The effects of fire frequency on nutrient pool sizes and the subsequent effects on grass quality in savanna grassland in Umfolozi Park.

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ABSTRACT

African savannas are subject to fires of differing frequency and intensity (regime). Nutrients like nitrogen and to a lesser extent, phosphorus, can be volatilised by the heat of the flames during these fires. This represents a potential loss to the system. Additional losses can occur as ash deposits are blown or washed away, and mineralised nutrients can also be leached out of the system. It is therefore proposed that very frequent fires will compound these losses leading to low soil nutrients and consequently low plant nutrient levels (poor fodder). Our results indicated the expected lowering plant nutrient levels with increasing fire frequency over time. However, we found that the soils of the very frequently burned sites (burns every 1-2 years) were unexpectedly high in nutrients. This indicates that these nutrients are not available to plants. This may be the result of cool fires not mineralising nutrients but killing soil microorganisms such that organic decay is very slow. In opposition, it may be that the soil microorganisms thrive in the post-fire environment and use up the available nutrients. Non-symbiotic organisms may use the ash as a substrate and fix nitrogen which would also be unavailable to the grass. Further study will be needed to ascertain exactly why one finds high-nutrient soils but low-nutrient plants at very high burning frequencies.

INTRODUCTION:

Savannas are vegetation cover, which covers extensive tracts of land globally and are subject to considerable socio-economic pressures (especially in Africa). They are the basis of the African livestock industry and in places where they support wildlife their function can dictate the success of tourism (Scholes and Walker 1993).

Since nitrogen and phosphorus are essential elements for plant growth (Scholes and Walker 1993), plotting their distribution helps to quantify environmental energy flows. One of the most important factors regulating the movement of these nutrients through the system is the processes which are able to liberate them from their bonds within carbon compounds, as this then makes them available for uptake by plants. It is noted by Scholes and Walker (1993), that other nutrients such as potassium, magnesium and calcium do not follow the carbon cycle closely and are able to leach out of living and dead material.

The carbon cycle has large fluxes to and from the atmosphere and is thus defined as an 'open' system. Nitrogen cycles also have a link with the atmosphere but to a much smaller extent than carbon. Phosphorus has a very small atmospheric flux and is almost entirely restricted to plant-soil interactions (Scholes and Walker 1993). These processes of exchange are very important in relation to the potential losses and rates of recovery after a loss event like fire. It is often documented that fire can affect soil nutrient concentrations. It does so by direct volatilisation or by oxidation of the organic nitrogen in the surface layers (Stock and Lewis 1986). 'Pyrodentrification' is the term Scholes and Walker (1993) use to describe the process whereby nitrogen is lost to the atmosphere as N_2 and N_2O. They note that the amount lost depends on the heat produced by the fire (a 600° C fire being able to burn all the nitrogen away). The heat of the fire also has the capacity to alter some physical properties of the soil which can influence the steps in the nutrient cycles. It must also be noted that the input of ash after a fire can further affect the pools and cycling of nutrients at the site (Stock and Lewis 1986). In short, when plant material is burned, carbon and the elements bound to it (nitrogen and phosphorus) are partially or completely released into the atmosphere. This ash can then be lost from the system in the wind or it can be deposited back onto the burned site. This means that there are potentially significant changes in soil nutrient levels after fires. As a direct consequence, any alterations in the fire regimes will impact on the soils.

Farmers and other managers have reasons to maintain some form of burning regime. These reasons include: to burn off unpalatable growth left over from the previous seasons growth; to stimulate growth in those seasons where there is a shortage of forage; to destroy parasites (ticks); and to control bush encroachment (alien or local) (Materechera *et al.* 1998). Farmers can be inclined to burn as the post-fire grasses are often more palatable and nutritious than unburned veld (Materechera *et al.* 1998) as the new growth is not in competition (light and nutrients) with the previous seasons growth (Mentis and Tainton 1984). Scholes and Walker (1993) found that, although the rate of accumulation at the burned site was initially lower than that at the unburned site, the total season's above-ground productivity in the burned veld was almost double that in the unburned veld.

Fires at varying intervals or even three or four fires over a 20-year period had no effects on the concentrations of carbon or nitrogen or on nitrogen and phosphorus availability in soils deeper than 2cm (Adams *et al.* 1994). However the concentrations of carbon, nitrogen, potentially mineralisable nitrogen and phosphatase activity within this 2cm soil horizon were significantly reduced by burning. This is important since grasses tend to root only in the top 20cm of soils in savannas (Materechera *et al.* 1998). The higher concentrations of inorganic phosphate after the fires is probably due to the partial sterilisation of the ground by the heat of the fire (Adams *et al.* 1994). Adams *et al.* (1994) found that in heathlands 17% of the carbon total and 27% of the nitrogen total were lost from the soil surface in repeatedly burned sites. These findings were mirrored by Materechera *et al.* (1998) who found burned sites to have lower organic carbon than unburned ones. Adams *et al.* (1994) calculated that the amount lost after a fire event exceeds the input from rain and sediment over a 20-year period. Stock and Lewis (1986) found that higher total nitrogen concentrations were found at increasing soil depths as time passed after a fire in fynbos. This they attributed to nitrogenous products becoming soluble after their thermal breakdown by the fire. This provides a further mechanism by which soil nutrient pools are decreased after fire events. These kinds of findings may be true for the savannas in which case one might expect decreasing nutrient content of the soils and hence the grasses which may result in a compositional change (Scholes 1990). This would have obvious repercussions on the management practices of that land.

There is very limited quantitative information available on the effects of fire regime on edaphics and plant yield/nutritional responses. In light of this, the aim of this project is to determine the extent of nutrient change in soils after differing fire histories for grasslands in Hluhluwe-Umfolozi Park in Kwazulu-Natal. The main questions being raised are: Is there any difference in the nutrient quality of soils which have had long-term exposure to different fire histories? If there is a loss (as predicted), do the nutrients re-establish in time after fires or is there a net loss compounded per fire? Are there thus any noticeable effects on the quality of the grasses and does this change with fire frequency?

