Biogeochemical niche construction in the forest-fynbos mosaic of Jonkershoek Nature Reserve, South Africa.

Raheem Dalwai

Supervisor: Lesego Khomo

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Table of contents

Abstract……………………………………………………………….……..……..…...…5

1. Introduction…………………………………………….……………………..…....6

1.1 Topographic and pedogenic factors controlling vegetation patterns ……….……..….......7

1.2 Implications of spatial distribution and textural variability in the forest-fy1nbos mosaic.7

1.3 Role of nutrients in determining vegetation patterns………………………………....8

1.4 Global importance of understanding forest-fynbos mosaics…………………….…..…11

1.5 Aims and objectives…….……...………….….…………………….………………….11

2. Materials and methods ……………………………………………………….….…13

2.1 Study site………………………………………………………………………………..13

2.2 Fieldwork……………………………………………………………………………….13

2.3 Dust and nutrient analysis………………………………………………………………14

2.3.1 X-ray Fluorescence analysis (XRF)……………………………………..……..14

2.3.2 Calculation of nutrient gain and loss (tau)……………………………………...15

2.3.3 Carbon and Nitrogen analysis (CNN)…….………………..………………………..15

2.3.4 Texture analysis………………………………………………..……………….15

2.4 Decomposition…………………………………………………………………………….16

2.5 Statistical analysis…………………………………………………………………………17

3. Results……………………………………………………………...………………… 18

3.1 Field observations in the forest and fynbos microhabitats…………………………...…18

3.2 Particle size distribution in Jonkershoek..………………………………….……..…….19

3.3 Particle size evidence for dust accretion……………………………………………..20

3.4 Nutrient distribution in Jonkershoek………………….………………….…..…..….…20

3.5 Loss and gain of nutrients relative to rock……......………......…………………………..21

3.6 Carbon and nitrogen cycling……………….………..………..………………...………...23

4. Discussion……………….……………………………….……………….…....………25

4.1 Microhabitats differentially affected by topographical processes……...……….……….…25

4.2 Implications of unique textures in the different patch types………...……….......…...…25

4.3 Factors affecting nutrient distribution in different patch types……….....……..……..….26

4.4 Implications of nutrient enrichment and depletion in different patch types……….......28

4.5 Sources of bedrock derived nutrients………………...……….…....…………...……29

4.6 Carbon and nitrogen cycling…..…..……………..………….......…..……......…...…30

4.7 Conclusions…...……..………….…..……..…………….…………………....…..…31

Acknowledgements……………………….…………………………..…………….........32

References ...…………………………........…………………………….…..……..…..………32

List of figures…………………………………………..…..…………………………...38

Figures……………………………………………………………...…………….……….41

Abstract

The south-western Cape of South Africa is dominated by fynbos vegetation with patches of forest restricted to rock screes and stream banks owing to the more favourable moisture status of these microhabitats. A detailed analysis of soil underlying forest and fynbos vegetation in Jonkershoek Nature Reserve was investigated. A total of nine soil pits were dug in forest and on fynbos slopes with high and low gradients. Pits were analysed by depth examining texture while soil was also sent for x-ray fluorescent analysis and carbon and nitrogen analysis. Evidence for dust deposition varied spatially, although this could be a result of the rapid erosion experienced during winter. Soil properties, mainly texture and nutrient concentration differed distinctly between forest and fynbos. I argue that these differences are caused by topographical diversity and maintained by vegetation which influences nutrient enrichment via dust accumulation and plant litter decomposition. Thus I concluded that soil texture favours nutrient retention in forest soil more than in fynbos soil enhancing the disparity between nutrients in the respective environments. By influencing litter decomposition and aeolian inputs of dust, vegetation is responsible for modifying its niche increasing the difference between fynbos and forest patches.

1. Introduction

Heterogeneous landscapes persist throughout the world producing diverse vegetation contributing to global biodiversity. The distribution of major vegetation types across the world is assumed to be determined by climate. However, large parts of the world which have climate suitable for closed forests support open vegetation instead (Bond, 2010). Studies conducted in savannas have questioned this assumption due to the coexistence of trees and grasses in one climate. In the fynbos biome, forests and shrublands coexist forming mosaic landscapes. Forests and fynbos are two ecologically distinct ecosystems composed of a suite of different species with different resource requirements. I find the coexistence of such distinct vegetation types within a single biome quite fascinating.

Fynbos plants normally grow on acidic, nutrient poor soils while forest plants usually require nutrient rich soils (Bengtsson et al., 2011). Forest patches within the fynbos recruit in moist areas such as riparian zones and screes in the landscape where fire cannot penetrate (Manders, 1990). Therefore, fynbos vegetation is more prone to the effects of fire. Despite the importance of fire, my study places emphasis on the biogeochemical aspect of niche construction and therefore, subsequently, I shall mention fire relatively infrequently. Nutrient poor soils cannot sustain forests even under high rainfall e.g. in south-western Australia (Bond, 2010). Therefore, in addition to moisture the mosaic landscape of forests and shrublands in the South-Western Cape may be a result of soil composition and nutrient availability.

1.1 Topographic and pedogenic factors controlling vegetation patterns

When climate and geology are uniform across a landscape, differences in vegetation patterns may be attributed to non-uniform biotic and abiotic factors. These include topography, soil composition, microorganism diversity and sunlight among others. Mosaic landscapes tend to be less pronounced where topography is less varied (Howard and Waring 1991). The physical processes dominant across the landscape affect forests and fynbos to different degrees due to differences in topography. Soil plays a crucial role in plant development through the supply of nutrients, water and anchorage. Soil varieties can be observed by recording the colour and texture together with the biota which are present on them. Soils which are organically enriched are usually black, while lighter soils are less enriched in carbon. Vegetation and animals respond to the differences in soil composition by utilising particular gradient ranges in environmental variables. For example, animals like termites are known to produce uniform mounds only when they are restricted to limited variation in climate and soil (Harris, 1956). Nutrient retention within the soil is influenced by soil texture and can affect the rate of sediment deposition. Clay-rich soils retain more water and nutrients than sandy soils which also lack organic matter for the same reason (Shachak et al., 2014).

1.2 Implications of spatial distribution and textural variability in the forest-fynbos mosaic

Fynbos vegetation occurs on gentle to steep slopes receiving seasonal rainfall as a moisture source. Steep slopes are more prone to weathering and erosion after a heavy rainfall event than gentle slopes. Eroded sediment tends to accumulate on the gentler slopes or be exported via drainage lines. Under these conditions, gentle slopes are expected to provide a more stable environment with deep and well defined soil horizons. Fynbos is also exposed to full sunlight and susceptible to frequent fires. Soils occurring on higher topographic positions in the landscape have a higher sand content while at lower positions the abundance of silt and clay is greater (Witkowski and Mitchell 1987). In addition, flat areas have fine-textured sand while at higher elevations medium textured sands prevail (Witkowski and Mitchell 1987). Fynbos soils are generally light indicating a lack of organic matter. Fynbos vegetation has adapted to growing on nutrient poor soils, producing poor quality above ground biomass hence the litter recycled is also of a poor quality (Read and Mitchell 1983).

By contrast, forests occur along the river or on screes. They recruit on slopes which vary in steepness and are exposed to perennial river flow which rapidly increases during winter (Slabbert et al., 2014). Forests may provide a less stable environment than fynbos with less pronounced and least developed soil horizons. Forests shade out light which provides a suitable microhabitat for many epiphytic species. Forest soils generally have more organic matter than soils elsewhere as more litter falls on the forest floor thereby decomposing and being recycled back into the system (Almendros et al., 2014). The forest has coarse, larger sized particles as high velocity water strips less resistant particles away. High below-ground biodiversity corresponds to high above-ground biodiversity (Slabbert et al., 2010). Therefore, being composed of a different suite of species, forests and fynbos are exposed to a different suite of microorganisms which alter soil chemistry and texture differently. Forest and fynbos vegetation have different resource requirements hence their respective soil compositions and textures are important determinants of vegetation distribution.

1.3 Role of nutrients in determining vegetation patterns

Nutrients are essential for all life forms be it plants, animals or microorganisms. All life on earth requires distinct amounts of macronutrients and micronutrients to ensure survival and reproduction. Most nutrients are derived from rocks while the atmosphere provides an additional nutrient reservoir for ecosystems (Bo et al., 2008). Weathered rocks release nutrients which enrich the surrounding soil and may be transported via aeolian processes across vast distances or locally (Fearnehough et al., 1996). In addition to weathering and aeolian deposits, the decomposition of plant litter further enriches soil with nutrients.

Aeolian deposition includes the deposition of dust which can occur on a global scale. Swap et al. (1992) showed that Saharan dust crosses the Atlantic and settles in the Amazon Basin maintaining nutrient balance in the tropical rain forest. Dust deposition has not been extensively studied in South Africa (SA). However, the findings of Soderberg and Compton (2007) showed that the fynbos ecosystem in the Cederberg Mountains of SA is enriched with nutrients through dust deposition. Dust particles are easily transported across the world and provide a source of nutrients. Dust fails to settle on landscapes with insufficient vegetation and will remain in suspension until it reaches a vegetated area where it will eventually settle and accumulate (Fearnehough et al., 1996). Therefore, steep slopes within the fynbos which have little or no vegetation should have a lower dust input than forest or highly vegetated areas in fynbos. Dust particles may be small or large but frequently occur within the range of 20-110µm. Dust settled on topsoil enriches surface soils to a greater degree than soils at depth (Fearnehough et al., 1996). Therefore, when there is a lot of dust then this size range becomes more abundant at the surface than at depth. Dust is composed of many nutrients some of which are essential for plant growth.

Essential nutrients include silicon (Si), magnesium (Mg), manganese (Mn), calcium (Ca), potassium (K), phosphorus (P) and nitrogen (N) while some of the most vital soil framework elements include aluminium (Al) and iron (Fe). Magnesium and Ca form deposits of dolomite which is a major component of sedimentary rock while Fe is released by the weathering of igneous rock (Cox, 1995). Iron is essential for microorganisms and plants as it aids plant health and defence and is used to produce chlorophyll (Lemanceau et al., 2009). Iron is acquired via both weathering and aeolian deposition occurring in high quantities in the soil. Plants require nutrients such as C, N, K, Mg and Mn for photosynthesis. Manganese ions activate several enzymes involved in Krebs cycle while K cations regulate the osmotic potential of plant cells. Magnesium ions have a specific role in the activation of enzymes involved in respiration and photosynthesis while P forms ATP and is used in metabolism. A lack of P will result in the hindering of plant growth (Gyaneshwar et al., 2002). Therefore, it is imperative that plants return P to the system to prevent plant growth being hindered.

Some of these elements are not absorbed by plants or aid in their growth but alter the rhizosphere and help retain or absorb nutrients essential for plant growth. Aluminium is one such element which may form a precipitate covering the root surface and is correlated with elevated amounts of P (Batty et al., 2002). Aluminium is usually found in small quantities in plants as it is not actively taken up. Nutrients and soil framework elements do not work in isolation but work together aiding plant growth and recruitment. The abundance of some nutrients is tightly correlated with each other as plants require specific quantities of nutrients relative to each other. The presence of Al in the soil enhances P uptake. Phosphorus is highly reactive to Ca, Al and Fe which may lead to its precipitation and become inaccessible to plants (Gyaneshwar et al., 2002). Some nutrients are more abundant than others in rock and aeolian deposits while plants absorb nutrients at different rates. Therefore, nutrient input and removal vary depending on the nutrient. Because forest and fynbos have different nutritional requirements they should also have differences in soil composition and nutrient fluctuation.

1.4 Global importance of understanding forest-fynbos mosaics

Forest patches within the fynbos biome are a significant feature of the landscape and their conservation is of paramount importance. Forests aid in lowering global CO_2 concentrations by absorbing large amounts of CO_2 from the atmosphere. Soil is one of the world's largest carbon reservoirs and it reduces pressure on oceanic ecosystems to absorb high concentrations of CO_2 from the atmosphere (Bohn, 1976). They ensure the production of oxygen, which in its absence all life would fail to exist. A range of disparate species inhabit forests which add to the high biodiversity of the region (Schwartzman et al., 2009). Both forest and fynbos house a vast number of species and play an important role in maintaining the efficient functioning of the ecosystem (Armstrong and Van Hensbergen 1994). By producing large amounts of plant litter for microorganisms to decompose, forests are responsible for returning nutrients back into the system providing a positive feedback. The forest canopy captures large amounts of dust which further enriches the soil. Fynbos vegetation has adapted to and require fire for recruitment (Edwards, 1984). The external morphology of fynbos vegetation is dry and lack thick barks hence promote frequent fires sweeping through. Thus, both forest and fynbos vegetation responds to environmental variables in an attempt to modify their niches for their own benefit.

