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INTERACTIVE EFFECTS OF WARMING AND ATMOSPHERIC NITROGEN DEPOSITION ON PLANT NET PRODUCTIVITY AND SPECIES COMPOSITION IN A TEMPERATE OLD FIELD

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INTERACTIVE EFFECTS OF WARMING AND ATMOSPHERIC NITROGEN DEPOSITION ON PLANT NET PRODUCTIVITY AND SPECIES COMPOSITION IN A TEMPERATE OLD FIELD

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by

Jennifer S. Hutchison

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of the requirement for the degree of
Master of Science

SCHOOL OF GRADUATE AND POSTDOCTORAL STUDIES

The University of Western Ontario
London, Ontario, Canada

CERTIFICATE OF EXAMINATION

Supervisor

_____

Dr. Hugh Henry

Supervisory Committee

_____

Dr. Paul Cavers

_____

Dr. Ben Rubin

Examiners

_____

Dr. Sheila Macfie

_____

Dr. Greg Thorn

_____

Dr. Ben Rubin

The thesis by

Jennifer Sharon <u>Hutchison</u>
entitled:

Interactive effects of warming and atmospheric nitrogen deposition on plant productivity and species composition in a temperate old field

is accepted in partial fulfillment of the
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ABSTRACT

Both climate warming and atmospheric nitrogen deposition are predicted to alter plant productivity and species composition over the next century; however, the extent to which their effects may interact is unclear. I measured plant productivity and species composition in response to warming (winter-only or year-round) and nitrogen in a temperate old field. I used shoot allometric relationships and spectral data to estimate productivity non-destructively, and sampled root biomass destructively, throughout two growing seasons. In 2007 there were no treatment effects on plant growth. However, in 2008, both warming and nitrogen addition increased aboveground productivity, and these effects were additive, resulting in an approximate doubling in aboveground plant biomass. Warming increased belowground biomass but no nitrogen effect was evident. Conversely, nitrogen addition increased plot greenness but greenness did not respond to warming. My results do not support the hypothesis that warming-induced changes to soil freezing dynamics over winter reduce plant productivity.

Keywords: atmospheric nitrogen deposition, *Bromus inermis*, climate change, NDVI, plant productivity, *Poa pratensis,* temperate old field, warming

CO-AUTHORSHIP STATEMENT

A manuscript will be submitted based on the content in Chapter 2 of this thesis, with Hugh Henry as the co-author.

DEDICACTION

I dedicate this to my family, especially my sister Christine, whose strength, determination, and ability to strive for the best despite the obstacles that come her way continue to inspire me each and every day.

ACKNOWLEDGEMENTS

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CHAPTER ONE: INTRODUCTION

1.1 Global climate change

Humans have accelerated global climate change as a result of agricultural and industrial intensification and the burning of fossil fuels for electricity, heating and transportation, all of which have increased the concentration of greenhouse gases in the atmosphere. Warming has generally been greater over land than the oceans, and the anticipated increase in the mean temperature of the earth's surface over the next century ranges between $1.1 - 6.4°$ C based on general circulation models, with the greatest warming occurring at high latitudes (Houghton *et al,* 2001; IPCC 2007). The intensity of warming will also vary seasonally, with greater warming occurring over the winter than over summer (IPCC 2007). To date, daily temperature records show a decrease in the number of very cold days and nights and an increase in the number of extremely hot days and warm nights for many regions of the world. The length of the frost-free season has increased in most mid- and high- latitude regions of both hemispheres, and in the northern hemisphere, this leads to an earlier start to spring (IPCC 2007).

Arctic and alpine systems are predicted to experience the greatest increase in warming, especially over winter, where an increase of 7-8 °C will occur by 2050 (Canadian Centre for Climate Modeling and Analysis 2006), and the responses of these systems to warming have been studied extensively (Clein and Schimel 1995; Schimel and Chapin 1996; Schimel *et al.* 2004; Schimel and Mikan 2005; Grogan and Jonasson 2003; Grogan *et al.* 2004; Larsen *et al.* 2002, 2007; Edwards *et al.* 2006; Miller *et al.* 2007; Buckeridge and

Grogan 2008). Temperature is a key factor that regulates many terrestrial ecosystem processes, such as soil respiration (Rustad *et al.* 2001), trace gas emissions (Muller *et al.* 2002), litter decomposition (Aerts *et al.* 2006), N mineralization and nitrification (Macdonald *et al.* 1995), and root dynamics (Gill and Jackson 2000, Weih and Karlsson 2002). However, the effects of temperature on ecosystems may be modified by changes in precipitation. Precipitation is expected to increase in some regions of the globe over the next century but unlike warming it will remain the same or decrease in many other regions (IPCC 2007). In addition, warming may reduce water availability independently of changes in precipitation by increasing evaporation rates and decreasing snow pack thickness. The effects of warming on plants may interact with other influential global-change factors, such as increased atmospheric CO_2 and changes in precipitation (Arft *et al.* 1999; Dukes and Mooney 1999; Kimball *et al.* 2002; Dunne *et al.* 2003; Penuelas *et al.* 2002).

