

**EMPIRICAL AND MODEL DERIVED RESPIRATION
RESPONSES TO CLIMATE IN DIFFERENT SOILS OF AN
ARID SOUTH AFRICAN ECOSYSTEM**

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A thesis submitted in partial fulfillment of the requirements for the degree
of Magister Scientiae in the Department of Biodiversity and Conservation
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May 2009

To Edmund and Marystella, for their love, patience and support



Keywords

Arid ecosystems

Artificial warming

Carbon dioxide

Climate change

Modeling

Nitrogen

Phosphorus

Precipitation exclusion

Soil organic matter

Soil respiration



Abstract

This study examined the magnitude of soil CO₂ efflux in an arid South African ecosystem, the flux responses as well as those of key limiting nutrients to soil temperature increases and moisture reductions consistent with a future climate change scenario, and compared measured soil respiration rates with those predicted with empirically and theoretically-based soil respiration models.

Measurements of soil respiration rate, temperature, moisture, N and P contents were conducted monthly over a 12-month period in natural environments and those artificially manipulated with replicated open-top warming chambers (average 4.1°C increase) and precipitation exclusion chambers (average 30.1% decrease in rainfall, 26.2% decrease in fog and dewfall) distributed in five different soil-vegetation units.

Measured soil respiration rates were over 3-fold less than those reported for temperate and tropical forest ecosystems with 61.5% of the total soil CO₂ efflux contributed by root respiration (derived from the differences between moderately vegetated and sparsely vegetated areas) in moderately vegetated soils. Massive increases (up to 15 times) in soil CO₂ efflux occurred during wet phases, but even these large CO₂ pulses were only comparable in magnitude with soil CO₂ effluxes reported for temperate semi-arid grasslands. There was considerable intra-annual and inter-site variability in the magnitude and direction of soil respiration and N and P responses to elevated temperatures and reduced precipitation levels with poor correspondence evident between soil CO₂ efflux and soil organic matter content. Soil CO₂ effluxes declined in response to precipitation exclusion by 7.1% over all sites and increased in response to warming by 42.1% over all sites. The large increase in response to warming was assisted by a 7.5% enhancement in soil moisture content due to precipitation interception by the chamber walls and its channelling to the soil surface. Relatively smaller respiration increases in response to warming occurred in moderately vegetated soils, these attributed to soil thermal insulation by the plant canopy cover. Soil P and N contents increased in response to warming by 11.3% and 13.3% respectively over all sites, with soil P declining in response to precipitation exclusion by 5.8% over all sites and soil N increasing in response to precipitation exclusion over all sites by 5.8%.

Standard least squares regressions quantified the relationships between soil respiration rate and measured soil physical and chemical properties, and their interactions for each of the 5 soil-vegetation units. These relationships were incorporated in an empirically-based soil respiration (EMR) model which was compared with a theoretically based generalized soil respiration model (GRESP). GRESP model functions included measured Q₁₀ coefficients at soil moisture contents above field capacity, these assumed reduced by half for dry conditions, and maximum retentive and field capacities of soils. EMR modelled soil

respiration rates displayed slightly better correspondence with measured soil respiration rates than GRESP modelled soil respiration rates. This apparent from the higher regression coefficients and lower sums of squared residuals, with EMR model residuals also more closely approximating normal distributions. However, despite the EMR model's slight superiority, it was concluded that more precise laboratory-based measurements of soil retentive and field capacities and their Q_{10} coefficients at different soil moisture contents could improve the GRESP model's accuracy thereby providing a more convenient and uncomplicated means of predicting respiration responses to current and future climates over a wide range of arid soil types



Declaration

I declare that *Empirical and model derived respiration responses to climate in different soils of an arid South African ecosystem* is my own work, that it has not been submitted before for any degree or examination in any other university, and that all the sources I have used or quoted have been indicated and acknowledged as complete references.

Justine Muhoro Nyaga

May, 2009

Signed



Acknowledgements

I am grateful to my supervisor, Dr Charles Musil, for his guidance and encouragement. The inspiration he offered in the course of writing and revising the drafts was invaluable without which the prompt completion of this work would not have been possible. I am also very grateful to him for obtaining funds for my research work, support and study, which made this work possible. I thank my second supervisor, Professor Lincoln Raitt for his valuable support and guidance in reviewing my chapter manuscripts. Many thanks to Dr. Brian Mantlana for the invaluable training offered in the use of Li-Cor 8100 Infrared gas Analyzer and in the initial field soil respiration measurements. My gratitude also goes to Mr. Stanley Snyders who assisted me with most of the technical work in the field. I also acknowledge the Climate Change & Bio-adaptation Group of SANBI, for material support especially with office space, vehicles, laboratory and internet facilities. My colleagues Mr Sheunesu Ruwanza, Mr Ignatious Matimati and Mr. Walter Maphangwa offered invaluable support and company in the course of this work. Special thanks go to my father Andrew Nyaga and my mother Jacinta Wangai who sacrificed a lot for my education. In addition, I thank all my brothers and sisters, and their families for their constant encouragement. Special thanks due to my wife Marystella and our son Edmund for their support and understanding.

This work was funded by the German Federal Ministry of Education and Research through BIOTA Southern Africa Phase III (Promotion number: 01LC0624A2). I am grateful to them for their financial support.

Table of Contents

Keywords.....	i
Abstract	ii
Declaration	iv
Acknowledgements	v
Table of Contents.....	vi
List of Tables	viii
List of Figures	ix
List of Appendices	x
Abbreviations	xi
Chapter 1: A review of soil respiration, elemental dynamics and responses to climate change	1
1.1. Introduction.....	1
1.2. Biophysical factors affecting soil respiration.....	2
1.3. Soil respiration models	3
1.4. Effects of climate change on soil respiration and elemental dynamics	6
1.4.1. <i>Temperature changes</i>	6
1.4.2. <i>Precipitation changes</i>	8
1.5. References	9
Chapter 2: Study rationale, sites, objectives and thesis structure..	21
2.1. Study rationale.....	21
2.2. Study area	21
2.3. Study sites	22
2.4. Study objectives	26
2.5. Thesis structure.....	26
2.4. References	27
Chapter 3: Effects of experimental warming and precipitation exclusion on CO₂ efflux and elemental content of different soils in an arid South African ecosystem.....	29
Abstract.....	29
3.1. Introduction.....	30
3.2. Materials and methods.....	32
3.2.1. <i>Study area and sites</i>	32
3.2.2. <i>Warming and precipitation exclusion treatments</i>	33
3.2.3. <i>Soil respiration</i>	34
3.2.4. <i>Soil environment</i>	34
3.2.5. <i>Soil organic and elemental content</i>	35
3.2.5. <i>Statistical analysis</i>	35
3.3. Results	35
3.3.1. <i>Warming and precipitation exclusion chamber environments</i>	35
3.3.2. <i>Soil respiration rate</i>	36

3.2.2.1 Effects of artificial warming.....	36
3.2.2.2 Effects of precipitation exclusion.....	37
3.2.2.3 Correspondence with soil organic matter content.....	37
3.3.2. Soil elemental content	37
3.2.2.1 Effects of artificial warming.....	37
3.2.2.2 Effects of precipitation exclusion.....	38
3.4. Discussion	39
3.5. References	44
Chapter 4: A comparison of empirical and theoretical based model predictions of CO₂ efflux in different soils of an arid South African ecosystem	60
Abstract.....	60
4.1. Introduction.....	60
4.2. Materials and methods.....	63
4.2.1. <i>Study sites</i>	63
4.2.2. <i>Warming and precipitation exclusion treatments</i>	64
4.2.3. <i>Soil respiration, moisture and nutrient assays</i>	64
4.2.4. <i>Model development</i>	65
4.2.4.1. Empirical model.....	65
4.2.4.1. GRESP model	66
4.2.5. <i>Model comparisons</i>	67
4.3. Results and Discussion	67
4.4. References	70
Chapter 5: Conclusions and recommendations	84
5.1. Main conclusions	84
5.2. Recommendations.....	84
5.3. References	84



List of Tables

Table 3.1. Average changes in soil surface temperatures, soil moisture levels, rainfall and fog and dewfall amounts in open top warming and precipitation exclusion chambers relative to those in the ambient environment. * derived from linear regressions of soil moisture content against rainfall and fog and dewfall amounts.....	52
Table 3.2. Statistics from an ANOVA (GLM) which tested the effects of artificial warming and precipitation exclusion treatments in different months and their interactions on soil respiration rates and elemental contents in 5 different soil-vegetation units. Variance ratios (F-statistics) presented in bold indicate significance at *P ≤ 0.05, **P ≤ 0.01, ***P ≤ 0.001.....	53
Table 3.3. Pearson correlation coefficients (r), t-statistics and significance levels for correspondence between measured soil respiration rates and soil organic matter contents in 5 different soil-vegetation units.....	54
Table 3. 4. Soil respiration rates reported for different ecosystems compared with those measured in an arid ecosystem in this study	55
Table 4.1. Soil moisture and respiration coefficients included in the GRESP model	75
Table 4.2. EMR model coefficients derived from least squares regressions of soil respiration rate against 11 environmental variables for 5 different soil-vegetation units	75
Table 4.3. Environmental variables selected by step wise regression for 5 different soil-vegetation units	76
Table 4.4. Correspondence (r ²) between measured and EMR and GRESP model predicted soil respiration rates for 5 different soil-vegetation units, non conformity (K-S statistic) of residuals to normal distributions, and sums of residuals squared (∑residuals ²). Significant at *P ≤ 0.05, **P ≤ 0.01, ***P ≤ 0.001.....	77
Table 4.5. Q ₁₀ coefficients derived from the EMR model for 5 different soil-vegetation units.....	78

List of Figures

Figure 2.1. Location, typical topography and vegetation of the Quaggaskop experimental site	23
Figure 2.2. Location, typical topography and vegetation of the Numees and Koeroegapvlakte experimental sites	25
Figure 3.1. Linear regressions of soil moisture content against rainfall and fog and dewfall frequency and amounts	56
Figure 3.2. Average monthly soil respiration rates measured in the ambient environment and in open top warming and precipitation exclusion chambers in 5 different soil vegetation units and total monthly rainfall amounts. Standard errors shown as bars.	57
Figure 3.3. Average monthly soil phosphorus contents measured in the ambient environment and in open top warming and precipitation exclusion chambers in 5 different soil vegetation units and total monthly rainfall amounts. Standard errors shown as bars. ..	58
Figure 3.4. Average monthly soil nitrogen contents measured in the ambient environment and in open top warming and precipitation exclusion chambers in 5 different soil vegetation units and total monthly rainfall amounts. Standard errors shown as bars. ..	59
Figure 4.1. Exponential regression of soil temperature against soil respiration rate at soil moisture levels above field capacity	79
Figure 4.2. Correspondence (r^2) between measured and EMR and GRESP modeled soil respiration rates in soils with sparse vegetation cover overlaid by quartz-gravel substrates (QG-SV) and goodness of fit of residuals to normal distributions.....	80
Figure 4.3. Correspondence (r^2) between measured and EMR and GRESP modeled soil respiration rates on soils with sparse vegetation cover overlaid by shale, phyllite and limestone derived substrates (SPL-SV) and goodness of fit of residuals to normal distributions.	81
Figure 4.4. Correspondence (r^2) between measured and EMR and GRESP modeled soil respiration rates on soils on soils with moderate vegetation cover overlaid by shale, phyllite and limestone derived substrates (SPL-MV) and goodness of fit of residuals to normal distributions.	82
Figure 4.5. Correspondence (r^2) between measured and EMR and GRESP modeled soil respiration rates on soils with moderate vegetation cover overlaid by quartzite, limestone and dolomite derived substrates (QLD-MV) and cenozoic alluvium, aeolian sand and calcrete derived substrates (ASC-MV) and goodness of fit of residuals to normal distributions.	83

List of Appendices

Appendix 1. Photos of open top warming, precipitation exclusion and control chambers used for manipulating soil temperature and moisture environments.....	86
Appendix 2. Photos of Infra-red gas analyser with sampling chamber interfaced with laptop computer used for measuring soil respiration rates in sparsely and moderately vegetated environment.....	87
Appendix 3. Photos of environmental sensors interfaced with loggers installed in ventilated radiation shields monitoring changes in soil moisture, temperature and apparent amounts of fog and dewfall at hourly interval.....	88



Abbreviations

ASC-MV	Cenozoic alluvium, aeolian sand and calcrete derived substrates – Moderate vegetation cover
BIOTA	Biological transect in Africa
EMR model	Empirical respiration model
GRESP model	General respiration model
IPCC	Inter-Governmental Panel on Climate Change
QG-SV	Quartz-gravel substrates – Sparse vegetation cover
QLD-MV	Quartzite, limestone and dolomite derived substrates – Moderate vegetation cover
SPL-MV	Shale, phyllite and limestone derived substrates – Moderate vegetation cover
SPL-SV	Shale, phyllite and limestone derived substrates – Sparse vegetation cover



Chapter 1: A review of soil respiration, elemental dynamics and responses to climate change

1.1. Introduction

Soils are the major reservoir of carbon in terrestrial ecosystems, containing more than two-thirds of the total carbon in the terrestrial part of the biosphere (Lin et al., 1999). They are important in the terrestrial carbon cycle due to their role in cycling and storage of carbon (Raich et al., 2002; Schimel et al., 1994). Soil respiration, also referred to as soil CO₂ efflux (Schlesinger and Andrews, 2000; Rustad et al., 2001), is an essential component of biosphere-atmosphere interactions (Lellei-Kovács et al., 2008). The flux of carbon from soils to the atmosphere in form of CO₂ represents the combined respiration of roots, mycorrhizae and soil micro and macro-organisms (Raich and Schlesinger, 1992; Rustad et al., 2000). It also includes to a lesser extent chemical oxidation of carbon compounds within the soil (Lloyd and Taylor, 1994). Soil respiration release of CO₂ from terrestrial ecosystems is one of the major pathways of carbon flux in the global carbon cycle (Schlesinger and Andrews, 2000), second only to gross primary productivity (Houghton and Woodwell, 1989; Raich and Schlesinger, 1992; Davidson et al., 2002) and accounts for about 25% of the global CO₂ exchange (Jia and Zhou, 2008). Almost 10% of the atmosphere's CO₂ passes through soils each year (Raich and Potter, 1995), which is more than 10 times the CO₂ released from fossil fuel combustion (Raich and Schlesinger, 1992; Schlesinger and Andrews, 2000; Raich and Tufekcioglu, 2000).

The production of CO₂ by soils is dependent to a large extent on microbial decomposition of soil organic matter which, like other chemical and biochemical reactions, is temperature and moisture dependant (Davidson and Janssens, 2006). The total organic matter in soils is a function of input from leaf and detritus material and output mainly as CO₂ efflux from the soil surface, though methane efflux and hydrological leaching of dissolved and particulate carbon compounds are also relevant (Davidson and Janssens, 2006). Decomposition of plant detritus in the litter layers is to an extent controlled by climate functions and substrate decomposition indices such as carbon-to-nitrogen ratios and lignin content (Meentemeyer 1978; Melillo 1982). Many attempts have been made with partial success to measure the three carbon pools, i.e. labile, recalcitrant and decomposed, in mineral soils through physical and chemical fractionation (Trumbore et al., 1996; Six, 2002), but these pools have however have remained as expressions of simplified models (Davidson and Janssens, 2006). However, multi-pool soil carbon models that simulate changes in soil

carbon stocks are preferred over models treating soil carbon as a single homogenous pool (Trumbore 2000; Powlson 2005).

1.2. Biophysical factors affecting soil respiration

Soil respiration is an integration of several ecosystem processes (Janssens and Pilegaard, 2003) with many factors reported to influence rates of soil CO₂ efflux. These include temperature (Singh and Gupta, 1977; Schleser 1982; Peterjohn et al., 1994; Kirschbaum 1996; Winkler et al., 1996), soil moisture (Howard and Howard, 1979; Singh and Gupta, 1977; Davidson et al., 1998), root biomass, litter inputs, microbial and soil nitrogen concentrations (Boone et al., 1998; Buchmann 2000; Fang and Moncrieff, 2001), vegetation and substrate quality (Tewary et al., 1982; Raich and Schlesinger, 1992), net ecosystem productivity (Schlesinger 1977; Raich and Potter, 1995), relative allocation of above- and below-ground net primary production (Boone et al., 1998), population and community dynamics of the above-ground vegetation and below-ground flora and fauna (Raich and Schlesinger, 1992) and land-use including disturbances such as fire (Ewel et al., 1987; Gordon et al., 1987; Weber 1990). Despite all these factors, studies have shown consistent positive relationships between soil respiration and temperature (Singh and Gupta, 1977; Reich and Schlesinger, 1992) with temperature often the best single predictor of soil respiration at any specific location (Singh and Gupta, 1977; Raich and Schlesinger, 1992), though there is no consensus on the form of the relationship (Lloyd and Taylor, 1994).

Although positive relationships have been reported between soil respiration and temperature at many sites (Lloyd and Taylor, 1994), the relationships are often weak or even negative when soil moisture is limiting (Bunnell et al., 1977). Such negative correlations between soil respiration and soil temperature have been observed in Mediterranean climate zones (Carlyle and Than, 1988, Luo et al., 1996, Wang et al., 1999, Ma et al., 2004), and in other areas where soil temperature increase coincides with drier soil conditions (Zak et al., 1999). Therefore, a sound estimation of soil respiration as a function of soil temperature and water content is crucial to the understanding of global climate change (Herbst et al., 2008). Inclusion of precipitation in soil respiration models does increase their predictive power (Mielnik and Dugas, 2000; Raich and Schlesinger, 1992), particularly in arid ecosystems (Tingley et al., 2006) where soil respiration often correlates significantly with both mean annual air temperature and precipitation and their interaction (Frank et al., 2002; Raich and Schlesinger, 1992). The controls exerted by temperature and moisture on soil respiration usually dominate (Raich and Potter, 1995) over other biotic and abiotic factors that contribute to soil CO₂ production (Rout and Gupta, 1989). In the absence of water stress, variation in soil temperature accounts for most of the seasonal and diurnal variation in soil CO₂ efflux, whereas in cases where water stress frequently occurs, soil CO₂ production can only be

correlated with soil moisture content (Rout and Gupta, 1989). Therefore, CO₂ release from the soil usually responds best to either temperature or moisture whichever is limiting at the time of measurement (Schlentner and Van Cleve, 1985).

1.3. Soil respiration models

The development of soil respiration models have assisted in understanding the regulation of soil respiration by influencing environmental factors and in quantifying the contribution of soil respiration to the global carbon budget (Ma et al., 2005). These models are of particular importance in examining how ecosystems may respond to changes in temperature, atmospheric CO₂, and precipitation (Zhou et al., 2008). Accurate modeling of soil respiration also plays a major role in the global carbon cycle, since models that are validated for present conditions may be used to predict soil CO₂ efflux under future boundary conditions, such as increased temperatures or elevated CO₂ levels (Herbst et al., 2008). Various modelling approaches have been applied to explain aspects of the global carbon cycle and to predict future soil respiration changes (Parton et al., 1998; Cramer et al., 2001). Most soil respiration models are based on empirical relationships between soil respiration, soil temperature (Lloyd and Taylor, 1994; Knapp et al., 1998; Fang and Moncrieff, 2001) and soil water content (Davidson et al., 2000) and their interaction (Oberbauer et al., 1992; Tang et al., 2005).

Theoretically-based respiration models propose that soil CO₂ efflux is fundamentally a cellular process and borrow a central principle from enzyme kinetics, namely the relationship between enzyme activity and temperature (Laidler 1997). Soil respiration increases with increasing temperature, and this relationship is usually described with exponential equations (Lloyd and Taylor, 1994). Soil temperature is the most important factor regulating soil respiration and also the most intensely studied factor (Lin et al., 1999, Winkler et al., 1996; Luo et al., 2001; Carlyle and Than, 1988). A temperature based respiration model for northern USA semi-arid grasslands reported differences between observed and predicted soil fluxes averaging only 1.5% (Frank et al., 2002). However, various models for soil and ecosystem respiration as functions of temperature have been proposed but no academic consensus exists (Lloyd and Taylor, 1994). Measured increases in soil respiration for every 10°C increase in temperature, designated Q₁₀, range from 1.3 to 5.6 (Raich and Schlesinger, 1992; Peterjohn et al., 1993; Simmons et al., 1996) with a Q₁₀ value of 2.0, a doubling of soil respiration for each 10°C rise in temperature, assumed for predictions of climate change. However, this value does not hold at high temperatures due to enzyme deactivation and acclimation of soil respiration to warming (Luo et al., 2001) with Q₁₀ also varying with the depth of the active soil layer (Swanson and Flanagan, 2001; Kirschbaum 1996). In fact, some studies even question the exponential relationship between soil respiration and

temperature (Liski et al., 1999; Johnson et al., 2000; Thornley and Cannell, 2001), though a wealth of data from soils and ecosystems around the globe does suggest otherwise (Singh and Gupta, 1977; Raich and Schlesinger, 1992).

Relationships between soil CO₂ efflux and moisture are often described by quadratic equations (Bunnell et al., 1977; Linn et al., 1984; Mielenik and Dugas, 2000), though linear, exponential and hyperbolic equations have also been used to describe soil respiration-moisture relationships (Norman et al., 1992; Davidson 1998; Liu et al., 2002; Schlentner and Van Cleve, 1985; Carlyle and Than, 1988). There also exists a strong interaction between soil temperature and soil moisture on the rate of soil respiration which is insensitive to soil moisture at temperatures below 5°C but relatively responsive to soil moisture at temperatures above 10°C (Carlyle and Than, 1988). A general soil respiration model combining soil temperature and soil moisture, designated GRESP (Bunnell and Tait, 1974), has been applied successfully to tundra, boreal forest and temperate bog ecosystems (Heal 1979). It has limitations in that it assumes that respiration equals zero at 0°C, that the relationship between soil respiration and temperature is exponential without an upper limit, and that Q₁₀ is constant. Variations of the GRESP model have been proposed, such as the BRESP model which adds an upper and lower limit of the response of soil respiration to temperature (Schlentner and Van Cleve, 1985) and the FRESP model which incorporates a Q₁₀ dependency on substrate moisture so that it can be applied to very dry conditions (Carlyle and Than, 1988).

