Regulation of soil-surface respiration in a grazed pasture in New Zealand

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Abstract

The work in this thesis investigated the regulation of soil-surface respiration (R_s) in a grazed pasture, located near Oxford, Canterbury, New Zealand. An environmentally controlled laboratory exercise was conducted to investigate how soil temperature (T_s) and root-zone volumetric water content (θ) interacted to regulate R_s. These data were used to develop a model that described R_s as a function of T_s and normalised θ (θ_n). Chamber measurements of R_s, carried out in the field approximately twice a month throughout the 2005 - 2006 growing season, were used to validate the R_s model.

A closed gas exchange system was used to measure the individual exchange rates of ecosystem respiration (R_e) and R_s, in order to gain knowledge of the contribution of R_s to R_e in this system. This knowledge was used to partition eddy covariance nighttime measurements of R_e into R_s and above-ground autotrophic respiration (R_{aa}). Eddy covariance soil-surface respiration (R_{sE}) measurements were compared to modelled estimates of R_s. Finally, the model of R_s and continuous field measurements of T_s and θ, were used to estimate total growing season R_s at the field site.

The laboratory exercise revealed that the influence of T_s on R_s was best described using an Arrhenius-type function, while the influence of θ_n on R_s was expressed with a linear function. The model determined that when $\theta_n > 0.90$, R_s remained constant. In the field, R_s measured with a respiration chamber, was strongly influenced by T_s, which ranged from a low of 12.2 °C to a high 20.1 °C throughout the measurement period. Values of θ_n at the field site, ranged from 1.00 to 0.59, but were generally > 0.90, and as such, rarely limited R_s. Maximum and minimum rates of R_s in the field were 11 and 6 μmol CO_2 m^{-2} s^{-1} respectively. The field soil-surface respiration rate, normalised to 10°C (R_{10}) was 4.7 μmol m^{-2} s^{-1}. The model developed in the laboratory exercise was able to explain half (r^2=0.52, P<0.05) of the variability observed in the field R_s measurements.

The partitioning exercise revealed that R_e was comprised of 84% R_s and 16% R_{aa}. There was a significant relationship between the contribution of R_s to R_e and leaf area index (L).

There were 62 nights of valid eddy covariance R_e data from the field site. Maximum and minimum nightly averaged R_e were 12 and 2 μmol m^{-2} s^{-1}, repetitively. Eddy covariance soil-surface respiration (R_{sE}) was determined by multiplying nocturnal eddy covariance R_e measurements by the fraction 0.84, as determined in the partitioning exercise. The eddy covariance soil-surface respiration measurements were generally lower than modelled R_s estimates. For nights of valid eddy covariance data, the model total R_s (44 mol CO_2 m^{-2}), was 57% greater than the total R_{sE} (28 mol m^{-2}). Total growing season R_s, as estimated by the chamber based model was 162 mol m^{-2} (1.94 kg C m^{-2}).

This study has shown that R_s in this temperate grazed pasture is a function of both T_s and θ_n, however, during the measurement period, θ_n rarely reached low enough levels to limit R_s.

Keywords: Carbon dioxide, carbon cycle, soil-surface respiration, pasture

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E_o	related to the energy of activation
GPP	gross primary productivity
L	leaf area index
NEE	net ecosystem exchange $NEE = GPP - R_e$
NPP	net primary productivity $NPP = GPP - R_a$
R_a	autotrophic respiration
R_{aa}	above-ground autotrophic respiration
R_{ab}	below-ground autotrophic respiration
θ	root-zone volumetric water content
θ_{max}	maximum value of θ_n
θ_n	normalised root-zone volumetric water content $\theta_n = \theta / \theta_{max}$
θ_c	value of θ_n above which θ_n no longer influences R_s
R_e	ecosystem respiration $R_e = R_{aa} + R_{ab} + R_h$ $R_e = R_{aa} + R_s$
R_h	heterotrophic respiration
R_s	soil-surface respiration $R_s = R_{ab} + R_h$
R_{sE}	eddy covariance soil-surface respiration
R_{sG}	soil-surface respiration with the grass clipped to the soil-surface
R_{10}	rate of respiration at 10 °C
T_s	soil temperature

1 Introduction

Humans have significantly perturbed the global carbon (C) cycle through the combustion of fossil fuels and the clearing of forests. These activities have transferred C from terrestrial storage on Earth, to the Earth's atmosphere mainly in the form of carbon dioxide (CO_2). As a consequence, atmospheric concentrations of CO_2 have increased from pre-industrial levels of approximately 280 µmol mol^{-1} to current levels of approximately 380 µmol mol^{-1} (Kennedy and Hanson 2006).

There is now a scientific consensus that the increases in concentrations of atmospheric CO_2 and other greenhouse gases are leading to a warming of the Earth's average surface temperature, which if continued unchecked could lead to profound and likely irreversible climate changes, such as increases in extreme weather and sea level rise (Houghton 2004).

Over the past century, the mean global surface temperature has increased by more than 0.5 °C (Houghton 2004). Under 'business-as-usual' conditions, with fossil fuel CO_2 emissions continuing to increase, global surface temperatures are expected to continue to rise by 2 – 3 °C by 2100 (Hansen 2005). According to recent studies (Hansen 2005; Overpeck *et al.* 2006), the Earth's past history suggests that a warming of 2 – 3 °C would lead to increased melting of ice from the Greenland ice sheet and ice sheets in west Antarctica and a portion of the ice sheet in east Antarctica, raising the sea level by up to 25 meters (Hansen 2005). Despite this risk, global fossil fuel emissions continue to climb at 1 – 1.5% per year (Houghton *et al.* 2001).

In the global C cycle there are four major reservoirs: the atmosphere, the oceans, terrestrial systems, and fossil fuels (Fig.1-1), and C may be transferred between reservoirs in seconds (e.g., the photosynthetic fixation of atmospheric CO_2 by plants) or over millennia (e.g., the accumulation of fossil C) (Houghton 2003). The largest C flux occurs through ecosystem photosynthesis, known as gross primary productivity (*GPP*), where plants convert atmospheric CO_2 into organic substances which make up plant tissues. Annually, *GPP* is approximately 120 Pg C. About half (60 Pg C) of the CO_2

taken in during photosynthesis is used in plant fixation and the other half (60 Pg C) is respired by the plant leaves, stems and roots to provide energy that supports growth and maintenance (Chapin *et al.* 2002). This respiration from plants is referred to as autotrophic respiration (R_a). Net primary production (*NPP*) is the rate of photosynthesis in excess of R_a (Jacobson *et al.* 2000), such that

$$NPP = GPP - R_a \tag{1.1}$$

Autotrophic respiration, which occurs in the presence of light and nocturnally, can be sub-divided into above-ground autotrophic respiration (R_{aa}), which originates from plant leaves and stems, and below-ground autotrophic respiration (R_{ab}), that originates from plant roots.

Heterotrophic respiration (R_h) occurs in the soil as a result of the microbial decomposition of soil organic matter (Davidson and Janssens 2006). Total ecosystem respiration (R_e) can thus be defined as,

$$R_e = R_{aa} + R_{ab} + R_h \tag{1.2}$$

Annually global R_e is estimated to be 117 Pg C, of which R_{aa} and R_{ab} together contribute 60 Pg C and R_h contributes approximately 58 Pg C (Fig. 1-2), although the relative contributions of R_{aa}, R_{ab}, and R_h to R_e vary in space and time (Houghton 2003). For instance, Chambers *et al.* (2004) estimated that in a tropical forest ecosystem, the average annual contribution of R_{aa}, R_{ab}, and R_h to R_e were 52, 19 and 29%. In a tropical savanna ecosystem in northern Australia, Chen *et al.* (2003) reported that R_{aa}, R_{ab}, R_h contributed 16, 42 and 42% to total R_e respectively.

Respiration is measured using respiration cuvettes and chambers, and the eddy covariance technique. Leaf cuvettes are placed over above-ground vegetation, and provide a direct measurement of R_{aa}. Soil-surface respiration chambers, placed on a vegetation free soil-surface, can be used to measure the combined respiration of R_{ab} and R_h. Since photosynthesis is exclusive to daylight hours, nocturnal measurements by eddy covariance systems, instrumented on towers above an ecosystem, can also

provide a direct measurement of total R_e. The techniques for measuring respiration are discussed in greater detail in sections 2.2 and 3.2.

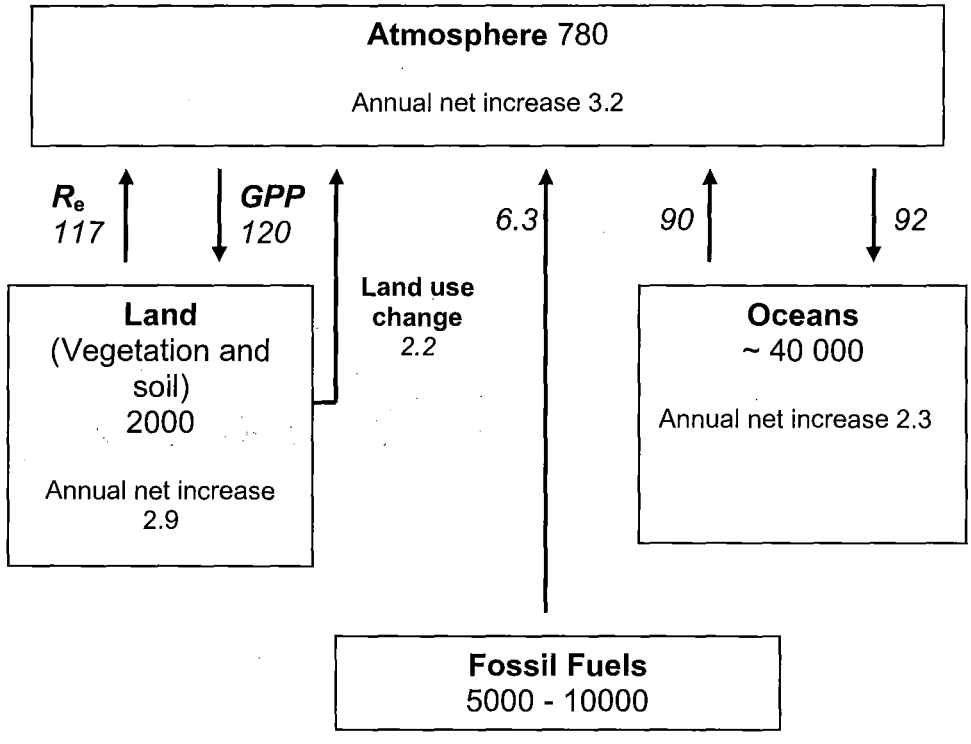

Figure 1-1 The biogeochemical carbon (C) cycle in simplified form. Shown are the C reservoirs (Pg C) and the annual fluxes of C (*Pg C* yr^{-1}) between these reservoirs. R_e is ecosystem respiration and *GPP* is gross primary productivity. The terrestrial biosphere is shown to be currently acting as a C sink. An annual atmospheric CO_2 concentration increase of approximately 3.2 Pg C is observed (Grace 2004).

It follows that net ecosystem exchange (*NEE*) is the whole ecosystem *GPP* minus total R_e, with *NEE* reflecting the annual budget balance of ecosystem C storage or loss (Chen *et al.* 2003).

$$NEE = GPP - R_e \tag{1.3}$$

Scientific inventories of the global C cycle have recognised an imbalance in the amount of anthropogenically produced C emissions and the rise in atmospheric CO_2. 'C sinks', which have been identified primarily as oceanic and terrestrial, are absorbing roughly half of the anthropogenic CO_2 emissions (White *et al.* 2000; Powlson 2005) (Fig. 1-1). Consequently, the biosphere as a whole is absorbing more CO_2 through photosynthesis than it is respiring, resulting in a substantial terrestrial C sink (Fig.1-3).

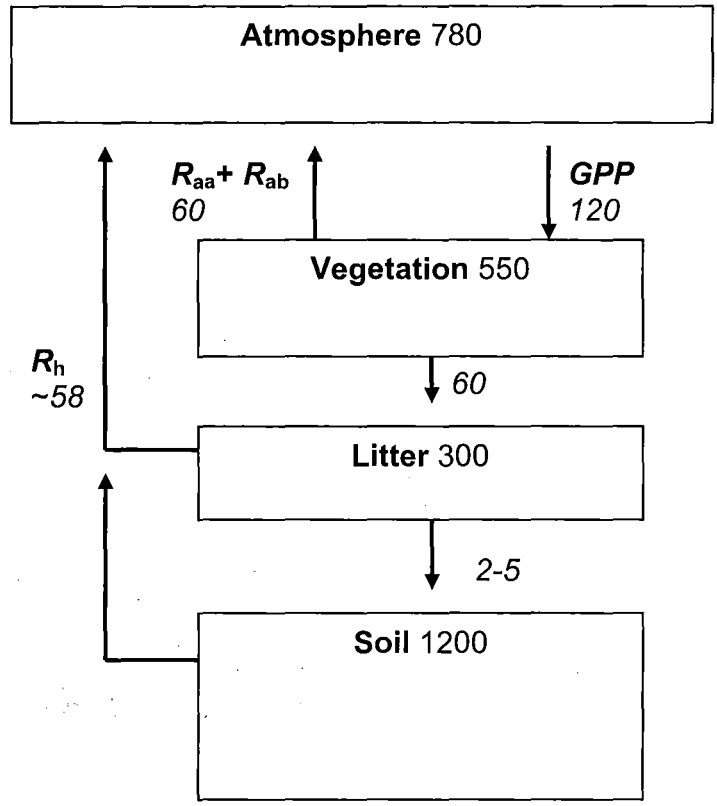

Figure 1-2 Carbon (C) exchange between the Earth's terrestrial biosphere and the atmosphere in simplified form. Shown are the C reservoirs (Pg C) and the annual fluxes of C between these reservoirs (*Pg C* yr^{-1}). R_{aa} is above-ground autotrophic-respiration, R_{ab} is below-ground autotrophic respiration, R_h is heterotrophic respiration and *GPP* is gross primary productivity (Houghton 2003).

