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**The effect of fire on the spatial distribution of  
total nitrogen, total phosphorus,  
soil organic matter and pH,  
and the Nitrogen acquisition patterns  
of pre and post-fire communities.**

**Botany Ecophysiology Honours Project**

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## Abstract

Fires can alter the soil nutrient contents and distribution through the deposition and redistribution of ash material over the soil surface. Geostatistics generates semivariograms which model the spatial distributional patterns of soil components. We compared the spatial distributions of total nitrogen, total phosphorus, soil organic matter and pH in a burnt and unburnt plot of mountain fynbos in the Silvermine Nature Reserve of the South Western Cape, South Africa. Fire did not alter the range of spatial dependence of total N, total P, and pH but significantly increased mean values of total P and pH in the burnt plot through the deposition of alkaline ash on the soil surface, where  $p = 0.009$  and  $p = 0.000002$  respectively, at the 5 % significance level. 'Fertile islands' under the canopy of reseeders were undetectable in our plots because regular burns of short fire intervals induce rapid community turnover which, prevents the long-term accumulation of nutrients under the canopy of shrubs. We analysed the foliar  $\delta^{15}\text{N}$  values of pre and post-fire communities, which reveal that seedlings of the Restionaceae in the burnt plot had significantly heavier  $\delta^{15}\text{N}$  signals relative to those in the unburnt plot ( $p = 0.0002$ ). Restionaceae acquire N from the surface layers of the soil. During combustion, the lighter isotopes of N are volatilised and leached, resulting in deposition of the heavier N isotopes on the soil surface which, results in enriched foliar  $\delta^{15}\text{N}$  signals of Restionaceae. Species of the Haemodoraceae, Penaeaceae and Thymelaeaceae, which form arbuscular mycorrhizal associations, had similar  $\delta^{15}\text{N}$  signals in the pre and post-fire community implying that bacterial and microbial populations are present 6 months after fire. Fire did not alter the spatial attributes of the soil components but increased total P and pH values through the deposition of alkaline ash. Thus fire did not alter the N acquisition patterns of pre and post-fire communities but enriched the  $\delta^{15}\text{N}$  signal of surface rooting Restionaceae.

### Keywords:

**Fire, nutrients, fynbos, geostatistics,  $\delta^{15}\text{N}$  signals.**

## Introduction

Wildfire converts aboveground organic matter into ash and charred materials (Boerner, 1982) and rapidly alters the amount, form and distribution of plant nutrients in ecosystems (Raison, 1979). Fire affects soil nitrogen through deposition of ash residues of combusted plant materials (Raison, 1979), oxidation of organic N in the surface layers of the soil (Stock and Lewis, 1986) and volatilisation of N (gaseous loss of N). Ash residues add readily available organic nutrients to the soil (Christensen & Muller, 1975). Stock & Lewis (1986) found increased total N, exchangeable  $\text{NH}_4\text{-N}$  concentrations at the soil surface immediately after fire, but these increases were only temporary (Stock & Lewis, 1986; Musil & Midgley, 1990). However, decreases in  $\text{NH}_4\text{-N}$  after fire have also been reported (DeBano et al. 1979). The ash remaining on the soil surface may be redistributed horizontally by wind or surface erosion, or downward by precipitation percolating through the soil (leaching) (Boerner, 1982). The redistribution of surface ash after fire, by wind or water, may alter the spatial distribution of soil nutrients (Grogan et al. 2000) and soil organisms. The effect of fire on the spatial variation and in turn the availability of soil nutrients in fynbos communities could have significant effects on the spatial arrangement of species in post-fire environments. According to Richards et al. (1997) soil nutrient availability could be important in determining the spatial distribution of species in nutrient-poor habitats such as kwongan in Australia and fynbos in South Africa.

In nutrient limiting soils such as desert ecosystems (Garner and Steinberger, 1989), semi-arid to arid grasslands, and steppe ecosystems, soil nutrients are concentrated in 'islands of fertility' under the canopy of shrubs (Crawford and Gosz 1982, Noy-Meir 1985). Soil nitrogen content decreases significantly as a function of the radial distance from the centre of the canopy of a desert-wash community (Garcia-Moya & McKell, 1970). The accumulation of nutrients under shrubs are a result of nutrient uptake, litter fall, and dry fall (deposition of fine dust from the atmosphere), soil processes such as erosion and deposition, and the presence of soil biota through mineralisation and decomposition (Whitford et al. 1997). Fynbos is adapted to fire and communities are composed of reseeders and resprouters. Resprouters may develop permanent 'islands of fertility' in its range of nutrient acquisition but reseeders generational 'movement' through the landscape may not allow for the development of 'fertile islands' under its canopy.

Furthermore, fire results in nitrogen losses from ecosystems through soil leaching and volatilisation, if the nutrients are not immediately absorbed by plants (DeBano & Conrad, 1978). Grogan et al. (2000) found that ash enhances plant N acquisition through stimulating primary production of

resprouting species, thereby decreasing N loss. Resprouting species respond to the transitory increases in N availability immediately after fire because of rapid immobilisation of N from surviving below ground root stocks. N acquisition by reseeding species is delayed by the onset of appropriate conditions required for germination. Furthermore, some species take up N indirectly through mycorrhizal associations whereas others acquire N directly from the soil or atmosphere ( $N_2$  fixers). Christensen & Muller (1975) found that bacteria and fungi were more abundant in burned than in unburned chaparral soils. Thus, increased N availability and increased microbial action after fire may affect N cycling processes in burnt ecosystems. Infact, Grogan et al. (2000) found that fire enriched plant  $^{15}N$  natural abundance values in a Californian bishop pine forest. Burning may increase soil nitrification, particularly on acidic soils since the deposition of alkaline ash favours nitrifying bacteria (Raison, 1979). Nitrification discriminates strongly against the  $^{15}N$  and can therefore result in enriched foliage  $^{15}N$  values (Grogan et al. 2000). According to Hogberg (1997) the surface layers of burnt soil are depleted in  $^{15}N$  natural abundance relative to the surface layers of unburnt soil. Fire consumes the surface layer thereby exposing mineral layers which are more enriched in  $^{15}N$ , resulting in enriched  $^{15}N$  in re-establishing plant communities. Fire not only consumes the more depleted surface layers of the soil but also deposits enriched  $^{15}N$  on the soil surface through the process of volatilisation. The process of volatilisation results in gaseous loss of the lighter N isotopes leaving the remaining soil relatively enriched in the heavier N isotope.

The first aim of this project is to determine the effect of fire on the spatial distribution of nitrogen, phosphorus, soil organic matter and pH in a fynbos community using geostatistics. Geostatistics forms the basis of procedures for analysis and estimation of spatially dependent variables (Trangmar et al. 1985). It enables spatial relationships among sample values to be quantified and used for interpolation of values at unsampled locations and accounts for both the structured and random characteristics of spatially distributed variables (Trangmar et al. 1985). It therefore allows for the modeling of spatial distributional patterns (Rossi et al. 1992). The second aim of this project is to determine the effect of fire on plant N acquisition by interpretation of  $\delta^{15}N$  values. We hypothesise that (i) fires redistribute nutrients concentrated in 'fertile islands' under shrubs, resulting in a homogeneous soil nutrient distribution in post-fire communities compared to heterogeneous soil nutrient distributions in pre-fire communities, (ii) the  $\delta^{15}N$  isotopic signals of post-fire vegetation are more positive (enriched in the heavier isotope) relative to the  $\delta^{15}N$  values of pre-fire vegetation.

## **Methods and materials**

### **Study area**

The study area is situated in the Silvermine Nature Reserve, within the fynbos biome of the Western Cape, South Africa. The Silvermine Nature Reserve is located at approximately 18° 23' 55" E and 34° 4' 30" S and is situated at the northern end of the Cape Peninsula (Kathan, 1981). Table mountain sandstone forms the underlying bedrock (Cole, 1966 taken from Kathan, 1981). The granite-derived soils of mountain fynbos soils are acidic with coarse to medium textured sand (Witkowski & Mitchell, 1987) and depths varying from 20 mm to 50 mm (Lambrechts, 1979 taken from Kathan, 1981). The study area is situated on the windward side of the mountain (north-facing), experiencing high winter rainfall (131.5 mm - 404.0 mm).