1.5 Aims and objectives

The aim of this study is to analyse the biogeochemistry of the forest-fynbos mosaic in order to determine the role soil plays in the coexistence of forest and fynbos vegetation in a single landscape. To do this, soil properties including texture, nutrient composition and processes which lead to nutrient fluctuation will be examined. I hypothesise that forest and fynbos soils are distinct in their texture and nutritional value, which produce disparate vegetation patches in a single landscape. Secondly, soil nutrient dynamics are affected by vegetation in an attempt to modify and sculpt the perfect niche. Finally, I hypothesise that soil nutrition is enhanced by decomposition of plant litter and through the input of aeolian deposits. An understanding of the role biogeochemistry plays in the forest-fynbos mosaic will aid in the management of the reserve and instil a greater appreciation for the important role soil plays in maintaining these pristine habitats. Studies examining soil properties from topsoil to bedrock are rare thus this study may serve as a baseline for future work on the subject.

2. Materials and methods

2.1 Study site

Sampling took place in the Jonkershoek Nature Reserve (33°55’51”S 18°51’16”E) which covers approximately 1400 hectares near Stellenbosch in the Western Cape, South Africa (Fig. 1). The region has a Mediterranean climate with hot dry summers and cool, wet winters (Garcia Quijano et al., 2007). It has a mean annual rainfall of 1296 mm (Midgley and Scott 1994) with 85% of it occurring between April and September (Versfeld and Donald 1991). February is the hottest month with a mean maximum temperature of 27.9°C while July is the coolest with a mean minimum temperature of 5.9°C (Heth and Donald 1978). Located within the highly biodiverse Cape Floristic Region (CFR), vegetation is dominated by fynbos while natural forest patches and pine plantations are less abundant. The underlying geology consists of sandstone and quartzite with intermittent thin shale bands of the Table Mountain Group (TMG) and some patches by granite (Midgley and Scott 1994). Soils are acid loam to sandy loam with a low bulk density. They are characterised as being either apedal or poorly developed soils (Garcia Quijano et al., 2007). The drainage lines are deep, rocky and generally underlain by TMG sandstone. Soils in the catchment are an accumulation of talus TMG sandstone which overlays a weathered granite mantle (Midgley and Scott 1994).

2.2 Fieldwork

Fieldwork was conducted on four days from 30th April 2014 to 21st June 2014. A total of nine soil pits were dug to bedrock using a shovel and pickaxe. Fynbos is composed of steep and shallow slopes with each being exposed to different degrees of physical weathering and erosion. Therefore, pits occurring on low (flats) and high (slopes) gradient slopes in the fynbos were sampled. By feeling the texture of the soil from the top to the bottom of the pit, the different horizons were determined and demarcated using pegs (Fig. 2B). A qualitative analysis of each horizon was conducted using the methods and definitions according to Schoeneberger et al. (1998). The characteristics examined included boundary, structure, texture, root and rock density and colour (Appendix A). To determine texture, roughly seven grams of soil was kneaded with water and pushed into a ribbon according to Schoeneberger et al. (1998) and characterised on the basis of proportion of clay, sand and silt. Using a Munsell Soil Colour Chart, a wetted ball of soil from each horizon was placed against the chart to determine soil colour. Roots and rock density were determined by observation. Samples of approximately 200g of soil was collected from each horizon (HS) and placed into air-tight plastic bags. Additional topsoil samples (TS) were collected within a 2m radius at each site using a 96cm^3 soil core. TS samples were collected to determine microbial release of CO_2 from the soil. These samples were also placed into air-tight plastic bags.

2.3 Dust and nutrient analysis

The bags of all HS samples were opened and the soil was stirred. They were placed into a 25°C room for seven days to be air-dried. Thereafter, they were sieved using a 2 mm mesh removing roots and stones.

2.3.1 X-ray Fluorescence analysis (XRF)

Approximately 10 g of each HS sample was combusted in a muffle furnace at 800°C for 8 hours. They were then finely ground for 10 minutes at 3000 rpm using a bead mill until they were powdered to a consistency of commercial flour. These samples were then sent to Geological Science Department at the University of Cape Town (UCT) for XRF analysis to determine major elemental composition and zirconium (Zr). Major elements tested included silicon (Si), aluminium (Al), iron (Fe), manganese (Mn), magnesium (Mg), calcium (Ca), sodium (Na), potassium (K), phosphorus (P) and sulphur (S).

2.3.2 Calculation of nutrient gain and loss (tau)

During weathering, elements are added or removed from soil and this fraction is tau (τ). The concentration of elements which are mobile may be misleading in determining loss or gain and therefore need to be compared to an immobile element. I used the immobile element Zr to calculate gain and loss of elements in soil using the formula below. The mobile element is X while I is the immobile element Zr.

$$\tau = \frac{Xsoil}{Xrock} \times \frac{Irock}{Isoil} - 1$$

2.3.3 Carbon and Nitrogen analysis (CNN)

Five grams of each HS sample were sent for CNN analysis to the Earth Science Department at the University of Stellenbosch where they determined carbon and nitrogen concentrations using an EA Euro 3000 elemental analyser.

2.3.4 Texture analysis

To determine water content, a subsample of each HS sample was weighed and placed into an oven at 105°C for 24 hours. A solution of 5% calgon was made by mixing 35 g of sodium hexametaphosphate ($[NaPO_3]_6$) with 1 L of reverse osmosis water. Calgon acts as a dispersing agent which aids in the separation of soil particles in solution. Forty grams of the HS samples was placed into a jar with 100 ml of the solution. The jars were sealed and placed on an end-over-end rotator for four hours. Thereafter, texture was analysed using the Bouyoucous hydrometer method (Witkowski and Mitchell 1987). To determine particle size, a 3 ml subsample of the solution was taken from the jars and poured into a Malvern Mastersizer 2000 particle size analyser (Malvern). For comparative purposes, particle size of HS samples not mixed with the solution were also analysed in the Malvern. Despite the Bouyoucous hydrometer method giving an accurate account of texture, the Malvern is more reliable as it also illustrates particle sizes of sands, silts and clays. Using the Bouyoucous hydrometer method, percentage sand, clay and silt was determined using the following equations:

$$\boldsymbol{Sand} = 100 - \frac{(R40-Rl)X100}{(Sample\ weight\ X\ Oven\ dry\ fraction)}$$

$$\boldsymbol{Clay} = \frac{(R7-Rl)X100}{(Sample\ weight\ X\ Oven\ dry\ fraction)}$$

$$\boldsymbol{Silt} = 100 - (Sand + Clay)$$

R40 = Hydrometer reading after 40 seconds

Rl = Hydrometer reading of water (blank)

R7 = Hydrometer reading after 7 hours

Oven dry fraction = Proportion of soil

2.4 Decomposition

All TS samples were weighed and then placed in paper plates. Soil was sieved to less than 2 mm removing leaves, stones and roots. Soil was then poured into jars and sealed before being placed into a 4°C room to halt decomposition. Samples were later weighed and soil moisture was used to standardise and equal the water content of all the samples. It is vital to keep the soils at the same temperature and moisture content because temperature and moisture are the most important controls on decomposition rate. Soils were placed into Mason jars to prevent any air from entering or escaping. Using soda lime which is mainly composed of:

- Calcium hydroxide, $Ca(OH)_2$ (~75%)
- Water, H_2O (~20%)
- Sodium hydroxide, NaOH (~3%)
- Potassium hydroxide, KOH (~ 1%),

CO_2 free air was pumped through each jar for five minutes and then sealed. Throughout the two-week duration of the experiment the Mason jars were kept in a 25°C room to simulate ambient temperature. The concentration of air in a tank filled with 1% CO_2 was measured using a LI-COR CO_2/H_2O gas analyser (LI-COR) each day to construct a calibration curve (Fig. 3). Thereafter, the air inside the jars was sampled using a syringe and inserted into the LI-COR to determine the CO_2 concentration.

2.5 Statistical analysis

All XRF, CNN and texture data were tested for normality using the statistical package "R" (64 bit) (R Core Team 2013). All tests were conducted using the aforementioned software. Pearson tests were run on XRF data determining correlation strength. Two-sampled t-tests were conducted to compare fynbos characteristics on slopes and flats. T-tests were also used to compare characteristics of fynbos with forest. In addition to R, Microsoft Excel 2010 was used to produce many of the figures.

3. Results

3.1 Field observations in the forest and fynbos microhabitats

Jonkershoek Nature Reserve has fynbos vegetation in both steep and low gradient slopes, and forest vegetation along the river and in screes. Forests occur within a bedrock-controlled and deeply incised river system lacking any fluvial deposits. The forest floor was dominated by plant litter while roots penetrate through gaps between rocks. Light penetrates to a small degree through the forest canopy. Forest soils were shallow but occurred on steep slopes which gave an impression of depth, but this was betrayed by the lack of soil development and well defined horizons (Appendix A). Soil texture in the forest was either sandy-clay or sandy-clay loam with dark colours at all depths indicating large inputs of organic matter. Rock fragments increased with depth in the forest while root prevalence decreased (Appendix A).

By contrast, fynbos contains shrubland vegetation which lack tall trees with large surface area canopies. Therefore, fynbos is exposed to full sunlight and lacks any dust capturing properties which the forest canopy may possess. Rivers flow periodically during the winter period of heavy rainfall. They flow along the slopes which promotes erosion and deposition of sediment into the flats. Fynbos slopes were shallow with bedrock occurring at 30-50 cm while fynbos flats were much deeper extending to depths greater than 150 cm. Fynbos soils had well-defined horizons on slopes and in flats. There were also considerable differences between the texture and colour of soils in each horizon. Fynbos was dominantly sandy while some horizons were characterised as sandy loam or loamy sand. The range of colours included light browns, light oranges, dark grey and even light grey-white similar to beach sand. In both fynbos slopes and flats, root prevalence decreased with depth while rock fragments increased.

3.2 Particle size distribution in Jonkershoek

In all patch types the soil was composed of different sized particles. These ranged from 9-2000 µm with particles less than 110 µm being very rare. There were noteworthy differences in the particle size distribution (PSD) between forest and fynbos (Fig. 4). Forest soils had a high proportion of very coarse and very fine particles while fynbos was dominated by intermediate sized particles. The bimodal nature of the forest PSD curve attests to this. Fynbos flats and slopes had a similar PSD suggesting that vegetation plays an important role in determining PSD (Fig. 4). Across all patch types, the high abundance of particles greater than 110µm illustrates the very sandy nature of all the soils. The PSD determined using the Malvern produced consistent results with the hydrometer method.

Both methods indicated that patches were dominated by sand with clay and silt occurring in much smaller quantities. The quantity of silt varied across different vegetation patches (f=9.484, df=39, $p<0.004$) and was most prevalent in forest and least abundant in flats (Fig. 5). Likewise differences were found in clay across the three patch types (f=6.379, df=42, $p=0.004$) with clay being most abundant in flats and least prevalent on slopes. Forest soils were composed of more clay and silt (16 % & 16 %) than fynbos slopes (10 % & 15 %) while flats were richer in clay but poorer in silt (20 % & 9 %). In all three patch types silt and clay were highly variable with depth. The variation in silt and clay abundance across depth accounts for the scatter, including the outlier of clay in the forest (Fig. 5).

3.3 Particle size evidence for dust accretion

Dust settles on the surface enriching topsoil to a greater degree than subsoil hence variation in particle size with depth could be expected. This trend was observed in the fynbos flats where there were more particles in the range 20-110 µm (putative dust) on the surface suggesting an input of "dust". Larger "dust" particles were more abundant than smaller particles as they are more easily captured by vegetation. This is because smaller particles are more prone to remain in suspension while larger particles tend to settle on vegetation. The shrublands in fynbos are not highly efficient in capturing "dust" hence smaller particles are less abundant. "Dust" decreased consistently with depth in all but one pit in the flats (Fig. 6). Ignoring the top horizon in this pit maintained the trend suggesting rapid erosion removed the "dust" in the top horizon of this pit. However, a similar trend was not observed in forest and on fynbos slopes as topsoil was not enriched in "dust".

3.4 Nutrient distribution in Jonkershoek

The concentration of elements in soil varied greatly across different vegetation patches in the landscape. Soil framework elements (Al and Fe) and most nutrients (K, P, N, Ca, Mn and Mg) occurred in higher quantities in forest than fynbos. Over 60% of some nutrients (K, P, N, Ca and Mg) were restricted to forest. Silica behaved differently in that there was more in the fynbos than the forest (Fig. 7). Silica is highly abundant in bedrock and therefore soils had high amounts of Si across all vegetation patches (>80%). There was no difference between the concentration of Si on fynbos slopes and flats (t=1.71, df=24, p=0.09). Weathering primarily enriches soil with nutrients thus high Si concentrations in rock maintain high Si concentrations in soil. However, nutrient concentration varied with patch type and nutrient suggesting there is an additional source of nutrients enriching soils. Such sources may include dust deposition and the decomposition of plant litter.