Existing models of soil respiration can be grouped in two categories that differ in temporal scale and methodology. Models like SOILCO₂ (Šimůnek and Suarez, 1993) and those of Cook et al. (1998) and Pumpanen et al. (2003) were developed to estimate soil CO₂ efflux at the scale of hours or days. These models focus on a physically based description of CO₂ transport in the soil. Typically, these models treat the CO₂ production in a simplified way by using an optimum respiration rate as a source term constant in time and/or space (Šimůnek and Suarez, 1993; Pumpanen et al., 2003). On the other hand, carbon turnover models like RothC (Coleman and Jenkinson, 2005), CENTURY (Parton et al., 1994) and CANDY (Franko et al., 1997) usually operate at the temporal scale of months to decades using pool concepts to account for microbiological carbon decomposition (Smith et al., 1997). RothC, like all other carbon turnover models, assumes that CO₂ production by microbial decomposition is immediately transferred to the atmosphere. Furthermore, carbon turnover models are mostly bulk models based on a conceptual approach (Smith et al., 1997; Molina and Smith, 1998). Although these models account for the influence of abiotic factors, soil temperature and soil water content on carbon decomposition (Smith et al., 2003), they do not resolve these variables over the depth of a soil profile. Usually, soil organic matter is partitioned into at least two pools or compartments, each characterized by different

decomposition rate constants. Typically, models in this category lack a feedback mechanism between local CO₂ concentration in the soil profile and microbial CO₂ production from carbon decomposition, though some CO₂ transport models of the first category also neglect this (Suwa et al., 2004; Hashimoto and Komatsu, 2006). The availability of combined CO₂ transport and carbon turnover models is still limited. Currently, there are three models that use a pool concept of carbon turnover in combination with a CO₂ transport module. One is PATCIS (Fang and Moncrieff, 1999), which applies a two-pool carbon concept but is focused on forest ecosystems, and requires soil water content and temperature as input. Another is PASTIS (Cannavo et al., 2006), which applies a combined C and N biotransformation module (Garnier et al., 2003). The third is the model of Jassal et al. (2004), which applies a two-pool carbon turnover concept with a CO₂ transport model similar to the model of Šimůnek and Suarez (1993). More recently, Herbst et al. (2008) coupled a model of water flux, heat and CO₂ transport (SOILCO₂, Šimůnek and Suarez, 1993) with the pool concept of a well-known and state-of-the-art carbon turnover model (RothC-26.3, Coleman and Jenkinson, 2005) to allow for a closed soil carbon balancing and a holistic description of soil carbon cycling and respiration.

Existing respiration models which include soil temperature (Fang et al., 1998; Janssens and Pilegaard, 2003), soil moisture (Davidson et al., 2000; Epron et al., 2004), their interactions (Tufekcioglu et al., 2001; Lee et al., 2002; Tang and Baldocchi, 2005), soil CO₂ diffusion coefficients and organic matter pool decomposition rates (Herbst et al., 2008) as parameter inputs to simulate large-scale temporal variability in soil respiration (Han et al., 2007) are limited. This is because they do not incorporate other bio-physical processes that directly or indirectly affect soil respiration (Davidson et al., 2006). These include photosynthesis, root and microbial respiration, soil physical properties and litter which regulate physical CO₂ diffusion processes (Bunnell et al., 1977; Cook and Orchard, 1983; Jia and Zhou, 2008) that differ across ecosystems (Ma et al., 2005). Broader-spectrum soil respiration models, which include interacting meteorological (water and temperature), soil nutrient and biophysical factors, are required to accurately evaluate soil respiration in different vegetation/terrestrial ecosystems at different temporal and spatial scales, and in more accurately predicting responses to climate change (Jia and Zhou, 2008). Some empirical models of carbon exchange do include factors, such as leaf area index in addition to air temperature and precipitation (Norman et al., 1992; Raich and Potter, 1995) and other more recent models as many relevant bio-physical factors as feasible to obtain a more precise parameterization, though most remain valid only for a limited number of ecosystems (Thornley and Cannell, 1997; Grant et al., 2003; Reichstein et al., 2003).

1.4. Effects of climate change on soil respiration and elemental dynamics

1.4.1. Temperature changes

Rising atmospheric CO₂ concentration due to land-use change and fossil fuel combustion has resulted in an increase in the global mean surface temperature by 0.76°C in the past 150 years and is predicted to increase by 1.5 to 6.4°C in the next 50 to 100 years (IPCC, 1996; IPCC, 2007). Temperature substantially impacts almost all aspects of terrestrial carbon (Luo 2007) and elevated global surface temperatures are likely to enhance carbon fluxes potentially feeding back to a build-up of atmospheric CO₂ concentration and climate dynamics (Schimel et al., 1996; Rustad et al., 2001; Luo et al., 2001; Luo 2007; Lellei-Kovács et al., 2008).

Climate warming influence on ecosystem and global carbon cycling is primarily through two major carbon fluxes, namely net primary production and heterotrophic respiration (Wan et al., 2005). The balance of these two determines whether ecosystems will act as carbon sources or sinks with climate change (Wan et al., 2005). Since temperature affects almost all chemical and biological processes (Wan et al., 2005), climate warming may directly influence carbon processes in terrestrial ecosystems through changes in plant photosynthesis, growth and soil respiration (Shaver 2000).

A variety of temperature-manipulation experiments around the world using electrical heating cables, vented and passively heated open-top field chambers and overhead lamps (Rustad et al., 2001; Zhou et al., 2006) have shown that soil respiration generally increases with warmer temperatures in relatively wet soils (Peterjohn et al., 1994; McHale et al., 1998). For example, Rustad et al. (2001) showed that experimental soil warming in the range 0.3 to 6.0°C above ambient, significantly increased soil respiration rates by 20%. Climatically induced changes in soil respiration far exceed the quantity of CO₂ released through combustion of fossil fuels (Jenkinson et al., 1992) and as a consequence may exacerbate or mitigate atmospheric increases of CO₂ with consequent feedbacks to climate change (Rustad et al., 2000; Schlesinger and Andrews, 2000). However, responses to experimental warming of other soil processes are more variable. For example, CH₄ production and oxidation, nitrogen cycling rates and losses, net carbon flux and plant productivity either increase, decrease, or remain unchanged with temperature and moisture variation (Van Cleve et al., 1990; Joslin and Wolfe, 1993; Peterjohn et al., 1994; Hobbie 1996; Lukewille and Wright, 1997; McHale et al., 1998).

Climate warming may also indirectly influence soil carbon dynamics by increasing nitrogen mineralization (Rustad et al., 2001). This in turn alters ecosystem biological diversity and rates and pathways of nitrogen cycling and loss (Tilman 1987; Barendse et al., 1993; Aber et al., 1995), by reducing soil water content through an enhancement of plant growth (Harte et al., 1995; Wan et al., 2002) and by shifting species composition and community

structure (Harte and Shaw, 1995; Shaver 2000). This affects soil respiration rates and release of carbon dioxide into the atmosphere (Schimel et al., 1995).

Nitrogen as well as phosphorus have long been recognized as limiting factors for plant growth and net primary productivity (Vitousek and Howarth, 1991; Luo 2006) and may play a critical role in regulating terrestrial carbon sequestration change (Wan et al., 2005). Increased soil nitrogen and phosphorus mineralization induced by climate warming may enhance primary productivity resulting in the effective transfer of these essential nutrients from the soil to plant biomass pools (Rastetter et al., 1997). In fact, several studies have shown that under adequate soil moisture conditions, experimental warming significantly increases nitrogen mineralization (Van Cleve et al., 1990; MacDonald et al., 1995; Hobbie 1996) in the upper organic soil horizon by up to 46% (Rustad et al., 2001) and mean above ground plant productivity (Jonasson et al., 1996) by up to 19%. Increased above ground plant productivity leads to an increase in soil carbon, since as much as half of the soil carbon fixed during photosynthesis (Högberg et al., 2001; Steinmann et al., 2004) is translocated from above- to below-ground plant parts. However, where N is non-limiting, further climate warming induced increases may exceed the ability of the ecosystem to assimilate them (Aber et al., 1995) and lead to saturation. This may potentially exacerbate global warming through reduced net ecosystem carbon sequestration resulting from diminished vegetation cover effected by the saturation, and the increased gaseous loss of oxides of nitrogen, such as NO and N₂O (Vitousek et al., 1997) which contribute to anthropogenic enhancement of the greenhouse effect (Albritton et al., 1995). Nitrous oxides also form important precursors of acid rain and photochemical smog that can be transported over long distances by wind (Chameides et al., 1994).

While mineralization and immobilization dynamics strongly regulate the availability and turnover of soil nitrogen (Binkley and Hart, 1989; Davidson et al., 1992; Stark and Hart, 1997), the dynamics of soil phosphorus are driven by competing mechanisms of adsorption/precipitation interactions, microbial assimilation and release, and extracellular enzyme activity (Cross and Schlesinger, 1995; Sanyal and De Datta, 1991; Stewart and Tiessen, 1987; Walbridge et al., 1991) with weathering, leaching and immobilization interacting to control phosphorus availability over the long term (Walker and Syers, 1976; Crews et al., 1995). Increased nitrogen inputs may also decrease phosphorus availability, measured as plant uptake (Salette and Huché, 1991; Duru et al., 1997) or soil extractable pools (Emmett et al., 1995; Gundersen 1998), with nitrogen fixers also altering soil properties by decreasing soil pH (Binkley and Sollins, 1990).

1.4.2. Precipitation changes

Changes in the amount and intensity of precipitation in most regions of the earth are also expected to accompany climate warming (IPCC, 2001). In mid and high latitudes of the northern hemisphere, precipitation increases of 7-12% already occurred during the 20th century (Borken et al., 2006). Further intensification of the hydrological cycle is expected to increase not only the frequency of wet spells and severe droughts but also change the land area of dry and wet ecosystems (IPCC, 2001). It is, however, unclear how fluxes and storage of carbon in terrestrial ecosystems will respond to extreme changes in precipitation (Borken et al., 2006). Soil moisture may limit or inhibit microbial decay of soil organic matter at high and low water contents, whereas root and microbial respiration within the rhizosphere may be less affected by low soil water contents, because many plants may compensate for soil water deficit in surface soils by water uptake from wetter, deeper soil depths (Borken et al., 2006).

Many laboratory studies have shown that drying of soils can limit heterotrophic respiration when water potential falls below a certain threshold (Cook and Orchard, 1983; Skopp et al., 1990). This threshold may vary from soil to soil and within the soil profile as soil organisms are differently adapted to water stress (Borken et al., 2006). Fungi for example are generally better adapted to water stress than bacteria (Swift et al., 1979). Some soil organisms may survive during dry periods in the form of cysts, capsules or spores, an important factor in top soils where frequent drying and wetting may occur (Borken et al., 2006), and promptly respond to wetting events within a few seconds (Borken et al., 2003). This is evident from the large peaks of gaseous emissions (mainly CO₂ and NO) that follow sudden changes from dry to wet phases in arid and semi-arid regions (Borken et al., 2003; Otter and Scholes, 2005).

A major difficulty in studying the effects of soil water content on soil respiration is that precipitation, temperature and evapo-transpiration often covary, and this makes it difficult to separate the effects of soil moisture and temperature on soil respiration (Davidson et al., 1998), since both have been identified as the main causes of variations in soil CO₂ efflux (Raich and Schlesinger, 1992; Schlentner and Van Cleve, 1985). Studies on soil moisture-CO₂ efflux relationships have been based on observations of both seasonal (Luo et al., 1996; Mielnick and Dugas, 2000) and spatial (Davidson et al., 1998) variations in soil water content. Although such studies were conducted in natural ecosystems without disturbing soil structure and plant growth, the observed relationships between soil moisture and CO₂ efflux were mostly confounded by other environmental factors due to considerable seasonal and spatial variations in soil temperature, root and microbial activities (Liu et al., 2002). Also, the effects of soil moisture on CO₂ efflux have been examined by artificially excluding precipitation in experimental micro ecosystems (Borken et al., 2006), but such studies are

often limited by corresponding changes in soil temperature and other biological and environmental conditions (Liu et al., 2002).

There also exist strong correlations between soil carbon and climate (Kirschbaum 1996). Various extensive analysis of soil carbon (Post et al., 1982, 1985; Jenny 1980) have shown that soil organic carbon is positively correlated with precipitation and negatively correlated with temperature for any given amount of precipitation. Seemingly, therefore, soil organic carbon content should decrease with climate warming (Shaver et al., 1992). Incorporation of this principle in soil organic matter models showed that future temperature increase could lead to the release of large quantities of carbon from the world's soils, (Schimel et al., 1990; Jenkinson et al., 1991; Thornley et al., 1991; Kirschbaum, 1993). Conversely, a similar analysis showed no loss of carbon with increasing temperature (Gifford 1992). Nevertheless, the general consensus is that elevated temperatures will lead to increases in both net primary productivity which provides the input to soil organic carbon, and the rate of soil organic matter decomposition which determines its loss (Kirschbaum 1996).

1.5. References

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Chapter 2: Study rationale, sites, objectives and thesis structure

2.1. Study rationale

The focus on carbon fluxes has mainly been on tropical ecosystems due to their dominant contribution to global carbon emission budgets. At the other end of the scale are arid and semi-arid environments which have long periods of no rainfall when microbial activity is low or non-existent. Global models indicate that carbon and other biogenic emissions from arid and semi-arid ecosystems are insignificant and the few carbon and nitrogen emission data available for these ecosystems indicate that emissions are much lower than in other ecosystems (Otter and Scholes, 2005). However, more important is how arid and semi-arid ecosystems will respond to environmental change. The sudden changes from dry to wet phases in arid and semi-arid regions makes them unique and potentially important, since the accumulation of nutrients in soils during the dry phase results in huge gaseous emissions during wet phases, which for NO_x has been reported a factor of 10 to 100 times higher than its dry season flux (Otter and Scholes, 2005). Although this gaseous pulsing after rainfall is considered insignificant at the global scale, regional studies suggest that pulsing events are extremely important for regional atmospheric chemistry (Otter and Scholes, 2005).

Apart from rainfall, which is a known limiting resource in arid regions (Kidron 2000), supplementary precipitation sources such as fog and dew, estimated to contribute up to 34% of the total hydrological input in some semi-arid regions (Dawson 1998), are crucial in understanding soil carbon fluxes and nutrient cycling in arid regions (Wilske et al., 2008). However, little is known about the effects of these supplementary precipitation sources on soil respiration processes (Jacobs et al., 2002). From a theoretical standpoint, dew amounts can reach up to 1.0 mm per night (Jacobs et al., 1990), while fog water input through droplet interception can reach tens of millimeters per night in some coastal ecosystems (Dawson 1998). Variation in soil surface wetting by dew and fog at a landscape scale is likely to result in variation in soil moisture content and nutrient supply and consequent soil respiration rates. This caused by nutrient input within this precipitation (Kulshrestha et al., 2005) and effects of soil moisture on soil microbial activity and nutrient cycling (Biederbeck 1977).

2.2. Study area

The study area was the succulent karoo biome, a semi-arid winter rainfall region in South Africa (Rutherford and Westfall, 1986) ranked among 34 global biodiversity hot spots (Myers et al., 2000; Mittermeier et al., 2000). The biome has the greatest botanical diversity

and the most abundant succulent vegetation of any arid region globally (Odendaal and Suich, 2007). It occupies an area of 112 000 km² on the arid fringes of the Cape Floristic Region and an area of 107,200 square kilometres along the western coastal regions of South Africa and Namibia including virtually all of the Richtersveld (Desmet et al., 1999). Globally, the succulent karoo biome is only comparable to four other geographically remote Mediterranean-climate regions, namely California in the western USA, central Chile, the European Mediterranean basin and Western Australia (Cowling et al., 1996). However, neither of these four regions is dominated by dwarf leaf-succulent shrubs making the succulent karoo unusual among winter-rainfall deserts (Mucina et al., 2006). Despite its significant reservoir of biodiversity, the natural vegetation in the succulent karoo is threatened by livestock grazing which is the main form of land use (Odendaal and Suich, 2007). This constitutes the greatest threat to biodiversity in the region, since it is incompatible with the maintenance of biodiversity and ecosystem processes (Desmet et al., 1999). Other forms of land use that threaten biodiversity in the region include mining, agriculture and illegal collection of succulents. These activities are likely to reduce plant biodiversity in the area which currently comprises 1,940 endemic plant species and 67 endemic plant genera (Desmet et al., 1999).



2.3. Study sites

Three study sites were selected, namely Quaggaskop situated in the southern Knersvlakte bioregion and Numees and Koeroegapvlakte situated in the northern Richtersveld bioregion of the succulent karoo biome.

The Quaggaskop site (31° 24.6' S, 18° 37.8' E) situated at an elevation of ±160 m, 20km north of north of the town of Vanrhynsdorp, has a mean annual precipitation of 145 mm and mean daily maximum air temperature of 25.7°C determined from the nearby Vredendal weather station (Climate of South Africa, 1986). Large parts of the Knersvlakte, an acknowledged centre of diversity and endemism (Hilton-Taylor 1994, 1996), are covered by quartz-gravel fields, an extra-zonal special habitat, which houses a globally unique specialized flora where specialized dwarf succulents dominate (Schmiedel and Jürgens, 1999; Schmiedel 2001, 2002). Inter-dispersed among the quartz-gravel fields are areas devoid of quartz covered with shale, phyllite and limestone derived substrates of the Nama Group (Schmiedel and Jurgens 1999) where larger succulent shrubs dominate (Figure 2.1).

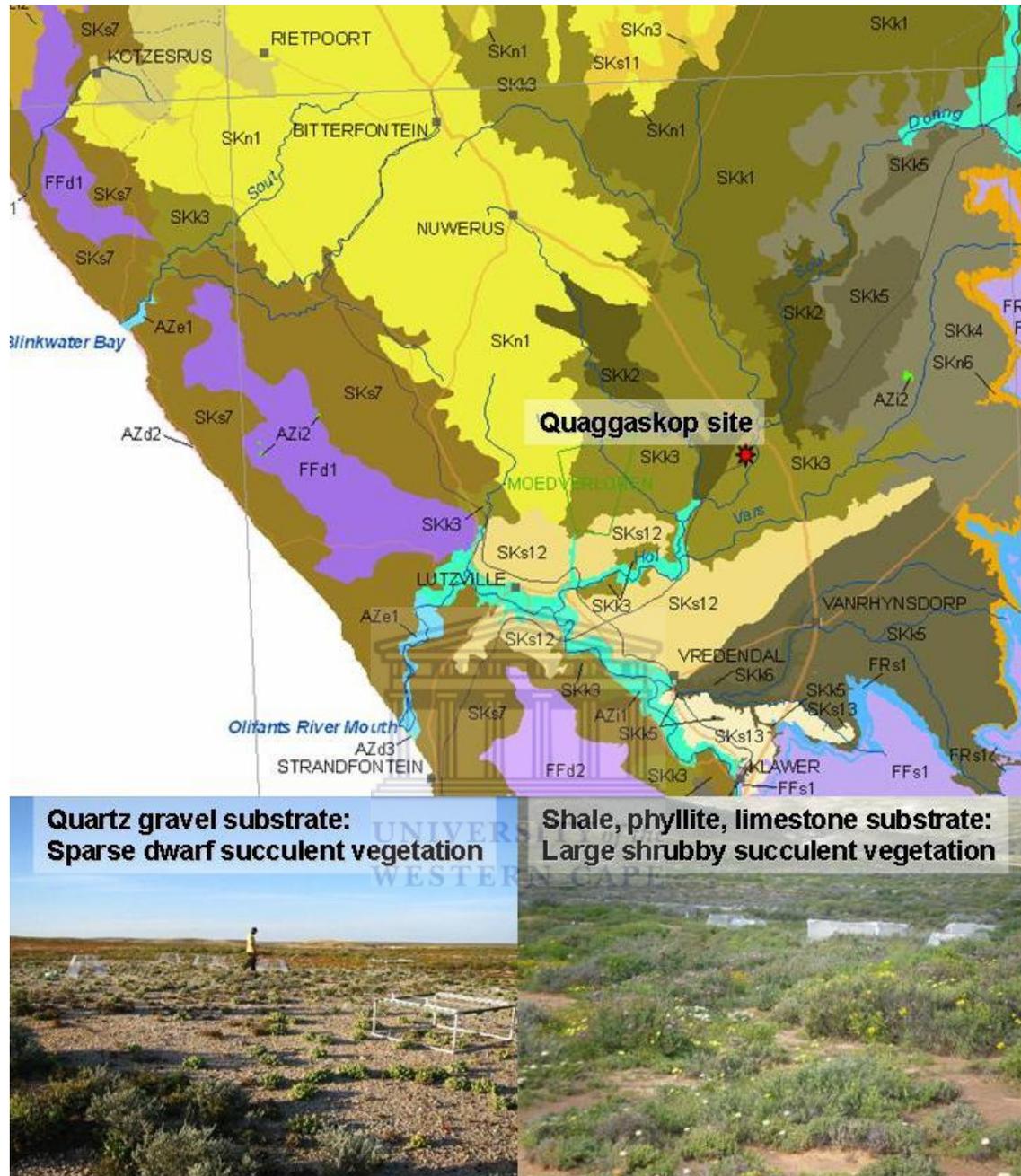
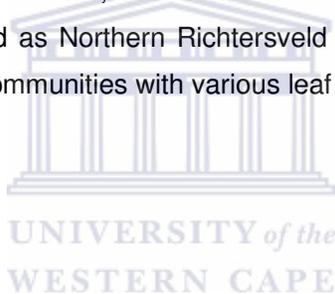


Figure 2.1. Location, typical topography and vegetation of the Quaggaskop experimental site

The Numees site (28° 18' 07.6" S, 16° 57' 50.4" E) is positioned approximately 12 km south-east of the Orange River at an altitude of 377 m (Figure 2.2). Maximum daily summer temperatures reach 50°C with a predominantly winter rainfall averaging 70 mm annum⁻¹ supplemented by coastal fogs occurring 40–50 days annum⁻¹ (Jürgens et al., 1999). The topography is highly diverse with steep slopes in the north and north-east with the remaining areas comprising predominantly hilly structures and dissected plains in allochthon unsorted substrates. Soils constitute meta-sediments of the Gariiep Supergroup which include quartzite, limestone and dolomite. The vegetation type is classified as Central Richtersveld Mountain Shrubland (Mucina et al., 2006) comprising diverse dwarf shrub communities with many leaf succulent species (Jürgens et al., 1999; Gotzmann 2002).

