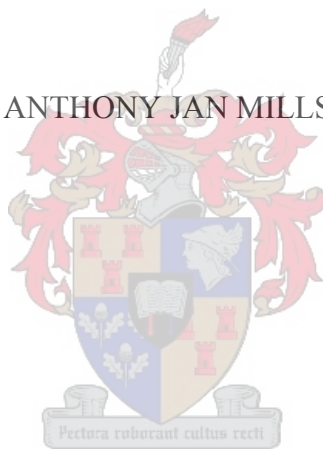


**RECIPROCAL RELATIONSHIPS BETWEEN
VEGETATION STRUCTURE AND SOIL PROPERTIES
IN SELECTED BIOMES OF SOUTH AFRICA**

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Declaration

I, the undersigned, hereby declare that the work contained in this dissertation is my own original work and that I have not previously in its entirety or in part submitted it at any university for a degree.

Signature:

Date:

ABSTRACT

The effects of different land use practices on soil quality in South Africa were investigated in five contrasting biomes, with a particular emphasis on the tendency of soils to crust and soil C content. Soil quality is a nebulous concept and its applicability in the South African landscape is scrutinised. A wide range of chemical and physical soil properties were examined. The tendency of soils to crust was assessed using modulus of rupture, water dispersible clay and a new method of laboratory infiltration which was verified with rainfall simulation. Crusting was greater in bare, exposed soils than soils under vegetation and varied with soil parent material. Differences in crusting are explained by factors relating to clay dispersion such as clay mineralogy, soil C, labile or readily oxidisable C, concentration of soluble salts, soil texture and exchangeable Na percentage (ESP). Results from long-term burn plots in savanna and grassland revealed that annual burning can increase the tendency of soils to crust. Greater crusting in burnt plots is ascribed to greater dispersion of clay, which in turn is attributed to a decline in soil C, a decline in EC and an increase in ESP. The loss of nutrients from burnt plots over time is ascribed to removal of ash in surface runoff. Calcium, Mg, and K were lost more readily than Na probably because plants take up these nutrients in greater concentration than Na. The net effect was an increase in ESP. Crusting on burnt plots may be self-perpetuating, because increased runoff is likely to increase the loss of soluble salts. Removal of vegetation due to cultivation, grazing or burning reduced soil C at all sites. Mean soil C in the 0-1 cm layer of unburnt plots in the Kruger National Park was more than three times greater than in burnt plots (2.7 vs 0.8%). The difference in soil C between treatments decreased with depth and illustrated that sampling to depths greater than a few centimetres can obscure effects of land use. The top few centimetres of soil have a disproportionate effect on soil infiltrability and nutrient cycling. This layer was named the *pedoderm*. Tree cover on burnt plots in the southern Kruger National Park is highly variable, and was hypothesised to be a function of herbivory pressure. Herbivores tended to congregate on plots with the greatest clay, Zn and Mn content and the lowest tree cover. It is suggested that soil properties determine the abundance of herbivores after fire, which in turn affects tree cover. In the Eastern Cape,

intensive stocking with goats transforms dense thicket to an open savanna. Soils from goat-transformed sites had a greater tendency to crust than soils from intact thicket, probably due to aggregate weakening associated with a decline in soil C. Mean soil C content of intact thicket was almost double that of goat-transformed thicket (5.6 vs. 3% to a depth of 10 cm) and is exceptionally high for a semi-arid region. The potential to sequester carbon in degraded thicket landscapes is thus considerable. Managing the land for greater sequestration of C will have the added benefit of increasing soil aggregate stability, reducing the tendency of soils to crust and therefore increasing the rate of water infiltration through the pedoderm. The benefits of such an approach have been recognised by specialists in soil conservation and rural land use for many decades, based largely on empirical observation. The results of this thesis provide a more quantitative basis for appreciating the effects of soil C across a broad spectrum of South African biomes.

UITTREKSEL

Die invloed van verskillende landgebruikspraktyke op grondkwaliteit in Suid-Afrika is in vyf kontrasterende biome ondersoek met spesifieke klem op die neiging van gronde om korste te vorm en die grond koolstofinhoud. Grondkwaliteit is 'n vae konsep en die toepassing daarvan in die Suid-Afrikaanse grondlandskap is noukeurig ondersoek. 'n Wye reeks van chemiese en fisiese grondeienskappe is ondersoek. Die neiging van korsvorming by gronde is beraam deur die gebruik van breukmodulus, waterdispergeerbare klei en 'n nuwe metode van laboratorium-infiltrasie wat met behulp van reënvalsimulasie gekontroleer is. Korsvorming was groter in kaal, blootgestelde gronde as in gronde met 'n plantbedekking en het gewissel volgens moeder materiaal. Verskille in korsvorming word verklaar deur faktore wat verband hou met kleidispergering soos byvoorbeeld kleimineralogie, grondkoolstof, labiele of maklik oksideerbare koolstof, konsentrasie oplosbare soute, grondtekstuur en uitruilbare natriumpersentasie (UNP). Resultate van langtermyn brandpersele in savanna en grasland het getoon dat jaarlikse brand die neiging tot korsvorming kan verhoog. Meer korsvorming in brandpersele word toegeskryf aan groter kleidispergering, wat waarskynlik verband hou met 'n afname in grondkoolstof, 'n afname in elektriese geleiding (EC) en 'n toename in UNP. Plantvoedingstowwe gaan oor tyd verlore uit brandpersele, waarskynlik deur die verwydering van as in oppervlak afloop. Kalsium, Mg en K gaan meer geredelik verlore as Na, waarskynlik omdat plante hierdie voedingstowwe in groter hoeveelhede opneem as Na. Die netto effek is 'n toename in UNP. Korsvorming op brandpersele kan self instand gehou word omdat verhoogde afloop die moontlike verlies van oplosbare soute kan verhoog. Verwydering van plantegroei deur bewerking, beweiding of brand het grondkoolstof op alle plekke verlaag. Die gemiddelde grondkoolstof in die 0-1 cm laag van ongebrande persele in die Kruger Nasionale Park was meer as drie maal groter as in brandpersele (2.7 vs 0.8 %). Die verskil in grondkoolstof tussen behandelings neem af met diepte wat daarop dui dat monsterneming tot dieptes groter as 'n paar sentimeters die effek van landgebruik kan verberg. Die boonste paar sentimeters van 'n grond het 'n oneweredige invloed op infiltrasie en voedingstofsirkulasie. Hierdie laag word die *pedoderm* genoem. Boombedekking op brandpersele in die suidelike

Kruger Nasionale Park is hoogs variërend. Die hipotese was dat dit 'n funksie van druk deur planteters is. Planteters neig om op persele met die hoogste klei, Zn- en Mn-inhoud en die laagste boom bedekking te versamel. Daar word voorgestel dat grondeienskappe die hoeveelheid planteters na 'n brand bepaal. Dit beïnvloed op sy beurt weer die boombedekking. In die Oos-Kaap het intensiewe bokboerdery digte bosruigtes verander na oop savannas. Gronde van bok-veranderde lokaliteite het 'n groter neiging tot korsvorming as gronde van onveranderde bosruigtes, vermoedelik as gevolg van verswakking van aggregate met 'n afname in grondkoolstof. Die gemiddelde grondkoolstof van onveranderde bosruigtes was byna dubbel soveel as die koolstof van bok-veranderde bosruigtes (5.6 vs 3 % tot 'n diepte van 10 cm) en buitengewoon hoog vir 'n semi-ariëde streek. Die potensiaal vir koolstof sekwestrasie in degradeerde bosruigte landskappe is dus aansienlik. Bestuur van land vir groter sekwestrasie van koolstof het die bykomende voordeel van verhoogde grond aggregaatstabiliteit, verlaging van die neiging tot korsvorming en daardeur 'n verhoging in die tempo van waterinfiltrasie deur die pedoderm. Die voordele van so 'n benadering is vir baie dekades deur spesialiste in grondbewaring en landelike landgebruik herken. Dit was grootliks gebaseer op empiriese waarneming. Die resultate van hierdie tesis bied 'n meer kwantitatiewe basis tot die verstaan van die invloed van grondkoolstof oor 'n breë spektrum van Suid-Afrikaanse biome.

I dedicate this thesis to: my grandmother, the late Jane Pijper, who regaled us with tales of her July school holidays spent in the Kruger National Park with James Stevenson-Hamilton, before the park was open to tourists; and also to my parents who took my siblings and me to the Kruger for many of our school holidays.

TABLE OF CONTENTS

Acknowledgements	
Introduction	
Chapter 1 Declining soil quality in South Africa: a literature review.....	1
1.1 Introduction	1
1.2 Understanding the causes and mechanisms of soil degradation	2
1.2.1 Why is SOM depleted when veld is cultivated, heavily stocked or burnt?.....	2
1.2.2 How does removal of vegetation reduce nutrient status?.....	3
1.3 Crust formation and soil quality	4
1.4 Land use practices and soil quality	8
1.4.1 Cultivation.....	8
1.4.2 Ranching.....	11
1.4.3 Forestry.....	12
1.4.4 Fire	13
1.4.4.1 Stimulation of microbial activity.....	13
1.4.4.2 Nutrient dynamics	14
1.4.4.3 The chemistry of crusting.....	15
1.5 Conclusions	16
Chapter 2 Frequent fires intensify soil crusting: physico-chemical feedback in the pedoderm of long-term burn experiments in South Africa	18
2.1 Introduction	18
2.2 Materials and methods	18
2.2.1 Study areas	18
2.2.1.1 Kruger National Park	19
2.2.1.2 Ukulinga Research Station	20
2.2.1.3 Fort Hare	21
2.2.2 Sampling.....	21
2.2.3 Laboratory methods.....	22
2.2.4 Statistical methods.....	24
2.3 Results	25
2.4 Discussion	26
2.4.1 Soil crusting and long-term burning.....	26
2.4.2 Feedback effects of crusting.....	48
2.5 Conclusions	49
Chapter 3 Soil carbon, crusting and goat farming in Xeric Succulent Thicket, Eastern Cape, South Africa	51
3.1 Introduction	51
3.2 Materials and methods	51
3.2.1 Study area.....	51
3.2.2 Sampling.....	55
3.2.3 Soil analyses.....	55
3.3 Results and discussion.....	55
3.4 Conclusions	63
Chapter 4 Soil carbon and vegetation in five contrasting biomes of South Africa.....	65
4.1 Introduction	65
4.2 Materials and methods	66

4.2.1 Study areas	66
4.2.1.1 West Coast Renosterveld	66
4.2.1.2 Central Nama Karoo.....	66
4.2.1.3 Xeric Succulent Thicket.....	67
4.2.1.4 Moist Upland Grassland.....	68
4.2.1.5 Mixed Lowveld Bushveld	68
4.2.2 Sampling.....	69
4.2.3 Soil analyses.....	69
4.2.4 Statistical analyses.....	70
4.3 Results	70
4.4 Discussion	71
4.5 Conclusions	80
Chapter 5 Factors affecting soil crusting in five contrasting biomes of South Africa	81
5.1 Introduction	81
5.2 Materials and methods	83
5.2.1 Study sites	83
5.2.2 Sampling.....	84
5.2.3 Soil analyses.....	86
5.2.4 Statistical analyses.....	86
5.3 Results	86
5.4 Discussion	87
5.4.1 West Coast Renosterveld	87
5.4.2 Central Nama Karoo.....	90
5.4.3 Xeric Succulent Thicket.....	95
5.4.4 Moist Upland Grassland.....	95
5.4.5 Southern Tall Grassveld.....	96
5.4.6 Mixed Lowveld Bushveld	97
5.5 Conclusions	97
Chapter 6 Interactive response of herbivores, soils and vegetation to annual burning in a South African savanna	99
6.1 Introduction	99
6.2 Materials and methods	101
6.3 Results	104
6.4 Discussion	114
6.5 Conclusions	116
Chapter 7 Reciprocal relationships between vegetation structure and soil properties in selected biomes in South Africa.....	117
7.1 Introduction	117
7.2 Fire, degradation of soil and the abundance of trees.....	117
7.3 A new theory on savanna structure: do productivity of plants and the Birch effect determine the distribution of trees across biomes?	124
7.4 Carbon sequestration, the Birch effect and soil redox	128
7.5 Carbon and soil crusting.....	131
7.6 Linking soil science and ecology in the future.....	132
7.7 Conclusions	135

References

LIST OF FIGURES

Figure 2.1 The location of the study areas (i.e. long-term burn experiment sites) in South Africa.....	19
Figure 2.2 The relationship between burnt plots and unburnt plots with respect to water-soluble ions (1:5) Ca, Mg, Na, K, NH ₄ , SO ₄ , Cl and NO ₃ in composite soil samples taken to a depth of 10 cm.....	27
Figure 2.3 The relationship between burnt plots and unburnt plots with respect to (a) (NH ₄)OAc-extractable cations Ca, Mg, Na, K; (b) electrical conductivity, sodium adsorption ratio and pH in a 1:5 soil-water extract; and (c) pH in KCl in composite soil samples taken to a depth of 10 cm.	28
Figure 2.4 The relationship between burnt plots and unburnt plots with respect to total C, total N, labile C, rate of soil respiration, C:N and Bray 2-extractable P. Results depicted are from composite soil samples taken to a depth of 10 cm, except for soil respiration which was determined from samples taken to a depth of 2 cm.....	29
Figure 2.5 The relationship between burnt plots and unburnt plots with respect to rate of laboratory infiltration, modulus of rupture, water dispersible clay, clay, silt, fine sand, medium sand and coarse sand. Results depicted are from composite soil samples taken to a depth of 10 cm, except for water dispersible clay which was determined from samples taken to a depth of 2 cm for Numbi and Napi plots (circles) and to a depth of 10 cm for all other plots.	30
Figure 2.6 Total carbon (a) and total nitrogen (b) as a function of soil depth and burning treatment at Numbi, Shabeni, Fayi and Napi burnt and unburnt plots in the southern Kruger National Park.	31
Figure 2.7 The electrical conductivity (1:5) in the profiles of burnt and unburnt plots in the southern Kruger National Park in 1 cm increments to 10 cm, 5 cm increments to 20 cm and a 10 cm increment to 40 cm. Error bars are the standard error of the difference between the two means.	32
Figure 2.8 pH (1:5) in the profiles of burnt and unburnt plots in the southern Kruger National Park in 1 cm increments to 10 cm, 5 cm increments to 20 cm and a 10 cm increment to 40 cm. Error bars are the standard error of the difference between the two means.	33
Figure 2.9 The distribution of water-soluble (a) and (NH ₄)OAc-extractable Ca (b) down profiles in burnt and unburnt plots in the southern Kruger National Park. Error bars depict minimum and maximum values.	34
Figure 2.10 The distribution of water-soluble (a) and (NH ₄)OAc-extractable Mg (b) down profiles in burnt and unburnt plots in the southern Kruger National Park. Error bars depict minimum and maximum values.	35
Figure 2.11 The distribution of water-soluble (a) and (NH ₄)OAc-extractable Na (b) down profiles in burnt and unburnt plots in the southern Kruger National Park. Error bars depict minimum and maximum values.	36
Figure 2.12 The distribution of water-soluble (a) and (NH ₄)OAc-extractable K (b) down profiles in burnt and unburnt plots in the southern Kruger National Park. Error bars depict minimum and maximum values.	37
Figure 2.13 Sodium adsorption ratios of 1:5 extracts (a) and exchangeable sodium percentage (ESP) (b) from profile samples in burnt and unburnt plots in the southern Kruger National Park. Error bars depict minimum and maximum values.	38
Figure 2.14 Rate of infiltration through soils from burnt and unburnt plots in the Numbi plots in the southern Kruger National Park using (a) rainfall simulation and (b) the laboratory method. Error bars are the mean difference between two replicates at each time interval	

for rainfall simulation infiltration and the mean standard error of three replicates at each time interval for laboratory infiltration.	39
Figure 2.15 Rate of infiltration through soils from burnt and unburnt plots in the Napi plots in the southern Kruger National Park using (a) rainfall simulation and (b) the laboratory method. Error bars are the mean difference between two replicates at each time interval for rainfall simulation infiltration and the mean standard error of three replicates at each time interval for laboratory infiltration.	40
Figure 2.16 Relationships between (a) laboratory and rainfall simulation infiltration, (b) water dispersible clay and laboratory infiltration, and (c) water dispersible clay and rainfall simulation infiltration, (d) laboratory infiltration in soils from unburnt and burnt plots; and (e) rainfall simulation infiltration in soils from unburnt and burnt plots.....	41
Figure 2.17 A broken crust on the Numbi annually burnt plot.	45
Figure 3.1 (a) <i>Portulacaria afra</i> on an intact thicket site; (b) <i>Pappea capensis</i> on a goat-transformed site; (c) crusting around <i>Portulacaria afra</i> at site 8; (d) fenceline contrast at site 1 (goat-transformed site on left, intact thicket site on right).	52
Figure 3.2 The geology of the Eastern Cape study area and location of the fenceline contrast sampling sites.	54
Figure 3.3 The relationship between goat-transformed and intact thicket sites with respect to electrical conductivity, water-soluble (1:5) Ca, Mg, Na, K, NH ₄ , SO ₄ , Cl and NO ₃ in composite soil samples taken to a depth of 10 cm.	56
Figure 3.4 The relationship between goat-transformed and intact thicket sites with respect to (a) (NH ₄)OAc-extractable cations Ca, Mg, Na, K; (b) sodium adsorption ratio and pH in a 1:5 soil-water extract; and (c) pH in KCl and water (1:2.5) in composite soil samples taken to a depth of 10 cm.	57
Figure 3.5 The relationship between goat-transformed and intact thicket sites with respect to total C, total N, labile C, total C:N, soil respiration in the laboratory, CO ₂ flux in the field and Bray 2-extractable P. Results depicted are from composite soil samples taken to a depth of 10 cm. The colours in the CO ₂ flux graph refer to site 1 (filled), site 3 (grey) and site 5 (open shapes).	58
Figure 3.6 The relationship between goat-transformed and intact thicket sites with respect to rate of laboratory infiltration, modulus of rupture, water dispersible clay, clay, silt, fine sand, medium sand and coarse sand. Results depicted are from composite soil samples taken to a depth of 10 cm.	59
Figure 4.1 The location of each study area used for investigating soil carbon stocks in five contrasting biomes of South Africa.....	67
Figure 4.2 The change in total C, N and C:N ratios with depth in the Central Nama Karoo. Three profiles are presented; two from predominantly shale-derived soils and one from a predominantly dolerite-derived soil. Where error bars are depicted, these are the standard errors of the mean	71
Figure 4.3 The change in total C, N and C:N ratios with depth in Dwyka sediment-derived soils and dolerite-derived soils on the Bokkeveld Plateau in West Coast Renosterveld. Where error bars are depicted, these are the standard errors of the mean.....	73
Figure 4.4 The change in total C, N and C:N ratios with depth in Xeric Succulent Thicket and Moist Upland Grassland in relation to land use and geology. In the thicket vegetation of the Eastern Cape, goat-transformed landscapes and intact landscapes dominated by the bush <i>Portulacaria afra</i> are compared. In the grassland of the southern Drakensberg, cultivated maize lands, kikuyu (<i>Pennisetum clandestinum</i>) pasture and virgin grassland (on sandstone and dolerite-derived soils) are compared. Where error bars are depicted, these are the standard errors of the mean.	74
Figure 5.1 The process of soil crusting, adapted from Bresson and Cadot (1992).	82

Figure 5.2 The location of the study areas used for an investigation into soil crusting in five contrasting biomes in South Africa.	84
Figure 5.3 Selected soil properties from the Southern Tall Grassveld study area at Ukulinga plotted against distance from the southern-most block on the long term burn experiment. Soils to the south are predominantly shale-derived. Soils to the north have a strong dolerite influence. Circles, diamonds and squares represent three replicates. Black-filled shapes are unburnt, grey-filled annually burnt and white-filled annually burnt and mown plots.	89
Figure 5.4 (a) Laboratory infiltration plotted against silt content for soils from the Central Nama Karoo (C.N.K.), West Coast Renosterveld (W.C.R.) and Xeric Succulent Thicket (X.S.T); and (b) laboratory infiltration plotted against modulus of rupture for the same soils depicted in (a).	90
Figure 6.1 The location of the long-term burn experiments in the southern Kruger National Park, South Africa.	102
Figure 6.2 Digital photographs used for image analysis of tree cover (with the software package eCognition 2.1) and the image analysis results for the Numbi and Kambeni burnt and unburnt plots.	107
Figure 6.3 Digital photographs used for image analysis of tree cover (with the software package eCognition 2.1) and the image analysis results for the Shabeni and Fayi burnt and unburnt plots.	108
Figure 6.4 Digital photographs used for image analysis of tree cover (with the software package eCognition 2.1) and the image analysis results for the Skukuza and Napi burnt and unburnt plots.	109
Figure 6.5 Digital photographs used for image analysis of tree cover (with the software package eCognition 2.1) and the image analysis results for the Mbyamiti and Nwaswitshaka burnt and unburnt plots.	110
Figure 6.6 The total number of impala and other herbivores sighted at the long-term burn plots in the southern Kruger National Park over the period June to September 1999 in <i>Terminalia</i> woodland (a) and <i>Combretum/Acacia</i> savanna (b). Data were transformed to depict a total of 19 visits at each site.	111
Figure 6.7 The relationships between tree impact factor and indices of herbivore abundance. Error bars depicted are standard errors of the mean.	111
Figure 6.8 The relationships between indices of herbivore abundance and total Zn. Error bars depicted are standard errors of the mean.	112
Figure 6.9 The relationships between indices of herbivore abundance and total Mn. Error bars depicted are standard errors of the mean.	112
Figure 6.10 The relationships between indices of herbivore abundance and total clay content. Error bars depicted are standard errors of the mean.	113
Figure 6.11 The number of trees (basal diameter > 7.6 cm) and shrubs (basal diameter > 91 cm) recorded from transects in annual burn plots of <i>Terminalia</i> woodland and <i>Combretum/Acacia</i> savanna in 1954 and 1996/7. Basal diameters of shrubs (which includes coppicing trees) refers to the distance between the two outermost stems.	113

LIST OF TABLES

Table 2.1: Paired t-test results for burnt and unburnt plot comparisons in the southern Kruger National Park and across all study sites.....	39
Table 2.2: Soil properties correlated with laboratory infiltration and water dispersible clay in granite-derived and basalt-derived soils in the Kruger National Park. Pearson correlation coefficients, n and p values are presented.....	40
Table 3.1: Soil properties correlated with laboratory infiltration, water dispersible clay and modulus of rupture in soils from goat-transformed and intact sites in the Xeric Succulent Thicket. Pearson correlation coefficients, n and p values are presented.....	58
Table 4.1: Total C and N to a depth of 10 cm in West Coast Renosterveld, Central Nama Karoo, Xeric Succulent Thicket, Moist Upland Grassland and Mixed Lowveld Bushveld. Mean bulk density was calculated from means of clay, silt and sand content in each vegetation type and soil carbon content for each profile, using algorithms developed by Saxton et al. (1986).....	72
Table 4.2: Estimated stocks of total soil C and N to a depth of 50 cm in West Coast Renosterveld, Central Nama Karoo, Xeric Succulent Thicket and Moist Upland Grassland. Three bulk density scenarios are depicted. A bulk density range was calculated for each profile from means and standard errors of clay, silt and sand content in each vegetation type and soil carbon content for each profile, using algorithms developed by Saxton et al. (1986).....	73
Table 5.1: Means and standard errors (se) of selected soil properties in West Coast Renosterveld (WCR), Central Nama Karoo (CNK), Xeric Succulent Thicket (XST), Moist Upland Grassland (MUG) and Mixed Lowveld Bushveld (MLB).....	87
Table 5.2: Soil properties strongly correlated with laboratory infiltration and water dispersible clay at each study site. Spearman rank correlation coefficients are presented, together with the number of samples (n) and p value (p).	
Table 6.1: Soil properties of annually burnt plots in the southern Kruger National Park.....	104
Table 6.2: Correlative relationships between impact of fire on tree cover, indices of herbivore abundance and soil properties. Pearson correlation coefficients are presented. Significant correlations ($p < 0.05$) are in bold.	105

APPENDICES

APPENDIX A: Chemical and physical soil properties of all samples from all study sites.

APPENDIX B: A manuscript in preparation by Milewski and Mills (2003) for submission to *Ecological Letters*. The manuscript is pertinent to Chapter 7.

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INTRODUCTION

The first records of an understanding of vegetation structure and soil date back to the Greek philosopher Aristotle (384-322 B.C.) and his student Theophrastus of Eresus (371-286 B.C.). Aristotle wrote, “As many flavours as there are in the flesh of different fruits, so many, it is plain, prevail also in the earth”. He viewed the soil as equivalent to a vast stomach that prepares and supplies the food of plants, which later became known as the humus theory of plant nutrition. Theophrastus was, however, probably the first person to document, in his *De caulis plantarum*, how different kinds of plants grow in, and are characteristic of, different abiotic environments. Only later, did Hans Jenny note that the relationship is reciprocal¹ and that soil type is a function of *biota*, climate, topography, parent material and the length of time of soil formation (Jenny, 1941). Jenny was particularly interested in how the growth of plants enables an accumulation of soil organic matter (Jenny, 1949; 1950). Aristotle, by contrast, highlighted how humus was important for plant growth and although Aristotle’s chemical understanding was rudimentary, numerous workers have subsequently shown how soil organic matter is critical for ecosystem functioning and productivity.

Soil organic matter tends to increase the aggregate stability of soils, thereby increasing the rate of water infiltration (Du Plessis and Shainberg, 1985; Haynes and Swift, 1990; Haynes, 1999; Robinson and Philips, 2001; Dominy and Haynes, 2002). It also increases the water and nutrient holding capacity of soils and is an important source of nutrients for plants (Wiltshire and Du Preez, 1993; Du Toit and Du Preez, 1995; Lal *et al.*, 1997). The return of plant material to soils is thus essential for maintaining soil quality (Gregorich *et al.*, 1994). Yet, there is a chicken and egg scenario, because soils also exert an effect on vegetation structure and ecologists (like Theophrastus) have long-recognised that plant communities are often determined by soil type (Werger and Coetzee, 1978). Plants are adapted to and consequently confined to a particular regime or envelope of physical factors which include temperature, water content, nutrients and oxygen. Soil properties affect all of these key physical factors and thus changes in soil properties induced by land management or natural variations in the landscape are likely to influence the distribution of plant species.

¹ “Reciprocal describes an equivalence, balance, equal counteraction, equal return, or equal sharing [not a mere cooperation of distinct forces, but an extremely powerful reciprocal action, each in turn firing the other and fired by it – C.E. Montague]” (Webster’s Third New International Dictionary, 1959).

Vegetation structure (reflected in the height and density of woody and herbaceous plants) is in many ways the essence of an ecosystem. It is the first gross parameter of an ecosystem that strikes the eye in a particular habitat; it is the parameter that enables us to judge whether we are encountering a grassland, savanna or tall forest. Vegetation structure not only determines how we classify habitats, it also determines what organisms are able to inhabit a particular area. Understanding what determines vegetation structure in a particular environment is thus at the heart of understanding the ecological functioning and the distribution of biodiversity within that habitat. Bird diversity for example, has been shown to be highly dependent on vegetation structure (Cody, 1986).

The effects of soils on vegetation structure may be gross and easily observed, such as the shift in plant species from sandy to clayey soils. In the southwestern Kruger National Park, for example, open grasslands are found on clayey, gabbro-derived soils, whereas dense *Terminalia* woodland with a tree canopy of ten to fifteen metres high occurs adjacent to the grasslands on sandy, granite-derived soils (Venter, 1990). Soils may also have more subtle effects on vegetation structure. Slight changes in soil pH or nutrient content can, for example, affect the distribution of a particular plant species (Coile, 1952; Abrams, 1985). In addition, soils may have indirect effects on plants. For example, the nutrient status of soils can affect the distribution of herbivores (Braithwaite *et al.*, 1983; Braithwaite, 1983; McNaughton, 1985; Van de Vijver, 1999), which in turn will alter plant community composition and hence vegetation structure (Trollope *et al.*, 1998).

Ecologists, like other scientists, have searched continuously for generalising abstractions or laws that explain their observations. If such laws exist then they should translate into an accurate prediction of ecosystem responses. The stakes are high, as the very success of ecology as a scientific discipline can be judged on whether such laws have been accurately identified. Some authors consider that the search for ecological laws has been fruitful (May and Seger, 1986), whereas others argue that evidence for the existence of natural ecological laws that can be used in a similar way to those in physics and chemistry is unconvincing (Hengeveld and Walter, 1999). Indeed, the management of ecosystems remains a highly contentious topic and advice on how to steer an ecosystem in a particular direction will vary from one ecologist to the next. Unlike physics and chemistry, prediction is not the hallmark of ecology. As Hengeveld and Walter (1999) note, “the only law-like processes that operate in ecology are constituted by the constraints posed by physical and chemical laws”. Theory

predominating in population, community and ecosystem ecology is, however, often divorced from physical and chemical processes operating within landscapes, and rather focus rather on biotic interactions (e.g. competition and predator-prey relationships). Hengeveld and Walter (1999) and Walter and Hengeveld (2000) suggest that ecology needs to change the prevalent paradigm of “demographic ecology” to a paradigm of “autecology”. Such a change in paradigm would see ecological focus shifting towards the abiotic environment as the primary controller of ecosystem structure, and biotic interactions would shift from the main players to “secondary modifiers” (Walter and Hengeveld, 2000). For ecological theory to be of value, it needs to be predictive. There is likely to be a greater chance of improving the predictive power of ecology if research focuses on predictive chemical and physical processes that control organisms, rather than interactions between organisms. The organism-interaction approach has to date yielded few, if any, ecological laws.

Soil science is grounded within the disciplines of chemistry and physics and has focussed for over a century on unravelling the interaction between plants and soils in an agricultural setting (Russell, 1988). Given that plant-soil interactions are a quintessential part of any ecosystem, soil science may be able to provide new insights and possibly theories for improving the predictive capacity of ecology. With this in mind, this thesis investigates the relationships between vegetation structure and soil properties, from the micro-scale of soil chemistry to the macro-scale of biomes.

Chapter 1 reviews the effect of land use on soil quality in South Africa, with a particular emphasis on soil crusting and soil organic matter. The semi-arid climate of most of South Africa dictates that water availability is critical for both ecosystem and agricultural productivity. The formation of a soil crust can reduce the rate of infiltration into soils by more than a thousand fold (McIntyre, 1958a; Hillel and Gardner, 1969; Levy and Rapp, 1999) and is consequently a process that land managers of semi-arid areas should judiciously avoid. Soil organic matter is in many ways an antidote to crusting or sealing in that it tends to bind soil aggregates and reduces the dispersion of clay (Cook *et al.*, 1992; Golchin *et al.*, 1995; Sumner, 1998). It is also a key indicator of soil health because it increases water and nutrient holding capacity, improves porosity and therefore aeration, and supplies nutrients via mineralisation (Gregorich *et al.*, 1994; Haynes, 1997).

Chapter 2 examines the soil chemistry of crusting in more detail and focuses on the effects of long-term burning in savanna and grassland biomes in South Africa. The interactions between vegetation structure, cation distribution, soil C and dispersion of clay reveal that frequent burning can potentially create a process of crusting that is self-perpetuating. One of the key objectives of this chapter was to investigate whether conventional sampling of soils to 5 or 10 cm obscures the effects of land use on soil quality. Soils in the Kruger National Park were sampled in 1 cm slices to a depth of 10 cm. It was hypothesised that this sampling strategy would reveal marked differences in soil properties from the top 0-1 cm layer to the 9-10 cm layer. A thin layer at the mineral soil surface, comprising only a few centimetres of soil, was deemed critical for plant productivity because of its disproportional influence on infiltration of water and supply of nutrients. This layer has been named the *pedoderm*. Chapter 3 is a case study from the Eastern Cape, where farming of goats has transformed a dense thicket vegetation into an open pseudo-savanna. The effects of this vegetation transformation on soil chemistry and crusting are investigated. In Chapter 4 the focus returns to soil organic matter and in particular the stocks of soil C that are present in selected South African biomes. The effect of different land use practices on C stocks is analysed and the processes behind the changes are discussed. Chapter 5 provides a similar overview across all study sites and biomes, but with a focus on soil crusting and how the removal of vegetation changes soil chemistry and thus the tendency of soils to crust. In Chapter 6, the percentage cover of trees in annually burnt plots in the Kruger National Park is quantified with image analysis software and is shown to be correlated with the abundance of herbivores and soil micronutrient content. Chapter 7 brings the preceding chapters together in a discussion on the effects of fire and agriculture on soil chemistry, crusting and carbon. The possible relationship between the Birch effect (Birch, 1958) and the abundance of trees across biomes is also discussed.

CHAPTER 1

DECLINING SOIL QUALITY IN SOUTH AFRICA: A LITERATURE REVIEW

1.1 Introduction

Ecosystem functioning and agricultural productivity are dependent on maintenance of the soil resource. Soil quality is defined in relation to use (Gregorich *et al.*, 1994) and any significant decline in quality therefore implies misuse of soils. The effects of inappropriate land use practices in South Africa have been in the spotlight of agricultural and political debates for centuries. The damage, however, has usually been quantified in terms of soil loss through erosion rather than in terms of more subtle indicators of quality in the soil that has remained intact. The development of policies to prevent and mitigate erosion in agricultural landscapes in South Africa began in 1923 with the Drought Investigation Commission report. This was followed by the Soil Erosion Advisory Council in 1930 and the Soil Conservation Act in 1946. The effect of these policies was effective control of erosion in many parts of the country (Donaldson, 2002). The control of erosion is, however, only the first step in managing the soil resource effectively. The second step requires an understanding of the changes in soil chemical and physical properties that may occur under different land use practices.

Soil quality has been typically equated with soil organic matter (SOM) or its associated indicator elements, C and N. Goldschmidt (1938), for example, reported on the "nitrogen problem in pasture soils on the Natal Sour Veld". Du Toit (1938) noted that because of widespread aridity and low humus content, South African soils generally "have an extremely delicate nature and lack resilience" in comparison to soils in temperate areas. And Penzhorn (1972) spoke of the "thin, vulnerable and unstable soil mantle" in South Africa. Only recently have quantitative studies begun to emerge: Du Toit *et al.* (1994) found that 5-90 years of cultivation in the Free State resulted in a loss of 10-73% of C and N relative to natural grassland. Similarly, Nel *et al.* (1996) found a 50% decline in C after 50 years of cropping a Hutton soil in Pretoria. The loss can be startlingly rapid. Lobe *et al.* (2001) recorded a 50% decline in C after only 3.5 years of cultivation in the Free State.

This review attempts to develop an understanding of how land use practices in South Africa have led to adverse changes in both chemical and physical properties of soils. In particular, it

seeks to explain why a decline in the receptiveness of soil to water infiltration, which in the context of the semi-arid South African landscape is probably the strongest single indicator of soil quality, is not necessarily a simple consequence of the parallel decline in SOM that accompanies many land use practices. Although the focus is on South African research, the review refers to work done in other parts of the world in order to retain a useful perspective of future research needs and possibilities.

1.2 Understanding the causes and mechanisms of soil degradation

1.2.1 Why is SOM depleted when veld is cultivated, heavily stocked or burnt?

Tillage is often highlighted as the main cause of SOM decline. This rests on the hypothesis that the disruption of soil aggregates leads to exposure of organic matter to microbial attack (Davidson, 1986). Evidence for this mechanism is, however, scarce. Significantly, several authors have shown that increases in soil respiration after tillage cannot account for even a small fraction of the SOM loss under cultivation (Rovira and Greacen, 1957; Hendrix *et al.*, 1988; Roberts and Chan, 1990; Reicosky *et al.*, 1997; Aslam *et al.*, 2000). The factors leading to SOM loss through tillage, intensive grazing or frequent burning are similar in many respects and can probably be attributed, mainly, to erosion and vegetation removal.

The effect of erosion in the absence of cultivation is fairly easily explained since the exponential decrease in SOM concentration with depth (Woods, 1989; Purnomo *et al.*, 2000) means that relatively little topsoil need be lost to substantially reduce the total SOM content. Vegetation removal effects are more complex. The direct effect is a reduction in inputs of litter and root biomass. Indirectly, however, the effect of temperature (Du Preez and Snyman, 1993), wetting and drying cycles (Birch, 1958; Savage and Vermeulen, 1983; Du Preez and Snyman, 1993; Jordaan and Rautenbach, 1996; Moyo *et al.*, 1998), possible inhibitory effects of plant roots on microbial activity and the sometimes excessive removal of N relative to C (Theron, 1951), may all contribute to a decline in SOM when vegetation is removed. Theron (1951) showed that grass leys had a reduced rate of mineralisation relative to fallow soils, which he ascribed to the release of antibacterial exudates from grass roots. He noted further that “an almost complete repression of mineralisation is particularly characteristic of permanent grass” and that under annual crops “the repression, if any, can take place only intermittently”.

In relation to N, Theron (1951) noted that “when the virgin soil is ploughed over, the agency ultimately responsible for maintenance of the organic matter, viz. the vegetation, is removed, the organic matter is rapidly oxidised, and nitrates are freely formed and lost through leaching and volatilisation...”. In addition, N can be exported from the site when crops are harvested, N can be volatilised when biomass is burnt, and N can be transferred by livestock from the veld into kraals. Because the C:N ratio will tend to return to its initial equilibrium (Theron, 1951), the result of an export of N is a net loss of soil C. Theron (1951) made this point quite explicitly and highlighted how this process leads to deterioration in soil quality in stating that “...the loss of nitrogen is accompanied by a corresponding loss of carbon...These losses are accompanied by a gradual deterioration of the crumb structure, amongst other evils”.

The decline in SOM in agricultural landscapes is thus multifaceted. The fundamental chemistry underlying the decline must, however, lie within soil redox. Photosynthesis reduces the carbon atoms and mineralisation oxidises the carbon back to a stable equilibrium state (McBride, 1994). The soil surface is a redox interface, between the oxidising atmosphere and the less oxidising and sometimes reducing soil matrix. As Bartlett (1999) notes, redox interfaces are where chemical action occurs. Birch (1958) ascribes the greater rate of mineralisation after wetting and drying to an increase in metabolically-active young microbes. Viewed in another light, wetting and drying results in an injection of oxygen into the soil matrix and “fans the microbial flame”. On wetting, dissolved oxygen moves into the soil in rainwater and on drying, atmospheric oxygen re-enters the soil pores. In this way a “bellows” effect is created.

1.2.2 How does removal of vegetation reduce nutrient status?

Vegetation enriches surface horizons with nutrients, either directly through litter (Frost and Edinger, 1991; Allsopp, 1999), indirectly by trapping atmospheric dust (Kellman, 1979; Vetaas, 1992; Bolton *et al.*, 1993) or providing cover for birds and mammals (Scholes and Archer, 1997). Belsky *et al.* (1989), for example, studied the effects of *Acacia tortilis* in Kenya and found that N, P, K, SOM and soil water content were greater under the canopy than outside it. Annual net primary productivity of grass was also greater under the canopy (7 t ha⁻¹ compared with 3.6 t ha⁻¹ outside the canopy).

Naidu *et al.* (1996) studied the effect of cultivation on soils in Australia, that prior to cultivation had supported indigenous *Eucalyptus* forest. They found that electrical conductivity (EC) was lower in cultivated lands in comparison to virgin forest soils. The ions that showed the greatest decline were Na^+ , K^+ and Cl^- . Naidu *et al.* (1996) attributed the decline in EC to greater leaching as a result of the removal of trees and a reduction in biochemical cycling of nutrients due to litter fall, through-flow and stem-flow. A forested landscape is likely to have less leaching due to the high evaporative demand of trees and the greater canopy interception of rainfall than non-forested landscapes (Blank and Fosberg, 1989). These interpretations were corroborated by Reynolds *et al.* (1988), who found that forested landscapes accumulated soluble salts in the soil profile. Attiwell and Leeper (1987) found that *Eucalyptus* canopy interception amounted to 10-30% of annual rainfall. Similar systematic studies are yet to be conducted on South African soils. An additional reason for a reduction in EC due to cultivation is the loss of nutrients due to cropping. Removal of vegetation can also, however, result in an accumulation of salts in certain parts of the landscape, such as has occurred in southwestern Australia. This has been ascribed to a rise in saline groundwater levels due to a reduction in transpiration that occurs with the removal of *Eucalyptus* woodlands (Peck and Hatton, 2003).

1.3 Crust formation and soil quality

Soil crusts or seals form when clay at the surface disperses and blocks soil pores and when exposed aggregates collapse and slake during wetting (McIntyre, 1958 a&b; Agassi *et al.*, 1981). This process is greatly enhanced under raindrop impact, as the energy input promotes dispersion and aggregate breakdown (Hillel, 1998). A crust on the soil surface need only be 0.1 mm wide to reduce the infiltration rate by a factor of 1800 (McIntyre, 1958a). Failure to account for the effect of crusting on infiltration can result in gross overestimation of water intake by the soil (McIntyre, 1958a; Hillel and Gardner, 1969; Levy and Rapp, 1999). This is especially true in arid areas, where high intensity rain events are the norm (Shainberg and Singer, 1985). Infiltration results obtained in laboratories should, however, be treated with some caution when extrapolating to the field, as infiltration in the field can be considerably greater than in the laboratory due to greater surface roughness and porosity of field soils (Bloem and Laker, 1994 a&b). Other factors affecting infiltration in the field include earthworm activity and the formation of biological crusts. Earthworm burrows increase macroporosity and thus infiltration, and are consequently often critical for maintaining soil

quality (Dlamini *et al.*, 2001; Haynes *et al.*, 2002). Biological crusts are a complex mosaic of living organisms, including algae, cyanobacteria (blue-green algae), bacteria, lichens, mosses, liverworts, and fungi, that grow on or just below the soil surface. These living crusts also affect soil porosity and can increase as well as decrease rates of infiltration relative to soils without the biological crust organisms (Belnap *et al.*, 2001; Warren, 2001). Mineral or physical crusts (which are the topic of a large part of this thesis) appear to be colonised by biological crust organisms in some areas (personal observation in the granitic landscapes of the southern Kruger National Park), however, the interaction and/or separation of processes leading to mineral vs biological crusting are rarely elucidated in the literature. The colonisation of mineral crusts by biological crust organisms may be a mechanism by which the potentially negative effects of mineral crusting (e.g. reduced infiltration and aeration) are alleviated in certain ecosystems. This is a topic worthy of further research.

The removal of vegetation during cultivation can have a marked effect on the crusting potential of soils by exposing the soil to raindrops and altering soil properties such that the soil becomes more prone to crusting (Meyer *et al.*, 1996). A study by Robinson and Philips (2001) of dispersive clay soils in southern Italy demonstrated that soils under woodland did not crust when exposed to simulated rainfall in a laboratory. In contrast, soils in the area that had been planted to wheat or exposed by overgrazing formed surface crusts under simulated rainfall. The greater crusting was linked to a decrease in aggregate stability, which in turn was related to a decline in SOM. The role of organic materials, such as polysaccharides and fungal threads, in binding soil aggregates has been highlighted by numerous authors (Tisdall and Oades, 1982; Powers and Skidmore, 1984; Haynes and Swift, 1990; Whitbread *et al.*, 1998; Puget *et al.*, 2000). Research using scanning electron microscopes (SEM) has confirmed that there is substantial loss of the binding agents around aggregates after cropping (Shepherd *et al.*, 2001). Invariably, a loss in SOM is correlated with a decrease in aggregate stability (Haynes, 1997; Haynes and Hamilton, 1999; Dominy *et al.*, 2002; Graham *et al.*, 2002a; Milne and Haynes, 2003, in press) and often an increase in clay dispersion (Cook *et al.*, 1992; Sumner, 1998). Different fractions of SOM, such as "readily mineralisable" or labile C, microbial biomass and soil enzymes are often highlighted as critical for maintaining soil quality i.e. soil stability and a supply of nutrients (Graham *et al.*, 2002b; Dominy *et al.*, 2002). The precise role of different fractions of SOM in soil quality are often, however, largely unknown (Sumner, 1998). The value of soil quality studies that analyse the effect of land use on numerous fractions of SOM, all of which tend to be strongly correlated, is

therefore questionable. Soil quality researchers should perhaps standardise their approach and select a few fractions of SOM and focus on the mechanism by which these fractions contribute to soil quality, to enable meaningful comparisons across study areas.

Robinson and Philips (2001) found that enhanced runoff and rapid erosion were evident in wheat lands and livestock-degraded lands, but not in woodlands. The study highlighted how soil degradation under agriculture can aridify a landscape due to a breakdown in soil structure and an increase in crusting and runoff. In particular, it is the top few centimetres of soil that are often of critical importance in terms of the supply of nutrients, maintenance of an open pore structure for infiltration of water and thus productivity of plants (Murphy *et al.*, 1998). The importance of this layer for a supply of nutrients to plants was demonstrated by Woods (1989), who found that mineralisation of N in the 0-1 cm layer was 18 times greater than in the 2-15 cm layer in the short grass steppe of Wyoming. The effect of this upper layer of soil on plant productivity was illustrated by Purnomo *et al.* (2000), who showed that the removal of the top few millimetres of soil in a wheat field at Wagga Wagga in Australia, resulted in a 47% reduction in grain yield.

Crusting is not, however, solely a function of vegetation cover, because texture and clay mineralogy also affect the tendency of a soil to crust. Stern *et al.* (1991a), for example, found that soils without smectite were more stable, less erodible and less susceptible to crust formation than smectitic soils. Indeed, kaolinitic soils in South Africa have been shown to be exceptionally stable, but even a small amount of smectite in a kaolinitic soil greatly increases susceptibility to crusting (Cass and Johnston, 1985; Levy and Van der Watt, 1988). Illitic soils also tend to be more susceptible to crusting than kaolinitic soils as Levy and Van der Watt (1988) demonstrated with rainfall simulation work. The effect of quantity of clay on crusting is less clear. Taylor and Fey (1988) pointed out that the degree of weathering affects crusting, with highly weathered soils tending to have greater clay content and more stable aggregates, which negate crusting. Shainberg (1992) also suggested that an increase in clay content tends to increase aggregate stability and thereby infiltration. In contrast, rainfall simulation work on forty five South African topsoils by Bloem and Laker (1994a) showed conclusively that an increase in clay content decreases infiltration. The authors noted that the soils most prone to crusting had at least one of the following properties: an exchangeable sodium percentage (ESP) greater than 2, a clay fraction dominated by smectite, a Ca:Mg ratio smaller than 1, or an organic matter content below 0.2%.

Studies on South African soils have contributed considerably to the understanding of crust formation. Du Plessis and Shainberg (1985), for example, showed that infiltration of water can be reduced in soils with an exchangeable sodium percentage (ESP) as low as 1 if the concentration of soluble salts is low enough, and that sesquioxides tend to reduce the effects of sodicity on the dispersion of clay. These authors noted that many arable soils in arid and semi-arid regions of the world contain 1-5% exchangeable Na which, until then, had not been considered problematic in terms of crusting. Crusting and erosion on such soils can be severe under irrigation with low EC water or after rainfall. Further insights were gained by Levy *et al.* (1986), who demonstrated how crusting is minimised whenever the solution concentration is high and monovalent cations are replaced by polyvalent ones, and by Frenkel *et al.* (1992), who showed that clay dispersion and hydraulic conductivity reduction do not generally occur at $ESP < 10$ provided that the EC of water used is $> 5-10 \text{ mmol}_c \text{ l}^{-1}$. In addition, the role of Mg in crust formation on South African soils has been highlighted by researchers such as Van der Merwe (1965) and Nel (1989), who showed that low Ca:Mg ratios enhance dispersivity and cause structural instability. Bloem and Laker (1994a) pointed out that soils with Ca:Mg ratios less than 1 are widespread in South Africa, because of the occurrence of Mg-rich mudstones and shales in areas where the rainfall is too low and erratic to effectively remove the Mg by leaching.

Some South African studies have also addressed the effect of iron oxides and organic matter on crusting. Ellis (1988) observed that bleached A horizons in the Central Nama Karoo had a greater tendency to crust than non-bleached A horizons. He suggested that Fe oxides are the critical ingredient for structural stability of these surface horizons and that a loss of Fe (during waterlogging and reducing conditions) results in greater crusting and sealing. Rainfall simulation work by Du Plessis and Shainberg (1985) showed that SOM promoted aggregate stability and increased infiltration while Frenkel *et al.* (1989) noted how adsorbed humic substances might neutralise positively charged clay surfaces, thereby reducing electrostatic attraction between clay micelles and increasing dispersion. Frenkel *et al.* (1992) found that organic anions had a greater dispersive effect on kaolinite than on smectite. They ascribed this effect to the greater ratio of positively charged, edge surface to negatively charged, planar surface, which results in a greater anion adsorption capacity. Interestingly, Bloem and Laker (1994a) and D'Huyvetter (1985) found that organic matter content did not contribute to multiple regression equations for predicting soil crusting and erodibility. Although organic

matter content may not correlate with clay dispersion or crusting across numerous soil types, there is considerable evidence showing that, for the majority of soils, aggregate stability and the rate of infiltration decrease when SOM is lost (Tisdall and Oades, 1982; Haynes *et al.*, 1991; Golchin *et al.*, 1995; Naidu *et al.*, 1996; Blair and Crocker, 2000). A cohesive theory on the effects of different fractions of organic matter on clay dispersion has yet to be developed (Sumner, 1998) and this remains as a substantial gap in our understanding of how soils degrade.

The effects of soil crusting on plant growth are varied. Besides reduced water infiltration, the strength and oxygen-excluding nature of crusts may impede root growth near the surface and curtail germination and growth of seedlings (Shainberg and Levy, 1994; Bristow, 1988; Hillel, 1998). Not all effects are detrimental. Sombroek (1986) noted that there may be a measure of protection against wind erosion and, sometimes, against water erosion. Valentin *et al.* (1999) studied banded vegetation in arid African landscapes and concluded that crusting between the bands promotes water runoff into adjacent bands of vegetation (a kind of natural water harvesting).

1.4 Land use practices and soil quality

1.4.1 Cultivation

Soil organic matter tends towards an equilibrium state through time, that is dependant upon the rate of input versus loss of organic matter (Jenkinson and Rayner, 1977). Land management that increases organic matter input usually results in an increase in soil C. Experiments at Rothamstead that started in 1852 have shown, for example, how the addition of farmyard manure (3 t C yr^{-1}) lead to an increase in soil C from $\sim 25 \text{ t ha}^{-1}$ to $\sim 90 \text{ t ha}^{-1}$ over 125 years (0-23 cm) (Jenkinson, 1990). Similarly, soil C of fallow lands at Rothamstead that were allowed to revert to deciduous woodland increased from $\sim 20 \text{ t ha}^{-1}$ to $\sim 60 \text{ t ha}^{-1}$ over the same time period (Jenkinson, 1990). Cultivation that does not include manuring, tends to result in a decline in soil C (Tisdall and Oades, 1982; Edwards *et al.*, 1992; Du Toit *et al.*, 1994; Francis *et al.*, 2001). The C lost from cultivated fields is a particular fraction of C which is easily mineralised. A large fraction of soil C is, however, extremely resilient to microbes and stable over periods of thousands of years. It is the presence of this stable C that explains why soil C in lands kept bare at Rothamstead (by handweeding) declined from $\sim 37 \text{ t}$

ha⁻¹ to only ~23 t ha⁻¹ over a period of one century (Jenkinson and Rayner, 1977). The rate of SOM loss also depends strongly on climate. Research on the Highveld has shown that in warmer, drier areas the initial rate of SOM loss was greater and an equilibrium was reached more rapidly than in cooler, wetter areas (Du Toit *et al.*, 1994; Du Toit and Du Preez, 1995). These studies showed a high rate of SOM loss during the first five years of cultivation with equilibrium being attained after about 35 years. The complexity of interacting factors affecting SOM and the range of SOM types (i.e. stable versus easily mineralised) has attracted a computer modelling approach for predicting the rate of decline or accumulation under particular land use practices. Such models have been successful for many systems, such as the experiments at Rothamsted (Jenkinson, 1990).

Loss of SOM from soils can result in substantial loss of CEC (Menzie and Gillman, 1997) and in reduced quantities of N, P and trace elements (Wiltshire and Du Preez, 1993; Du Toit and Du Preez, 1995; Lal *et al.*, 1997). Wiltshire and Du Preez (1993) showed, for example, that cultivation in the Free State resulted in the loss of 30-50% of total N, while Prinsloo *et al.* (1990) found that cultivation reduced N in the top 15 cm of soil from 1.8 to 0.5 t ha⁻¹. Declines of this magnitude threaten the sustainability of crop production in the area (Du Toit and Du Preez, 1995). Although the decline in SOM is usually highlighted as the main reason behind the decline in N and P reserves, studies on soils subjected to long periods of cultivation have shown that in many cases soil N losses can be accounted for by removal of N by crops (Goldschmidt, 1938; Haas *et al.*, 1957), especially where no organic manures or fertilizers have been added. Du Toit and Du Preez (1995) found, however, that losses of C were consistently greater than losses of N in cultivated lands of the highveld. The net result was a lower C:N ratio in cultivated soils than in virgin soils.

Crop production entails the removal of plant materials and hence nutrients from the landscape. Unless these nutrients are returned as fertilizer, a "nutrient mining" situation may develop, whereby soil fertility is depleted over time. Fertilization, in contrast, can increase nutrient levels beyond that of virgin soils and potentially improve soil quality as a result. The effects of crop production on nutrient status are thus highly varied and are a function of soil type, crop type and management (Scotney and Dijkhuis, 1990). Du Preez and Wiltshire (1997), for example, found that K decreased whereas P and Zn levels increased under dryland cultivation in central regions of South Africa. At Cedara, Miles and Hardy (1999) found that Italian ryegrass production removed 518 kg K ha⁻¹ yr⁻¹. The removal of nutrients can also

have effects on soil structure. Calcium, for example, is an aggregating force in many soils and removal of Ca via cropping (or via leaching) could reduce soil structural stability. Chapter 2 in this thesis reports on how depletion of Ca in topsoils, as a result of frequent burning, increases the tendency of soils to crust. It remains to be shown whether removal of Ca via cropping is having a similar effect in South African agricultural landscapes.

The role of SOM in governing plant available P in soils is not well understood (Du Preez and Claassens, 1999; Dalal and Chan, 2001). In general, a reduction in labile P has been closely associated with SOM losses in South Africa (Van Zyl and Du Preez, 1997; Du Preez and Claassens, 1999) and Kenya (Nziguheba *et al.*, 2000). On the South African Highveld, Du Preez and Claassens (1999) found that 30% of labile P was lost as a result of cultivation. They point out, however, that inorganic P fertilizers are converted to stable soil P forms and can be viewed as a long-term P pool for plants. Phosphorus fertilization in their study area thus mitigated the loss of labile P fertility. Van Zyl and Du Preez (1997) showed that inorganic P increased in cultivated fields in 94% of cases investigated, while organic P decreased in 42% of cases. The concentration of inorganic P was greater than organic P in cultivated fields, while the reverse was true for virgin soils.

The loss of organic matter from soils under cultivation is not inevitable. The deterioration of soil quality depends on the type of tillage, fertilizer and irrigation management. Nel *et al.* (1996) reported that the SOM decline after 50 years of cropping on a Hutton soil in Pretoria was less severe under manure treatments, as well as balanced treatments of N, P and K fertilizer. Unbalanced fertilization (e.g. NP and NK) resulted in similar SOM declines (~50%) to the no-fertilizer treatments. In some cases, cultivated fields develop a greater SOM content than adjacent virgin veld (Du Preez and Wiltshire, 1997). The reasons for such an effect are not always clear-cut but have been ascribed to irrigation and fertilization, which enhances growth and increases organic matter return to the soil (Du Preez and Wiltshire, 1997). Irrigation and fertilization are also likely to increase mineralisation of SOM and thus the net effect on SOM is not consistent (Du Preez and Wiltshire, 1997).

The potential for increasing the concentration of soil C beyond those of virgin veld raises the possibility of using soils for C sequestration. The semi-arid climate that predominates over most of South Africa limits, however, the potential for sequestering C both in biomass and soils. Robles and Burke (1998) found that the cessation of cultivation in semi-arid soils of

Wyoming, under an annual rainfall of 420 mm, resulted in an extremely slow recovery of soil C. Short grass steppe was re-established on the old lands and, after 6 years, no change in total soil C was evident. A slight increase in labile C was detected, but in terms of total C sequestration, no statistically significant gain was evident. South African ecosystems are likely to have a similar rate of soil C recovery and thus meaningful C sequestration could only be expected after decades of restoration. The slow return of soil C in semi-arid environments may be one reason why no-till agriculture has not been found to increase C sequestration in South African soils (Van der Watt, 1987). This lack of evidence for C sequestration under no-till may, however, simply reflect a lack of research and insufficient sampling (Van der Watt, 1987). Innovation could potentially overcome obstacles to C sequestration in the semi-arid climate of South Africa. Garcia *et al.* (1998), for example, demonstrated that restoration of vegetation and soil C in semi-arid conditions was improved if terraces were built to prevent surface runoff and if manure was added to improve nutrient status. Recent findings suggest that planting the indigenous, succulent bush *Portulacaria afra* might be another way of improving C sequestration and soil quality, as surprisingly high organic C levels (>5%) have been reported in the top 10 cm of soil under *P. afra* in the semi-arid Eastern Cape (see Chapter 3). Irrigation of crops in semi-arid areas will also tend to increase soil C.

1.4.2 Ranching

Plants in semi-arid environments tend to serve as nutrient hotspots (Schlesinger *et al.*, 1990; Roos and Allsopp, 1997). The removal of vegetation by livestock results in a net depletion of nutrient/SOM reserves in the landscape (Allsopp, 1999). The processes by which SOM is lost when vegetation is removed have been discussed above. Du Preez and Snyman (1993) highlighted some of these processes and demonstrated the relationship between veld condition and SOM. Three veld conditions (poor, moderate and good) were established in an experiment in a *Themeda-Cymbopogon* grassland of the Free State, with basal cover decreasing linearly with veld condition. After 15 years, the poor and moderate veld had 25% and 16% less organic matter, respectively, than the good veld. This was ascribed to significantly lower biomass production and greater soil temperatures in the poor and moderate veld in comparison to the good veld. The reduced biomass production resulted in less organic matter return to the soil and the greater temperatures presumably increased the rate of decomposition through direct effects on the rate of microbial metabolism, as well as promotion of the Birch effect, due to an increased number of wetting and drying cycles.

Undoubtedly J.J. Theron would have invoked repression of mineralisation by plants in the good veld as the primary reason for maintenance of SOM (Theron, 1951; 1963), but this explanation is surprisingly absent from literature in the past few decades. Perhaps it should be revisited.

In another study on livestock effects on soils, Mworira *et al.* (1997) found that a high stocking rate in a Kenyan savanna resulted in reduced soil water content and greater bulk density in comparison to savannas with a low stocking rate. Similar results were obtained by Seidlheko *et al.* (1993) in semi-arid rangelands of Texas. Rangelands exposed to high, in comparison to low stock densities, had reduced aggregate stability, a reduced rate of infiltration (22 vs 41 mm hr⁻¹) and lower hydraulic conductivity (61 vs 139 mm hr⁻¹). If soil quality deteriorates to the extent that plant growth and germination are adversely affected, then a shift in ecosystem state may occur and veld recovery may become extremely difficult to achieve (Du Preez and Snyman, 1993). Preservation of vegetation cover would certainly seem to be a cardinal requirement for maintaining soil quality in rangelands.

1.4.3 Forestry

Planting trees such as *Pinus* and *Eucalyptus* spp. invariably alters many soil properties. Soils under plantations typically become more acidic (Morris, 1986; Du Toit, 1993; Nowicki, 1997; Sagggar *et al.*, 2001; Jaiyeobu, 1998; Clough, 1991), the effect usually being ascribed to uptake of basic cations into the forest biomass (Reuss and Johnson, 1986; Fey *et al.*, 1990). Pine needle litter contains acidic organic compounds that are released into the soil during decomposition (Scholes and Nowicki, 1998), although the contribution of this process to overall acidification is not clear and it may be a red herring.

Another common effect in many forest plantations in South Africa is an increase in available nitrate (Echeverría, 2000; Fey, 2001). The cause of greater soil nitrate concentration under pine plantations in comparison to natural grasslands is potentially complex. The size of the soil nitrate pool represents the net effect of various nitrate fluxes: inputs via mineralisation and precipitation, and outputs via denitrification, leaching and uptake by plants and microbes. Evapotranspiration by plantations tends to create a drier soil environment (Irving, 1941) which is likely to increase the rate of mineralisation in comparison to moister grassland soil. The wetter conditions under grasslands may also lead to more denitrification and leaching of

N. The combined effect would be to enlarge the nitrate pool under pines. If greater nitrate levels in pine plantations signify mineralisation of natural humus from the earlier grassland vegetation, then the implication is that soil quality is being degraded through humus destruction caused by the desiccating effect of the trees. This hypothesis needs to be explored. Alternative hypotheses are that the relatively low concentration of nitrate in the grassland soils may be a function of a low rate of nitrification (Echev rria, 2000), immobilisation of nitrate by soil microbes (Botha, 1963) or retardation of mineralisation by antibiotic exudates released from grass roots (Theron, 1951; 1963). Inhibition of nitrification has been documented in climax ecosystems of both North America and Europe (Rice and Pancholy, 1972), and soils in pine plantations on the Mpumalanga escarpment have a greater rate of net mineralisation than soils in adjacent grassland (personal communication, M.C. Scholes).

Such an increase in the rate of mineralisation under forest plantations is likely to be reflected in SOM values. SOM has been reported to decline under plantation forestry (Irving, 1939; Jones and Richards, 1977; Jaiyeobu, 1998). Irving (1939) found that soil N content was "considerably lower" in *Eucalyptus* plantations than adjacent highveld grasslands at Frankenwald. Jaiyeobu (1998), working in Nigerian savannas, found that SOM was reduced (from 2.5% to 1.5% in the top 15 cm of soil) in young pine plantations of 2-5 years. In older pine plantations, SOM content was, however, similar to that of adjacent virgin soils. In contrast, studies on the eastern escarpment have shown that plantation soils can have greater soil C than adjacent grasslands (Nowicki, 1997; Echev rria, 2000) although these studies probably did not make a sufficient distinction between partly decomposed surface litter and mineral soil horizons. Research directed at plantations of different ages (such as in the acidification study of Sugarman, 1998) may prove fruitful in terms of clarifying how plantations alter soil C cycling over time. The idea that natural humus becomes degraded after trees are planted, despite the overall augmentation of biomass, is an entertaining one.

