INFLUENCE OF MICRO-ENVIRONMENTAL CONDITIONS ON ECOSYSTEM EXCHANGES IN THE AFRO-ALPINE ZONE OF MOUNT KILIMANJARO, TANZANIA

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A DISSERTATION SUBMITTED IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE OF MASTER OF SCIENCE IN WILDLIFE MANAGEMENT AND CONSERVATION OF SOKOINE UNIVERSITY OF AGRICULTURE. MOROGORO, TANZANIA.

ABSTRACT

This study was carried out in the alpine ecosystem of Mount Kilimanjaro (*ca*, 4000 m a.s.l), from July 2012 to August 2012 with the aim of assessing the influence of micro-environmental conditions on ecosystem exchanges of CO_2. A total of 18 plastic soil frames with either single or combination of dominant species were used to determine and estimate the net ecosystem exchange of CO_2 (FNEE) and ecosystem respiration (Reco), biomass and leaf area of dominant species, and to establish temporal and spatial variation on ecosystem CO_2 exchanges. To achieve that, manually operated closed gas exchange chambers referred to as light chamber to measure net ecosystem exchange of CO_2 (FNEE) and dark chamber to measure ecosystem respiration (Reco) were used. Later, the above ground plant biomass in each soil frame was harvested for leaf area and biomass determination. Leaf area and biomasses were obtained using digital scanner and through oven drying at 80 ^{0}C for 48 hours respectively. In order to assess temporal and spatial variations, soil frames were located in three subplots for repetition and measurement rounds were carried out from morning (0800 hours) to evening (17.00 hours). Both correlation and regression analysis were used to assess diurnal dependencies of CO_2 concentrations on the environmental variables. The CO_2 fluxes were correlated to Photosynthetic Active Radiation (PAR) at (R^2>0.95). The mean daily FNEE ranged from 1.3398 µmol m^{-2} s^{-1} to -6.2150 µmol m^{-2} s^{-1} and Reco from 1.3474 µmol m^{-2} s^{-1} to 4.6695 µmol m^{-2} s^{-1} while green biomass ranged from 302.2 gm^{-2} to 48.81 gm^{-2}. The highest CO_2 fluxes were evident in combination of species. Subsequently, PAR, air and soil temperatures explain most temporal variability of CO_2 fluxes. Nonetheless, micro-environmental conditions created by vegetation structures that increased the leaf area for canopy level light utilization and green biomass seemed also to play important roles on CO_2 exchanges.

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DECLARATION

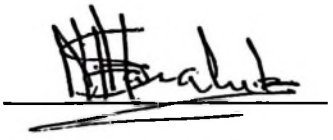
I, SALUM RAMADHANI KULUNGE, do hereby declare to the Senate of Sokoine University of Agriculture that this dissertation is my own original work done within the period of registration and that it has neither been submitted nor being concurrently submitted in any other institution.

28/10/13

Salum Ramadhani Kulunge — Date

(MSc. Wildlife Management and Conservation)

The above declaration is confirmed by



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Prof. Shombe N. Hassan — Date

(Supervisor)

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In the end, I would like to pay my tribute to my loving parents, my wife, son and daughters whose prayers and affection strengthened me to go forward.

DEDICATION

This work is dedicated to my father Mzee Ramadhani Mussa Kulunge, my beloved wife Kuruthumu Omar, and my beloved son and daughters Khalifa Salum, Neema Salum and Najma Salum for their everlasting love, patience, tolerance and encouragement throughout the time I was undertaking my studies.

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LIST OF ABBREVIATIONS AND ACRONYMS

a.s.l	Above sea level
CO_2	Carbon dioxide
FNEE	Photosynthetic net ecosystem exchanges of CO_2
GPP	Gross Primary Production
KINAPA	Kilimanjaro National Park
MAB	Man and Biosphere Reserve
PAR	Photosynthetic Active Radiation
Reco	Ecosytem respiration of CO_2
SUA	Sokoine University of Agriculture
TANAPA	Tanzania National Parks
VPD	Vapour Pressure Deficit

CHAPTER ONE

1.0 INTRODUCTION

1.1 Background Information

Humid tropical alpines are considered to be one of the unique terrestrial ecosystems that sustain biodiversity as well as provide important ecosystem services like carbon storage and surface water (Buytaert *et al.*, 2011). Such mountain environments are critical to sustaining the biosphere. They are sensitive to changes in atmospheric composition, soil carbon deposition and other climate factors such as the drying effect of wind and temperature. Therefore, humid tropical alpines are potentially subjected to rapid change and degradation (Li *et al.*, 2008a).

In humid tropical alpines, dry and rainy seasons increase and decrease respectively, above 3800 m and frost occurs almost every night (Bodner and Beck, 1987) while daily temperature fluctuations dominate (Li *et al.*, 2008a). As a result, most alpine species are adapted to both micro-environments of drought and freezing temperatures throughout the year. When plant tissues freeze, ice is formed in gaps between cells, which draw water from protoplasts (Körner, 2003) whereas soil's coldness hampers water uptake of roots resulting into spatial species heterogeneity (Korner and Paulsen, 2010). Overall, frost retards plant metabolic processes in response to activation energy (Riutta *et al.*, 2006), and animal activity. Subsequently, there is decreased photosynthesis due to stronger difficulties for water flux and lower stomata conductance for CO_2 diffusion (Piper, 2010). Therefore, the exposure of afro-alpine environment to high amplitude of diurnal temperature change, but little seasonal variation has a pronounce effect on plant net productivity and thus wildlife feeding patterns (Cavieres *et al.*, 2000; Piper *et al.*, 2010). Plants and wild animals in the alpine tolerate low nutrient availability, low partial

pressures of CO_2 and intense ultraviolet radiation (Llambí *et al.*, 2003; Körner, 2003). For that matter, the concept of environmental stress in the afro-alpine ecosystem is worth being understood (Callaway, 2007; Cavieres and Badano, 2009) for effective management and conservation of such wildlife ecosystem.

Factors influencing the carbon uptake capacity within humid tropical alpines include the amount of green biomass and the physiological activity or reaction rates as determined by temperature (Lindroth *et al.*, 2007; Kikvidze *et al.*, 2011). On the other hand, the characteristics of vegetation mosaic reflect resource availability and correlate with aspects of Carbon balance and water use (Gilmanov *et al.*, 2007). Similarly, respiration is influenced by aboveground biomass, the associated belowground biomass and temperature. Low temperature reduces evapo-transpiration rates because of the high frequency of fog, cloud cover and high relative humidity (Buytaert *et al.*, 2011). Consensus views by Owen *et al.* (2007) and Moore *et al.* (2009) are being developed to provide estimates of net ecosystem exchanges of CO_2 associated with gross primary production and ecosystem respiration. These support the derivation of ecosystem model parameters for use in spatial generalizations of vegetation/atmosphere CO_2 exchange.

Understanding the carbon cycle and its dynamics in afro-alpine ecosystems is important because it provides an indicator of stability or change such as response to environmental stress or altered land use, energy balance and water use by vegetation (Otieno *et al.*, 2009; Li *et al.*, 2008b). The net ecosystem exchange of CO_2 is composed of the differences between the uptake through photosynthesis and the release through respiration (Lindroth *et al.*, 2007). These two processes probably may also represent the two largest CO_2 exchanges in the alpine ecosystem.

1.2 Research Problem and Justification

Humid tropical alpine environments provide important services both at local and global scales (Buytaert *et al.*, 2011; Li *et al.*, 2008a) particularly, carbon storage and water supply for wildlife sustenance, cities, agriculture and hydro-power. The services are at a decrease due to increased warming and land use change (Rohr and Killingtveit, 2003). The impacts of decreasing services can be transmitted to large areas and influence wildlife populations via aboveground plant productivity, and the hydrological link between upland and lowland areas (Tenhunen *et al.*, 2009). However, the most intractable threats come from the total disappearance of wildlife habitats due to different reasons including climate change. In recent decades, climate change has emerged as another threat to mount Kilimanjaro ecosystem the repercussions would be extremely serious to the biodiversity and ecosystem services including tourism activities (Hemp, 2006).

Despite the roles in ecosystem exchanges of CO_2, insufficient information exist on the ecological processes in the alpine regions in the West Eurasian and North American mountain Systems (Kikvidze *et al.*, 2011; Anthelme *et al.*, 2011; Tenhunen *et al.*, 2009; Li *et al.*, 2008b) and in Mount Kenya (Schulze *et al.*, 1985) with no mention on the state of the matter for the alpine zone of Mount Kilimanjaro. Scanty information is attributable partly to the logistic difficulties of carrying out comprehensive ecological studies in such complex terrain. Meanwhile, it is critical to improve our knowledge and understanding primarily on net ecosystem exchange of CO_2 characterized by gross primary productivity, total ecosystem respiration and biomass in the alpine region of Mt. Kilimanjaro. Therefore, this study sought to determine the causal relationships between the CO_2 exchange components i.e., gross primary productivity (GPP), ecosystem respiration (Reco) and biomass according to micro-environmental changes to see what drives ecosystem exchanges of CO_2. The findings through quantitative description of ecosystem-

scale characteristics will enhance our understanding, prediction of plant species performance and may help management of the alpine ecosystem, which forms part of the Kilimanjaro National Park, a Biosphere reserve as well as world heritage site.

1.3 Research Objectives and Hypothesis

1.3.1 General objective

The study seeks to investigate the influence of micro-environmental conditions on ecosystem exchanges of CO_2 in the afro-alpine zone of Mt. Kilimanjaro, Tanzania.

1.3.2 Specific objectives

(i) To assess net ecosystem exchanges of CO_2 and ecosystem respiration

(ii) To determine the biomass and Leaf area of dominant plant species

(iii) To evaluate the effect of temporal and spatial variation in abiotic factors on ecosystem exchanges of CO_2

1.4 Research Hypotheses

H_o: Micro-environment conditions have no influence on ecosystem exchanges of CO_2 and ecosystem respiration in the afro-alpine zone.

H_A: Micro-environment conditions determine ecosystem exchanges of CO_2 and ecosystem respiration in the afro-alpine zone.

CHAPTER TWO

2.0 LITERATURE REVIEW

2.1 Tropical Alpine Ecosystem

Despite common features of alpine ecosystems such as reduction in air temperature, pressure and relative humidity, and increasing solar radiation (Korner, 2003). Tropical alpine environments are characterized by unique environmental characteristics (especially in their most humid part) resulting from bio-geographical and climatic specificities (Li *et al.*, 2008a; Malhi *et al.*, 2010). Among these are a lack of clear seasonality, the absence of prolonged dry periods and marked day to day climatic variation (Buytaert *et al.*, 2011; Antheleme *et al.*, 2011; Korner, 2003). Consequently, tropical mountains have evolved singular plant communities characterized by a continuous vegetative period and exceptional taxonomic and functional diversity (resulting from both physiological and morphological adaptations) even within a given plant growth form like the cushion plants *Helichrysum newnii* (Antheleme *et al.*, 2011). Managing mountain biodiversity has increasingly been recognized as a global responsibility in recent decades (Malhi *et al.*, 2010; Hofer, 2005). Climate change may further increase the pressure for more conservation as well as for more intensive resource use in mountains (Kikvidze *et al.*, 2011; Otieno *et al.*, 2009). Innovative concepts and approaches are thus required to reconcile biodiversity conservation with development (Anthelme *et al.*, 2011; Tenhunen *et al.*, 2009).

Furthermore, the importance of integrated ecosystem research in mountain areas provided the focus of the UNESCO programme "Man and the Biosphere" (MAB) reserves. MAB's goal number one is to protect and maintain terrestrial ecosystems that are threatened by intensification of economic development (Tenhunen *et al.*, 2009). Developmental needs

result into changes in the composition and structure of the vegetation and ecosystem processes, altering ecological stability and causing change in wild animal species and/or disappearance (Li *et al.*, 2008b).