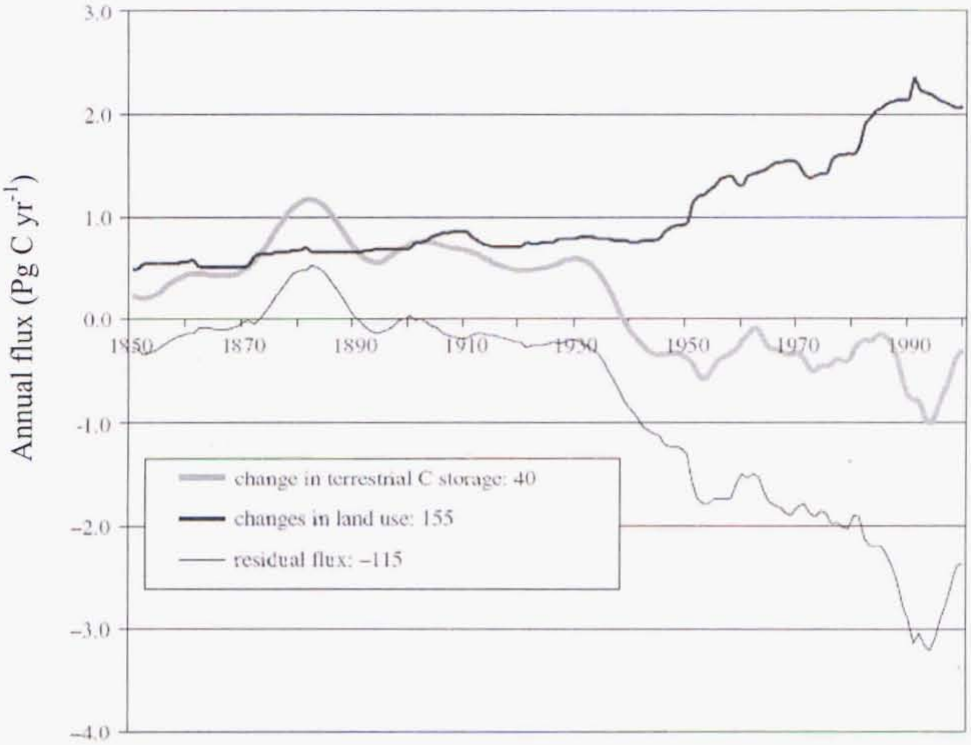

Figure 1-3 The net change in terrestrial carbon (C) storage (including changes in land-use) (thick grey line), the flux of C from changes in land-use (black line), and the difference between the net flux and the flux from change in land-use (thin grey line). Positive values indicate a terrestrial C source and negative values indicate a terrestrial C sink. From: Houghton (2003) pp.485.

Many mechanisms are thought to be responsible for the increasing size of the terrestrial C sink. Briefly, those that are thought to be most important include:

(1) *CO_2 fertilisation effect*. The approximately 30% increase in the atmospheric CO_2 concentration since pre-industrial times is having a fertilisation effect on terrestrial ecosystems (Grace and Rayment 2000). This occurs because most plants respond to elevated concentrations of atmospheric CO_2 by increasing rates of photosynthesis and growth (Grace 2004). However, it is not currently known if this fertilisation effect will result in a long-term increase in terrestrial C storage, because measurements have

demonstrated that the effects of higher concentrations of CO_2 on plant growth are often reduced or absent over long time periods (Oren *et al.* 2001).

(2) *Nitrogen fertilisation*. Human activity has increased the amount of biologically active forms of nitrogen present in ecosystems. This has occurred through the production and use of fertilisers, the cultivation of atmospheric nitrogen fixing legumes, and through the combustion of fossil fuels (Houghton 2003). The increase in the availability of nitrogen has led to increased plant growth and hence, terrestrial C storage (Grace and Rayment 2000; Melillo *et al.* 2002). However, the long term effects of nitrogen deposition on the terrestrial C balance remain unclear.

(3) *Climate change and variability*. The increase in the global surface temperature during the last few decades has led to a prolonged growing season in the middle and high latitude ecosystems, which has generally resulted in an increase in *NPP* at these latitudes. However, measurements of CO_2 exchange in these ecosystems do not consistently show a net C uptake, presumably because warmer soils have higher rates of respiration (Grace and Rayment 2000).

(4) *Forest regrowth*. The large scale regrowth of forests following disturbance by humans in the past has also led to an increased terrestrial C sink. This is particularly so in the Northern Hemisphere where processes such as fire suppression, the growth of forests on land abandoned after agriculture, and the growth of forests previously harvested is leading to increased forest C storage (Houghton 2003).

Large quantities of C are located in the terrestrial biosphere with rapid exchange occurring between the atmosphere, terrestrial biota and soils (Fig.1-2). The world's soils hold approximately twice as much C (1500 Pg - including soil-surface litter) as the atmosphere (780 Pg) and two-thirds of terrestrial ecosystem C (Powlson 2005). In grasslands, the C stored in litter, recalcitrant and labile soil C pools accounts for over 90% of total ecosystem C (Ryan and Law 2005). As respiration from the Earth's soils is the second largest flux in the annual global carbon budget, following *GPP* (Powlson 2005), changes in soil C dynamics have the potential to influence the C balance at local,

regional and global scales (Chen *et al.* 2002). Consequently, quantifying how the soil-surface respiration rate is regulated by the environment is critical.

Soil-surface CO_2 respiration (R_s) is a sensitive indicator of the metabolic activity of the soil and the rate of conversion of soil organic matter to atmospheric CO_2 (Rochette *et al.* 1997). It is a complex process, as it includes both the below-ground autotrophic respiration of plant roots and rhizomes (R_{ab}), and the heterotrophic decomposition of soil organic compounds and detritus (R_h) (equation 1.4). Studies examining the relative contribution of R_{ab} and R_h to R_s indicate that R_{ab} can account for as little as 10 percent to > than 90 percent of total R_s depending on vegetation type and season of the year (Hanson *et al.* 2000).

$$R_s = R_{ab} + R_h \tag{1.4}$$

Global R_s is estimated to be approximately 76.5 Pg C per year (Conant *et al.* 2004). Therefore relatively small changes in the net amount of C flowing in and out of soils have the potential to influence atmospheric CO_2 concentrations (Powlson 2005) and as a result, global climate. At the present time, there is considerable uncertainty about changes in R_s as CO_2 continues to accumulate in the atmosphere (Cramer *et al.* 2001; Steffen *et al.* 2001) and the climate continues to warm (Norby and Lou 2004). Research points to a short-term C sink which will weaken and eventually switch to become a C source (Grace and Rayment 2000; Powlson 2005), thus exacerbating global warming in a feed forward response.

Many studies, in a variety of ecosystems, have demonstrated that the main cause of change in the R_s rate is soil temperature (T_s) (Lloyd and Taylor 1994; Conant *et al.* 2004; Trumbore 2006). For example, Fang and Moncrieff (2001) found that soils from both a farmland and a Sitka spruce site in Scotland showed an exponential increase in respiration with increasing T_s over a 10 to 30 °C temperature range. The influence of T_s on R_s is often described using an Arrhenius type equation, such as that developed by Lloyd and Taylor (1994) (see chapter 2). Recently, Davidson *et al.* (2006a) noted that current functions used to describe the response of respiration to temperature, such as that developed by Lloyd and Taylor (1994) are somewhat inadequate, since respiration

from soils is comprised of CO_2 generated from several temperature sensitive processes. These include enzyme activity, diffusion of oxygen and soluble C substrates through soil air and water and across cellular membranes, and growth of root tissues and microbial populations, which can have multiplicative effects on total R_s (Davidson *et al.* 2006b).

Root-zone volumetric water content (θ) has also been found to play a role in the regulation of R_s (Davidson *et al.* 2006a). The effect of θ on R_s has been described by linear, logarithmic, quadratic, and parabolic functions of root-zone water content expressed as either soil matric potential, soil gravimetric or volumetric water content, soil water holding capacity, soil water-filled pore space, precipitation indices, and depth to water table (Davidson *et al.* 2000). Some studies such as those conducted by Conant *et al.* (2004), on a series of soils from semi-arid sites in the USA, and Reichstein *et al.* (2003), who performed an analysis on R_s from17 different forest and shrubland sites in Europe and North America have found that the temperature response of R_s is reduced as the θ decreases. Xu *et al.* (2004) observed that when θ fell below 0.15 m^3 m^{-3} at an oak/grass savanna in the USA, R_e (and therefore presumably R_s) almost shut down.

Root-zone volumetric water content can limit R_s in two ways, either by limiting aeration when θ is high, or by stressing plant root and soil microbial communities when it is low (Rey *et al.* 2002). Low θ can limit microbial respiration because both the diffusion of extracellular enzymes produced by microbes for breaking down organic matter and the diffusion of soluble C substrates that can be assimilated by the microbial cells must occur in the presence of water (Davidson *et al.* 2006b). In plants, low θ can lead to loss of tissue turgor, stomatal closure, and leaf shedding, which can result in substantial reductions in root respiration per unit biomass or loss in total respiratory biomass (Aber and Melillo 1991). Borken *et al.* (2006) note that root respiration may be less affected by low θ than microbial respiration if plants can compensate for low surface θ by up-taking water from wetter soil, deeper in the soil profile. Thus, the temperature sensitivity of R_s can become less under dry conditions, mainly due to the limited diffusion of C solutes in thin soil water films (Davidson *et al.* 2006b). Consequently, models of R_s, in environments where the soil water content can become limiting, need to incorporate the response to θ.

Since grasslands cover one-third of the Earth's land surface, and store between 10 – 30% of the world's soil carbon (Risch and Frank 2006), they are an important component of the global terrestrial C cycle. In broad terms grasslands are defined as ecosystems where the dominant vegetation component is comprised of herbaceous species (Jones and Donnelly 2004). Recently, several studies have examined the regulation of grassland R_s. Franzluebbers *et al.* (2002) investigated the spatial and temporal determinants of R_s from a tallgrass prairie in Kansas, USA, using nighttime exposure of static chambers to alkali absorption. The study determined the main drivers of R_s to be soil organic C, soil temperature (T_s), θ, and plant growth rate. Verburg *et al.* (2005) conducted an experiment comparing the R_s from soil cores collected from a tallgrass prairie in Oklahoma, USA, and found that a combined T_s and θ regression explained 64% of the observed variation in respiration rates. Other R_s studies have been conducted on semi-arid grasslands and savannas. Tang and Baldocchi (2005) reported that the seasonal pattern of R_s in an oak-grass savanna ecosystem in California, USA, was driven by both T_s and θ.

Despite the recent interest in quantifying R_s from grasslands, relatively few studies have been published on R_s from temperate pastures. In particular there is a lack of data from intensively managed temperate pastures (Byrne *et al.* 2005). In one temperate, natural grassland study in Yellowstone National Park, USA, which was primarily concerned with the effects of ungulate grazing, Risch and Frank (2006) measured CO_2 exchange over a site grazed by elk, bison and pronghorn. They compared R_s rates from sites inside and outside long term ungulate enclosures, in dry to mesic conditions, and found that temporal and spatial variations in R_s were ultimately related to variability in θ. They reported no differences in respiration rates between grazed and un-grazed sites.

In New Zealand, pastures occupy 6.67 x 10^4 km^2 (26%), forming the largest single land cover type (Trotter *et al.* 2004). However, to date, there have been no known detailed studies of how R_s is regulated by T_s and θ in pastoral systems in New Zealand. Nieveen *et al.* (2005) conducted a study on the C exchange of a pasture over a drained peat soil in New Zealand, but examined only total R_e (using the eddy covariance technique). Hunt *et al.* (2002) also used the eddy covariance technique to measure total

R_e from a New Zealand tussock grassland, but did not measure R_s independently. Hunt *et al.* (2004), also in a grazed New Zealand tussock grassland, did measure R_s with a soil respiration chamber, but focused on the effects of drought and rainfall, and only measured R_s immediately before and after a rainfall event. Because pastures are the primary land cover type in New Zealand, quantifying the respiration from these soils is critical in determining the C balance of New Zealand.

In a recent review of ecosystem respiration, Trumbore (2006) noted, that while the variables which regulate respiration are well known, the specific details of how ecosystem respiration and R_s depend on these variables, at any given time, are still largely unknown. Trumbore (2006) comments that the "problem is both with a lack of a theory of respiration that explains how all the driving variables may interact, as well as in obtaining relevant data to test models based on theory". Hence, in order to construct global carbon budgets, detailed information at the local scale is needed from a diverse range of ecosystems and climate zones (Rayment and Jarvis 2000; Law *et al.* 2001; Raich *et al.* 2002).This will allow a theory of ecosystem respiration and R_s to be developed and, as a result, better models of future ecosystem and global C budgets. This study will contribute to filling the current gap in R_s data from temperate cattle-grazed pastures.

1.1 Nature and scope of thesis

This study was a component of a long term programme conducted by Landcare Research, investigating changes in C cycling as pastures are converted to shrubland. This thesis contributed to the overall study by quantifying rates of R_s in a New Zealand grazed pasture and investigating the seasonal regulation of R_s by environmental variables. The principal objectives were to:

1. Quantify rates of R_s in a New Zealand grazed pasture.

2. Measure seasonal variation in R_s in relation to T_s and θ.

3. Model R_s and validate modelled rates of respiration against field measurements.

4. Estimate total growing-season R_s

1.2 Thesis structure

Chapter 2 describes a controlled laboratory experiment undertaken to measure R_s over a range of T_s and θ values. These measurements were used to construct a model of R_s which was then validated against R_s measurements made in the field under natural environmental conditions. The results of a partitioning exercise to determine the contribution of R_s to R_e are presented in **Chapter 3**. The soil-surface respiration model, developed in Chapter 2, was validated against partitioned nocturnal eddy covariance respiration data made available through the Landcare Research programme and the R_s model was used to estimate the total growing season R_s from the field site. **Chapter 4** presents final conclusions and future work.

2 Soil temperature and root-zone water content regulation of soil-surface respiration in a New Zealand grazed pasture

2.1 Introduction

The terrestrial biosphere currently absorbs approximately one-third of all anthropogenic CO_2 emissions (Schimel *et al.* 2001). Since the Earth's climate is regulated to a high degree by the atmospheric CO_2 concentration (Houghton 2001), it is critical to understand what regulates carbon (C) exchange between the world's terrestrial ecosystems and the atmosphere. Soil respiration at the soil-surface (R_s) comprises CO_2 production from both plant roots, and the microbial decomposition of soil organic compounds and detritus (Reth *et al.* 2005). After photosynthesis, R_s constitutes the largest exchange of C between the terrestrial biosphere and the atmosphere (Reichstein *et al.* 2005). Thus a small increase in the rate of R_s could potentially have a large impact on atmospheric CO_2 concentrations. While C exchange has been studied over a range of grassland ecosystems, including an oak-grass savanna (Tang and Baldocchi 2005), a northern temperate grassland (Flanagan and Johnson 2005), and a tall-grass prairie (Franzluebbers *et al.* 2002), there remains a need for information on the regulation of R_s in temperate, intensively grazed pastures (Byrne *et al.* 2005). In New Zealand, the respiration from pastoral soils is a potentially important component of the terrestrial C cycle, because pastoral ecosystems comprise almost 30% of New Zealand's terrestrial surface area (Trotter *et al.* 2004). Thus, it is important to quantify the R_s flux density from pastoral systems in New Zealand, in order to understand what potential changes in the seasonal R_s rate might occur in relation to climatic changes.