### **Field sampling**

Sample collection took place approximately 6 months after the fire, on the 6 July 2000. We deliberately sampled after the first winter rains in order to allow for the movement of ash until it is washed into the soil by the first rains. In addition, Christensen & Muller (1975) found that bacterial and fungal plate counts show increases in the wet season, with peaks in abundance within 2-5 months post-fire (Reenen et al. 1992). Our results therefore account for physical and biological processes affecting post-fire community succession.

We selected a plot in the burnt area and an adjacent plot in the unburnt area of similar slope and exposure. Topographically uniform sites were selected to avoid gradient driven effects in the geostatistical analysis. The gradient at both sites was measured using a clinometer. The gradient at the burnt site was 4.5° whereas the gradient at the unburnt site was 6°. We established an 8 X 8 plot of 64 sampling points in a burnt and an unburnt site. According to Raison, (1979) most effects of fire are manifested in the topsoil. Thus at every one metre interval of the grid, a soil corer was used to take a soil sample 7.5 cm in diameter and 5 cm deep. For each sample we noted the vegetation type found closest to the sample as well as whether it was taken from beneath the vegetation or from bare soil. We mapped the distribution of vegetation in relation to the sampling grid in order to relate the spatial distributions of nutrients with the spatial arrangement of the vegetation.

### **Laboratory analysis**

The soil samples were dried in the oven at 107 °C for 72 hours. Each sample was mixed and sieved through a 2 mm mesh. Total nitrogen was determined using Kjeldahl Digestion method, which

converts  $\text{NO}_3\text{-N}$  to  $\text{NH}_4\text{+N}$ , the  $\text{NH}_4\text{+N}$  is then determined colorimetrically (Smith, 1980). Total phosphorus was determined using the Triacid Digestion method (Grimshaw, 1985) and the Murphy & Riley (1962) method was used for the colorimetric assay. pH was determined using 0.01 M Calcium Chloride and a pH meter (Rowell, 1994). Soil organic matter was determined by the muffle furnace method (Rowell, 1994) where soil organic matter is lost upon ignition when heated to a temperature of  $420^\circ\text{C}$  for 16 hours.

### **Geostatistical analysis**

Spatial variability of total N, total P, soil organic matter and pH taken from soil samples from the burnt and unburnt plot, were measured by comparison of semivariograms generated with geostatistical techniques. For each soil component, of the burnt and unburnt plots, we derived semivariograms using the geostatistical package, Geopack V1.0e Tecsoft Inc. and generated contour plots using Statistica, 2000. According to Trangmar et al. (1985) the semivariogram describes the spatial patterns where the semivariance increases with distance between paired sample locations, rising to a more or less constant values (the sill) at a given separation distance, called the range of spatial dependence (lag distance). Samples separated by distances greater than the range of spatial dependence are not related whereas those separated by distances closer than the range are spatially related. In other words, it measures the average variance found in comparison of samples taken at increasing distance from one another (Gallardo et al. 2000). The semi-variogram is based on the following equation:

$$2\gamma^*(h) = 1/n \sum [g(x) - g(x + h)]$$

where  $h$  represents the distance between samples, the mean differences between samples is referred to as  $\gamma^*(h)$  and the variance of these differences as  $2\gamma(h)$ ,  $g$  represents grade (value determined at that point),  $x$  denotes the position of one sample in the pair and  $(x + h)$  the position of the other, and  $n$  is the number of sample pairs (Clarke, 1979). It assumes that the mean and variance values of the samples are determined only by the relative spatial orientation of those samples, known as the 'Intrinsic Hypothesis' (Clarke, 1979). Thus it also accounts for error variance referred to as the nugget value (Clarke, 1979). This is the result given when a sample in the same position is resampled and a different value obtained. Theoretically, the resampled sample should not vary relative to itself, but in reality variation does occur. This variation is referred to as the error variance. The size of patches of varying nutrient concentrations are determined and a visual representation and spatial arrangement are identified by means of contour plots revealing the gradients followed by each soil component in each plot.

Contour plots were generated for each soil component in the burnt and the unburnt plot with Statistica, 2000. Vegetation maps were generated using Corel Draw, showing the relative locations of the vegetation types in both plots. The relationships between the spatial arrangement and soil components were then determined through comparison with the contour plots.

The values obtained for each soil component are normally distributed and have similar variances. The mean values for each soil component from the burnt and unburnt plot were tested for significance at the 5 % level using students t-test by means of Statistica, 2000. The soil components for each plot were regressed using correlation matrices of Statistica, 2000, in order to compare the relationship of the soil components between both plots.

### **Foliar isotope collection**

For isotopic analysis we collected 3 specimens of leaf material from species present in the burnt plot and the unburnt plot. The burnt plot was dominated by seedlings of the Restionaceae and Proteaceae skeletons. Other seedlings of the Haemodoraceae, Penaeaceae, Thymelaeaceae and Cyperaceae were present in the burnt plot. The unburnt plot was dominated by species of the Proteaceae and Restionaceae. Other species of the Haemodoraceae, Penaeaceae, Thymelaeaceae, Ericaceae and Asteraceae were present in the unburnt plot.

The leaf material collected for isotopic analysis was ground using the ball mill grinder. The  $\delta^{15}\text{N}$  values and C:N ratios of samples were determined on a VG Micromass 602E mass spectrometer. Species were grouped according to family and the mycorrhizal status was noted. We then compared the  $\delta^{15}\text{N}$  values and C:N ratios for those families present in the post (burnt) and pre-fire (unburnt) communities.

### **Statistical analysis**

The  $\delta^{15}\text{N}$  and C:N ratios obtained for each family follow a normal distribution and have similar variances, which allows us to perform an analysis of variance (ANOVA) using Statistica, 2000. The values obtained for each family were analysed for significant differences, between the burnt and unburnt plot, at the 5 % significance level.

## Results

The burnt and unburnt plot were very similar in terms of the mean total N, total P and soil organic matter contents across the plots. pH of the burnt and unburnt plots showed differences. Table 1 shows the results.

Table 1. The mean, standard deviations and P values of the students t-tests of total N, total P, soil organic matter and pH of the burnt and the unburnt plot. \*P < 0.05

|   | BURNT PLOT |         | UNBURNT PLOT |         | T-TEST    |
|---|------------|---------|--------------|---------|-----------|
|   | MEAN       | STD.DEV | MEAN         | STD.DEV | P         |
| <b>Total N (mg N g<sup>-1</sup> soil)</b> | 0.535      | 0.140   | 0.555        | 0.165   | 0.461106  |
| <b>Total P (µg P g<sup>-1</sup> soil)</b> | 29.90      | 7.95    | 26.84        | 4.90    | 0.009741* |
| <b>SOM (%)</b>                            | 2.52       | 0.66    | 2.65         | 0.71    | 0.287962  |
| <b>pH</b>                                 | 4.0        | 0.3     | 3.8          | 0.1     | 0.000002* |

### Semivariograms and contour plots

Semivariograms for N, P, soil organic matter and pH were adjusted to a spherical model (Figure 1-4). Table 2 summarises the range of spatial dependence, the sill (constant variance with increasing distance) and the nugget (error variance) found for the soil components sampled.

Table 2. The result of the semivariograms showing the range of spatial dependence, the sill and the nugget for total N, total P, soil organic matter and pH in the burnt (B) and unburnt (UB) plots. (\*estimated value and ND - not determined) (Fig. 1-4)

|                | RANGE (m) |        | SILL   |        | NUGGET |       |
|----------------|-----------|--------|--------|--------|--------|-------|
|                | B         | UB     | B      | UB     | B      | UB    |
| <b>Total N</b> | 1.4       | 1.6    | 0.017  | 0.019  | 0.003  | 0     |
| <b>Total P</b> | 2.5       | 2.3    | 36.214 | 27.400 | 16     | 5     |
| <b>SOM</b>     | 1.3*      | 248.1? | ND     | 7.095  | ND     | 0.275 |
| <b>pH</b>      | 1.5       | 1.4    | 0.073  | 0.012  | 0      | 0.001 |

According to Table 2, the range of spatial dependence for total nitrogen, total phosphorus, and pH are similar in the burnt and unburnt plots. Unfortunately, we could not fit a model to the soil organic matter data for the burnt plot and the range of spatial dependence was therefore estimated from the semivariogram. However, the semivariograms for soil organic matter are unreliable. We therefore

assessed the effect of fire on the spatial components of soil organic matter by interpretation of the contour plots and regression analyses.