METHODS:

SITE:

This study was conducted in the Hluhluwe-Umfolozi Park. This reserve covers an area of 96 453 ha and is located in Kwazulu-Natal, South Africa (28°00′-28°26′ S; 31°43′-32°09′ E. see Figure 1).

SAMPLING:

On the 7th July 1999 we drove through Umfolozi, stopping at stands of open grassland dominated by *Themeda*. This was done in order to avoid differences caused by species effects. *Themeda* is easily identifiable and is resistant even to frequent fires (Trollope 1984) and thus should be found across the range of burn histories. At each site a soil sample was taken with a corer to a depth of 15cm. This was thought to be the best representative depth as previous studies suggested that fire effects had little or no long term impact on soils deeper than 2cm (Stock & Lewis 1986, Adams *et al.* 1994, Materechera *et al.* 1998), and that grasses tend to root only within the top 20cm of soil

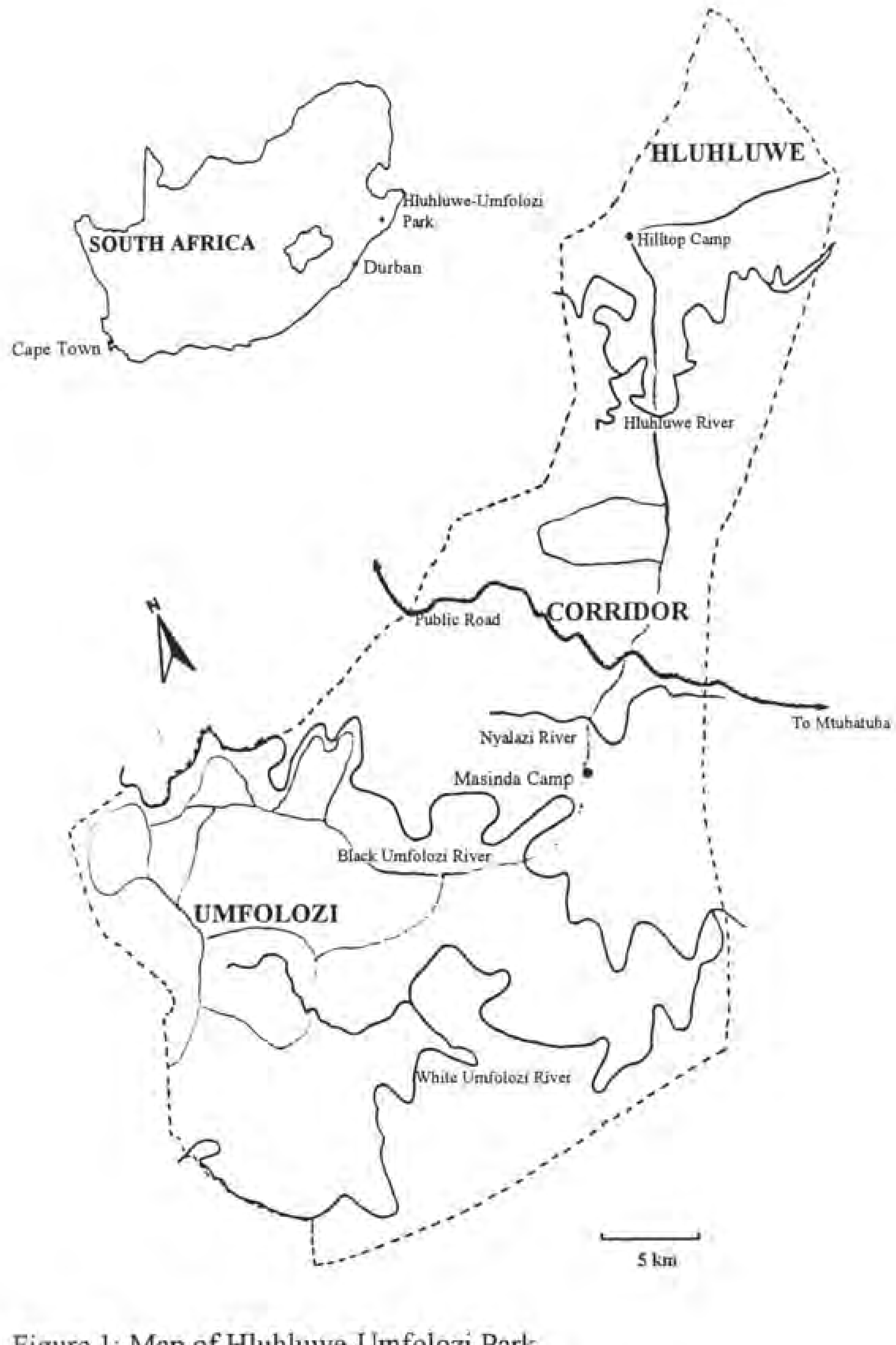


Figure 1: Map of Hluhluwe-Umfolozi Park

(Materechera *et al.* 1998). These samples were stored in labeled plastic bags which were folded and sealed on site. We also took a cutting of the *Themeda* grass growing next to the site of soil sampling. These were stored in brown paper bags. This procedure was repeated three times per site to provide the replicates. 26 sites were sampled (A-Z), therefore the total number of samples was 78 (n = 78 for all results). A GPS was then used to get the coordinates of the site. These coordinates were later fed into the computer at the research center to give us the exact fire history of each site from the GIS program installed there (roads were used as fire breaks). These are reported as the number of times the stand has burned since 1949. For the purposes of the analysis these were then further divided into four groups:

- 1 = 5 - 8 burns in the last 40 years
- 2 = 9 - 12 burns
- 3 = 13-16 burns
- 4 = 17-20 burns

Category 1 implies that there has been a fire through that site every 5 to 8 years. Category 2 burns every 3 to 4 years, 3 burns every 2.5 to 3 years and category 4 has burned every 2 years since 1949.