It is well documented that R_s increases exponentially with increasing soil temperature (T_s) (Lloyd and Taylor 1994). However, root-zone volumetric water content (θ) has also been shown to regulate R_s (Borken *et al.* 2006). For instance, several studies in a variety of ecosystems have reported the temperature response of R_s to be limited at low θ (Davidson *et al.* 2000; Conant *et al.* 2004). Davidson *et al.* (2000) found that R_s rates decreased with low θ for both Amazonian pasture and forest soils. In a

North American prairie study, Franzluebbers *et al.* (2002) found that when water-filled pore space was < 0.4 m^3 m^{-3}, increasing T_s had little effect on R_s, but when water-filled pore space was > 0.4 m^3 m^{-3}, increasing T_s positively influenced R_s. Very high values of θ can also reduce R_s, due to limitations on oxygen diffusion (Linn and Doran 1984). In a study on a temperate mixed-hardwood forest, Davidson *et al.* (1998), found that when θ was > 0.12 m^3 m^{-3}, R_s decreased with increases in θ, and when θ was > 0.7 m^3 m^{-3} R_s was usually very low (less than 1.6 µmol m^{-2} s^{-1}). In a review of previous R_s studies, none of which took place over an intensively grazed temperate pasture, Davidson *et al.* (2000) noted that the optimal rate of soil CO_2 production frequently occurs at relatively intermediate θ, often near field capacity and declines at wetter and drier soil conditions.

Since soil temperature and root-zone volumetric water content often co-vary in the field, determining the relative influence each factor has on R_s has been problematic (Borken *et al.* 2006). This study attempts to overcome this challenge by undertaking a laboratory study using pasture soils collected from the field, and controlling T_s and θ independently. This technique proved to be successful when determining R_s in a tallgrass prairie in Oklahoma, USA (Verburg *et al.* 2005). Laboratory studies are a useful way of determining the relative influence each of these variables has on R_s, as respiration measurements can be made across a wide range of either T_s or θ.

The objectives of this portion of the study were to:

- Conduct a laboratory experiment to determine how R_s from a New Zealand cattle-grazed pasture was regulated by T_s and θ.
- Use these relationships to develop a model of R_s.
- Validate the model of R_s against field measurements of R_s.

2.2 Methods

2.2.1 Site description

The field measurements were carried out in an established cattle-grazed pasture, located near Oxford in Canterbury, New Zealand (latitude 43.3° S, longitude 172.2° E, elevation above sea level 34m) (Plate 2.1). The pasture was dominated by perennial ryegrass (*Lolium perenne* L.) with the remaining vegetation comprised of white clover (*Trifolium repens* L.),yorkshire fog (*Holcus lanatus* L.), creeping bent (*Agrostis stolonifera* L.) and browntop (*Agrostis capillaris* L.). During the measurement period cattle grazed the pasture three times, from 9 October to 22 October 2005, from 25 November to 8 December 2005, and from 3 February to 16 February 2006.

The soil was a Taitapu Typic Orthic Gley (New Zealand soil classification) (Hewitt 1998), poorly drained, with a perched water table. This type of soil typically develops on wet sites and in depressions at the bases of hills. For much of the year, the water table is near to the surface and the soil profile has a pale subsoil colour. At field capacity, the root-zone volumetric water content (θ) is approximately 0.49 m^3 m^{-3}. The average C:N ratio (0 – 300 mm soil depth) is 14.2. Mixed forests comprised of *Nothofagus* and *Podocarpus* species were present at this location before conversion to pasture, more than a century ago. The underlying zonal soils are derived from greywacke and tertiary rocks with a covering of loess, which developed during the last glaciation (18 – 20 000 years ago). Soil pH is typically 5.3. At depths > 300 mm, the soil becomes white and mottled.

At Darfield, located 20 km from the field site, the mean 30 year annual air temperature is 11.7 °C (NIWA 2006). The climate is characterized by cool, moist winters (average daily air temperature 7 °C) and warm summers (average daily air temperature 16 °C and average daily maximum air temperature 22 °C). The average yearly rainfall is 782 mm with the rainfall being evenly distributed throughout the year (NIWA 2006).

Plate 2-1 Study site during the growing season measurement period.

2.2.2 Soil-surface respiration measurements made in the field

In order to measure R_s in the field (section 1.1, objective 1), 24 soil collars were made from PVC pipe (100 mm in diameter and 150 mm in length). These were permanently inserted to a depth of 125 mm into the soil-surface of the pasture, at spaced intervals of 10 m. This left exposed above the soil-surface a 25 mm soil 'collar' upon which a CO_2 respiration chamber could be placed, as described below.

Immediately prior to CO_2 respiration measurements, the grass growing inside the collars was clipped to 20 mm above the soil-surface using hand shears. Clipping was done to ensure that the respiration measurements would be comprised almost entirely of soil-surface respiration (equation 1.4), and not include above-ground autotrophic

respiration from above-ground vegetation. The CO_2 flux density was measured using a portable closed-chamber attached to an infrared gas analyser (models SRC-1 and EMG-1, PP Systems, Hitchin, UK). The chamber was placed on each of the 24 PVC collars in turn. Measurements of the CO_2 fluxes were conducted approximately every two weeks, beginning in September 2005 and continuing until March 2006. Each respiration measurement was conducted over a period of 2 min.

Since the pasture had been clipped to a height of 20 mm, the measured CO_2 exchange was equivalent to soil-surface respiration, and is subsequently referred to as R_s. It should also be noted here that further measurements (see section 3.3.1 chapter 3) confirmed that cutting the pasture to a height of 20 mm effectively removed the above-ground autotrophic respiration component of the R_s measurement.

Soil temperature (T_s) at 50 mm depth, was measured by inserting a thermistor directly into the soil next to the PVC collars during each R_s measurement. The value of root-zone volumetric water content (θ) was continuously determined, and recorded at 30 min intervals, using electronic probes (ThetaProbe, Delta-T, Cambridge, UK) linked to a data-logger (CR10X Campbell Scientific) at depths of 50, 100 and 300 mm at one location in the pasture. For analysis purposes, the θ measurements at each depth were integrated to provide a single θ value over the 0 – 300 mm soil profile. To integrate θ, values at the 50, 100 and 300 mm depths, which represented 0 – 75, 75 – 200, and 200 – 300 mm of the soil profile, were multiplied by the proportion of the profile they measured (25, 41.6 and 33.3% respectively) and then the values were added together.

2.2.3 Laboratory measurements of soil-surface respiration

In order to reveal how T_s and θ interacted to regulate R_s (section 1.1, objective 2), a laboratory study was conducted. To achieve this, thirteen intact soil cores, 300 mm in length and 200 mm in diameter, were removed from the pasture by inserting PVC pipes (300 mm long and 200 mm diameter) into the soil-surface and then carefully digging around the casings (Plate 2.2). The soil cores, inside their casings, were removed from the pasture while the soils were wet and near field capacity. While still in the field, PVC collars, (100 mm diameter, 70 mm long), were inserted into the surface of the cores to a

depth of 50 mm. The base of the casings were covered with mesh (2 mm) to ensure containment of the soil cores and yet allow excess water to drain. The soil cores were then transported to the laboratory so that R_s could be measured in controlled conditions in a growth cabinet.

Plate 2-2 One of thirteen soil cores used in laboratory study being dug out of the pasture.

Prior to being placed in the growth cabinet (Temperzone, Temperzone Ltd., Auckland, New Zealand) (dimensions: 0.90 x 1.2 x 1.8m), the thirteen soil cores were saturated by immersing in water for approximately four hours, thus allowing water to percolate throughout the core. The cores were then placed on a rack in the growth cabinet, where excess water was allowed to drain for two days, so that at the beginning of the experiment the cores were considered to be at their maximum water holding capacity. Herbage on the soil cores was left as it was when the cores were removed from the field.

In the growth cabinets water loss from the soil cores occurred via evaporation from the soil-surface and plant transpiration. The rate of water loss was controlled by varying humidity in the growth cabinets as required. In order to dry the soil cores the humidity was reduced to 15%, while to maintain θ at fixed values, the humidity was increased to 80%. At any given time when measurements of R_s were made, the humidity in the growth cabinet was maintained within narrow limits (70-80%). For each set level of θ, R_s was measured at T_s values of approximately 5, 10, 15, 20, 25 and 30 °C.

The values of T_s were measured using thermocouples placed in the centre of three of the cores while the values of T_s were controlled by adjusting the air temperature of the growth cabinet. As per the field measurements, when respiration measurements were made T_s was measured with a thermistor at 50 mm depth from the soil-surface. This process was repeated until respiration measurements had been made at a broad range of T_s (5 - 30 °C) and under wet to dry soil conditions that constituted seven levels of θ (~0.1 – 0.5 $m^3\ m^{-3}$).

The volume of the soil cores were measured at the beginning of the laboratory study. On the day of each R_s measurement, the cores were weighed to determine their mass, so that the exact water content could be calculated subsequently. Following the experiment, the soil cores were oven-dried and weighed again to determine the oven-dry soil mass. These data were used to calculate the soil bulk density for each core (ρ_{soil}), which enabled the value of θ to be determined during any particular R_s measurement as follows:

$$\rho_{Soil} = M_s / V_t \quad (2.1)$$

where M_s is the mass of soil and V_t is the total core volume.

$$V_w = M_w / \rho_{water} \quad (2.2)$$

where V_w is the volume of water, M_w is the mass of water (g) and ρ_{water} is the bulk density of water; assumed to be 1000 kg m^{-3}.

$$\theta = V_w / V_t \quad (2.3)$$

where θ is the root-zone volumetric water content.

As with the field R_s measurements, the grass on the soil cores in the growth cabinets was clipped to a height of 20 mm before respiration measurements were made. However, the grass was not clipped more than once a week, to avoid unwanted clipping effects, such as those identified by Wan and Luo (2003). These researchers conducted a clipping experiment in a tallgrass North American prairie, and showed that clipping reduced below-ground substrate supply and as a result, led to reduced rates of R_s. Bremer *et al.* (1998) also found that in a tallgrass prairie in Kansas, USA, clipping typically reduced R_s by 21 – 49% by the second day after clipping.

2.2.4 Data Analysis

To determine the influence of T_s and θ on R_s, a non-linear regression model (section 1.1, objective 3) was constructed that included an Arrhenius-type function for the T_s response (Lloyd and Taylor 1994) and a linear function for the θ response (the selection of a linear θ function is discussed in section 2.3.1).

During the laboratory study, the bulk density of the individual soil cores varied considerably, from 0.46 to 1.13 m^3 m^{-3}. Reichstein *et al.* (2003) noted that θ was not a good measure of water availability when soils of different texture were compared. Thus,

it was decided to use a normalised root-zone water content (θ_n), defined as the root-zone volumetric water content available relative to the maximum root-zone volumetric water (θ_{max}) (equation 2.4) for each individual core. The water content function of the equation also included a parameter, θ_c defined as the θ_n value at which a further increase in θ_n no longer influences respiration, so that when $\theta_n > \theta_c$, equation 2.5 was utilised, however when $\theta_n < \theta_c$, equation 2.6 was utilised.

$$\theta_n = \theta / \theta_{max} \tag{2.4}$$

$$R_s = R_{10} e^{E_o\left[\frac{1}{56.02} - \frac{1}{T_s - 227.13}\right]} \tag{2.5}$$

$$R_s = R_{10} e^{E_o\left[\frac{1}{56.02} - \frac{1}{T_s - 227.13}\right]} \cdot \left[\frac{\theta_n}{\theta_c}\right] \tag{2.6}$$

R_{10} is the base respiration rate at 10 °C, T_s is the soil temperature (K) and E_o is a parameter related to the energy of activation (K).

The model adopted was a non-linear mixed effects model, fit by maximum likelihood (Pinheiro and Bates 2000). This model was used as it allowed for random differences between the soil cores, correctly adding their variability into that of parameter estimates. The model allowed R_{10} to have a component of variation from the soil cores, and considered correlation between successive measurements on the same soil core, correctly lessening the influence of individual measurements, particular those close together in time. Finally, the model allowed for greater variability at higher levels of R_s, which was observed in the data (Note: this type of model does not provide an r^2 or r^2 equivalent value).

2.3 Results

2.3.1 Laboratory measurements of soil-surface respiration

In the laboratory experiment, R_s increased markedly with increases in T_s (Fig. 2-1). The temperature response of R_s was greater when θ_n was relatively high. To determine the nature of the response of R_s to θ_n, R_s measurements were normalised to 10 °C (R_{10}). To do this for each soil core, R_s measurements were grouped into classes of θ_n (0.80 – 0.90, 0.70-0.79, 0.60-0.69, 0.50-0.59, 0.40-0.49, 0.30 – 0.39 and <0.30) and equation 2.5 was fitted to the R_s measurements in each class (Fig.2-2). A linear function best described the increase in R_s with θ_n until a threshold value of 0.90 (θ_c), after which point a further increase in θ_n no longer had an influence on respiration.

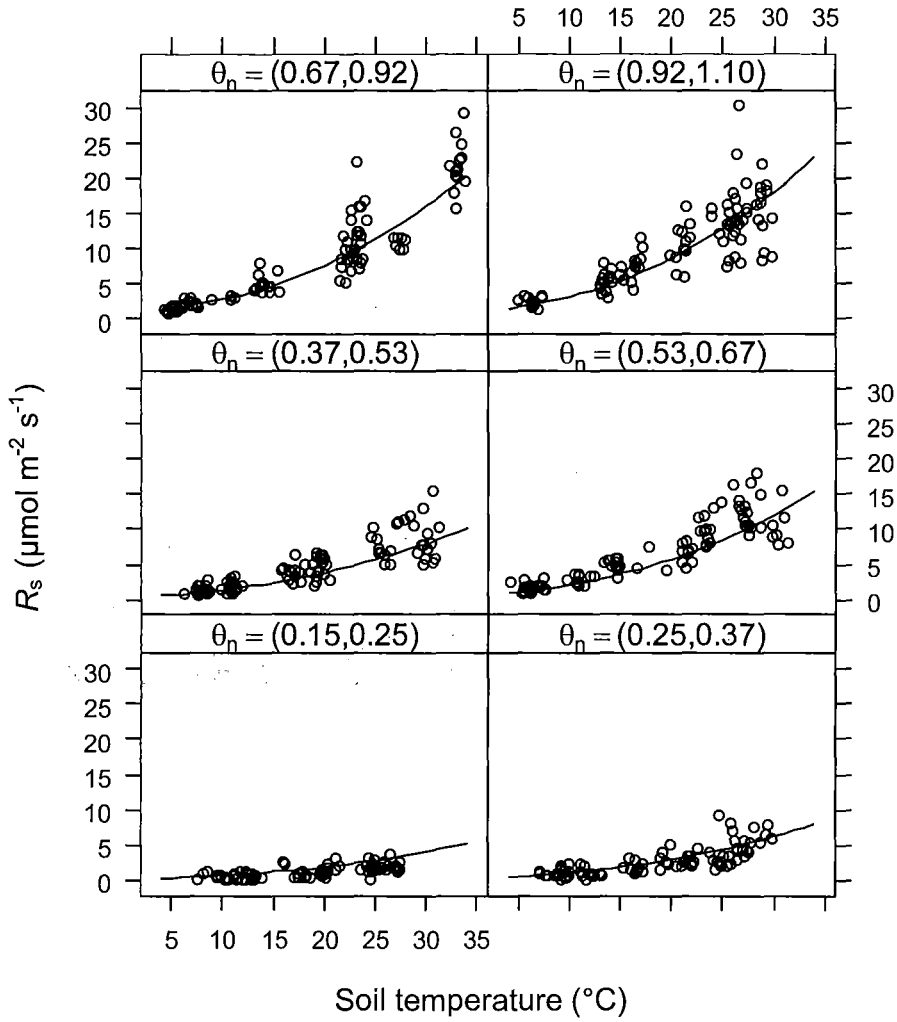

Figure 2-1 Laboratory measurements of R_s (soil-surface respiration) of all soil cores in relation to soil temperature at a depth of 50 mm, at six different classes of θ_n (normalised root-zone water content) (numbers in brackets represent the range of θ_n in each class). The line is fitted using the model (equations 2.5 and 2.6).