1.2 Warming treatments in field experiments

Techniques used to study soil warming in the field include open-top chambers (Henry and Molau 1997; Arft *et al.* 1999), polyethylene tents (Wookey *et al.* 1993), buried warming cables (Peterjohn *et al.* 1994), heated, fluid-filled tubes on the soil surface (Hillier *et al.* 1994; Marion *et al.* 1997), passive night-time warming (Hollister & Webber 2000), and overhead infrared heaters (Nijs *et al.* 1996). Of these techniques, overhead heaters are the most appropriate because they mimic natural warming by heating soil from above (Shen and Harte 2000). Snow removal experiments have also been used to simulate climate warming (Groffman *et al.* 2001; Fitzhugh *et al.* 2001).

However, unlike natural snow melt, which usually occurs in combination with above-freezing air temperatures, snow removal may expose soils and over-wintering plants to unrealistically intense soil freezing (Henry 2008).

1.3 Effects of warming on herbaceous plants

1.3.1 Phenology

Global climate change could alter plant phenology significantly because temperature influences the timing of development (Walther *et al.* 2002; Penuelas *et al.* 2002; Badeck *et al.* 2004). With warmer air temperatures, an earlier snowmelt can also play a role in driving plant phenological changes. For example, Inouye *et al.* (2000) found that flowering date advanced with a lower snowpack depth or with an earlier snowmelt date in a subalpine meadow, and advanced flowering time has also been associated with a total lower snowfall, shallower snowpack or with an earlier snowmelt in other subalpine, alpine and arctic systems (Inouye and McGuire 1991; Shaver and Kummerow 1992; Walker *et al.* 1995).

Growing season length in the northern hemisphere, particularly at higher latitudes, where temperature rise has been the greatest (Myneni *et al.* 1997), has had an estimated increase of 1.1-4.9 days per decade within the last 50 years (Menzel 2003). While climate warming may lead to an earlier spring emergence and hence an earlier onset of flowering (Bradley *et al.* 1999; Primack *et al.* 2004), phenological flowering responses to climate change may often be species specific (Galen and Stanton 1995). Early flowering species tend to be the most responsive to warming (Fitter and Fitter 2002). Conversely,

in alpine meadow forbs, warming delayed the flowering date (Dunne *et al.* 2003), and

flower production by early flowering forbs has decreased with the lower winter snow

accumulation and earlier spring melt resulting from warming treatments (Saavedra *et al.*

2003). In a grassland ecosystem, warming accelerated the onset of flowering (Cleland *et al.* 2006), and led to an increase in growing season length for some species (Dukes *et al.* 2005).

1.3.2 Productivity

Warming treatments in field experiments tend to increase plant biomass, and this

increase is linked to early germination as well as the lengthening of the growing season

(Arft *et al.* 1999). Press *et al.* (1998) reported an increase in productivity of 125% in

response to warming. In a meta-analysis of ecosystem-level warming experiments,

warming increased aboveground plant productivity by approximately 19% (Rustad *et al.*

2000). This response was greatest in cold ecosystems, with the strongest response in the

tundra sites. The direct effects of warming on plants are likely to be most pronounced in

systems where primary productivity is strongly limited by the brevity of the snow-free

growing season, and where spring snowmelt serves as an environmental cue that initiates

growth and flowering (Walker *et al.* 1995, Henry and Molau 1997). However, adverse

effects of climate warming on the productivity of plant communities could be due to

increased by temperature stress (White *et al.* 2000). Warming has had a negative effect

on productivity in some systems (De Boeck *et al.* 2008), and no net effect in others

(Chapin *et al.* 1995, Chapin and Shaver 1996). Furthermore, different groups of plants

may respond differently within an ecosystem, as demonstrated in a study by Arft *et al.*

(1999), in which herbaceous species responded more strongly and consistently by increasing vegetative growth than did woody species.

The responsiveness of herbaceous species to warming may be attributed to their more flexible morphology and greater ability to take up nutrients (Shaver *et al.* 1992). In general, changes in species composition in response to increased temperatures will depend on changes in nutrient availability and competitive interactions among species (Callaghan and Jonasson 1995). Warming of the soil can increase rates of microbial processes such as litter decomposition (Hobbie and Chapin 1996; Van Cleve *et al.* 1990), thereby increasing the availability of nutrients (Rustad and Fernandez 1998). Rates of nitrogen mineralization are expected to increase as soils warm (Rustad *et al.* 2001), and with rising temperatures nutrient uptake by roots will also increase (BassiriRad 2000).