SAMPLE ANALYSIS:

Soil: Each soil sample was sieved through a 2mm mesh after having been air-dried. Total N was determined using 1.0g of the air-dried and sieved soil put through Kjeldahl digestion with 1ml of distilled water and 3ml of acidified salicylic acid (34g l^{-1} salicylic acid in concentrated H_2SO_4). In accordance with Bremner (1965) as revised in Stock & Lewis (1986), a selenium-catalyst tablet was added with 0.2g thiosulphate in order to include the assay of nitrite and nitrate. After digestion the sample was made up to 50ml with distilled water and nitrogen content determined by a phenol-hypochlorite method (Foster 1994a). The samples were read by a B&L Spectronic 21 spectrophotometer at 635nm. Results are expressed in mg N per g of sample.

Total P was determined with 0.2g of soil in 1ml distilled water. Digestion took place, as above, on an aluminium-block digester, with the addition of 3.5ml triacid mix (HNO_3:$HCLO_4$:H_2SO_4). After the digestion the samples were made up to 25ml with distilled water and the phosphorus content determined, after reaction with Murphy and

Riley reagent, with the same spectrophotometer as above reading at 882nm wavelength (Foster 1994b). As above, results are in mg/g.

20g of soil per sample were added to a jar, to which 50ml 0.01M $CaCl_2$ was also added. Soil pH was then determined on these samples using a pH meter. Method as per Rowell (1994).

Organic matter content was calculated as the mass lost by a sample upon ignition at 450 °C over 20 hours. These samples were previously dried at 105 °C for 24 hours in a forced-draught oven to remove any soil moisture remaining after the air-drying. Results are expressed as percentage organic matter per sample.

Plant: Since the ratio of shoot-to-leaf changes for different heights of *Themeda* and we were only interested in the nutrient content of the leaves, the leaves of all the plant samples were manually removed from the stems. This leaf material was then dried at 70 °C in a forced-draught oven for at least 48 hours. At least 2g of dried material was then ground in a Whiley mill through a 40 mesh. 0.1g of this was then subjected to the same Kjeldahl digestion method described for the soil to determine its nitrogen content. A further 0.1g was then put through the triacid digestion and Murphy and Riley method for phosphorus analysis. As before, the results display nitrogen and phosphorus as milligrams of nitrogen/phosphorus per gram of sample substrate.

STATISTICAL ANALYSIS:

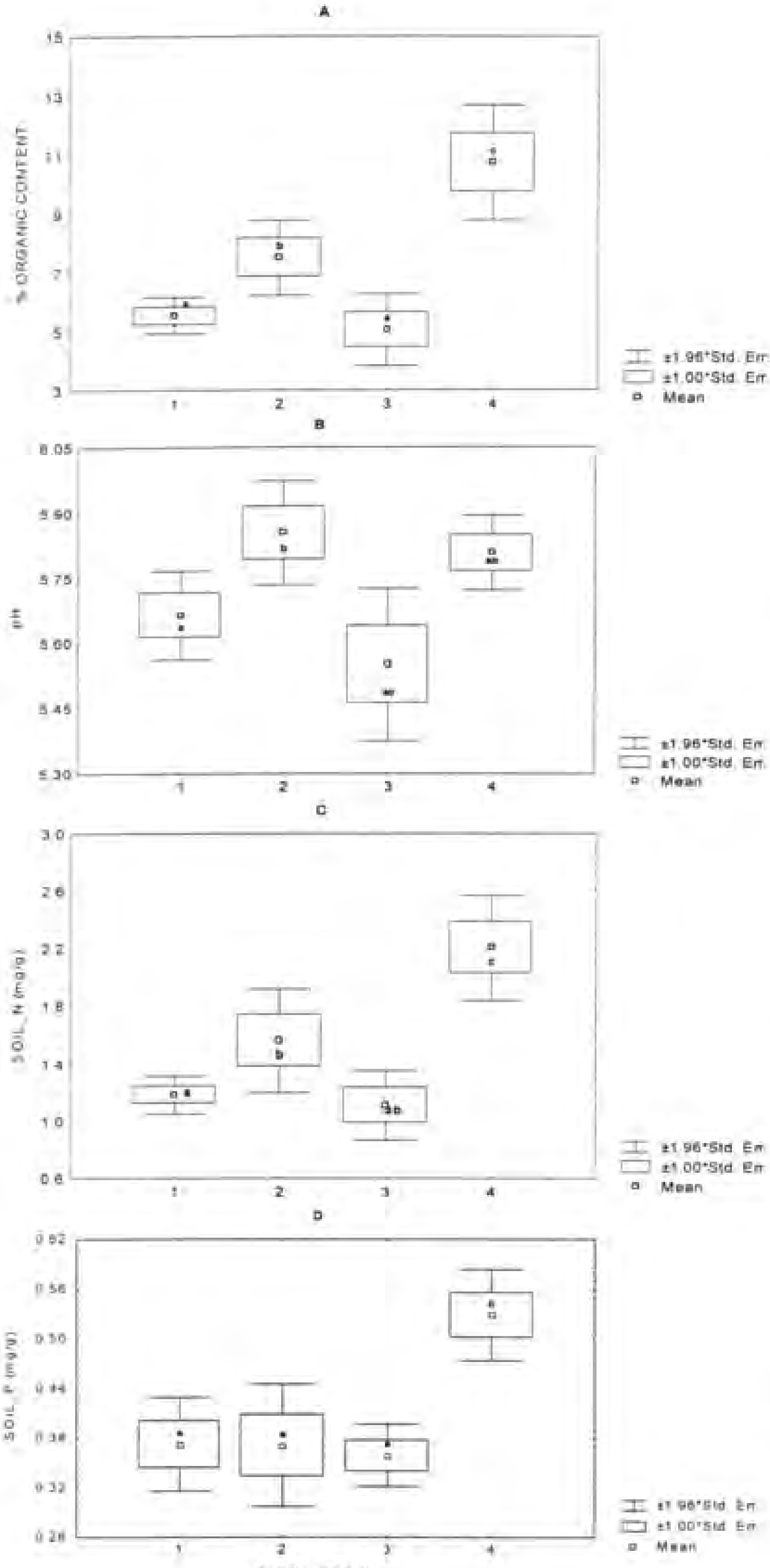
Data were put into spreadsheets in Excel and imported into Statistica 5.1 where they underwent analysis of variance, after being checked for normality. Unfortunately the data could not support a 2-way ANOVA so one-way ANOVA's were run comparing the burn history category to the various measured variables for both plant and soil. Box-and-whisker plots show the mean (of the variances), the standard error and 1.96* the standard error. On the graphs, different lower-case letters in the boxes represent statistically different means at $p<0.05$ (these were determined by a Least Significant Difference [LSD] post-hoc test for planned comparisons).