1.4.4 Fire

1.4.4.1 Stimulation of microbial activity

SOM tends to decline in landscapes that are burnt regularly (Jones *et al.*, 1990; Seastedt *et al.*, 1994; Bird *et al.*, 2000; Parker *et al.*, 2001). There are several possible reasons for this

decline. Firstly, the removal of vegetation will tend to increase mineralisation of organic matter for reasons such as the Birch and “bellows” effect discussed earlier. Knapp *et al.* (1998) recorded a 20-55% increase in CO₂ flux after burning in tall grass prairie, with unburnt prairie averaging 10 μmolCO₂ m⁻² s⁻¹ and burnt prairie 15 μmolCO₂ m⁻² s⁻¹. At the same site, O’Lear *et al.* (1996) showed that the decomposition of wooden dowels was faster in burnt sites than unburnt sites. Greater soil temperature in burnt prairie was deemed the driving variable with respect to CO₂ flux in these studies. Secondly, soil microbes tend to respond favourably to the increase in soil pH from ash addition (Greenwood, 1968; Knapp *et al.*, 1998). This is probably a redox effect, with greater pH favouring oxidation. An increase in pH also tends to increase labile C concentration, which will generally favour microbial growth (Curtin *et al.*, 1998). Thirdly, SOM may actually combust. This is, however, an unlikely factor in savannas and grasslands where soil temperature during fires probably does not achieve the heights required (Giovannini *et al.*, 1990). Inputs of organic matter to the soil are reduced by burning because of the combustion of above-ground biomass and leaf litter.

1.4.4.2 Nutrient dynamics

Fire has a considerable effect on nutrient cycling but there is little agreement over the effect of fire on nutrient concentration (Raison, 1979). In the absence of fire, vegetation is either consumed by herbivores or returns over time to the soil surface and is decomposed by microbes. By contrast, fire deposits aboveground nutrients as ash onto the soil surface. Depending on soil texture and the post-fire climatic conditions, this flush of nutrients may or may not be reincorporated into the soil profile. Materechera *et al.* (1998) reported that annual burning for several decades at Fort Hare resulted in an increase in soil pH and basic cation concentration. On the other hand, Chapter 2 in this thesis shows that basic cations are often depleted under long-term annual burning regimes. Because nutrients may be lost in surface runoff (Gimeno-Garcia *et al.*, 2000), the tendency of the soil to crust and the intensity of rainfall after the fire are critical factors affecting the distribution of nutrients in the post-fire environment.

Most investigations into the effects of fire on soil nutrients report a post-fire flush of nutrients, including P, K, Ca and Mg (Ahlgren and Ahlgren, 1960; Tomkins *et al.*, 1991; Stromgaard, 1992; Blank and Zamudio, 1998). The loss of N to volatilisation can, however, be considerable. DeBano *et al.* (1979) showed that in chaparral soils, 50% of N in the top 20

mm of soil was volatilised when soil temperature reached 200°C at 10 mm. Even in low-intensity fire regimes, N losses may exceed N inputs via N fixing and atmospheric deposition. Cook (1994) reported that under annual burning in northern Australian savannas, annual N losses greatly exceed inputs and that N reserves are depleted over time. The proportion of N volatilised is dependent on fire intensity and in grassland and savanna fires, it is unlikely that 100% of N within the burning biomass will be volatilised (Debell and Ralston, 1970; Lewis, 1974). There is consequently often a short-term increase in N availability in the post-fire environment due to nitrate and ammonium ions present in ash (Viro, 1974; Choromanska and De Luca, 2001). Stock and Lewis (1986), for example, found that fire resulted in an input of 66 kg ha⁻¹ of N and a flush of ammonium in dry coastal fynbos on the West Coast of South Africa. The nitrate concentration in the soil profile was greater for 9 months after fire. These authors concluded that fire is an effective mineralising agent in the fynbos ecosystem.

1.4.4.3 The chemistry of crusting

Dyrness and Youngberg (1957) noted that fire may combust SOM thereby reducing aggregate stability and promoting the formation of a soil crust, the net result of which is a reduction in infiltration. Philips (1930) had earlier observed increased runoff in burnt areas of South African savannas and had called for further research into the effects of fire on the permeability of soils and surface runoff. His call appears to have been heeded and his findings corroborated, as increased runoff in burnt treatments in comparison to unburnt treatments were subsequently reported by Compton (1934), Thompson (1937), Cook (1939), Sim (1943), Scott (1955) and Bijker *et al.* (2001). By contrast, Edwards (1961) showed that unburnt treatments in the Tall Grassveld of Natal had greater runoff than burnt treatments, possibly due to a thatch effect. Burning season can also affect rate of runoff. Studies by Everson *et al.* (1989) showed that spring burning in the Highland Sourveld of the KwaZulu-Natal Drakensberg was likely to cause greater soil loss than winter burning. Lower soil loss under winter burning than spring burning was attributed to greater grass cover during spring rains.

With respect to soluble salts, Philips (1930) reported that fire adds "...appreciable amounts of K salts to the soil..." and that "...in silty and clay soils, the salts of K result in puddling and impair aeration and drainage". This reference to "puddling" is perhaps the first reference to fires inducing crusting in South Africa, although whether it was the effect of K specifically or

of ash alkalinity that promoted dispersion is debatable. The relationship between crusting, monovalent ions and electrical conductivity had not been established in 1930. Although Na is commonly cited as the primary dispersion-inducing ion, K can also increase dispersion as noted by McBride (1994). Philips (1930) was thus perceptive when invoking such chemical effects in interpreting the physical response of soil to burning. Subsequent research on highveld soils at Frankenwald showed that a decline in extractable cations in annually burnt plots was directly related to rainfall in the month following the burn. White and Grossman (1972) suggested that this decline in nutrient status was due to the removal of ash by surface runoff. They concluded that greater runoff on annual burn plots was due to the absence of surface litter and a reduced capacity of the soil to absorb and retain water. This work was corroborated by studies in the Kruger National Park presented in this thesis (see Chapter 2), where the infiltrability of soils was lower in burnt than unburnt plots (means of 19 and 35 mm hr⁻¹, respectively). This observation was ascribed to the preferential loss of Ca, Mg and K in ash and surface runoff, which results in reduced ionic strength of the soil solution and a greater ESP (17 versus 8%) in the 0-1 cm layer of burnt plots in comparison to unburnt plots. The net effect of these changes was a potentially intensifying effect of greater dispersion of clay and hence greater crusting on the burnt plots.

1.5 Conclusions

Soil quality has many facets. Despite evidence that there is considerable acidification and nutrient depletion in South African soils, perhaps the most challenging of facets is the capacity of the soil to absorb rainwater and, in the process, to erode less and to offer more water to the plant. At the risk of overstating the obvious, soil quality and soil structure (especially surface structure) are, in our rain-starved landscape, virtually synonymous. Structural stability depends on many things including electrolyte concentration, which is affected by burning and runoff. The quality of soil and vegetation are interdependent. When plants are removed, soil deterioration commences on many fronts. At the surface, soil aggregates are exposed to the force of raindrops, clay disperses, pores become blocked, and runoff, soil loss and soil aridity are intensified. The first few centimetres of undisturbed topsoil hold disproportionately more humus, nutrients and salts than the underlying layers. Consequently even a small loss of surface soil can initiate a decline in soil quality that becomes self-sustaining. It is this very thin layer of organic-rich surface soil, evident in uncultivated land, as well as minimally tilled cropland and pasture, on which future soil

quality research should concentrate. The conservation and replenishment of N is all important for retaining humus and maintaining soil quality. As J.J. Theron stated, half a century ago: "It is on this foundation that conservation farming must rest" (Theron, 1951).

CHAPTER 2
FREQUENT FIRES INTENSIFY SOIL CRUSTING:
PHYSICO-CHEMICAL FEEDBACK IN THE PEDODERM
OF LONG-TERM BURN EXPERIMENTS IN SOUTH AFRICA

2.1 Introduction

Grasslands and savannas in South Africa burn frequently and consequently fire is often utilised for manipulating the condition of the veld. The response of vegetation to fire depends on the intensity of the burn and extent of physical damage, but may also depend on how soil properties have been altered. Frequent burning of veld, for example, can reduce the rate of infiltration of rainwater into soil (Philips, 1930; Daubenmire, 1968; Schacht *et al.*, 1996; Bijker *et al.*, 2001). Under semi-arid conditions, an increase in runoff is likely to affect the recruitment and resprouting of plants after fire. Several explanations might be suggested for a decline in infiltration after fire. Firstly, soil organic matter, which usually increases soil aggregation and consequently the rate of infiltration (Dyrness and Youngberg, 1957; Pikul and Zuzil, 1994; Sumner, 1998), tends to decline in veld that is burnt frequently (Bird *et al.*, 2000). Secondly, ash particles may block pores at the soil surface (Mallik *et al.*, 1984). Thirdly, the removal of vegetation increases the exposure of soil to raindrop impact, which will increase breakdown of aggregates, dispersion of clay and thus soil crusting (Hillel, 1998). It is not known, however, whether frequent burning affects dispersion of clay and hence crusting of soils. The objective of this study was to determine whether veld burning changes soil chemistry in a manner that increases the tendency of the soil to crust and promote runoff. Soils were sampled from long-term burning experiments in Mpumalanga, KwaZulu-Natal and the Eastern Cape, South Africa and the effects of annual burning and fire exclusion on soil chemistry, clay dispersion and the rate of infiltration were investigated.

2.2 Materials and methods

2.2.1 Study areas

Fire exclusion and annual burn treatments were investigated at nineteen sites across South Africa. Fifteen of the sites were situated in the Kruger National Park, Mpumalanga (four at

Numbi; four at Napi; four at Satara; and three at Mopane); three at Ukulinga Research Station, Kwa-Zulu Natal; and one at Fort Hare, Eastern Cape (Figure 2.1).



Figure 2.1 The location of the study areas (i.e. long-term burn experiment sites) in South Africa.

2.2.1.1 Kruger National Park

The long-term burn plots in the Kruger National Park are situated in Mixed Lowveld Bushveld (Low and Rebelo, 1996) and range in elevation from 300 to 700 m above sea level (23°-25°S; 31°-32°E). The vegetation types can be further divided as follows: Pretoriuskop Sourveld at Numbi (predominantly *Terminalia sericea*); Mixed Bushwillow Woodlands at Napi (predominantly *Combretum apiculatum* and *Acacia nigrescens*); Knob Thorn/Marula Savanna at Satara (predominantly *Acacia nigrescens* and *Sclerocarya birrea*); and Mopane Shrubland at Mopane (predominantly *Colophospermum mopane*) (Venter, 1990). The climate is strongly seasonal with a mean annual temperature range of 21.1-23.3°C (mean monthly temperature 16-28°C). Rains fall predominantly in summer and mean annual rainfall varies from 687 mm at Numbi in the southwest to 404 mm at Letaba in the central region of the park. Soils in the southern burn plots are derived from Nelspruit granite and soil forms

include Hutton, Bainsvlei, Clovelly, Cartref and Avalon (Soil Classification Working Group, 1991). In the terminology of the World Reference Base classification system these soils include Rhodic Lixisols, Paraplinthic Cambisols, Dystric Regosols and Paraplinthic Lixisols (FAO, 1998). Soils in the burn plots in the central region of the park are derived from basalt and soil forms include Shortlands, Swartlands, Mayo and Milkwood. In the terminology of the World Reference Base classification system these soils include Rhodic Nitisols, Haplic Luvisols and Leptic Phaeozems. The long-term burn experiment began in 1955 and comprises seven-hectare plots with different frequencies and seasons of burns (Van Wyk, 1971). Soils were sampled from unburnt plots and plots burnt annually in August. These treatments were located within a string of 13 different treatments and were not further than 3 km apart.

2.2.1.2 Ukulinga Research Station

The research station is situated within the Southern Tall Grassveld (Tainton and Mentis, 1983) at an elevation of ~840 m a.s.l. (29°40`S; 30°20`E). The climate is strongly seasonal with a mean annual temperature of 17.6°C (mean monthly temperature of 13.2-21.4°C). The annual rainfall is 710 mm falling predominantly in summer (Tainton, 1981). The parent material of the soils on site is mainly Ecca Group shale of the Pietermaritzburg formation, with some influence of dolerite through colluvial action in the northern plots. The experimental plots run south to north, with soil depths varying from <15 cm in the southern plots to over 60 cm in the northern plots. The shallower soils are mainly of the Mispah form and the deeper soils are of the Swartland and Westleigh forms. In the terminology of the World Reference Base classification system these soils include Dystric Leptosols, Chromic Luvisols and Haplic Plinthisols, respectively. Long-term burning trials have been in operation for 47 years, in an effort to determine the effect of fire frequency, fire season and mowing on the grassland ecosystem (Tainton and Mentis, 1983). Forty four different treatments were established in triplicate in plots measuring 13.7 m by 18.4 m. Unburnt plots, plots burnt annually in August, and plots burnt annually in August as well as mowed annually in late summer, were sampled. For purposes of comparison with the Kruger National Park sites, results from unburnt plots and annually burnt plots (i.e. unmown plots) are presented.

2.2.1.3 *Fort Hare*

The University of Fort Hare experimental plots are situated outside the town of Alice in the Eastern Thorn Bushveld (Low and Rebelo, 1996) in the Eastern Cape (32°50'S; 26°50'E). The site is ~700 m a.s.l. and the mean annual rainfall is ~500 mm, falling predominantly in summer. The soils of the region are derived from Beaufort Group mudstones/sandstones of the Adelaide subgroup. Karoo dolerite intrusions into the sedimentary rocks also occur and will affect soil properties at these specific localities. The predominant soil form on the experimental plots is a Glenrosa (Dystric Regosol in the World Reference Base classification). Long-term burning/grazing trials have been in operation for 28 years. The following three treatments have been implemented, without replication: (i) a treatment of 0.6 ha grazed heavily with cattle at the end of the growing season after the first frost i.e. post 20th May; (ii) a goat treatment of 1 ha grazed heavily with cattle at the end of the growing season after the first frost (i.e. post 20th May) plus continuous stocking of goats at ± 1 mature goat per ha; and (iii) an annual burn treatment of 0.6 ha which is burnt at the end of winter before the first spring rains (July/August). All 3 treatments were sampled, but for purposes of comparison with the Kruger National Park sites, only treatments (ii) and (iii) are presented in the results.

2.2.2 *Sampling*

Composite topsoil samples were taken from burnt and unburnt plots at all sites to a depth of 10 cm using a soil auger. Each composite sample comprised 15 to 20 subsamples taken randomly from each plot. In the Kruger National Park burn plots, subsamples were taken at ~20 m intervals across the middle of each plot. Soil type varied across plots, but for the purposes of this study it was assumed that changes in soil chemistry due to annual burning would be reflected in composite topsoil samples. In addition, composite samples to a depth of 2 cm were taken from all plots at Numbi and Napi for comparing the methods of laboratory and rainfall simulation infiltration. These samples were taken randomly across each plot with a spade and each composite comprised approximately 20 subsamples. Three soil pits were dug on each plot at the four sites at Numbi and four sites at Napi. Samples were taken from these profiles at 1 cm intervals to a depth of 10 cm; at 5 cm intervals to 20 cm; and a subsoil sample at approximately 40 cm.

2.2.3 Laboratory methods

Soils were air-dried and sieved to <2 mm. The following analyses were undertaken on composite samples taken to a depth of 10 cm: electrical conductivity (EC) and pH in 1:5 soil extracts (Rhoades, 1982); pH in KCl and water (1:2.5); water-soluble (1:5) cations (Rhoades, 1982) and ammonium acetate-extractable cations (the centrifuge procedure described by Thomas, 1982) using atomic absorption spectrometry; water-soluble (1:5) anions by ion chromatography; extractable P using a Bray-2 extract as described by Bray and Kurtz (1945); total C and N by complete combustion using a Eurovector Euro EA Elemental Analyzer; and labile C (or readily oxidisable C) with a modified Walkley-Black method using (i) 5 ml and (ii) 10 ml of dilute sulphuric acid, instead of 20 ml, as described by Chan *et al.* (2001).

pH in KCl and water were determined by mixing 10 g of air dry soil with 25 ml of 1M KCl and distilled water, respectively. pH of saturated pastes were determined on Kruger National Park samples. Distilled water was added to approximately 200 g of soil, until the mixture showed the characteristics of a saturated paste. pH readings were taken after 1 hour.

Soil respiration or “readily mineralisable C” was measured on composite samples to 2 cm, by incubating soil samples in a growth chamber and measuring the CO₂ flux using a Licor LI-6400 Portable Photosynthesis System and 6400-09 Soil CO₂ flux chamber in a similar manner to Gewin *et al.* (1999). Ten millilitres of distilled water were added to 50 g of air-dry, <2 mm soil in a porcelain crucible; the soil was then incubated for 1 hour at 35°C in a growth chamber, and the CO₂ flux measured immediately after removal from the growth chamber. Each CO₂ flux measurement took ~3 minutes. During the development of this method, it was found that incubations of 4-5 hours gave similar results to incubations of 1 hour. The shorter time period of 1 hour was selected to enable more rapid processing of samples. Samples were removed from the growth chamber in order to measure CO₂ flux because the Licor equipment did not fit in the growth chamber. It was assumed that the effect of cooling (by transferring samples from the growth chamber environment of 35°C to room temperature of ~20°C) on CO₂ flux was uniform for all samples.

Clay content was determined by the hydrometer method, sand content by sieving and silt by difference. The clay fraction was dispersed using a Calgon dispersing solution of sodium hexametaphosphate and sodium carbonate. Organic matter was removed by oxidation with

hydrogen peroxide (Soil Classification Working Group, 1991). Electrical conductivity and pH in 1:5 extracts were measured on all samples collected at 1 cm depth intervals. Water-soluble ions, (NH₄)OAc-extractable cations, total C and total N were measured on samples collected from profiles at three Numbi sites and one Napi site at depths of 1, 2, 4, 7, 12.5 and 17.5 cm. Due to cost constraints, not all samples and profiles could be analysed. These particular analyses were performed to investigate possible mechanisms behind infiltration differences between burnt and unburnt plots. Profiles that were likely to yield the greatest differences between treatments were consequently selected. Two profiles at each burnt and unburnt plot were selected for water soluble ions and (NH₄)OAc-extractable cations analysis. One profile at each burnt and unburnt plot was selected for total C and N analysis. Selection was based on EC measurements. Profiles were ranked according to their mean EC. Profiles with a high mean EC were selected from unburnt plots and profiles with a low mean EC were selected from burnt plots.

The exchangeable sodium percentage (ESP) was calculated from (NH₄)OAc-extractable cation concentrations as follows: $ESP = [Na^+]/([Ca^{2+}] + [Mg^{2+}])$. The sodium adsorption ratio (SAR) of 1:5 extracts was calculated using solution concentrations expressed in units of millimoles of charge per liter according to the following equation (McBride, 1994):

$$SAR = \frac{[Na^+]}{\sqrt{\frac{1}{2}([Ca^{2+}] + [Mg^{2+}])}}$$

Infiltration through simulated crusts (i.e. laboratory infiltration) was determined as follows: a 16 g sample of air-dry, <2 mm soil was agitated vigorously with 80 ml distilled water in a 120 ml cylinder on a reciprocal shaker at 150 cycles per minute for 5 minutes. Three 5 g samples of the same soil were packed as tightly as possible into three separate 10 ml disposable plastic syringes by subjecting them to maximum hand pressure beneath a sawn-off syringe plunger. A 1 mm layer of cotton wool was placed at the base of the syringes before adding the dry soil. The base of the syringes were then placed in 1 cm of distilled water to allow water to move up into the syringe and saturate the soil. The agitated soil suspension was left to settle for 5

minutes after which a 30 ml aliquot was carefully taken from the settled suspension using a pipette immersed to a depth of 15 cm to prevent disturbance of the settled sediment. The 30 ml aliquot was divided into three 10 ml aliquots by pipetting it into three 20 ml bottles. Each 10 ml aliquot was then pipetted gently into one of the prepared syringes up to the 10 ml mark, at the same time blocking the base of the syringe by finger pressure to prevent premature drainage. The syringes were then placed in a rack above a beaker on a digital balance and the bases of the syringes were released to allow drainage into the beaker. The rate of water release from the syringes was recorded as the mass increase of the receiving beakers over time.

Rainfall simulation work was conducted as follows: air dry, <2 mm soil samples were packed 2 cm deep, over a 4 cm layer of coarse sand in 30 by 50 cm perforated trays. The trays were then placed in a rainfall simulator at a slope of 5° (Morin *et al.*, 1967). The soil samples were saturated through the bottom of the trays and then subjected to a rain intensity of 45 mm hr⁻¹ for 60 minutes. The volume of water percolating through the tray was determined, from which infiltration rate could be then be calculated. Two replicates were performed on each sample.

Water dispersible clay was determined following a method similar to that of Miller and Baharuddin (1986). An 8 g soil sample was agitated vigorously with 40 ml distilled water in a 50 ml centrifuge tube on a reciprocal shaker at 150 cycles per minute for 5 minutes. The tubes were then placed vertically on a laboratory bench and a 2 ml sample was pipetted from a depth of 2 cm after 2 hours. The dispersed clay content was determined gravimetrically after drying at 110 °C. Modulus of rupture was determined as described by Richards (1953).

2.2.4 Statistical methods

Unistat 5.0 was used for performing paired t-tests between burnt and unburnt plots as well as correlations between selected soil properties. Pearson correlation coefficients were used because linear patterns were observed in many of the xy scatter plots and outliers were not evident. Data in the correlation analyses were assumed to have a bivariate normal distribution. To standardise the data across all study sites, paired t-tests were performed on the percentage difference between burnt and unburnt plots i.e. unburnt plots had a value of 100 and burnt plot values were calculated accordingly.

2.3 Results

A comparison of soils from burnt and unburnt plots (Figures 2.2-2.5) shows that composite samples taken to a depth of 10 cm from burnt plots had significantly lower (paired t-test on percentage differences, $p < 0.05$, $n = 19$) laboratory infiltration rate (with a mean decrease of 19%), EC of 1:5 extracts (13%), water-soluble K (14%), water-soluble NH_4 (39%), total C (13%), total N (16%) and labile C (16%). Burnt plots had significantly higher pH in KCl, water dispersible clay (37%) and modulus of rupture (55%, $n = 4$). Soil respiration in samples taken to a depth of 2 cm was lower in burnt plots at all of the eight sites analysed (means of 21 vs 36 $\text{ng C g}^{-1} \text{ s}^{-1}$, $p < 0.01$).

Results from samples at 1 cm intervals revealed that the greatest differences between burnt and unburnt plots were in the 0-1 cm layer (Figures 2.6-2.13). Soils from 0-1 cm in burnt plots had significantly lower (paired t-test, $p < 0.05$, $n = 4$) total C (means of 0.8 vs 2.7% for burnt and unburnt plots, respectively) (Figure 2.6), total N (0.07 vs 0.23%) (Figure 2.6), $(\text{NH}_4)\text{OAc}$ -extractable Ca (7 vs 17 $\text{mmol}_c \text{ kg}^{-1}$) (Figure 2.9), Mg (2 vs 7 $\text{mmol}_c \text{ kg}^{-1}$) (Figure 2.10), K (0.8 vs 1.5 $\text{mmol}_c \text{ kg}^{-1}$) (Figure 2.12), significantly greater exchangeable sodium percentage (17 vs 8%) (Figure 2.13) and similar $(\text{NH}_4)\text{OAc}$ -extractable Na (Figure 2.11).

Rainfall simulation on composite samples taken to a depth of 2 cm demonstrated that burnt plots crusted more rapidly than unburnt plots (means of 19 vs 35 mm hr^{-1}) (Figures 2.14 & 2.15). These results were corroborated by the laboratory infiltration results (Figures 2.14 & 2.15). An increase in crusting over time (i.e. a reduced rate of infiltration) is evident in soils from burnt plots for both rainfall simulation and laboratory infiltration. A crusting response during laboratory infiltration is evident in soils from all unburnt plots, but is not evident for four of the unburnt plot soils during rainfall simulation over 60 minutes. The rate of laboratory infiltration over the whole ten minutes was correlated with water dispersible clay, and with the rate of infiltration under rainfall simulation over 60 minutes (Figure 2.16).

Rates of laboratory infiltration were several times greater than simulated rainfall infiltration and a linear regression line for Figure 2.16a does not go through the origin, indicating that for zero infiltration under simulated rainfall, there is still a measurable laboratory infiltration rate ($\sim 50 \text{ mm hr}^{-1}$). A possible explanation for this difference is in the laboratory infiltration

method, water moves preferentially down the sides of the syringe tubes where channels of pores may be larger and more continuous i.e. the plastic and soil interface. Despite a possible “leak” where soil aggregates are not flush with the plastic surface, the strong correlation between laboratory and simulated rainfall infiltration indicates that this laboratory method is a useful way of ranking soils in terms of their tendency to form a crust of seal which impedes infiltration. The postulated preferential flow down the sides of the syringe suggests that rates of infiltration in the field are likely to be less than the rates recorded with the laboratory method. Field infiltration can, however, be extremely variable due to the presence of channels made by earthworms, moles or other soil dwellers.

Statistical analyses, including paired t-tests between soil properties from burnt and unburnt plots, and Pearson correlation coefficients between selected soil properties are presented in Table 2.1.

2.4 Discussion

2.4.1 Soil crusting and long-term burning

The results indicate that for the majority of soils sampled from long-term burn experiments in South Africa, frequent burning changes soil chemistry in a manner that increases the tendency of the soil to crust. Soils crust or seal when dispersed clay moves into and blocks pores in the soil surface (McIntyre, 1958b). The tendency of a soil to crust is thus to a large extent related to the dispersibility of the clay fraction. It is suggested here that changes in soil chemistry brought about by frequent burning may act on crusting by affecting the dispersibility of clay. Rates of infiltration in the laboratory and under rainfall simulation were strongly correlated and were lower in soils from burnt plots than unburnt plots (Figures 2.5, 2.14, 2.15 & 2.16). The rates of laboratory and rainfall simulation infiltration were also positively correlated with water dispersible clay (Figure 2.16). These correlations validate the use of laboratory infiltration as a suitable method for assessing the tendency of soils to crust.

Greater crusting on burnt plots than unburnt plots is ascribed to three main changes in the chemistry of soils brought about by frequent burning that were likely to increase the dispersion of clay. Firstly, the electrical conductivity (EC) of 1:5 extracts was lower in burnt than in unburnt plots (Figures 2.3 & 2.7). Secondly, the exchangeable sodium percentage

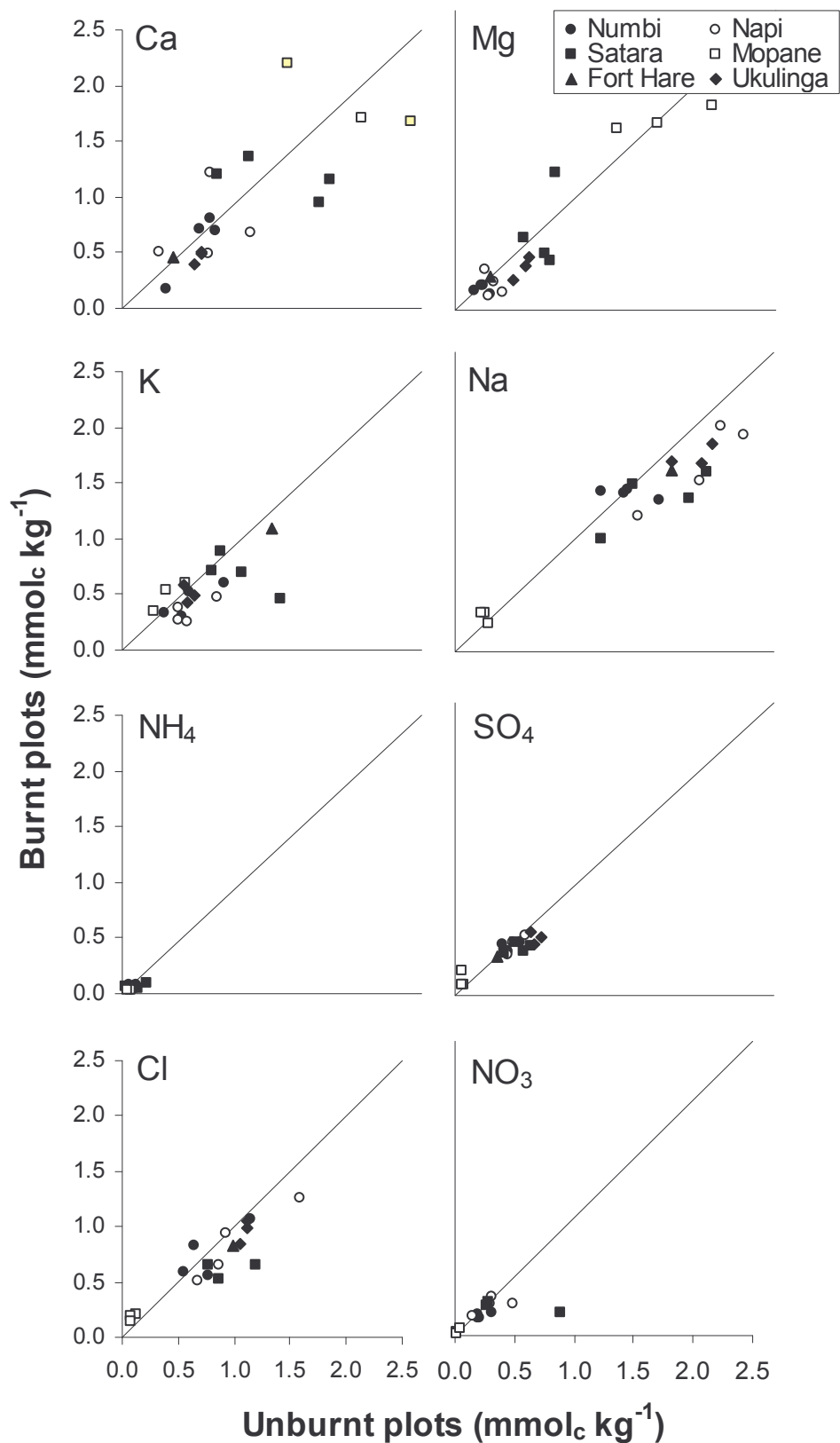


Figure 2.2 The relationship between burnt plots and unburnt plots with respect to water-soluble ions (1:5) Ca, Mg, Na, K, NH₄, SO₄, Cl and NO₃ in composite soil samples taken to a depth of 10 cm.

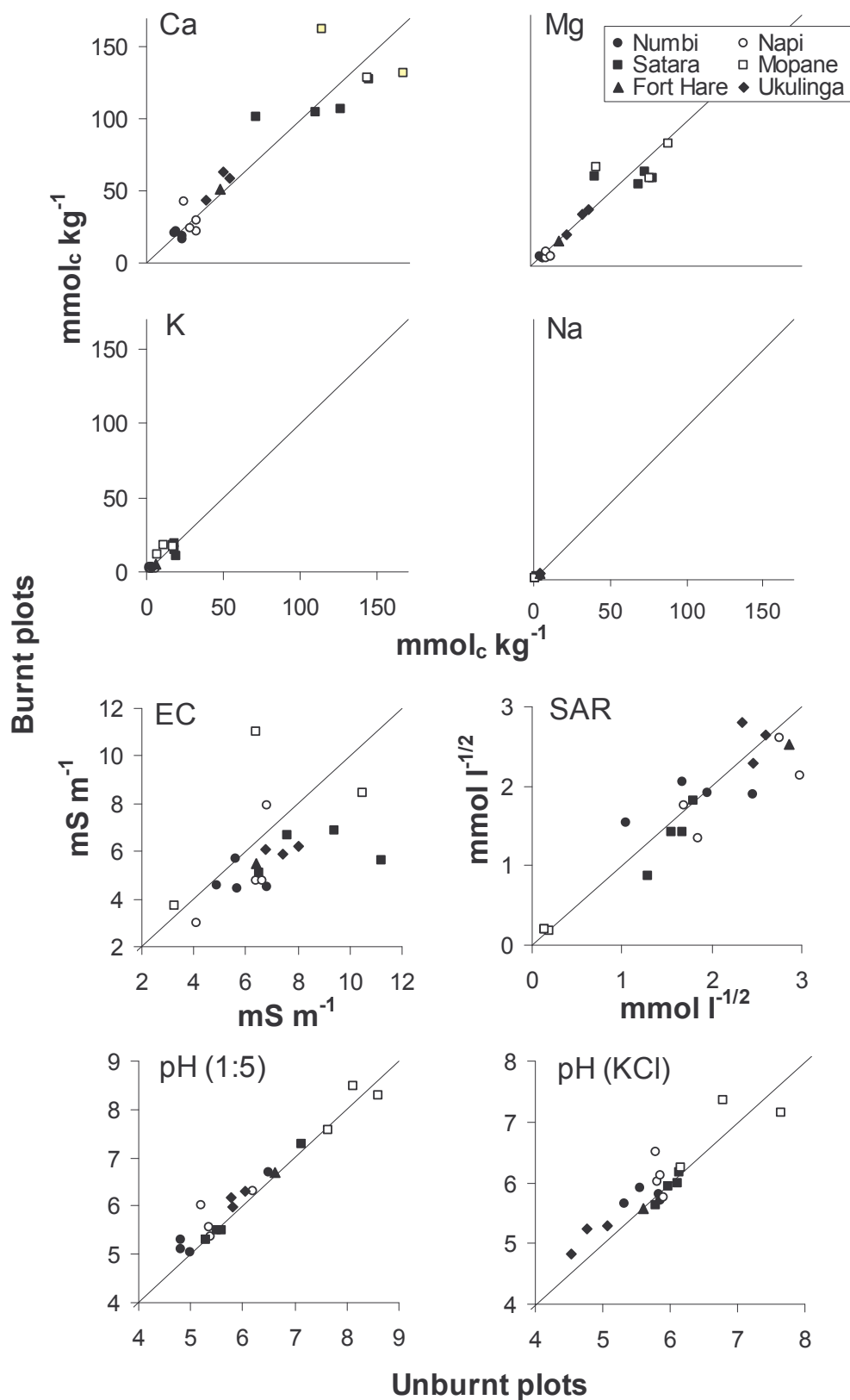


Figure 2.3 The relationship between burnt plots and unburnt plots with respect to (a) $(\text{NH}_4)\text{OAc}$ -extractable cations Ca, Mg, Na, K; (b) electrical conductivity, sodium adsorption ratio and pH in a 1:5 soil-water extract; and (c) pH in KCl in composite soil samples taken to a depth of 10 cm.

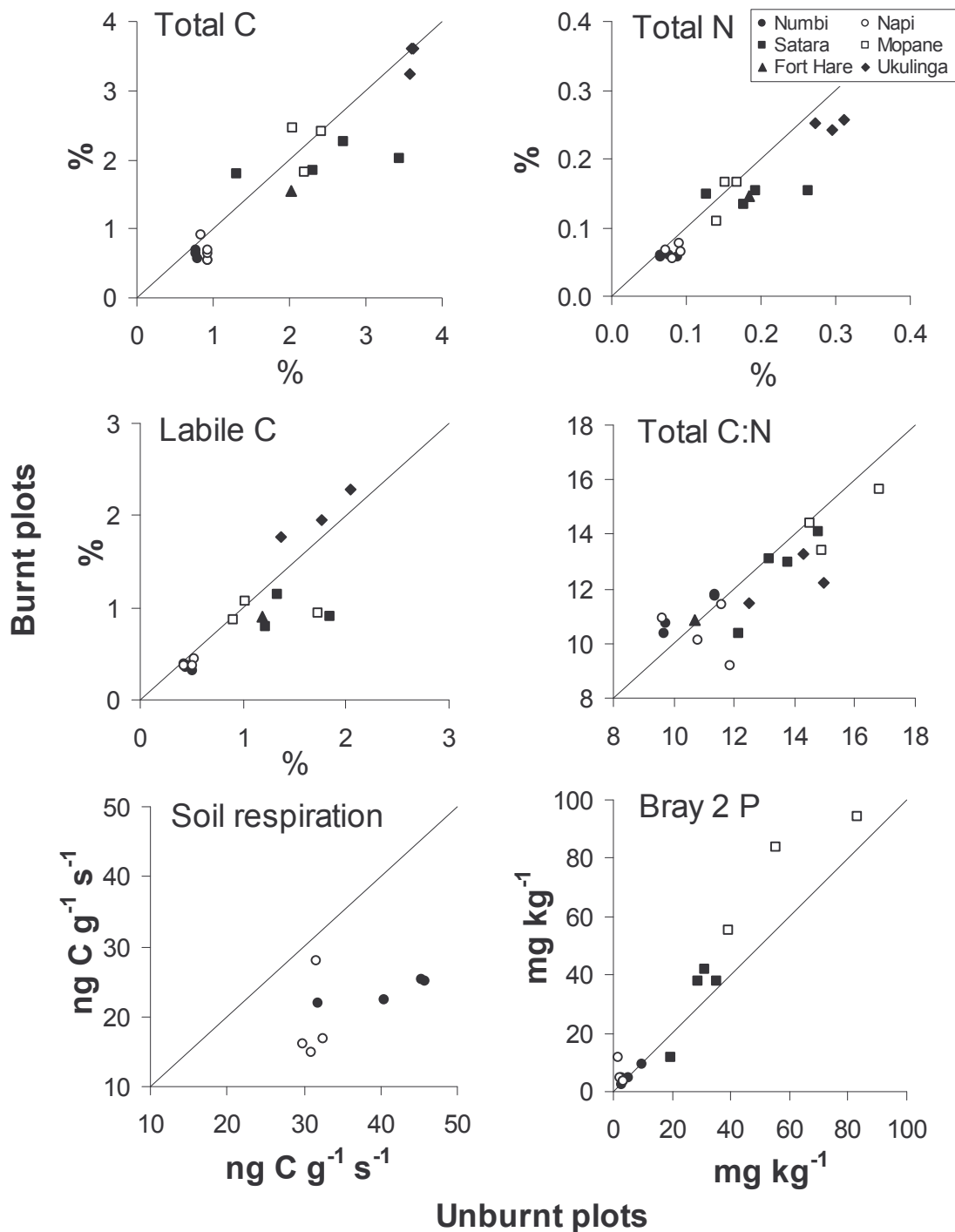


Figure 2.4 The relationship between burnt plots and unburnt plots with respect to total C, total N, labile C, rate of soil respiration, C:N and Bray 2-extractable P. Results depicted are from composite soil samples taken to a depth of 10 cm, except for soil respiration which was determined from samples taken to a depth of 2 cm.

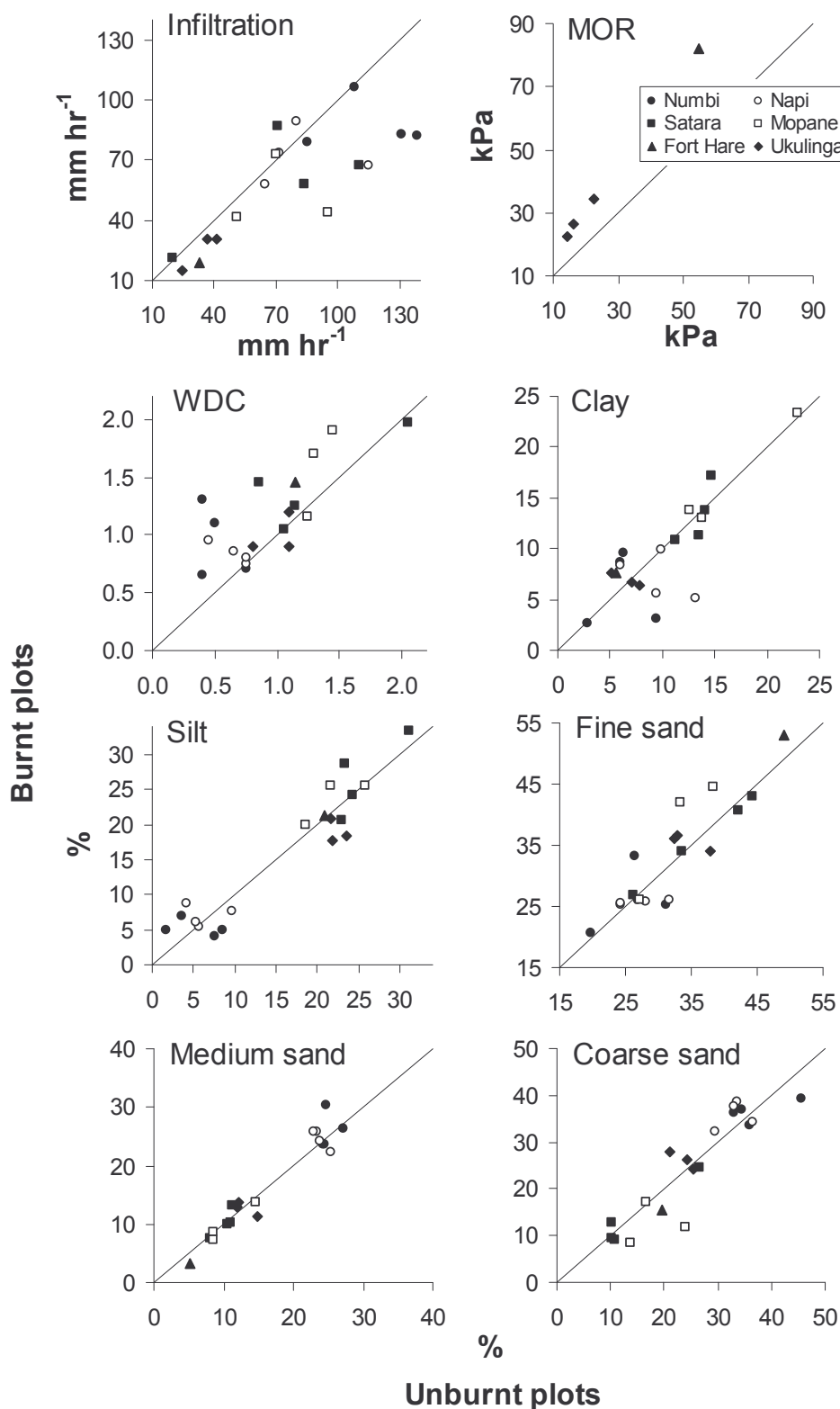


Figure 2.5 The relationship between burnt plots and unburnt plots with respect to rate of laboratory infiltration, modulus of rupture, water dispersible clay, clay, silt, fine sand, medium sand and coarse sand. Results depicted are from composite soil samples taken to a depth of 10 cm, except for water dispersible clay which was determined from samples taken to a depth of 2 cm for Numbi and Napi plots (circles) and to a depth of 10 cm for all other plots.

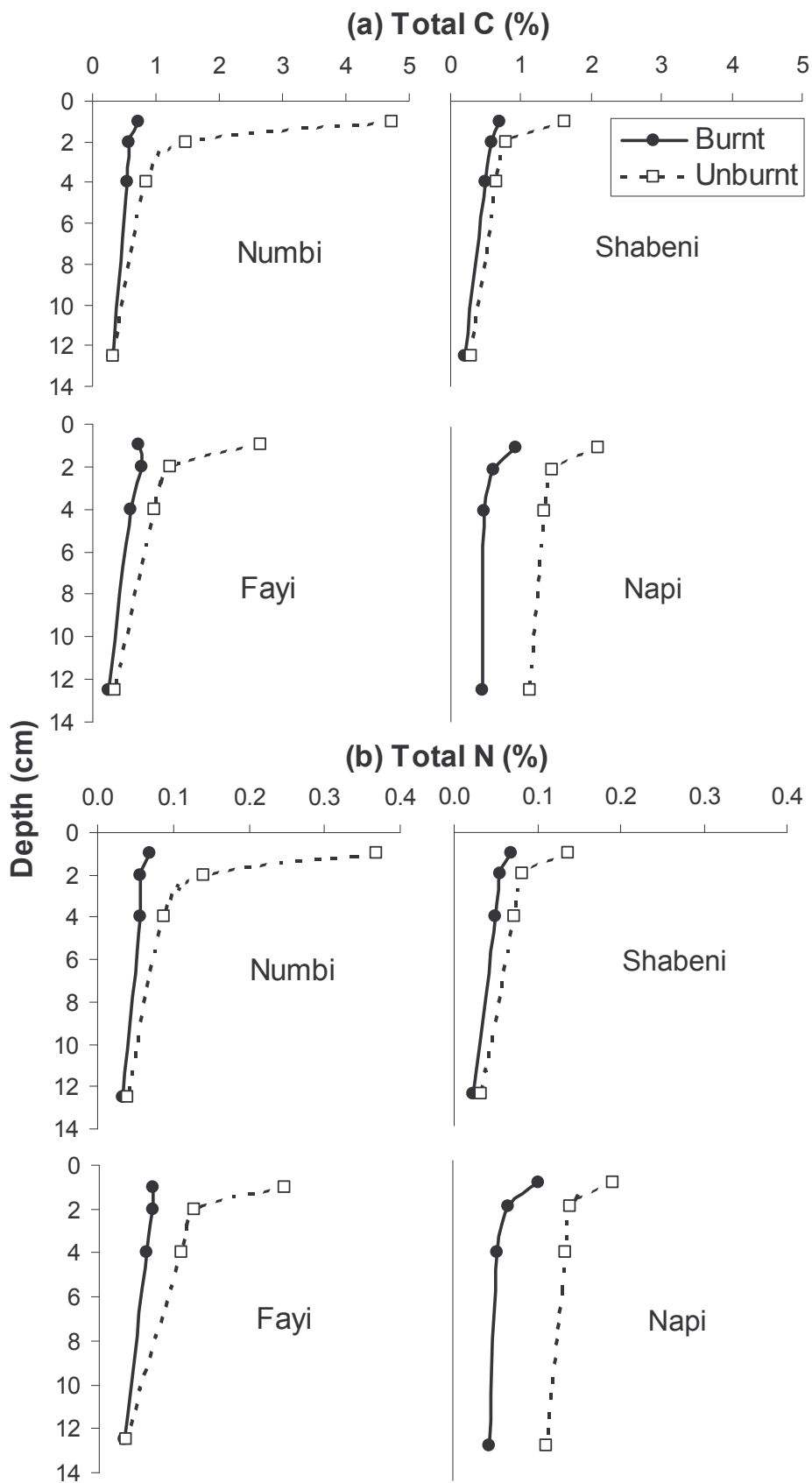


Figure 2.6 Total carbon (a) and total nitrogen (b) as a function of soil depth and burning treatment at Numbi, Shabeni, Fayi and Napi burnt and unburnt plots in the southern Kruger National Park.

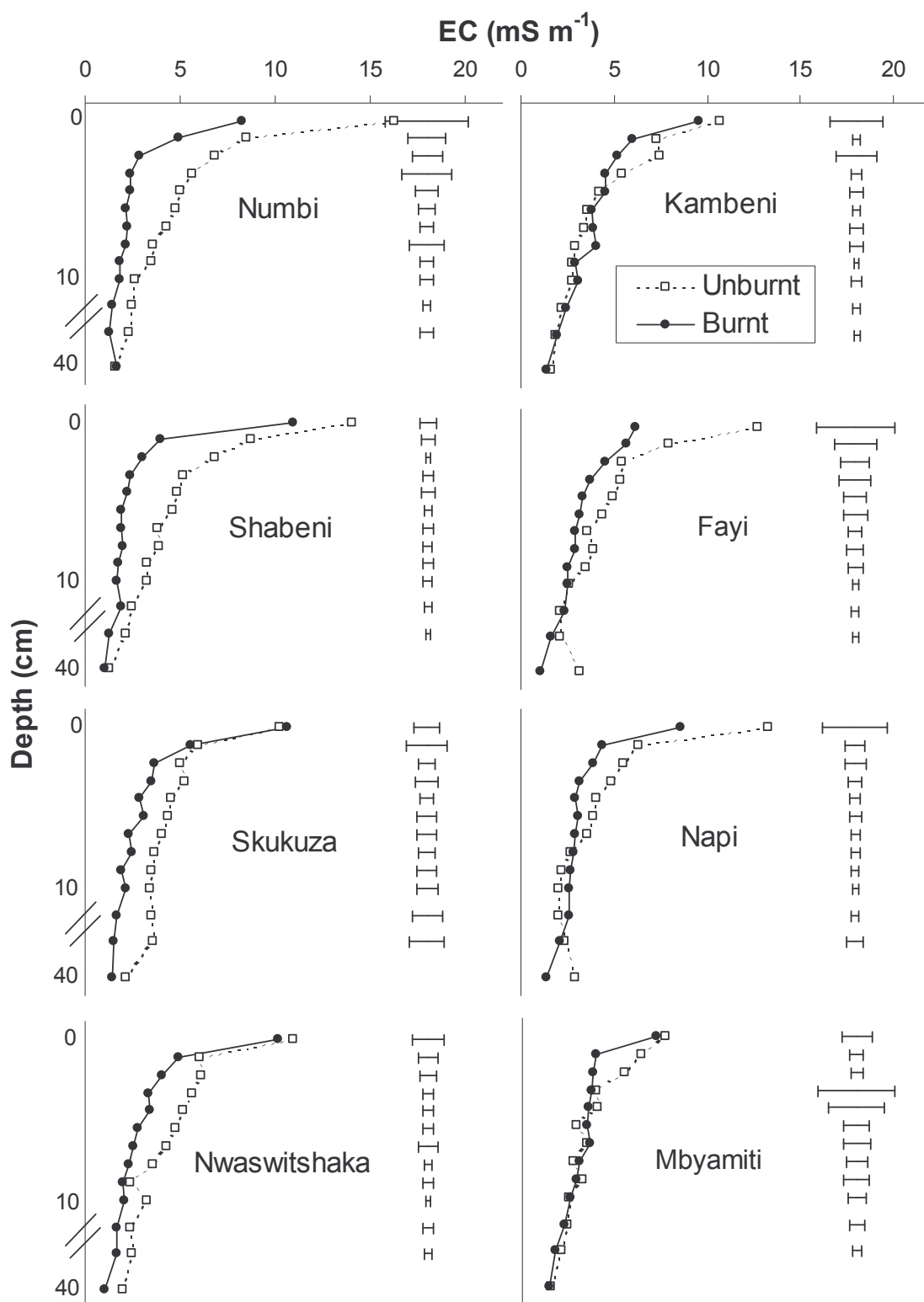


Figure 2.7 The electrical conductivity (1:5) in the profiles of burnt and unburnt plots in the southern Kruger National Park in 1 cm increments to 10 cm, 5 cm increments to 20 cm and a 10 cm increment to 40 cm. Error bars are the standard error of the difference between the two means.

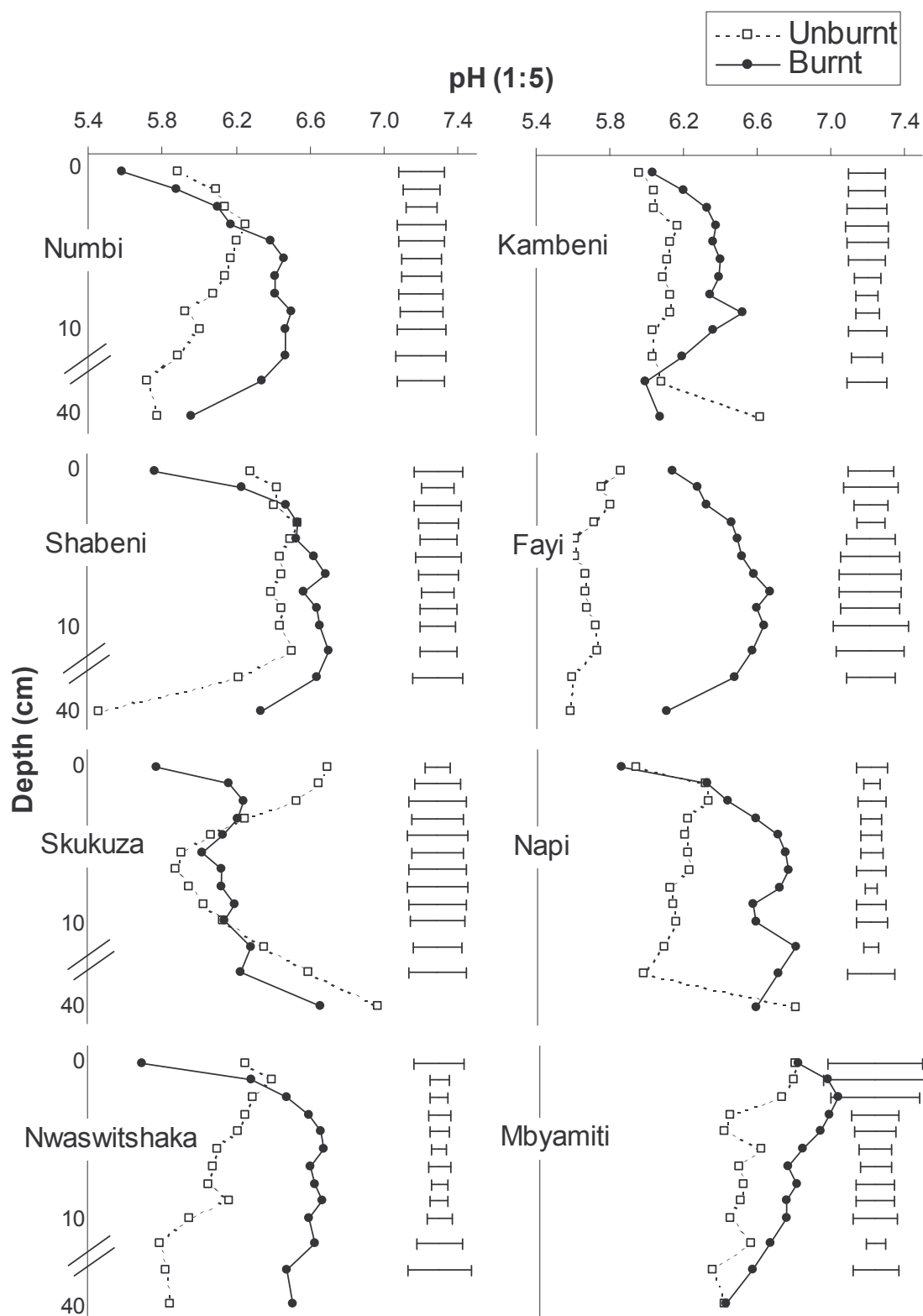


Figure 2.8 pH (1:5) in the profiles of burnt and unburnt plots in the southern Kruger National Park in 1 cm increments to 10 cm, 5 cm increments to 20 cm and a 10 cm increment to 40 cm. Error bars are the standard error of the difference between the two means.

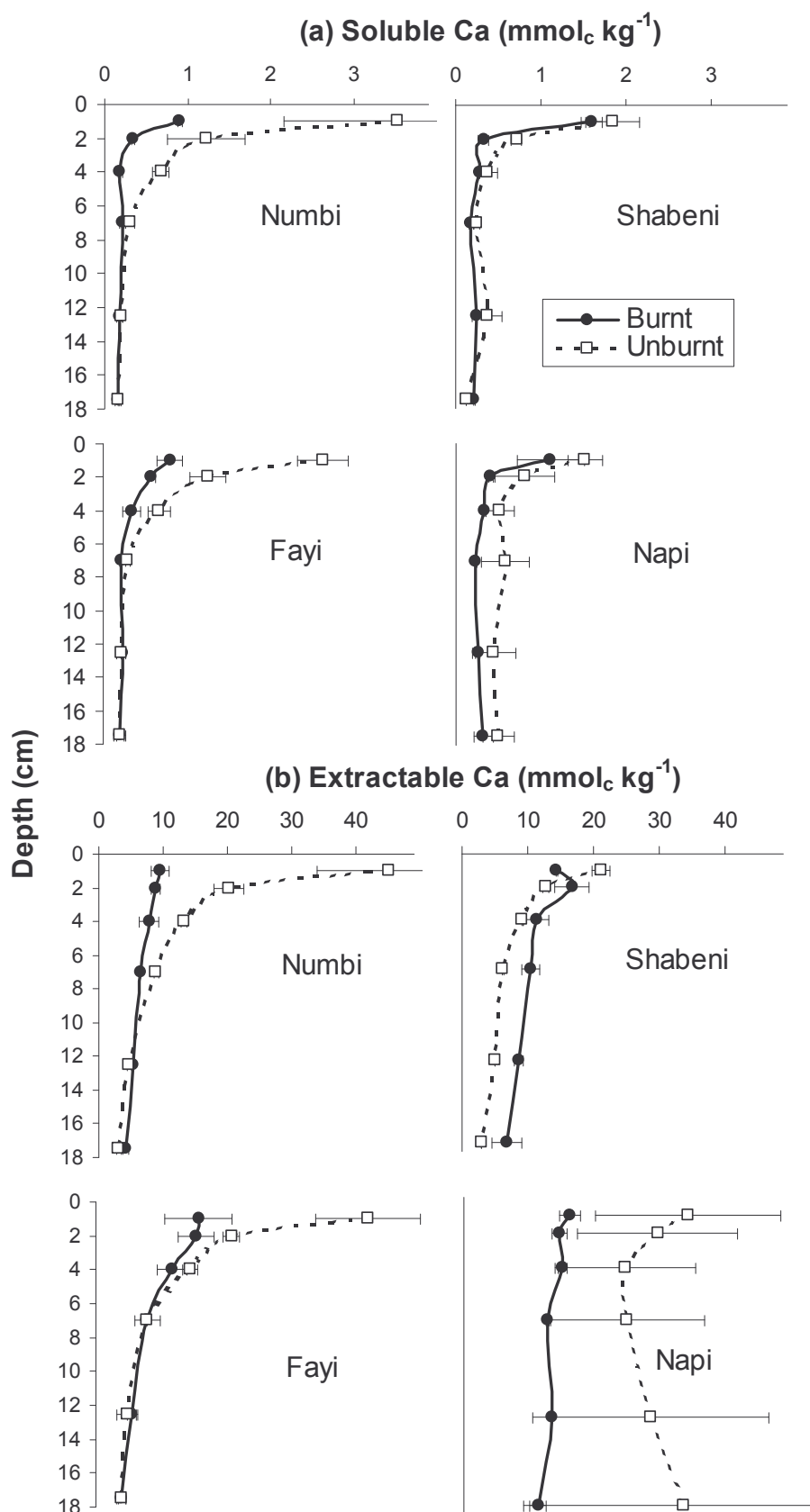


Figure 2.9 The distribution of water-soluble (a) and $(\text{NH}_4)\text{OAc}$ -extractable Ca (b) down profiles in burnt and unburnt plots in the southern Kruger National Park. Error bars depict minimum and maximum values.

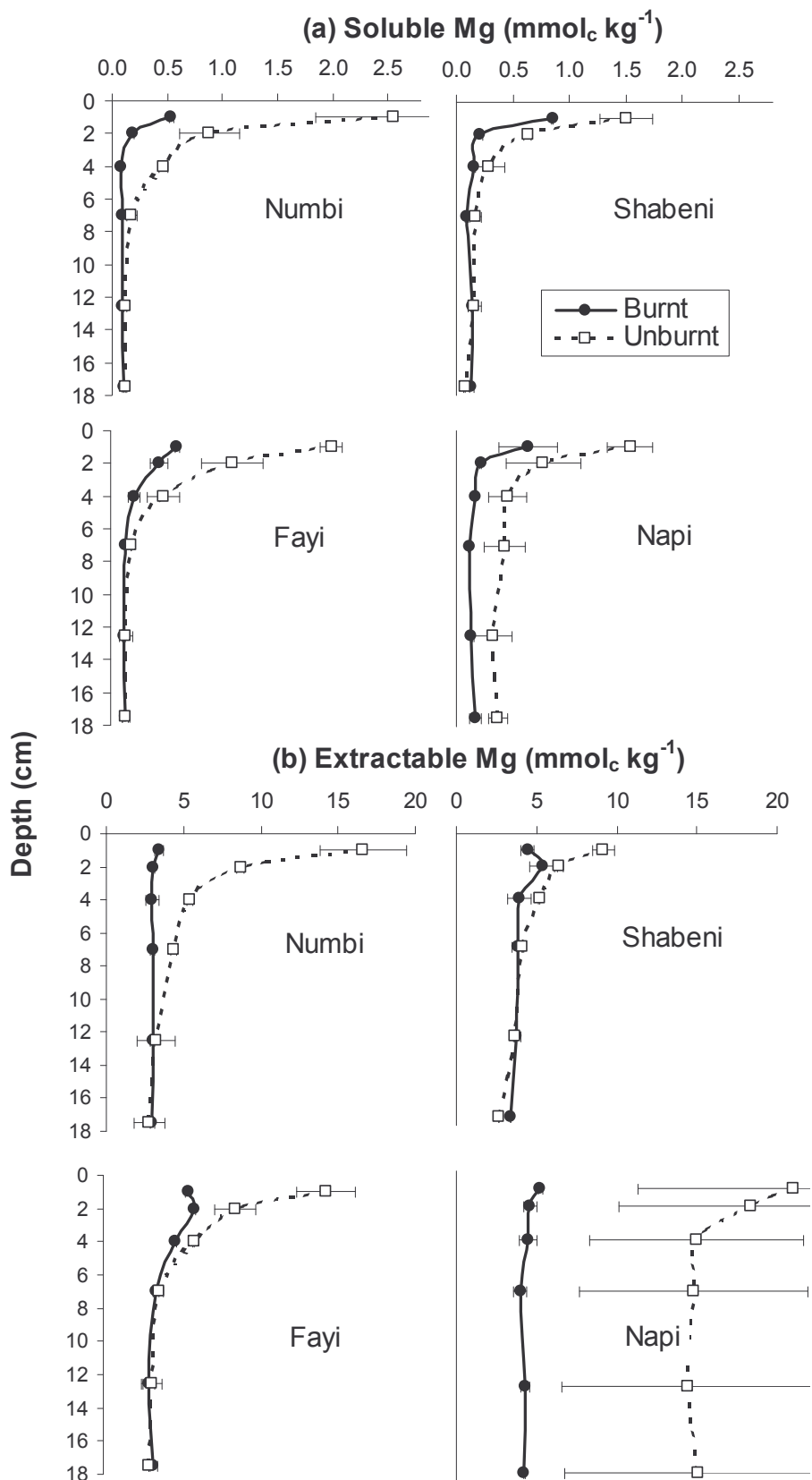


Figure 2.10 The distribution of water-soluble (a) and $(\text{NH}_4)\text{OAc}$ -extractable Mg (b) down profiles in burnt and unburnt plots in the southern Kruger National Park. Error bars depict minimum and maximum values.