Warming-induced increases in plant productivity may be a direct effect of increased rates of photosynthesis at higher temperatures (Korner and Larcher 1988), although warmer temperatures may also increase evapotranspiration, thereby increasing water stress. When mineral nutrients or water are limiting, plants allocate more to root growth than to shoot growth (Stitt and Scheible 1998). Root phenology is linked to both temperature and soil moisture (Tierney *et al.* 2003). In arctic ecosystems root production may increase in response to warming (Sullivan and Welker 2005). Warming may also lead to an increase in root production in other systems (Majdi and Ohrvik 2004), with increased root carbon-allocation (Carlen *et al.* 1999). However, Edwards *et al.* (2004) reported that warming itself, without soil drying, had a negative effect on root biomass in temperate grasslands through increased root death. Batts *et al.* (1998) also observed that

while root biomass as a percentage of total plant biomass increased with increasing CO_2, it decreased with increasing air temperature.

1.3.3 Shifting plant range and diversity

Climate warming is expected to affect species abundance and distribution (Iverson and Prasad 1998). Plants have had clear responses to warming with a northward extension of species' distributions in northern, cold/wet and southern, warm/dry ecosystems (Myneni *et al.* 1997; Parmesan and Yohe 2003; Menzel *et al.* 2006). However, as distributions extend northward, suitable habitat and soil conditions may not be available, and mutualistic associations with organisms such as mycorrhizal fungi and pollinators may not be maintained properly. Climate-warming effects on plant phenology could further disrupt relationships between plants and their mutualists. Generally, in long-term warming experiments, plants increase in cover and height while diversity and evenness decrease (Walker *et al.* 2006). In these experiments, species richness has decreased as a result of the loss of the less abundant species (Chapin *et al.* 1995; Walker *et al.* 2006).

1.4 Nitrogen as a limiting element in ecosystems

The atmosphere contains approximately 78% nitrogen in the form of dinitrogen gas, yet this form of nitrogen is not directly available to most organisms. Instead, nitrogen fixation must first occur, breaking up the stable triple covalent bond between the two nitrogen atoms to produce ammonia (NH_3) or nitrate (NO_3^-). This reaction can be accomplished by both industrial and natural processes but it is energetically costly.

Biological nitrogen fixation is only performed by a select group of microorganisms (White 1993). Nitrogen demand in plants is high relative to other mineral nutrients; nitrogen is an important component of many important structural, genetic and metabolic compounds in plant cells, and it is a major component of chlorophyll, amino acids and proteins (Taiz and Zeiger 1991). As a consequence of the short supply of nitrogen to plants and their high nitrogen demand, nitrogen is the major limiting nutrient influencing most terrestrial ecosystems, influencing ecosystem diversity, species composition and nutrient cycling and retention (Vitousek and Howarth 1991; Vitousek *et al.* 1997; Aerts and Chapin 2000; Clark and Tilman 2008).

Nitrogen deposition is the input of reactive nitrogen compounds from the atmosphere to the biosphere, either in the form of wet deposition (rain and snow) or dry deposition (dust particles). Due to human activities such as agricultural and industrial intensification, which add more reactive nitrogen to the environment (Vitousek *et al.* 1997), global reactive N is projected to increase from 156 Tg N yr^{-1} in the 1990s to 270 Tg N yr^{1} by 2050 (Galloway *et al.* 2004). The dominant forms of reactive nitrogen in the atmosphere are ammonium and nitrate, with the former predominant near agricultural areas and the latter in the vicinity of urban and industrial areas (Sickles and Shadwick 2007).

1.5 Ecosystem effects of increased atmospheric nitrogen deposition

1.5.1 Productivity

Both the short- and long-term effects of nitrogen addition, both chronic and acute, have been studied extensively, and nitrogen additions alter primary production and

nutrient cycling in most terrestrial ecosystems (Matson *et al.* 2002). Competition for light tends to increase with nitrogen addition (Wilson and Tilman 1991), and this may be of advantage for tall or fast growing species (Aerts 1999). For example, increased dominance of grasses over forbs can result from long term nitrogen fertilization (van Heerwaarden *et al.* 2003; Gusewell 2005), and increased nitrogen can also increase the water-use efficiency of woody invaders in temperate grasslands (Bert *et al.* 1997). However, large nitrogen additions to forest systems have also led to nitrogen saturation, leading to increased nitrogen leaching and tree mortality (Magill *et al.* 2000).