Figure 6a and 6b shows that total N is homogeneously distributed in both the burnt and unburnt plots. Figure 7a and 7b reveals that total P in the burnt plot is more heterogeneously distributed relative to total P in the unburnt plot. Figure 8a and 8b shows that the soil organic matter content across the burnt and unburnt plots are homogeneously distributed. Figure 9a and 9b shows that the burnt plot is comprised of a greater degree of variation relative to the unburnt plot which means that pH in the burnt plot is heterogeneously distributed and pH in the unburnt plot is relatively homogeneously distributed. The semivariograms indicate patch sizes of related soil components whereas contour plots provide visual representations of the class gradients of soil component variability across the plots. The discrepancy between semivariograms and contour plots are not contradictory because the contour plots do not differentiate between spatially dependent and independent values as does the semivariogram, but merely reveals class gradients of soil components in the plots.

### **The spatial arrangement of Protea skeletons in the burnt plot, live Proteas and Ericas in the unburnt plot**

Seedlings of the Restionaceae are evenly scattered throughout both the burnt and the unburnt plot (Figure 5a and 5b) and are therefore not included in the comparative analysis. Table 3 compares the total N, total P, soil organic matter and pH values of the soil beneath Protea skeletons in the burnt plot, with the corresponding soil component values of the soil beneath live Proteas and Ericas in the unburnt plot.

Table 3. The range of total N, total P, soil organic matter and pH of the soil beneath Protea skeletons in the burnt plot and live Proteas and Ericas in the unburnt plot (Fig. 5-9)

|                                     | VEGETATION           |                              |
|-------------------------------------|----------------------|------------------------------|
|                                     | B (Protea skeletons) | UB (Live Proteas and Ericas) |
| <b>N (mg N g<sup>-1</sup> soil)</b> | 0.5 - 0.6            | 0.5 - 0.6                    |
| <b>P (µg P g<sup>-1</sup> soil)</b> | 20.0 - > 47.0        | 26.0 - 32.0                  |
| <b>SOM (%)</b>                      | 2.5 - 3.0            | 2.5 - 3.0                    |
| <b>pH</b>                           | 3.9 - 4.4            | 3.7 - 3.9                    |

According to Table 3, fire did not alter the total N contents surrounding combusted Proteas as the range of total N values of the soil beneath Protea skeletons in the burnt plot are the same as the range of total N values of the soil beneath live Proteas and Ericas in the unburnt plot. However, total P values of soil beneath Protea skeletons in the burnt plot is more variable relative to the range of total P values found beneath live Proteas and Ericas in the unburnt plot. Fire did not alter the soil organic matter content beneath Proteas skeletons in the burnt plot and live Proteas and Ericas in the unburnt plot. However, fire increased the range of pH values of the soil beneath Proteas skeletons relative to the range of pH values found beneath live Proteas and Ericas in the unburnt plot.

### **The relationships between soil components**

From the regression analyses we found that soil organic matter is strongly correlated with total nitrogen in the burnt and the unburnt plot where the coefficient of determination,  $r = 0.77$  and  $r = 0.88$  respectively (Figure 10a and 10b). Soil organic matter is also correlated with total phosphorus in both plots where  $r = 0.50$  and  $r = 0.42$  respectively (Figure 11a and 11b). Total phosphorus and total nitrogen were correlated in both plots where  $r = 0.48$  and  $r = 0.46$  respectively (Figure 12a and 12b).

In the burnt plot, soil organic matter regressed with pH, phosphorus regressed with pH and nitrogen regressed with pH are weakly correlated, where  $r < 1.6$ . In the unburnt plot, soil organic matter regressed with pH, phosphorus regressed with pH and nitrogen regressed with pH are weakly correlated where  $r = -0.21$ ,  $r = 0.01$ ,  $r = -0.25$  respectively. As result of the weak correlations found amongst these variables we excluded the graphs.

### **$\delta^{15}\text{N}$ natural abundance values of fynbos species in a burnt plot (post-fire community) and an unburnt plot (pre-fire community) in the Silvermine Nature Reserve**

Foliar  $\delta^{15}\text{N}$  values of species present in the burnt and unburnt plots show similar enrichment patterns, as indicated by the overlapping  $\delta^{15}\text{N}$  values (Figure 13). Species common to both the burnt and unburnt plots, of the Restionaceae, Haemodoraceae, Penaeaceae and Thymelaeaceae. Species of the Restionaceae, in the burnt and unburnt plot, spanned a broad range of  $\delta^{15}\text{N}$  values. On average, species in the burnt plot had significantly more positive ( $p = 0.0002$ ) foliar  $\delta^{15}\text{N}$  signals, ( $SD = 1.110 \text{ ‰}$ ), whereas species in the unburnt plot had more negative foliar  $\delta^{15}\text{N}$  values ( $0.10 \text{ ‰}$ ,  $SD = 0.874 \text{ ‰}$ ). The  $\delta^{15}\text{N}$  values for non-mycorrhizal species of the Restionaceae have a more positive  $\delta^{15}\text{N}$  values than species which obtain N indirectly through mycorrhizal associations. Species of the Haemodoraceae and Penaeaceae spanned a narrow range of  $\delta^{15}\text{N}$  values and foliar

$\delta^{15}\text{N}$  values obtained in the burnt plot and the unburnt plots are not significantly different ( $p = 0.309$ ,  $p = 0.934$ ) respectively. Foliar  $\delta^{15}\text{N}$  values, of species of the Thymelaeaceae, in the burnt plot had on average more negative values ( $-0.68\text{‰}$ ,  $\text{SD} = 1.753\text{‰}$ ) relative to those obtained in the unburnt plot ( $0.99\text{‰}$ ,  $\text{SD} = 0.624\text{‰}$ ) but as a result of inadequate sample sizes, these values could not be tested for significance.

Species of the Proteaceae, Ericaceae and Asteraceae were present only in the unburnt site (pre-fire community). Foliar  $\delta^{15}\text{N}$  values for non-mycorrhizal Proteaceae were on average more negative,  $-0.68\text{‰}$ , ( $\text{SD} = 0.616\text{‰}$ ) than expected, based on the findings of Stock et al. (1995) where the  $\delta^{15}\text{N}$  signal for *Protea repens* was  $4.71\text{‰}$ . The  $\delta^{15}\text{N}$  values of species of the Ericaceae, associated with ericoid mycorrhizal (Allsopp & Stock, 1993), had on average,  $-4.08\text{‰}$ , ( $\text{SD} = 1.323\text{‰}$ ), which is within the expected range for Ericaceae. The  $\delta^{15}\text{N}$  of species of the Asteraceae, associated with arbuscular mycorrhizal (Allsopp & Stock, 1993), had average  $\delta^{15}\text{N}$  values of  $0.59\text{‰}$  ( $\text{SD} = 0.306\text{‰}$ ). Species of the Cyperaceae, not associated with mycorrhizae (Allsopp & Stock, 1993), were present only in the burnt plot. The  $\delta^{15}\text{N}$  values were on average  $1.90\text{‰}$ , ( $\text{SD} = 0.306\text{‰}$ ).

#### **C:N ratios of fynbos species present in burnt (post-fire) and unburnt (pre-fire) communities in the Silvermine Nature Reserve**

The C:N ratios of families in the post and pre-fire communities show different patterns (Figure 14). Species of the Restionaceae, Haemodoraceae, Penaeaceae and Thymelaeaceae had lower C:N ratios in the burnt plot compared to species present in the unburnt plot. Species of the Restionaceae show some overlap of values but on the burnt plot had on average and significantly ( $p = 0.001$ ) lower C:N ratios ( $31.55$ ,  $\text{SD} = 9.553$ ) compared to averaged ratios obtained in the unburnt plot ( $66.08$ ,  $\text{SD} = 35.255$ ). The C:N values obtained for species of the Haemodoraceae showed no significant differences between the burnt and unburnt plot ( $p = 0.187$ ). The C:N ratios for species of the Penaeaceae were significantly ( $p = 0.022$ ) lower ( $46.74$ ,  $\text{SD} = 10.053$ ) in the burnt plot, relative to the ratios obtained in the unburnt plot ( $65.93$ ,  $\text{SD} = 7.836$ ). The C:N ratios for species of the Thymelaeaceae were lower values in the burnt plot ( $37.59$ ,  $\text{SD} = 0.700$ ) relative to those obtained in the unburnt plot ( $73.74$ ,  $\text{SD} = 7.596$ ) but as a result of an inadequate sample size, we could not test for significance.

