Productivity, decomposition and carbon sequestration of *Chionochloa* species across altitudinal gradients in montane tussock grasslands of New Zealand

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General abstract

Anthropogenic activities are drastically altering Earth's terrestrial, aquatic and atmospheric processes and altering carbon (C) and nutrient cycling. Carbon sequestration, which can be negative feedback to climate change, may help mitigate humanity's impacts on Earth's climate. Carbon sequestration is a natural process occuring when the fixation of C is greater than the release of C back to the atmosphere from a specified system over an annual timeframe, minimally. Investigation of annual plant productivity, decomposition and alterations in relationships between productivity and decomposition across altitudinal and climate gradients will provide insight into C sequestration driven by environmental and plastic responses of species to climate change. This research investigates how alterations in climate influence ecoclinal populations of *Chionochloa* species' in terms of their productivity, decomposition, as well as C and nutrients, across altitudinal gradients on Mounts Tongariro and Mangaweka, Central North Island, New Zealand. Further, impacts on the C sequestration are investigated through alterations in productivity to decomposition ratios (P:D). Reciprocal translocations of living *Chionochloa* plants and litter decomposition bags were performed across plots every 100m in elevation (equivalent to 0.6^{o}C mean annual lapse rate). Trends were analysed based on experimental plots of origin and destination, and were compared with *in situ* plants and home site transplants. Productivity of downslope transplants increased at lower elevation plots (i.e. in warmer climates). Leaf litter experienced greater mass loss based on litter translocation to higher elevations on Mount Tongariro and at lower elevations on Mount Mangaweka likely owing to precipitation and temperature gradients respectively. The chemical and constituent composition of leaves and decomposed litter following translocation indicates strong environmental effects on both the plastic responses of plants in growth and the alterations in mass loss from decomposition. Despite chemical and constituent differences in *Chionochloa* species' tissues and decomposed litter across gradients, the P:D ratios were greater in warmer environments of lower altitudinal plots. The increased productivity observed outweighs the less-climatically responsive decomposition, indicating greater C sequestration in New Zealand's tussock grasslands is likely to occur with warming associated with climate change, providing an environmental and economic imperative for conservation of these indigenous grassland systems.

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Contents

Chapter 1

General Introduction

Chionochloa rubra on a recently burnt location in the Kaimanawa Ranges

Māori proverb
"*Ehara I te aurukōwhao, he takerehāia*."
"It's not a small leak, but a huge hole in the hull."
(in reference to a major disaster)

Background

Anthropogenic activities are altering Earth's climate (IPCC, 2013) which has important ramifications for biogeochemical processes, such as carbon (C) and nutrient cycling and ultimately C sequestration (Tate, 1992). "It is extremely likely [>95% chance] that human influence on climate caused more than half of the observed increase in global average surface temperature from 1951–2010" (IPCC, 2013). Since the start of the Anthropocene (the current Epoch, considered to have begun with the Industrial Revolution; Crutzen, 2002; Revkin, 2011), anthropogenic activities have increased the transfer of C from inert storage into the atmosphere via the release of carbon dioxide (CO_2) and other greenhouse gases (GHGs; Crutzen, 2002; Lövbrand *et al*., 2009). Average global temperatures have increased by 0.74 ºC over the last century (1906-2005), and are expected to rise by another 0.46-1.65ºC in the next 50 years (IPCC, 2007). There is a strong correlation between increased concentrations of greenhouse gas (GHGs) and increasing global temperatures (IPCC, 2007).

New Zealand's average surface temperatures have risen by approximately 0.9^{o}C since 1900 (IPCC, 2014). According to model projections, climate change is predicted to increase New Zealand's average surface temperatures between 0.8 to 3.5^{o}C (above the 1986 – 2005 average) by 2100, if stringent measures are not implemented to limit global GHG emissions (IPCC, 2014). Based on the average of 6 C emissions scenarios and 12 climate models, the predicted temperature increases for most of New Zealand will equate to 0.9^{o}C by 2040 and 2.1^{o}C by 2090 (MfE, 2008; Figure 1a,c). The projected changes in New Zealand's climate by 2100 are likely to result in: (1) increases in average surface temperatures (ranging from 0.75^{o}C in the south to 2.2^{o}C in the north, compared to the 1990 average), (2) significant shifts in precipitation patterns with major variation across regions of New Zealand (Figure 1b,d); (3) tripling of land area which is frost-free in spring and autumn by 2090 (IPCC, 2014); (4) approximately a 10% increase in strong winds; (5) fewer days of frosts; (6) decrease in snowfall; (7) shortened duration of seasonal snow lie; and (8) rise in snowline (MfE, 2008). These predicted changes in climate are likely to influence ecosystem processes and functioning across New Zealand.

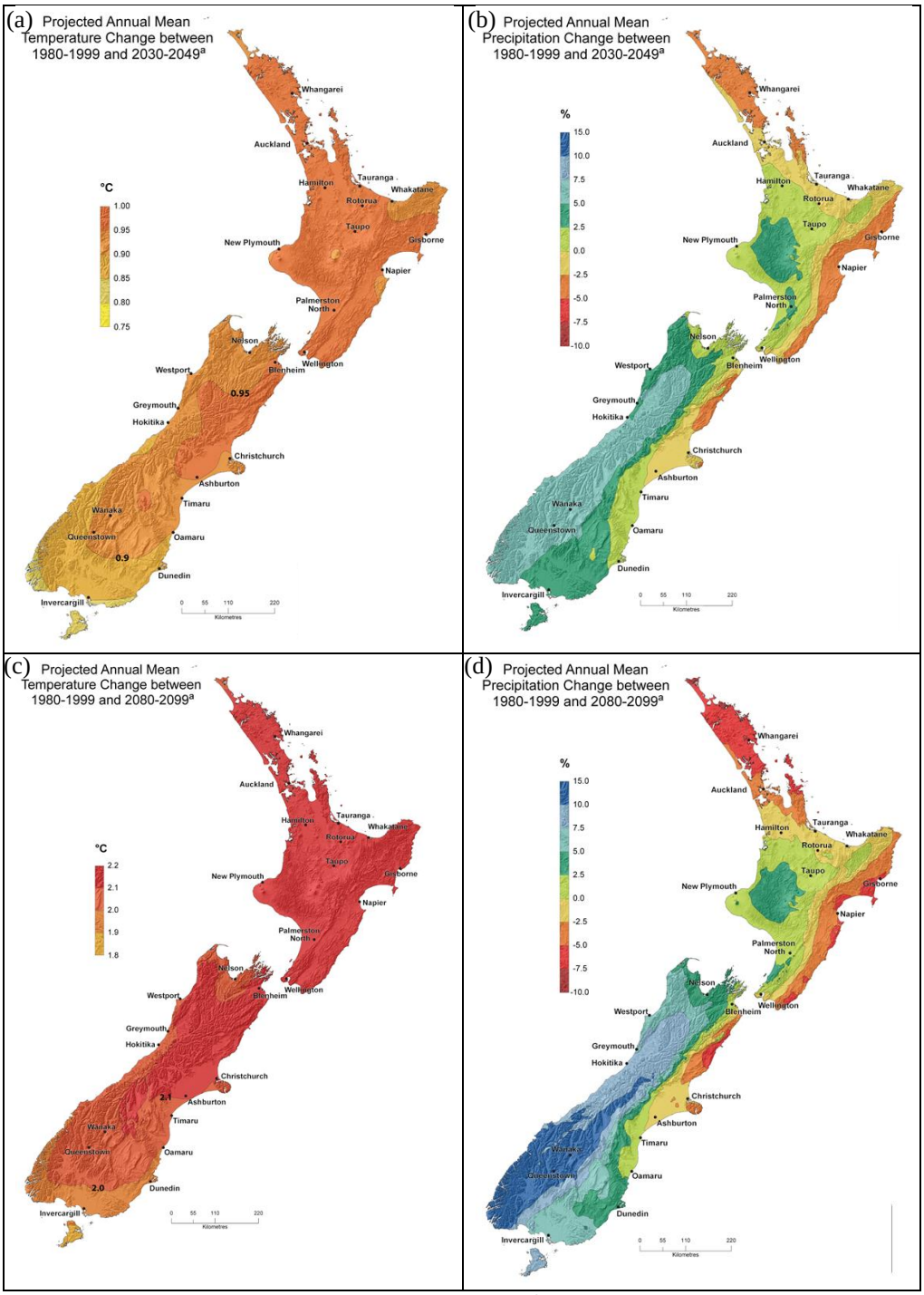

Figure 1: Projected average changes in temperature (^{o}C; a, c) and precipitation (%; b, d) for 2030 – 2049 (i.e. 2040 average) and for 2080 – 2099 (i.e. 2090 average) from the 1980 – 1999 (i.e. 1990 average) averages for New Zealand. Projections are based on averages from 6 emissions scenarios and 12 climate models (images from NIWA, 2014).

The increased concentrations of these GHGs in the Earth's atmosphere and elevated mean global temperature have raised concerns about the effects of warmer climates on biological processes (Hinckley and Tierney, 1992; Ennis and Marcus, 1996). Climate change is impacting terrestrial locations across the planet, but more intensely at high latitude and

altitude regions (IPCC, 2007). The rates of warming in these systems is predicted to be two to three times higher than increases of 20th century temperatures (Guisan and Theurillat, 2000; Cavieres and Sierra-Almeida, 2012), making these ecosystems especially vulnerable to impacts of climate change (Nogués-Bravo *et al*., 2007; Colwell *et al*., 2008). The vegetation of montane ecosystems is especially sensitive to climate change (Pauli *et al*., 1996) because of high vulnerability to alterations in abiotic conditions (Beniston, 2003).

There has been substantial investigation of responses of different species and ecosystems to climate change (Shaver *et al*., 2000; Rustad *et al*., 2001), though the ability of montane plant species to adjust to alterations in climate is uncertain (Byars *et al*., 2007). Changes in abiotic conditions occur across montane altitudinal gradients with increasing elevation, typically resulting in decreases in temperature, alterations in precipitation patterns (Körner, 2007), and increases in abiotic stress (Callaway *et al*., 2002). Temperature changes with altitude on mountains, resulting in mean annual lapse rates ranging from 0.55 – 0.65^{o}C per 100m in elevation (Rolland, 2003 and references therein). Precipitation commonly increases with elevation yielding increases in productivity (Wu *et al.*, 2014) and decomposition (Murphy *et al.*, 1998). Climate change will increase at local scales and will likely alter C and nutrient cycling resulting in increased productivity (Halloy & Mark, 2003) and decomposition (Sundqvist *et al*., 2011a; 2011b). It is uncertain whether productivity or decomposition will be more responsive to climate change and result in positive or negative feedback loops to atmospheric C (Kirschbaum, 2000).

Climate and abiotic stress can influence ecosystem processes and functioning (Callaway et al., 2002; Körner, 2007) since climate and stress play a major role in determining plant species' composition (Chapin, 1991), and select for and elicit different plant ecophysiological traits, which can in turn influence terrestrial C and nutrient cycling (Violle *et al*., 2007). The growth rates and allocation patterns of plant species may directly influence the amount and chemical composition of C that plants put into the soil, as well as the fate of that C within the soil (Chapin, 2003; Lavorel *et al*., 2007). Changes in climate may disrupt the current balances of soil carbon cycling,

storage and sequestration in terrestrial environments (Tate, 1992). Aside from recent anthropogenic disturbances, the C cycle is driven by the removal, release and storage of C between the biosphere and atmosphere (Falkowski *et al*., 2000). The key components of this C exchange between the biosphere and atmosphere are plant fixation of atmospheric CO_2 (i.e. net removal of CO_2 from the atmosphere into temporary storage within plant tissues via photosynthesis), decomposition (i.e. breakdown of tissues and organic compounds by microbes or fungi and release of CO_2 back into the atmosphere) and C sequestration (i.e. the storage of C in inert forms so it is not readily released back to the atmosphere). Climate change via alterations in temperature and precipitation patterns will likely impact all 3 of these components since the transfer of C through terrestrial ecosystems and the amount deposited into the soil is functionally correlated with photosynthesis efficiency, plant productivity and the decomposition potential of the litter (Buyanovsky *et al.*, 1987; Seastedt *et al*., 1994).

The chemical composition of the plant litter produced owing to allocation patterns can directly influence the rates of decomposition owing to litter quality and chemistry, which in turn can influence C dynamics in the soil (Hobbie, 1996 and references therein). Plant species with high growth rates primarily allocate C to photosynthetically active structures that are low in cellular density and high in nutrients, making the litter easily decomposable; species with low growth rates, on the other hand, tend to be long lived and produce nutrient-poor litter (Aerts & Chapin, 1999). Such litter is often more recalcitrant to decomposition owing to its chemical and constituent composition, as plants with a genetic disposition to tolerate elevated environmental stresses may have higher production of phenolic compounds and lignin, acting as stress regulators (Kim *et al*., 2008). The breakdown of lignin, and other recalcitrant compounds, is a slow process that eventually results in humic substances which can further increase soil C sequestration through complexes formed with other organic molecules within the soil (Hättenschwiler & Vitousek, 2000). This can aid in C sequestration because of increased residence times within the soil (Boer *et al*., 2005). Carbon sequestration may play a vital role in mitigating the

effects of elevated atmospheric CO_2 concentrations and the impending threats of climate change (Lal, 2004 and references therein).

Carbon sequestration is one of the most important topics in regards to climate change today (Krna & Rapson, 2013) as it is a natural process of removing and storing the ever increasing CO_2 from the atmosphere. The vagueness of C sequestration definitions in the literature necessitates a more robust definition. Authors commonly neglect to specify the type of C sequestration or duration of C sequestration, both of which are critical in terms of C budgeting and accounting, especially with the ever increasing anthropogenic release of CO_2 and impending consequences of climate change. In subsequent chapters a definitive definition of C sequestration is proposed and tested across altitudinal gradients (via investigation of relationships of productivity and decomposition).

Model system and species

Montane systems are ideal locations for exploration of adaptive differentiation across climate gradients (Gonzalo-Turpin & Hazard, 2009), since there are gradual changes in climate across short horizontal distances (Körner, 2007). A consequence of temperature and precipitation gradients, such as occurs on mountains, is the presence of adaptive plant forms either as ecoclines or ecotypes (Warren *et al*., 2006; Liancourt et al., 2013). Ecoclinal species across altitudinal gradients are likely to respond differently to changes in abiotic conditions and translocation is one means of investigating their responses. Transplantation experiments across montane altitudinal gradients date back to the late 1800's (Turesson, 1922 and references therein) and are still being used in field experiments today (Grassein *et al*., 2014; Read *et al*., 2014; Souther *et al*., 2014) to assess ecoclinal differences and to determine how environmental conditions and genotypic variation interact on phenotypic responses of plants (Bennington *et al*., 2012 and references therein).Thus mountains can serve as ideal locations for investigating the range of species responses to different climates to assess responses that may occur under future climate change scenarios.

Grasslands make up approximately one-fifth of global terrestrial systems (24 x 10^6 km^2) and contain >10% of global C stocks (Eswaran *et al.*, 1993). In New Zealand, approximately 60% of land area is composed of indigenous or introduced grassland species (Wardle, 1991); of these grasslands, approximately one fifth are modified indigenous short- and tall-tussock grassland communities, primarily located on the South Island (Mark & McLennan, 2005). Grasslands store a vast majority of their C within soils which have relatively long turnover times ranging from 100 to 10,000 years, and thus changes in environmental conditions that impact C sequestration and storage in grasslands will be of substantial duration and have long-lived effects on the global C cycle (Parton *et al*., 1995).

Native tussock grasslands were chosen as the model system for this research because they are an important C store in New Zealand (Trotter *et al*., 2004) and globally (Scurlock & Hall, 1998). Species within the genus *Chionochloa* (tussocks) were the model species because they are long lived perennials, have extensive altitudinal ranges, express differences in growth across montane gradients, are often the dominant species (Mark, 1965a, b, & c). Mark (1969) found reduction in leaf elongation rates of *C. rigida* when transplanted to higher altitudes and the opposite trend when planted to lower altitudes. Revealing *Chionochloa* species can express plasticity in growth responses to changes in environmental conditions across altitudinal gradients, making them the ideal species to assess the potential impacts of climate change and how this may impact C sequestration in New Zealand's tussock grasslands. Stress across altitucinal gradients not only alters growth, but changes in stress can also influence the chemical and constituent composition of leaves, increased production of secondary metabolites (Kim *et al*., 2008), which may provide living plants with additional tolerance to environmental stress, and also aid in C sequestration because of recalcitrance to decomposition and prolonged residence times of litter within the soil (Boer *et al*., 2005). Few studies have investigated the decomposition of plant material from species within the genus *Chionochloa*. Williams *et al*. (1977) is the only published study, to my knowledge, that examined decomposition of *Chionochloa* species. However they did not investigate how the role of climatic and altitudinal gradients can influence

decomposition of the litter. Nor have there been any previous studies that investigated the relationships between productivity and decomposition across altitudinal gradients in regards to C sequestration.

Research aim

The aim of this research was to investigate alterations in productivity and decomposition of *Chionochloa* species and the relationships of these parameters via the productivity to decomposition ratio (P:D) across altitudinal gradients as a means to interpret the potential range of impacts of changes in climate on endogenous C sequestration in New Zealand's tussock grasslands. The use of the P:D ratio is not a novel concept as Kirschbaum (2000) mentions a similar application of the approach presented here with modelling of positive and negative feedbacks to climate warming based on net primary productivity and decomposition of soil organic matter. The use of the P:D ratios in this research investigates the interactions of productivity and decomposition primarily at the leaf level to determine how aboveground processes can influence C sequestration of *Chionochloa* species across altitudinal gradients.

Research questions

Question 1: What does C fixation within and release of C from a system indicate for C sequestration? There is a need for a strong definition of C sequestration which allows for assessment of alterations in productivity and decomposition, especially since alterations occur to both these processes with climate change.

Question 2: How does productivity, decomposition and the productivity to decomposition ratio (P:D) of *Chionochloa* species vary across altitudinal gradients and what are implications of climate change on these processes of ecoclinal populations?

Question 3: How does productivity, decomposition and the P:D ratios of *Chionochloa* species vary in response to reciprocal translocation across altitudinal gradients and what implications does this have for climate change?

Question 4: Are there differences in the chemical and constituent composition of *Chionochloa* species tissues from different environments across altitudinal gradients and how does this influence productivity, decomposition and P:D ratios in response to climate warming?

Question 5: What are the implications of alterations in productivity, decomposition and P:D ratios with climate change in New Zealand's tussock grasslands?

Approach

An herb was chosen for this research, because herbs have no somatic C sequestration (*sensu* Krna & Rapson, 2013), which would complicate the issue of measuring productivity. A grass species was chosen because it has modular growth units, called tillers, themselves made up of repeating, linearly-elongating units called leaves, simplifying measurements. Tussock (bunch) grasses are long-lived, with an upright growth form, and species of the genus *Chionochloa* possess a wide range of temperature tolerances and are known to show variation in growth and allocation patterns throughout their altitudinal ranges (Mark, 1965a; 1965b). *Chionochloa rubra* (red tussock) and *Chionochloa pallens* (mid ribbed snow tussock) are endemic, indigenous and widespread in alpine environments in New Zealand (Connor, 1991; Connor & Lloyd, 2004). These species are found along altitudinal gradients, where changes in climatic conditions occur with changes in elevation and are considered grassland dominants in montane environments of New Zealand (Mark, 1969). The above situation was used to test relationships of the P:D ratio with climate change across altitudinal gradients.

Productivity of *in situ* and translocated *Chionochloa* species across altitudinal gradients (via reciprocal translocation) was measured to assess differences in growth and the potential implications of climate change. Decomposition of *Chionochloa* species' litter was performed with full reciprocal translocation experiments to assess changes in mass loss across altitudinal gradients as a proxy for climate change. The chemical and constituent composition of *Chionochloa* litter and tissues was investigated

as a means to understand how C and nutrient cycling may be altered in living tissue and decomposing litter with alterations in climate across altitudinal gradients. Ultimately the aim of this research was to interpret and assess the interactions of productivity and decomposition via P:D ratios of *in situ* and translocated plants and litter decomposition of *Chionochloa* species across altitudinal gradients, used as a proxy for climate change, to understand how future alterations in Earth's climate may impact endogenous C sequestration in New Zealand's tussock grasslands.

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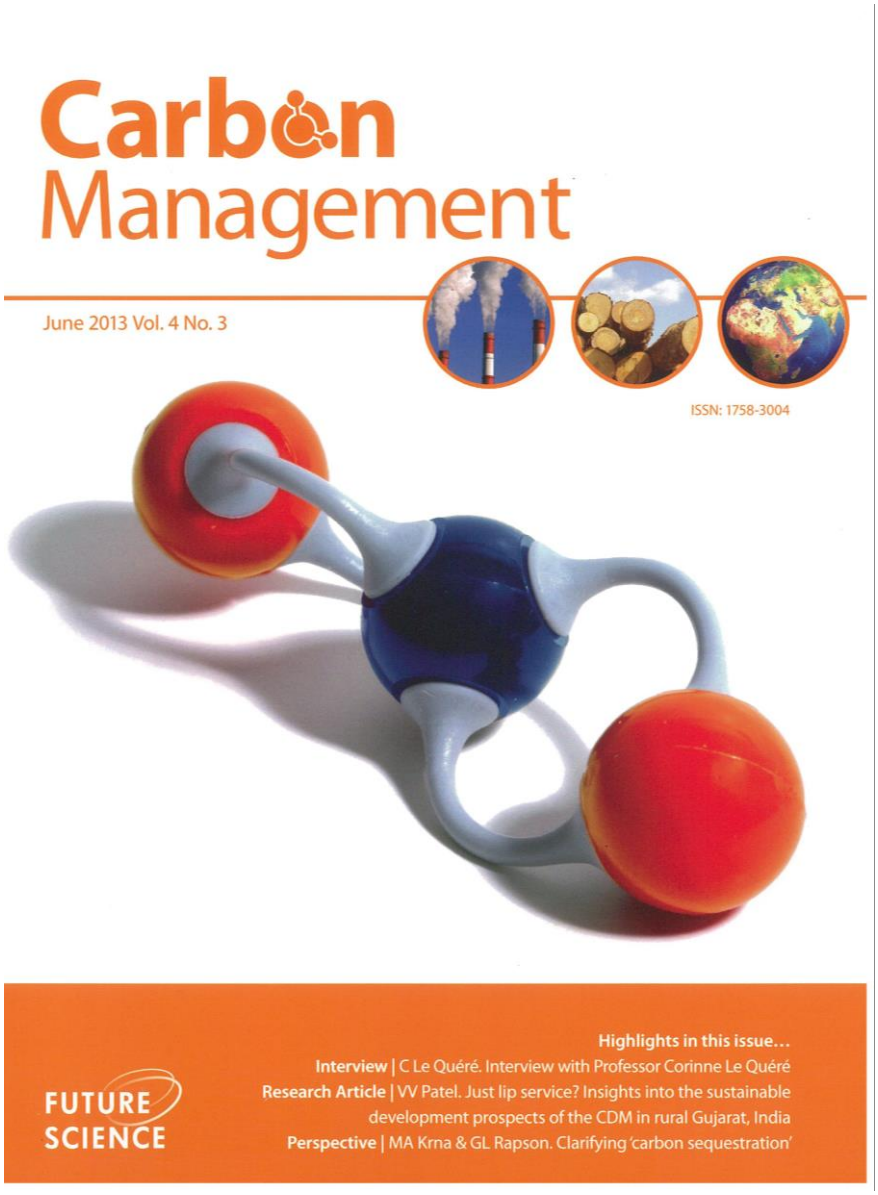
Chapter 2

Clarifying ‘carbon sequestration’



Māori proverb
“*Hōhonu kakī, pāpaku uaua*”
“Long on words, short on actions”

Clarifying 'carbon sequestration'

Carbon Management (2013) 4(3), 309–322

Matthew A Krna[1,2] & Gillian L Rapson*[1]

Despite widespread use in the literature, there seems to be little consensus on what the term 'carbon (C) sequestration' means. We differentiate between endogenous C, which fluxes within a system, and exogenous C, which fluxes between systems. Here we define 'endogenous C sequestration' as occurring when C fixation to release ratio is greater than one ($fixation_{(a,s)}/release_{(a,s)}$ >1), expressed at the briefest, annually (a) and budgeted within a specified system (s). We distinguish between sequestered C (stored for >1 year) and temporarily utilized biologic C (i.e., labile C present within a living organism), developing equations for herbaceous and woody plant systems. Standardized expression of C sequestration with incorporation of descriptors, for example '$somatic\ C\ sequestration_{(10\ year,\ forest)}$', clarifies the location, timescale and system being considered and should allow for increased transparency and improved communication for climate change debates and C budgeting.

Climate change, via increasing global temperatures and alterations of precipitation patterns, may impact biological processes [1,2] and ecosystem responses [3,4], including carbon (C) sequestration [5]. 'C sequestration' is one of the most important concepts in studies of climate change today, yielding approximately 9,690,000 and 36,153 results in the search engines of Google™ and Web of Knowledge, respectively (as of 8 April 2013) [101]. However, there is still ambiguity over what is actually meant by the term. Clearly a simple definition with greater explanatory power is needed because of the significance of C sequestration for the climate change issue [6] and the importance of clarity in C accounting aimed at reducing CO_2 emissions and moderating anthropogenic alterations of the global C cycle.

C sequestration & climate change

Aside from small inputs of C from space via meteorites and minute outputs into space of low-molecular weight C compounds [7], as well as deployment of extra-planetary hardware, the amount of C on planet Earth is effectively constant [8]. The major C pool is sedimentary rock, including marine deposits, at around 66–100 billion Gt. Geologic C sequestration has been achieved with considerable success by nature over the past 3 billion years with storage of C within the Earth's surface as, for example, natural gas, oil or coal (i.e., black C) [9].

Within the biosphere however, and particularly since the Holocene, humans have been altering C and nutrient cycling across the Earth's aquatic and terrestrial ecosystems. Humans are insatiably exploiting the geologic C storage by consuming oil, coal and natural gas to obtain energy, and as a byproduct, releasing GHGs into the atmosphere that were once sequestered securely beneath the Earth's surface [10]. Based on isotopic analyses of gases trapped in ice cores, Sapart *et al.* deduced that anthropogenic releases of C-containing GHGs, from land use changes and combustion of coal and wood during the Roman Empire and the Chinese Han Dynasty, as well as postmediaeval population expansion, were great enough to alter the Earth's climate [11]. Since the Anthropocene (considered to have started with the Industrial Revolution [12,13]), anthropogenic activities have drastically increased the transfer of C from inert storage into the atmosphere, via release of CO_2 and other GHGs [12,14]. Of the GHGs,

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Key terms

Carbon sequestration: Occurs when nontemporarily utilized biologic C fixed from the atmosphere is greater than the release of C to the atmosphere, over a specified time period and within a given system.

Endogenous carbon sequestration: When C is stored within the system in which it was fixed.

CO_2 has the greatest atmospheric concentration (~390 ppm [15]) and a long atmospheric residence time (>100 years [16,17]). Approximately 9 Pg (1 Pg = 10^{15} g = 1 Gt) of C is currently accumulating in the atmosphere per year from land use change and fossil fuel combustion [18]. Warming trends over recent decades have exceeded those of the past two millennia [19], and average global temperatures have increased by 0.74°C over the last century (1906–2005), and are expected to rise by another 0.46–1.65°C within the next 50 years [10], accelerating climate change [16,20,21]. Alterations in precipitation patterns have also been noted and are expected to continue; however, model predictions are highly variable and less certain than projected temperature trends [10]. Since CO_2 accounts for 63% of GHG emissions [10,22], reducing C emissions and increasing C sequestration rates are likely to be effective mitigation strategies for climate change [5,10,23]. But what does 'C sequestration' actually mean (Figure 1)?

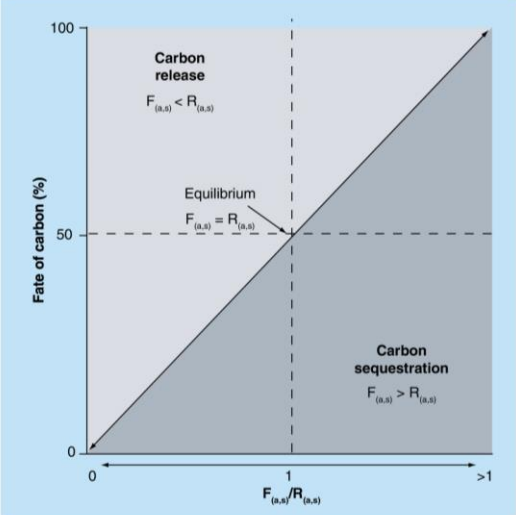


Figure 1. Fate of carbon within a system on an annual timescale in relation to the ratio of fixation to release. C that has been sequestered (dark gray) and released C (light gray).
$F_{(a,s)}$: Total C fixation per annum (a) within a system (s); $R_{(a,s)}$: Total C release from that system.

Definitions of 'C sequestration'

The Oxford Online Dictionary definition of 'definition' is: "A statement of the exact meaning of a word, especially in a dictionary", or "An exact statement or description of the nature, scope, or meaning of something" [102]. Confusion about the definition of C sequestration is therefore to be deplored.

Knowledge of C cycling has been around for many decades [24]. However, the term 'C sequestration' originated only two decades ago with international panels discussing CO_2 and climate change [25]. The IPCC first used the term 'C sequestration' in their 1990 report entitled *Climate Change: The IPCC Response Strategies* [26], but did not define what they meant by it until their *Second Assessment Report* in 1995 [27]. Neither did a report by the FAO of the UN clarify the issue, stating that *"the potential scope of C sequestration can be captured in the efforts by various organizations to define it"* [28]. Examination of a range of definitions, implications and/or explanations of C sequestration shows there is little obvious congruence in meanings (Table 1). Most usages vary in their elements of scale, system under study and storage locations considered, as well as covering unspecified time periods (Table 1). Geoengineers, for example, Wilson *et al.*, use the term in a C management sense (Table 1) [29]. While usage of C sequestration concepts is internally consistent for individual studies, the variability in definitions between studies hampers communication and comparison. We feel a solid and uniform definition needs to be developed and utilized.

Definitive definition of 'endogenous C sequestration'

We define, following the example of Odum, the process of 'endogenous C sequestration' as occurring when C fixed from the atmosphere into stores is greater than the release of C to the atmosphere, over a specified time period (minimally annual, due to high within-system variability) and within a specified system [30]. Expression of this definition as an equation is:

$$\text{Endogenous C sequestration}_{(a,s)} = F_{(a,s)}/R_{(a,s)} > 1$$

Equation 1

where $F_{(a,s)}$ = total annual (a) fixation into storage of C within a specified system (s) and $R_{(a,s)}$ = total annual release of C within that system. Subscripts should be utilized and varied to suit time periods and systems under study at the authors' discretion. C is being sequestered as long as $F_{(a,s)} > R_{(a,s)}$, where the amount of C stored by the system exceeds the amount of C released (Figure 1). Once $F_{(a,s)} = R_{(a,s)}$ the C flux has reached equilibrium. When $F_{(a,s)} < R_{(a,s)}$, then C is being depleted from the system and no sequestration occurs.

Table 1. Definitions of carbon sequestration from selected sources and their fit (+ or -) with criteria of our proposed definition.

Source	Definitions, implications or explanations of 'C sequestration'	C fixation (or similar process)	Release of CO_2 (e.g., respiratory)	Annual time scale	Endo-geneity	Exo-geneity	Ref.
Winjum *et al.*	"Forests also have high rates of ecosystem productivity, and therefore of C sequestration, compared with most other terrestrial ecosystems (i.e., the amount of C photosynthesized is greater than that respired)"	+	+	-	+	-	[80]
IPCC	"Carbon sequestration at the ecosystem level depends not only on plant photosynthesis, respiration and growth, but also on the fluxes of carbon out of litter and soil carbon pools"	+	+	-	+	-	[81]
US Department of Energy	"Carbon sequestration in terrestrial ecosystems is either the net removal of CO_2 from the atmosphere or the prevention of CO_2 net emissions from the terrestrial ecosystems into the atmosphere"	+	+	-	-	-	[82]
Jacobs	"Terrestrial ecosystems remove atmospheric carbon dioxide by plant photosynthesis during the day, which results in plant growth (roots and shoots) and increases in microbial biomass in the soil. Plants release some of the stored carbon back into the atmosphere through respiration. When a plant sheds leaves and roots die, this organic material decays, but some of it can be protected physically and chemically as dead organic matter in soils, which can be stable for up to thousands of years"	+	+	-	+	-	[83]
FAO and references therein	"One activity mentioned is carbon sequestration – retaining in the geosphere carbon that would otherwise escape into the atmosphere. Carbon sequestration can occur in several sites: biomass, forests, wetlands, geologic formations and soils, among others"	-	-	-	+	-	[28]
US EPA	"Terrestrial, or biologic, carbon sequestration is the process by which trees and plants absorb carbon dioxide, release the oxygen, and store the carbon. Geologic sequestration is one step in the process of carbon capture and sequestration (CCS), and involves injecting CO_2 deep underground where it stays permanently"	+	-	-	-	+	[84]
Hambleton	"The conversion by plants, through photosynthesis, of atmospheric CO_2 into organic carbon compounds. Also called carbon fixation"	+	-	-	-	-	[85]
US Department of Energy	"Carbon sequestration can be defined as the capture and secure storage of carbon that would otherwise be emitted to or remain in the atmosphere. The idea is (1) to keep carbon emissions produced by human activities from reaching the atmosphere by capturing and diverting them to secure storage, or (2) to remove carbon from the atmosphere by various means and store it"	+	-	-	-	-	[86]
Resources for the Future	"[T]he capturing of carbon – in a carbon sink, such as the oceans, or a terrestrial sink such as forests or soils – so as to keep the carbon out of the atmosphere"	+	-	-	-	-	[87]
US Department of Agriculture	CO_2 "capture and sequestration (CCS) is a set of technologies that can greatly reduce CO_2 emissions from new and existing coal- and gas-fired power plants and large industrial sources"	+	-	-	-	-	[88]
Soil Science Society of America	"Carbon sequestration refers to the storage of carbon in a stable solid form…The amount of carbon sequestered at a site reflects the long-term balance between carbon uptake and release mechanisms"	+	+	-	+	-	[89]

Table 1. Definitions of carbon sequestration from selected sources and their fit (+ or -) with criteria of our proposed definition (cont.).

Source	Definitions, implications or explanations of 'C sequestration'	C fixation (or similar process)	Release of CO_2 (e.g., respiratory)	Annual time scale	Endo-geneity	Exo-geneity	Ref.
Lal	"Carbon sequestration implies transferring atmospheric CO_2 into long-lived pools and storing it securely so it is not immediately reemitted"	+	-	-	-	-	[66]
Voronin and references therein	"By definition, the photosynthetic carbon sequestration corresponds to the photosynthetic carbon budget during the current growth period. It represents photosynthesis over the growth period minus respiratory losses of photosynthetically fixed carbon during the current year in the autotrophic tissues of plant…and minus decarboxylation of current-year photosynthates during phloem transport"	+	+	+	+	-	[31]
Jastrow *et al.*	"Accumulation of soil organic C (SOC) requires a positive imbalance between inputs to and outputs from soil organic matter stocks. Carbon accrual can be driven by an increase in photosynthetically derived C inputs, a decrease in C losses, or both. Decomposition, leaching, runoff, and erosion can all contribute to losses from any given location, but the latter three processes also have the potential to add to C inputs elsewhere"	+	+	-	-	+	[34]
Hutchinson *et al.*	"Carbon sequestration can be defined as persistent increase in C storage (in soil or plant material or in the sea)"	-	-	-	+	-	[90]
Wilson *et al.*	Carbon capture and sequestration "is conceptually simple: capture CO_2 emissions from fossil-fuel-burning sources and inject the CO_2 into deep geologic formations, thereby sequestering large volumes of buoyant CO_2 underground (geologic sequestration) and avoiding atmospheric emissions"	-	-	-	-	+	[29]
Lal	"Carbon sequestration implies transfer of atmospheric CO_2 into other long-lived global pools including oceanic, pedologic, biotic and geological strata to reduce the net rate of increase in atmospheric CO_2"	-	-	-	-	+	[63]
Powlson *et al.*	"Any increase in the C content of soil resulting from a change in land management might be referred to as sequestration, in that additional C is held on to in the soil and is separated from other parts of the ecosystem."	-	-	-	+	-	[91]
Srivastava *et al.* and references therein	"Carbon sequestration is usually measured in terms of the total carbon stored in the soil but how much carbon is stored, and for how long this carbon can be stored, depends upon the pools (active/labile vs recalcitrant/passive) and their recycling… form of stabilization (chemical/physical)… and physical location (inter/intra-aggegate vs free)… of the carbon in the soil"	-	-	-	+	-	[92]
Wikipedia	"Carbon sequestration is the process of capture and long-term storage of atmospheric carbon dioxide"	-	-	-	-	-	[103]
Oxford Online Dictionary	"A natural or artificial process by which carbon dioxide is removed from the atmosphere and held in solid or liquid form"	-	-	-	-	-	[102]
Our definition	"We define 'endogenous C sequestration' as when non-TUB C fixed from the atmosphere is greater than the release of C to the atmosphere, over a specified time period (minimally annual) and within a given system"	+	+	+	+	NA	

There seems to be a lack of consensus in the literature over the period for which C has to be immobilized before it is considered to be sequestered (Table 1). Authors will reference time as 'long', 'long-lived' or 'not immediately'. Only one of the definitions in Table 1 that we list (Voronin) includes a component of annualized C budgets [31]. A more precise temporal basis should be integrated explicitly into definitions and explanations of C sequestration. It makes sense to annualize C sequestration as in our definition because, from a C accounting point of view, both fixation and release of CO_2 are often heavily influenced by environmental parameters that vary on annual timescales [32], such as precipitation and temperature [33].

A system-level definition is needed to estimate impacts on C sequestration, since individual systems respond differently to climate change. We define a system as any arbitrarily delimited unit that is effectively closed for C fluxes. Therefore, the scale of the system depends on the processes of C exchange that are under consideration. Within a system many other processes, smaller in magnitude than the studied ones, either balance out or can be taken as constant, unless they interact in some way. The system under study must be at the discretion of authors, but it is nonetheless essential they communicate its general properties.

A number of authors have definitions of C sequestration that omit or overlook the capture of C, apparently because they are focusing on only a specific part of the C sequestration process (Table 1). However, it is the essential initial step to C sequestration. In most systems the major contributors to C fixation are plants. Decomposition is frequently included in definitions of C sequestration (Table 1), perhaps recognizing its ecological association with soil C storage. Respiration from decomposition results when organic material fixed by photosynthesis is detached or isolated from the plant, and becomes accessible to decomposer organisms, which progressively transform it, extracting energy and nutrients and releasing CO_2 as a byproduct. In our definition, C substrate that is not released, for example by decomposition after 1 year, adds to the amount of C sequestered.

Most nongaseous C does not naturally move far from the system where it was fixed. Equation 1 relates to endogenous C sequestration (i.e., within a system), but C also fluxes (influx and efflux) between systems, when it can be designated as exogenous. Jastrow *et al.* included leaching, and water-borne and physical erosion, as C fluxes to other systems [34]. Animal-vectored translocations of C include worldwide ones such as those by invading species (migrations are mostly intra-annual) or anthropic activities such as freighting oil [34]. Since influxing exogenous C is produced outside of the specified system, it falls outside the $F_{(a,s)}/R_{(a,s)}$ relationship of the host system, altering the ratio without necessarily affecting the overall C sequestration rate. If substantial, exogenous C needs to be accounted for separately, and the closure of the system re-evaluated.

Key term

Temporarily utilized biologic carbon: Temporarily utilized biologic C is labile C present within the body of an organism and should be distinguished from sequestered C.

Fates of fixed endogenous C

Equation 1 is globalized, applying to all systems involving C compounds. In terrestrial ecosystems, plants are the most common fixers of CO_2, so Equation 1 also applies to systems composed largely of annual plants, such as some deserts. Annuals live less than 1 year, retreating into seeds, which are negligible from a C accounting point of view, over the harsh season.