2.2 Ecological Characteristics of Kilimanjaro Afro-alpine Zone

Ecologically, Kilimanjaro ecosystem is outstandingly unique (UNEP *et al.*, 2006; Hemp, 2006). Climate has formed distinct ecological zones affecting wildlife species along the gradient like the alpine zone which starts from 3800 m above sea level with varying conditions (Cavieres and Badano, 2009). The alpine environment is stressful throughout the year (Martin *et al.*, 2007). Stressful environments are best defined as those in which producers are limited by the environment in their ability to convert energy to biomass (Maestre *et al.*, 2008) thus reducing the quality of wildlife habitats.

The outcome of biotic interactions along productivity-based stress gradients may vary depending on the stress tolerance and competitive ability of the interacting species (Körner and Paulsen, 2010). Focus on vegetation development in response to daily change in micro climate influencing the potential for CO_2 uptake and gross primary productivity (Li *et al.*, 2008a) is required. The ecosystem exchange of CO_2 in the alpine is composed of several significant fluxes and parameters (Lindroth *et al.*, 2007). The fluxes include carbon, water and nutrient cycles while the parameters are species composition, biomass and leaf area (Gilmanov *et al.*, 2007). Given the taxonomic and micro habitat diversity in the alpine zone, mono-specific studies are at risk to reflect curiosity rather more than general principles (Körner, 2003). Parameters that define the capacity of ecosystems for carbon absorptions (GPP) and emissions (Reco) are key components in models of carbon dynamics (Owen *et al.*, 2007; Dhital *et al.*, 2010).

2.3 Alpine Micro-environmental Conditions

Micro-environmental heterogeneity is important for the distribution and diversity of plants (Cavieres, 2005; Hemp, 2006). Sources of micro-environmental variation include canopy heterogeneity, inter- and intra-specific relations, edaphic conditions (pH, litter) and topography (Li *et al.*, 2008b; Hofer, 2005; Reichstein *et al.*, 2003). Among these variables, canopy heterogeneity is suggested as an important source of variation since it can modify variables such as light intensity, temperature, soil and seed dispersal (Hussein *et al.*, 2009; Zhao *et al.*, 2010). Climatic change is expected to have pronounced effects on these micro-environment conditions (Antheleme *et al.*, 2011; Tenhunen, *et al.*, 2009). Future warming is predicted to enhance evaporation, promote surface drying and impact on net ecosystem exchanges of CO_2 and respiration (Martin *et al.*, 2007).

The dominant growth forms in the alpine are the cushion-forming plants such as the genera *Herychrusm*, *Snecio*, *Festuca* and *Lobelia* facilitating other plants by creating biogenic habitats (Cavieres and Badano, 2009). The dominant shrub species are of the genus *Herychrysum* having a continuous layer of grasses and herbs in the understory influenced by gradients in habitat factors (Hemp, 2006). However, cushion plants (*H. newnii*) may contribute to the ecosystem exchanges of CO_2 through inhibiting temperature regime and photosynthetic capacity (Kikvidze *et al.*, 2011). Cushion plant increases leaf area (LA), average leaf light utilization efficiency, length of the active period for carbon uptake and sensitivity of stomata to changes in soil moisture (Owen *et al.*, 2007). The leaf area influences surface flux exchanges and other micro-environmental boundaries interactions (Moore *et al.*, 2009). Leaf area affects ecosystem respiration estimates, soil respiration through light-response functions analysis hence reducing the gross photosynthetic uptake (Gilmanov *et al.*, 2007).

CHAPTER THREE

3.0 METHODOLOGY

3.1 Study Area

Mount Kilimanjaro lies in northern Tanzania between 2° 45' and 3° 25'S and between 37° 00' and 37° 43'E. It is the highest mountain in Africa, rising to 5895 m a.s.l. The mountain has three main volcanic peaks: Kibo (5895 m), Mawenzi (5149 m) and Shira plateau (3962 m). Also, the whole mountain above 2700 m, covering an area of 1831.81 km^2 comprises the Kilimanjaro National Park (KINAPA) that was established in 1977. KINAPA was inscribed on the World Heritage site list in 1987 (TANAPA, 2006; UNEP *et al.*, 2006). Rainfall and temperature decreases with increase in altitude.

The study location was within the alpine zone, which starts from the transition of the ericaceous zone *ca.* 3790 m a.s.l, up to 5000 m (Niemela and Pellikka, 2004; TANAPA, 2006). The zone receives little rainfall, less than 250 mm per annum (Hemp, 2006). Furthermore, it experiences extreme daily temperature fluctuations up to 26.7°C from day to night. The zone is characterized by low vegetation of 10–50 cm tall dwarf shrubs, often growing as hemispherical cushions; tussock grasses and herbs arising just a few centimeters from ground level (Niemela and Pellikka, 2004; Anthelme *et al.*, 2011). The lichens and mosses are also common in the alpine zone (Hemp, 2006).

3.1.1 Study species

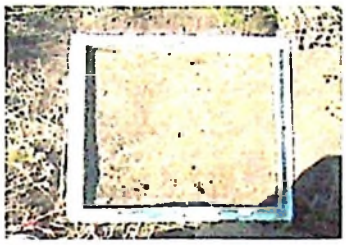
Alpine plants of Mt. Kilimanjaro include genera of *Helichrysum, Festuca, Alchemilla, Senecio* and *Lobelia* (Hemp, 2006). *Helichrysum newnii* is a shrub in the family Asteraceae whose stature mainly raises to about 0.5 m forms a rounded bush (cushions) which is often wider than higher; the leaves are narrow 6 mm to 22 mm long. *H. newii*

have been found at an attitude as high as 5760 m (Hemp, 2006). A tussock grass *Festuca abysinica* in the family Poaceae is among the upper montane dwarf grasses found above 2800 m a.s.l. Their leaves are 15 mm to 60 mm long; leaf-sheaths smooth and glabrous on surface. In addition, the herbaceous perennial plant *Alchemilla johnstonii* found in the family Rosaceae is the dominant plant creeping under the cushions. *A. johnstonii* is a carpet clump forming whorl basal long stalked fan shaped leaves covered with soft hairs, showing high degree of water resistance. Overall many plant species within the zone are endemic and becomes more specially adapted to harsh climate conditions exhibiting striking specializations (Hemp, 2006). Among the dominant plants only *H. newnii*, *F. abysinica* and *A. johnstonii* were included for chamber measurements. The *H. newnii* covers about one third of the alpine ecosystem hence it has been considered as important component due to their abundance worth for this study. The *H. newnii* supports the *A. johnstonii* and *F. abysinica* growing on the understory. Other plant species found in the zone but non-dominant were *Luzula abysinica*, *A. argyrophylla* and *H. citirspinum.* These three were not included in biomass measurements due to time and human resource constraints.

3.2 Experimental Design and Sampling Procedure

A sample block of 100 m x 100 m was delineated within the alpine zone. Corners of the plot were marked with poles. The 100 m x 100 m plot was divided into five grid squares of 20 m x 20 m subplots. Later on, three subplots (20 m x 20 m grid) were systematically selected depending on the possibility of having a combination of dominant species to include in the chamber measurement for CO_2. The subplots were about 60 m to 80 m apart for repetitions.

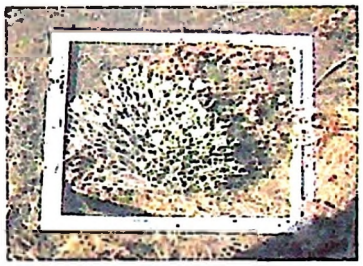
Within each of the three subplots, six plastic soil frames (38 cm x 38 cm x 10 cm) having single and combination of dominant species were established. The soil frames were named as none (bare soil), hel (*Helichrysum newnii*), fest *(Festuca abysinica*), alch (*Alchemilla johnstonii*), helalch (*H. newnii and A. johnstonii*) and helalchfest (*H. newnii, A. johnstonii and F. abysinica*) (Plate 1). Both light chamber and dark chamber measurement rounds were done on the five soil frames of single dominant species (hel, fest, alch) and combination of dominant species (helalch and helalchfest) for net ecosystem exchange of CO_2 and Ecosystem respiration respectively, while none (bare soil) soil frame was established only for the dark chamber to measure soil respiration. The plastic soil frames ensure closed air tight system, stability of the chamber and spatial establishment of the measuring plot.



none (bare soil)

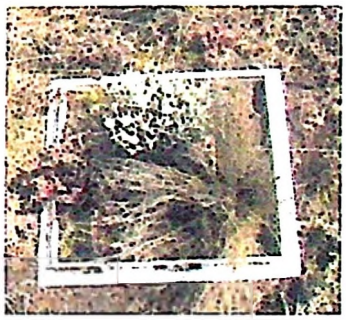
hel (*Helichrysum newnii*)

fest (*Festuca abysinica*)



helalch (*Helichrysum newnii* and *Alchemilla johnstonii*)

alch (*Alchemilla johnstonii*)



helalchfest (*Helichrysum newnii. Alchemilla johnstonii* and *Festuca abysinica*)

Plate 1: Soil frames having bare soil (none), single dominant species (alch, hel and fest) and combination of dominant species (helach and helalchfest) included in the chamber measurements for CO_2 fluxes

3.3 Data collection

3.3.1 Measurement of net ecosystem exchange of CO_2 and ecosystem respiration

During data collection, 18 days were set for a series of measurements for Net Ecosystem Exchange of CO_2 (FNEE) and Ecosystem Respiration (Reco). The measurement procedure used manually operated closed gas exchange chambers of the same size referred to as light chamber to measure net ecosystem exchange of CO_2 (FNEE) and dark chamber to measure ecosystem respiration (Reco). Infra-Red Gas Analysers (LI-820, LI-COR, Nebraska, USA) were used to measure the concentration of the gas exchanges over time. The use of Infra-Red Gas analyser is recommended for use with closed gas exchange chamber (Light and Dark chambers) method on a finer spatial scale (Chojnicki *et al.*, 2010).

The light chamber, 40 cm x 40 cm x 54 cm, (Plate 2) was constructed of transparent plexiglass (3 mm XT type 20070 and light transmission 95%). Contrary, the dark chamber (Plate 3) was constructed of opaque PVC, covered with an opaque insulation layer and reflective aluminium foil. In each chamber, a thermometer (Digital thermometer, Conrad, Hirschau, Germany) was installed in order to measure air temperature inside and outside the chamber during measurements. Both light and dark chambers were placed on plastic soil frames that were inserted into the ground 0.05 m deep, nine days before measurement days to ensure that each system had no air leakage. Six plastic soil frames were placed at each of the three subplots. This number is based on logistic considerations (minimize movement time to maximize frequency of sampling rotations) and the desire to obtain comparisons between soil frames (replicate). However, the effect at subplot location was not followed up as all three subplots could not be sampled on the same day and time due to limited human resource and equipment, but the subplots served as replicates.

Each plastic soil frame was further sealed to the chamber with a flexible rubber gasket and the chamber firmly secured using elastic bands fastened onto the ground from two sides. Following Droesler (2005), each chamber was tested for leakage wherever it was possible to do so to ascertain that the system remained air tight. The excessive air pressure into the chamber was avoided through a 12 mm diameter opening at the top of the chamber before the chamber is placed onto the soil frame. Thereafter, the opening was closed before on set of CO_2 flux measurement. Mixing of air within the dark and light chambers was provided by three and four fans respectively, yielding a wind speed of about 1.2 ms^{-1}. Inflow and outflow flexible tubes of 3 m long and 0.32 cm diameter (Bev-A-Line, LI-COR, USA) were used for connecting the chambers to an Infra-Red Gas Analyser (LI-820, LI-COR, Nebraska, USA) (Plate 4). Changes in chamber CO_2 concentration over time was assessed with a portable, battery operated pump IRGA (LCA2, ADC, UK). Influence of the concentration change on estimated gas exchange rates was avoided by mounting frozen ice packs (0.33264L) on the backside of the dark and light chambers in the air flow (Plate 5). The frozen ice packs also prevented any rapid build-up of water vapour in the chamber during measurements. Temperature during measurements was stabilized within 2°C relative to ambient air temperatures inside and outside of the chambers.