There were strong correlations between elements, all positive except when Si was involved (Fig. 9). This means more Si was associated with less of each of the other elements.

However, more of any of the other elements meant more of all the others. This suggests that the processes controlling the abundance of Si in the landscape are vastly different from those affecting other elements. Rocks in Jonkershoek are dominated by Si up to 90%. Therefore, any incoming Si is negligible in comparison to inputs from the weathering of these rocks. The positive correlations between the other nutrients indicate a common origin or a common process governing their concentrations. Calcium was least correlated with Al and Fe suggesting that Ca comes from a different source or is controlled by a different process (Fig. 9). Since Fe and Ca are both essential for plant growth and are taken up in similar quantities, the poor correlation between them suggests that the “dust” enriching these soils is richer in Fe than Ca. Potassium, Mg and P are essential to plant growth as well and showed strong, positive correlations ($r^2 > 0.91$) suggesting they are removed and replenished at relatively similar rates.

3.5 Loss and gain of nutrients relative to rock

The loss and gain of nutrients differed with nutrient, patch type and depth (Fig. 10). Rock-derived elements were gained in the forest while they were lost in fynbos. However, in both forest and fynbos, Si was lost. Nutrient loss or gain was more variable in forest soils than fynbos soils. The amount gained differed with nutrient as forest gained over ten times more Ca than any other nutrient (K, P and Mg). The source of Ca could be marine aerosols or carbonates from the dry interior of the country. Silica was the only nutrient which was lost in forest indicating either a high input or low utilization of silica by forest biota or relatively low inputs in “dust” (Fig. 10). Fynbos slopes and flats were similar but showed slight differences in Ca. Some surface horizons showed a gain in Ca in fynbos soils suggesting plant litter decomposition and “dust” enriches topsoil with more Ca than subsoil.

There were strong, positive correlations between the losses and gains of nutrients with the exception of Si which showed no correlation. Because Si is highly abundant in rock and soil, its removal from soil becomes negligible. By contrast, other nutrients are less abundant in bedrock and thus removing small quantities from the soil show large losses. The relationship between the loss of Ca and Fe+Al was relatively weak, similar to the relationship in the raw elements. Thus, the large gains in Ca cannot be explained by the same process as the more subdued gains in Fe+Al. Apart from Ca, Al+Fe showed strong correlations with other elements (Fig. 11). The loss and gain of P was strongly correlated with that of K and Mg due to the fundamental role they play in plant growth as they are absorbed and replenished at relatively similar rates.

Elemental loss patterns against Si also suggest origin either via marine aerosols, "dust", *in situ* weathering or tight nutrient cycling by plants. There were large gains in Al particularly in forest patches and these were associated with comparatively large Si losses relative to bedrock suggesting aeolian deposits are likely aluminosilicates or clay. The loss or gain patterns in fynbos was consistence with aeolian deposition since Si was generally lost, but less so in flats and also less so in the surface horizons, the locus of the "dust" (Fig. 12). Furthermore, slopes did not exhibit the least Si losses at the surfaces because of the erosive nature of these landscape positions. The loss of Fe across fynbos soils was associated with Si loss, but in forest soil there was no relationship between Fe and Si losses. Low Fe loss in forest soils was associated with high Si loss while high Si loss was associated with high Fe loss in fynbos soils. There were substantial gains in K particularly in forest patches while fynbos showed K loss. Because fynbos and forest vegetation differ in biomass, decomposition of plant litter can be expected to enrich soils with K to a greater degree in the forest. Fynbos flats had consistent loss in both Si and K while slopes experienced lower losses. These slopes were located within close proximity to the forest thus "dust" enriching the forest may have blown there or been intercepted by fynbos vegetation. Large gains in Mg were apparent in forest patches which were associated with large losses in Si. Fynbos slopes experienced lower losses in Mg which corresponded to increased losses in Si. Similar to K, these slopes were close to the forest and thus may benefit from forest nutrients. By contrast, the loss experienced in the flats showed no correlation to the loss of Si. There were large gains in P particularly in forest patches while fynbos experienced a loss. Both gains and losses showed no correlation to the loss of Si. Similarly, Ca experienced large gains in forest and losses in fynbos. However, slopes showed minor gains as it is located within close proximity to the forest. Calcium gains and losses were poorly correlated with the losses in Si suggesting a disparate origin (Fig. 12).

3.6 Carbon and nitrogen cycling

In all patch types the concentration of C and N decreased with depth (Fig. 13). Unlike most nutrients, C and N do not occur in rock. Therefore, soils become enriched with C and N via decomposition of plant litter, “dust” and fixation of N in the soil via microbes. The decrease with depth was relatively similar on slopes and flats in fynbos as they are both derived from the decomposition of similar plant litter across fynbos patches. Forest soils were more enriched with C and N probably because of high biomass decomposition in the soil. The low concentrations of C and N in fynbos soils cause fynbos to be more susceptible to hindered plant growth and leaf chlorosis while high concentrations in forest soils facilitate forest expansion.

Decomposition rates were significantly greater in forest than fynbos. Forest soils produced 70 mg C m^{-2} day^{-1} while fynbos slopes and flats produced 6 mg C m^{-2} day^{-1} and 2.3 mg C m^{-2} day^{-1} respectively (Fig. 14). The breakdown of organic matter by microbes released more

CO_2 in the forest due to a more favourable temperature and moisture content. The large canopy provides shade for forest-dwelling biota and maintains relatively constant temperatures throughout the day. By contrast, fynbos is exposed to high levels of sunlight and thus susceptible to diurnal temperature variations. Because decomposition is carried out by bacteria and fungi, the rate of decomposition is greatly affected by temperature and moisture. By maintaining a relatively constant temperature throughout the day, forest maintains relatively constant decomposition rates. However, decomposition rates in fynbos may fluctuate diurnally as they are exposed to temperatures which exceed 25°C, the temperature at which decomposition begins to decelerate. In addition, water in fynbos is scarce as the vegetation has adapted to living in dry conditions. Thus, low moisture content in soil may hinder the effectiveness of soil microbes during decomposition. Because temperature and moisture content in forest soils are more favourable for decomposition, the breakdown of dead organic material is greater and thus enriches the rhizosphere by releasing large quantities of C, N and other essential nutrients making them available to plant roots.

4. Discussion

4.1 Microhabitats differentially affected by topographical processes

Jonkershoek Nature Reserve (JNR) is underlain by mixed granite, shale and sandstone and has a uniform climate, so the vegetation has to be mostly uniform. Therefore, the forest-fynbos mosaic consisting of trees and shrubs is due to factors other than the geology and climate. Topographical variation in the valley results in low and high gradient slopes differentially affected by physical processes such as erosion producing a variety of microhabitats in the landscape. After heavy rainfall, high gradient slopes are exposed to rapid erosion (Weyman, 1973), while low gradient slopes experience low intensity erosion providing a relatively stable environment. The co-location of these microhabitats results in the co-existence of fynbos and forest vegetation. Fynbos and forest vegetation modify their niches in turn making their respective habitats even more disparate. These niches differ by a number of characteristic features including soil texture and nutrient status among others.

4.2 Implications of unique textures in the different patch types

Vegetation patches have different particle sizes with fynbos soils being sandier than forest soils. Compared to smaller particles such as clay and silt, sand has a low surface area to volume ratio thus having a low cation exchange capacity (CEC) hence lacks the ability to hold positively charged ions (Khaled and Stucki 1991). Because many important plant nutrients (K, Ca and Mg) occur as positively charged ions in the soil, plant growth may be hindered. The sandy nature of fynbos soils possess little cohesion between particles and are susceptible to run-off with nutrients. Both fynbos slopes and flats contain sandy soils despite being exposed to different degrees of weathering and erosion. By contrast, forest soils are distinctly less sandy containing more clay and silt even though erosion and weathering are key processes in the bedrock-controlled river the forest inhabits. When studying soil texture in JNR, Manders (1990) produced similar results indicating that forest soils had a finer texture and were less sandy than fynbos soils. Thus, the argument that vegetation constructs and alters its niche is given more weight by this study. If vegetation was not as important as weathering then the contrasting rates of weathering on fynbos slopes and flats would result in differences in soil texture in each of these patches types. However, their vegetation is similar and so are their soils. The less sandy nature of forest soils provides a suitable capture and storage mechanism for nutrients. Silts and clays are abundant in forest soils and have a high CEC hence have strong cohesion between particles. Despite being exposed to large amounts of water, the high CEC in forest soils is maintained as clay prevents soil from draining quickly even after periods of heavy rainfall. Clay is essential in maintaining stable conditions in the rhizosphere as it is able to maintain pH (Stotzky and Rem 1966). The negative charge of clay particles attracts positive ions which cause the enrichment of nutrients in the rhizosphere. Therefore, the sandy nature of fynbos soils is shown to be less capable of storing nutrients than forest soils.

4.3 Factors affecting nutrient distribution in different patch types

The high levels of rock abrasion which forest soils are exposed to are responsible for increasing the input of nutrients via weathering, but these nutrients are soon washed away. More importantly, forest soils become enriched through aeolian deposition and litter decomposition. Thus, differences in weathering, aeolian deposition and litter decomposition account for the nutrient differences between forest and fynbos. The low concentration of nutrients in fynbos soils was consistent with the findings of Midgley et al. (2012). The amount of nutrients in the soil is determined by the balance in nutrient input and output. Forest vegetation removes large quantities of nutrients out of the soil as they have high nutrient requirements to produce high biomass. By contrast, fynbos vegetation removes a lower concentration of nutrients from the soil as they have a lower demand for nutrients. Therefore, one would expect fynbos soil to be more nutrient rich than forest soil assuming the main source of nutrients was through weathering of bedrock. However, the opposite is true since forest soils have a greater concentration of nutrients. Thus, forest soils experience a greater nutrient input through aeolian deposits and litter decomposition than fynbos. Nutrient concentration differences are further enhanced by the sandy soils in fynbos which lack cohesion between particles and thus are unable to retain nutrients as much as forest soils.

Aeolian deposition is an important source of soil nutrient enrichment and strong evidence for dust deposition was shown in the fynbos flats. The concentration of dust sized particles was significantly greater in topsoil compared to lower soil profiles. But similar trends were not seen in fynbos slopes nor in forest soils. This is expected because fynbos slopes are shallow and thus there is no real variation with depth. In addition, wind and water are responsible for transporting sediment downslope which then settles and accumulates in the flats. Thus, dust is unable to accumulate on the surface of slopes in a similar way as it does in flats. Similarly, forest soils are susceptible to sediment removal due to water disturbance in the rainy season. Also, forest soils lack well-defined horizons because they are continuously cut by the river and hence all soil horizons have similar surface exposure. Dust captured in the canopy is washed down trees to the soil through rainfall.

Fearnehough et al. (1998) showed that dust would remain in suspension if there was insufficient vegetation to settle on. This is what happens in the fynbos shrublands where dust remains in suspension until it reaches the forest canopy. I found substantially more dust in forest soils than fynbos soils which supports the argument that vegetation plays a crucial role in niche modification. Fearnehough et al. (1998) suggested that vegetation and topography are strongly affected by the accumulation of aeolian deposits. My results are consistent with theirs since the amount of dust deposited in each patch type is determined by the dominant vegetation. My study was conducted during winter, the time when slopes are most susceptible to erosion and run-off. Had I been in the field during the dry summer, fynbos slopes might have still had a veneer of dust in the topsoil.

4.4 Implications of nutrient enrichment and depletion in different patch types

Fynbos vegetation does not require large quantities of nutrients hence they are able to persist on nutrient poor soils (Bengtsson et al., 2012). However, forest expansion may lead to the capture of dust which would normally settle on fynbos thus making fynbos soils even more nutrient poor. Whether fynbos vegetation will be able to persist on such soils is something to ponder. Nutrients are essential for plant growth and with a lower concentration of nutrients available, fynbos vegetation may be more susceptible to wilting than forest vegetation. If P was a limiting factor, plant growth would be hindered and vegetation would be stunted with slender stems lacking wood (Taiz and Zeiger 2002). It is essential that plant growth is not hindered as this would be detrimental if a plant was not at the correct level of maturity when a fire swept through. Low amounts of Fe and Mn may cause leaf chlorosis while a shortage in Mg can cause chlorosis between leaf veins. The high amount of Si in both fynbos and forest soils can serve as an alternative to lignin which strengthens cell walls making vegetation less susceptible to logging (Taiz and Zeiger 2002). Each nutrient serves a unique function and plants require them all in the correct amounts. Therefore, if a nutrient is too scarce plants may face difficulty in growth and survival. This is true for both fynbos and forest as a change in nutrient input in either system may cause it to flourish or fail.