In such a closed system the atmospheric CO_2 concentration can be accepted as constant on an annual scale due to homogenous mixing – noting, scale wise, that urban areas are domed by locally elevated CO_2 concentrations [35]. The contribution of animals to biomass within such a system is functionally negligible, and can mostly be ignored from a C sequestration point of view, although this may not apply to rangeland or agricultural systems. While microbial respiration is well understood, the contribution of microbes to CO_2 dynamics through fixation [36,37] and also release (e.g., as a byproduct of processes such as methanogenesis [38]) is poorly understood at the system scale. We can assume that C release due to processes such as photodegradation and biogenesis of volatile organic chemicals is small and constant within such a system, although there is increasing evidence this might not always be so [39,40]. The same caveats apply to processes of C loss other than respiration, such as oxidation into inorganic C. When these processes are important in the C cycle at particular scales and in particular systems they will need to be incorporated into definitions of C sequestration, following Chapin *et al.* [24].

However, the situation is different for woody systems (w). Photosynthetically captured C that has been retained within such a system for >1 year can be allocated either to sequestered C or temporarily utilized biologic C (TUB C), which is C present within a living organism, and used in growth (Figure 2). Note that the concept of net ecosystem carbon balance does not distinguish sequestered C from TUB C, but we believe this to be a valuable distinction [24]. TUB C differs from sequestered C in that it is not in storage, is labile and accessible within the organism, but is not available for decomposition. Once the organism dies or tissue detaches from the organism that material becomes available to decomposers that progressively transform it, releasing CO_2 as a by-product.

The amount of C fixed photosynthetically by plants is gross primary productivity (GPP). However,

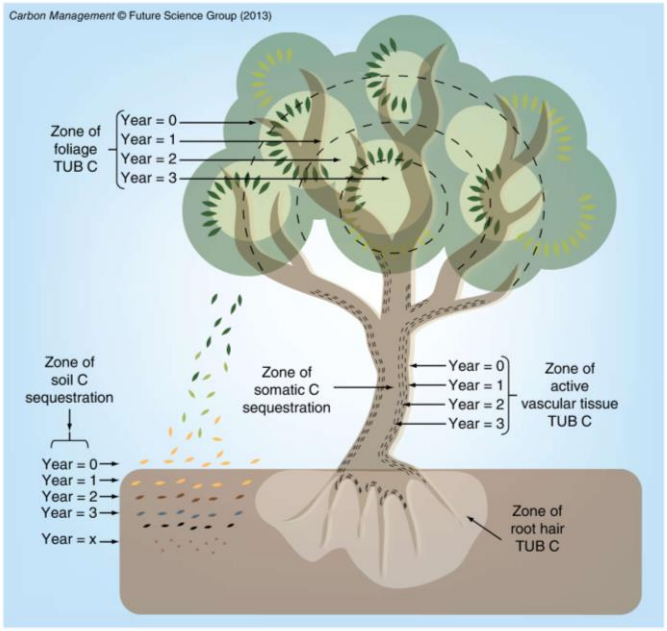


Figure 2. Emplacement of temporarily utilized biologic carbon, and storage of soil and somatic carbon in a woody system. The example tree is an evergreen broadleaved tree. TUB C is present in the active wood, rooting zone (including root hairs) and in the foliage. Sequestered C is present in the inactive wood and in the soil.
TUB: Temporarily utilized biologic.

plant productivity is more conventionally and conveniently measured as net primary productivity (NPP; i.e., gross photosynthesis minus autotrophic respiration). Therefore:

$$NPP_{(a,w)} = GPP_{(a,w)} - RA_{(a,w)}$$

Equation 2

where $RA_{(a,w)}$ is total annual autotrophic respiration of C by woody perennial plants. So $F_{(a,w)}$, which is total annual storage of sequestered C in a woody system, is:

$$F_{(a,w)} = GPP_{(a,w)} - RA_{(a,w)} - TUB\ C_{(a,w)} + soil\ C_{(a,w)}$$

Equation 3

where soil $C_{(a,w)}$ is the annual amount of C being sequestered in the soil. It is derived from material, including former TUB C, having undergone a year's decomposition (Figure 3). Further:

$$R_{(a,w)} = RD_{(a,w)}$$

Equation 4

where $R_{(a,w)}$ is the nonautotrophic respiratory release of C, that is, $RD_{(a,w)}$ or decomposer respiration. Therefore:

$$\text{Endogenous C sequestration}_{(a,w)} = F_{(a,w)}/R_{(a,w)} > 1 = (NPP_{(a,w)} - TUB\ C_{(a,w)} + soil\ C_{(a,w)})/RD_{(a,w)} > 1$$

Equation 5

The caveats above regarding annual plants apply here too, noting also that flowers, seeds, fruits and root hairs do not contribute to sequestered C, except, briefly, for long-lived seeds such as coconuts and perhaps for sexual reproductive structures in perennial monocarpic species.

So it is only the portion of fixed C not used to sustain the year's growth that can become sequestered. In woody systems C is laid down in secondary xylem and xylem parenchyma as part of the annual growth cycle of the vascular cambium, and is usually active for 2–3 years before ceasing to function, and becoming sequestered. This can be labeled 'somatic C sequestration'; that is, the storage of C within the nonfunctional tissues of a living woody plant (e.g., heartwood, detectable via the 'aluminum reaction' [41]). This store is biologically inert and the tree has no capacity to access it. Effectively:

$$Somatic\ C_{(a,w)} = NPP_{(a,w)} - TUB\ C_{(a,w)}$$

Equation 6

In addition to increasing TUB C, forests undergoing successional development are annually increasing the amount of C sequestered, both within the soil and in heartwood. At successional climax, as the demographic structure of the forest stabilizes, somatic C sequestration reaches an equilibrium point; that is, $F_{(a,w)} = R_{(a,w)}$ (Figure 4). Somatic C in tree trunks, limbs and large roots is usually released only when the organism dies (such deaths balancing on a system scale), although heartwood of a living tree may undergo partial decomposition, due to the presence of fungi or other wood-decomposing organisms. Even

Key terms

Somatic carbon sequestration: Storage of functionally inert C in woody structures; cannot occur in grassland systems.

Climax: If climax vegetation ever exists, it is vegetation that is stable in terms of C dynamics.

Recalcitrant: Recalcitrant materials are resistant to decay, but it may only be the environment that makes them so.

forests as old as 800 years can continue to take up C [42]. At climax, when most of the system has sequestered all the C of which it is capable, soil C sequestration may still be on ongoing, perhaps due to past disturbances affecting the rate of accumulation of material in the slowly decaying soil pools [43]. In cyclic succession such as in kauri (*Agathis australis*) forests, podzols may protect buried soil C from decomposition, allowing further soils to develop on top [44].

Equation 5 also applies in herbaceous perennial systems (hps), such as grasslands, but with the modification that there is no above-ground sequestration of C, all photsynthetically fixed C going into TUB C, where it is used to construct active biomass (NPP - TUB C ≈ 0). In fact TUB C is the only source of all biomass increment in such systems, and when above-ground biomass (or standing crop as it is agriculturally known) is at equilibrium, the system can only sequester C in the soils through litter. Effectively then:

$$F_{(a,hps)} = NPP_{(a,hps)} - TUB\ C_{(a,hps)} + soil\ C_{(a,hps)} \approx soil\ C_{(a,hps)}$$

Equation 7

So:

$$\text{Equilibrium endogenous C sequestration}_{(a,hps)} = soil\ C_{(a,hps)}/RD_{(a,hps)} > 1$$

Equation 8

Unfortunately situations that perturb the above equations are common. For example, volcanoes can release large amounts of CO_2 into the biosphere, exogenously altering the atmospheric CO_2 concentrations in addition to anthropogenic activities [45]. Additionally, forests (the woody perennial systems above) are frequently disturbed in various ways, including by fires with concomitant effects on C release and cycling [46], making C accounting more difficult (e.g., Amiro *et al.* [47]). Indeed, for some forests ongoing disturbance is an essential feature of regeneration dynamics, for example *Nothofagus* forest in New Zealand [48]. Such systems are best evaluated on larger temporal and spatial scales, allowing for patchiness of seral stages. The same applies to managed forests, especially those grown for timber extraction, which are harvested on a rotational basis and are inevitably exogenously leaky [49].

Stability of sequestered C

C sequestration as a process is accepted by practitioners and other authors [50,51]. However, the general public may be misled by the term and assume that sequestered C is in reality always locked up in a stable and inert form. Sequestered C may reside within a store or pool, to which C is constantly being added and removed. Effectively an individual C atom has a residence time within the C pool (Figure 3), with the whole pool continuously turning over at rates of up to thousands of years [52].

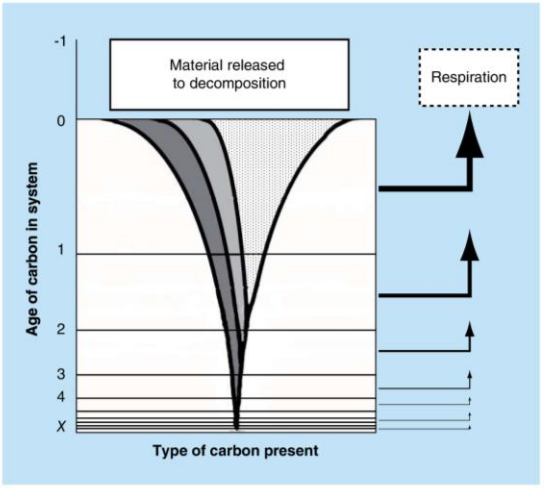


Figure 3. Depiction of residence times of chemical components of sequestered soil carbon. The arrows depict fluxes of C out of the system from decomposer respiration. Compounds highly recalcitrant to decomposition, for example lignin (dark gray), more readily decomposed compounds, for example starch (light gray), and easily decomposed compounds, for example amino acids (stippling).

The process of C turnover within storage locations is exemplified by C sequestration in soils (Figure 3). Litter is constantly being added to the soil from NPP and CO_2 is being released by decomposer organisms. The funnel in Figure 3 portrays varying longevity of different C-based compounds in soil. A C compound's decomposition rate depends largely upon its chemical bonds, as well as the biological and physical processes within the storage pool [53–56]. Compounds such as sugars, amino acids or compounds with high nitrogen or phosphorus concentrations (i.e., low C to nitrogen or phosphorus ratios) are first to decompose (Figure 3), resulting in high respiration rates. Complex carbohydrates, starches and celluloses persist for intermediate periods, while compounds that are highly recalcitrant to decomposition, such as secondary metabolites including lignin, tannins and polyphenolics, may aid in soil C sequestration because of their prolonged residence times within the soil [57], noting that recalcitrance may be largely an ecosystem property, rather than a molecular one [58–60]. Thus, decomposition rates can vary from system to system

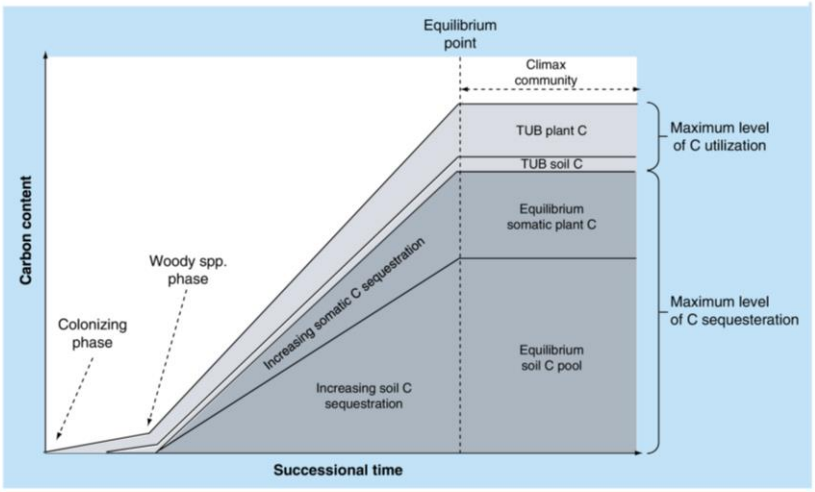


Figure 4. Carbon sequestration (dark gray area) or carbon utilization (light gray area) throughout natural succession of a woody system. The vertical dashed line represents establishment of a climax community, a point of equilibrium where C sequestration is no longer increasing. Note: relationships may be curvilinear and/or distances between portions of the graph may vary depending on systems and environmental variables.
TUB: Temporarily utilized biologic.

and over time. Cycling of C can be further affected by climatically driven positive and negative feedbacks [10,61,62]. Climate change may further affect the growth rates and allocation patterns of producers (C fixers) and directly influence the amount and chemical composition of C entering a pool such as the soil, as well as its fate there [54,55].

Taxonomy of C sequestration storage

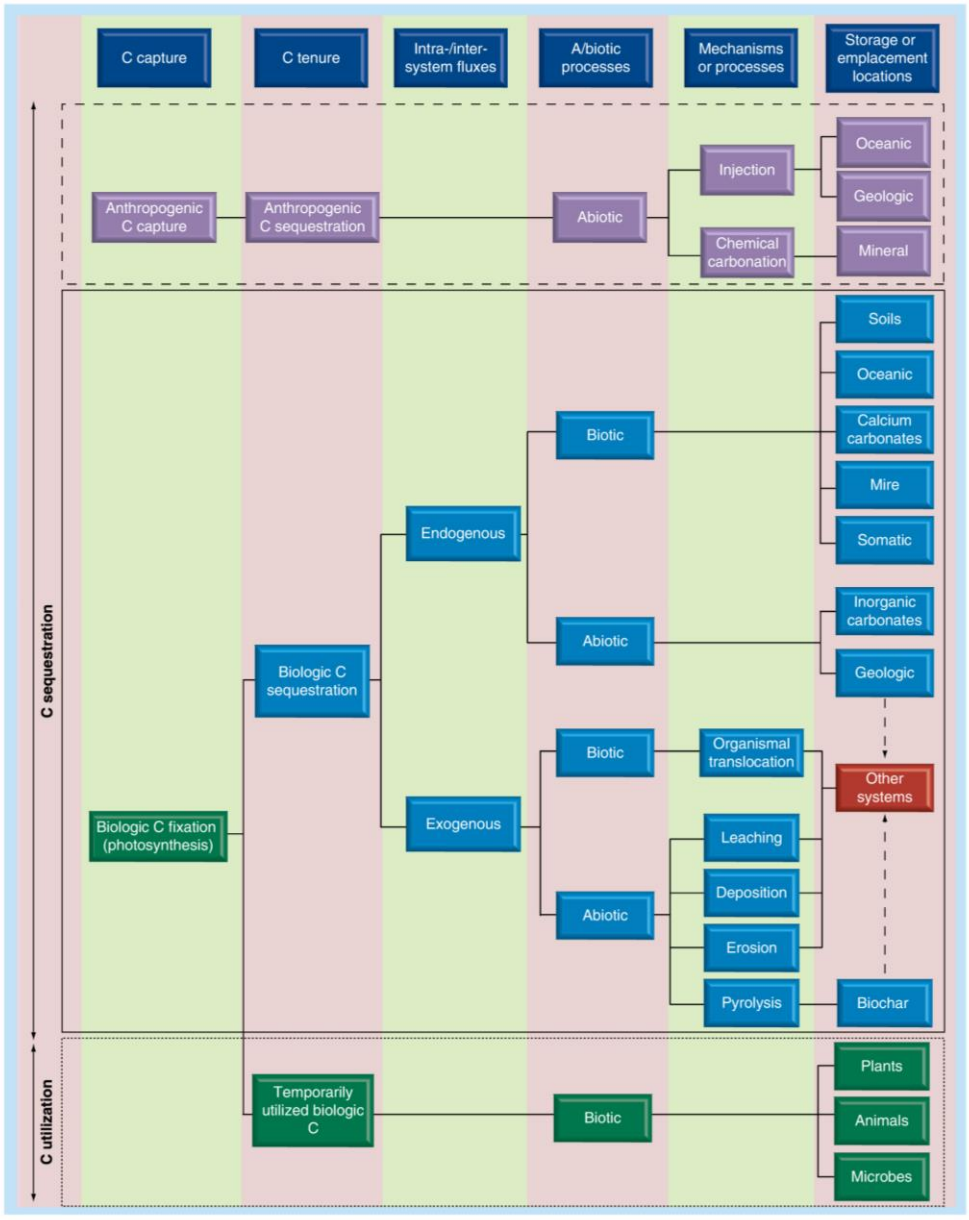
The storage locations of sequestered C are mostly interpretable from the context of any particular piece of literature. However it is sensible to devise a taxonomy that clarifies those locations for others and simplifies comparisons between studies. Addition of attributive nouns gives precise meaning to the location of sequestered C being addressed by authors. We incorporate pre-existing concepts from Jastrow *et al.* and Lal into a taxonomic hierarchy of storage locations of fixed C, introducing others here because they categorize storage locations that have been less than clearly defined [34,63]. We therefore propose the taxonomy in Figure 5, and encourage other authors to use these terms routinely.

Removal of CO_2 from the atmosphere can occur by anthropogenic C capture as depicted in the upper dashed box of Figure 5. Lal, and Zoback and Gorelick describe the sequestration techniques of oceanic and geologic injection as well as mineral carbonation, but development is still needed for these to be sustainable mitigation options for climate change [63,64].

Removal of CO_2 from a system primarily occurs naturally via photosynthesis (Figure 5, central solid box). TUB C is present within a living organism but is being used for growth (Figure 5, dotted box) and so is outside the sequestered pool. When photosynthates have been present inaccessibly within the system for >1 year, they should be categorized as sequestered C (Figure 3).

We maintain that C sequestration can be categorized via abiotic or biotic processes of storage, similar to Lal [63]. Abiotically, inorganic carbonates are present in soils as either primary carbonates that originated from parent rock material or as secondary carbonates formed when

Figure 5. Taxonomy and categorisation of storage and emplacement locations for carbon. Upper (dashed) box: anthropogenic C storage; central (solid) box: sequestrational storage of biologically fixed C; lower (dotted) box: temporarily utilized biologic C utilization and emplacement in organisms; titled columns (separated by color): fate of C from capture through to storage or utilization; dashed arrows: anthropogenic exogenous movement of biochar or biologically sourced geologic C to other systems.


C capture
C tenure
Intra-/inter-system fluxes
A/biotic processes
Mechanisms or processes
Storage or emplacement locations
C sequestration
C utilization
Anthropogenic C capture
Anthropogenic C sequestration
Abiotic
Injection
Chemical carbonation
Oceanic
Geologic
Mineral
Biologic C fixation (photosynthesis)
Biologic C sequestration
Endogenous
Exogenous
Biotic
Abiotic
Biotic
Abiotic
Soils
Oceanic
Calcium carbonates
Mire
Somatic
Inorganic carbonates
Geologic
Organismal translocation
Other systems
Leaching
Deposition
Erosion
Pyrolysis
Biochar
Temporarily utilized biologic C
Biotic
Plants
Animals
Microbes

dissolved CO_2 precipitates carbonates and bicarbonates with Ca^{2+} and Mg^{2+} ions [65]. Biotic endogenous C sequestration occurs in a wide range of locations, some of which were addressed by Lal and others are introduced here (Figure 5) [63].

Soil C sequestration is a natural endogenous process, which can be enhanced via anthropogenic manipulation, which is an economic option because the estimated size of the global soil organic C pool alone is, at 2500 Gt, approximately 3.3- and 4.5-times larger than the atmospheric and biotic C pools, respectively [66]. Most global circulation models project climate change scenarios, which will result in elevated temperatures and alterations in precipitation patterns, influencing soil C sequestration rates, in common with rates in many other stores [67].

Oceanic C sequestration occurs naturally through photosynthesis of microorganisms known as phytoplankton [68], which are estimated to fix approximately 45 Pg C $year^{-1}$ [69]. Sequestration results when particulate organic matter formed by dead phytoplankton is deposited on the ocean floor, although only 0.2 Pg C $year^{-1}$ is sequestered, orders of magnitude smaller than soil C sequestration [70]. However, since oceans cover 71% of the Earth's surface, phytoplankton removal of CO_2 into oceanic storage locations is still important for C sequestration [15].

Biological formation of calcium carbonate is where C is naturally sequestered and retained in an inorganic form, such as in shells of eggs and molluscs [71] and stromatolites formed by cyanobacteria [72]. Similarly, phytoliths (silicated 'plant opals') contain up to 5.8% occluded C and accumulate in the soil, resisting decomposition [73]. It is unknown to what degree C sequestration occurs in such forms on an annual basis.

Mires store C as peat, totalling 455 Pg, and are considered to be one of the most stable stores of surficial terrestrial C [74]. Even here, there is still turnover of C, resulting in changes in degree of peat decomposition over time (Figure 3) [75]. However, this is extremely slow and there is a practically linear relationship between the time of C deposition and the volume of peat C that is sequestered (normally expressed as depth of a core) over centuries or even millennia; for example, Li *et al.* [76]. Future climate change could alter the stability of this pool [74].

Somatic C sequestration is the storage of C within the trunks and branches of trees (not to be confused with TUB C; Figure 2). It is the most readily manageable of the C stores, since trees sequester C naturally.

Exogenous C storage is not well understood, but probably only landscape-scale displacement and emplacement events make significant contributions to system C sequestration. Another method of anthropogenic C sequestration occurs through pyrolysis of biotically captured organic material to form biochar [7,77], which is then moved to other systems via anthropic means (Figure 5), although there is debate over how successful a mitigation strategy this might be [78,79].

Usage of our proposed terminology

We encourage the common scholarly practice of defining a term or concept at its first mention and subsequently using abbreviations or codes to facilitate better communication between authors. One of the most commonly considered systems for C sequestration is forest, which exhibits soil C sequestration, somatic C sequestration and deposition of TUB C, although the latter two are not usually distinguished in publications. Examples of the recommended use of our proposed terminology are described below:

- If authors are referring to soil (organic) C sequestration within a system that has undergone reforestation over the last decade, they could use phraseology such as '$\text{soil C sequestration}_{(10\text{year, reforest})}$';
- '$\text{Exogenous abiotic C sequestration}_{(1\text{ year, mire})}$' refers to C produced in another system that has been moved via abiotic processes into a mire system and retained for 1 year;
- When discussing the amount of C retained in a forested system for two decades, authors could use formulations equivalent to:
  - $\text{Total C sequestration}_{(20\text{ year, forest})} = \text{somatic C}_{(20\text{ year, forest})} + \text{soil C}_{(20\text{ year, forest})}$;
  - $\text{Total C retained} = \text{total C sequestration}_{(20\text{ year, forest})} + \text{TUB C}_{(20\text{ year, forest})}$.

This totals the soil and somatic (e.g., heartwood of trees) C sequestered within a forest system, as well as the TUB C, over a period of two decades.

Conclusion

It is still uncertain how increased atmospheric CO_2 concentrations and climate change will alter biological processes pertaining to endogenous C sequestration. It is certain that mitigation of climate change is a highly important objective and priority for scientists, policymakers and land managers alike. In order to clarify communication and implement proper climate change mitigation strategies, clear definition of the type of C sequestration being addressed is urgently needed. In addition, annualizing C fluxes within specifically defined systems will also allow for better C accounting and more pragmatic C trading. Differentiation between C sequestration and TUB C is also imperative

to avoid biasing results and obstructing comparisons between studies. Utilization of our definition of endogenous C sequestration types should improve humanity's odds of ameliorating and overcoming the impending threats posed by elevated atmospheric CO_2 concentrations and climate change.

Future perspective

It is our hope that this work will stimulate others, better placed than we are, to develop robust and widely applicable definitions of C sequestration methods and stores. This could usefully be lead by explorations of the definitionally induced confusions and uncertainties present in applications of current definitions.

There is also a need for finer scale research into the many small processes other than photosynthesis and decomposer respiration, which affect the size and lability of C in both natural and anthropogenic systems, and their interactions with the known processes.

For herbaceous perennial systems based on modular structures that have high turnover rates (although >1 year), for example tussock or bunch grasses, there needs clear understanding of the *in situ* duration of C, as individual atoms, and an evaluation of the biospheric gains from temporarily placing C into TUB C in a permanent system.

The implications of disturbance in ecosystems for C dynamics require greater exploration, including the anthropogenic exogenous movements of C, both deliberately and as a byproduct of human activities. Part of this should include better categorization of exogenous storage locations.

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No writing assistance was utilized in the production of this manuscript.

Executive summary

Background
- Carbon (C) sequestration, often used in the literature, is a poorly defined term, though it is an important concept in the global C cycle and in climate change mitigation.

C sequestration & climate change
- CO_2 is the most important of the GHGs, encouraging management of its concentration in the atmosphere.

Definitions of 'C sequestration'
- Currently the concept is poorly defined.
- Table 1 exemplifies the need for a robust definition of the term.

Definitive definition of 'endogenous C sequestration'
- 'Endogenous C sequestration' occurs when ratio of C fixation into storage (F) and C release (R) is greater than one ($F_{(a,s)}/R_{(a,s)} > 1$), expressed annually (a) within a specified system (s).
- Other processes within a system are likely to be stable or balanced in comparison.
- Exogenous C sequestration refers to storage outside the system of C fixation.

Fates of fixed endogenous C
- For herbaceous perennial systems (hps), endogenous C sequestration occurs when soil $C_{(a,hps)}$/decomposer respiration$_{(a,hps)} > 1$.
- For woody systems a portion of net primary productivity is used as temporarily utilized biologic C: that is, labile C.
- Somatic C sequestration refers to C locked up in nonfunctional wood of trees.

Stability of sequestered C
- Even sequestered C turns over all the time, although less so for some stores than others.

Taxonomy of C sequestration storage
- Temporarily utilized biologic C is emplaced in organisms, but should not be considered to be sequestered.
- Storage locations for sequestered C can be defined based upon mechanisms of C capture and processing.

Usage of our proposed terminology
- Subtexts to C terminology clarify meanings and improve communication.
- For example 'exogenous abiotic C sequestration$_{(1\ year,\ mire)}$' refers to C sourced from outside the system and then stored for 1 year within a mire system.

Conclusion
- This article demonstrates that terminology needs to be and can be improved.
- Improvement of C sequestration definitions would facilitate better understanding and communication in climate change debates.

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GRADUATE RESEARCH SCHOOL

STATEMENT OF CONTRIBUTION
TO DOCTORAL THESIS CONTAINING PUBLICATIONS

(To appear at the end of each thesis chapter/section/appendix submitted as an article/paper or collected as an appendix at the end of the thesis)

We, the candidate and the candidate's Principal Supervisor, certify that all co-authors have consented to their work being included in the thesis and they have accepted the candidate's contribution as indicated below in the *Statement of Originality*.

Name of Candidate: Matthew Aaron Krna

Name/Title of Principal Supervisor: Dr. Gillian L. Rapson

Name of Published Research Output and full reference:

Krna, M. A., & Rapson, G. L. (2013). Clarifying 'carbon sequestration'. Carbon Management, 4(3), 309-322.

In which Chapter is the Published Work: Chapter 2

Please indicate either:

- The percentage of the Published Work that was contributed by the candidate:

  and / or

- Describe the contribution that the candidate has made to the Published Work:

  Matthew Aaron Krna reviewed the literature and compiled drafts and Dr. Gillian L. Rapson discussed concepts and helped with polishing the final draft.

Candidate's Signature — 13-4-2015 Date

Jarek Reid - Acting H.O.I
Principal Supervisor's signature — 13.4.2015 Date
on behalf of G. Rapson

Chapter 3

How does an altitudinal gradient impact relationships between productivity and decomposition of *Chionochloa rubra* on Mount Tongariro?

Chionochloa rubra on Mount Tongariro's north face (October 2012)

Phrase from the anthem of Māori in the Central North Island
"*Tongariro te maunga*,"
"Tongariro is our (sacred) peak,"
(Ngāti Poneke, 1967)

Abstract

Altitudinal gradients express natural, usually gradual changes in climatic conditions which provide opportunities to examine species' ecological and evolutionary responses to environmental influences. The relationships between plant productivity and decomposition across altitudinal gradients can provide insight on carbon (C) cycling in a changing climate. In this experiment, *in situ* aboveground plant productivity and leaf litter decomposition (full reciprocal translocation) of *Chionochloa rubra* were examined at 8 plots across a ≈700m elevational gradient on Mount Tongariro's northern face. The productivity to decomposition ratio (P:D) of *C. rubra* was calculated across all plots and for 300m sub-sections (1.8^{o}C Δ/300m). Biotic and abiotic parameters were analysed to generate an envirometric gradient across the 8 plots. Litter that did not undergo decomposition treatments (initial litter) from each plot was analysed for chemical and constituents and soils from each plot were analysed for C, nitrogen (N) and phosphorous (P) to 30cm in depth. The average soil C, N and P concentrations (mg/g) were 41, 122 and 117% lower, respectively, at the uppermost plot compared to the lowest plot. Individual tiller and whole plant productivity of *C. rubra* after 2 years declined with increasing elevation, and was 41 and 33% lower, respectively, at higher altitudes; however productivity as g/g/yr (i.e. relative growth) rate did not express this trend. The N and P concentrations (mg/g) of initial litter were 49% greater and 29% lower, respectively, at upper plots compared to lower plots, whereas no trend was observed with C. The lignin and total phenolic concentrations of initial litter (mg/g) at tb he lowest plot was 9 and 25% greater, respectively, than the uppermost plot. After 3 years of decomposition, the mass loss of *C. rubra* litter was 15% greater at higher altitudes than lower. The P:D ratios across the altitudinal gradient decreased with increasing altitude, with lower plots having 140% greater P:D ratios than the uppermost plot. There was a 37% difference in the P:D ratios of lower sub-sections and higher sub-sections of the gradient. A decline in productivity is often observed within a species with increasing elevation and/or stress along altitudinal gradients and differences in the chemical and constituent composition of leaves and subsequent leaf litter can result. The chemical and constituent composition of the litter indicates differences in litter quality across the gradient, which may impact decomposition processes and soil C and nutrient concentrations. Litter decomposition is more strongly influenced by the location where it decomposed, instead of its location of origin, implying that environmental parameters may be more influential than underlying genetics and plant allocation patterns across the gradient. The decline in the P:D ratios ascending the gradient indicates less productivity is needed per unit decomposition for C sequestration and more C sequestration occurs at lower altitudes. Climate change is likely to impact plant productivity and decompositional processes as well as C and nutrient cycling and thus may have important ramifications for C sequestration in New Zealand's alpine tussock grasslands.

Key words: carbon sequestration, montane, grassland, red tussock, stress gradient

Introduction

Climate change is impacting terrestrial locations across the planet, but more severely at high latitude and altitude regions (IPCC, 2007). The vegetation of montane ecosystems is especially sensitive to climate change (Pauli *et al*., 1996) because of high vulnerability to alterations in abiotic conditions (Beniston, 2003), such as evapostranspiration rates, temperature and precipitation patterns (Walther *et al*., 2002) and changes in seasonality (Beniston, 2003). The rate of future warming in these systems is predicted to be two to three times higher than 20th century temperature recordings (Guisan & Theurillat, 2000; Cavieres & Sierra-Almeida 2012), making these ecosystems vulnerable to impacts of climate change (Nogués-Bravo *et al*., 2007; Colwell *et al*., 2008). One of the primary challenges we are currently facing with climate change in terrestrial ecosystems is uncertainty whether it will lead to the sequestration and storage of more atmospheric C in the terrestrial biosphere, a negative feedback to climate change, or to result in the release of C back into the atmosphere, a positive feedback (Davidson & Janssens, 2006). A better understanding of C fixation into storage and C release within specified systems over at least an annual time frame is needed to evaluate actual carbon sequestration (Krna & Rapson, 2013), especially across environmental gradients.

Plant community composition and species' traits are largely determined by climate (Chapin, 1991), since climate selects for specific plant ecophysiological traits (Violle *et al*., 2007), alters growth rates and allocation patterns (Chapin, 2003), and elicits different plant responses from different species (Peñuelas *et al*., 2004). Changes in climate can alter plant productivity (Wu *et al*., 2011), litter decomposition (García-Palacios *et al*., 2013) and biogeochemical cycles (Bardgett *et al*., 2013) such as carbon (C) and nutrient cycling within a system. This may result from alterations in species' growth rates and allocation patterns of C and nutrients. Alterations of chemical composition of plant tissues and litter (i.e. increased concentrations of secondary metabolites such as lignin, tannins and phenolics) may influence decomposability and ultimately C and nutrient cycling (Asner *et al*., 1997; Chapin, 2003; Lavorel *et al*., 2007). Thus, predicting ecosystem and species' responses to climate change is complex,

as these responses encompass a multitude of complex interactions and effects of alterations in abiotic conditions both within and between species (Walther *et al*., 2002). Alpine environments are ideal locations for early detection and investigation of climate change signals (Beniston, 2003) and plant species' responses to changes in climate (Körner, 2003).

Stress typically increases when ascending montane altitudinal gradients (Callaway *et al*., 2002) and local-scale adaptation of plants can occur along these gradients (Mark, 1965a; McGraw & Antonovics, 1983; Byars *et al*., 2007; Laincorut & Tielbörger, 2009), playing an important role in ecological and evolutionary processes (Leimu & Fischer, 2008; Hereford, 2009). High altitude plant species are often "stress-dominated" where abiotic factors, primarily climate, are foremost in eliciting alterations in individual species' responses (Pauli *et al*., 1996). Ecotypically differentiated plant populations also perceive and respond to environmental conditions differently and thus might have varying degrees of vulnerability to changes in climate (Harte *et al*., 2004; Beierkuhnlein *et al*., 2011). How alpine plant populations will respond to and differ in their responses to climate change is unknown (Pearson & Dawson, 2003; Harte *et al*., 2004; Lavergne *et al*., 2010), as are the impacts that these changes may have on productivity, decomposition and C and nutrient cycling in alpine systems. Factoring in ecotypic differentiation (i.e., local genetic variation and adaptation within species to different environmental conditions) in alpine environments can further confound predictions of plant responses to climate change (Laincorut & Tielbörger, 2009). However, a situation in which there is no known ecotypic differentiation is preferable when examining trends along gradients, so background differences in genetics can be ignored, and here ecoclinal or population-based patterns are preferred.

Plant taxa with varying tolerances to differing degrees of environmental stresses can differ in their chemical and constituent composition (Kim *et al*., 2008), which can influence both productivity (owing to allocation patterns) and decomposition rates (owing to litter quality). Litter decomposition consists of three primary components that work in a hierarchical manner: climate > litter quality > soil organisms (Aerts, 1997; 2006; Lavelle *et al*., 1993; Swift *et al*., 1979). Changes in

climate not only directly impact a plant species' productivity (Körner, 2007) and decomposition (Coûteaux *et al*., 1995; Lavelle *et al*., 1993), but can also influence the quality of litter produced, its decomposability and subsequent C and nutrient concentrations as well as C sequestration (Hobbie, 1996).

In montane systems, New Zealand especially, temperature decreases with increasing elevation whereas precipitation and ultra-violet (UV) radiation increase with increasing elevation (Körner, 2007). Temperature and precipitation are dominant drivers of ecosystem functioning, however other factors (i.e. UV radiation, soil properties and other species presence) can also influence ecosystem processes. A multifaceted description of abiotic and biotic conditions, creating an envirometric gradient with principal component analysis, may provide more explanatory power of differences in productivity and decomposition than altitudinal or temperature gradients alone.

Species of snow-tussock within the genus *Chionochloa* possess a wide range of temperature tolerances and often show variation in growth and allocation patterns throughout their altitudinal ranges (Mark, 1965a; 1965b). In upland tussock grasslands, the levels of stress plants are exposed to vary along altitudinal gradients (Holdsworth & Mark, 1990 and references therein) and can influence growth rates and productivity (Mark, 1965a). Species within the genus *Chionochloa* in New Zealand's tussock grasslands often express phyenotypic and ecotypic differentiation along altitudinal gradients with greater growth rates and reproductive development at lower altitudes (Mark, 1965c), including *Chionochloa rubra* (red tussock), a long lived and slow growing indigenous montane grass species that inhabits a wide range of locations across alpine environments in New Zealand.

The aim of this research is to determine the relationships of productivity and decomposition of *C. rubra* along an expansive altitudinal gradient and how these responses may vary across an environmental gradient, and so influence C and nutrient cycling. Because these relationships may not be simply related to the altitudinal gradient, a number of site characteristics were obtained to clarify the environmental gradient's effect on productivity and decomposition. In this experiment *in situ* plant

productivity and leaf litter decomposition of *C. rubra* (red tussock) were investigated. A full reciprocal translocation of litter types across the gradient was performed to investigate how litter origin and destination of litter would influence decomposition and relationships with productivity across an altitudinal gradient of changing climate. Alterations in climate are highly likely to impact plant productivity, decomposition and ultimately C and nutrient cycling. Climate models predictions range from 1.5 to 6.2^{o}C increases in temperature since pre-industrial times (IPCC, 2014). This research will provide a better understanding of how alterations in climate and other abiotic and biotic factors may influence C and nutrient cycling in the tussock grassland across the gradient, and thus give clues as to the potential impact of climate change.

Methods

Study site

Tongariro National Park (TNP) was New Zealand's first national park. It was established in 1887 and became a United Nations Educational, Scientific and Cultural Organization (UNESCO) dual World Heritage Site in 1990, owing to its volcanic features and Maori cultural significance. The National Park is located in the Volcanic Plateau of New Zealand's North Island. Vegetation is podocarp-broadleaved forest in the stable lowland areas, beech forest in higher and more disturbed areas. Subalpine and alpine vegetation develops in areas less exposed to volcanic disturbances (Atkinson, 1985). Extensive swards of tussock grassland occur as a pyric successional phase or across recently disturbed zones. Prevailing winds tend to be westerly and north-westerly, which typically brings precipitation (as snow and/or rain) to northern and western parts of the park on at least half of the days of the year (DoC, 2013). Owing to topographical features and geographic location, weather conditions in TNP can be highly variable within and between years.

The location chosen for this experiment was Mount Tongariro's north face, on two ridgelines (approximately 1km) west of Ketetahi Hut and the Tongaririo Crossing track. This location possesses one of the largest and continuous gradients of alpine tussock grasslands in New Zealand

dominated by *C. rubra*, spanning an altitudinal gradient of approximately 700m (beginning just above the current volcanic treeline at ≈980m and reaching its uppermost limit at ≈1700m in elevation).

Species' description

There are 25 species within the genus *Chionochloa* (commonly referred to as 'snow grasses' or 'snow tussocks'), an Australasian genus (Mark, 2012), 23 of which are endemic to New Zealand (Connor & Lloyd, 2004), and seventeen of which inhabit sub-alpine and alpine zones (Mark 2012; NZPCN 2013). The dominant *Chionochloa* species of tussock present on Mount Tongariro is *C. rubra* subsp. *rubra* var. *rubra* Zotov, commonly referred to as 'red tussock' owing to its red to reddish-brown hue.

Experimental Design

Eight experimental plots (15 x 30m, along the contour) were established in February, 2011 and incrementally spaced approximately every 100m in elevation (Figure 1). Most plots had similar slopes, aspects and were positioned along the same ridgeline, where *C. rubra* was abundant. However, plot 7 was positioned on the face of the neighbouring ridgeline, approximately 300m to the east, due to sparseness of *C. rubra* at that altitude.

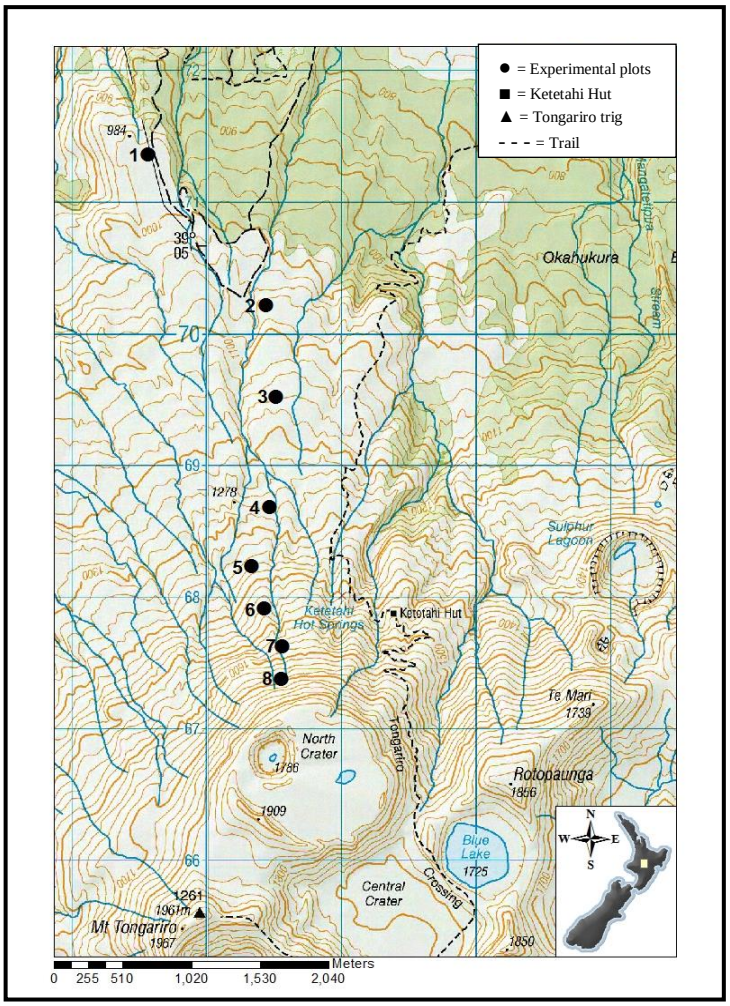

Figure 1: Topographic map (map source = LINZ 1:50 000, sheet numbers BH34 and BH35, datum = D_WGS_1984) depicting the eight experimental plots, incrementally spaced every ≈100m in altitude, on Mount Tongariro's north face. Inset map of New Zealand shows general location of Tongariro National Park.