Light and dark chamber measurements were conducted cyclically on hourly intervals from morning 0800 to 1700 hours during measurement days. Once the rate of concentration change on the air tight system was approximately steady, data were recorded every 15 seconds for a period of 2 minutes and 15 seconds before shifting to the next soil frame. One measurement round comprised of the light and dark chambers measurements rotations. Eight to nine measurement rotations were accomplished on individual days and the gas exchange data compiled together with the micro-environment

data of soil, air and inside chamber temperatures, and Photosynthetic Active Radiation (PAR) within the chamber (Plate 6). The measurements were carried out from Wednesday, 11 July to Sunday, 19 August 2012, at 6-day interval. Low temperature (sometimes frost on leaves) in the morning and evening prevented starting and continuation of the observations with chambers, since low temperature showed water vapour dilution effect on CO_2 fluxes (Li *et al.*, 2008).

During data collection, one day, Thursday 15 August 2012 was reserved for the measurement of soil frames having combination of dominant species that were not included in the chamber measurement analysis for this study just to see the diurnal variations on CO_2 exchanges for these combination i.e. *H. newnii* and *F. abyisinica* (helfest) and *A. johnstonii* and *F. abysinica* (alchfest).

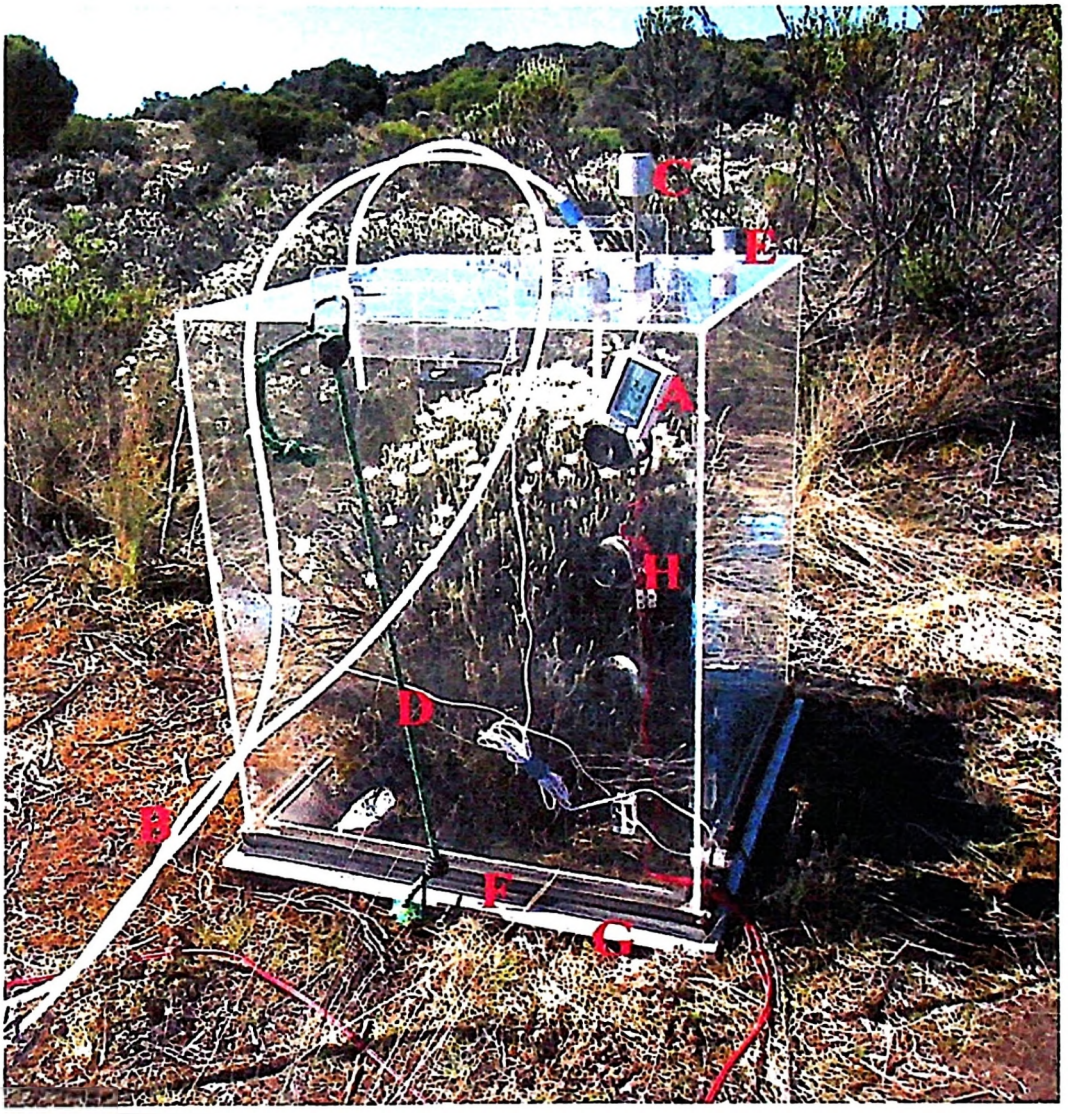


Plate 2: Light chamber (light transmission 95%) mounted on *Helichrysum newnii* for measuring net ecosystem exchange of CO_2 (FNEE), A = digital thermometer; B = flexible inflow and outflow pipes; C = fan rod; D = elastic band; E = opening (12mm); F = rubber gasket; G = Soil frame, and H = fan

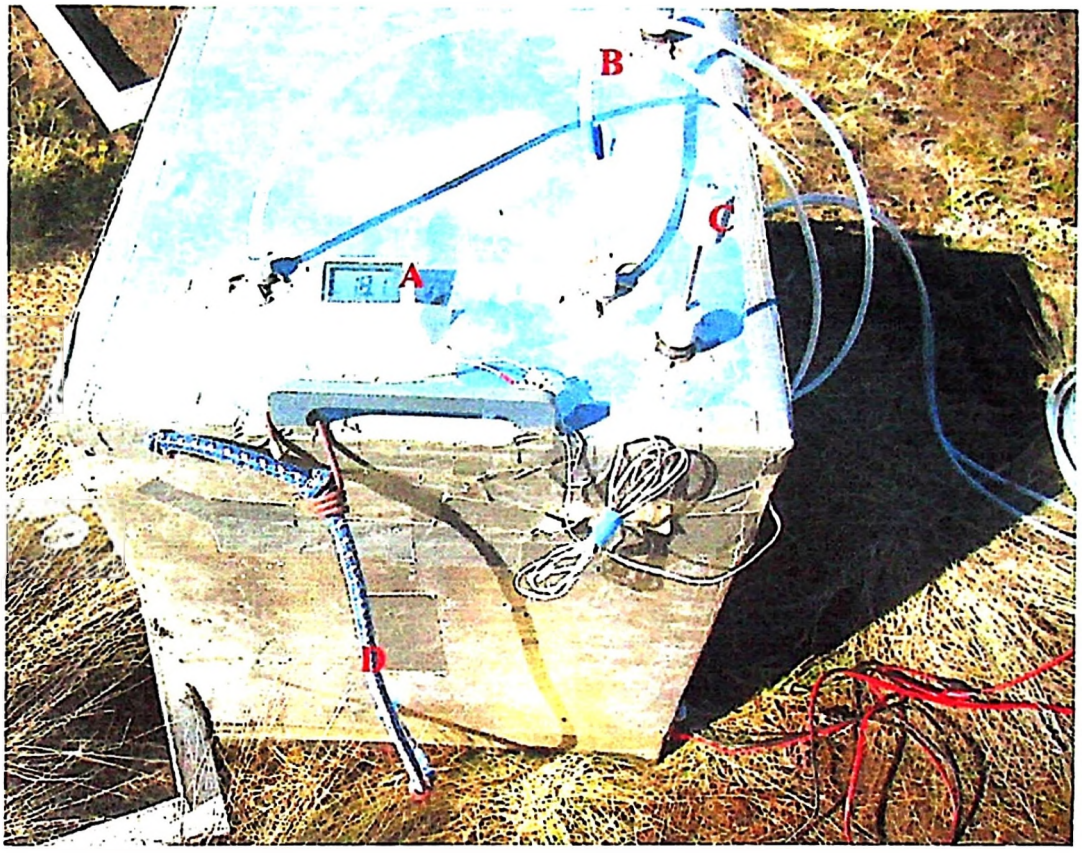


Plate 3: **Dark chamber (Opaque, PVC insulation layer and reflective aluminium foil) for measuring ecosystem respiration (Reco); A = digital thermometer; B = Inflow and outflow tubes; C = fan rod, and D = elastic bands**

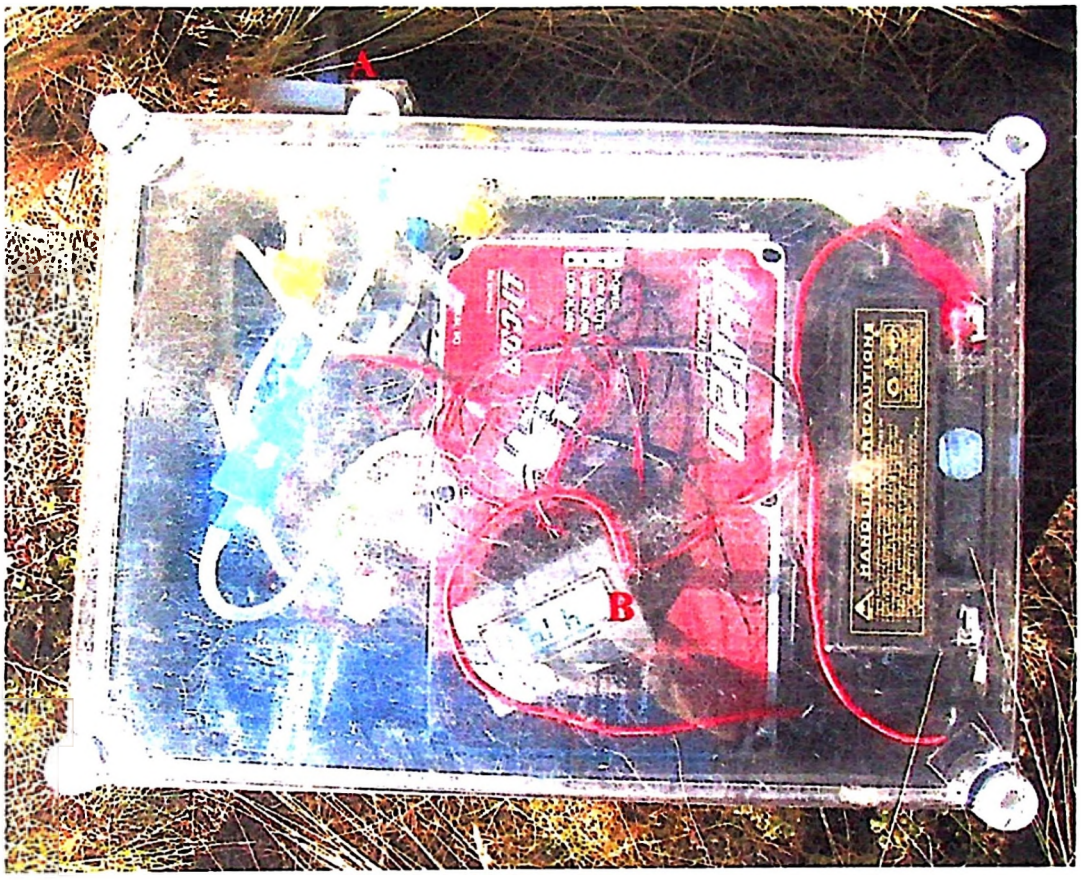


Plate 4: **Infra-Red Gas Analyzer (LI-820, LI-COR, Nebraska, USA), A = A connection for inflow and outflow tubes to the chamber and B = digital reader for CO_2 concentrations (ppm)**

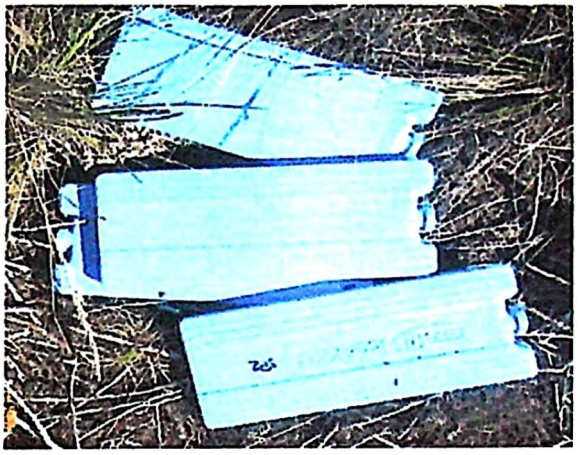


Plate 5: Cool packs (ice box) to be mounted on the backside of the light and dark chamber

Plate 6: A plastic soil frame (*Alchemilla johnstonii*) having, A = digital thermometer (Einstich thermometer, Conrad, Hirschau, Germany) for measuring soil temperature at 0.1 m and, B = a light sensor (LI-190 Quantum sensor, LI-COR, USA) for measuring Photosynthetic Active Radiation (PAR)

3.3.2 Determination of biomasses and Leaf area of single and combination of dominant species

After gas exchange measurements, all the aboveground biomass within soil frames in each of the three subplots were harvested, and sorted out in the laboratory into green leaf and green stem. Thereafter the samples (green leaf and green stem) were oven dried in paper bags at 80^0C for 48 hours and weighed to determine dry biomass for each vegetation compartment. Leaf area of green leaves were measured using a digital scanner before being oven dried as an index of amount of light energy use by the plant.