While aboveground biomass often responds positively to nitrogen additions, most fertilization studies on nitrogen-limited sites show that increasing nitrogen availability does not increase fine root biomass (Nadelhoffer 2000), although root turnover and production may increase (Gundersen *et al.* 1998; Nadelhoffer 2000). Nitrogen addition can also decrease the activity of nitrogen-fixing organisms and decrease mycorrhizal root tips (Parrent *et al.* 2006). Treseder (2008) also found that nitrogen tends to suppress fungal growth rates, and in areas of Europe most affected by nitrogen deposition a decline in fruiting by mycorrhizal fungi has been observed (Arnolds 1991).

1.5.2 Plant species diversity

While short-term nitrogen additions can increase plant productivity without changing plant diversity or plant composition, long term nitrogen enrichment decreases plant species richness, increases biomass and shifts the composition of vegetation to a few dominant species with high tissue quality (Aerts and Berendse 1988; Huenneke *et al.*

1990). Nitrogen deposition has been repeatedly observed to reduce grassland diversity by increasing the dominance of common species (Huenneke *et al.* 1990). Forb diversity has been found to decline following nitrogen additions in temperate grasslands (Goldberg and Miller 1990; Foster and Gross 1998) and in California grasslands (Zavaleta *et al.* 2003). Soil nitrogen content can affect plants during the spring by inhibiting the establishment of new seedlings while promoting the growth of other species (Foster and Gross 1998). Nitrogen additions can also affect plant flowering phenology. For example, nitrogen addition to a grassland ecosystem caused accelerated flowering in most forbs and delayed flowering in grasses, while flowering in *Vicia sativa*, a N-fixing forb, was unresponsive to nitrogen addition (Dunne *et al.* 2003).

1.6 Potential interactive effects of nitrogen and warming on plant productivity

As described above, both climate warming and nitrogen addition can increase plant productivity. Although the effects of warming and increased nitrogen deposition have been additive in some systems, such as California annual grasslands (Shaw *et al.* 2002), there is some evidence that climate warming over winter can accelerate ecosystem nitrogen losses in colder systems (Campbell *et al.* 2005). In particular, increased nitrogen mineralization at a time when plant roots may be largely inactive (Miller *et al.* 2007), coupled with changes to soil freezing dynamics, such as an increased frequency and intensity of freeze-thaw cycles (Isard and Schaetzl 1998; Groffman *et al.* 2001), may lead to increased nitrogen leaching predominately as NO_3^- (Fitzhugh *et al.* 2001; Yanai *et al.* 2004; Joseph and Henry 2008) and nitrogen trace-gas losses (Chen *et al.* 1995; Muller *et al.* 2002; Matzner and Borken 2008). Therefore, warming over winter may exacerbate

nitrogen limitation, which would decrease the response of primary productivity to warming in field experiments under current levels of nitrogen addition. In contrast, warmer temperatures in the future will be combined with increased nitrogen availability, and excess nitrogen may enable a much stronger plant-growth response to warming. Nevertheless, the effects of soil freeze-thaw cycles on soil nitrogen retention and plant-root damage have been quite variable among studies (Henry 2007). While the lysis of soil microbial cells and damage to fine roots can occur in response to severe freeze-thaw cycles (Tierney *et al.* 2001), in some cases an increased frequency of freeze-thaw cycles has contributed to an increase plant productivity over the following growing season (Kreyling *et al.* 2008).

1.7 Measuring plant productivity in long-term global change experiments

Although primary productivity is a useful integrative measure of ecosystem response to global change treatments, the estimation of this variable is not simple. In particular, the potential for temporal variation in annual peak biomass among species, coupled with biomass losses to seed set, decomposition of senesced tissues and herbivory often necessitates the use of multiple biomass estimates over the growing season to estimate annual productivity (Fahey and Knapp 2007). For long-term field experiments, destructive biomass harvests (the removal of all biomass from a sampling area) may not be practical. Numerous non-destructive methods for biomass estimation have been developed, including the pin-intercept method (Jonasson 1988) and the use of allometric equations to convert measurements of shoot height into shoot mass (Niklas 1994). Although these non-destructive methods are effective, they are also time consuming, and

a more rapid alternative is the use of spectral measures to estimate aboveground biomass at the plot level. The most broadly applied spectral index used to estimate plant biomass is the normalized difference vegetation index (NDVI) (Rouse *et al.* 1974), and this measure has been used to estimate grassland productivity (Gamon *et al.* 1995). NDVI integrates two spectral features of photosynthetic tissues: low reflectance in the red wavelengths and high reflectance in the infrared portions of the spectrum (Pineiro *et al.* 2006). Because NDVI is sensitive to the total chlorophyll content and fractional photosynthetic energy absorption of canopies (Choudhury 1987; Asrar *et al.* 1989; Myeni and Williams 1994), it serves as a reliable spatial and temporal indicator of canopy greenness, senescence, and phenology in grassland ecosystems (Goetz 1997; Tiezen *et al.* 1997; Huemmrich *et al.* 1999). It has proven to be a valuable tool in detecting and quantifying changes in plant and even ecosystem processes associated with climate change (Braswell *et al.* 1997).