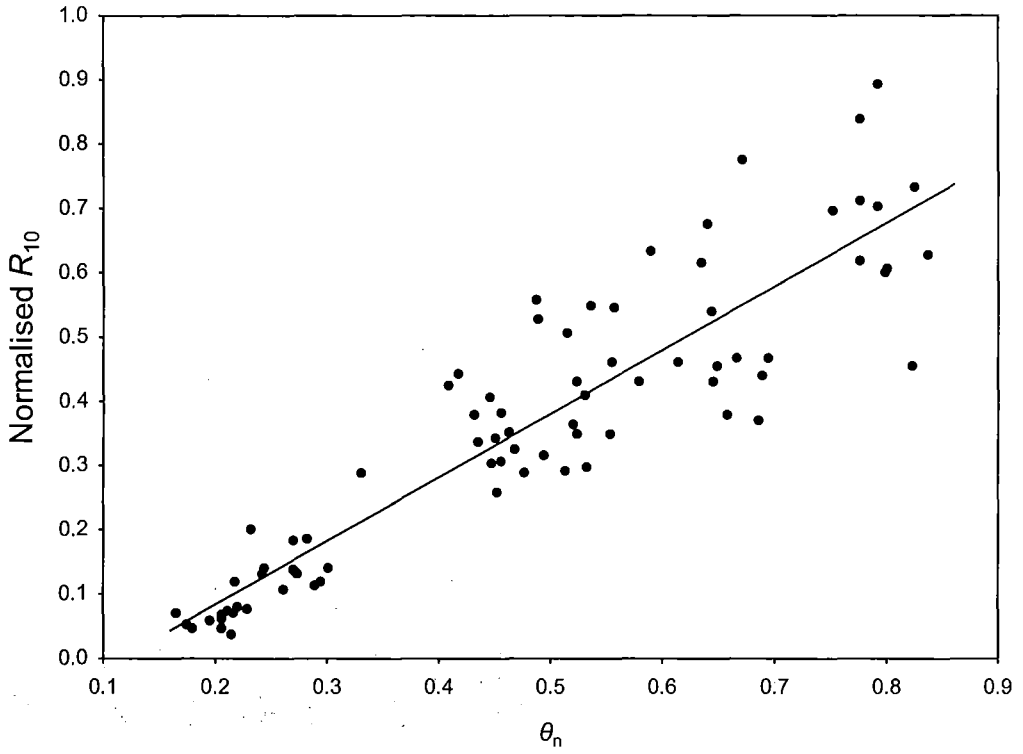

Figure 2-2 Soil-surface respiration normalised to 10°C (R_{10}) and θ_n (normalised root-zone volumetric water content) when θ_n is < 0.90 (θ_c). R_{10} values are normalised to the maximum R_{10} value. R_{10} values were determined by fitting equation 2.5 to respiration measurements in θ_n classes of 0.80 – 0.90, 0.70-0.79, 0.60-0.69, 0.50-0.59, 0.40-0.49, 0.30-0.39 and <0.30, in each of the thirteen soil cores. r^2 = 0.84; y = -0.1141+0.9891*x.

2.3.2 Modelling of laboratory measurements

Using the relationships between R_s and T_s and θ_n established in the laboratory, a non-linear mixed effects model was developed, fitted with maximum likelihood, using equations 2.5 and 2.6 (section 2.2.4). The parameters generated by the model are presented in Table 2-1.

Table 2-1 Fitted parameters (± standard errors) derived from the soil-surface respiration model. R_{10} is the soil-surface respiration rate at 10 °C. E_o is related to the energy of activation, and θ_c is the threshold point at which a further increase in normalised root-zone water content no longer has an influence on soil-surface respiration.

R_{10} (μmol m^{-2} s^{-1})	E_o (K)	θ_c
3.19 ± 0.2	369.2 ± 8.5	0.90 ± 0.04

2.3.3 Field measurements of soil-surface respiration

When the first two field R_s measurements were made in the late winter, T_s was 13 °C. During the spring and early summer, T_s increased rapidly to 20 °C and stayed near this temperature until early autumn, when T_s fell to 15 °C prior to the last measurement in March (Figure 2-3a). Field root-zone water content measurements were converted to θ_n so that they were directly comparable to the laboratory measurements of θ_n. To normalised θ, the value of θ during each field measurement day was divided by the maximum θ value (θ_{max}) reached during field measurements. Maximum θ was 0.48 m^3 m^{-3}. Normalised root-zone water content values commenced at near maximum water holding capacity in September and remained high (> 0.90) throughout the early summer. In January, θ_n values fell relatively rapidly and reached a low of approximately 0.55 in early February. Soil θ_n values then fluctuated, due to intermittent rainfall, for the remainder of the measurement period. R_s ranged from 6 to 8 μmol m^{-2} s^{-1} during the late winter and gradually increased as spring progressed into summer, when R_s reached a maximum rate of 11 μmol m^{-2} s^{-1}. During February and March, R_s fell slightly to rates of approximately 9 μmol m^{-2} s^{-1} (Fig. 2-3b).

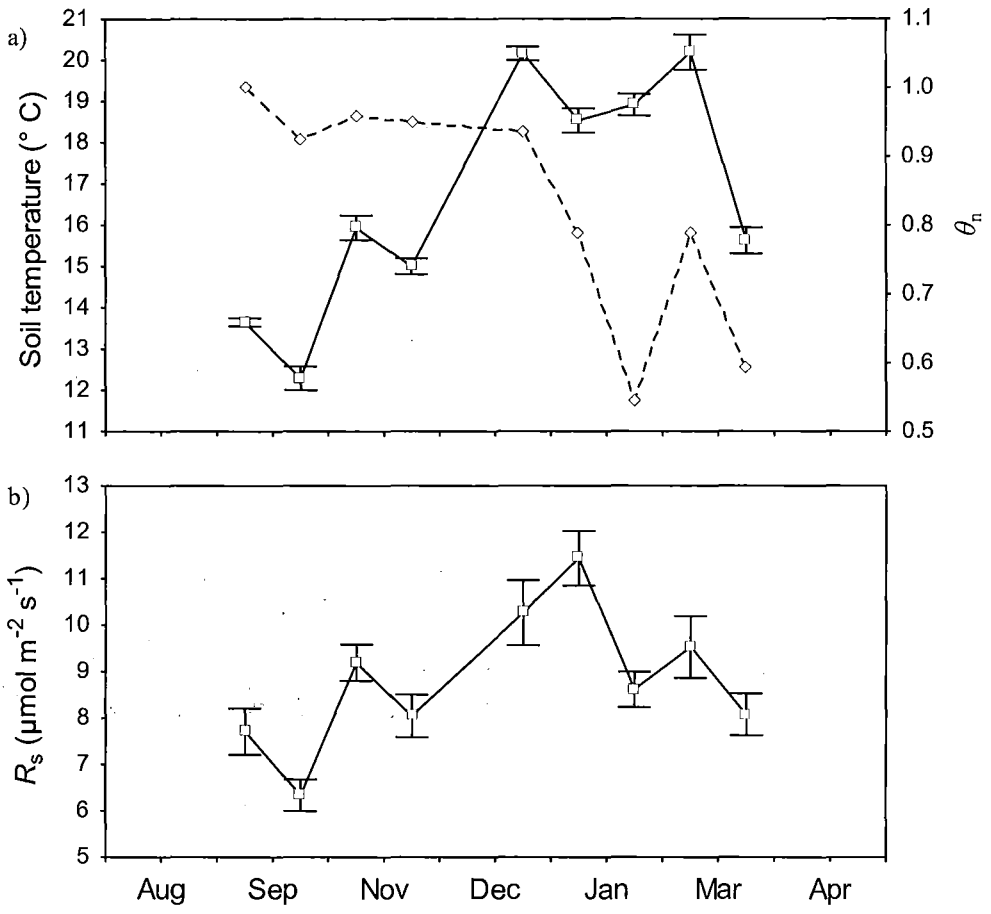

Figure 2-3 (a) Field measurements of soil temperature at 50 mm (square points connected with solid line) and θ_n (normalised root-zone water content) (diamond points connected with dashed line) and, (b) R_s (soil-surface respiration) measurements from September 2005 to March 2006. Individual points represent averages of measurements made at 24 collars and bars represent standard errors.

2.3.4 Modelling soil-surface respiration in the field

The model developed as a result of the laboratory experiment, was used to predict R_s with inputs of T_s (at 50 mm depth) and θ_n (0 – 300 mm soil depth) data that were measured in the field. Thus, a prediction of R_s in the field could be made using the laboratory model. The R_{10} value used in the model, during this exercise, was established by calculating the average of field R_s measurements made when T_s was close to 10 °C. The field measured R_{10} value was 4.7 µmol m^{-2} s^{-1}, was higher than the R_{10} laboratory

fitted value of 3.19 μmol m^{-2} s^{-1}, indicating that R_s was greater in the field than in the laboratory. Thus, if the laboratory fitted value of R_{10} was used to run the model, the model would have underestimated measured field R_s. Hence, the field measured R_{10} value was used to run the model. There was a significant regression relationship (r^2 =0.52, P <0.05) between the rates of actual measured field R_s and the rates of modelled field R_s (Fig. 2-4). A concordance correlation test was also performed which measured the variation of the linear relationship between values of measured and modelled R_s, from the line of unity (Lin 1989). The concordance correlation coefficient measures both how far each observation deviates from the line to the data (precision), and also how far this line deviates from the line through the origin (accuracy) (Lin 1989). The concordance correlation coefficient was 0.66. Differences between modelled and measured R_s became greater in the latter part of the summer when θ_n in the field fell bellow approximately 0.8.

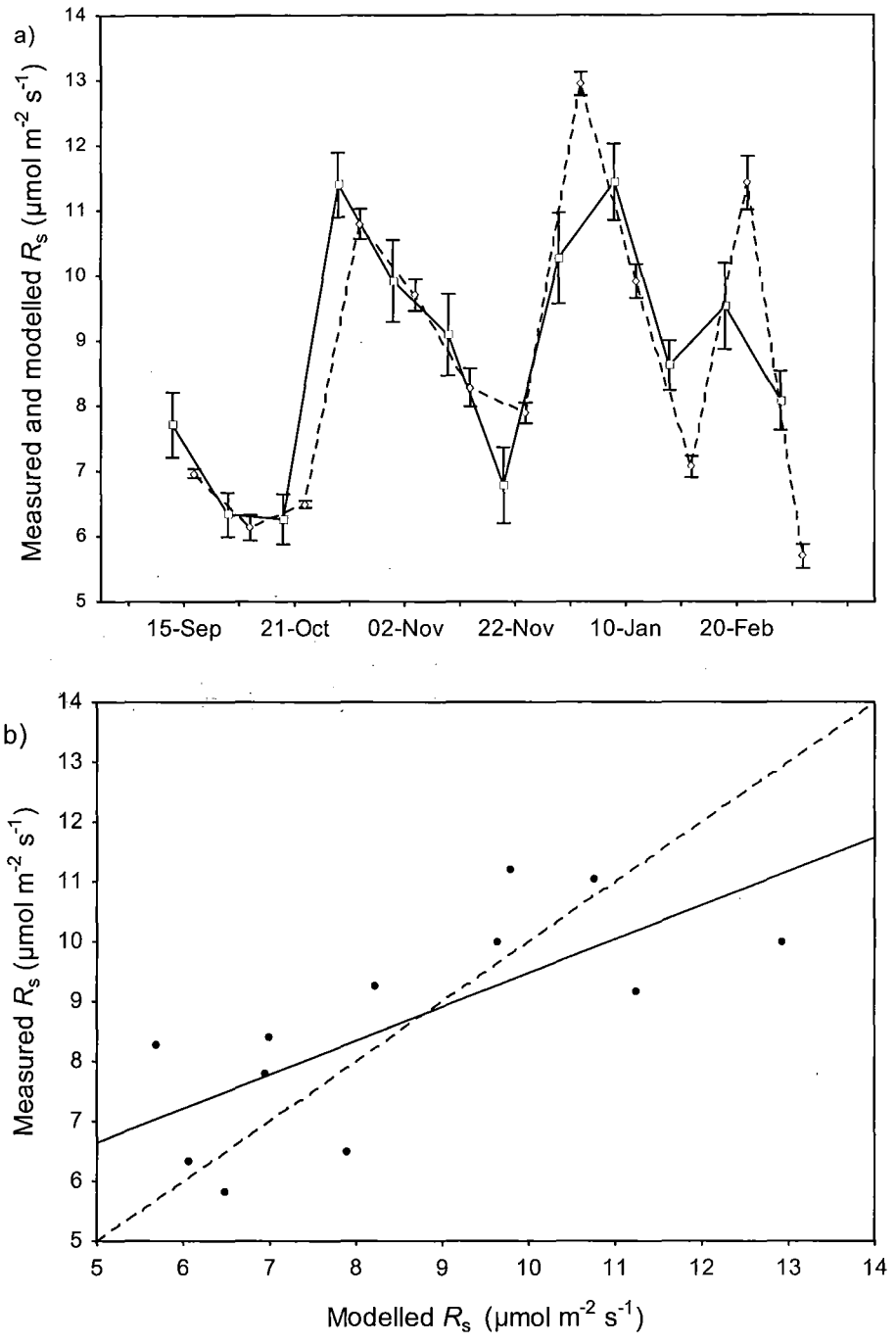

Figure 2-4 (a) Field measured soil-surface respiration (R_s) (dashed line, n=24) and modelled soil-surface respiration (R_s) (solid line) throughout the year and standard error bars. Modelled values are slightly offset measured values of R_s to avoid overlap. (b) Field measured and modelled rates of soil-surface respiration (R_s) r^2= 0.52; P<0.05. Dashed line represents the line of unity. The concordance correlation coefficient was 0.66, indicating agreement between measured and modeled R_s.