3.3.3 Quantification of temporal and spatial variation in abiotic factors on ecosystem CO_2 exchanges

Temporal and spatial variations from 0800 to 1700 hours both within and outside the soil frame were measured. The soil frames formed the basis for spatial variations. Within the soil frame air temperature inside and outside the chambers (light and dark), soil temperature at 0.1 m deep (using Einstich thermometer, Conrad, Hirschau, Germany), soil moisture (using ECH$_2$O-logger (*Em* 50)) and soil pH (using pH-meter) were measured at the start and end of CO_2 fluxes measurements for a period of 2 minutes and 15 seconds. Moreover, Photosynthetic Active Radiation (PAR) was measured using LI-190 Quantum sensor, LI-COR, USA for light chamber measurements. On the other hand, air temperature, humidity and Vapour pressure deficit were measured using funky device VAISALA HMP45A, Helsinki, Finland at vertical profiles from soil surface; 0.1 m, 1 m, 2 m within and outside the cushion plants (*H. citrispinum* and *H. newnii*) outside the soil frame. Additional spatial measurement was soil depth on each soil frame (38 cm x 38 cm) using a 0.5 m rod deepened at nine points of each soil frame and averaged. The basis for measuring within the soil frame was to determine the micro-environmental variation between the soil frames while measurements outside the soil frame provided the overall

environmental condition for the study area. Measurements within and outside the cushion plants (*H. newnii*) were geared towards describing the micro-environmental differences between the two strata.

3.4 Data Summary and Statistical Analysis

R statistical package was used for data computation and statistical analysis.

3.4.1 Net ecosystem exchange of CO_2 and ecosystem respiration

Empirical descriptions of the measured time series FNEE fluxes were validated in terms of temporal linearity of CO_2 concentration (Chojnicki *et al.*, 2010). Subplots were not included in the analysis as the data were not taken on the same day and time. The correlation coefficient (R^2) was calculated for each measurement series (two minutes and fifteen seconds) on a single and combination of dominant plant species. If $R^2 > 0.95$ then CO_2 flux rate (FCO_2) was calculated using the following equation:

$$FCO_2 = k * (T_0/T_1) * (V/A) * (P_1/P_0)*(dc/dt^{-1}) \quad \text{..... (1)}$$

Where:

FCO_2 refers to CO_2 flux [mgCO2 m^{-2} h^{-1}];

k refers to gas-constant at 273.15 K = 0.536 =[µg C $µl^{-1}$];

T_1 refers to mean air temperature inside the chamber [K];

T_0 refers to air temperature 273.15 [K];

V refers to chamber volume (Chamber volume + Vsoil Inequality – Vcool packs) [L];

A refers to area of soil frame [m^2];

P_0/P_1 refers to partial air pressure assumed to be stable during measurement period;

dc/dt refers to CO_2 concentration change in chamber estimated using linear regression [mg CO_2 m^{-2} h^{-1}].

Gross Primary Production (GPP) or total amount of carbon fixed during photosynthesis by plant in an ecosystem:

GPP = Reco – FNEE.....(2)

Where:

Reco refers to Ecosystem Respiration [μmol m^{-2} s^{-1}]

FNEE refers to Net Ecosystem Exchange [μmol m^{-2} s^{-1}]

Reco and FNEE were calculated using the following formulas:

Soil respiration (Rsoil) = CO_2 released from the bare soil

Reco = CO_2 released from the soil (Rsoil) + plant (Rplant)..... (3)

FNEE = GPP + Reco..... (4)

Analysis of net ecosystem exchange of CO_2 and ecosystem respiration of single and combination of dominant species were done using regression analysis describing the time dependent change in CO_2 concentration in both light and dark chambers. Data were individually fitted to the corresponding dataset.

3.4.2 Estimation of biomass and leaf area of dominant species

The green dry biomasses for single and combination of dominant species within the soil frames were used to normalize FNEE per unit green biomass on the basis of leaf area as an indicator of canopy light utilization.

3.4.3 Temporal and spatial variation in abiotic factors on ecosystem CO_2 exchanges

Regression analysis was made on CO_2 flux components i.e. FNEE and Reco in order to assess diurnal dependencies of CO_2 concentrations (Equation 1) on five environmental variables i.e. air and soil temperatures, Photosynthetic Active Radiation (PAR), humidity and Vapour Pressure deficit (VPD). Also, the spatial aspect was related to the deferring CO_2 fluxes and micro-environment in each soil frame.

CHAPTER FOUR

4.0 RESULTS

4.1 An Overview on Environmental Conditions

The variation of weather conditions between days was detected on days with clear sky, cloudy, sunny and windy days. The highest and lowest mean daily Photosynthetic Active Radiation (PAR) recorded were between day nine and day thirty one respectively (Fig. 1).

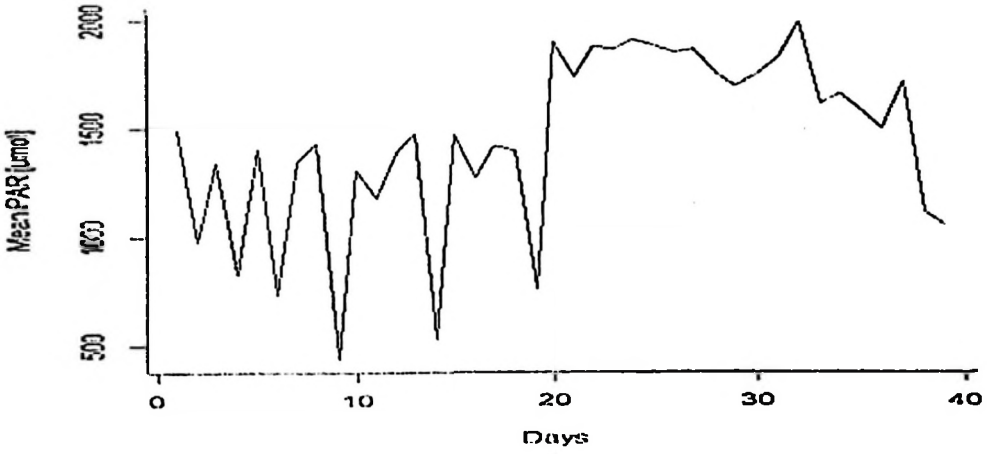


Figure 1: Mean daily Photosynthetic Active Radiation (PAR) during data collection days from Wednesday, 11 July 2012 to Monday, 20 August 2012

The highest mean diurnal daily temperature profiles at 2 m above the vegetation ranged from $6^0C - 26^0C$ (Fig 2). To the contrary, the lowest mean ranges were from $5^0C - 15^0C$ and from $5^0C - 12.9^0C$ at 1 m outside and within the cushion plant (*H. newnii*) respectively (Fig. 3 and 4).

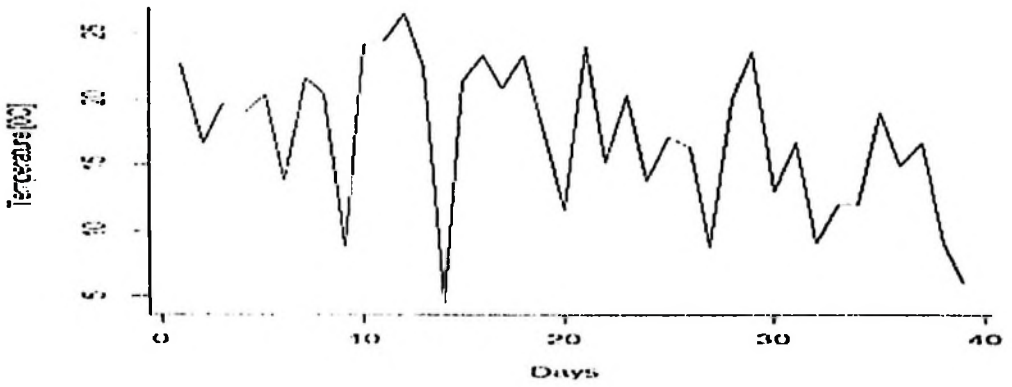


Figure 2: Mean daily diurnal variations of air temperature above vegetation at 2 m from the soil surface, from Wednesday, 11 July 2012 to Monday, 20 August 2012

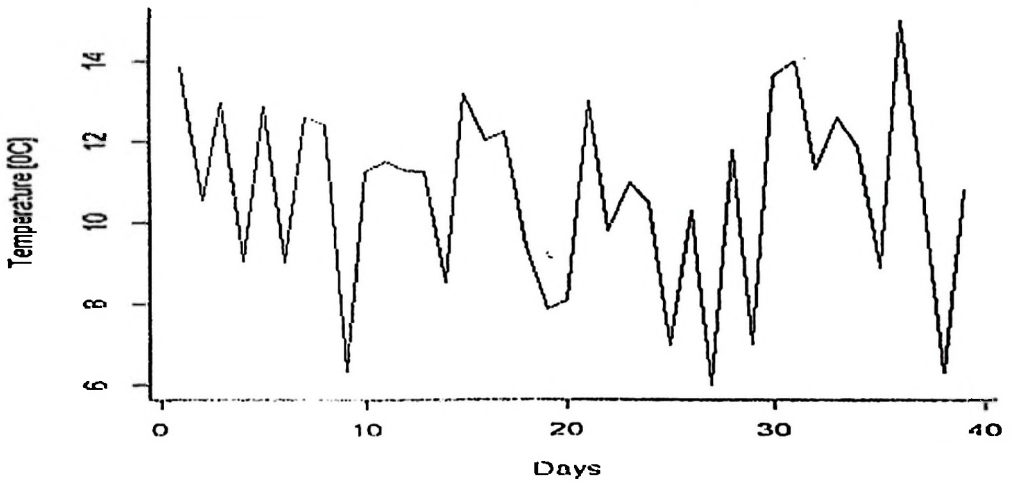


Figure 3: Variations of mean daily diurnal air temperature at 1 m from soil surface, free of vegetation (outside the cushion plant) from Wednesday, 11 July 2012 to Monday, 20 August 2012

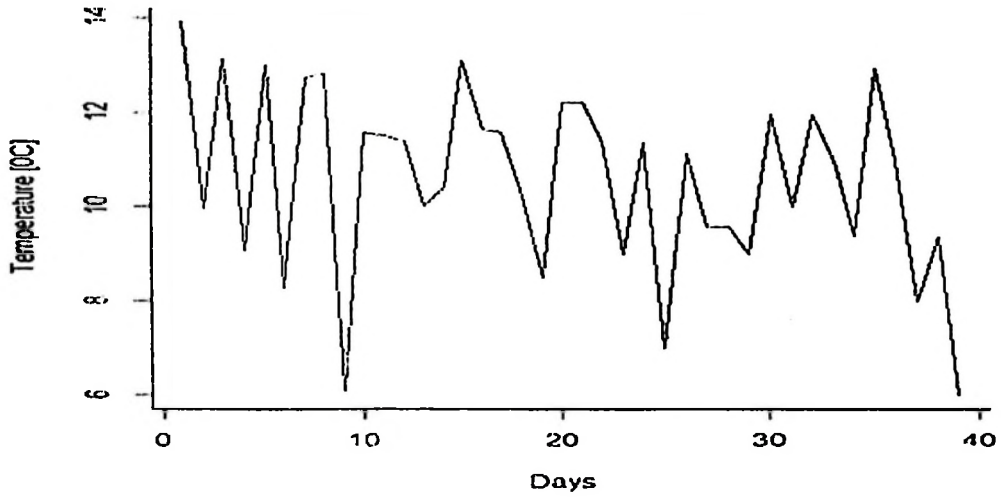


Figure 4: Mean daily diurnal air temperature at 1 m within the cushion plant *Helichrysum newnii* from Wednesday, 11 July 2012 to Monday, 20 August 2012

Moreover, the study revealed that temperature variations negatively influence humidity but positively influence Vapor pressure deficit (Appendix 1). The maximum and minimum soil temperatures at 0.1 m depth were found on day 6 and 14 respectively (Fig. 5).

