The influence of fire severity on recruitment of fynbos
with particular emphasis on seed size: a field study in
the Cape Peninsula

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Abstract

Fifty-two sites throughout the Cape Peninsula area burnt in the January 2000 fires were sampled to investigate the effects of fire severity on the recruitment of invasive and fynbos plants with particular emphasis on seed size. Four hundred fynbos species were divided into big- (>10mg) and small-seeded (<10 mg) species. Different measurements of burnt plant skeletons were examined to find the most appropriate indicator of the biological effects of a fire. It was found that the measurement of thinnest branch diameter of plant species with similar growth forms can be used as estimates of fire severity. Seedling density of fynbos species decline with an increase in fire severity, whereas recruitment of alien seedlings is not affected by fire severity. Big-seeded species and seedlings showed no significant correlation with fire severity, whereas the density of small-seeded species and seedlings correlated significantly with fire severity. It is likely that variations in fire severity that influences the depth to which seeds are killed will affect the ability of small seeds to emerge. High severity burns may thus have a different community composition by favouring the survival of big-seeded species.
Introduction

Fire is a key disturbance factor in many Mediterranean ecosystems and is an important selective agent of life-history traits. Most plant species characteristic of fynbos vegetation are considered adapted to survive fires (Bond and van Wilgen, 1996). These plants survive fire by resprouting and/or germination of soil and canopy-stored seeds (Bond and van Wilgen, 1996). Over 300 species of fynbos plants have serotinous (canopy-stored) seeds (Fraser 1990), whilst 20% (1300 species) of all fynbos plant species are buried in the soil by ants (Bond and Slingsby 1983). Overall nonsprouting plants that regenerate from soil-stored seeds are the largest component in terms of species numbers and biomass in the fynbos (Cowling et al., 1987). Thus understanding how fire affects the recruitment of seed regenerating plants is an important informant in prescribed burning practices.

Intense heat shock, chemicals leached from charred wood (Keeley, 1991) and soil heating (van der Venter and Esterhuizen, 1988) improve germination of soil-stored seeds. Although high soil temperatures provide the germination cue for many seeds, threshold intensities exist above which mortality results (Richardson and van Wilgen, 1986; Núñez and Calvo, 1999). It has been suggested that seed size is an adaptive trait to fire, as larger seeds are more likely to survive after heat shocks (Escudero, Núñez and Perez-Garcia, 2000). Bond, Honig and Maze (1999) showed that larger seeds are able to emerge from deeper soil depths (40mm) than smaller seeds. Big-seeded species are thus favoured in high intensity fires that kill seeds in the surface soil layers, by having the extra resources to emerge from deeper down (Bond et al., 1999).

Small-seeded species will thus only recruit successfully after low intensity burns and big-seeded species that are able to emerge from deeper soil depths will be able to survive more intense fires (Bond et al., 1999; Delgado et al., 2001). Very few field studies have been done to support this hypothesis. Many of the myrmecochorous (ant-dispersed) seeds are large (10 by 6 mm to 2 by 2mm) and are buried in ant’s nests 4 to 7 cm below the soil surface (Bond and Slingsby, 1983).

High intensity burns may thus favour ant-dispersed species. Seedling recruitment of two myrmecochorous species (*Leucospermum conocarpodendron* and *Mimetes fimbrifolius*)
was strongly correlated to fire intensity (Bond, Le Roux and Erntzen, 1990). Musil and de Wit (1990) showed that seeding perennials in a sand plain lowland fynbos community with large mainly myrmecochorous seeds emerged sooner after fire and from greater depths than species with smaller seeds. Richardson and van Wilgen, (1986) showed a shift from resprouters to seeders after high-intensity fires in areas that had been cleared of alien trees and shrubs.