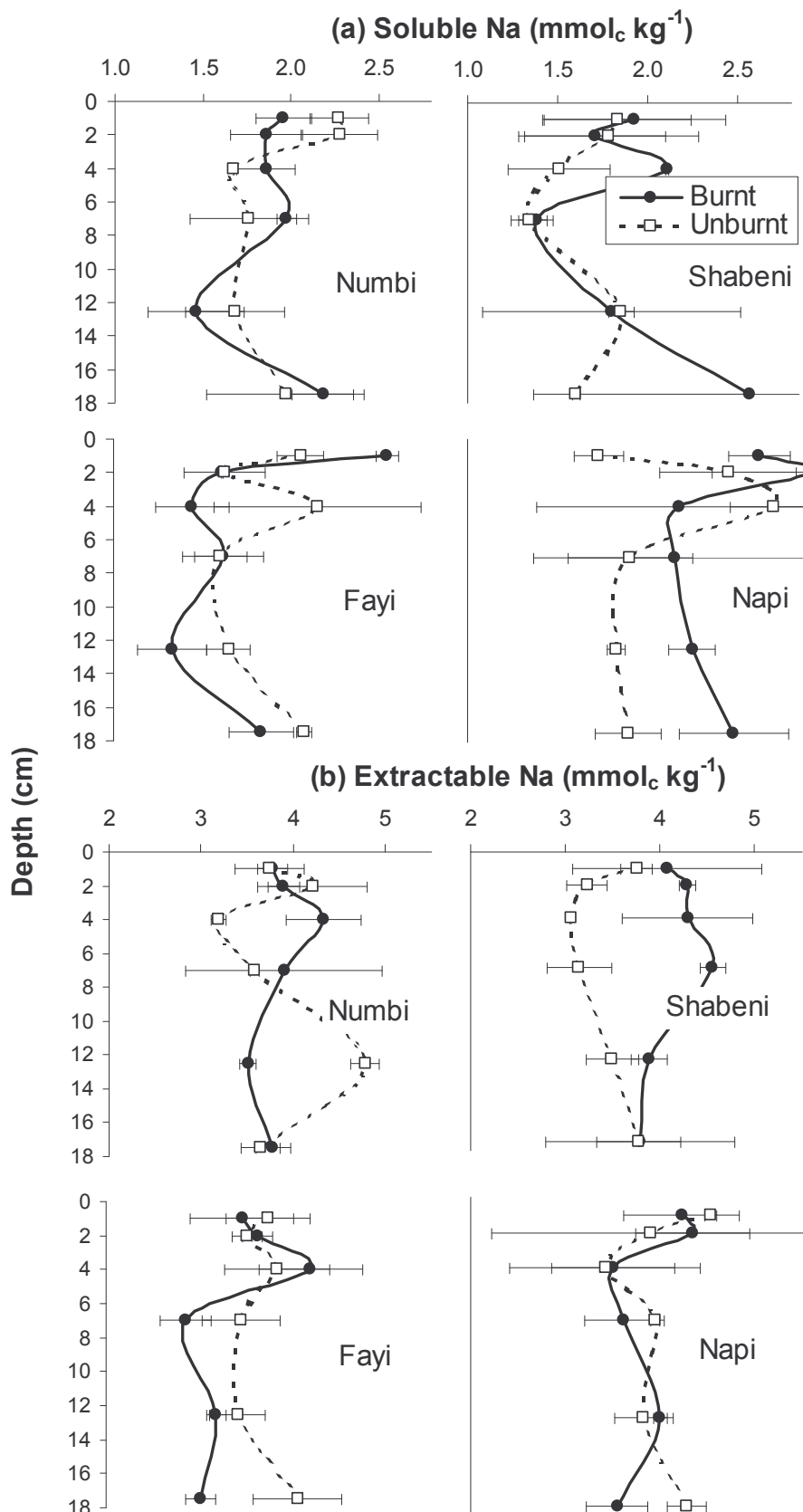


Figure 2.11 The distribution of water-soluble (a) and $(\text{NH}_4)\text{OAc}$ -extractable Na (b) down profiles in burnt and unburnt plots in the southern Kruger National Park. Error bars depict minimum and maximum values.

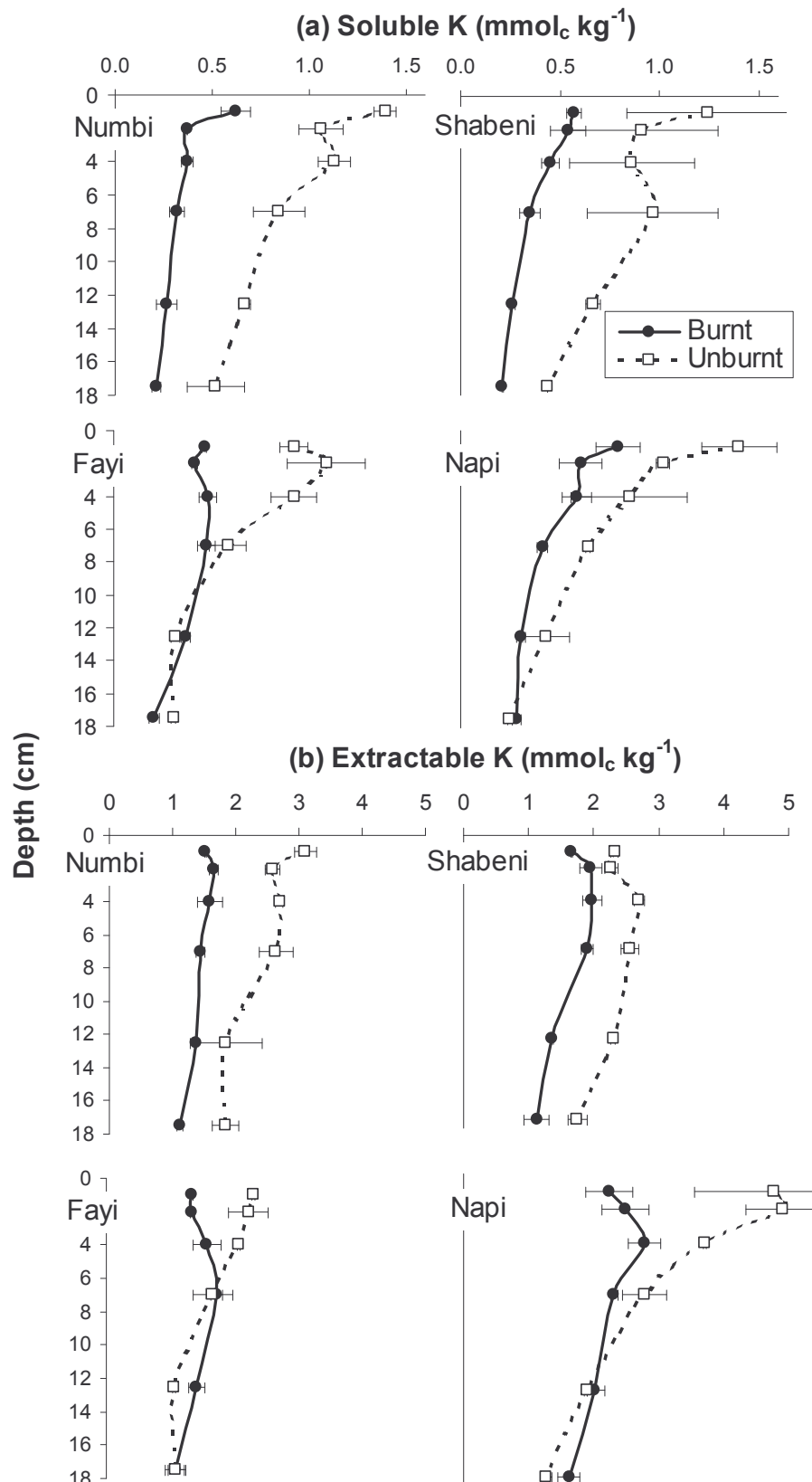


Figure 2.12 The distribution of water-soluble (a) and $(\text{NH}_4)\text{OAc}$ -extractable K (b) down profiles in burnt and unburnt plots in the southern Kruger National Park. Error bars depict minimum and maximum values.

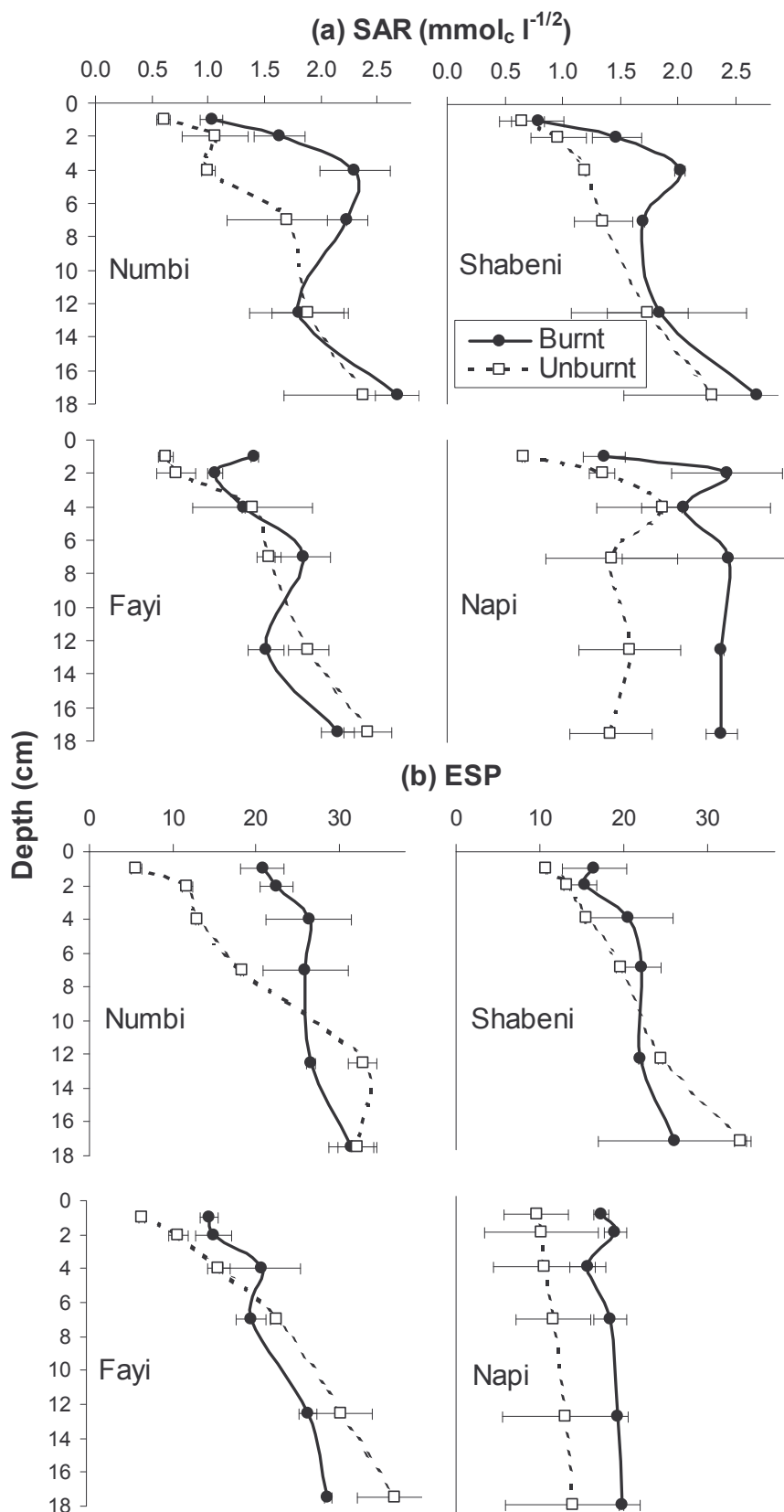


Figure 2.13 Sodium adsorption ratios of 1:5 extracts (a) and exchangeable sodium percentage (ESP) (b) from profile samples in burnt and unburnt plots in the southern Kruger National Park. Error bars depict minimum and maximum values.

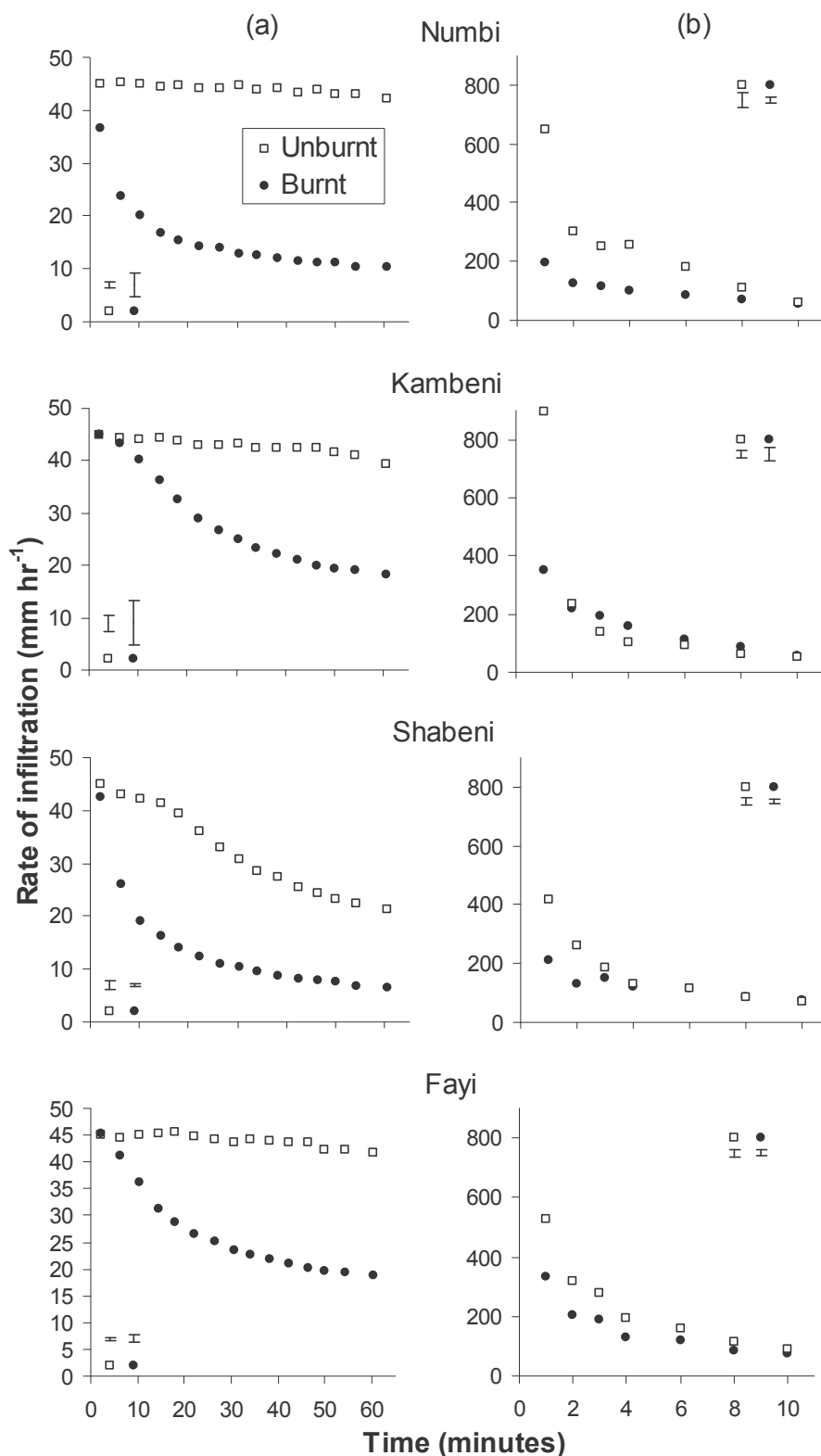


Figure 2.14 Rate of infiltration through soils from burnt and unburnt plots in the Numbi plots in the southern Kruger National Park using (a) rainfall simulation and (b) the laboratory method. Error bars are the mean difference between two replicates at each time interval for rainfall simulation infiltration and the mean standard error of three replicates at each time interval for laboratory infiltration.

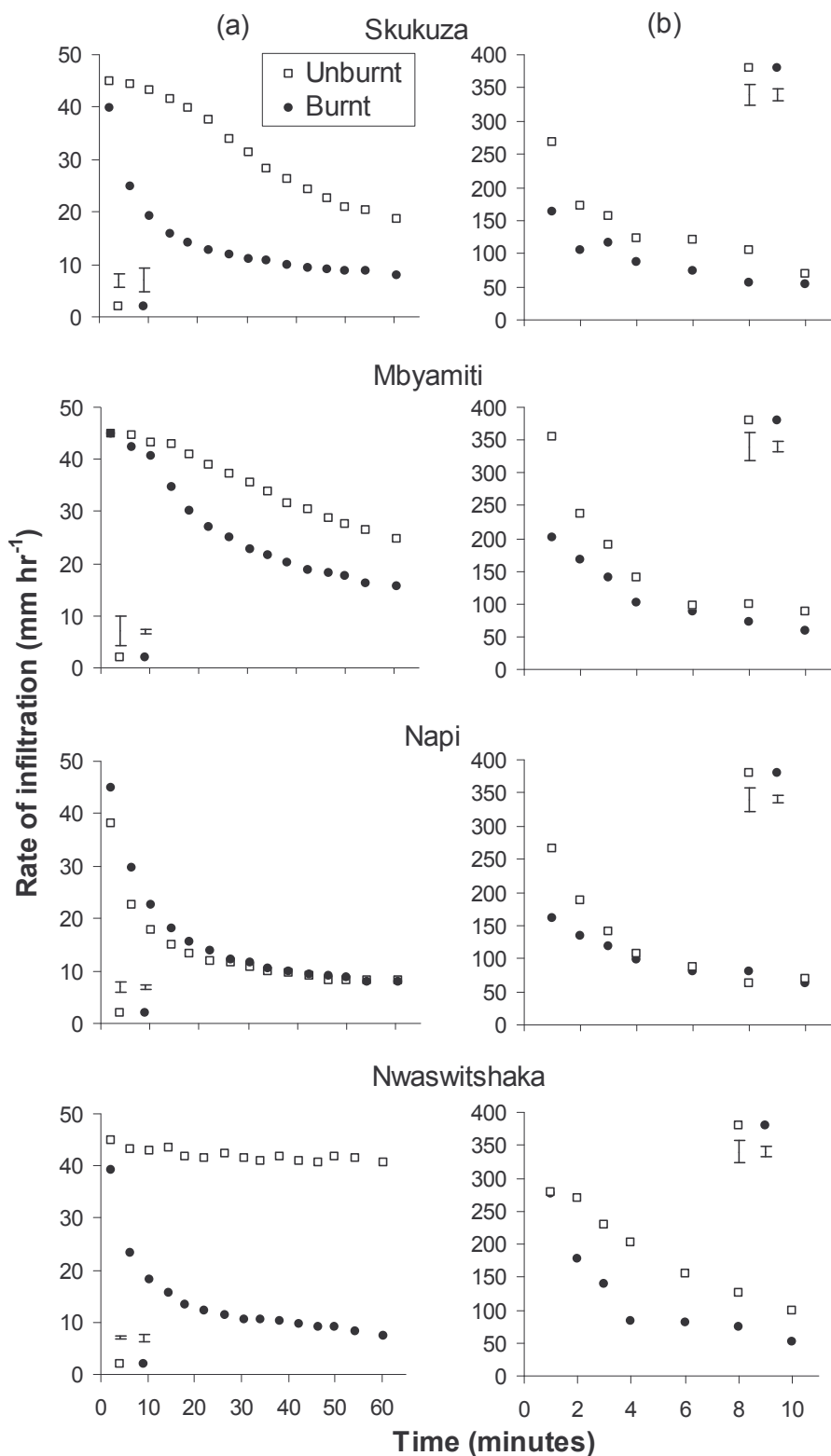


Figure 2.15 Rate of infiltration through soils from burnt and unburnt plots in the Napi plots in the southern Kruger National Park using (a) rainfall simulation and (b) the laboratory method. Error bars are the mean difference between two replicates at each time interval for rainfall simulation infiltration and the mean standard error of three replicates at each time interval for laboratory infiltration.

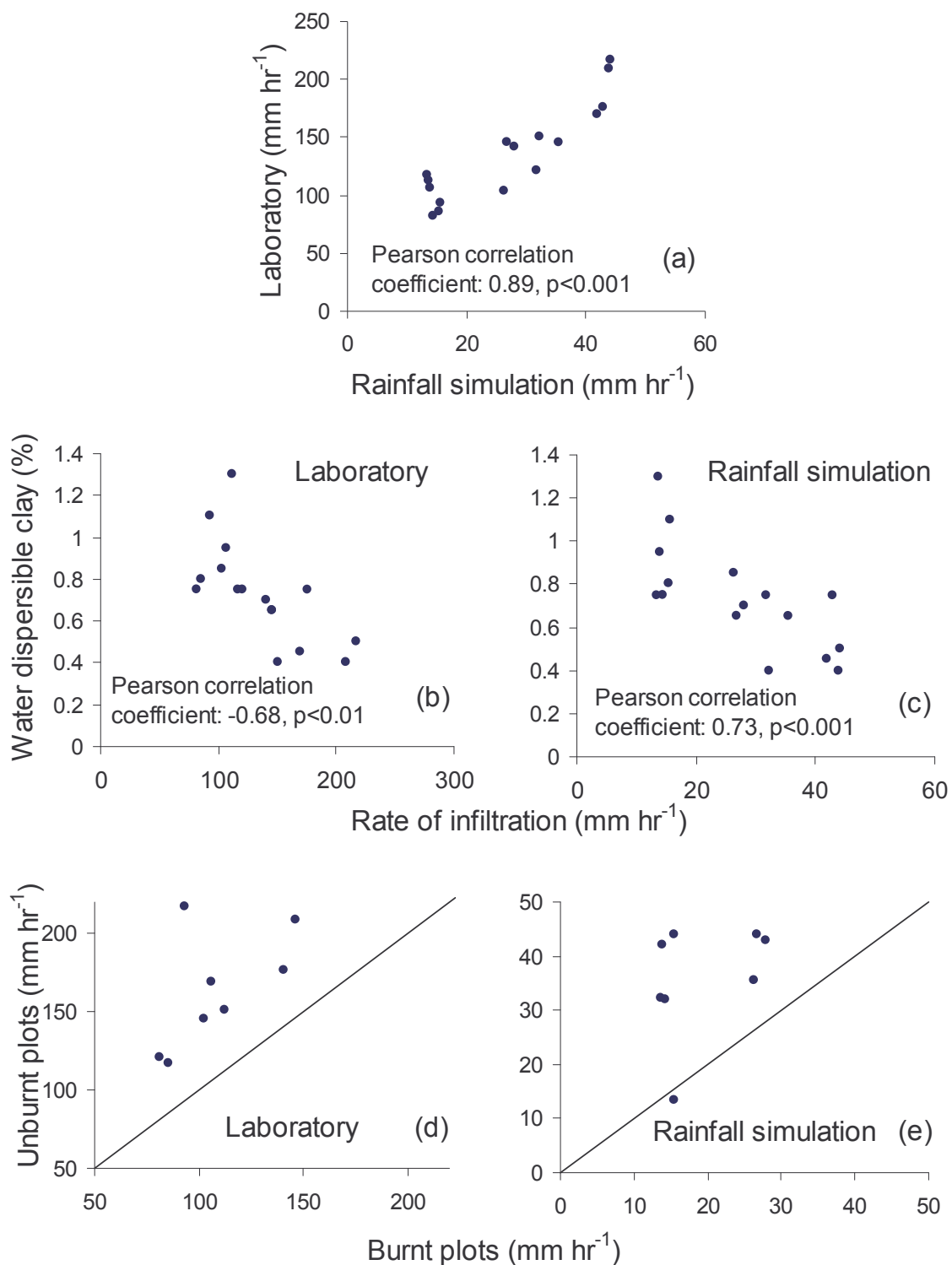


Figure 2.16 Relationships between (a) laboratory and rainfall simulation infiltration, (b) water dispersible clay and laboratory infiltration, and (c) water dispersible clay and rainfall simulation infiltration, (d) laboratory infiltration in soils from unburnt and burnt plots; and (e) rainfall simulation infiltration in soils from unburnt and burnt plots.

Table 2.1: Paired t-test results for burnt and unburnt plot comparisons in the southern Kruger National Park and across all study sites.

	Composite samples taken from a depth of 0-10 cm in burnt and unburnt plots on granite-derived soils in the southern Kruger National Park (Numbi and Napi sites)		Composite samples taken from a depth of 0-10 cm in burnt and unburnt plots in grasslands and savannas in South Africa (all sites).		Composite samples taken from a depth of 0-2 cm in burnt and unburnt plots on granite-derived soils in the southern Kruger National Park (Numbi and Napi sites).	
	p value	Difference ¹	p value	Difference ¹	p value	Difference ¹
Electrical conductivity	0.04	-16	0.047	-13	0.02	-36
Soluble K	0.002	-30	0.04	-14	0.04	-26
Soluble NO ₃	0.04	-17	0.02	-39	0.001	-50
Extractable Mg	0.02	-27	0.07	-10	0.02	-37
Infiltration	0.07	-16	0.001	-19	0.005	-40
Water dispersible clay	0.045	69	0.01	37	0.02	-34
Total C	0.005	-21	0.0003	55	0.02	-34
Labile C - 10ml	0.020	-20	0.013	-13		
Labile C - 5ml	0.001	-21	0.030	-15		
Total N	0.001	-22	0.008	-16		
pH (1:5)	0.03	0.3	0.068	-5		
pH (saturated paste)	0.02	0.2	0.0001	-17		
			0.01	0.2		

¹ Difference is the mean percentage difference between unburnt and burnt plots for all variables other than pH, where the mean absolute difference is reported. Percentage differences were calculated by subtracting burnt from unburnt plot values and using unburnt plot values as the denominator.

Table 2.2: Soil properties correlated with laboratory infiltration and water dispersible clay in granite-derived and basalt-derived soils in the Kruger National Park. Pearson correlation coefficients, n and p values are presented.

	Laboratory infiltration			Water dispersible clay		
	Correlation	n	p value	Correlation	n	p value
Soluble NH ₄	0.56	12	0.029	Total C ¹	14	0.001
Medium sand	0.47	16	0.033	Total C ²	16	0.011
Labile C 5ml	0.47	15	0.039	Total N ²	16	0.010
Total N ¹	0.47	14	0.046	Soluble K	16	0.019
Total C ¹	0.46	14	0.048	Soluble NH ₄	12	0.029
Electrical conductivity	0.41	16	0.060	Clay	16	0.040
Water dispersible clay	-0.37	16	0.076	Labile C 5ml	15	0.043
Soluble K	0.35	16	0.093	Infiltration	16	0.076
C:N	0.36	15	0.094	pH (saturated paste)	16	0.099
Total C ²	0.23	16	0.190	Electrical conductivity	16	0.105
Basalt-derived soils in the central Kruger National Park (Satara and Mopane sites)						
	Laboratory infiltration			Water dispersible clay		
	Correlation	n	p value	Correlation	n	p value
Total C ²	0.68	14	0.004	Infiltration	14	0.004
Water dispersible clay	-0.67	14	0.004	Medium sand	14	0.013
Soluble NO ₃	0.62	14	0.009	Soluble PO ₄	11	0.015
Labile C 10ml	0.61	14	0.010	pH (1:5)	14	0.022
Total N ²	0.57	14	0.016	Coarse sand	14	0.037
Coarse sand	-0.51	14	0.031	Extractable Mg	14	0.039
Medium sand	0.51	14	0.032	Soluble NO ₃	14	0.048
Extractable Mg	0.47	14	0.045	Labile C 10ml	14	0.049
Labile C 5ml	0.46	13	0.055	Total C ²	14	0.056
Fine sand	0.42	14	0.065	Soluble Na	14	0.091
Soluble NH ₄	0.44	12	0.076	Labile C 5ml	13	0.101
pH (1:5)	-0.40	14	0.081			

1 & 2: Total carbon and nitrogen analyses were performed twice on the same soils. The first analyses (1) were undertaken in early 2000 and the second analyses (2) were undertaken in early 2002.

(ESP) in the top centimetre of soil (sampled at four of the paired plots), was significantly greater in burnt than unburnt plots (Figure 2.13). And thirdly, total C, labile C and soil respiration were significantly lower in burnt than unburnt plots (Figures 2.4 & 2.6). As expected, the percentage of water dispersible clay was greater in burnt plots than in unburnt plots (Figure 2.5).

The changes in concentration of soluble salts, ESP and organic matter status on burnt plots can be ascribed to several processes. In the subsequent paragraphs each one of these changes is addressed, with the order of discussion not inferring any ranking of importance. With respect to concentration of soluble salts, it is noted that crusting in the field was evident on the majority of burnt plots particularly those on granite-derived soils in the southern Kruger National Park (Figure 2.17), and it is suggested therefore that the main mechanism for the decline in EC on burnt plots is the removal of ash (and the salts therein) by surface runoff, as has been reported by several workers in other biomes. Gimeno-Garcia *et al.* (2000), for example, demonstrated that annual burning in Mediterranean shrublands increased the quantity of soluble salts lost in surface runoff. Prior to this, Lewis (1974) had shown that 70% of all ions in ash were removed by 80 mm of rain over a 30 day period in a South Carolina pine forest. Work on the South African highveld by White and Grosman (1972) showed that a decline in $(\text{NH}_4)\text{OAc}$ -extractable cations in annually burnt plots was directly related to the rainfall in the month following the burn. They concluded that the decline in nutrient status was due to the removal of ash by surface runoff. It is suggested that this decline in nutrient status may affect clay dispersion by changing the nature of the diffuse double layer around clay micelles in the soil solution. As EC of the soil solution decreases, this layer becomes more diffuse and the electrostatic repulsion between clay micelles increases (Shainberg, 1992; Curtin *et al.*, 1994). The export of nutrients in ash is thus one way in which fire can potentially increase the dispersion of clay and thus the tendency of surface soils to crust.

Clay dispersion is highly sensitive to small changes in ESP (Du Plessis and Shainberg, 1985) and consequently the increase in ESP from a mean of 8% to a mean of 17% in the top centimetre of soil in burnt plots of the southern Kruger National Park is potentially most illuminating in terms of understanding how frequent fires may affect clay dispersion and hence crusting. The data presented in Figures 2.9-2.13 show that the response of Na to frequent burning was very different to the responses of Ca, Mg and K. Concentrations of



Figure 2.17 A broken crust on the Numbi annually burnt plot.

water-soluble and $(\text{NH}_4)\text{OAc}$ -extractable Ca, Mg and K in the top 0-1 cm were several times lower in burnt plots than unburnt plots, whereas no differences in the concentration of Na were apparent. The increase in ESP thus appears to be due to preferential removal of Ca, Mg and K from the burnt plots. A possible explanation is that nutrients are exported from burnt sites in ash, which would explain why Na was less affected by fire than Ca, Mg and K. The mean foliar concentration of Ca, Mg, Na and K in leaves of *Hyperthelia dissoluta* sampled at Numbi were 0.45, 0.22, 0.04 and 1.28%, respectively (unpublished data). Sodium is not an essential nutrient for plant growth and consequently foliar concentration of Na tends to be considerably lower than nutrients such as Ca, Mg and K (Whitehead, 2000). It is suggested therefore that the increase in ESP is largely due to preferential removal of Ca, Mg and K from the soil profile by plants and the loss of these nutrients when ash is washed off-site by surface runoff.

Organic matter is yet another factor likely to affect dispersion of clay and thus crusting in the burnt plots. Soil organic matter tends to decline in landscapes that are burnt regularly (Jones *et al.*, 1990; Seastedt *et al.*, 1994; Bird *et al.*, 2000; Parker *et al.*, 2001). The data in this study corroborate these findings, with total C, total N, labile C and soil respiration in incubated samples showing a consistent trend of being lower in burnt plots than unburnt plots. The

decrease in total C in the top 0-1 cm layer as a result of veld burning in the southern Kruger National Park is particularly noteworthy, with means of 0.8 and 2.3% for burnt and unburnt plots, respectively (Figure 2.6). This surface layer of soil, which is referred to here as the *pedoderm*², affects ecosystem functioning in a disproportionate manner as it controls water and air entry into the soil. Crusts on the soil surface may be less than 0.1 mm wide but can reduce the infiltration rate by a factor of 1800 (McIntyre, 1958a). Furthermore, the rate of nutrient release through mineralisation in the top few centimetres of the soil tends to be several times greater than deeper layers (Woods, 1989; Purnomo *et al.*, 2000) and consequently this layer can have a profound effect on the nutrition of plants. Although long-term burning may appear to have negligible effects on soils sampled to a depth of 10 cm (Figures 2.2-2.5), such a sampling strategy may mask quite marked effects in the pedoderm, as is evident in Figures 2.6-2.13.

The thin layer at the soil surface is also a redox interface between a potentially reducing soil environment and the oxidising atmosphere. Bartlett (1999) points out that redox interfaces are where much of the chemical action in nature takes place: where "...C, N, and S transform...from one redox state to another and back again...". The mineralisation of organic matter is largely controlled by redox, as organic matter is composed of reduced carbon, which will tend to move via oxidation towards a more stable state, such as CO₂. Redox also affects N status, because even moderately reducing conditions ($-4 < pe < 12$, where $pe = -\log[e^-]$ and expresses a hypothetical "electron activity" in solution) favour denitrification i.e. the reduction of NO₃⁻ to N₂ (McBride, 1994). The structure of the pore spaces at the soil surface determines whether oxygen moves freely into its organic-rich interior and whether mineralisation of organic matter is either promoted by a supply of oxygen or inhibited by a lack of oxygen. The pH of the surface soil will also affect mineralisation, as redox is pH dependent (McBride, 1994).

The decline in total C and N as a result of frequent burning is attributable to several processes operating simultaneously, many of which can be linked to redox. Firstly, the removal of vegetation tends to increase the number of wetting and drying cycles in the soil surface, due to greater soil temperature (Savage and Vermeulen, 1983) and less interception of rainfall in the exposed post-fire environment (Moyo *et al.*, 1998). This in turn increases the rate of

² Pedoderm is a new name put forward in this thesis. It is the interface between the atmosphere and the soil body and refers to the top few centimetres of mineral soil.

mineralisation of organic matter, a process known as the Birch effect (Birch, 1958). The Birch effect is attributed to the promotion of young, metabolically-active microbes (Birch, 1958), but is perhaps also a function of redox. When soils dry out, soil pore spaces become aerated, soil oxygen levels increase and when the soil rewets, microbes utilise this replenished oxygen. Rewetting also replenishes oxygen in the form of dissolved oxygen in the rainwater. Wetting and drying a soil can thus be likened to the fanning of a flame: it injects oxygen into the soil matrix.

A second explanation for soil C and N declines after burning is based on a fundamental chemical principle that the rate of chemical reactions increases with temperature. Soil temperature tends to increase after burning because of greater exposure to sunlight and this is likely to increase microbial activity. Knapp *et al.* (1998), for example, recorded a 20-55% increase in CO₂ flux after burning in tallgrass prairie, with unburnt prairie averaging 10 μmol CO₂ m⁻² s⁻¹ and burnt prairie 15 μmol CO₂ m⁻² s⁻¹. At the same site, O'Lear *et al.* (1996) showed that the rate of decomposition of wooden dowels was greater in burnt sites than unburnt sites. Soil temperature was greater in burnt prairie than unburnt prairie and differences in CO₂ flux were attributed to this temperature difference. A third explanation for a decline in soil C and N is that soil microbes tend to respond favourably to the increase in soil pH (caused by the deposition of alkaline ash) in the post-fire environment (Greenwood, 1968; Knapp *et al.*, 1998). This is again related to redox, as oxidation is favoured at high pH. An increase in pH also tends to increase labile C concentration which will tend to favour microbial growth (Curtin *et al.*, 1998).

A fourth explanation is that the soil organic matter may combust during veld burning. Combustion of soil organic matter begins at 220°C (Giovannini *et al.*, 1990) and combustion of grasses in savannas can generate a temperature of 700°C (Van de Vijver, 1999). Mineral soil is, however, a poor conductor of heat and thus combustion of soil organic matter, if it occurs at all, is likely to be limited to the top few centimetres of soil (Scotter, 1970). The maximum soil temperature recorded at a depth of 2.5 cm in a hot *Eucalyptus* forest fire, for example, was only 275°C (Beadle, 1940), and soil temperature in fires in *Pinus palustris* savannas in the southeastern United States was only 135°C just below the soil surface (Heyward, 1938). In chaparral fires much of the biomass is close to the ground and the temperature at the soil surface may exceed 700°C, but at a depth of 2.5 cm in the soil is rarely above 200°C (DeBano *et al.*, 1977). A fifth possible factor affecting soil C loss in burnt plots

is a reduction in plant roots and consequently root exudates which inhibit mineralisation (Theron, 1951; 1963). The role of root exudates in maintaining soil organic matter is largely unknown, probably because it is difficult to disentangle from the effects of temperature, soil water content and plant litter inputs. Lastly, inputs of organic matter to the soil are reduced by burning because of the combustion of above-ground biomass and leaf litter.

Carbon in virgin soils (i.e. undisturbed soils) tends to increase aggregate stability and reduce clay dispersion (Cook *et al.*, 1992; Sumner, 1998, Chan *et al.*, 2001). The chemical principles behind the flocculating or dispersing effect of organic compounds is, however, largely unknown and soil organic matter has in some cases been shown to increase dispersion of clay (Sumner, 1998). The role of soil organic matter depends to a large extent on the type of organic matter present, but in general an aggregating effect in virgin veld can be expected. The decline of soil organic matter in burnt plots is thus likely to be a major contributing factor to the increase in clay dispersion and crusting.

The relationship between infiltration rate, water dispersible clay and soil C is evident from Pearson correlation coefficients (Table 2.2). In granite-derived soils of the Kruger National Park, infiltration and water dispersible clay were significantly correlated ($p < 0.05$) with total C (Pearson correlation coefficients of 0.46 and -0.75, respectively). In basalt-derived soils of the Kruger National Park, infiltration was significantly correlated with total C (0.68) and water dispersible clay was significantly correlated with labile C (-0.46). This range in correlation coefficients of 0.46-0.75 equates to r^2 values of 0.21-0.56, which mean that the regression of y on x can only account for a range of 21% to 56% of the variation in y. Such a range is not unexpected, as several factors are likely to be at play. What the results indicate is that soil C is probably one of the main factors (if not *the* main factor) influencing clay dispersion and crusting in these savannas. Where organic matter is depleted, such as under a regime of frequent burning, crusting is likely to become more severe.

2.4.2 Feedback effects of crusting

With reference to biological systems, “feedback” is defined (Websters Third International Dictionary, 1959) as “the potential reversion of the effects of a given process to its source or to a preceding stage so as to reinforce or modify it”. A feedback effect may develop for example, whereby the depletion of soil C over time results in greater clay dispersion, further

crusting and reduced return of C to the soil because of less production of biomass in a crusted, arid soil. Other feedback effects that promote soil crusting are also likely to take place under a regime of frequent burning. Firstly, fire reduces vegetation cover and increases the exposure of the soil surface to raindrop impact. This alone is likely to increase the extent of crusting in the landscape, due to increased clay dispersion and aggregate breakdown arising from the mechanical energy imparted by falling raindrops (Hillel, 1998). Such a breakdown in soil structure is likely to reduce plant growth and prevent the development of an effective plant cover for shielding the soil from raindrop impact. Secondly, the greater the crusting, the greater the runoff of rainwater and loss of ash from the site of the burn. The greater the export of nutrients in the ash, the greater the decline in EC and the greater the increase in ESP. The process thus does a full circle back to greater clay dispersion and crusting as a result of chemical changes initiated by the crusting in the first place. The phenomenon of crusting on burnt plots is thus potentially a situation that can feed on itself and snowball towards greater crusting, spurred on by a declining EC, increasing ESP and declining soil organic matter.

The feedback effect of frequent burning on crusting may lead to a new equilibrium within the ecosystem, and a change in the state of the ecosystem. The abiotic environment of the ecosystem in a crusted state versus an uncrusted state is likely to be very different. The crusted state would tend to be drier due to greater surface runoff and greater soil temperatures, and nutrient cycling would tend to be faster, driven by a Birch effect and a greater rate of mineralisation. The crusted ecosystem state may thus be expected to support plants such as grasses which are not only adapted to relatively dry environments, but also occur in areas where mineralisation of soil organic matter and thus nutrient cycling is rapid. Woody vegetation in savannas may, in contrast, be excluded from the crusted environment due to a relatively low tolerance of aridity.

2.5 Conclusions

The top few centimetres of soil, or pedoderm, is potentially of critical importance for ecosystem functioning in semi-arid areas as it contains an inordinately high organic C concentration, which affects aggregate stability, water infiltration, aeration and nutrient cycling. The soil C in the 0-1 cm layer of unburnt plots was 248% greater than in burn plots and was 225% greater in the 0-1 cm layer than the 4-5 cm layer in unburnt plots. Marked

differences between burnt and unburnt plots are evident in the 0-1 cm layer but are often not apparent in composite samples of 0-10 cm. Composite sampling of soils to greater depths than a few centimetres in semi-arid systems is thus likely to dilute the properties of the pedoderm and thereby confound and obscure any interpretation of how soils may be affecting ecosystem structure and function.

The results discussed in the preceding sections suggest that frequent burning can increase the tendency of soil to crust and that feedback effects may occur which could enhance the crusting effect. There are three potential feedback loops operating in parallel. Crusting promotes runoff and therefore (i) results in a drier soil climate and sparser vegetation which (a) promotes mechanical dispersion of clay through raindrop impact and (b) decreases soil organic matter and therefore aggregate stability, and (ii) removes salts which further promotes clay dispersion and crusting.

The study also highlights how plants may degrade soil quality by changing the distribution of Na, Ca and Mg within the soil profile. Plants remove greater quantities of Ca and Mg than Na from the soil and consequently if plant material is removed from a particular site (whether by fire or herbivory), the exchangeable Na percentage of surface layers will increase. This in turn is likely to increase clay dispersion and hence soil crusting. In the next chapter, the focus is again on the effects of vegetation removal on soil properties. The study area is located in the Xeric Succulent Thicket of the Eastern Cape and vegetation was removed by goats, not fire. Interestingly, the effects of vegetation removal by goats and fire on soil properties are very similar.

CHAPTER 3

SOIL CARBON, CRUSTING AND GOAT FARMING IN XERIC SUCCULENT THICKET, EASTERN CAPE, SOUTH AFRICA

3.1 Introduction

Vegetation returns organic matter to the soil, protects the soil from raindrop impact and cools the soil surface through shading. Consequently, patches of vegetation are usually hotspots of soil organic matter and nutrients, especially in semi-arid regions (Schlesinger *et al.*, 1990). The removal of vegetation tends to deplete soil organic matter and because aggregate stability is often a function of soil organic matter (Oades, 1993), the structure of the soil is also likely to deteriorate. This deterioration may manifest itself in the form of soil crusting or sealing and enhanced surface runoff. Furthermore, crusting would tend to increase when vegetation is removed because of increased exposure to raindrop impact. The Xeric Succulent Thicket in the Eastern Cape, South Africa is an unusual vegetation type for a semi-arid environment because, in its virgin state, there is an almost complete cover of dense vegetation, predominantly the succulent shrub *Portulacaria afra*. The thicket biome has been used for farming goats since the early 1900's. Intensive stocking with goats destroys the *P. afra* and transforms the thicket to an open "pseudo-savanna" dominated by annual grasses and karroid shrubs (Lechmere-Oertel *et al.*, 2002, in preparation). The effect that this transformation has had on soil properties is unknown. It was hypothesised that the removal of *P. afra* by goats would cause a deterioration in soil quality, reduce soil organic matter content and increase the tendency of the soil to crust. To test this hypothesis soil properties from eight fence-line contrasts between intact thicket and goat-transformed sites, within a region of about 700 km², were investigated.

3.2 Materials and methods

3.2.1 Study area

The study area is situated west of Kirkwood in the Eastern Cape, at an elevation of 300-500 m a.s.l. (33°30`S; 25°20`E). It has a warm, semi-arid climate with evenly distributed annual rainfall of 250-400 mm and an annual coefficient of variation of 135%. The vegetation is

characterised by a matrix of the succulent shrub *Portulacaria afra*, which is interspersed with spinescent bushes (e.g. *Azima tetracantha*, *Gymnosporia polycantha*, *Putterlickia pyracantha*,

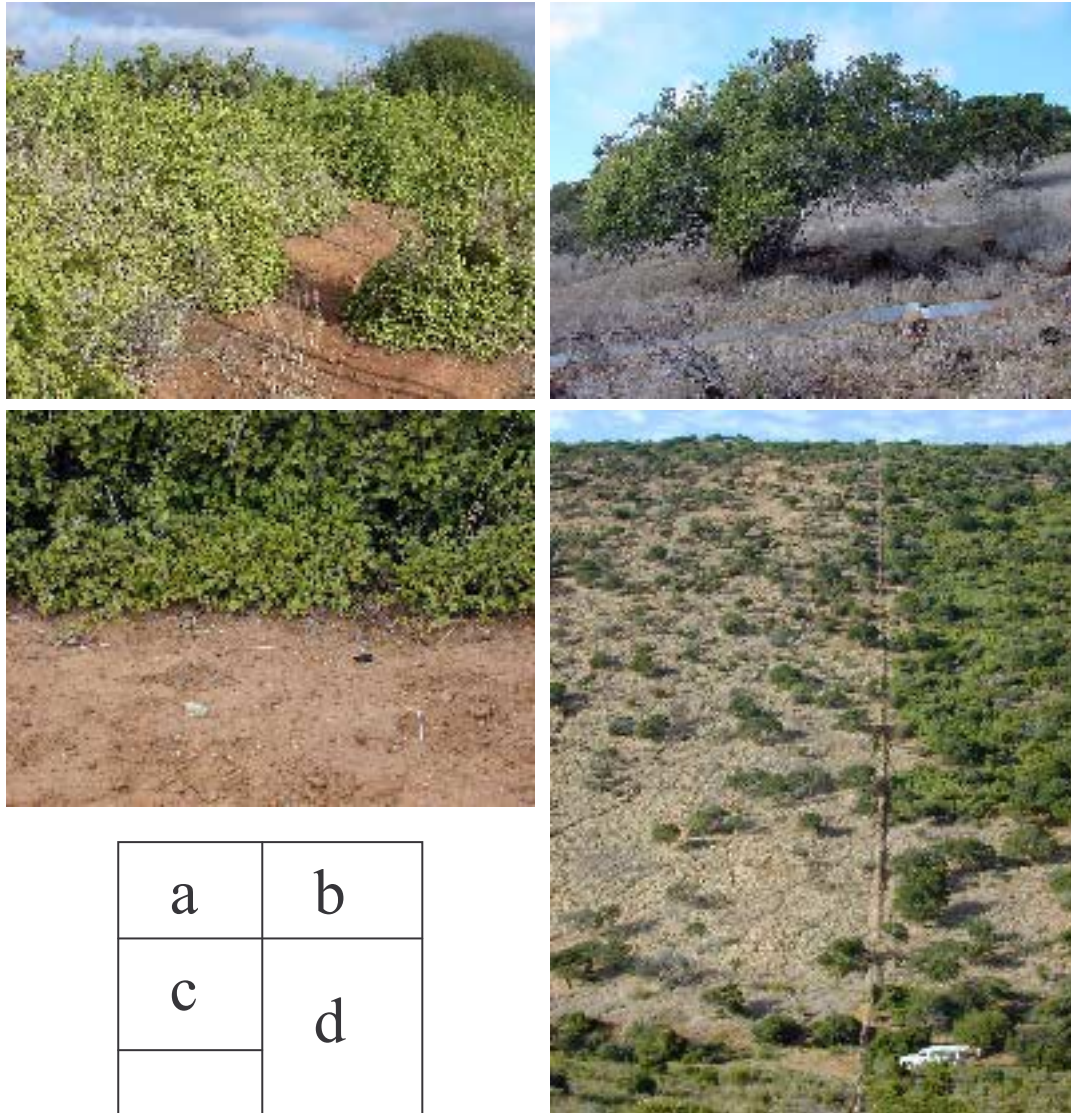


Figure 3.1 (a) *Portulacaria afra* on an intact thicket site; (b) *Pappia capensis* on a goat-transformed site; (c) crusting around *Portulacaria afra* at site 8; (d) fenceline contrast at site 1 (goat-transformed site on left, intact thicket site on right).

Rhigozum obovatum, *Rhus longispina*) and low-growing trees (<5 m) (e.g. *Pappia capensis*, *Euclea undulata*, *Schotia afra*). This vegetation type has been termed Xeric Succulent Thicket (Low and Rebelo, 1996; Everard, 1987) and more recently “Sundays River Thicket” (Vlok and Euston-Brown, 2002). It is referred to as Xeric Succulent Thicket in this thesis. In

goat-transformed sites, the shrubs and trees are replaced by ephemeral or weakly perennial grasses and karroid shrubs, often dominated by the alien chenopod saltbush (*Atriplex lindleyi* subsp. *inflata*). In goat-transformed sites, the tree component (predominantly *Pappea capensis*) is the only remnant of the original thicket and has been termed “pseudo-savanna” (Lechmere-Oertel *et al.*, 2002, in preparation). The vegetation of intact sites and goat-transformed sites, as well as the succulent shrub *P. afra*, are depicted in Figure 3.1.

The study sites lie in a broad valley, flanked by the Groot-Winterhoekberge mountain range to the south and the Klein-Winterhoekberge to the north. These ranges are made up of the Table Mountain group of quartzitic sandstones of the Nardouw subgroup and the Peninsula formation. In the valley there is an assortment of sedimentary rocks from the Bokkeveld and Uitenhage groups (Figure 3.2). Bokkeveld shales, sandstones and siltstones of the Ceres and Traka subgroups lie on the southern side of the valley, and Uitenhage mudstones, sandstones and conglomerates of the Kirkwood formation lie on the northern side of the valley.

To investigate the effect of goat farming on soil properties, eight fenceline contrasts of intact thicket and goat-transformed thicket were selected (five on north facing slopes [10-20°] and three on flat ground). Goat-transformed sites had been browsed for 20-80 years by domestic livestock, predominantly boer goats (*Capra hircus*) and angora goats (*Capra angoriensis*). Accurate stock density data were not available for any sites and it was assumed that the existence of a distinct fence-line contrast in vegetation was evidence that long-term stocking history had differed. Sites 1-5 were located on the lower slopes of the Groot-Winterhoek Mountains and accessed from the gravel road between Uitenhage and Steytlerville and sites 6-8 were located on flat ground adjacent to the tarred road between Uitenhage and Kirkwood (Figure 3.2). Bokkeveld Group shale is the dominant underlying geology of sites 1-5 and Uitenhage Group sediments underlie sites 6-8. A calcrete layer was often encountered at a depth of 30–75 cm at sites 6-8. The parent material of any particular soil profile in the study area is likely to be a mixture of transported material and weathered bedrock. Soil forms identified in the study area include Mispah, Augrabies, Klapmuts, Valsrivier, Oakleaf, Glenrosa and Addo (Soil Classification Working Group, 1991). In the terminology of the World Reference Base classification system the soils include Calcaric Cambisols, Calcic Luvisols, Rhodic Luvisols and Calcaric Regosols (FAO, 1998).

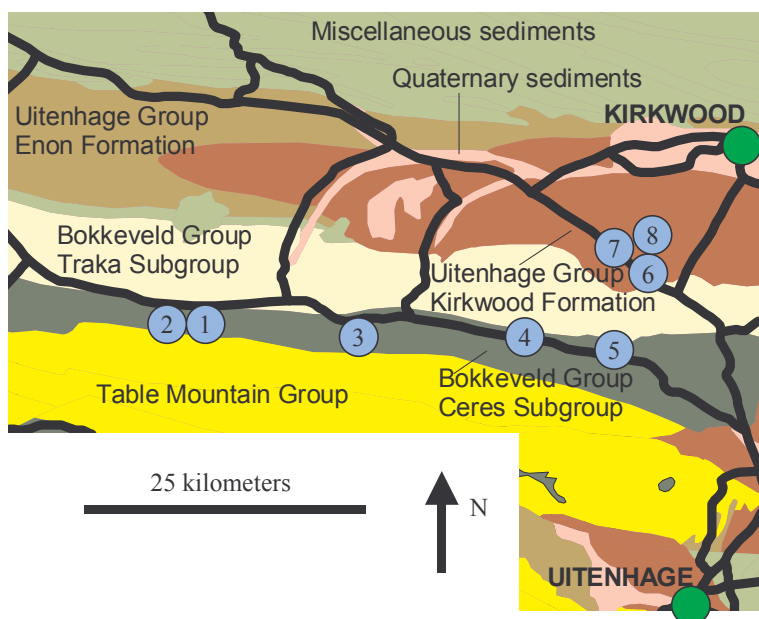
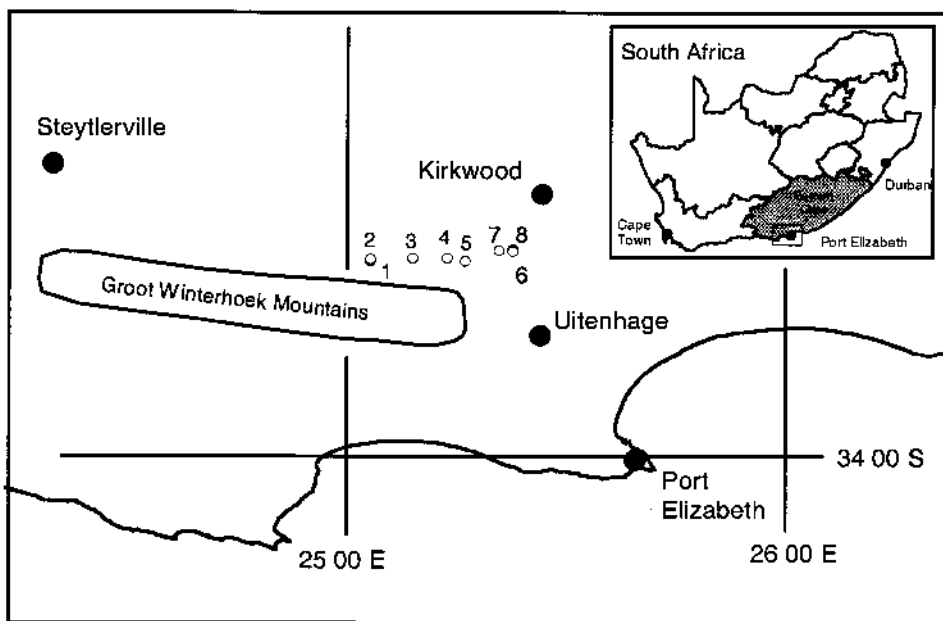


Figure 3.2 The geology of the Eastern Cape study area and location of the fenceline contrast sampling sites.

3.2.2 Sampling

One hectare plots were laid out on each side of the fence and two composite topsoil samples were taken from each plot to a depth of 10 cm using a soil auger. Composite samples comprising fifteen to twenty subsamples were taken randomly from under *P. afra* in intact sites and from open, grassy areas in goat-transformed sites. A soil pit was dug to a depth of 50 cm in each plot and samples were taken at 10 cm intervals for C analysis. Soil CO₂ flux measurements were undertaken in March 2001 at sites 1, 3 and 5. Six soil collars were laid out in both goat-transformed sites and intact thicket sites, 3 under trees and 3 in the open. Carbon dioxide flux measurements were taken from each collar in the early morning (6-9 am), late morning (9 am-12 pm), early afternoon (12-3 pm) and late afternoon (3-6 pm).

3.2.3 Soil analyses

A full description of methods of soil analysis is given in Chapter 2. In brief, the following analyses were undertaken on composite samples taken to a depth of 10 cm: electrical conductivity (EC) and pH in 1:5 soil extracts; pH in KCl and water (1:2.5); water-soluble (1:5) and ammonium acetate-extractable cations; water-soluble (1:5) anions; Bray 2-extractable P; total C and N; labile C; soil respiration in the laboratory; particle size distribution; modulus of rupture; laboratory infiltration and water dispersible clay. Statistical analyses were performed using the software package Unistat 5.0. A paired t-test was undertaken to detect significant differences ($p < 0.05$) between goat-transformed and intact thicket sites.

3.3 Results and discussion

A comparison of soil properties in paired plots of intact *P. afra* thicket and goat-transformed sites is presented in Figures 3.3-3.6. Associated with the change of intact thicket to pseudo-savanna, a significant decrease (paired t-test, $p < 0.05$) was found in total C (respective means of 5.6 vs 3.0%), total N (0.33 vs 0.24%), labile C (2.8 vs 1.5%), CO₂ flux (1.9 vs 0.5 $\mu\text{mol m}^{-2} \text{s}^{-1}$), soil respiration in the laboratory (144 vs 79 $\text{ng C g}^{-1} \text{s}^{-1}$), C:N (16.6 vs 12.5), (NH₄)OAc-extractable Mg (55 vs 28 $\text{mmol}_c \text{kg}^{-1}$), medium plus coarse sand (33 vs 26%) and laboratory infiltration rate (51 vs 19 mm hr^{-1}). By contrast, a significant increase was found in modulus of rupture (16 vs 34 kPa), silt content (9 vs 11%), pH in water (6.7 vs 7.7), water-soluble Ca

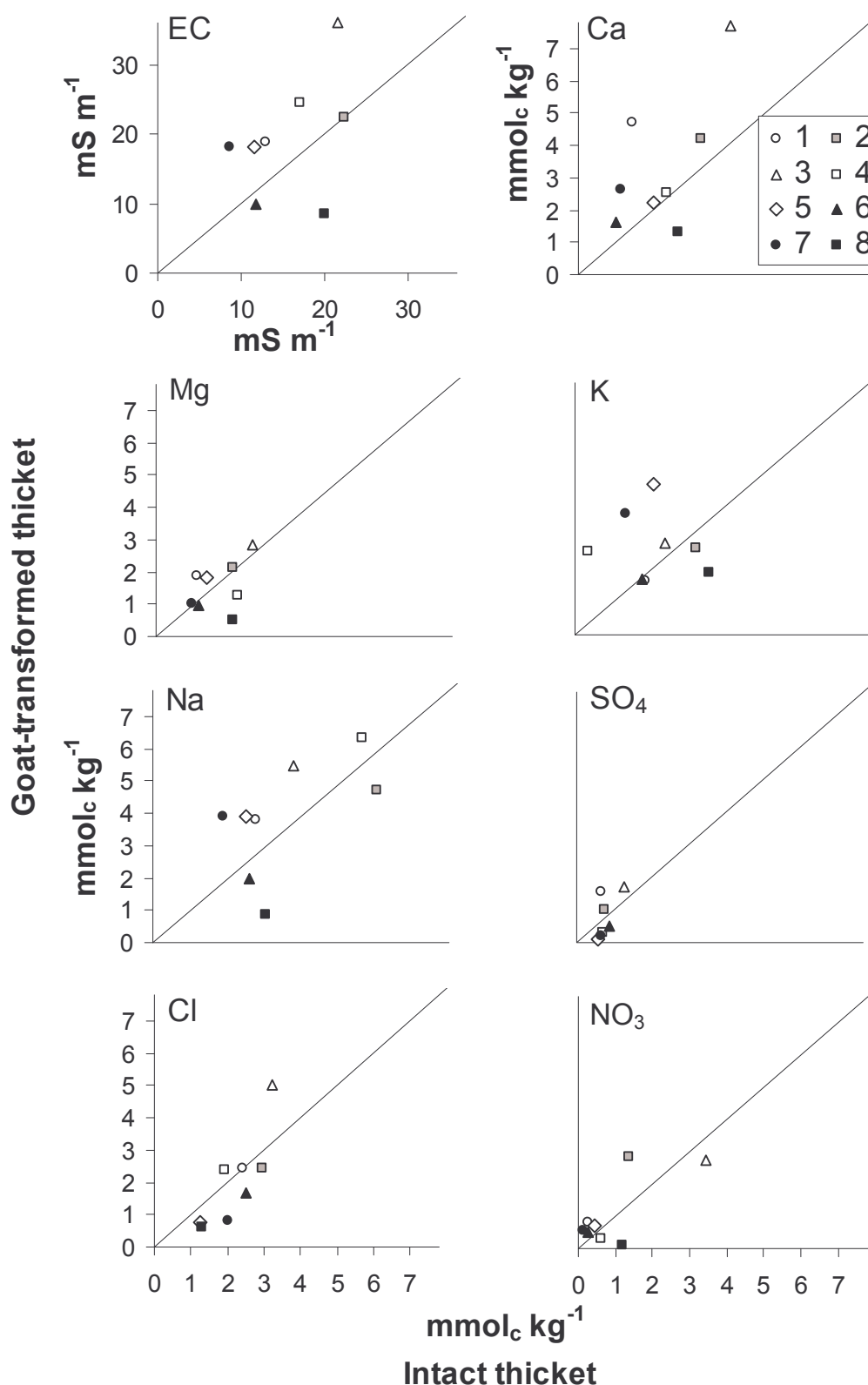


Figure 3.3 The relationship between goat-transformed and intact thicket sites with respect to electrical conductivity, water-soluble (1:5) Ca, Mg, Na, K, NH₄, SO₄, Cl and NO₃ in composite soil samples taken to a depth of 10 cm.

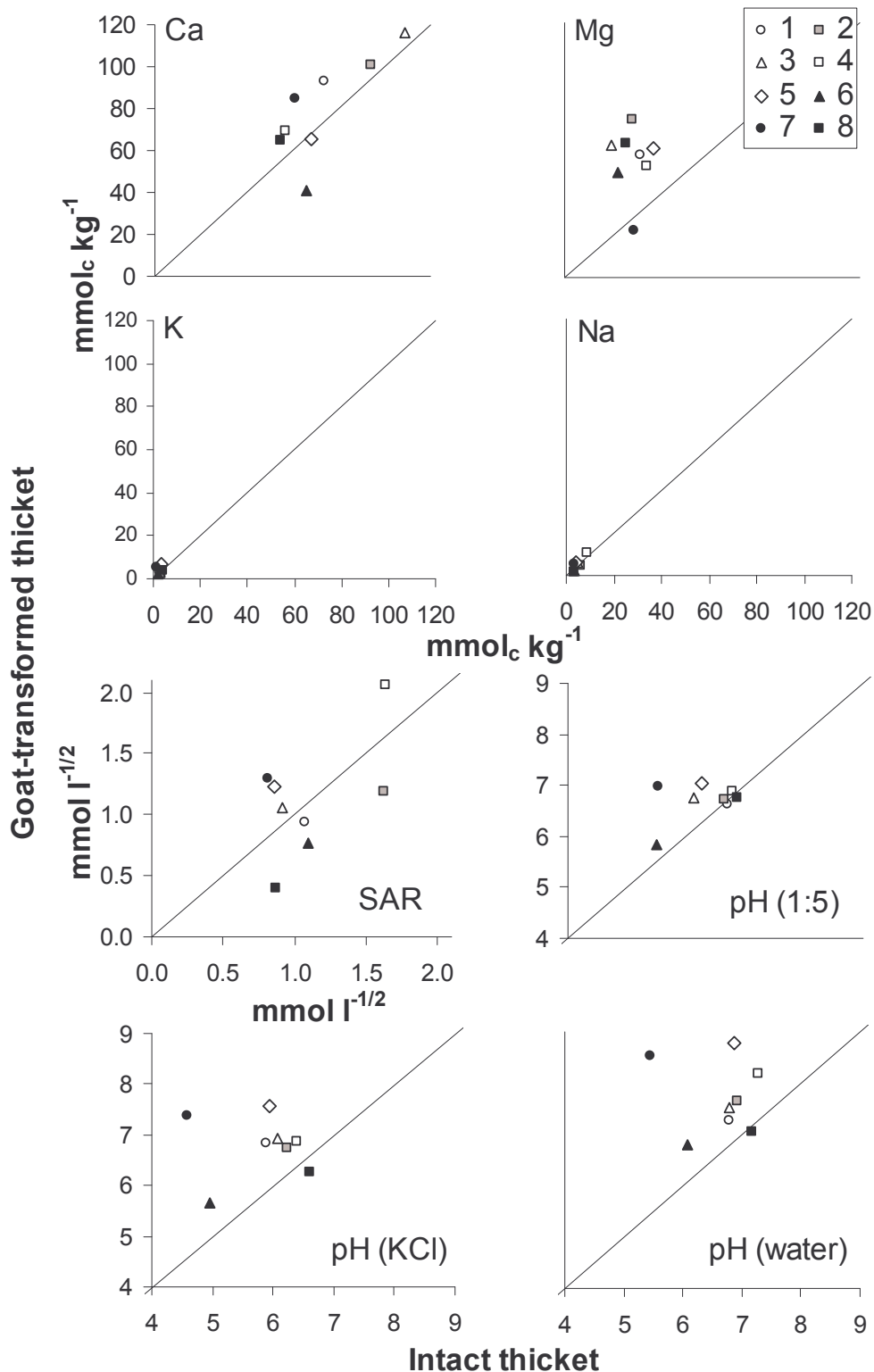


Figure 3.4 The relationship between goat-transformed and intact thicket sites with respect to (a) $(\text{NH}_4)\text{OAc}$ -extractable cations Ca, Mg, Na, K; (b) sodium adsorption ratio and pH in a 1:5 soil-water extract; and (c) pH in KCl and water (1:2.5) in composite soil samples taken to a depth of 10 cm.