Unfortunately, we cannot compare the ratios of post and pre-fire communities for species of the Proteaceae, Ericaceae, Asteraceae and Cyperaceae since species belonging to these families were not present in both plots. However, species of the Proteaceae, Ericaceae and Asteraceae, present

only in the unburnt plot, had values of, 88.50, (SD = 27.709); 71.65, (SD = 8.973); 39.86, (SD = 7.496) respectively. Species of the Cyperaceae, present in the burnt plot had on average a C:N ratio of 27.70, (SD = 6.595).

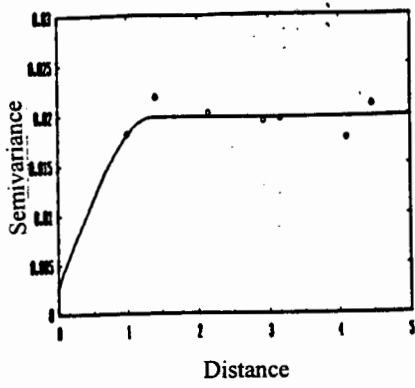


Figure 1a. Semivariogram for total N (mg N / g soil) in the burnt plot.

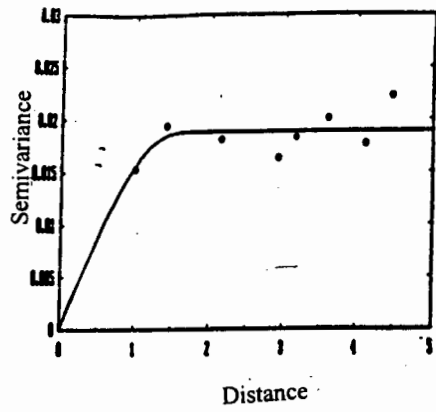


Figure 1b. Semivariogram for total N (mg N / g soil) in the unburnt plot.

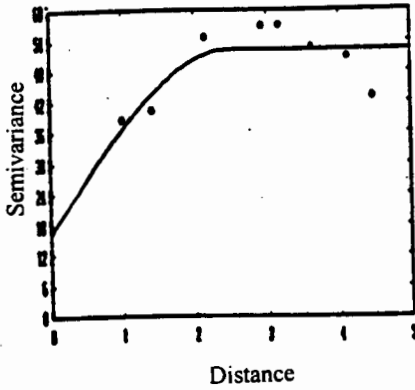


Figure 2a. Semivariogram for total P (ug P / g soil) in the burnt plot.

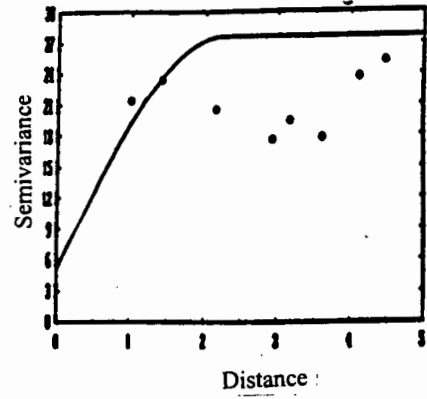


Figure 2b. Semivariogram for total P (ug P / g soil) in the unburnt plot.

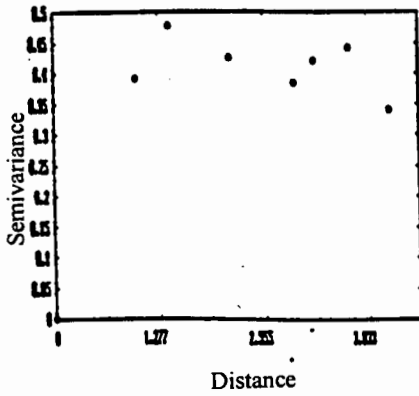


Figure 3a. Semivariogram for soil organic matter (%) in the burnt plot.

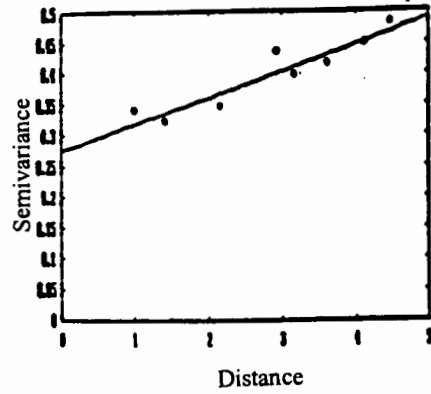


Figure 3b. Semivariogram for soil organic matter (%) in the unburnt plot.

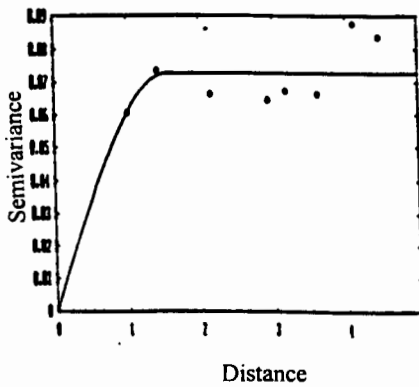


Figure 4a. Semivariogram for pH in the burnt plot.

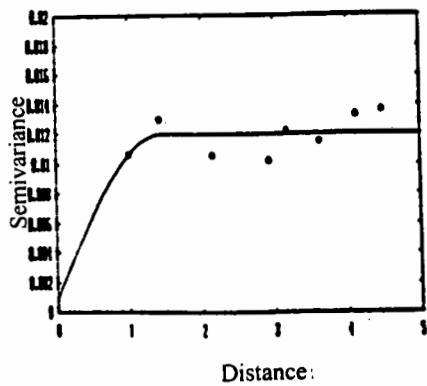


Figure 4b. Semivariogram for pH in the unburnt plot.

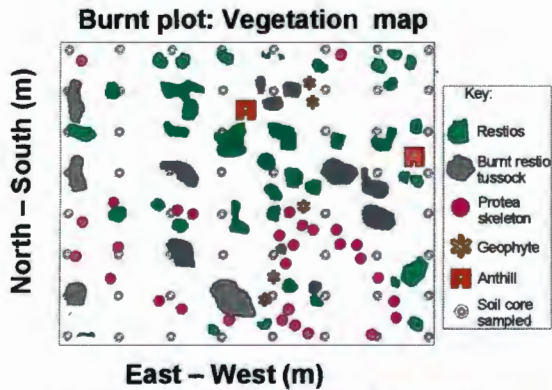


Figure 5a. Vegetation map of the burnt plot in a fynbos community.

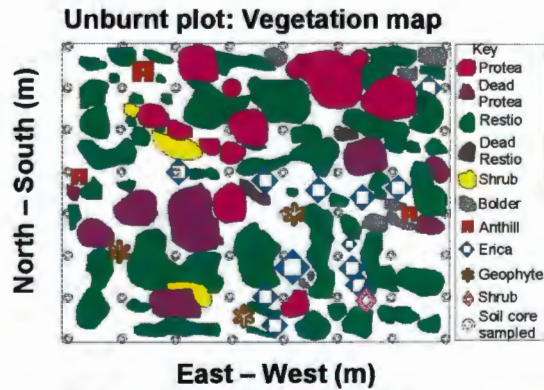


Figure 5b. Vegetation map of the unburnt plot in a fynbos community.

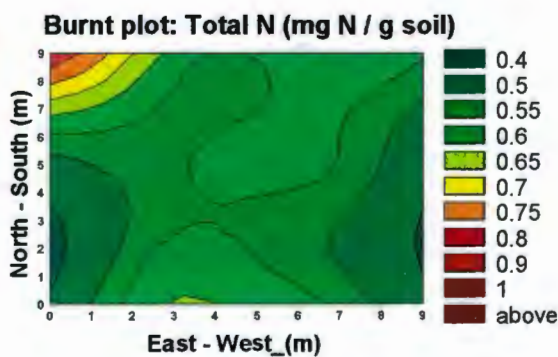


Figure 6a. Soil contour map of the burnt plot for total soil Nitrogen content (mg N / g soil) in a fynbos community.

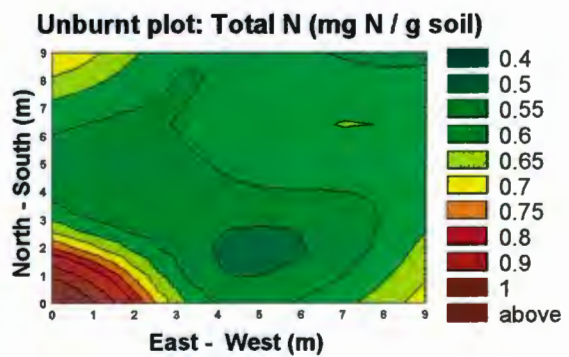


Figure 6b. Soil contour map of the unburnt plot for total soil Nitrogen content (mg N / g soil) in a fynbos community.