In January 2000, fires burnt nearly 8 000 hectares across the Cape Peninsula. Hot daily temperatures (on the second day of the fire a maximum temperature of 41 °C was recorded) and preceding gale-force winds decreased moisture content of plants, rendering even young stands of fynbos highly flammable. These unusually hot fires motivated an investigation on the effects of fire intensity on the regeneration of fynbos. The effects of alien plants and global warming may increase the “natural” fire intensities (van Wilgen 1984) for which fynbos vegetation is adapted. As part of a long-term study on fire severity and the effects of invasive plant clearing methods on the regeneration of fynbos, the effects of fire intensity on recruitment and particularly the potential relationship between seed size and fire intensity were investigated.

Post-hoc measure of fire severity

One of the important tasks was to find a post-hoc measure of fire intensity that could be used across a wide range of sites as an estimate of fire intensity. Fire intensity is measured as energy released per meter of fire front (Bond and van Wilgen, 1996). The most commonly used measure of fire intensity is Byram’s fireline intensity: \( I = Hw \). Where \( I \) is the fireline intensity (kW m\(^{-1}\)), \( H \) is the heat yield of the fuel (Jg\(^{-1}\)), \( w \) is the mass of fuel load consumed (g m\(^{-2}\)), and \( r \) is the rate of the fire spread (ms\(^{-1}\)) (Bond and van Wilgen, 1996).

Although fire intensity is useful in estimating the behaviour of a fire, it has been argued that the ecological impact of a fire is better categorized by estimating fire severity (Keeley and Fotheringham, unpubl. report, Whelan 1995). This is because a slow-moving fire that consumes more biomass than a fast-moving fire can have the same fire-line intensities but different severities (Bond 2000). Fire severity is a distinct but related concept to fire intensity and is often measured as the amount of biomass that is consumed in a fire.
Post hoc indicators of fire severity include measuring minimum branch diameters remaining on burnt plants after a fire (Moreno and Oechel, 1989; Perez and Moreno, 1998). In a South African study, the amount of green and dead material in Proteaceae canopies was used as estimates of fire severity (Bond et al., 1990).

The measure of smallest twig diameter as an estimate of fire severity (Moreno and Oechel, 1989) is based on the assumption that thinner branches will remain on burnt vegetation in lower intensity fires as compared to high intensity fires. There are a number of difficulties in using minimum branch diameter as a measure of fire severity. In homogeneous communities where stands are often dominated by a single species, the response of a single species across a range of fire severities can be measured. It becomes more difficult to measure fire severity in heterogeneous environments where one species is not dominant throughout the landscape because twig diameter of different species might not have comparable architectures. Furthermore some plant species with large leaves (like many Leucospermum spp.) never have very thin branches. Therefore, the same twig diameter for a burnt ericoid and proteoid may indicate very different fire severities. This problem, as well as other methods of measuring skeletal remains was investigated to establish the best post-burn biological estimate of fire severity.
Study area

The Cape Peninsula lies in the southwest corner of the Cape Floristic Kingdom. It covers an area of around 470 km² that includes the entire Peninsula Mountain Chain and the western portion of the Cape Flats. The Cape Floral Kingdom is the world’s smallest and, for its size, richest of the six recognized plant kingdoms, with over 8500 plant species occurring in a very small area (90 000 km²). The Peninsula flora, comprising over 2285 species, is the richest for any similar-sized area both in the Cape Floral Kingdom and elsewhere in the world.

The Peninsula geology has representative samples of all the major formations of the Cape Floral Kingdom: quartzitic sandstones of the Table Mountain Group, Malmesbury Group shales, granites of the Cape Suite and a lowland mantle of Quaternary sands. The climate is Mediterranean with warm, dry summers and cold, wet winters. Rainfall varies considerably in different parts of the Cape Peninsula, from 1900 mm on top of Table Mountain (1083 m), 1340 mm at Kirstenbosch, to 457 mm and 305 mm at Signal Hill and Cape Point respectively.

Study sites

Fifty-two sites were chosen throughout the area burnt in the January 2000 fires. Sites were selected according to geology, geographical location, accessibility, altitude, vegetation type, alien plant cover, including cleared alien sites where debris had been removed or stacked on-site before the fires. Some sites were not fully representative of the full range of criteria and some inaccessible sites could not be sampled.