The Koeroegapvlakte site (28° 14' 08.4" S, 17° 01' 32.4" E) is located in the north bounding sinuosity of the Orange River at an altitude of 635 m (Figure 2.2). The mainly winter precipitation varies between 50-100 mm annum⁻¹. The topography of the typical inner mountain basin comprises an alluvial plain with a mean inclination of 5%. Soils are of high salinity and consist of cenozoic alluvium, aeolian sand and calcrete layers (Petersen 2008). The vegetation type is classified as Northern Richtersveld Scorpionstailveld (Mucina et al., 2006) comprising dwarf shrub communities with various leaf succulent species.



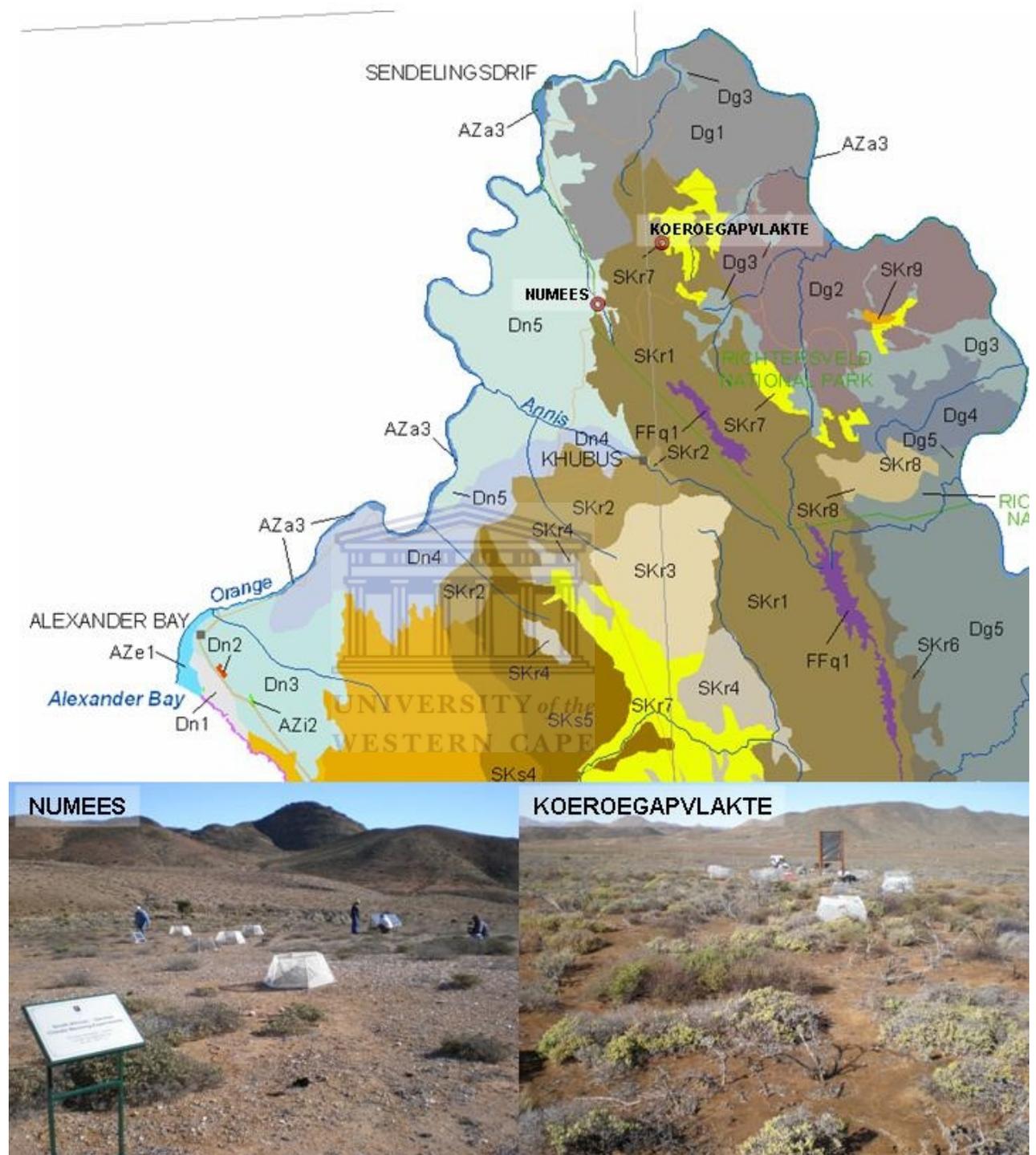


Figure 2.2. Location, typical topography and vegetation of the Numees and Koeroegapvlakte experimental sites

2.4. Study objectives

The main objectives of this study were to measure responses of soil CO₂ efflux and key soil elemental concentrations to changes in temperature and precipitation consistent with future climate change scenarios in an arid South African ecosystem and incorporate these in an empirical-based model. The following key questions were addressed:

1. Are soil CO₂ effluxes as small as in those other arid ecosystems and insignificant compared to those in tropical and temperate climate ecosystems
2. How substantial are pulses in soil CO₂ efflux during wet phases relative to total annual CO₂ efflux
3. What is the relative contribution of root respiration to soil CO₂ efflux
4. Are soil CO₂ effluxes correlated with soil organic matter content
5. To what extent will soil CO₂ effluxes and soil N and P concentrations be altered by changes in temperature and precipitation, inclusive of fog and dew, consistent with future climate change scenarios
6. Can soil CO₂ effluxes be predicted as accurately with a generalized theoretically-based soil respiration model as with an empirically-based soil respiration model

2.5. Thesis structure

The thesis comprises five chapters. The first chapter includes a comprehensive review of soil respiration and elemental dynamics and responses to climate change based on 232 independent sources of reference. The second chapter presents the study rationale, provides a description of the study area and sites and lists the main objectives and key questions. The third chapter describes the results obtained from measurements of soil respiration rate conducted in natural and in temperature and precipitation modified micro-environments in five different soil-vegetation units. The fourth chapter determines whether measured soil respiration rates in different soil vegetation units are predicted more accurately with an empirically-based soil respiration model than a generalized theoretically-based soil respiration model. The fifth chapter presents study conclusions and recommendations. Chapters three and four are presented as scientific manuscripts, the literature references and citations presented in accordance with provisions of the Journal of Environmental and Experimental Botany.

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Chapter 3: Effects of experimental warming and precipitation exclusion on CO₂ efflux and elemental content of different soils in an arid South African ecosystem

Abstract

The magnitude of soil CO₂ effluxes in arid South African ecosystems and their responses, as well as those of key limiting nutrients, to soil temperature increases and moisture reductions consistent with future climate change scenarios are unknown. These were examined empirically by measuring soil respiration rates and N and P contents monthly over a 12 month period in natural environments and those artificially manipulated with replicated open-top warming chambers (average 4.1°C increase) and precipitation exclusion chambers (average 30.1% decrease in rainfall, 26.2% decrease in fog and dewfall) distributed over five different soil vegetation units. Measured soil respiration rates were over 3 times less than those reported for temperate and tropical forest ecosystems with 61.5% of the total soil CO₂ efflux contributed by root respiration in moderately vegetated soils. Massive increases (up to 15 times) in soil CO₂ efflux occurred during wet phases, but even these large CO₂ pulses were only comparable in magnitude with soil CO₂ effluxes reported for temperate semi-arid grasslands. There was considerable intra-annual and inter-site variability in the magnitude and direction of soil respiration and N and P responses to elevated temperatures and reduced precipitation levels with poor correspondence evident between soil CO₂ efflux and soil organic matter content. Soil CO₂ effluxes declined in response to precipitation exclusion by 7.1% over all sites and increased in response to warming by 42.1% over all sites. The large increase in response to warming was assisted by a 7.5% enhancement in soil moisture content due to precipitation interception by the chamber walls and its channelling to the soil surface. Relatively smaller respiration increases in response to warming occurred in moderately vegetated soils, these attributed to soil thermal insulation by the plant canopy cover. Soil P and N contents increased in response to warming by 11.3% and 13.3% respectively over all sites, with soil P declining in response to precipitation exclusion by 5.8% over all sites and soil N increasing in response to precipitation exclusion over all sites by 5.8%.

3.1. Introduction

Atmospheric concentrations of green house gases such as carbon dioxide (CO₂), methane (CH₄) and nitrous oxide (NO₂) due to human activities since the industrial revolution have led to an increase in the global mean surface temperature by 0.76°C in the past 150 years, and this is expected to increase by 1.5 to 6.4°C in the next 50 to 100 years (IPCC, 1996). These temperature increases are likely to impact on the amount, intensity and frequency of precipitation as well as evapotranspiration in most regions of the earth (IPCC, 2001). Temperature and moisture are known to regulate a wide range of terrestrial biogeochemical process, including soil respiration (Raich and Schlesinger, 1992), litter decomposition (Hobbie 1996), N mineralization and nitrification (MacDonald et al., 1995), denitrification (Malhi et al., 1990), CH₄ emission (Crill 1991), fine root dynamics (Gill and Jackson, 2000), plant productivity (Warren-Wilson 1957), and plant nutrient uptake (BassiriRad 2000). Future climate change is expected to increase not only the frequency of severe droughts and wet spells but also to change the land area of dry and wet ecosystems (IPCC, 2001). It is however not clear how soil CO₂ fluxes and nutrient storage in terrestrial ecosystems are expected to respond (Borken et al., 2006).

Being a major contributor to atmospheric CO₂, soil respiration is a major component of the global carbon budget (Schimel 1995; Raich and Tufekcioglu, 2000). Its high percentages in the global carbon budget (Han et al., 2007) means that relatively small climatic-induced changes in soil respiration would have large effects on atmospheric CO₂ concentrations and the global carbon budget with potential feedbacks to climate change (Reichstein et al., 2003; Sánchez et al., 2003). For example, a 20% increase in soil respiration has been estimated to contribute 2 to 3 times more CO₂ to the atmosphere than the amounts released per year by combined fuel and land-use changes (Lal et al., 1995).

Many studies have relied on empirical-based models which use soil temperature (Fang et al., 1998; Janssens and Pilegaard, 2003), soil moisture (Davidson et al., 2000 Epron et al., 2004) and their interaction (Tufekcioglu et al., 2001; Lee et al., 2002; Tang and Baldocchi, 2005) to simulate large-scale temporal variability in soil respiration (Han et al., 2007). Besides soil temperature and soil moisture, root biomass, net primary productivity (NPP), litter inputs, microbial populations, root nitrogen concentrations, soil texture, substrate quantity and quality have all been shown to have effects on soil respiration (Boone et al., 1998; Buchmann 2000; Fang and Moncrieff, 2001). Soil respiration is not only a physiological response to soil temperature and soil moisture, but an integration of several ecosystem processes (Janssens and Pilegaard, 2003). Despite this complexity, the significant relationships found between soil respiration, soil temperature and soil moisture in several studies (Schleser 1982; Raich and Schlesinger, 1992) indicates that climate warming together with altered precipitation amounts, as predicted by future African climate change

scenarios (Hulme et al., 2001), is expected to lead to a substantial changes in the amounts of carbon released from soils into the atmosphere (Rustad et al., 2001).

A variety of temperature-manipulation experiments around the world have shown that soil respiration generally increases with warmer temperatures in relatively wet soils (Peterjohn et al., 1994; McHale et al., 1998). For example, Rustad et al. (2001) showed that experimental soil warming in the range 0.3 to 6.0°C above ambient, significantly increased soil respiration rates by 20%. However, many laboratory studies have showed that drying of soils can limit heterotrophic respiration when water potential falls below a certain threshold (Cook and Orchard, 1983 and Skopp et al., 1990). In fact, it is difficult to separate the effects of soil moisture and temperature on soil respiration since precipitation, temperature and evapotranspiration often co-vary (Davidson et al., 1998). Changes in precipitation, evapotranspiration and soil water content have all been shown to affect soil respiration and decomposition (Borken et al., 2006). The response of other ecosystem processes to these climate change-related temperature-moisture variations is more variable. For example, CH₄ production and oxidation, nitrogen cycling rates and losses, net carbon flux and plant productivity either increase, decrease, or remain unchanged with temperature and moisture variation (Van Cleve et al., 1990; Joslin and Wolfe, 1993; Peterjohn et al., 1994; Hobbie 1996; Lukewille and Wright, 1997; McHale et al., 1998).

Soil elemental supply, particularly concentrations of key limiting nutrients, such as nitrogen and phosphorus (Vitousek et al., 1997), and the nature and quantity of soil organic carbon are also likely to be influenced by a future climate change (Rustad et al., 2001). Increased soil nitrogen and phosphorus mineralization induced by climate warming enhance primary productivity resulting in the effective transfer of these essential nutrients from the soil to plant biomass pools (Rastetter et al., 1997). In fact, several studies have showed that under adequate soil moisture conditions, experimental warming significantly increases nitrogen mineralization (Van Cleve et al., 1990; MacDonald et al., 1995; Hobbie 1996) in the upper organic soil horizon by up to 46% (Rustad et al., 2001) and mean above ground plant productivity (Jonasson et al., 1996) by up to 19%. Increased above ground plant productivity leads to an increase in soil carbon, since as much as half of the soil carbon fixed during photosynthesis (Högberg et al., 2001; Steinmann et al., 2004) is translocated from above- to below-ground plant parts. However, where N and P are non-limiting, further climate warming induced increases may exceed the ability of the ecosystem to assimilate them (Aber et al., 1998) and lead to saturation. This may potentially exacerbate global warming through reduced net ecosystem carbon sequestration resulting from diminished vegetation cover effected by the saturation, and the increased gaseous loss of nitrogen as NO and N₂O which are both greenhouse gases (Vitousek et al., 1997).

The focus on carbon fluxes has mainly been on tropical ecosystems due to their dominant contribution to global carbon emission budgets. At the other end of the scale are arid and semi-arid environments which have long periods of no rainfall when microbial activity is low or non-existent. Global models indicate that carbon and other biogenic emissions from arid and semi-arid ecosystems are insignificant and the few carbon and nitrogen emission data available for these ecosystems indicate that emissions are much lower than in other ecosystems (Otter and Scholes, 2005). However, more important is how arid and semi-arid ecosystems will respond to environmental change. The sudden changes from dry to wet phases in arid and semi-arid regions makes them unique and potentially important, since the accumulation of nutrients in soils during the dry phase results in huge gaseous emissions during wet phases for which NO has been reported a factor of 10 to 100 higher than its dry season flux (Otter and Scholes, 2005). Although this gaseous pulsing after rainfall is considered insignificant at the global scale, regional studies suggest that pulsing events are extremely important for regional atmospheric chemistry (Otter and Scholes, 2005). Also, the role of supplementary precipitation sources such as fog and dew, which have been reported to contribute up to 34% of the total hydrological input in some semi-arid regions (Dawson 1998) are crucial in understanding soil carbon fluxes and nutrient cycling in arid regions (Wilske et al., 2008). Indeed, recent lysimeter-based measurements in an arid South African ecosystem have shown that the amount of water contributed to soils by fog and dew over an 8-month recording period comprised 75% of the mean annual rainfall (Matimati 2009). The contribution of fog and dewfall to total hydrological input is also expected to decline with increased night time temperatures accompanying global warming. Consequently, this study examined the effects of experimental warming and reduced precipitation including fog and dew on soil respiration and key limiting soil elements in an arid ecosystem.

3.2. Materials and methods

3.2.1. Study area and sites

The study area was the succulent karoo biome, a semi-arid winter rainfall region in South Africa (Rutherford and Westfall, 1986) ranked among 34 global biodiversity hot spots (Myers et al., 2000; Mittermeier et al., 2004). Within this biome, three study sites were selected, namely Quaggaskop situated in the southern Knersvlakte bioregion and Numees and Koeroegapvlakte situated in the northern Richtersveld bioregion.

Quaggaskop ($31^{\circ} 24.6''$ S / $18^{\circ} 37.8''$ E) at an elevation ± 160 m has a mean annual precipitation of 145 mm and mean daily maximum air temperature of 25.7°C determined from the nearby Vredendal weather station (Climate of South Africa 1986). Large parts of the Knersvlakte, an acknowledged centre of diversity and endemism (Hilton-Taylor 1994, 1996),

are covered by quartz-gravel fields, an extra-zonal special habitat, which houses a globally unique specialized flora where specialized dwarf succulents dominate (Schmiedel and Jürgens, 1999; Schmiedel 2001, 2002). Inter-dispersed among the quartz-gravel fields are areas devoid of quartz covered with shale, phyllite and limestone derived substrates of the Nama Group (Schmiedel and Jurgens, 1999) where larger succulent shrubs dominate.

Numees (28° 18' 07.6" S / 16° 57' 50.4" E) occurs approximately 12 km south-east of the Orange River at an altitude of 377 m. Maximum daily summer temperatures reach 50°C with a predominantly winter rainfall averaging 70 mm per annum supplemented by coastal fogs occurring 40–50 days annum⁻¹ (Jürgens et al., 1999). The topography is highly diverse with steep slopes in the north and north-east with the remaining areas comprising predominantly hilly structures and dissected plains in allochthon unsorted substrates. Soils constitute meta-sediments of the Gariep Supergroup which include quartzite, limestone and dolomite. The vegetation type is classified as Central Richtersveld Mountain Shrubland (Mucina et al., 2006) comprising diverse dwarf shrub communities with many leaf succulent species (Jürgens et al., 1999; Gotzmann 2002).

Koeroegapvlakte (28° 14' 08.4" S / 17° 01' 32.4" E) is located in the north bounding sinuosity of the Orange River at an altitude of 635 m. The mainly winter precipitation varies between 50-100 mm annum⁻¹. The topography of the typical inner mountain basin comprises an alluvial plain with a mean inclination of 5%. Soils are of high salinity and consist of cenozoic alluvium, aeolian sand and calcrete layers (Petersen 2008). The vegetation type is classified as Northern Richtersveld Scorpionstailveld (Mucina et al., 2006) comprising dwarf shrub communities with various leaf succulent species.

3.2.2. Warming and precipitation exclusion treatments

Ambient environments were artificially manipulated (Appendix 1) at each site to simulate elevated temperatures and reduced precipitation amounts anticipated with future climate warming (Hulme et al., 2001). Daytime passive heating of soils was achieved with clear acrylic (transmission down to 280 nm) hexagonal open-top chambers (basal diameters: 120 cm between parallel sides) of 50 cm height. Such open-top chambers have been applied extensively in the International Tundra Experiment (ITEX) organized to investigate how soils and vegetation in arctic tundra and high alpine regions may be affected by global warming (Henry and Molau, 1997), and their efficacy as analogues of climate warming has received biotic validation (Hollister and Weber, 2000). Demarcated plots of equivalent open-top chamber basal dimensions enclosed by 5 cm high steel fencing with a 40cm diameter mesh comprised the controls which represented ambient conditions. Vertical and horizontal precipitation by fog, dew and rainfall was partly excluded from the soils by chambers 1.2 m long x 1.2 m wide x 0.5 m high whose roofs were clad with louvered clear acrylic and whose

sides were clad with 60% light transmitting shade cloth. At all 3 sites, warming, precipitation exclusion and control chambers, replicated three times, were positioned at random in 5 different soil-vegetation units. These included:

1. Soils with sparse vegetation cover overlaid by quartz-gravel substrates (QG-SV)
2. Soils with sparse vegetation cover overlaid by shale, phyllite and limestone derived substrates (SPL-SV)
3. Soils with moderate vegetation cover overlaid with shale, phyllite and limestone derived substrates (SPL-MV)
4. Soils with moderate vegetation cover overlaid with quartzite, limestone and dolomite derived substrates (QLD-MV)
5. Soils with moderate vegetation cover overlaid with cenozoic alluvium, aeolian sand and calcrete derived substrates (ASC-MV)

The first three soil-vegetation units occurred at the Quaggaskop site, the fourth at the Numees site and the fifth at the Koeroegapvlakte site.

3.2.3. Soil respiration

Polyvinyl chloride (PVC) soil collars with an internal diameter of 10 cm and a length of 5cm were installed at the centers of each of the warming, precipitation exclusion and control chambers leaving a 1cm rim extending above the soil surface. Commencing one month after collar installation, two morning and two afternoon measurements of soil respiration rate were taken (Appendix 2) in each chamber with a Li-Cor 8100 infrared gas analyzer (Li-Cor BioSciences, Lincoln, Nebraska, USA). Measured soil respiration rates as $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ were converted to $\text{g C m}^{-2} \text{ d}^{-1}$. At the Quaggaskop site, soil respiration measurements were performed at monthly intervals spanning the 12 month period from July 2007 to June 2008. At the remote Numees and Koeroegapvlakte sites, soil respiration measurements were restricted to the early spring month of September 2007 and mid winter month of July 2008.