Site Characteristics

Data loggers (HOBO Pendant® Temperature/Light Data Logger model 8K - UA-002-08), programmed to record temperatures every minute and log averages every two hours, were positioned 10cm above the soil surface on the southern (shaded) side of wooden stakes in April 2012 at each plot. Data loggers were removed from plots in June 2013. Missing data were derived from overall trends to establish a full annual record across all plots.

Soil cores (2.8cm diameter; n=6-8) were randomly collected to 30cm in depth from locations just outside each plot in March 2013, following methods described in Allen *et al*. (1989). These soil cores were divided into 10cm segments (0-10, 10-20 and 20-30cm below the soil surface) in the field, and transported to Massey University and stored at -20°C. After

thawing and drying at room temperature, soils were sieved to 2mm to remove roots and then finely ground with a mortar and pestle, prior to analysis. Carbon and N analyses of soil samples (*n*=1; 0-10, 10-20 and 20-30cm depths) was performed using flash combustion analysis with a Leco furnace (Laboratory Equipment Corporation, St Joseph, Michigan, USA) and soil phosphorous (P) analyses (*n*=1; 0-30cm) were performed following the Kjeldahl method at Landcare Research, Palmerston North, New Zealand.

Productivity

To investigate productivity, leaf elongation, dieback and tip-loss were measured on 5 randomly selected tillers of *in situ C. rubra* plants (*n*=10 per plot; Figure 2a) that were randomly selected at each plot. Monitored tillers were marked with coloured paperclips and the youngest exposed leaf from each marked tiller was then marked with a coloured loop (Figure 2b). Leaf lengths of live and dead portions of each monitored tiller were measured from the ligule. If leaves were too immature to have developed a ligule, then the ligule from the next oldest leaf was used for determining leaf lengths. The number of tillers per plant was recorded. Measurements were performed for 6 censuses and harvested on the final census.

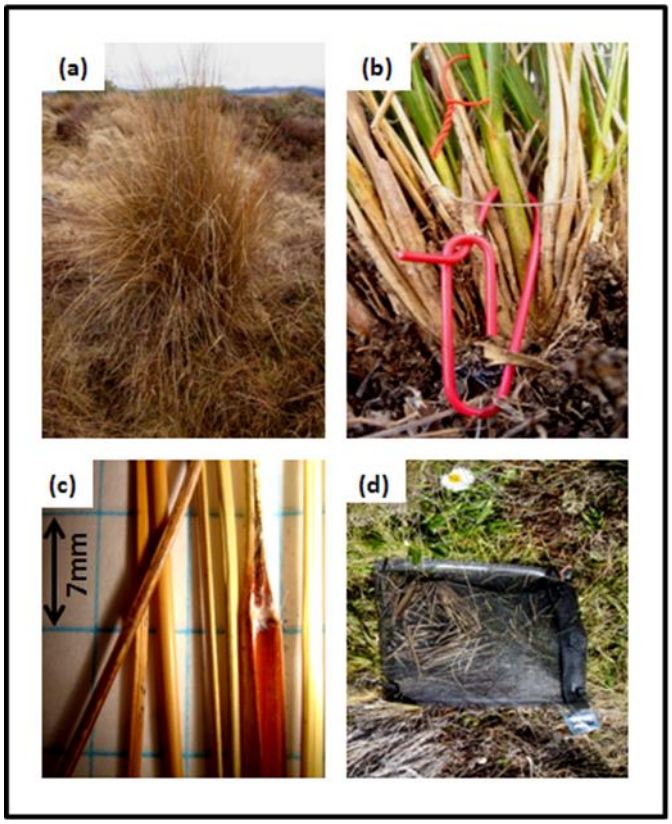

Figure 2: (a) *Chionochloa rubra* (at plot 4; altitude = 1265m) on Mount Tongariro, (b) tiller and young leaf marked with paperclip and loop respectively, (c) initial *C. rubra* leaf litter, and (d) decomposition bag in field.

At the conclusion of censuses, in late autumn (June 2013), marked tillers were harvested (at the base of the tiller, just above the roots) and stored at -20°C. After thawing, individual harvested leaves were classified into age classes based on order of leaf emergence. They were separated into living and dead portions and sheaths and their lengths measured prior to being dried at 60°C for 72hrs in a drying oven and segments weighed. These lengths and weights were used to derive power functions for each leaf age class at each plot. Power functions are commonly used with growth and decay data because they can fit regression lines to linear, curvilinear and/or exponential data without providing negative values. These functions were used to transform the live and dead leaf lamina and sheath lengths from each census into weights between censuses, since transitions of a blade of grass were assumed to sequentially pass through these phases.

Censuses were combined to form 2 annual time periods. After transformations of leaf lengths to biomass, a macro created in Microsoft

Excel© was used to calculate the amount of productivity, and expressed three ways. Productivity per tiller was determined by summing the productivity per leaf within that tiller and expressed as grams per year (g/yr). Productivity per plant was calculated by multiplying average productivity per tiller by the total number of tillers present and expressed as g/yr. The productivity per unit biomass, as grams of productivity per grams of biomass per year (g/g/yr; i.e. relative growth rate - RGR) was calculated by dividing the tiller productivity by the measured tiller biomass of the living portion at final harvest as a proxy for tiller weight at the start of the measurements, since grasses in general and *Chionochloa* in particular are known to have remarkably constant tiller weights (Couso *et al*., 2012).

Linear mixed effect models (LMEs) were used to determine significant differences in the mean annual productivity per tiller, per plant and from RGR using the lme procedure in the nlme package (by Pinheiro *et al*., 2014) in R (R Core Development Team, 2010). LMEs were utilized because of fixed effects (productivity being dependent on altitude), the levels of nesting (plant > tiller > year), and temporal pseudoreplication of the random effects within the experimental design. Significant differences ($P \leq 0.05$) were determined using Tukey's HSD (Honest Significant Difference) posthoc test using the HSD.test function in the agricolae package (De Mendiburu, 2012) in R (R Core Development Team, 2010).

Leaf litter decomposition

Litter chosen for full reciprocal translocation (Figure 3) decomposition was the youngest-most-fully-dead leaves that were still attached to tillers of non-experimental plants at each plot. Litter was excised, pooled per plot, cut into ≈5cm segments (Figure 2c), and 3.0g placed in litter decomposition bags (20cm x 25cm in size) made of black-nylon mesh (2mm pore size; Figure 2d). A total of 1461 decomposition bags were produced comprising 8 plots of litter origin by 8 plots of litter destination with 4-6 replicates and 4 annual collection periods (3 completed to date). In March of 2011, at each plot, bags were pinned to randomly selected patches of bare ground or low-lying vegetation in inter-tussock spaces, and left to decompose. Subsamples of this initial litter (i.e. did not

undergo decomposition treatments in the field) were collected for chemical and constituent analyses and for fresh-to-dry-weight conversions. Annual collections of decomposition bags occurred in March of 2012, 2013 and 2014 and bags were promptly stored at -20°C. After thawing, litter from each bag was sorted to remove attached soil and non-*Chionchloa* plant material, dried at 60°C for 72hrs, weighed, and mass loss calculated. Decomposition is expressed as averages of mass loss (on a g/g basis) of decomposed litter to initial biomass for home plots, and based on litter origin and destination.

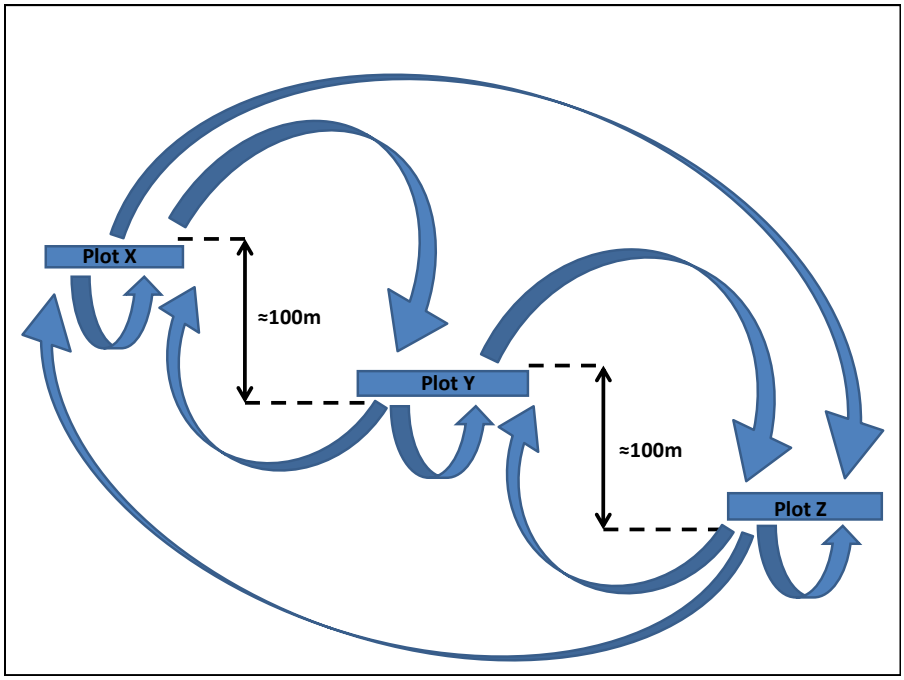

Figure 3: Simplified diagram of full reciprocal translocation of decomposition bags across only 3 plots (labelled X, Y and Z) incrementally spaced approximately every 100m in elevation (indicated by black dashed lines and vertical arrows). The blue arrows represent the translocation of decomposition bags from litter origin (arrow base) to litter destination (arrow point) of 4-6 replicates for decomposition for all possible combinations of translocations when using only 3 plots. Note: there were a total of 8 plots spanning a ≈700m altitudinal gradient on Mount Tongariro.

A 3-Way Analysis of Variance (ANOVA) was used to determine the significant differences and interactions of litter origin, litter destination and time on the mass loss of *C. rubra* litter as a function of plot location. A two-way ANOVA was used to determine plot and year differences and interactions for the mass loss of home plot decomposition, litter origin and litter destination. One-way ANOVAs were used to determine significant differences for home plot decomposition, litter destination and litter origin

for year 3 decomposition. All ANOVAs were followed by Tukey's HSD post-hoc test to determine differences at the $P \leq 0.05$ level using the HSD.test function in the agricolae package (De Mendiburu, 2012) in R (R Core Development Team, 2010).

Leaf litter chemical and constituent composition

Oven-dried (60°C) subsamples of *C. rubra* initial litter (i.e. litter which has not undergone decomposition in the field) of the original bulk-litter samples from the 8 plots were used for analyzing chemical and constituent composition. Samples were finely ground to 1mm with an impact grinder and re-dried for one hour at 105°C. Total organic carbon and nitrogen (N) analysis of leaf litter was performed on a Leco furnace. Combustion of a sample releases carbon dioxide (CO_2) and nitrogen (N) gases and the gaseous concentrations of these are used to calculate C and N concentrations (mg/g) based on dried sample weight. Phosphorus (P) concentrations of litter were determined following the Kjeldahl method and expressed as a concentration (mg/g) of the sample dry weight. Acid-detergent fibre (AD-fibre), cellulose and lignin concentrations were determined using an acid detergent fibre-sulphuric acid procedure following the methods of Rowland and Roberts (1994), the three resulting fractions expressed as concentrations (mg/g) of sample dry weight.

Condensed tannins and total phenolics (from the lowest, middle and highest plots - plots 1, 4 and 8 respectively) were assessed following methods of Broadhurst & Jones (1978) and Price & Butler (1977) respectively. The chemical and constituent compositions of the litter are expressed as concentrations (mg/g) based on sample weight. These chemical and constituent analyses of the initial litter were performed at Landcare Research, Palmerston North, New Zealand. Carbon to N ratios (C:N), C to P ratios (C:P), N to P ratios (N:P) and lignin to N ratios (L:N) were calculated and linear regression was used to examine trends across plots.

Litter decomposition half-life

The half-life of decomposing litter was determined from the decay rate coefficient derived from the slope of log transformed decomposition

rate (Olson; 1963), which is appropriate when the litter is confined and there are no annual additions of litter (Sundarapandian & Swamy, 1999). The equation is:

$$X/X_o = e^{-kt} \qquad \text{Equation 1}$$

where X is the mass of litter remaining at time t, X_o is the original litter mass, e is the base of the natural logarithm, k is the decay rate coefficient, and t is time. Olson's (1963) decay rate coefficient (k) was originally derived from the equation in Jenny *et al*. (1949) for "loss constants", which are expressed as the remaining fraction of the original mass. Assuming k is constant, k can be derived from the following natural logarithmic equation:

$$k = -\ln(X/X_o) \qquad \text{Equation 2}$$

The decay rate coefficients (k) were determined on *C. rubra* litter samples that experienced three years of decomposition in the field. The equation from Bockheim *et al*. (1991) was used to determine the half-life $t_{(0.5)}$ of *C. rubra* litter:

$$t_{(0.5)} = \ln(0.5)/(-k) = -0.693/(-k) \qquad \text{Equation 3}$$

A one-way ANOVA was used to determine significant differences for annual half-lives based on year 3 decomposition values of *C. rubra's* litter for home plot, litter origin and destination. These ANOVAs were followed by Tukey's HSD post-hoc test to determine differences at the $P \leq 0.05$ level using the HSD.test function in the agricolae package (De Mendiburu, 2012) in R (R Core Development Team, 2010).

Productivity to Decomposition Ratio

To revaluate the relationship between productivity and decomposition, the P:D ratios were determined for each of the 8 plots using the rational of the equation for endogenous C sequestration from Krna & Rapson (2013), based on their C fixation to release ratio:

$$F_{(a,s)}/R_{(a,s)} \quad \text{Equation 4}$$

where $F_{(a,s)}$ is the fixation of C into storage over a specified time period, minimally annual (*a*), within a specified system (*s*), and $R_{(a,s)}$ is the release of C over the specified time and within the system. In this experiment, P:D ratios were obtained from all combinations of the three different measurements expressing productivity (per tiller, per plant and RGR) and decomposition (home plot, litter origin and litter destination). The P:D ratios were plotted against the altitudes of plots and also against plots positioned along the envirometric gradient (defined here as a gradient constructed from biotic and abiotic environmental components derived from axis 1 of Principal Component Analysis; PCA; described in more detail below).

Linear regression analysis of P:D ratios was performed with first-order polynomials, and were positioned along either the altitudinal or the envirometric gradient (see below for details). Regression analysis was performed in R (R Core Development Team, 2010) to compare 1st and 2nd order polynomials to determine if the slopes of the P:D ratios were linear or curvilinear.

Envirometric Gradient

To establish a multifaceted environmental gradient (*envirometric gradient*), environmental and floristic components of each plot were assessed. Plant diversity and percent coverage of all vascular and non-vascular plant species were recorded in March 2013 by establishing 4 x 4m quadrats just outside of experimental plots. Coverage was determined as each species' shadow at solar zenith. Bare ground, rocks, wood debris, litter and hare faecal pellet coverage were also recorded. Plant species were grouped into functional groups (woody, herbaceous, cushion, moss and lichen) and used as *in situ* phytometers to express changes in stress across the gradient. Measured environmental characteristics were grouped into the categories climate, geographical, litter coverage and soil characteristics, and along with coverage were analysed independently with principal component analyses (PCA) in CANOCO© (Ter Braak & Smilauer, 1998). Variables

with the strongest eiganvalue from each of these PCAs was then used to perform a final PCA to construct an envirometric gradient based on ordination space of plots along axis 1 (Appendix 1).

To reduce the number of parameters used to construct the final envirometric gradient to be analysed with PCA (Appendix I; Eigenvalue of axis 1 = 0.965), parameters were subdivided into categories of litter, climate, geological, *in situ* phytometers, or soil characteristics. The preliminary PCA showed the parameters with the greatest contributions to Axis 1 were litter coverage (eigenvalue of axis 1 = 0.879), precipitation (0.999), woody species coverage (0.589) and average soil N (0.983) were selected. Altitude had the strongest effect of the geological variables (eigenvalue of axis 1 = 1.0), but this parameter heavily influenced the final PCA and was consequently omitted from the analysis because of circularity. On axis 1, plots 1 and 8 had the greatest distance apart with plots 5, 2 and 3 grouping near plot 1 (in that order) and plots 4, 6 and 7 ordered near plot 8. The distance along Axis 1 was taken as the envirometric gradient, and examined along with altitude.

Comparisons of P:D ratios for projected warming

A 0.6^{o}C mean annual lapse rate (Halloy & Mark, 2013) was used to make comparisons of the P:D ratios for plots that were ≈300m in difference across the gradient (sub-sections from the total ≈700m gradient; e.g. from Plot 4 to Plot 1) to assess how a 1.8^{o}C warming (the conservative end of model projections for temperature increases, IPPC, 2014) would impact the P:D ratios of *C. rubra* across on Mount Tongariro. Average *in situ C. rubra*'s productivities from both ends of the ≈300m and average translocated mass losses of 3 year decomposed *C. rubra* leaf litter corresponding to the ≈300m gradient were used. The average of the "From" (i.e. litter origin) and "To" (i.e. litter destination) P:D ratios were calculated to deduce potential differences in C sequestration that may occur with predicted climate change.

Results:

Productivity

Average annual productivity per tiller of *C. rubra* declined with increasing altitude across both years ($P \leq 0.05$). Plants at the highest altitude plot (plot 8) had 41.1% significantly lower average productivity per tiller compared to the lowest 4 plots ($P \leq 0.05$). Plants a plot 7 (altitude = 1565m) was an exception to this trend (Figure 4a), having 47.2 and 85.6% greater average productivity per tiller than plots 6 and 8 respectively. Plants at the lowest altitude plots, plots 1 and 2, had 45.1 and 40.2% greater average productivity per tiller respectively compared to higher altitude plots (plots 3-8). Average productivity per tiller did not significantly differ between middle plots (plots 3, 4, 5 and 6).

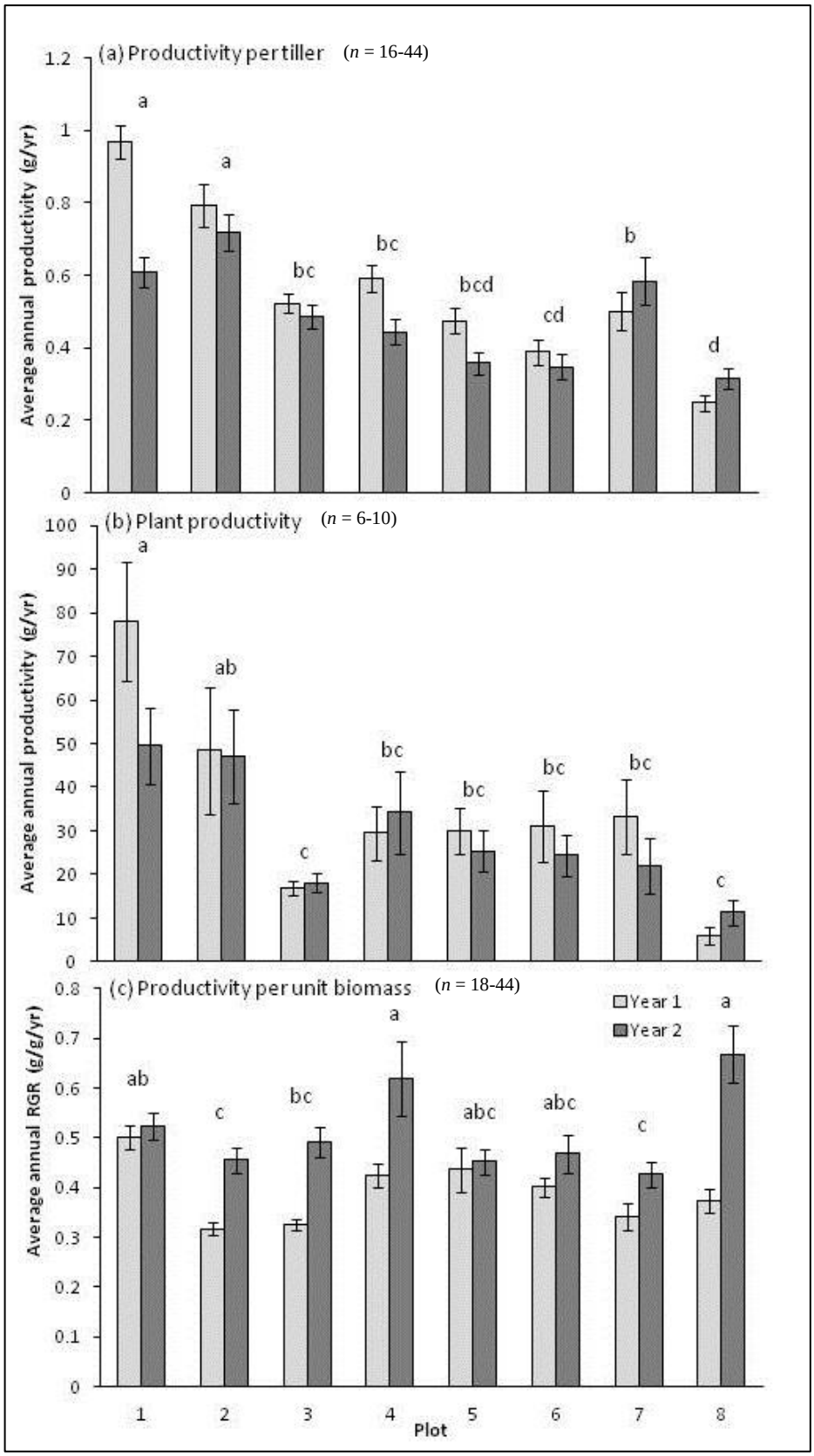

Figure 4: Mean ± S.E. annual aboveground productivity per (a) tiller, (b) plant and (c) unit biomass of *Chionochloa rubra* leaves for years 1 (light grey) and 2 (dark grey) across the 8 plots on Mount Tongariro. Different letters denote significant differences at the $P \leq 0.05$ level.

When average annual productivity was expressed per plant, the trends in productivity observed along the altitudinal gradient was weaker, but still followed the same direction (Figure 4b). Average plant productivity across both years at plot 1 did not significantly differ with that of plot 2; however it was 100.1% greater than higher altitude plots (plots 3-8; $P \leq 0.05$). Average plant productivity did not differ between plots 4, 5, 6 and 7. The average plant productivity of plots 3 and 8 were 63.4 and 80.0% lower than that of the lowest two plots.

The average annual productivity per unit biomass (Figure 4c) ranged from 0.56 to 0.38g/g/yr and did not follow trends of decreasing productivity with increasing altitude observed with the productivity per tiller or plant across plots. The lowest, middle and uppermost plots (plots 1, 4 and 8) had the greatest average productivity per unit biomass and did not significantly differ, however they were 31.3% greater than plots 2 and 7 ($P \leq 0.05$). There were no differences in the average productivity per unit biomass for plots 2 through 7, excluding plot 4, which was significantly different to plots 2, 3 and 7 ($P \leq 0.05$).

Decomposition

Leaf litter origin (where plot litter was taken "From"), destination (where plot litter was plated out "To") and time (in "Years") were independently significantly different, and significant interactions were observed between litter origin and year as well as litter destination and year (Table 1). The average total mass losses of decomposing *C. rubra* litter for years 1, 2 and 3 respectively were 0.179 (±0.002 SE; $n = 349$), 0.299 (±0.003 SE; $n= 355$) and 0.459g/g (±0.005 SE; $n = 345$; Figure 5). Mass loss of year 2 decomposition was 67.0% greater than year 1 ($P \leq 0.001$) and mass loss of year 3 decomposition was 53.5% greater than year 2 ($P \leq 0.001$). Annual difference in mass loss between years 1 and 2 was 0.122g/g (±0.003 SE; $n = 335$) and mass loss between years 2 and 3 was 0.158g/g (±0.005; $n= 327$).

Table 1: Analysis of variance table of mass loss of decomposing leaf litter of *Chionochloa rubra* after a full reciprocal translocation for 1, 2 and 3 years of decomposition across the 8 plots on Mount Tongariro. Significance levels are denoted by *** ($P \leq 0.001$), ** ($P \leq 0.01$), and * ($P \leq 0.05$).

	Df	Sum Sq	Mean Sq	F value	P value	Significance
From	7	0.098	0.01398	3.419	0.001305	**
To	7	0.103	0.01472	3.600	0.000791	***
Year	2	0.577	0.28833	70.518	< 2e-16	***
From:To	49	0.088	0.00179	0.438	0.999737	
From:Year	14	0.106	0.00759	1.857	0.027564	*
To:Year	14	0.164	0.01173	2.868	0.000307	***
From:To:Year	98	0.337	0.00343	0.840	0.861435	
Residuals	819	3.349	0.00409			

The mass loss from home plot decomposition did not significantly differ between plots, only between years ($P \leq 0.001$; Figure 5a). Mass loss based on litter origin was greatest with litter originating from the lower two and the uppermost plots, while litter originating from plot 6 had the lowest mass loss across all three years of decomposition (Figure 5b). The destination of litter revealed significant trends in mass loss across the plots after three years of decomposition. Litter translocated to the upper plots (plots 4-8) had 14.6% greater mass loss than that of the lower 3 plots ($P \leq 0.001$; Figure 5c).

The decompositional half-lives of home-transplanted *C. rubra* leaf litter across the 8 plots did not reveal any significant differences ($P = 0.255$; Appendix I). The mean half-life was 3.6 years. Based on leaf litter origin, litter from plot 6 had 25.9 and 37.3% longer half-lives than that from plots 1 and 8 respectively, and plot 4's half-life was 27.6% greater than plot 8 ($P \leq 0.05$). Based on litter destination, lower plots have longer half-lives than upper plots. Litter decomposing at plot 2 had 25.7 and 26.2% greater half-lives than that at plots 4 and 6 respectively, and litter decomposing at plot 3 had 29.6 and 30.2% greater half-lives than that at plots 4 and 6 respectively ($P < 0.05$).

Litter chemical and constituent composition

The chemical composition of *C. rubra's* initial leaf litter (i.e. litter from bulk samples of each plot which did not undergo decomposition treatments in the field) revealed trends across the altitudinal gradient (Table

2). Its C content slightly increased with increasing altitude (r^2 = 0.948), litter C content from the uppermost plot was 1.4% greater than the lowest plot. An increasing trend of the N content of initial litter with increasing altitude was also observed (r^2 = 0.822); litter N of plot 8 was 48.8% greater than plot 1. Phosphorous content of initial litter decrease with increasing altitude, although this relationship was weakly correlated (r^2 = 0.271). The initial litter from the lowest plot had 40.6% greater P content than the uppermost plot. The lowest and highest plots had 66.8 and 18.3% greater P content respectively than plot 3, which had the lowest percent P of all plots.

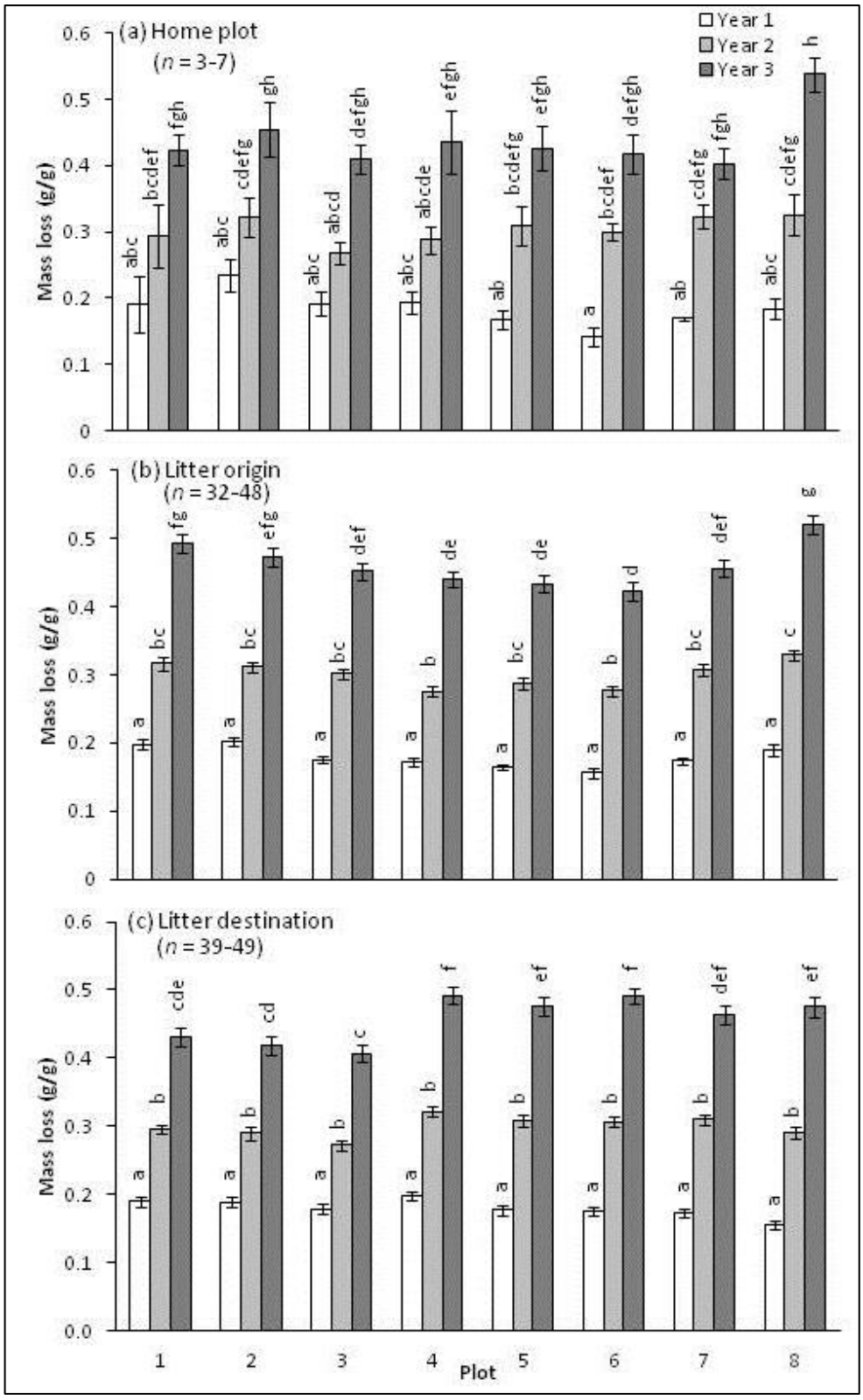

Figure 5: Mean ± S.E. mass loss of decomposing *Chionochloa rubra* litter for decomposition (a) at home plot, (b) by litter origin and (c) by litter destination across the 8 plots. Different letters denote significant differences at the $P \leq 0.05$ level.

The carbonaceous constituent composition of *C. rubra* litter also revealed trends along the altitudinal gradient (Table 2). The litter percent AD-Fibre decreased with increasing altitude (r^2 = 0.879); the AD-Fibre content of plot 1 was 7.8% greater than plot 8. The percent cellulose of litter did not differ substantially across plots (r^2 = 0.341). The percent lignin content of litter had a slight tendency to decrease with increasing elevation (r^2 = 0.1756), plot 4 had the greatest lignin content and was 6.0 and 15.0% greater than plots 1 and 8 respectively. The L:N of litter decreased with increasing altitude (r^2 = 0.735), the L:N of litter from plot 1 was 61.4% greater than plot 8. The L:P of litter from plot 4 was greatest and was 66.3 and 27.9% greater than plots 1 and 8 respectively.

Table 2: Chemical and constituent composition of initial leaf litter of *Chionochloa rubra* (i.e. did not undergo decomposition treatments in the field) (n = 1) and decompositional half-lives (n = 39-46) based on 3 years of decomposition in the field. Different superscript letters denote significant differences at the $P \leq 0.05$ level.

Parameter	Plot 1	Plot 2	Plot 3	Plot 4	Plot 5	Plot 6	Plot 7	Plot 8
Altitude (m)	986	1066	1162	1252	1368	1469	1565	1679
Carbon (C; mg/g)	469.99	469.99	469.98	472.23	472.69	474.72	476.66	476.50
Nitrogen (N; mg/g)	2.05	2.63	2.59	2.61	2.85	2.79	3.23	3.05
Phosphorous (P; mg/g)	0.097	0.072	0.058	0.062	0.063	0.060	0.066	0.069
C:N (C to N ratio)	229.56	178.75	181.71	181.03	165.70	170.33	147.79	156.49
C:P (C to P ratio)	4850.58	6517.78	8090.79	7648.58	7563.04	7918.41	7245.27	6937.03
N:P (N to P ratio)	21.13	36.46	44.53	42.25	45.64	46.49	49.02	44.33
Tannins (mg/g)	< 2.0	--	--	< 2.0	--	--	--	< 2.0
Phenolics (mg/g)	6.79	--	--	6.25	--	--	--	5.45
AD-Fibre (mg/g)	430.24	425.70	411.10	416.90	409.79	409.3	406.5	399.2
Cellulose (mg/g)	338.80	320.70	302.20	337.14	301.60	264.76	312.61	329.59
Lignin (L; mg/g)	73.70	72.10	72.50	78.13	77.22	74.21	69.20	67.93
L:N (L to N ratio)	36.00	27.43	28.03	29.94	27.07	26.63	21.45	22.31
L:P (L to P ratio)	760.72	1000.18	1248.10	1265.18	1235.56	1237.91	1051.58	988.92
Home Half-life (years)	3.60^{a}	3.62^{a}	4.00^{a}	3.94^{a}	3.92^{a}	3.96^{a}	3.76^{a}	2.75^{a}
From Half-life (years)	3.21^{bc}	3.46^{abc}	3.62^{abc}	3.75^{ab}	3.94^{ab}	4.04^{a}	3.61^{abc}	2.94^{a}
To Half-life (years)	3.89^{abc}	4.03^{ab}	4.15^{a}	3.20^{c}	3.37^{bc}	3.19^{c}	3.52^{abc}	3.58^{abc}

Soil carbon and nutrients

The average soil C concentration of the three soil depths decreased with increasing soil depth, where 0-10cm, 10.1-20 and 20.1-30 averaged 58, 41 and 34 mg/g respectively (Appendix 1). The average of all soils from plots of the top 10cm of soil had a 43.0 and 71.7% greater C content than

10-20 and 20-30cm depths respectively, and the percent TOC of the 10-20cm depth was 20.1% greater than the 20-30cm depth. The soil C averages of all soil depths for plots 7 and 8 were 12.8 and 27.0% lower respectively than all lower plots.

The average soil N concentration of the three soil depths from all plots also decreased with increasing soil depth. The top 10cm of soil had a 25.2 and 40.9% greater soil N than 10.1-20 and 20.1-30cm depths respectively, and the percent TON of the 10-20cm depth was 12.6% greater than the 20-30cm depth. There was a trend of decreasing soil N with increasing altitude.

The average C:N of the three 10cm soil depths from all plots decreased with increasing depth, where 0-10, 10.1-20 and 20.1-30 averaged 220, 196 and 190 mg/g respectively (Appendix 1), as C:N in the 10.1-20cm depth was 3.3% greater than the 20.1-30cm depth. There was a trend of increasing soil C:N with increasing altitude up to plot 7; however the average of the C:N of the 3 depths of plot 8 was 17.5% lower than that of plot 7.

The percent soil P decreased with increasing altitude (Appendix 1). The soil C:P and N:P across the altitudinal gradient both expressed a concave curve across the plots, although this was more strongly observed with the C:P ($R^2 = 0.812$).

Productivity to decomposition ratio

The P:D ratios of *C. rubra* decreased at higher altitudes and along the envirometric gradient when expressed on a per tiller or per plant basis (Figure 6). Second order polynomials did not significantly fit the P:D data better than 1st order polynomials, except for one (Figure 6f; $P = 0.0669$). The P:D ratios, expressed as productivity per tiller and per plant for the three types of decomposition (home plot, litter origin and litter destination), decreased with increasing altitude and across the environmental gradient (Figure 6a-d). However, when productivity of the P:D ratios were expressed as RGR for the three types of decomposition, no trends were expressed (Figure 6e-f).

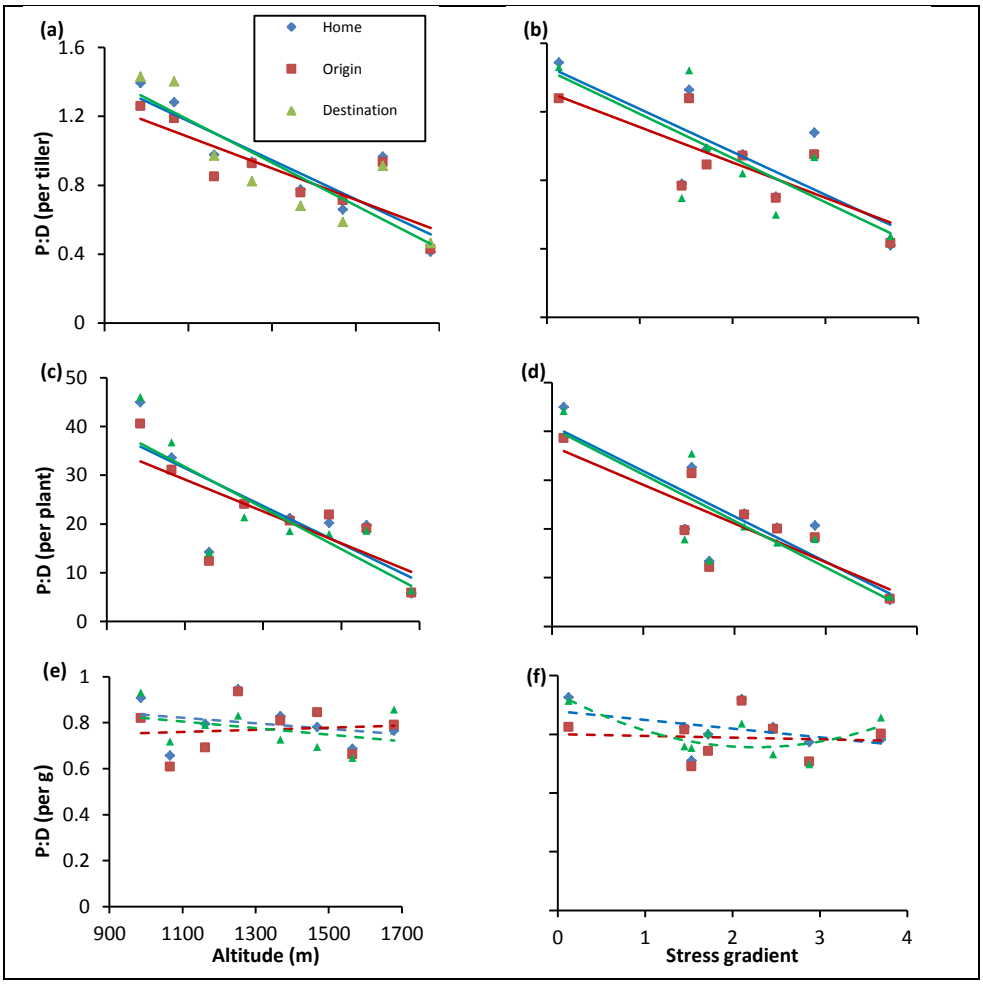

Figure 6: Regression of the mean productivity to decomposition ratio (P:D) of *Chionochloa rubra* across the 8 plots on Mount Tongariro plotted against altitude and the envirometric gradient (constructed from axis 1 from PCA). Productivity is expressed as calculated averages of two years of productivity for g on a tiller basis, for g on a plant basis and per g of biomass. Decomposition is expressed as the annual average of mass loss (g) per g of initial weight after 3 years of decomposition of leaf litter from home plot decomposition, where litter originated from and destination of where litter was plated to. Solid lines denote significant regression and dashed lines denote non-significant regression.