Study sites were permanently marked with steel pegs at the corners of the six, 100 m² plots, within the 600 m² site (Fig. 1). GPS co-ordinates of the top right corner (plot 1) of the site was taken and the site location was marked on 1: 50 000 topographic maps. In this study, a subset of the sites to compare vegetation recovery between fynbos (19 sites) and invasive species (22 sites) was used. Sites where invasives had been cleared before the fires or where aliens were stacked on site after clearing were included. The plots in invaded areas included sites where invasive plants comprised 50% or more of the total plant biomass before the fire.
Methods

Sampling methods were taken from Keeley (1998). Each site is 600 m², subdivided into six 100 m² plots, with two 1 m² plots inside each 100 m² plot (Fig. 1). The upper (up slope) right hand corner (if one is facing down the slope) was always taken as plot number 1 (100 m²), and the 1 m² subplots within Plot 1 was labelled as a and b. The plots (1 to 6) and 1 m² subplots (a to f) were labelled in a similar sequence as shown in figure 1. Abiotic variables were sampled for the whole site; the six 10 m 10 m plots were sampled for burnt plant-skeletal remains characteristics, species diversity and recovery data. Various characteristics (Table 1) were measured for two burnt plant skeletons in each 1 m 1 m subplots (12 per site) for all 52 sites. The % cover, density (number of seedlings per species) and regeneration mode (resprouter, reseeder or both) of all species were also recorded for each subplot.

Figure 1 Each site (20 m 30 m) was laid out in a “Whittaker” design and divided into six 10 m 10 m subplots. Two 1 m 1 m plots were marked within each subplot.

This study focuses on data collected for skeletal remain characteristics and seedling density at the 1 m 1 m subplots level. The term subplot will be used to refer to a 1 m 1 m plot.
**Post-hoc measure of fire intensity**

Table 1. Summary of the measurements taken for two burnt plant skeletons in 12 1m × 1m subplots per site as a measure of fire severity

<table>
<thead>
<tr>
<th>Measurement</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>The two nearest canopy skeleton genus &amp; species</td>
<td></td>
</tr>
<tr>
<td>Smallest twig remaining on two nearest canopy</td>
<td></td>
</tr>
<tr>
<td>skeleton (diameter, cm) below and above knee height (0.5m)</td>
<td></td>
</tr>
<tr>
<td>% of nearest shrub and canopy skeleton remaining</td>
<td></td>
</tr>
<tr>
<td>below and above knee height (0.5m)</td>
<td></td>
</tr>
<tr>
<td>Basal diameter of two nearest skeletons</td>
<td></td>
</tr>
<tr>
<td>Actual height of two nearest shrub skeletons</td>
<td></td>
</tr>
<tr>
<td>Extrapolated height (height before fire) of two nearest shrub skeletons</td>
<td></td>
</tr>
<tr>
<td>Number of charred stumps (present/absent)</td>
<td></td>
</tr>
<tr>
<td>Maximum diameter charred stumps (cm)</td>
<td></td>
</tr>
</tbody>
</table>

The various measurements taken from burnt plant skeletons remaining after the fire are summarized in table 1 and illustrated in figure 2. The two plant skeletons nearest to the centre of the subplot were measured. The diameter (cm) of the smallest twig remaining on the two burnt plants below and above 0.5m (that is from approximately below knee height to the soil surface and above knee height) was recorded. The assumption is that thinner twigs will remain on the plant after a low severity fire than after a high severity fire. Similarly, the percentage woody biomass of the burnt skeletons above and below knee height (0.5m) was recorded. Again, it is assumed more biomass will remain after a low compared to a high severity fire.