3.2.4. Soil environment

Hourly measurements of soil volumetric water contents were obtained with ECH₂O-TE sensors, interfaced with data loggers (EM-50, Decagon Devices Inc. USA), buried 20 mm beneath the soil surface in open-top warming and precipitation exclusion chambers and controls. Simultaneous measurements of soil surface temperature were obtained with thermocouples, shielded from direct solar radiation in perforated plastic tubes, placed on the soil surface (Appendix 3). Fog and dewfall amounts were recorded with leaf wetness resistance sensors located 10 cm above the soil surface and rainfall amounts with tipping bucket gauges. They were all interfaced with miniature data loggers (Watch Dog 450, Spectrum Technologies Inc., Plainfield, Illinois, USA). Measured leaf wetness resistances

(range: 0 to 15 units) were converted to apparent fog and dewfall amounts in mm using a published formula (Musil et al., 2009) and soil volumetric water contents were converted to gravimetric moisture contents by dividing these by measured bulk densities of oven dried soils.

3.2.5. Soil organic and elemental content

Soils for organic and elemental analysis were dried at 30°C in a forced draft oven and sieved to ≤ 2 mm particle size. Approximately 50 g soil sub samples for organic matter assay were weighed, ashed at 400°C in a muffle furnace and reweighed. P concentrations in 5 g soil sub samples were analyzed according to the method of Bray and Kurtz (1945) following extraction of soil soluble P using a Bray-II extract. N concentrations in 5 g soil sub samples were measured with an Auto-Analyser (SP428, Nitrogen Analyser LECO Corporation, USA) following soil combustion as described by Clesceri et al., (1998). Soil organic matter contents were expressed as percent dry mass. Measured N (% N) and P (mg kg^{-1} P) concentrations in the soil samples were expressed uniformly as m mol kg^{-1} dry soil mass.

3.2.5. Statistical analysis

Analyses of variance (Generalized Linear Model) tested the effects of experimental warming and precipitation exclusion in different months and their interactions on measured soil respiration rates, elemental and organic matter contents in each of the 5 different soil and vegetation units. Least squares regressions examined linear relationships and Pearson correlation coefficients tested for correspondence between measured soil respiration rates and other parameters. These were at three different levels of significance, thus $*P \leq 0.05$ for least significance, $**P \leq 0.01$ for moderate significance and, $***P \leq 0.001$ for high significance.

3.3. Results

3.3.1. Warming and precipitation exclusion chamber environments

Maximum daily soil surface temperatures in the open top warming chambers ranged annually between 0.9°C and 8.1°C above ambient with an annual average increase of 4.1°C (Table 3.1). Those in the fog exclusion chambers ranged annually between 2.9°C below ambient and 3.3°C above ambient with an annual average decrease of 0.3°C. Minimum daily soil surface temperatures in the open top warming chambers ranged annually between 2.3°C and 3.7°C above ambient with an annual average increase of 3.0°C (Table 3.1). Similar increases occurred in the precipitation exclusion chambers where minimum daily soil surface

temperatures ranged annually between 2.4°C and 3.5°C above ambient with an annual average increase of 2.9°C.

Measured changes in soil moisture levels in the open top warming and precipitation exclusion chambers were variable. During the wet winter (June to August) period, increased soil moisture levels averaging 16.2% were apparent in the open-top warming chambers and decreased soil moisture levels averaging -18.2% were evident in the precipitation exclusion chambers. However, during the dry summer (December to February) period, increased soil moisture levels of similar magnitude averaging 7.4% in the open top warming chambers and 5.8% in the precipitation exclusion chambers were apparent. On an annual basis, soil moisture levels increased by an average of 7.5% in the open top warming chambers and decreased by an average of -5.4% in the precipitation exclusion chambers (Table 3.1).

Both rainfall and apparent fog and dewfall frequencies and amounts were significantly ($P \leq 0.001$) linearly related to soil gravimetric moisture contents (Figure 3.1). The regression functions describing these linear relationships estimated changes in rainfall and fog and dewfall amounts in the open top warming and precipitation exclusion chambers. Over the wet winter (June to August) period, increased rainfall amounts averaging 26.8% above ambient and fog and dewfall amounts averaging 23.3% above ambient were apparent in the open top warming chambers and decreased rainfall amounts averaging 30.1% below ambient and fog and dewfall amounts averaging 26.2% below ambient were evident in the precipitation exclusion chambers (Table 3.1). However, during the dry summer (December to February) period, both rainfall and fog and dewfall increased by similar average amounts in the open top warming chambers (rainfall 12.2% and fog and dewfall 10.6% above ambient) and precipitation exclusion chambers (rainfall 9.7% and fog and dewfall 8.4% above ambient). On an annual basis, rainfall and fog and dewfall amounts were elevated on average by 12.4% and 10.8% respectively in the open top warming chambers and reduced by 8.9% and 7.8% respectively in the precipitation exclusion chambers (Table 3.1).

3.3.2. Soil respiration rate

3.2.2.1 Effects of artificial warming

Overall soil respiration rates increased significantly ($P \leq 0.05$) with artificial warming in the QG-SV (16.3% increase), SPL-SV (25.4% increase) and ASC-MV (167.5% increase) soil vegetation units (Table 3.2, Figure 3.2). Also, a significant ($P \leq 0.05$) interaction between warming and month on soil respiration rate was observed in the QG-SV soil-vegetation unit (Table 3.2) where the magnitude and direction of soil respiration changes differed between months (Figure 3.2). In this soil vegetation unit, significantly ($P \leq 0.05$) increased soil respiration rates were observed during the warm summer months of December to February (106.7% increase) coinciding with an out of season precipitation event, and a significantly

reduced respiration rate observed during the cold winter month of June (54.2% decrease) which coincided with a reduced precipitation amount (Figure 2).

3.2.2.2 Effects of precipitation exclusion

Overall soil respiration rates decreased significantly ($P \leq 0.05$) with precipitation exclusion in the SPL-SV (25.5% decrease) and SPL-MV (32.0% decrease) soil vegetation units (Table 3.2). The decreased respiration rates were apparent throughout most of the year in the SPL-MV soil vegetation unit and more prominent in the SPL-SV soil vegetation unit from late autumn (May) to early spring (September) months (41.8% decrease) when precipitation levels, and the amounts excluded by the chambers, were high (Table 3.1, Figure 3.2). Also, a significant ($P \leq 0.05$) interaction between precipitation exclusion and month on soil respiration rate was observed in the QG-SV soil-vegetation unit (Table 3.2). In this soil-vegetation unit, significantly ($P \leq 0.05$) increased soil respiration rates (Figure 3.2) were observed only during the warm summer months of January and February (86.7% increase) and the early spring month of September (77.6% increase).

3.2.2.3 Correspondence with soil organic matter content

Soil respiration rates were significantly ($P \leq 0.05$) positively correlated with soil organic matter contents in only two of the five soil vegetation units with a significant negative correlation ($P \leq 0.01$) between soil respiration rate and soil organic matter content also observed in the ASC-MV soil vegetation unit (Table 3.3).

3.3.2. Soil elemental content

3.2.2.1 Effects of artificial warming

Overall soil phosphorus increased significantly ($P \leq 0.05$) with artificial warming in the SPL-SV (40.1% increase), SPL-MV (3.7% increase) and QLD-MV (9.9% increase) soil vegetation units only (Table 3.2, Figure 3.3), the increases of greater magnitude in the sparsely vegetated SPL-SV than the moderately vegetated SPL-MV and QLD-MV units. Also, a significant ($P \leq 0.001$) interaction between warming and month on soil phosphorus was observed in the SPL-SV soil-vegetation unit (Table 3.2). Here, the magnitude of soil phosphorus increases differed between months (Figure 3.3) with the largest increases apparent in April (40.1% increase) and the smallest in October (11.3% increase).

Overall soil nitrogen contents increased significantly ($P \leq 0.001$) with artificial warming (Table 3.2, Figure 3.4) in the SPL-MV soil vegetation unit only (19.1% increase). Also, significant ($P \leq 0.05$) interactions between warming and month on soil nitrogen were observed in all, except the ASC-MV soil-vegetation unit (Table 3.2). In the sparsely

vegetated QG-SV and SPL-SV soils, significant changes in soil N content in response to warming differed throughout the year. For example, in the QG-SV soil vegetation unit significantly, increased soil N contents occurred in March (36.4% increase), April (11.1% increase), June (11.8% increase), July (41.7% increase) and October (22.2% increase) and significantly decreased soil N contents occurred in January (12.5% decrease), February (23.6% decrease), and November (11.8% decrease) while in the SPL-SV soil vegetation unit significantly increased soil N contents occurred in August (7.7% increase) and October (67.7% increase) and significantly decreased soil N contents (Figure 3.4) occurred only in February (16.7% decrease) and May (18.4% decrease). In the moderately vegetated SPL-MV soil-vegetation unit, N levels were significantly increased in all months except October (39.8% decrease) with the increases of greater magnitude in the wetter winter of June (42.9% increase) and July (50.0% increase) than the drier summer months of January (14.8% increase) and February (13.3% increase).

3.2.2.2 Effects of precipitation exclusion

Overall soil phosphorus decreased significantly ($P \leq 0.05$) with precipitation exclusion (Table 3.2, Figure 3.3) in the SPL-SV (11.8% decrease) and SPL-MV (12.7% decrease) soil vegetation units and increased significantly ($P \leq 0.001$) in the QLD-MV soil vegetation unit (13.9% increase). Also, a significant ($P \leq 0.05$) interaction between precipitation exclusion and month on soil phosphorus was observed in the QG-SV soil-vegetation unit only (Table 3.2, Figure 3.3), the magnitude of soil phosphorus changes displaying considerable intra-annual variation, ranging from a 5.8% increase in early spring September to a 27.5% decrease in late spring (November).

Overall soil nitrogen contents increased significantly ($P \leq 0.001$) with precipitation exclusion (Table 3.2, Figure 3.4) in the QG-SV (23.6% increase) and QLD-MV (23.9% increase) soil vegetation units, and declined significantly ($P \leq 0.01$) with precipitation exclusion in SPL-MV (12.5% decrease) soil vegetation unit. Also, significant ($P \leq 0.05$) interactions between precipitation exclusion and month on soil nitrogen were observed in all, except the SPL-SV soil-vegetation unit (Table 3.2). In the sparsely vegetated QG-SV soil vegetation unit, N levels increased significantly ($P \leq 0.05$) in all months except January (0.1% decrease), February (23.6% decrease) and November (11.8% decrease) with the increases of largest magnitude evident in the wetter late autumn and winter months of May to August (40.1% increase). However, in the moderately vegetated SPL-MV soil unit, significantly ($P \leq 0.05$) reduced soil N levels were observed in the drier and warmer spring and summer months of October (47.4% decrease), November (19.9% decrease), January (11.1% decrease), February (26.7% decrease) and March (21.1% decrease). Similarly in the moderately vegetated ASC-MV site, significantly ($P \leq 0.05$) reduced soil N levels were

observed in the drier and warmer September month (18.8% decrease). This contrasted with the significantly ($P \leq 0.05$) increased soil N levels observed in the moderately vegetated QLD-MV soil unit during the drier and warmer September month (57.7% increase).

3.4. Discussion

The recorded mean annual 4.1°C increase in maximum daily soil surface temperature in the open top warming chambers closely approximated the mean annual temperature increase of 4.5°C (means of 7 GCM models) predicted by the SRES A2-high climate sensitivity scenario for the succulent karoo biome towards the end of the century (Hulme et al., 2001). In contrast, maximum daily soil surface temperatures in the precipitation exclusion chambers averaged 0.3°C below ambient which was in the range 0.2°C to 0.4°C reported for canopy precipitation exclusion chambers in a Massachusetts forest (Borken et al., 2006). Estimated average changes in winter rainfall (30.1% decrease) and fog and dewfall (26.2% decrease) in the precipitation exclusion chambers also closely approximated the SRES A2-high climate sensitivity scenario prediction of a 26% reduction in winter (June to August) precipitation for the succulent karoo biome (Hulme et al., 2001). In contrast, increases in both winter rainfall and fog and dewfall averaging 28.8% and 23.3% respectively were apparent in the open top chambers. These increases presumably a consequence of interception of additional rainfall and fog and dewfall by the open-top chamber walls and their channelling to the soil surface (Musil et al., 2009). The average annual 7.5% increase in soil moisture content corresponding with a mean annual 4.1°C soil temperature increase in the open top warming chambers of this study contrasted with a previously reported average 67% reduction in soil moisture content accompanying an average 2.4°C elevation in soil temperature in a global network of soil warming experiments (Rustad et al., 2001).

Measured soil respiration rates in the different soil vegetation units of this study were over 3 orders of magnitude less than those reported for temperate and tropical forest ecosystems (Table 3.4). During wet phases, soil respiration rates displayed massive increases which were up to 15 orders of magnitude greater than those during dry phases (Figure 3.2). However, these large wet phase pulses in soil respiration rate were only comparable in magnitude with those reported for temperate semi-arid grasslands and some bare agricultural soils (Table 3.4). These findings concur that arid ecosystem soils are relatively minor sources of CO₂ emissions (Otter and Scholes, 2005). An average, 61.5% of the total soil CO₂ efflux in moderately vegetated soils was contributed by root respiration, this evident from a comparison of soil respiration rates in the sparsely and moderately vegetated SPL-SV and SPL-MV soil-vegetation units respectively. This percentage was only slightly higher than the reported 53% contribution by root respiration to total soil CO₂ efflux in the Duke forest in USA (Hui and Luo, 2004).

The general pattern of increased soil respiration rates in response to warming and diminished soil respiration rates in response to precipitation exclusion concurred with previously reported soil respiration responses to moisture and temperature variations (Schleser 1982; Raich and Schlesinger, 1992). The observed average 42.1% increase in soil respiration rate over all sites in response to the 4.1°C temperature increase was relatively higher than the reported average 20% increase in soil CO₂ efflux in response to an 0.3 - 0.6°C warming in high tundra, low tundra, grassland, and forest biomes (Rustad et al., 2001) as well as a reported 25.8% increase in soil CO₂ efflux in response to a mid-day temperature increase of 4°C in an Alaskan boreal forest (Bergner et al., 2002). All these findings contrasted with a reported 7 - 15% reduction in soil CO₂ efflux in response to a 1.6°C temperature increase in a semi-arid temperate Pannonian sand forest-steppe (Lellei-Kovács et al., 2008). The observed average 7.1% reduction in soil CO₂ efflux over all sites in response to both rainfall and fog and dewfall exclusion was less than the reported 10 - 30% reduction in soil respiration rate in canopy precipitation exclusion experiments in a Harvard forest (Borken et al., 2006).

Enhanced soil respiration rates in response to warming were observed during both the wetter winter and spring months in the ASC-MV vegetation unit and throughout the year in the SPL-SV vegetation except during early autumn and winter months when levels of precipitation were high and soil moisture levels were close to saturation which are known to inhibit soil respiration (Borken et al., 2006; Wang and Fang, 2008). These enhanced soil respiration rates supported previous experimental studies that overwhelmingly indicate that elevated temperatures result in increased carbon dioxide emissions from soils (Lloyd and Taylor, 1994; Trumbore 1996; Kätterer et al., 1998; Holland et al., 2000). However, they did not entirely concur with reports that such increased carbon dioxide emissions from soils are due largely to microbial decomposition of soil organic matter (Davidson and Janssens, 2006), since measured soil respiration rates were poorly correlated with soil organic matter content with significant positive correlations apparent in only two of the five soil vegetation units. Also, significantly increased soil respiration rates in response to warming were observed in the QG-SV soil-vegetation unit, but these were confined to those warm summer months that coincided with out of season precipitation events. In contrast, decreased soil respiration rates in response to warming were also observed in the QG-SV soil-vegetation unit during those cold winter months that coincided with reduced precipitation levels. These diverse respiration responses to warming reflected the strong interaction between soil temperature and soil moisture in regulating soil respiration rates in arid ecosystems, with respiration rates limited by soil moisture at high temperatures and *vice versa* (Schlentner and Van Cleve, 1985; Davidson et al., 1998). Noteworthy, in this regard was the absence of any significant respiration response to warming in the moderately vegetated SPL-MV soil vegetation unit

and the substantially higher (over 3 orders of magnitude) soil respiration rate in this soil vegetation unit than its sparsely vegetated counterpart (SPL-SV soil vegetation unit) which exhibited consistently reduced soil respiration rates in response to warming. These anomalies can be attributed to soil thermal insulation by the larger plant canopy cover and the added contribution of root respiration to soil microbial respiration in the SPL-MV soil vegetation unit (Frank et al., 2002).

It has been proposed that soil moisture is the most important factor limiting soil respiration in dry ecosystems (Kidron 2000). This proposal supported by the diminished soil respiration rates observed in the precipitation exclusion chambers throughout most of the year in the SPL-MV soil vegetation unit and the proportionately larger decreases in soil respiration rate observed in the precipitation exclusion chambers in the SPL-SV soil-vegetation unit during the late autumn to spring period when precipitation levels, and the amounts excluded by the chambers, were high. These findings concurred with reported reductions in soil respiration rate in canopy precipitation exclusion chambers in a deciduous American forest (Borken et al., 2006), though in another study no net effect on soil respiration rate was observed over a 3-year period in canopy precipitation exclusion chambers in an Amazonian forest, despite a clear treatment effect on N₂O and CH₄ fluxes, and on tree growth and mortality (Davidson et al., 2004). A seeming contradiction to the above-mentioned findings were the elevated soil respiration rates recorded in the precipitation exclusion chambers during the warm summer and early spring months in the QG-SV soil-vegetation unit. One explanation for this ostensible contradiction was a reduced evaporative water loss from the cooler quartz gravel substrates due to their reflective properties (Schmiedel and Jurgens, 1999), a situation which alongside high summer temperatures possibly optimized soil respiration (Rout and Gupta, 1989; Schlentner and Van Cleve, 1985).

Various studies have demonstrated that like soil respiration (Singh and Gupta, 1977; Raich and Schlesinger, 1992) the mobilization and net mineralization of nitrogen and phosphorus in soils is affected by both temperature and moisture (Kowalenko et al., 1978; Kladviko and Keeney, 1987; Malhi et al., 1990; Rustad et al., 2001). Both field and laboratory (Cassman and Munns, 1980) studies have demonstrated that the extent to which temperature affects microbial decomposition and nutrient mineralization is dependent on soil water content (Kowalenko et al., 1978), with a definitive interaction established between temperature and soil water content on net mineralization (Kladviko and Keeney, 1987). In this study, concentrations of both phosphorus and nitrogen in soils were significantly altered by artificial warming and precipitation exclusion but the magnitude and direction of change differed intra-annually and in different soil types. The observed increase in soil phosphorus concentrations in response to warming in the SPL-SV, SPL-MV and QLD-MV soil vegetation

units seemingly complied with a reported increase in extractable phosphorus forms with soil drying (Snyder and Slaton, 2002). This proposal partly supported by the absence of any significant increase in soil phosphorus concentrations in response to warming in the relatively more moist quartz gravel substrates in the QG-SV soil-vegetation unit, which due to their reflective properties are cooler (Schmiedel and Jurgens, 1999) and subject to less evaporative water loss. Also, the relatively smaller increases in soil phosphorus concentrations in response to warming observed in the moderately vegetated SPL-MV soil vegetation unit than in the sparsely vegetated SPL-SV soil vegetation unit possibly also reflected a smaller thermal impact on soil drying induced by the larger vegetation canopy cover as well as phosphorus uptake by plant roots. However, these hypotheses were seemingly rebutted by the generally diminished soil phosphorus concentrations in response to precipitation exclusion observed in the SPL-SV and SPL-MV soil vegetation units but not in the QLD-MV soil vegetation unit where soil phosphorus concentrations also increased in response to precipitation exclusion. Noteworthy, was that the largest percentage reductions in soil phosphorus and nitrogen concentrations in response to precipitation exclusion occurred in both the SPL-SV and SPL-MV soil vegetation units during May when the highest rainfall amounts were recorded. These reduced phosphorus concentrations possibly due to nutrient leaching were exacerbated during periods of high rainfall, as well as to P immobilization (Walker and Syers, 1976; Crews et al., 1995) and N adsorption by moist organic matter, a known sink for nitrogen within terrestrial ecosystems (Compton and Cole, 2001).

Although several studies have shown that increased temperatures stimulate N mobilization (Rustad et al., 2001; Jonasson et al., 1993; Marion et al., 1997) by increasing the rates of microbial decomposition and mineralization (Henry and Molau, 1997), other studies have indicated that both temperature and moisture are important drivers of this mineralization process (Gonclaves and Caryle, 1994). This alongside decomposition of detritus material and root activity, which are also known to stimulate nitrogen mineralization (Paul et al., 2003) may explain the increased soil N concentrations in response to warming observed throughout most of the year in the SPL-MV soil vegetation unit and the reduced N concentrations in response to precipitation exclusion, the largest reductions apparent during those warm spring and summer months with low rainfall amounts. However, the overall 13.3% increase in soil N concentration for all sites in response to a 4.1°C warming observed in this study was less than the average 46% increase in nitrogen mineralization in response to a 0.3 - 0.6°C warming reported for high tundra, low tundra, grassland, and forest biomes (Rustad et al., 2001). This temperature increase also led to an overall increase in soil P concentration of 11.3% for all sites, with precipitation exclusion resulting in an overall 5.8% decrease in soil phosphorus and a similar overall 5.8% increase in soil nitrogen for all sites.

However, there was considerable intra-annual and inter-site variability in soil nitrogen responses to warming and precipitation exclusion, these presumably due to differences in soil temperature, moisture retention and leaching properties and consequent microbial decomposition and mineralization rates.