4.5 Sources of bedrock derived nutrients

Because plants require particular amounts of nutrients, the concentration of each nutrient is tightly linked together as they do not work in isolation. Some nutrients show stronger correlations than others as they are used for a similar process. The concentration of one nutrient affects the concentration of the next. This is especially true for P limited systems such as fynbos where the dearth of P leads to low utilization of available N (Power et al., 2010). The high amount of Al in forest soils promotes the uptake of P which aids plant growth (Batty et al., 2002). However, P-deficiency may cause plant stress and Al toxicity may present plants with problems (Leiser et al., 2014). Nutrients (K, P and Mg) performing a role in similar enzymatic processes tend to be strongly correlated. Calcium and Fe are both important for plant growth but are not tightly correlated. Van Wesemael (1993) found that the concentration of N, P and Ca increased rapidly upon decomposition while Fe and Al did not show a similar trend. Therefore, Ca and Fe are poorly correlated as decomposition increases the concentration of Ca and Fe differently.

The concentration of nutrients in the soil does not remain constant. It fluctuates as nutrients are removed via absorption through plant roots and leaching which exports them. Nutrient removal varies with depth as shallow roots cannot reach nutrients in deep soil (Wang et al., 2014). This is especially true in flats where roots are confined to the top 50 cm of pits extending deeper than 150 cm (Appendix A). The concentration of nutrients in fynbos soils was significantly lower than in the parent material illustrating nutrient loss. For most nutrients, forest soils gained nutrients as the soils were richer in nutrients than parent rock. Soderberg and Compton (2007) found that bedrock near Citrusdal, Western Cape was composed of more than 98% Si and I found similar results in JNR. The high concentrations of Si found in bedrock cause soils to be rich in Si. Most of the Si which plants absorb from soil comes from bedrock and less from external sources thus soils show a loss in Si as bedrock is far more concentrated in Si than soils. Because of this high concentration in bedrock, vegetation plays a negligible role of enriching soils with Si. However, vegetation plays a significant role in enriching soils with other nutrients especially those which are less abundant in bedrock.

4.6 Carbon and nitrogen cycling

Carbon and nitrogen are two of the most important structural components of plants which are not derived from rock. Therefore, weathering of bedrock does not lead to soil enrichment in these two elements. Many enzymatic processes in plant cells require both C and N thus these elements work in combination and hence share a strong relationship. Carbon and N decrease with depth as their inputs are purely from the surface as they do not receive inputs from weathered bedrock. Despite plants removing large quantities from shallow soil horizons, there is a constant supply of nutrients as plant litter is recycled returning these nutrients back into the system.

Decomposition in the forest was much greater than in fynbos which allows more nutrients to be returned and further enrich forest soils. Despite fynbos soils being less enriched than forest, they still become enriched to a greater degree than they would be in the absence of decomposition of plant litter. Ashton et al. (2005) found that invaded sites showed more rapid decomposition rates than pristinely vegetated sites. In JNR, fynbos is the dominant vegetation type and thus forest can be described as invading the fynbos biome. A change in the litter which enters the system results in a change in decomposition rates (Ashton et al., 2005). Thus, vegetation plays an important role in the enrichment of soils showing more pronounced effects in forest. In the absence of vegetation, soils in both forest and fynbos would have a lower concentration of nutrients and be primarily enriched through weathering with nutrient concentrations increasing with depth.

Studies examining soil by depth extending further than the top 30 cm is rare in the field of ecology. Therefore, comparable data was scarce and seldom obtainable. Further studies should be conducted in forest-fynbos mosaics across the country to determine whether the phenomena observed is confined to JNR. Studies focussing on differences in species assemblages within fynbos may account for differences between low and high gradient slopes in fynbos. More significant dust data may be obtained if the study was conducted in summer when rainfall and erosion is less pronounced. By studying the diversity of microorganisms in the soil may shed some light on how they interact with vegetation above ground. It is unclear whether the dust in JNR comes from a local or global source. Further studies should study and analyse isotopes to determine the source of the dust.

4.7 Conclusions

My study shows compelling evidence for dust deposition influencing soil nutrient dynamics which is further affected by vegetation in the fynbos biome. Had there been no vegetation in the valley, there would be very little soil differences in the landscape. This is because the topographic diversity of steep and gentle slopes as well as the riverine habitat produces baseline heterogeneity which leads to minor differences in patch types. These differences are intensified as patch types have been further modified by vegetation, which captures dust and produces plant litter for decomposition which further enrich soil nutrients. Weathered bedrock plays a minor role in soil nutrient enrichment while vegetation plays a more significant role through plant litter decomposition and dust capture. Nutrient retention is favoured by soil texture in forest while fynbos leaks more nutrients. Decomposition rates are greater in the forest as plant litter is more nutrient rich and relatively more abundant than in fynbos. Continued dust deposition and plant litter decomposition will further enhance the differences between these two habitats, which may result in forest expansion and fynbos contraction.

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List of figures

Figure 1: Study area. A) South Africa. B) Cape Point in the Western Cape, South Africa. C) Jonkershoek Nature Reserve with sample sites included where: 1 includes the sites in forest, 2 includes fynbos flats and 3 fynbos slopes, (Map source: Google Earth, 2014). D) Photograph of study site at Jonkershoek Nature Reserve showing the forest-Fynbos mosaic.

Figure 2: A) Soil pit. B) Soil pit with pegs inserted demarcating soil horizons.

Figure 3: CO_2 LI-COR calibration curve showing CO_2 volume with corresponding peak CO_2 concentrations for each day of the two-week experiment

Figure 4: Particle size distribution across vegetation patch type. Colour lines illustrate patch type while the solid black line indicates clay and silt to the left, and sand to the right

Figure 5: Percentage silt and clay across different vegetation patch types. Each distribution includes the entire soil pit containing all horizons from topsoil to bedrock. Clay and silt was determined using the hydrometer method.

Figure 6: “Dust” distribution across depth in the flats. The legend to the right indicates depth in cm.

Figure 7: Nutrient distribution across vegetation patches. The figure illustrates how each nutrient is distributed across the landscape and how much is in each patch type.

Figure 8: Soil framework element distribution across vegetation patches. The figure illustrates how each element is distributed across the landscape and how much is in each patch type.

Figure 9: Correlations between rock-derived elements in soil. The lower-left half indicates point density of the raw data. The upper-right half are r^2 for the model curve shown in the corresponding scatter plot.

Figure 10: The proportion of elements remaining from parent material across all three vegetation patch types, calculated using Zr as an immobile index element (TAU). The figure illustrates proportion change with values above the solid line indicating nutrient gain and values below indicating nutrient loss.

Figure 11: Correlations between tau values of rock-derived elements. The lower-left half indicates point density of the raw data. The upper-right half are r^2 for the model curve shown in the corresponding scatter plot.

Figure 12: Correlations of Si with Al, Fe, K, Mg, P and Ca. Yellow markers indicate forest samples while red indicate slopes and green show flats. The x-axis shows the proportion change in Si while the y-axis shows proportional change in each of the aforementioned elements.

Figure 13: Carbon and nitrogen depth plots across vegetation patches. The top three graphs are fynbos flats, middle three are fynbos slopes, bottom three are forest. The red markers indicate nitrogen while green markers indicate carbon. Depth is illustrated on the y-axis in cm while the x-axis illustrates the percentage of carbon and nitrogen.

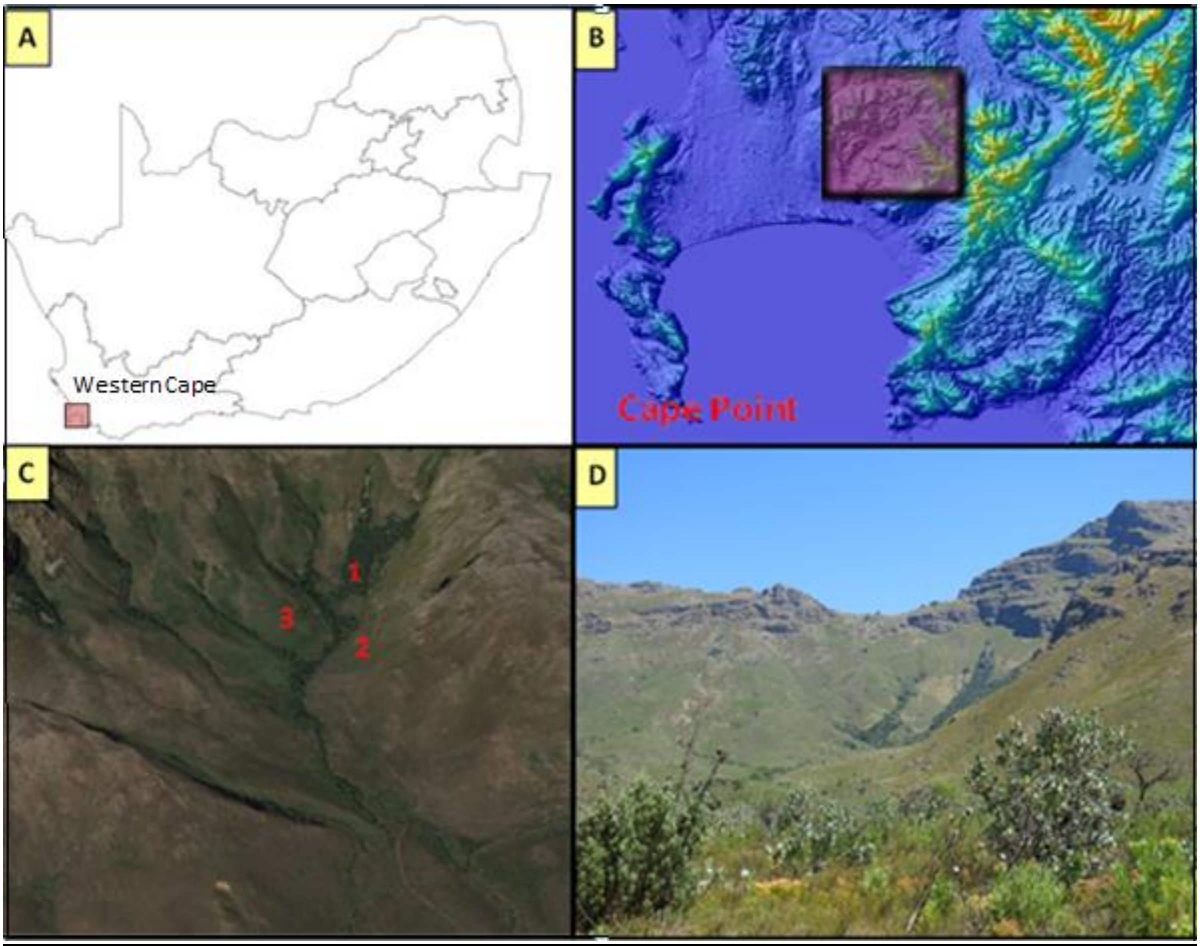
Figure 14: Decomposition rate across different vegetation patch types. The figure illustrates soil respiration by microbes in topsoil indicating how much carbon is being released per day.

Figure 15: Conceptual links amongst soil forming processes and soil nutrient enrichment in a landscape. Long-term controls on soil properties and weathering are geology and rainfall upon which soil forming processes act. Nutrients are released from primary minerals in rock

via weathering and are leached away from extreme depths. Rainfall transports surface material enhancing erosion. Nutrients are further added by decomposing plant litter and through the capture of dust. These processes are present in both forest and fynbos.