Destructive root harvests do not necessarily provide a useful estimate of root productivity since root turover is high, and the peak biomass of roots may only represent 60% of annual root productivity (Robinson 2004). To provide a clearer measure of root production, images collected from rhizotrons are used. This method monitors root growth without being destructive (Jackson *et al.* 2001), and root systems can be monitored over time.

1.8 Objective and Hypothesis

My objective was to examine the interactive effects of climate warming and N deposition on plant productivity and species composition in a temperate old field. Warming treatments were applied all year round or during the winter (November to April) using overhead infrared heaters, resulting in an increase of 2-3 °C at the soil surface; and these treatments were crossed with a N addition treatment (6 g m^{-2} y^{-1}) in a split plot design. While the all-year warming treatment was applied to simulate projected warming scenarios for this region, the winter-only warming treatment was designed to isolate the effects of winter warming from the year-round warming effects.

I hypothesized that earlier snowmelt and a lengthening of the growing season would result in increased primary production is response to warming, and that N addition would also increase primary productivity. However, I predicted that these effects would be non-additive, based on the assumption that nitrogen limitation would intensify in plots experiencing warming over winter. I hypothesized that grasses would respond more strongly than forbs to the warming and nitrogen addition treatments, and finally that treatment effects on NDVI would correspond closely with effects on aboveground biomass.

CHAPTER TWO: MATERIALS AND METHODS

2.1 Site description

I conducted my research at an old-field site in London, Ontario, Canada (43° 01'

46" N, 81° 12' 52" W) between June 2007 and November 2008. The site was a former

agricultural field, and had not been ploughed, fertilized or mowed for over 20 years. The

soil was classified as a well to imperfectly drained silt loam glacial till (Hagerty and

Kingston 1992), and had an average pH of 7.5 (Terry Bell, unpublished data). The

vegetation at the site was dominated by the perennial grasses *Poa pratensis* L. (Kentucky

blue grass) and *Bromus inermis* Leyss. (smooth brome), while the forb *Cirsium arvense*

L. (Canada thistle) and the legume *Lotus corniculatus* L. (bird's-foot trefoil) were also

common, but patchy. The forbs *Asclepias syriaca* L. (common milkweed), *Aster*

ericoides L. var. *ericoides* (heath aster), and *Solidago canadensis* L. var. *scabra* Torr.&

A. Gray (tall goldenrod) also were present at lower density. The mean annual

temperature for the site is 7.5 ± 0.8 °C, with a low monthly mean of -6.3 ± 2.8 °C

(January) and a high monthly mean of 20.5 ± 1.1°C (July), and a mean annual

precipitation of 818 mm (Canadian Climate Normals 1971-2000, Environment Canada,

National Climate Data and Information Archive, The London International Airport).

2.2 Design of warming and N addition experiment

The field manipulations consisted of three warming treatments (warming all year, warming over winter only, and un-warmed control) crossed with two N treatments (added N and control) organized in a randomized block split-plot design (n=10), with warming administered at the plot level and N treatments assigned to two spatially-separated circular subplots within each plot (Fig. 2.1). In each treatment was a reserve plot, which was not used. Each of the 60 subplots was 113 cm in diameter and extended outwards by an additional 10 cm into a buffer zone that also received the experimental treatments. Plots were warmed by 150 W ceramic infrared heaters (Zoo-Med Laboratories, San Luis Obispo, CA, USA), suspended 50 cm above plot centers. These heaters simulated solar heating without giving off photosynthetically active radiation (Harte *et al.*1995). In the fertilized plots, we added a pulse of aqueous ammonium nitrate in late March at a rate of $2 \text{ g m}^{-2} \text{ y}^{-1}$, and in late May we added additional ammonium nitrate in the form of slow-release pellets (Florikan ESA, Sarasota, FL, USA) at a rate of $4 \text{ g m}^{-2} \text{ y}^{-1}$. These rates were designed to approximate projected increases in atmospheric deposition in this region by the year 2050 (Galloway *et al.* 2004). We began warming the plots in late November 2006, and we monitored the microclimatic effects on the soil using 107-BAM-L temperature probes at both 1 and 5 cm depth and CS616-L time-domain reflectometry probes (for estimating soil moisture) located at depths of 0-15 cm and 0-30 cm (both probes from Campbell Scientific Canada Corp., Edmonton, AB, Canada). All soil temperature and moisture data were recorded year-round, on an hourly basis (Fig. 2.2). We conducted winter warming treatments from 20 Nov. 2006 to 11 Apr. 2007, and again from 15 Nov. 2007 to 7 Apr. 2008. Both winters were approximately 2°C warmer than

recent climate normals and the second winter featured anomalously high precipitation