3.5. References

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Table 3.1. Average changes in soil surface temperatures, soil moisture levels, rainfall and fog and dewfall amounts in open top warming and precipitation exclusion chambers relative to those in the ambient environment. * derived from linear regressions of soil moisture content against rainfall and fog and dewfall amounts

Month	Max daily temp °C		Min daily temp °C		Soil moisture % change		*Rainfall % change		*Fog & Dewfall % change	
	Warm	Prec-Ex	Warm	Prec-Ex	Warm	Prec-Ex	Warm	Prec-Ex	Warm	Prec-Ex
Jan	8.1	-0.5	3.7	3.2	4.5	10.9	7.5	18.0	6.5	15.7
Feb	6.8	-0.2	3.4	2.9	13.6	6.4	22.5	10.6	19.6	19.2
Mar	5.3	-1.2	3.6	3.3	7.6	15.3	12.6	25.3	10.9	22.0
Apr	3.1	-0.9	3.7	3.5	0.7	11.4	1.2	18.9	1.0	16.4
May	1.5	2.6	2.5	2.7	34.9	-38.7	57.8	-64.0	50.2	-55.7
Jun	0.9	3.3	2.8	2.7	30.9	-24.2	51.1	-40.1	44.5	-34.8
Jul	2.2	-0.5	2.6	2.4	-3.1	-14.9	-5.1	-24.7	-4.5	-21.5
Aug	1.7	-0.2	2.3	2.8	20.8	-15.4	34.4	-25.5	29.9	-22.2
Sep	2.4	-1.2	2.6	3.1	-0.2	-2.6	-0.3	-4.3	-0.3	-3.7
Oct	4.3	-2.9	2.7	2.9	-18.4	-7.3	-30.5	-12.1	-26.5	-10.5
Nov	6.1	-1.7	2.9	2.9	-5.1	-4.8	-8.4	-7.9	-7.3	-6.9
Dec	7.1	-0.5	3.0	2.7	4.1	0.2	6.8	-0.3	5.9	0.3
Year	4.1	-0.3	3.0	2.9	7.5	-5.4	12.4	-8.9	10.8	-7.8

Table 3.2. Statistics from an ANOVA (GLM) which tested the effects of artificial warming and precipitation exclusion treatments in different months and their interactions on soil respiration rates and elemental contents in 5 different soil-vegetation units. Variance ratios (F-statistics) presented in bold indicate significance at *P ≤ 0.05, **P ≤ 0.01, ***P ≤ 0.001.

Site/ Soil-Vegetation Unit	Warming			Precipitation exclusion		
	Soil CO ₂ efflux	Soil Phosphorus	Soil Nitrogen	Soil CO ₂ efflux	Soil Phosphorus	Soil Nitrogen
QUAGGASKOP						
QG-SV						
Treatment	F _{1,142} = 3.2	F _{1,142} = 1.2	F _{1,142} = 3.5	F_{1,142} = 4.5*	F _{1,142} = 0.9	F_{1,142} = 46.9***
Month	F_{11,142} = 43.2***	F_{11,142} = 41.7***	F_{11,142} = 26.3***	F_{11,142} = 57.1***	F_{11,142} = 12.7***	F_{11,142} = 26.9***
Treatment x Month	F_{11,142} = 1.9*	F _{11,142} = 0.4	F_{11,142} = 2.0*	F_{11,142} = 2.4*	F_{11,142} = 1.0*	F_{11,142} = 2.8**
SPL-SV						
Treatment	F_{1,135} = 4.8*	F_{1,135} = 72.2***	F _{1,135} = 3.8	F_{1,126} = 5.2*	F_{1,126} = 4.1*	F _{1,126} = 1.7
Month	F_{11,135} = 3.3***	F_{11,135} = 23.5***	F_{11,135} = 10.23***	F_{11,126} = 5.9***	F_{11,126} = 15.0***	F_{11,126} = 8.6***
Treatment x Month	F _{11,135} = 1.3	F_{11,135} = 5.8***	F_{11,135} = 2.3*	F _{11,126} = 1.8	F _{11,126} = 0.78	F _{11,126} = 1.7
SPL-MV						
Treatment	F _{1,143} = 0.1	F_{1,143} = 4.0*	F_{1,143} = 19.5***	F_{1,141} = 19.7***	F_{1,141} = 17.1***	F_{1,141} = 11.2**
Month	F_{11,143} = 22.7***	F_{11,143} = 43.6***	F_{11,143} = 10.6***	F_{11,141} = 30.5***	F_{11,141} = 17.1***	F_{11,141} = 15.4***
Treatment x Month	F _{11,143} = 1.2	F _{11,143} = 1.8	F_{11,143} = 3.8***	F _{11,141} = 1.4	F _{11,141} = 1.2	F_{11,141} = 3.1***
NUMEES						
QLD-MV						
Treatment	F _{1,127} = 0.1	F_{1,127} = 6.1*	F _{1,127} = 0.4	F _{1,84} = 0.1	F_{1,84} = 11.8***	F_{1,84} = 12.3***
Month	F _{1,127} = 0.1	F_{1,127} = 166.6***	F_{1,127} = 29.5***	F _{1,84} = 2.6	F_{1,84} = 50.4***	F_{1,84} = 27.2***
Treatment x Month	F _{1,127} = 0.4	F _{1,127} = 0.3	F_{1,127} = 6.1*	F _{1,84} = 1.0	F _{1,84} = 2.3	F_{1,84} = 6.8*
KOEROEGAPVLAKTE						
ASC-MV						
Treatment	F_{1,97} = 11.1**	F _{1,97} = 2.8	F _{1,97} = 0.4	F _{1,91} = 0.5	F _{1,91} = 0.4	F _{1,91} = 0.6
Month	F _{1,97} = 0.3	F_{1,97} = 43.4***	F _{1,97} = 0.0	F_{1,91} = 38.6***	F_{1,91} = 46.4***	F _{1,91} = 1.0
Treatment x Month	F _{1,97} = 1.8	F _{1,97} = 2.8	F _{1,97} = 1.8	F _{1,91} = 1.0	F _{1,91} = 0.4	F_{1,91} = 7.8**

Table 3.3. Pearson correlation coefficients (r), t -statistics and significance levels for correspondence between measured soil respiration rates and soil organic matter contents in 5 different soil-vegetation units.

Soil-Vegetation Unit	r	t -statistic	Significance level
QUAGGASKOP			
QG-SV	0.094	$t_{1, 213} = 1.379$	$P \geq 0.05$
SLP-SV	0.298	$t_{1, 194} = 4.352$	$P \leq 0.001$
SPL-MV	0.027	$t_{1, 212} = 0.399$	$P \geq 0.05$
NUMEES			
QLD-MV	0.177	$t_{1, 144} = 2.152$	$P \leq 0.05$
KOEROEGAPVLAKTE			
ASC-MV	-0.188	$t_{1, 147} = -2.322$	$P = \leq 0.01$



Table 3. 4. Soil respiration rates reported for different ecosystems compared with those measured in an arid ecosystem in this study

ECOSYSTEM	Soil respiration rate g CO ₂ m ⁻² d ⁻¹	Source
ARCTIC		
Tundra (Sweden)	11.52	Sjögersten & Wookey (2002)
TEMPERATE GRASSLANDS		
Steppe (Mongolia)	0.64 - 7.32	Jia & Zhou. (2008)
Semi arid grassland (Mandan, USA)		Frank et al. (2002)
Non-grazed mixed grass	3.50	
Grazed mixed grass	4.30	
Grazed wheat grass	4.00	
Tall grass prairie (Texas, USA)	3.97	Mielnik & Dugas (2000)
Mixed semi arid steppe & sand forest	0.36 – 6.36	Lellei-Kovács et al. (2008)
TEMPERATE FORESTS		
Siberian Taiga forest	1.56 – 34.30	Sawamoto et al. (2000)
Alaskan Boreal forest	2.41 – 3.25	Bergner et al. (2002)
Mixed conifer forest (Nevada, USA)		Ma et al. (2004)
Open forest canopy	7.95 – 17.88	
Ceanothus dominated patches	3.58 – 11.53	
Duke forest simulated (USA)	5 - 25	Hui & Luo (2004)
Mountain birch forest (Sweden)	14.88	Sjögersten & Wookey (2002)
Scots Pine forest	15.98	Zha et al. (2007)
TROPICAL FORESTS		
Tropical forest (Malaysian Peninsula)		
Primary forest	19.94	Adachia et al. (2006)
Secondary forest	20.11	
Oil Palm Plantation	23.18	
AGRICULTURAL ECOSYSTEMS		
Maize farm (Jinzhou, China)	5.25 – 19.36	Han et al. (2007)
Bare soil (Bornim, Germany)	2.95	Herbst et al. (2008)
Peat soil (Finland)	15.6	Koizumi et al (1999)
Sandy soil (Finland)	7.2	Koizumi et al. (1999)
ARID ECOSYSTEMS		
Arid succulent karoo (South Africa)		
Quartz-gravel sparse vegetation	0.11 – 1.68	This study
Shale, phyllite, limestone sparse vegetation	0.38 – 2.18	This study
Shale, phyllite, limestone medium vegetation	0.40 – 6.15	This study
Quartzite, limestone, dolomite medium vegetation	1.69 – 2.05	This study
Cenozoic alluvium, calcrete medium vegetation	1.39 – 2.85	This study

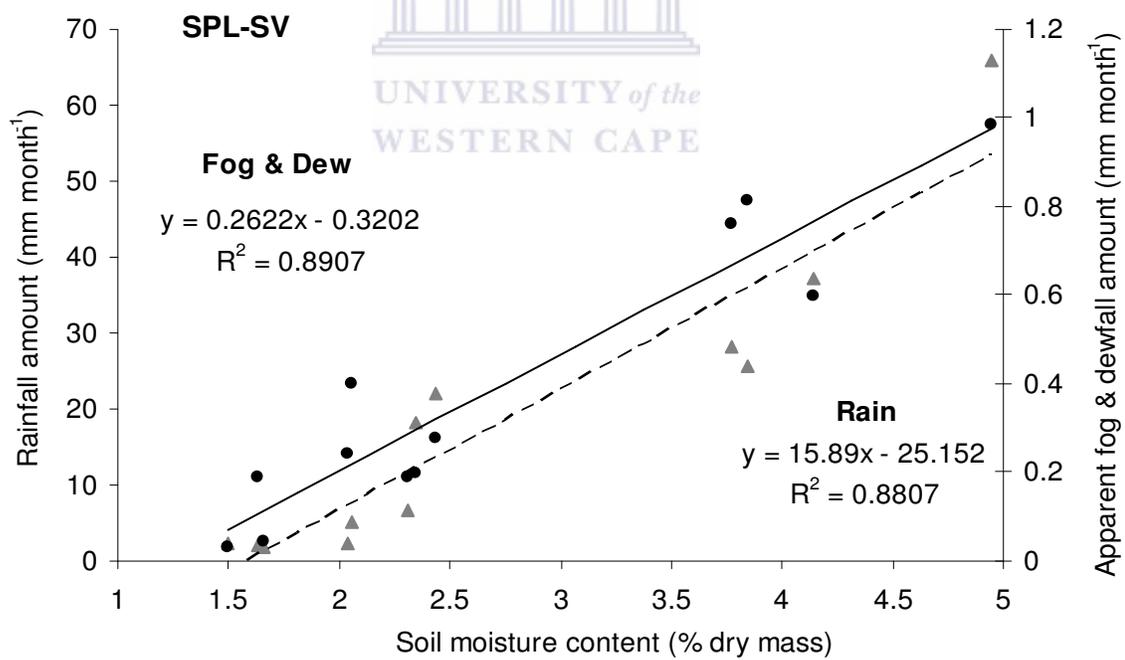
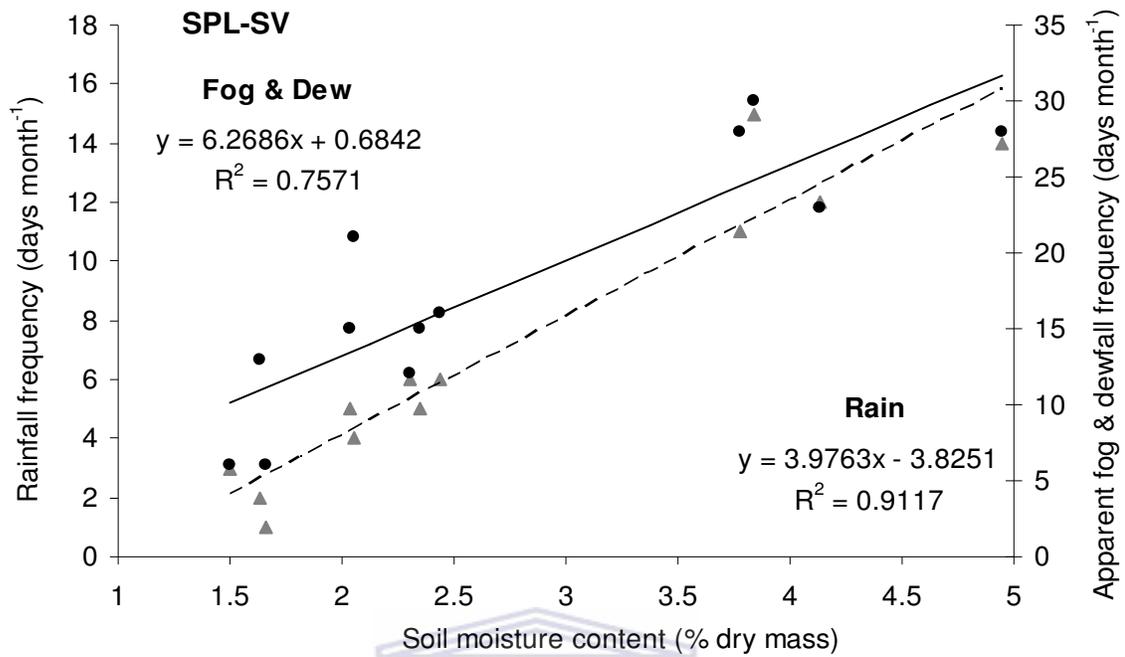


Figure 3.1. Linear regressions of soil moisture content against rainfall and fog and dewfall frequency and amounts.

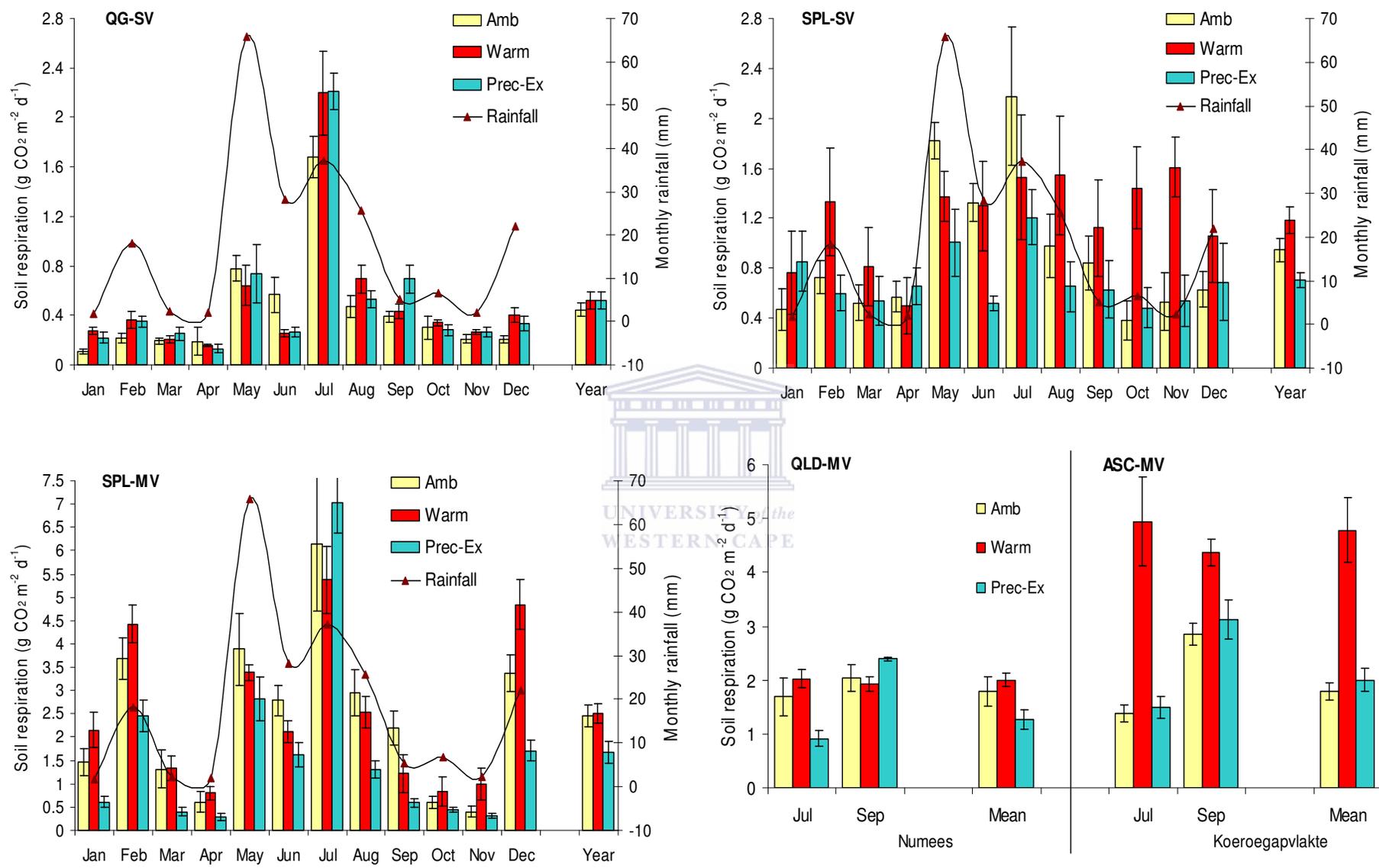


Figure 3.2. Average monthly soil respiration rates measured in the ambient environment and in open top warming and precipitation exclusion chambers in 5 different soil vegetation units and total monthly rainfall amounts. Standard errors shown as bars.

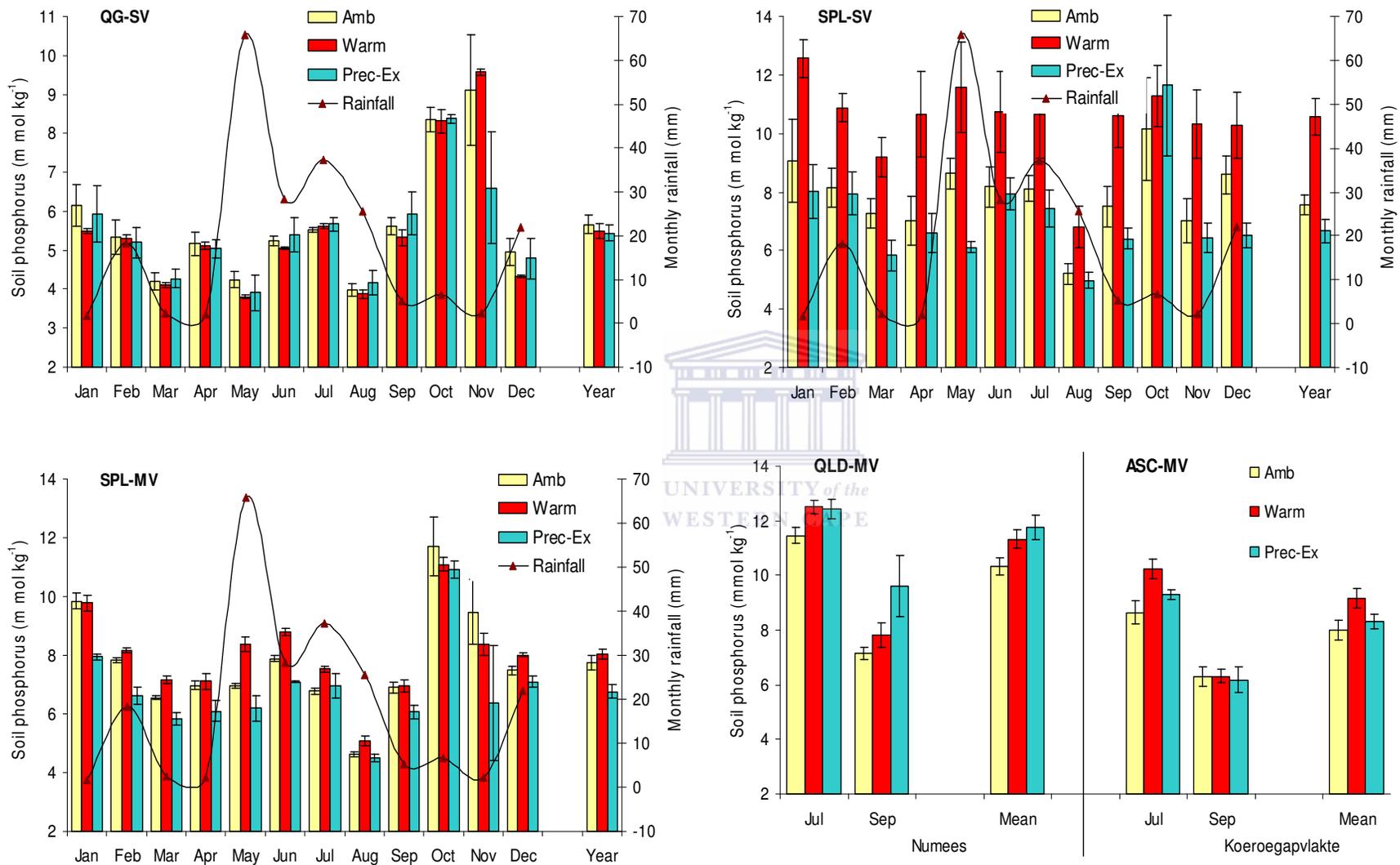


Figure 3.3. Average monthly soil phosphorus contents measured in the ambient environment and in open top warming and precipitation exclusion chambers in 5 different soil vegetation units and total monthly rainfall amounts. Standard errors shown as bars.