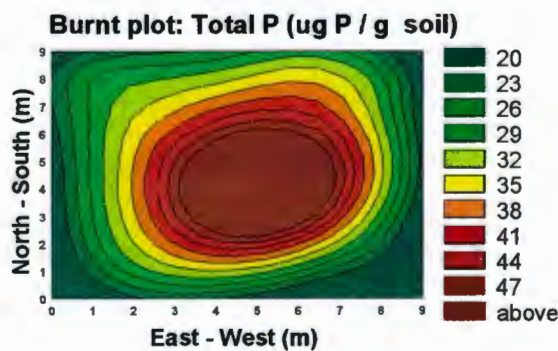


Figure 7a. Soil contour map of the burnt plot for total soil Phosphorus content (ug P / g soil) in a fynbos community.

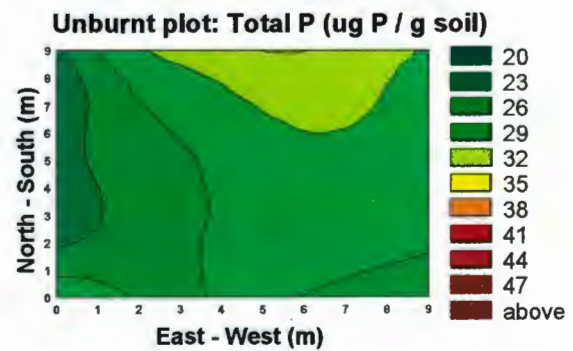


Figure 7b. Soil contour map of the unburnt plot for total soil Phosphorus content (ug P / g soil) in a fynbos community.

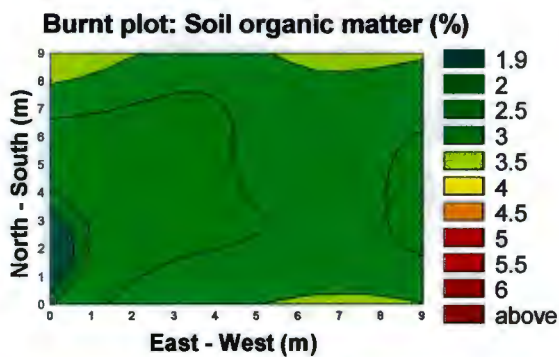


Figure 8a. Soil contour map of the burnt plot for soil organic matter (%) in a fynbos community.

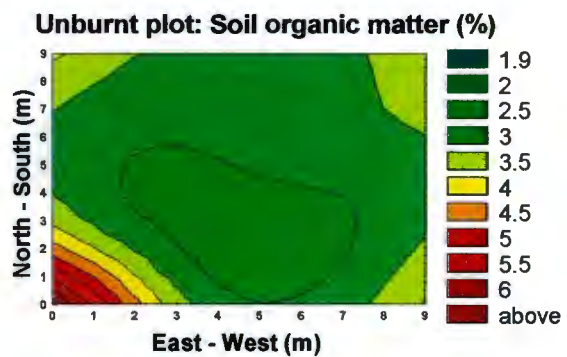


Figure 8b. Soil contour map of the unburnt plot for soil organic matter (%) in a fynbos community.

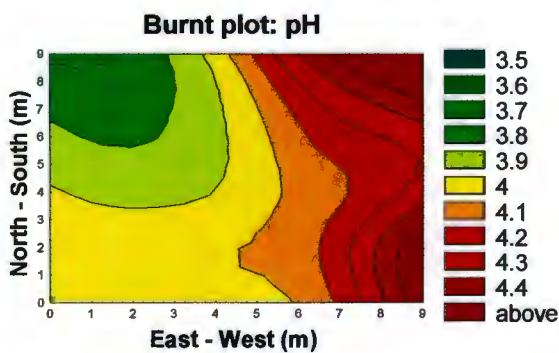


Figure 9a. Soil contour map of the burnt plot for pH in a fynbos community.

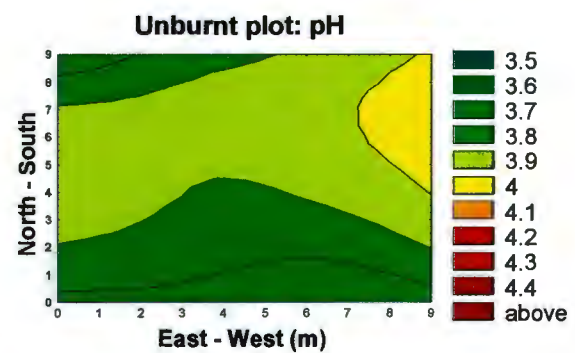


Figure 9b. Soil contour map of the unburnt plot for pH in a fynbos community.

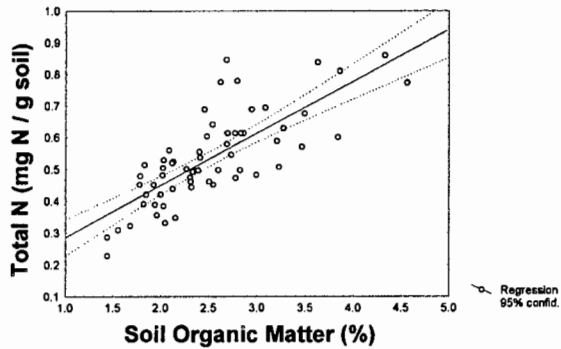


Figure 10a. Regression analyses for Soil organic matter (%) and Total Nitrogen (mg N / g soil) in the burnt plot where,  $y = 0.12128 + 0.16384x$  and  $r = 0.76899$ .

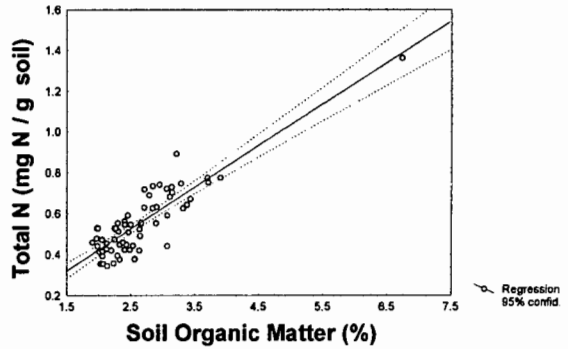


Figure 10b. Regression analyses for Soil organic matter (%) and Total Nitrogen (mg N / g soil) in the unburnt plot where,  $y = 0.01327 + 0.20415x$  and  $r = 0.87680$ .

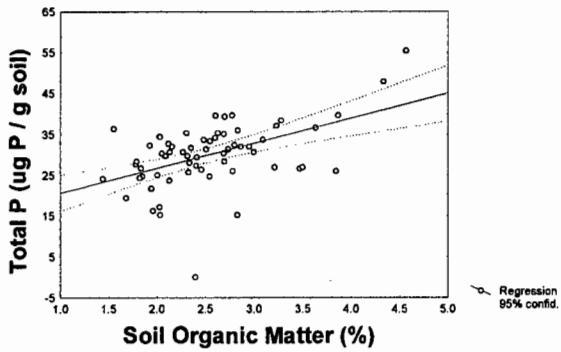


Figure 11a. Regression analyses for Soil organic matter (%) and Total P (ug / g soil) in the burnt plot where,  $y = 14.538 + 6.0914x$  and  $r = 0.50224$ .

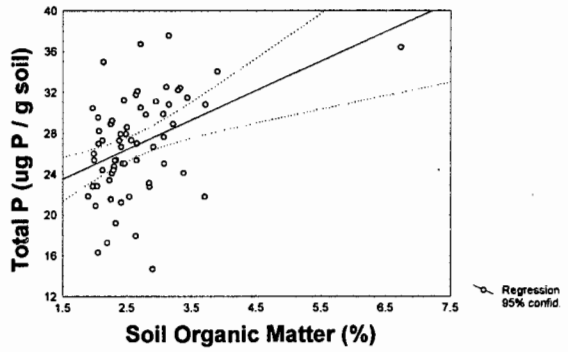


Figure 11b. Regression analyses for Soil organic matter (%) and Total P (ug P / g soil) in the unburnt plot where,  $y = 19.205 + 2.8788x$  and  $r = 0.41668$ .