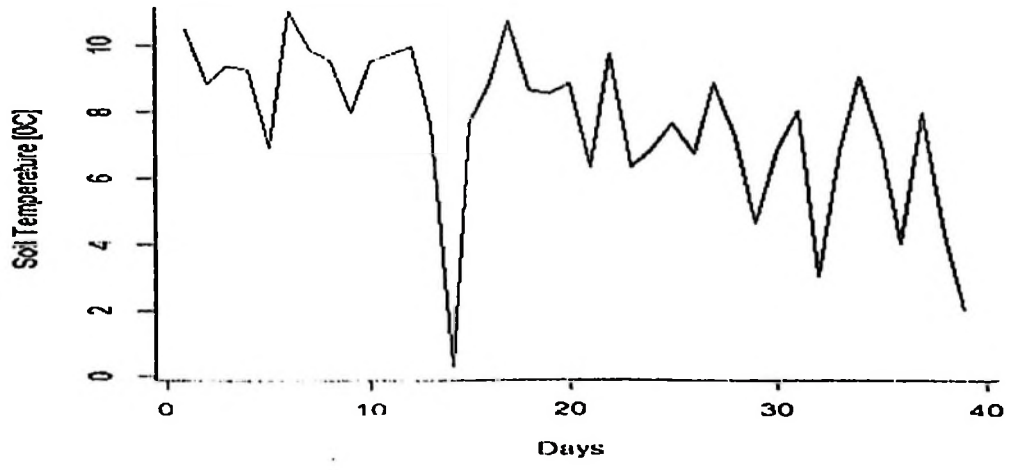


Figure 5: Mean daily soil temperature at 0.1 m from Wednesday, 11 July 2012 to Monday, 20 August 2012

4.2 Net ecosystem exchange of CO_2 and ecosystem respiration

An increase in CO_2 concentration with time was detected from the ecosystem respiration (Reco) measurement (dark chamber, Fig. 6) alongside a decreasing trend in concentration of the gas as depicted from the measurement of Net Ecosystem Exchange of CO_2 (FNEE) (Light chamber, Fig. 7) for all measurements of single and combination of dominant species. There was about 100 ppmv depletion measured at the highest PAR conditions. The coefficient of linear correlations (R^2) between the CO_2 concentration and time ranged from 0.7226 to 0.9874, for each measurement in both chambers.

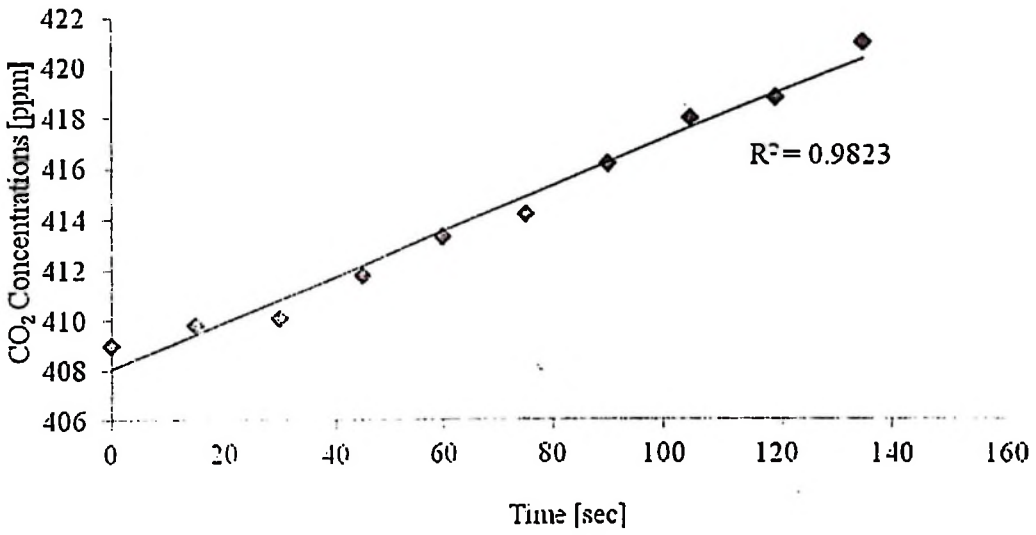


Figure 6: CO_2 concentration as per dark chamber measurement from Wednesday, 11 July 2012 to Monday, 20 August 2012

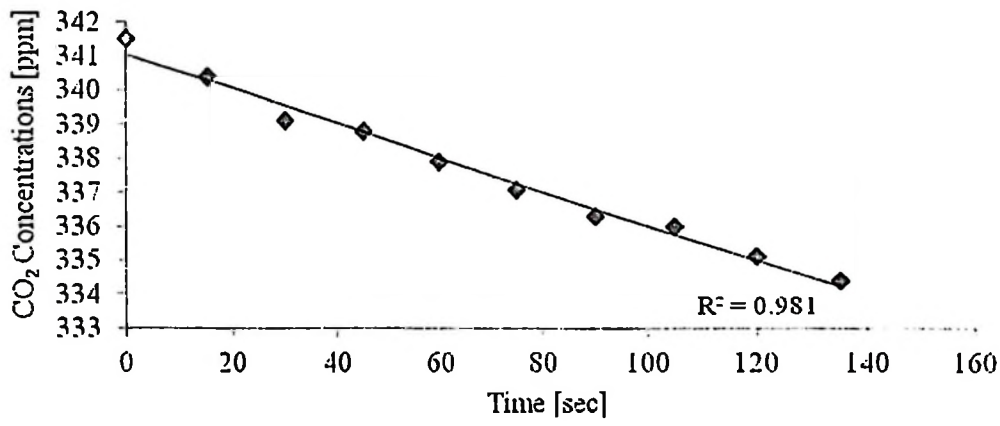


Figure 7: CO_2 concentration in light chamber from Wednesday, 11 July 2012 to Monday, 20 August 2012

H. newnii had the highest daily mean FNEE release recorded on Wednesday, 11 July 2012 while a soil frame with combination of dominant species of *H. newnii* and *A. johnstonii* recorded the lowest release on Friday, 17 August 2012 (Table 1). Reco were highest for a soil frame with combination of dominant species of *H. newnii* and *A. johnstonii* recorded on Thursday, 26 July 2012 (Table 2) whereas plant respiration was also highest for combination of species of *H. newnii* and *A. johnstonii* on Wednesday, 11 July 2012 (Table 3).

Based on data collection days, the study observed slight fluctuations in Reco levels. For example, the highest mean daily Reco on Wednesday, 11 July 2012 ranged from 2.44 μmol $m^{-2}s^{-1}$ to 4.26 μmol $m^{-2}s^{-1}$ and the lowest on Sunday, 19 August 2012 which ranged from 1.35 to 2.20 μmol $m^{-2}s^{-1}$ (Table 2).

Combination of *H. newnii* and *A. johnstonii* had the highest mean daily GPP recorded on Wednesday, 11 July 2012 while *A. johnstonii* recorded the lowest GPP on Thursday, 12

August 2012 (Table 4). Moreover, the mean daily GPP/Reco ratio of the ecosystem on Sunday, 12 August 2012 was smaller than for Wednesday, 11 July 2012 and Tuesday, 17 July 2012 (Appendix 2).

Table 1: Mean daily Net Ecosystem Exchanges of CO_2 (FNEE) for soil frames of single dominant species *Alchemilla johnstonii* (alch); *Festuca abysinica* (fest); *Helichrysum newnii* (hel), and combination of dominant species *Helichrysum newnii*, *Alchemilla johnstonii* and *Festuca abysinica* (helalchfest); and *Helichrysum newnii* and *Alchemilla johnstonii* (helalch)

Date	Subplot	alch	fest	hel	helalchfest	helalch
11/7/2012	I	-0.9306	-0.9332	1.3398	-1.7643	-4.9512
17/7/2012	I	-0.3560	-1.4180	0.6481	-2.2591	-4.7369
07/26/2012	I	-0.3004	-0.8022	0.9207	-1.4407	-3.9358
01/8/2012	I	-0.5918	-0.4334	0.6052	-2.1887	-4.3599
11/8/2012	I	1.0605	-0.8266	0.6827	-1.7178	-4.5500
17/8/2012	I	-0.5080	-1.5921	0.0523	-3.2731	-6.2150
12/7/2012	II	0.3634	-2.0692	0.2208	-2.6065	-2.3129
18/7/2012	II	0.6959	-1.5981	-0.1621	-2.0516	-1.1546
27/7/2012	II	0.2728	-1.1963	-0.7636	-1.7593	-0.9991
02/8/2012	II	0.7751	-2.0637	-0.1483	-1.8765	-1.6803
12/8/2012	II	1.3306	-1.6967	0.0806	-1.3507	-1.0355
18/8/2012	II	0.5186	-2.1262	-0.5090	-2.6347	-1.8120
13/7/2012	III	-1.4403	-1.5784	-0.1698	-0.2723	-2.4538
19/7/2012	III	-2.3287	-3.5492	-1.1752	-0.7949	-2.6248
28/7/2012	III	-0.3326	-1.7632	-0.4152	0.1250	-1.1353
03/8/2012	III	-0.2471	-1.7836	-0.4636	-0.0015	-1.8800
13/8/2012	III	0.2547	-1.5906	-1.1477	0.6013	-1.0882
19/8//2012	III	-1.0360	-1.5206	-1.5576	-0.6740	-2.0421

The mean FNEE uptake is highest for the combination of species *H. newnii* and *A. johnstonii* (helalch) and it varied significantly from other single or combination of species (p= 0.025; F=15.06; df. 4). The difference was detected between combination of species, helalchfest and helalch (p= 0.0027; F= 4.4356; df.1).