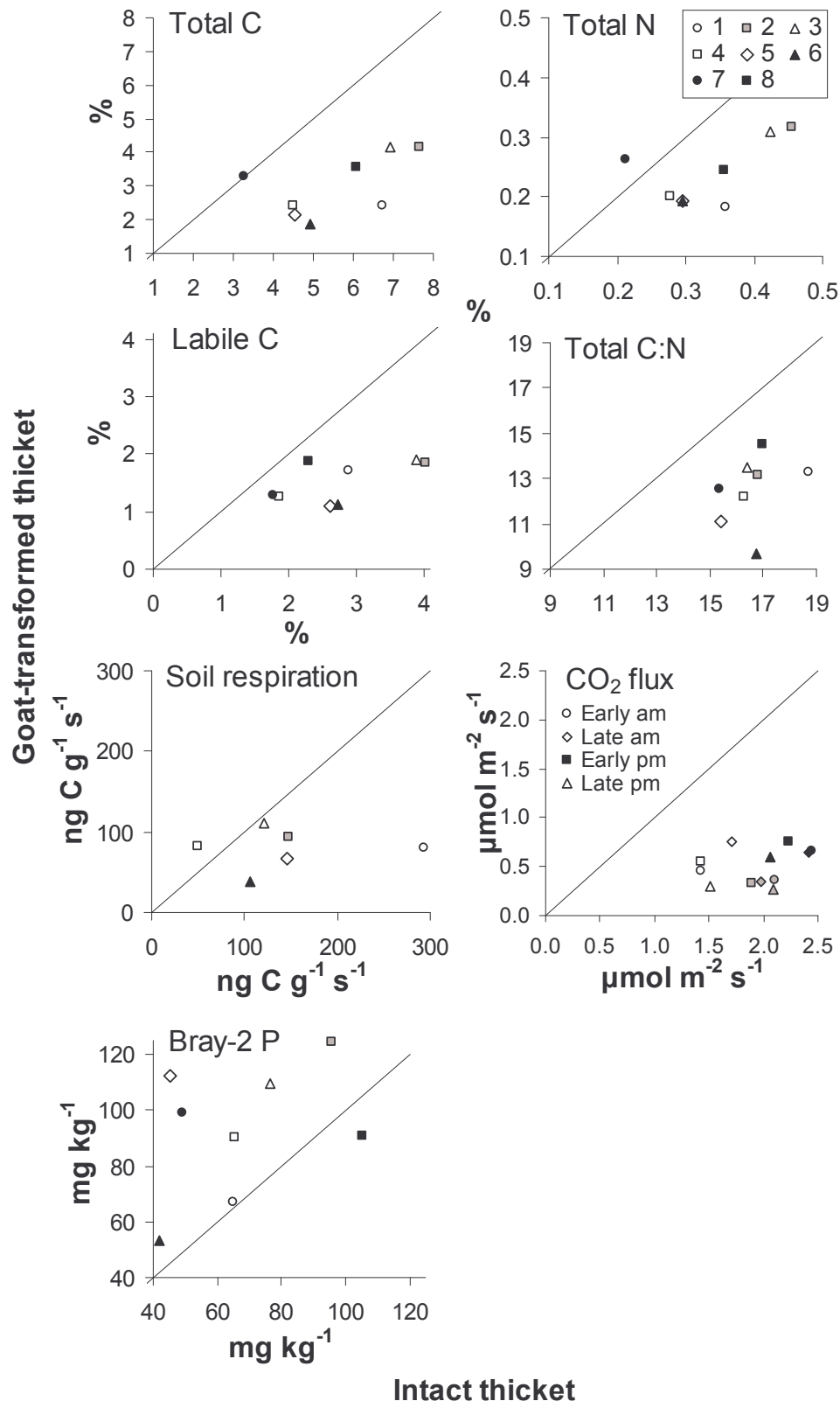


Figure 3.5 The relationship between goat-transformed and intact thicket sites with respect to total C, total N, labile C, total C:N, soil respiration in the laboratory, CO₂ flux in the field and Bray 2-extractable P. Results depicted are from composite soil samples taken to a depth of 10 cm. The colours in the CO₂ flux graph refer to site 1 (filled), site 3 (grey) and site 5 (open shapes).

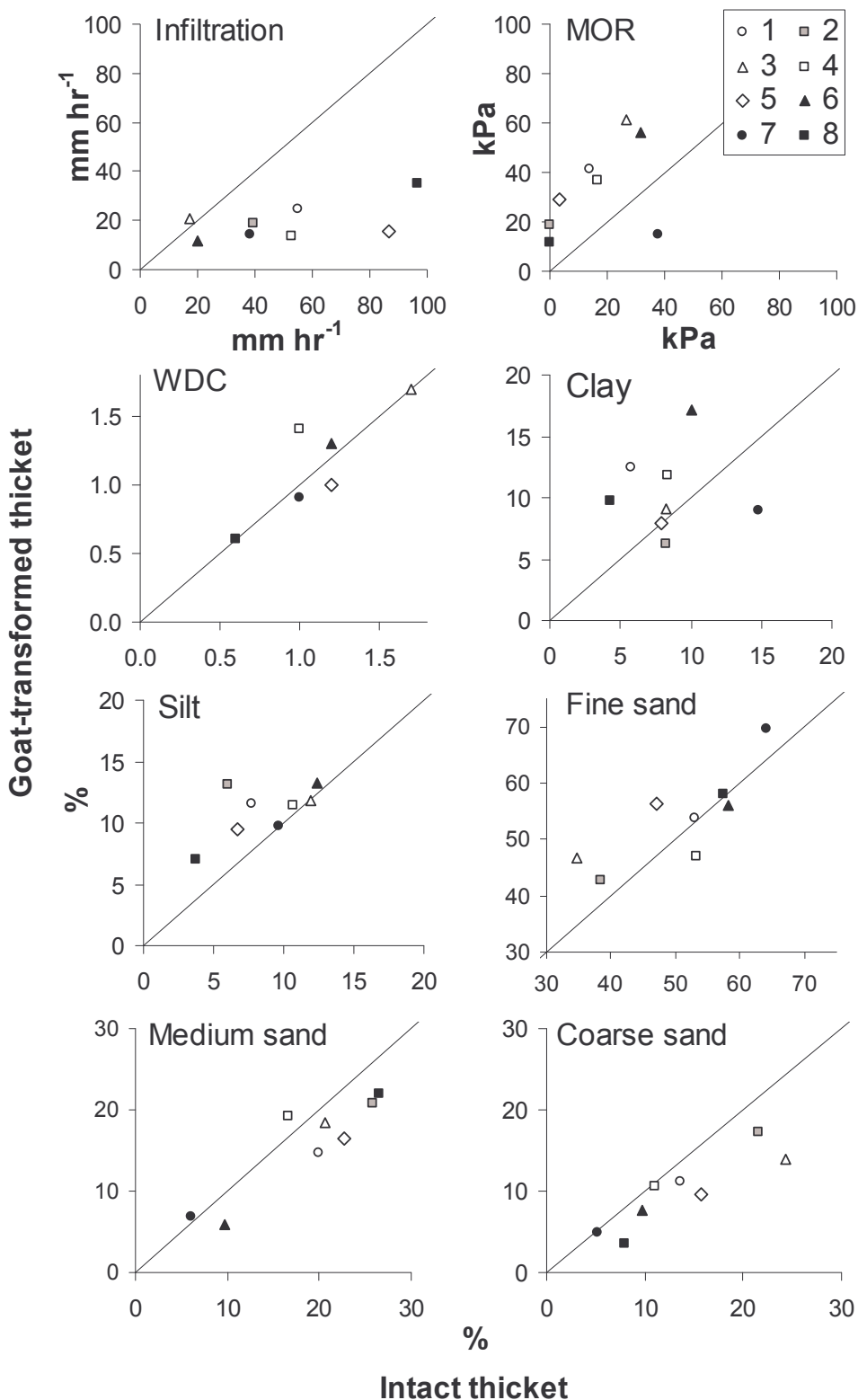


Figure 3.6 The relationship between goat-transformed and intact thicket sites with respect to rate of laboratory infiltration, modulus of rupture, water dispersible clay, clay, silt, fine sand, medium sand and coarse sand. Results depicted are from composite soil samples taken to a depth of 10 cm.

(2.3 vs 3.4 mmol_c kg⁻¹), and Bray-2 extractable P (68 vs 93 mg kg⁻¹). The Pearson correlation coefficients for soil properties correlated with infiltration, water dispersible clay, and modulus of rupture are presented in Table 3.1.

Table 3.1: Soil properties correlated with laboratory infiltration, water dispersible clay and modulus of rupture in soils from goat-transformed and intact sites in the Xeric Succulent Thicket. Pearson correlation coefficients, n and p values are presented.

	Correlation	n	p value
<u>Laboratory infiltration</u>			
Silt	-0.69	32	<0.0001
MOR	-0.61	32	0.0001
CO ₂ flux	0.60	12	0.020
C:N	0.58	31	0.0003
Water dispersible clay	-0.46	30	0.005
Medium sand	0.45	32	0.005
<u>Modulus of rupture</u>			
Clay	0.67	32	<0.0001
Silt	0.63	32	0.0001
Infiltration	-0.61	32	0.0001
CO ₂ flux	-0.60	12	0.019
Medium sand	-0.57	32	0.0004
Total C	-0.56	31	0.0005
<u>Water dispersible clay</u>			
Silt	0.65	30	0.0001
Soluble Ca	0.64	29	0.0001
Coarse sand	0.62	30	0.0001
Fine sand	-0.60	30	0.0002
Infiltration	-0.46	30	0.005
Soluble NO ₃	0.43	30	0.008

The removal of *P. afra* by goats reduced soil organic matter content and increased the tendency of the soil to crust. Four possible explanations for the decline in soil organic matter are suggested. Firstly, the return of organic matter to the soil via leaf litter (present as a dark layer often several centimetres thick under *P. afra*) and the sloughing of roots are reduced when *P. afra* is removed. Secondly, the removal of the dense bush cover results in greater soil surface temperature (Lechmere-Oertle, unpublished data) and reduced interception of rainfall by vegetation, both of which will tend to increase the number of wetting and drying cycles in the surface soil. This in turn will greatly increase the rate of mineralisation of soil organic matter (Birch, 1958, Theron, 1963). Thirdly, the removal of the *P. afra* canopy

increases the exposure of surface litter to UV light which will tend to increase the rate of photodegradation of leaf litter (Moorhead and Callaghan, 1994). And fourthly, the vegetation may be actively repressing mineralisation of organic matter, possibly through antibacterial exudates, as postulated by Theron (1951; 1963). The C data presented suggest that the C sequestration potential of Xeric Succulent Thicket is large relative to that of other semi-arid regions.

The organic C content above 5% in the surface soils of intact thicket is extremely high for a semi-arid region, and may be due to the nature of the *P. afra* bush. The effect *P. afra* cover has on the abiotic environment and hence the rate of mineralisation is likely to be a major factor in the retention of organic matter in the soil. As discussed above, *P. afra* probably reduces the rate of mineralisation by shading the soil surface and intercepting rainfall. The mean daily maximum soil temperature over the period March 2001 to March 2002 was 12°C lower in intact sites under *P. afra* than in degraded sites in open grassy areas (mean maximum temperature of 23.2 vs 35.1°C, $p < 0.001$ student t-test, Lechmere-Oertel, unpublished data). The rate of mineralisation of soil organic matter tends to be highest at approximately 37°C (Jenkinson, 1981) and goat-transformed sites are likely to reach this optimum temperature more frequently and for more sustained periods than the shaded *P. afra* sites. The interception of rainfall in the *P. afra* canopy could conceivably reduce the amount of rainfall reaching the mineral soil by over 50%. Thurow *et al.* (1987), for example, found that only 54% of annual precipitation reached the mineral soil under oak canopies in Texas. The remainder was intercepted by the canopy or litter layer and evaporated. They demonstrated further that below a 5 mm rain event hardly any water reached the soil. During fieldwork on 24 July 2001, soil under *P. afra* bushes was observed to be dry after rainfall events of 41 mm (22 July) and 7 mm (23 July), whereas soil in open, bare areas away from bushes was wet to a depth of 60 mm. The lack of visible soil moisture below 60 mm in bare areas after 48 mm of rain may have been due to high evaporation from the exposed surface and/or limited infiltration due to crusting. Dry soil under *P. afra* was possibly due to stem flow or flow of water off the shrub canopy and onto surrounding bare areas. This explanation is, however, highly speculative and requires further investigation. Whether the chemical composition of the litter or antibacterial exudates from roots renders the *P. afra* organic matter especially stable is also still to be explored. Watt and Breyer-Brandwijk (1962) report that certain varieties of *P. afra* have a high tannin concentration. Such tannins may preserve leaf litter and partly explain the large stocks of C in intact thicket sites.

Soil organic matter may also have declined on the goat-transformed sites because of greater erosion on these sites than on the intact thicket sites. The greater tendency of soil on goat-transformed sites to crust (discussed below) suggests that runoff and erosion would indeed have been greater on these sites. Erosion may have removed the surface layer of soil, which is the most organic-rich layer in the profile, and could explain the precipitous decline in soil C in the 0-10 cm layer in goat-transformed sites. The decrease in the C:N ratio (Figure 3.5) as a result of goat-induced transformation to pseudo-savanna is consistent with both an erosion-induced decline in soil C, as well as a microbially-mediated decline in organic matter. This is because the C:N ratio in the soil profiles sampled decreased with depth (see Chapter 5) and mineralisation results in a lowering of the C:N ratio. It is thus difficult to separate out the effects of erosion versus soil microbes on the soil C content of goat-transformed sites.

Soil from goat-transformed sites showed a greater tendency to crust than soil from intact sites. This is evident because laboratory infiltration was lower and modulus of rupture was greater in soil from goat-transformed sites than intact sites (Figure 3.6). The reason for an increase in crusting on goat-transformed sites appears to be related to soil C status and soil texture as opposed to other factors affecting clay dispersion and crusting. Water dispersible clay did not show a consistent pattern between sites and thus factors affecting dispersion can not be invoked to explain infiltration and modulus of rupture differences recorded. Indeed, EC showed a trend of being greater in goat-transformed sites and thus increased dispersion due to EC effects were not expected. In addition, the sodium adsorption ratio of 1:5 soil suspensions and the exchangeable sodium percentage (ESP) did not show consistent responses to transformation of the vegetation. An increase in sodicity is consequently an unlikely reason for the reduction in infiltration. In contrast, total C, total N, labile C, CO₂ flux and soil respiration in the laboratory were all significantly lower in goat-transformed than in intact sites (Figure 3.5). The aggregate stability of soil and hence the resistance of a soil to crusting has been linked to soil C. The precise mechanism behind the aggregating effect of C on soil is unknown (Sumner, 1998), but numerous studies have shown strong correlations between measures of aggregate stability and soil C, in particular labile C (Tisdall and Oades, 1982; Du Plessis and Shainberg, 1985; Haynes and Swift, 1990; Golchin *et al.*, 1995; Blair and Crocker, 2000; Chan *et al.*, 2001). The role of C in soil aggregation may be linked to the interaction between organic molecules and clay micelles. Cook *et al.* (1992), for example, showed that water dispersible clay and total C were positively correlated in Australian

vertisols. Irrespective of the precise mechanism, the decrease in infiltration and increase in modulus of rupture in goat-transformed sites is likely to be primarily due to a decrease in soil C and its associated soil aggregating effect.

The soil properties most strongly correlated with laboratory infiltration, water dispersible clay and modulus of rupture are presented in Table 3.1. These Pearson correlation coefficients give some indication as to which soil properties play a role in the soil crusting process in this environment. The strong correlation of silt, medium sand and water dispersible clay with infiltration suggests that soil texture is also a critical aspect for understanding the tendency of these soils to crust. Silt and fine sand are commonly cited as the main size fractions that promote crusting (Bradford and Huang, 1992). Silt was strongly correlated with infiltration (-0.69), and was significantly greater on goat-transformed sites than intact sites. In addition, the concentration of coarse sand was lower on goat-transformed sites and may also have affected the rate of laboratory infiltration. The mechanism by which silt content may increase and coarse sand may decrease on goat-transformed sites as a result of transformation is not clear.

In addition to changes in organic matter status and tendency of the soil to crust, other noteworthy changes in soil chemical properties as a result of transformation of intact thicket to pseudo-savanna are an increase in pH, water-soluble Ca, Bray 2-extractable P and a decrease in (NH₄)OAc-extractable Mg. It is suggested that the increase in pH and Ca on goat-transformed sites may be due to the exposure of calcareous subsoil layers through erosion.

3.4 Conclusions

The transformation of *P. afra* thickets into pseudo-savanna by goats reduced soil C by 46 %, soil N by 27% and increased the tendency of the soils to crust. The dense and almost complete cover that *P. afra* affords the soil in this biome is most unusual for a semi-arid region receiving 250-400 mm of rainfall per annum. It is suggested that it is this plant that is largely responsible for the remarkably high total soil C levels in the area. The concentration of labile C under *P. afra* is also considerable, being greater than 4% at some sites, which suggests that much of the soil C in intact sites may be due to accumulation of relatively undecomposed leaf litter. The reduction in the C:N ratio after transformation also indicates that a large proportion of the organic matter in the intact surface soils has not undergone

humification. Whether the reason for the extreme accumulation of C is due to the adsorption of particularly stable organic compounds by the mineral soil, repression of the Birch effect due to interception of rainfall and soil shading, the release of antibacterial exudates by *P. afra* roots or a high concentration of tannin in the *P. afra* leaf material remains an interesting and challenging research topic. What is evident is that the removal of the *P. afra* cover results in a major decline in soil quality in terms of organic matter status and soil crusting. In the next chapter this theme of soil degradation is explored further, with the focus shifting to how the removal of vegetation affects soil C in five contrasting biomes in South Africa.

CHAPTER 4

SOIL CARBON AND VEGETATION IN FIVE CONTRASTING BIOMES OF SOUTH AFRICA

4.1 Introduction

The present increase in atmospheric CO₂ and associated concerns of global warming have turned the attention of the world community towards the global carbon cycle. Sequestering C into biomass or soil could buy time to address the problem and slow down the increase in atmospheric CO₂. The production of biomass in a predominantly semi-arid country such as South Africa is, however, often limited by the availability of water. This limits the accumulation of soil C. Consequently, the stocks of soil C per unit area in dry South African landscapes are typically lower than in temperate, mesic regions. Soil with a cover of vegetation tends to have a greater concentration of soil C than exposed soil because plants return organic matter to the soil via leaf litter or sloughing of roots and they may suppress mineralisation by releasing antibacterial exudates (Theron, 1951; 1963). Plants also minimise the Birch effect (increased mineralisation catalysed by wetting and drying of the soil) by shading and cooling the soil surface and by intercepting rainfall, both of which reduce the number of wetting and drying cycles in topsoil. The removal of vegetation through ploughing, grazing, browsing or burning reduces the return of organic matter to the soil and can increase the rate of mineralisation. Declines in soil C due to cultivation have been documented in grasslands of the highveld (Du Toit *et al.*, 1994; Nel *et al.*, 1996) but the extent to which land use practices affect soil C in other South African regions is largely unknown. Five vegetation types were selected, namely West Coast Renosterveld, Central Nama Karoo, Xeric Succulent Thicket, Moist Upland Grassland and Mixed Lowveld Bushveld, and the stocks of soil C under vegetation, in the open and in lands that had either been cultivated, browsed, planted to pasture or frequently burnt, were determined.

4.2 Materials and methods

4.2.1 Study areas

4.2.1.1 West Coast Renosterveld

This study area is situated on the Bokkeveld plateau, near the town of Nieuwoudtville in the Northern Cape (31°20'S; 19°10'E), approximately 300 km north of Cape Town at an elevation of 800 m above sea level (a.s.l.) (Figure 4.1). The climate of the region is strongly seasonal with a mean annual temperature of 15.9°C (mean monthly temperature 9.2-22.2°C) and a mean annual rainfall of 350 mm, mostly falling in the winter months of May to August. Soils on the plateau can be broadly divided into those derived from Dwyka sediments (shale and tillite) and those derived from Karoo dolerite. Soil forms on the plateau typical of the Dwyka sediment-derived soils include Estcourt, Valsrivier, Glenrosa, Sterkspruit, Klapmuts and Swartland; those typical of the dolerite-derived soils include Arcadia, Shortlands and Augrabies (Soil Classification Working Group, 1991). In the terminology of the World Reference Base classification system, the Dwyka sediment-derived soils include Eutric Planosols, Hyperochric Rhodic Luvisols, Skeletic Leptosols, Abruptic Hyperochric Cutanic Luvisols and Albic Luvisols; and the soils of the dolerite-derived soils include Chromic Vertisols, Chromi-Calcic Vertisols, Vertic Leptosols, Grumic Vertisols, Calcic Vertisols, Rhodi-Eutric Nitisols and Calcaric Cambisols (FAO, 1998). The predominant land uses on the plateau are sheep farming and wheat production. Old wheat lands on some farms have been planted to *Medicago* to serve as winter pasture for sheep. The vegetation on Dwyka sediment-derived soils is characterised by numerous geophyte species (predominantly in the family Iridaceae), the renosterbos (*Elytropappus rhinocerotis*) and Cape wire grass (*Merxmullera stricta*).

4.2.1.2 Central Nama Karoo

This study area is situated 30 km west of Beaufort West in the Western Cape (32°15'S; 22°50'E) at 1100 m a.s.l. (Figure 4.1). The climate of the region is strongly seasonal with a mean annual temperature of 17.4°C (mean monthly temperature 11.3-23.4°C) and a mean annual rainfall of 225 mm, mostly falling in the summer months. Soils in the region are derived from Beaufort Group sediments and Karoo dolerite. Soil forms identified in the area

include Addo, Oakleaf, Augrabies, Prieska, Garies, Kimberley and Valsrivier. In the terminology of the World Reference Base classification system the soils include Aridic Calcisols, Aridic Cambisols, Calcic Luvisols, Petric Calcisols and Chromic Luvisols. The predominant land uses in the region are livestock and game farming. The vegetation is characterised by small bushes (e.g. *Pentzia incana*) and grasses (e.g. *Stipagrostis* spp.).

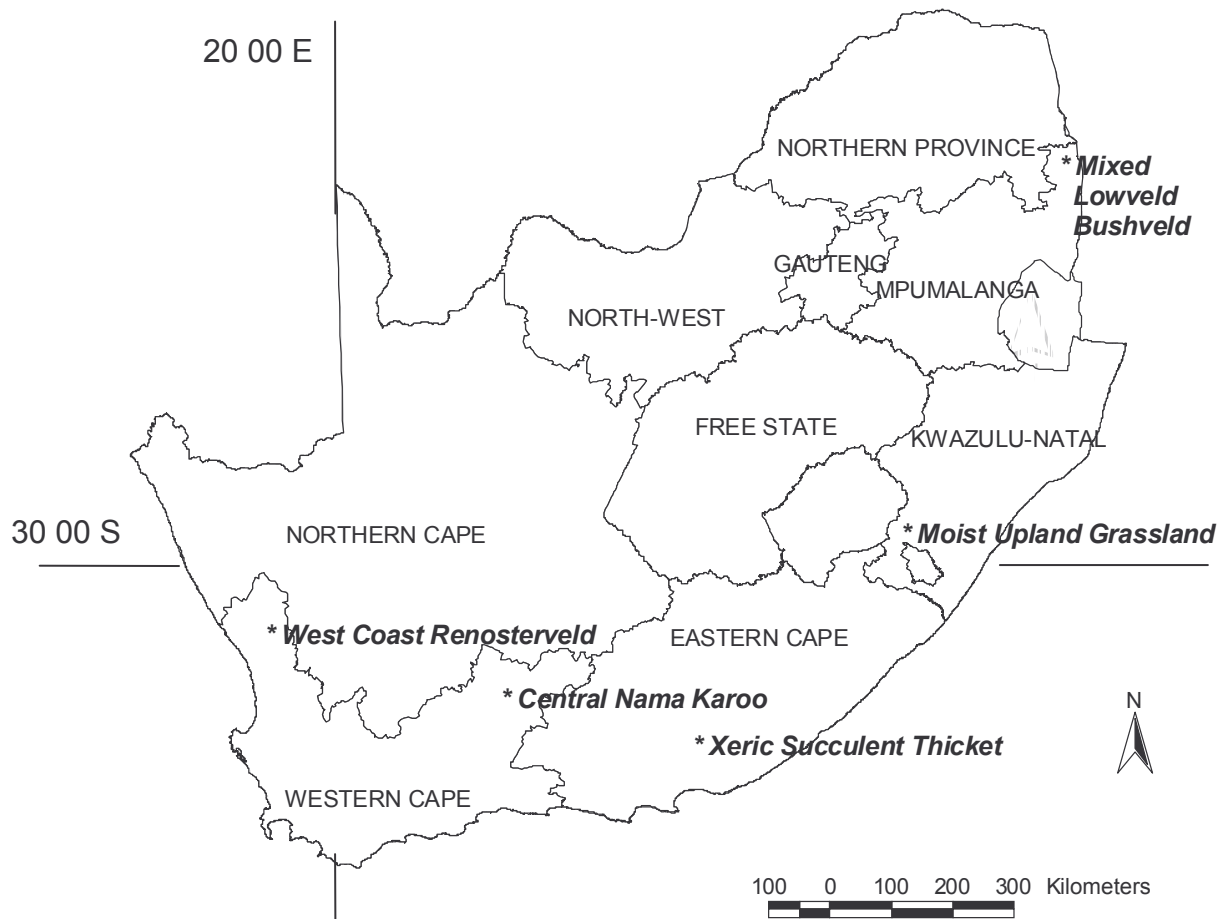


Figure 4.1 The location of each study area used for investigating soil carbon stocks in five contrasting biomes of South Africa.

4.2.1.3 Xeric Succulent Thicket

The study area is situated in a broad valley west of Kirkwood, Eastern Cape (33°30'S; 25°20'E), at an elevation of 300-500 m a.s.l. (Figure 4.1). The climate of the region is strongly seasonal with a mean annual temperature of 17.6°C (mean monthly temperature 12.3-22.4°C) and a mean annual rainfall of 250-400 mm distributed evenly through the year.

Bokkeveld shales, sandstones and siltstones of the Ceres and Traka subgroups lie on the southern side of the valley and Uitenhage mudstones, sandstones and conglomerates of the Kirkwood formation lie on the northern side of the valley. Soil forms identified in the valley include Augrabies, Klapmuts, Valsrivier, Oakleaf, and Glenrosa. In the terminology of the World Reference Base classification system the soils include Calcaric Cambisols, Calcic Luvisols, Rhodic Luvisols and Calcaric Regosols. The vegetation of the area is characterised by the bush *Portulacaria afra*, which forms a dense thicket ~3 m in height. The predominant land use in the region is goat farming.

4.2.1.4 Moist Upland Grassland

This study area is situated in the foothills of the southern Drakensberg, near the town of Underberg, KwaZulu-Natal (29°45`S; 29°30`E) at an elevation of ~1700 m a.s.l. (Figure 4.1). The climate of the region is strongly seasonal with a mean annual temperature of 15.1°C (mean monthly temperature 9.2-19.2°C) and a mean annual rainfall of 1050 mm, mostly falling in the summer months. Beaufort mudstones and sandstones of the Tarkastad subgroup are the predominant rock types and are interspersed with Karoo dolerite outcrops. Soil forms identified in the study area include Sepane, Oakleaf, Tukulu, Glenrosa, Hutton and Clovelly. In the terminology of the World Reference Base classification system the soils include Gleyic Luvisols, Rhodic Cambisols, Chromic Luvisols, Gleyic Cambisols, Haplic Regosols, Rhodic Acrisols and Chromic Acrisols. Land in the region is utilised for beef production, dairy farming, maize cultivation, conservation of grassland and timber production. The grasslands are characterised by numerous geophytes and grasses (e.g. *Eucomis* spp. and *Themeda triandra*).

4.2.1.5 Mixed Lowveld Bushveld

This study area comprises the long-term burn experiments (Van Wyk, 1971) in the Kruger National Park, Mpumalanga (23°-25°S; 31°-32°E) at 300-700 m a.s.l. (Figure 4.1). The climate is strongly seasonal with a mean annual temperature range of 21.1-23.3°C (mean monthly temperature 16-28°C). Rains fall predominantly in summer and mean annual rainfall varies from 687 mm at Pretoriuskop in the south west to 404 mm at Letaba in the central region of the park. Soils in the southern burn plots are derived from Nelspruit granite and soil forms include Hutton, Bainsvlei, Clovelly, Cartref and Avalon. In the terminology of the

World Reference Base classification system these soils include Rhodic Lixisols, Paraplinthic Cambisols, Dystric Regosols and Paraplinthic Lixisols. Soils in the burn plots in the central region of the park are derived from basalt and soil forms include Shortlands, Swartlands, Mayo and Milkwood. In the terminology of the World Reference Base classification system these soils include Rhodic Nitisols, Haplic Luvisols and Leptic Phaeozems. The long-term burn experiment began in 1955 and consists of 7 ha plots with different frequencies and seasons of burns. Soils were sampled from unburnt plots and plots annually burnt in August. The vegetation is a savanna characterised by *Acacia* and *Combretum* spp. in the south and central regions, and *Terminalia sericea* in the southwest near Pretoriuskop.

4.2.2 Sampling

Composite samples, comprising 15-20 subsamples, were taken to a depth of 10 cm from beneath vegetation and in open areas (as detailed in Table 4.1). Profile samples were taken at 0-2 cm, and thereafter at 10 cm intervals to the base of the B horizon in West Coast Renosterveld (Dwyka sediment-derived soils and dolerite-derived soils) and in Xeric Succulent thicket. In the Moist Upland Grassland and Central Nama Karoo bulk samples were taken using an auger at 10 cm intervals to a depth of 50 cm. In the Mixed Lowveld Bushveld samples were taken from profiles at 1 cm intervals to 10 cm, 5 cm intervals to 20 cm and at 40 cm (see Chapter 2). Stocks of C and N in tonnes per hectare to different depths were estimated at each site. Bulk density was calculated from the texture and C content of the 0-10 cm layer, using algorithms developed by Saxton *et al.* (1986) (and accessed at www.pedosphere.com). An accurate estimate of bulk density at the scale of hectares is extremely difficult to make, as bulk density varies both horizontally and vertically. The algorithms of Saxton *et al.* (1986) generate an approximate bulk density that can be used to place the C and N percentage values in a C sequestration context.

4.2.3 Soil analyses

Soils were air-dried, sieved to <2 mm and total C and N were determined by complete combustion using a Eurovector Euro EA Elemental Analyzer. An analysis of the contribution of inorganic and organic C to total C was not undertaken as free carbonates were absent from the majority of soil samples collected (as determined by adding 10% hydrochloric acid and checking for effervescence). Where effervescence was observed (usually in a calcareous B

horizon) soil C concentration was often double the mean concentration of non-effervescing samples taken at the same depth (as is evident in two of the samples taken at 45 cm in the Central Nama Karoo in Figure 4.2).

4.2.4 Statistical analyses

Statistical analyses were performed using the software package Unistat 5.0. A graphical investigation showed that the condition for an ANOVA of a normal distribution was not always met in the data from renosterveld on Dwyka sediments as well as Moist Upland Grassland and consequently a nonparametric approach was taken. A Kruskal-Wallis test was applied to data from renosterveld on Dwyka sediments (4 groups: vegetation, open, *Medicago*, wheat) and grassland (7 groups: grassland-dolerite, grassland-sandstone, maize, ryegrass, *Eragrostis*, kikuyu, pine). Significant differences between groups ($p < 0.05$) were detected using a t-distribution multiple comparison (Conover, 1980). Data from renosterveld on dolerite and the Central Nama Karoo were analysed using a student t-test. Data from paired contrasts in Xeric Succulent Thicket and burnt versus unburnt plots in bushveld (two separate analyses: granite and basalt) were analysed using a paired t-test. Differences were deemed significant where $p < 0.05$.

4.3 Results

Stocks of soil C and N to a depth of 10 cm and 50 cm are presented in tonnes per hectare in Table 4.1 and 4.2, respectively. The stocks of soil C and N varied across regions in the following order: Xeric Succulent Thicket > Moist Upland Grasslands > West Coast Renosterveld > Mixed Lowveld Bushveld > Central Nama Karoo. Land under cultivation with wheat/maize, farmed intensively with goats and burnt frequently, had lower soil C and N than virgin veld. Stocks of C and N were also greater in soils under a cover of woody vegetation than in open, exposed soils. The distribution of C and N, as well as the C:N ratio down selected soil profiles, are presented in Figures 4.2-4.4 for Central Nama Karoo, West Coast Renosterveld, Xeric Succulent Thicket and Moist Upland Grassland.

Comparable data from Mixed Lowveld Bushveld are presented in Chapter 2 (Figure 2.6). Soil C and N, as well as the C:N ratio, declined in all profiles, except for two profiles in the Central Nama Karoo, which showed an increase in total C at a depth of 30-40 cm. This

pattern of increasing total C with depth is ascribed to a calcrete layer. Samples taken at 1 cm intervals in the Mixed Lowveld Bushveld showed that the concentrations of C and N at 0-1 cm are several times greater than at depths below 4 cm (see Chapter 2).

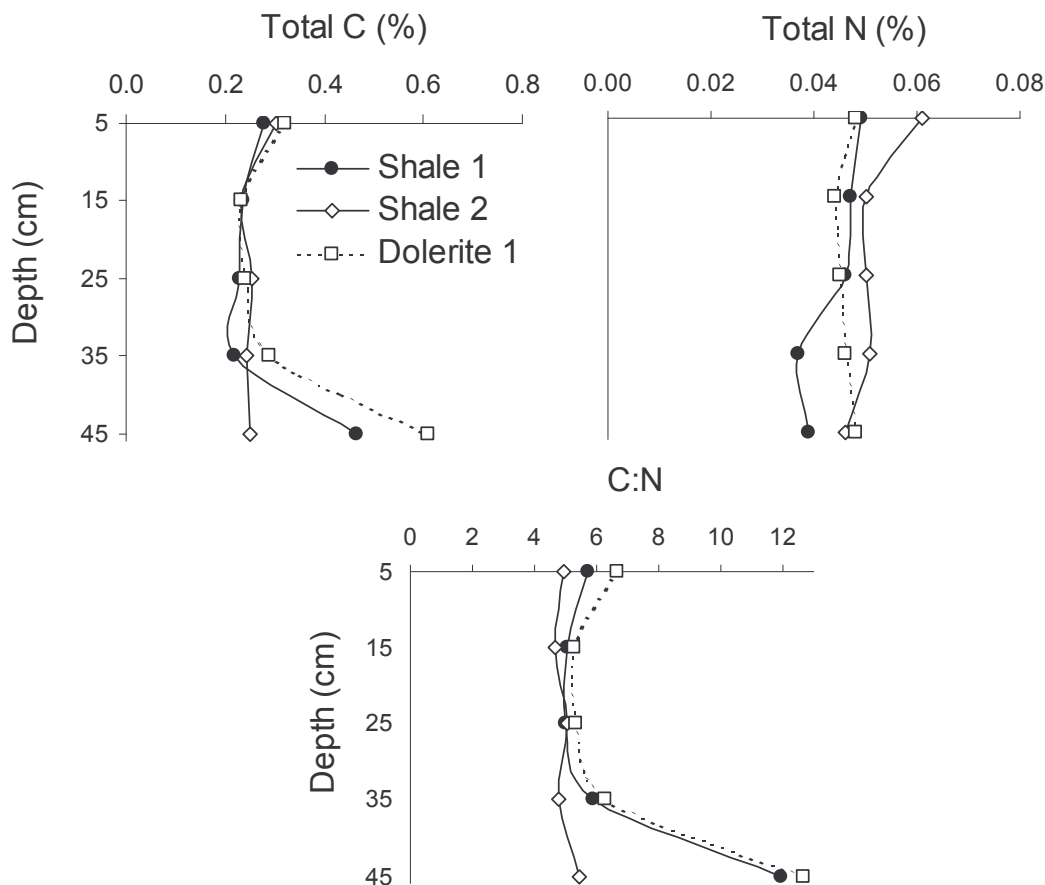


Figure 4.2 The change in total C, N and C:N ratios with depth in the Central Nama Karoo. Three profiles are presented; two from predominantly shale-derived soils and one from a predominantly dolerite-derived soil. Where error bars are depicted, these are the standard errors of the mean

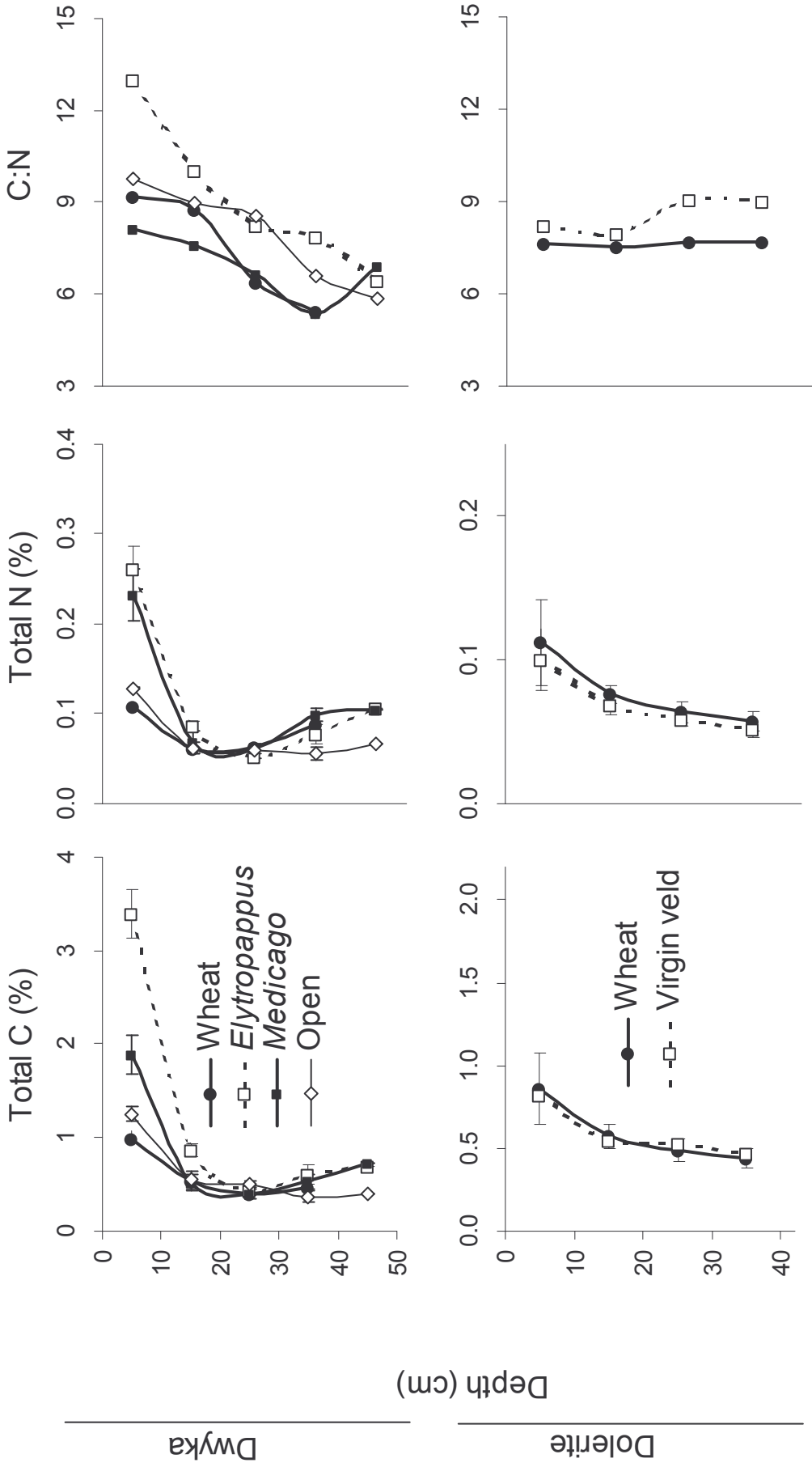
4.4 Discussion

Stocks of C in the top 50 cm of soil ranged from 21 t ha^{-1} in Central Nama Karoo to 168 t ha^{-1} in Xeric Succulent Thicket. Land use practices such as cultivation, livestock production and veld burning, that reduce the cover of vegetation in space or time, were associated with lower stocks of soil C and N than those of benchmark sites in virgin veld, particularly in the top 10 cm of soil. Declines in soil C due to cultivation were proportionately greater in renosterveld than mesic grassland. At Nieuwoudtville, soil C under renosterbos was greater than in wheat fields (means of 65 vs 37 t ha^{-1} in the top 50 cm of soil, $p < 0.05$), whereas in the Underberg

region, soil C under virgin grassland was not significantly different from soil C under maize cultivation (164 vs 153 t ha⁻¹). A consistently lower soil C percentage in maize fields did, however, suggest that soil C was being lost under maize cultivation (the small sample size of n=3 was probably insufficient for detecting a significant difference). Soil C is lost from cultivated fields due to a greater rate of mineralisation and reduced returns of organic matter to the soil (Edwards *et al.*, 1992; Du Toit *et al.*, 1994; Francis *et al.*, 2001).

The possible reasons for a greater rate of mineralisation in cultivated fields in comparison to virgin veld include: greater aeration of the soil due to tillage; exposure of previously protected organic matter; increased wetting and drying of the soil surface which maintains the microbial population in a young, metabolically active state (Birch, 1958); a reduced concentration of microbe-inhibiting, root exudates (Theron, 1951; 1963); and greater soil temperature due to exposure to the sun (Savage and Vermeulen, 1983). The climate at Nieuwoudtville is warmer and drier than Underberg and consequently the Birch effect and raised soil temperature are likely to have a greater effect on microbial metabolism and hence the rate of mineralisation. Du Toit *et al.* (1994) and Du Toit and Du Preez (1995) found that declines in soil C under cultivation on the highveld were greatest in areas that were relatively warm and dry as opposed to cool and moist. The data from Nieuwoudtville and Underberg corroborate this observation. Greater rates of mineralisation due to changes in land use are not, however, restricted to cultivated sites. Whenever vegetation is removed by grazing, browsing or fire, soil microbial activity is likely to increase.

Livestock, if managed ineffectively, can degrade the condition of veld by reducing the cover of vegetation, which in turn will tend to reduce soil C (Du Preez and Snyman, 1993). The effect of goats at the Eastern Cape study site in Xeric Succulent Thicket is especially noteworthy. Soil C under *P. afra* in intact sites was greater than in goat-transformed pseudo-savanna sites (means of 71 and 40 t ha⁻¹ in the top 10 cm of soil). The total amount of C and N in the soil mantle in the Xeric Succulent Thicket is exceptionally high for a semi-arid environment (means of 168 t C ha⁻¹ and 13 t N ha⁻¹ in the top 50 cm of soil). The annual rainfall at Nieuwoudtville is comparable to the Eastern Cape study site (250-400 mm) and consequently stocks of soil C were expected to fall within a similar range. Stocks of soil C and N were greatest under renosterbos at Nieuwoudtville (means of 65 t C ha⁻¹ and 7 t N ha⁻¹ in the top 50 cm of soil), yet were only about half of the C and N found in the Xeric Succulent Thicket. Indeed, the mean mass of C lost from the top 10 cm of soil in thicket vegetation



Vest

Coast Renosterveld. Where error bars are depicted, these are the standard errors of the mean.

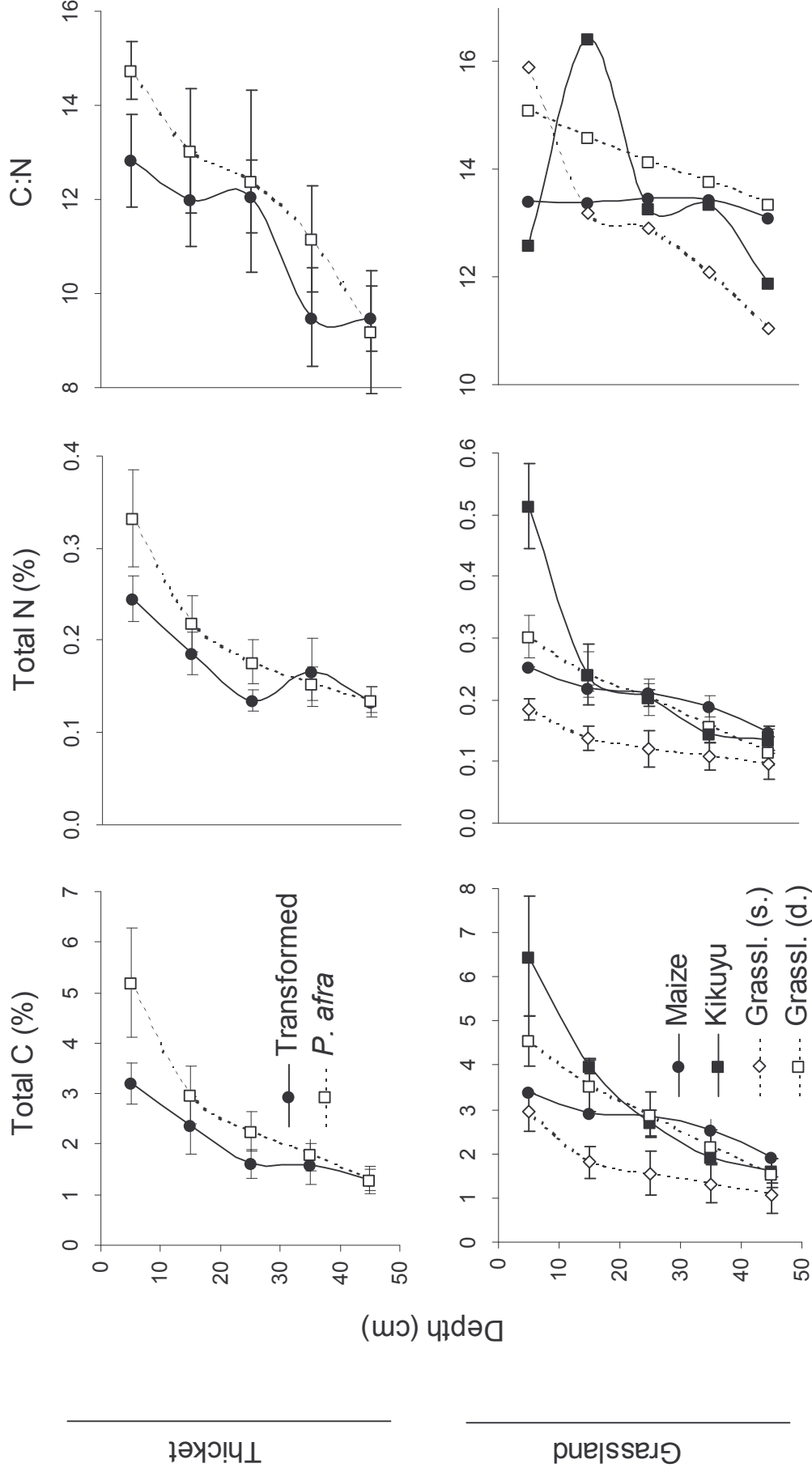


Figure 4.4 The change in total C, N and C:N ratios with depth in Xeric Succulent Thicket and Moist Upland Grassland in relation to land use and geology. In the thicket vegetation of the Eastern Cape, goat-transformed landscapes and intact landscapes dominated by the bush *Portulacaria afra* are compared. In the grassland of the southern Drakensberg, cultivated maize lands, kikuyu (*Pennisetum clandestinum*) pasture and virgin grassland (on sandstone and dolerite-derived soils) are compared. Where error bars are depicted, these are the standard errors of the mean.

Table 4.1 Total C and N to a depth of 10 cm in renosterveld, karoo, thicket, grassland and bushveld. Mean bulk density was calculated from means of clay, silt, sand and carbon content for each sampling site, using algorithms developed by Saxton et al. (1986).

Location	Soil sampling site	Geology	(%) C	(%) N	(%) C	(%) N	(%) C	(%) N	(%) C	(%) N	se	se	BD (g cm ⁻³)		
West Coast Renosterveld	<i>Elytropappus rhinocerotis</i>	Dwyka tillite	1.8	0.14	a	0.13	0.006	a	28	2	a	1.9	0.08	8	
	Open soil	Dwyka tillite	1.0	0.09	b	0.09	0.005	b	15	1	b	1.4	0.08	16	
	Medicago	Dwyka tillite	1.1	0.13	b	0.11	0.004	b	16	2	b	1.6	0.07	6	
	Active wheat cultivation	Dwyka tillite	1.1	0.16	b	0.10	0.006	b	16	2	b	1.5	0.09	4	
	Virgin veld	Dolerite	1.0	0.1	a	0.11	0.01	a	12	1	a	1.4	0.12	6	
Central Nama Karoo	Active wheat cultivation	Dolerite	0.8	0.1	a	0.09	0.01	a	9	2	a	1.1	0.08	5	
	<i>Pentzia incana</i>	Shale	0.4	0.03	a	0.06	0.003	a	7	0.5	a	1.1	0.05	12	
	Open soil	Shale	0.3	0.02	b	0.05	0.002	b	5	0.3	b	0.9	0.04	12	
	<i>Stipagrostis</i> grass spp.	Dolerite	0.6	0.15	a	0.05	0.002	a	9	2.6	a	0.9	0.04	6	
	Open soil	Dolerite	0.2	0.01	b	0.04	0.001	b	4	0.2	b	0.7	0.03	6	
Individual plots	A vondale 3	Shale	0.2			0.04			3.3			0.7		1	
	Kamferskraal 3	Shale	0.2			0.04			3.6			0.7		1	
	Elandsfontein 4	Dolerite	0.3			0.05			4.7			0.8		1	
	Bleakhouse 2	Dolerite	0.2			0.05			4.1			0.9		1	
Xeric Succulent Thicket	Intact <i>Portulacaria afra</i>	Shale/sandstone	5.6	0.53	a	0.33	0.028	a	71	7	a	4.2	0.36	8	
	Goat-transformed sites	Shale/sandstone	3.0	0.32	b	0.24	0.019	b	40	4	b	3.1	0.25	8	
Moist Upland Grassland	Grassland	Shale/dolerite	4.7	0.38	bc	0.31	0.023	b	54	4	bc	3.5	0.26	9	
	Grassland	Sandstone	2.2	0.21	a	0.15	0.009	a	27	3	a	1.8	0.12	3	
	Maize	Shale/dolerite	3.5	0.36	ab	0.27	0.024	ab	41	4	ab	3.2	0.29	3	
	Communal old maize lands	Shale/dolerite	2.4			0.18			29			2.2		1	
	Kikuyu	Shale/dolerite	6.0	0.81	c	0.47	0.051	c	69	9	c	5.3	0.58	3	
	Ryegrass	Shale/dolerite	4.6	0.31	bc	0.35	0.025	bc	54	4	bc	4.1	0.30	3	
	Pine plantations	Shale/dolerite	4.5	0.67	bc	0.30	0.046	b	52	8	abc	3.5	0.54	3	
	Fragrostis	Shale/dolerite	5.2	0.75	bc	0.37	0.043	bc	60	9	bc	4.2	0.49	3	
	Mixed Lowveld Bushveld	Unburnt savanna	Nelspruit granite	0.9	0.03	a	0.08	0.004	a	14	0.4	a	1.3	0.06	8
	Annual burning	Nelspruit granite	0.7	0.04	b	0.06	0.003	b	11	0.6	b	1.0	0.04	8	
Unburnt savanna	Basalt		2.4	0.25		0.17	0.017		28	3		2.1	0.20	7	
	Annual burning	Basalt	2.1	0.11		0.15	0.008		25	1		1.8	0.09	7	

BD = mean bulk density for each land use; se = standard error of the mean; n = number of samples; Significant differences (p<0.05) between means were determined by a Kruskal Wallis test (t-distribution for multiple comparison) for renosterveld (on Dwyka sediments) and grassland; a paired t-test for thicket, bushveld on granite and bushveld on basalt; and a student t-test for renosterveld on dolerite and karoo (dolerite and shale). Where letters are different, means were significantly different at the 95% confidence interval.

Table 4.2 Estimated stocks of total soil C and N to a depth of 50 cm in renosterveld, karoo, thicket and grassland. Three bulk density scenarios are depicted. A bulk density range was calculated for each profile from means and standard errors of clay, silt and sand content in each vegetation type and soil carbon content for each profile, using algorithms developed by Saxton *et al.* (1986).

Vegetation type	Land use/sampling site	Geology	Carbon to a depth of 50 cm in tonnes per hectare			Nitrogen to a depth of 50 cm in tonnes per hectare			p > 0.05	n	se										
			BD 1 (minimum)	BD 2 (mean)	BD 3 (maximum)	Carbon (BD1)	Carbon (BD2)	Carbon (BD3)				Nitrogen (BD1)	Nitrogen (BD2)	Nitrogen (BD3)							
West Coast Renosterveld	<i>Elytropappus rhinocerotis</i>	Dwyka tillite	1.44	1.51	1.59	62	6	65	6	68	6	3	3	a							
	Open soil	Dwyka tillite	1.47	1.53	1.62	38	3	40	3	42	3	3	3	ab							
	Medicago	Dwyka tillite	1.46	1.53	1.61	44	6	46	6	48	6	4	4	ab							
	Active wheat cultivation	Dwyka tillite	1.47	1.54	1.63	36	0.3	37	0.4	39	0.4	3	3	b							
Virgin veld		Dolerite	1.18	1.23	1.30	33	5.3	34	5.5	36	5.8	4	4								
	Active wheat cultivation	Dolerite	1.19	1.24	1.31	33	4.9	34	5.1	36	5.4	3	3								
Central Nama Karoo	Avondale 3	Shale	1.62	1.70	1.85	26	27	30													
	Kamferskraal 3	Shale	1.62	1.70	1.86	20	21	23													
	Elandsfontein 4	Dolerite	1.61	1.69	1.84	29	31	34													
	Bleakhouse 2	Dolerite	1.59	1.67	1.82	48	50	54													
Xeric Succulent Thicket	Intact <i>Portulacaria afra</i>	Shale/sandstone	1.21	1.27	1.35	161	25	168	26	178	27	8	8								
	Goat-transformed sites	Shale/sandstone	1.26	1.32	1.40	125	15	131	16	140	17	8	8								
Moist Upland Grassland	Grassland	Shale/dolerite	1.09	1.15	1.24	155	21	164	22	177	23	8	8	ab							
	Grassland	Sandstone	1.16	1.23	1.33	91	27	97	29	105	31	3	3	a							
	Maize	Shale/dolerite	1.12	1.18	1.27	144	7	153	8	164	8	3	3	ab							
	Kikuyu	Shale/dolerite	1.08	1.14	1.22	189	22	199	23	214	24	3	3	b							
	Ryegrass	Shale/dolerite	1.10	1.17	1.26	160	23	169	24	182	26	3	3	ab							
	Pine plantations	Shale/dolerite	1.10	1.17	1.25	162	29	172	31	185	33	3	3	ab							
Eragrostis		Shale/dolerite	1.09	1.15	1.24	174	39	184	40	198	43	3	3	b							
		Shale/dolerite	1.09	1.15	1.24	174	39	184	40	198	43	3	3	b							

BD = mean bulk density for each land use; se = standard error of the mean; n = number of samples; significant differences ($p < 0.05$) between means were determined by a Kruskal Wallis test (t-distribution for multiple comparison) for renosterveld (on Dwyka sediments) and grassland; a paired t-test for thicket; and a student t-test for renosterveld on dolerite and karoo. Where letters are different, means were significantly different at the 95% confidence interval.

after goat-induced transformation to an open pseudo-savanna is more than the total mass of C in the soil profile in open areas of renosterveld.

Although the effect of livestock on stocks of soil C in other vegetation types was not investigated directly, a comparison of stocks of soil C under vegetation and in adjacent open soil can give an indication of the potential effect of livestock on soil C. In renosterveld, soil C under renosterbos was about one and three quarters times greater than in adjacent open soil (means of 28 versus 15 t ha⁻¹ to a depth of 10 cm, p<0.01). Consequently, for every 1 ha of renosterbos removed by livestock, approximately 13 tonnes of C are likely to be lost from the top 10 cm of soil. In contrast, for every 1 ha of *Pentzia incana* bushes removed by livestock in the Central Nama Karoo, only 2 tonnes of C are likely to be lost from the top 10 cm of soil. Soil C under *Pentzia incana* bushes was about one and a half times greater than in adjacent open soil (7 vs 5 t ha⁻¹).

In addition to climate, land use and vegetation type, soil parent materials can affect stocks of soil C. In Moist Upland Grassland, stocks of C in soils with reddish colours (usually indicating an influence of dolerite) were almost double those in soils with greyish colours (derived predominantly from sandstone) (respective means of 164 vs 97 t C ha⁻¹ in the top 50 cm of soil). The reason for this effect of parent material is not apparent in the data collected. The texture, (NH₄)OAc-extractable cation concentrations, pH and EC of these soils were similar (unpublished data). The data, however, corroborate Sumner (1957), who found that the soil C content of dolerite-derived soils in KwaZulu-Natal was greater than that in Beaufort sediment-derived soils. An explanation for soil C differences may lie in differences in clay mineralogy and sesquioxide content. Dolerite-derived soils will, in particular, tend to have a greater sesquioxide content than sedimentary-derived soils (Sumner, 1957; Olson *et al.*, 2000). This may be the primary reason for greater soil C in dolerite-derived soils, as sesquioxides are powerful binders and thus preservers of soil C (Zech *et al.*, 1997; Percival *et al.*, 2000). Percival *et al.* (2000) studied the soil C distribution across New Zealand and showed that pyrophosphate-extractable Al was strongly correlated with soil C content across all soil types. They concluded that chemical stabilisation of organic matter by sesquioxides is the key process controlling accumulation of soil C in New Zealand.

The effect of parent materials on stocks of soil C is also evident in the Mixed Lowveld Bushveld of the Kruger National Park. Stocks of C in burnt plots in basalt-derived, clayey

soils were double those in granite-derived, sandy soils (means of 28 vs 14 t ha⁻¹ to a depth of 10 cm), despite a greater mean annual rainfall in the region with granite-derived soils. This result is similar to that of Bird *et al.* (2000) who found that the concentration of C in clay soils in a tropical savanna ecosystem at Matopos, Zimbabwe was double that of C in sandy soils (10 vs 5 t ha⁻¹ to a depth of 5 cm). The effect of fire on stocks of soil C to a depth of 10 cm in the Kruger National Park were not as pronounced as that found by Bird *et al.* (2000). Stocks of C were 27% greater in unburnt plots than burnt plots on granite-derived soils (14 vs 11 t ha⁻¹ to a depth of 10 cm) and were consistently (but not significantly) greater in unburnt plots than burnt plots on basalt-derived soils (28 vs 25 t ha⁻¹). In comparison, Bird *et al.* (2000) found in the Matopos, Zimbabwe that soil C in the 0-5 cm interval in unburnt plots was 40-50% greater than burnt plots. The comparably larger effect of fire on soil C in Matopos may be a reflection of the narrower sampling interval (0-5 cm as opposed to 0-10 cm in the Kruger National Park). Indeed, differences in soil C between burnt and unburnt plots in the Mixed Lowveld Bushveld were greatest in the 0-1 cm layer. Soil C in the 0-1 cm layer in unburnt plots was two and half times greater than in burnt plots (Figure 2.6) and highlights how sampling to depths greater than a few centimetres can obscure differences related to land use. The reduction in soil C as a result of burning can be attributed to reduced returns of organic matter and to an increase in soil microbial activity due to the Birch effect and greater soil temperatures (Birch, 1958; Knapp *et al.*, 1998). It is also inevitable that, immediately after fire, the alkalinity of ash will raise pH in the first few centimetres of surface soil where the organic matter is most concentrated, stimulating microbial activity and organic matter oxidation (Greenwood, 1968). Interestingly, pH in the top centimetre of soil in the southern Kruger National Park was consistently lower in burnt plots than unburnt plots (Figure 2.8). This is ascribed to the generation of acidity during organic matter oxidation (Russell, 1988). Another possible factor affecting soil C loss in burnt plots is a reduction in plant roots and root exudates. Theron (1951; 1963) showed that N mineralisation was greatly reduced under grass swards and suggested that root exudates may be inhibiting mineralisation. This hypothesis warrants further investigation, particularly for furthering an understanding of how to manage soil C sequestration.

The pattern of decreasing C:N ratio with depth in most profiles (Figures 4.2-4.4) is a result of several factors. Litter on the soil surface (which may include woody material) is likely to have a greater C:N ratio than organic matter inputs from root die-off, deeper in the soil profile. Organic matter that moves via invertebrate activity from the soil surface to deeper in

the soil profile is likely to be older and more decomposed than surface organic matter. Decomposition and thus nutrient cycling is likely to be more rapid at the surface than at depth because of greater aeration, greater temperature and greater activity of soil invertebrates (such as earthworms) at the surface than at depth. Despite this greater rate of decomposition and thus loss of C from the surface, the C:N ratio remains relatively high because of continual input of fresh litter. The decrease in C:N is particularly pronounced in Xeric Succulent Thicket and suggests that the unusually high concentration of C in the surface soil is predominantly fine plant material that has only partly decomposed. Virgin veld in renosterveld, thicket, grassland and bushveld biomes had a consistently greater C:N ratio in surface soils in comparison to soils in adjacent cultivated, goat-transformed or frequently burnt landscapes. This suggests that these land uses reduce the input of fresh organic matter with a high C:N ratio and/or increase the rate of mineralisation, thereby reducing the C:N ratio of organic matter in surface soils.