(Table 2.1). The growing season in 2007 was 1.4°C warmer than recent climate normals

and anomalously dry, whereas the mean temperature and precipitation over the 2008

growing season were closer to normal (Table 2.1). The temperature of the soil at 1 cm

depth in the warmed plots was raised by between 1 to 4 °C relative to ambient plots over

the snow-free season, whereas warmed plots sometimes reached colder temperatures than

ambient plots when the snow was melted in the former but the latter remained protected

by snow (Fig. 2.2).
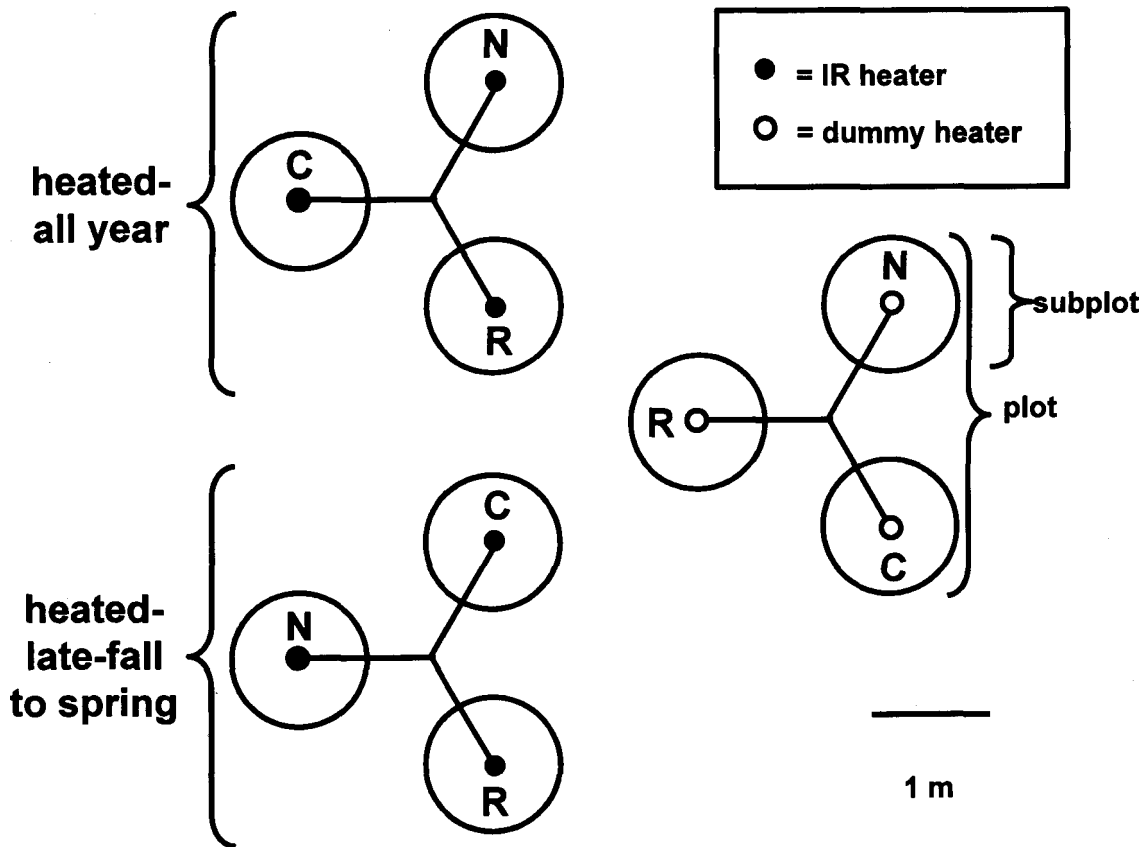
Figure 2.1 Experimental design showing 1 of 10 blocks. Groups of 3 heaters represent

plots, and are warmed year-round, during the winter only, or are exposed to ambient

temperatures with dummy heaters as controls. Subplots consist of those receiving N