Table 2: Mean daily Ecosystem Respiration (Reco) for soil frames of single dominant species *Alchemilla johnstonii* (alch); *Festuca abysinica* (fest); *Helichrysum newnii* (hel), and combination of dominant species *Helichrysum newnii*, *Alchemilla johnstoni* and *Festuca abysinica* (helalchfest), and *Helichrysum newnii* and *Alchemilla johnstonii* (helalch)

Date	Subplot	alch	fest	hel	helalchfest	helalch
11/7//2012	I	2.8523	2.4444	2.4886	2.9776	4.2697
17/7/2012	I	2.4235	2.1350	1.9497	2.6235	3.6380
26/7/2012	I	2.6639	2.5581	1.9726	3.3335	4.6695
01/8/2012	I	2.2296	1.9779	1.6340	2.6146	3.4712
11/8/2012	I	4.0414	2.7959	1.9021	3.5598	3.8790
17/8/2012	I	2.4664	2.2229	1.3474	2.4326	2.8760
12/7/2012	II	2.3438	3.4299	2.4867	3.4733	3.2063
18/7/2012	II	1.9607	2.7481	2.0929	2.9413	2.6064
27/7/2012	II	1.4887	2.2785	1.7541	2.2324	2.1400
02/8/2012	II	1.8286	2.5662	1.9938	2.8627	2.5574
12/8/2012	II	2.1254	3.3135	2.2901	3.4187	3.0280
18/8/2012	II	1.7131	3.0368	1.9277	2.8470	2.6570
13/7/2012	III	3.2093	3.3640	2.3813	2.9461	4.2964
19/7/2012	III	2.2067	2.2801	1.7057	2.1704	2.7512
28/7/2012	III	3.1587	2.8740	2.0733	2.5117	3.7710
03/8/2012	III	2.0609	2.1632	1.4091	1.5920	2.8912
13/8/2012	III	2.9475	2.3546	1.8625	2.4479	3.2503
19/8/2012	III	1.9652	1.7726	1.3586	1.7438	2.2071

Table 3: Mean daily plant respiration for single dominant plant species *Alchemilla johnstonii* (alch); *Festuca abysinica* (fest); *Helichrysum newnii* (hel) and combination of dominant plant species *Helichrysum newnii*, *Alchemilla johnstonii* and *Festuca abysinica* (helalchfest); *Helichrysum newnii* and *Alchemilla johnstonii* (helalch), and Soil respiration for bare soil frame (none)

Date	Subplot	alch	fest	hel	helalchfest	helalch	none
11/7//2012	I	1.6110	1.2032	1.2473	1.7363	3.0285	1.2412
17/7/2012	I	1.1327	0.8448	0.6588	1.3326	2.3476	1.2908
26/7/2012	I	0.8552	1.9999	1.0160	2.1142	1.7804	1.4642
01/8/2012	I	0.5857	1.6713	0.9125	1.8859	1.5983	1.5768
11/8/2012	I	1.2373	1.3941	0.6502	1.1276	1.7317	1.3966
17/8/2012	I	1.7188	1.8182	0.8988	1.4383	2.7244	1.5264
12/7/2012	II	0.3778	1.1499	0.6004	1.2411	1.1013	1.1736
18/7/2012	II	1.2105	1.2818	0.6741	1.3275	1.7022	1.3791
27/7/2012	II	0.9260	1.0016	0.2820	0.3774	1.5952	1.4287
02/8/2012	II	1.3266	0.7788	-0.1961	1.0272	1.7929	1.8387
12/8/2012	II	1.0315	0.3848	-0.4179	0.7871	1.3240	2.0115
18/8/2012	II	1.7488	1.3890	1.5896	1.3354	1.6866	0.9105
13/7/2012	III	2.3191	2.1032	2.9239	1.8159	2.3191	1.4369
19/7/2012	III	1.6187	0.6513	2.4437	1.1483	1.6187	2.1395
28/7/2012	III	0.7041	1.9207	0.7925	2.0498	1.7323	1.5991
03/8/2012	III	0.6023	1.9228	0.8358	1.7446	1.4606	1.1953
13/8/2012	III	1.0663	0.4735	-0.0185	0.5668	1.3691	1.8811
19/8/2012	III	0.7502	0.5575	0.1435	0.5287	0.9920	1.2150

Table 4: Mean daily Gross Primary Productivity (GPP) for soil frame of single dominant species *Alchemilla johnstonii* (alch); *Festuca abysinica* (fest); *Helichrysum newnii* (hel), and combination of dominant species *Helichrysum newnii*, *Alchemilla johnstonii* and *Festuca abyssinica* (helalchfest), and *Helichrysum newnii* and *Alchemilla johnstonii* (helalch)

Date	Subplot	alch	fest	hel	helalchfest	helalch
11/7/2012	I	3.7829	3.3778	1.1487	4.7420	9.2210
17/7/2012	I	2.7796	3.5538	1.3022	4.8826	8.3750
26/7/2012	I	2.9644	3.3604	1.0514	4.7742	8.6053
01/8/2012	I	2.8215	2.4114	1.0288	4.8033	7.8311
11/8/2012	I	2.9809	3.6222	1.2194	5.2776	8.4290
17/8/2012	I	2.9744	3.8151	1.2950	5.7058	9.0910
12/7/2012	II	1.8991	5.4987	2.2658	6.0799	5.5192
18/7/2012	II	1.4328	4.3186	2.2383	4.9193	3.6665
27/7/2012	II	1.2159	3.4749	2.5177	3.9918	3.1392
02/8/2012	II	1.0535	4.6299	2.1422	4.7395	4.2377
12/8/2012	II	0.7947	5.0102	2.2095	4.7694	4.0636
18/8/2012	II	1.1944	5.1630	2.4367	5.4817	4.4691
13/7/2012	III	4.6497	4.9424	2.5512	3.2186	6.7503
19/7/2012	III	4.5355	5.8294	2.8810	2.9654	5.3761
28/7/2012	III	3.4914	4.6373	2.4886	2.3866	4.9064
03/8/2012	III	2.3081	3.9468	1.8727	2.4179	4.7713
13/8/2012	III	2.6928	3.9452	3.0103	1.8466	4.3386
19/8/2012	III	3.0014	3.2932	2.9163	2.4179	4.2492

4.3 Biomass and Leaf Area of Single and Combination of Dominant Species

Biomass changed differently among the measured soil frames. The highest green biomass was observed for subplot I with the combination of dominant species of *H. newnii* and *A. johnstonii* and the lowest also for sub plot I with *F. abysinica* (Table 5).

On the other hand, the highest leaf area was observed for a soil frame with combination of dominant species of *H. newnii* and *A. johnstonii* in subplot I while the lowest was for *A. johnstonii* in subplot II. Both single dominant species *H. newnii* and a soil frame with combination of dominant species of *H. newnii* and *A. johnstonii* in subplot I had the highest dry biomass (Table 5). Also biomass was related to FNEE and Reco (Fig. 9).

Table 5: Leaf area and biomass for harvested species used for FNEE and Reco measurements

Sub plot	Species/soil frames	Leaf area [gm^{-2}]	Green biomass [gm^{-2}]	Dry biomass [gm^{-2}]
I	*A. johnstonii*	760.9	76.03	75.23
I	*F. abysinica*	778.5	48.81	115.4
I	*H. newnii*	2203.6	232.13	264.16
I	*H. newnii, A. johnstonii* and *F. abysinica*	1276.1	127.66	151.18
I	*H. newnii* and *A. johnstonii*	3342.3	302.2	205.31
II	*A. johnstonii*	334.4	68.26	37.49
II	*F. abysinica*	666.9	63.53	100.28
II	*H. newnii*	1498.6	112.48	92.98
II	*H. newnii, A. johnstonii* and *F. abysinica*	1399.6	113.34	110.47
II	*H. newnii* and *A. johnstonii*	1146.3	66.7	46.78
III	*A. johnstonii*	533.8	58.48	40.54
III	*F. abysinica*	676	77.52	139.75
III	*H. newnii*	1677.7	92.63	93.31
III	*H. newnii, A. johnstonii* and *F. abysinica*	1776.7	197.71	227.44
III	*H. newnii* and *A. johnstonii*	1455.6	150.18	146.8

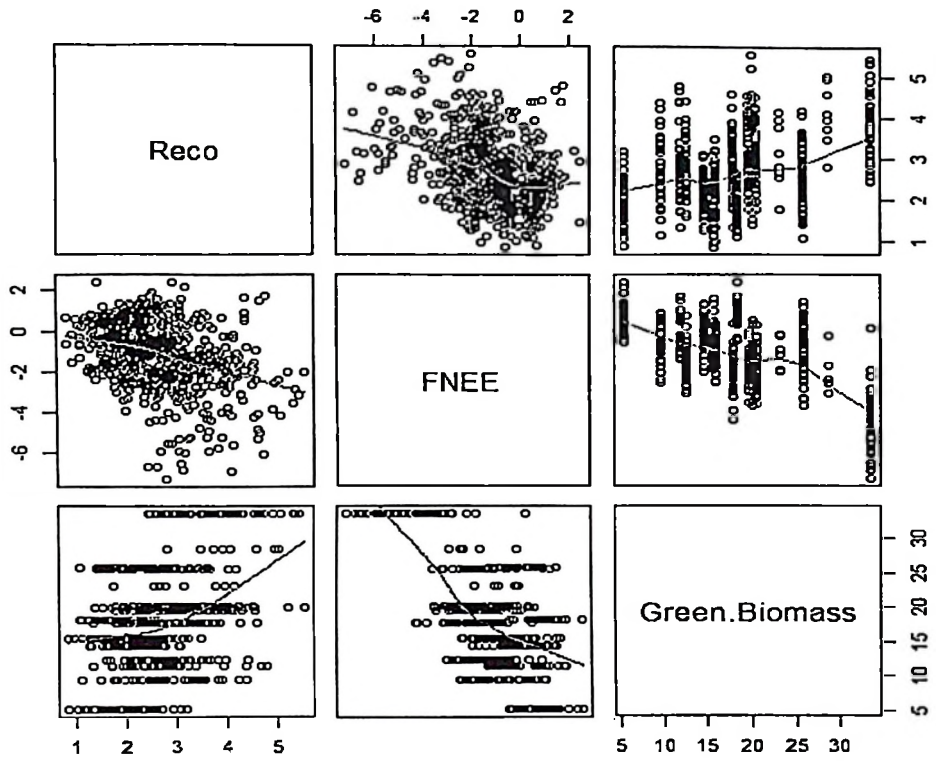


Figure 8: Data model for the influence of Green Biomass on FNEE and Reco of single and combination of dominant species

4.4 Temporal and Spatial Variation in Abiotic Factors on Ecosystem CO_2 Exchanges

The study reveals several important and consistent patterns emerging from the observed daily measurements of net ecosystem exchanges of CO_2 (FNEE), air temperature inside the chamber and PAR reached peak in the afternoon (Fig. 10-12) followed by a gradual decline. Contrary ecosystem respiration (Reco) and soil temperature peaked in the late afternoon (Fig. 13) after which they declined abruptly.

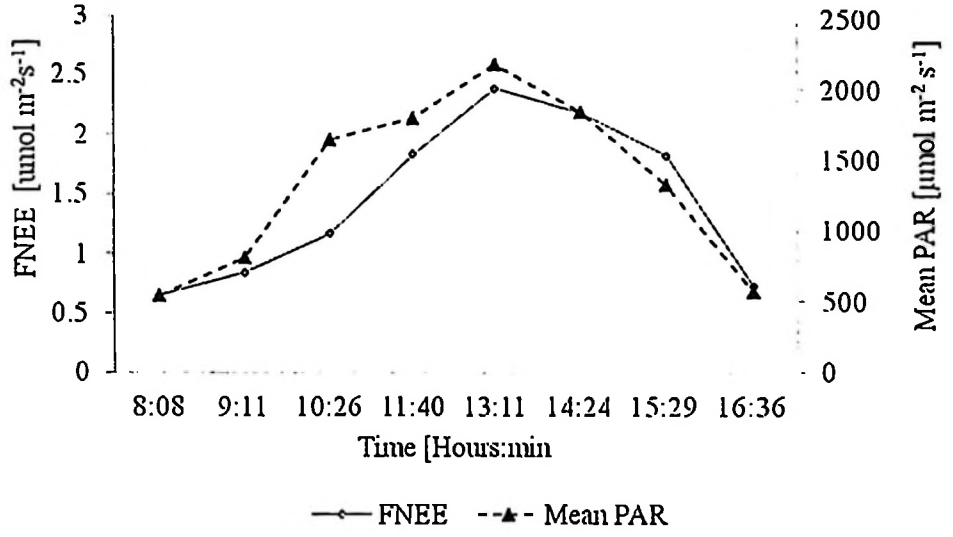


Figure 9: FNEE (CO_2 flux) and PAR measured using light chamber as depicted from Wednesday, 11 July 2012 to Monday, 20 August 2012

