resulted in much greater fire intensities at the invaded sites. The fact that this does not affect seedling species number is surprising, particularly as there are large effects on the number of seedling individuals. It is likely that the decrease in number of individuals will ultimately have an effect on species number, however, particularly as species numbers and individual numbers are highly correlated. The reduction in seedling numbers suggests that the first part of the proposed hypothesis is true i.e. more seeds are killed where fire is most intense. It was not possible to relate seedling emergence to seed size.

As mentioned previously, it is important to distinguish between invasion effects due directly to competition such as shading of native plants by the taller invasives, and those due to increased fuel loads. The results of the study on fire intensity effects potentially helps to distinguish the effects of the two components. At the Villiersdorp site, where the data for the comparison between invaded and uninvaded sites was collected, there appears to be no significant relationship between fire intensity and seed germination. This suggests that the differences between invaded and uninvaded sites are due purely to competition effects before the fire. However results of intensity effects on germination at the Franschhoek site contradict this. In this case the species number showed a significant decline with increasing fire intensity and the relationship between number of individuals and intensity was logarithmic and significant.

These results are difficult to explain purely in terms of fire intensity. Although the climatic conditions at the time of the Villiersdorp wildfire are unknown, soil moisture conditions in February are likely to have been drier than at the Franschhoek site which was burned after heavy rains and one would therefore expect *greater* effects of intensity on seedling emergence at the Villiersdorp site. It is impossible to compare pre-fire fuel loads at the two sites, but post-burn observations of rock fragmentation and termitaria shattering at the two sites do not reveal any pronounced differences in intensities.

A factor in which the two sites differed markedly, however, is the duration of alien invasion prior to the fires. While the Franshhoek site was invaded for approximately 47 years prior to the fire, the Villiersdorp site had only been invaded recently (within one fire cycle; approximately 12 years). Holmes and Cowling (1997) studied vegetation recovery after clearing all vegetation from sites in uninvaded, recently invaded (1-2 fire cycles) and long-invaded stands (25+ years). They found that species richness was almost as high in the recently invaded stands as in the uninvaded fynbos. This may explain why, at the Villiersdorp site, there was no significant difference in number of species between invaded (mean=11.8; SD=2.4) and uninvaded sites (mean = 12.8; SD=3.5). Holmes and Cowling (1997) also found that seedling species richness declined steeply with stage of invasion. This is also consistent with the results of this study which show the Villiersdorp site had a mean species richness of 12.62 species per plot (SD=3.45) while the longer-invaded Franschhoek site had a mean of 4.8 species per plot (SD= 2.95).

The relationships between resprouter abundances and fire intensities at the Franschhoek and Villiersdorp sites, like seedling abundances, seem contradictory. While number of resprouters decreases with increased fire intensity at the Villiersdorp site, there seems to be no relationship between the two variables at the Villiersdorp site. Holmes and Cowling (1997) found that in both uninvaded and recently invaded fynbos, resprouters formed about half the canopy cover, but that resprouter cover was insignificant at the long-invaded sites. The gradient in number of resprouters with intensity at the Franschhoek site may thus be due to the effects of different invasion densities at the site and not due to the fire intensity itself. This is in agreement with the findings of and experiment by Beadle (1940) which showed that plants possessing lignotubers are rarely killed by fire. Percentages of resprouter cover at the Villiersdorp site are similar to the value found by Richardson and Van Wilgen (1996) after a fire in a *Hakea* invaded area. The trend in decrease in resprouter number with increased soil moisture at the time of the fire, though insignificant, may indicate that moist heat has negative effects on resprouter survival.

The similarities between many of the findings of this study and those of Holmes and Cowling (1997) indicate that much of the observed vegetation response within sites is determined by the directs effects of alien invasion. While increased fire intensities as a result of felled alien fuel may be influencing seed and resprouter mortality as hypothesised, these effects play only a minor, secondary role in determining post-invasion community structure.

Another possible explanation for the apparent contradiction in seedling emergence results from the two sites is that, while both sites were rocky, the Villiersdorp site was markedly rockier than the Franschhoek site. Rocks have high thermal inertia and would therefore have been unlikely to reach high temperatures during the fire. As a result, they may have kept soil immediately surrounding them cool and deflected heat from certain soil patches during the fire, thereby providing refugia for the seeds. This heterogeneity of heating may have allowed more seeds to escape mortality at the Villiersdorp site than the more uniform heat to which soil-stored seeds at the Franschhoek site were exposed.

Sites at which aliens had been felled prior to the fire showed higher fire intensities as well as lower seed germination and resprouter cover. This is despite the fact that fynbos in felled sites was free from alien competition for at least 6 months prior to the fire. This suggests that fire intensity is responsible for the changes, though the other results from this study decrease confidence in this conclusion. Another possibility is that the dense litter layer that remained after felling shaded the soil to the extent that flowering or even germination of the indigenous vegetation was repressed. The differences in post-fire germination may therefore be due to pre-fire differences in the abundance of soil-stored seed.