Appendix A. Horizon field properties and soil profile locations of sampled pits

Appendix B. Major element and zirconium composition of soil samples across patch types



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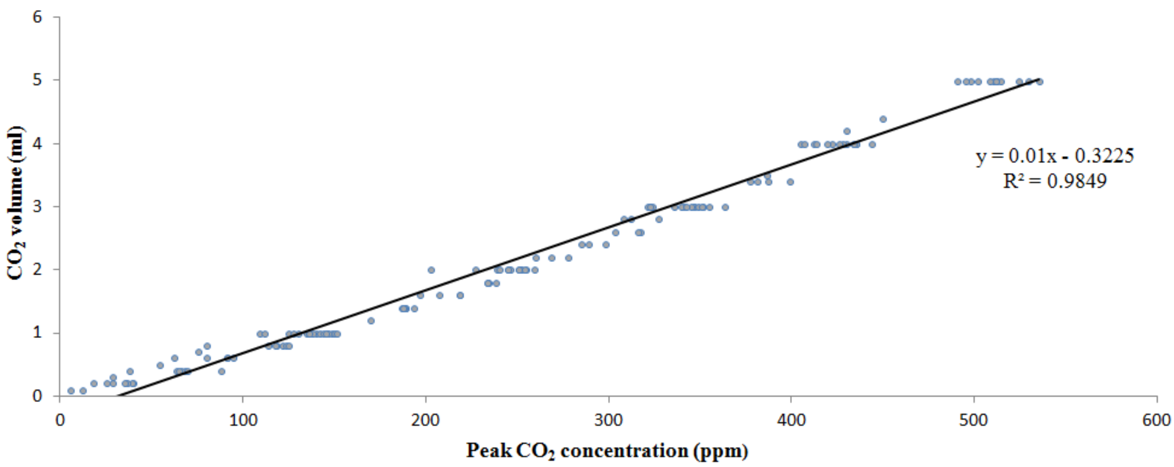

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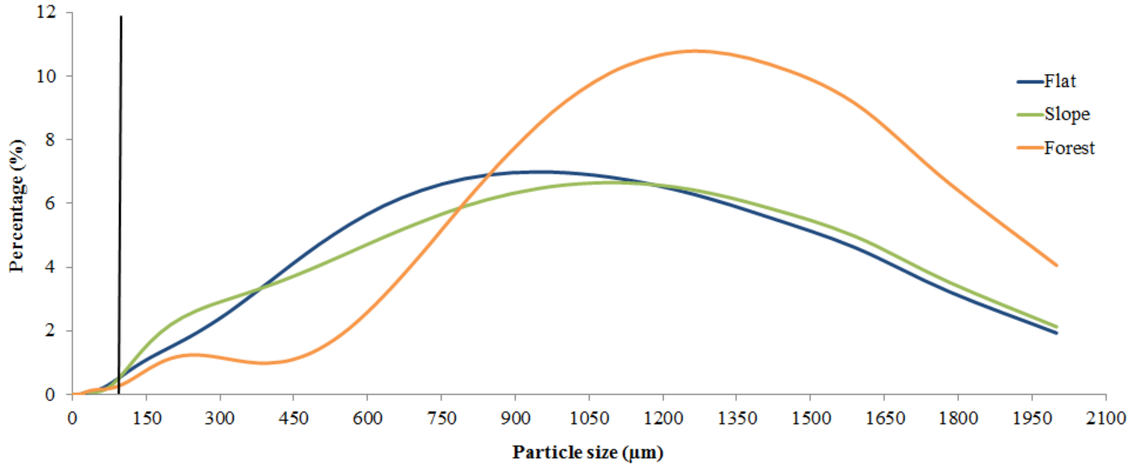

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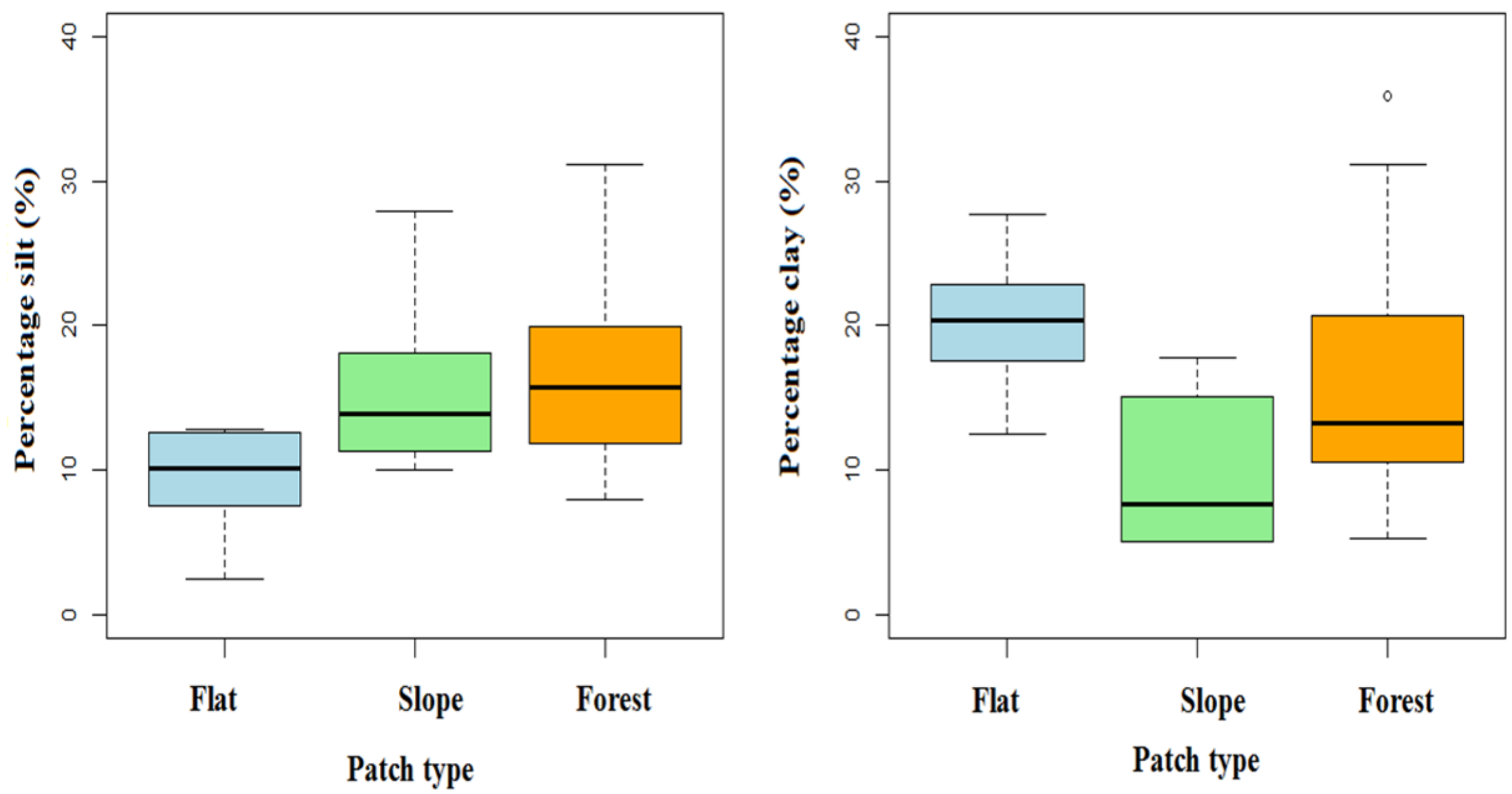

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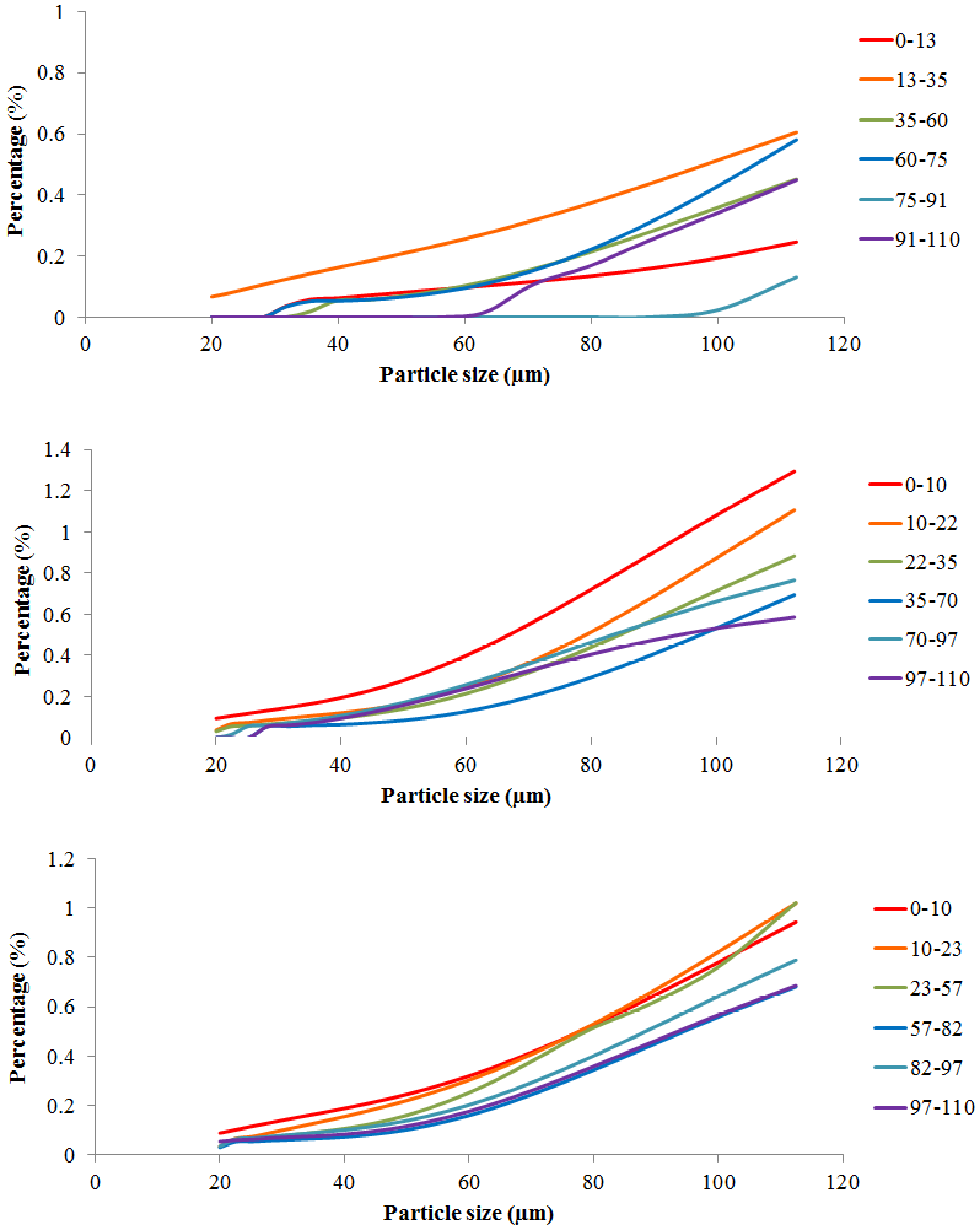
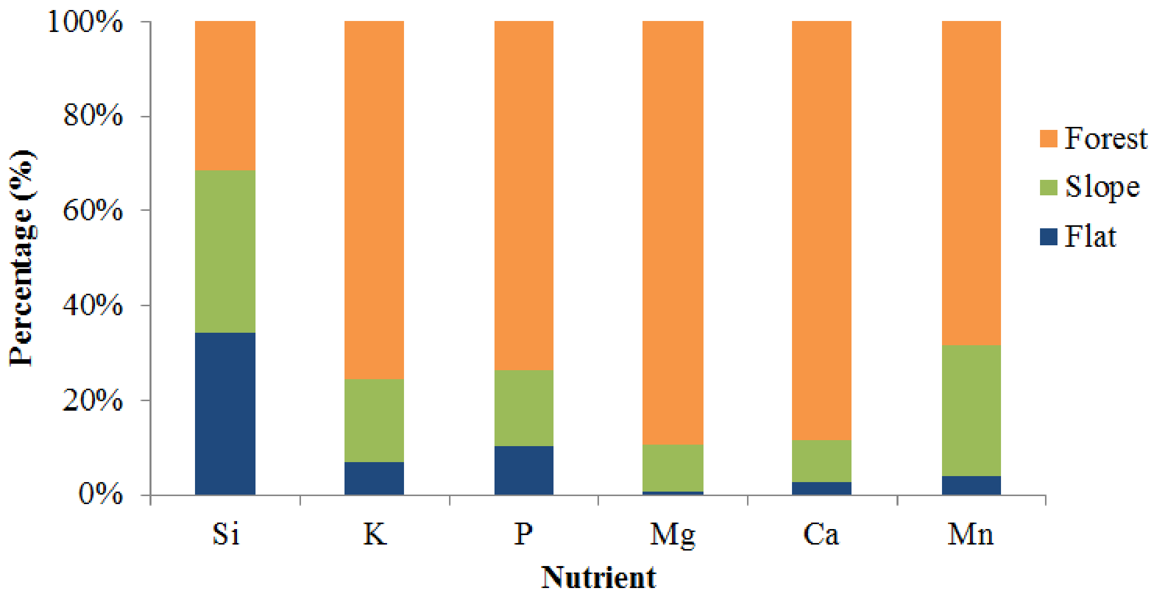


Figure 6: "Dust" distribution across depth in the three pits in the flats. The legend to the right indicates depth in cm.