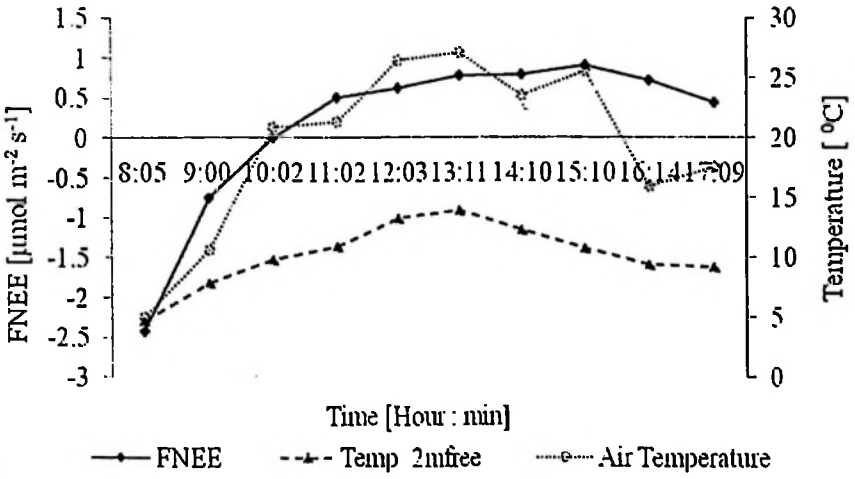


Figure 10: FNEE (CO_2 flux), temperature at 2 m above and air temperature measured from Wednesday, 11 July 2012 to Monday, 20 August 2012

Plate 7: Frozen surface of *Alchemilla johnstonii* in the morning (photo taken on Wednesday, 11 July 2012)

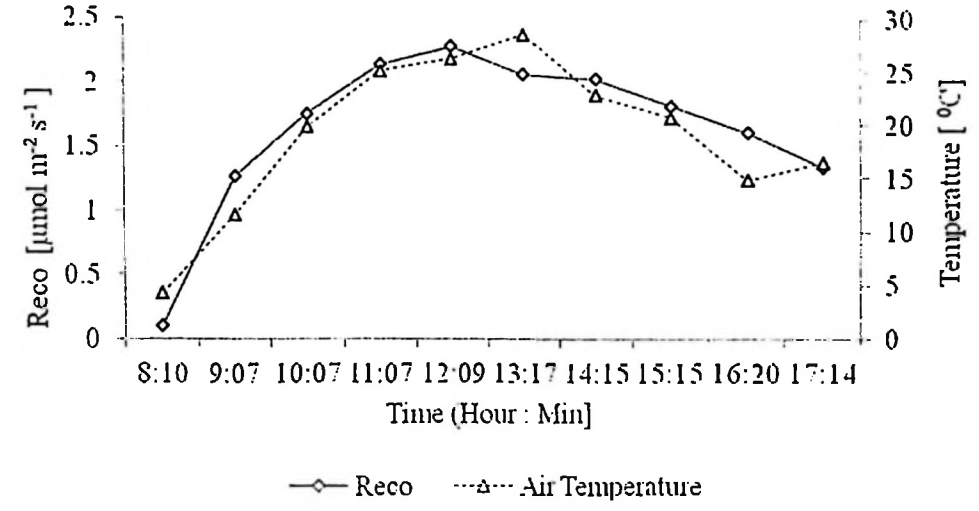


Figure 11: Reco (CO2 flux) and air temperature (inside chamber) measured from Wednesday, 11 July 2012 to Monday, 20 August 2012

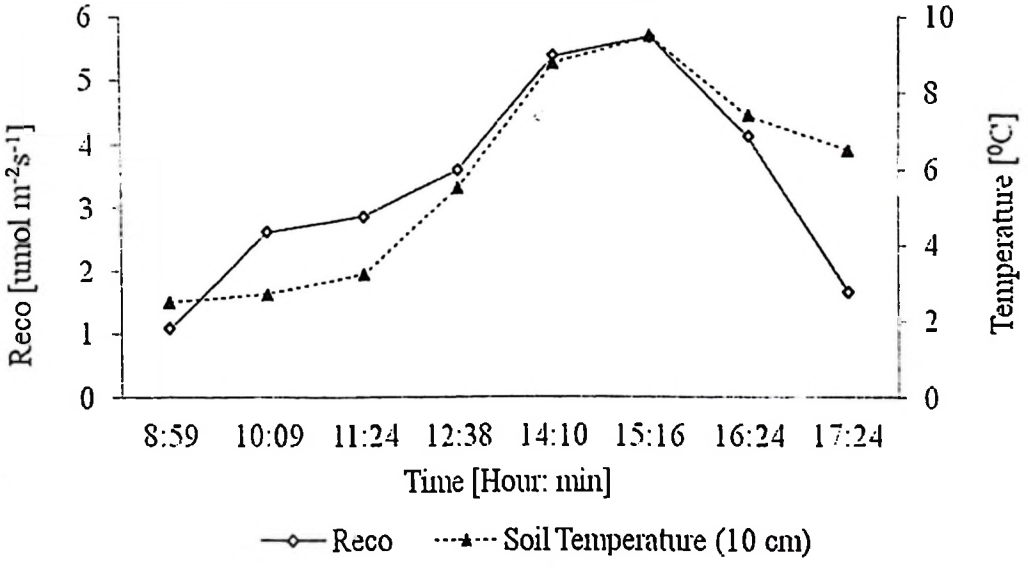


Figure 12: Reco and soil temperature at 0.1 m deep for *Helichrysum newnii* from Wednesday, 11 July 2012 to Monday, 20 August 2012

The study noted that soil pH in the alpine is slightly acidic 5.4 (Table 6). The highest mean soil depths was observed for soil frames with combination of dominant species *H. newnii, A. johstonii* and *F. abysinica* in subplot III while the lowest was observed in a soil frame with single dominant species *F. abysinica* in subplot I (Table 6).

Table 6: Spatial variation in soil pH, and soil depth (± S.d = Standard deviation) for soil frames of single dominant species *Alchemilla johnstonii* (alch); *Festuca abysinica* (fest); *Helichrysum newnii* (hel), and combination of dominant species *Helichrysum newnii, Alchemilla johnstonii* and *Festuca abysinica* (helalchfest); and *Helichrysum newnii* and *Alchemilla johnstonii* (helalch)

Subplot	Species /Soil frame	Soil pH	Mean soil depth (cm) ± S.d
I	*A. johnstonii*	5.53	30.1 ± 12.8
I	*F. abysinica*	5.3	20 ± 9.3
I	*H. newnii*	5.25	34.4 ± 4.6
I	*H. newnii, A. johnstonii* and *F. abysinica*	5.64	15.7 ± 11
I	*H. newnii* and *A. johnstonii*	5.4	39.7± 7.8
II	*A. johnstonii*	5.34	34.1 ± 3.5
II	*F. abysinica*	5.47	42.5 ± 4.3
II	*H. newnii*	5.5	23.9 ± 6.3
II	*H. newnii, A. johnstonii* and *F. abysinica*	5.35	37.2 ± 9.5
II	*H. newnii* and *A. johnstonii*	5.42	41.3 ± 4
III	*A. johnstonii*	5.3	27.7 ± 5.2
III	*F. abysinica*	5.69	28.1 ± 8
III	*H. newnii*	5.52	32.6 ± 5.7
III	*H. newnii* and *A. johstonii*	5.25	34.1 ± 10.1
III	*H. newnii, A. johstonii* and *F. abysinica*	5.58	43 ± 1.9

CHAPTER FIVE

5.0 DISCUSSION

5.1 An Overview on Environmental Conditions

Diurnal sequences of PAR, air temperature profiles and soil temperature at 0.1 m depth showed major variation over the day i.e. morning and evening values were low while afternoon hours were high. This complies with the reported general relationship of daily temperature changes in the humid alpine zone characterized by low night temperature and frost every night of the year (Schulze *et al.*, 1985, Fetene *et al.*, 1997, Owen *et al.*, 2007 and Buytaert *et al.*, 2011). However, low morning and evening temperatures were evident. During afternoon between 1200 hours and 1400 hours in some days PAR, and temperature were over 2400 μmol m^{-2} s^{-1} quantum and 38^{0}C respectively. In general temperatures were low within the cushion plant *H. newnii* as compared to outside the cushions. Such observed variations reflect the spatial differences of micro-environmental conditions of PAR, soil moisture and even nutrients. This substantiates the facilitations of the cushion plant *H. newnii* to other species under the cushion (Cavieres *et al.*, 2005). Also, it was revealed that temperature variations affect environmental conditions of Vapour Pressure Deficit and humidity (Appendix 1). Chojnicki *et al.*, 2010 and Hussain *et al.*, 2009 showed that PAR and temperature variations affect the plant CO_2 fluxes by increasing or limiting the photosynthetic metabolic activity. However, cloudy sky conditions reduce vapor pressure deficit (VPD) and temperature (Otieno *et al.*, 2009) enhancing canopy level photosynthesis (Li *et al.*, 2008b) while reducing ecosystem respiration (Hussein *et al.*, 2009) and evapo-transpiration (Cavieres *et al.*, 2005) in the alpine ecosystem hence increased in FNEE and GPP.

5.2 Net Ecosystem Exchange of CO_2 and Ecosystem Respiration

The increasing CO_2 concentration in the dark chamber demonstrates respiration activity while the decreasing CO_2 concentration in the light chamber implies that assimilation prevails over respiration in the alpine zone (Fig.6 and 7). The FNEE ranged between positive values and negative values (Table 1). According to Zhao *et al.* (2009), positive (release) and negative (uptake) values of FNEE are evidently influenced by diurnal variations of PAR. Release (emissions) is the results of plant (autotrophic) and soil (heterotrophic) respiration while uptake (assimilation) is realised through plant photosynthetic process (Equation 3 and 4).

This study illustrates that combination of dominant species i.e. *H. newnii* and *A. johnstonii* supports the most uptake of CO_2. The species *A. johnstonii* grows under *H. newnii* to maximize energy for survival and growth. Yet, the daily maximal rates of CO_2 uptake and releases were moderately low when compared with those of other species studied elsewhere (Körner, 2003; Hussain *et al.*, 2009 and Otieno *et al.*, 2009). The low CO_2 uptake rate may be related to the low nutritional status of the alpine plants (Schulze *et al.*, 1985). Also, cloudy skies and poor PAR favour net Carbon uptake of temperate ecosystems (Zhang *et al.*, 2011). Cloudiness in this study is used in a very general sense referring to the presence and quantity of clouds/fog in the sky. However, it is certain that CO_2 exchange at canopy level may decrease with elevation due to low partial pressure (Li *et al.*, 2008a).

Additionally, combination of species *H. newnii* and *A. johnstonii* recorded higher Reco value (Table 2). Similar results were published by Cavieres *et al.* (2005) and Hussain *et al.* (2009), where species combination had higher Reco and the decrease in temperature affected respiration rates directly. The daily maximum Reco during the days with sunny

and clear sky were generally observed around 1400 hours to 1500 hours. There was a time lag of two to three hours from the highest FNEE to compensate to the warming of soil temperature (Li *et al.*, 2008a). At this time of day, soil temperature at 0.1 m reached its maximum of 6^0C (Fig. 12). Indeed, increasing temperature affected the physiological status (transpiration) of the species and the soil microbial activity (Li *et al.*, 2008b). Low temperature increases the frequency of fog in contact with plants reducing respiration activity (Zhang *et al.*, 2008).

On the other hand, the higher GPP for the combination of species is linked with higher availability of energy that can be used by the plant (Cavieres *et al.*, 2005). Positive relationships between FNEE and GPP and/or fitness have been shown for several species (Otieno *et al.*, 2009; Zhao *et al.*, 2009; and Chojnick *et al.*, 2010) including non-native species (Cavieres *et al.*, 2005). Unlike single species, that had low FNEE and GPP values these results evidenced that combination of *H. newnii* and *A. johnstonii* perhaps raised the corresponding leaf-level photosynthetic capacity.