RESULTS:

SOILS: Figure 2. shows all the soil parameters across the four burn history categories. Sites which burned 9 to 12 times over the last 40 years (category 2) have higher organic content, pH and soil nitrogen. There is a general trend for these values to drop in the next category (13-16 burns). In the frequently burned sites, almost all the soil parameters are seen to rise (pH also rises but is not statistically different from the other burn histories at $p<0.05$). This is the only category in which a rise in soil phosphorus is noticeable and statistically relevant. Except for pH values, there is a general trend for the nutrients and organic matter content to rise with increasing fire frequency over the long-term. Only phosphorus is relatively unaffected until this threshold, but the other indicators all show a slight elevation in burn category 2. This then recedes back before rising again in response to very frequent fires over the long term. It is noteworthy that nitrogen and phosphorus track the soil organic content and that pH is also weakly correlated with these two (R^2 values for the correlations being 0.477, 0.237 & 0.164 respectively).

The ratio of soil nitrogen to phosphorus shows a similar trend to the one mentioned above, although none of the means are statistically different from each other (Figure 3. **A**).

GRASS: Plant nitrogen is clearly lower for increasing fire frequency. Little change is noticeable between categories 1 and 2, but thereafter the concentration of nitrogen in the leaves of *Themeda triandra* decreases markedly (Figure 4. **A**). Figure 4. **B** shows the mean values for plant phosphorus. These do not follow the trends as seen above for plant nitrogen. Here phosphorus is seen to be depleted with a slight rise in category 4 (frequent burns). The range of these values in the frequently burned sites is quite large, which may indicate contamination but the lowest value is still higher than that of burn category 3, which supports the trend observed. Local contamination may have occurred if some of the acid boiled over in the digestion process as this could



ANOVA Results:
$F(3,74) = 15.64$; $p = 0.000$

ANOVA Results:
$F(3,74) = 4.28$; $p = 0.007$

ANOVA Results:
$F(3,74) = 12.62$; $p = 0.000$

ANOVA Results:
$F(3,74) = 5.99$; $p = 0.001$

gure 2: Means of Soil Organic Matter for each of the burn history categories (**A**), Means of pH across e burn history categories (**B**). Means of soil nitrogen (**C**) and soil phosphorus (**D**) for each burn ategory. Different lower case letters in the boxes indicate statistically different means ($p<0.05$) after -way AVOVA and LSD post-hoc tests have been applied.