Occasionally land use practices can result in an increase in soil C. This effect is evident in kikuyu pastures established on what was previously Moist Upland Grassland. Stocks of soil C in kikuyu pastures were consistently (but not significantly) greater in the top 10 cm than in virgin grassland (69 vs 54 t ha⁻¹). The lack of a significant difference between carbon stocks in kikuyu pastures and grassland is probably a function of small sample size (n=3). The beneficial effects of pastures in terms of increasing soil organic matter and maintaining soil structure are well documented (Tisdall and Oades, 1982; Haynes *et al.*, 1991; Francis *et al.*, 2001). A trend of greater soil C in kikuyu pastures is probably due to: increased shading of the soil surface which reduces the rate of mineralisation; greater productivity of the grass sward in comparison to virgin veld and hence greater returns of organic matter; fertilization of pastures with N, P and S (Campbell *et al.*, 1991; Paustian *et al.*, 1992) which allows for a potential accumulation of soil C (given that soil C:N, C:P and C:S ratios tend towards their initial equilibrium ratios); and a possible repression of mineralisation due to release of antibacterial exudates from grass roots (Theron, 1951; 1963). In particular, fertilization with N is likely to increase sequestration of soil C, due to greater plant productivity and equilibration of soil C:N ratio. Burke *et al.* (1997) summarised this notion by noting that “N is required for the capture of C”.

4.5 Conclusions

The potential of landscapes in South Africa to sequester C from the atmosphere is largely a function of climate, parent material and the cover of vegetation. Where vegetation has been removed due to cultivation, goat farming or frequent burning, stocks of soil C tended to decline. The C:N ratio also declined in the upper part of the soil mantle under these land uses, which suggests that inputs of fresh organic matter were reduced and/or that the rate of mineralisation had increased. The effect of vegetation removal on soil C content is most evident in semi-arid areas. In thicket near Kirkwood, for example, farming with goats resulted in almost a halving of soil C (a mean loss of 31 t C ha⁻¹) to a depth of only 10 cm. Similarly, in bushveld in the Kruger National Park, annual burning resulted in a loss of about three quarters of the soil C in the 0-1 cm layer in comparison to unburnt plots. The results highlight how land use effects on stocks of soil C are often most evident in the top few centimetres of the soil profile. Where natural ecosystems have been restored to increase soil C sequestration (to gain international C credits), stocks of soil C tend to increase slowly and are difficult to measure (Robles and Burke, 1998). By focusing on the 0-1 cm layer, C sequestration accountants and soil quality researchers may reveal short-term effects that are likely to be obscured by sampling to greater depths. Such short-term effects on soil C at the surface may provide important clues for longer term trends at greater depths. Soil C is at present under the world spotlight because of its role in C sequestration, yet the beneficial effects of soil C go beyond mitigating atmospheric pollution. In the next chapter the effect of vegetation removal (and the associated loss of soil C) on soil crusting is investigated in five contrasting biomes in South Africa.

CHAPTER 5

FACTORS AFFECTING SOIL CRUSTING IN FIVE CONTRASTING BIOMES OF SOUTH AFRICA

5.1 Introduction

“...clay expansion and dispersion are the precursors of degradation...”

McBride (1994, p.282).

Soil crusts or crusts form when clay at the surface disperses and when exposed aggregates slake and collapse during wetting (McIntyre, 1958 a&b; Agassi *et al.*, 1981). This process is greatly enhanced under raindrop impact, as the energy input promotes dispersion and aggregate breakdown (Levy *et al.*, 1986). McIntyre (1958 a&b) demonstrated that it is the movement of dispersed clay into the soil which results in clogging of macropores and the formation of a crust. The tendency of a soil to crust is thus in part a function of the tendency of clay to disperse or flocculate, which in turn is a function of clay mineralogy, pH, salt concentration, the exchangeable sodium percentage (ESP) and soil organic matter. Dispersion is often highlighted as the dominant process behind soil crusting, yet some degree of re-flocculation of dispersed clay, as it migrates through the pores, may be necessary for an effective crust to form (Frenkel *et al.*, 1992). Indeed, Bresson and Cadot (1992) showed that it is silt-size particles that form bridges across soil pores and ultimately clog the pores at a depth of <1 mm below the soil surface (Figure 5.1).

Failure to account for the effect of crusting on infiltration can result in gross overestimation of water intake by the soil (McIntyre, 1958a; Hillel and Gardner, 1969; Vandervaere *et al.*, 1998; Levy and Rapp, 1999; Levy, 2000). This is especially true in arid areas, where high intensity rain events are the norm (Shainberg and Singer, 1985). McIntyre (1958a) measured the permeability of different layers within a single crust. The permeability of the skin crust 0.1 mm thick, a washed-in layer just below the crust, and the underlying soil were 0.02, 0.2 and 36 mm hr⁻¹, respectively. The skin crust thus reduced infiltration by a factor of 1800. As a result of reduced water infiltration, plants may have limited access to soil water on crusting soils. The hard physical structure of hardsetting crusts can also impede root growth near the soil surface. This may curtail germination and growth of seedlings as young roots are especially vulnerable (Ahmad and Roblin, 1971; Finlay *et al.*, 1994; Shainberg and Levy,

1994). In addition, soil aeration is greatly reduced under crusts, with an oxygen-deficient layer often forming just below the crust surface, which reduces germination success and seedling survival. In soils which exhibit a strong crusting tendency, seedling emergence often occurs only through the crust cracks, which can doom an entire crop from the very outset (Hillel, 1998). The effects of crusts are not, however, all detrimental to plant growth. As Sombroek (1986) notes, depending on the strength of the crust, there may be a measure of protection against wind erosion and sometimes against water erosion. Valentin *et al.* (1999) observed that in arid landscapes in Africa, crusted bare bands often promote water runoff into bands of vegetation and concluded that it is the crusting between bands that makes the system sustainable.

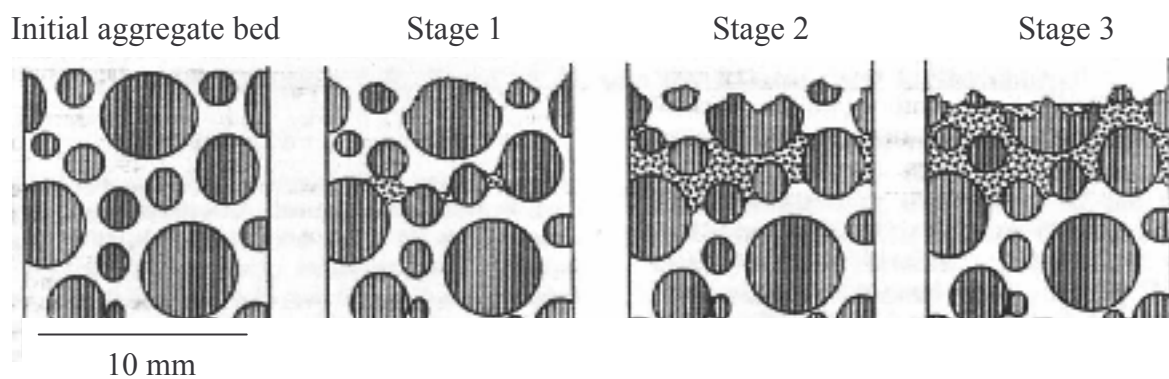


Figure 5.1 The process of soil crusting, adapted from Bresson and Cadot (1992).

Bradford and Huang (1992) noted that crusting can occur on most soils, except for those with high coarse sand and very low silt and clay contents. Crusting is particularly common in the sandy topsoils, characteristic of many semi-arid savannas (Oster *et al.*, 1992). A high silt content also tends to favour crusting and reduces infiltration (Bradford and Huang, 1992). In general, the crusting process is favoured on soils with a balanced mixture of coarse, medium, fine and very fine sand particles, together with silt and clay percentages between 5 and 10%. This enables close packing of particles. Stabilising constituents like humus and iron compounds reduce the tendency of a soil to crust or improve the rate of infiltration through the crust (Sombroek, 1986). Pikul and Zuzel (1994), for example, demonstrated that the greater the organic C concentration within a soil crust, the greater the crust porosity and the greater the mean pore diameter. Du Plessis and Shainberg (1985) also found that soil organic matter promoted aggregate stability and increased the rate of infiltration under rainfall simulation.

Clay mineralogy is another factor affecting soil crusting. Oster *et al.* (1980) observed that soils with illitic clay were more prone to dispersion than soils with montmorillonitic clay and Levy and Van der Watt (1988) demonstrated that illitic soils were more susceptible to crusting than kaolinitic soils. Kaolinitic soils were shown to be the most stable soils, but even a small amount of smectite among the kaolinite greatly increased their susceptibility to crusting (Cass and Johnston, 1985; Levy and Van der Watt, 1988; Stern *et al.*, 1991a).

South Africa is predominantly a semi-arid region and the infiltration of rainfall into the soil profile is critical for productivity in natural ecosystems as well as agricultural systems. This study investigated the factors related to the tendency of soils to crust in West Coast Renosterveld, Central Nama Karoo, Xeric Succulent Thicket, Moist Upland Grassland, Southern Tall Grassveld and Mixed Lowveld Bushveld. It was hypothesised that the tendency of soils to crust (quantified by laboratory infiltration and modulus of rupture) would be a function of water dispersible clay. This follows from work by Stern *et al.* (1991b), who found that water dispersible clay and runoff under rainfall simulation were strongly correlated across a wide range of soil types in South Africa. Furthermore, it was hypothesised that water dispersible clay and thus crusting would be related to clay mineralogy, pH, salt content, soil organic matter content and the exchangeable sodium percentage. The effect of a vegetation cover on the tendency of soils to crust was examined in each habitat.

5.2 Materials and methods

5.2.1 Study sites

A list of the vegetation types and location of each study site is presented below and depicted in Figure 5.2. For a detailed description of each study area, refer to Chapter 4 for sites 1-5 and Chapter 2 for site 6.

- 1) West Coast Renosterveld, on the Bokkeveld plateau, approximately 300 km north of Cape Town, near the town of Nieuwoudtville, Northern Cape (31°20`S; 19°10`E).
- 2) Central Nama Karoo, 30 km west of Beaufort West, Western Cape (32°15`S; 22°50`E).
- 3) Xeric Succulent Thicket, in a broad valley west of Kirkwood in the Eastern Cape (33°30`S; 25°20`E).

- 4) Moist Upland Grassland, in the foothills of the southern Drakensberg, near the town of Underberg, KwaZulu-Natal ($29^{\circ}45'S$; $29^{\circ}30'E$).
- 5) Mixed Lowveld Bushveld, within the long-term burn experiment in the Kruger National Park, Mpumalanga ($23^{\circ}-25^{\circ}S$; $31^{\circ}-32^{\circ}E$).
- 6) Southern Tall Grassveld, at the Ukulinga Research Station, Pietermaritzburg, KwaZulu-Natal ($29^{\circ}40'S$; $30^{\circ}20'E$).

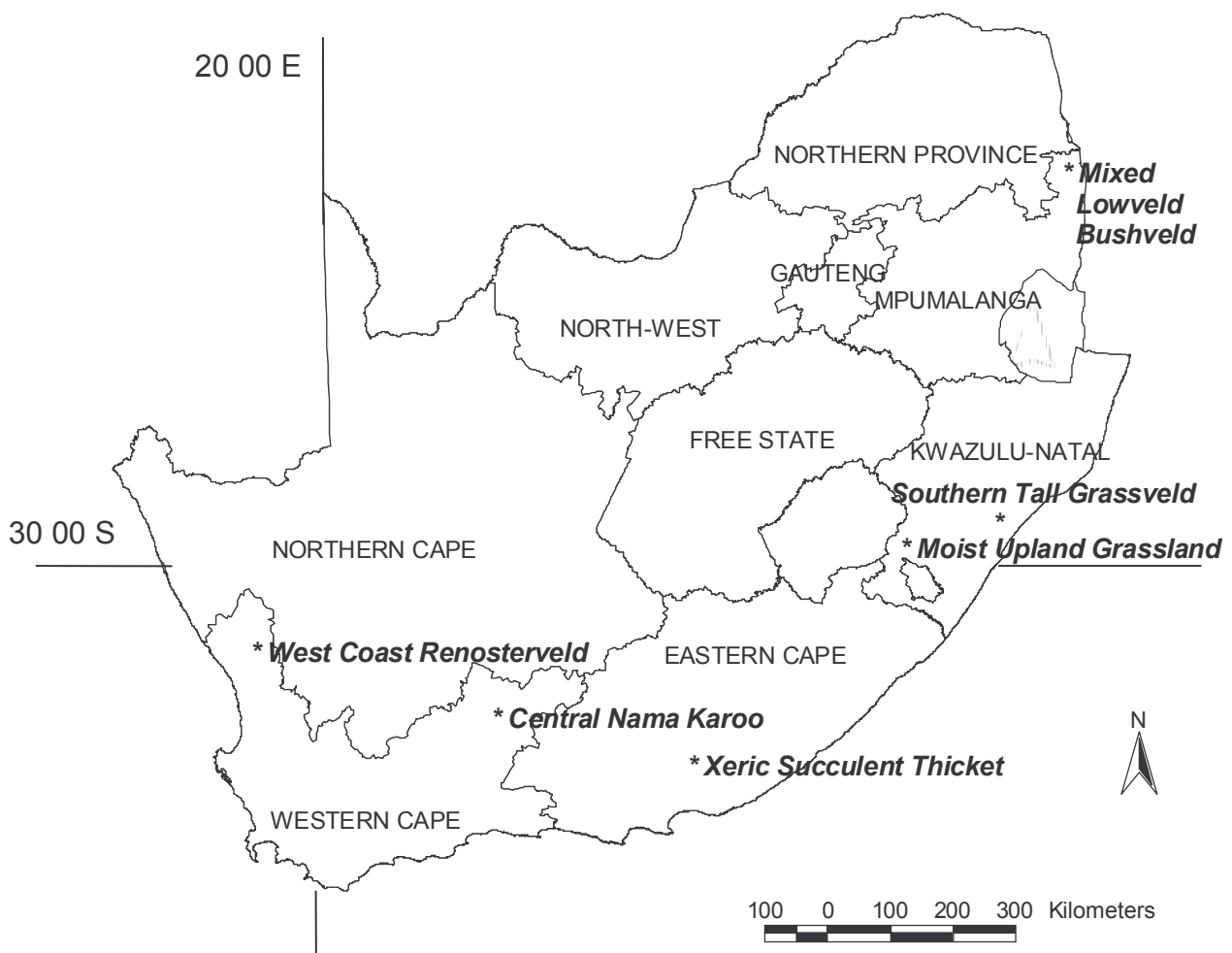


Figure 5.2 The location of the study areas used for an investigation into soil crusting in five contrasting biomes in South Africa.

5.2.2 Sampling

Composite samples, comprising 15-20 subsamples, were taken with an auger to a depth of 10 cm as described below:

(a) *West Coast Renosterveld* - soils were sampled from (i) open renosterveld i.e. on exposed, bare ground outside of bush clumps (n=7); (ii) below *Elytropappus rhinocerotis* bushes (n=11); (iii) in old wheatlands planted to *Medicago* (n=6); and (iv) in cultivated wheat lands (n=4). All sites were at least 500 m apart.

(b) *Central Nama Karoo* - dolerite- and shale-derived soils were sampled from beneath *Pentzia incana* bushes and *Stipagrostis* grass species as well as from adjacent bare, exposed ground (n=12 for dolerite-derived soils and n=6 for shale-derived soils). All sites were at least 500 m apart.

(c) *Xeric Succulent Thicket* - intensive stocking with goats removes the dominant trees and shrubs and transforms the dense thicket (~3 m tall) to an open “savanna”, with a few scattered trees and a groundcover dominated by annual grasses and forbs. Soils were sampled from one hectare plots in (i) intact thicket and (ii) goat-transformed savanna at eight fenceline contrasts. All sites were at least 1 km apart.

(d) *Moist Upland Grassland* - dolerite-derived soils were sampled in (i) grazed indigenous grassland (n=10); (ii) cultivated maize lands (n=3); (iii) kikuyu (*Pennisetum clandestinum*) pastures (n=3); (iv) ryegrass (*Lolium* spp.) pastures (n=3); (v) pine plantations (*Pinus* spp.) (n=3); (vi) *Eragrostis* pastures (n=3). All sites were at least 400 m apart.

(e) *Southern Tall Grassveld* - the predominant parent material on site is Ecca Group shale of the Pietermaritzburg formation, with some influence of dolerite through colluvial action in the northern plots. The experimental plots run south to north, with soil depths varying from <15 cm in the southern plots to over 60 cm in the northern plots. Long-term burning trials have been in operation for 47 years, in an effort to determine the effect of fire frequency, fire season and mowing on the grassland ecosystem (Tainton & Mentis 1983). Forty four different treatments were established in triplicate in plots measuring 13.7 m by 18.4 m. Unburnt plots, plots burnt annually in August and plots burnt annually in August as well as mowed in mid-summer were sampled (i.e. n=3 for each treatment).

(f) *Bushveld* – this site comprised the Kruger National Park long-term burn experiment, which started in 1955 and consists of treatments of differing frequency and season of burns in seven-hectare plots (van Wyk 1971). Soils in the southern burn plots (i.e. Numbi and Napi plots) are derived from Nelspruit granite and the central burn plots (i.e. Satara and Mopane plots) are derived from basalt. Soils were sampled from unburnt plots and plots burnt annually in August at fifteen locations (n=8 for granite-derived soils and n=7 for basalt-derived soils). The annually burnt and unburnt treatments were located within a string of 13 different treatments and were not further than 3 km apart. All strings were at least 5 km apart.

Subsamples for each composite sample were taken at ~20 m intervals across the middle of each seven hectare plot. Soil type varied across plots, but for the purposes of this study it was assumed that composite samples of topsoils would reflect sufficient differences between treatments to enable an investigation into the tendency of soil to crust. Vegetation structure in unburnt plots ranged from dense to open woodlands while annually burnt plots were less wooded i.e. more open and grassy. Rain falls predominantly in summer and mean annual rainfall varies from 687 mm at Numbi in the southwest to 404 mm at Letaba in the central region of the park.

5.2.3 Soil analyses

A full description of the methods of soil analysis is given in Chapter 2. In order to assess the tendency of soils to crust and to investigate soil properties related to crusting, the following analyses were undertaken on composite samples taken to a depth of 10 cm: laboratory infiltration whereby a 1:5 soil water suspension was leached through a packed soil column; water dispersible clay; electrical conductivity (EC); pH in KCl; modulus of rupture; particle size distribution; total C; labile C; and ammonium acetate-extractable cations.

5.2.4 Statistical analyses

Statistical analyses were performed using the software package Unistat 5.0. The statistical significance of differences between means were calculated using a one way ANOVA for samples from West Coast Renosterveld and Moist Upland Grassland (Tukey-HSD test for detecting significant differences between groups); a paired t-test for samples from Xeric Succulent Thicket and Mixed Lowveld Bushveld; and a student t-test for samples from the Central Nama Karoo. Differences were deemed significant where $p < 0.05$. Correlation analyses between various soil properties were performed using non-parametric methods (Spearman Rank correlation analysis) because non-linear patterns were observed in some of the xy scatter plots.

5.3 Results

In Table 5.1 means and standard errors are presented for the following soil properties pertaining to soil crusting: laboratory infiltration, water dispersible clay, EC, pH (KCl), MOR,

silt, clay, sand, total C, labile C and ESP for West Coast Renosterveld, Central Nama Karoo, Xeric Succulent Thicket, Moist Upland Grassland and Mixed Lowveld Bushveld. Results from the Southern Tall Grassveld long-term burn experiments (including laboratory infiltration, water dispersible clay, pH (KCl), MOR, labile C and total C) are presented in Figure 5.3 and depict the transition from a shale influence in the south to the dolerite influence in the north, as well as the effects of fire exclusion, annual burning, and annual burning plus mowing. Correlation analysis showed positive relationships between laboratory infiltration and MOR; and laboratory infiltration and silt content in Central Nama Karoo, West Coast Renosterveld and Xeric Succulent Thicket. These relationships are depicted in Figure 5.4. Soil properties strongly correlated with laboratory infiltration and water dispersible clay at each study site are presented in Table 5.2.

5.4 Discussion

5.4.1 West Coast Renosterveld

The tendency of soils to crust was greater in soils from open, bare ground than soils from under natural vegetation. Laboratory infiltration in open soils was about one and a half times, modulus of rupture about a half and water dispersible clay about 80% of that in soils under vegetation (Table 5.1). An unexpected result was that infiltration in soils from wheat lands was comparable with soils from under vegetation. By contrast, soils from old wheat lands (planted with *Medicago*) had about four times lower infiltration than soils from under natural vegetation. The data in Table 3 suggest that EC and soil C are probably the key factors influencing clay dispersion, aggregate stability and thus crusting. Soils with a vegetation cover had a greater EC, total C and labile C content than open soils and soils from old wheat lands. Soils with a vegetation cover had a greater EC and greater soil C, both of which are likely to increase flocculation of clay (Shainberg and Singer, 1985; Du Plessis and Shainberg, 1985; Cook *et al.*, 1992; Hillel, 1998; Sumner, 1998), and thereby reduce crusting and improve infiltration. Soils from wheat lands had a similar EC to soils from under natural vegetation (possibly as a result of fertilization), which may have imparted a greater aggregate stability to these soils in comparison to the more electrolyte-deficient soils from bare ground. A study by Robinson and Philips (2001) of dispersive clay soils in southern Italy produced similar results to this investigation. These authors demonstrated that soils under woodland did not crust when exposed to simulated rainfall in a laboratory. In contrast, soils in the area

that had been ploughed or exposed by overgrazing did form surface crusts under simulated rainfall in a laboratory. The crust formation was linked to a decrease in aggregate stability, which in turn was related to a decline in soil organic matter. Enhanced runoff and rapid erosion were evident in wheatlands and livestock degraded lands, but not in the woodlands.

Similar results have been obtained in other studies. In Australia, Naidu *et al.* (1996) found that soils previously under *Eucalyptus* woodland became more dispersive after cultivation and Golchin *et al.* (1995) showed that the tendency of different soils for hardsetting and crusting as a result of structural collapse was reflected in MOR, which was significantly greater in cultivated soils than their virgin counterparts. In India, Bajracharya *et al.* (1996), working on Alfisols found that water dispersible clay was greater in tilled soils than in virgin soils. The tilled soils had a greater propensity to crust and had a lower rate of infiltration than the virgin soils. In Nigeria, Abubakar *et al.* (1996) demonstrated that soils from fallow lands that reverted back to natural vegetation, were less prone to crusting than cultivated lands. And in South Africa, Fuls (1992) noted that removal of vegetation in grassland by excessive livestock grazing resulted in crust formation and reduced soil water content.

Correlation analyses showed that pH (1:5), soil carbon and medium sand were strongly correlated with laboratory infiltration ($p < 0.01$) (Table 5.2). Total and labile C were positively correlated with infiltration, possibly due to an aggregating effect which increases crust porosity. This was demonstrated by Pikul and Zuzel (1994) who found that the greater the organic C concentration within a soil crust, the greater the crust porosity and the greater the mean pore diameter. Medium sand was also positively correlated with infiltration. This fraction of sand may play a role by increasing pore size at the soil surface (in comparison to fine sand). Soil pH (1:5) was negatively correlated with infiltration, possibly because negative charge density and thus clay dispersion tends to be greater at high pH (Chorom *et al.*, 1994). The EC of a 1:5 soil suspension is also reflected in pH to some extent because of the displacement of H^+ ions from exchange sites by soluble cations. A high pH (1:5) may therefore be associated with greater clay dispersion due to both EC and pH effects on interparticle repulsion.

The tendency of Dwyka sediment-derived soils to crust (as quantified by laboratory infiltration and modulus of rupture) was greater than other shale-derived soils from the Central Nama Karoo and Xeric Succulent Thicket sites (Figure 5.4). Given that silt often

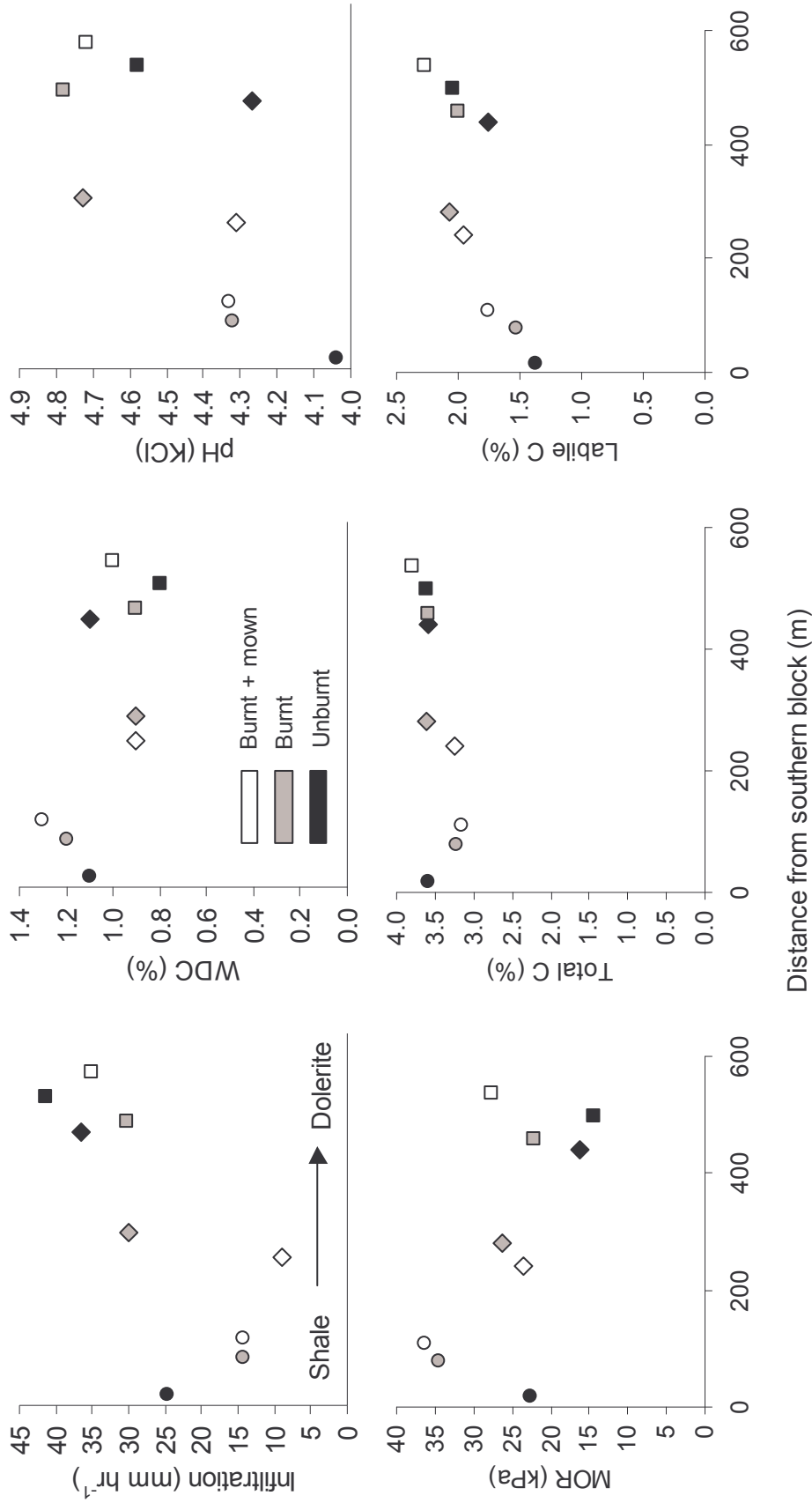


Figure 5.3 Selected soil properties from the Southern Tall Grassveld study area at Ukulinga plotted against distance from the southern-most block on the long term burn experiment. Soils to the south are predominantly shale-derived. Soils to the north have a strong dolerite influence. Circles, diamonds and squares represent three replicates. Black-filled shapes are unburnt, grey-filled annually burnt and white-filled annually burnt and mown plots.

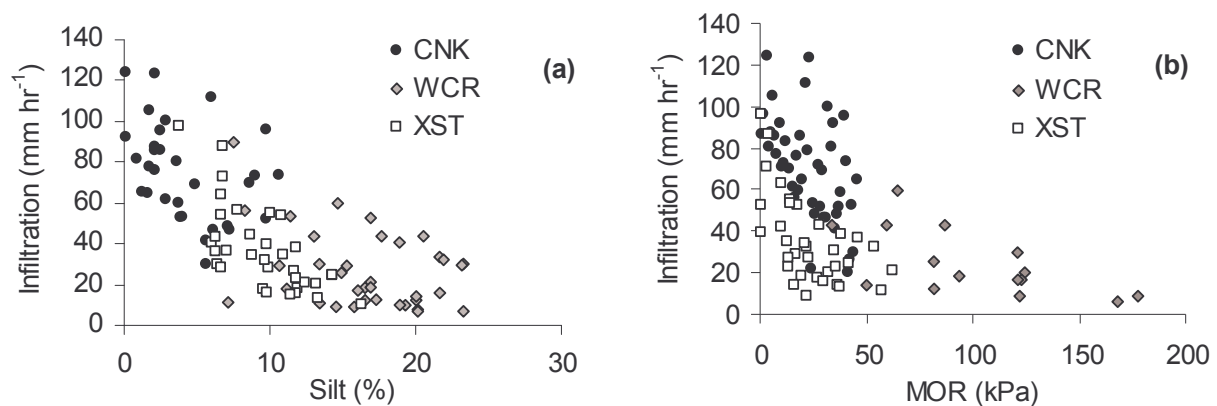


Figure 5.4 (a) Laboratory infiltration plotted against silt content for soils from the Central Nama Karoo (C.N.K.), West Coast Renosterveld (W.C.R.) and Xeric Succulent Thicket (X.S.T); and (b) laboratory infiltration plotted against modulus of rupture for the same soils depicted in (a).

plays an important role in the blockage of pores and crust formation (Bradford and Huang, 1992), the greater silt content of the Dwyka-sediment derived soils (Figure 5.4) is a likely contributing factor to the pattern of greater crusting in West Coast Renosterveld.

5.4.2 Central Nama Karoo

In the Central Nama Karoo, laboratory infiltration in shale-derived soils sampled in the open was approximately half the laboratory infiltration of all other soils sampled (i.e. shale and dolerite-derived soils sampled from beneath vegetation and dolerite-derived soils sampled in the open). These results are not unexpected as the greater permeability of dolerite-derived soils in comparison to Beaufort sediment-derived soils has been demonstrated by Sumner (1957) in KwaZulu-Natal. The lower rate of infiltration (i.e. greater crusting) of these shale-derived soils in the open in comparison to other soils is likely to be related to a combination of factors. Sumner (1957) showed, for example, that Beaufort sediment-derived soils had a greater exchangeable Mg content and less pore space than dolerite-derived soils. He suggested that the Mg may cause dispersion, poor structure and less pore space in the Beaufort sediment-derived soils and thereby retard infiltration. The water-soluble and

Table 5.1: Means and standard errors (se) of selected soil properties in West Coast Renosterveld (WCR), Central Nama Karoo (CNK), Xeric Succulent Thicket (XST), Moist Upland Grassland (MUG) and Mixed Lowveld Bushveld (MLB).

Vegetation	WCR		CNK		XST		MUG				MLB							
Geology	Dwyka		Shale		Dolerite		Mixed		Mixed				Granite		Basalt			
	<i>Elytro./Merx.</i>	Open	<i>Pentzia</i>	Open	<i>Stip./Pentzia</i>	Open	<i>P. afra</i>	Transformed	Grassland	Maize	Ryegrass	Eragrostis	Kikuyu	Pine	Unburnt	Burnt	Unburnt	Burnt
Infil. (mm hr⁻¹)	44	16	80	46	84	83	51	19	36	9	12	47	62	51	99	80	72	56
se	4	2	5	4	5	6	10	3	4	2	5	13	2	10	10	5	11	8
n and p<0.05	8a	17b	12a	12b	6a	6a	8a	8b	10ab	3a	3a	3b	3b	3b	8a	8b	7a	7b
WDC (%)	2.2	2.6	1.4	2.0	1.2	1.4	1.1	1.1	1.5	1.2	1.4	0.8	0.7	0.9	0.6	0.9	1.3	1.5
se	0.1	0.2	0.1	0.2	0.1	0.1	0.1	0.2	0.3	0.3	0.3	0.2	0.2	0.1	0.1	0.1	0.1	0.1
n and p<0.05	11	16	12a	12b	6a	6a	8	6	10	3	3	3	3	3	8a	8b	7a	7b
EC (mS m⁻¹)	12.1	6.1	5.3	5.9	4.7	3.6	15.8	30.7	5.8	8.7	9.8	5.9	16.2	6.2	5.9	5.0	7.8	6.8
se	2.7	0.6	0.4	0.9	0.4	0.3	1.8	10.2	0.3	0.9	1.7	0.7	2.5	0.2	0.3	0.5	1.0	0.9
n and p<0.05	11a	16b	12	12	6	6	8	8	10a	3a	3a	3a	3b	3a	8	8	7	7
pH (KCl)	5.1	5.3	6.2	6.4	5.9	5.8	5.8	6.8	4.2	4.1	4.1	4.1	4.2	3.9	5.2	5.4	5.9	5.9
se	0.1	0.1	0.1	0.1	0.1	0.1	0.2	0.2	0.07	0.08	0.09	0.07	0.10	0	0.1	0.1	0.2	0.2
n and p<0.05	11	16	12	12	6	6	8a	8b	9	3	3	3	3	3	8	8	7	7
MOR (kPa)	64	121	34	29	19	28	16	34										
se	6	17	5	9	5	9	5	7										
n and p<0.05	8a	4b	7	9	6	3	8a	8b										
Silt (%)	17	18	3	6	5	5	9	11	15	18	24	22	10	11	6	6	15	17
se	1.0	1.2	0.9	0.7	1.7	2.2	1.1	0.7	1	6	8	1	3	5	0.9	0.6	2	3
n and p<0.05	11	15	8	7	5	5	8a	8b	10	3	3	3	3	3	8	8	4	4
Clay (%)	8	10	5	8	4	5	8	10	42	35	26	29	46	47	8	7	22	22
se	0.4	0.7	0.5	1.2	1.0	1.5	1.1	1.2	6	5	6	3	10	17	1.1	1.0	2	3
n and p<0.05	11	15	8	7	5	5	8	8	10	3	3	3	3	3	8	8	4	4
Sand (%)	75	72	92	86	91	90	83	79	43	47	50	50	44	42	86	87	62	61
se	1.3	1.8	0.9	0.8	0.7	0.9	1.9	1.5	6	6	10	3	7	12	1.1	1.3	0.5	1
n and p<0.05	11	15	8a	7b	5a	5a	8	8	10	3	3	3	3	3	8	8	4	4
Total C (%)	1.7	1.0	0.42	0.28	0.56	0.23	5.6	3.0	4.3	3.5	4.6	4.6	6.0	4.5	0.9	0.7	2.4	2.1
se	0.1	0.1	0.03	0.02	0.15	0.01	0.5	0.3	0.4	0.4	0.3	0.3	0.8	0.7	0.03	0.04	0.2	0.1
n and p<0.05	11a	16b	12ab	12b	6a	6b	8a	8b	10	3	3	3	3	3	8a	8b	7	7
Labile C (%)	0.9	0.5	0.26	0.17	0.16	0.11	2.8	1.5	2.5	1.7	2.4	2.8	3.5	2.3	0.5	0.4	1.3	0.9
se	0.1	0.05	0.02	0.03	0.02	0.02	0.3	0.1	0.2	0.1	0.2	0.3	0.5	0.3	0.02	0.03	0.2	0.05
n and p<0.05	11a	16b	8a	12ab	6ab	5b	8a	8b	10ab	3a	3ab	3ab	3b	3ab	7a	8b	6	7
ESP	2.7	2.4	2.5	2.7	2.4	2.4	4.0	4.0	4.3	2.8	3.1	3.1	3.2	4.2	4.0	3.8	2.6	2.6
se	0.1	0.1	0.1	0.1	0.3	0.1	0.2	0.3	0.1	0.2	0.2	0.2	0.3	0.4	0.3	0.2	0.3	0.2
n and p<0.05	11	16	12	12	6	6	8	8	10a	3b	3bc	3b	3bc	3ac	8	8	7	7

Key to Table 5.1: Infil. = laboratory infiltration; WDC = water dispersible clay; EC = electrical conductivity in a 1:5 soil extract; MOR = modulus of rupture; ESP = exchangeable sodium percentage; *Elytro./Merx.* = soils sampled below *Elytropappus rhinocerotis* and *Merxmuellera stricta*; *Stip./Pentzia* = soils sampled below *Stipagrostis grass spp.* and *Pentzia incana* bushes; *P. afra* = soils sampled below *Portulacaria afra*; Transformed = soils sampled in the open in goat-transformed sites; n and p<0.05 refer to the number of samples (n) and significant differences between means, as determined by student t-test for West Coast Renosterveld; one way ANOVA (post hoc Tukey HSD) for Central Nama Karoo and Moist Upland Grassland; paired t-test for Xeric Succulent Thicket, granite Mixed Lowveld Bushveld and basalt Mixed Lowveld Bushveld. Where letters are different, means were significantly different (p<0.05). Where no letters are presented, means were not significantly different (p>0.05).

Table 5.2: Soil properties strongly correlated with laboratory infiltration and water dispersible clay at each study site. Spearman rank correlation coefficients are presented, together with the number of samples (n) and p value (p).

Laboratory Infiltration				Water dispersible clay			
Renosterveld	Cor.	n	p		Cor.	n	p
pH (1:5)	-0.65	37	0.0000	Total clay	0.56	39	0.0001
Total carbon	0.50	37	0.0009	Total carbon	-0.39	40	0.0067
Medium sand	0.49	36	0.0014	Medium sand	-0.33	39	0.0216
Labile carbon	0.44	37	0.0035	Silt	0.29	39	0.0351
Total clay	-0.40	36	0.0078	Fine sand	-0.25	39	0.0658
EC	0.39	37	0.0089	pH (1:5)	-0.23	37	0.0893
Modulus of rupture	-0.60	15	0.0095	Infiltration	-0.23	37	0.0893
ESP	0.32	37	0.0262	Labile carbon	-0.21	40	0.0999
Karoo dolerite							
Total clay	0.50	11	0.0596	ESP	-0.53	14	0.0268
Silt	-0.44	11	0.0887	Medium sand	0.45	12	0.0701
Modulus of rupture	-0.39	12	0.1068	Fine sand	-0.45	12	0.0732
Coarse sand	-0.30	11	0.1850	Total carbon	-0.35	14	0.1086
Karoo shale							
Silt	-0.87	13	0.0000	Infiltration	-0.59	22	0.0021
Water dispersible clay	-0.59	22	0.0021	Silt	0.72	13	0.0028
Total clay	-0.71	13	0.0035	Total carbon	-0.55	22	0.0039
ESP	0.51	22	0.0074	Total clay	0.70	13	0.0040
Total carbon	0.48	22	0.0111	ESP	-0.44	22	0.0203
Fine sand	0.61	13	0.0134	pH (KCl)	0.41	22	0.0290
Medium sand	0.50	13	0.0397	Labile carbon	-0.43	18	0.0390
Labile carbon	0.42	18	0.0432	Modulus of rupture	0.36	21	0.0560
pH (KCl)	-0.37	22	0.0472	Fine sand	-0.46	13	0.0578
Thicket							
Silt	-0.6758	32	0.0000	Coarse sand	0.4244	32	0.0077
Modulus of rupture	-0.6266	32	0.0001	Fine sand	-0.4238	32	0.0078
Medium sand	0.4419	32	0.0057	Silt	0.3873	32	0.0143
EC	-0.4306	32	0.0069	Infiltration	-0.3022	32	0.0464
pH (1:2.5)	-0.4028	32	0.0111	Modulus of rupture	0.2883	32	0.0548
pH (KCl)	-0.3758	32	0.0170	EC	0.2691	32	0.0682
Total carbon	0.3393	32	0.0287	Labile carbon	0.2401	32	0.0928
Water dispersible clay	-0.3022	32	0.0464				
Labile carbon	0.2878	32	0.0551				
Upland grassland							
Labile carbon	0.50	31	0.0023	Infiltration	-0.37	31	0.0189
Modulus of rupture	-0.57	21	0.0035	ESP	0.23	31	0.1106
Total carbon	0.46	31	0.0046				
Water dispersible clay	-0.37	31	0.0189				
Total clay	0.24	31	0.0928				
Bushveld granite							
Medium sand	0.53	16	0.0171	Labile carbon	-0.64	15	0.0053
EC	0.40	16	0.0639	Total carbon	-0.52	16	0.0201
Water disp. clay	-0.34	16	0.1023	Total clay	0.42	16	0.0537
Labile carbon	0.33	15	0.1130	EC	-0.41	16	0.0592
Silt	-0.30	16	0.1326				
ESP	0.27	16	0.1554				
Bushveld basalt							
Total clay	0.77	8	0.0133	Infiltration	-0.56	14	0.0189
Silt	-0.74	8	0.0183	pH (1:5)	0.54	14	0.0240
Water dispersible clay	-0.56	14	0.0189	Coarse sand	-0.54	8	0.0841
Total carbon	0.55	14	0.0214	Labile carbon	-0.38	13	0.0992
Tall grassveld							
Medium sand	-0.84	9	0.0023	ESP	0.87	9	0.0013
Total carbon	0.83	9	0.0026	Labile carbon	-0.70	9	0.0170
Coarse sand	-0.73	9	0.0123	Total carbon	-0.67	9	0.0236
Silt	0.72	9	0.0149	pH (1:2.5)	-0.66	9	0.0256
Total clay	0.72	9	0.0149	Modulus of rupture	0.59	9	0.0478
Modulus of rupture	-0.67	9	0.0249	pH (KCl)	-0.50	9	0.0873
ESP	-0.48	9	0.0937	Coarse sand	0.48	9	0.0960
Labile carbon	0.45	9	0.1110	Infiltration	-0.45	9	0.1148
Water dispersible clay	-0.45	9	0.1148				

(NH₄)OAc-extractable Mg of shale and dolerite-derived soils were not significantly different in the Central Nama Karoo and thus Mg differences could not be invoked to explain the greater crusting of shale-derived soils in the open. Water dispersible clay was greatest in the shale-derived open soils (despite a relatively high EC) and is probably a function of the greater total clay content but may also be a function of pH and ESP. pH and ESP were also greatest in the shale-derived open soils. In addition, the total silt plus clay fraction was consistently greater in shale-derived open soils than in the other soils. Within shale-derived soils, silt content was strongly correlated ($p < 0.01$) with laboratory infiltration (negative) and water dispersible clay (positive) (Table 5.2). The silt and clay fraction tends to block pores during crust formation (Bradford and Huang, 1992) and consequently a greater concentration of this fraction is likely to enhance crusting. Sumner (1957) also found that dispersion of clay was greater in Beaufort sediment-derived soils than dolerite-derived soils. He ascribed this difference to greater dispersion and hydration of Beaufort sediment clays.

The mineralogy of the clay fraction in shale-derived soils as opposed to dolerite-derived soils is also likely to be more conducive to effective blockage of pores and thus crusting. Weathering of shales tends to produce 2:1 layer silicates, such as illite and vermiculite, whereas weathering of dolerite tends to produce 1:1 layer silicates, such as kaolinite (Sumner, 1957; Olson *et al.*, 2000). Sumner (1957), for example, showed that Beaufort sediment-derived topsoils in KwaZulu-Natal had illite and illite-montmorillonoid mixed layer minerals, whereas dolerite-derived topsoils had only kaolinite. 2:1 layer silicates tend to be more susceptible to crusting than 1:1 layer silicates (Levy and Van der Watt, 1988), possibly because the platy structure of 2:1 layer silicates enables the development of a more effective crust than the more aggregated and massive structure of 1:1 layer silicates such as kaolinite (McBride, 1994; Hillel, 1998). As Hillel (1998) notes: "Owing to its relatively large particles and low specific surface, kaolinite exhibits less plasticity, cohesion, and swelling than most other clay minerals". Apart from 2:1 layer silicate differences, the shale-derived soils are also likely to have less Fe than the dolerite-derived soils (Ellis, 1988) (evident in the redder coloration of the dolerite-derived soils). Sumner (1957) showed that the Fe oxide content of dolerite-derived soils was approximately double those of Beaufort sediment-derived soils. Fe oxides tend to increase soil structural stability (Hillel, 1998) and on the basis of this difference alone, the dolerite-derived soils are likely to be less susceptible to crusting than the shale-derived soils. Indeed, Sumner (1957) showed that aggregate stability in dolerite-derived soils in KwaZulu-Natal was strongly correlated with Fe₂O₃ content.

Despite this greater susceptibility of shale-derived soils to crust, laboratory infiltration of shale-derived soils beneath bushes was similar to laboratory infiltration of dolerite-derived soils. This may have been related to labile C, which was greatest in shale-derived soils beneath bushes and which may have provided a measure of soil structural stability. Total carbon and labile carbon were positively correlated with laboratory infiltration and negatively correlated with water dispersible clay ($p < 0.05$) in shale derived soils (Table 5.2). Soil C has been linked to a reduction in clay dispersion and an increase in aggregate stability (Cook *et al.*, 1992; Sumner, 1998; Chan *et al.*, 2001). Sumner (1957) found that aggregate stability of dolerite-derived and Beaufort sediment-derived topsoils were similar, despite the greater Fe oxide content of dolerite-derived soils. He concluded that soil C, which was strongly correlated with aggregate stability, provided a strong aggregating effect in the Beaufort sediment-derived topsoils.

The greater clay and silt content of shale-derived soils in the open (in comparison to the other soils sampled) may be related to effects of erosion. Ludwig *et al.* (1997) note that plants are resource sinks in semi-arid regions, collecting water runoff and the sediment within the runoff. At this study site, bushes were generally elevated above the open soil and it is difficult to conceive of water being trapped by the plants. However, wind erosion may result in soil being trapped in the bush canopies and thereby change the particle size distribution. The sand content of shale-derived soils below bushes was consistently greater than soils in the open (Table 5.1), which suggests that the sand size fraction is preferentially trapped by bushes during wind erosion events. The same pattern is not evident in the dolerite-derived soils, which reflects a possibly greater resilience of these soils to wind erosion. The removal of soil in open areas may also have exposed deeper layers of soil with a greater clay content. Duplex soils, such as the Valsrivier form, were identified in shale areas, suggesting that erosion between bushes may in part be responsible for the greater clay content of shale-derived soils in the open.

Dolerite-derived soils tended to be deeper than shale derived soils (0.5 m vs > 1.5 m deep; personal observation) which is probably a function of greater weatherability (Sumner, 1957). The water content of the soils may in turn affect the type of vegetation that predominates. Bushes such as *Pentzia incana* were prevalent on shale-derived soils and grasses (*Stipagrostis* spp.) were abundant on the dolerite-derived, deeply-weathered soils. Bushes at this site may

be adapted to more arid conditions than the grasses and consequently predominate on the crusting, shale-derived soils.

5.4.3 *Xeric Succulent Thicket*

Soils from goat-transformed sites showed a greater tendency to crust than intact thicket sites. This is evident because laboratory infiltration was lower and modulus of rupture was greater in soils from transformed sites (Table 5.1). The reason for an increase in crusting on transformed sites appears to be related to soil C status and soil texture as opposed to other factors affecting clay dispersion and crusting. Water dispersible clay did not show a consistent pattern between sites and thus factors affecting dispersion could not be invoked to explain the infiltration and modulus of rupture differences recorded. In contrast, total C and all measures of labile C showed marked decreases as a result of transformation (Figure 3.5). The lower infiltration and greater modulus of rupture of soils from goat-transformed sites in comparison to intact sites is thus probably due to a decrease in soil organic matter and an associated decrease in soil aggregate stability.

The correlation relationships in Table 5.2 give some indication as to which soil properties may play a role in soil crusting in thicket. The significant correlation of silt (negative) and medium sand (positive) with infiltration suggests that soil texture data are critical for understanding the tendency of these soils to crust. Silt and fine sand are commonly cited as the main size fractions that promote crusting (Bradford and Huang, 1992). Silt content was highly correlated with infiltration ($r = 0.68$). It was also significantly greater in the degraded pseudo-savanna than adjacent thicket, although in the absence of a suitable explanation such textural differences cannot be attributed to a transformation of the vegetation cover.

5.4.4 *Moist Upland Grassland*

In the Moist Upland Grassland, the tendency of soils to crust (as measured by laboratory infiltration) was as follows: maize fields (9 mm hr^{-1}) > ryegrass pastures (12 mm hr^{-1}) > virgin veld (36 mm hr^{-1}) > *Eragrostis* pastures (47 mm hr^{-1}) > pine plantations (51 mm hr^{-1}) > kikuyu pastures (62 mm hr^{-1}). The rate of laboratory infiltration of soils under maize and ryegrass was significantly lower ($p < 0.05$, one way ANOVA) than soils under *Eragrostis*, pines and kikuyu. Total and labile C were positively correlated with infiltration across all

soils sampled in upland grassland ($p < 0.01$) (Table 5.2). Greater crusting under maize may be due to a lower total C and labile C content, and consequently less aggregate stability, but this effect is not evident in the ryegrass pastures. The textural data show that two of the ryegrass pastures were siltier than other soils, which may explain the greater crusting under ryegrass, as high silt contents are often associated with greater soil crusting (Bradford and Huang, 1992). Milne and Haynes (2003, in press) did show, however, that aggregate stability and soil C were often lower in ryegrass pastures than undisturbed vegetation in the Eastern Cape. Cultivation of ryegrass, which entails tillage, is thus likely to result in a deterioration of soil structure and potentially greater crusting.

Soils under kikuyu pastures had about one a half times greater soil C and close to double the EC of virgin grasslands. The accumulation of soil C in kikuyu pastures in South Africa has recently been highlighted by Milne and Haynes (2003, in press) and Dominy and Haynes (2002). An increase in soil C and EC tends to increase aggregation, reduce dispersion and reduce crusting. This effect is evident in the water dispersible clay data, as there was 52% less dispersed clay in kikuyu pastures than in virgin grasslands. The fertilization of kikuyu pastures (inorganic fertilizer application, as well as livestock dunging and urinating) is another factor which may have improved infiltration. The beneficial effect of fertilization on infiltration (Oster *et al.*, 1992; Pikul and Zuzel, 1994) has been ascribed to a greater ionic strength of the soil solution which promotes flocculation of clays, as well as increased return of organic matter to the soil.

5.4.5 Southern Tall Grassveld

In the Central Nama Karoo, laboratory infiltration in open soils was lower in soils derived from shale than from dolerite. In the long-term burn experiments in the Southern Tall Grassveld, a similar trend is evident (Figure 5.3). Laboratory infiltration was lower and modulus of rupture greater on soils derived predominantly from shale (in the southern plots) than on soils with an influence of dolerite (in the northern plots) (means of 18 vs 36 mm hr⁻¹ in southern and northern treatments, respectively). In addition, the treatment effects of annual burning and annual burning plus mowing were greater (i.e. a proportionately greater reduction in rate of infiltration compared to unburnt treatments) on the southern shale-derived soils than on the northern dolerite-derived soils. These findings corroborate work done in KwaZulu-Natal by Sumner (1957) who noted that “The soils derived from the Beaufort and Ecca Series

exhibit a marked susceptibility to erosion by water whereas those derived from dolerite are reasonably stable". A number of factors are likely to contribute to the greater crusting of shale-derived soils in comparison to dolerite-derived soils. Water dispersible clay was greater in the shale-derived soils (despite a lower pH) than dolerite-derived soils. Total C was strongly correlated with infiltration ($p < 0.01$) (Table 5.2) and labile C content was lower in shale-derived soils than dolerite-derived soils (Figure 5.3). The aggregating effect of labile C (Chan *et al.*, 2001) may have decreased clay dispersion and increased infiltration in the dolerite-derived soils more than in the shale-derived soils. In addition, the mineralogy of shale-derived versus dolerite-derived soils, as mentioned in the Central Nama Karoo section of this chapter, is likely to have played a role in the crusting differences. Soil aggregate stability and thus soil structure is likely to be weaker in shale-derived soils than dolerite-derived soils, due to a lower Fe content and the presence of 2:1 layer silicates (as opposed to 1:1 silicates in dolerite-derived soils).

5.4.6 Mixed Lowveld Bushveld

Rates of laboratory infiltration under rainfall simulation were lower in soils from burnt plots than unburnt plots in the southern Kruger National Park (see Chapter 2). This effect is ascribed to three main changes in the chemistry of soils that were likely to increase the dispersion of clay. Firstly, the electrical conductivity of 1:5 extracts (EC) was significantly lower in burnt than in unburnt plots (see Chapter 2). Secondly, the exchangeable sodium percentage (ESP) in the top centimetre of soil (sampled at 4 of the paired plots), was significantly greater in burnt than unburnt plots. And thirdly, the total C and measures of labile C were significantly lower in burnt than unburnt plots. As expected, the percentage of water dispersible clay was significantly greater in burnt plots than unburnt plots. For a discussion on the mechanisms behind these changes in soil chemistry, see Chapter 2.

5.5 Conclusions

The tendency of soils to crust in all vegetation types was greater in open areas than under a canopy of vegetation. The differences in soil crusting are ascribed to effects of total C, labile C, pH, soluble salt concentration, soil texture, clay mineralogy and ESP, all of which affect the dispersion of clay and hence the blocking of soil pores. In West Coast Renosterveld, for example, water dispersible clay was greater in the open than under vegetation and this is

attributed to a lower soluble salt and C content of open soils. Water dispersible clay was also greater in burnt than unburnt plots in the Mixed Lowveld Bushveld. This is attributed to not only lower soluble salt and C content, but greater ESP of soils from burnt plots. In addition, soils under vegetation tended to have greater sand and lower silt contents than open soils, which is probably another contributing factor to differences in crusting. The tendency of soils to crust was also related to parent material, possibly due to different clay mineralogy and Fe oxide content. Dolerite-derived soils, in particular, had a greater rate of laboratory infiltration than soils derived from shales, as is evident in both the Southern Tall Grassveld and Central Nama Karoo. This is attributed to a greater Fe oxide and a lower 2:1 layer silicate content of dolerite-derived soils in comparison to shale-derived soils. In the next chapter, the investigation into reciprocal relationships between vegetation structure and soil properties moves back to the granitic landscapes of the southern Kruger National Park. Data are presented which suggest that herbivores actively seek micronutrients in these nutrient-poor landscapes and that it is the abundance of herbivores in the post-fire environment that controls the survival of tree seedlings in annually burnt plots.

CHAPTER 6**INTERACTIVE RESPONSE OF HERBIVORES, SOILS AND VEGETATION TO ANNUAL BURNING IN A SOUTH AFRICAN SAVANNA**

6.1 Introduction

Trees in South African savannas have evolved with, and hence are adapted to fire. Trollope *et al.* (1998) and Higgins *et al.* (2000) report that trees >3 m tall in the Kruger National Park are generally resistant to fire. The recruitment of trees is, however, affected by fire, as trees below this height tend to be burnt back to their base. Long-term burn experiments were established on the granite-derived soils in the southern Kruger National Park in 1954 to determine the effect of burning on savanna ecology (Figure 6.1) (Van Wyk, 1971). Aerial photography in 2000, of plots that had been burnt every August since 1955, revealed that annual burning has not had a consistent effect on tree cover. As will be described in this chapter, in some plots tree cover is relatively dense in comparison with other plots which have a minimal cover of trees. These observations suggest that mortality of trees due to damage from fire is not the major factor influencing tree cover in this granitic landscape. It is, however, acknowledged that fire intensity may have varied within the same treatments and is also likely to have played a role in determining the current vegetation structure of the plots. Nevertheless, it is probable that factors other than fire intensity also affect the vegetation structure in these long-term burn experiments, herbivory in particular.

Bell (1978) suggests that vegetation structure across Africa (in regions receiving >400 mm of rainfall) is largely controlled by the density of herbivores, which in turn is a function of soil fertility. He postulates that the removal of trees by elephants (*Loxodonta africana*) can open up woodlands and allow smaller herbivores such as antelope to maintain an open grassland. Subsequent studies have shown that elephants reduce tree height and density in the Kruger National Park (Trollope *et al.* 1998) and that browsing by small antelope reduces tree sapling growth in the Serengeti (Belsky, 1984). McNaughton (1988) notes that “Africa’s abundant large herbivores are very heterogeneously distributed, both geographically and regionally” and that “within a region, some localities contain dense animal concentrations although areas nearby may be virtually unoccupied.” During field work at the long-term burn sites in the southern Kruger National Park it was noted that some localities were frequented by herbivores whilst apparently similar environments were largely devoid of animals.

McNaughton (1988) notes that tropical forages are often chronically deficient in mineral elements and suggests that soil mineral content is an important determinant of the spatial distribution of animals within the Serengeti National Park, Tanzania.

It was postulated that intensity of post-fire browsing on burnt plots in the Kruger National Park, could affect tree cover, and that the abundance of herbivores may be related to the nutrient status of the soil. Herbivores are especially likely to select the most nutrient-rich patches in a landscape if the soils are nutrient-poor (Braithwaite *et al.* 1983). Braithwaite (1983) found, for example, that in a *Eucalyptus* forest in New South Wales, 63% of arboreal animals on the site occupied a region of slightly richer soils which comprised only 9% of the total area. The granite-derived sandy soils of the southern Kruger National Park are poor in total N, (NH₄)OAc-extractable cations and Bray 2-extractable P, yet concentrations of these nutrients were similar across the burn sites. It was consequently postulated that micronutrients such as Zn and Cu may affect herbivore densities more than major nutrients in this environment.

Micronutrient-deficient soils are not uncommon. Cook (1994) reported that some areas of Kakadu National Park in Australia are deficient in Zn and Cu for mammals, while Grant *et al.* (1996) concluded from a study in Namibian rangelands that certain areas were deficient in P, I and Cu. Studies by Tracy and McNaughton (1995) showed that forage in the Serengeti was deficient in Na and Zn, particularly for lactating and growing ungulates. Sutton *et al.* (2000), also working in Kenya, found that 78% of grass samples in Shimba Hills National Park contained Zn levels below a critical threshold for cattle. Whether herbivores actively seek out micronutrients in nutrient-poor environments is largely unknown. A study by Stafford (1997) suggested that this may be the case for Sambar deer (*Cervus unicolor*) in New Zealand. The deer occasionally ventured from grasslands into pine plantations to strip and eat pine bark. A nutritional investigation into this behaviour concluded that the deer had a Cu deficiency and that ingestion of pine bark may have been an attempt to alleviate the deficiency. With these studies in mind, the relationship between tree cover, the abundance of herbivores and the concentration of Zn, Cu and other micronutrients on long-term burn experiments in the Kruger National Park was investigated.

6.2 Materials and methods

The study was carried out in the southern Kruger National Park, Mpumalanga (25°S; 31°-32°E; Figure 6.1) and comprises the long-term burn experiments conducted since 1955. The burn experiment consists of sixteen sites and thirteen treatments at each site. Each treatment is a rectangular plot approximately seven hectares in extent, separated from adjacent treatments as well as the surrounding bush by a 4-5 m firebreak. The present investigation was confined to the eight sites in the south of the park, near Numbi Gate and Skukuza rest camp. The vegetation is classified as Mixed Lowveld Bushveld (Low & Rebelo, 1996). The soils in the region are nutrient-poor sands derived from porphyritic granite and include Hutton, Bainsvlei, Clovelly, Cartref and Avalon (Soil Classification Working Group, 1991) and in the terminology of the World Reference Base classification system: Rhodic Lixisols, Paraplinthic Cambisols, Dystric Regosols and Paraplinthic Lixisols (FAO, 1998).

Composite soil samples to a depth of 10 cm were taken from all eight August-annual-burn plots in the long-term burn experiments described by Van Wyk (1971). Each composite sample was based on 15-20 samples taken at about 20 m intervals across the middle of each plot, using an auger. Soil type varied across plots, but for the purposes of this study it was assumed that composite samples of topsoils from these granitic sands would reflect sufficient differences between sites to enable an investigation into the effects of soil chemistry on herbivory and tree cover. Four of the plots are situated on the western side of the Kruger National Park where rainfall is about 650 mm per annum and the vegetation is a woodland dominated by the tree *Terminalia sericea*. The other four plots are situated further east, where rainfall is about 500 mm per annum and the vegetation is a savanna dominated by *Combretum* and *Acacia* species (mostly *Acacia exuvialis* and *Combretum apiculatum* subsp. *apiculatum*). The climate is strongly seasonal with a mean annual temperature range of 21.1-23.3°C (mean monthly temperature 16-28°C) and with rain falling predominantly in summer.

Soils were air-dried and sieved to <2 mm. Electrical conductivity (1:5 extract) and pH (1:5 extracts, saturated paste and 1:2.5 KCl 1M suspension) were determined on all samples (Rhoades, 1982). Water-soluble and ammonium acetate-extractable cations were analysed using atomic absorption spectrometry (Rhoades, 1982; Thomas, 1982). Total Zn, Mn, Co, Cu, Se and Mo were analysed by ICP-MS after digestion of a 50 mg soil sample with HF and HNO₃. Bray 2-extractable P was determined as described by Bray and Kurtz (1945). Total C

and N were analysed by complete combustion using a Eurovector Euro EA Elemental Analyzer. Clay content was determined by the hydrometer method, sand content by sieving and silt by difference. The clay fraction was dispersed using a Calgon dispersing solution of sodium hexametaphosphate and sodium carbonate. Organic matter was removed by oxidation with hydrogen peroxide (Soil Classification Working Group, 1991).