Comparisons of P:D ratios for potential warming

Across ≈300m sub-sections of the total ≈700m altitudinal gradient, the average of *C. rubra* productivity of higher altitudinal plots (i.e. From) and lower altitudinal plot (i.e. To), reveals that a 300m downslope translocation to a warmer environment results in a 40% greater productivity than higher elevations (Table 3). The greatest difference in productivity between sub-sections of the gradient was found between Plot 5 and Plot 2 (0.35g/yr) and the smallest difference was observed between Plot 7 and Plot 4 (-0.05g/yr). The average productivity of lowest altitudinal sub-section (Plot 4 → Plot 1) was 40% greater than that of the highest altitudinal sub-

section (Plot 8 → Plot 5). The mass loss of *C. rubra* litter after 3 years of decomposition following translocation was 45% greater at higher sub-sections compared to lower sub-sections of the gradient. The average P:D ratios at lower sub-sections (i.e. To) was 43% greater than higher altitudinal sub-sections (i.e. From). The P:D ratios based on productivity of upper (i.e. From) and lower (i.e. To) reveal lower sub-sections (Plot 4 → Plot 1) have 148 and 185% greater P:D ratios than upper sub-sections (Plot 8 → Plot 5), respectively. The P:D ratios based on differences in the productivity across sub-sections of the gradient reveal the lowest sub-section P:D ratios (Plot 4 → Plot 1) is 284% greater than that of uppermost sub-section (Plot 8 → Plot 5). Of these, greatest difference in P:D ratios was observed for the second lowest sub-section (Plot 5 → Plot 2; 0.85) and the lowest difference in P:D ratios was observed for the second highest sub-section (Plot 7 → Plot 4; -0.09). The P:D ratios based on averages in productivity across sub-sections of the gradient, the lowest sub-section (Plot 4 → Plot 1) expresses a P:D ratio 171% greater than the uppermost sub-section (Plot 8 → Plot 5), a 37% difference between these sub-sections.

Table 3: Productivity (Prod) to decomposition (Decomp) ratios (P:D) on a per tiller basis calculated from average *in situ Chionochloa rubra* productivity over 2 years (g/yr) of plots ≈300m difference in elevation (with "From" being higher altitude plot than "To"), the difference between the productivities (To minus From), the average of the "From" and "To" productivities, and mass loss of its leaf litter following 3 years of decomposition (g/g) after translocation downslope ≈300m in altitude. The productivity to decomposition ratios (P:D) ratios are calculated based on averages of *in situ* productivities of "From" and "To" plots and corresponding translocated decomposition averages.

Translocation (From → To)	**Prod** (From)	**Prod** (To)	**Prod** (Difference)	**Decomp** (Translocated)	**P:D** (From)	**P:D** (To)	**P:D** (Difference)
Plot 4 → Plot 1	0.49	0.78	0.29	0.40	1.24	1.96	0.73
Plot 5 → Plot 2	0.40	0.75	0.35	0.45	0.97	1.82	0.85
Plot 6 → Plot 3	0.37	0.50	0.14	0.37	0.99	1.36	0.37
Plot 7 → Plot 4	0.54	0.49	-0.05	0.51	1.07	0.97	-0.09
Plot 8 → Plot 5	0.29	0.40	0.11	0.58	0.50	0.69	0.19
Average	0.42	0.59	0.17	0.45	0.95	1.36	0.41

Discussion

Carbon sequestration occurs when the fixation of C from the atmosphere into storage is greater than the release of C to the atmosphere from storage (through autotrophic or microbial respiration from decomposition) within a specified system over a designated time period (Krna & Rapson, 2013). No other studies have previously investigated P:D ratios (Web of Science© search for "productivity to decomposition ratio" or "ratio of productivity to decomposition" yielded no records as of 2 December 2014) in relation to altitude or environmental gradients to examine C cycling and sequestration. In this study, C sequestration is inferred to increase with increasing P:D ratios of *C. rubra* along a ≈700m altitudinal stress gradient on Mount Tongariro. The P:D ratios decline with increasing altitudinal and environmetric stress (when expressed on a per tiller or per plant basis), indicating more C sequestration occurs at higher altitudes per unit productivity. Indications of a slight curvature in the P:D ratio relationship based on origin and expressed on a per g basis may suggest gains in C sequestration are not monotonic, and mid-altitudinal ranges for *Chionochloa* may sequester less C than expected from an altitudinal or stress gradient.

Productivity

On Mount Tongariro's montane gradient, there was a significant decrease in productivity of *in situ C. rubra* plants (when expressed on a per tiller or per plant basis) with increasing elevation. This trend in reduced *Chionochloa* species' productivity and leaf elongation rates across increasing altitudinal gradients is well supported in the literature (Mark, 1965c, Mark & Bliss, 1970; Greer, 1979; Williams *et al*., 1982) and others have found similar trends with other species in montane environments across gradients (Michalet *et al*. 2014; Callaway *et al*., 2002; Kikvidze *et al*., 2005). These trends are likely attributed to cooler temperatures, reduced growing season and increased duration of snow cover at higher altitudes, which can result in lower productivity (Körner, 2007 and references therein) owing to greater stress at higher elevations of altitudinal gradients (Callaway *et al*., 2002).

Meta-analyses across montane-altitudinal gradients reveal increased productivity which is often attributed to reduced stress experienced by plants with decreasing elevation at lower altitudes (Michalet *et al*. 2014; Callaway *et al*., 2002; Kikvidze *et al*., 2005). This trend has also been observed with non-*Chionochloa* species in New Zealand's tussock grasslands (Lee *et al*., 1987) and within the genus *Chionochloa* (Mark, 1965a, 1965b, 1965c; Mark and Bliss, 1970; Greer, 1979; Williams *et al.* 1982). The reduction in productivity with increasing elevation is likely attributed to not only differences environmental characteristics but also to differences within species; i.e. ecotypic differentiation resulting from local acclimation and/or adaptation to environmental differences across altitudinal gradients. Ecotypic differentiation in productivity may result in differences in decomposability and mass loss of litter owing to alterations in allocation patterns of C and nutrients within leaves.

Decomposition

Climate is the primary factor that influences the decomposition of plant litter (Coûteaux *et al*., 1995; Lavelle *et al*., 1993), and elevated temperatures typically result in increased decomposition rates of plant litter (Wasley *et al*., 2006). This was demonstrated along an altitudinal gradient in

northern Sweden where mass loss of litter was significantly lower in the colder climate at higher altitudes (Sundqvist *et al*., 2011a; 2011b). However, Murphy *et al*. (1998) found precipitation to be the prominent driver along a semiarid montane gradient in northern Arizona and mass loss was increased at higher altitudes because of greater moisture availability; they concluded that warmer temperatures and increased precipitation would elevate decomposition rates. Bryant *et al*. (1998) analysed aboveground plant litter decomposition rates across temperature and moisture gradients in alpine tundra of Colorado over three years and found increased precipitation and soil moisture to increase mass loss of litter across the environmental gradient more so than temperature. On Mount Tongariro greater mass loss was expected at lower altitudes because of warmer climate, however the mass loss of *C. rubra* based on litter destination increased with altitude which is most likely attributed to the observed increase in precipitation ascending the gradient.

Effects of litter destination examine plastic differences in decomposition resulting from environmental characteristics across the gradient. It appears to influence decomposition rates more than litter origin. Across altitudinal gradients, environmental factors can play a role in plant litter decomposition (Murphy *et al*., 1998). Litter decomposition consists of three primary components that work in a hierarchical manner, namely: climate > litter quality > soil organisms (Aerts, 1997; 2006; Lavelle *et al*., 1993; Swift *et al*., 1979). To stress the importance of these three components, Hobbie (1996) found warmer temperatures in the Arctic tundra increased decomposition rates of plant litter and this was influenced by the litter quality of the plant species which can influence N release into the soil via soil organisms (Hobbie, 1996 and references therein). The three primary components of litter decomposition can vary across montane environmental gradients. Differences in climate across altitudinal gradients can influence plant allocation patterns and thus result in differences in litter quality, decomposability and chemical composition (Chapin, 2003; Lavorel *et al*., 2007) and microbial communities can also vary across altitudinal gradients (Yuan *et al*., 2014). Murphy *et al*. (1998) and Sundvist *et al*. (2011a; 2011b) both investigated decomposition across altitudinal gradients in semiarid and

subarctic tundra environments respectively, to determine litter quality and effects of climate on decomposition; they found differing results. Their findings are most likely attributed to not only the different species examined, but more importantly the environments in which the experiments were performed. On Mount Tongariro there was an increase in mass loss of *C. rubra* leaf litter after 3 years with increasing elevation and precipitation following translocation based on litter destination, but these differences were minimal (< 0.1g difference between upper and lower plots). The effects of mass loss based on litter origin suggest there may be slight chemical and/or structural differences (since mid-altitudinal range plots have the lowest rates of mass loss) in the litter across the altitude and stress gradients.

Envirometric and altitudinal stress gradients

Changes in stress along alpine gradients (typically greater at higher altitudes) can influence ecosystem processes and functioning (Callaway *et al*., 2002; Körner, 2007), which can in turn influence plant productivity (Sundqvist *et al*., 2013), decomposition (Zhu *et al*., 2012) and C sequestration (Ward *et al*., 2014). Expressions of gradients in montane systems often differ in the types of data that are used in the literature (e.g. geographical, abiotic and environmental parameters utilized in defining the gradient). On a global scale, Kikvidze *et al*. (2005) investigated 18 different plant communities across subalpine and alpine ecosystems and observed both linear and curvilinear correlative links between abiotic conditions (temperature and precipitation) and biotic components (productivity, species richness, plant interactions and spatial patterns). In this study on Mount Tongariro, both means of expressing a stress gradient for plotting P:D ratios (altitude, and the envirometric gradient) yielded similar trends with regression analysis. However there were slight differences in the responses of the P:D ratios across the two means of expressing the gradient.

Altitude is most often the major variate that affects abiotic characteristics which influence ecosystem processes on mountains (Korner, 2007). Michalet *et al*. (2014) and Callaway *et al*. (2002) both performed global-scale meta-analyses to examine plant interactions along altitudinal

gradients in montane systems using high and low altitude as indicators for exposure to levels of plant stress. In this study, the indicator of stress (altitude vs. envirometric gradient) was dependent on the means by which productivity was expressed. Expression on a per tiller basis provides a better fit to the data than productivity expressed on a per plant basis, yet similar trends were still observed. However, when the productivity of the P:D ratios is expressed as RGR (on a per g basis), neither gradient detects any trends. This indicates that the P:D ratio is not only dependent on the means by which productivity is expressed but also, though to a much lesser extent, on the type of stress gradient used to express differences across this montane tussock grassland.

After removing altitude from PCA analyses (because it drowned out other environmental variables), the prominent drivers of the envirometric gradient on Mount Tongariro were precipitation and percentages of soil N, and percent coverages of litter and woody species. In low and mid latitude regions, precipitation often increases with altitude (Beniston, 2005), as found in New Zealand tussock grasslands (Holdsworth & Mark, 1990 and references therein); hence the increase in precipitation with increasing altitude on Mount Tongariro (Appendix 1) was not unexpected. Changes in plant species' composition occurs along altitudinal gradients (Gerald & Jürgen, 2007 and references therein) can indicate changes in stress owing to individual species ecophysiolgical limits, traits and tolerances to changes in environmental variables across gradients (Violle *et al*., 2007). The use of *in situ* plant taxa for indicators of changes in stress along altitudinal gradients (Halloy, 1989) often reveals a decrease in woody species (Breshears, 2006 and references therein) and an increase in mat/cushion species with increasing elevation (Cavieres *et al*., 2006). Similar trends have been observed in New Zealand's tussock grasslands (Walker *et al*., 2004 and references therein). In this study, woody species' coverage was greatest at lower altitudes and the coverage of mat species was greatest at higher altitudes. On Mount Tongariro, the percent soil N decreased with increasing altitude and the soil C:P (which also had a strong influence on PCA) tended to increase with increasing altitude. The range of the soil C:P on Mount Tongariro indicates this system has a soil fraction categorised as "slow",

which may indicate this system is P limited because of retarded P cycling (Parton *et al*., 1988). However, despite the use of such biotic and abiotic variates to construct the envirometric gradient, it appears as though altitude, the simpler variate to measure, expresses the gradient just as well, making altitude a powerful proxy for environmental stress across montane gradients. The differences in the P:D ratios from their different means of expression (altitude and envirometric gradients) may result from alterations in allocation patterns of plant growth (which can also influence litter quality and decomposition) owing to changes in the levels of stress plants are exposed to across the gradient.

Chemical and constituent composition of litter

Climate can influence plant ecophysiological traits and responses, which can impact growth rates and allocation patterns, feeding back to influence the chemical composition of litter (Chapin, 2003; Lavorel *et al*., 2007; Hobbie, 1996). Primary productivity declines in plants with altitudinal changes; this is often associated with chemical and structural differences of plants observed along an altitudinal gradient (Waide *et al*., 1998). Plants with a genetic disposition to tolerate elevated environmental stresses often have higher production of lignin and phenolic compounds (Kim *et al*., 2008) which can provide plants with additional tolerance to environmental stress (Boer *et al*., 2005).

In *C. rubra*, the concentration of tannins is below detectible limits, and this has been observed by others for this species (pers. com Tarnia Hodges). The concentrations of lignin and total phenolics of *C. rubra* litter decreased with increasing altitude, however the ratios of productivity per concentrations of lignin and total phenolics reveal a strong increase with increasing altitude. This indicates that more productivity at higher altitudes may be utilized in production of these compounds to ameliorate or cope with increasing stress across the gradient, which may influence the P:D ratios. The increased production of these stress response compounds in reaction to increasing stress is likely to come at a cost to the plant owing to resource allocation, and ultimately resulting in reduced productivity.

Under conditions of nutrient limitation, plants produce less biomass than would occur if nutrients were not limiting (Chapin *et al*., 1986). In this experiment, the lower productivity of *C. rubra* at the highest plot is not likely due to N limitation, owing to an increase in N concentrations with altitude. Rather P limitation may be the contributing factor, as a decrease in P concentrations within leaf tissues which may indicate plants are not N limited (Aber *et al*. 1989).

The chemical composition of plant litter, such as C, N, P and lignin concentrations as well as C:N, C:P and L:N ratios, can also strongly influence and are good indicators of decomposition rates (Lavelle et al., 1993; Coûteaux *et al*., 1995; Hobbie, 1996; Aerts, 1997 and references therein; Murphy *et al*., 1998). Chemical analysis of *C. rubra's* litter revealed an increase in C, N, C:P, N:P and L:P, as well as a decrease in the C:N, P, L:N, AD-fibre, cellulose and lignin with increasing altitude. The increase in C, N, C:P and L:P as well as the decrease in C:N, would indicate that litter from higher altitude plots should be more readily decomposed than that from lower altitude plots. However, the ratios of year 3 home plot litter decomposition rates to the above parameters may suggests otherwise, indicating a decrease in decomposability of the litter with increasing altitude. Thus, the chemical and constituent composition of *C. rubra* litter may impact the decomposition portion of the P:D ratio. Shifts in the balances between N and P in grassland systems may play important roles in regulating plant growth in grassland systems (Phoenix *et al*., 2003) as well as C and nutrient cycling through decomposition of litter and incorporation into the soil.

Soil carbon and nutrients

Soil nutrient concentrations on Mount Tongariro may also be contributing factors influencing the P:D ratios across the gradient. Carbon, N and P cycling restrain a majority of ecosystem processes; soil P is primarily derived from weathering of local parent material, whereas soil N is mainly supplied by organic matter decomposition (He *et al*., 2008 and references therein). Cooler temperatures, when ascending gradients, can result in nutrient limitation because of inhibited N mineralization and result

in a lower N supply rate available to plants as at higher altitudes in Nez Zealand tussock grasslands (Craine & Lee, 2003 and references therein; Wang *et al*. 2004). On Mount Tongariro, there was a decrease in soil N, P and N:P ratios, and increase in C:N and C:P ratios with increasing altitude. This suggests that soil nutrients may also be a contributing factor to the decline of the P:D ratio with increasing altitude.

Implications for climate change

Cold ecosystems (i.e. Arctic, Antarctic and alpine environments) that push the boundaries of low temperature limitations of plant life are particularly sensitive to climate change (Pounds *et al*., 1999; Walther *et al*., 2002). Both temperature and precipitation are likely to be impacted with climate change (although there are greater uncertainties with model predictions of precipitation alterations). Even though montane plants are well adapted (because of continuous exposure to extreme climatic conditions), they are still highly sensitive to alterations in climate (Bugmann, 2001), as this alters the nature and/or levels of stress. Changes in stress along altitudinal gradients can therefore influence ecosystem processes and plant community structure (Sunqvist *et al*., 2013). This may be modified by shifts in ecophysiological responses to stress, which may result in alterations in productivity, decomposition and C and nutrient cycling, ultimately impacting C sequestration.

A decline in *C. rubra* P:D ratios based on averages of productivity across 300m subsections of the gradient reveal a 37% difference between lower and uppermost sub-sections was observed on Mount Tongariro. This was performed using only *in situ* plant responses for an estimate of potential climate change impacts on productivity. The productivity of *C. rubra* will increase with warmer temperatures. The decomposition of its leaf litter does not appear to be as influenced by temperature (more likely precipitation in this system). Thus a 1.8^{o}C temperature change and alterations in precipitation patterns will impact endogenous C sequestration of *C. rubra* in New Zealand's tussock grasslands. With increasing productivity and little change in the decomposition rates of *C. rubra* in warmer environments, it is likely that the P:D ratios of *C. rubra* will increase with climate change and

result in more C sequestration, thus generating a positive feedback for C cycling for New Zealand tussock grasslands.

Future studies

The findings presented here indicate grater alterations in productivity than decomposition of *C. rubra* along an altitudinal gradient; investigation of this trend in other species within the genus *Chionochloa* is needed to better understand C and nutrient cycling in New Zealand's alpine tussock grasslands. The transplantation of living *C. rubra* plants was not permitted at this World Heritage Site. Investigation of *Chionochloa* species' responses to alterations in abiotic conditions via transplantation of living *Chionochloa* plants across altitudinal gradients will provide better insights as to how climate change will influence the productivity portion of the P:D ratios; allowing for the examination of plastic and genetic variation in response to changes in climate across gradients, and potential changes in C and nutrient cycling in New Zealand's tussock grasslands.

Conclusions

The soil nutrients, productivity, litter decomposition as well as litter chemical and constituent composition all influence the P:D ratio of *C. rubra*. Its decline at higher altitudes indicates less productivity occurs per unit decomposition for C sequestration at the cooler environments. Productivity appears to be the driving force of the P:D ratio rather than decomposition based on comparisons of slope directions from regression analysis of productivity and decomposition. The decline of *C. rubra's* P:D ratio was strongest when productivity was expressed per tiller and per plant; little variation was detected when expressed as RGR, indicating RGR and decomposition may be in balance in this system owing to a near constant rate of tiller and leaf turnover within the genus *Chionochloa*. Climate change will alter plant productivity, litter decomposition, as well as soil C and nutrient cycling. Alterations to any of these parameters will shift the P:D ratio and influence the C sequestration potential of *C. rubra* in New Zealand's tussock grasslands.

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Appendix I. Parameters investigated to create the envirometric stress gradient; bold parameters were used to create the final stress gradient with principal component analysis.

Parameter	Plot 1	Plot 2	Plot 3	Plot 4	Plot 5	Plot 6	Plot 7	Plot 8
Altitude (m)	986	1066	1162	1252	1368	1469	1565	1679
Precipitation (mL)	**467.0**	**557.5**	**568.5**	**589.0**	**546.5**	**613.0**	**637.0**	**690.0**
Average Temperature (^{o}C)	9.72	8.46	8.47	8.28	7.79	7.38	7.28	6.21
Average Max Temperature (^{o}C)	35.58	30.44	29.86	29.28	29.16	31.66	32.87	29.34
Average Min Temperature (^{o}C)	-6.08	-5.01	-5.44	-3.95	-3.20	-4.14	-3.58	-3.61
Slope (degrees)	0	2	5	15	19	16	31	35
Northing (degrees)	-39.07	-39.08	-39.09	-39.10	-39.10	-39.10	-39.11	-39.11
Non-*Chionochloa* litter cover (%)	0.5	0.5	1	0.5	2	0.5	0.5	1
Chionochloa litter cover (%)	4	0.5	0.5	1	1	1	1	1
Wood cover (%)	0.5	1	0.5	0.5	0.5	0.5	0.5	0.5
Litter cover (%)	4.5	1	1.5	1.5	3	1.5	1.5	2
All litter cover (%)	**5**	**2**	**2**	**2**	**3.5**	**2**	**2**	**2.5**
Species diversity (%)	15	29	26	25	27	23	22	24
Chionchloa rubra cover (%)	22	7	5	8	7	3	3	2
All moss species cover (%)	5	1	15.5	20	6	8	14.5	11.5
Racamitrium & all moss cover (%)	27	8	20.5	28	13	11	17.5	13.5
Racimitrium ÷ all moss cover (%)	0.18	0.12	0.75	0.71	0.46	0.72	0.82	0.85
Grass species cover (%)	23.5	16	6.5	12	22	16	25.5	38
Lichen species cover (%)	0	0	1	3	0	0	0	0
Herbaceous species cover (%)	3	9	12.5	15	6.5	10.5	9.5	12.5
Woody species cover (%)	**67**	**74.5**	**67**	**41.5**	**36**	**48.5**	**33**	**38**
Mat species cover (%)	0	0.5	1.5	7	3	6	4	2
Soil C 0-10cm (mg/g)	67.52	61.25	55.68	55.72	64.07	70.23	55.42	36.64
Soil C 10-20cm (mg/g)	40.24	39.13	47.00	42.43	42.26	42.90	33.31	38.45
Soil C 20-30cm (mg/g)	30.62	37.75	49.59	35.84	30.90	36.19	28.12	22.75
Soil C average 0-30cm (mg/g)	46.13	46.04	50.76	44.66	45.74	49.77	38.95	32.62
Soil N 0-10cm (mg/g)	4.25	3.97	2.83	2.13	2.63	2.93	1.90	1.67
Soil N 10-20cm (mg/g)	2.95	3.38	2.86	1.71	1.79	1.87	1.46	1.79
Soil N 20-30cm (mg/g)	3.16	3.22	2.54	1.70	1.37	1.39	1.22	1.23
Soil N average 0-30cm (mg/g)	**3.46**	**3.52**	**2.74**	**1.84**	**1.93**	**2.06**	**1.53**	**1.56**
Soil C:N 0-10cm	15.85	15.41	19.65	26.12	24.28	23.95	29.13	21.82
Soil C:N 10-20cm	13.60	11.57	16.38	24.75	23.53	22.85	22.75	21.42
Soil C:N 20-30cm	9.67	11.70	19.49	21.05	22.53	26.00	22.90	18.48
Soil C:N average 0-30cm	13.04	12.89	18.51	23.98	23.45	24.27	24.93	20.57
Soil P 0-30cm (mg/g)	0.39	0.27	0.30	0.19	0.22	0.19	0.18	0.18
Soil C:P 0-30cm	117.13	167.43	167.26	234.81	204.20	251.30	206.95	178.40
Soil N:P 0-30cm	0.0003	0.0002	0.0002	8.1E-05	0.0001	7.9E-05	9.1E-05	0.0001

Chapter 4

Ecoclinal trends in productivity and decomposition of *Chionochloa pallens* across an altitudinal gradient and implications for carbon sequestration

Chionochloa pallens on Mount Mangaweka (June, 2012)

Māori proverb

"*He kura kāinga e hokia; he kura tangata e kore e hokia.*"

"The treasure of the land will persist; human possessions will not."

(in Brougham *et al*., 2005)

Abstract

Recent and projected alterations in Earth's climate have raised concerns about impacts on biological processes, especially those pertaining to carbon (C) cycling and sequestration. Ecoclinal differentiation of *Chionochloa* species can occur across altitudinal gradients, allowing assessment of the influence of climate on genotypic and phenotypic responses of these species to changes in climate. The plasticity of plant responses to alterations in abiotic conditions are still governed, to some degree, by underlying genetics; however it is expected that climate change will influence terrestrial C and nutrient cycling because of alterations to productivity and decomposition. Productivity and decomposition of *Chionochloa pallens*' tissues were investigated via full-reciprocal translocation across five plots incrementally spaced every ≈100m in altitude on Mount Mangaweka, Ruahine Range, NZ. Productivity costs of transplanting, measured against home site transplants, averaged 41.6%. Productivity, expressed per tiller, per gram or per plant, of *in situ C. pallens* declined with increasing altitude and plants of lower plots had 135.6% greater productivity than upper plots (P<0.05). Average productivity of *C. pallens* transplants differed based on location of transplant origin (P<0.001) and destination (P<0.001); however no interactions were detected. The greatest productivity with respect to translocation was observed when *C. pallens* was transplanted to the lowest plot across the altitudinal gradient. Productivity based on transplant origin most regression slopes increased with altitude compared to transplants based on destination, indicating plasticity of responses in *C. pallens*' productivity across the gradient. Decomposition of *C. pallens'* leaf litter based on plot of origin did not differ between plots within years; however, based on plot of destination, the two lowest plots (1 & 2) had 1.3 times greater mass loss (g/g) than the uppermost plot (P<0.001) after 2 years of decomposition. The alterations to productivity and decomposition support the notion that phenotypic and ecoclinal variation to alterations in climate occurs across the altitudinal gradient and climate change may impact *C. pallens*' C sequestration. The ratio of aboveground productivity to decomposition (P:D ratio) of *C. pallens* indicates transplant destination is more important than origin of plants and litter. It appears as though climate change will alter these interactions and result with increased P:D ratios. Alterations to environmental conditions associated with climate change appear to positively impact *C. pallens'* productivity and decomposition, and will ultimately result in more endogenous C sequestration occurring for *C. pallens*.

Key words: mid-ribbed snow tussock, montane, temperate grassland, ecocline, plasticity

Introduction

Earth's terrestrial, aquatic, geologic and atmospheric processes are highly influenced by climate. These processes are highly complex and interrelated, where alterations to one or more components can result in repercussions throughout biogeochemical cycles. Changes in Earth's climate is being exacerbated by the elevated and ever increasing concentration of carbon dioxide (CO_2) as well as other greenhouse gases (GHGs) in Earth's atmosphere. There has been international and intergovernmental advocacy to limit the increase of global average surface temperatures by 2^oC, compared to pre-industrial levels, (Vautard *et al*., 2014) by reducing GHG emissions. These levels are based off evidence presented from the 2nd Assessment Report by the Intergovernmental Panel on Climate Change (IPCC, 1995).

The highest ever recording of atmospheric CO_2 concentrations occurred in March 2014 at Mauna Loa, HI, USA reaching 400ppm (NASA, 2014; NOAA, 2014a). Global average temperature recordings in 2014 also reveal Earth has experienced some of its warmest months on record (i.e. May, June, August and September; NOAA, 2014b). The strong correlation between increasing atmospheric CO_2 concentrations and increasing global temperatures is well known. This was brought to heightened attention through Mann *et al.* (1998)'s analysis of global temperatures and climate forcing over six centuries, with a single graph often referred to as "the hockey stick". Earth System Models following this have predicted with high confidence that, within the 21st century, positive feedbacks between climate and the carbon (C) cycle will increase. This elevated atmospheric CO_2 will alter terrestrial and oceanic C sinks (IPCC, 2013). The resulting changes to climate via alterations in temperatures and precipitation patterns (both of which are strong determinants of biological processes), will have strong impacts on ecosystems across the planet. Consequently, C sequestration has become a key concept for climate change mitigation.

High latitude and altitude regions are predicted to be most affected by climate change according to most global circulation models (IPCC, 2007). Approximately one quarter of Earth's terrestrial surface is composed of mountains (Barthlott *et al*., 1996), the vegetation of which is especially

threatened by climate change (Pauli *et al*., 1996; Körner, 1999; Theurillat & Guisan, 2001; Beniston, 2003; Gonzalo-Turpin & Hazard, 2009 and references therein; La Sorte & Jetz, 2010) owing to montane vegetation's high vulnerability to alterations in abiotic conditions (Beniston, 2003). The adaptive potential of montane plant species to adjust to alterations in climate is uncertain (Byars *et al*., 2007). The long term consequence from climate change may be shifts in range limits of such vegetation (Lenoir *et al*. 2008). Understanding species' limits, distributions and physiological limitations across montane topographical gradients is essential for predicting species' responses to climate change (Violle *et al*., 2007; Eckhart *et al*., 2011 and references therein).

Across montane gradients stress is typically greater at high elevations than at lower elevations (Callaway *et al*., 2002). Temperature is a primary factor that changes with altitude on mountains, resulting in mean annual lapse rates ranging from 0.55 – 0.65^{o}C (Rolland, 2003 and references therein) and precipitation often increases with elevation. Increased precipitation yields increases in productivity (Wu *et al.*, 2014) and decomposition (Murphy *et al.*, 1998), as well as increases in temperature results in increased productivity (Halloy and Mark, 2003) and decomposition (Sundqvist *et al*., 2011a; 2011b) across altitudinal gradients. A consequence of temperature and precipitation gradients is formation of adaptive plant forms either as ecoclines or even ecotypes (Warren *et al*., 2006; Liancourt et al., 2013). This makes montane regions ideal locations for exploration of adaptive differentiation owing to their steep environmental gradients (Gonzalo-Turpin & Hazard, 2009). Climate change may shift selective pressures on local variation of plant species' characteristics across altitudinal gradients. Local variation can arise from differing environmental effects on phenotypic variation (or underlying genetic variation). Regardless of the type of variation that occurs, alterations in climate across gradients can affect ecosystem functioning.

Changes in climate may disrupt the current balances of soil carbon cycling, storage and sequestration in terrestrial environments (Tate, 1992). Carbon sequestration is an important process of the C cycle and one of the most important concepts in studies of climate change (Krna & Rapson,

2013). This process may play a vital role in mitigating the effects of elevated atmospheric CO_2 concentrations and the impending threats of climate change (Lal, 2004a and references therein). To stress its importance, the global soil C pool (2500 Gt) is approximately 3.3 and 4.5 times larger than the atmospheric and biotic C pools respectively (Lal, 2004b). Endogenous C sequestration occurs when non-temporarily utilized biologic C fixed from the atmosphere is greater than the release of C within a specified system over a defined time period (Krna & Rapson, 2013). Soil C sequestration is determined by abiotic factors (topography, mineralogy and texture) and by living organisms and their interactions with different climate factors (De Deyn *et al*., 2008) which are likely to change across altitudinal gradients.

Montane gradients can influence ecosystem processes (Callaway *et al*., 2002; Körner, 2007) such as plant productivity (Sundqvist *et al*., 2013) and litter decomposition (Zhu *et al*., 2012), ultimately influencing biogeochemical cycling (Bardgett *et al*., 2013) and C sequestration (Ward *et al*., 2014). The aim of this research is to interlink these processes and endogenous C sequestration along an altitudinal gradient, with an assumed 0.6^{o}C/100m altitudinal mean annual lapse rate (Halloy and Mark, 2003 and references therein), as a proxy for climate change. The use of a long lived perennial species, demonstrating differences in growth forms and possibly ecotypic differentiation across its montane altitudinal range, allows for better assessment of climate change impacts across the gradient.

Ecotypic differentiation and ecoclines occur with plant species of montane environments owing to local genetic variation and adaption to environmental conditions across species' altitude ranges (Byars *et al*., 2007; Eckhart *et al*., 2004), and responses by different eco-forms across these gradients is an important factor to consider when predicting alterations to biological processes resulting from climate change (Laincourt *et al*., 2013). One means of testing ecoclinal differences is through the use of reciprocal transplantation experiments to determine how environmental conditions and genotypes interact on phenotypic responses of plants (Bennington *et al*., 2012 and references therein). Such effects have long been documented and studied via transplantation experiments dating back to the late 1800's

(Turesson, 1922 and references therein) and are still being used in field experiments today (Grassein *et al*., 2014; Read *et al*., 2014; Souther *et al*., 2014).

Above the New Zealand treeline resides a belt of vegetation often dominated by tussock or bunch grasses of the genus *Chionochloa* (Mark, 2012). Reciprocal transplant experiments with *Chionochloa* species across altitudinal gradients in New Zealand have been used to investigate ecoclinal alterations in growth (Mark, 1965a; Mark 1965b; Mark, 1965c). Since ecoclinal plant populations may perceive and respond to alterations in environmental conditions differently, and may express differences in productivity, changes in climate will likely influence their physiological responses and influence rates of litter decomposition and C sequestration.

In this experiment, a full reciprocal translocation was performed to assess the productivity, decomposition and endogenous C sequestration of *Chionochloa pallens* over 2 years, across 5 plots incrementally spaced approximately every 100m in elevation on Mount Mangaweka, Ruahine Forest Park, Central North Island, New Zealand. Regression analysis was used to examine the environmental influence and plasticity of a potential ecoclinally differentiated population of *C. pallens*, to assess differences in productivity and litter decomposition arising from alterations in environmental characteristics across the gradient. *In situ* productivity and home plot decomposition of *C. pallens* were compared with a full-reciprocal translocation of plants and litter decomposition bags based on locations they originated from and locations they were translocated to across the 5 plots. This was performed as a means investigate how alterations in climate influence productivity, decomposition and C sequestration.

Endogenous C sequestration is considered to occur "when C fixed from the atmosphere into stores is greater than the release of C to the atmosphere, over a specified time period (minimally annual, due to high within-system variability) and within a specified system" (Krna & Rapson, 2013). A modified version of Krna & Rapson's (2013) $F_{(as)}/R_{(as)}$ equation (i.e. Fixation to Release ratio over an annual time period within a specified system) was used with the productivity to decomposition ratio (P:D ratio) of

C. pallens to investigate how endogenous C sequestration in New Zealand's tussock grasslands may be impacted with climate change.

Questions (Q) and Hypotheses (H)

Background: Leaf elongation and dieback of *Chionochloa* species varies across altitudinal gradients in New Zealand's tussock grasslands (Mark, 1965a), indicating productivity of *Chionochloa* species varies across altitudinal gradients.

Q1: How will productivity of *in situ C. pallens* plants differ along the altitudinal gradient and how will translocation of plants across the gradient influence shifts in productivity and what will this reveal about its plasticity?

H1: The productivity of *in situ C. pallens'* plants will decrease with increasing altitude, translocations will yield increases in productivity when higher altitude plant populations are transplanted to lower altitudes, and reductions in productivity after translocation to higher altitudes. The responses of *C. pallens* at the extremes of the gradient will express the greatest changes in productivity and be most plastic in response to transplantation into different environments.

Background: The decomposition of plant litter can vary along altitudinal gradients (Murphy *et al.*, 1998; Zhu *et al*., 2012) where mass loss can be influenced across temperature (Walsey *et al*., 2006) and precipitation gradients (Sundqvist *et al.*, 2011a; 2011b; 2013), such as occurs across altitudinal gradients in New Zealand montane systems.

Q2: How will the mass loss of *C. pallens'* litter following decomposition after translocation across the altitudinal gradient be altered and will litter origin or destination have a greater impact on mass loss?

H2: The decomposition of *C. pallens*' litter originating from upper altitude plots will have lower mass loss compared to lower altitude plots. Decomposition based on litter destination to higher altitude plots will have lower mass loss compared to

lower altitude plots. Litter destination will have a greater impact on mass loss than origin of litter as decomposition is primarily climate driven.

Background: Climate change will likely influence plant producitivity, litter decomposition, C and nutrient cycling and ultimately C sequestration. The findings of experiments on *Chionochloa rubra* from Mount Tongariro (Chapter 3) indicate a decrease in P:D ratios with increasing altitude and that productivity was the more prominent driver of the P:D ratios than decomposition.

Q3: How will alterations to *C. pallens'* productivity and decomposition following translocation along the altitudinal gradient influence the P:D ratioss and what implications will this have for endogenous C sequestration with projected climate change scenarios?

H3: There will be a reduction in the P:D ratios with increasing altitude and the alterations in *C. pallens'* productivity will be more pronounced than decomposition and be the primary driver of the P:D ratios, and the P:D ratios will be lowest at higher altitude plots indicating less productivity will be needed per unit decomposition for endogenous C sequestration. Projected warming associated with climate change will increase *C. pallens*' P:D ratios and thus more C should be retained within the system.

Methods

Site description

The Ruahine Range is a non-volcanic mountain range of New Zealand's Central North Island, spanning 110km northeast – southwest from inland Hawke's Bay region to the Manawatu Gorge. The basement geology and landforms of the Hikurangi Range (a range within the Ruahine Range) are described as "undulating and dissected greywacke terrain" (Rogers and McGlone, 1989). The location chosen for this experiment was on Mount Mangaweka (1731m, the highest point of the Hikurangi and Ruahine Ranges) in Ruahine Forest Park. Treeline is at approximately 1320m in

elevation where scrubland transitions into tussock grasslands which span bioclimatic zones from cool temperate to subalpine (Körner *et al*., 2011), up to the summit of the range.

In March 2011, five plots (30 x 20m) were established on Mount Mangaweka; plots were incrementally spaced approximately every 100m in elevation. To achieve plots with similar slopes and aspects, they were positioned along the south face of the ridgeline leading from Purity Hut to Wooden Peg, though Plot 5 (the uppermost plot) was located near the summit. All plots were located at least 5m to the south of the Purity Hut Track (Plots 1-4) and the uppermost plot (Plot 5) was located 12m vertically below the summit of Mount Mangaweka's south face (Figure 1).

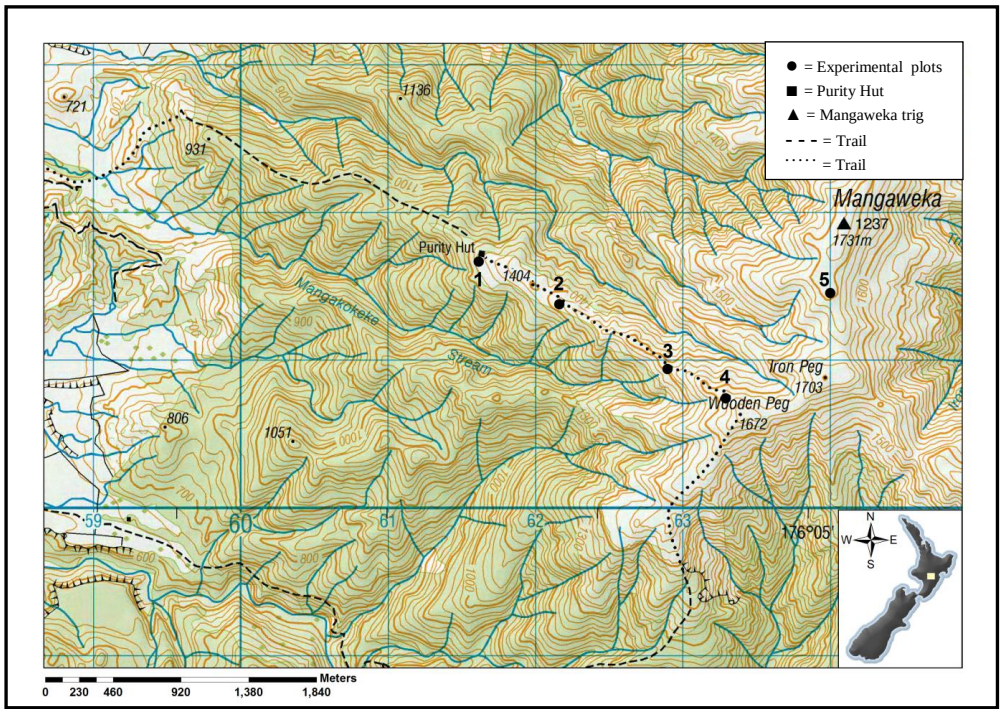

Figure 1: Topographic map (map source = LINZ 1:50 000, sheet number BK36, datum = D_WGS_1984) across five experimental plots, incrementally spaced every ≈100m in elevation, on Mount Mangaweka (yellow box within inset map of New Zealand shows general location of Ruahine Forest Park).