additions (N), control (C), and reserve plots (R) which were not used.
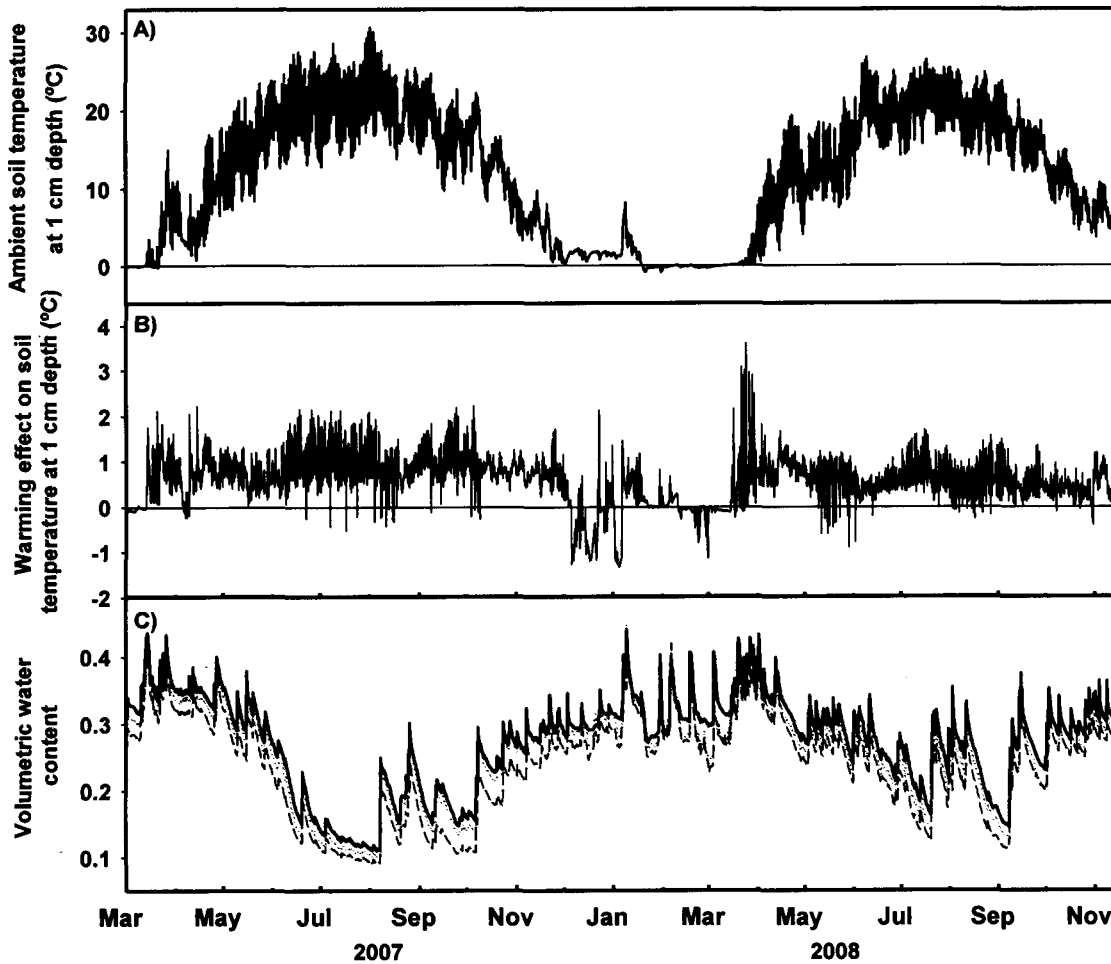
Figure 2.2 A) Soil temperature at 1 cm depth for ambient plots (n=20), B) the difference

in soil temperature between plots warmed year-round (n=20) and ambient plots (n=20)

and C) volumetric water content from plots warmed year-round (n=20)(dashed line),

winter warmed (n=20) (dotted line) and ambient plots (n=20) (solid line), all pooled over

N treatments over the course of the experiment.

Table 2.1. Mean temperature (±SD) and total precipitation over the 2006-2007 and 2007-2008 winters Nov. to 1 Apr.) and the 2007 and 2008 plant growing seasons (1 Apr. to 31 Oct.) for the experimental site relative to 1971-2000 climate normals (Environment Canada, National Climate Data and Information Archive).