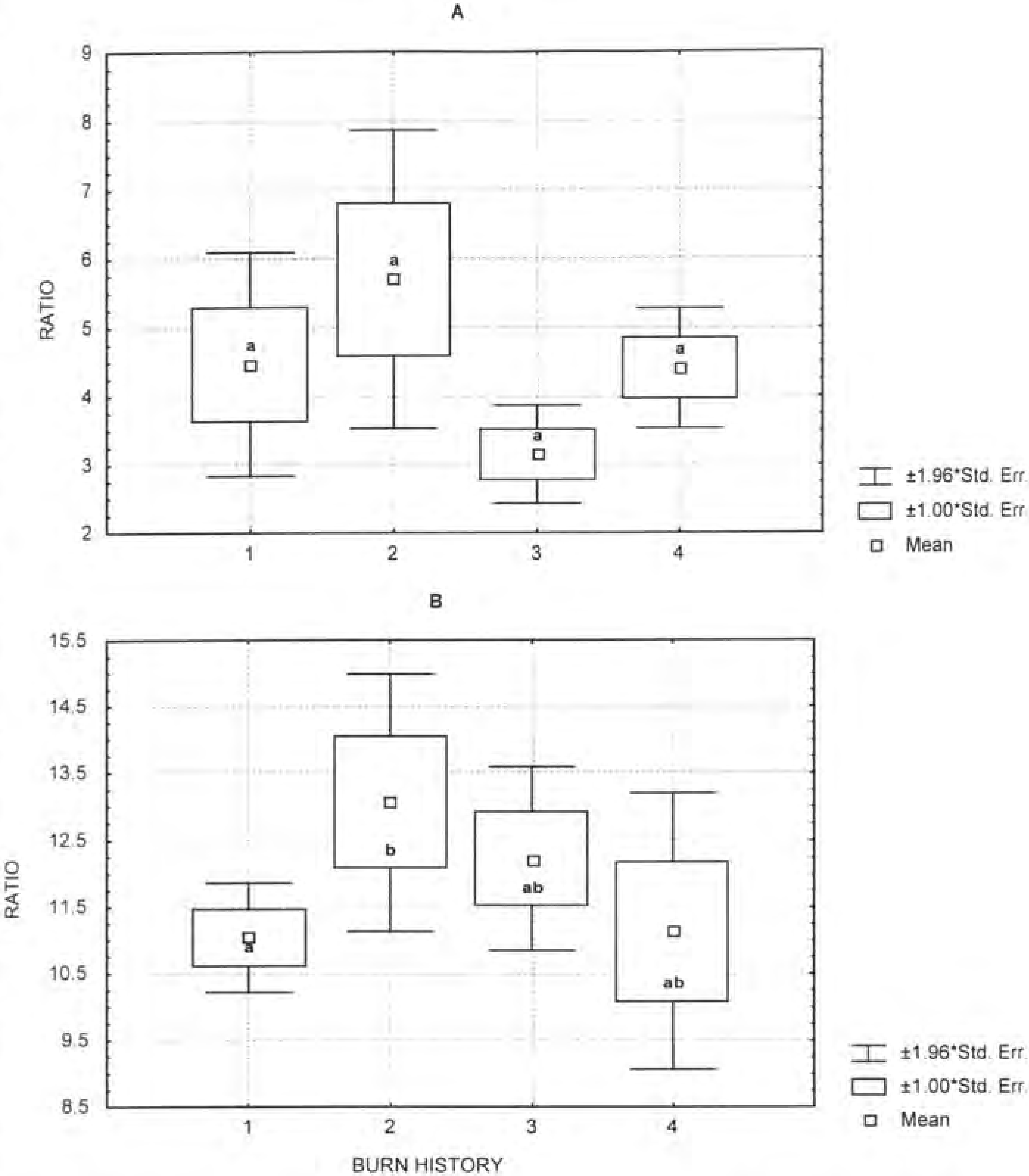


Figure 3: Means of soil nitrogen to phosphorus ratios (**A**) F{3,74} = 1.12; p = 0.35; and plant nitrogen to phosphorus (**B**) F{3,74} = 1.60; p = 0.2, for the range of burn histories after a 1-way ANOVA. Statistically different means were determined by a post-hoc LSD test and are denoted by different lower-case letters ($p<0.05$).

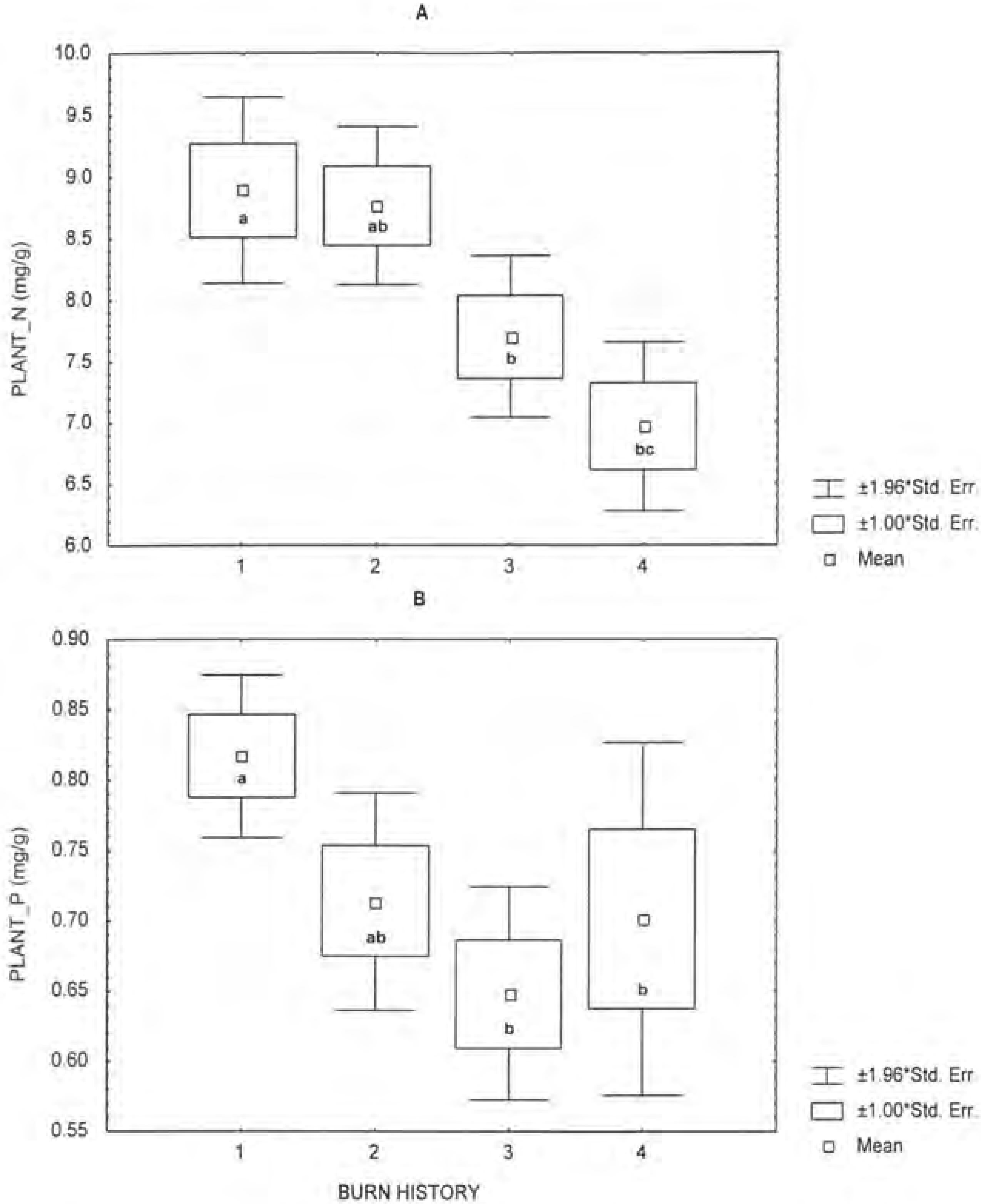


Figure 4: Means of plant nitrogen (**A**) $F\{3,74\} = 5.78$; $p = 0.0013$; and plant phosphorus (**B**) $F\{3,74\} = 2.92$; $p = 0.04$, for the range of burn histories after 1-way ANOVA test. Different lower-case letters indicate statistically different means ($p<0.05$), determined using a Least Significant Difference (LSD) post-hoc test for planned comparisons.