The number of charred stumps (where biomass was completely removed) in a subplot was counted and it was assumed that the number of charred stumps should increase with fire severity. The maximum diameter of the two plant skeletons and that of the charred stumps inside one subplot were measured. It is assumed that with an increase in fire intensity, individuals with larger stem diameters will survive the fire better than individuals with smaller stem diameters. The height of the two burnt skeletons after the fire was recorded.
Figure 2 The different characteristics measured for two burnt plant skeletons that occurred in the same subplot (1m²). (a) and (e) are the actual and extrapolated heights measured. The number of charred stumps within the subplot was also counted. Thinnest branch diameters and % woody skeleton remaining was estimated above and below 0.5 m.
The height before the fire was estimated from examining the size of the basal diameter of the skeleton and surrounding sunburnt vegetation. From this, a height ratio was calculated (actual: extrapolated). Where actual = extrapolated height, the height ratio is a 100% which indicates a low severity fire. Where the extrapolated height >> than the actual height, the height ratio is close to 0%, which indicates a high severity fire.

Four properties were defined that would make a post-hoc measure of fire severity useful as an indicator of the biological effects of a fire:

1. It should be useful over a wide range of fire severities. It should thus represent a continuum from low to high severity.
2. It should give consistent results in an area exposed to the same fire intensity.
3. It should be useful for predicting biological response variables.
4. It should be linked, theoretically and empirically, with physical variables of fire severities.

To test whether the characteristics measured for different burnt plant skeletons gave consistent results when exposed to similar fire severities (Prediction 2), the different bioassays of two plant skeletons that occurred in the same subplot were correlated using multiple regressions. This is based on the assumption that skeletons occurring in the same subplot (1m by 1m) would have experienced very similar fire severities and hence measured skeletal characteristics on separate plants in the same subplot should correlate.

Post-burn skeletal measurements (Table 1) of ericoids (mostly Erica spp., Cliffortia spp. and Pelargonium spp.) occurring in the same subplot as proteoids (Leucadendron spp., Minetes spp., and Rhus spp.) were correlated with each other. This was repeated where two ericoid, two proteoid, two alien (Hakea spp., Acacia spp., and Pinus spp.) or an ericoid and an alien plant skeleton occurred in the same subplot.
**Seedling regeneration**

Species were divided into two categories: big-seeded (> 10mg) and small-seeded (<10mg) (approximately 400 species) (Trinder-Smith, Bond *pers. comm.*). The total number of big- and small-seeded species and seedlings as well as the total number of fynbos and alien seedlings were counted for each subplot (1m²).

**Statistical analysis**

The Mann Whitney U test was applied to test for significant differences in vegetation regeneration between fynbos and alien sites. The relationship between fire severity and seed size within fynbos and alien sites was investigated. Regression analyses did not prove useful as the scatter of data points often formed a triangular shape (Fig. 3). This pattern is especially common for field data and is expected from the theory of limiting factors (Thomson *et al.*, 1996).

The response variable often shows a limited range of points when the limiting factor exerts a strong effect. Where the effect of the controlling factor is weaker, the response variable may take on larger or smaller points, depending on other limiting factors. In such “factor-ceiling” distributions, regression analysis is inappropriate because variance of the response changes with values of the limiting factor. Various approaches to overcome this statistical problem exist (Scharf *et al.*, 1998; Garvey *et al.* 1998). A test (proposed by Bond *et al.* 2001)) based on the null hypothesis that data points are equivalently distributed below and above the median of the independent variable (limiting factor) was used. Each graph is divided into four quarters along the median line of each axis and the number of data points in each quadrat is counted (see Fig. 3 and 4 below). The number of points in each block was counted directly from excel worksheets to overcome data points that overlay in graphs.

The calculated median value of the limiting factor included a large proportion of low severity fires. As this study was more concerned with the effects of low versus high severity fires, the 75% quartile value instead of the median for the independent variable was used.
Figure 3 The number of data points above the median of the x-axis is significantly different from the number of data points below the median. This indicates where the limiting factor has a strong effect (above the median) the response variable have a smaller range of points. Where the limiting factor has a weaker effect, the response variable takes on a larger range of points depending on other limiting factors.

Figure 4 The number of data points in each quadrat (as shown on the graph) is not significantly different from above and below the median of the x-axis. This indicates that the response variable is not controlled by the limiting factor.