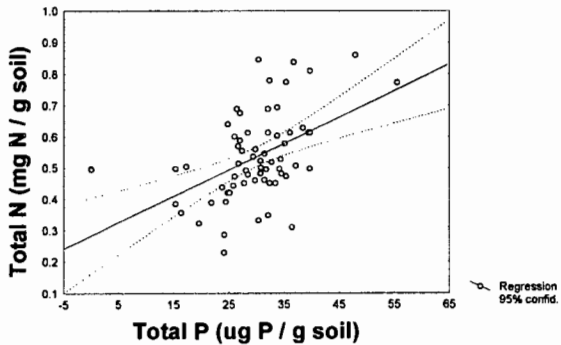


Figure 12a. Regression analyses for total Phosphorus (ug P / g soil) and total Nitrogen (mg N / g soil), in the burnt plot where  $y = 0.28226 + 0.00844x$  and  $r = 0.48034$ .

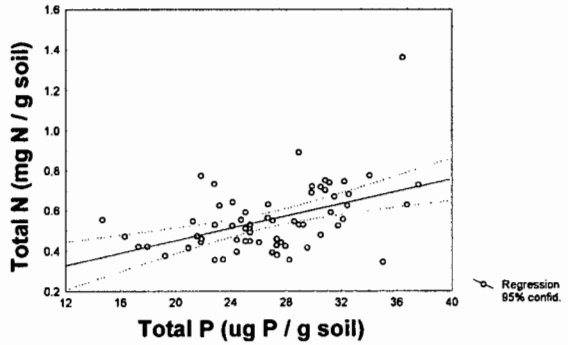
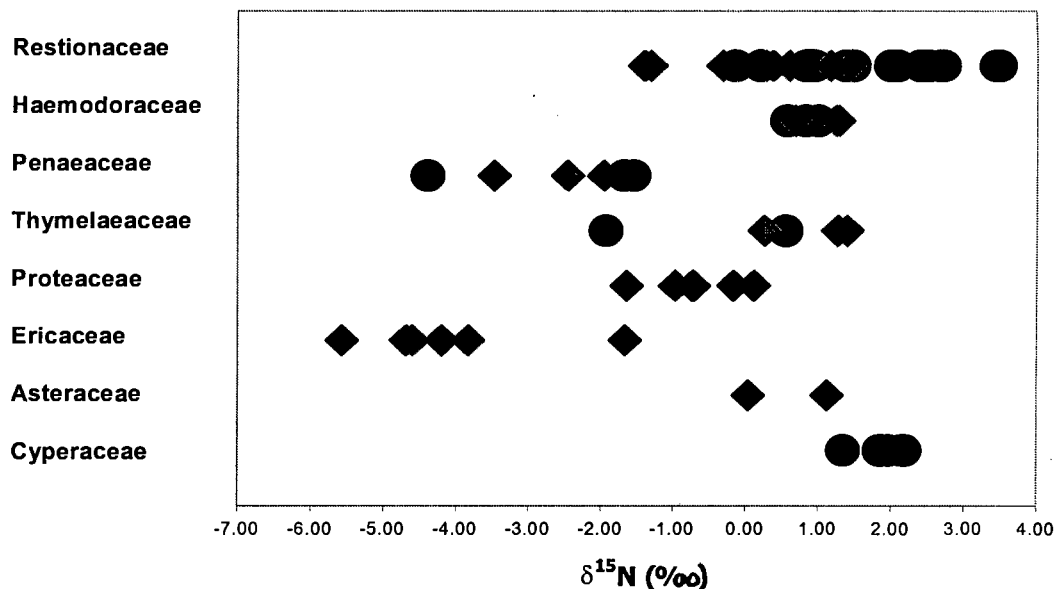
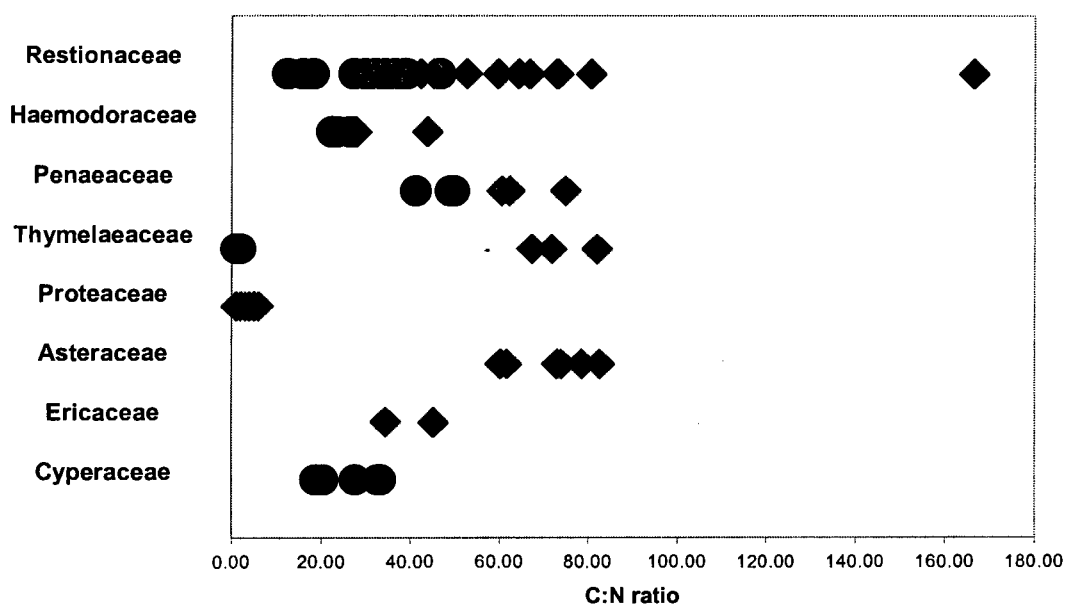


Figure 12b. Regression analyses for total Phosphorus (ug P / g soil) and total Nitrogen (mg N / g soil) in the unburnt plot where  $y = 0.14154 + 0.01539x$  and  $r = 0.45667$ .



**Figure 13.** Foliar  $\delta^{15}\text{N}$  values of fynbos families, taken from Silvermine Nature Reserve in the Cape Floristic Region. The black circles represent the isotopic N signature of species present in a burnt plot (post-fire community, ~6 months). The grey diamonds represent the isotopic N signature of species present in a nearby unburnt plot. Species belonging to the families Restionaceae, Haemodoraceae, Penaeaceae and Thymelaeaceae were present in burnt and unburnt sites. Species belonging to the families of Proteaceae, Ericaceae and Asteraceae were present only in the unburnt plot whereas species belonging to the family Cyperaceae were present only in the burnt plot.



**Figure 14.** C:N ratios of fynbos families taken from the Silvermine Nature Reserve in the Cape Floristic Region. The black circles represent the C:N of species present in the burnt plot (post-fire community ~6 months). The grey diamonds represent the C:N of species present in a nearby unburnt plot. Species belonging to the families Restionaceae, Haemodoraceae, Penaeaceae and Thymelaeaceae were present in the burnt and unburnt plot. Species belonging to the families Proteaceae, Ericaceae and Asteraceae were present only in the unburnt plot whereas species belonging to the family Cyperaceae were found only in the burnt plot.

## Discussion

### **Does fire affect the spatial components of a fynbos community?**

According to the results of this study, the range of spatial dependence for total nitrogen, total phosphorus and pH are similar in both the burnt and the unburnt plots (Fig. 1-4). It appears that fire does not combust plant material in a manner sufficiently chaotic, to alter the spatial components of the soil, and the rain and wind did not redistribute ash material over the surface of the plot. Ash is deposited near the source of combusted material resulting in similar ranges of spatial dependence in the burnt and unburnt plot. Our regression analysis of total nitrogen and soil organic matter (Fig 10a,b), contour plots (Fig. 6, 8) and tests of significance (Table 1) shows that soil organic matter and nitrogen are homogeneously distributed throughout the burnt and the unburnt plots. Thus fire did not alter the homogeneous distribution of soil organic matter and total N in the burnt and unburnt plot. However, the contour plots (Fig. 7, 9) and tests of significance (Table 1) reveal that total P and pH in the burnt plot are significantly higher relative to the unburnt plot. Thus fire induced increased heterogeneity of total P and pH in the burnt plot relative to the unburnt plot.