The lack of any differences in seedling germination or resprouting between north-facing and south-facing slopes was also unexpected as differences in overall greenness of the two sides of the valley were observable from a distance. The soil moisture conditions at the time of the Villiersdorp fire are unknown. Although there are differences in rainfall on the opposite aspects, the fire occurred during the dry season and if it followed a particularly hot, dry period, as is likely for a wildfire, then soil moisture content of the upper soil layers was likely to be similar.

The results of this study indicate that alien invasion does not necessarily lead to large decreases in fynbos biodiversity. Similar findings were reported by Kruger and Van Wilgen (1981 in Richardson and Van Wilgen 1986) after a fire in felled *Hakea* stands in Zachariashoek. There is, however, evidence from other studies that disastrous effects can occur. Richardson and Van Wilgen (1986) found drastic decreases in vegetation cover, species number and resprouters after a wildfire in felled *Hakea* stands in the Wemmershoek area and similar results were found by Van Wilgen and Holmes (1986 in Richardson and Van Wilgen 1986) after piles of *Acacia cyclops* were burnt. Breytenbach (1986) described similar findings and from a nursery experiment, he discovered that seedling numbers decreased substantially in *Hakea*-invaded sites.

It is unlikely that the inconsistencies between the results of these studies are due to erroneous study methods as similar study methods used by the same author have indicated both negligible (Van Wilgen and Kruger 1981) and severe effects (Richardson and Van Wilgen 1986) at different sites. It is more probable that the inconsistent results are due to differences in fire characteristics and/or site differences. Fuel loads in the Franshhoek experimental burn were far lower than those simulated for the Wemmershoek fire (Richardson and Van Wilgen 1986). Heavy logs were placed in piles in the study of *Acacia cyclops* (Van Wilgen and Holmes 1986). Soils in the Wemmershoek area were deep and the area was not rocky so the lack of seed refugia may be responsible for the more severe effects of fire at the Wemmershoek site.

The broad range of findings from the few fire-intensity related studies in fynbos highlight the difficulties involved in measuring and comparing fire intensity in the field, (particularly as it is affected by so many variables). It must also serve as a warning against rigidly applying the findings of one study to the entire fynbos biome. Conclusions at this time are tentative and must be treated as such. Each new study, however, is a step to understanding the nature of fire intensity and its ecological effects.

Management implications

The direct effects of alien invasion i.e. competition with indigenous vegetation, appear to play the dominant role in decreasing fynbos biodiversity in the areas investigated in this study. The first priority of management should therefore be to remove alien vegetation as soon as possible. The indirect effects of invasion i.e. increased fire intensities, seem to play a minor role in comparison. However, the marked direct effects of invasion make ensuring the survival of the maximum number of remaining species during fire all the more important in fynbos which is already depleted in species richness.

In areas where pines have been felled, the mass of fuel per square meter provides a good indication of the intensity with which a fire will burn. Based on this, as well as on climatic factors, managers should decide on fire control measures and manpower needed during the fire.

The number of seeds and resprouters killed can be reduced by minimising soil temperatures during fires. The following actions can help managers to reach this goal:

1. Burning in autumn i.e. at the beginning of the wet season, or shortly after heavy rains when fuel moisture contents are high (though fuel is sufficiently dry to ignite) will keep heat released from fuel well below its potential maximum. Lower fire intensities will result and this keeps soil temperatures down. Though high soil moisture may have negative effects on seeds due to the action of steam, it's primary effect is to reduce soil temperatures during fires.

2. At the time of burning, fuel less than 25mm in diameter should ideally be moist, compacted and situated close to the ground as this fuel then burns with a lower intensity than when placed

above the ground. In this position, it may act to some extent as an insulating layer between fire and the soil. Fuel should not be concentrated in piles or in one particular area, and should preferably be spread evenly over the planned burn site. Where possible, large logs should be elevated so that they are not in contact with the soil. This will reduce conductive heating of the soil while logs smoulder for long periods after the fire.

The above actions will help to decrease post-fire soil erosion as well as reducing the induction and movement of water repellency in soils. The evenly distributed, partially burnt logs will act to some extent as erosion blocks during rains after the fire.

3. The processes responsible for the strong negative effects of felled aliens compared to standing aliens are not resolved. However, this study's results clearly show that burning standing aliens has significantly fewer biodiversity costs than burning felled aliens. *Pinus pinaster* releases seeds at approximately six years of age (Bond pers. comm.). Stands should therefore be burnt before they reach this age, and reinvasion by seedlings should not result. In stands older than 6 years, biodiversity costs of burning twice within 6 years must be weighed against those associated with using the 'slash and burn' strategy and burning felled aliens.

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