Species' description

Chionochloa pallens Zotov (1963) subsp. *pallens* is one of the most widely distributed tussock-grass species in New Zealand and is present in montane regions across both the North and South Islands of New Zealand (Connor, 1991). On the North Island, its distribution is on mountain ranges from Raukumara Range southward (Connor, 1991; Mark, 2012) through the Ruahine and Tararua Ranges and it is classified as having a low alpine

altitudinal range of 1100 – 1800m (Mark, 2012). A detailed floristic description of *C. pallens* is provided by Connor (1991). Owing to the usually prominent yellow midrib (giving *C. pallens* its yellowish hue) on the lamina's abaxial surface, *C. pallens* is commonly known as the "mid-ribbed snow tussock" (Connor, 1991). On Mount Mangaweka the percent coverage of *C. pallens* plants and surface leaf litter ranges from 74.5 to 40.5% and 0.8 to 2.5% respectively (Table 1). It has apparent differences in growth forms across altitudinal gradients (Figure 2). No research has previously been performed that indicates ecotypic differentiation or presence of an ecocline with this species. The presence of ecoclinal variation within this species across an altitudinal gradient would allow for better extrapolation of impacts climate change may have on productivity, decomposition and C sequestration.

Table 1: Percent coverage of *Chionochloa pallens* plants and litter across the 5 plots, incrementally spaced every ≈100m in elevation, on Mount Mangaweka.

	Plot 1	Plot 2	Plot 3	Plot 4	Plot 5
Altitude (m)	1325	1420	1520	1622	1719
C. pallens plant cover (%)	49.5	40.5	36.5	74.5	46.0
C. pallens litter cover (%)	2.5	0.8	0.8	4.0	2.0

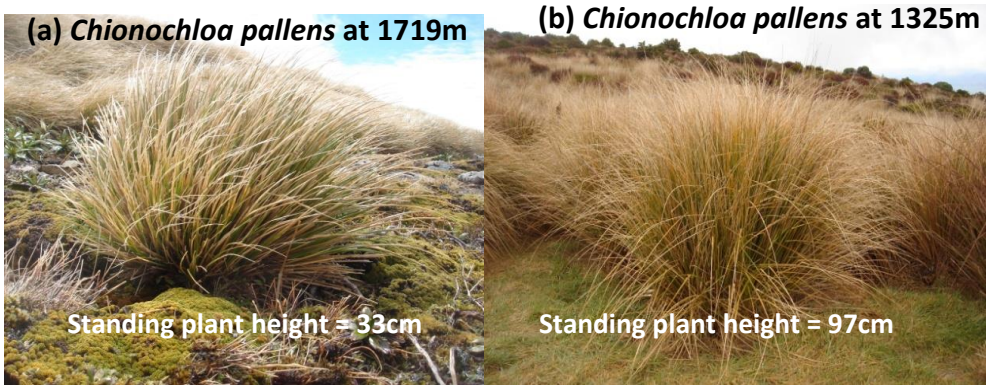

Figure 2: Images of *Chionochloa pallens* growing *in situ* at (a) Plot 5 (altitude = 1719m) and (b) Plot 1 (altitude = 1325m) depicting differences in growth forms at both ends of its altitudinal range on Mount Mangaweka.

Soil properties

Soil cores (2.8cm diameter; n=6) were randomly collected to 30cm in depth from locations just outside each plot in November 2012, following methods described in Allen *et al*. (1989). These soil cores were divided into 10cm segments (at 0-10, 10-20 and 20-30cm depths below the soil surface)

in the field, and transported to Massey University and stored in a freezer at -20°C. The 10cm soil core segments were bulked, broken up and dried at 60°C for 168hr and constant biomass was obtained. After drying, soils were sieved to 2mm to remove roots and then finely ground with a mortar and pestle, prior to C and nutrient content (mg/g) analyses. Carbon and N content of soil samples (0-10, 10-20 and 20-30cm depths) was performed using flash combustion analysis with a Leco furnace (Laboratory Equipment Corporation, St Joseph, Michigan, USA) and soil phosphorous (P) analyses (0-30cm) were performed following the Kjeldahl method at Landcare Research, Palmerston North, New Zealand.

Soil bulk density (Db) samples (n = 4) were obtained at 10, 20 and 30cm below the soil surface with soil bulk density rings (4.7cm diameter, 2.0cm height, 34.7cm^3 volume) at 4 locations just outside each of the 5 experimental plots. Samples were individually placed into labelled zip-lock bags, transported to Massey University and promptly stored at -20°C prior to weighing. After thawing, field moist soils were weighed and then dried at 60°C for 168hrs until constant biomass was obtained and recorded. Soil bulk density was calculated for tonnes per hectare (t/ha) as was C, N and P across the 3 soil depths.

Productivity

Productivity of *C. pallens* populations and their responses to translocation across the gradient were investigated on *in situ* and experimental transplants. Transplants were randomly selected within plots of origin, and were excavated with spades to collect approximately 7225cm^3 (17cm x 17cm x 25cm deep) of roots and surrounding soil. Transplants were transported in nylon bags to plots and replanted in holes created from earlier tussock excavations. Existing holes were reused to minimize disturbance and could be considered to be, microsite-wise, appropriate locations for transplants. This resulted in six treatments per plot (*in situ* plants , home plot transplants and transplants from the four other plots; n = 6).

Productivity was examined on two to five randomly selected vegetative tillers of all *in situ* and transplanted *C. pallens* plants at each plot (treatments = 6 per plot; 6 replicate plants per treatment). In early November

2011, monitored tillers of experimental plants were marked with coloured paperclips and young leaves from each tiller were marked with a corresponding coloured loop made from plastic-coated wire 1mm wide. Lamina lengths (i.e. the leaf above the ligule) of live and dead portions of each monitored tiller were measured from the ligule. If young leaves had not developed a ligule, then the ligule from the next oldest leaf was used for determining lamina lengths. The number of tillers and inflorescences per plant was also monitored. Tillers that were grazed, died or became reproductive during the course of the experiment were omitted from subsequent analyses. Leaf elongation, dieback, tip-loss and leaf loss were calculated between the six sequential census dates, since transitions of a blade of grass are assumed to sequentially pass through these phases. For the final analysis, censuses were combined to form 1 biennial time period (early November 2011 to late October 2013) to assess productivity of *C. pallens* over as long a period as possible.

In late October 2013, the final census date, the marked tillers were harvested from the field (i.e., cut at base of tiller, just above the roots), bagged intact and stored at -20^{0}C. After thawing, leaves were classified into age classes based on order of leaf emergence, and were measured and separated into segments of live tissue, dead tissue and sheaths prior to being dried at 60^{0}C for 72hrs and weighed (Figure 3). For *in situ* and transplanted *C. pallens* experimental plants, lengths and weights of live and dead leaf portions were used to derive power function equations ($y = ax^b$) for length to biomass conversions for each leaf age class of each treatment. Power functions can fit regression lines to linear, curvilinear and/or exponential data without providing negative values and are commonly used with growth and decay data (Prof. Ian Henderson, pers. com.). Analysis of Variance (ANOVA) was used on the *a*- and *b*-values of the power functions to determine significant differences between leaf age classes according to the plots of origin of transplants, and of plots which of destinations for transplants. For sheaths, live and dead leaf segments, plots of origin had different b-values at the $P<0.08$ level and therefore plots of origin were used for length to biomass transformations for all censuses (note: no significant differences were found for *a*-values; data not shown). Leaves were also

grouped into 3 categories (A = youngest, B = 2nd and 3rd youngest, and C = all older leaves) because of lack of significant variation within these categories in terms of a- and b-values. The power functions were then used in a macro created in Microsoft Excel© to convert the lengths of live and dead laminae and sheaths from each census into biomass equivalents. Tip-loss, dieback and leaf elongation between census dates were then used to calculate productivity. Productivity at each plot was assessed as averages over the two years, expressed per tiller, per whole plant (multiplying average tiller productivity by the number of tillers at each census date) and as relative growth rate of each tiller (RGR; average annual tiller productivity divided by the biomass of the final harvested tiller).

Figure 3: *Chionochloa pallens*' leaves from 1 tiller (originating from Plot 3; 1520m in elevation) and newly produced tillers (bases not in line with vertical ruler) organized by emergence from oldest to youngest (top to bottom) prior to length measurements, drying and weighing of living and dead portions used for biomass transformations.

Linear mixed effect models (LMEs) were used to determine significant differences in the mean biennial productivity per tiller, per plant (multiplying by tiller number) and RGR (dividing by tiller weight) for *in situ* and translocated *C. pallens* plants using the lme procedure in the nlme package (by Pinheiro *et al*., 2014) in R (R Core Development Team, 2010). LMEs were utilized because of the fixed effects (productivity dependent on altitude), the levels of nesting (plant > tiller > census date) and temporal pseudoreplication of the random effects within the experimental design. Significant differences ($P \leq 0.05$) were determined using Tukey's HSD

(Honest Significant Difference) posthoc test using the HSD.test function in the agricolae package (De Mendiburu, 2014) in R (R Core Development Team, 2010).

Decomposition

Decomposition of *C. pallens'* leaf litter and roots were examined via full reciprocal litter bag translocation experiments across the five plots, in October 2011. For leaf litter decomposition, the youngest-most-completely-dead leaves of *C. pallens* were cut from living, non-experimental plants at each of the five plots for use in decomposition treatments. Live roots of *C. pallens* were collected by excavating plants similar to experimental plants, cleaning roots free of soil and other organic materials and drying roots with paper towels. Litter was bulked per site, then sub-samples were formed into replicates, six of which were used for calculating the average fresh-to-oven-dry-weight differences for conversions of litter that was placed to decompose in the field (i.e. litter that did not undergo decomposition treatments in the field; "initial litter" henceforth). Roots and leaf litter for decomposition treatments were cut into 5cm lengths and 3.00g of each were then placed into a decomposition bag (20 x 25cm) made of black-nylon mesh with 2mm pore size. A total of 675 leaf litter bags were made for a full-reciprocal translocation across the 5 plots with 6 replicates for placement on bare ground or low-lying vegetation ("surface-plated", henceforth) and 3 replicates for placement 5cm below the soil surface ("buried", henceforth), with 3 collection periods. A total of 225 root decomposition bags were made for a full-reciprocal translocation across the 5 plots with 3 replicates for placement 5cm below the soil surface with 3 annual collection periods. Note, only 2 annual collections of decomposition bags has been performed to date, as the final collection is still undergoing treatment in the field and is to be collected after 4 years.

In October 2011, within randomly selected inter-tussock spaces, decomposition bags were plated out and secured to the ground. Annual collections of decomposition bags occurred in October of 2012 and 2013 and bags were promptly stored at -20^{0}C. After thawing in small subsets, litter from each bag was sorted to remove soil and non-*Chionochloa* plant

material. Litter was then dried at 60°C for 72hrs, weighed, and mass loss calculated. Decomposition is expressed as average mass loss (g/g).

A Four-Way Analysis of Variance (ANOVA) was used to examine decomposition interactions with litter origin, litter destination, time and depth for surface-platted litter and buried litter. Three-Way ANOVAs were used to determine significant differences in decomposition for *C. pallens* surface-platted litter, buried litter and roots to assess interactions of litter origin, litter destination and time on the mass loss as a function of plot location. Two-way ANOVAs were used to determine plot and year differences and interactions for the mass loss for home plot, litter origin and litter destination decomposition treatments. Student's t-test were used to compare differences between lowest and uppermost plots for mass loss, under surface decomposition treatments, based on plot of litter origin, destination and home plot mass loss across both years of decomposition in the field, as the two ends of the gradient expressed the greatest differences in decomposition. Tukey's HSD post-hoc test was used to determine differences at the $P \leq 0.05$ level using the HSD-test function in the agricolae package (De Mendiburu, 2012) in R (R Core Development Team, 2010).

Productivity to Decomposition Ratio

To further assess relationships and interactions of productivity and decomposition across the gradient, the P:D ratios were calculated for the 5 plots using the ideology of the C fixation to release equation for endogenous C sequestration from Krna & Rapson (2013). The C fixation is expressed as productivity (g) over 2 years and C release is expressed as mass loss (g) after 2 years of decomposition. In this experiment, P:D ratios were obtained from all combinations of treatments from the full reciprocal translocation of living plants and surface leaf litter of *C. pallens* using three different means of expressing productivity (per tiller, per plant and RGR). As references for the physical impacts of transplocation, the P:D ratios of *in situ C. pallens* plants were obtained using averages of *in situ* plant productivity to corresponding home-site surface litter decomposition treatments. The P:D ratios of transplanted *C. pallens* plants were obtained using averages of productivity per plot as a ratio of corresponding transplanted surface litter

decomposition treatments from full reciprocal translocation along the altitudinal gradient. The P:D ratios of transplants were analysed based on plant and litter origin (i.e. plots they originated from) and destination (i.e. plots they were translocated to). Regression analysis was performed with the anova-function in R (R Core Development Team, 2010) for fitting polynomial regression models of 1st and 2nd order to determine if the slopes of the P:D ratios across the plots were linear or curvilinear. Second order polynomials did not provide significantly better fits to the data (allowing for decreased degrees of freedom) compared with 1st order polynomials and thus 1st order linear regression lines were used.

Downslope P:D ratio comparisons

The P:D ratios of home plot and downslope transplants were used for comparisons across an assumed mean annual lapse rate of 0.6^{o}C per 100m across the 400m altitudinal gradient. Regression analysis was performed by plotting the P:D ratios of home plot (0^{o}C temperature change) and downslope transplants (ranging from 0.6 to 2.4^{o}C temperature change) against lapse rate temperature changes across the gradient. This was performed to assess how alterations in temperature under predicted climate change scenarios will influence the interactions of *C. pallens*' productivity and decomposition, and its C sequestration potential across the gradient.

Results

Soil Properties

Soil C, N and P concentrations (mg/g) decreased with increasing soil depth and increasing elevation (Table 2). Soil C ranged from 87.4 to 227.4mg/g at 20-30cm in soil depth at Plot 5 and the upper 10cm of soil at plot 1 respectively. Soil N ranged from 5.2 to 12.2mg/g at 20-30cm in soil depth at Plot 5 and the upper 10cm of soil at plot 1 respectively. Soil P ranged from 0.43 to 0.96mg/g at 20-30cm in soil depth at Plot 5 and the 10-20cm depth of soil at plot 1 respectively. Soil C:N increased with depth but decreased with increasing altitude and ranged from 16.4 to 21.8. Soil C:P tended to decrease with soil depth and was greatest at Plots 3 and 4, and ranged from 152.5 to 279.8. Soil N:P tended to decrease with soil depth and

Plot 3 had the greatest N:P; the N:P across the plots ranged from 15.2 to 8.1, being highest at the top 10cm depth at Plot 3 and lowest at the 20-30cm depth of Plot 1. Soil bulk density increased with soil depth and altitude (data not shown), however no detectable trends were observed with soil depth or altitude for the calculated C, N, P t/ha (Appendix 1).

Table 2: Soil carbon (C), nitrogen (N) and phosphorous (P) concentrations (mg/g; n = 1) and ratios at 10cm soil depths across the 5 plots incrementally spaced ≈100m in elevation on Mount Mangaweka.

Plot	Altitude (m)	Soil depth (cm)	C (mg/g)	N (mg/g)	P (mg/g)	C:N	C:P	N:P
1	1325	0.0 – 10.0	227.36	12.21	0.93	18.62	244.47	13.13
		10.1 – 20.0	174.91	8.96	0.96	19.52	182.20	9.33
		20.1 – 30.0	149.12	6.84	0.85	21.80	175.44	8.05
2	1420	0.0 – 10.0	181.80	10.55	0.82	17.23	221.71	12.87
		10.1 – 20.0	140.54	8.10	0.76	17.35	184.92	10.66
		20.1 – 30.0	110.91	6.15	0.73	18.03	151.93	8.42
3	1520	0.0 – 10.0	200.92	11.37	0.75	17.67	267.89	15.16
		10.1 – 20.0	159.41	8.61	0.57	18.51	279.67	15.11
		20.1 – 30.0	148.18	7.56	0.56	19.60	264.61	13.50
4	1622	0.0 – 10.0	199.85	11.25	0.78	17.76	256.22	14.42
		10.1 – 20.0	152.59	8.21	0.59	18.59	258.63	13.92
		20.1 – 30.0	145.96	7.80	0.62	18.71	235.42	12.58
5	1719	0.0 – 10.0	138.06	8.4	0.73	16.44	189.12	11.51
		10.1 – 20.0	94.73	5.73	0.51	16.53	185.75	11.24
		20.1 – 30.0	87.39	5.24	0.43	16.68	203.23	12.19

Productivity

Productivity was greatest at lower sites. Average productivity on a per tiller basis of *in situ C. pallens* plants from Plots 1 and 2 was 184.1 and 135.6% greater respectively than for upper plots (P<0.05; Figure 4a; Appendix 2). From comparison of biannual averages of *in situ* and home plot transplants of *C. pallens* plants, transplantation reduces productivity by 41.6%. Mean productivity on a per tiller basis of *C. pallens* transplants differed significantly based on plant origin (P<0.001) and destination (P<0.001); however no significant interactions were detected (Appendix 3).

Transplants tended to have the lowest productivity when transplants originated from the lowest plot (Figure 4b). On a per plant basis average

productivities of *in situ C. pallens* plants from Plots 1 and 2 were 316.1 and 234.2% greater respectively than upper plots ($P<0.05$; Figure 4c; Appendix 4). Mean productivity on a per plant basis of *C. pallens* transplants differed significantly based on plant origin ($P<0.001$) and destination ($P<0.001$); however no significant interactions were detected ($P>0.05$; Appendix 5). The average productivity on a per plant basis of the uppermost and lowest plots revealed the greatest variation of translocation based on origin and destination (Figure 4d). Average productivity based on RGR of *in situ C. pallens* plants did not differ between the five plots ($P>0.05$; Figure 4e; Appendix 6). However the trends were similar, with values for plots 1 and 2 being 59.4 and 94.9% greater respectively than the upper plots, and these plots, when used as destinations compared with origins, were significantly different (Fig 4f).Mean productivity based on per gram of harvested biomass of *C. pallens* transplants differed significantly based on origin ($P<0.001$) and destination ($P<0.01$); however no significant interactions were detected ($P>0.05$; Figure 4f; Appendix 7).

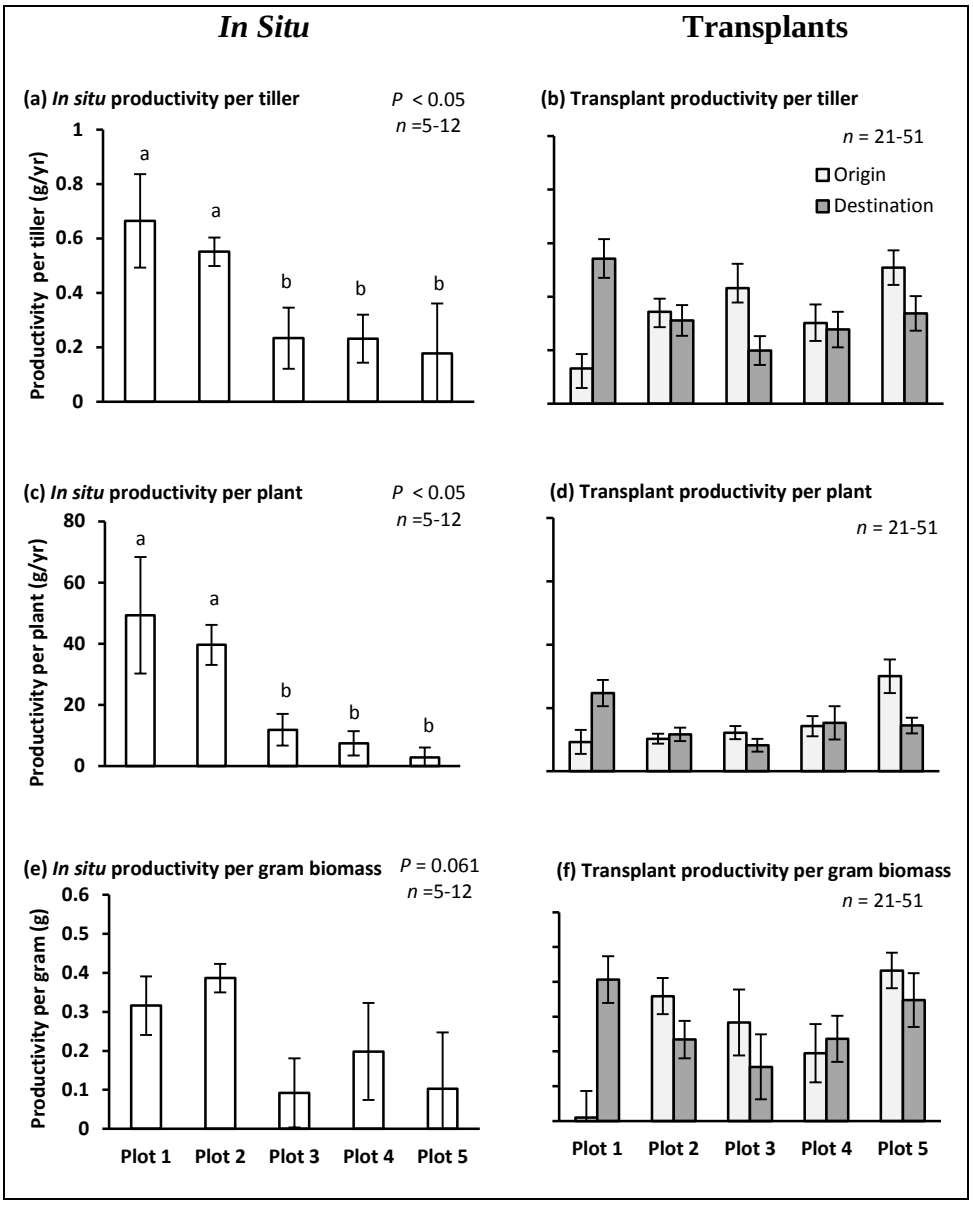

Figure 4: Average productivity per tiller (a,b), per plant (c,d), and per gram of harvest biomass (e,f) of *in situ* (white bars; column 1) and transplants from full-reciprocal translocation of *C. pallens* plants (light grey bars= data sorted by plant origin; dark grey bars= plant destination; column 2) across the five plots incrementally spaced every ≈100m in elevation on Mount Mangaweka. Error bars are SE, *n* refers to the number of tillers, and different letters denote significant differences at the $P \leq 0.05$ level.

Regression analysis of *in situ C. pallens* productivity expressed per tiller, per gram (RGR) and per plant reveals a decline with increasing altitude (Figure 5a-c). Regression lines of *in situ* productivity expressed per tiller and per plant provide better fits to data than per gram based on r^2 values (averaging 0.7739). A more detailed analysis of *C. pallens* following translocation across the altitudinal gradient reveals plot of origin to almost all have positive linear regression slopes, opposite to what was observed with trends found with *in situ C. pallens* plants (blue regression lines in Figure 5d-r). However, after translocation depicted by plot of destination, most (11 out of 15) regression lines are negative, similar to trends observed with *in situ C. pallens* plants (red regression lines in Figure 5d-r).

Based on comparisons of regression slopes of productivity after translocation, the location of transplant destination is 2.75 times more influential in shifting slope direction than the location of origin across the gradient. Negative slopes are observed with *in situ* plants, where as positive slopes are found based on transplant origin and both negative and positive slopes were observed with transplant destination. The down-slope translocation of *C. pallens* enhanced productivity and plants originating from the higher altitude plots had greater increases in productivity when translocated to lower altitudes.

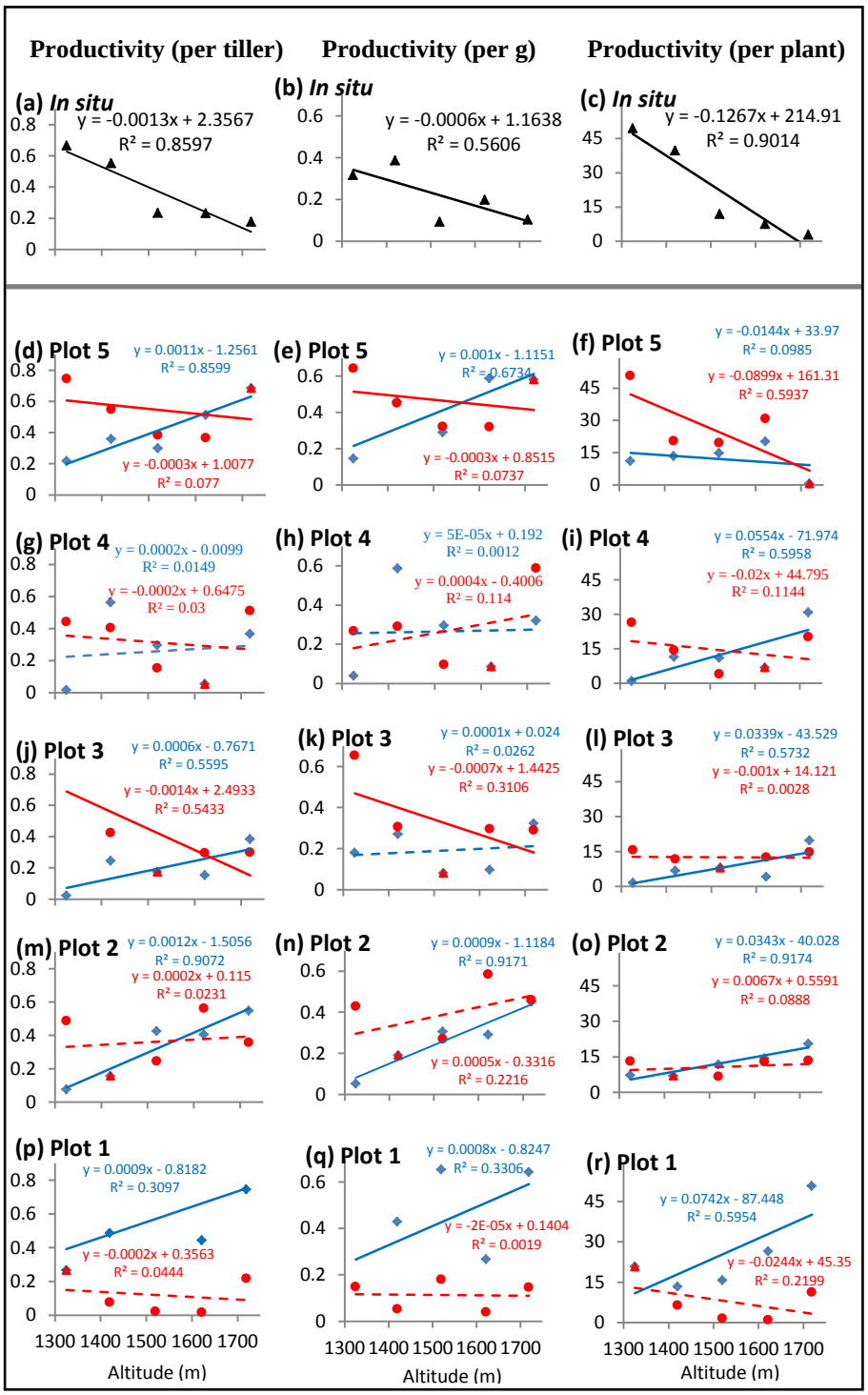

Figure 5: Mean productivity of *Chionochloa pallens* over 2 years expressed as averages per tiller (column 1), per gram of final harvest biomass (column 2), and per plant (column 3) of *in situ* and transplants following full-reciprocal translocation across 5 plots incrementally spaced ≈100m in elevation (*n* = 4-12). **Black** regression lines and data points are i*n situ* productivity (a-c). **Blue** regression lines and data points indicate transplants averaged over plot of origin **Red** regression lines and data points indicate transplants averaged over plot of destination. Regression lines with r^2 values<0.3 are dashed.

Decomposition

The full reciprocal translocation of *C. pallens* leaf litter under surface-plated and buried ("depth"; 5cm below soil surface) decomposition treatments (across the five plots on Mount Mangaweka over 2 years of decomposition) revealed significant differences in mass loss (g/g) between years ($P<0.001$) and between plots of translocation destination ($P<0.001$), and there was a slight interaction between years and placement of litter (on soil surface or buried; $P=0.06$; Appendix 8). Surface-platted litter decomposition revealed only plot location of litter destination and year to be significantly different ($P<0.001$); however the plot location from which litter originated was not significant, and no interactions were detected ($P>0.05$; Appendix 9).

Decomposition of *C. pallens* leaf litter on the surface revealed differences in plot ($P<0.01$) and year ($P<0.001$); however no interactions were observed ($P>0.05$; Figure 6a; Appendix 10). The home plot surface-platted decomposition across all five plots revealed no differences in mass loss of *C. pallens'* litter within years ($P > 0.05$; Figure 6a). However, comparison of the lowest and uppermost plots across both years showed Plot 1 to have 46.8% greater mass loss than Plot 5 ($P<0.05$; Appendix 11).

No treatment effects were observed with mass loss of surface-plated *C. pallens'* litter based on its origin, from the full reciprocal translocation, across both years ($P>0.05$), as, predictably, year 2 had a 52.4% greater mass loss than year 1 ($P<0.001$; Figure 6b; Appendix 12). There was no significant differences in mass loss based on litter origin between the lowest and uppermost plots ($P>0.05$; Appendix 13).

The mass loss of *C. pallen's* surface-plated litter based on plot of litter destination revealed no differences across treatments in the first year ($P > 0.05$; Figure 6c). However, after the second year of decomposition, the mass loss from the lowest plot was 25.3% greater than that for the upper three plots ($P < 0.05$), and mass loss of litter at Plot 2 was 35.9% greater than at Plot 5 ($P < 0.05$; Appendix 14). Comparing the mass loss based on plot of destination, the lowest and uppermost plots across both years showed Plot 1 to have 26.9% greater mass loss than Plot 5 ($P<0.01$; Appendix 15).

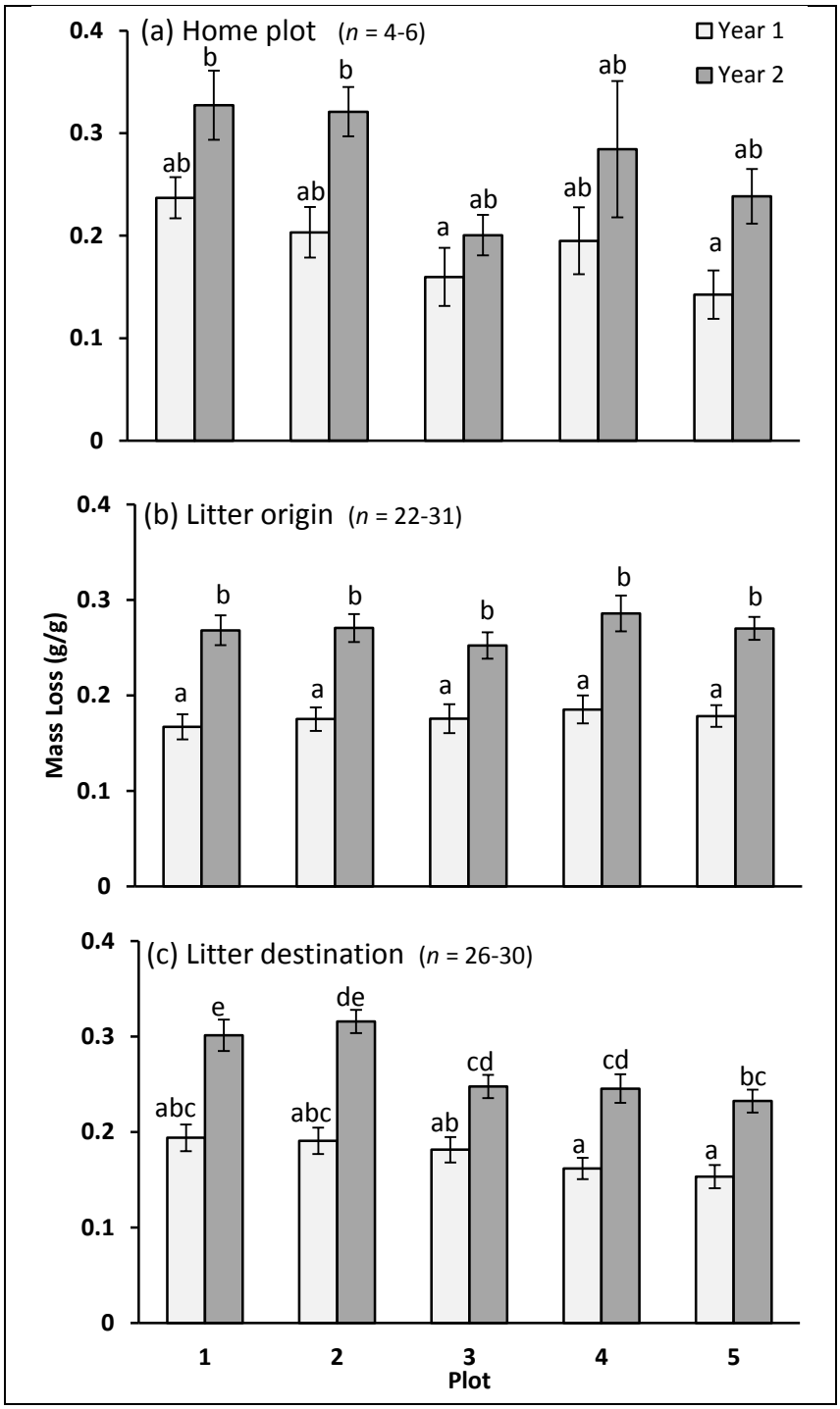

Figure 6: Mass loss (g/g) of *C. pallens'* leaf litter, under surface-plated decomposition treatments, after one and two years (light and dark grey respectively) of decomposition from full reciprocal translocation treatments across five plots (incrementally spaced every ≈100m in elevation) on Mount Mangaweka. Error bars are standard error and different letters represent significant differences at the $P \leq 0.05$ level.

Linear regression analyses of *C. pallens'* mass loss (g/g) after one and two years of surface-plated decomposition following full reciprocal translocation treatments across the five plots on Mount Mangaweka indicates the location of litter destination (i.e. environmental characteristics across plots) is 3.5 times more influential on decomposition rate than the location of litter origin (i.e. leaf litter characteristics across plots; Figure 7a-e; slope equations and r^2 values for linear regression are presented in Appendix 16). Regression analysis of mass loss based on litter origin revealed negative slopes over both years of decomposition in the field, significantly differed across all but one plot along the altitudinal gradient. Regression analysis of mass loss based on litter destination expressed a shift in direction of linear regression slopes from negative at the lowest plot (e.g. Fig 7e) to being positive at higher altitude plots (e.g. Fig 7a).

From regression analysis of mass loss of surface-plated litter after 2 years of decomposition; comparisons of regression slopes for home plot, location of origin and location of destination, shows that the location of litter destination is 10 times more influential in shifting slope direction than the location of origin across the gradient.

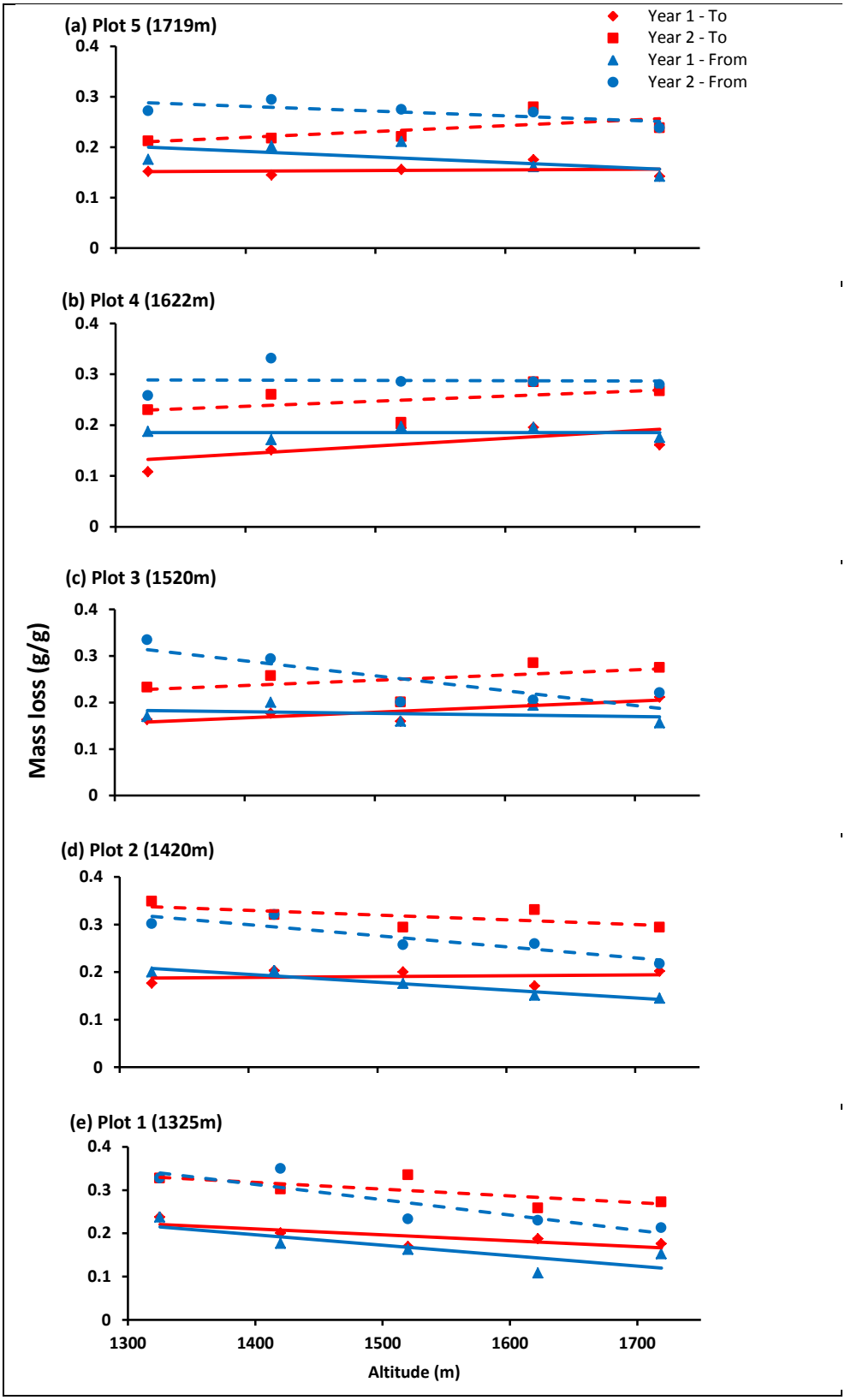

Figure 7: Mass loss (g/g) of *Chionochloa pallens* leaf litter, under surface decomposition treatments, after one and two years (solid and dashed lines respectively) of decomposition from full-reciprocal translocation (n = 4-7) across five plots incrementally spaced every ≈100m in elevation. **Blue** regression lines are mass loss based on plot of litter origin. **Red** regression lines are mass loss based on plot of litter destination. Slope equations and r^2 in Appendix 16.

Annual differences in mass loss of buried decomposition treatments of *C. pallens* leaf litter following full reciprocal translocation revealed the mass loss after two years of decomposition was 75.9% greater than one year (P<0.001; Appendix 17). No other treatment effects or interactions for buried decomposition were significant. The average mass loss of all buried decomposition treatments was 7.8% less and 6.6% more for years 1 and 2 compared with surface-plated decomposition treatments over these years.

Root mass loss under translocation treatments averaged 0.22g/g for both years 1 and 2. No differences or interactions were observed in mass loss for any of the root decomposition treatments across both years (P>0.05; Figure 8; Appendix 18).