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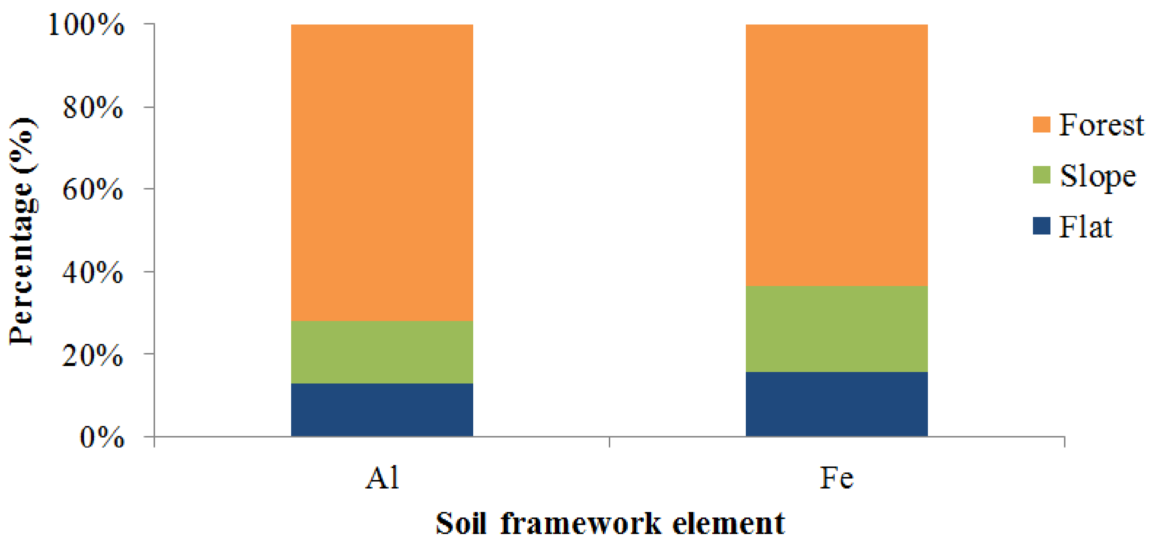

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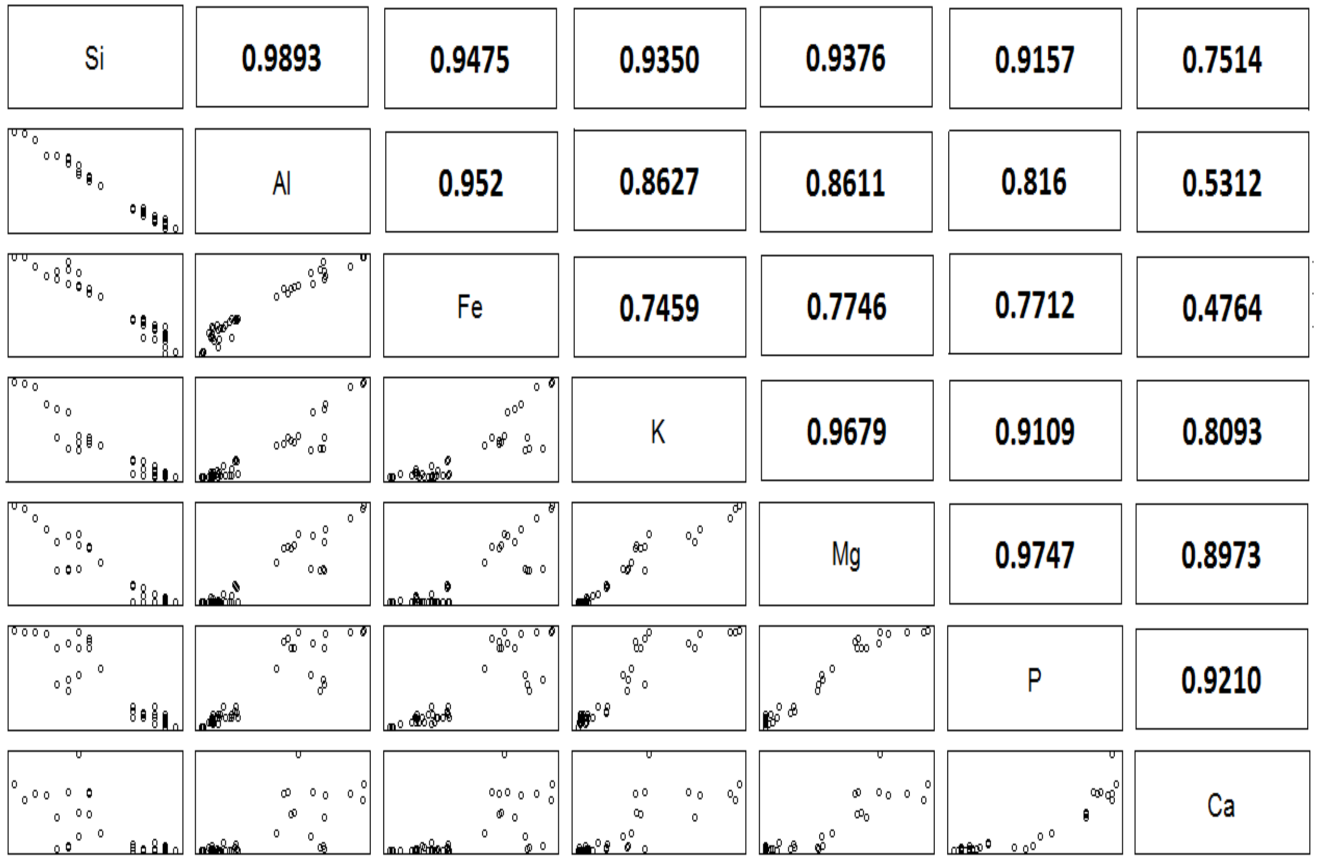

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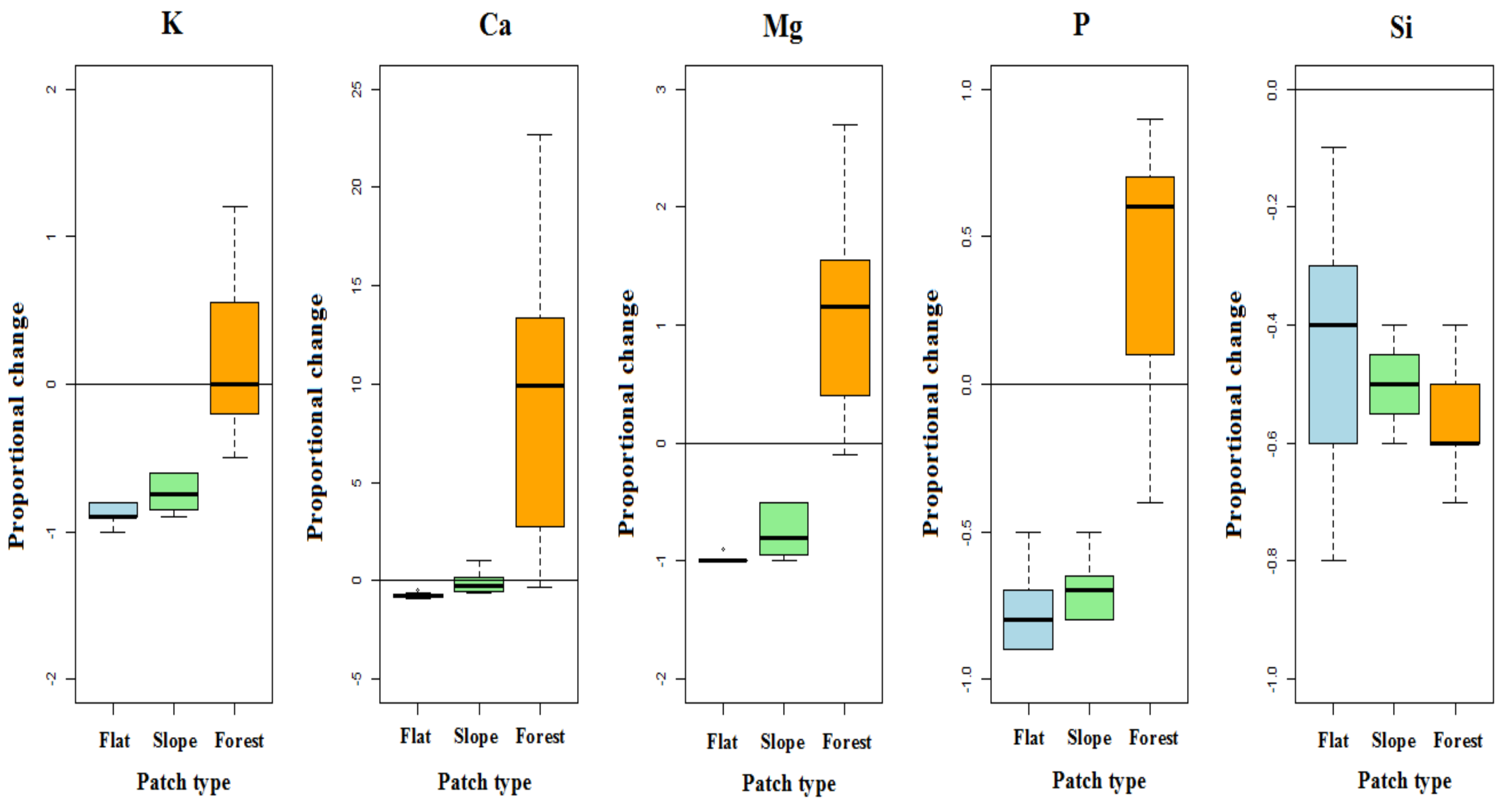

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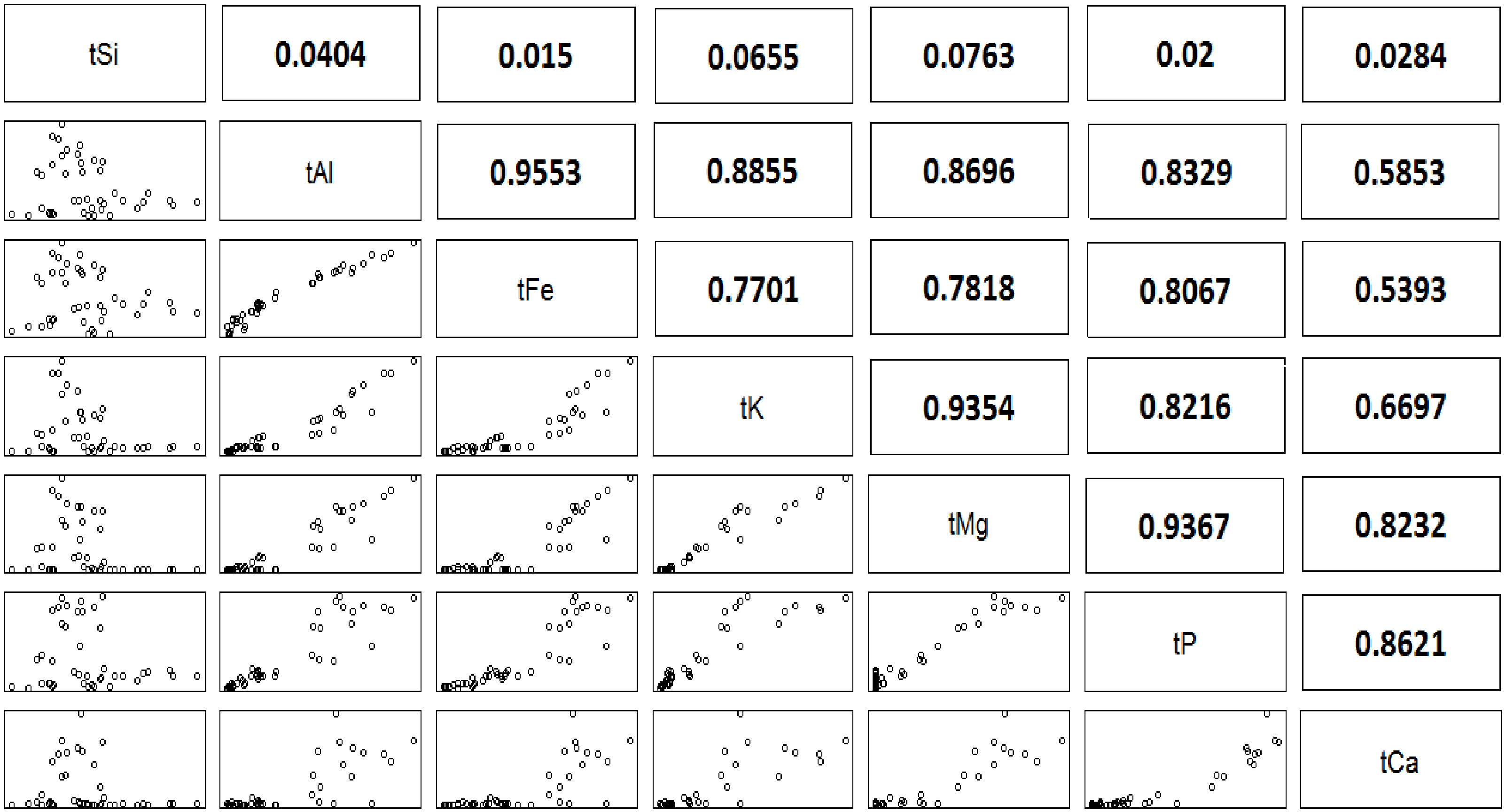