2.4 Discussion

2.4.1 Laboratory measurements

The laboratory experiment allowed the response of soil surface respiration to T_s and θ_n to be determined. Equation 2.5 provided an accurate description of the response of R_s to soil temperature. The value of θ_c of 0.90 fitted by the respiration model indicated that at θ_n less than this value R_s was limited by θ. Low θ can limit R_s by stressing microbial communities and plant roots (Rey *et al.* 2002). Many other studies have also reported respiration limitations as θ decreased (Reichstein *et al.* 2005; Davidson *et al.* 1998). For instance, Risch and Frank (2006) reported that in a temperate natural grassland, spatial and temporal variability in R_s was ultimately related to variability in θ, which ranged from a high of ~30% in May to a low ~10% in August, which when normalised by myself (following the procedure described in section 2.2.4), ranged from a θ_n of 1 – ~0.33 and averaged ~0.7 throughout the growing season, which, results from this study suggest, is well within the range where low θ limits R_s. In a Canadian prairie, Flanagan and Johnson (2005) reported that the Q_{10} (proportional change in respiration with a 10° C change in temperature) of ecosystem respiration (R_e) decreased with declining soil water availability. In this current study, R_s was not limited when θ_n was > θ_c.

2.4.2 Field measurements of soil-surface respiration

Compared to other temperate grassland respiration studies, field R_s rates were relatively high in this study. The R_{10} of 4.7 µmol m^{-2} s^{-1} is comparable to the value of 4.27 µmol m^{-2} s^{-1} reported for a mountain meadow in Austria (Wohlfahrt *et al.* 2005), but higher than the ecosystem respiration (R_e) R_{10} value of 2.44 µmol m^{-2} s^{-1} reported by Nieveen *et al.* (2005) for a grazed New Zealand pasture over a drained peat soil. Bolstad and Vose (2005) reported R_s values at 10°C of approximately 2 µmol m^{-2} s^{-1} at pastoral sites in the southern Appalachian Mountains, USA. Soil-surface respiration rates were also much lower at grazed and ungrazed sites in a temperate grassland in Yellowstone National Park, USA, which reached maximum rates of ~4 µmol m^{-2} s^{-1} in the autumn at a T_s of approximately 15 °C (Risch and Frank 2006). Flanagan and Johnson (2005) reported a maximum R_{10} value of 3.6 µmol m^{-2} s^{-1} for R_e in well watered soils in a Canadian temperate grassland. One explanation for the relatively high R_{10}

found in this study is that θ remained high throughout most of the measurement period and rarely reached levels low enough to have a limiting effect.

2.4.3 Comparison of modelled and measured soil-surface respiration in the field

The respiration model developed, using equations 2.5 and 2.6, fitted the field R_s data well. Using regression analysis, the model was able to explain 52% of the variation in field R_s measurements. The concordance correlation coefficient was 0.66, indicating good agreement between measured and modelled R_s, but some deviation from the line of unity. The model generally underestimated R_s when θ_n was less than ~0.8. It is possible that during periods of dry soil-surface conditions in the field, some grass roots are able to compensate for this by accessing soil water from deeper down the soil profile. Many grass roots were observed at soil depths of 300 mm. Other differences between the modelled and measured field respiration rates are possibly due to the field R_s responses to T_s and θ_n being confounded by other factors such as variations in radiation, vegetation development and C allocation and precipitation (Risch and Frank 2006; Trumbore 2006: Salimon *et al.* 2004).

At the field site, cattle periodically grazed the pasture. There are several possible mechanisms by which grazing can affect R_s. The removal of above-ground vegetation by grazing results in reduced photosynthesis (Bremer *et al.* 1998), which can reduce R_s since below-ground autotrophic respiration is partially dependent on plant C allocation below-ground (Flanagan and Johnson 2005). Heterotrophic respiration is also influenced by the supply of root exudates, which may decline following grazing (Garcia 1992). Following grazing many grass species relocate C assimilate to regrowing shoots at the expense of roots, so less C is translocated to the roots (Bremer *et al.* 1998). Crider (1955) reported that the removal of half or more of the foliage from several grass species caused root growth to stop for up to six weeks.

In this study the effects of grazing on R_s via reduced above-ground biomass could not be determined. This was because the grass inside the soil collar was cut to 20 mm prior to R_s being measured (approximately every two weeks), which meant that the

length of the grass growing inside the soil collar did not vary greatly over the measurement period, regardless of whether the pasture had been grazed. Furthermore, the soil collars were placed relatively deep (130 mm) into the soil to prevent them from being damaged by cattle stepping on them. Since 90% of root biomass occurred within the top 100 mm of the soil horizon, the majority of the root respiration included in the R_s measurements must have originated from the roots of the grass growing inside the embedded soil collars. Thus, roots from grass growing outside the soil collars, which was not clipped, and hence would be expected to be affected by dramatic reductions in above-ground biomass due to grazing, would only occur at depths greater than 130 mm.

Previous studies have found grazing can cause R_s to increase or decrease, while other studies have reported no effects. For instance, Bremer *et al.* (1998) conducted a clipping experiment to simulate grazing and found that clipping reduced annual R_s by 17.5% due to reduced vegetative photosynthesis. LeCain *et al.* (2000), over a three year period found no seasonal difference in R_s between cattle grazed and un-grazed semi-arid sites in Wyoming, USA, but found that in the early spring, R_s was greater in grazed than ungrazed sites. LeCain et al. (2000) attributed this to better light penetration and a warmer soil surface in the grazed sites, which led to a higher rate of R_s. Risch and Frank (2006) found no effect of grazing by elks, bison and pronghorn on R_s in a temperate grazed grassland study, and suggested that soil water stress during the measurement period and a lower than usual grazing intensity could have reduced the effects of grazing on R_s in that study.

Consideration was also given to the possibility that R_s might vary due to urine deposition from when the cattle were grazing in the pasture. Urine can increase soil pH, nitrogen replete soil patches and increase microbial availability of soil organic matter (Kelliher *et al.* 2005). Kelliher *et al.* (2005) conducted a laboratory incubation experiment where they applied urea applications to soil samples collected from a temperate dairy cattle-grazed pasture near Lincoln, New Zealand, and found that microbial respiration increased by up to 5 times that of control soils a day after urea application. They reported that microbial respiration remained high for 4 days, and returned to pre-treatment levels after 6 days. A study in which Clough *et al.* (2003) applied synthetic urine to soils sampled from a temperate sheep-grazed grassland near Lincoln, New

Zealand, reported that over 9 days after urine application, total R_s was 4.3 times greater than that of control soils. In this present study, there was no noticeable effect on R_s from possible urine application by the cattle, although it is not known whether the cattle urinated on or near the R_s collars embedded in the pasture. The lack of a noticeable urination effect might be because R_s measurements were generally made more than a week after the site had been grazed. However, on 21 October R_s was measured while the cattle were in the pasture grazing and there was no significant change in R_s in relation to the previous and subsequent days on which measurements took place.

For more complete testing of the laboratory based model under field conditions, a wider range of θ_n is required. Inter-annual variability in rainfall could result in a wide range of θ at the field site, but periods of prolonged drought are rare. This suggests, therefore, that changes in R_s at this field site can be explained largely by T_s, except under extreme drought conditions in exceptional years.

2.4.4 Conclusions

The results of the laboratory study showed that both T_s and θ_n regulated R_s in this cattle grazed temperate pasture. In the laboratory, θ_n had a limiting effect on respiration when θ_n fell below 0.90. However, in the field study the water limitation effect was minor, due to other factors such as grass roots accessing deeper soil water and high, well distributed rainfall. Thus, seasonal changes in R_s at the site are explained almost entirely by T_s. R_s rates at this temperate grazed pasture are relatively high compared to those reported for other temperate grasslands, which might be due to the non water limiting conditions which persist for much of the year at this site. The soil-surface respiration model suggests that if the field site were to experience drier soil-surface conditions than experienced throughout this study period, R_s would likely be reduced due to θ limitations.

3 Measurement and modelling of soil-surface respiration from a grazed temperate pasture during the growing season

3.1 Introduction

Net ecosystem CO_2 exchange (*NEE*) is determined from the difference between the photosynthetic CO_2 input from the atmosphere to the ecosystem, which occurs via photosynthesis, and the CO_2 outputs from the ecosystem due to ecosystem respiration (R_e) (equation 1.3). The magnitude of *NEE* is relatively small compared to the opposing photosynthetic and ecosystem respiration CO_2 fluxes (section 1, Fig.1-1). Ecosystem respiration comprises CO_2 from both above-ground and below-ground components. The above-ground CO_2 source occurs as a result of autotrophic respiration (R_{aa}) which takes place through plant components. The below-ground CO_2 source occurs as soil-surface respiration (R_s) which is the result of heterotrophic decomposition of soil organic compounds and detritus (R_h), along with root autotrophic respiration (R_{ab}) (Reth *et al.* 2005). Soil-surface respiration is the second largest CO_2 flux in the global carbon cycle (Reichstein *et al.* 2005), thus it is extremely important to understand how this is regulated by environmental variables to predict future impacts of global climate change on carbon budgets for ecosystems (Law *et al.*1999a).

Common methods for measuring R_s include chambers placed on the soil-surface and the eddy covariance technique for whole ecosystem exchange. Chamber measurements can provide useful information on the spatial variation of R_s and how it responds to environmental variables. In chapter 2 chamber measurements under controlled laboratory conditions were used to show how R_s in a New Zealand grazed pasture was regulated by soil temperature (T_s) and root-zone volumetric water content (θ). This knowledge was subsequently used to develop a model to determine the response of R_s to driving environmental variables.

Eddy covariance systems measure the covariation between vertical wind velocities and CO_2 concentrations, providing a direct measure of *NEE* across the canopy

– atmosphere interface (Baldocchi 2003). During the nocturnal period, when photosynthesis is absent, the eddy covariance technique provides a direct measurement of R_e. Nocturnal measurements of respiration using eddy covariance have an advantage over chamber measurements in that they reduce the inherent uncertainties that are involved with scaling up chamber measurements over time and space (Law *et al.* 1999b).

Eddy covariance nighttime measurements also provide a useful means of evaluating chamber based respiration models. This requires the up-scaling of chamber measurements. Alternatively, a comparison of techniques could involve the down-scaling of eddy covariance data to the chamber based measurements.

The contribution of R_s to R_e has been measured in many ecosystems. For example, Wohlfahrt *et al.* (2005) used eddy covariance and chamber measurements in a mountain meadow in the Austrian Alps to show that the contribution of R_s to R_e varied from 100% in the winter to 40% in the summer following changes in the presence of above-ground vegetation. The contribution of R_s to R_e, measured using respiration chambers, ranged from 50% to 77% during the growing season at grazed and un-grazed grassland sites in Yellowstone National Park, USA (Risch and Frank 2006). In the study by Risch and Frank (2006) R_s, was almost constant over the growing season, however above-ground autotrophic respiration (R_{aa}) closely followed changes in soil and air temperature and vegetation development.

In New Zealand grazed pastures, the contribution of R_s to R_e is not known, thus the objectives of this part of the study were to:

- Determine the contribution of R_s to R_e,
- Determine if measuring soil-surface respiration with the surface grass clipped to 20 mm above the soil-surface (as conducted in chapter 2) differs significantly from measuring soil-surface respiration with the grass clipped right to the soil surface,
- Compare chamber based modelled estimates of R_s with eddy covariance R_e measurements that have been partitioned into R_s and R_{aa}, and

- Use continuous half-hourly soil temperature and root-zone water content measurements to estimate total growing-season R_s.

3.2 Methods

3.2.1 Site description

The study was conducted in an established cattle-grazed pasture, located near Oxford in Canterbury, New Zealand (latitude 43.3° S, longitude 172.2° E, elevation above sea level 34m). The pasture was dominated by perennial ryegrass (*Lolium perenne* L.). Other vegetation included white clover (*Trifolium repens* L.),yorkshire fog (*Holcus lanatus* L.), creeping bent (*Agrostis stolonifera* L.) and browntop (*Agrostis capillaris* L.). During the measurement period cattle grazed the pasture three times, from 9 October to 22 October 2005, from 25 November to 8 December 2005, and from 3 February to 16 February 2006.

The soil was a Taitapu Typic Orthic Gley (New Zealand soil classification) (Hewitt 1998), poorly drained, with a perched water table. This type of soil typically develops on wet sites and in depressions at the bases of hills. For much of the year, the water table is near to the surface and the soil profile has a pale subsoil colour. In this soil, field capacity, expressed as root-zone volumetric water content (θ), occurs at 0.49 m^3 m^{-3}. The average C:N ratio (0 – 300 mm depth) was 14.2. Mixed *Nothofagus* and *Podocarpus* forests were present at this location before conversion to pasture, more than a century ago. The underlying zonal soils are derived from greywacke and tertiary rocks with a covering of loess, which developed during the last glaciation (18 – 20 000 years ago). The soil pH was 5.3. At depths greater than 300 mm, the soil became white and mottled.

At Darfield, located 20 km from the field site, the 30 year mean annual air temperature is 11.7 °C (NIWA 2006). The climate is characterized by cool, moist winters (average daily air temperature 7 °C) and warm summers (average daily air temperature 16 °C and average daily maximum air temperature 22 °C). The average yearly rainfall is 782 mm with the rainfall being evenly distributed throughout the year (NIWA 2006).

3.2.2 Determining the contribution of soil-surface respiration to ecosystem respiration

A partitioning exercise was conducted in spring 2005. At nine replicate sites, a closed gas exchange system was used to measure *NEE*, R_e, R_s and soil-surface respiration with the grass clipped to ground level (R_{sG}). The system consisted of a clear dome chamber (height 200 mm) placed on a collar (diameter 340 mm, height 100 mm) inserted 20 mm into the soil surface at random locations in the pasture, attached to an infrared gas analyser (Li-6200, Li-Cor, Lincoln, NE, USA) (Plate 3.1). The dome chamber had a height of 200 mm, which was high enough to fit over the pasture without disturbing the system and the soil collars contained a rubber seal to ensure leaks were minimised during CO_2 exchange measurements. By measuring the flux densities mentioned above, it was possible to calculate the contribution of R_s to R_e.

The first measurement, made in natural daylight conditions, determined *NEE*. This was achieved by simply placing the air-flushed dome chamber onto the appropriate collar and then recording the time and concentration of CO_2 every 30 seconds for a total period of 2.5 min. This enabled the flux density to be calculated as,

$$Q = \frac{\Delta c}{\Delta t} \cdot \frac{v}{a} \tag{3.1}$$

where Q is the CO_2 flux density, Δc is the change in CO_2 concentration, Δt is the change in time, v is the volume of the total chamber and a is the ground area occupied by the chamber. For each measurement the flux density was calculated as the mean of three measurements.

Following the *NEE* measurement, the chamber was opened, the headspace flushed with air, the dome replaced and an opaque canvas covering was placed over the chamber. The canvas covering ensured that no light entered the chamber thus making sure the only flux was R_e, as photosynthesis does not occur in the dark. The measurement of R_e was made in the same manner as described above for *NEE*.