### **Are 'fertile islands' a characteristic feature of mountain fynbos?**

The results of this study have raised interesting differences between the spatial patterns of ecosystems subjected to the regular disturbance of fire and those ecosystems, which are not subjected to fire events. Based on the 'fertile islands' concentrated under the canopy of shrubs in semi-arid to arid regions (Schlesinger et al 1996), inherent in our hypothesis was the assumption that 'fertile islands' exist in unburnt fynbos. However, the contour plots reveal that total N, total P, soil organic matter and pH of pre-fire communities are relatively homogeneously distributed. These results refute the existence of 'fertile islands' in pre-fire communities. Stock and Lewis (1986) found no apparent lateral difference of total N between bare patches of soil and the soil of rhizosphere regions of a coastal fynbos ecosystem. However, they found significant lateral differences in  $\text{NH}_4\text{-N}$  and  $\text{NO}_3\text{-N}$  concentrations. These differences were attributed to N utilisation patterns and soil microclimates beneath species, which implies that 'fertile islands' may not be detectable by measuring total N and the lack of evidence for 'fertile islands' in this study may not mean that it does not exist. ✓

Nevertheless, the fire event, which occurred approximately 6 months prior to sampling, did not induce homogeneity in the burnt plot because homogeneity of the sampled soil nutrients may be a

characteristic feature inherent to ecosystems subjected to regular disturbance events such as fire and grazing. Thus regular burns may maintain homogeneity of soil nutrients but not induce homogeneity of soil nutrients. The absence of 'fertile islands' in the fynbos community of the Silvermine Nature Reserve may be influenced by the fire interval. Stock et al (1999) found that long-lived species show greater concentration effects under the canopies but short-lived perennials species of the Namaqualand region have more ephemeral 'fertile islands' because of rapid community turnover. In the Silvermine Nature Reserve where fires occur approximately every 15 years, there may not be sufficient time between fires, for the formation of fertile islands because community turnover is rapid. Re-establishment distribution patterns of post-fire reseeders communities are therefore not influenced by pre-fire soil components but may be a function of seed dispersal strategies and other competitive interactions. Fynbos communities, which have not burned for longer periods of time such as Jonkershoek, which has not burned for 21 years (Stock & Allsopp 1992), may have had sufficient time for the development of 'fertile islands' under the canopy of reseeders. In such cases, a fire may break up 'fertile islands' under shrubs, thereby influencing the post-fire community distributional patterns.

#### **Why does fire affect different nutrients differently?**

According to Boerner (1982) nutrient elements in biomass and detritus may be lost to the atmosphere, deposited as ash on the soil surface, or remain as incompletely burned skeletons or detritus. Fire did not alter the spatial attributes of nitrogen and soil organic matter of the soil whereas phosphorus and pH showed increasing variability in the burnt plot relative to the unburnt plot (Fig. 6-9). Stock & Lewis (1986) estimated that 76 % of a total of 39 274 kg ha<sup>-1</sup>, was consumed by the fire and only 66 kg ha<sup>-1</sup> were added to the soil by ash deposition. Protea skeletons may have retained small quantities of N but large quantities N may have been lost through the process of volatilisation and ash containing N may have leached from the soil leaving no significant differences in the mean N values of the surface layers of the burnt and unburnt plots (Table 1). Furthermore, DeBano et al (1979) found that approximately 67 % of the total N in the litter and soil was lost during an intense burn over dry soil, opposed to a loss of less than 25 % when the soil and litter was moist. At the time of the fire (January, 2000), it was a relatively dry Summer and temperatures were unusually high. Thus conditions may have been conducive to high levels of N loss. Stock & Lewis (1986) found that total N concentrations increase with depth as a result of leaching. We sampled only the surface 5 cm, which means that we were unable to detect N if it had already leached after the first Winter rains. In addition, fire increased the soil pH of the burnt plot.

Raison (1979), found that the deposition of alkaline ash during fire increases soil pH. Increased soil pH is favourable to microbial populations which then re-immobilise N, reducing soil levels of available N (Raison, 1979). The combination of factors explained may account for the similarity of total N differences in the surface layers of the soil.

In the burnt plot total phosphorus was spatially heterogeneous (Fig. 7a,b) and had significantly higher mean values relative to the unburnt plot (Table 1). The volatilisation temperatures of P are greater than that of N. N volatilises at approximately 200°C whereas volatilisation of P requires temperatures greater than 500°C (Boerner, 1982). Thus the intensity of the fire may have reached temperatures sufficient to volatilise N but not P. An ash accumulation central to burnt ratio tussocks (Fig. 5a) may have returned large quantities of P, to the soil resulting in more heterogeneous distributions in the burnt plot relative to that of total N. DeBano & Conrad (1978) found that after a fire in the Southern California chaparral, practically all the P in the plant material was deposited on the soil surface as ash. Smaller twigs have higher concentrations of P, which are released during burning leaving only 8 % of P in charred materials (DeBano & Conrad, 1978). Furthermore, P is relatively immobile in soils and thus may not have leached as N may have leached after the rains. However, it is also possible that fire did add N to the soil just as it did P, through the effect of ash deposition, but rapid regrowth of fire-adapted species in the burnt plot may have minimised N losses from the system (Boerner, 1982) and Witkowski & Mitchell (1987) found that microbial activity is primarily accountable for the accumulation of soil organic phosphorus. Thus vegetation regrowth rates and microbial populations which, according to Christensen and Muller (1975) are more abundant after fire, affect the soil nutrient components. Thus the P contents in the burnt plot were higher because P is generally not susceptible to volatilisation (DeBano & Conrad, 1978), leaching and losses of P are prevented through microbial activity.

Regardless of these differences both soil total N, total P and soil organic matter are strongly correlated in the burnt and the unburnt plot but pH is very weakly correlated with total N, total P, and soil organic matter in the burnt and unburnt plot (Fig. 10-12). It appears that the most significant difference induced by fire in the burnt plot is the increased variability of soil pH (Fig 9a, b and Table 1) as a result of alkaline ash deposition on the soil surface.

## **How does fire influence the $\delta^{15}\text{N}$ signals and what can we infer about pre and post-fire N acquisition?**

Species of Restionaceae show significant differences in  $\delta^{15}\text{N}$  values between the burnt and the unburnt plot whereas species of Haemodoraceae, Penaeaceae and Thymelaeaceae do not have significantly different  $\delta^{15}\text{N}$  values between the burnt and unburnt plots (Fig. 13). Species of Restionaceae acquire N directly from the surface layers of the soil and do not form mycorrhizal associations whereas species of the Haemodoraceae, Penaeaceae and Thymelaeaceae are associated with arbuscular mycorrhizae (Allsopp & Stock, 1993). During fire, fractionation occurs which means that the lighter isotopes of N are volatilised or leached, while the heavier isotopes of N are deposited on the soil surface (Grogan, 2000). Species of the Restionaceae acquire N from the surface layers of the soil, which is composed of the heavier isotopes of N, accounting for the significantly more positive  $\delta^{15}\text{N}$  values of Restionaceae in the burnt plot relative to the unburnt plot.

Mycorrhizal and bacterial populations are often more abundant after a fire as a result of increased alkalinity (Christensen & Muller, 1975, Raison, 1979), which may account for the similarity of  $\delta^{15}\text{N}$  signals of the Haemodoraceae, Penaeaceae and Thymelaeaceae between the burnt and the unburnt plots (Figure 13). Thus the  $\delta^{15}\text{N}$  of surface rooters is more positive in a post-fire community but generally the pathway of N acquisition 6 months after fire is not different from the N acquisition pathway of pre-fire communities.

However, the N pulse which occurs immediately after fire (Stock and Lewis, 1986, Musil and Midgely, 1990) increases the C:N ratios of post-fire communities relative to pre-fire communities in the Restionaceae, Penaeaceae and Thymelaeaceae (Fig. 14). Furthermore, seedlings generally initiate growth with low C:N ratios and in later stages of development possess a greater degree of carbon relative to that of the seedling stage. Haemodoraceae may not have significantly lower C:N ratios in the burnt plot possibly because of delayed seedling emergence, which may have occurred after the transient N pulse. The lower C:N ratios in the unburnt plot are because individuals in the unburnt plot are at a later stage of development, which means that a greater degree of carbon is produced for structural growth and support.