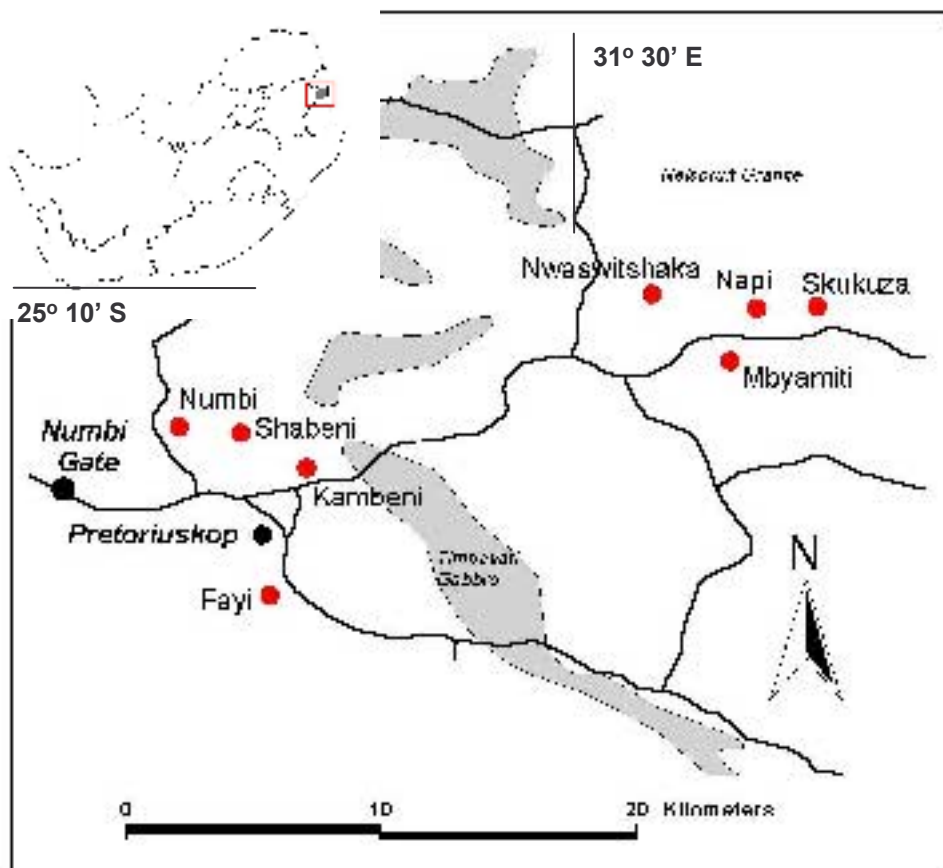


Figure 6.1 The location of the long-term burn experiments in the southern Kruger National Park, South Africa.

A survey was conducted over the period July to September 1999 to determine the abundance of herbivores at each site. Although herbivore numbers in a particular area are likely to change over time, an assumption was made in this study that the congregation of herbivores in specific localities (as documented by McNaughton [1988] in the Serengeti) is consistent over time. Consequently it was assumed that a three month survey could give an indication of the herbivore pressure in a specific locality over a longer period (possibly spanning several decades). Each long-term burn site was visited at least 18 times over this period and the number of herbivores present at each site was documented. The survey was conducted by

driving the length of the experiment in the firebreak adjacent to the 13 plots at each site and noting the number of herbivores on each treatment plot. All surveying was conducted in daylight hours. Impala (*Aepyceros melampus*) were more abundant than any other herbivore and could conceivably affect the mortality of tree seedlings given that they both browse and graze (Skinner and Smithers, 1990). General herbivore abundance was estimated by calculating the mass of herbivores sighted per visit. Herbivore mass for individual species was obtained from Skinner and Smithers (1990). Elephants and white rhinoceros (*Ceratotherium simum*) were sighted irregularly and skewed the data because of their great mass. Four herbivore indices of abundance were consequently used for correlation analyses with tree cover changes and soil micronutrients: i) mass of herbivores <1500 kg per visit (i.e. excluding elephant and white rhinoceros); ii) mass of herbivores per visit (including elephant and white rhinoceros); iii) total number of herbivores sighted per visit; and iv) number of impala sighted per visit. Digital aerial photographs taken from a low-flying helicopter in October 2000 were used for estimating the percentage of bare or grass covered area and the percentage of tree-covered area of annually burnt and unburnt plots. This was achieved using the object-oriented image analysis software eCognition 2.1 and the GIS software ArcMap 8.2. The impact of each annual burn treatment on tree cover at each site (tree impact factor) was scored by subtracting the percentage tree cover in the annual burn plots from the percentage tree cover in the forested unburnt plots. It was assumed that the unburnt plots represented an area of maximum tree cover potential for each site and that the difference between this “tree potential” and the tree cover on annual burn plots provided an index of the impact of annual burning on tree cover. In addition, tree and shrub data that were collected from transects on the annual burn plots in 1954, prior to the start of the experiment, were compared with data collected from the same transects in 1996 (*Terminalia* plots) and 1997 (*Combretum/Acacia* plots). All trees and shrubs were recorded from two transects of 300 m by 2 m running across the diagonals of each plot and categorised according to basal diameter. The basal diameter of shrubs was recorded as the distance between the two outermost stems. Multi-stemmed (coppicing) trees were categorised as shrubs, even though height of these “shrubs” could be in excess of 8 m. For this reason, a composite index of “tree cover” was difficult to extract from this data, and the aerial photographs were deemed a more accurate way of presenting the effect of fire and herbivores on tree versus open areas under grass.

Relationships between the tree impact factor, herbivore abundance indices and soil properties were determined with correlation and regression analyses using Unistat 5.0. The long-term

burn experiments were originally designed for an analysis of variance, but in this study it was noted that identical fire treatments had different effects on vegetation structure. Given that herbivore numbers vary from plot to plot, replication of treatments is assumed to be confounded by a herbivory effect and consequently a correlative approach was used for determining relationships across plots. Such an approach resides within a “confirmation” as opposed to “falsification” philosophy of science, which is recognised as appropriate for testing ecological theory (Pickett *et al.* 1994; Ford 2000). Determining whether significant correlations reflect causality would require further investigation. The significance of correlations was assessed using Pearson correlation coefficients as linear patterns were observed in many of the xy scatter plots and outliers were not evident. Data used in the correlation analyses were assumed to have a bivariate normal distribution. The graphical display of relationships includes a linear regression line with an associated r^2 value. The lack of fixed independent variables in this study violates a condition for Model I regression analysis and the analyses presented are therefore Model II regressions. Sokal and Rohlf (1995) suggest that if there is a causality relationship between variables, then a simple linear regression is appropriate for a Model II regression. The assumption was made in this study that there are causality relationships between the variables for which Model II regression relationships are presented.

6.3 Results

Aerial photographs of the annual burn and fire exclusion plots and the eCognition depiction of tree cover and open areas at each site are presented in Figures 6.2-6.5. Table 6.1 presents soil properties of each site and Figure 6.6 depicts the total number of herbivores sighted over the survey period. The tree impact factor was positively correlated with mass of herbivores <1500 kg ($r^2=0.65$, $n=8$, $p<0.001$) (Figure 6.7) and the latter was in turn strongly correlated with total Zn ($r^2=0.64$, $n=8$, $p<0.001$) (Figure 6.8). Other indices of herbivore abundance also showed significant relationships with soil properties and are presented in Table 6.2. In particular, the number of impala at each site was positively correlated with total Mn ($r^2=0.73$, $n=8$, $p<0.001$) (Figure 6.9) and total clay content ($r^2=0.72$, $n=8$, $p<0.001$) (Figure 6.10). The total number of herbivores was also positively correlated with total clay content ($r^2=0.75$, $n=8$, $p<0.001$). A summary of tree and shrub data collected from transects in 1954 and 1996/7 is presented in Figure 6.11. A marked decline in the number of trees with basal diameters > 7.6 cm is evident from 1954 to 1996/7 for all plots except Kambeni (the plot with the lowest

herbivore abundance), which showed a slight increase in this class of trees. Kambeni is also the plot with the greatest number of large shrubs and coppicing trees (Fig. 6.11c). Shrubs and coppicing trees showed an increase in the *Terminalia* plots from 1954 to 1996, but the response in the *Combretum/Acacia* plots was not uniform. A trend of decreasing tree/shrub density (1954 data in particular) with increasing herbivore pressure (as determined from the survey in 2000) is evident in Figures 6.11a&b.

Table 6.1: Soil properties of annually burnt plots in the southern Kruger National Park.

	<i>Terminalia</i> woodlands				<i>Combretum/Acacia</i> savanna			
	Numbi	Kambeni	Shabeni	Faai	Skukuza	Napi	Mbayamiti	Nwasitsaka
Electrical conductivity and pH								
EC (mS m ⁻¹)	4.4	5.7	4.5	4.5	3.0	4.8	7.9	4.8
pH (1:5)	5.1	5.3	5.1	6.7	6.3	5.4	6.0	5.6
pH saturated paste	6.5	6.5	6.4	6.5	6.8	6.4	7.0	6.8
pH KCl	5.2	5.4	5.2	5.3	5.5	5.3	6.0	5.6
Soluble ions (mmol_c kg⁻¹)								
Na	1.3	1.4	1.3	1.3	1.8	1.4	1.9	1.1
K	0.3	0.5	0.3	0.6	0.5	0.3	0.4	0.2
Ca	0.7	0.8	0.7	0.2	0.5	0.5	1.2	0.7
Mg	0.2	0.2	0.2	0.1	0.2	0.1	0.3	0.2
NH ₄	0.05	0.08	0.08	nd	nd	0.03	0.04	0.05
Cl	0.6	0.8	0.6	1.1	1.3	0.6	0.9	0.5
NO ₃	0.2	0.2	0.2	0.1	0.2	0.3	0.3	0.3
SO ₄	0.4	0.4	0.4	0.4	0.5	0.4	0.5	0.3
Extractable cations (mmol_c kg⁻¹)								
Na	0.9	1.1	0.9	0.9	0.9	1.0	1.0	1.0
K	1.9	2.0	2.7	2.0	2.1	2.3	3.5	2.0
Ca	17	22	21	19	22	24	43	29
Mg	5.1	6.4	6.8	5.3	6.4	5.2	9.6	6.4
Total metals (mg kg⁻¹)								
Zn	75	48	50	46	48	37	69	49
Mn	329	257	378	273	267	267	488	429
Co	3.9	4.3	5.5	3.4	2.5	2.4	4.4	3.3
Cu	6.0	5.1	8.2	10.6	6.7	4.1	7.9	5.3
Se	nd	nd	0.1	0.2	nd	0.4	nd	nd
Mo	0.3	0.2	0.3	0.1	0.1	0.1	0.2	0.1
Extractable P								
Bray-2 P (mg kg ⁻¹)	10	11	8	4	6	6	28	6
Soil organic matter								
Total carbon (%)	0.64	0.68	0.57	0.54	0.64	0.65	0.90	0.69
Total nitrogen (%)	0.056	0.060	0.059	0.056	0.055	0.067	0.076	0.064
Soil texture								
Clay	10	3	9	3	5	6	10	8
Silt	7	5	5	4	5	9	6	8
Fine Sand	21	25	26	33	25	26	26	26
Medium Sand	24	30	24	26	26	22	24	26
Course Sand	39	36	37	34	39	38	34	32

Table 6.2: Correlative relationships between impact of fire on tree cover, indices of herbivore abundance and soil properties. Pearson correlation coefficients are presented. Significant correlations ($p < 0.05$) are in bold.

	Tree cover	Herb. all (kg)	Herb. excl. ele. (kg)	Herb. no.	Impala no.
Tree cover		0.67	0.80	0.59	0.41
Herb. all (kg)	0.67		0.68	0.47	0.25
Herb. excl. ele. (kg)	0.80	0.68		0.80	0.63
Herb. no.	0.59	0.47	0.80		0.96
Impala no.	0.41	0.25	0.63	0.96	
EC	0.16	-0.33	-0.15	0.21	0.35
pH (1:5)	-0.16	-0.10	-0.07	-0.02	0.04
pH (sat. paste)	-0.20	-0.29	0.02	0.51	0.68
pH (KCl)	-0.15	-0.43	-0.10	0.40	0.60
Na	0.24	-0.01	0.08	0.25	0.28
K	-0.13	-0.06	-0.16	-0.42	-0.44
Ca	0.21	-0.13	0.10	0.48	0.56
Mg	0.30	-0.08	0.26	0.51	0.56
Cl	-0.09	-0.09	-0.08	-0.15	-0.14
NO ₃	-0.16	-0.49	-0.35	0.21	0.41
SO ₄	0.25	0.42	0.28	0.24	0.16
Extractable Na	-0.71	-0.87	-0.81	-0.56	-0.35
Extractable K	0.38	0.14	0.05	0.47	0.52
Extractable Ca	-0.04	-0.34	-0.16	0.41	0.59
Extractable Mg	0.10	-0.05	-0.02	0.46	0.57
Zn	0.70	0.28	0.80	0.79	0.74
Mn	0.21	0.13	0.26	0.76	0.85
Co	0.36	0.46	0.20	0.26	0.19
Cu	0.36	0.54	0.32	0.25	0.16
Se	0.04	0.05	-0.35	-0.46	-0.51
Mo	0.64	0.65	0.61	0.41	0.23
Bray-2 P	0.37	-0.13	0.16	0.50	0.58
Total carbon	0.07	-0.42	-0.03	0.42	0.58
Total nitrogen	0.02	-0.39	-0.26	0.25	0.42
Clay	0.53	0.39	0.59	0.87	0.85
Silt	-0.07	-0.35	-0.07	0.12	0.22
Fine Sand	-0.30	-0.05	-0.40	-0.38	-0.33
Medium Sand	-0.61	-0.49	-0.45	-0.52	-0.43
Course Sand	0.46	0.33	0.38	-0.04	-0.23

Tree cover = tree cover % on unburnt plots less tree cover % on burnt plots; Herb. all = mass of herbivores per visit; Herb. excl. ele. = mass of herbivores (excluding elephant and white rhino) per visit; Herb. no. = number of herbivores sighted per visit; Impala no. = number of impala sighted per visit.

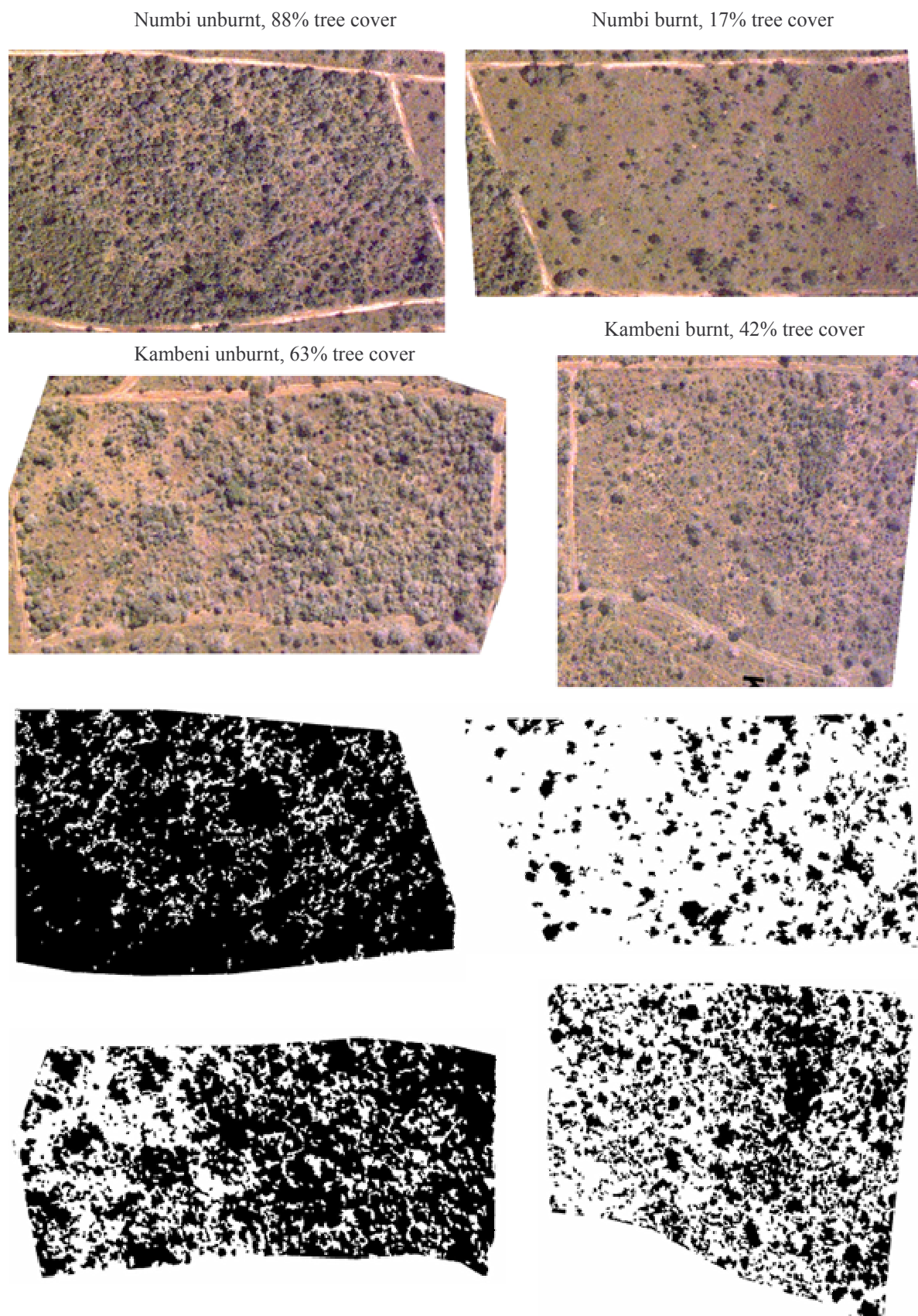


Figure 6.2 Digital photographs used for image analysis of tree cover (with the software package eCognition 2.1) and the image analysis results for the Numbi and Kambeni burnt and unburnt plots.

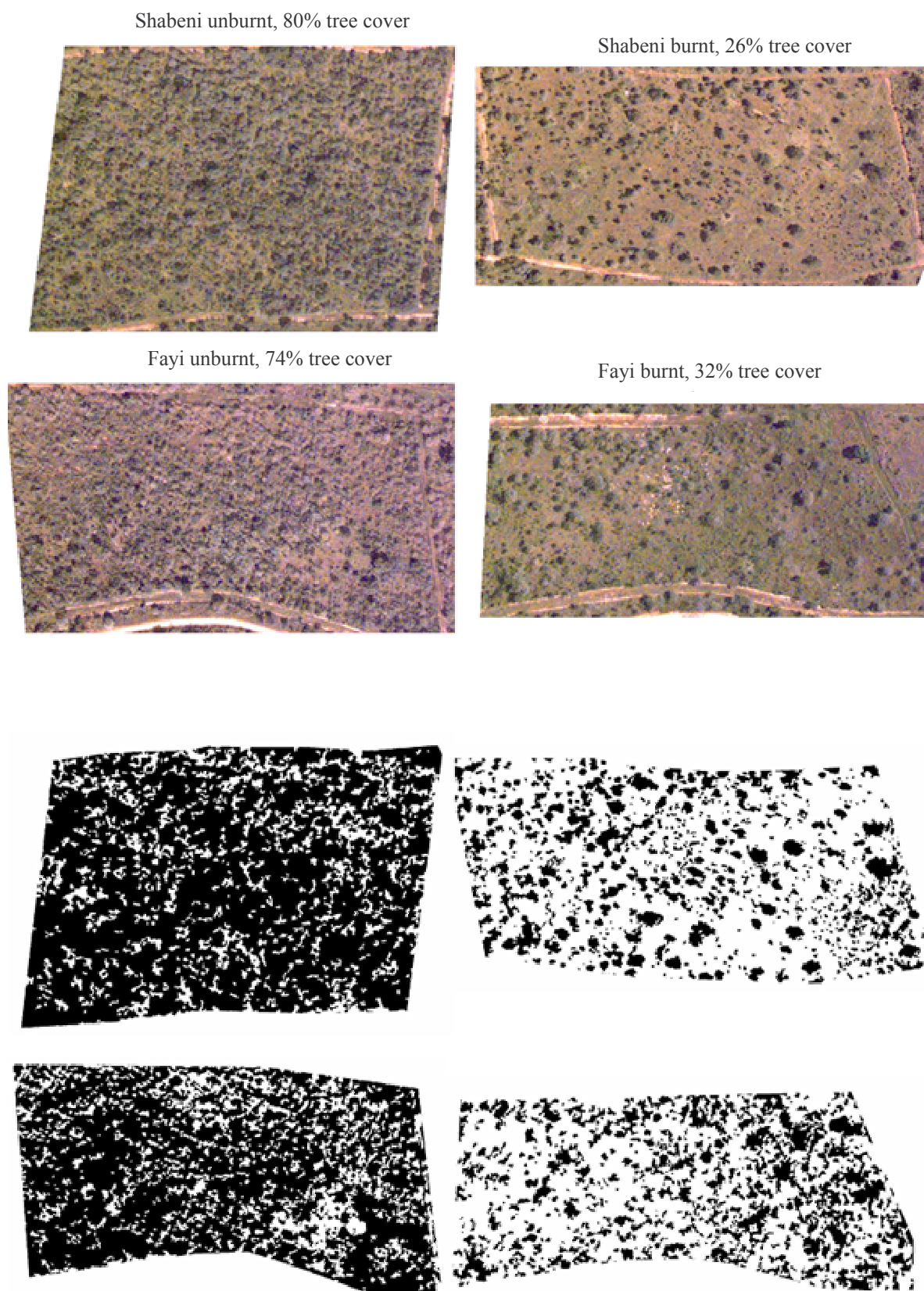


Figure 6.3 Digital photographs used for image analysis of tree cover (with the software package eCognition 2.1) and the image analysis results for the Shabeni and Fayi burnt and unburnt plots.

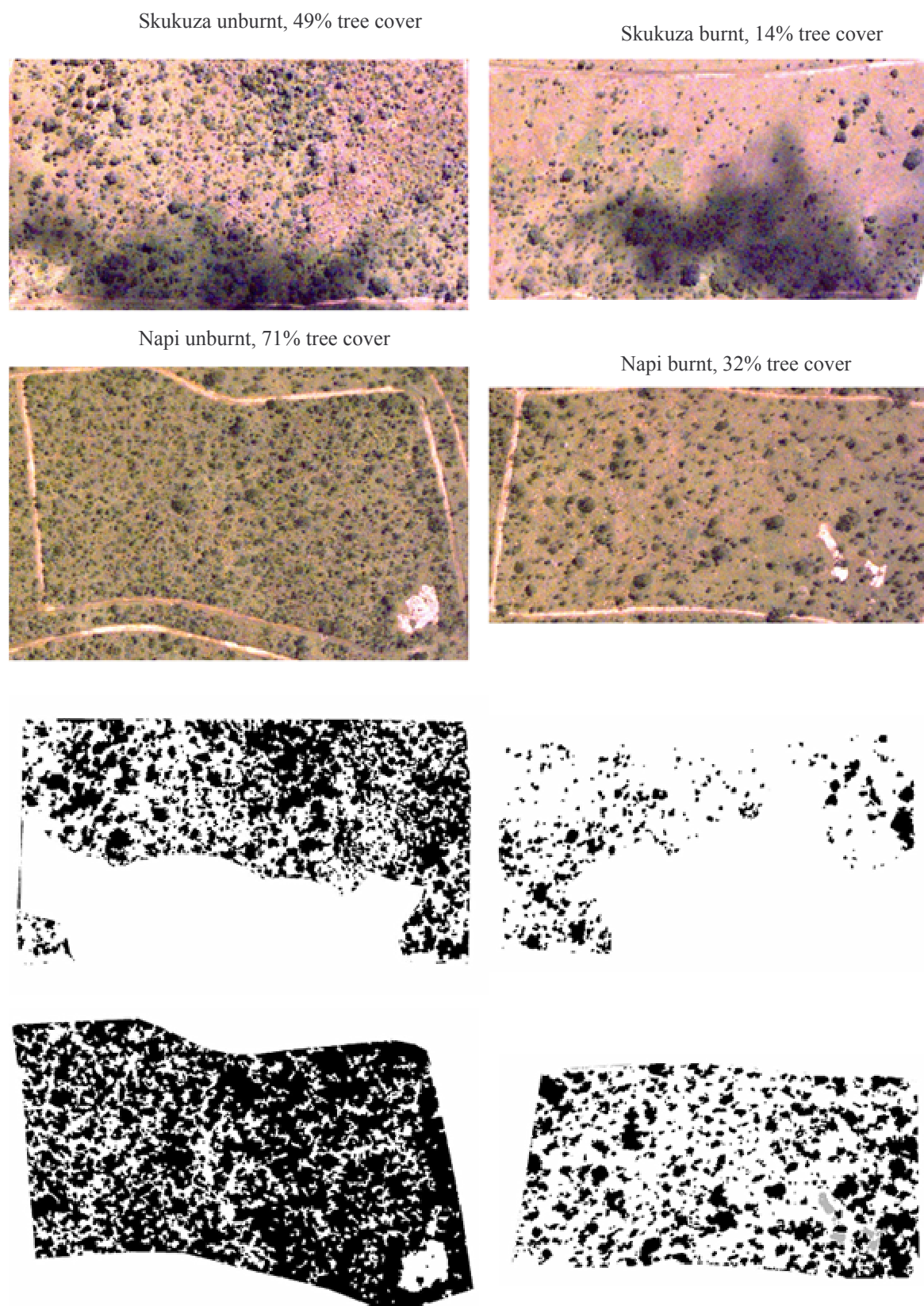


Figure 6.4 Digital photographs used for image analysis of tree cover (with the software package eCognition 2.1) and the image analysis results for the Skukuza and Napi burnt and unburnt plots.

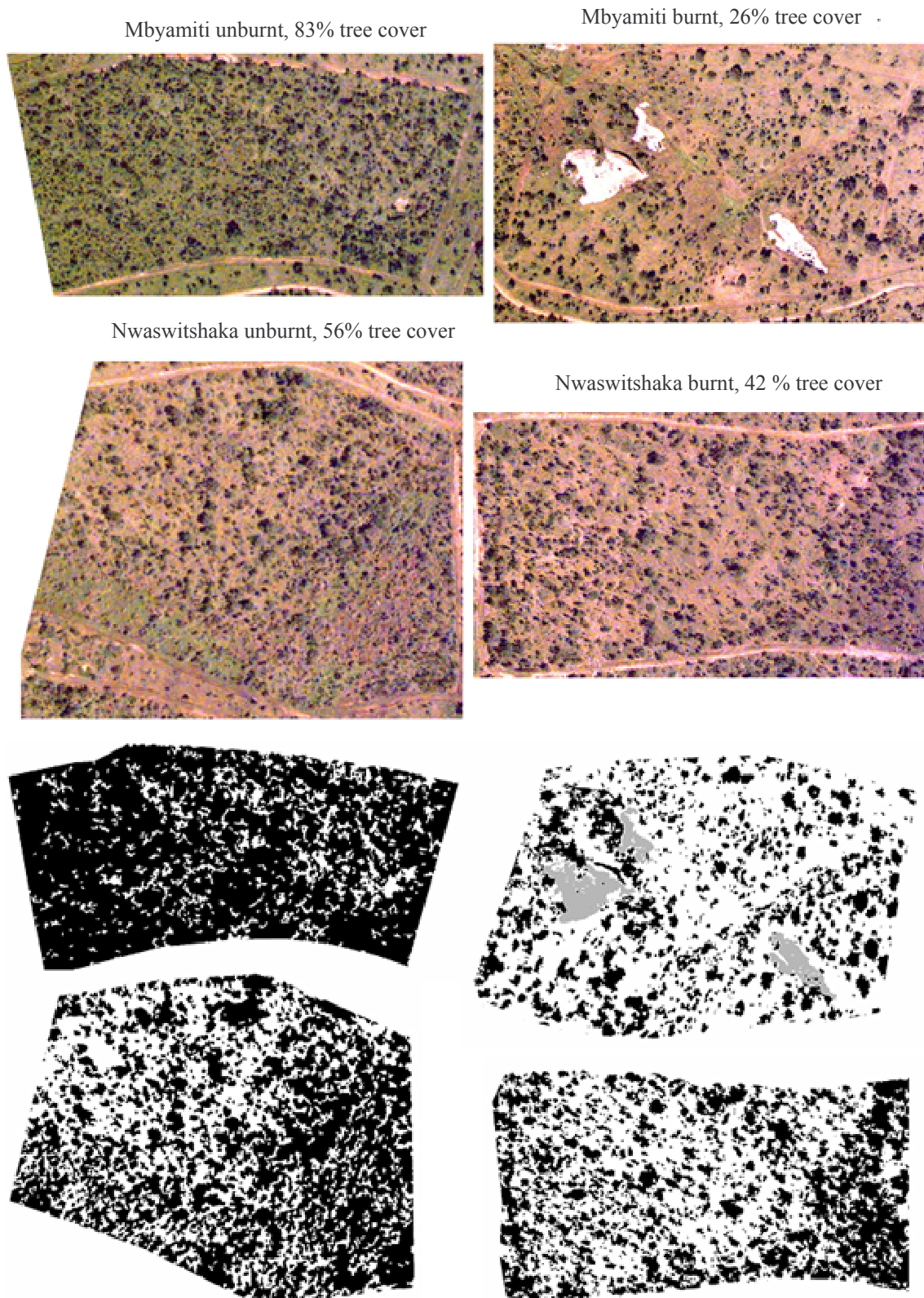


Figure 6.5 Digital photographs used for image analysis of tree cover (with the software package eCognition 2.1) and the image analysis results for the Mbyamiti and Nwaswitshaka burnt and unburnt plots.

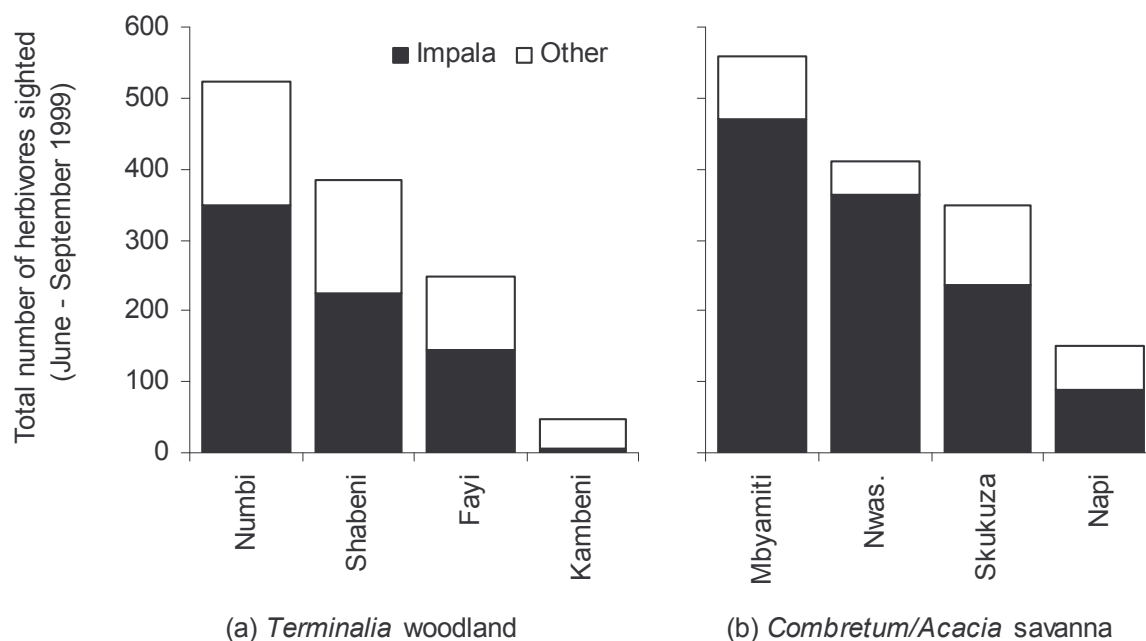


Figure 6.6 The total number of impala and other herbivores sighted at the long-term burn plots in the southern Kruger National Park over the period June to September 1999 in *Terminalia* woodland (a) and *Combretum/Acacia* savanna (b). Data were transformed to depict a total of 19 visits at each site.

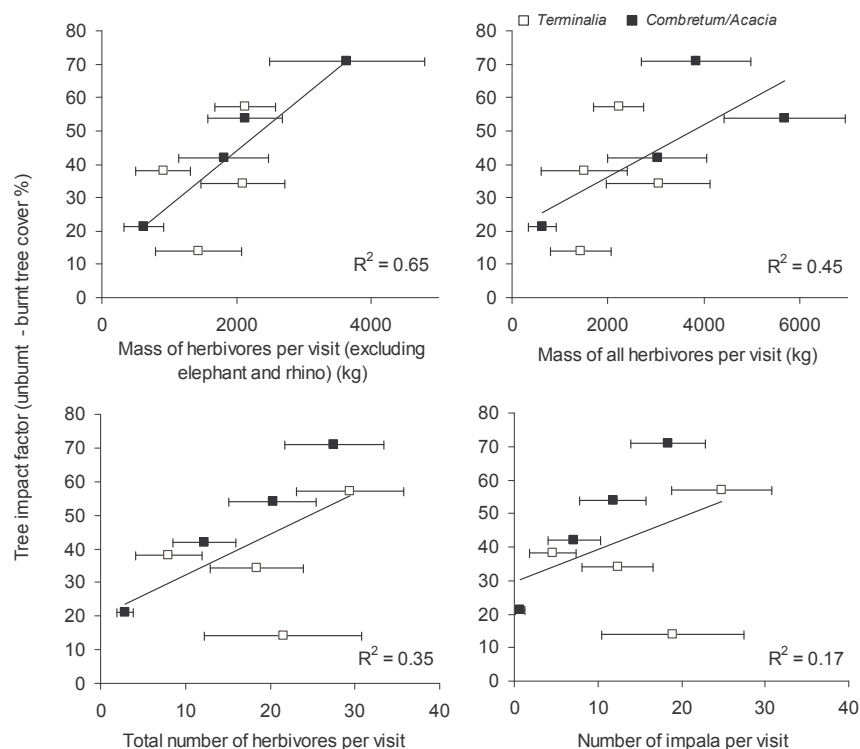


Figure 6.7 The relationships between tree impact factor and indices of herbivore abundance. Error bars depicted are standard errors of the mean.

Chapter 6: Soils, herbivory, fire and survival of trees in the Kruger National Park

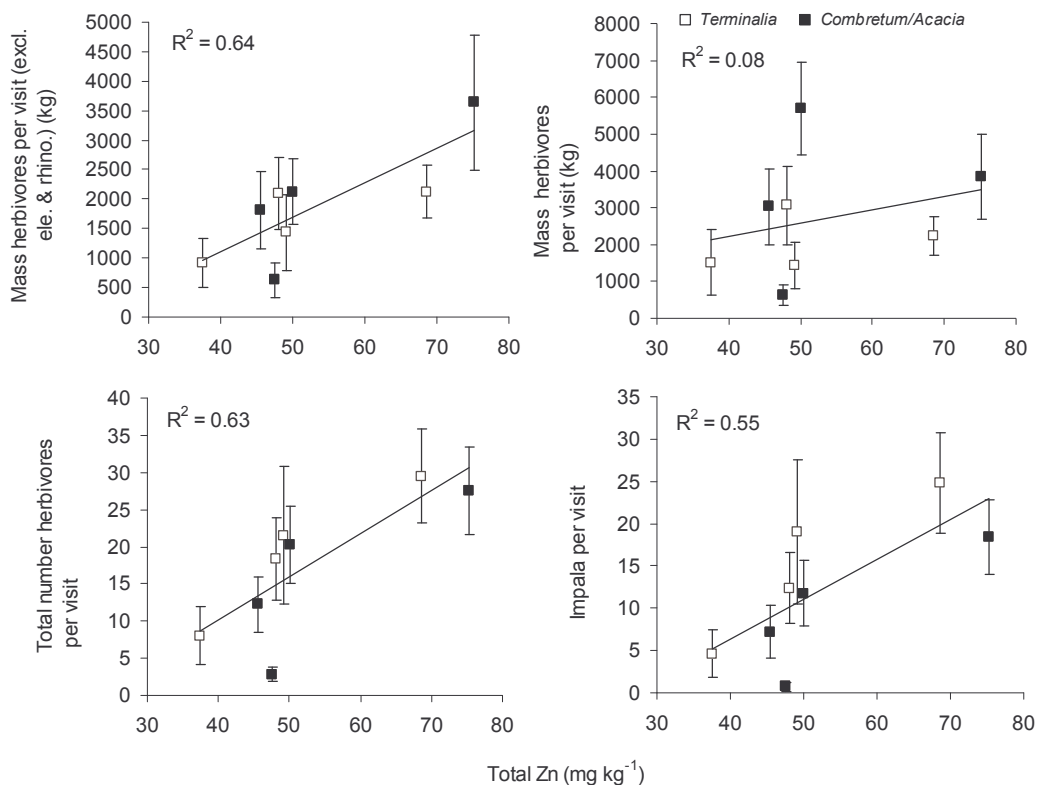


Figure 6.8 The relationships between indices of herbivore abundance and total Zn. Error bars depicted are standard errors of the mean.

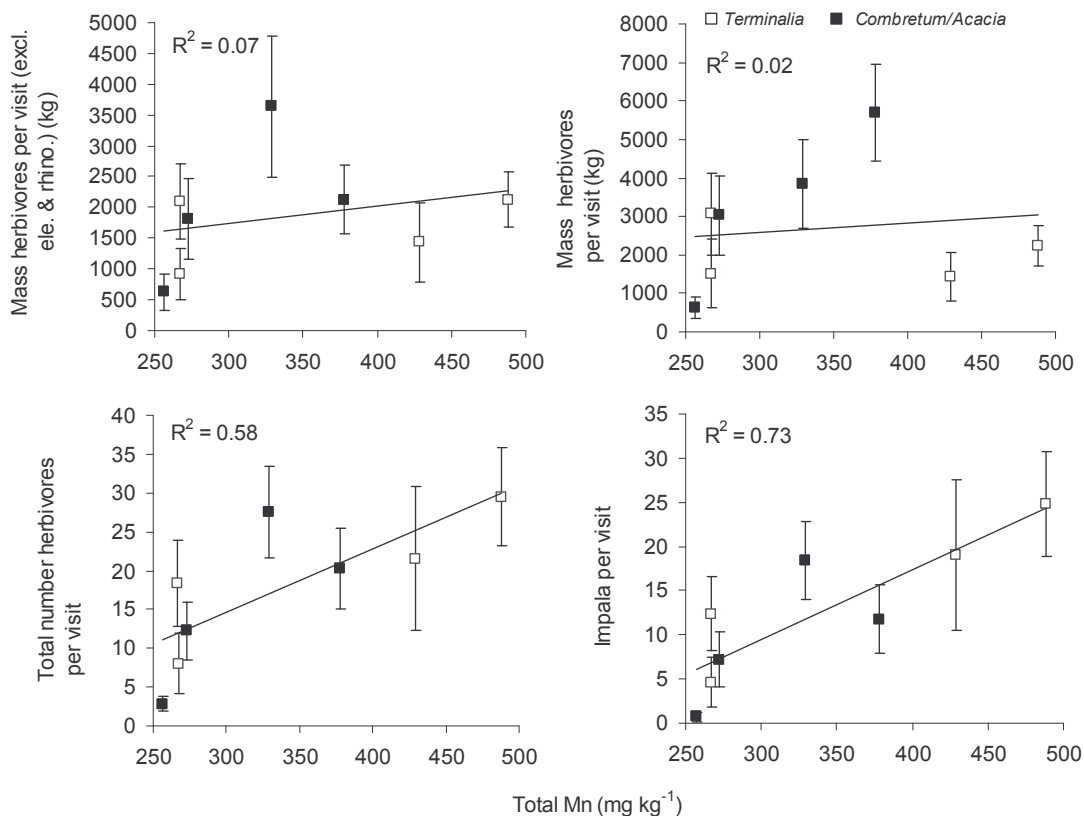


Figure 6.9 The relationships between indices of herbivore abundance and total Mn. Error bars depicted are standard errors of the mean.

Chapter 6: Soils, herbivory, fire and survival of trees in the Kruger National Park

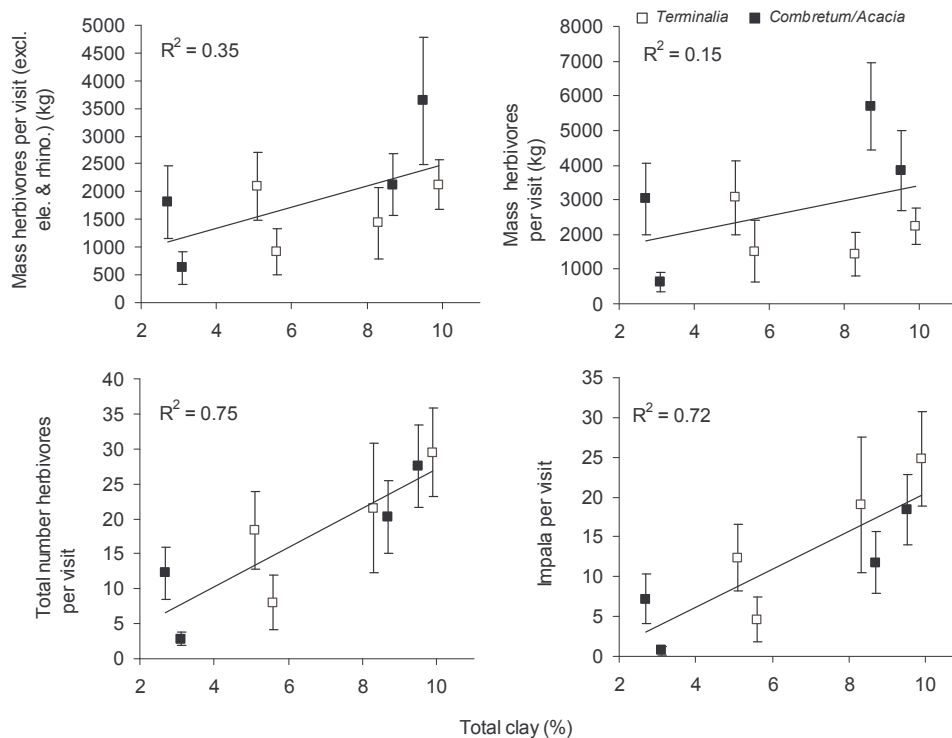


Figure 6.10 The relationships between indices of herbivore abundance and total clay content. Error bars depicted are standard errors of the mean.

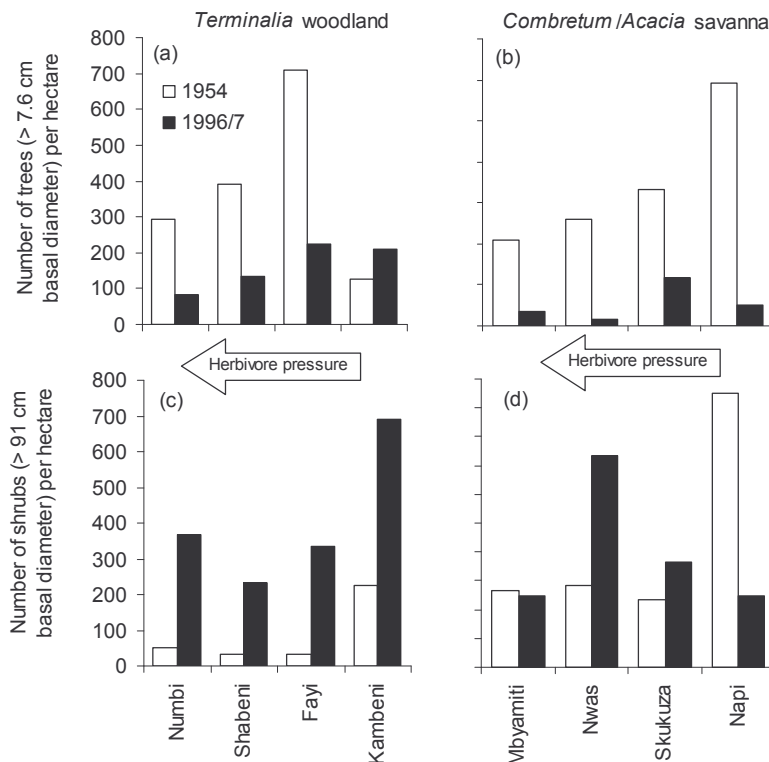


Figure 6.11 The number of trees (basal diameter > 7.6 cm) and shrubs (basal diameter > 91 cm) recorded from transects in annual burn plots of *Terminalia* woodland and *Combretum/Acacia* savanna in 1954 and 1996/7. Basal diameters of shrubs (which includes coppicing trees) refers to the distance between the two outermost stems.

6.4 Discussion

The postulates that (i) the intensity of browsing determines the persistence of trees in the post-fire environment and (ii) that the abundance of herbivores is a function of soil properties were both supported by the results of this study. Firstly, the tree impact factor (the difference between unburnt and burnt plot tree cover) was positively correlated with both the mass of herbivores < 1500 kg and with other indices of herbivore abundance (Figure 6.7). The tree impact factor at the four *Terminalia* plots, in particular, showed a distinct linear relationship to total number of herbivores (as well as number of impala) (Figure 6.7) and suggests that the two habitat types respond differently to herbivory and burning. Tree/shrub data collected in 1954 and 1996/7 also suggest this differing response in the two habitats. Large trees in the *Combretum/Acacia* plots showed a greater decline over time than the *Terminalia* plots (Figures 6.11a&b), and large shrubs (and coppicing trees) showed a uniform trend of increasing with time on the *Terminalia* plots whereas the response was not uniform in the *Combretum/Acacia* plots (Figures 6.11c&d). A possible explanation for the greater resilience of trees and shrubs to annual burning in the *Terminalia* plots, is the greater mean annual rainfall that occurs in the *Terminalia* woodland. The drier environment of the *Combretum/Acacia* savanna may prevent tree/shrub recruitment and reduce tree survival to a greater extent than in the moister *Terminalia* woodland. The inclusion of these two distinct habitat types within the same correlation analyses is problematic. Nevertheless, general patterns and relationships did emerge, notably the relationship between herbivore abundance and soil nutrient content.

The postulate that herbivore abundance may be a function of soil properties and possibly the status of micronutrients such as Zn was also supported by the data and indicates that the postulate is worthy of further investigation. The mass of herbivores <1500 kg was positively correlated with total Zn (Figure 6.8); the total number of herbivores was positively correlated with total clay content (Figure 6.10) and the number of impala at each site was positively correlated with total Mn (Figure 6.9) and total clay content (Figure 6.10).

Clay content may affect how attractive the site is for herbivores in numerous ways. The clay content of a soil affects both water content and nutrient availability, both of which in turn may affect the quality and production of forage. The effect of clay content on the availability of water for plant roots is complex. Clay can bind water and prevent water uptake. It may also

increase the water holding capacity of the soil, but at the same time reduce infiltration of rainwater. It is thus difficult to predict the effects that a shift in clay content from 3 to 10% in these granite-derived sandy soils may have on forage production. Nutrient availability tends to increase with clay content. Herbivores access nutrients either from foliage (which will tend to reflect the nutrient status of the soil) or through ingestion of soil, either via geophagia or by eating soiled foliage. Healy (1973) reports that geophagia can potentially supplement herbivore diets with micronutrients, especially given that chemical conditions in the alimentary tract tend to increase the availability of trace elements such as Zn and Mn.

If access to nutrients, whether they be macro or micronutrients, limits herbivore productivity, then herbivores are likely to have evolved a mechanism over time for seeking out that nutrient in their environment. If herbivores in the southern Kruger National Park are indeed congregating in areas that yield a greater supply of the most limiting nutrients in their diet, then Zn and Mn are possible candidates for the most limiting nutrients, given their strong correlations with indices of herbivore abundance. The congregation of herbivores on soils with greater clay content may not, however, be driven in a focussed, law-of-minimum fashion. It may be that soils with a greater clay content offer the herbivores a suite of advantages that include greater nutrient availability and a grass cover that flushes more frequently due to a more favourable soil water regime.

In the *Terminalia* woodland and *Combretum/Acacia* savannas, aerial photography reveals that a dense cover of trees can persist under a regime of annual burning. It is suggested here that the extent of tree cover after frequent burning in this environment is largely determined by the intensity of browsing. If herbivores are attracted *en masse* to the post-fire environment, then tree seedlings may be browsed and killed and adult trees may be damaged by larger herbivores. Elephants certainly have the capability to transform woodlands into grasslands and savannas (Cummings, 1982, Belsky *et al.* 1989; Trollope *et al.* 1998), but even small ungulates can reduce the growth of small trees (Belsky, 1994). Skinner and Smithers (1990) report that impalas eat a very wide range of browse plants, with the list of species taken dependent on the availability of the species in a particular area. They state further that the fine twigs and fresh leaves of *Acacia* spp. are a common item in the diet of impala in most areas and, where available, fine twigs and leaves of *Combretum* spp., *Grewia* spp., *Ziziphus* spp., *Maytenus* spp., *Dichrostachys* spp. and *Terminalia* spp. are also eaten. All of these tree genera are present in the study area and consequently impala are likely to be a major force affecting tree establishment and persistence. An abundance of herbivores in the post-fire

environment is likely to favour grasses over trees, such as is evident at Numbi. In contrast, if herbivores are not abundant within a particular area and are not attracted to the post-fire environment, then tree seedlings may establish, coppicing trees and shrubs may grow out of the fire zone (i.e. >3m) and adult trees may survive despite the effects of frequent fire. This is the postulated course of events at Kambeni, resulting in a relatively dense cover of trees and shrubs despite a regime of annual burning for 47 years. The tree and shrub data collected in 1954 and 1996 show that the density of large trees has increased at Kambeni and that large shrubs (which include coppicing trees) are approximately double the density of other *Terminalia* plots. Another pattern to emerge from the transect data in 1954 and 1996/7 is a trend of decreasing tree/shrub density (1954 data in particular) with increasing herbivore pressure (as determined from the survey in 2000) (Figure 6.11). This suggests firstly that the abundance of herbivores shapes vegetation structure in the southern Kruger National Park, not only in annually burnt plots, but in the landscape as a whole. Secondly, it suggests that the congregation of herbivores in localised regions (as reported by McNaughton [1988]) is a consistent phenomenon on a timescale of half a century.

6.5 Conclusions

Herbivores appear to be a major factor determining the extent of tree/shrub cover in the long-term annual burn plots of the southern Kruger National Park. This is suggested by the strong correlation between the tree impact factor and mass of herbivores <1500 kg. It is postulated further that the congregation of herbivores in localised areas may be related to soil nutrient content. Indices of herbivore abundance were positively correlated with total Zn, total Mn and total clay content of surface soils. The congregation of herbivores on plots with greater clay content may be due, along with other factors such as soil water availability, to greater availability of micronutrients such as Zn and Mn. In the next chapter, the links between the preceding chapters are brought together in a discussion on the reciprocal relationships between vegetation structure and soil properties across all study sites. A new theory is presented on savanna structure and how the abundance of trees in a landscape may be affected by the rate of mineralisation of soil organic matter. In particular, it tackles the question: “Why are trees excluded from mesic grasslands, yet occur in xeric savannas?”

CHAPTER 7

RECIPROCAL RELATIONSHIPS BETWEEN VEGETATION STRUCTURE AND SOIL PROPERTIES IN SELECTED BIOMES IN SOUTH AFRICA

7.1 Introduction

The relationships between vegetation structure and soil properties are multifaceted. For the purposes of this thesis, soil organic matter and the tendency of soil to crust were chosen as two key soil properties on which to focus, because of their relevance, particularly in a semi-arid country such as South Africa, to ecosystem functioning and agricultural productivity. In this chapter, interactions between soil organic matter, soil crusting and vegetation are discussed in the context of all the study sites. The discussion ranges from the quantitative effects of vegetation structure on soil chemistry to a more speculative hypothesis on how the Birch effect (Birch, 1958) may influence the abundance of trees across biomes.

7.2 Fire, degradation of soil and the abundance of trees

Fire alters vegetation structure, is an integral part of the ecology of the bushveld and grassland biomes in South Africa (Bond, 1997; O'Connor and Bredenkamp, 1997; Scholes, 1997; Higgins *et al.*, 2000) and is frequently used as a tool in veld management. Despite the ubiquitousness of fire in South African ecosystems, the effects of frequent fire on soil properties and the possible consequences of these soil changes for plant growth are largely unknown. In Chapter 2 it was shown that annual burning can alter soil physico-chemical properties and potentially affect the regeneration of plants in the post-fire environment. The soil organic matter content of soils was lower in annually burnt plots than in unburnt plots. This effect of fire can be ascribed to (i) a loss of organic matter through combustion and thus less return of organic matter to soils, (ii) greater soil temperatures in the exposed burnt plots and therefore greater microbial activity (Savage and Vermeulen, 1983; O'Lear *et al.*, 1996; Knapp *et al.*, 1998), (iii) combustion of soil organic matter in the top few centimetres of soil (Hains, 1926; Austin and Baisinger, 1955; Ahlgren and Ahlgren, 1960), (iv) greater microbial activity in burnt plots due to frequent wetting and drying of the soil surface – a result of less interception of rainfall by vegetation and greater soil temperature and therefore evaporation (Birch, 1958), (v) a possible reduction in microbe-inhibiting root exudates (Theron, 1951; 1963), and (vi) an increase in soil alkalinity (which favours microbial growth) (Greenwood,

1968; Curtin *et al.*, 1998; Knapp *et al.*, 1998). The difference in soil organic matter content between burnt and unburnt plots in the Kruger National Park was greatest in the top few centimetres of soil. It is this thin surface layer or *pedoderm* that is likely to be of critical importance for the regeneration of plants after fire. The pedoderm has a greater soil organic matter content than deeper layers (Chapter 2) and consequently mineralisation and supply of nutrients such as N and P is likely to be disproportionately greater in this surface layer than deeper in the profile (Woods, 1989; Purnomo *et al.*, 2000). It is also the membrane that “receives”, “transfers” and adsorbs nutrients from the decomposing leaf litter that lies above the mineral soil. Furthermore, water and oxygen enter the soil profile through this membrane and thus the stability of the membrane pores affects the water content and redox status of the soil profile (McIntyre, 1958a; Agassi *et al.*, 1981; Hillel, 1998). If these soil pores become blocked due to the breakdown of soil aggregates, then infiltration into the soil is impeded and surface runoff is likely to occur (Levy and Rapp, 1999). Soil organic matter tends to promote soil aggregate stability (Du Plessis and Shainberg, 1985; Golchin *et al.*, 1995; Haynes, 1999) and consequently a decrease in organic matter may reduce the stability of soil pores and decrease the rate of infiltration of water into the soil profile (Robinson and Philips, 2001).

Indeed, it was shown that soils from burnt plots in the Kruger National Park, Ukulinga and Fort Hare all have a greater tendency to crust (i.e. a lower rate of infiltration through the soil surface) than soils from adjacent, unburnt plots. The significance of this is that not only are soils more likely to crust or seal after fire due to exposure of the soil surface to raindrop impact (McIntyre, 1958 a&b; Hillel, 1998), but that subtle chemical changes that come about after long-term burning render the soils more prone to clay dispersion and thus crusting. This finding has potential application in the broader context of land degradation as a whole. The question should be asked: if the removal of vegetation by fire alters soil chemistry in such a way that the soil has a greater tendency to degrade (i.e. a soil more prone to clay dispersion, crusting, aggregate breakdown and hence erosion), then does the removal of vegetation by livestock or farmers have a similar effect on soil chemistry? The answer may lie within an understanding of how and why soil chemistry is altered by long-term burning regimes.

In Chapter 2 it was shown how soil properties at different depths in the granite-derived soils of the southern Kruger National Park are altered by frequent burning. Soils were sampled at 1 cm depth intervals and it was this approach that revealed how the removal of vegetation by fire changes the distribution and relative quantities of individual cation species within the soil

profile. Previous bulk sampling to a depth of 10 cm had obscured major differences between burnt and unburnt plots that became markedly apparent with the 1 cm depth interval sampling strategy. The results showed that burnt plots had lower concentrations of water-soluble and (NH₄)OAc-extractable Ca, Mg and K, particularly in the top few centimetres of soil. By contrast, concentrations of water-soluble and (NH₄)OAc-extractable Na in these layers were similar in burnt and unburnt plots. This finding provides an explanation for why soils in burnt plots have a greater tendency for clay dispersion and crusting. The sodium adsorption ratio and exchangeable sodium percentage were greater in the surface soils of burnt plots than unburnt plots. Such a change in soil chemistry is likely to increase the tendency of clay to disperse (Du Plessis and Shainberg, 1985; Bloem and Laker, 1994a). Long-term burning can thus reduce organic matter in surface soils, but it can also decrease the proportion of Ca and Mg to Na. Both of these effects are likely to create a soil with less resilience to raindrop impact, i.e. a soil more prone to aggregate breakdown, clay dispersion, crusting and hence erosion.

The question then remains, will removal of vegetation by livestock or crop harvesting potentially increase the sodium adsorption ratio of surface soils? The answer lies within an understanding of why Ca, Mg and K are reduced in concentration relative to Na. In Chapter 2 it was suggested that Ca, Mg and K are removed from burnt plots over time because plants take up greater quantities of these cations than they do Na (Whitehead, 2000), and that the Ca, Mg and K-rich ash in the post-fire environment is often lost from the site by surface runoff or is blown off the site (White and Grosman, 1972). Sodium, by contrast, remains in the soil and is not cycled into plants and hence ash. Consequently, the removal of vegetation over time by livestock or cropping, could have a similar effect to long-term burning on the sodium adsorption ratio, *if* the vegetation is removed from the site. Where vegetation is left on the soil surface, or is recycled through livestock and deposited as dung and urine, Ca and Mg are unlikely to leave the site. If, however, livestock are kraaled at night and dung is concentrated in a certain area, and/or vegetation is cropped and taken off site, then there is likely to be an export of Ca and Mg and an increase in the sodium adsorption ratio over time. Such an effect may only be revealed by sampling in thin slices through the top few centimetres of soil, as this is where root density and thus nutrient extraction are greatest. A focus on this surface layer or pedoderm is thus an interesting direction for future research aimed at unravelling the complexities of land degradation.

Unfortunately, the approach of sampling at centimetre intervals was adopted only towards the end of this study and hence the majority of fieldwork was undertaken using bulk samples to a depth of 10 cm. In the Eastern Cape, where the effect of vegetation removal by goats was investigated, it was shown that, like frequent burning, intensive goat farming resulted in a marked decrease in soil organic matter in the top 10 cm of soil. It is suggested that the processes behind the decline in organic matter are similar to the processes operating in long-term burn plots (i.e. a reduction in the return of organic matter to the soil, an increase in soil temperature, an increase in the number of wetting and drying cycles, and a possible reduction in microbe-inhibiting root exudates). The tendency of soils to crust was also greater in goat-transformed sites than intact thicket sites. This change in soil chemistry is attributed to the aggregate-weakening effect of a decline in organic matter, particularly labile C. The sodium adsorption ratios of bulk samples to 10 cm were similar in goat-transformed and intact thicket sites and consequently changes in proportions of Ca and Na did not appear to be part of the process of greater crusting in goat-transformed sites. Water-soluble and (NH₄)OAc-extractable Ca were actually consistently greater in goat-transformed sites than intact sites. Goats recycle nutrients, such as Ca, in dung and urine and consequently there is less likely to be a loss of nutrients from goat-transformed sites than from burnt plots, where ash can be lost in wind or water runoff. Investigation into soil chemistry in the top centimetre of soil may, however, be instructive for future research in this environment.

The alteration of vegetation structure by both annual burning and goat farming had similar effects on soil properties, i.e. a reduction in soil organic matter and an increased tendency of the soil to crust. Such changes in soil properties are likely to affect plant growth and thus ecosystem responses to fire and goats. An increased tendency to crust, for example, will result in greater runoff, a drier soil profile and greater erosion. The dominance of drought-adapted ephemeral grasses and karroid shrubs on goat-transformed sites in the Eastern Cape (Lechmere-Oertel *et al.*, 2002, in preparation) may therefore be partly explained by the greater soil temperatures, as well as greater runoff, that would be expected on these sites. Similarly, in the Kruger National Park, greater runoff on burnt plots may favour shallow-rooted grasses over deeper-rooted woodland tree species in the region.

The effect of fires on vegetation structure is, however, extremely complex and soil crusting is only one factor in a milieu of interacting factors that include damage by fire, soil texture, nutrients, herbivory and climate (Scholes and Walker, 1993; Walker and Noy-Meir, 1982;

Westoby *et al.*, 1989; Frost, 1996; Scholes and Archer, 1997). Higgins *et al.* (2000) propose that savanna structure in the post-fire environment is dependent upon the intensity of fire and, most importantly, rainfall. They argue that tree seedlings will only recruit into mature trees if there is sufficient water for growth to outrival grasses and that water is limiting in most years in many savanna environments. It is therefore only in the occasional wet year that tree seedlings are able to escape the zone where fire and competition by grasses prevent their growth into mature trees. The findings in this thesis add to this theory by demonstrating that frequent fire can increase crusting of soils and therefore increase the aridity and drought stress experienced by tree seedlings at a particular site. Fire can therefore potentially promote grasses over trees through several mechanisms, such as (i) direct damage to trees, and (ii) an increase in aridity due to greater soil crusting, as well as removal of litter, and thus increased evaporation from the soil surface (Kelly and Walker, 1976; Cass *et al.*, 1984; Fischer and Turner, 1978; Van de Vijver, 1999).

An additional mechanism by which fire can alter vegetation structure is by attracting herbivores to the post-fire environment. Fire tends to result in a flush of green grass with a greater nutrient content than unburnt grass (Christensen, 1977; McNaughton, 1985; Van de Vijver, 1999). Herbivores may limit tree seedling recruitment by browsing leaves and stems (Skinner and Smithers, 1990). This effect is not included in the model of savanna structure proposed by Higgins *et al.* (2000). They suggest instead that herbivores reduce fire intensity by reducing the fuel load of grass and that this will favour tree seedling recruitment. This is contrary to the results presented in Chapter 6 which show that the difference in tree cover between unburnt and burnt plots in the southern Kruger National Park is strongly correlated with the abundance of herbivores at each site. It is suggested in this chapter that the intensity of herbivory is the primary factor governing tree seedling survival and therefore tree cover in the post-fire environment of these granitic landscapes. It is also noted that the abundance of herbivores was strongly correlated with clay content, total Zn and total Mn in topsoils of the eight burnt plots. This combined dataset, showing correlations between tree cover, herbivore abundance and micronutrients, although not demonstrating cause and effect, points towards an intriguing scenario for vegetation structure in the southern Kruger National Park. The model put forward in Chapter 6 for vegetation structure (i.e. the percentage of grass cover versus tree cover) in these post-fire environments is as follows: (i) herbivore productivity and vigour in this nutrient-poor, granitic landscape are limited by micronutrients such as Zn and Mn; (ii) herbivores, in search of flushes of nutrient-rich foliage in the post-fire environment

(McNaughton, 1985; Moe *et al.*, 1990; Wilsey, 1996) concentrate in areas where micronutrients are most available; (iii) the micronutrients may be accessed via geophagia (Healy, 1973) and/or ingestion of plant material; and (iv) where soils are relatively rich in micronutrients, tree seedlings are browsed before they reach maturity and hence a grassland-like environment is created. The Numbi annual burn plot was the archetype “grassland” site, with the greatest concentration of Zn and Mn relative to other sites in the region and was also the plot which attracted the greatest number of herbivores (Figures 6.2 & 6.6). By contrast, the Kambeni annual burn plot had the lowest concentration of Zn and Mn, attracted the fewest herbivores, and is surprisingly wooded, despite being burnt every August for 47 years.