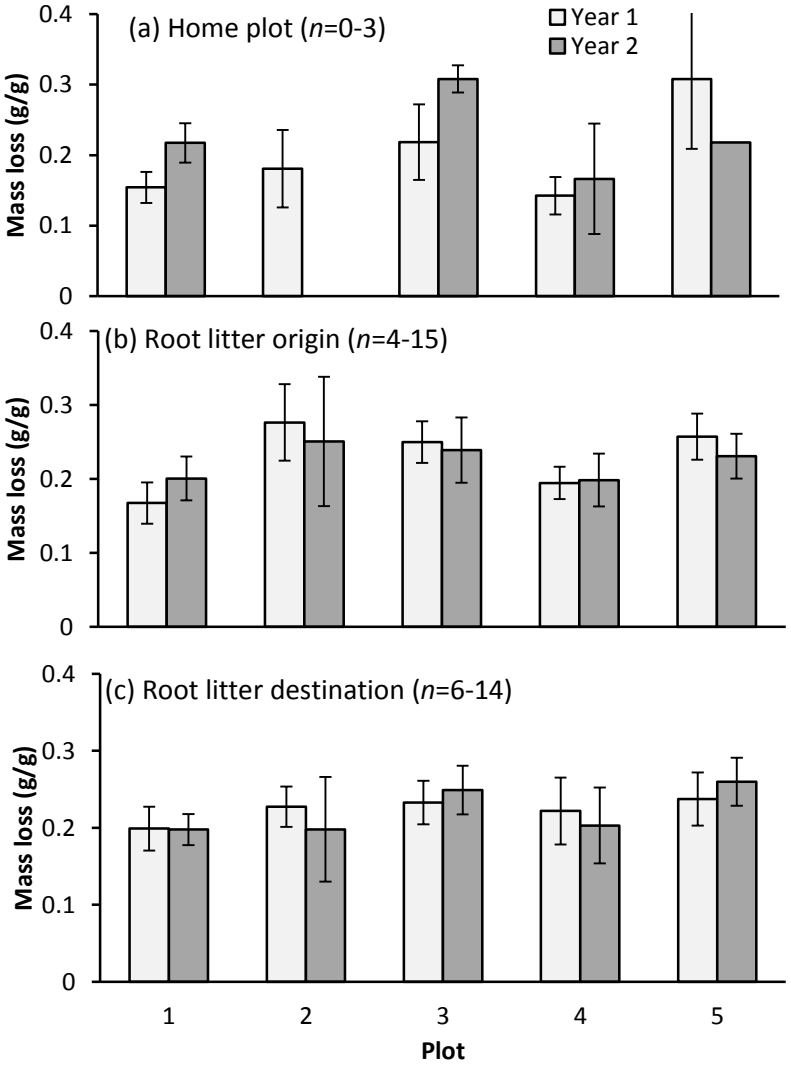

Figure 8: Mass loss (g/g) of *C. pallens*' root litter after one and two years of decomposition, white bars and grey bars respectively, following reciprocal translocation of across 5 plots incrementally spaced every ≈100m in elevation on Mount Mangaweka. Note: no home plot decomposition bags were obtained for year two at Plot 2.

Productivity to decomposition ratio

The P:D ratios of *in situ C. pallens* productivity to home plot decomposition based on per tiller, per g and per plant bases all decrease with increasing altitude, with the slowest decrease arising from P:D ratios on a per gram basis (Figure 9a-c and 10a-c). The fit of regression lines per tiller and per plant fit the data much better than the P:D ratios on a per gram basis, based on r^2 values. The P:D ratios of translocated *C. pallens* plants based on plot of origin are highly variable in the direction of their slopes and based on r^2 values the fits of the curve to the data are not very strong (Figure 9d-r). However, those based on plot of destination are not as variable in the direction of their slopes (all are increasing with increasing altitude) and based on r^2 values the fit of regression lines to the data is much stronger than those based on plots of origin (Figure 10d-r). Based on locations of origin and destination of surface litter mass loss of P:D ratios, analysis shows that the location of litter destination is 8 times more influential in shifting slope direction than the location of origin across the gradient, indicating a stronger environmental response than a physiological response.

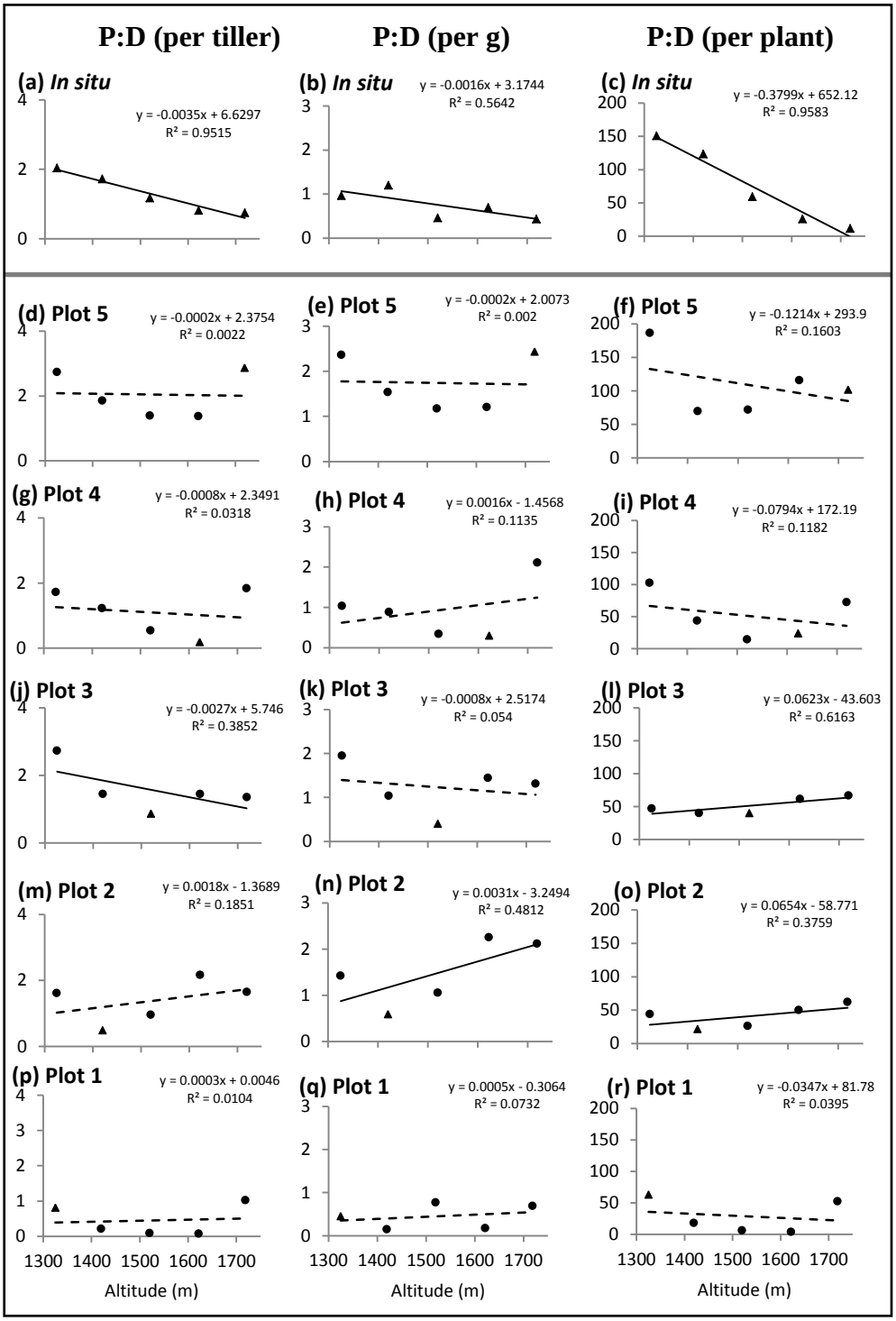

Figure 9: Productivity to decomposition ratios (P:D) based on plot of **origin** across 5 plots incrementally spaced ≈100m in elevation on Mount Mangaweka**.** Here 2 years of productivity is expressed as averages per tiller (column 1), per gram of final harvest biomass (column 2), and per plant (column 3), while decomposition is expressed as averages of mass loss after 2 years of decomposition following full-reciprocal translocation. *In situ* P:Ds (a-c) are expressed as productivity of *in situ* plants and home plot decomposition. Plot P:Ds (d-r) are expressed as productivity of plants and decomposition of leaf litter originating from indicated plots translocated to all plots (▲ indicates P:Ds of *in situ* or home plot translocation and home plot decomposition). Dashed lines indicate r^2 values < 0.3.

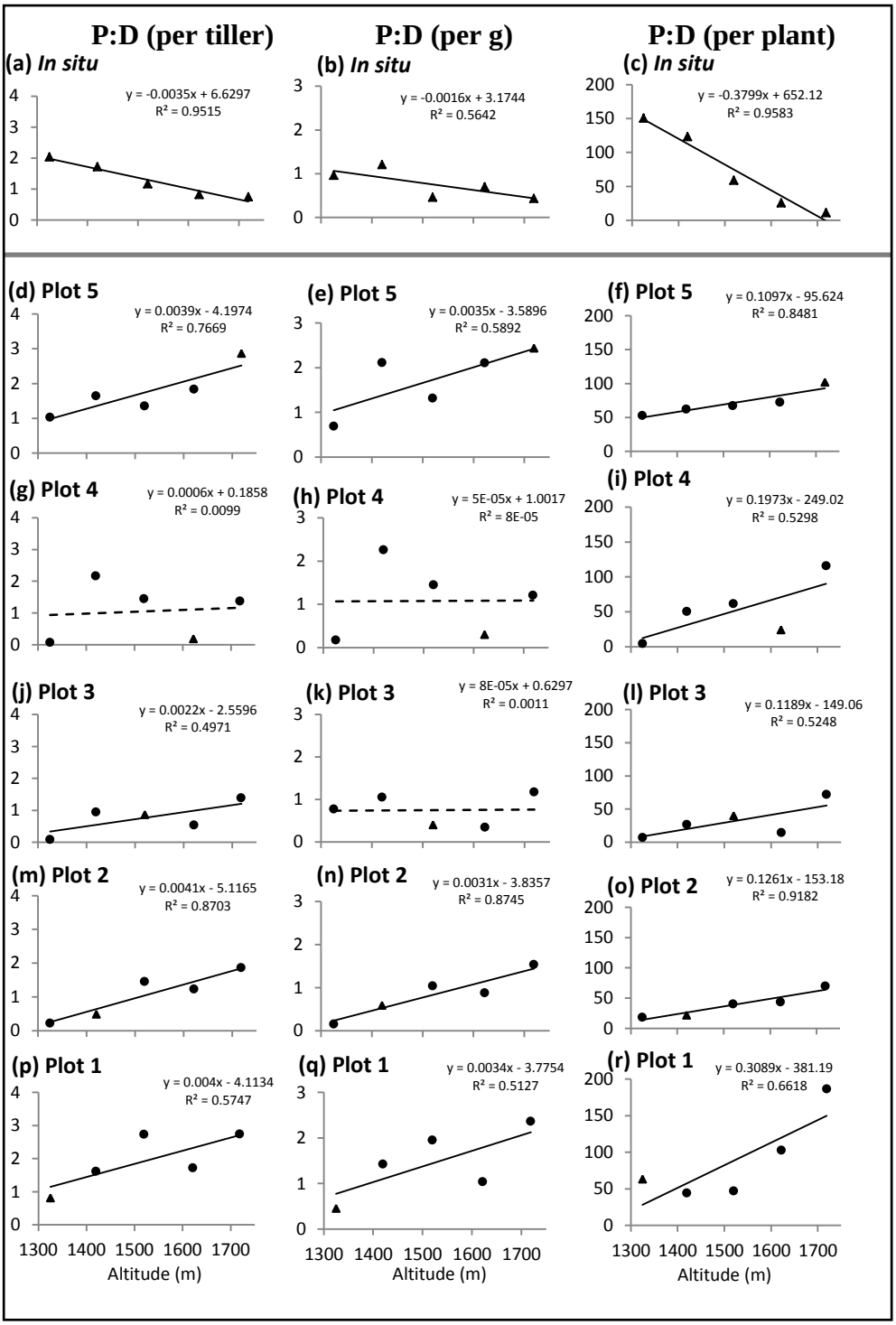

Figure 10: Productivity to decomposition ratios (P:D) based on plot of **destination** where 2 years of productivity is expressed as averages per tiller (column 1), per gram of final harvest biomass (column 2), and per plant (column 3); decomposition is expressed as averages of mass loss after 2 years of decomposition following full-reciprocal translocation across 5 plots incrementally spaced ≈100m in elevation on Mount Mangaweka. *In situ* P:Ds (a-c) are expressed as productivity of *in situ* plants and home plot decomposition. Plot P:Ds (d-r) are expressed as productivity of plants and decomposition of leaf litter translocated to indicated plots originating from all plots (▲ indicates P:Ds of *in situ* or home plot translocation and home plot decomposition). Dashed lines indicate r^2 values < 0.3.

Downslope P:D ratio comparisons

Based on averages of P:D ratios from tiller productivity of home plot and downslope transplants across the altitudinal gradient, there is an increase in *C. pallens*' P:D ratios with increasing temperatures (Figure 11; Appendix 19). Linear regression trends observed using all downslope transplants combinations had a slope of 0.6, a y-intercept of 1, and not a very strong fit to the data (r^2=0.28). Changes in temperatures of 0, 0.6, 1.2, 1.8, and 2.4^{o}C (based on a mean annual lapse rate of 0.6^{o}C per 100m in elevation) across the plots on Mount Mangaweka, result in average P:D ratios of *C. pallens* of 1.05, 1.24, 1.78, 1.79 and 2.74 respectively. This trend reveals a temperature increase of 2^{o}C can result in 160% greater P:D ratios when compared with the P:D ratios of transplants experiencing no change in temperature.

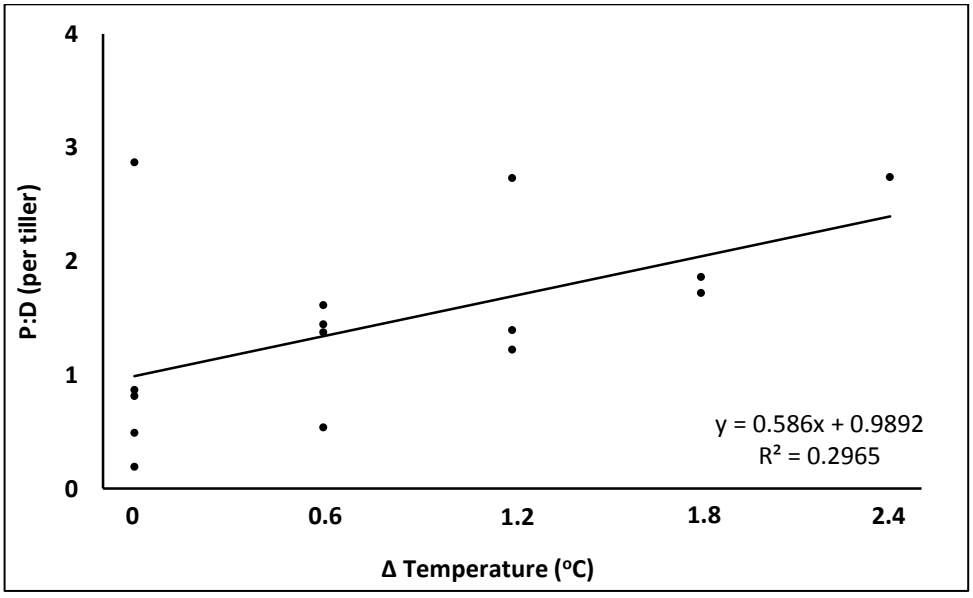

Figure 11: Linear regression of tiller productivity to decomposition ratios (P:D) of downslope translocated *Chionochloa pallens* plants plotted against a change (Δ) in temperature (^{o}C) corresponding to a lapse rate of 0.6^{o}C/100m with elevation across the ≈400m altitudinal gradient on Mount Mangaweka.

Discussion

Summary of main findings

The productivity of *in situ C. pallens* decreases with altitude on Mount Mangaweka and the productivity of transplants was least when translocated to highest-altitude plots. This variation in productivity across the gradient reveals a degree of plasticity in growth responses of *C. pallens*

to variation in environmental conditions across the gradient; this was expressed greatest by the end members across the gradient. The mass loss of *C. pallens*' surface-plated litter, based on location of litter origin, indicated litter decomposability on the surface may not differ greatly across the altitudinal gradient. However, litter translocated to lower plots had greater mass loss after two years of decomposition than litter placed at upper plots, likely a result of temperature. Linear regressions for litter origin revealed negative slopes for all but one treatment, whereas those for litter destination were positive for the higher altitude plots. The differences observed in mass loss across the gradient indicate that environmental influences may be more important on *C. pallens'* litter decomposition than litter quality. The productivity to decomposition ratios (P:D) based on the origin of *C. pallens* productivity and decomposition were highly variable and no discernible trends were observed. However the P:D ratios based on destination increased with increasing altitude, productivity varies more with altitude and litter decomposition was less variable. The P:D ratios of *C. pallens* downslope transplants reveal a substantial increase of ≈160% across a 2.4^{o}C temperature gradient. These findings suggest greater amounts of productivity are needed per unit decomposition when translocated into warmer climates. Thus warmer temperatures projected to be associated with climate change may greatly alter the relationships of productivity and decomposition of *Chionochloa* in the tussock grasslands of New Zealand and result in greater increases in productivity than decomposition thus leading to more C sequestration.

Ecoclinal variation

In New Zealand's montane tussock grasslands, *Chionochloa* species possess a vast range of temperature tolerances, expressing variation in growth patterns across their altitudinal ranges and sometimes exhibiting ecoclinal variation across altitudinal gradients (Mark 1965c). Based on alterations in productivity and shifts in slopes of *C. pallens* plants, both *in situ* and following translocation, there appears to be ecoclinal variation across this altitudinal gradient. This indicates *C. pallens'* plasticity to alterations in environmental conditions across the gradient. Mark (1965a;

1965b; 1965c) found populations of *Chionochloa* species to differ in plant size, leaf elongation, leaf production, functional life of leaves and reproductive development across altitudinal gradients. In this experiment, *C. pallens* plant populations across the ≈400m altitudinal gradient on Mount Mangaweka reveal a shift in growth forms, standing plant height and productivity, suggesting the presence of ecoclinal differentiation. The presence of this potential *C. pallens* ecocline provides more explanatory power of how climate change may impact species across gradients owing to differences within a single species across its range of environmental tolerances. This can reveal the potential range of shifts in productivity that a species may express experiencing predicted climate change scenarios. Assessing variation in these parameters across altitudinal gradients where ecoclinal populations differ in responses will allow investigation of plasticity of responses to environmental changes.

A commonly used method to assess responses of plant responses across gradients is through comparisons of growth, biomass and/or productivity changes to environmental stress via co- and countergradient responses (Eckhart *et al.*, 2004). Cogradient variation occurs when environmental and genetic components of variation work in the same direction, and/or selection alters reaction norms in the same direction of environmental effects on expression of phenotypic traits (Antonovics, 1976; Sultan, 1987, Eckhart *et al.*, 2004). On the other hand, countergradient variation arises when genetic influences on traits oppose those of the environment and/or when phenotypic variation is not adaptive (Eckhart *et al.*, 2004). Differences in *C. pallens*' productivity reveal a combination of co- and countergradient variation, however based on productivity following transplant destination it appears that cogradient variation is the prominent driving force owing to *C. pallens* plasticity in growth responses to changes in environmental conditions across the gradient.

Productivity

Greater productivity is typically found at lower altitudes, owing to lower levels of environmental stress, compared to higher altitudes; this finding has been well supported through meta-analyses (Callaway *et al.*,

2002; Kikvidze *et al*., 2005; Michalet *et al*. 2014). With respect to *Chionochloa*, Mark (1965a, 1965b and 1965c) utilized reciprocal translocation of *Chionochloa rigida* across altitudes to investigate plasticity of responses to changes in environmental conditions and found population-based variation in flowering and seasonal growth. Leaf elongation of *C. rigida* was reduced when transplanted to higher altitudes, and greater rates of leaf elongation occurred when transplanted to lower altitudes (Mark, 1969),–indicating temperature responses and some degree of both genetic control and phenotypic plasticity. These findings are similar to what was observed with productivity of *C. pallens* in this experiment. Translocation across the gradient revealed alterations in *C. pallens'* productivity to be most pronounced at the highest and lowest ends of the altitudinal gradient and intermediate alterations of middle plots, indicating an ecoclinal shift in productivity, as expected.

Transplantation experiments across altitudinal gradients often yield differing results owing to differences in abiotic conditions driving ecosystem processes. Bastida *et al.* (2014 and references therein) found performance of *Aquilegia vulgaris* in the southern Iberian Peninsula to be better at home plots and when transplanted to higher altitudes, attributing poorer performance of *A. vulgaris* at lower altitudes to lower water availability. In this experiment, the productivity of *in situ C. pallens* declines with increasing altitude, most likely attributed to changes in temperature. These differing slopes indicate how genetics (transplants of origin) and environmental factors (transplants of destination) can influence productivity across the gradient. Alterations in productivity of *C. pallens* following translocation across the gradient indicate some degree of phenotypic plasticity in growth patterns with increases in productivity and decomposition with increasing temperature, and thus such plasticity can respond to alterations in climate which are well known to affect plant productivity in grassland systems (Carlyle *et al*., 2014 and references therein).

Decomposition

Both climate and underlying plant genetics can affect the quality of litter produced and thus its decomposability (Chapin, 2003; Lavorel *et al*., 2007; Hobbie, 1996). Environmental factors across altitudinal gradients play an important role in decomposition of plant litter (Murphy *et al*., 1998). The mass loss of litter has been found to be lower in colder climates at higher altitudes (Sundqvist *et al*., 2011a; 2011b). However, precipitation may also be a prominent driver in decomposition (Murphy *et al*., 1998). Both temperature and precipitation are likely to be affected with climate change (IPCC, 2013). The genetic tendencies of plants to tolerate elevated environmental stress have been shown to have increased production of phenolic compounds and lignin (Kim *et al*., 2008), compounds with high C content. These C compounds often provide plants with additional tolerance to environmental stress and may aid in C sequestration because of the litter's recalcitrance to decomposition (de Boer *et al*., 2005). The type of litter produced can be influenced by differences in growth forms and biomass allocation patterns, and thus influence the litter quality and chemistry (Hobbie, 1996). Litter decomposition is primarily influenced by climate and secondly by the chemical composition of litter (Coûteaux *et al*., 1995; Lavelle *et al*., 1993). Thus, the chemical composition of litter can directly influence rates of decomposition, which in turn can influence C dynamics in the soil (Hobbie, 1996 and references therein). This has yet to be investigated as a factor for influencing the decomposability of *C. pallens*' litter across altitudinal gradients.

In this experiment, the mass loss of *C. pallens'* litter was significantly higher at low altitude plots compared to higher altitude plots. This was further supported with regression analysis and comparisons of slopes, where environmental influences affect mass loss of *C. pallens'* litter more than underlying litter quality across the plots. Climate can elicit ecophysiological responses which affect growth rates, allocation patterns, chemical and constituent composition of the litter and ultimately influence its decomposability (Chapin, 2003; Lavorel *et al*., 2007; Hobbie, 1996). However, the location of origin of *C. pallens'* litter did not reveal any differences within years, indicating litter traits across the gradient may not

be as influential on decomposition as environmental characteristics across the gradient.

Plant litter decomposition rates are often increased along gradients of increasing temperature and precipitation. Here, temperature appears to be more influential in decomposition of *C. pallens* litter compared to precipitation. Bryant *et al*. (1998) analysed leaf litter decomposition rates across temperature and moisture gradients in alpine tundra of Colorado over three years and found increased precipitation and soil moisture to increase mass loss of litter across the environmental gradient more than temperature. However, along altitudinal gradients (500 and 1000m in elevation) in northern Sweden, Sundqvist *et al*. (2011a; 2011b) found mass loss of litter from two contrasting plant functional types was significantly higher at lower elevations, they highlighted the importance of temperatures on decomposition. These findings in relation to temperature are similar to what was observed in this experiment, on Mount Mangaweka after two years of decomposition, based on litter destination, with greater mass loss at lower altitudes was observed.

The overall findings regarding mass loss based on locations of origin and destination significant differences indicate the environment where decomposition occurs along the altitudinal gradient is more influential on mass loss of *C. pallens'* leaf litter than the location where litter was produced. This was also supported with regression analysis which revealed litter destination location was more influential than origin. These findings indicate although there may be differences in litter across the gradient, the nature of the decomposition environment outweighs the chemical and/or structural differences in litter quality. However, a more in depth look at patterns arising with individual treatments via linear regression analysis of *C. pallens'* mass loss based on litter origin revealed predominantly negative slopes, indicating lower decomposability of litter from higher than lower altitude plots. These findings may indicate that differences in litter traits with plot of origin do exist and quality of *C. pallens* litter along this altitudinal gradient may have the potential to influence decompositional processes, meriting further investigation. Knowledge of the chemical and constituent composition of *C. pallens'* plant tissue, and both initial and

decomposed litter following translocation is still needed to better understand implications this will have on C and nutrient cycling in the tussock grasslands of New Zealand.

Soil properties

Changes in environmental conditions across altitudinal gradients can influence C and nutrient cycling within montane ecosystems. Leifeld *et al*. (2005) found percent soil organic carbon (SOC) to decrease with increasing depth within soil profiles of arable, temporary grasslands and permanent Swiss agricultural grasslands and an increase in SOC with increasing altitudes spaced every 100m in elevation. The decrease in soil C with increasing depth within the soil profile was also observed with findings presented here, however a decrease in soil C with increasing altitude was observed on Mount Mangaweka. The discrepancies with changes in soil C may be attributed to differences in soil types and landuse; Leifeld *et al.* (2005) investigated agricultural soils, whereas Mount Mangaweka is a non-agricultural temperate grassland.

Soil nutrients and plant uptake of nutrients can vary across altitudinal gradients. Wang *et al.* (2004) investigated soil organic matter (SOM), N, P and plant productivity alterations in response to environmental differences across a 595m altitudinal gradient in an alpine gradient and found greater concentrations of SOM, N and P at lower altitudes compared with higher altitudes. Their findings of greater soil N and P at lower altitudes compared with higher altitudes are similar to trends observed with soil N and P across the altitudinal gradient on Mount Mangaweka. The decrease in soil N and P with increasing depth may be attributed to differences in plant rooting zones and nutrient uptake or pedological differences within the soil profile. The decrease of the average soil C:N and increase of the average soil C:P with increasing altitude on Mount Mangaweka may indicate that N is more limited at lower altitudes whereas P may be more limited at higher altitudes.

Endogenous C sequestration in a changing climate

Changes in plant productivity and decomposition of dominant species within such a system due to alterations in climate may impact C and nutrient cycling within that ecosystem. This highlights the importance of Krna and Rapson's (2013) concept of endogenous C sequestration which accounts for gains and losses of C within a specified system over an annual time scale based on the ratio of C fixation to release ($F_{(as)}/R_{(as)}$). Here, a version of their F_{as}/R_{as} equation was used with *C. pallens'* ratio of productivity to decomposition (i.e. P:D). Across altitudinal gradients productivity is typically greater at lower altitudes (Callaway *et al*., 2002; Kikvidze *et al*., 2005; Michalet *et al*. 2014; Körner, 2007 and references therein), as is litter decomposition (Sundqvist *et al*., 2011a; 2011b; 2013). Logically, one may assume either greater productivity or reduced decomposition rates would result in greater endogenous C sequestration. But these processes are seldom either in concert with each other or independent, so they confound the issue of endogenous C sequestration across altitudinal gradients. Thus, examination of alterations of the P:Ds via a full reciprocal translocation of living *C. pallens* plants and leaf litter across the gradient on Mount Mengaweka provides evidence of how alterations in climate may influence endogenous C sequestration.

The P:D ratios of *in situ C. pallens'* plants and home plot decomposition decreased with increasing altitude, indicating less productivity is needed per unit decomposition for a standard amount of endogenous C sequestration, all else being equal in terms of the biotic and abiotic environment. Regression analysis and comparison of slopes from home transplants of *C. pallens*' plant P:D ratios, origin and destination of transplants indicates destination to cause greater alterations in slopes than origin, further supporting the importance of climate on productivity and decomposition. Considering there were smaller differences in slopes between comparisons of home and transplant origin P:Ds, this indicates that there may also be some degree of counter-gradient variation occurring and that ecoclinal differences in productivity and decomposition exist. However the environment appears to be the primary driver of productivity and decomposition along this altitudinal gradient, supporting cogradient

variation in *C. pallens*' P:D ratios. In contrast, the P:D ratios based on plot of destination show an increase with increasing altitude, these trends being opposite of that observed with *in situ* productivity and home plot decomposition of *C. pallens'* plants and litter. Thus, more productivity per unit decomposition is needed when translocated to lower altitudes. This stresses the importance climate change can have on alterations of two key and interrelated components (productivity and decomposition) on C cycling and sequestration. The increase in P:D ratios with downslope translocation of *C. pallens* indicate that with predicted warming, *C. pallens* will more likely sequester more C which may shift balances of C and nutrient cycling in New Zealand's tussock grasslands.

Conclusions

Climate change will alter the relationships of plant productivity and litter decomposition, which will impact C cycling and sequestration in New Zealand's montane tussock grasslands. It appears as though ecoclinal differences are present in *C. pallens* productivity and this will likely eventually result in differences in litter decomposability which will impact endogenous C sequestration in New Zealand's tussock grasslands. The productivity of *C. pallens* is greatest at lower altitudes of warmer environments. The mass loss by decomposition of surface-plated litter of *C. pallens'* does not appear to be significantly influenced by litter origin. However, the location of litter destination across the altitudinal gradient does significantly impact decomposition, stressing the role environment has on decomposition of *C. pallens*. However, regression analysis of locations of litter origin indicates lower mass loss of litter originating from higher altitudes. The P:D ratios of downslope translocation into warmer environments indicates that more productivity per unit decomposition to occur and thus greater C sequestration mediated by *C. pallens* is likely under the projected climate change scenarios.

Future Studies

Continued monitoring of productivity as well as analysis of chemical and constituent composition of transplants is desired, as it can take years for

plants to acclimate to changes in environmental conditions as well as for transplants to recover from physiological shock from transplantation (Close *et al*., 2005 and references therein). Greater stress experienced by plants at higher altitudes can result in alterations of allocation patterns and production or up-regulation of protective compounds (i.e. lignin, tannins and phenolics) which are also recalcitrant to decomposition thus slowing decompositional processes and increasing C sequestration. The alterations observed in the productivity and decomposition of *C. pallens* when translocated across this altitudinal gradient raise two questions. How will the chemical and constituent composition of leaves from transplants be altered after translocation, and how will this affect their decomposition? What implications will alterations in chemical and constituent composition of *C. pallens'* tissue and litter after translocation have on C sequestration in New Zealand's tussock grasslands in a changing climate?

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Appendix 1: Soil carbon (C), nitrogen (N) and phosphorous (P) concentrations expressed as tons per hectare (t/ha) at 10cm depths from the soil surface across the 5 plots, incrementally spaced every ≈100m in elevation, on Mount Mangaweka.

Plot	Altitude (m)	Soil depth (cm)	C (t/ha)	N (t/ha)	P (t/ha)
1	1325	10	64.18	3.45	0.26
		20	61.68	3.16	0.34
		30	58.85	2.70	0.34
2	1420	10	55.96	3.25	0.25
		20	74.28	4.28	0.40
		30	63.51	3.52	0.42
3	1520	10	62.53	3.54	0.23
		20	64.90	3.51	0.23
		30	60.11	3.07	0.23
4	1622	10	105.80	5.95	0.41
		20	64.07	3.45	0.25
		30	98.70	5.27	0.42
5	1719	10	66.26	4.03	0.35
		20	49.50	3.00	0.27
		30	53.59	3.21	0.26

Appendix 2: One-way ANOVA table for *in situ* productivity of *Chionochloa pallens* expressed on a per tiller basis across the five plots incrementally spaced ≈100m in elevation on Mount Mangaweka. DF indicates degrees of freedom, Sum Sq denotes sum of squares and Mean Sq indicates mean squares. Significance denoted by *corresponds to $P \leq 0.05$.

	DF	Sum Sq	Mean Sq	F-value	P-value	
In situ	4	1.794	0.4484	2.771	0.0401	*
Residuals	40	6.474	0.1618			

Appendix 3: Two-way ANOVA table for transplant productivity of *Chionochloa pallens* expressed on a per tiller basis across the five plots incrementally spaced ≈100m in elevation on Mount Mangaweka. 'From' indicates location of plant origin and 'To' indicates location of plant destination after full reciprocal translocation across plots. DF indicates degrees of freedom, Sum Sq denotes sum of squares and Mean Sq indicates mean squares. Significance denoted by '***' corresponds to $P \leq 0.001$.

	DF	Sum Sq	Mean sq	F-value	P-value	
From	4	3.202	0.8005	5.064	0.0007	***
To	4	3.751	0.9377	5.932	0.0002	***
From:To	16	2.443	0.1527	0.966	0.4959	
Residuals	176	27.882	0.1581			

Appendix 4: Two-way ANOVA table for transplant productivity of *Chionochloa pallens* expressed on a per plant basis across the five plots incrementally spaced ≈100m in elevation on Mount Mangaweka. 'From' indicates location of plant origin and 'To' indicates location of plant destination after full reciprocal translocation across plots. DF indicates degrees of freedom, Sum Sq denotes sum of squares and Mean Sq indicates mean squares. Significance denoted by '***' corresponds to $P \leq 0.001$.

	DF	Sum Sq	Mean Sq	F-value	P-value	
From	4	11475	2868.8	6.354	<0.0001	***
To	4	8495	2114.7	4.684	0.0013	***
From:To	16	3734	233.4	0.517	0.9361	
Residuals	176	79463	451.5			

Appendix 5: One-way ANOVA table for *in situ* productivity of *Chionochloa pallens* expressed on a per plant basis across the five plots incrementally spaced ≈100m in elevation on Mount Mangaweka. DF indicates degrees of freedom, Sum Sq denotes sum of squares and Mean Sq indicates mean squares. Significance denoted by '*' corresponds to $P \leq 0.05$.

	DF	Sum Sq	Mean Sq	F-value	P-value	
In situ	4	15742	3936	2.832	0.0366	*
Residuals	41	56969	1389			

Appendix 6: One-way ANOVA table for *in situ* productivity of *Chionochloa pallens* expressed as relative growth rate across the five plots incrementally spaced ≈100m in elevation on Mount Mangaweka. DF indicates degrees of freedom, Sum Sq denotes sum of squares and Mean Sq indicates mean squares. Significance denoted by '.' corresponds to $P \leq 0.1$.

	DF	Sum Sq	Mean Sq	F-value	P-value	
In situ	4	0.671	0.16774	2.454	0.0609	.
Residuals	41	2.802	0.06834			

Appendix 7: Two-way ANOVA table for transplant productivity of *Chionochloa pallens* expressed as relative growth rate across the five plots incrementally spaced ≈100m in elevation on Mount Mangaweka. 'From' indicates location of plant origin and 'To' indicates location of plant destination after full reciprocal translocation across plots. DF indicates degrees of freedom, Sum Sq denotes sum of squares and Mean Sq indicates mean squares. Significance denoted by '***' corresponds to $P \leq 0.001$ and '**' corresponds to $P<0.01$.

	DF	Sum Sq	Mean Sq	F-value	P-value	
From	4	4.29	1.0717	5.353	0.0004	***
To	4	3.16	0.7897	3.944	0.0043	**
From:To	16	2.62	0.1640	0.819	0.6627	
Residuals	176	35.23	0.2002			

Appendix 8: Four way analysis of variance (ANOVA) table for mass loss (g/g) of *Chionochloa pallens'* leaf litter following full reciprocal translocation across the five plots (incrementally spaced every ≈100m in elevation) on Mount Mangaweka. "From" indicates litter origin, "To" indicates litter destination, "Year" refers to annual time period and "Depth" refers to decomposition bags being buried 5cm below soil or occurring on the surface. DF indicates degrees of freedom, Sum Sq denotes sum of squares and Mean Sq indicates mean squares. Significance denoted by '***' corresponds to $P \leq 0.001$ and '**.**' corresponds to $P \leq 0.1$.

	Df	Sum sq	Mean Sq	F-value	P-value	
From	4	0.0218	0.0055	0.951	0.4346	
To	4	0.2025	0.0506	8.813	<0.0001	***
Year	1	1.1218	1.1218	195.333	<0.0001	***
Depth	1	0.0000	0.0000	0.003	0.9567	
From:To	16	0.1064	0.0067	1.158	0.3009	
From:Year	4	0.0176	0.0044	0.764	0.5491	
To:Year	4	0.0198	0.0050	0.864	0.4860	
From:Depth	4	0.0332	0.0083	1.444	0.2192	
To:Depth	4	0.0023	0.0006	0.102	0.9818	
Year:Depth	1	0.0210	0.0210	3.652	0.0569	.
From:To:Year	16	0.0414	0.0026	0.450	0.9675	
From:To:Depth	16	0.1062	0.0066	1.156	0.3024	
From:Year:Depth	4	0.0138	0.0035	0.060	0.6620	
To:Year:Depth	4	0.0166	0.0041	0.720	0.5784	
From:To:Year:Depth	16	0.0758	0.0047	0.083	0.6568	
Residuals	322	1.8492	0.0057			

Appendix 9: Three way analysis of variance (ANOVA) table for mass loss (g/g) of *Chionochloa pallens* surface decomposition following full reciprocal translocation across five plots on Mount Mangaweka. "From" denotes litter origin, "To" denotes litter destination and "Year" denotes annual time period. DF indicates degrees of freedom, Sum Sq denotes sum of squares and Mean Sq indicates mean squares. Significance denoted by '***' corresponds to $P \leq 0.001$.

	Df	Sum Sq	Mean Sq	F value	P value	
From	4	0.0054	0.0014	0.269	0.897	
To	4	0.1544	0.0386	7.638	<0.0001	***
Year	1	0.6003	0.6003	118.753	<0.0001	***
From:To	16	0.0947	0.0059	1.171	0.293	
From:Year	4	0.0069	0.0017	0.341	0.850	
To:Year	4	0.0293	0.0073	1.448	0.219	
From:To:Year	16	0.0537	0.0034	0.664	0.828	
Residuals	230	1.1626	0.0015			

Appendix 10: Two way analysis of variance (ANOVA) table for mass loss (g/g) of *Chionochloa pallens* surface decomposition following full reciprocal translocation across five plots on Mount Mangaweka. "Home" indicates home plot litter destination and "Year" indicates annual time period for decomposition. DF indicates degrees of freedom, Sum Sq denotes sum of squares and Mean Sq indicates mean squares. Significance denoted by '***' corresponds to $P \leq 0.001$ and '**' corresponds to $P \leq 0.01$.

	DF	Sum Sq	Mean Sq	F-value	P-value	
Home	4	0.07854	0.01964	4.072	0.0068	**
Year	1	0.09602	0.09602	19.913	<0.0001	***
Home:Year	4	0.00890	0.00222	0.461	0.7637	
Residuals	44	0.21216	0.00482			

Appendix 11: Student's T-test for mass loss of *Chionochloa pallens* surface home plot decomposition of Plots 1 and 5 following full reciprocal translocation across five plots on Mount Mangaweka. "Home" indicates home plot litter destination. DF indicates degrees of freedom, Sum Sq denotes sum of squares and Mean Sq indicates mean squares. Significance denoted by '***' corresponds to $P \leq 0.05$.

	DF	Sum Sq	Mean Sq	F-value	P-value	
Home	1	0.0511	0.025552	4.519	0.024	*
Residuals	20	0.1131	0.005655			

Appendix 12: Two way analysis of variance (ANOVA) table for mass loss (g/g) of *Chionochloa pallens* surface decomposition following full reciprocal translocation across five plots on Mount Mangaweka. "From" indicates litter origin and "Year" indicates annual time period. DF indicates degrees of freedom, Sum Sq denotes sum of squares and Mean Sq indicates mean squares. Significance denoted by '***' corresponds to $P \leq 0.001$.

	DF	Sum Sq	Mean Sq	F-value	P-value	
From	4	0.0054	0.0014	0.246	0.912	
Year	1	0.5997	0.5997	108.200	<0.0001	***
From:Year	4	0.0058	0.0014	0.260	0.904	
Residuals	270	1.4965	0.0055			

Appendix 13: Student's T-test for mass loss of *Chionochloa pallens* surface decomposition of Plots 1 and 5 based on plot of origin ("From") following full reciprocal translocation across five plots on Mount Mangaweka. "Home" indicates home plot litter destination. DF indicates degrees of freedom, Sum Sq denotes sum of squares and Mean Sq indicates mean squares.