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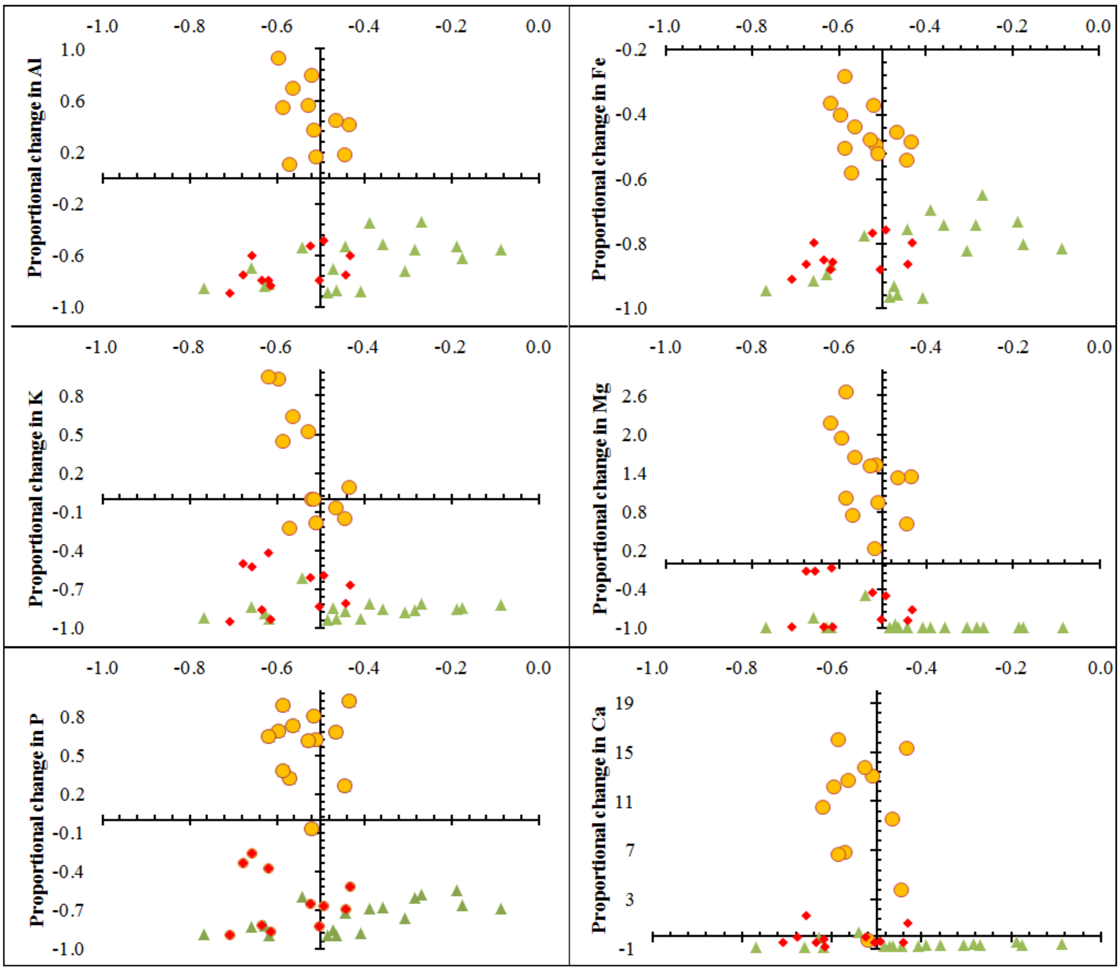

Figure 12: Correlations of Si with Al, Fe, K, Mg, P and Ca. Yellow markers indicate forest samples while red indicate slopes and green show flats. The x-axis shows the proportion change in Si while the y-axis shows proportional change in each of the aforementioned elements.

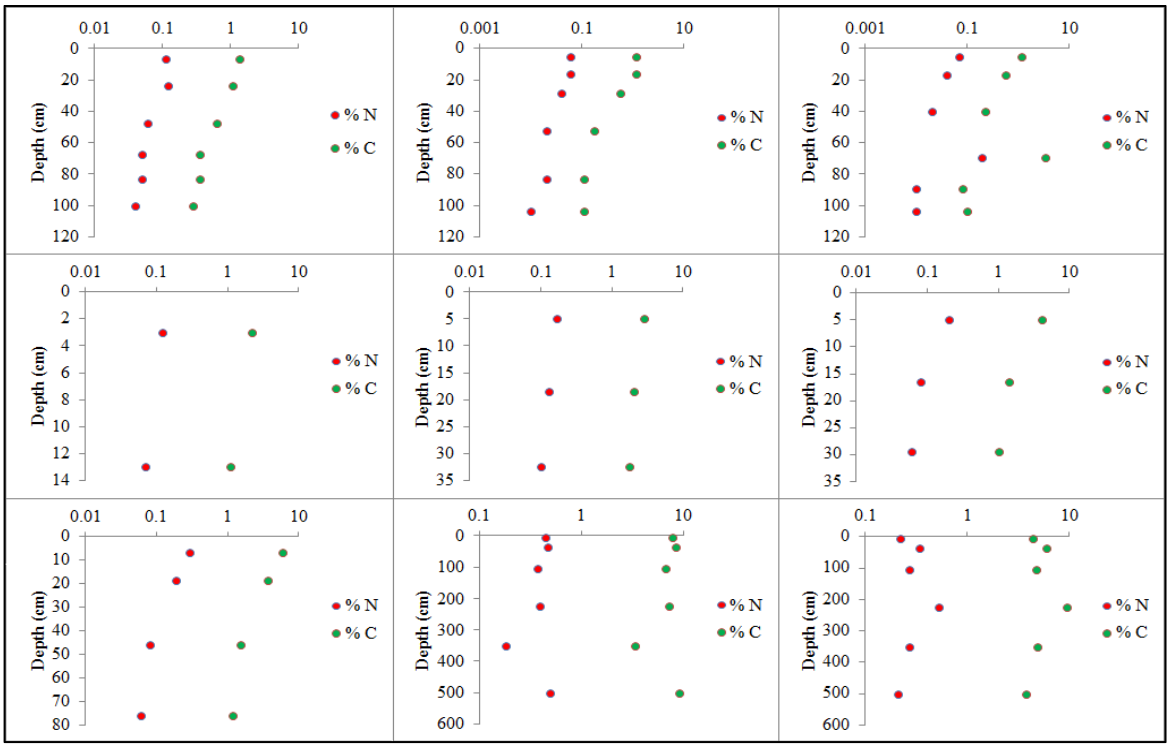

Figure 13: Carbon and nitrogen depth plots across vegetation patches. The top three graphs are fynbos flats, middle three are fynbos slopes, bottom three are forest. The red markers indicate nitrogen while green markers indicate carbon. Depth is illustrated on the y-axis in cm while the x-axis illustrates the percentage of carbon and nitrogen.

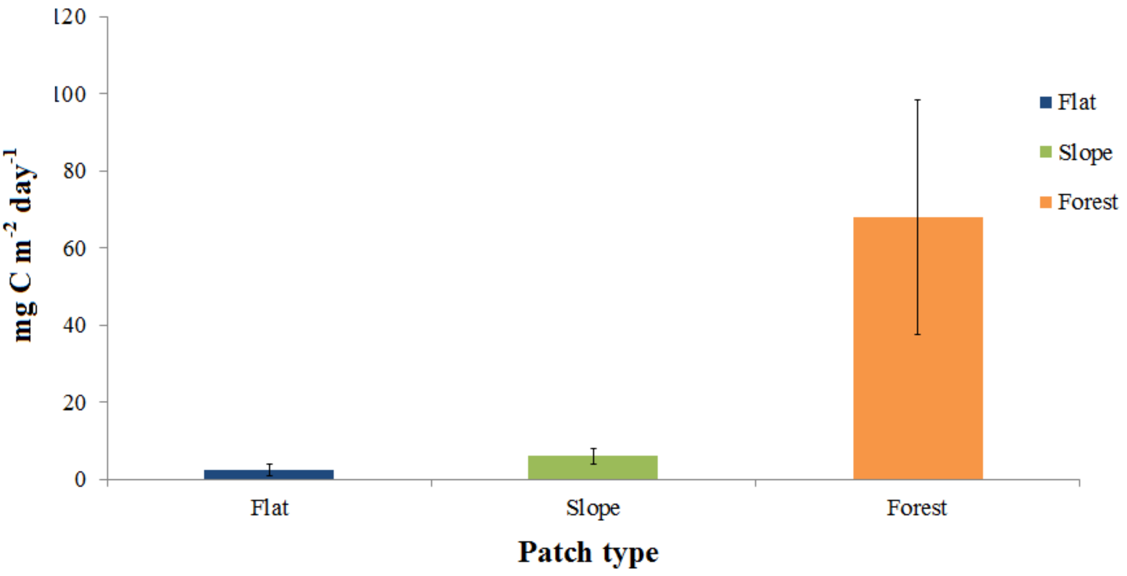

Figure 14: Decomposition rate across different vegetation patch types. The figure illustrates soil respiration by microbes in topsoil indicating how much carbon is being released per day.

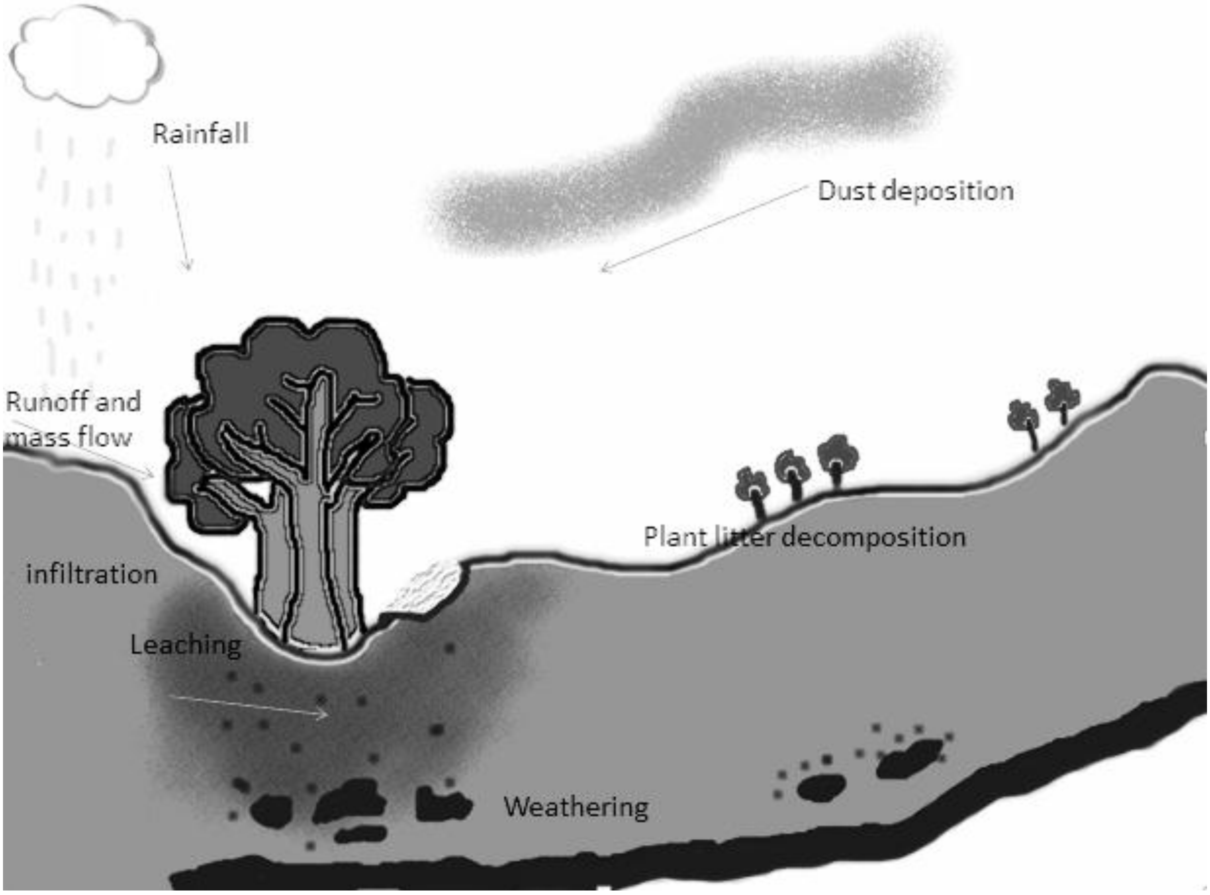

Figure 15: Conceptual links amongst soil forming processes and soil nutrient enrichment in a landscape. Long-term controls on soil properties and weathering are geology and rainfall upon which soil forming processes act. Nutrients are released from primary minerals in rock via weathering and are leached away from extreme depths. Rainfall transports surface material enhancing erosion. Nutrients are further added by decomposing plant litter and through the capture of dust. These processes are present in both forest and fynbos.