Directly after R_e had been measured, the chamber was opened and the grass was clipped inside the soil collar to a height of 20 mm above the soil-surface and R_s was measured as described above. The clipping was done to the same level as conducted in chapter 2 (sections 2.2.2 and 2.2.3).

Finally, R_{sG} was measured as above, after clipping the remaining 20 mm of grass right down to the soil-surface.

As each CO_2 exchange measurement was being conducted, soil temperature was measured using a thermistor placed in the soil at a depth of 50 mm. During *NEE* measurements leaf temperature was also measured using a thermistor. Root-zone volumetric water content was measured as described in section 3.2.4.

Grass clipped prior to the R_s and R_{sG} measurements was collected so that above-ground biomass and leaf area index (L) could be determined for each of the nine replicates. A biomass sub-sample was taken from the harvested clippings from each replicate. This was then scanned to determine the sub-sample leaf surface area. The sub-samples and the remaining clippings were then dried for 48 hours at 70 °C, and weighed to determine total above-ground biomass and L for each replicate.

Plate 3.1 System used to measure net ecosystem exchange (section 3.2.2). The dome CO_2 exchange chamber can be seen on top of a soil collar previously inserted 20 mm into the ground. A battery powering the infrared gas-analyser can be seen near the chamber.

3.2.3 Eddy covariance ecosystem respiration measurements

Ecosystem respiration (R_e) data were collected, from September 2005 (early spring) – January 2006 (late autumn) with a closed-path, eddy-covariance system. The instrumentation consisted of a three-axis sonic anemometer (Solent, R3, Gill Instruments, Lymington, Hampshire, UK) mounted at a height of 4 m above the pasture (Plate 3.2). An air sampling suction pump, with a flow rate of 6 L min^{-1}, pulled air through Decabon tubing (ID 4 mm), through a heat exchanger and then a closed-path,

fast-response infrared gas analyser (Li-6262, Li-Cor, Lincoln, NE, USA) which measured the concentration of both CO_2 and water vapour. The analyser was kept in a temperature controlled box and nitrogen gas was bled through the reference side of the analyser at 0.03 L min^{-1}. Calibration of the CO_2 analyser was done infrequently, but when carried out drift was usually very small. The sampling tube was not heated because the lowered internal pressure caused by the inclusion of a 1 μm filter reduced the dew point and prevented condensation formation. All wind and CO_2 data were collected at 20 Hz (EddyMeas, Max-Planck-Institute for Biogeochemistry, Jena, Germany). Post-processing procedures used the analysis package developed by R. Clement at the University of Edinburgh (EdiRe) to determine 30 minute averages and closely followed the steps described by Moncrieff et al. (1997) and Aubinet et al. (2000). Changes in the average half-hour CO_2 concentration stored in the air space below the sonic anemometer were calculated but found to be insignificant. By convention, the flux of CO_2 away from the surface (respiration) is positive.

As this study was only interested in measurements of respiration in the absence of photosynthesis, only nighttime data were used. These data were further screened for suitable wind direction, when the wind was from the east or west (thus passing over the field site), and when sufficiently turbulent, the threshold value u^* (friction velocity) > 0.3 m s^{-1}, well within the range of 0.1 -0.6 m s^{-1} often used to produce reliable nighttime data (Baldocchi 2003). For analysis purposes, data meeting these criteria were grouped by individual nights to attain nightly averages of R_e. Only nightly averages of R_e that included three or more valid 30 min measurements, on nights when the cattle were not grazing the site were considered. The eddy covariance system was run by Dr. John Hunt of Landcare research, and nocturnal data were made available for this study.

Plate 3.2 Eddy covariance system used to measure CO_2 exchange. The sonic anemometer can be seen attached to the top of the tower. The gas analyser is located inside the temperature controlled box.

3.2.4 Measurements of root-zone water content and soil temperature

Data for root-zone volumetric water content (θ) and soil temperature (T_s) were measured half-hourly at 50, 100 and 300 mm soil depth from August 2005 to April 2006 using automated probes (ThetaProbe, Delta-T, Cambridge, UK) linked to data loggers (ML2 CR10X, Campbell Scientific, Logan, USA).

For analysis purposes, θ measurements were integrated to provide a single value for 0 – 300 mm. To integrate θ, values at the 50, 100 and 300 mm depths, which

represented 0 – 75, 75 – 200, and 200 – 300 mm of the soil profile, were multiplied by the proportion of the profile they measured (25, 41.6 and 33.3% respectively) and then the values were added together. When soil samples were analysed, it was found that the bulk density of the soil varied considerably, from 0.456 to 1.132 $m^3 m^{-3}$. Thus, we decided to use a normalised value of root-zone water content (θ_n), defined as the amount of θ present relative to the maximum value (θ_{max}).

$$\theta_n = \theta / \theta_{max} \tag{3.2}$$

3.2.5 Modelling soil respiration

The model of R_s, developed in chapter 2, was used to model growing season R_s in the field using half-hourly measurements of T_s and θ_n (section 3.2.4). Where,

$$R_s = R_{10} e^{E_o\left[\frac{1}{56.02} - \frac{1}{T_s - 227.13}\right]} \cdot \left[\frac{\theta_n}{\theta_c}\right] \tag{3.3}$$

R_{10} is the base respiration rate at 10 °C, T_s is the soil temperature (K) and E_o is a parameter related to the energy of activation (K). θ_c is the point at which a further increase in θ_n no longer influences respiration. When θ_n was greater than θ_c, the term (θ_n / θ_c) is set to 1. The model is a non-linear mixed effects model, fitted by maximum likelihood (Pinheiro and Bates 2000) (see section 2.2.4 for further details).

3.2.6 Biomass measurements

Twenty replicate samples for total aboveground biomass were collected once a month by Tony McSeveny (Landcare Research) by clipping vegetation to ground level within a 0.5 m x 0.5 m plots. The plots were placed randomly throughout the pasture. Sub-samples were collected from each main sample to determine the percentage of grass, herb and dead biomass within each replicate. The sub- and main samples were dried in an oven at 70 °C for 48 h and then weighed to determine above-ground biomass.

3.3 Results

3.3.1 Determination of the contribution of soil-surface respiration to ecosystem respiration

On the four days used to determine the contribution of R_s to R_e, leaf temperature and T_s averaged 19.7 and 15.6 °C respectively (Table 3-1). Normalised root-zone water content, measured next to the eddy covariance system, averaged 0.92 which was above the threshold θ_c value of 0.90 (as determined in section 2.3.2), indicating that root-zone water content was not limiting respiration at this time.

Table 3-1 Leaf and soil temperatures, and normalised root-zone water content (θ_n) (0 – 300 mm) during the days of the partitioning experiment.

	Leaf temperature (°C)	**Soil temperature (°C) (50 mm depth)**	θ_n
14 November	24.0	15.6	0.91
16 November	18.3	14.6	0.93
17 November	13.3	15.0	0.93
18 November	23.0	17.3	0.92

Averages of the partitioned CO_2 fluxes measured with the clear chamber, showed that the *NEE* was negative, indicating a net uptake of CO_2 by the ecosystem (Table 3-2). Ecosystem respiration and R_s were 13.8 and 11.1 µmol m^{-2} s^{-1}, indicating that 84% of R_e was comprised of respiration from the soil-surface. This implies that the remaining 16% of R_e was due to R_{aa}. Rates of R_{sG} were slightly lower then R_s and comprised 80% of R_e. Among the nine replicates there was a significant relationship between the contribution of R_s to R_e and L (Fig. 3-1).

Table 3-2. Direct measurements of net ecosystem exchange (*NEE*), ecosystem respiration (R_e), soil-surface respiration with the grass clipped to 20mm (R_s), and soil-surface respiration with the grass clipped to soil surface (R_{sG}) and the contribution of R_s to R_e, R_{aa} to R_e, and R_{sG} to R_e, and standard errors (SE). n = 10.

	CO_2 exchange	**SE**
NEE	-5.6 µmol m^{-2} s^{-1}	1.2
R_e	12.9 µmol m^{-2} s^{-1}	1.0
R_s	10.8 µmol m^{-2} s^{-1}	0.80
R_{sG}	10.5 µmol m^{-2} s^{-1}	1.0
R_s / R_e	84%	0.0
R_{aa} / R_e	16%	0.0
R_{sG} / R_e	80%	0.023

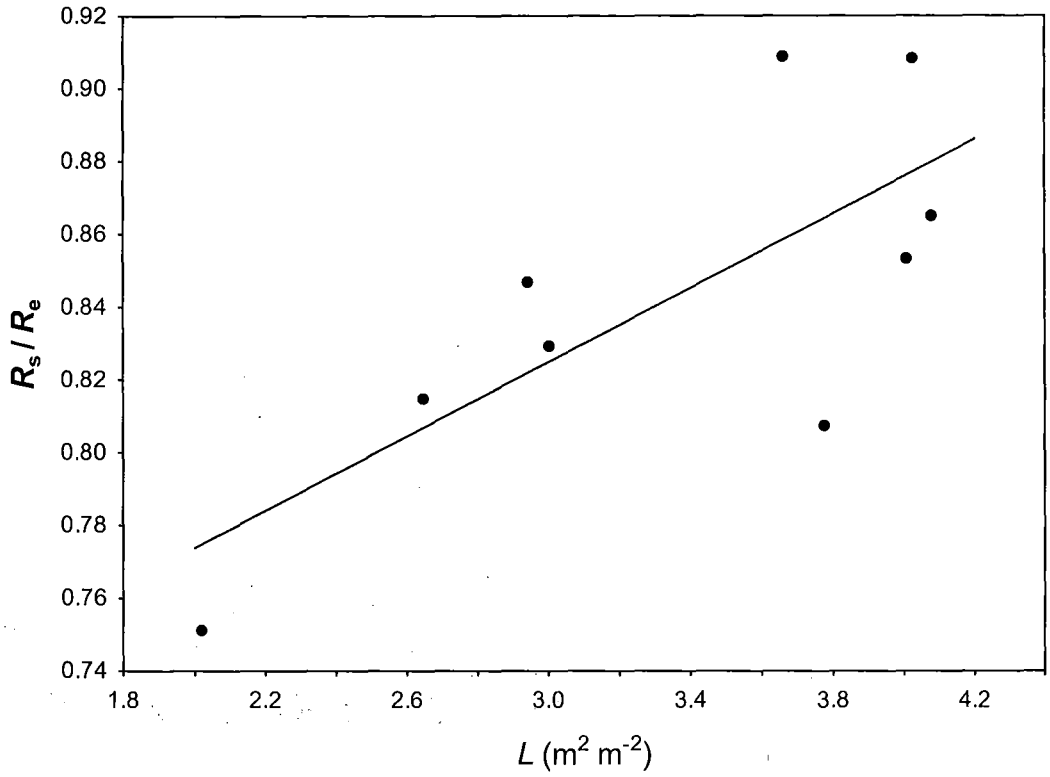

Figure 3-1 The relationship between the ratio of R_s to R_e and leaf area index (L) for each of the nine replicates in the CO_2 exchange partitioning exercise. r^2 = 0.557; y = 0.672 + 0.051*x.

3.3.2 Eddy covariance nighttime respiration measurements

There was a total of 58 nights where the nocturnal eddy covariance ecosystem respiration data met the selection criteria outlined in section 3.2.3. When the measurement period began in September 2005, the nighttime T_s was 11 °C (Fig. 3-2). As spring progressed, T_s quickly increased to approximately 17 °C and reached peaks of 20 °C during mid-summer. In early autumn, T_s began to decrease to approximately 16 °C at the end of the measurement period. Maximum θ during the measurement period was 0.49 m^3 m^{-3}. From spring through to the early summer period, θ_n was between 0.9 and 1. In mid-summer θ_n began to decrease but following a rainfall event it quickly returned to near field capacity. During the late summer θ_n gradually fell and reached a low of approximately 0.57 by early autumn.

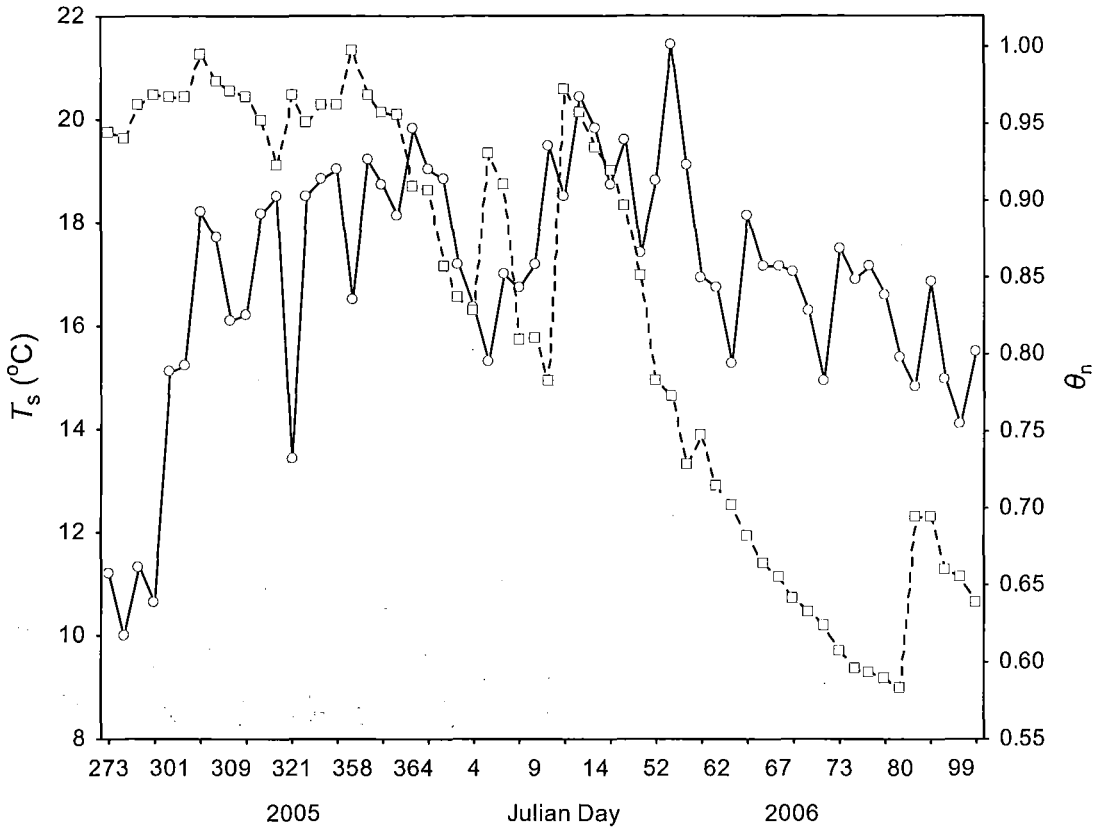

Figure 3-2 Nocturnal nighttime averages of field site soil temperature (T_s) (solid line) at 50 mm depth and normalised root-zone water content (θ_n) (dashed line) over the measurement period.