The structure of savannas and, in particular, the unlikely coexistence of two extremely different plant forms - trees and grasses - has been debated at length in the literature (Westoby *et al.*, 1989; Scholes and Archer, 1997). This has been termed the “savanna problem” by Sarmiento (1984). Walter (1971) proposed that trees and grasses occupy separate rooting niches in savannas and that this enables their coexistence. He suggested that trees have sole access to water in deeper soil horizons, while grass roots dominate topsoils and compete successfully with tree roots for water near the soil surface. Recently Higgins *et al.* (2000) provided an opposing hypothesis, suggesting that tree recruitment takes place in unusually wet years and that the coexistence of trees and grasses is essentially a reflection of alternating climatic conditions that in some years favour grasses and in other years favour trees. This is a compelling idea, yet it ignores an inescapable truism that many grasslands worldwide have wetter climates than adjacent savannas (Appendix B, Figure 1). If trees are limited by water availability in savannas and only recruit in relatively wet years, then why are grasslands with wetter climates not dominated by trees? Higgins *et al.* (2000) suggest that fire intensity is greater in mesic grasslands than in dry savannas because of greater biomass production and that trees are excluded from the landscape due to fire. In the paragraph below evidence is presented which shows that even extremely intense fires are unlikely to exclude trees. This is followed by a new theory, based on the Birch effect, explaining why savannas often occur in areas that are drier and warmer than grasslands.

The plant kingdom is extremely flexible in terms of structure and size. It is not unusual for a single plant family to range in size from ground-dwelling herbs to trees 20 m in height (e.g. Asteraceae, Euphorbiaceae). Plants are therefore unlikely to be constrained by genetic limitations, in terms of evolving into trees in particular landscapes. A corollary to this

statement is that if the physical environment is favourable for tree growth, then trees will ultimately evolve from the genetic stock in that landscape. The argument, for example, that tall trees are not present in some South African landscapes, such as the fynbos biome (Richardson and Cowling, 1992) because of an accident of history and because tree immigration may have been prevented due to geographic isolation (Richardson *et al.*, 1992), could be dismissed on the grounds of extreme flexibility within plant families. The fynbos biome is one of the most plant speciose regions in the world (Cowling *et al.*, 1997). It is therefore highly unlikely that such a system would be constrained by genetic limitation. As Richardson *et al.* (1992) note: “For some reason that we cannot explain, a guild of pioneer trees has not evolved in the fynbos flora”.

Returning to the question of tree exclusion from grasslands: if trees across the planet have evolved mechanisms for coping with intense fire, then there is inconsistency in the argument that trees can be excluded from certain regions due to damage by fire (unless it can be shown that these fires are more frequent and intense than other forested areas). Fire (often frequent and intense) is an integral part of the ecology of forests in many parts of the world (Ahlgren and Ahlgren, 1960; Kozlowski and Ahlgren, 1974; Rundel, 1981; Keeley and Fotheringham, 2002). In the *Pinus* woodlands/savannas of the southeastern United States, for example, the highly flammable ground cover of *Aristida* grass commonly burns at frequencies of 2-8 years (Wells, 1928; Christensen, 1977; Wilson *et al.*, 2002). Interestingly, the tallest and most massive plants ever known (*Sequoia*, *Sequoiadendron*) are fire-prone conifers (Enright and Ogden, 1995). Mutch and Parsons (1998) note that fire intervals during 1700-1900 in the Giant Forest area of Sequoia National Park were 7 to 10 years. In the angiosperm realm, some of the tallest known plants are ash eucalypts (e.g. *Eucalyptus regnans*), which are also well adapted to fire (Ashton, 1981; Beadle, 1981; Florence, 1996). *Eucalyptus* spp. in Australia are not only adapted to intense fire, but propagate it with volatile oils and stripping bark, so that the tree canopies ignite in a green state. Ward *et al.* (2001) demonstrated through analysis of grasstree (*Xanthorrhoea*) trunks that fires in the dry *Eucalyptus* forest region of southwestern Australia probably occurred every 3–5 years. In northern Australia, Liedloff *et al.* (2001) note that under a regime of frequent fire, *Eucalyptus* savannas/woodlands have ground layers dominated by annual grasses which “produce copious quantities of highly flammable fuel that perpetuate frequent, hot fires”. Williams *et al.* (2002) report that frequent fire can increase tree mortality in northern Australian savannas but also note that annual, intense fires in a mesic savanna at Kapalga did not reduce the bank

of tree seedlings or saplings in all of the major tree species. In the African tropics, the tallest woodlands (e.g. Miombo dominated by *Brachystegia*) are also fire-prone and have grassy understories which burn regularly (Trapnell, 1959; Werger and Coetzee, 1978; O'Connor and Bredenkamp, 1997).

Fire, it seems, can perpetuate a forested ecosystem and it is evident that even intense fires do not exclude trees from many ecosystems. Trees are thus unlikely to be excluded from grasslands due to damage by fire. Such an argument undermines the tremendous flexibility of plants and trees to adapt to regimes of frequent and intense fires. It is undeniable that in most grasslands, fire exclusion experiments do tend to result in encroachment of woody species (Titshall *et al.*, 2000). This does not, however, demonstrate that it is damage by fire *per se* that excludes trees from grasslands. Fire also changes the physical environment within which plants are growing by reducing the cover of vegetation, exposing the soil surface to sunlight, reducing the interception of rainfall and in some cases increasing the tendency of soils to crust. The fire exclusion experiments may therefore merely be indicating that fire can, under certain climatic and soil conditions, create a physical environment that favours grasses over trees. It is commonly *assumed* that damage by fire excludes trees from grasslands (Rundel, 1981; Higgins *et al.*, 2000). As discussed above, because trees have evolved to cope with intense and frequent fire in numerous habitats across the earth, it follows that a specific set of physical changes in the post-fire grassland environment, rather than damage to trees by fire, may be the primary reason for exclusion of trees in grasslands. A hypothesis and some supporting data on how the physical environment can favour either trees or grasses is presented below.

7.3 A new theory on savanna structure: do productivity of plants and the Birch effect determine the distribution of trees across biomes?

In order to tackle the questions: “why do trees and grasses coexist in savannas without one group outrivalling the other?” and “why do savannas tend to occur in drier and warmer regions than grasslands?” the fundamental differences in environmental preferences between trees and grasses need to be ascertained. A possible explanation may lie within a theory recently developed by Milewski and Mills (in preparation, Appendix B). The theory proposes that the fundamental difference between trees and grasses is in the ratio of *plant productivity:nutrient uptake* and that this difference can potentially explain why trees occur in

some biomes and not others. In brief, trees are composed largely of wood which is relatively nutrient-poor, whereas grasses are composed largely of foliage and fine roots which are comparatively nutrient-rich. All other things being equal, in environments where nutrients are cycled rapidly through soil organic matter (and in the process made available for plant uptake) there is the potential for plants to form nutrient-rich tissues i.e. herbaceous tissues. By contrast, in environments where nutrient cycling is restricted and the availability of nutrients for plant uptake is limited at certain times, plants may be limited to producing nutrient-poor tissues i.e. wood. An exception to this rule may be tropical rainforests where nutrient cycling is rapid, but nutrients are easily leached, productivity of plants is exceptionally great and consequently nutrient-poor tissues are likely to develop. An assumption underpinning this theory is that although an increase in height may be beneficial for plants in terms of outrivaling neighbouring and competing plants through shading, in general, height is costly because of the energetic costs involved in transporting water (xylem vessels presumably require reinforcing as pressure within the vessels increases), counteracting gravity (growth of support structures) and maintaining sapwood (Tyree and Sperry, 1988; Yoder *et al.*, 1994; Ryan and Yoder, 1997). Thus, if plants are able to maximise productivity in a particular environment, yet still take up sufficient nutrients to form nutrient-rich tissues, then the habitat that evolves in that environment will be dominated by herbaceous plants and the vegetation will be short. The assumption here is that woody plants would not compete effectively in this environment because they incur the costs of gravity and tissue maintenance, whereas herbaceous plants do not incur these costs. If, however, plants maximise their productivity in a particular landscape, yet are unable to take up sufficient nutrients to form nutrient-rich tissues, then herbaceous plants by definition cannot compete and woody plants will emerge as the dominant plants in the landscape.

Figure 4 in Appendix B presents net primary productivity of forests and grasslands on six continents plotted against the annual net uptake of N and provides a test for the productivity:nutrient hypothesis described above. As predicted from the productivity:nutrient hypothesis, in habitats of similar productivity, absolute nutrient uptake (in this case N uptake) is greater in grasslands than in forests. The graph suggests that the availability of nutrients, relative to the productivity of the system, may well be an important factor determining the vegetation structure of biomes. It is important to note here that availability of many nutrients is largely divorced from the nutrient content of parent materials and soil types. Most of the N (and often most of the P) taken up by plants in natural systems is made available through the

mineralisation of soil organic matter. Although the source of P in soils is originally the soil parent material, the strong sorption of PO_4 in soils often dictates that plants can only access P when it is released from soil organic matter. Mineralisation therefore tends to be the rate limiting step in the process of nutrient supply to plants from soils. Understanding the dynamics of the mineralisation of soil organic matter may thus be the key for unlocking an understanding of vegetation structure across biomes. It is suggested below that the vegetation structure in savannas and grasslands can be understood by examining differences in the timing of mineralisation and thus nutrient supply to plants.

The rainfall in many characteristic grasslands of the world, such as the Highveld of South Africa, the Tallgrass Prairies of North America, the Pampas of South America and the Serengeti plains in East Africa ranges from approximately 400-1200 mm per annum. During the growing season in these systems, the water content in the top 10 cm of soil is likely to fluctuate from moist to relatively dry over a period of hours or days, depending on the amount of rainfall and temperature (Scholes and Walker, 1993). It is this top layer of soil that holds a disproportionate amount of soil organic matter (Figure 2.6) and thus the water content in this layer of soil greatly affects the supply of nutrients to plants via mineralisation (Woods, 1989). In 1958, Birch demonstrated that the rate of mineralisation of soil organic matter is greater in soils which are wetted and dried than in soils which are kept permanently moist or dry. Nutrient supply to plant roots is thus likely to be greatest where the water content in the top 10 cm of soil fluctuates, but is not kept moist or dry for extended periods (e.g. weeks at a time). It is suggested here that many of the grasslands in the world have this optimal mineralisation regime, whereby the top 10 cm of soil (with the greatest concentration of organic matter) has a fluctuating water content, that maximises the rate of mineralisation and therefore the supply of nutrients to grass roots. It is this environment of maximal mineralisation that promotes the formation of plants with nutrient-rich tissues i.e. grasses.

By contrast, savannas such as in the Kruger National Park tend to be drier and warmer than the adjacent Highveld grasslands and consequently the top 10 cm of soil in these savannas is likely to be dry for longer periods than in the grasslands. Mineralisation ceases when soils dry out, because the mineralising microbes become desiccated and die (Scholes and Walker, 1993). If mineralisation in the top layer of soil ceases because of desiccation, yet plants can continue to grow because of water availability at greater depths in the soil profile, then the supply of nutrients to plant roots is likely to be limited and plants may be confined to

producing nutrient-poor tissues i.e. wood. Thus, it may be that the drier climates prevalent in savannas, effectively switch off mineralisation and thus the nutrient supply from topsoils, and in the process favour the growth of woody species.

In regions with less rainfall than savannas, soil profiles may be dry even at depth in the growing season. Plants may have access to water only in the topsoil and shortly after rainfall. In such systems, mineralisation of soil organic matter is likely to be maximised when the plants are growing and thus the production of nutrient-rich tissues is possible and a low grassland or herbaceous shrubland is likely to develop, i.e. a desert system. By contrast, as climates become progressively wetter than in mesic grasslands, topsoils may become saturated for extended periods of time and nutrient supply may be restricted as a result (Birch, 1958). So in higher rainfall regions, not only is there greater plant productivity, but nutrient supply from mineralisation may be limited. Both these effects are likely to result in nutrient-poor tissues and consequently, a dominance of woody plants would be expected.

Given the above reasoning, it is conceivable that the primary effect of fire on vegetation structure may operate through its effects on soil water content, plant productivity and mineralisation of soil organic matter. In the post-fire environment there is less vegetation cover than before the fire, and this results in greater soil temperature (Savage and Vermeulen, 1983; Van de Vijver, 1999), less interception of rainfall by vegetation, and consequently a greater number of wetting and drying cycles in the topsoil. These effects are likely to increase the rate of mineralisation of soil organic matter and therefore the supply of nutrients to plant roots. In addition, greater evaporation from the soil surface may result in less water penetrating to depth, which in turn may reduce plant productivity on the site (Van de Vijver, 1999). The combination of a reduced overall productivity of plants due to water limitations and a greater supply of nutrients due to enhanced mineralisation is likely to promote the growth of nutrient-rich tissues i.e. grasses. In areas where herbivores are abundant, vegetation continues to be removed in the post-fire environment and the rate of mineralisation is likely to remain elevated. In addition, herbivores increase the rate of nutrient cycling through dung and urine deposition (Frank and Groffman, 1998; McNaughton *et al.*, 1997), thus further promoting the growth of nutrient-rich plant tissues. Soil texture is also likely to affect the rate of mineralisation and therefore vegetation height. Clayey soils have a greater water-holding capacity than sandy soils and thus mineralisation in the pedoderm, especially in semi-arid areas, is likely to extend for longer periods in clayey soils than sandy soils. This

reasoning may help to explain why an open grassland with short scattered trees occurs on clayey gabbro-derived soils in the southern Kruger National Park, near Pretoriuskop and a 10-15 m high *Terminalia* woodland occurs on immediately adjacent sandy, granite-derived soils (Venter, 1990). It is interesting to note that the Numbi burnt plot, which was the most open grassland-like plot, was also the plot with the greatest clay content. The open vegetation structure of Numbi may therefore be an interaction of several factors that include: (i) an increased rate of mineralisation of soil organic matter due to the removal of vegetation by fire and herbivores; (ii) direct damage of tree seedlings by herbivores attracted to the relatively micronutrient-rich site; (iii) soil crusting which results in water loss and drought stress for tree seedlings; and (iv) greater mineralisation due to greater water holding capacity of clayey soils, and therefore the promotion of nutrient-rich tissues.

Although the productivity:nutrient hypothesis predicts that the height of vegetation is a function of plant productivity and the rate of mineralisation of soil organic matter, it does not imply that where soil organic matter content is great, vegetation should be short and herbaceous. It is rather the rate of soil organic matter turnover in the topsoil of ecosystems that is relevant in terms of the supply of nutrients to plant roots. Indeed, one of the shortest vegetation types in this study, the Central Nama Karoo, had the lowest soil organic matter content of all study sites. Despite the low soil organic matter content, when plants are growing after rain in this system, the soil organic matter that *is* present, is likely to be mineralising rapidly. Although the bushes in the Central Nama Karoo are relatively woody, the wood:leaf ratio is likely to be less than taller vegetation types, such as the Mixed Lowveld Bushveld. The Central Nama Karoo is thus, in comparison to savannas or forests, a relatively nutrient-rich vegetation type that may depend on the rapid mineralisation that occurs in the pedoderm immediately after rainfall.

7.4 Carbon sequestration, the Birch effect and soil redox

The rate of mineralisation of soil organic matter has potential consequences for not only the woodiness of vegetation, but also the topical issue of C sequestration. The global community has in recent years focussed on how to maximise C sequestration in order to buy time for replacing fossil fuel technologies and to mitigate the rise in atmospheric carbon dioxide. To increase sequestration of C in soil, two approaches are possible: either increase the organic matter inputs and/or reduce the rate of mineralisation. There is another potential benefit of

reducing the rate of mineralisation: according to the productivity:nutrient hypothesis of vegetation height, if mineralisation is reduced, so too is the supply of nutrients to roots and consequently plant growth is likely to yield nutrient-poor tissues (i.e. wood). Wood is more inert and stores C for a longer period than herbaceous material and is thus beneficial in terms of sequestering C.

Management practices that increase the rate of mineralisation of soil organic matter will tend to lose soil C to the atmosphere. This effect is evident across all study sites. For example, long-term burning in bushveld and grassland biomes resulted in a decrease in soil C. The greatest difference in soil C between burnt and unburnt plots recorded in this study was in the top centimetre of soil in the southern Kruger National Park (0.8 vs 2.7 % total C). As discussed above, fire is likely to increase the rate of mineralisation, especially in the top few centimetres of soil and highlights how fire suppression can increase C sequestration (Tilman *et al.*, 2000) through above-ground C, as well as soil C accumulation. Fire also affects soil C by reducing the return of organic matter to the soil and also potentially combusting soil C in the top few centimetres of soil. Because soil is a poor heat conductor, direct combustion of soil organic matter during the fire is only likely to occur in extremely intense fires (Ahlgren and Ahlgren, 1960), but this effect in savannas and grasslands is largely unquantified.

Other management practices that, like fire, result in the removal of vegetation cover, will also tend to increase the rate of mineralisation of soil organic matter and reduce the return of organic matter to the soil. For example, in the top 10 cm layer of soil: in Xeric Succulent Thicket, goat-transformed sites had 27 t ha⁻¹ less C than intact thicket; West Coast Renosterveld soils in the open had 11 t ha⁻¹ less C than soils under *Elytropappus* bushes; Central Nama Karoo soils in the open had 2 t ha⁻¹ less C than soils under *Pentzia* bushes; and Moist Upland Grassland soils under maize cultivation had 11 t ha⁻¹ less C than virgin grassland soils. These results highlight how removing vegetation either through fire, livestock farming or cultivation results in a loss of soil C. There are numerous possible processes operating simultaneously that result in loss of C, some of which are contentious and all of which are difficult to disentangle in order to ascertain which is the dominant effect. Although it is often assumed that tillage results in exposure of previously protected soil C to microbes (Phillips and Phillips, 1984), the evidence for such an effect is scarce (Rovira and Greacen, 1957; Hendrix *et al.*, 1988; Roberts and Chan, 1990; Reicosky *et al.*, 1997; Aslam *et al.*, 2000). It is proposed here that the key driving force behind the decrease in soil C under

all the management practices discussed above, is an increase in the rate of mineralisation of soil organic matter due to greater soil temperature (Savage and Vermeulen, 1983), the Birch effect operating due to a greater number of wetting and drying cycles (Birch, 1958) and possibly less suppression of soil microbes by plant exudates (Theron, 1951; 1963). Reduced return of organic matter to the soil is also an important consideration but the major decline of soil C after vegetation removal is often rapid (Bird *et al.*, 2000; Lobe *et al.*, 2001). Because annual C inputs from vegetation tend to be 10 to 100 fold less than the total soil C store, the loss of up to 50% of total C after only a few years of veld burning or tillage (Bird *et al.*, 2000; Lobe *et al.*, 2001), suggests that the rate of mineralisation as opposed to a change in the level of organic input is the primary factor involved in soil C losses. Vegetation not only shades the soil and reduces soil temperature, but also intercepts a considerable amount of rainfall (Thurow *et al.*, 1987; Van de Vijver, 1999; Le Maitre, 1999). This intercepted rainfall evaporates from the leaf surface and does not reach the soil surface. The effect of rainfall interception on the rate of mineralisation of soil organic matter has not to the author's knowledge been investigated, yet is likely to be of critical importance for modelling losses of soil C after the removal of vegetation. In light rains, up to 100% of rainfall can be intercepted by vegetation/leaf litter and consequently the soil surface does not wet and dry. In contrast, a soil exposed by fire, grazing or tillage will wet and dry after the lightest of showers. The Birch effect (i.e. a proliferation of metabolically active microbes) will take hold in such environments. Birch himself, pointed out in 1958 that "Any agricultural practice that enhances soil drying such as burning, exposure by ploughing...or bare fallowing should hasten the loss of soil carbon...".

Enhanced mineralisation due to wetting and drying was ascribed by Birch (1958) to high metabolic activity of young bacterial populations that develop after each wetting. It is tentatively suggested here that the chemistry that underlies the Birch effect may also be governed by redox. Mineralisation entails the oxidation of reduced carbon atoms and consequently, the rate of mineralisation will increase as the soil environment becomes more oxidising. Although Birch's (1958) experiments were conducted in respirometers, where "aeration and moisture conditions are virtually ideal", it is postulated here that bacteria may still have experienced localised regions of anaerobiosis within the substrate over time. Oxygen (O₂) is depleted in a water-saturated soil because of its low solubility in water and its consumption by continued biological activity. McBride (1984) notes that when soil flooding occurs, "...a high organic matter level in soils usually means that the electron acceptors are

overwhelmed by microbial activity, and the E_h decreases rapidly.” When water evaporates or drains out of the soil, O_2 re-enters the pores, the redox potential increases and oxidation can commence again (McBride, 1984). Frequent wetting and drying of the soil surface may therefore be switching the redox status from a reducing state to an oxidising state, especially in the pedoderm, which tends to be organic-rich. In particular, frequent drying will aerate soil pores that were previously waterlogged and in this way a “bellows” effect may be created whereby oxygen is injected into the soil matrix. In addition, rainwater entering the soil carries “new” oxygen in dissolved form into the pores (Hillel, 1998) and draws air downward by suction as it gravitates into the soil. When the soil rewets, microbes proliferate in the oxygen-rich environment and increase the rate of mineralisation, until the concentration of oxygen once again drops to an equilibrium level. The Birch effect may therefore be associated with a young, metabolically-active microbe population as well as a change in redox status over time. The top few centimetres of soil are a redox interface (Bartlett, 1999) between the potentially reducing soil environment and the oxidising atmosphere. By curbing oxygenation of the soil matrix through this thin surface layer, managers can reduce mineralisation and increase soil C. This can be achieved by maintaining a cover of vegetation which insulates the soil surface with a litter layer, reduces the number of wetting and drying cycles via rainfall interception and takes up oxygen in the soil through roots.

7.5 Carbon and soil crusting

The loss of C from exposed soils has ramifications aside from effects on C sequestration and atmospheric carbon dioxide levels. As mentioned earlier in the discussion, labile C in particular appears to play an important role in maintaining soil aggregate stability and reducing the dispersion of clay (Golchin *et al.*, 1995). If labile C is lost (and by definition this is the fraction of C most likely to be removed from soils due to mineralisation) then aggregate stability is compromised, dispersion of clay increases, crusting is promoted and infiltration into the soil is reduced. Thus a potential feedback effect develops because reduced infiltration results in reduced plant growth. A vegetation cover maintains soil organic C levels (i.e. shading, rainfall interception, return of organic matter, possible release of microbe-inhibiting exudates) and consequently, by removing vegetation and stimulating mineralisation, a spiralling process of degradation becomes possible. Such a spiral includes: loss of organic matter, greater crusting, reduced infiltration, reduced plant growth and in this way the spiral can self-perpetuate. Indeed, results from this study demonstrate that where vegetation is

removed, soils become more prone to crusting. It is important to note that this increased tendency to crust reflects a change in the chemical composition of the soil and does not pertain to the greater exposure of soils to raindrop impact, although raindrop impact will indeed exacerbate the crusting of exposed soils. The increased tendency to crust is ascribed to predominantly a loss of soil C, as mentioned above, but also to a decrease in Ca and Mg relative to Na, in the case of annual burning effects in the southern Kruger National Park. An increased tendency of exposed soils to crust is a consistent finding within this study and is evident in West Coast Renosterveld near Nieuwoudtville, Central Nama Karoo near Beaufort West, Xeric Succulent Thicket near Kirkwood, Moist Upland Grassland near Underberg, Southern Tall Grassveld near Pietermaritzburg, Eastern Thorn Bushveld near Fort Hare and Mixed Lowveld Bushveld in the Kruger National Park.

7.6 Linking soil science and ecology in the future

The research presented in this thesis has inevitably unearthed more questions than it has answered. The immense complexity of natural systems often precludes satisfactory testing of ideas, and ecologists are thus often in danger of falling into the trap of forming untestable hypotheses, that according to Popper (1959) have no place in science. Indeed, ecology, with its lack of predictive “laws” sits rather uncomfortably within the hard sciences of chemistry and physics. Hayek (1991), in his book “*Fatal Conceit*”, suggests that economists who believe that they can predict the direction of economies are fatally conceited because the complexity and unpredictability of human interaction prevents accurate prediction. If Hayek had applied his mind to natural systems he may well have concluded that ecologists fall into the same trap as economists. Nevertheless, ecosystems do respond to climate and management changes and consequently ecologists will continue to endeavour to understand why certain changes take place. The recent concern over atmospheric CO₂ and global climate change has resulted in the world community turning to ecologists to find out how C is cycled through ecosystems. This focus has in many ways exposed how little is known about the flow of energy and elements through ecosystems. It is suggested in this thesis that an understanding of nutrient cycling and the dynamics of mineralisation in particular, may unlock a greater understanding of the distribution of biomes across the planet. Furthermore, it will enable more effective management of atmospheric CO₂.

Sequestration of carbon in soils is a contentious issue. Recent research has shown that planting forests in many parts of the world is likely to result in a net release of carbon into the atmosphere. This is because preparation of land for planting may result in large losses of C through soil respiration (Page *et al.*, 2002; Paul *et al.*, 2002). This thesis has emphasised the complexity of soil water content and redox dynamics and how these may impact on soil C accumulation or loss. Even the loss of soil C due to tillage is not fully understood – is it due to the exposure of previously protected soil C to oxygen or due to greater wetting and drying as suggested in this thesis? The release of root exudates which suppress mineralisation is yet another factor that may control soil C: an idea put forward by Theron in 1951, yet one which remains largely unexplored half a century later.

Understanding the dynamics of soil C is critical not only for balancing the world carbon budget but also for effective management of soil organic matter and thereby increasing productivity in agricultural systems. Agriculture in semi-arid regions and in regions where people do not have access to fertilizer stand to benefit from a greater understanding of soil C dynamics. Organic farming is also, by definition, dependent on nutrient release from organic matter.

This thesis has emphasised that perhaps the key gap in our understanding of soil C dynamics is the extent to which the Birch effect results in a loss of soil C after changes in landuse. Experiments could be conducted to establish whether it is (i) greater soil temperatures, (ii) greater drying of surface soils, (iii) more frequent wetting of surface soils, (iv) reduced concentrations of microbe-inhibiting root exudates, or (v) exposure of previously protected soil C, that is the primary cause of soil C loss after tillage, frequent burning, or removal of vegetation by livestock or harvesting.

Another potentially rewarding research direction in the field of soil quality is to investigate the role of Ca in land degradation. Chapter 2 showed that removal of Ca from the surface soils of burnt plots may have increased the tendency of soils to crust. If Ca can be preferentially lost in ash after fires then it is conceivable that Ca can be lost by cropping and livestock farming. A careful analysis of Ca distribution in surface layers may reveal that soil crusting, land degradation, and the aggregating effect of divalent cations are intricately linked.

The productivity:nutrient hypothesis is a rather bold attempt at trying to understand vegetation height across biomes, while avoiding Hayek's fatal conceit. The hypothesis is preliminary and requires rigorous testing if it is to develop further. One such test may be to measure the productivity of a wide variety of biomes, identify those biomes where productivity is comparable, and then test the mineralisation rate of a standard bulk soil sample in these locations over a period of several years. The hypothesis predicts that the rate of mineralisation will be in the order of grasslands>savannas>forests. It may also be possible to model mineralisation in surface soils, as well as plant productivity, from long-term climate data and in this way undertake a desktop test of the hypothesis. Soil water dynamics are, however, exceptionally complex and field validation would be something that Leonardo da Vinci (1452-1519) would have advocated. He is reputed to have said, "Remember when discoursing about water to adduce first experience and then reason".

Chapter 3 presented soil C data which shows that veld dominated by *Portulacaria afra* has an inordinately great quantity of soil C for a semi-arid environment. The reasons for this accumulation are not understood and may be related to the chemical composition of the foliage (i.e. some chemical resistance to decomposition) or to the structure of the bush. The dense nature of the bush results in much rainfall interception and this could slow the rate of decomposition in comparison to less dense vegetation. The use of *P. afra* as a carbon sequestrator may increase the income-earning potential of semi-arid landscapes. Carbon is presently being sold on international markets for up to US\$20 per tonne. Dense *P. afra* habitats in the Xeric Succulent Thicket have in excess of 80 t ha⁻¹ above-ground C in biomass and in excess of 150 t ha⁻¹ below-ground C in soil. In addition, *P. afra* is palatable and could potentially support game-ranching operations. Future research efforts could focus on the mechanism of C accumulation under *P. afra*, by establishing soil water dynamics and the rate of mineralisation under *P. afra* in exposed soils and under other plant species.

Finally, clay dispersion and soil crusting may warrant further investigation with regard to the effect of crusting on vegetation distribution and ecosystem functioning. The distribution of plants is a function of climate and, in particular, rainfall. Yet the penetration of rainwater into the soil matrix will vary from one location to another. Especially in semi-arid systems, where soil surfaces are often exposed to raindrop impact, the inherent tendency of the soil to crust can have a great bearing on ecosystem function and thus plant distribution. This inherent tendency of soils to crust is largely a function of soil texture, clay dispersibility and clay

mineralogy. An interesting research direction in the future may therefore be to correlate plant distribution with clay mineralogy. Soil texture is often correlated with individual plant species distribution and this is ascribed to the effects that texture has on soil water content and nutrient availability. Clay mineralogy in semi-arid regions will potentially provide even stronger correlations due to its effect on soil crusting and rainfall infiltration.

7.7 Conclusions

Soils and plants interact in a myriad of ways. This thesis has detailed a few of these interactions in selected biomes in South Africa. Investigation into the effect of long-term burning on soil properties demonstrated that the removal of vegetation can increase dispersion of clay and soil crusting. This is ascribed to an increase in the exchangeable sodium percentage and a decrease in labile C in the pedoderm. Long-term burning also resulted in a decrease in soil organic matter across all study sites. This is ascribed to reduced organic matter inputs, but most importantly to an increase in the rate of mineralisation of soil organic matter. Increased mineralisation is likely to take place due to greater soil temperature, an increased number of wetting and drying cycles (Birch effect), an increase in soil pH and a possible reduction in microbe-inhibiting root exudates. Given that mineralisation is the *oxidation* of soil organic matter, it is likely to be first and foremost a function of soil redox. The Birch effect, for example, may operate through a “bellows” effect which “fans the microbial flame” when oxygen is injected into the soil matrix after drying and in rainwater when the soil rewets. The removal of vegetation as a result of livestock farming and cultivation had similar effects to frequent burning on soil C. Where soils were exposed, soil C decreased, dispersion of clay increased and the tendency of soils to crust was greater. This result was consistent across all study sites and highlights how a cycle of degradation can develop if plant cover is not judiciously maintained. The rate of infiltration of water through a crusted soil surface can be thousands of times lower than an uncrusted soil and consequently crusting creates a relatively arid soil environment. Such aridity induced by crusting is likely to reduce plant growth and perpetuate the cycle of degradation.

The greater tendency of soils to crust in the post-fire environment is likely to lead to greater runoff which has ramifications for plant growth and may favour shallow-rooted grasses over deeper-rooted trees. Vegetation structure in annually burnt plots in the southern Kruger National Park is, however, likely to be dependent on more than just soil water effects. The

reduction of tree cover on burnt plots was correlated with herbivore numbers which suggests that herbivory may be the limiting factor for tree seedling recruitment. The abundance of herbivores is in turn possibly a function of soil properties. Clay content, total Zn and total Mn were positively correlated with herbivore numbers and indicates that herbivores may be actively seeking limiting nutrients in these nutrient-poor, granitic landscapes.

Savanna structure is, however, likely to be more complex than the effects that damage by fire, soil crusting and herbivores have on tree seedling survival. Many grasslands have climates more mesic than savannas, yet trees are excluded from these regions. There is inconsistency in the argument that intense fires exclude trees, because intense and frequent fires occur in numerous forested ecosystems e.g. *Pinus* in the southeastern United States, *Brachystegia* in central Africa and *Eucalyptus* in northern Australia. A more fundamental reason needs to be invoked for the exclusion of trees from mesic grasslands and the inclusion of trees in relatively xeric savannas. The productivity:nutrient hypothesis, which proposes that biome structure is largely a function of the potential productivity of plants in the landscape relative to the potential supply of nutrients to plant roots, is presented as a model for understanding the effects of climate, soil and fire on savanna structure. Where nutrient supply is limited, nutrient-poor tissues (i.e. wood) are produced and trees establish. This may be the case in savannas, because topsoils dry out during the growing season and the supply of nutrients from mineralisation of soil organic matter is often limited. Mesic grasslands in comparison, because of the Birch and “bellows” effect, are likely to have a maximal rate of mineralisation of soil organic matter throughout the growing season, which favours the production of nutrient-rich tissues (i.e. herbaceous materials). The primary mechanism by which fire excludes trees in mesic grasslands may therefore be through exposing the soil surface to sunlight and rainfall, thereby increasing the rate of mineralisation and supply of nutrients to plant roots in surface soils, as opposed to direct damage inflicted by fire on tree seedlings.

Reciprocal relationships between plants and soils lie at the heart of understanding ecological functioning of landscapes. This thesis has highlighted a few of the complex interactions and potential feedback effects that take place, from the effect of fire on sodium adsorption ratios to the effect of vegetation cover on dispersion of clay. In order to manage ecosystems effectively, an understanding of why certain plants have evolved in a particular landscape is essential. Ecology is still some distance away from understanding the fundamental abiotic forces that underpin plant distributions and often resorts to the dangerous notion of “an

accident of history". Such a notion dooms ecology to a game of guessing ecosystem responses as opposed to predicting responses based on an understanding of the basic chemical and physical driving principles. The question of why trees are excluded from mesic grasslands yet are present in semi-arid savannas is, for example, a fundamental ecological question that warrants intensive research, rather than assumptions about fire damage to trees. The productivity:nutrient hypothesis suggests that processes such as mineralisation of soil organic matter affect the structure of vegetation across biomes and highlights the role that soil science could play in the field of ecology in the future. In grasslands and savannas, the pedoderm often holds a disproportionately large amount of soil organic matter. It is this thin soil layer, the redox interface between earth and atmosphere, that affects water infiltration through soil crusting, the Birch effect through wetting and drying, the transfer of nutrients from surface litter to mineral soil and thus the availability of water and nutrients to plants. Future studies of the intricate relationships between soil quality and vegetation structure are likely to be rewarded most by concentrating on the character of the pedoderm.

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Appendix A: Chemical and physical soil properties of all samples from all study sites.**Key A to Appendix A: Sample numbers, names and locations.**

No.	Site name	Sample location	No.	Site name	Sample location
West Coast Renosterveld - Dwyka tillite sediments			Nama Karoo - Calcrete		
1	2Ltal	Active wheat field	59	ACB1	Below bushes
2	Kklf	Active wheat field	60	ACB2	Below bushes
3	Wheat One	Active wheat field	61	ACB3	Below bushes
4	Wheat Two	Active wheat field	62	EB2	Below bushes
5	De Lande	Open soil in virgin veld	63	ECB1	Below bushes
6	Flower Reserve Tillite	Open soil in virgin veld	64	ECB2	Below bushes
7	Glnr Open	Open soil in virgin veld	65	ECB3	Below bushes
8	Long Open	Open soil in virgin veld	66	KB5	Below bushes
9	Lnren	Open soil in virgin veld	67	ACO1	Open soil
10	Matjiesfontein	Open soil in virgin veld	68	ACO2	Open soil
11	Papren Open	Open soil in virgin veld	69	ACO3	Open soil
12	Sheeps Leg	Open soil in virgin veld	70	ECO1	Open soil
13	Top	Open soil in virgin veld	71	ECO2	Open soil
14	Treepad	Open soil in virgin veld	72	ECO3	Open soil
15	Unbr Open	Open soil in virgin veld	73	EO2	Open soil
16	Brn Open	Open soil in virgin veld	74	KO5	Open soil
17	Mnd Open	Open soil in virgin veld	Central Nama Karoo - Dolerite		
18	Mound	Open soil in virgin veld	75	BO1	Open soil
19	Niels House	Open soil in virgin veld	76	BO2	Open soil
20	Lpren Open	Open soil in virgin veld	77	BO5	Open soil
21	Rtol open	Open soil in virgin veld	78	EO1	Open soil
22	Ltol	Open soil in virgin veld	79	EO3	Open soil
23	Brn Elytro	<i>Elytropappus rhinocerotis</i>	80	EO4	Open soil
24	Mnd Elytro	<i>Elytropappus rhinocerotis</i>	81	EO5	Open soil
25	Glnr Elytro	<i>Elytropappus rhinocerotis</i>	82	BG1	<i>Pentzia incana/Stipagrostis</i> spp.
26	Long Elytro	<i>Elytropappus rhinocerotis</i>	83	BG2	<i>Pentzia incana/Stipagrostis</i> spp.
27	Mnd Unbnt El.	<i>Elytropappus rhinocerotis</i>	84	EB1	<i>Pentzia incana/Stipagrostis</i> spp.
28	Papren Elytro	<i>Elytropappus rhinocerotis</i>	85	EB3	<i>Pentzia incana/Stipagrostis</i> spp.
29	Unbr Elytro	<i>Elytropappus rhinocerotis</i>	86	EB4	<i>Pentzia incana/Stipagrostis</i> spp.
30	Lpren Elytro	<i>Elytropappus rhinocerotis</i>	87	EB5	<i>Pentzia incana/Stipagrostis</i> spp.
31	Long Merx	<i>Merxmuellera</i> spp.	88	BG5	<i>Pentzia incana/Stipagrostis</i> spp.
32	Unbr Merx	<i>Merxmuellera</i> spp.	Central Nama Karoo - Shale		
33	Brn Merx	<i>Merxmuellera</i> spp.	89	AO1	Open soil
34	Rtol Patch	Below geophyte spp.	90	AO2	Open soil
35	Horn	<i>Medicago</i> field	91	AO3	Open soil
36	Horizon One	<i>Medicago</i> field	92	AO4	Open soil
37	Horizon Two	<i>Medicago</i> field	93	AO5	Open soil
38	House	<i>Medicago</i> field	94	BO3	Open soil
39	Lucerne	<i>Medicago</i> field	95	BO4	Open soil
40	Stmnd	<i>Medicago</i> field	96	KO1	Open soil
West Coast Renosterveld - Dolerite			97	KO2	Open soil
41	2Ldal One	Active wheat field	98	KO3	Open soil
42	2Ldal Two	Active wheat field	99	KO4	Open soil
43	Kwdal	Active wheat field	100	AB1	<i>Pentzia incana</i>
44	Smdal	Active wheat field	101	AB2	<i>Pentzia incana</i>
45	Gldl	Open soil virgin veld	102	AB3	<i>Pentzia incana</i>
46	Camel Dolerite One	Open soil virgin veld	103	AB4	<i>Pentzia incana</i>
47	Idol	Open soil virgin veld	104	AB5	<i>Pentzia incana</i>
48	Ldol	Active wheat field	105	BB3	<i>Pentzia incana</i>
49	Flower Reserve Dolerite	Open soil virgin veld	106	BB4	<i>Pentzia incana</i>
50	Rdol Open	Old wheat field	107	KB1	<i>Pentzia incana</i>
51	Rdol Patch	Old wheat field (geophyte)	108	KB2	<i>Pentzia incana</i>
52	Chnd Bulb	Under geophyte spp.	109	KB3	<i>Pentzia incana</i>
53	Chnd Grass	Under geophyte spp.	110	KB4	<i>Pentzia incana</i>
54	Chnd Open	Open soil virgin veld			
55	Ind	Open soil virgin veld			
56	Lndol	Open soil virgin veld			
57	Koppie	Dolerite koppies			
58	Brunsvigia Koppie	Old wheat field			

No.	Site name	Sample location	No.	Site name	Sample location
Xeric Succulent Thicket					
111	IB1	Intact <i>Portulacaria afra</i>	169	VIVK	Kikuyu pasture
112	IB2	Intact <i>Portulacaria afra</i>	170	MKIK	Kikuyu pasture
113	IB3	Intact <i>Portulacaria afra</i>	171	VIVR	Ryegrass pasture
114	IB4	Intact <i>Portulacaria afra</i>	172	VIVRB	Ryegrass pasture
115	IB5	Intact <i>Portulacaria afra</i>	173	MRYE	Ryegrass pasture
116	IB6	Intact <i>Portulacaria afra</i>	174	GRAP	Pine plantation
117	IB7	Intact <i>Portulacaria afra</i>	175	HIMP	Pine plantation
118	IB8	Intact <i>Portulacaria afra</i>	176	PCOLE	Pine plantation
119	TB1	Goat-transformed <i>Pappaea capensis</i>	177	MASSG	Wet grassland grazed by cattle
120	TB2	Goat-transformed <i>Pappaea capensis</i>	178	MASSP	<i>Dactylis glomerata</i> pasture
121	TB3	Goat-transformed <i>Pappaea capensis</i>	Mixed Lowveld Bushveld - Nelspruit granite		
122	TB4	Goat-transformed <i>Pappaea capensis</i>	179	Numbi C	Unburnt plot
123	TB5	Goat-transformed <i>Pappaea capensis</i>	180	Numbi AB	Annually burnt plot
124	TB6	Goat-transformed <i>Pappaea capensis</i>	181	Kambeni C	Unburnt plot
125	TB7	Goat-transformed <i>Pappaea capensis</i>	182	Kambeni AB	Annually burnt plot
126	TB8	Goat-transformed <i>Pappaea capensis</i>	183	Shabeni C	Unburnt plot
127	IO1	Intact thicket - open soil	184	Shabeni AB	Annually burnt plot
128	IO2	Intact thicket - open soil	185	Faai C	Unburnt plot
129	IO3	Intact thicket - open soil	186	Faai AB	Annually burnt plot
130	IO4	Intact thicket - open soil	187	Skukuza C	Unburnt plot
131	IO5	Intact thicket - open soil	188	Skukuza AB	Annually burnt plot
132	IO6	Intact thicket - open soil	189	Napi C	Unburnt plot
133	IO7	Intact thicket - open soil	190	Napi AB	Annually burnt plot
134	IO8	Intact thicket - open soil	191	Mbay C	Unburnt plot
135	TO1	Goat-transformed thicket	192	Mbay AB	Annually burnt plot
136	TO2	Goat-transformed thicket	193	Nwas C	Unburnt plot
137	TO3	Goat-transformed thicket	194	Nwas AB	Annually burnt plot
138	TO4	Goat-transformed thicket	Mixed Lowveld Bushveld - Basalt		
139	TO5	Goat-transformed thicket	195	Satara C	Unburnt plot
140	TO6	Goat-transformed thicket	196	Satara AB	Annually burnt plot
141	TO7	Goat-transformed thicket	197	Moray C	Unburnt plot
142	TO8	Goat-transformed thicket	198	Moray AB	Annually burnt plot
143	IO7TER	Termite mound	199	Nwanetsi C	Unburnt plot
144	IO8TER	Termite mound	200	Nwanetsi AB	Annually burnt plot
Moist Upland Grassland - Sandstone					
145	COMF	Grassland - commercial cattle	201	Lind C	Unburnt plot
146	MISS	Grassland - communal cattle	202	Lind AB	Annually burnt plot
147	COLES	Grassland grazed by wildlife	203	Mooiplaas C	Unburnt plot
148	CSUN	Grassland grazed by wildlife	204	Mooiplaas AB	Annually burnt plot
Moist Upland Grassland - Dolerite					
148	COTD	Grassland - commercial cattle	205	Dsondo C	Unburnt plot
149	GRAG	Grassland - commercial cattle	206	Dsondo AB	Annually burnt plot
150	LARG	Grassland - commercial cattle	207	Tsende C	Unburnt plot
151	VIVG	Grassland - commercial cattle	208	Tsende AB	Annually burnt plot
152	COMFD	Grassland - communal cattle	Eastern Thorn Bushveld		
153	MISD	Grassland - communal cattle	209	AB1	Annually burnt plot
154	VILL	Grassland - communal cattle	210	AB2	Annually burnt plot
155	COLEAB	Grassland grazed by wildlife	211	C1	Unburnt plus cattle
156	COLED	Grassland grazed by wildlife	212	C2	Unburnt plus cattle
157	HIMG	Grassland grazed by wildlife	213	GC1	Unburnt plus goats and cattle
158	CAMP	Grasslands grazed by wildlife	214	GC2	Unburnt plus goats and cattle
159	LARM	Commercial maize	Southern Tall Grassveld		
160	VIVM	Commercial maize	215	R1A1	Unburnt plot
161	COMFC	Communal maize	216	R1A2	Annually burnt plot
162	JMAIZE	Commercial maize	217	R1D2	Annually burnt plus mowing
163	CMAIZE	Communal maize	218	R2A1	Unburnt plot
164	COMO	Communal maize - old land	219	R2A2	Annually burnt plot
165	JERA	<i>Eragrostis ley</i>	220	R2D2	Annually burnt plus mowing
166	ERAL	<i>Eragrostis ley</i>	221	R3A1	Unburnt plot
167	ERAHL	<i>Eragrostis ley</i>	222	R3A2	Annually burnt plot
168	LARK	Kikuyu pasture	223	R3D2	Annually burnt plus mowing

Key B to Appendix A

No.	Sample number. For sample name and location refer to key A.
Inf	Laboratory infiltration (mm hr^{-1}). Description of method in Chapter 2.
EC	Electrical conductivity of a 1:5 soil water extract (mS m^{-1}).
pH1:5	pH in water (1:5).
pHK	pH in 1M KCl (1:2.5).
pHW	pH in water (1:2.5).
WDC	Water dispersible clay (%). Description of method in Chapter 2.
MOR	Modulus of rupture (kPa), as determined by Richards (1953).
S Ca	Water soluble Ca ($\text{mmol}_c \text{kg}^{-1}$ in a 1:5 soil water extract). Determined by atomic absorption using a Varian SpectrAA-250 Plus.
S Mg	Water soluble Mg ($\text{mmol}_c \text{kg}^{-1}$ in a 1:5 soil water extract). Determined by atomic absorption using a Varian SpectrAA-250 Plus.
S K	Water soluble K ($\text{mmol}_c \text{kg}^{-1}$ in a 1:5 soil water extract). Determined by atomic absorption using a Varian SpectrAA-250 Plus.
S Na	Water soluble Na ($\text{mmol}_c \text{kg}^{-1}$ in a 1:5 soil water extract). Determined by atomic absorption using a Varian SpectrAA-250 Plus.
S NH ₄	Water soluble NH ₄ ($\text{mmol}_c \text{kg}^{-1}$ in a 1:5 soil water extract). Determined by ion chromatography using a Dionex DX120.
S Cl	Water soluble Cl ($\text{mmol}_c \text{kg}^{-1}$ in a 1:5 soil water extract). Determined by ion chromatography using a Dionex DX120.
S NO ₃	Water soluble NO ₃ ($\text{mmol}_c \text{kg}^{-1}$ in a 1:5 soil water extract). Determined by ion chromatography using a Dionex DX120.
S SO ₄	Water soluble SO ₄ ($\text{mmol}_c \text{kg}^{-1}$ in a 1:5 soil water extract). Determined by ion chromatography using a Dionex DX120.
E Ca	(NH ₄)OAc-extractable Ca ($\text{mmol}_c \text{kg}^{-1}$). Determined by atomic absorption using a Varian SpectrAA-250 Plus.
E Mg	(NH ₄)OAc-extractable Mg ($\text{mmol}_c \text{kg}^{-1}$). Determined by atomic absorption using a Varian SpectrAA-250 Plus.
E K	(NH ₄)OAc-extractable K ($\text{mmol}_c \text{kg}^{-1}$). Determined by atomic absorption using a Varian SpectrAA-250 Plus.
E Na	(NH ₄)OAc-extractable Na ($\text{mmol}_c \text{kg}^{-1}$). Determined by atomic absorption using a Varian SpectrAA-250 Plus.
P	Bray2-extractable P (mg kg^{-1}), as determined by Bray and Kurtz (1945).
Cu	Di-ammonium EDTA-extractable Cu (mg kg^{-1}). Determined by atomic absorption using a Varian SpectrAA-250 Plus.
Zn	Di-ammonium EDTA-extractable Zn (mg kg^{-1}). Determined by atomic absorption using a Varian SpectrAA-250 Plus.
Clay	Clay content (%). Determined by the hydrometer method.
Silt	Silt content (%). Determined by the hydrometer method.
F sand	Fine sand content (%). Determined by sieving.
M Sand	Medium sand content (%). Determined by sieving.
C sand	Coarse sand content (%). Determined by sieving.
C	Total carbon (%). Determined by a Eurovector Euro EA Elemental Analyser.
N	Total nitrogen (%). Determined by a Eurovector Euro EA Elemental Analyser.
C/N	The ratio of carbon:nitrogen.
LC 5	Labile carbon (%). Determined by a modified Walkley Black method, using 5 ml sulphuric acid.
LC 10	Labile carbon (%). Determined by a modified Walkley Black method, using 10 ml sulphuric acid.
CO ₂ F	Carbon dioxide flux in the field ($\mu\text{mol m}^{-2} \text{s}^{-1}$). Determined by a Licor LI 6400 Portable Photosynthesis System and 6400-09 Soil CO ₂ flux chamber.

No.	Int	EC	pH _{1.5}	pHK	pHW	WDC	MOR	S Ca	S Mg	S K	S Na	S NH ₄	S Cl	S NO ₃	S SO ₄	E Ca	E Mg	E K	E Na	P	Cu	Zn	Clay	Silt	F sand	M Sand	C sand	C	N	C/N	LC ₅	LC ₁₀	CO ₂ F	
1	40	4.6	6.0	5.7	6.5	3.7		0.13	0.06	0.98	0.42	0.59	0.08	0.16	32	7	7.8	2.0	60				9	19	35	19	19	1.0	0.09	10.9	0.6			
2	33	16.9	5.9	5.1	5.9	3.7		0.67	0.67	0.95	1.59	3.01	3.17	0.96	24	13	4.4	5.7	31				9	22	40	18	11	0.7	0.08	8.8	0.4	0.9		
3	89	9.7	6.8	5.6	6.3	1.4		1.51	1.22	0.37	0.86	0.17	0.76	0.43	33	8	2.4	2.3	26				5	8	32	33	22	1.0	0.10	10.6	0.5	1.1		
4	30	20.3	6.8	5.6	6.1	1.8		1.20	2.06	1.32	0.35	0.57	0.08	0.30	0.08	43	17	4.9	2.1	42				7	13	40	20	20	1.5	0.11	13.4	0.4	1.1	
5	11	1.9	7.3	5.1	6.4	2.6		1.99	1.82	0.23	0.68	0.08	0.22	0.04	18	9	2.7	1.5	10				8	7	47	19	19	0.5	0.06	9.3	0.3	0.6		
6	7	5.5	7.5	6.3	6.9	2.8		1.05	0.75	0.79	0.36	0.18	0.42	0.07	0.18	37	18	4.5	2.0	14				13	20	42	13	12	0.8	0.09	8.7	0.4	0.9	
7	18	7.4	6.9	5.6	6.8	1.8		93	1.03	0.80	0.77	0.56	0.15	0.18	0.52	0.10	32	12	5.9	1.7	21				8	17	44	13	19	1.1	0.11	10.2	0.5	1.0
8	6	3.2	6.9	4.9	6.7	3.1		167	0.61	0.48	0.19	0.58	0.07	0.17	0.14	0.10	29	11	2.8	2.0	14				12	20	42	15	11	0.8	0.09	9.6	0.3	0.8
9	29	4.9	6.1	5.0	6.2	3.0		0.24	0.14	0.60	0.52	0.63	0.50	0.19	39	17	5.3	2.1	10				15	23	37	13	12	1.9	0.14	13.4	0.9	1.8		
10	4	10.3	6.9	4.6	6.0	3.1		2.02	1.05	0.26	0.82	0.07	0.15	0.04	19	10	2.8	1.4	9									0.7	0.07	10.3	0.2	0.8		
11	29	6.7	6.0	5.1	6.2	0.5		0.23	0.20	0.68	0.51	0.94	0.72	0.19	20	9	6.4	2.3	17				9	15	43	17	16	1.1	0.10	10.7	0.5	1.3		
12	6	4.1	7.1	5.3	6.3	2.3		1.27	1.17	0.62	0.41	0.15	0.12	0.08	33	16	4.3	1.8	17				12	23	38	11	16	1.0	0.10	9.9	0.4	1.0		
13	12	5.4	7.0	5.3	6.3	3.1		1.07	1.41	0.77	0.92	2.70	0.90	0.80	33	13	4.8	2.0	11				8	17	41	13	21	1.0	0.09	11.1	0.4			
14	29	4.1	7.0	5.3	6.4	1.8		1.26	1.22	0.44	0.95	0.07	1.39	1.30	0.49	10	3	1.0	0.7	8				5	11	34	29	21	0.8	0.07	11.4	0.3	0.9	
15	15	3.6	6.9	4.7	6.5	3.7		0.64	0.44	0.22	0.59	0.08	0.13	0.17	0.08	39	12	3.0	1.6	10				13	22	39	13	13	0.7	0.07	10.4	0.4	0.9	
16	21	7.1	7.1	5.5	6.9	2.5		124	0.95	0.73	0.52	0.31	0.16	0.06	0.28	0.08	32	12	4.2	1.2	14				9	17	40	16	19	1.6	0.10	16.4	0.8	1.1
17	7	0.6	6.5	5.2	6.7	3.3		98	0.93	0.82	0.38	0.50	0.10	0.14	0.21	0.06	31	11	3.3	1.5	13				8	16	51	15	12	0.9	0.08	10.2	0.5	0.9
18	11	5.6	7.1	5.3	6.2	1.8		1.04	1.03	0.41	0.32	0.25	0.10	0.18	0.05	37	16	4.4	1.6	19				7	20	46	15	12	1.0	0.11	9.5	0.5	1.1	
19	17	9.8	7.1	5.5	6.5	2.8		1.90	1.75	0.30	0.82	0.07	0.16	0.07	46	16	5.2	2.3	17				9	17	45	15	15	1.0	0.11	9.3	0.5	0.9		
20	28	10.9	5.9	5.4	6.3	3.6		0.44	0.45	0.74	1.12	2.46	0.47	0.72	33	21	5.1	5.1	44				11	23	36	14	16	0.9	0.09	9.6	0.3	0.9		
21	9	5.6	7.4	5.7	7.1	0.0		177	0.83	0.69	0.50	0.62	0.10	0.07	0.21	0.07	33	12	4.3	1.5					42	15	12	0.7	0.07	9.3	0.2	0.7		
22	55	6.1	6.1	6.1	6.8	2.9		0.41	0.16	0.87	0.54	0.70	0.08	0.22	34	7	4.6	2.1	49				9	8	44	20	20	0.9	0.08	10.4	0.3	0.9		
23	25	8.5	6.8	5.5	6.8	2.4		81	1.16	1.04	0.86	0.68	0.23	0.26	0.23	0.19	31	14	5.2	2.2	14				9	15	42	17	17	1.5	0.10	14.4	0.8	1.5
24	7	7.7	6.8	5.3	6.6	2.6		82	1.04	0.90	0.51	0.71	0.09	0.09	0.16	0.06	36	13	4.1	1.8	17				9	18	45	16	12	1.4	0.11	12.8	0.7	1.6
25	43	10.4	6.8	5.9	7.0	1.5		33	1.01	0.91	0.96	1.03	0.22	0.31	0.74	0.11	38	13	6.9	2.0	20				8	13	46	19	15	1.6	0.13	12.4	0.8	1.4
26	14	5.4	6.5	4.8	6.1	2.0		49	1.03	0.92	0.57	0.72	0.13	0.20	0.19	0.09	36	16	4.7	2.1	10				8	20	45	18	9	2.2	0.14	16.2	1.3	2.3
27	54	6.7	4.9	6.3	1.9			59	0.87	0.70	0.57	1.00	0.08	0.92	0.43	0.34	41	16	4.0	2.2	13				8	20	46	17	10	2.1	0.13	16.6	1.0	2.3
28	52	11.6	6.0	4.9	5.7	2.1		0.77	0.65	1.09	0.79	2.04	0.86	0.61	32	18	5.1	3.4	16				7	11	43	23	15	2.4	0.15	16.1	1.3	2.5		
29	43	6.3	6.7	5.0	6.3	1.7		59	0.84	0.54	0.61	0.51	0.07	0.15	0.18	0.07	33	47	5.1	2.3	12				6	18	49	16	11	2.0	0.13	15.5	1.1	1.9
30	31	4.8	6.1	5.0	6.1	3.2		0.15	0.11	0.66	0.46	0.52	0.55	0.14	27	19	6.7	2.0	39				11	22	34	14	19	1.4	0.11	12.1	0.9	1.5		
31	43	23.0	6.4	5.0	6.5	2.3		87	3.44	4.43	1.05	3.00			36	18	4.5	3.0	14						44	17	10	1.5	0.12	13.4	0.6	1.6		
32	52	17.2	6.1	4.8	5.8	2.1		2.68	3.18	1.07	1.77	0.15	5.04	0.52	0.73	31	15	4.6	2.7	12				7	17	49	15	12	1.3	0.09	14.7	0.8	1.5	
33	59	33.2	6.3	5.1	6.1	1.9		65	5.54	6.45	1.92	2.94	0.18	7.36	7.43	0.85	43	47	5.6	3.7	19				43	17	16	1.2	0.11	11.1	0.6	1.4		
34	17	8.3	7.0	5.9	7.1	3.2		122	1.08	0.87	0.76	0.51	0.21	0.14	0.19	0.11	34	11	5.0	2.1	60				49	17	13	0.8	0.08	9.9	0.3	0.8		
35	12	12.6	7.2	6.3	6.6	2.5		82	1.96	1.39	1.00	0.71	0.30	0.30	0.95	0.19	47	15	5.2	2.3	127				9	17	42	19	14	1.7	0.13	13.3	0.8	1.2
36	8	11.3	7.4	5.9	6.8	2.3		1.09	1.19	0.95	1.50	3.22	3.98	0.85	51	17	3.6	3.8	96				8	16	45	15	17	1.0	0.11	8.8	0.4	1.1		

West Coast Renosterveld - Dwyka tillite sediments

No.	Inf	EC	pH1.5	pHK	pHW	WDC	MOR	S Ca	S Mg	S K	S Na	S NH ₄	S Cl	S NO ₃	S SO ₄	E Ca	E Mg	E K	E Na	P	Cu	Zn	Clay	Silt	F sand	M Sand	C sand	C	N	C/N	LC5	LC10	CO ₂ F					
37	10	5.4	7.0	5.1	6.2	2.6	2.00	1.17	0.41	0.81	0.10	0.29	0.06	37	16	2.9	2.9	87	17	1.0	0.10	9.7	0.4	1.1	16	17	1.0	0.10	9.7	0.4	1.1							
38	16	6.6	7.1	5.5	6.4	1.6	120	2.16	1.71	0.35	1.43	0.11	0.23	0.36	0.15	39	11	4.9	1.6	67	0.9	1.3	6	16	46	20	13	0.8	0.10	8.3	0.4	0.9						
39	8	9.1	6.0	5.7	6.6	3.7	0.81	0.52	0.68	0.63	1.10	1.09	0.37	53	23	4.8	2.4	113	17	18	0.8	0.10	8.6	0.4	15	16	1.0	0.11	9.9	0.5	1.0							
40	9	6.7	7.3	5.7	6.6	2.3	121	2.22	1.27	0.38	0.80	0.09	0.18	0.21	0.05	45	17	5.8	2.2	110	1.2	1.2	9	19	41	15	16	1.0	0.11	9.9	0.5	1.0						
West Coast Renosterfeld - Dolerite																																						
41	38	6.8	6.7	6.4	7.5	2.2	1.19	0.74	0.38	2.25	3.68	1.54	322	121	11.8	8.7	20	5.3	0.8	23	20	48	5	4	0.7	0.09	8.4	0.3	0.6									
42	40	7.6	6.6	6.4	7.5	2.4	1.21	0.68	0.55	2.03	5.75	1.00	0.52	338	107	13.0	7.2	18	11	21	60	5	3	0.6	0.08	7.1	0.2	0.5										
43	69	7.5	6.9	6.4	7.5	1.7	0.97	0.44	0.25	3.29	3.48	2.32	1.06	388	101	15.6	8.9	12	19	19	57	3	1	0.7	0.08	8.7	0.3											
44	45	6.9	6.9	5.7	7.4	1.6	1.96	1.11	0.26	2.33	1.72	2.51	0.64	291	117	13.0	6.1	23	4.4	0.9	38	17	33	9	4	1.2	0.11	11.3	0.8	1.2								
45	68	11.1	7.2	5.6	7.0	1.7	2.00	1.93	0.42	1.32	0.96	206	278	7.3	7.7	17	14	25	52	7	2	1.0	0.10	9.7	0.7	1.1												
46	26	12.2	8.3	6.2	7.2	2.3	1.35	1.85	1.08	1.01	3.44	6.08	4.82	2.87	283	160	14.2	6.9	17	10	25	58	5	2	1.0	0.11	8.9	0.3	0.9									
47	49	8.6	6.7	6.2	7.2	1.8	1.80	1.03	0.60	1.64	3.83	3.32	0.92	262	123	16.2	5.0	8	39	17	37	4	3	0.7	0.09	8.1	0.3	0.7										
48	42	5.4	6.8	5.7	7.0	3.0	0.78	0.66	0.38	2.28	4.33	3.06	0.88	234	115	13.6	5.0	15	34	28	32	4	2	0.6	0.08	7.5	0.1	0.4										
49	48	9.3	7.9	5.8	7.0	1.7	1.16	0.99	0.44	0.68	0.79	1.76	3.53	0.85	187	128	13.0	5.0	26	10	20	59	7	4	1.1	0.12	9.3	0.6	1.0									
50	58	20.4	7.2	6.0	7.6	1.8	3.27	2.81	0.94	1.71	0.94	7.58	4.85	2.57	288	160	10.4	5.5	60	22	23	38	9	7	1.1	0.12	9.9	0.4	1.1									
51	73	19.6	7.1	5.7	7.2	2.2	2.89	2.89	0.78	1.43	0.82	5.48	4.48	1.79	217	144	9.7	5.0	58	12	22	47	10	8	4.1	0.39	10.4	2.1	4.0									
52	23	20.0	7.9	7.3	8.7	2.5	2.5	4.40	1.82	0.82	1.63	0.64	10.2	0.82	336	128	11.2	6.0	52	2.9	0.8	21	26	38	7	7	1.7	0.15	10.9	0.9								
53	54	35.1	7.3	7.1	8.1	2.3	23	4.98	2.58	1.64	2.04	1.97	10.3	31.1	2.72	306	120	17.3	7.9	355	3.7	1.7	15	26	46	7	6	2.8	0.28	10.2	1.3	3.2						
54	32	21.5	7.8	7.3	8.8	3.4	53	3.77	1.60	1.06	3.31	0.59	8.80	0.75	309	124	13.8	10.8	48	2.9	0.8	22	19	45	7	7	1.7	0.16	10.5	0.6	1.6							
55	117	6.1	6.7	6.0	7.5	2.1	1.00	0.53	0.41	2.21	4.17	3.27	1.07	285	109	15.0	6.8	9	9	17	64	6	5	0.8	0.09	8.7	0.9	0.6										
56	50	9.0	6.9	5.7	7.5	1.4	1.66	1.31	0.15	1.88	0.58	3.91	4.93	1.27	216	158	12.9	5.6	15	12	22	56	7	3	1.4	0.16	9.2	0.5	0.7									
57	86	27.4	7.7	7.1	8.0	0.8	3.96	2.18	2.98	3.56	1.41	5.09	16.3	5.45	330	97	16.1	10.0		2.4	0.7	7	15	35	16	27												
58	47	15.4	8.7	6.3	7.8	1.4	2.25	1.50	0.97	3.13	4.85	11.5	2.14	407	89	15.4	5.1	10					12	25	57	4	2	0.9	0.10	9.2								
Nama Karoo - Calcrete																																						
59	65	10.5	8.2	7.7	8.7	1.6	2.55	0.65	0.88	0.63	0.29	0.12	0.18	65	4	2.1	2.5	69	7	1	71	14	7	1.2	0.08	14.4	0.5	1.1										
60	111	7.1	7.7	7.8	8.7	0.5	0	2.41	0.63	0.82	0.44	0.25	0.22	0.16	52	8	1.6	1.0	42			10	6	60	17	7	0.7	0.07	9.5	0.5	0.7							
61	79	7.5	8.1	7.5	8.7	1.3	31	2.40	0.83	1.24	0.54	0.23	0.20	36	9	2.3	1.0	41	1.8	1.5			4	7	59	14	15	1.2	0.10	12.2	0.7	1.1						
62	48	11.5	8.4	7.5	8.5	1.7	3.75	0.88	1.19	0.74	0.15	0.43	74	6	2.6	3.7	45					5	2	58	24	17	0.5	0.05	9.5	0.2	0.6							
63	123	9.2	8.1	7.6	8.4	0.9	0	2.71	0.86	0.92	0.57	0.12	0.27	35	4	1.3	2.3	28					1	4	74	15	6	0.6	0.07	8.7	0.2	0.4						
64	22	8.8	8.0	7.1	8.5	2.1	31	2.48	0.96	1.06	0.58	0.11	0.35	35	12	2.3	2.8	49	1.5	1.3			1	4	74	15	6	0.6	0.07	8.7	0.2	0.4						
65	53	10.8	8.3	7.4	8.3	0.7	6	3.04	0.92	1.31	0.56	0.27	0.47	0.26								8	3	62	16	11	0.3	0.05	7.4	0.2	0.5							
66	86	8.0	7.8	7.4	8.0	1.4	11	0.89	0.82	0.60	1.67	0.18	0.19	0.60	20	9	2.0	2.9	20			10	2	66	13	10	1.6	0.08	19.1	0.4	0.7							
67	38	9.6	8.3	7.8	8.8	2.5	8	3.93	0.73	0.56	0.55	0.39	0.13	0.14	80	5	1.8	2.8	61			9	3	66	15	7	0.9	0.07	12.9	0.3	0.6							
68	46	12.0	8.3	7.8	8.9	2.7	34	3.46	0.74	0.79	0.47	0.22	0.28	0.12	75	5	2.1	3.1	43			6	3	66	15	7	0.9	0.07	12.9	0.3	0.6							
69	53	7.3	7.6	7.5	8.6	2.3	29	2.27	0.74	0.87	0.33	0.17	0.10	0.06	39	5	2.1	2.7	53			6	3	56	23	13	0.6	0.06	10.0	0.4	0.6							
70	85	9.7	8.4	7.8	8.8	1.9	3.76	0.90	0.47	0.26	0.12	0.09	61	10	1.2	0.6	25					6	3	56	23	13	0.6	0.06	10.0	0.4	0.6							
71	32	9.4	8.3	7.4	7.7	1.9	39	2.97	0.87	0.64	0.47	0.26	0.41	58	14	2.0	2.5	55	1.4	0.6			6	3	56	23	13	0.9	0.08	11.5	0.2	0.8						