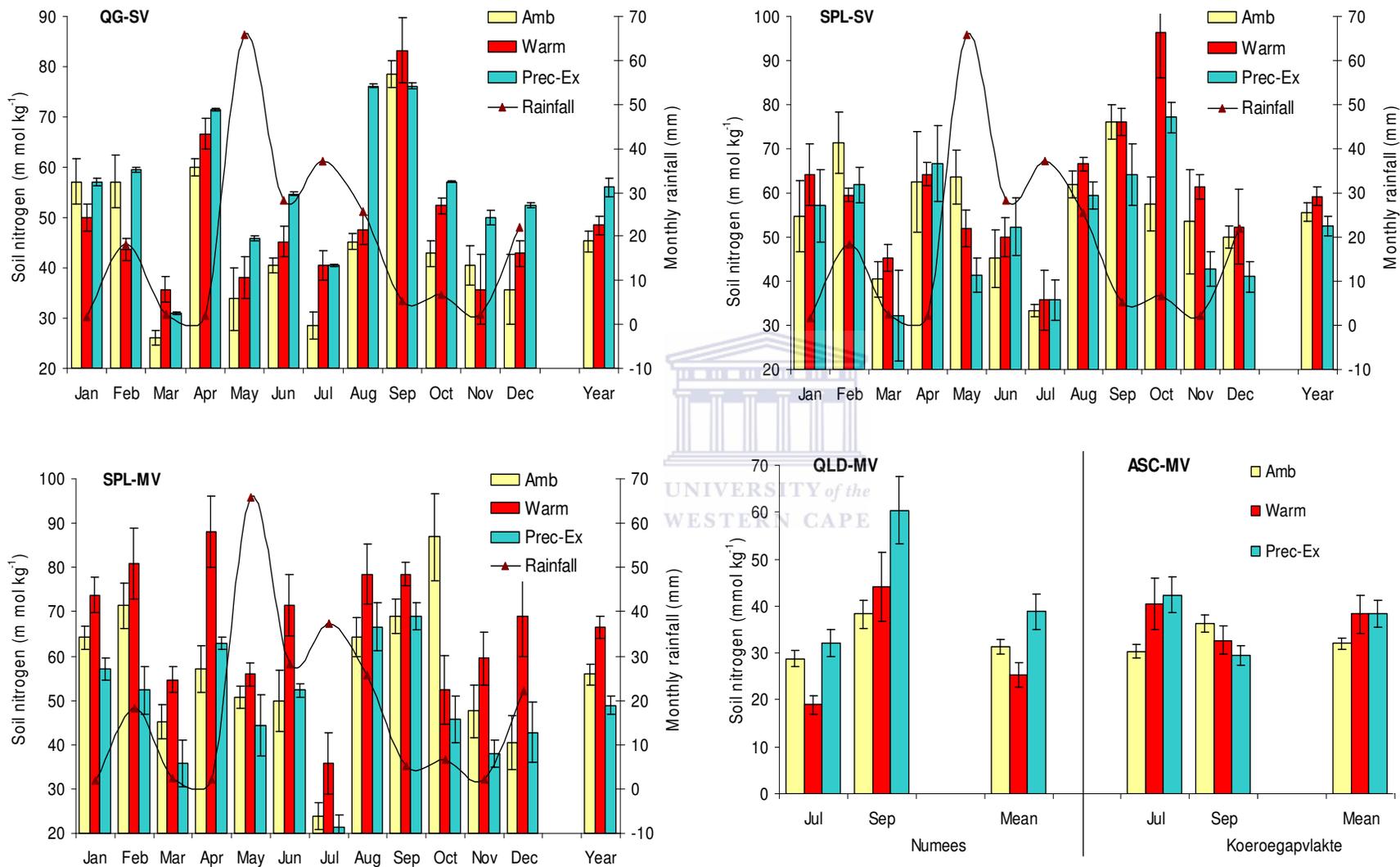


Figure 3.4. Average monthly soil nitrogen contents measured in the ambient environment and in open top warming and precipitation exclusion chambers in 5 different soil vegetation units and total monthly rainfall amounts. Standard errors shown as bars.

Chapter 4: A comparison of empirical and theoretical based model predictions of CO₂ efflux in different soils of an arid South African ecosystem

Abstract

An empirically-based soil respiration (EMR) model was compared with a theoretically based generalized soil respiration model (GRESP). Input data for the EMR model comprised monthly measurements over a 12-month period of soil respiration rate, temperature, moisture and nitrogen and phosphorus contents in natural and artificially manipulated soil environments located in five different soil-vegetation units. Artificial manipulation of soil environments comprised the elevation of soil surface air temperatures and partial exclusion of rainfall, fog and dewfall from soils using warming and precipitation exclusion chambers. Standard least squares regressions quantified the relationships between soil respiration rate and measured soil physical and chemical properties, and their interactions for each of the 5 soil-vegetation units. Requisite functions for the GRESP model included Q_{10} respiratory coefficients, derived from exponential regressions of measured soil respiration rate against soil temperature at soil moisture contents at or above field capacity for each soil vegetation unit, these assumed reduced by half for dry conditions, and the maximum retentive and field capacities of soils obtained from buried soil moisture sensors. EMR modelled soil respiration rates displayed slightly better correspondence with measured soil respiration rates than GRESP modelled soil respiration rates. This apparent from the higher regression coefficients (r^2) and lower sums of squared residuals, with EMR model residuals also more closely approximating normal distributions than the GRESP model residuals in all 5 soil vegetation units. Despite the apparent superiority of the EMR over the GRESP model, more precise laboratory-based measurements of soil retentive and field capacities and their Q_{10} coefficients at different soil moisture contents could improve the GRESP model's accuracy thereby providing a more convenient and uncomplicated means of predicting respiration responses to current and future climates over a wide range of arid soil types

4.1. Introduction

Carbon dioxide is a significant anthropogenic greenhouse gas and its global atmospheric concentration has increased from its pre-industrial value of about 280ppm to 379 ppm³ in 2005 (IPCC, 2007). Raich and Potter (1995) estimated that approximately 10% of the atmosphere's CO₂ passes through soils every year which is approximately 10 times more than the CO₂ released from fossil fuel combustion (Raich and Potter, 1995). At a global

scale, soil carbon in terrestrial ecosystems far exceeds that within aboveground biomass (Ehleringer et al., 2000). It's released by respiring micro-organisms, roots and mycorrhizae (Raich and Schlesinger 1992) and constitutes a major component of the annual biospheric CO₂ contribution to the atmosphere (Schimel 1995). Soil CO₂ efflux is driven mainly by soil temperature and moisture and their interaction (Raich and Schlesinger, 1992; Rout and Gupta, 1989; Liski et al., 2003) with soil moisture being the main limiting factor in arid ecosystems (Tingley et al., 2006; Viliam and Jan, 2006).

Existing models of soil respiration can be classified in two groups that differ in temporal scale and methodology. The first group contains models which estimate soil CO₂ efflux at the scale of hours or days and treat CO₂ production in a simplified way by using an optimum respiration rate as a source term constant in time and/or space (Šimůnek and Suarez, 1993; Cook et al., 1998; Pumpanen et al., 2003). The second group comprises carbon turnover models which operate at the temporal scale of months to decades using pool concepts to account for microbiological carbon decomposition (Franko et al., 1997; Smith et al., 1997 Parton et al., 1994; Coleman and Jenkinson, 2005).

Theoretically-based respiration models propose that soil CO₂ efflux is fundamentally a cellular process and borrow a central principle from enzyme kinetics, namely the relationship between enzyme activity and temperature (Laidler 1997). Soil respiration increases with increasing temperature, and this relationship is usually described with exponential equations (Lloyd and Taylor, 1994). Soil temperature is the most important factor regulating soil respiration and also the most intensely studied factor (Lin et al., 1999; Winkler et al., 1996; Luo et al., 2001; Carlyle and Than, 1988). A temperature based respiration model for northern USA semi-arid grasslands reported differences between observed and predicted soil fluxes averaging only 1.5% (Frank et al., 2002). However, various models for soil and ecosystem respiration as functions of temperature have been proposed but no academic consensus exists (Lloyd and Taylor, 1994). Measured increases in soil respiration for every 10°C increase in temperature, designated Q₁₀, range from 1.3 to 5.6 (Raich and Schlesinger, 1992; Peterjohn et al., 1993; Simmons et al., 1996) with a Q₁₀ value of 2, a doubling of soil respiration for each 10°C rise in temperature, is assumed for predictions of climate change. However, this value does not hold at high temperatures due to enzyme deactivation and acclimation of soil respiration to warming (Luo et al., 2001) with Q₁₀ also varying with the depth of the active soil layer (Swanson and Flanagan, 2001; Kirschbaum 1996). In fact, some studies even question the relationship between soil respiration and temperature (Liski et al., 1999; Johnson et al., 2000; Thornley and Cannell, 2001), though a wealth of data from soils and ecosystems around the globe does suggest otherwise (Singh and Gupta, 1977; Raich and Schlesinger, 1992).

Soil moisture is another important factor influencing soil respiration. Soil CO₂ efflux is usually low under dry conditions due to low root and microbial activities, but increases with soil moisture to a maximum level and thereafter declines due to a limitation of oxygen diffusion and suppression of CO₂ emissions. As a consequence, the relationship between soil CO₂ efflux and moisture is often described by quadratic equations (Bunnel et al., 1977; Linn et al., 1984; Mielnik and Dugas, 2000), though linear, exponential and hyperbolic equations have also been used to describe soil respiration-moisture relationships (Norman et al., 1992; Davidson 1998; Liu et al., 2002; Schlentner and Van Cleve, 1985; Carlyle and Than, 1988). There also exists a strong interaction between soil temperature and soil moisture on the rate of soil respiration which is insensitive to soil moisture at temperatures below 5°C but relatively responsive to soil moisture at temperatures above 10°C (Carlyle and Than, 1988). A general soil respiration model combining soil temperature and soil moisture, designated GRESP (Bunnel and Tait, 1974), has been applied successfully to tundra, boreal forest and temperate bog ecosystems (Heal 1979). It has limitations in its assumptions that respiration equals zero at 0°C, the relationship between soil respiration and temperature is exponential without an upper limit, and that Q₁₀ is constant. Variations of the GRESP model have been proposed, such as the BRESP model which adds an upper and lower limit of the response of soil respiration to temperature (Schlentner and Van Cleve, 1985) and the FRESP model which incorporates a Q₁₀ dependency on substrate moisture so that it can be applied to very dry conditions (Carlyle and Than, 1988). Other factors, such as leaf area index (Norman et al., 1992), air temperature and precipitation have also been added as variables to soil respiration models (Raich and Potter, 1995).

Models for soil respiration at present include only the effects of water and temperature, while the biological and soil factors controlling soil respiration and their interactions with water and temperature have as yet not been considered. Broader-spectrum soil respiration models which include interacting meteorological (water and temperature), soil nutrient and biological factors are required to accurately evaluate soil respiration in different vegetation/terrestrial ecosystems at different temporal and spatial scales, and in more accurately predicting responses to climate change (Jia and Zhou, 2008). Consequently, this study examined broader spectrum soil respiration models derived from empirical data obtained in different soils and vegetation units of an arid ecosystem and compared predictions from these with those from a previously published theoretically based general soil respiration model.

4.2. Materials and methods

4.2.1. Study sites

There were three study sites, namely Quaggaskop situated in the southern Knersvlakte bioregion and Numees and Koeroegapvlakte situated in the northern Richtersveld bioregion in the western part of the Ai-Ais Tranfrontier National Park. Both bioregions are included in the succulent karoo biome, a semi-arid winter rainfall region in South Africa (Rutherford and Westfall, 1986) ranked among 34 global biodiversity hot spots (Myers et al., 2000; Mittermeier et al., 2000).

Quaggaskop (31° 24.6" S / 18° 37.8" E) at an elevation ±160 m has a mean annual precipitation of 145 mm and mean daily maximum air temperature of 25.7°C determined from the nearby Vredendal weather station (Climate of South Africa, 1986). Large parts of the Knersvlakte, an acknowledged centre of diversity and endemism (Hilton-Taylor 1994, 1996), are covered by quartz-gravel fields, an extra-zonal special habitat, which houses a globally unique specialized flora where specialized dwarf succulents dominate (Schmiedel and Jürgens, 1999; Schmiedel 2001, 2002). Inter-dispersed among the quartz-gravel fields are areas devoid of quartz covered with shale, phyllite and limestone derived substrates of the Nama Group (Schmiedel and Jurgens, 1999) where larger succulent shrubs dominate.

Numees (28° 18' 07.6" S / 16° 57' 50.4" E) occurs approximately 12 km south-east of the Orange River at an altitude of 377 m. Maximum daily summer temperatures reach 50°C with a predominantly winter rainfall averaging 70 mm annum⁻¹ supplemented by coastal fogs occurring 40–50 days annum⁻¹ (Jürgens et al., 1999). The topography is highly diverse with steep slopes in the north and north-east with the remaining areas comprising predominantly hilly structures and dissected plains in allochthon unsorted substrates. Soils constitute meta-sediments of the Gariep Supergroup which include quartzite, limestone and dolomite. The vegetation type is classified as Central Richtersveld Mountain Shrubland (Mucina et al., 2006) comprising diverse dwarf shrub communities with many leaf succulent species (Jürgens et al., 1999; Gotzmann 2002).

Koeroegapvlakte (28° 14' 08.4" S / 17° 01' 32.4" E) is located in the north bounding sinuosity of the Orange River at an altitude of 635 m. The mainly winter precipitation varies between 50-100 mm annum⁻¹. The topography of the typical inner mountain basin comprises an alluvial plain with a mean inclination of 5%. Soils are of high salinity and consist of cenozoic alluvium, aeolian sand and calcrete layers (Petersen 2008). The vegetation type is classified as Northern Richtersveld Scorpionstailveld (Mucina et al., 2006) comprising dwarf shrub communities with various leaf succulent species.

4.2.2. Warming and precipitation exclusion treatments

In order to provide added flexibility to the model for predicting future trends in soil respiration, ambient environments were artificially manipulated (Appendix 1) at each site to simulate elevated temperatures and reduced precipitation amounts anticipated with future climate warming (Hulme et al., 2001). Artificial heating of soils was achieved with clear acrylic (transmission down to 280 nm) hexagonal open-top chambers (basal diameters: 120 cm between parallel sides) of 50 cm height. Daytime elevation of soil surface air temperatures in these chambers averaged 4.1°C above ambient with a concomitant reduction in fog and dew precipitation averaging 41.5%. Such open-top chambers have been applied extensively in the International Tundra Experiment (ITEX) organized to investigate how soils and vegetation in arctic tundra and high alpine regions may be affected by global warming (Henry and Molau, 1997), and their efficacy as analogues of climate warming has received biotic validation (Hollister and Weber, 2000). Reduction of fog and dew precipitation from soils averaging 48.9% without a concomitant elevation in daytime soil surface air temperatures (average 0.3°C decrease), was achieved with 120 cm square chambers of 50 cm height whose roofs were clad with louvered clear acrylic and whose sides were clad with 60% light transmitting shade cloth. Demarcated plots of equivalent open-top chamber basal dimensions enclosed by 40cm high steel fencing with a 5 cm diameter mesh comprised the controls which represented ambient conditions. At all 3 sites, warming, precipitation exclusion and control chambers, replicated three times, were positioned at random in different soil-vegetation units. These included soils with sparse vegetation cover overlaid by 1. quartz-gravel substrates (QG-SV) and 2. shale, phyllite and limestone derived substrates (SPL-SV), and soils with moderate vegetation cover overlaid with 3. shale, phyllite and limestone derived substrates (SPL-MV), 4. quartzite, limestone and dolomite derived substrates (QLD-MV), and 5. cenozoic alluvium, aeolian sand and calcrete derived substrates (ASC-MV). The first three soil-vegetation units occurred at Quaggaskop, the fourth at Numees and the fifth at Koeroegapvlakte.

4.2.3. Soil respiration, moisture and nutrient assays

Polyvinyl chloride (PVC) soil collars with an internal diameter of 10 cm and a length of 5cm were installed at the centers of each of the warming, precipitation exclusion and control chambers leaving a 1cm rim extending above the soil surface. Commencing one month after collar installation, several morning and afternoon measurements of soil respiration rate were taken (Appendix 2) with a Li-Cor 8100 infrared gas analyzer (Li-Cor BioSciences, Lincoln, Nebraska, USA) and soil temperatures simultaneously recorded with thermocouple probe. Measured soil respiration rates as $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ were converted to $\text{g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$. At the Quaggaskop site, soil respiration measurements were performed at monthly intervals

spanning the 12 month period from July 2007 to June 2008. At the remote Numees and Koeroegapvlakte sites, soil respiration measurements were restricted to the early spring month of September 2007 and mid winter month of July 2008.

After each set of respiration measurements, soil samples were collected and sealed in 40cm³ sample bottles for moisture and elemental analysis. Gravimetric soil moisture contents, expressed as percentages of soil dry mass, were computed from the measured fresh and dry masses of the soils following soil drying in a forced draft oven at 60°C (Garretson 1999). Also, in each of the five soil-vegetation units, hourly measurements of soil volumetric water content over the entire 12-month recording period were obtained with ECH₂O-TE sensors buried 20 mm beneath the soil surface in the warming, precipitation exclusion and control chambers which were interfaced with data loggers (EM-50, Decagon Devices Inc. USA). Volumetric water contents were converted to gravimetric moisture contents by dividing these by measured bulk densities of oven dried soils. Also, simultaneous measurements of soil surface air temperature were obtained with thermocouples, shielded from direct solar radiation in perforated plastic tubes (Appendix 3), fog and dew precipitation with leaf wetness sensors located 10 cm above the soil surface, and rainfall amounts with tipping bucket gauges all of which were interfaced with miniature data loggers installed in radiation shields (Watch Dog 450, Spectrum Technologies Inc., Plainfield, Illinois, USA). Measured leaf wetness resistances (range: 0 to 15 units) were converted to apparent fog and dew precipitation amounts in mm using a published formula (Musil et al., 2009).

Soils for elemental analysis were dried at 30°C in a forced draft oven and sieved to ≤ 2 particle size. P concentrations in 5 g soil sub samples were analyzed according to the method of Bray and Kurtz (1945) following extraction of soil soluble P using a Bray-II extract. N concentrations in 5 g soil sub samples were measured with an Auto-Analyser (SP428, Nitrogen Analyser LECO Corporation, USA) following soil combustion as described by Clesceri et al., (1998). Measured N (% N) and P (mg kg⁻¹ P) concentrations in the soil samples were expressed uniformly as m mol kg⁻¹ dry soil mass.

4.2.4. Model development

4.2.4.1. Empirical model

The relationship between measured soil respiration rate and soil temperature, soil moisture, N and P concentrations and their interactions at different times of the day were quantified for each of the five different soil-vegetation units applying standard least squares regression approaches. The empirical respiration model was defined as:

$$EMR = T+SMC+N+P+ T.SMC + T.N + T.P + SMC.N + SMC.P + N.P + AM.PM \dots\dots\dots 1.$$

where:

EMR = soil respiration rate ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)

T = soil temperature ($^{\circ}\text{C}$)

SMC = gravimetric soil moisture content ($\text{g H}_2\text{O g}^{-1}$ dry soil x 100)

N = soil N concentration mmol kg^{-1}

P = soil P concentration mmol kg^{-1}

AM.PM = morning (AM) and afternoon (PM) scored as 0 and 1 respectively.

An added stepwise regression (forward selection) was applied for selection of significant model variables. Modeled soil respiration rates were converted to $\text{g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$ by multiplying them by 3.9744, i.e. $[46 \times 60 \times 60 \times 24]/10^5$

4.2.4.1. GRESP model

The relationship between soil respiration rate and soil temperature and moisture has been quantified in a generalized respiration model, designated GRESP, developed by Bunnell and Tait (1974). This model has been applied successfully to tundra, boreal forest and temperate bog ecosystems (Heal 1979), and was applied as a basis for comparison with the empirically based soil respiration model developed in this study. It is defined as:

$$\text{GRESP} = \frac{M}{M + a_1} \times \frac{a_2}{M + a_2} \times a_3 \times a_4^{(T-10)/10} \dots\dots\dots 2$$

where:

GRESP = soil respiration rate ($\text{g CO}_2 \text{ m}^{-2} \text{ h}^{-1}$)

T = soil temperature ($^{\circ}\text{C}$)

M = gravimetric soil moisture content ($\text{g H}_2\text{O g}^{-1}$ dry soil x 100)

a_1 = % soil moisture content at half field capacity

a_2 = % soil moisture content at half maximum retentive capacity

a_3 = theoretical maximum respiration rate at 10°C when moisture is non-limiting

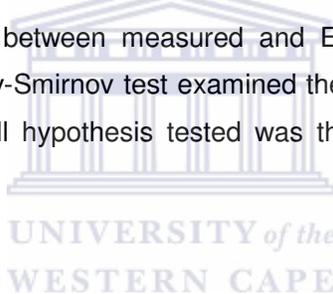
a_4 = Q_{10} coefficient (sensitivity to temperature)

The maximum retentive and field capacities of soils in each of the 5 soil-vegetation units (Table 4.1) were obtained from the average soil moisture contents, expressed as percentages of soil dry mass, recorded by the ECH₂O-TE moisture sensors during and 3-days after respectively significant rainfall amounts (Israelson and West, 1922; Veihmeyer and Hendrickson, 1931). The Q_{10} respiratory coefficients for each of the 5 soil-vegetation

units were derived from exponential regressions of measured soil respiration rates against soil temperature at soil water contents at or above field capacity (Figure 4.1). Under dry conditions (soil moisture contents below 2.5%) existing from late spring (November) through to early autumn (April), the Q_{10} respiratory coefficients incorporated into the model were reduced by half due to their reported dependency on soil moisture (Carlyle and Than, 1988). The highest soil respiration rates measured at soil temperatures at or close to 10°C in the different soil-vegetation units at soil water contents at or above field capacity were assumed the theoretical maximum soil respiration rates at 10°C when moisture is non-limiting (Table 4.1). Modeled soil respiration rates were converted to $\text{g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$ by multiplying them by 24.

4.2.5. Model comparisons

Least squares regressions examined correspondence between measured soil respiration rates and those predicted by the EMR and GRESP models for each of the 5 different soil-vegetation units. The two models were compared using common sums of squared residuals (differences between measured and EMR and GRESP modelled soil respiration rates). A Kolmogorov-Smirnov test examined the goodness of fit of the residuals to normal distributions. The null hypothesis tested was that the residuals fitted a normal distribution.