The average ecosystem respiration rate for the 58 nights of valid data was 6.98 μmol m^{-2} s^{-1} and ranged from a high of 11.8 μmol m^{-2} s^{-1} in late December, 2005 to a low of 1.9 μmol m^{-2} s^{-1} in February, 2006 (Fig. 3-3).

Since the partitioning exercise revealed that 84% of R_e is comprised of R_s, the nocturnal eddy covariance data was multiplied by this fraction to obtain eddy covariance estimates of soil-surface respiration (R_{sE}) (Fig. 3-3). R_{sE} data were compared with chamber based modelled rates of R_s. R_{sE} rates that varied between 2.3 and 9.8 μmol CO_2 m^{-2} s^{-1} throughout the late spring and early summer periods. During the early autumn, R_{sE} rates were relatively low, as they were limited by reductions in both T_s and

θ_n. Throughout the entire measurement period, the maximum and minimum R_{sE} rates reached were 9.9 and 1.6 μmol m^{-2} s^{-1}.

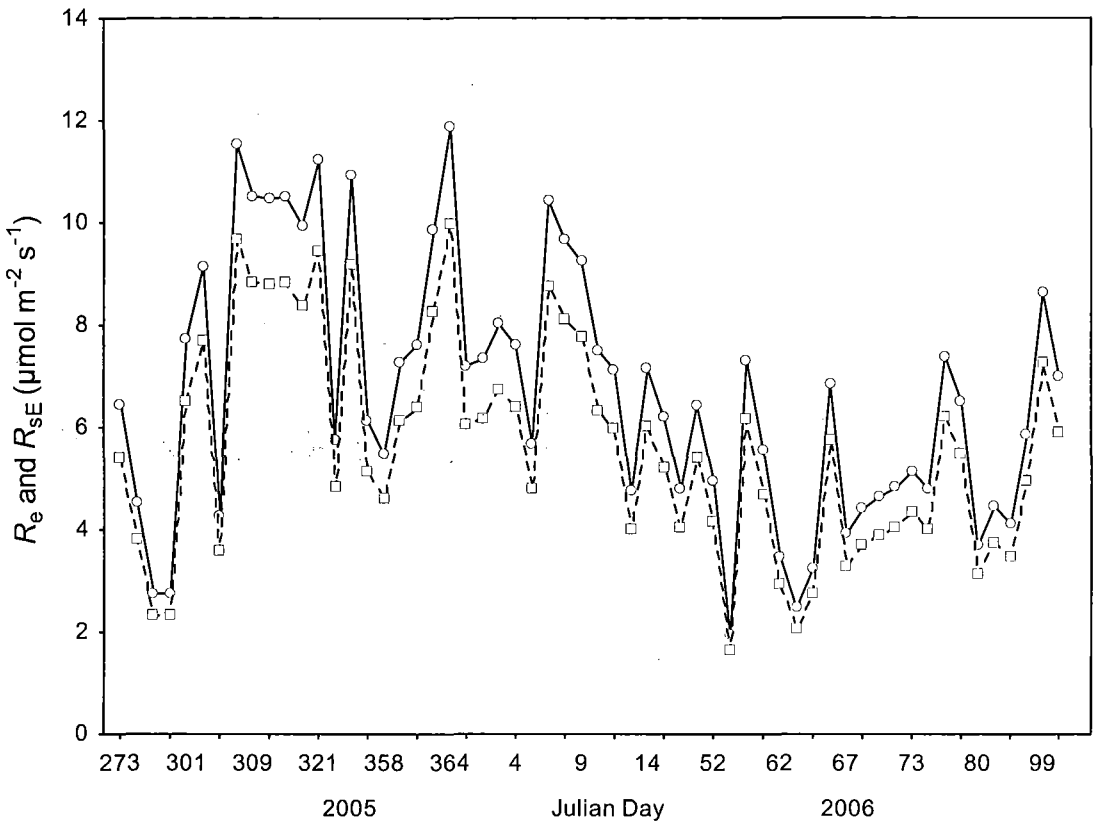

Figure 3-3 Nocturnal nighttime averages of ecosystem respiration (R_e) (solid line) and eddy covariance soil-surface respiration (R_{sE}) (dashed line) over the measurement period. R_{sE} was calculated by multiplying R_e by the fraction 0.84, as determined in the partitioning exercise.

Any influence of L on R_{sE} was not able to be determined due to the large amount of overlap in the standard errors of L data and normalised measurements of R_{sE} (Fig. 3-4). R_{sE} were normalised to 10 °C, by using equation 3.3 (with the root-zone water content term set to 1). Normalised R_{sE} data were only considered for this analysis if

measurements were made within a week of biomass collection and if the cattle did not enter the pasture to graze within that week.

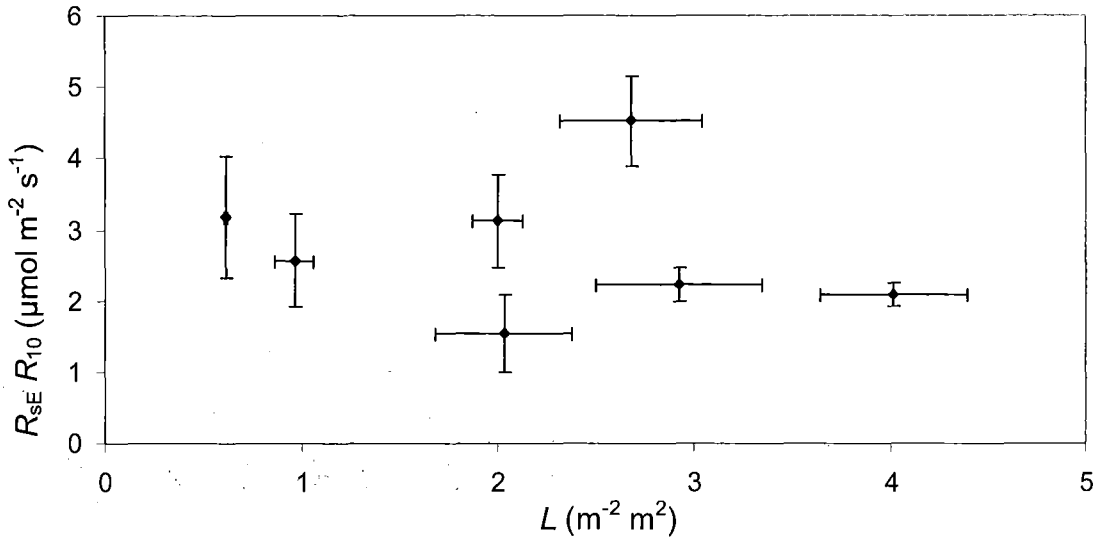

Figure 3-4 Eddy covariance estimates of soil-surface respiration (R_{sE}) normalised to 10 °C and leaf area index (L). R_{10} values are averages of acceptable nights of R_{sE} data occurring within a week of biomass measurements (providing cattle were not grazing within that week). L measurements represent the average of twenty replicate measurements. Bars show the standard errors on both axes.

3.3.3 Modelling soil-surface respiration measurements

In Chapter 2, a chamber-based model was developed to estimate R_s as a function of T_s and θ_n (equation 3.3). The parameters used to run the model are presented in Table 3-3. When this model was applied to the entire period of valid nighttime eddy covariance measurements, using soil temperature and root-zone water content data collected at the site, resulting values were consistently higher than R_{sE}, but generally followed the same pattern (Fig. 3-5). The integrated sum for the R_{sE} and modelled R_s for the total 58 nights

of valid measurements are presented in Table 3-4. The total model R_s was greater than the total R_{sE} by 16 mol m^{-2} (57%) (Table 3-4).

Table 3-3 Fitted parameters for the chamber based soil-surface respiration model as determined in chapter 2. E_o is related to the energy of activation, θ_c is the point at which root-zone water content no longer influences respiration. The R_{10} value comes from direct soil-surface respiration measurements made in the field at 10°C with a closed chamber.

R_{10} (μmol m^{-2} s^{-1})	E_o (K)	θ_c
4.7	369.2	0.90

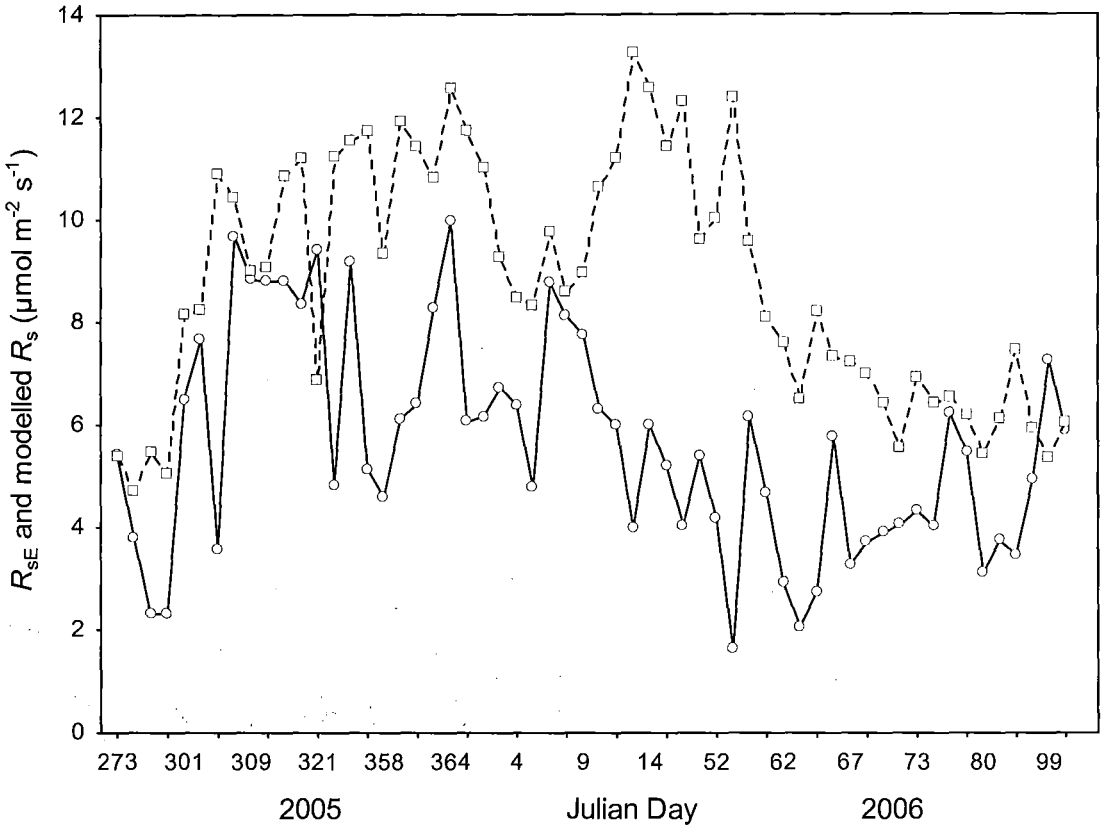

Figure 3-5 Eddy covariance soil-surface respiration (R_{sE}) (solid line) and modelled soil-surface respiration (R_s) (dashed line) over the measurement period. r^2 = 0.1481.

Table 3-4 Total eddy covariance soil-surface respiration (R_{sE}) and estimates using the chamber based model of R_s for the 58 nights of valid measurements.

	R_{sE}		**Modelled R_s**
(mol m^{-2})	(kg C m^{-2})	(mol m^{-2})	(kg C m^{-2})
28	0.34	44	0.53

3.3.4 *Estimating total growing season soil-surface respiration at the field site*

The continuous field site measurements of T_s and θ_n and the model of R_s developed in Chapter 2 were used to estimate total growing season R_s (12 August 2005 to 28 April 2006 (Fig. 3-6) (see appendix). There was a 10 day data gap from day 259 -268 due to instrumentation malfunction. The model, averaged over 24 h periods, ranged from a high of 13.29 µmol m^{-2} s^{-1} in December to a low of 2.98 µmol m^{-2} s^{-1} in August. Total growing season R_s is estimated to be 162 mol m^{-2} (1.94 kg C m^{-2}) for the 249 day measurement period.

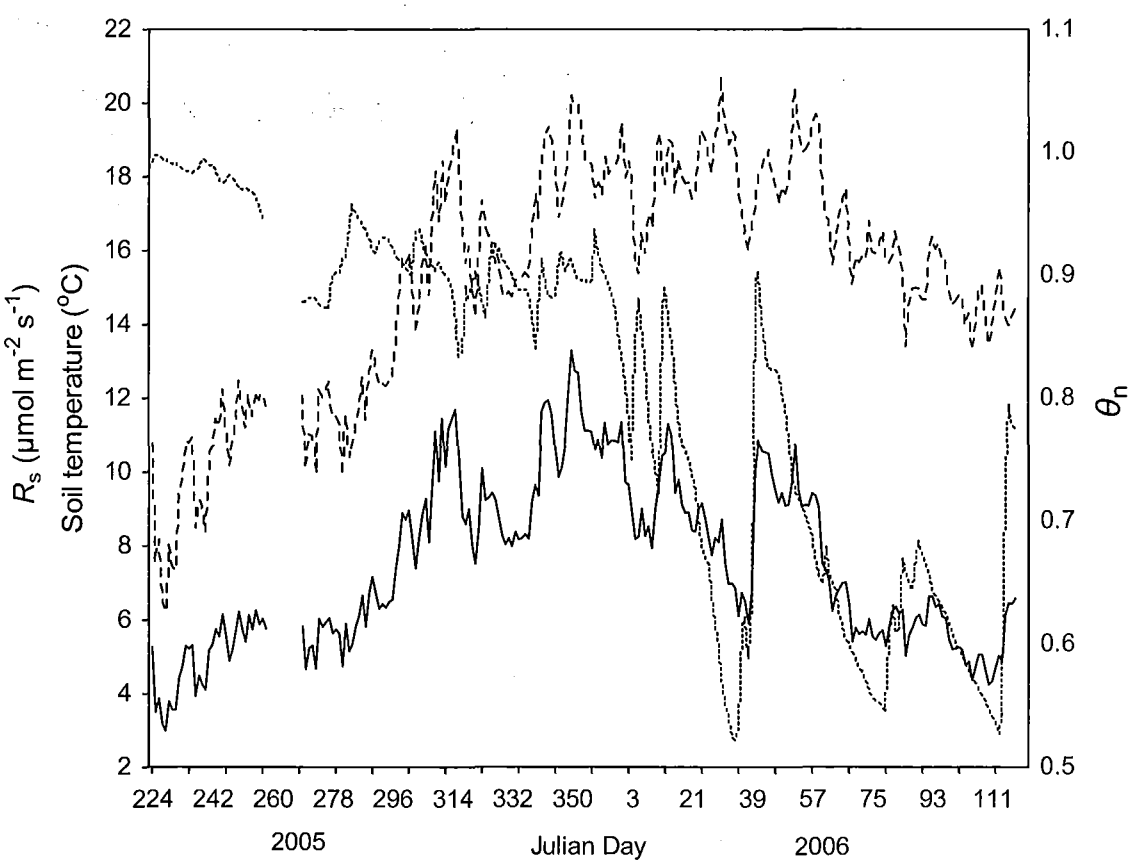

Figure 3-6 Growing season soil temperature (°C) at 50 mm (dashed line) and modelled soil-surface respiration (black line) on the left axis, and normalised root-zone water content (θ_n) (dotted line) on the right axis. The gap in the data from days 259 -268 is due to equipment malfunction.