	DF	Sum Sq	Mean Sq	F-value	P-value
From	1	0.0005	0.000512	0.071	0.791
Residuals	113	0.8185	0.007243		

Appendix 14: Two way analysis of variance (ANOVA) table for mass loss (g/g) of *Chionochloa pallens* surface decomposition following full reciprocal translocation across five plots on Mount Mangaweka. "To" indicates litter destination and "Year" indicates annual time period. DF indicates degrees of freedom, Sum Sq denotes sum of squares and Mean Sq indicates mean squares. Significance denoted by '***' corresponds to $P \leq 0.001$.

	DF	Sum Sq	Mean Sq	F-value	P-value	
To	4	0.1547	0.0387	7.853	5.32E-06	***
Year	1	0.5916	0.5916	120.107	<2E-16	***
To:Year	4	0.0310	0.0078	1.576	0.181	
Residuals	270	0.3300	0.0049			

Appendix 15: Student's T-test for mass loss of *Chionochloa pallens* surface decomposition of Plots 1 and 5 based on plot of origin ("From") following full reciprocal translocation across five plots on Mount Mangaweka. "Home" indicates home plot litter destination. DF indicates degrees of freedom, Sum Sq denotes sum of squares and Mean Sq indicates mean squares. Significance denoted by '**' corresponds to $P \leq 0.01$.

	DF	Sum Sq	Mean Sq	F-value	P-value	
To	1	0.0741	0.07409	10.02	0.00201	**
Residuals	109	0.8062	0.00740			

Appendix 16: Linear regression analysis of mass loss of Chionochloa pallens leaf litter after one and two years of decomposition treatments of a full reciprocal translocation across the five plots on Mount Mangaweka. Litter origin denotes plot where litter originated from and litter destination denotes plot where litter was translocated to in the field.

Plot	Altitude (m)	Year	Treatment	Regression equation	r^2	*n*
1	**1325**	**1**	**Litter origin**	y = -0.0002x + 0.5337	0.6526	5-6
			Litter destination	y = -0.0001x + 0.4018	0.6391	4-6
		2	**Litter origin**	y = -0.0004x + 0.8087	0.7728	5-6
			Litter destination	y = -0.0002x + 0.5369	0.5348	4-6
2	**1420**	**1**	**Litter origin**	y = -0.0002x + 0.4265	0.9166	4-6
			Litter destination	y = 2E-05x + 0.1647	0.0301	4-7
		2	**Litter origin**	y = -0.0002x + 0.6246	0.8014	4-6
			Litter destination	y = -1E-04x + 0.4691	0.4229	4-7
3	**1520**	**1**	**Litter origin**	y = -3E-05x + 0.229	0.0737	5-7
			Litter destination	y = 0.0001x + 0.0007	0.7020	4-6
		2	**Litter origin**	y = -0.0003x + 0.7375	0.6945	5-7
			Litter destination	y = 0.0001x + 0.0777	0.2713	4-6
4	**1622**	**1**	**Litter origin**	y = 4E-07x + 0.1844	3.00E-05	4-6
			Litter destination	y = 0.0002x - 0.067	0.4319	4-6
		2	**Litter origin**	y = -5E-06x + 0.2954	0.0009	4-6
			Litter destination	y = 0.0001x + 0.0963	0.2465	4-6
5	**1719**	**1**	**Litter origin**	y = -0.0001x + 0.3453	0.3637	4-6
			Litter destination	y = 1E-05x + 0.1368	0.0188	5-6
		2	**Litter origin**	y = -9E-05x + 0.4128	0.5368	4-6
			Litter destination	y = 0.0001x + 0.0572	0.4401	5-6

Appendix 17: Analysis of variance (ANOVA) table for mass loss (g/g) of *Chionochloa pallens* buried decomposition following full reciprocal translocation across five plots on Mount Mangaweka. "From" indicates litter origin, "To" indicates litter destination and "Year" indicates annual time period. DF indicates degrees of freedom, Sum Sq denotes sum of squares and Mean Sq indicates mean squares. Significance denoted by '***' corresponds to $P \leq 0.001$.

	DF	Sum Sq	Mean Sq	F-value	P-value	
From	4	0.0452	0.0113	1.514	0.205	
To	4	0.0516	0.0129	1.728	0.151	
Year	1	0.5460	0.5460	73.167	<0.0001	***
From:To	16	0.1160	0.0072	0.971	0.494	
From:Year	4	0.0263	0.0066	0.880	0.479	
To:Year	4	0.0083	0.0021	0.279	0.891	
From:To:Year	16	0.0616	0.0038	0.516	0.993	
Residuals	92	0.6866	0.0075			

Appendix 18: Analysis of variance (ANOVA) table for mass loss (g/g) of *Chionochloa pallens* root decomposition following full reciprocal translocation across five plots on Mount Mangaweka. "From" indicates litter origin, "To" indicates litter destination and "Year" indicates annual time period. DF indicates degrees of freedom, Sum Sq denotes sum of squares and Mean Sq indicates mean squares.

	Df	Sum Sq	Mean Sq	F-value	P-value
From	4	0.0902	0.22547	1.944	0.118
To	4	0.0262	0.006561	0.566	0.689
Year	1	0.0002	0.000152	0.013	0.909
From:To	16	0.1728	0.010802	0.932	0.541
From:Year	4	0.0240	0.005990	0.517	0.724
To:Year	4	0.0321	0.008021	0.692	0.601
From:To:Year	13	0.1670	0.012845	1.108	0.375
Residuals	49	0.5682	0.011596		

Appendix 19: Average tiller productivity, decomposition and productivity to decomposition ratios (P:D) on a per tiller basis of downslope and home plot translocated *Chionochloa pallens* plants across the 5 plots, incrementally spaced every ≈100m in elevation assuming a 0.6°C/100m mean annual lapse rate for change (Δ) in temperature (°C) with altitude on Mount Mangaweka.

Translocation (From → To)	Δ Temperature (°C)	Productivity (g/yr)	Decomposition (g/g)	P:D (ratio)
5 → 4	0.6	0.3666	0.2667	1.3745
5 → 3	1.2	0.3832	0.2749	1.3937
5 → 2	1.8	0.5474	0.2943	1.8599
5 → 1	2.4	0.7454	0.2721	2.7391
4 → 3	0.6	0.1536	0.2850	0.5389
4 → 2	1.2	0.4047	0.3311	1.2221
4 → 1	1.8	0.4439	0.2580	1.7207
3 → 2	0.6	0.4248	0.2940	1.4448
3 → 1	1.2	0.9142	0.3347	2.7316
2 → 1	0.6	0.4866	0.3018	1.6125
5 → 5	0	0.6844	0.2385	2.8696
4 → 4	0	0.0543	0.2846	0.1908
3 → 3	0	0.1741	0.2005	0.8683
2 → 2	0	0.1569	0.3209	0.4889
1 → 1	0	0.2666	0.3274	0.8143

Chapter **5**

Alterations in chemical and constituent composition of a *Chionochloa pallens* ecocline across an altitudinal gradient

Chionochloa pallens on Mount Mangaweka, New Zealand (October, 2013)

Māori proverb

"Whāia te iti kahurangi ki te tūohu koe me he maunga teitei."

"Aim for the highest cloud so if you miss it, you will hit a lofty mountain."

Abstract

Anthropogenic activities are altering terrestrial, aquatic and atmospheric processes pertaining to C and nutrient cycling. Owing to the interrelatedness of C and nutrients, alterations in climate can disrupt C and nutrient cycling in terrestrial systems owing to changes in productivity, decomposition and the chemical and constituent composition of plant tissues. Ecological stoichiometry allows for the investigation of alterations to balances of chemical, notably carbon (C), nitrogen (N) and phosphorous (P), in ecological interactions and processes; its usage extends from productivity to decomposition to soil mineralization and C sequestration. In order to investigate alterations of these components and interactions, a full-reciprocal translocation of *Chionochloa pallens* plants and litter was performed across five plots incrementally spaced every ≈100m in altitude on Mount Mangaweka, Ruahine Range, NZ. Soils were analysed for percent C, N, and P at 0-10, 10-20 and 20-30cm depths across the 5 plots. Green leaf tissue from *in situ* and translocated plants, roots from resident plants, as well as initial leaf litter and 2 year decomposed leaf litter following translocation were analysed for percentages of C, N, P, AD-fibre, cellulose, lignin (L) and pertinent ratios. Trends of the above parameters for soils and plant tissues were analysed and compared with linear regression. The percent C, N and P of soils decreased with increasing altitude and increasing soil depth. The percent C, N, AD-fibre of *C. pallens*' roots increased with increasing elevation; whereas the lignin percentage, C:N and L:N ratios tended to decrease with increasing elevation. Regression of leaf chemical and constituent composition of transplants based on location of origin was more closely similar to that of *in situ*; whereas regression of these parameters based on destination expressed a greater difference in comparison. This indicates plasticity and ecoclinal differentiation in C and nutrient composition of *C. pallens*' tissues owing to differing allocation patterns in response to alterations in abiotic condition across the altitudinal gradient. Trends observed with chemical and constituent analyses of 2 year decomposed litter reveal increased decomposability based on translocation of litter destination, when translocated to lower altitudes, compared to translocation based on litter origin. This finding is supported by the increase in mass loss found at lower altitudes. Despite increased mass loss and decomposability of *C. pallens* litter when translocated to lower altitudes, the increased productivity observed outweighs the decomposition resulting in increased productivity to decomposition ratios (P:D) and greater C sequestration.

Key words: ecological stoichiometry, reciprocal translocation, montane, tussock grassland

Introduction

The increased concentrations of greenhouse gases (GHGs) in Earth's atmosphere, elevated average global temperatures and alterations in climate, have all raised concerns about their effects on biological processes (Hinckley & Tierney, 1992; Ennis & Marcus, 1996). "It is extremely likely (>95% chance) that human influence on climate caused more than half of the observed increase in global average surface temperature from 1951–2010" (IPCC, 2013). The current atmospheric carbon dioxide (CO_2) concentration is 401.5ppm (as of March 2015; NOAA, 2015) and Jones (2013) was correct with her prediction of average atmospheric CO_2 concentrations passing 400ppm in the few years following her publication. Average global temperatures have increased by 0.74ºC over the last century (1906-2005), and are expected to rise by another 0.46-1.65ºC in the next 50 years (IPCC, 2007). The correlations between elevated GHGs concentrations, increasing global temperatures and alterations to climate have been well modelled with global circulation models (GCMs); however how alterations in climate will influence different systems and species responses is still under investigation. There has been substantial effort to investigate different ecosystems' responses to climate change and increasing global temperatures (Shaver *et al*., 2000; Rustad *et al*., 2001), as this may disrupt carbon (C) and nutrient cycling in terrestrial systems.

Carbon sequestration is a highly important part of the C cycle and one of the most important concepts in studies of climate change (Krna & Rapson, 2013) since changes in climate may disrupt the balances of soil carbon cycling, storage and sequestration in terrestrial environments (Tate, 1992). Carbon sequestration has an important role in mitigating the effects of elevated atmospheric CO_2 concentrations and the impending threats of climate change (Lal, 2004a and references therein). Alterations in climate are likely to influence N and P cycling, as these are typically the most limiting elements for terrestrial vegetation and mineralization of these elements is an important nutrient source for plants (Manzoni *et al*., 2010 and references therein). The tight coupling of C and nutrients in terrestrial systems suggests that alterations to key nutrients would in turn influence C cycling, since it is primarily driven by abiotic factors (topography,

mineralogy, nutrients and texture) and by interactions living organisms and their environment (De Deyn *et al*., 2008).

In terrestrial systems, the cycling of C and nutrients are complex and tightly interlinked ecosystem processes; alterations to one cycle can have repercussions on others. Anthropogenic activities are disrupting C and nutrient cycling; increased concentrations of GHGs into the atmosphere, notably CO_2, methane (CH_4) and nitrous oxide (N_2O), result in alterations in climate and increased nitrogen (N) deposition (Ambus & Robertson, 2006). Increased N deposition has increased the availability of N relative to other nutrients; thus some systems which were N limited are now enriched, resulting in deficiencies of phosphorus (P) or other mineral elements (Güsewell, 2004 and references therein). Elevated CO_2 and temperatures often result in increased plant growth and leaf C content, and increased CO_2 can yield relative reductions in leaf N content (Veteli *et al*., 2002), which would likely alter C sequestration owing to reduced leaf decomposability. The logic of studies of nutrient use efficiency (NUE) of plants implies plants evolved (and thus have acclimated and/or adapted to) different efficiencies for production of biomass per unit of assimilated nutrient (McGroddy *et al*., 2004 and references therein) and is likely to differ across geographic gradients (Reich & Oleksyn, 2004). Nutrient availability greatly influences plant metabolic processes, since plant growth is primarily limited by the availability of N and P (Güsewell, 2004). These two elements are considered the most limiting elements for terrestrial plants as they are highly important in regulation of plant metabolic processes (Reich & Oleksyn, 2004). Enzymatic activity is driven by N in plant proteins and P regulates protein synthesis; and temperature is likely to influence these processes (Reich & Oleksyn, 2004). Owing to these influences on plants and their physiological responses, biogeographic gradients of N and P are likely to occur across temperature gradients (Reich & Oleksyn, 2004), which is also likely to influence C cycling along temperature gradients.

However, decomposition is often greater under elevated temperatures which would likely result in reduced C sequestration. These differences in productivity and decomposition under warmer climates create a double-edged sword, where both positive and negative feedbacks to

atmospheric CO_2 concentrations are likely to occur with climate change, and soil organic C would be influenced (Kirschbaum, 2000) as well as soil nutrients (Bardgett & Wardle, 2010). The alterations in climate and soil nutrients are likely to influence plant productivity owing to alterations in nutrient availability and assimilation. Terrestrial C cycling is not only influenced by nutrient cycling but can also be influenced by climate, since climate influences, and selects for, specific plant ecophysiological traits (Violle *et al*., 2007; Lavorel *et al*., 2007). The transfer of C through an ecosystem and the amount that becomes deposited into the soil is functionally correlated with photosynthesis efficiency, plant productivity and litter decomposition potential (Buyanovsky *et al*., 1987; Seastedt *et al*., 1994). Plant growth rates and allocation patterns may directly influence the amount, and chemical composition, of C deposited into soil, and the fate of that C within the soil (Chapin, 2003; Lavorel *et al*., 2007). Plant species with high growth rates primarily allocate C to photosynthetically active structures that are low in cellular density and high in nutrients, making leaf litter more easily decomposed; whereas species with low growth rates tend to be long lived and produce nutrient-poor litter recalcitrant to decomposition (Aerts & Chapin, 2000). Plants with genetic dispositions to tolerate elevated environmental stress can increase production of phenolic compounds and lignin (Kim *et al*., 2008). These C compounds are considered to provide plants with additional tolerance to environmental stress and to aid in C sequestration because of increasing the litter's recalcitrance to decomposition (de Boer *et al*., 2005). The type of litter produced can be influenced by differences in growth forms, biomass allocation patterns and litter quality and chemistry (Hobbie, 1996). Litter decomposition is primarily influenced by climate and the chemical composition of litter (Coûteaux *et al*., 1995; Lavelle *et al*., 1993). Thus, the chemical composition of litter can directly influence rates of decomposition, which in turn can influence C and nutrient dynamics in the soil (Hobbie, 1996 and references therein).

In montane systems, altitudinal gradients provide a unique opportunity to investigate plant responses to changes in abiotic conditions that vary with alterations in elevation (Körner, 2007), often over relatively

short horizontal distances (Beniston, 2003). Temperature is one of the most important factors influencing species across altitudinal gradients (Körner, 2007) and numerous studies report about elevation/temperature alterations on plant growth (Hoch & Körner, 2012 and references therein). Abiotic stress is typically greater at high elevations (Callaway *et al*., 2002), owing to lower temperatures and greater, more desiccating winds, than at lower elevations. Changes in climate, across altitudinal gradients, can influence plant ecophysiological traits and responses (Violle *et al*., 2007), and the local acclimation or adaptation of plants can result in ecoclinal differentiation within species. Growing season temperatures and duration are likely to influence geographic patterns of leaf N and P, thus genotypic variation resulting from local adaptation to temperatures may influence N and P concentrations within leaves (Reich & Oleksyn, 2004). Owing to variation in selective pressures across alpine ecosystems, montane regions are ideal locations for exploration of adaptive differentiation such as occurs in ecotypes and ecoclines, owing to steep environmental gradients (Eckhart *et al*., 2004; Byars *et al*., 2007; Gonzalo-Turpin & Hazard, 2009). The responses of different ecotypes and/or ecoclinal differentiation across these gradients are important factors when predicting alterations to biological processes resulting from climate change (Liancourt *et al*., 2013). Genotypic variation resulting from local adaptation to temperatures may influence N and P concentrations within leaves (Reich & Oleksyn, 2004) thus resulting in alterations leaf C, N and P stoichiometry. These alterations to leaf C and nutrients are likely to influence the decomposability of the litter as alterations to C:N and C:P ratios are influential in litter decomposition (Manzoni *et al*., 2010) as are the impacts of climate change (Elser *et al*., 2000a; Reiche & Oleksyn, 2004; Ordoñez *et al*., 2009; Liu *et al*., 2013, and references therein).

Ecological stoichiometry as defined by Sterner & Elser (2002) is "the balance of multiple chemical substances in ecological interactions and processes". The primary elements involved in ecological stoichiometry are C, N and P and their ratios are used to investigate how the ecology of organisms is shaped by their nutrient content; and the applicability of ecological stoichiometry extends from growth to decomposition to organic

matter mineralization (Sterner & Elser, 2002). Both N and P are considered the most important limiting elements for vegetation in terrestrial systems (Vitousek, 1984), and the amount of these nutrients available to plants influences plant productivity, litter decomposition (Manzoni *et al*., 2010) and C sequestration (Hessen *et al*., 2004; Kirkby *et al*., 2013). Reductions in and/or lower C and nutrient ratios indicate increased decomposability of the litter (Melillo *et al*., 1982); if these ratios decrease with decreasing altitude it would imply less C sequestration is likely to occur through the decomposition component of the P:D ratio with predicted warming associated with climate change. However, a better understanding of altitudinal patterns of leaf stoichiometry is needed (Zhao *et al*., 2014), as is the influence of climate on genotypic and plastic responses within ecoclinal species, as this will expose the range of responses capable within a species (and so avoiding inter-specific differences) and impacts on C and nutrient cycling under the threat of climate change.

In this study, a ≈400m altitudinal gradient of montane tussock grassland was used to assess alterations in soil nutrients and differences in the chemical and constituent composition of an ecoclinal population of *Chionochloa pallens*, via a full reciprocal translocation of plants and leaf litter decomposition bags. Increased temperatures and soil nutrients are common with decreasing elevation in montane systems and are likely to have differing influences on stoichiometry within plant tissues and the decomposability of litter from an ecocline owing to adaptation to local environmental conditions. How will the chemical and constituent composition of *C. pallens* be affected by changes in climate (via repositioning on an ecoclinal gradient) and what implications will this have on productivity, decomposition and endogenous C sequestration?

Methods

Species' description

Chionochloa pallens Zotov (1963) subsp. *pallens* is commonly referred to as the "mid-ribbed snow tussock", owing to the typically prominent yellow midrib on the lamina's abaxial surface (Connor, 1991). A detailed floristic description of *C. pallens* can be found in Connor (1991). It

is one of the most widely distributed tussock-grass species, present in montane regions across both the North and South Islands of New Zealand (Connor, 1991). On the North Island, its distribution extends from the Raukumara Range and southward (Connor, 1991; Mark, 2012) through the Ruahine and Tararua Ranges. It is classified as having a low alpine altitudinal range of 1100 – 1800m (Mark, 2012).

Site description

The Ruahine Range spans 110km northeast – southwest from inland Hawke's Bay region to the Manawatu Gorge and is a non-volcanic mountain range of New Zealand's Central North Island. The basement geology and landforms of the Hikurangi Range (a range within the Ruahine Range) are "undulating and dissected greywacke terrain" (Rogers and McGlone, 1989). The location chosen for this experiment was in the Hikurangi Range on Mount Mangaweka (1731m, the highest point of the Ruahine Range) in Ruahine Forest Park. Treeline is at approximately 1320m in elevation where scrubland transitions into tussock grasslands which span bioclimatic zones from cool temperate to subalpine (Körner *et al*., 2011), to the mountain summit.

Experimental design

Five plots (30 x 20m; incrementally spaced approximately every 100m in elevation) were established in March 2011, on Mount Mangaweka. Across the ≈400m gradient a 0.6^{o}C/100m mean annual lapse rate was assumed (Halloy and Mark, 2003 and references therein). Plots had similar slopes and aspects due their position along the ridgeline from Purity Hut (1325m) to 50m below Wooden Peg (1672m) and Plot 5 (the uppermost plot) was located on the south face of the summit. All plots were located on the south face of the ridgeline at least 5m to the south of the Purity Hut Track (Plots 1-4) and the uppermost plot (Plot 5) was located 12m vertically below the summit (see Figure 1 of Chapter 4). A full reciprocal transplantation of living *C. pallens* plants (*n*=6) and surface-plated decomposition bags of *C. pallens*' leaf litter (i.e. on bare soil surface or on low-lying vegetation; *n*=6) was performed across the 5 plots. Translocations

were initiated in March 2011 for living *C. pallens* plants and, in October 2011 for decomposition bags (see Chapter 4 for details). Growth of tillers was monitored on six occasions over a two year period. Monitored tillers from monitored *in situ* and translocated plants, decomposition bags and soils were collected in October 2013 and promptly stored at -20^{o}C prior to analyses. Leaf elongation rates were converted into biomass estimates (see Chapter 4 for details).

Soil Analyses

Soil cores (n = 6) were collected to 30cm in depth below the organic horizon from random locations outside the 5 plots in October 2013, following methods described in Allen *et al*. (1989). Cores were divided into 10cm segments (0-10.0, 10.1-20.0 and 20.1-30.0cm below the soil surface) and stored at -20^{0}C. Soil cores were combined to form a bulk sample and air-dried at room temperature for 5 days. After drying 10cm cores, soils were sieved to 2mm and finely ground with a mortar and pestle, prior to chemical analyses. Total organic C and N was assessed at each of the 3 depths (n=1) with flash combustion analysis using a Leco furnace (Leco, 2003; Laboratory Equipment Corporation, St Joseph, Michigan, USA). Soil phosphorus (P) was analysed at each of the 3 depths (n=1) following the Kjeldahl method, described by Blakemore *et al*. (1987) and Taylor (2000), at Landcare Research, Palmerston North, New Zealand. Soil C, N and P are expressed as percentages, and the C:N, C:P and N:P ratios were calculated.

Tissue chemical and constituent composition

Chemical and constituent analyses (n = 1) were performed on bulked samples of *C. pallens*' young leaves (produced since commencement of the experiment from tillers of both *in situ* and translocated plants), roots, initial leaf litter, and "2 year decomposed litter" (litter as decomposed by 2 years after full reciprocal translocation) which were collected from each of the 5 plots. Chemical (C and N) and constituent (lignin, cellulose and acid-detergent fibre; AD-fibre henceforth) composition was performed on green portions of the youngest 4 leaves of both *in situ* and transplanted *C. pallens* plants (i.e. leaves grown following implementation of experiment), on

Chionochloa "initial litter" (i.e. litter before undergoing decomposition in the field), on 2 year decomposed litter, and on *C. pallens* roots. Phosphorous was also analysed for the initial and 2 year decomposed litter of *C. pallens*. Tissues were oven-dried (60^0C) for 48hr and were finely ground to pass through a 1mm screen and re-dried for one hour prior to chemical and constituent analyses, similar to methods described by Campbell and Plank (1997). Total organic C and N analysis of leaf litter was performed on a Leco CNS2000 Analyzer (Leco, 2003) and is expressed as percent of sample dry weight. Phosphorus (P) concentrations of initial litter and 2 year decomposed litter were determined following the Kjeldahl wet oxidation process (Blakemore *et al*., 1987) and are expressed as percentages of sample dry weight. Cellulose, AD-fibre, and lignin concentrations were determined with an acid detergent fibre-sulphuric acid procedure following the methods of Rowland & Roberts (1994), and are expressed as percent of sample dry weight. These chemical and constituent analyses of *C. pallens'* living leaves, leaf litter and roots were performed at Landcare Research, Palmerston North, New Zealand. Carbon to N ratios (C:N), carbon to P ratios (C:P), lignin to N ratios (L:N), lignin to P ratios (L:P) and N to P ratios (N:P) were determined. Linear regression analyses (with first order polynomials and subsequent R^2-values) was used to explain trends of *C. pallens*' *in situ* leaves and initial litter from plots, as well as of leaves, and 2yr decomposed litter following translocation across the plots based on plots of origin and destination. The chemical and constituent composition of up- and downslope translocations from reciprocal translocations were also assessed.

Modelling of productivity, decomposition and P:D ratios

For the downslope components of the translocation experiment, including the translocation to the home site, parameters influencing the measured variables for productivity, decomposition and the P:D ratio were investigated. Tested response and explanatory variables are listed in Table 1. These were selected after removal of highly-correlated ($r>0.8$) variables, and those with collinearity (including the source altitude for translocations). To describe the translocations, the altitude the transplant was moved to and

the decrease in altitude were used for all analyses. For all other parameters, the difference between the site of origin and the site the transplants were moved to was calculated, since the focus was on the impact of changes in the growth environment. This generated zeros for all home site translocations. For productivity, soil parameters were used, as these directly affected the transplants, and the nutrient composition of young, green leaves was used as these reflect its relations with the soil. For decomposition, soil parameters were used along with the condition of the initial litter plated out. For the P:D ratio soil parameters were used as these are the only variables affecting both productivity and decomposition processes.

The goodness of fit was evaluated using Akaike Information Criterion via the procedure step (B. Ripley) in the package Stats in R (R Core Team, 2012). The procedure searches (in both directions) for appropriate models of the response variables, presenting those with the lowest AICs. Where models were not significantly different from the best model (the global model), then the simplest model is accepted. No interaction terms were calculated, due to low degrees of freedom.

Table 1: Response and explanatory variables tested for goodness of fit using AIC.

Response variables	**Explanatory variables (and explanation)**
Productivity Per tiller Per plant Per gram	ToAlt - Altitude translocation was to AltDrop - Change in altitude for translocation N0to10 - N in top 10 cm of soil P0to10 - P in top 10 cm of soil ISP - P in green leaf of the plant ISCtoN - C:N in green leaf of the plant ISCtoP - C:P in green leaf of the plant ISCell - Cellulose concentration in green leaf of the plant ISLignin - Lignin concentration in green leaf of the plant
Decomposition Decomposition after 2 years Half life	ToAlt - Altitude translocation was to AltDrop - Change in altitude for translocation P0to10 - P in top 10 cm of soil CtoN0to10 - C:N ratio in top 10 cm of soil CtoP0to10 - C:P ratio in top 10 cm of soil ILC - C concentration in the initial litter ILP - P concentration in the initial litter ILLignin - Lignin concentration in the initial litter
P:D ratio for Decomposition after 2 years Per tiller Per plant Per gram	ToAlt - Altitude translocation was to AltDrop - Change in altitude for translocation P0to10 - P in top 10 cm of soil CtoN0to10 - C:N ratio in top 10 cm of soil CtoP0to10 - C:P ratio in top 10 cm of soil

Results

The percent soil C, N and P decreased with increasing depth of soil, as well as with increasing altitude (Figure 1). Soil C ranged from 22.7% in the upper 10cm of soil at plot 1 to 8.7% at 20-30cm at Plot 5. The average slopes of the regressions of percent soil C (0-30cm depth) across the altitudinal gradient was 0.015 and 0. 016 steeper than those of the percent soil N and P respectively, indicating a greater decline in soil C with increasing altitude than soil nutrients. Soil N ranged from 0.5% at 20-30cm in soil depth at Plot 5 to 1.2% in the upper 10cm of soil at plot 1. Soil P ranged from 0.04% at 20-30cm in soil depth at Plot 5 to 0.09% in the 10-20cm depth of soil at Plot 1. The soil C:N ratio increased with depth but decreased with increasing altitude and ranged from 16.4 to 21.8 throughout the soil profile and with increasing altitude. The C:P of the top 10cm of soil ranged from 152.5 to 279.8, tending to decrease with soil depth, and was greatest at mid altitude plots (Plots 3 and 4) . The soil C:P of lower depths (10-20 and 20-30cm) increased with increasing altitude. Soil N:P tended to decrease with soil depth and Plot 3 had the greatest N:P; the N:P across the plots ranged from 15.2 to 8.1, being highest at the top 10cm depth at Plot 3 and lowest at the 20-30cm depth of Plot 1.

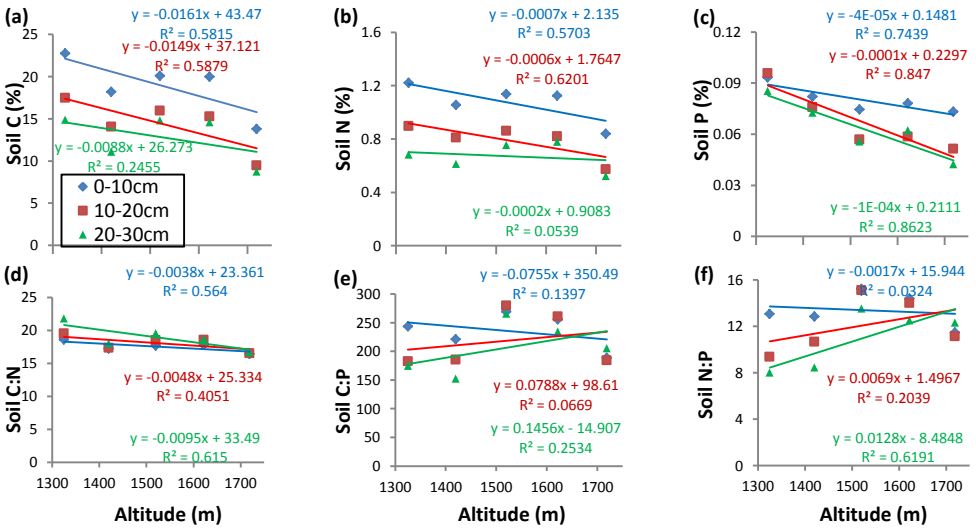

Figure 1: Soil total carbon (C), nitrogen (N), phosphorus (P) expressed as percentages and ratios (*n*=1), across the 5 plots (incrementally spaced every ≈100m in altitude) on Mount Mangaweka. Blue lines and points are 0-10.0cm in depth, Red lines and points are 10.1-20.0cm in depth, and green lines and points are 20.1-30.0cm in depth of soil profile.

The decomposition of *C. pallens*' roots reported in Chapter 4 revealed a slow rate of decomposition but no differences between years or across the altitudinal gradient. The percent C and N of *C. pallens*' roots tended to increase with increasing elevation, especially so for the percent N (Figure 2). The percent root AD-Fibre and cellulose had slight tendencies to increase with increasing elevation; however linear regressions did not reveal a strong fit to the data. Lignin (L) concentrations of *C. pallens*' roots ranged from 14.6% at the uppermost plot to 18.3% at the middle plot (Plot 3). There was a decrease in both the root C:N and L:N ratios with increasing elevation and these trends strongly fit the data. The C:N ranged from 1142 at the lowest altitude (Plot 1) to 86 at the uppermost altitude (Plot 5) and the L:N ranged from 369 at Plot 1 to 26 at Plot 5.

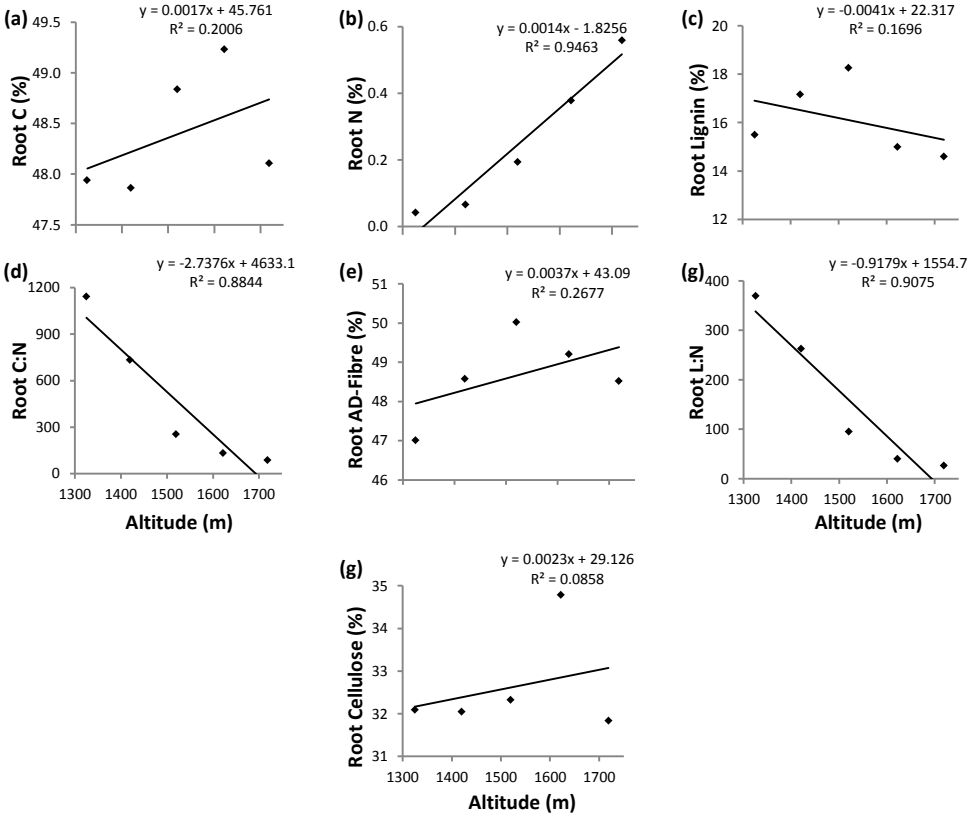

Figure 2: Linear regressions of *Chionochloa pallens*' roots for percent carbon (C), nitrogen (N), lignin (L), AD-Fibre, and cellulose, expressed as percentages, and pertinent ratios of (n=1) across the 5 plots (incrementally spaced every ≈100m in altitude) on Mount Mangaweka.

For *in situ C. pallens*' young leaves the percent C and lignin tended to decrease with increasing elevation across the 400m altitudinal gradient, whereas the percent N tended to increase (Figure 3). There were minimal differences between the average percent of C, N, AD-fibre and cellulose of young leaves from *in situ* and transplanted *C. pallens*', whereas the percent lignin of transplanted *C. pallens* was 36% greater than *in situ* (Table 2). The C:N of young leaves of *in situ* plants was 6.5% greater than leaves of translocated plants. The L:N of young leaves of *in situ* plants was 26.9% lower than leaves of translocated plants. Comparisons of regression slopes of the chemical and constituent composition of young leaves from *in situ* and translocated *C. pallens* across the altitudinal gradient indicate the location of plant destination is more influential on shifting the slope direction than the location of origin (Figure 3).

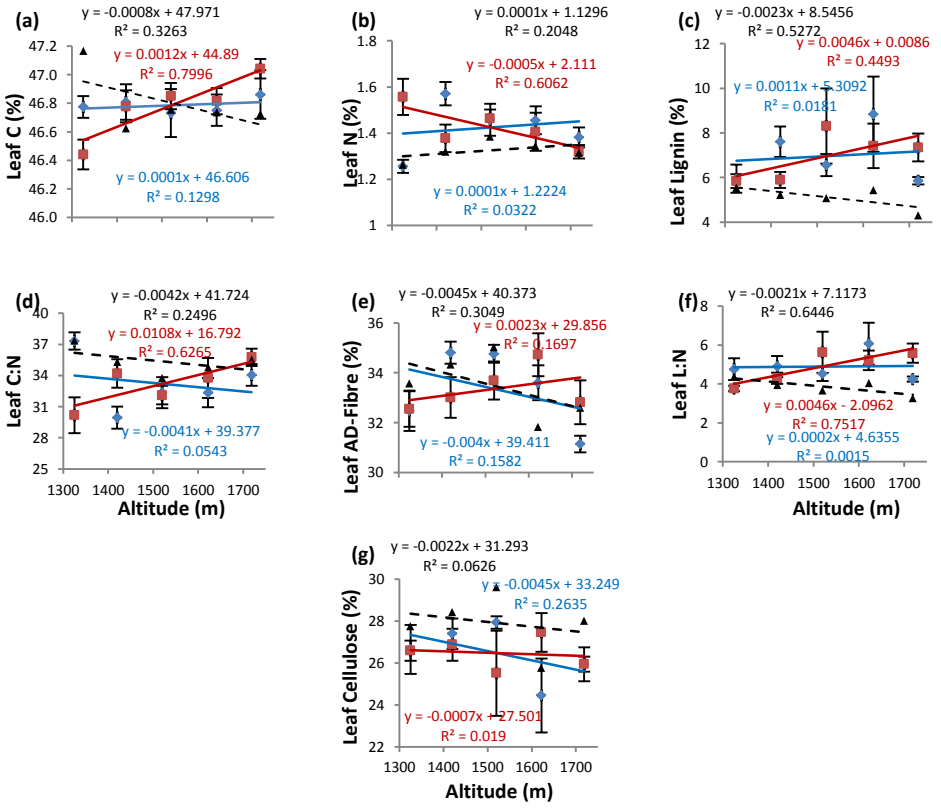

Figure 3: *Chionochloa pallens*' young leaves, linear regression analysis of carbon (C), nitrogen (N), lignin (L), AD-Fibre, and cellulose expressed as percentage of green leaf tissue, and ratios of *in situ* leaves (black; *n*=1) and leaves that emerged following translocation (*n*=5; blue and red denote translocated plants based on origin, and destination respectively) across the 5 plots on Mount Mangaweka. Error bars are standard error.

Table 2: *Chionochloa pallens*' leaves, average percent leaf chemical (Carbon and Nitrogen) and constituent (AD-Fibre, cellulose, and lignin) composition of *in situ*, all translocated plants and up- and downslope transplants across the 400m altitudinal gradient on Mount Mangaweka. Values are expressed as percentage of dry biomass.

	Carbon (%)	**Nitrogen (%)**	**AD-Fibre (%)**	**Cellulose (%)**	**Lignin (%)**	**C:N**	**L:N**
In situ	46.80	1.33	33.47	27.91	5.11	35.35	3.86
Translocated	46.79	1.42	33.36	26.47	6.96	33.20	4.90
Upslope	46.86	1.36	33.93	27.20	6.94	34.76	5.10
Downslope	46.63	1.49	32.65	25.82	6.81	31.53	4.58

For the initial litter of *C. pallens* the percent C decreased with increasing elevation ranging from 47.2 to 46.6 at the lowest and highest plots respectively (Figure 4). Following 2 years of decomposition after translocation, there were slight increase in the percent C compared with the initial, and the differences in percent C between the uppermost and lowest plots was minimal. After 2 years of decomposition the percent N and P were 680 and 167% greater, compared to initial litter concentrations. The initial lignin contents were unchanged with increasing elevation, ranging from 7.8 to 8.5% from plots 1 and 5 respectively, whereas there was a decrease in the AD-fibre and cellulose with increasing elevation. Most of the parameters of the chemical and constituent composition of *C. pallens*' litter after 2 years of decomposition based on origin more closely resembled regression trends to that of the initial litter. Suggesting that translocation across the gradient and environmental factors are influential in altering leaf litter chemistry.