Appendix A. Horizon field properties and soil profile locations of sampled pits

Patch Type	Depth (cm)	Horizon	Latitude (m)	Longitude (m)	Boundary	Structure	Texture	Moist colour	Roots	Rock frequency (%)
Fynbos Flat	0-13	A	6236568	311177	AS	1gr vf, f	sl	10YR3/2	2 vf,f	5
	13-35	Bw1			CW	2vf,f sbk 1 vf,f gr	sl	10YR3/3	2vf,f	5
	35-60	Bw2			CW	1vf,f gr	sl	10YR4/4	1vf,f 1m	5
	60-75	Bw3			GS	1vf,f gr	sl	10YR4/6	1vf	5
	75-91	Bw4			GS	1vf,f gr	sl	10YR5/8	-	5
	91-110	Bw5			-	2 vf,f gr	sl	10YR4/6	-	5
Fynbos Slope	0-6	A			VAI	2m, sbk	sl	10YR3/4	3vf,f	50
	6-20	Bw1	6236846	310911	VAI	1f, sbk	sl	10YR3/4	2vf,f	80
	20 +	CR			-	m	-	-	1vf	100
Fynbos Flat	0-10	A			VAI	2m sbk	ls	10YR4/6	3vff	0
	10-22	2C	6236768	3110882	VAI	m	s	-	3mbff	90
	22-35	3Bw1			AS	2m sbk	s	10YR4/6	2mvff	0
	35-70	3Bw2			GS	1f, sbk	s	10YR6/8	2vff	0
	70-97	3Bw3			GS	SG	s	10YR6/8	2vf	0
	97-110	3Bw4			N/A	SG	s	10YR6/6	1vf	0
Fynbos Flat	0-10	A			CS	2m sbk	sl	10YR4/3	2vff	5
	10-23	Bw1	6236496	310801	CS	1f, sbk	ls	10YR5/3	1vff	10
	23-57	Bw2			GS	1vf, sbk	ls	10YR5/4	1mbff	0
	57-82	Bw3			GS	1m gr	ls	10YR5/4	1vf	0
	82-97	Bw4			GS	1m gr	ls	10YR5/4	1vf	0
	97-110	Bw5			N/A	SG	ls	10YR6/4	1vf	0
Fynbos Slope	0-10	A	6236144	310440	AS	1f, sbk	scl	10YR3/3	3vff 1co	10
	10-27	Bw1			AS	2f, sbk	scl	10YR3/3	2vff 1vc	20
	27-38	Bw2			AW	2f, m sbk	sl	10YR3/4	1vff	40
	38-50	BC			-	-	sl	10YR3/4	1vf	80
Fynbos Slope	0-10	A	6236139	310440	AS	1f, sbk	scl	10YR3/4	3vff 1co	0
	10-23	Bw1			AS	2f, sbk	scl	10YR 3/3	2vff 1vc	0
	23-36	Bw2			AW	2f, m sbk	sl	10YR3/2	1vff	20
	36-44	BC			-	-	-	-	1vf	100
Forest	0-13	A	6236887	311037	AS	1 vf,f, gr	scl	10YR3/3	1m,co 3vf,f	10
	13-24	Bt1			CS	2 vf,f sbk	scl	10YR3/3	1m,co 3vf,f	30
	24-68	Bt2			GW	2 f, m sbk	sc	5YR4/6	1m,co 3vf,f	50
	68-84	Bt3			VAW	2 m sbk	sc	2.5YR 4/4	1 vf	70
	84 +	R			-	m	-	-	-	100
Forest	0-10	-	6235958	310544	-	-	-	-	-	-
	10-60	-			-	-	-	-	-	-
	60-150	-			-	-	-	-	-	-
	150-300	-			-	-	-	-	-	-
	300-400	-			-	-	-	-	-	-
	400-500	-			-	-	-	-	-	-
Forest	0-10	-	6235947	310499	-	-	-	-	-	-
	10-60	-			-	-	-	-	-	-
	60-150	-			-	-	-	-	-	-
	150-300	-			-	-	-	-	-	-
	300-400	-			-	-	-	-	-	-
	400-500	-			-	-	-	-	-	-

Appendix B. Major element and zirconium composition of soil samples across patch types

	weight (%)																		ppm
Depth (cm)	**Si**	**τSi**	**Al**	**τAl**	**Fe**	**τFe**	**Mn**	**τMn**	**Mg**	**τMg**	**Ca**	**τCa**	**K**	**τK**	**P**	**τP**	**S**	**τS**	**Zr**
0-13	44	-0.19	1.08	-0.54	0.43	-0.73	0.01	-0.99	0.01	-1.00	0.01	-0.46	0.11	-0.85	0.01	-0.55	0.00	-0.25	191
13-35	44	-0.28	1.17	-0.56	0.47	-0.74	0.10	-0.76	0.01	-1.00	0.01	-0.64	0.12	-0.86	0.01	-0.60	0.00	-0.56	216
35-60	43	-0.36	1.40	-0.51	0.51	-0.74	0.01	-0.99	0.01	-1.00	0.01	-0.67	0.13	-0.86	0.01	-0.68	0.01	0.01	236
60-75	43	-0.44	1.55	-0.53	0.56	-0.76	0.14	-0.75	0.01	-1.00	0.01	-0.76	0.14	-0.87	0.01	-0.72	0.01	-0.13	272
75-91	43	-0.27	1.67	-0.34	0.61	-0.65	0.14	-0.67	0.01	-1.00	0.01	-0.69	0.14	-0.82	0.01	-0.58	0.01	0.15	207
91-110	42	-0.39	1.92	-0.35	0.62	-0.70	0.10	-0.79	0.01	-1.00	0.01	-0.68	0.17	-0.82	0.01	-0.69	0.00	-0.41	242
0-6	45	-0.63	0.82	-0.84	0.37	-0.90	0.19	-0.78	0.01	-1.00	0.03	-0.13	0.18	-0.89	0.01	-0.82	0.01	-0.44	426
6-20	44	-0.63	1.06	-0.79	0.52	-0.85	0.14	-0.84	0.01	-1.00	0.01	-0.57	0.22	-0.86	0.01	-0.82	0.01	-0.44	422
0-10	45	-0.71	0.69	-0.90	0.39	-0.91	0.15	-0.86	0.01	-1.00	0.02	-0.53	0.09	-0.96	0.01	-0.90	0.00	-0.82	540
10-22	45	-0.61	0.82	-0.84	0.49	-0.86	0.10	-0.87	0.01	-1.00	0.01	-0.84	0.10	-0.94	0.01	-0.87	0.00	-0.77	410
22-35	44	-0.62	0.86	-0.83	0.46	-0.87	0.01	-0.99	0.01	-1.00	0.00	-0.87	0.10	-0.93	0.00	-0.89	0.01	-0.41	406
35-70	45	-0.31	0.78	-0.72	0.34	-0.82	0.01	-0.99	0.01	-1.00	0.01	-0.72	0.10	-0.88	0.01	-0.76	0.01	0.04	228
70-97	45	-0.18	0.88	-0.62	0.32	-0.80	0.01	-0.99	0.01	-1.00	0.01	-0.67	0.11	-0.85	0.01	-0.66	0.00	-0.75	192
97-110	45	-0.09	0.93	-0.56	0.27	-0.81	0.01	-0.99	0.01	-1.00	0.01	-0.63	0.12	-0.82	0.01	-0.69	0.01	0.37	173
0-10	44	-0.77	1.14	-0.86	0.30	-0.95	0.10	-0.92	0.01	-1.00	0.01	-0.88	0.19	-0.92	0.01	-0.89	0.01	-0.64	668
10-23	43	-0.66	1.65	-0.70	0.31	-0.92	0.01	-0.99	0.98	-0.85	0.01	-0.86	0.27	-0.84	0.01	-0.83	0.00	-0.89	445
23-57	45	-0.47	1.07	-0.71	0.17	-0.93	0.01	-0.99	0.27	-0.94	0.01	-0.79	0.17	-0.85	0.00	-0.86	0.01	-0.21	300
57-82	46	-0.46	0.46	-0.88	0.10	-0.96	0.01	-0.99	0.01	-1.00	0.01	-0.79	0.08	-0.93	0.00	-0.89	0.01	-0.21	302
82-97	46	-0.48	0.41	-0.89	0.09	-0.97	0.01	-0.99	0.01	-1.00	0.01	-0.80	0.08	-0.94	0.00	-0.90	0.00	-0.39	314
97-110	45	-0.41	0.40	-0.88	0.07	-0.97	0.01	-0.99	0.01	-1.00	0.01	-0.76	0.08	-0.93	0.00	-0.88	0.00	-0.82	267
0-10	42	-0.54	1.82	-0.54	0.61	-0.77	0.49	-0.23	2.42	-0.49	0.03	0.35	0.47	-0.62	0.01	-0.60	0.01	-0.26	322
10-27	42	-0.52	1.77	-0.53	0.60	-0.77	0.29	-0.53	2.51	-0.45	0.02	-0.13	0.46	-0.61	0.01	-0.65	0.00	-0.69	310
27-38	43	-0.49	1.86	-0.49	0.60	-0.76	0.20	-0.66	2.17	-0.51	0.01	-0.44	0.46	-0.59	0.01	-0.68	0.01	-0.20	297
0-10	44	-0.43	1.30	-0.61	0.46	-0.80	0.81	0.51	1.12	-0.72	0.04	1.03	0.34	-0.67	0.01	-0.53	0.01	-0.12	272
10-23	45	-0.44	0.85	-0.75	0.32	-0.87	0.25	-0.55	0.42	-0.90	0.01	-0.55	0.20	-0.82	0.01	-0.70	0.00	-0.66	283
23-36	45	-0.50	0.80	-0.79	0.31	-0.88	0.12	-0.81	0.59	-0.87	0.01	-0.56	0.19	-0.84	0.01	-0.83	0.00	-0.85	319
0-13	37	-0.66	4.99	0.08	1.33	-0.58	0.49	-0.35	4.91	-0.13	0.08	1.68	0.68	-0.53	0.03	-0.26	0.01	-0.37	378
13-24	36	-0.68	5.53	0.16	1.50	-0.54	0.35	-0.54	5.02	-0.13	0.03	-0.08	0.74	-0.50	0.02	-0.34	0.01	-0.39	390
24-68	36	-0.62	5.41	0.34	1.37	-0.51	0.27	-0.59	4.57	-0.07	0.02	-0.30	0.73	-0.42	0.02	-0.38	0.01	-0.28	331
68-84	35	-0.52	5.57	0.79	1.35	-0.37	0.39	-0.24	4.66	0.22	0.01	-0.35	0.97	-0.01	0.02	-0.08	0.00	-0.44	256
0-10	37	-0.51	4.46	0.36	1.14	-0.49	0.83	0.55	10.06	1.52	0.50	22.74	1.02	0.00	0.05	0.80	0.01	1.13	269
10-60	38	-0.43	4.04	0.41	1.02	-0.49	0.88	0.87	8.16	1.33	0.30	15.31	0.97	0.08	0.04	0.91	0.01	1.22	236
60-150	38	-0.51	3.84	0.16	1.09	-0.52	0.73	0.34	7.85	0.94	0.30	12.98	0.85	-0.19	0.04	0.62	0.01	0.75	273
150-300	37	-0.46	4.28	0.44	1.11	-0.46	0.49	0.01	8.37	1.31	0.20	9.54	0.87	-0.07	0.04	0.68	0.01	-0.02	243
300-400	38	-0.57	4.18	0.11	1.09	-0.58	0.56	-0.10	8.01	0.73	0.19	6.80	0.91	-0.23	0.04	0.31	0.01	0.23	311
400-500	39	-0.44	3.54	0.18	0.95	-0.54	0.49	0.00	5.88	0.60	0.09	3.79	0.79	-0.16	0.03	0.26	0.00	-0.23	247
0-10	36	-0.53	5.08	0.56	1.17	-0.48	0.73	0.36	9.94	1.50	0.31	13.67	1.55	0.52	0.04	0.61	0.01	0.78	268
10-60	35	-0.58	5.58	0.55	1.23	-0.51	0.73	0.23	8.82	1.00	0.18	6.62	1.63	0.44	0.04	0.38	0.01	-0.20	296
60-150	34	-0.56	5.64	0.69	1.29	-0.44	0.81	0.49	10.76	1.64	0.29	12.62	1.71	0.64	0.04	0.72	0.01	0.39	274
150-300	33	-0.59	6.70	0.92	1.44	-0.40	0.93	0.63	12.46	1.93	0.29	12.17	2.11	0.93	0.05	0.69	0.01	1.33	286
300-400	32	-0.62	7.19	1.00	1.57	-0.37	0.95	0.61	13.92	2.17	0.26	10.43	2.19	0.94	0.05	0.64	0.01	-0.03	295
400-500	31	-0.58	7.25	1.27	1.58	-0.28	1.10	1.10	14.26	2.65	0.35	15.95	2.24	1.24	0.05	0.88	0.01	1.18	263