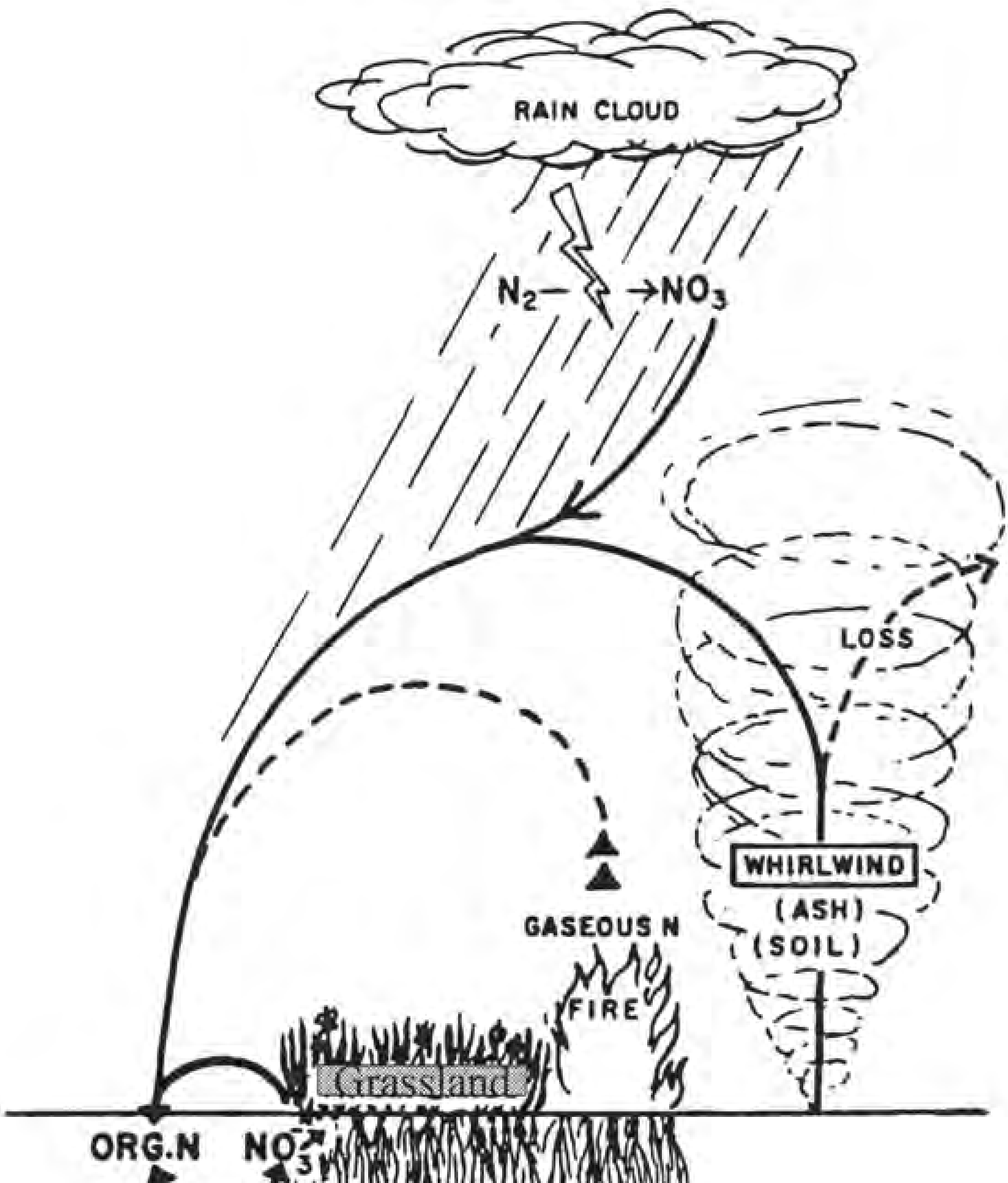


Figure 6: Schematic diagram indicating sources and sinks of nitrogen.

have landed in an adjacent tube. Values in the boiled-over tubes would be falsely low, but those into which the splattered acid landed would be falsely high.

Plant nitrogen to phosphorus ratios indicate a rise from category 1 to 2, followed by a slightly significant drop with increasing fire frequency (Figure 3. **B**).

Lastly, in Figure 5. **A**, one can see how there is no significant difference over the first three burn categories. Those sites which have burned every 2 years since 1949, show a very high ratio of soil nitrogen to plant nitrogen. This means that there is much nitrogen in the soil but little in the plant material. Similarly, the ratio for soil to plant phosphorus tends to increase with increasing fire frequency. As with nitrogen, it is only in the very frequently burned sites that this becomes significantly different. A high ratio is again indicative of high soil phosphorus but low plant phosphorus observed at that site

DISCUSSION:

The results of this study clearly demonstrate how, soil nitrogen values and to a lesser extent soil pH values, track soil organic content. Concentrations of Ca, Mg and K in the ash after fires have the effect of raising the pH of the soil (Materechera *et al.* 1998). On the other hand, organic matter acidifies the soil by releasing humic acids and soluble CO_2. At our sites these two processes would appear to be functioning simultaneously, which would help to explain the marginally significant pH readings which appear not to follow the above trend very closely. pH values only differ by 0.6 between the extremes and are not significantly correlated with any other parameter of soil and/or plant nutrition. Although mineralisation can be aided by raised pH readings, the lack of significant correlation warrants their exclusion from further discussion. It is interesting that the values for soil organic matter, and consequently those for nitrogen and phosphorus, show a sudden elevation associated with the threshold of very frequent burns over the long term. At the same time, these nutrient values in the leaves of the *Themeda* show a decreasing trend with increasing fire frequency. These seemingly conflicting results certainly warrant further attention.