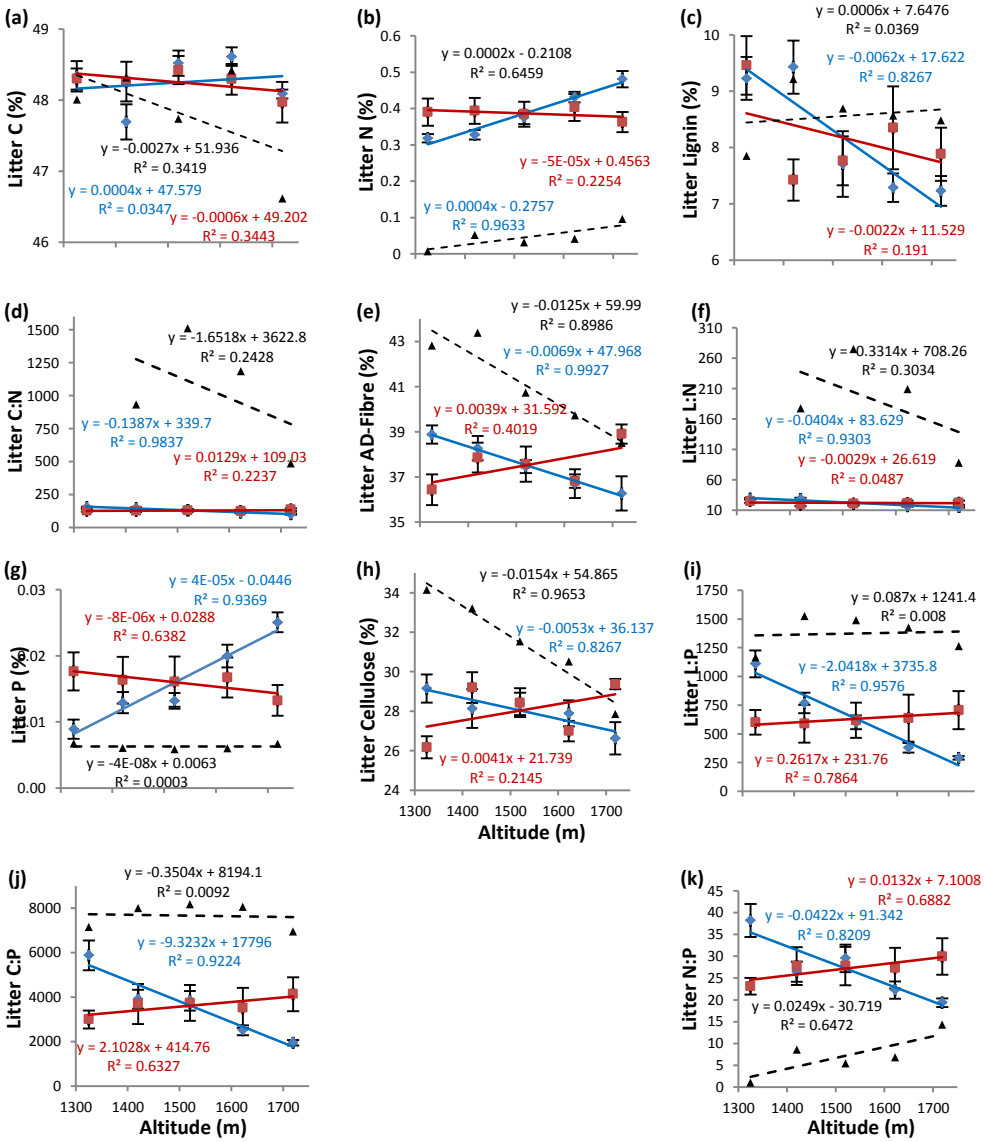

Figure 4: *Chionochloa pallens*' litter, linear regression analysis of leaf litter carbon (C), nitrogen (N), phosphorus (P), lignin (L), AD-Fibre, and cellulose, expressed as percentages, and pertinent ratios for initial values prior to decomposition (black; *n*=1), and after 2 years of decomposition following translocation (blue and red denote translocated litter based on origin (*n*=5) and destination (*n*=5) respectively) across the 5 plots (incrementally spaced every ≈100m in altitude) on Mount Mangaweka. Error bars are standard error.

There were slight increases in the percentages of C, N and P of *C. pallens*' litter after two years of decomposition in the field, following translocation across the plots, compared to initial litter that did not undergo decomposition (Table 3). The percent AD-Fibre and cellulose decreased after decomposition and were more pronounced with the downslope translocation. The percent lignin decreased after decomposition and upslope translocation compared to initial litter, however little change in percent lignin was detected compared with downslope translocation and initial litter. The C:N, L:N, C:P and L:P ratios of decomposed litter all decreased compared to those of initial litter, whereas the N:P ratio increased following decomposition. These stoichiometric ratios were greatest for downslope translocation compared to upslope.

Table 3: Averages of *Chionochloa pallens*' leaf litter chemical [percent carbon (C), nitrogen (N), phosphorus (P)], constituent [AD-Fibre (AD-F), cellulose (Cel), lignin (L)] and subsequent ratios; of initial litter (n = 5), all decomposition treatments after 2 years (n = 25) and decomposed litter following translocation up- (n = 10) and downslope (n = 10) across the 400m altitudinal gradient on Mount Mangaweka. Values are expressed as percentages of dry biomass and subsequent ratios.

	C (%)	**N (%)**	**P (%)**	**AD-F (%)**	**Cel (%)**	**L (%)**	**C:N**	**L:N**	**C:P**	**N:P**	**L:P**
Initial litter	47.8	0.05	0.006	41.04	31.5	8.56	2289	389.9	7661	7.2	1373
Decomposed	48.3	0.39	0.016	37.52	28.0	8.18	129	22.1	3614	27.2	629
Upslope	48.3	0.44	0.02	36.27	26.9	7.87	113	18.8	2513	21.87	424
Downslope	48.1	0.34	0.01	38.43	28.8	8.59	144	26.0	4759	32.6	859

The AIC analysis of the fit of relevant parameters to various aspects of the performance of tissues with respect to their downslope movement reveals potential impacts of climate change. Productivity is largely modelled by aspects of phosphates, and the altitude which plants were translocated to (Table 4). The phosphates' coefficients are the largest component of the relationship. Decomposition is variously related to chemical composition of the soil, and less so by altitude. The P:D ratio is largely affected by the phosphates and also the soil at the destination site, as well as the change in altitude across the gradient.

Table 4: Outcomes from AIC testing of models, with accepted model being the simplest model which is not significantly different from the model with the lowest AIC. The first coefficient is for the Intercept, and the others for the explanatory variables of the accepted model, in that order. See Table 1 for explanation of response and explanatory variables for abbreviations used for the accepted model.

Response variable	Delta AICc	Accepted model	Coefficients
Productivity			
Per tiller	-21.458	Intercept ToAlt P0to10	-0.6401 0.000601 31.0852
Per plant	-57.728	Intercept N0to10 ISP	10.650 77.883 801.221
Per gram	-59.728	Intercept ToAlt P0to10	-0.786 0.00067 25.00292
Decomposition			
Decomposition after 2 years	-21.458	Intercept ToAlt AltDrop CtoN0to10 CtoP0to10 ILP ILLignin	-2.945 -0.0515 15.74 176.3 359.0 35390000 22620
Half life	-44.16	Intercept ToAlt	-1.265 0.00399
P:D ratio for Decomposition after 2 years			
Per tiller	-14.238	Intercept ToAlt P0to10	-3.893922 0.003219 112.709846
Per plant	-6.484	Intercept AltDrop P0to10 CtoN0to10 CtoP0to10 NtoP0to1	426.81 3.832 -606600 34550 -2263 37220
Per gram	-20.968	Intercept ToAlt P0to10	-4.1661 0.0033 94.668

Discussion

There was a decrease in the percent soil C, N and P with increasing soil depth and increasing elevation across the 400m altitudinal gradient on Mount Mangaweka. The root and leaf C:N and L:N ratios of home plot/*in situ C. pallens* plants decreased with increasing elevation. The percent C of leaves and litter decomposition from downslope translocated *C. pallens* plants were greater than that of upslope translocation, whereas the opposite trend was observed with 2yr decomposed litter. The C:N and L:N ratios of leaves from downslope transplants decreased, whereas the L:N of decomposed litter increased with downslope translocation. There was a decrease in the C:N, C:P, L:P and N:P ratios of decomposed litter with downslope translocation. Reductions in these ratios indicate increased decomposability of the litter and thus less C sequestration may be likely to occur through the decomposition component of the P:D ratio with regional warming associated with climate change. Based on comparisons of leaves and litter at the *in situ*/home plots with those of translocations, it appears as though there is some degree of resource allocation differentiation across the ecocline. Of the C and nutrients within the soil and plant tissues, P is the nutrient which is most influential on productivity, mass loss and the P:D ratios across this 400m altitudinal gradient.

Across montane altitudinal gradients the changes in environmental conditions that occur can influence C and nutrient cycling within these ecosystems. Soil organic carbon (SOC) often decreases with increasing soil depth as was observed in arable, temporary grasslands and permanent Swiss agricultural grasslands (Leifeld *et al*., 2005), and on Mount Mangaweka. Leifeld *et al*. (2005) reported an increase in SOC with increasing altitudes, opposite to trends observed on Mount Mangaweka where a decrease in SOC with increasing altitude was observed, more similar to findings of Wang *et al*., (2004). The discrepancies with changes in SOC may be attributed to differences in soil types and land-use practices; Leifeld *et al.* (2005) investigated agricultural soils, whereas Mount Mangaweka is a non-agricultural high-altitude temperate grassland. This decline in soil C at higher altitudes may be attributed to a decline in productivity and

decomposition as was reported in Chapter 4, which would likely influence the soil nutrients.

Soil nutrients can vary across altitudinal gradients, and often decline with elevation (Aerts & Chapin, 1999), which can influence productivity and decomposition of plant material. Lower decomposition rates in cooler environments, i.e. higher altitudes, are most often attributed to lower microbial metabolic activity of decomposers, which ultimately lowers soil nutrients and availability for plants (Brady & Weil, 2008). Wang *et al.* (2004) investigated soil organic matter (SOM), N, P and plant productivity across a 595m altitudinal gradient of alpine meadows. They found greater concentrations of SOM, N and P at lower altitudes compared with higher altitudes, similar to trends observed here with soil N and P declining with ascent along the altitudinal gradient on Mount Mangaweka. Although Wang *et al.* (2004) found a decline of soil nutrients with increasing altitude; they attributed the primary differences in plant productivity across the altitudinal gradient to differences in temperatures. Soil nutrient leaching is often associated with increased precipitation in montane systems which reduces soil nutrient concentrations (Benner & Vitousek, 2010). The increased precipitation at higher elevations in New Zealand montane systems (Leopold *et al*., 2014 and references therein) is a potential cause for the decrease in soil nutrients with increasing elevation on Mount Mangaweka. The decrease of the average soil C:N and increase of the average soil C:P with increasing altitude on Mount Mangaweka may indicate that N is more limited at lower altitudes, whereas P may be more limited at higher altitudes.

Leaf C of *in situ C. pallens* decreased with increasing elevation; however following translocation there was an increase in leaf C based on transplant destination with increasing elevation on Mount Mangaweka. This trend of increasing leaf C with increasing altitude has been observed by others. Hoch & Körner (2012) performed a global meta-analysis of high altitude tress and found leaf C to increase with altitude. Zhao *et al*. (2014) assessed 175 species (which were grouped based on plant growth forms: trees, shrubs and herbs) across an 1800m altitudinal gradient on Changbai Mountain in China. They found all growth forms to have increased leaf C

with increasing altitude and suggested this resulted from an increase in non-structural C compounds (i.e. starch, low molecular weight sugars and storage lipids). Owing to higher stress and less favourable growth conditions experienced by plants at high altitudes (i.e. colder temperatures, increased freeze-thaw cycles, shorter growing season and increased desiccating winds), higher non-structural C concentrations may be accumulated to balance cellular osmotic pressure and resist freezing (Hoch & Körner, 2012; Millard *et al*., 2007; Hoch *et al*., 2002). However, other workers have demonstrated increased production of lignin and polyphenolics to occur with increasing environmental stress as (Kim *et al*., 2008; de Boer *et al*., 2005). The lignin concentrations of *in situ C. pallens* decreased with increasing altitude; however following translocation there was an increase in leaf C based on transplant destination with increasing elevation. This increase in leaf lignin and C following translocation to higher altitudes indicates warmer temperatures associated with climate change will likely to reduce the leaf C content of *C. pallens*.

The initial litter N of *C. pallens* tended to increase with increasing elevation, whereas the initial litter P remained constant across the gradient. Following translocation of litter and 2 years of decomposition, results for plots of origin revealed increases in the N and P and decreases in the C:N, C:P, L:N and L:P. Different stoichiometric patterns have been observed with leaf N and P across altitudinal gradients. Some studies found leaf N and P to decline with increasing elevation (Körner, 1989; Soethe *et al*., 2008; Hoch & Körner, 2012; Macek *et al.*, 2012), while others have observed opposite trends (Köhler *et al*., 2006; Macek *et al*., 2009; Sundqvist *et al*., 2011; Shi *et al*., 2012; Fisher *et al*., 2013). These differences may be attributed to the different species examined and nutrient availability within the systems being studied. Here the litter N:P ratio of *in situ C. pallens* increased with increasing altitude on Mount Mangaweka and this was also observed after 2 years of decomposition based on plot of destination. Across a 500m altitudinal gradient in subarctic tundra of northern Sweden, Sundqvist *et al*. (2011) found leaf N:P to increase with altitude. This trend of increasing leaf N:P with increasing altitude was also observed along a 1800m altitudinal gradient on Changbai Mountain, China (Zhao *et al.*, 2014)

and along an 1830m elevational gradient in NW Himalayas (Macek *et al*., 2012). Altitudinal patterns of leaf N, P and N:P may be influenced by slowing of plant metabolic rates and nutrient availability as well as these interactions (Zhao *et al*., 2014). Within a plant species, the leaf N and P concentrations of plants from low temperature regions may be greater than those from warm temperatures owing to increased demand of N and P for metabolic processes which is likely influence productivity of the species, while leaf N and P should decline monotonically with increasing temperature (Reich & Oleksyn, 2004) as temperature declines with increasing elevation across altitudinal gradients.

When plants within the same species from different populations (native to different temperatures) are planted in a common garden, those from colder environments tend to have greater leaf N and P concentrations compared with plants from warmer environments (Chapin & Oechel, 1983; Reich *et al*., 1996; Oleksyn *et al*., 1998). However, opposite trends between leaf stoichiometric traits of temperature and altitude have also been observed (Zhao *et al*., 2014). On Mount Mangaweka, there was increase of *in situ C. pallens*' leaf and litter N, while no trends were observed with litter P; however, based on origin the litter N and P increased with increasing elevation, resulting in differences in leaf stoichiometry. Alterations in plant growth rate correspond to changes in leaf stoichiometry, where the need for RNA under rapid growth alters leaf P content and thus alters C:P and N:P ratios (Elser *et al*., 2000a; 2000b; 2003). Reductions in N:P may occur with increasing temperatures owing to effects of acclimation and/or adaptation to different temperatures (Reich & Oleksyn, 2004). Low temperatures retard decomposition rates and mineralization of organic matter, thus reducing N and P availability in the soil and thus likely reducing leaf N and P (Reich & Oleksyn, 2004). The C:N, C:P, L:N and L:P ratios are indicators of litter quality and decomposability (Melillo *et al*., 1982; Manzoni *et al*., 2010). Greater mass loss of *C. pallens*' litter were observed at lower altitudes after 2 years of decomposition based on destination of translocation (see Chapter 4); and the lower ratios of C and lignin to nutrients indicate increased decomposability (Melillo *et al*., 1982). Suggesting environmental effects influence the leaf litter chemistry of *C. pallens*' leaf litter through

decomposition. Temperature-related genotypic variation may influence N and P concentrations within leaves (Reich and Oleksyn, 2004). Based on plots of origin and destination for young leaves and decomposed litter of *C. pallens* following translocation, there tends to be a decrease in the C:N, L:N, C:P and N:P when translocated to warmer temperatures. Lower C:N, L:N and lignin concentrations indicate increased decomposability of the litter (Melillo *et al*., 1982) which was observed with increased mass loss of *C. pallens* litter at lower altitudes (see Chapter 4).

Leaf constituents, such as lignin, cellulose, phenolics and tannins, are composed of primarily of C molecules; these compounds within plant tissues can be produced in greater concentrations when plants experience higher abiotic stress (Kim *et al*., 2008). The increased lignin concentrations of transplants compared with *in situ* plants indicates that plants may still be experiencing stress from transplantation shock, as it can take years for plants to recover (Bond *et al*., 2004). The increased production of these compounds would likely result in increased C sequestration owing to recalcitrance to decomposition (de Boer *et al*., 2005). There was a greater concentration of lignin in *C. pallens*' leaves when translocated to the higher stress, higher altitude, environments, indicating that lignin may not only aid in amelioration of stress but also in C sequestration. The greater C:N of *C. pallens* roots at lower altitudes suggests reduced decomposability at lower altitudes.

The C:N and L:N ratios of *in situ C. pallens* plants' leaves, roots and initial litter all decline with increasing elevation, suggesting a decrease in the decomposability of these tissues from cooler environments. However following translocation based on destination, these parameters (as well as the C:P, N:P and L:P) tended to decrease in *C. pallens*' decomposed litter with increasing temperatures at lower altitudes. Reductions in these ratios indicate increased decomposability of the litter (Melillo *et al*., 1982), thus less C sequestration may be likely to occur through the decomposition component of the P:D ratio with predicted warming associated with climate change.

Higher replication of the chemical and constituent components of *C. pallens*' tissues and decomposed litter is desirable. However, the chemical

and constituent analyses of soils and plant tissue are both costly and time consuming, resulting in low replication and the green tissue from youngest leaves (produced after initiation of translocation) are low in weight and would require greater numbers of plants to be translocated and measured. Continued monitoring of translocated plants would allow for further assessment of productivity and chemical and constituent analyses, until these plants cease experiencing shock from transplantation. Decomposition analysis of litter produced from transplanted tussocks would provide further insight as to how decomposition will be influenced by climate change. The use of soil and ecosystem C models, such as the RothC or CENTURY models is needed further investigate how alterations with predicted climate change will influence C cycling and sequestration in New Zealand's tussock grasslands.

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Chapter 6

General Discussion

Celmisia in a sea of *Chionochloa* on Mount Bruce, New Zealand (2013)

Māori proverb
"*Anei tātou nā ko te pō anā tātou nā he rā ki tia*."
"Here we are in the night, but day is on the way."
(There is light at the end of the tunnel)

Discussion

Changes in environmental conditions associated with climate change will likely impact carbon (C) cycling and sequestration (Kirschbaum, 2000; Powlson *et al*., 2011), including in New Zealand's montane tussock grasslands owing to changes in projected temperature and precipitation patterns (NIWA, 2014; IPCC, 2014). High altitude regions are predicted to be one of the areas most affected by climate change according to most global circulation models (IPCC, 2007). In these systems, when descending altitudinal gradients the precipitation decreases whereas temperature increases. Temperature is a primary factor that changes with altitude on mountains (Körner, 2007), resulting in mean annual lapse rates ranging from 0.55 – 0.65^{o}C (Rolland, 2003 and references therein). Precipitation is more variable than temperature patterns across altitudinal gradients (Körner, 2007), but is typically greater at higher elevations in montane regions of New Zealand (Craine & Lee, 2003). Temperature and precipitation are likely to be altered with climate change (NIWA, 2014; IPCC, 2014), both of which are key components of biological processes (Campbell & Reece, 2001), and influence C and nutrient cycling in terrestrial systems (Wu *et al*., 2011). Alterations to C and nutrient cycling in terrestrial systems are likely to impact C sequestration owing to changes in plant productivity, litter decomposition and C sequestration (Kirschbaum, 2000).

In the research presented here, alterations in productivity and decomposition of *Chionochloa* species occurs across altitudinal gradients yielding greater productivity to decomposition ratios (P:D) at warmer climates of lower altitudes. This indicates that more C sequestration occurs at the lower and warmer altitudes, indicating that projected warming associated with climate change will likely increase C sequestration in grassland systems as was found in this research. Across the altitudinal gradients, on both Mounts Tongariro and Mangaweka, there were similarities and differences in both *Chionochloa* species' productivity, decomposition and P:D ratios, which are likely attributed to differences in soil nutrient availability, alterations in leaf litter chemistry and changes in climate (Table 1). These differences observed within species responses across the gradient indicate that ecoclinal differentiation is likely present

and provided an opportunity to investigate a range of responses possible from ecoclinal populations within a species to alterations in climate.

Table 1: General comparisons and changes with decreasing altitude (environmental warming) for trends observed with *Chionochloa* species on Mounts Tongariro and Mangaweka with *in situ* plants and home plot decomposition treatments.

Parameter	**Mount Tongariro**	**Mount Mangaweka**
Species	*Chionochloa rubra*	*Chionochloa pallens*
Mountain type	Volcanic	Non-volcanic
Altitudinal range	700m (986 – 1679m)	400m (1325 – 1719m)
Range of temperature change	4.2^{o}C	2.4^{o}C
Soil C, N, P (0-30cm)	Increases	Increases
Soil C:N (0-30cm)	Decreases	Increases
Soil C:P (0-30cm)	Decreases	Decreases
Productivity (P)	Increases	Increases
Decomposition (D)	Decreases	Increases
Litter decomposability	Chemistry differs	Chemistry differs
P:D ratio	Increases	Increases
Litter C, N, P	Increases	Increases
Litter N	Decreases	Decreases
Litter P	Increases	Increases
Litter C:N	Increases	Increases
Litter C:P	Decreases	Decreases
Litter lignin	Increases	Decreases

The productivity of *C. rubra* and *C. pallens* (obtained from leaf elongation, dieback and tip-loss measurements) increased at lower elevations of warmer climates across the altitudinal gradients on Mounts Tongariro and Mangaweka respectively. Similar trends have been observed with increased leaf elongation rates of *Chionochloa* species at lower altitudes (Mark, 1965a; 1965b; 1965c; 1969), as was found in the research presented here prior to transformation of leaf elongation data into productivity. The *in situ* productivity of *C. pallens* and *C. rubra* was significantly greater at lower elevation in the warmer environments in New Zealand montane systems. On Mounts Tongariro and Mangaweka, *Chionochloa* species at the lower altitude plots had 40.2 and 135.6% greater average productivity per tiller than higher elevation plots respectively. Abiotic factors such as climate and nutrient availability have been shown to increase productivity when descending altitudinal gradients (Raich, *et al*., 1997; Takyu *et al*., 2003). In addition to differences in climate conditions across the gradients (primarily temperature and precipitation), one of the causes that would influence *Chionochloa's* productivity is the decline in soil

nutrients (N and P) with increasing altitude (Stevens, 1992). From the translocation of *C. pallens* plants on Mount Mangaweka, the productivity based on plot of origin indicates plants from higher altitudes are more productive, and thus may be more plastic in responses to changes in environment. The productivity based on plot of destination shows plant performance is best at warmer plots (i.e. lowest altitude plot), implying a strong environmental control of temperature.

One of the primary factors that influence the decomposition of plant litter is climate (Coûteaux *et al*., 1995; Lavelle *et al*., 1993), where increased decomposition results from elevated temperatures (Wasley *et al*., 2006) and/or increased precipitation (Murphy *et al*., 1998; Bryant *et al*., 1998). The decomposition of *Chionochloa* leaf litter revealed differences based on location of litter destination across the gradients on Mounts Tongariro and Mangaweka. Decomposition of *Chionochloa* litter based on location origin did not express significant differences in treatments following full reciprocal translocations across plots on Mounts Tongariro and Mangaweka, indicating no sign of genetic or plastic differentiation. However, treatment effects for decomposition based on litter destination were apparent after 2 and 3 years for Mounts Mangaweka and Tongariro respectively (indicating environmental control), although differing trends were observed. On Mount Tongariro there was a decrease in mass loss of *C. rubra* leaf litter with decreasing altitude, which is likely attributed to a declining precipitation gradient. This finding is similar to what Murphy *et al*. (1998) found, where precipitation was determined to be the prominent driver of decomposition along a semiarid montane gradient in northern Arizona; mass loss increased at higher altitudes because of greater moisture availability. It was concluded that warmer temperatures and increased precipitation would likely increase decomposition rates (Murphy *et al*., 1998). On Mount Mangaweka there was an increase in the mass loss of *C. pallens*' leaf litter with decreasing altitude, which is likely attributed to a temperature gradient. This trend was also observed along an altitudinal gradient in northern Sweden, where mass loss of multiple species' litter was significantly greater in the warmer climates of lower altitudes (Sundqvist *et al*., 2011a; 2011b). The differences in decomposition of *C. pallens* and *C.*

rubra suggest environmental influences to be the prominent driver of decomposition; however leaf litter chemistry also plays an important role in decomposition (Hobbie, 1996).

Reduced temperatures can lower mineralization of organic matter, reducing soil N and P availability and likely reducing leaf N and P (Reich & Oleksyn, 2004). The differences in decomposition across the gradients on Mounts Tongariro and Mangaweka may be attributed to differences in the chemical composition of the initial litter (i.e. litter which had not undergone decomposition). During decomposition, *C. rubra*'s litter on Mount Tongariro tended to increase in C and N content and decrease in P, whereas the content of *C. pallens*' litter on Mount Mangaweka decreased in C, increased in N, and the P was more variable in expression within litter. The use of ecological stoichiometry in this study provided insight into the importance of nutrient concentrations within the soil, leaves and litter in regards to productivity and decomposition. However the use of isotopic labelling and isotopic tracers within these three components could provide better insight into the C and nutrient cycling (Di *et al*., 2000 and references therein) across environmental gradients and how climate change may further alter these interactions. In addition, the use of eddy covariance would provide direct measurements of C exchange between terrestrial systems and the atmosphere and would allow for assessment of alterations to the net ecosystem C balance (Serrano-Ortiz *et al*., 2014) across the altitudinal gradients.

Across montane gradients, lower temperatures associated with higher altitudes increase the abiotic stress which plants experience and can result in not only reduced productivity (Callaway *et al*., 2002) and decomposition (Murphy *et al*., 1998), but also an increase production of lignin and phenolics. These can act as protective compounds to increased stress (Kim *et al*., 2008) which in turn retard decomposition and increase C sequestration (de Boer *et al*., 2005). On Mount Tongariro, the lignin concentration of *C. rubra*'s initial litter decreased at the colder environment whereas the opposite trend was found on Mount Mangaweka with *C. pallens*. These findings likely contribute to the observed differences in mass loss of *Chionochloa* species across the gradients.

Despite the differences in *Chionochloa* litter's chemical composition and decomposition rates across gradients, there was still a decline in P:D ratios with increasing altitude for both *C. rubra* and *C. pallens* on Mounts Tongariro and Mangaweka respectively. This indicates that more productivity occurs per unit decomposition at lower altitudes of warmer environments, thus resulting in more C sequestration occurring with *Chionochloa* species. There is a fine balance to positive and negative feedbacks with climate change and alterations in productivity and decomposition can influence C sequestration based on which factor is most influenced by warming (Kirschbaum, 2000). A negative feedback would likely occur when the temperature sensitivity of productivity is less than the temperature sensitivity of decomposition. Since *Chionochloa* species' productivity increase outweighed its decomposition responses at warmer locations (lower altitudes), this indicats a negative feedback on climate change will occur with climate change, since more C is being removed from the atmosphere. However, on Mount Mangaweka the decomposition of *C. pallens*' litter also increases when moved to warmer environments, indicating a positive feedback to climate change owing to more C being released from decomposition. The plasticity of *Chionochloa* species response of increased productivity with warming outweighs the increase in decomposition associated with warming as indicated by an increasing P:D ratio descending the altitudinal gradient to warmer climates. This indicates that predicted warming, within the 2^{o}C temperature increases predicted to occur at the end of the century (NIWA, 2014; IPCC, 2014), associated with climate change will increase the C sequestration potential of *Chionochloa* species.

The amount of C sequestration of *Chionochloa* is likely to vary not only because of changes in environmental conditions, but also because of different responses of ecoclinal populations across the gradients, as was observed in response parameters of productivity, decomposition as well as the chemical and constituent composition of the litter. It is possible to calculate the relative importance that plasticity has in response to the genetic and environmental components (Schlichting, 1986) However, this was not the primary focus of this research, but would make for an interesting follow

up study with use of data collected for this research. The importance of using ecoclinal populations of *Chionochloa* across gradients was to understand the range of variation in the above parameters that is possible within a species across altitudinal climate gradients, but more importantly how these responses would impact C sequestration. The responses observed in the P:D ratios between both species of Chionochloa were unaffected by differences between the species, still indicating C sequestration to be greatest at warmer locations.

The means by which C sequestration potential of *Chionochloa* species was assessed with calculated P:D ratios of productivity and decomposition, has both its advantages and limitations. Transplantation shock can reduce the productivity of transplants which are likely to take years to recover and to express physiological adaptations to the new environment (Close *et al.*, 2005 and references therein). Thus, not only were the transplants experiencing new climates but they were also suffering from transplantation, calculated as reducing productivity up to 40%. The transplantation of plants across altitudinal gradients did alter the climatic conditions; but some soil, soil nutrients and soil microbes were also translocated from the locations of plant origin. The microbial community is likely to adapt to the new environmental conditions over time, and the soil nutrients are likely to rebalance with time; however the impacts that this will have on productivity are unknown and further monitoring is needed. Non-destructive monitoring of tillers over multiple years was needed as a means to assess the leaf elongation, dieback and tip-loss, all of which were included in the calculations for productivity based on leaf length to biomass transformations. Further investigation into the dieback and tip-loss would provide clarification of the rates at which litter is entering the system. The rates of dieback in some *Chionochloa* species have been shown not to vary with altitude (Mark, 1969). However, tip-loss is likely to vary across the gradient owing to increased winds and freeze thaw cycles at higher altitudes and a likely increased rate of herbivory from mammal sand invertebrates at lower altitudes likely attributed to increased density at lower elevations (Hodkinson, 2005).

Owing to the limitations of the research, some key belowground processes were unable to be investigated. The investigation of root productivity and turnover would have provided better insight and a more holistic C and nutrient accounting and C sequestration (Gill & Jackson, 2000) occurring by *Chionochloa* species. In grassland systems, root turnover and decomposition play an important part in C sequestration (Scurlock & Hall, 1998). In this study, root decomposition of *C. pallens* did not indicate any significant differences across treatments or years. The C content of *C. pallens*' roots tended to increase with increasing elevation across the gradient on Mount Mangaweka. The percent lignin concentration of initial roots was 5.3 times greater than that of initial leaf litter, which would likely increase C sequestration within the soil. The residence time of root C within soils is typically longer than that of shoot material and the amount of root C incorporated into the soil through root turnover processes are a of the total soil C (Rasse *et al*., 2005). However, a decrease in soil C was observed with increasing elevation.

The use of litter bags (black nylon mesh with a 2mm pore space) to assess decomposition of roots and leaf litter not only excluded many invertebrates (allowing for primarily microbial and fungal decompositional processes), but also likely altered the microenvironment within the decomposition bags by increasing the ambient temperature and excluding ultra-violet radiation, both of which would alter the "natural" decomposition process (Boulton & Boon, 1991 and references therein). The decomposition bags also minimized litter contact with the substrate (i.e. soil surface, low-lying vegetation, and/or other litter), which would also influence decomposition rates (Boulton & Boon, 1991). However, the same methods of decomposition were used across all plots on Mounts Tongariro and Mangaweka; thus the error of these limitations to this method was evenly distributed across all treatments. When tip-loss of *Chionochloa* occurs, the dead portions of the leaves are often observed embedded within the base of the tussock or other neighbouring vegetation which would likely influence the microclimates of different regions of the embedded leaves and alter decomposition of these regions.

The decomposition portion of research presented in previous chapters underestimates the true annual contribution of decomposition of the leaf litter occurring within the system, since tip loss was only calculated for the years of the experiment and much older litter present from previous years would still be decomposing. Less recalcitrant compounds (i.e. those which are more easily decomposed with low C:N and/or C:P ratios such as amino acids and sugars) will likely be removed from the system first via decomposition, whereas highly recalcitrant compounds will remain for much longer duration and aid in C sequestration (see Figure 3 in Krna & Rapson, 2013 and references therein). The decomposition half-life is important as a means to extrapolate these contributions to the release of C from decomposition, as this provides a more complete system-level estimate of decomposition.

For the downslope translocations, scaling up the P:D ratios to the system level, as productivity (₱) and decomposition (Ð) per unit area (as $g/m^2/yr$), required multiplication of productivity and tip-loss (i.e. the litter contributed annually by the system to the substrate) per plant by plant density at each plot. The decay rate coefficients (k) of the half-lives for litter decomposition were used to estimate the amount of mass loss annually over 50yrs of decomposition, reflecting the contribution to C loss from the system, of litter which would logically have been added to the system by the plants in years previous to the experimental period, and would be well past the initial period of mass loss measured here.

For the downslope translocations, the ₱:Ð ratio was plotted against temperature changes experienced assuming a mean annual lapse rate of 0.6^oC per 100m in elevation. As the temperature warms, the ₱:Ð increases almost 40-fold (Figure 1). Thus, for a constant unit of C loss (via decomposition), a substantial increase in productivity occurs resulting in more C being added to the system than is being removed based on aboveground processes. The rates of productivity are more greatly impacted with warming than the rates of decomposition of *Chionochloa* litter. Thus with warming of 2^oC under predicted climate change scenarios for New Zealand, the expectation is greater C sequestration will occur in the tussock grasslands owing to greater increases in productivity than decomposition.

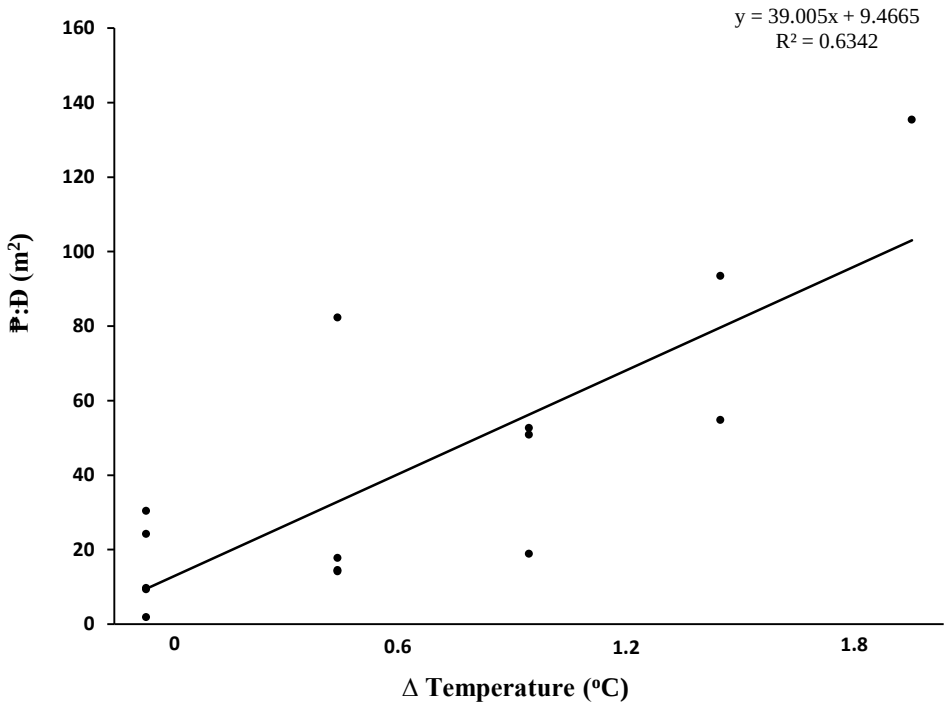

Figure 1: Productivity (Ꝑ) to decomposition (Đ) ratios of *Chionochloa pallens* scaled up to m^2 across the change (Δ) in temperatures, assuming a 0.6°C mean annual lapse rate, across the 5 plots on Mount Mangaweka.

Owing to the plasticity of responses of *Chionochloa*'s growth, productivity and leaf chemistry to changes in climate conditions, differing responses of ecoclinal populations are likely to occur with climate change. The decomposition of *Chionochloa* litter is primarily environmentally controlled as no significant differences were observed in mass loss based on location of litter origin across the gradients. In the short-term, *Chionochloa* populations of higher altitudes are likely to express responses to climate change similar to those of lower altitudes (and plants translocated from other altitudes in these experiments are likely to acclimate their productivity similar to *in situ* plants) owing to plasticity of responses. It can take years, even for perennial tussocks, to replace all its home plot tissues with one appropriate to the destination plot. In the mid-term, prolonged acclimation to "new" environmental conditions of *Chionochloa* is likely to result in genetic shifts, which could be similar to current genomics of lower altitude populations. There is likely to be differing lag times in the adjustment of soils as the microbial community will adapt quickly, but the soil C and nutrient stoichiometry is likely to take longer to stabilize. In the long-term,

with all else remaining constant (which is highly unlikely since, "the only thing that is constant is change" according to Heraclitus *circa* 500BC), populations will stabilize to climax communities and the P:D ratios should stabilize as somatic C sequestration reaches equilibrium (Krna & Rapson, 2013). However this may take centuries to occur since climate change is an ongoing process and residence times of C within tussock grassland soils can persist for centuries (Tate *et al*., 1995).

The research presented here is primarily at the leaf and plant level. Scaling up to the ecosystem level (which is different research approach that may be hampered by community variability, would provide a more holistic estimate of C sequestration in New Zealand's tussock grasslands), since these systems are considered an important C store both in New Zealand (Trotter *et al*., 2004) and globally (Scurlock & Hall, 1998). Thus, alterations to climate that influence the C sequestration of the system would likely have important ramifications at local and global scales. *Chionochloa* species are typically the dominant species in the tussock grasslands (Mark, 1969) and thus may even be considered the keystone species in regards to C sequestration in these systems. However, other plant species (even microbial, fungal, and/or herbivore species) within these systems will contribute to the overall C and nutrient dynamics. Belowground processes (i.e. fine root turnover, root exudates and root productivity) are also important to consider with C sequestration in grassland systems (Burke *et al*., 1998 and references therein). Analysis into the composition of fungal and microbial communities across the gradients would provide a better understanding of decompositional processes observed across the gradients, as well as soil microbial C and respiration, since their role in decomposition can influence C and nutrient cycling (Six *et al*., 2006).

Kirschbaum's (2000) equation, similar to the P:D ratio used in this study, indicates the applicability of his equation to an array of systems; and the P:D ratio used here is also applicable to other systems and species. Annuals complete their life cycle within a year and the amount of C sequestration is likely to be low owing to their high decomposability, as they primarily allocate to photosynthetic structures that are easily decomposable (Aerts & Chapin, 1999); thus their contribution to C

sequestration is likely to be minimal and investigations into this should look at a shorter time frame than one year. On the other hand, species with low growth rates tend to be long lived and produce nutrient-poor litter (Aerts & Chapin, 1999), as is the case with some woody species. However, when factoring in the C sequestration potential and contributions of woody species, temporarily utilized biologic C and somatic C needs to be accounted for, and removed from being classified as sequestered, as this C is still accessible to the plant and should not be classified as sequestered C (Krna & Rapson, 2013).

Future studies

Meta-analysis of productivity and decomposition experiments, performed across altitudinal and environmental gradients, could assess how the P:D ratios of different species in different environments across a global scale can impact C sequestration in response to climate change. New Zealand's biogeography of 25 different *Chionochloa* provides a unique opportunity for investigation of the responses of productivity and decomposition of other species within this genus, while minimising genetic differences, across both altitudinal and latitudinal gradients, as climate change is likely to impact gradients across latitudes in dissimilar fashions (Rind, 1998). The encroachment of woody species and an increase in the altitude of the treeline is likely to influence resource availability, C dynamics, species composition as well as productivity and decomposition (Lett & Knapp, 2005 and references therein). Future investigation to alterations in C and nutrient cycling occurring via encroachment of woody species will be needed in the near future. The use of soil and ecosystem C models, such as the RothC or CENTURY models, is needed to further investigate how alterations with predicted climate change will influence C cycling and sequestration in New Zealand's tussock grasslands. Since soils play a vital role in mitigating the effects of elevated atmospheric CO_2 concentrations with C sequestration (Lal, 2004a), considering the global soil C pool (2500 Gt) is approximately 3.3 and 4.5 times larger than the atmospheric and biotic C pools respectively (Lal, 2004b).

Conclusions

The average surface temperatures of New Zealand in 2090 are likely to increase by 2^{o}C above the 1990 average temperatures, which is likely to alter precipitation patterns across the nation (NIWA, 2014; IPCC, 2014). Findings and results presented here suggest it will likely result in greater C sequestration in New Zealand's tussock grasslands. Warmer temperatures at lower environments yield increases in *Chionochloa* productivity and as well as decomposition, but precipitation may also be an important driver of decomposition. Despite the environmental contributions to decomposition, it appears as though productivity is more influenced by changes in climate, owing to plasticity of responses, than decomposition which is primarily environmentally mediated. Across the gradient on Mount Mangaweka, the variation in responses of *C. pallens* plants in regards to growth and nutrient content and leaf and litter stoichionmetry suggest ecoclinal differentiation, and allows for a better assessment of the range of responses available within a species to alterations in climate. Translocation to warmer environments increases the P:D ratio of *Chionochloa* species and thus projected warming associated with climate change will likely increase C sequestration in New Zealand's tussock grasslands, providing an economic imperative to the conservation of these spectacular systems.

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