No.	Int	EC	pH _{1.5}	pHK	pHW	WDC	MOR	S Ca	S Mg	S K	S Na	S NH ₄	S Cl	S NO ₃	S SO ₄	E Ca	E Mg	E K	E Na	P	Cu	Zn	Clay	Silt	F sand	M Sand	C sand	C	N	C/N	LC ₅	LC ₁₀	CO ₂ F
143	33	15.2	5.2	4.6	5.5	1.3	53	4.70	1.24	0.76	0.58	4.95	0.36	0.51	61	9	0.8	0.6	36	4		22	11	59	4	4						1.9	
144	30	29.0	5.4	5.7	6.5	1.4	35	5.44	2.89	1.81	3.71	3.98	7.03	1.16	45	30	2.0	4.0	38			5	10	69	16	1						1.6	
Moist Upland Grassland - Sandstone																																	
145	36	6.1	5.8	4.0	5.3	1.2	0	0.27	0.15	0.69	1.39	0.98	0.13	0.48	11	7	4.1	2.7	6			33	15	26	14	12	3.5	0.23	15.3	1.9	1.9	1.3	
146	37	5.3	6.1	4.0	5.5	0.7	8	0.25	0.12	0.92	1.34	0.74	0.02	0.37	15	11	4.3	3.6	3			30	2	54	8	6	1.9	0.14	13.4	1.3	1.6	1.2	
147	21	5.6	5.9	4.1	5.6	1.2	16	0.34	0.18	0.75	1.17	0.69	0.06	0.29	24	12	3.9	3.2	5			22	26	34	8	11	2.6	0.17	15.7	1.6	2.7	1.6	
148	12	5.7	6.3	4.3	5.7	0.5	37	0.38	0.21	1.32	1.36	0.96	0.11	0.43	28	14	3.5	2.6	4			23	21	33	20	3	2.1	0.13	15.7	1.2	2.5	1.7	
Moist Upland Grassland - Dolerite																																	
148	31	6.3	6.0	4.3	5.8	1.4	14	0.22	0.13	1.05	1.42	1.08	0.09	0.47	22	15	6.5	3.0	2			27	17	31	22	4	2.0	0.16	12.4	1.4	2.0	1.6	
149	35	6.0	6.0	4.0	5.4	1.3	0	0.25	0.19	0.61	1.41	0.99	0.10	0.44	17	12	5.7	3.6	1			72	16	12	1	0	5.8	0.36	16.1	3.0	5.8	1.1	
150	48	6.3	6.4	4.1	5.5	0.7	0	0.19	0.12	0.86	1.31	0.90	0.11	0.49	18	12	7.6	3.4	2			58	12	15	7	7	5.0	0.33	15.0	3.4	5.4	1.2	
151	53	6.6	5.7	4.1	5.4	0.7	0	0.21	0.16	1.01	1.20	1.00	0.15	0.46	18	13	7.4	3.3	4			9	16	52	18	5	6.0	0.36	16.6	2.8	5.8	1.1	
152	43	6.3	6.1	4.2	5.8	1.7	14	0.54	0.45	0.72	1.45	0.99	0.07	0.44	41	41	7.7	3.1	3			57	24	5	9	5	3.6	0.26	14.1	2.3	3.8	0.4	
153	33	6.0	5.8	4.2	5.5	0.6	0	0.20	0.14	0.88	1.34	0.90	0.08	0.48	18	13	5.2	3.2	3			37	11	50	1	1	2.6	0.18	14.6	1.5	2.9	2.1	
154	14	2.6	5.6	4.4	5.6	1.2		0.24	0.23	0.37	1.39	0.95	0.08	0.46	22	17	2.9	1.6	2			16	14	Total sand:70			5.1	0.35	14.4	2.9			
155	25	6.4	5.7	4.1	5.4	3.6	3	0.23	0.19	0.82	1.34	1.11	0.10	0.43	19	14	6.5	3.6	3			39	16	19	12	15	4.0	0.29	14.1	2.2	4.0		
156	13	5.8	5.8	4.1	5.4	1.8	0	0.18	0.14	0.54	1.36	1.13	0.14	0.41	13	8	3.4	2.7	4			44	14	18	10	14	5.5	0.32	17.0	3.5	5.5	1.7	
157	52	5.7	6.0	4.0	5.3	2.0	0	0.26	0.18	0.59	1.33	1.00	0.14	0.42	11	6	3.2	3.5	1			49	10	37	4	0	3.9	0.23	16.7	2.1	4.0	0.9	
158	31	2.8	5.9	4.6	5.8	0.8		0.23	0.20	0.87	0.96	1.12	0.00	0.37	22	16	8.1	1.7	2			22	20	Total sand:58			5.1	0.36	14.3	2.9			
159	7	8.4	5.5	4.0	5.0	1.8	13	0.77	0.56	0.65	1.16	0.85	1.37	0.59	17	9	3.7	3.0	1			44	14	24	12	5	3.0	0.24	12.5	1.6	3.2	0.9	
160	13	10.5	5.6	4.1	5.1	0.9	0	0.87	0.72	1.11	1.28	0.91	1.92	0.57	19	11	5.1	2.8	52			30	29	36	3	2	3.3	0.25	12.9	1.8	3.0	0.9	
161	9	5.7	5.7	4.1	5.5	1.0	81	0.44	0.27	0.80	1.10	0.75	0.25	0.62	32	14	3.6	2.5	18			29	11	51	4	6	1.5	0.13	11.4	0.8	1.0	0.5	
162	8	7.3	5.2	4.3	5.3	0.8		9.11	3.76	1.92	1.74	1.76	0.92	28	9	2.8	1.5	15			32	11	Total sand:58			4.2	0.32	13.2	1.6				
163	10	4.2	5.4	4.4	5.6	1.8		0.63	0.50	1.04	1.17	0.72	0.90	0.40	19	9	1.6	1.5	1			23	8	Total sand:69			0.9	0.09	9.3	0.4			
164	4	4.8	6.4	4.5	6.1	0.8	31	0.41	0.30	0.32	1.33	0.77	0.15	0.34	59	39	3.2	3.3	3			19	25	32	11	13	2.4	0.18	13.1	1.4	1.7	0.9	
165	58	5.7	5.2	4.3	5.5	0.9		0.85	0.69	0.17	1.34	0.91	1.81	0.21	20	9	1.2	1.9	4			27	21	Total sand:52			6.2	0.43	14.6	3.2			
166	20	4.8	5.1	4.1	5.2	1.0		1.35	0.99	0.63	1.14	2.39	1.17	0.40	19	8	1.8	1.7	11			34	22	Total sand:43			3.7	0.28	13.1	2.1			
167	63	7.2	4.9	4.0	4.9	0.5		0.84	0.66	0.35	1.11	0.87	1.79	0.28	9	5	2.2	2.0	5			24	23	Total sand:53			5.6	0.39	14.3	3.0			
168	67	18.3	5.6	4.3	5.2	0.4	0	1.22	1.29	2.60	1.46	1.94	3.41	0.67	36	24	8.7	3.3	51			41	14	14	18	14	4.4	0.37	12.1	2.7	4.8	2.6	
169	61	18.9	5.3	4.1	5.0	1.1	0	1.48	1.72	1.71	1.55	2.55	3.33	0.55	27	19	6.3	3.6	23			65	4	30	1	0	6.8	0.50	13.7	3.6	6.3	3.6	
170	60	11.3	5.5	4.4	5.6	0.6		0.52	0.49	2.38	1.72	3.21	1.10	0.67	32	18	14.6	1.8	19			33	13	Total sand:55			6.9	0.54	12.8	4.3			
171	1	13.1	6.3	4.0	4.9	1.7	13	1.50	0.85	0.55	1.61	1.59	2.40	0.30	28	11	2.8	3.2	55			17	33	48	1	1	5.0	0.40	12.5	2.5	4.4	4.1	
172	14	9.2	5.7	4.0	5.1	0.8	6	0.89	0.71	0.43	1.67	0.87	1.73	0.44	33	17	2.6	3.8	51			38	30	32	1	0	4.9	0.36	13.8	2.8	5.1	3.0	
173	20	7.1	5.0	4.3	5.1	1.7		0.71	0.47	0.89	0.82	0.64	2.08	0.28	9	3	3.6	1.7	50			24	9	Total sand:67			4.0	0.31	12.9	1.9			
174	36	6.3	5.7	3.9	5.1	0.7	0	0.21	0.26	0.52	1.43	1.08	0.16	0.57	9	11	3.6	3.1	1			76	3	14	7	1	5.4	0.35	15.4	2.7	5.3	0.7	
175	48	6.6	5.9	4.0	5.2	0.9	0	0.24	0.18	0.72	1.49	0.99	0.26	0.50	13	10	4.4	3.4	15			45	12	31	5	8	3.2	0.21	15.0	1.7	1.5	0.5	
176	69	5.8	5.3	4.1	5.4	1.1		0.56	0.50	0.81	1.38	1.13	0.26	0.55	22	16	6.3	2.2	1			19	20	Total sand:61			4.9	0.35	14.0	2.6			

No.	Inf	EC	pH1:5	pHK	pHW	WDC	MOR	S Ca	S Mg	S K	S Na	S NH ₄	S Cl	S NO ₃	S SO ₄	E Ca	E Mg	E K	E Na	P	Cu	Zn	Clay	Silt	F sand	M Sand	C sand	C	N	C/N	LC5	LC10	CO ₂ F		
177	22	7.8	5.8	3.9	5.2	2.0	0	0.22	0.16	0.69	1.65	1.20	0.18	0.49	14	8	4.8	3.4	9	85	3.6	3.7	8	23	51	14	4	7.3	0.49	14.8	4.3	7.0	1.0		
178	31	7.4	5.8	4.2	5.5	1.1	0	0.69	0.37	0.58	1.44	0.81	1.04	0.31	55	18	3.6	3.7	85	3.6	3.7	85	33	15	24	21	8	5.3	0.39	13.7	2.4	5.5	1.2		
Mixed Lowveld Bushveld - Nelspruit granite																																			
179	131	5.7	5.0	5.4	0.5	0.5	0.65	0.21	0.50	1.61	0.11	0.77	0.18	0.42	23	8	2.7	0.9	11	1.3	0.9	6	4	20	25	46	0.8	0.07	11.8	0.5	0.9				
180	83	4.4	5.1	5.2	1.1	1.1	0.71	0.20	0.31	1.27	0.05	0.55	0.15	0.38	17	5	1.9	0.9	10	2.5	0.7	10	7	21	24	39	0.6	0.06	11.4	0.4	0.6				
181	108	5.6	4.8	5.1	0.8	0.8	0.73	0.23	0.56	1.35	0.06	0.64	0.31	0.41	19	9	3.8	1.1	3	1.5	1.1	10	2	31	25	33	0.8	0.07	11.7	0.4	0.7				
182	106	5.7	5.3	5.4	0.7	0.7	0.80	0.21	0.52	1.36	0.08	0.83	0.20	0.37	22	6	2.0	1.1	11	1.8	1.2	3	5	25	30	36	0.7	0.06	11.4	0.4	0.7				
183	85	4.9	4.8	4.8	0.4	0.4	0.78	0.15	0.35	1.14	0.12	0.54	0.19	0.38	19	6	2.2	0.9	5	1.3	1.3	6	9	27	24	34	0.8	0.08	10.4	0.5	0.9				
184	79	4.5	5.1	5.2	1.3	1.3	0.69	0.16	0.34	1.34	0.08	0.58	0.18	0.43	21	7	2.7	0.9	8	3.2	1.5	9	5	26	24	37	0.6	0.06	9.7	0.4	0.8				
185	138	6.8	6.5	5.3	0.4	0.4	0.37	0.28	0.85	1.32	1.15	0.20	0.51	23	7	2.5	1.3	10	1.0	0.8	3	8	27	27	36	0.9	0.09	10.7	0.5	0.8					
186	82	4.5	6.7	5.3	0.7	0.7	0.17	0.13	0.60	1.32	1.07	0.15	0.45	19	5	2.0	0.9	4	1.5	0.5	3	4	33	26	34	0.5	0.06	9.7	0.3	0.5					
187	65	4.1	6.2	5.3	0.8	0.8	0.30	0.30	0.80	2.27	1.59	0.15	0.55	32	13	6.2	1.6	7	0.5	1.3	6	24	23	34	0.9	0.08	11.4	1.0							
188	58	3.0	6.3	5.5	0.8	0.8	0.50	0.23	0.48	1.80	1.25	0.16	0.52	22	6	2.1	0.9	6	1.8	0.8	5	5	25	26	39	0.6	0.06	11.6	0.2	0.6					
189	115	6.4	5.4	5.4	0.8	0.8	0.71	0.26	0.48	1.93	0.08	0.87	0.30	0.42	29	10	3.1	0.9	5	1.9	0.6	10	4	28	25	33	0.8	0.07	10.9	0.4	0.7				
190	67	4.8	5.4	5.3	0.8	0.8	0.49	0.12	0.27	1.43	0.03	0.65	0.26	0.36	24	5	2.3	1.0	6	1.7	0.8	6	9	26	22	38	0.6	0.07	9.6	0.4	0.8				
191	72	6.8	5.2	5.3	0.6	0.6	0.74	0.24	0.47	2.08	0.06	0.92	0.31	0.46	24	9	2.8	1.0	15	3.0	0.5	10	5	24	24	37	0.8	0.09	9.2	0.5	0.8				
192	73	7.9	6.0	6.0	0.8	0.8	1.22	0.34	0.38	1.89	0.04	0.94	0.33	0.46	43	10	3.5	1.0	28	4.3	1.8	10	6	26	24	34	0.9	0.08	11.9	0.5	0.6				
193	80	6.6	5.4	5.4	0.5	0.5	1.08	0.37	0.55	1.44	0.09	0.67	0.49	0.42	32	12	3.3	1.0	8	1.4	0.7	6	10	32	23	30	0.9	0.09	10.1	0.5	0.9				
194	89	4.8	5.6	5.6	1.0	1.0	0.68	0.15	0.25	1.13	0.05	0.51	0.26	0.34	29	6	2.0	1.0	6	1.6	0.5	8	8	26	26	32	0.7	0.06	10.8	0.4	0.6				
Mixed Lowveld Bushveld - basalt																																			
195	84	7.6	5.3	5.5	1.1	1.1	1.06	0.53	0.75	1.39	0.13	0.77	0.27	0.47	125	77	17.2	1.6	151	1.8	2.3	21	17	Total sand:62	62	2.7	0.19	14.1	1.3	2.2					
196	58	6.7	5.3	5.4	1.2	1.2	1.35	0.60	0.72	1.40	0.05	0.66	0.25	0.45	107	59	18.0	2.4	147	1.6	2.5	21	20	Total sand:59	59	2.3	0.15	14.8	1.1	1.8					
197	71	9.4	5.5	5.6	0.9	0.9	1.65	0.74	1.00	1.97	0.03	1.20	0.28	0.59	109	71	18.7	2.1	107	1.0	1.7	23	14	Total sand:63	63	2.3	0.18	13.0	1.2	1.9					
198	87	6.9	5.5	5.7	1.5	1.5	0.95	0.41	0.69	1.50	0.06	0.66	0.28	0.43	105	64	15.2	1.9	149	1.1	1.4	29	11	Total sand:60	60	1.9	0.13	13.8	0.8	1.1					
199	110	11.2	5.6	5.6	1.1	1.1	1.74	0.70	1.32	1.84	0.21	0.86	0.88	0.54	143	68	19.0	2.4	96	1.7	6.4					3.5	0.26	13.1	1.8	3.0					
200	67	5.6	5.5	5.5	1.0	1.0	1.16	0.47	0.46	1.28	0.10	0.53	0.20	0.38	128	55	10.3	1.7	106	1.9	2.5					2.0	0.15	13.2	0.9	1.7					
201	20	6.5	7.1	5.3	2.0	2.0	0.80	0.78	0.82	1.15	0.11	1.77	0.08	0.39	71	40	18.5	3.0	41	1.9	2.8					1.3	0.13	10.4							
202	21	5.1	7.3	5.1	2.0	2.0	1.20	1.15	0.89	0.95	0.86	0.04	0.36	102	61	18.7	2.5	15	2.2								1.8	0.15	12.2	0.8	1.3				
203	51	10.5	8.6	7.2	1.5	1.5	4.82	1.26	0.36	0.23	0.02	0.13	0.02	0.06	332	41	10.9	1.1	213	1.4	0.4	17	21	Total sand:63	63	2.4	0.17	14.4	1.0	1.7					
204	41	8.5	8.3	6.7	1.9	1.9	3.35	1.52	0.54	0.32	0.20	0.03	0.09	264	67	18.1	1.3	267	1.7	0.8	16	25	Total sand:59	59	2.4	0.17	14.5	1.1	1.9						
205	95	3.3	7.6	5.7	1.2	1.2	2.00	2.01	0.53	0.27	0.07	0.08	0.01	0.05	143	87	17.3	1.4	117	1.4	1.8	28	10	Total sand:61	61	2.2	0.14	15.7	0.9	1.8					
206	43	3.7	7.6	5.8	1.2	1.2	1.70	1.71	0.60	0.23	0.02	0.19	0.02	0.20	128	83	16.4	1.4	136	1.2	0.9	22	13	Total sand:65	65	1.8	0.11	16.8	0.9	1.5					
207	70	6.4	8.1	6.3	1.3	1.3	2.76	1.58	0.26	0.21	0.05	0.08	0.04	0.05	226	74	7.6	1.2	210	1.7	0.6					2.0	0.15	13.4	1.7	1.7					
208	72	11.0	8.5	6.9	1.7	1.7	4.38	1.55	0.34	0.33	0.02	0.14	0.07	0.10	326	59	11.1	1.3	188	2.9	0.4					2.5	0.17	14.9	0.9	1.9					
Eastern Thorn Bushveld																																			
209	16	5.4	6.5	5.1	6.6	1.6	76	0.53	0.35	1.14	1.41	0.84	0.33	0.33	51	17	4.8	3.8	8							1.5	0.15	10.7	0.9	1.8					
210	21	5.6	7.0	5.1	6.5	1.3	89	0.40	0.21	1.05	1.61	0.82	0.32	0.32	51	18	5.4	4.0	4							3	15								
211	24	6.5	6.4	5.0	6.4	1.0	54	0.55	0.25	1.12	1.64	0.92	0.12	0.36	45	20	6.7	3.1	6									2.1	0.20	10.7			2.3		

Appendix B: Manuscript to be submitted to Ecology Letters (July 2003)

A first theory on the height of vegetation across biomes

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Height of vegetation is unexplained by water supply, but may be explained by the rate of net energy fixation (E) divided by rate of uptake of nutrients (n). Net photosynthetic rate is gross photosynthetic rate minus respiration rate. Since respiration consumes simple carbohydrates, E is the rate of production of complex polymers of carbohydrates, and translates approximately to net primary productivity. A large E/n would produce nutrient-poor (tall, woody) vegetation, and a small E/n nutrient-rich (short, herbaceous) vegetation. Above-ground net primary productivity of fast-growing forests is matched by productive tropical grasslands (>20 t ha⁻¹ yr⁻¹). Rates of nutrient turnover, and not merely productivity, thus distinguish tall from short vegetation.

Keywords: vegetation height, net productivity, mineralization, organic matter, savanna, forest, grassland, nutrient cycling

The height of vegetation is a most visible and obvious ecological parameter, yet there is no consistent theory to explain why some vegetation types are tall and others short (Woodward 1992).

Ecologists are accustomed to perceiving a gradient from well-watered valleys with tall trees to deserts with stunted shrubs (Walter 1979). The height of vegetation is, however, poorly correlated with indices of water availability across ecosystems (Fig. 1). Holdridge's (1947) depiction of world plant formations also indicates this anomaly by showing that forests and grasslands occur under apparently similar temperature and moisture regimes. Fig. 1 shows that within the range of 300-1000 mm mean annual rainfall on well-developed soils, vegetation varies from forests >25 m high to grasslands <1 m high. A comparison of savannas and grasslands in Fig. 1 illustrates that trends in height of vegetation may actually run counter to the availability of water to roots. Although wooded savannas are several times taller than grasslands, savannas extend to regions warmer and drier than grasslands. Similarly, the widespread vegetation under mean annual rainfall ~250 mm in southwestern Australia is eucalypt woodland ~15 m high (Milewski 1981), whereas the adjacent mesic (>600 mm per year) coastal plain 100 km away is dominated by mallee-heath (~3 m high), representing an 80% decrease in height of vegetation despite a 240% increase in mean annual rainfall (Beard 1990).

It has been widely assumed that the advantage of height is that tall plants can reach the light of the canopy, thus overshading and outcompeting low plants (Grime 1979; Thompson 1987; Begon & Harper 1990). However, it remains unexplained why this process has not occurred in many ecosystems in which vegetation remains low despite an apparently ample supply of water. If light were the controlling resource, then all vegetation types would be expected to maximize their height. It is difficult to conceive that mesic grasslands and shrublands, such as mallee-heath in southwestern Australia, and Moist Upland Grassland and Mountain Fynbos in South Africa, represent maximum heights under their copious mean annual rainfall of >600, >1000 and >2000 mm, respectively (Walter 1979; Richardson & Cowling 1992; O'Connor & Bredenkamp 1997). Tilman (1988) notes that the most competitive plants are not necessarily those dominating the light source but are often the plants that optimise the uptake as well as allocation of nutrients. An integrated understanding of how competition for nutrients, water or light affects vegetation height remains, however, elusive and is often anecdotal and site specific. The co-existence of trees and grasses in savannas has, for example, been explained by separation of rooting zone, with trees monopolising water deep in the soil profile and grasses water in the topsoil (Walter, 1971; Walker & Noy-Meir, 1982).

Neglect of anomalies such as the marked variation in vegetation height across apparently similar moisture conditions has led several authors to question whether, after the practice of ecology for more than a century, the approach of ecologists has been conceptually sound (Pickett et al 1994; Ford 2000). Pickett *et al.* (1994) encourage ecologists to return to fundamental questions and to balance the reductionist approach by particular efforts to integrate ecological understanding across different domains and disciplines. Ford (2000) calls for an emphasis on "why-type questions" and "progressive synthesis", whereby theories are continually refined and tested using confirmation as well as falsification. Both Pickett *et al.* (1994) and Ford (2000) emphasise that progress in ecology depends on a continual welcoming of new theories. They also remind us that new theories, by their very nature, will challenge the credulity of peer reviewers, at least initially. To these exhortations we would add that ecological theories should elucidate cause and effect, that they are inherently uncertain, and that their formulation should be based on a combination of the facts available, parsimonious assumptions, and rationales that are both sound and internally consistent.

Here, we offer a first theory to explain observed patterns in the height of vegetation across biomes. The potential power of this approach is considerable because it promises a conceptual basis for understanding the structure of ecosystems across the planet. Height is perhaps the most important parameter of structure, even if it is used on a relative basis only (i.e. forests are taller than shrublands which in turn are taller than grasslands). The height of vegetation not only assists classification of biomes, it also affects the dynamics and diversity of organisms in them. Understanding what determines structure of vegetation in a particular environment lies at the heart of understanding ecological functioning and the distribution of biodiversity across landscapes. Bird diversity, for example, has been shown to depend on relative height of vegetation, with a greater species-richness of birds occurring in tall than short vegetation due to a greater availability of distinct niches (Cody, 1986).

The importance of the relationship of productivity to mineralization was perhaps first realized by Darwin in his book *Natural Selection*. Darwin stated that “the fairest measure of the amount of life being probably the amount of chemical composition and decomposition within a given period” (cited in Stauffer, 1975). Was Darwin hinting that the structure of vegetation could be explained by the relative dynamics of two main resources, energy and nutrients? We take this apparent hint further and suggest that the height of vegetation across biomes can be explained by the ratio E/n , where the rate of net energy fixation through carbon compounds (E) is divided by the rate of uptake of nutrients by vegetation (n). E is the rate of fixation of energy by photosynthesis (excluding the energy metabolised in various plant tissues) and corresponds to the energy available for fixation in complex polymers of carbohydrates, as opposed to sugars and starches. E is therefore synonymous with the net photosynthetic rate, which in turn is equal to the gross photosynthetic rate minus the rate of respiration that inevitably accompanies production of structural materials in the plant. Net primary productivity, in terms of dry matter, is largely structural energy in terrestrial ecosystems, with small contributions (on a mass basis) of metabolisable energy (simple carbohydrates) and nutrients. Therefore, E translates approximately into net primary productivity on a dry matter basis in biomes on land, despite the inclusion of nutrients in the plant matter produced.

We contend further that the inherent concentration of nutrients in soil parent materials is likely to be subordinate to the rate of release of nutrients from soil organic matter by fungi and microbes (hereafter termed microbial mineralization), and that the rate of uptake of nitrogen (N) and other nutrients is likely, in timescales of several years, to be strongly correlated with the rate of mineralization of organic matter by fungi, microbes, herbivores or fire. This means that an infertile soil with relatively low soil organic matter content can have a high “ n ”, if its limited stock of nutrients is rapidly recycled (Stock & Lewis, 1988; Canals *et al.* 2003), whereas a fertile, organic-rich soil can potentially have a low “ n ”, if the large stock of nutrients is cycled slowly (Davidson *et al.* 1992). Nitrogen is not necessarily representative of all nutrients, but is the subject of this initial analysis because of the availability of data for N .

We theorize that a large E/n is likely to promote the production of nutrient-poor (tall, woody) vegetation and a small E/n , nutrient-rich (short, herbaceous) vegetation. Tall vegetation is inherently nutrient-poor at the scale of the whole biomass, owing to the nutrient-poverty of fibrous structural tissues (Beadle & White, 1968). Short vegetation, by contrast, is inherently nutrient-rich because of the minimal contribution of lignin to herbaceous tissues, and is therefore likely to have a greater nutrient requirement than tall vegetation in a dynamic sense. This is depicted in the hypothetical comparison of a forest and grassland in Fig. 2. A feedback effect likely occurs, whereby mineralization is retarded under ligneous litter in woody vegetation and promoted under non-ligneous litter in herbaceous vegetation (Rayner & Boddy 1988; Knops *et al.* 2002; Schroter 2003).

The ratio of the rates of net photosynthesis to nutrient uptake may, for example, explain why the tallest trees are far taller in temperate than in tropical climates (Walter 1979; Carder 2002). E/n is likely to be larger in temperate forests than in tropical forests because gross photosynthesis is most rapid at moderate temperatures whereas microbial mineralization and plant respiration are most rapid at high temperatures (Larcher 1975; Howard & Howard 1993; Lloyd & Taylor 1994; Specht & Specht 1999) (Fig. 3).

A conceptually sound theory should be precise in its definitions of axioms, assumptions, and postulates (Ford 2000). A fundamental assumption in our theory is that there is an optimal height for vegetation in any particular environment, and that convergent evolution ensures that natural habitats (if given sufficient time) will attain the optimum height. In other words, the height of vegetation in two identical abiotic environments on different continents will be identical even if the floras are very different. We reject the assumption that the height of vegetation is constrained by the collective genetic resources available in a particular environment, i.e. we assume that genotypic and phenotypic flexibility within plant families ensures that a change from tall trees to short herbaceous plants or vice versa across an evolutionary timescale is quite feasible. Several other assumptions warrant mention. i) The natural vegetation of any environment is dominated by the most competitive plant species to emerge from the process of natural selection. ii) The most competitive plants are likely to be those with the most rapid metabolism, regardless of body size or investment in structural organs. iii) Organic matter may be produced at a maximum rate on a sustainable basis in all environments, but small plants would be more productive (and therefore more competitive) than large plants in certain environments, regardless of having inferior biomass. This is corroborated by Fig. 4, which shows that the productivity of short vegetation is not necessarily inferior to that of tall vegetation. iv) An increase in height brings various disadvantages, e.g. the risk of xylem cavitation, and the maintenance of structural tissues (Deshmukh 1986). These costs may set proximate, if not ultimate, limits to vegetation height (Ryan & Yoder 1997). v) Plants are likely to maximize their uptake of nutrients in any ecosystem, inasmuch as this increases metabolic rates, productivity and competitiveness.

Given the above reasoning and assumptions, we hypothesised that the N requirement of tall, woody vegetation would be less than that of shorter, herbaceous vegetation of comparable productivity, and that productivity of grasslands could rival that of forests. We predicted that uptake of N would be less in forests than grasslands of comparable productivity. An analysis of the available literature confirmed this prediction. Fig. 4 shows that N uptake of forests is approximately half that of grasslands of equivalent productivity and that above-ground net primary productivity of fast-growing forests is matched by the most productive tropical grasslands ($>20 \text{ t ha}^{-1} \text{ yr}^{-1}$). This indicates that a main difference between these two ecosystems is not productivity as much as rates of N uptake and hence turnover (Hart *et al.* 1993).

Productivity in all vegetation types is likely to be affected by the supply of nutrients, but what differs among ecosystems is the degree to which the nutrients taken up are diluted by structural fibre (nutrient-free energy) in the biomass produced. Nutrient-poor tissues (i.e. wood) are, for example, likely to build up in environments where for every 150 kg of biomass produced, 1 kg of N is taken up. By contrast, nutrient-rich tissues (i.e. herbaceous matter) are likely to be competitive in environments where, for every 150 kg of biomass produced, 3 kg of N are taken up. These calculations resemble those used to assess 'nutrient-use efficiency' in plant growth (Vitousek 1984), except that our approach uses ratios calculated for whole plants, not just foliage.

Despite their great biomass, forests take up N far more slowly than grasslands of equivalent productivity do. Productive grasslands take up at least twice as much N ($>300 \text{ kg ha}^{-1} \text{ yr}^{-1}$) as do forests, while fixing energy at a similar rate in terms of dry matter. Even grasslands of modest productivity exceed forests of extremely fast-growing eucalypts in their rates of uptake of N (Fig. 4). Data currently available from various European forests and plantations provide a preliminary direct test of the effects of E/n on carbon sequestration. Height of vegetation is positively correlated with the ratio of net primary productivity to the rate of mineralization of soil organic matter (Fig. 5) (Schulze 2000). There is a need to collect data on both height and density of trees from a large number of mature stands, before a general pattern can be confirmed.

The greater height of dry savannas than moist grasslands is potentially explained by E/n. At high temperatures, microbial mineralization is potentially rapid, but the topsoil tends to be frequently desiccated to the point of inactivation of decomposers (Scholes & Walker 1993). Savanna trees can, however, continue to photosynthesize even if topsoils are dry, by tapping water from subsoils (Walter 1971) (Fig. 6). We postulate that grasslands tend to be restricted to latitudes and altitudes which are cool enough to prevent prolonged desiccation of topsoils, thereby ensuring a largely uninterrupted supply of nutrients via mineralisation.

The abrupt border between alpine grasslands and forests is evident at treelines across continents at a mean temperature of $\sim 6 \text{ }^\circ\text{C}$ during the growing season (Hoch & Korner 2003). E/n may explain this sudden switch from trees to herbaceous plants, inasmuch as conversion of sugars to lignin is largely restricted to temperatures above $6 \text{ }^\circ\text{C}$, whereas microbial mineralization proceeds at close to $0 \text{ }^\circ\text{C}$ (Aragno 1981; Berry & Raison 1981; Lloyd & Taylor 1994; Hoch *et al.* 2002). The considerable reduction of E/n at temperatures below $6 \text{ }^\circ\text{C}$ potentially explains the transition to alpine grasslands at this temperature (Fig. 7).

Various environmental factors, such as episodicity of rainfall, seasonal waterlogging, wind, fire, and herbivory, affect height of vegetation (Tinley 1982). However, this may be *via* their effects on E/n, rather than through physical damage or anoxia *per se*. Wind, for example, reduces net photosynthetic rate by reducing the rates of gross photosynthesis, transpiration, and translocation of energy from leaf to stem (Grace 1977; Nobel 1981). It simultaneously boosts the rate of respiration, owing mainly to the repair of tissues shaken and disrupted by wind at a microscopic scale (Todd *et al.* 1972; Clemente & Marler 2001). Chronic wind may thus limit E/n by reducing the rate of net energy fixation without necessarily reducing the rate of microbial mineralization.

Future analyses of E/n promise to resolve the confusing effects of fire on height of vegetation. Frequent fires maintain grasslands and shrublands (e.g. fynbos), yet are also compatible with trees in e.g. miombo woodlands in Africa and eucalypt woodlands in Australia (Trapnell 1959; Kozłowski & Ahlgren 1974; Rundel 1981; Williams *et al.* 2002). Fire exposes soil to solar warming, thus potentially boosting microbial mineralization (O'Lear *et al.* 1996; Knapp *et al.* 1998) and releases nutrients from biomass (Stock *et al.* 1988). Boosting of n and reduction of E/n would, we hypothesize, maintain grasslands. By the same token, microbial mineralization is likely to be inhibited by either waterlogging and its consequent anoxia, or surface desiccation, maintaining seasonally wet forests or dry woodlands despite frequent fires.

Although fire results in the mineralization of N to nitrate and ammonium, it also depletes N greatly by volatilization (Rundel 1981; Cook 1994). Extremely intense fires, such as occur in tall eucalypt and conifer forests, are likely to volatilize a greater proportion of organic N, and a greater absolute quantity of N per unit area, than grass fires. It is thus possible that fires intense enough to volatilize most of the nutrients in the biomass boost E/n in the long term, whereas fires mild enough to conserve nutrients and promote microbial mineralization do the opposite. The effect of fire on E/n and height of vegetation is thus probably a function of the intensity as well as frequency of combustion and how fire interacts with climate and drainage.

Height of vegetation has been surprisingly poorly defined (i.e. no consensus has been reached on how to measure vegetation height across biomes) given its prime importance as a parameter of ecosystems. The lack of a suitable definition

indicates the unfortunate reluctance of biologists to embrace height of vegetation as a predictable parameter. We suggest the following definition: “the height of vegetation in a given environment is the mean height of the 50 tallest living plants in a hectare in mature vegetation”. This definition prevents extreme individuals, such as emergent trees in tropical forests, lone trees in savannas and/or vegetation in a temporarily low state (e.g. after fire) from unduly affecting the overall height recognized for the mature stand.

Fire-prone vegetation is periodically reduced to a height approaching zero. We contend that it is the height of the mature vegetation that indicates the relevant height of vegetation under the particular abiotic regime. Fire and other disturbances such as flooding can, however, change the abiotic environment in numerous ways (e.g. nutrient availability, light availability, soil temperature) and thus the optimal height for a particular habitat can potentially fluctuate through time. Plants could conceivably track this change in optimal height throughout the process of succession from post-fire herbaceous plants to tall trees i.e. the rate of increase in height may be a function of the change in optimal height, as determined by changing abiotic factors, through the cycle.

It is unlikely that any terrestrial ecosystem can be effectively managed until the gross dimensions of its dominant plants have been rendered predictable. E/n not only offers an explanation in terms of fundamental principles of the physical environment, but may provide a common denominator among ecosystems, by which apparently disparate biotic and abiotic factors ultimately resolve into a simple ratio, i.e. the rate of net energy fixation divided by the rate of nutrient uptake. We acknowledge that the pattern we describe, of correlation between height of vegetation and the ratio of energy to nutrients incorporated in the vegetation, may be an effect and not a cause. However, ecologists have the following choice: 1) to continue to assume that the pattern of height of vegetation across the Earth is accidental or inscrutable, and that the ratio of energy to nutrients in vegetation is a mere consequence of this pattern, or 2) to test the possibility that this ratio is actually a driving force. We contend that the latter option is worth pursuing, because only by investigating underlying causality can true understanding be attained. Inevitably, theories such as this cannot be tested by a few researchers, but require the critical attention of the ecological community.

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Figure legends

Figure 1 Relationship between approximated mean heights of vegetation in different biomes and indices of water availability, including mean annual rainfall (a) and mean annual rainfall less Thornthwaite Potential Evapotranspiration (b). Climatic data were obtained from the South African Weather Bureau, Bureau of Meteorology Australia (<http://www.bom.gov.au>) and World Climate website (<http://www.worldclimate.com>). The location of each data point is submitted as supplementary information.

Figure 2 Hypothetical comparison of the nitrogen (N) requirement of a forest and a grassland that both produce 10 t (dry matter) $\text{ha}^{-1} \text{yr}^{-1}$.

Figure 3 Hypothetical comparison of rates of photosynthesis and mineralization in temperate and tropical forests over the average day (during the growing season in the case of temperate forest). The difference in temperatures results in different rates of mineralization in the soils. However, net photosynthetic rates are similar, because of the greater costs of plant respiration under warm than under cool conditions. Net photosynthetic rate is derived from a hypothetical annual net productivity of 10 t (dry matter) ha^{-1} in both vegetation types. The rates of N mineralization are derived from a hypothetical annual N mineralization of $\sim 40 \text{ kg N ha}^{-1}$ in the temperate forest and $\sim 120 \text{ kg N ha}^{-1}$ in the tropical forest

Figure 4 Differences between forests and grasslands in above-ground net primary productivity and rate of uptake of N. Data were calculated from the literature and are submitted as supplementary information. Karri = *Eucalyptus diversicolor* F. Muell., Douglas fir = *Pseudotsuga menziesii* Mirb. Franco, Jarrah = *Eucalyptus marginata* Donn ex Sm., Shorea = *Shorea robusta* Gaertn. Tropical pastures received no fertilization since establishment.

Figure 5 Relationship between height of vegetation in European forests (including immature stands) and the ratio of net primary productivity to the modeled rate of mineralization of soil organic matter. Data were taken from Schulze (2000). Soils were incubated in the laboratory to determine the rate of mineralization under various temperature and water regimes. The mean annual rate of mineralization was then modeled using measurements of temperature and water content from soils in the field.

Figure 6 Hypothetical comparison of rates of photosynthesis and mineralization in savanna and grassland under the same regime of rainfall and soil moisture, but different regimes of temperature. The course of photosynthesis and mineralization is followed for five days after a given rainfall event during the growing season. Photosynthesis in the savanna remains rapid, because roots can exploit moisture deep in the soil where mineralization is negligible. However, the warmth of the savanna climate desiccates topsoils, curtailing mineralization. Accumulation of wood is explained by the ratio of photosynthesis to mineralization, which even on day 1 in savanna exceeds that on any day in grassland. Net photosynthetic rate is derived from a hypothetical annual net productivity of $\sim 5 \text{ t (dry matter) ha}^{-1}$ in the savanna and $\sim 4 \text{ t (dry matter) ha}^{-1}$ in the grassland. The rate of N mineralization is derived from a hypothetical annual N mineralization of $\sim 50 \text{ kg N ha}^{-1}$ in the savanna and $\sim 60 \text{ kg N ha}^{-1}$ in the grassland.

Figure 7 Hypothetical rates of energy fixation and N mineralization in a forest below the treeline and in an alpine grassland above the treeline over a twelve hour period during the growing season. Below a mean growing season temperature of 6°C , lignification (fixation of chemical energy into lignin) is limited more than mineralization, so that E/n decreases. The rate of N mineralization is derived from a hypothetical rate of $\sim 20 \text{ kg N ha}^{-1}$ in the forest and $\sim 15 \text{ kg N ha}^{-1}$ in the alpine grassland. The rate of energy fixation is derived from a hypothetical annual net productivity of $\sim 2.5 \text{ t (dry matter) ha}^{-1}$ in the forest and $\sim 1 \text{ t (dry matter) ha}^{-1}$ in the alpine grassland.

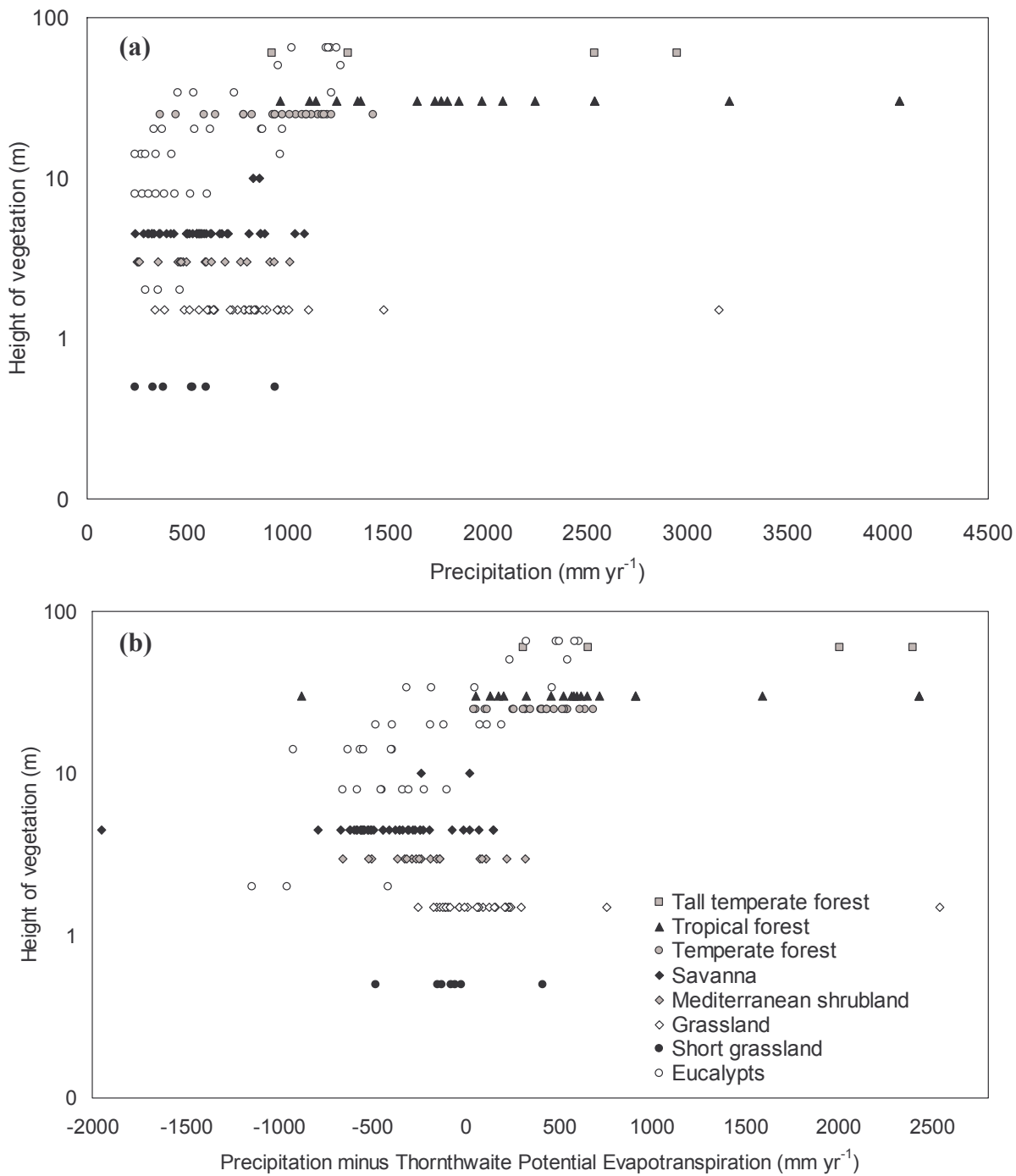


Figure 1

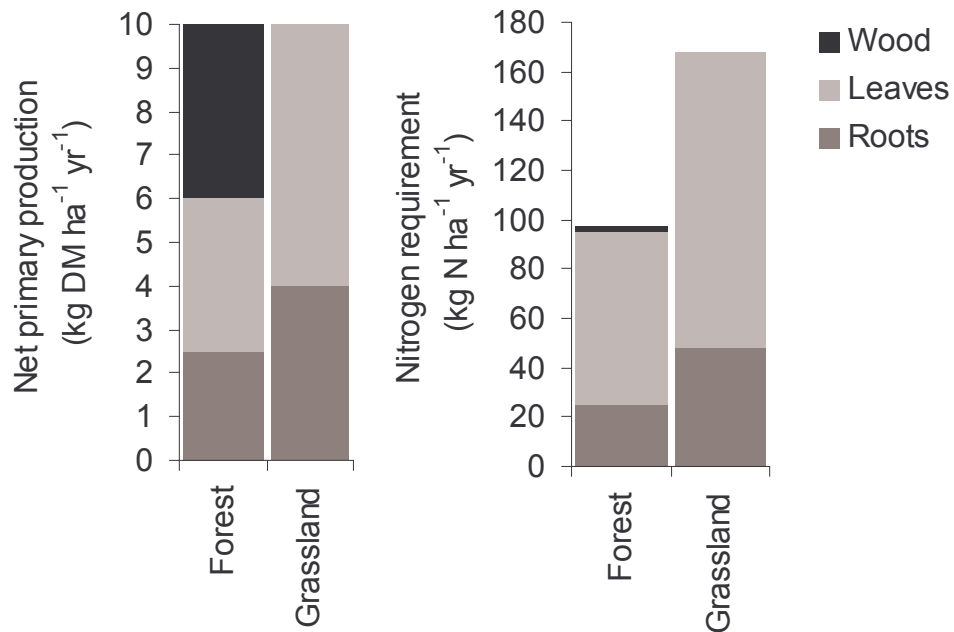


Figure 2

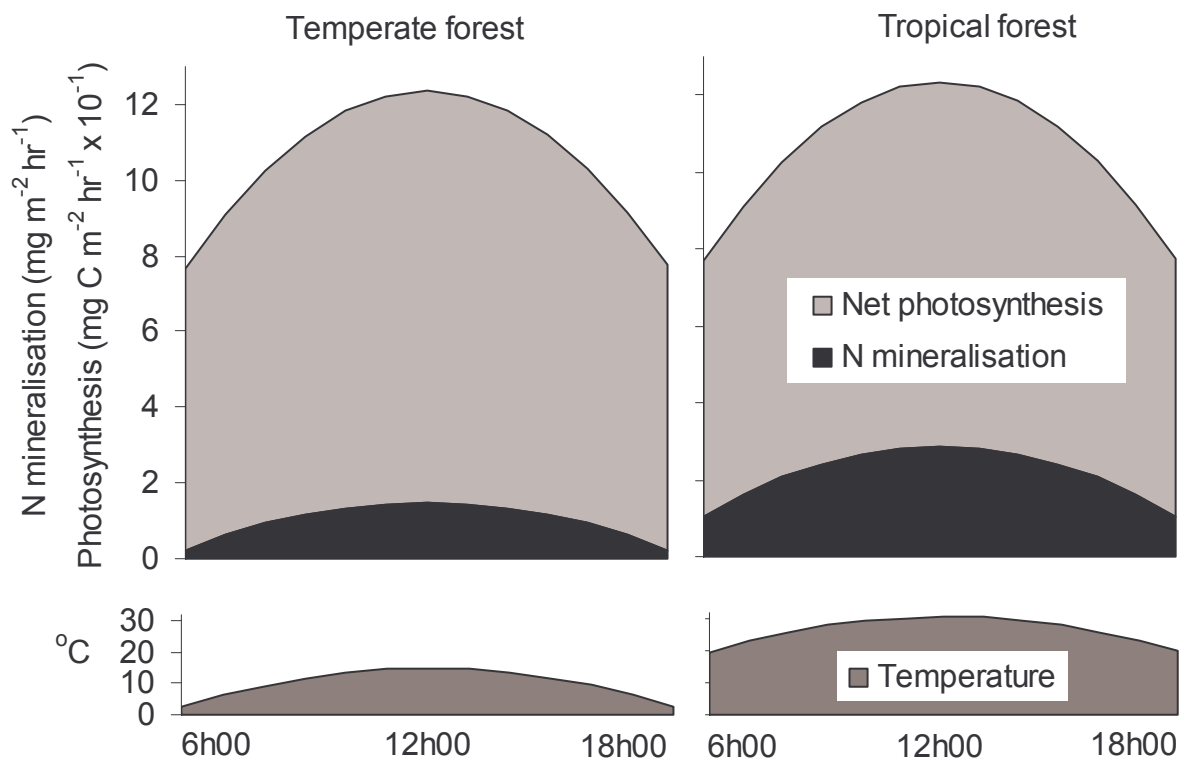


Figure 3

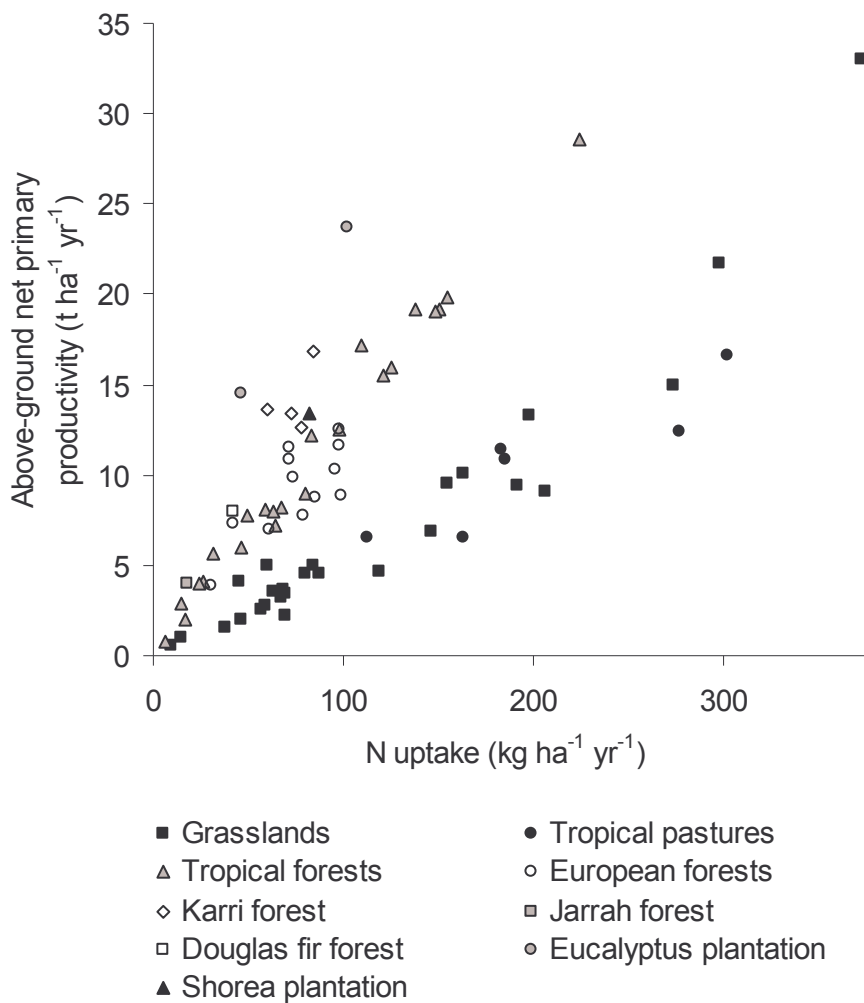


Figure 4

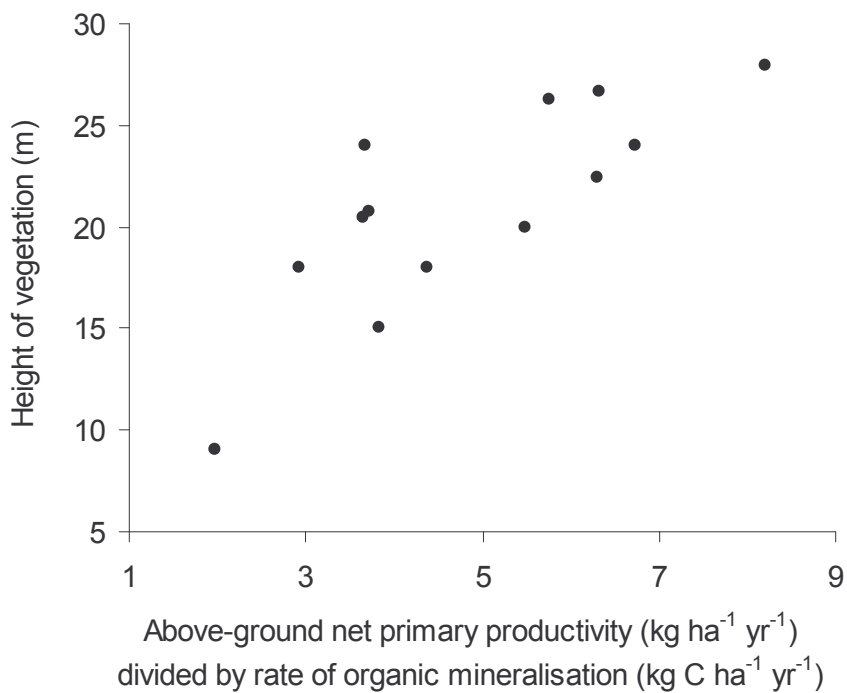


Figure 5

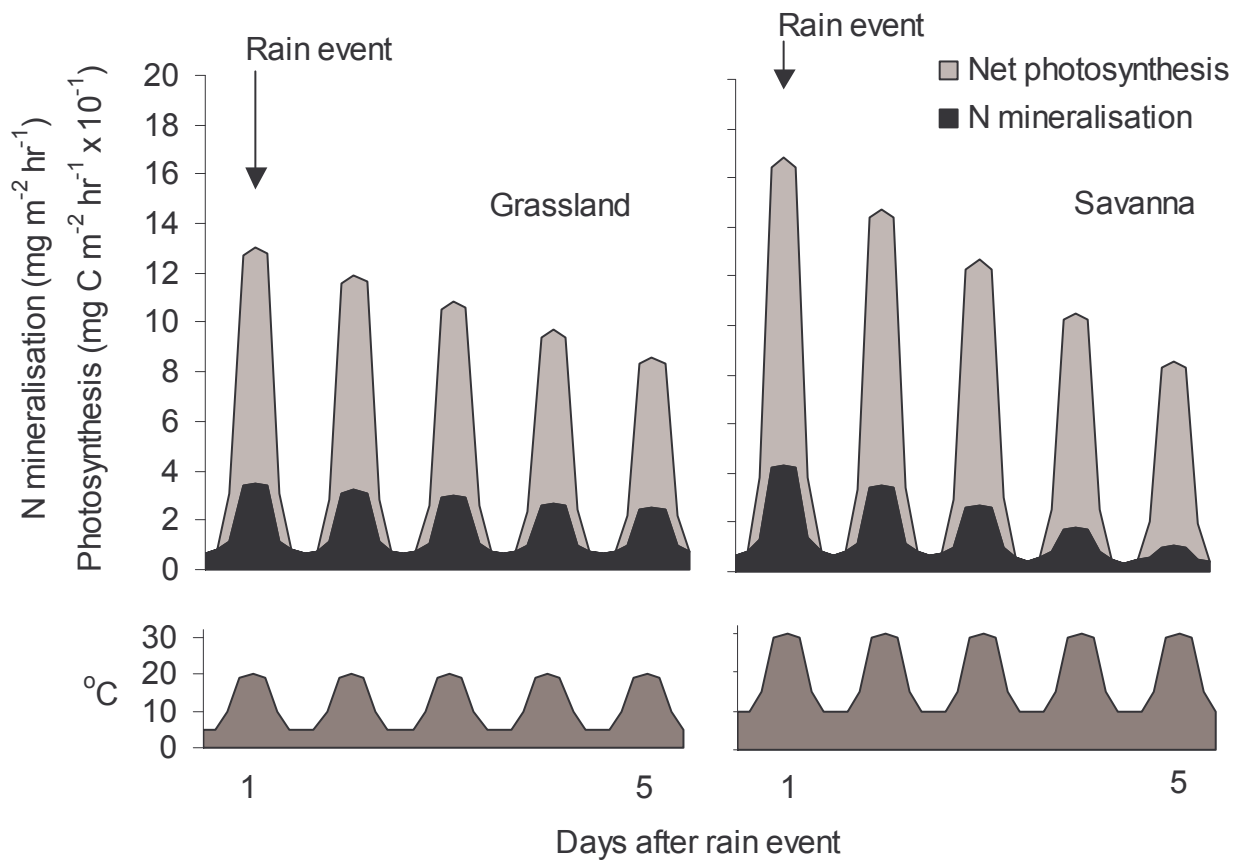


Figure 6

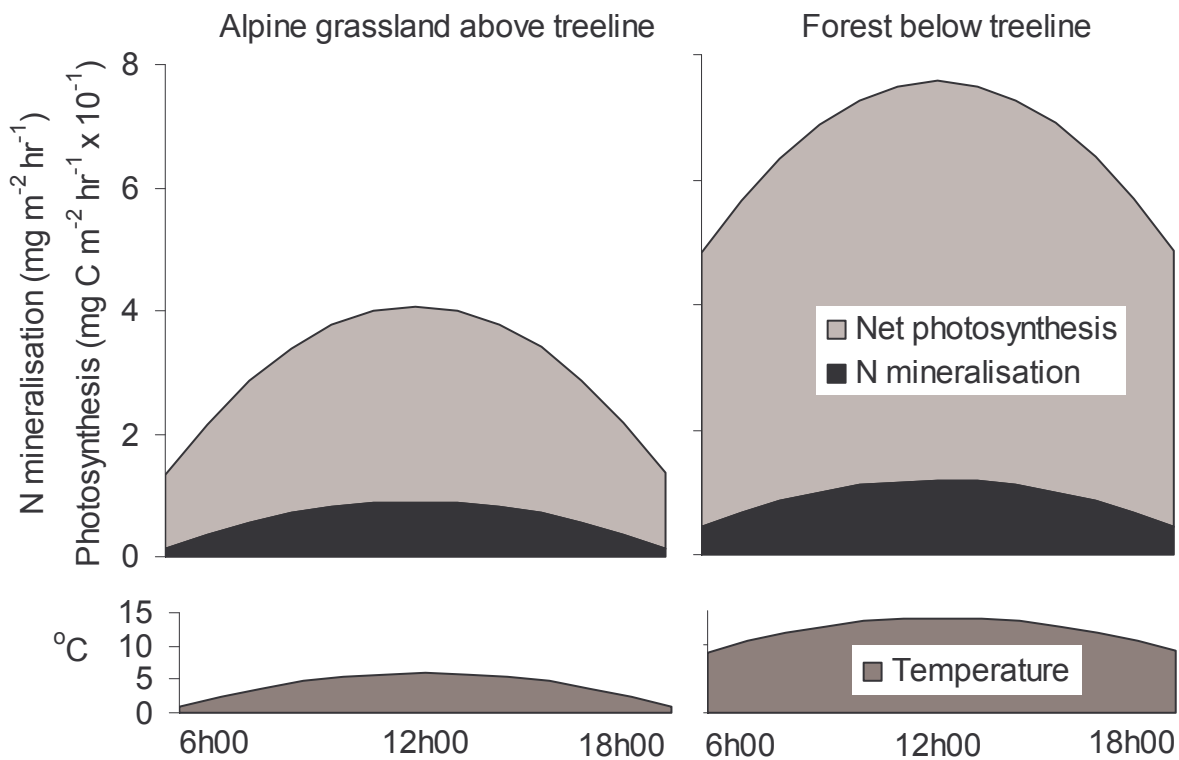


Figure 7