4.3. Results and Discussion

The stepwise regressions selected a different complement of model variables for each of the 5 soil-vegetation units with only P and the interaction between soil temperature and moisture content (T.SMC) common to 3 of the 5 soil-vegetation units (Table 4.3). Therefore, rather than the variable sub sets selected by the stepwise regression, the full complement of 11 environmental variables were included in the EMR model, the coefficients of which are presented in Table 4.2. This decision was also supported by reports that significance tests based on stepwise procedures lead to greatly inflated Type I error rates, *i.e.* the probability of erroneously rejecting a true null hypothesis (Mundry and Nunn, 2009).

Both the EMR and GRESP modelled soil respiration rates corresponded comparatively well with measured soil respiration rates and adequately resolved the high peaks in soil CO_2 flux (up to 15-fold increase) measured after rainfall events (Figures 4.2 to 4.5), which were of a similar order of magnitude to after rainfall pulses reported for NO and NO_2 in arid other arid ecosystems (Otter and Scholes, 2005). These large pulses in soil CO_2 flux commencing immediately after rain events attributed to an enormous stimulus to microbial activity resulting from an accumulation of nutrients in the soil during the dry season, a feature which makes arid regions unique and also potentially important as sources of CO_2

feeding back to increasing atmospheric CO₂ (Otter and Scholes, 2005). They are, like in other arid and semi arid areas, sinks for carbon-based compounds during dry seasons but change to sources of the same during wet periods. After rains, not only do soil microbes become active, but the vegetation is also revived (Otter and Scholes, 2005). However, during the drier late spring to early autumn (November to April) period, the EMR modelled soil respiration rates tended to over estimate soil respiration rates in quartz gravel substrates with sparse vegetation cover (Figure 4.2) whereas the GRESP model tended to under estimate soil respiration rates on all substrates with moderate vegetation cover. The latter, a possible consequence of the contribution to total soil respiration of root respiration and leaf fall detritus decomposition (Otter and Scholes, 2005).

Overall, correspondence between measured and EMR modelled soil respiration rates was better than that between measured and GRESP modelled soil respiration rates for all 5 soil-vegetation units. This apparent from the higher regression coefficients (r^2) and lower sums of squared residuals originating from the EMR modelled soil respiration rates (Table 4.4, Figures 4.2 to 4.5), though the latter alone are considered inadequate criteria for evaluating comparative goodness of different models describing soil respiration relationships to the environment (Tuomi et al., 2008). However, the residuals from the EMR modelled soil respiration rates also more closely approximated normal distributions than the residuals from the GRESP modelled soil respiration rates. This evident from the lower K-S test statistic values consistently obtained from the EMR model than GRESP model residuals (Table 4.4). In two of the 5 soil-vegetation units, namely SPL-MV and ASC-MV, the EMR model residuals were insignificantly different ($P \geq 0.05$) from normal distributions (Figure 4.4 and 4.5). These findings concur with recommendations that modelling soil respiration responses to climate should be based on empirical data from a wide range of habitats to obtain closer correspondence between models and experiments (Luo et al., 2007).

Despite the apparent superiority of the EMR model over the GRESP model, the GRESP model has certain practical advantages. The coefficients included in the GRESP model are easier to determine and the model's broad applicability has been demonstrated in tundra, boreal forest and temperate bog ecosystems (Heal 1979). Nevertheless, the reported dependence of Q_{10} on soil moisture (Carlyle and Than, 1988) presents a limitation to the GRESP model's applicability in arid ecosystems, a feature apparent in all Q_{10} based models which poorly estimate soil respiration relationships to the environment (Tuomi et al., 2008). The assumption applied in this study that Q_{10} coefficients under dry conditions were half those in moist soils was supported by the EMR model derived Q_{10} coefficients which ranged from 0.9 in dry to 2.4 in moist soils of the 5 different soil-vegetation units (Table 4.5). This Q_{10} range's upper limit is above the Q_{10} range of 1.17 to 1.65 reported for three desert communities (Zhang et al., 2008) but compares favourably with the Q_{10} range of 0.77 to 2.60

reported by Carlyle and Than (1988) in Ordovician phyllites podzolic soils under a *Pinus radiata* plantation in Australia with the highest Q_{10} of 2.4 conforming with Q_{10} values of 2.0 and 2.4 reported for moist A-horizon humus soils by Wiant (1967) and Raich and Schlesinger (1992) respectively. However, substantially higher Q_{10} ranges of 3.4 to 5.6 have been reported for soils from a temperate hardwood forest (Davidson et al., 1998), these possibly exacerbated by added root respiration which is known to elevate Q_{10} values (Davidson et al., 1998). Nevertheless, more precise laboratory-based measurements of soil retentive and field capacities and their Q_{10} respiratory coefficients at different soil moisture contents could improve the GRESP model's accuracy thereby providing more convenient and uncomplicated means of predicting respiration rates responses to current and future climates over a wide range of soil types in arid regions.



4.4. References

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Table 4.1. Soil moisture and respiration coefficients included in the GRESP model

	QG-SV	Quaggaskop SPL-SV	SPL-MV	Numees QLD-MV	Koeroegapvlakte ASC-MV
Soil moisture					
Retentive capacity (% dry mass)	15.0951	12.9025	23.0781	12.5507	9.9150
Field capacity (% dry mass)	5.5950	4.7822	8.5538	7.2137	5.6988
Soil respiration					
Maximum CO ₂ flux at 10°C (g m ⁻² h ⁻¹)	0.0414	0.0513	0.1586	0.1292	0.1358
Q ₁₀ at ≥ field capacity	2.2984	2.3707	2.3316	2.8151	2.2796
Q ₁₀ dry conditions	1.1492	1.1853	1.1658	-	-



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Table 4.2. EMR model coefficients derived from least squares regressions of soil respiration rate against 11 environmental variables for 5 different soil-vegetation units

Variable	QG-SV	Quaggaskop SPL-SV	SPL-MV	Numees QLD-MV	Koeroegapvlakte ASC-MV
Intercept	0.2069	-0.0069	0.8124	0.1561	3.5343
T	-0.0068	0.0053	-0.0197	-0.0723	-0.0519
SMC	-0.0493	0.0120	-0.1332	0.0170	-0.0645
P	0.0061	0.0294	-0.1049	-0.0057	-0.1478
N	-0.0014	-0.0011	-0.0047	0.0587	-0.1007
T*SMC	0.0032	0.0018	0.0015	-0.0016	0.0021
T*P	-0.0000	-0.0007	0.0038	0.0106	0.0009
T*N	0.0001	0.0000	0.0002	-0.0007	0.0015
P*SMC	-0.0011	-0.0000	0.0196	-0.0031	-0.0060
N*SMC	0.0002	-0.0001	0.0013	0.0007	0.0009
P*N	-0.0001	-0.0000	-0.0001	-0.0046	0.0070
AM/PM	0.0005	-0.0851	-0.0277	0.1728	-0.0037

Table 4.3. Environmental variables selected by step wise regression for 5 different soil-vegetation units

Variable	QG-SV		Quaggaskop SPL-SV		SPL-MV		Numees QLD-MV		Koeroegapvlakte ASC-MV	
	r ²	F-ratio	r ²	F-ratio	r ²	F-ratio	r ²	F-ratio	r ²	F-ratio
T	0.7947	272.3***							0.8742	160.9***
SMC	0.7818	379.8***								
P			0.3972	42.2***	0.5957	61.3***			0.8536	205.6***
N									0.7872	175.1***
T.SMC	0.7459	625.3***	0.3193	91.0***	0.4711	188.9***				
T.P					0.5057	107.9***				
T.N									0.5177	154.6***
P.SMC							0.0633	9.9***	0.8629	176.3***
N.SMC					0.5292	78.7**	0.1698	9.9***		
P.N					0.5693	69.1***			0.5812	99.2***
AM.PM			0.3684	56.3***			0.1278	10.7***		

Table 4.4. Correspondence (r^2) between measured and EMR and GRESP model predicted soil respiration rates for 5 different soil-vegetation units, non conformity (K-S statistic) of residuals to normal distributions, and sums of residuals squared ($\sum \text{residuals}^2$). Significant at * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$.

Parameter	QG-SV	Quaggaskop SPL-SV	SPL-MV	Numees QLD-MV	Koeroegapvlakte ASC-MV
n	216	216	216	154	154
EMR	$R^2 = 0.7610^{***}$	$r^2 = 0.4276^{***}$	$r^2 = 0.6195^{***}$	$r^2 = 0.3168^{***}$	$r^2 = 0.8816^{***}$
GRESP	$R^2 = 0.7224^{***}$	$r^2 = 0.2295^{***}$	$r^2 = 0.4070^{***}$	$r^2 = 0.0037$	$r^2 = 0.2491^{***}$
n	216	216	216	154	154
EMR	K-S = 1.401*	K-S = 1.691**	K-S = 0.897	K-S = 1.559*	K-S = 0.703
GRESP	K-S = 2.811***	K-S = 2.936***	K-S = 3.663***	K-S = 1.853**	K-S = 2.486***
$\sum \text{residuals}^2$					
EMR	27.5	74.2	320.2	270.9	189.4
GRESP	24.0	119.2	1374.5	536.0	1639.8

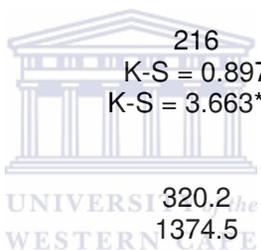


Table 4.5. Q_{10} coefficients derived from the EMR model for 5 different soil-vegetation units

Month	QG-SV	SPL-SV	SPL-MV	QLD-MV	ASC-MV
Jan	0.9	1.1	1.2	-	-
Feb	1.0	1.2	1.3	-	-
Mar	1.3	1.1	1.6	-	-
Apr	1.0	1.2	1.6	-	-
May	2.3	1.3	1.8	-	-
Jun	2.2	1.1	2.1	-	-
Jul	1.4	1.1	1.4	1.6	1.7
Aug	1.2	1.7	1.6	-	-
Sep	1.2	1.3	1.7	0.6	1.1
Oct	1.0	1.4	1.5	-	-
Nov	1.0	2.4	2.3	-	-
Dec	1.1	1.1	1.2	-	-



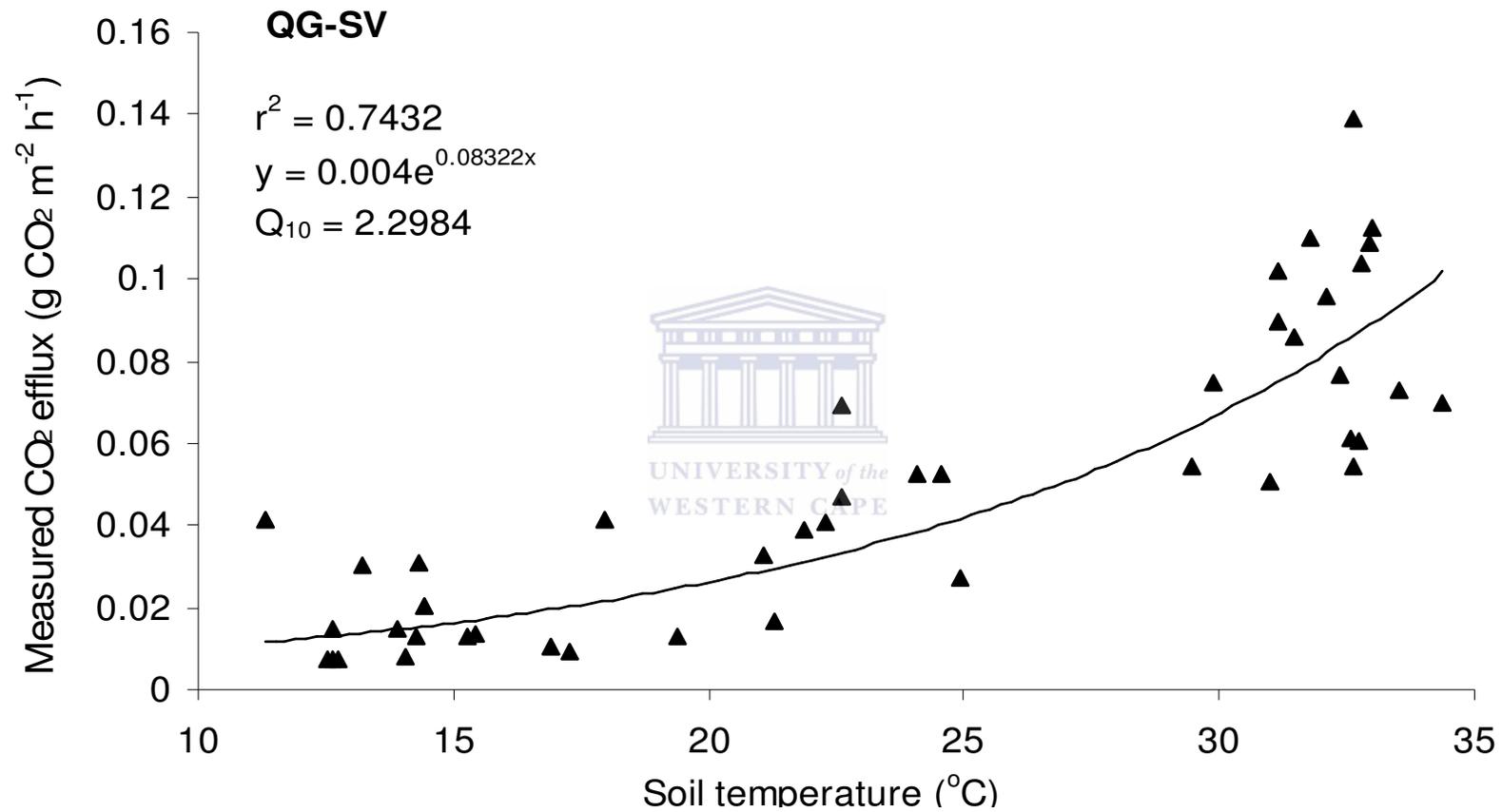


Figure 4.1. Exponential regression of soil temperature against soil respiration rate at soil moisture levels above field capacity

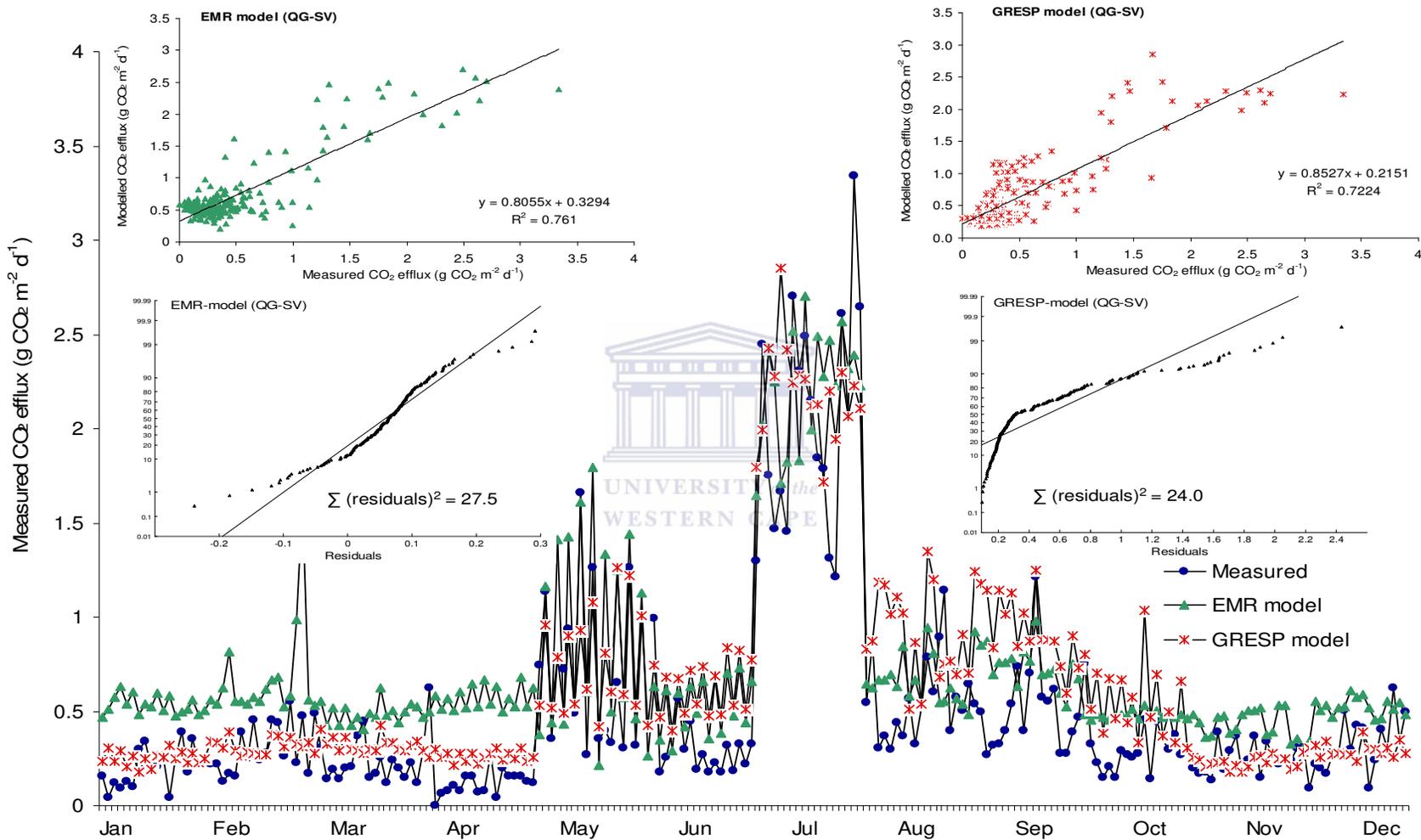


Figure 4.2. Correspondence (r^2) between measured and EMR and GRESP modeled soil respiration rates in soils with sparse vegetation cover overlaid by quartz-gravel substrates (QG-SV) and goodness of fit of residuals to normal distributions.

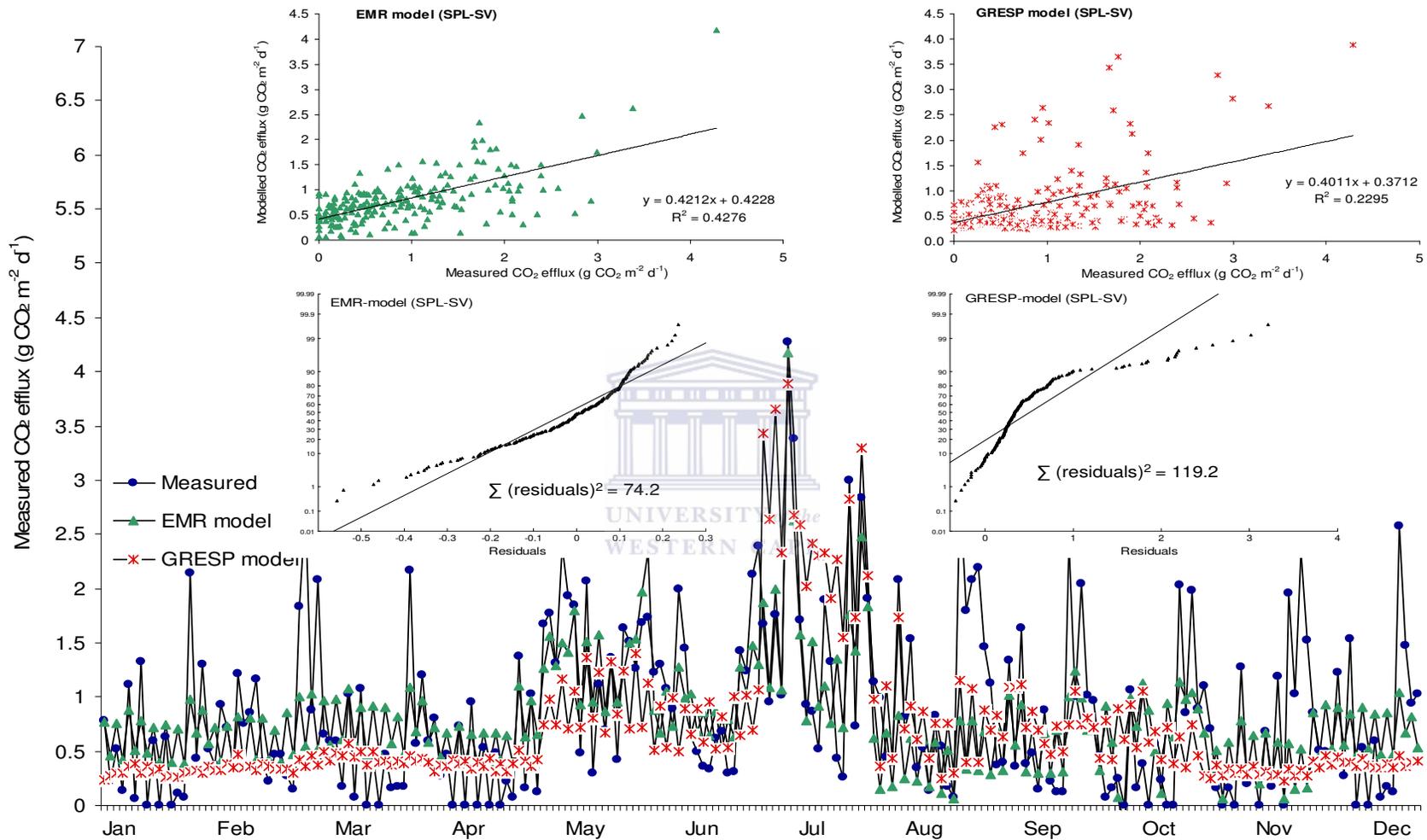


Figure 4.3. Correspondence (r^2) between measured and EMR and GRESP modeled soil respiration rates on soils with sparse vegetation cover overlaid by shale, phyllite and limestone derived substrates (SPL-SV) and goodness of fit of residuals to normal distributions.