## Conclusion

Firstly, the semivariograms for nitrogen, phosphorus and pH shows that fire and the erosive forces of wind and rain did not serve to alter the spatial attributes of the soil components. Furthermore, 'fertile islands' do not appear to exist in mountain fynbos communities possibly because of short fire intervals which induce rapid community turnover, preventing the concentration of nutrients under canopies of reseeders as found under the canopies of longer lived species. Thus fire does homogenise soil components of fynbos and maintains homogeneity through relatively short fire intervals. Ash deposition increased the total P content of the burnt plot because P requires very high temperatures to volatilise as opposed to N. It appears that the main effect of fire results in an increase of the soil pH of the burnt plot through the deposition of alkaline ash on the soil surface. Secondly, fire did not alter the N acquisition of seedlings in post-fire communities, 6 months after fire. As hypothesised, species of Restionaceae had more positive  $\delta^{15}\text{N}$  values as a result of acquiring N from the surface layers of the soil. Surface layers of the soil are enriched in heavier N isotopes, as a result of volatilisation and leaching of the lighter isotopes. However, our evidence supports the hypothesis for surface rooters only since families which acquire N through mycorrhizal associations, continue to do so 6 months after fire resulting in the similar  $\delta^{15}\text{N}$  values in both pre and post-fire communities. Thus the only significant effect of fire is that it significantly raised the total P and pH of the soil through the ash effect which may have stimulated bacterial populations and that surface rooters acquire N enriched in heavier isotopes as a result of leaching and volatilisation of the lighter isotopes during combustion and deposition of enriched N isotopes on the soil surface.

## Recommendations

We recommend that the spatial arrangement of the post-fire community is analysed in order to determine the accuracy of the semivariogram results. Larger sampling plots could be analysed at a sampling interval less than a metre since the semivariograms reveal ranges of spatial dependence just over a metre. In order to examine the increasing variability over a smaller scale we should sample every 30 cm. We could measure the contents of  $\text{NH}_4\text{-N}$  and  $\text{NH}_3\text{-N}$  separately in order to clarify the status of fertile microsites in mountain fynbos. We could also look into the behaviour of animals in the study area as excreta were observed mostly on boulders. It is possible that regions surrounding boulders would be enriched in nutrients relative to other areas. As a result of the abundance of anthills it may be necessary to investigate the effects of anthills on the spatial

distributions of soil components. From this analysis it appears that anthills have no effects on soil components but it requires more detailed studies. Furthermore, the isotopic N signals could be tested at a time sooner after fire in order to determine whether fire alters the N cycling pathway of seedlings prior to the abundance of mycorrhizal and bacterial populations, which usually occurs after rain. In addition the duration of the heavier  $\delta^{15}\text{N}$  signals of the Restionaceae could be monitored in order to determine the duration of the effects of the deposition of heavier isotopes on foliar  $\delta^{15}\text{N}$  signals.

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## References

- Allsopp, N., Stock, W. D. 1993. Mycorrhizal status of plants growing in the Cape Floristic Region, South Africa. Bothalia 23(1): 91-104
- Boerner, R. E. J. 1982. Fire and Nutrient cycling in Temperate Ecosystems. Bioscience 32: 187-192
- Christensen, N., Muller, C. H. 1975. Effects of fire on factors controlling plant growth in *Adenostoma* chaparral. Ecological Monographs 45: 29-55
- Clarke, I. 1979. Practical Geostatistics. Applied Science Publishers Ltd. London
- Crawford, C. S., Gosz, J. R. 1982. Desert ecosystems: their resources in space and time. Environmental Conservation 9: 181-195
- DeBano, L. F., Conrad, C. E. 1978. The effect of fire on nutrients in a chaparral ecosystem. Ecology 59(3) 489-497
- DeBano, L. F., Eberlein, G. E., Dunn, P. H. 1979. Effects of burning on chaparral soils: I. Soil Nitrogen. Soil Sci. Soc. Am. J. 43: 504-509
- Gallardo, A., Rodriguez-Saucedo, J. J., Covelo, F., Fernandez-Ales, R. 2000. Soil nitrogen heterogeneity in a Dehesa ecosystem. Plant and Soil 222: 71-82
- Garcia-Moya, E., McKell, C. M. 1970. Contribution of shrubs to the nitrogen economy of a desert-wash plant community. Ecology 51(1): 81-88
- Garner, W., Steinberger, Y., 1989. A proposed mechanism for the formation of 'fertile islands' in the desert ecosystem. Journal of Arid Environments 16: 257-262
- Grimshaw, H. M. 1985. The determination of total P in soils by acid digestion. In: Chemical Analysis in Environmental Research. Rowland, A. P (eds). Pp. 92-95. ITE Symposium No. 18, Natural Environmental Research Council, Cumbria.
- Grogan P., Bruns, T. D., Chapin III, F. S. 2000. Fire effects on ecosystem nitrogen cycling in a Californian bishop pine forest. Oecologia 122: 537-544
- Hogberg, P. 1997. Tansley Review No. 95 <sup>15</sup>N natural abundance in soil-plant systems. New Phytologist 137: 179-203
- Kathan, L. 1981. A study of certain ecological aspects pertaining to a *Leucadendron laureolum* community at the Silver Mine Nature Reserve, South Africa. Master of Science, Department of Botany, University of Cape Town.
- Murphy, J., Riley, J. P. 1962. A modified single-solution method for the determination of phosphate in natural waters. Analytical Chim. Acta 27: 31-36
- Musil, C. F., Midgley, G. F. 1990. The relative impact of invasive Australian acacias, fire and season on the soil chemical status of a sand plain lowland fynbos community. South African Journal of Botany 56(4): 419-427

- Noy-Meir, I. 1985. Desert ecosystem structure and function. Pp 93-103 in M. Evenari et al., editors. Hot deserts and arid shrublands. Elsevier Science, Amsterdam, The Netherlands.
- Raison, R. J. 1979. Modification of the soil environment by vegetation fires, with particular reference to nitrogen transformations: A Review. Plant and Soil 51: 73-108
- Reenen, C. A., Visser, G. J., Loos, M. A. 1992. Soil microorganisms and activities in relation to season, soil factors and fire. In: Van Wilgen B, Richardson, D. M., Kruger, F. J., Van Hensbergen H. J (eds). Fire in South African mountain fynbos. Springer, Berlin Heidelberg New York, pp 258-272
- Richards, M. B., Stock, W. D., Cowling, R. M., 1997. Soil nutrient dynamics and community boundaries in the Fynbos vegetation of South Africa. Plant Ecology 130: 143-153
- Rossi, R. E., Mulla, D. J., Journel, A. G., Franz, E. H., 1992. Geostatistical tools for modeling and interpreting ecological spatial dependence. Ecological Monographs 62(2): 277-314
- Rowell, D.L. 1994. Organic materials - Alive and Dead (Ch. 3, p48) and Soil Acidity and Alkalinity (Ch. 8 p159-161) in: Soil Science: Methods and Applications.
- Schlesinger, W. H., Raikes, J. A., Hartley, A. E., Cross, A. F., 1996. On the spatial patterns of soil nutrients in desert ecosystems. Ecology 77(2): 364-374
- Smith, V. R. 1980. A phenol-hypochlorite determination of ammonium-nitrogen in Kjeldahl digests of plant tissue. Comm. Soil Science Plant Analysis 11: 67-94
- Stock, W. D., Allsopp, N. 1992. Functional perspectives of ecosystems. Ed. Cowling, R. In. The ecology of Fynbos, Nutrients, Fire and Diversity. Oxford University Press. Cape Town.
- Stock, W. D., Dlamini, T. S., Cowling, R. M., 1999. Plant induced fertile islands as possible indicators of desertification in a succulent desert ecosystem in northern Namaqualand, South Africa. Plant Ecology 142: 161-167
- Stock, W. D., Lewis, O. A. M., 1986. Soil nitrogen and the role of fires as a mineralising agent in a South African coastal fynbos ecosystems. Journal of Ecology. 74: 317-328
- Trangmar, B. B., Yost, R. S., Uehara, G. 1985. Application of geostatistics to spatial studies of soil properties. Advances in Agronomy 38: 45-65?
- Whitford, W. G., Anderson, J., Rice, P. M. 1997. Stemflow contribution to the 'fertile island' effect in creosotebush, *Larrea tridentata*. Journal of Arid Environments 35: 451-457
- Witkowski, E. T. F., Mitchell, D. T. 1987. Variations in soil phosphorous in the fynbos biome, South Africa. Journal of Ecology 75: 1159-1171