3.4 Discussion

3.4.1 Partitioning sources of respiration

Soil-surface respiration was the dominant contributor (84%) to R_e in this temperate pasture ecosystem. The 16% of ecosystem respiration not attributed to R_s was attributed to the respiration of above-ground grasses (R_{aa}). The small 4% difference between the contribution of soil-surface respiration with the grass clipped to 20 mm above the soil surface (R_s) and soil-surface respiration with the grass clipped right to the soil-surface (R_{sG}) provides support to the technique of clipping the grass to 20 mm above the soil-surface (used in chapter 2) to attain a robust measurement of soil-surface respiration.

It is possible that the contribution of R_s to R_e varies throughout the year, as R_{aa} and R_s could respond differently to variations in T_s and θ_n (Davidson *et al.* 2006b). However, the limited data sets obtained in this study were not able to answer this question. In a study in a mountain meadow in the Austrian Alps, which used the eddy covariance technique to measure R_e and a respiration chamber to measure R_s, Wohlfahrt *et al.* (2005) reported that the contribution of R_s to R_e varied from 100% in the winter, when above-ground grasses were absent, to 40% in mid – summer. In this study, T_s rarely fell below 10 °C and above-ground vegetation was always present and green, so such a dramatic change in the contribution of R_s to R_e would not be expected. Risch and Frank (2006) used respiration chambers to measure R_s and R_e at grazed and un-grazed sites in a temperate grassland in Yellowstone National Park, USA, and found that the contribution of R_s to R_e ranged from 50 to 77% during the growing season (May – September). Risch and Frank (2006) found that R_s did not vary much throughout the growing season, with the exception of May when all CO_2 exchange rates were low (likely due to an undeveloped canopy), but R_e generally followed seasonal changes in L.

In this study, the finding that the contribution of R_s to R_e amongst the nine replicates was significantly related to L was expected. As L increased, the contribution of R_s to R_e also increased, indicating that R_s responded to changes in above-ground leaf area. This occurs because evidence suggests that below-ground autotrophic respiration (roots) is partially dependent on plant growth and development, photosynthesis and carbon allocation patterns (Flanagan and Johnson 2005). The heterotrophic respiration

component of R_s is also partially dependent on the supply and quality of respiratory substrate provided by plants, particularly plant roots (Raich and Schlesinger 1992; Wan and Luo 2003). Thus, both R_{ab} and R_h decrease as L decreases, resulting in a reduced contribution of R_s to total R_e.

3.4.2 Measured and modelled soil-surface respiration

The soil-surface respiration model developed in Chapter 2, consistently estimated higher rates of R_s than R_{sE} measurements (Fig. 3-5). Other studies have also reported higher chamber-based estimates of respiration when compared to eddy covariance measurements (e.g. Law *et al.* 2001; Law *et al.* 1999a; Law *et al.* 1999b; Lavigne *et al.* 1997; Goulden *et al.* 1996). However, there is a dearth of such studies in grazed pasture systems. In a ponderosa pine forest in Oregon, USA, Law *et al.* (1999b), reported that eddy covariance measurements of R_e were 50% lower than chamber based models of R_e (the sum of chamber based models of R_s, foliage respiration and wood respiration), with weak correlation between the measured eddy covariance respiration and modelled respiration (r^2= 0.14). Nocturnal eddy covariance measurements of R_e were on average 23%, 35% and 27% lower than chamber based estimates in a ponderosa pine forest, a mixed temperate forest and boreal coniferous forests (Law *et al.* 1999a; Goulden *et al.* 1996 and Lavigne *et al.* 1997). There was however, good agreement between eddy covariance and chamber based respiration measurements in a different ponderosa pine forest study by Law *et al.* (2001).

Two factors can often lead to eddy covariance measurements underestimating nocturnal respiration. One factor is low wind conditions during the nightime (Law *et al.* 2000a), which we attempted to avoid by only including for analysis nocturnal fluxes which occurred under relatively turbulent conditions (u^* >0.3 m s^{-1}). The second is a possible systematic bias error due to the lack of an energy balance closure often observed in eddy covariance studies (Baldocchi 2003), i.e. the sum of latent and sensible heat measured with the eddy covariance technique often does not match independent measurements of energy available. Baldocchi (2003) notes that since tests of surface energy balance closure at some sites are 10 – 30% too small to close the surface energy budget, it is possible that CO_2 exchange measurements are also

10 – 30% underestimated. Although this energy balance gap might be due to different eddy covariance and independent energy measurement footprints (Wilson *et al.* 2002), it is a possible explanation for at least some of the difference between the modelled R_s and R_{sE} values observed in this study. Law *et al.* (2000b) noted that due to the lack of agreement between chamber and eddy covariance respiration measurements, estimates of respiration with either technique remain uncertain.

Moncrieff *et al* (1996) demonstrated that the overall sampling error over a year long eddy covariance dataset is ± 1.2 mol m^{-2} y^{-1} (53 g C m^{-2} y^{-1}). Thus, the method of Moncrieff *et al.* (1996) was used to estimate the random error for the total estimate of R_{sE} in this current study. This error was extremely small (0.002%) in relation to the total estimate of R_{sE}.

In this study, the effect of *L*on R_{sE} was not able to be determined, as there was too much overlap in the standard errors of the weekly average rates of R_{sE} (from nights of valid measurements occurring within a week of biomass collection for *L* measurements), and *L* measurements (Fig. 3-4). It would be expected that R_s would be partially dependent on *L*, for reasons stated in section 3.4.1 (i.e. both below ground autotrophic and heterotrophic respiration being depending on plant C allocation below ground).

3.4.3 Estimating total growing season soil-surface respiration

The total growing-season soil-surface respiration estimate of 1.95 kg C m^{-2} for this site is relatively high compared to other studies conducted in various types of grasslands. For instance, Bolstad and Vose (2005) estimated total annual R_s to be 1.09 kg C m^{-2} y^{-1} at pasture sites with an average annual soil temperature of 13 °C, in the Appalachian Mountains, USA. Total growing season and annual R_s was reported to be 0.39 and 0.53 kg C m^{-2} in a semi-arid grassland in Colorado, USA (Pendall *et al.* 2003), and Chen *et al.* (2003) reported total annual R_s to be 1.43 kg C m^{-2} in a northern Australian tropical savanna. These studies were done in ecosystems that experienced cold, freezing winters or in semi-arid environments, which differ considerably from this temperate, intensively managed pasture, with mild winters and evenly distributed seasonal rainfall.

In a study conducted in a more similar environment, Byrne *et al.* (2005) estimated total annual R_e in new and permanent temperate grasslands in southern Ireland to be 2.0 and 2.52 kg C m^{-2}, and total growing season R_e (May – September) to be 1.17 and 1.5 kg C m^{-2}, which although estimated for the total ecosystem respiration, are closer to values estimated in this study. In a New Zealand grazed pasture, Nieveen *et al.* (2005) calculated total annual R_e to be 1.35 kg C m^{-2} , although that pasture was over a drained peat soil (bulk density of 335 kg m^{-3}), which is much less than the value for the soil found at this site (average bulk density 682 kg m^{-3}).

The high growing season R_s in this study was probably due to the large number of days included in the growing season (249 days) and the non-limiting root-zone water content conditions which persisted at this site throughout much of the growing season. Prolonged droughts, which might act to limit R_s were also absent during the measurement period as rainfall was well distributed. As a result, at this site, R_s is largely a function of T_s.

3.4.4 Conclusions

The partitioning exercise was able to determine the relative contribution of R_s to R_e successfully. This enabled nocturnal eddy covariance measurements of total ecosystem respiration (R_{sE}) to be partitioned into R_{aa} and R_s components. When compared against values of R_s estimated by the model developed in Chapter 2, R_{sE} values were consistently lower, but generally followed the same pattern. It is not known whether the R_{sE} values were underestimates or the modelled R_s values were overestimates of soil-surface respiration, but other studies have shown that eddy covariance measurements of respiration often underestimate respiration compared to chamber-based models. The soil-surface respiration model was successful in estimating total-growing season respiration at this pastoral site (1.95 kg C m^{-2}), which was of a similar magnitude compared to seasonal and annual respiration estimates reported in other grassland studies.

4 Conclusions and future work

4.1 Conclusions

Previous studies have shown that soil-surface respiration is primarily regulated by soil temperature (T_s) and root-zone water content (θ). However, relatively few studies have investigated how these two environmental variables regulate R_s in temperate grazed pastures. This thesis addressed this data-gap by investigating the regulation of R_s by either T_s or θ in a temperate grazed pasture in New Zealand. This investigation was able to achieve the objectives of this thesis, as follows,

- Objective 1 *Quantify rates of R_s in a New Zealand grazed pasture*

Field rates of soil-surface respiration were successfully quantified using a variety of techniques, including field chamber measurements, laboratory chamber measurements, and partitioned nocturnal eddy covariance measurements. The soil-surface respiration rate (R_s) at 10 °C, measured in the field using a respiration chamber, was 4.7 μmol m^{-2} s^{-1}. This was higher than reported by the very small number of other studies that have examined temperate pasture systems, probably due to the favourably long growing season at the field site.

- Objective 2 *Measure seasonal variation in R_s in relation to T_s and θ*

The laboratory exercise was able to determine the individual influence of either soil temperature or root-zone water content on R_s in this pasture ecosystem. An Arrhenius-type function described the influence of T_s on R_s, while a linear function described the influence of θ. The value of θ_c determined that θ had a limiting effect on R_s up until a normalised root-zone water content (θ_n) of 0.90, after which point a further increase in θ_n no longer influenced R_s. This is the first time the effects of soil temperature and root-zone water content on R_s have been reported for an intensively grazed pasture in New Zealand.

- Objective 3 *Model R_s and validate modelled rates of respiration against field measurements*

Using measurements of soil-surface respiration, soil temperature and normalised root-zone water content made in the laboratory exercise, and equations 2.5 and 2.6, a model of R_s was constructed. To run the model, the R_{10} parameter was established by using an average of field measurements of R_s made around 10 °C. A good fit was achieved between the model and the laboratory data (Fig. 2-1).

When validated against field chamber measurements of R_s, the model of R_s was successfully able to predict changes in R_s based on changes in T_s and θ_n (Fig. 2-4). Differences between modelled and measured R_s generally occurred when θ_n began to decline to values less than 0.90 (θ_c). At these values of normalised root-zone water content the model applied a θ limitation effect, however in the field, the θ limitation was not as apparent. This may have been due to grass roots compensating for low soil-surface water content by accessing water from deeper down the soil profile.

In order to validate the model of R_s against nocturnal eddy covariance measurements of respiration, a partitioning exercise was conducted. The partitioning exercise determined the contribution of R_s to R_e was 84%. This exercise also confirmed that measuring R_s with the grass clipped to 20 mm above the soil-surface, as conducted in the laboratory exercise and in the field, adequately removed R_{aa} from the R_s measurement.

Nocturnal eddy covariance soil-surface respiration (R_{sE}) measurements were consistently less than modelled rates of R_s. It is not known why this was the case. It is possible the lack of energy balance closure often observed in eddy covariance studies (Baldocchi 2003) led to an underestimation of R_{sE} (see section 3.4.2).

- Objective 4 *Estimate total growing-season R_s*

By using the model of R_s and continuous field measurements of T_s and θ, this investigation was able to estimate a total growing season R_s of 1.94 kg C m^{-2}.

4.2 Future work

Based on the results from this thesis there is clearly a need for more extensive research to be undertaken on the regulation of R_s in this ecosystem. Since all field measurements were conducted over just a single growing season, there were certain limitations to this investigation. For instance, the CO_2 exchange partitioning exercise was only performed during the spring/summer period. However, the contribution of R_s to R_e could vary throughout the year, as found in other studies (e.g. Davidson *et al.* 2006b), thus it would be useful to perform the partitioning exercise seasonally.

Throughout the field measurement period, root-zone water content conditions were relatively wet, which meant that the model of R_s could not be fully tested over a wide range of wet to dry soil conditions. Performing this study over multiple growing seasons, might allow the model to be more fully tested over a broader range of environmental conditions, including drought, which might not occur annually in this pasture.

A variety of techniques was used to measure and model R_s in this study. The laboratory exercise provided a very successful means of determining how soil temperature and root-zone water content regulate R_s across a broad range of T_s and θ. This would be highly difficult to replicate in the field, where other factors, such as variations in radiation, vegetation development and precipitation (Risch and Frank 2006; Trumbore 2006: Salimon *et al.* 2004), which can be kept relatively constant in a growth cabinet, could confound the individual influences of T_s and θ. Also, during the growing season that this study was conducted over, the ranges of T_s and θ were much narrower than the ranges allowed for in the laboratory exercise.

The eddy covariance technique has an advantage over respiration chambers of being able to measure CO_2 exchange continuously at the ecosystem level (Hutley *et al.* 2005). Thus, nocturnal eddy covariance measurements of ecosystem respiration incorporate spatial variations in respiration throughout the field site, not necessarily captured with chamber measurements. Nocturnal eddy covariance respiration rates were lower than modelled rates of R_s, which were based on laboratory measurements,

but generally followed changes in T_s and θ. It would be useful to examine the differences between eddy covariance respiration measurements and chamber based modelled rates of R_s. For instance, chamber measurements of R_s could be made nocturnally, thus allowing measurements to be directly comparable to eddy covariance nighttime values.

Soil-surface respiration was measured after removing above-ground autotrophic respiration by clipping the grass to 20 mm above the soil surface, both in the field and in the laboratory. This level was chosen because if clipped any shorter, the grass might have died. It is not known how this clipping might have influenced R_s, although previous studies by Wan and Luo (2003) and Bremer *et al.* (1998) showed that clipping significantly reduced rates of R_s (see section 2.2.3). Also, the specific effects of grazing on R_s in the field site were not able to be determined, although the partitioning exercise demonstrated that as leaf area index (L) increased, the contribution of R_s to R_e also increased. Future work, which involved the measuring of R_s immediately before, and after grazing or clipping events, might more clearly indicate the effects of grazing, above-ground biomass and L have on R_s.

In this thesis, the regulation of total R_s by T_s and θ in a temperate pasture was determined. However, it is possible that below-ground autotrophic respiration (R_{ab}) and heterotrophic respiration (R_h) respond differently to changes in T_s and θ. A more extensive investigation could determine the individual responses of R_{ab} and R_h to T_s and θ. Such an investigation requires additional techniques and tools, such as stable isotopes, to enable R_s to be partitioned into below-ground autotrophic and heterotrophic components (Yakir and Sternberg 2000).

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