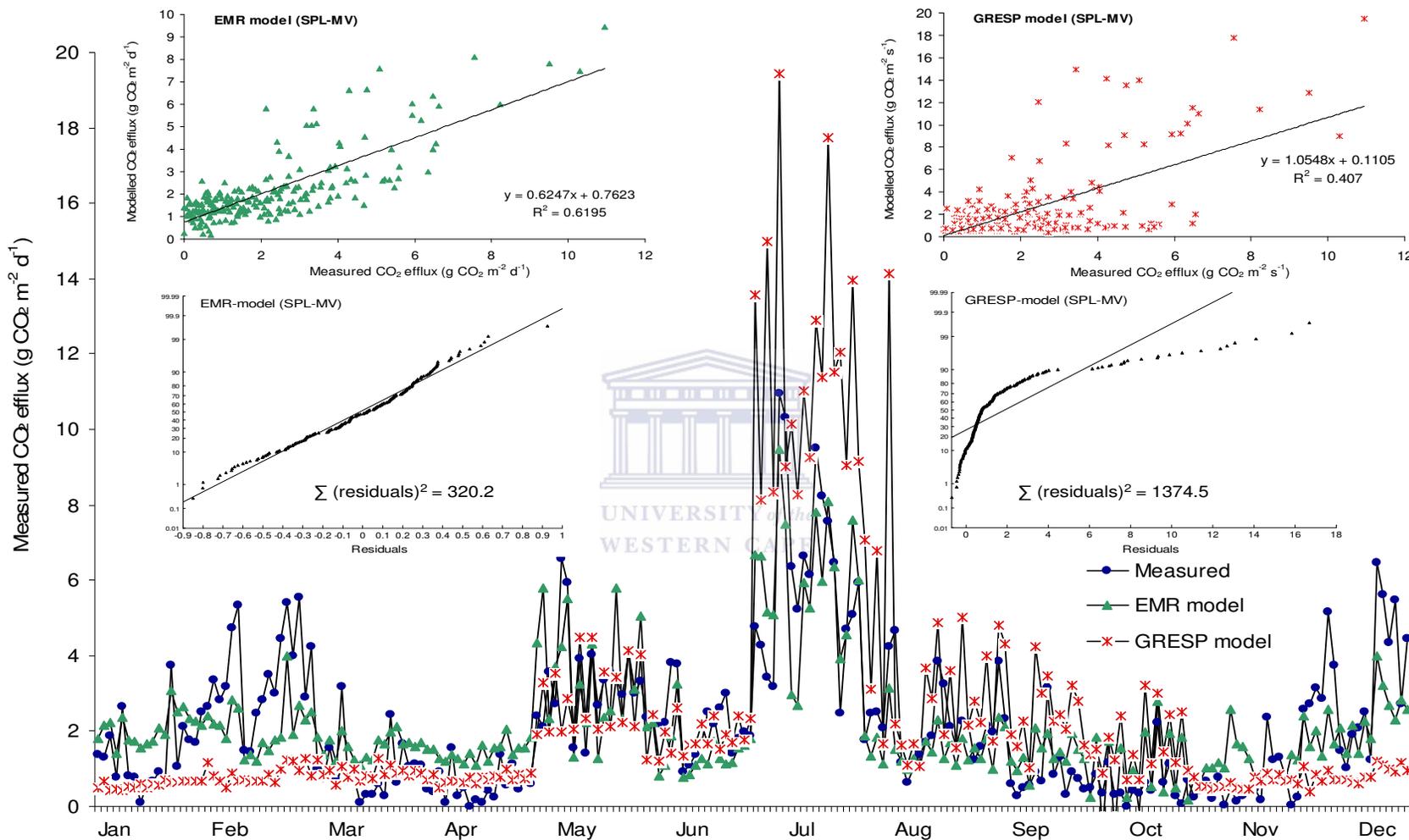


Figure 4.4. Correspondence (r^2) between measured and EMR and GRESP modeled soil respiration rates on soils on soils with moderate vegetation cover overlaid by shale, phyllite and limestone derived substrates (SPL-MV) and goodness of fit of residuals to normal distributions.

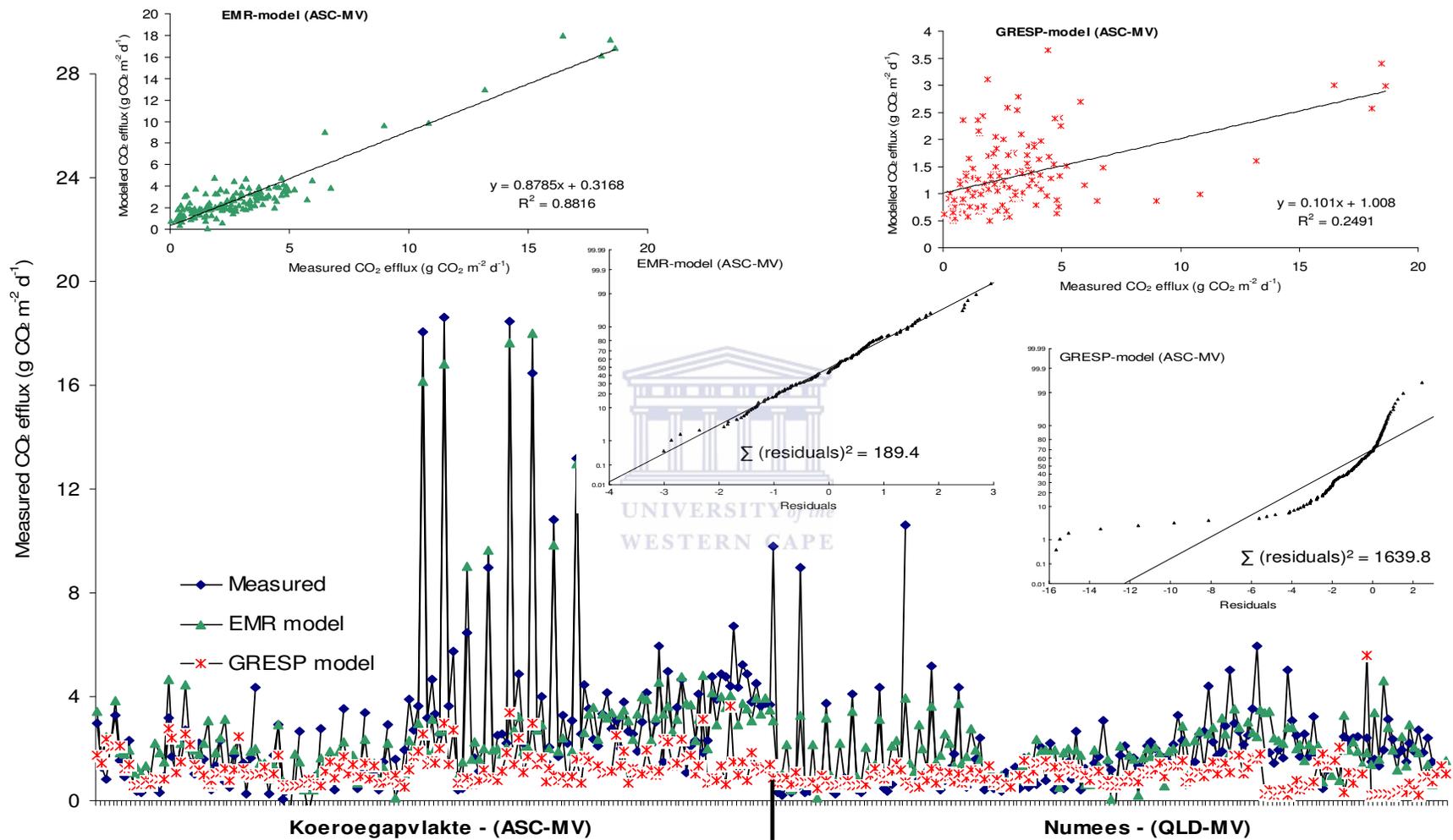


Figure 4.5. Correspondence (r^2) between measured and EMR and GRESP modeled soil respiration rates on soils with moderate vegetation cover overlaid by quartzite, limestone and dolomite derived substrates (QLD-MV) and cenozoic alluvium, aeolian sand and calcrete derived substrates (ASC-MV) and goodness of fit of residuals to normal distributions.

Chapter 5: Conclusions and recommendations

5.1. Main conclusions

The main study conclusions are as follows:

1. South African arid ecosystem soils are indeed minor CO₂ emission sources comparable only to semi-arid grasslands during wet phases.
2. The proportional contribution of root respiration to total soil CO₂ efflux in South African arid ecosystems is similar to that of forest ecosystems.
3. The observed poor correspondence between soil CO₂ efflux and soil organic matter content in South African arid ecosystems indicate that soil CO₂ emissions are not largely dependent on microbial decomposition of soil organic matter.
4. The relatively smaller increases in soil CO₂ efflux in response to warming observed in moderately than sparsely vegetated soils indicate that inappropriate land use may exacerbate climate warming impacts by reducing soil thermal insulation provided by the vegetation canopy.
5. Open top warming chambers are not appropriate analogues of climate warming as their walls intercept additional rain, fog and dew precipitation and channel these to the soil surface thereby also artificially elevating soil moisture levels.
6. The theoretically-based generalized soil respiration model (GRESM) is inferior to an empirically-based model, but nevertheless if refined could potentially provide a more convenient and uncomplicated means of predicting responses of respiration rates to current and future climates over a wide range of soil types in arid regions.

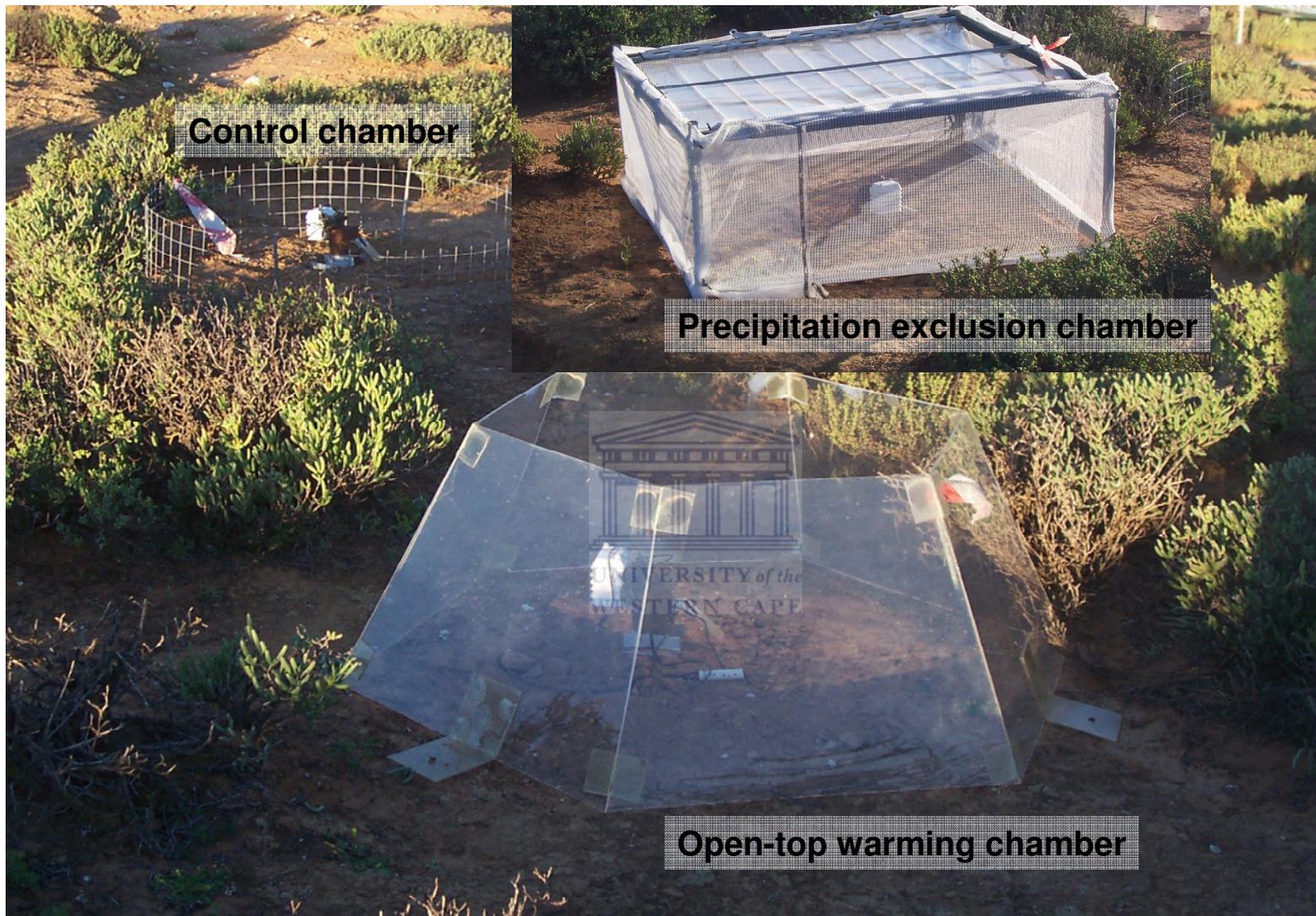
5.2. Recommendations

Inappropriate land use practices, especially livestock grazing which is the main form of land use in the arid South African succulent karoo, as well as mining, agriculture and illegal collection of succulents constitute the greatest threat to the natural vegetation (Odendaal and Suich, 2007). These land use practices and related human activities alter vegetation cover, soil organic matter content and other chemical and physical soil properties (Fernandes et al., 2002; Wang and Fang, 2009) that impact on terrestrial ecosystem responses to atmospheric CO₂ enrichment (Reich et al., 2006). Therefore, further research on the effects that different land use practices have on soil carbon and elemental dynamics and their responses to climate change is required. In this regard, the design of the open-top warming chambers need to be improved by including gutters around their bases to channel intercepted precipitation away from the soil in the interior of these chambers.

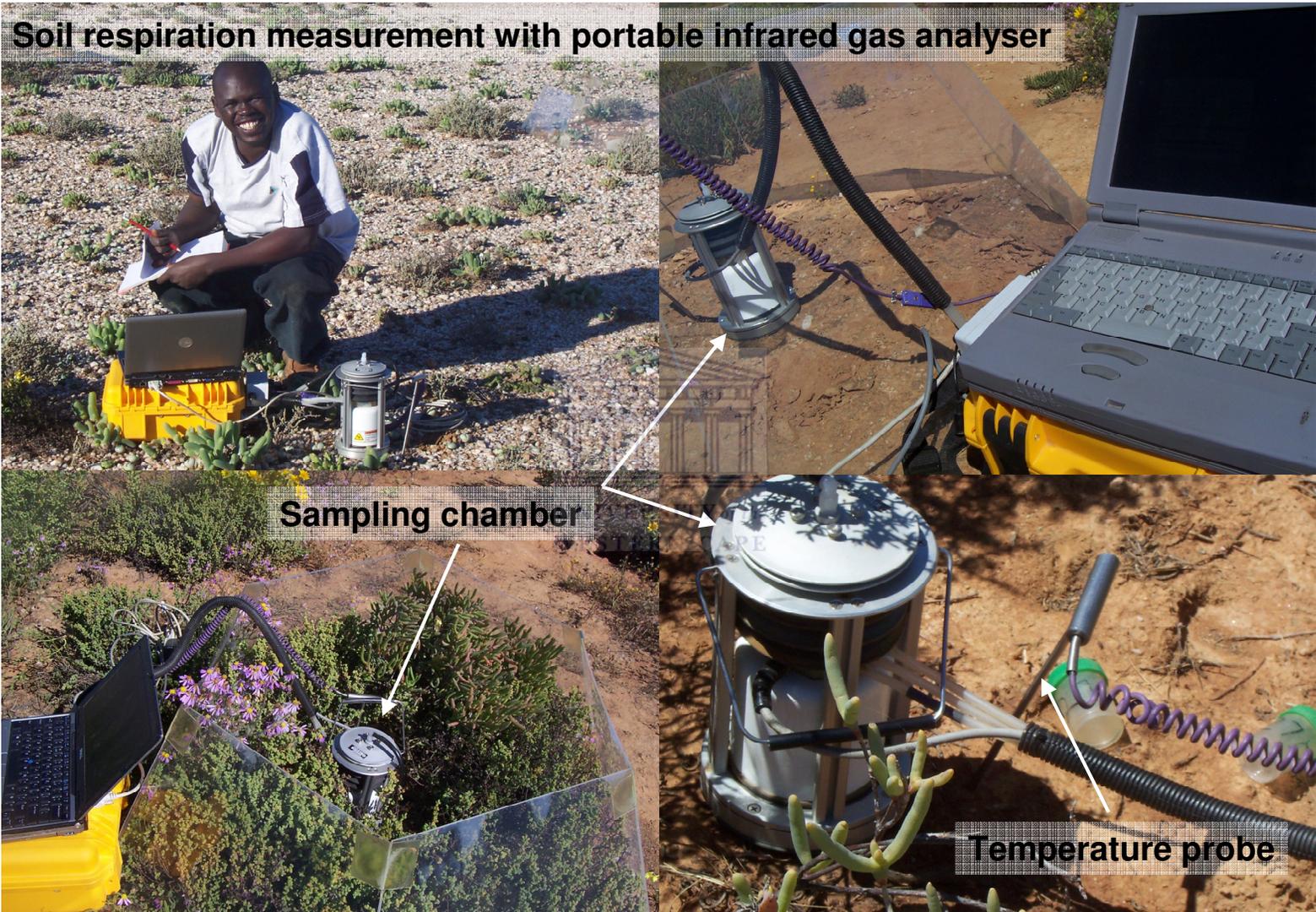
5.3. References

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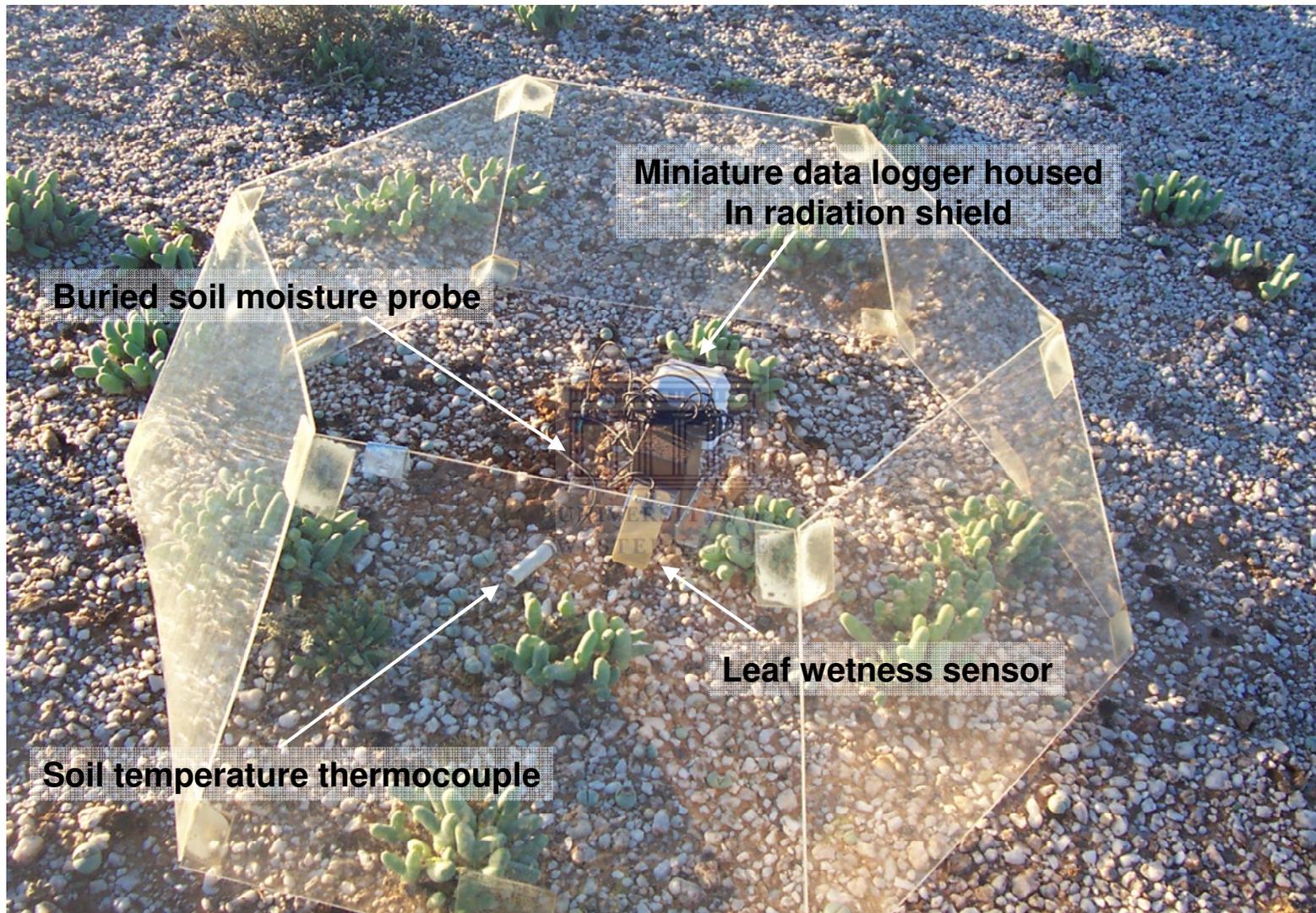




Appendix 1. Photos of open top warming, precipitation exclusion and control chambers used for manipulating soil temperature and moisture environments



Appendix 2. Photos of Infra-red gas analyser with sampling chamber interfaced with laptop computer used for measuring soil respiration rates in sparsely and moderately vegetated environment



Appendix 3. Photos of environmental sensors interfaced with loggers installed in ventilated radiation shields monitoring changes in soil moisture, temperature and apparent amounts of fog and dewfall at hourly interval



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