Prediction: Nutrient Loss

It is widely predicted that nutrients (especially volatile ones such as nitrogen and, to a lesser extent phosphorus) would be steadily depleted from the soil with increasing fire frequency and compounded over the long term (Debano & Conrad 1978, Cass *et al.* 1984, Stock & Lewis 1986, Scholes & Walker 1993, Materechera *et al.* 1998). The logic being that the heat of the fires releases these nutrients from their carbon bonds in organic material which causes them to be lost to the atmosphere (Scholes & Walker 1993, Materechera *et al.* 1998). Nutrients, which survive this volatilisation but are a component of the ash, may then be blown away from the site by winds, which can now reach the surface of the soil because the covering vegetation has been removed by the fire (Cass *et al.* 1984). – see Figure 6 (Barber 1984). Furthermore, it has been predicted that rains subsequent to the fire will cause leaching of the nutrients still remaining at the site (Stock & Lewis 1986). The overall effect of the above processes is an initial 'flush' of higher soil nutrients (ash deposits and mineralised organic matter), followed by a steady decrease in available nutrients.

This kind of nutrient loss was the hypothesis we were expecting to confirm with this study. The plant nutrient levels are lower with increasing fire frequency as expected, but this was predicted to have been a consequence of low soil nutrient levels. Contrary to this, our results indicate significantly elevated soil nutrients which appear to manifest only after a threshold limit in the burn regime (very frequent fires over many years). The ratios of nitrogen to phosphorus indicate that (in this system at least), volatilization of nutrients by fire is not a significant influence (Figure 3). Since phosphorus is less volatile than nitrogen (Debano & Conrad 1978, Stock & Lewis 1986, Kutiel & Inbar 1993), N:P ratios should demonstrate negative linear relationships with increasing fire frequency (relatively more phosphorus means a lower ratio). Our data show this effect only very weakly in plant matter and no significant effect at all for soils (Figure 3). This indicates that the fires (certainly the most recent ones) have not successfully volatized significant amounts of nitrogen, which is suggestive of 'cool' fires. Alternatively, the nitrogen in this system may be rapidly replaced subsequent to fires.

High Soil Nitrogen:

It has been reported in some habitats that soil nitrogen can be increased after a fire – particularly plant-available nitrogen (Stock & Lewis 1986, Prieto-Fernandez 1993, Kutiel & Inbar 1993). This is due to the addition of ash which was formerly a pool of inaccessible nutrition for plants. This mineralisation of organic material is able to provide a 'flush' of available nutrients into the soil by releasing these nutrients from their bonds to carbon. However, it has also been reported that this source of now-soluble nutrients is vulnerable to precipitation which may wash them away, or cause them to be leached to deeper soil profiles (Stock & Lewis 1986, Dumontet *et al.* 1996). Nevertheless, a buildup of soil nutrients is possible in this way.

The heat of the fire is capable of breaking down the high-nitrogen, anti-herbivore tannins and phenols employed by some plants, and charcoal has the ability to adsorb these chemicals into its structure (Moore 1996, Wardle *et al.* 1998). When these materials are present in organic litter, they impede the function of microorganisms which in turn hinders the breakdown process, which translates to lower nitrogen availability for plant roots (Moore 1996. Wardle *et al.* 1998). Fires in this situation provide better access to these stored nutrients and can thus increase soil (available) nutrient pools.

The above two situations describe scenarios which should be beneficial to plants rooted in these soils after fires. In both instances, the fire releases a pool of nutrients into the soil which are readily available for uptake by plants. One would naturally expect the plants here to show correspondingly high values for these nutrients in their leaves. Our burn histories do not reflect this pattern. The elevation in soil nutrients is accompanied by a lowering of leaf nutrition with increasing fire frequency (Figure 4).

Microbes the key?

The survival and success of microorganisms after fires is a debatable point as some authors report their inability to revive after fires (Garcia-Oliva *et al.* 1999). Dumontet *et al.* (1996) conclude how "even 11 years after the fire the microbial biomass is far from recovery of the same value as the unburned site". The intense heat of the fires (around 250° C but as high as 600° C – Trollope 1984) has the potential capacity to kill the microorganisms responsible for the breakdown of organic matter (Cass *et al.* 1984). These populations are known to re-establish after fires (Moore 1996) but over many years of frequent burns, their populations may have been damaged irreparably such that they are no longer able to successfully break down unburned organic matter before the next burn. It may be possible that many frequent fires has the ability to sterilise the soil. This would lead to organic matter build-up but low available nutrition for plant roots. Our data seems to support this notion in that we observed what appeared to be high levels of nitrogen and phosphorus in the soils of the most frequently burned sites (Figure 2 C & D). At the same time, however, these same sites showed decreasing amounts of these nutrients in the leaves of the grass (Figure 5 A & B). This would suggest that the soil nutrition is in a form which is not readily accessible to the roots of these plants.

However, most authors agree that the soil microbial community is not adversely affected over the long term (Cass *et al.* 1984, Stock & Lewis 1986). Soil conducts heat very poorly. It also has a high latent heat and cannot burn over 100° C until the soil moisture has been boiled off. It is for these reasons that the flush of heat associated with fires tends not to penetrate very deeply into the soil horizon (temperature changes of greater than 10° C only occurred in the top 15cm of soil - Cass *et al.* 1984). It would seem then, that the microorganismal communities would be able (at least partially) to survive these fires. Such deleterious effects on these populations of microorganisms were seen as so minimal and of such short duration as to be declared unimportant by Cass *et al.* (1984) and Trollope (1984). Therefore, if microorganismal communities are as resilient as papers suggest, then some other explanation of our data is preferable.

Fire Intensity:

Our data clearly indicate significantly elevated soil organic matter and consequently elevated soil nitrogen and phosphorus in conjunction with depleted values for the same nutrients in the leaves, at the very frequently burned sites. Something has happened here which has caused the accumulation of nutrients in the soil in a form which is obviously inaccessible to the roots of the plants. This is further illustrated in Figure 5 (A & B) which show the ratios of soil nitrogen/phosphorus to plant nitrogen/phosphorus. There is a statistically significant jump as one crosses the fire frequency threshold mentioned earlier. This sudden elevation is further evidence that the soil at these sites contains unusually high levels of nutrient relative to the plant material growing in them.