5.3 The Biomasses and Leaf Area of Single and Combination of Dominant Species

The study revealed that the green biomass and leaf area influence FNEE and GPP through enhancing the photosynthetic surface area (Fig. 8). Reco was also closely associated with leaf area. This is in agreement with the fact that sequestered carbon in an ecosystem is governed by biomass and leaf area (Chojnicki *et al.*, 2010; Anthelme *et al.*, 2011). The mean daily maximum net CO_2 uptake for combination of dominant species of *H. newnii* and *A. johnstonii* indicated that the diurnal variations in FNEE perhaps depended mainly on leaf area and biomass (Table 1 and Table 5).

The interaction of growth forms of the species, species combination and leaf area account for the creation of micro-environmental conditions. Growth forms such as creeping herb (*A. johnstonii)* and tussock grass (*F. abysinica*), and under the cushion plant (*H. newnii*) not only increase moisture content and nutrient but also increases leaf surface area for PAR absorption and biomass production. However, there is evidence that green biomass is the results of long term carbon fixation through photosynthesis (Li *et al.,* 2008b). Subsequently, the higher leaf area and biomass exhibited by the combination of dominant species is associated with the higher CO_2 fluxes to maintain respiration of plant organs and soil assimilation (Polley *et al.*, 2011 and Otieno *et al.,* 2009).

5.3 Temporal and Spatial Variation in abiotic Factors on Ecosystem CO_2 Exchanges

5.3.1 Temporal variations on ecosystem CO_2 exchanges

On clear sky days, FNEE uptake increased from sunrise and reached maximum around noon (1100 to 1400 hours). The daily peaks of CO_2 uptake changed on daily basis depending on the prevailing air temperature and light (PAR) conditions (Fig. 9 and 10). Other studies such as Zhao *et al.* (2010) and Chojnicki *et al.* (2010) found similar results which where influenced by PAR and temperature in the alpine of the Qinghai-Tibetan Plateau and Poland respectively. Furthermore, Reco values differed depending on the soil and air temperature as the soil gets warmer in the late afternoon is when the rate of respiration also increased. The variation of mean daily Reco reflects different temperature sensitivities for autotrophic and heterotrophic respiration (Li *et al.,* 2008a and Otieno *et al.,* 2009). For example, the lowest Reco values on Sunday, 19 August 2012 that ranged from 1.35 to 2.20 $\mu mol\ m^{-2}\ s^{-1}$ (Table 2) were influenced by the cloudy weather. On this day it was sunny, but from 1100 hours there was a cloud cover of about 90%. According to Otieno *et al.* (2009) and Zhao *et al.* (2010), Reco has been reported to decrease with decrease in soil, air and leaf temperature under cloudy sky conditions.

Since the mean daily GPP/*R*eco ratio of the ecosystem on Sunday, 12 August 2012 was smaller than for Friday, 17 August 2012 and Sunday, 19 August 2012 (Appendix 2). This indicates that the ecosystem released more carbon on Sunday, 12 August 2012 than on Friday, 17 August 2012 and Sunday, 19 August 2012. This seemed to be influenced by the daily variation in PAR and temperatures (Chojnick *et al.*, 2010 and Li *et al.*, 2008a). Moreover, the effect of temperature on Reco is widely documented by several authors including Martin *et al.* (2007); Hussain *et al.* (2009) and Cavieres *et al.* (2005). The authors concur that soil temperature has influence on respiratory activities of the plant. Temperature stimulates the microbial activity, increase plant metabolic rates and organic matter decomposition hence increased ecosystem respiration. This interaction reveals that temperature is the most important Reco controlling factor since when temperature dropped rapidly and plant surfaces froze (Plate 7), Reco also declined drastically.

5.3.2 Spatial variations in ecosystem CO_2 exchanges

The soil is shallow (ca. 20-30 cm) and slightly acidic (Table 6) characterised by finer particles overlying the volcanic rock. Soil development tends to decrease with altitude limiting roots activity to upper soil layers hence reduce ecosystem respiration (Buytaert *et al.*, 2011 and Li *et al.*, 2008a). Soil depths facilitate soil respiration (Table 3 and 6) by boosting aerobic conditions, roots nutrient allocation and organic matter decomposition (Hussain *et al.*, 2009). This result is consistent with Zhao *et al.* (2010) that soil depth and nature of soils creates spatial heterogeneity in the availability of nutrients and micro-environment that could have profound influence on ecosystem parameters and functioning. This further substantiates the importance of soil depth in ecosystem respiration through increased autotrophic and heterotrophic respiration (Otieno *et al.*, 2009). From this study, it has been shown that individuals growing within cushions

(herein referred to as combination of species) have a better photosynthetic performance than those individuals growing alone. Interestingly, the highest GPP also reveals that there is more energy within the cushion (Table 4). These results agree with the hypothesis that micro-environment conditions determine ecosystem exchange of CO_2 and ecosystem respiration in the afro-alpine zone.

There are numerous explanations to this; *H. newnii* is best adapted to the fluctuations of alpine climatic conditions and that the low height and dense canopy create suitable micro-environment for other species (Korner, 2003). Also, cushion plant *H. newnii* maintain soil moisture, has low humidity, low air and soil temperatures (Husain *et al.*, 2009). The species appears to be important to reduce evaporation demand by increasing soil moisture and nutrient content for the species underneath (Antheleme *et al.*, 2011). Humid conditions support high productivity and carbon allocation to the soil due to low organic carbon decomposition (Zhao *et al.*, 2010). In fact Hussain *et al.* (2009) informed that cushions reduce environmental stress for the undergrowth and may encourage green biomass accumulation under the canopies. However, the relative increase in leaf area can produce more dry matter through photosynthesis. The study suggests that leaf area controls the ecosystem capability for assimilation and resource requirements, which corresponds with Zhao *et al.* (2010). Leaf area, biomass and temperature certainly influence the ecosystem components parameters of FNEE and Reco as depicted within the combination of dominant species (Li *et al.*, 2008a).

CHAPTER SIX

6.0 CONCLUSIONS AND RECOMMENDATIONS

6.1 Conclusions

This study is consistent with the existence of diversity of micro-environmental conditions and interactions taking place in affecting the ecosystem exchanges of CO_2 in the humid tropical alpine environment elsewhere. The CO_2 exchanges were more influenced by the changing abiotic factors of PAR, which seemed to control FNEE while temperature had much control on daily Reco changes. Moreover, the study substantiates that micro-environment created by *H. newnii* increases biomass and leaf area as well as enhancing nutrient supply that account for herbage production within the ecosystem for CO_2 exchanges. Indeed, the study supports that the alpine ecosystem is a sink of atmospheric CO_2, increased temperature may reduce the sinking capacity of this ecosystem.

6.2 Recommendations

Based on the importance of the afro-alpine zone in terms of the biodiversity and ecosystem services further studies are required on the long term ecosystem exchanges of CO_2 to enhance our understanding on eco-physiological process within the zone where climate warming impacts are forecast to be pronounced and detected early on.

(i) Alpine plants survived harsh environmental conditions for long time hence they are a valuable research tool for leaning the consequences of climate change.

(ii) Monitoring of CO_2 exchanges in the long-term will enhance deep knowledge for advising policy makers and conservation authorities on the effect of climate change on the alpine biota.

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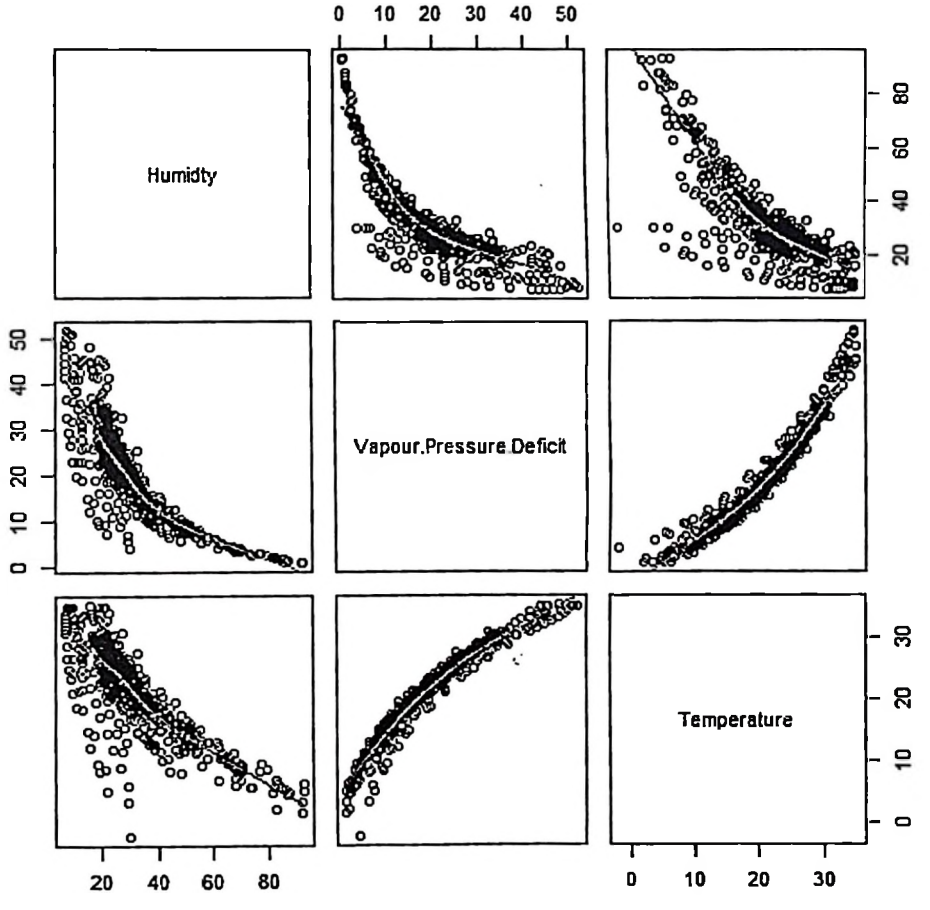
APPENDICES

Appendix 1: Data model for the influence of temperature on Vapour Pressure Deficit and air humidity from Wednesday, 11 July 2012 to Monday 20 August 2012



Appendix 2: Ratio of GPP to Reco for species on respective days for single dominant species *Alchemilla johnstonii* (alch); *Festuca abysinica* (fest); *Helichrysum newnii* (hel), and combination of dominant species *Helichrysum newnii*, *Alchemilla johnstonii* and *Festuca abysinica* (helalchfest), and *Helichrysum newnii* and *Alchemilla johnstonii* (helalch)

Date	alch	fest	hel	helalchfest	helalch
11/7/2012	1.326275	1.381783	0.461615	1.592545	2.15960
17/7/2012	1.146913	1.663981	0.667901	1.861098	2.30203
26/7/2012	1.112783	1.313602	0.533139	1.432271	1.84288
1/8/2012	1.265432	1.219115	0.629659	1.837107	2.25600
11/8/2012	0.737541	1.295679	0.641054	1.482569	2.17298
17/8/2012	1.206675	1.716246	0.961126	2.345524	3.16102
15/8/2012	2.135899	1.319224	1.536889	1.623565	2.13589
12/7/2012	0.810269	1.603488	0.911184	1.750460	1.72133
18/7/2012	0.730759	1.571489	1.069442	1.672482	1.40675
27/7/2012	0.816706	1.525056	1.435362	1.788090	1.46690
2/8/2012	0.5761210	1.804169	1.074404	1.655501	1.65702
12/8/2012	0.373930	1.512052	0.964798	1.395088	1.34199
18/8/2012	0.6972438	1.700129	1.264058	1.925433	1.68197
13/7/2012	1.4487844	1.469194	1.071340	1.092447	1.57113
19/7/2012	2.0552445	2.556557	1.688979	1.366283	1.95406
28/7/2012	1.1053422	1.613502	1.200293	0.950197	1.30108
3/8/2012	1.1190412	1.8245149	1.329069	1.518777	1.65027
13/8/2012	0.9171277	1.6755275	1.616225	0.7543420	1.33485
19/8/2012	1.5191889	1.8578350	2.146531	1.3865588	1.92526