Bearing in mind that the fires in Umfolozi do not appear to have volatilised significant amounts of nitrogen and that the survival of the microbial community appears to be without question, what could be the cause of the phenomenon observed at our frequently burned sites?

I believe that an answer could be the intensity of the fires experienced at the sites in question. This is not to say that these fires are necessarily 'cool' fires burning in the absence of large amounts of biomass, but that they are sufficiently lacking in energy for certain critical processes to occur.

- Firstly, and most importantly, the heat of the fires is not enough to induce volitisation. This should be clear, given the evidence put forward and means that there are apparently not experiencing the great losses in nutrients (particularly nitrogen) that we had been expecting. As a consequence, the post-fire soil is not experiencing a compounding depletion of nitrogen or phosphorus.
- Secondly, the heat of the fire is below the ignition temperature of the organic materials and/or the duration of the fire is not long enough to burn all of the organic accumulation. So the post-fire deposit consists largely of partially broken down organic material. This material would raise the organic content (and hence the nutrient levels) in the soil at the burned site. But this pool of nutrients released into the soil is not readily available to plants as it has not been mineralised. Other authors have found similar results. Prieto-Fernandez *et al.* (1993) found that most of the additional nitrogen observed in their soils after a fire was in organic form which implies the rise in total N in the burned sample was due to the "permanence in the ash of incompletely burned plant residues". Likewise, a study by Christensen

(1973) found that the ash deposition contained 38% organic matter of which only 128.3 ppm could be attributed to available nitrogen forms (NO_3-N & NH_4-N).

The above two points explain the data in this study by presenting a mechanism which will provide high soil nutrients but low plant realised nutrition, in sites subjected to a long history of frequent burns. At these sites there is less biomass accumulation due to the low mineralisable nutrient fraction in the soil. Therefore, the fires here burn with less intensity and are subsequently unable to release much plant-available nitrogen into the soil. They succeed in partially burning the grass cover, but leave a high organic fraction in the ash. In this dry environment, this organic matter is not readily broken down but persists in the soil alongside the root masses of old grasses (also not removed by the fire). These tillers of old, dead grass occupy space which cannot support new growth. So because the fire does not remove them, they build up in number and help to further lower the fuel load for the next fire (which will again be too 'cool' to mineralise these stores of inaccessible nutrients).
The result is that frequently burned patches will exhibit high soil nutrient values, but the plants growing in them will reflect the low availability of these pools.

REVISITING MICROORGANISMS:
The high survivability of microorganisms following a fire reported by previous researchers into this phenomenon, suggests another explanation to the 'cool fires' proposition. As mentioned earlier, the data indicate high soil nitrogen and phosphorus but low values for these nutrients in the plants, indicating that the soil nutrition is unavailable to the plants despite its proximity. Given the above, we are able to suggest that the fire regime threshold change represents a switch in nutrient cycling within the system, in favour of the microbial community. After the fire, conditions suit the microbes in the soil very well Christensen & Muller 1975), especially in terms of nutrient competition with plants (as the latter are less able to rapidly capitalise on the flush of nutrients – Stock & Allsopp 1992). In this scenario, the flush of post-fire nutrients encourages the rapid development of the soil microbial community which then use up the available nutrients as they grow and multiply (Lewis 1986).

This is especially feasible given the high carbon to nitrogen ratio that the grass medium must provide. Having to utilise a carbon source so low in nutrients (particularly nitrogen), means that the microbes could use up all the available nitrogen in the soil, including the flush after the ash deposition (Lewis 1986). This would effectively 'lock up' these nutrients making them unavailable to plants, but allowing them to show up in our analysis.

Non-symbiotic nitrogen fixing bacteria (*Clostridium*, *Azotobacter*, etc) may be a significant portion of this effect. Our data suggest that volitisation is not a major issue in this savanna, but it could be the case that the nitrogen lost in the fire is rapidly replaced by these non-symbiotic nitrogen fixers. They are stimulated by the flush of substrate (ash) after the fire and by oxidising this new organic material, are able to fix atmospheric nitrogen (Lewis 1986). These would also have the effect of raising the level of soil nitrogen as measured in this study, while making it inaccessible to plant roots.

CONCLUSION:

We are now faced with two possible explanations for the very frequently burned sites' nutrient balance. Firstly the inificient breakdown of plant organic matter by 'cool' fires and the possible (although unlikely given cool fires) negative long-term effects on beneficial soil microorganisms, leaves the nutrient pool in the soil and inaccessable to plants. Secondly, the flush of nutrients and organic matter promotes the soil microbial community such that it is able to utilise the nitrogen in its growth, making it unavailable for the grasses. Non-symbiotic nitrogen fixers may be a significant proportion of this microbial community and could 'hide' the fact that nitrogen was indeed volatilised in the fire. In this scenario, the threshold fire regime has caused the productivity of the system to shift dramatically in favor of the microbes.

Whatever the cause, the effect is high soil nitrogen which is not available to the plants, causing the latter to have nutrient-poor leaves. We can therefore conclude that frequent burning lowers the quality of the grasses, which is especially relevant when considering these sites in terms of management. Infrequent burns may enable trees and thicket species to dominate the landscape (Scholes & Archer 1997), which is a negative impact if the management aim is to provide fodder for large grazers (wild or domestic). There seems to be a threshold burning frequency associated with the grasslands in Umfolozi, after which soil nutrients suddenly rise while those in plants continue to decline. When sites are burned at a high frequency (more often than once every 2.5 years) for long periods of time, the fodder they produce probably becomes unpalatable and not very nutritious owing to the low nutrient status of the leaves of the grasses there. This would negatively impact range managers concerned with supporting livestock or wild game.

In order to ascertain the cause of the low plant nutrient levels, further study is needed which should focus both on the microbial community's and the plants' responses over time to fires. If the intensity of these fires can be observed or calculated, they would add greatly to the results, being able to demonstrate or disprove the 'cool' fire proposition.

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