	1971-2000	2007	2008
Mean winter temperature (°C)	-2.4 (3.9)	-0.9 (5.3)	-0.4 (3.0)
Total winter precipitation (mm)	392	364	568
Mean growing season temperature (°C)	14.5 (5.4)	15.9 (5.2)	15.1 (5.1)
Total growing season precipitation (mm)	595	373	489

2.3 Plant productivity estimates

In 2007, I estimated aboveground biomass for each species on 7 Aug. and 18 Oct. from a 10 cm × 10 cm quadrat in each subplot of the experiment. For the grasses, I counted the number of tillers within the quadrat and recorded their heights. I recorded the number and height of inflorescences separately. I collected approximately 30 tillers and inflorescences of each grass, selecting from a wide range of heights, outside of the experimental plots on each sampling date, dried the samples at 70 °C for at least 48 h, then weighed them. I then plotted the logarithm of mass against height for each sampling date and fit a regression line to describe the shoot mass to height allometry (*B. inermis*, mean $r^2 = 0.82$; *P. pratensis*, mean $r^2 = 0.76$). I used these equations to estimate the aboveground biomasses of the tillers and inflorescences in the quadrats. I also estimated percent cover for each plant species within each quadrat. I used a similar sampling method in 2008, with the exception that aboveground biomass was estimated monthly (Apr. through Oct.) from permanent 113 cm^2 rings established in each subplot. In addition, given that the forbs were rarely present in the sampling quadrats in 2007, percent cover for each forb species was estimated for the entire subplot.

Given that there was little evidence of herbivory on the grasses at the site, I used aboveground biomass measures to estimate aboveground productivity. The grass *B. inermis* exhibited two clear phases of growth and senescence over fall. Therefore, I estimated productivity in this species by adding the mid-summer peak in leaf and inflorescence biomass to the late fall biomass estimates. For *P. pratensis*, which experienced leaf senescence over summer and fall more uniformly at our site, I counted

and measured all leaves (green and senesced) at each sampling point, and carried over inflorescence biomass values to all dates following seed set.

To estimate root biomass, I sampled soils from each subplot using a 2 cm diameter × 15 cm deep corer on 6 Nov., 2007 and 22 Apr. and 11 Jul. 2008. I also collected a subset of thirty samples from 15 cm to 30 depth on 6 Nov., 2007, but discontinued these measures for the later sampling dates based on their low biomass relative to the roots in the top 15 cm of soil (< 5%). I soaked the soil cores in water and separated the roots from the soil particles using a 35 mesh sieve (0.5 mm openings), then dried them at 70 °C for at least 48 h. Given the potentially high turnover rate of roots in soil (Robinson 2004), I made no effort to estimate root productivity from the biomass measures.

2.4 NDVI sampling

I used a portable spectrophotometer (FieldSpec Handheld, Analytical Spectral Devices, Boulder, CO, U.S.A.) to obtain weekly measures (weather permitting) of the normalized difference vegetation index (NDVI) from each plot from spring melt through to the first snowfall. I performed spectral measures on cloudless days when the wind speed was not sufficient to sway the plant shoots, within one hour of noon. Each recorded spectrum was the mean of ten spectra obtained with the fibre optic suspended 1 m above the soil, using a 20° field of view foreoptic, to give a 30 cm diameter circle of view. I calculated NDVI as (NIR-RED)/(NIR+RED), with NIR (near infrared)= the average reflectance from 720 - 740 nm and RED (visible red) = the average reflectance from 660 - 680 nm.

2.5 Statistical analyses

For analyzing treatment effects on the dependent variables, I used a randomized block split-plot ANOVA that included warming as a fixed between-plot factor, nitrogen addition as a fixed within-plot factor, the interaction term for their treatment combination and block number as a random factor. To account for repeated measures of the subplots, I also added date as a fixed factor, along with all treatment interactions with date, and subplot as a random factor. Error terms for significance tests were as specified in Kirk (1995) and I ran the analyses using the REML method of the Fit Model platform in JMP 4.0 (SAS Institute Inc., Cary, NC, USA). Biomass data were log-transformed prior to analysis to satisfy the assumptions of normality and homogeneity of variances. For the NDVI data, I performed repeated-measures analysis within each of the main plant growth phases (1. green-up and early-season growth, 2. peak green biomass, and 3. senescence; phases separated by dotted lines in Fig. 3.6), since the relative contributions of the main factors driving the NDVI values (leaf cover vs. leaf greenness) varied across the summer.

CHAPTER THREE: RESULTS

3.1 Productivity and cover estimates

In 2007, there were no significant effects of warming or N deposition on aboveground productivity (P_N=0.74, P_W=0.87 and $P_{W \times N}$=0.94) or root biomass (P_N=0.87, P_W=0.74 and $P_{W \times N}$=0.10). Averaged across all plots, aboveground productivity and root biomass were 707 ± 51 g m^{-2} (*B. inermis* - 553 ± 59 g m^{-2}; *P. pratensis* - 133 ± 10 g m^{-2}) and 77 ± 6 g m^{-2} (*B. inermis* and *P. pratensis*), respectively. However, in 2008, both warming and nitrogen addition increased aboveground productivity significantly (P_W=0.015 and $P_{N \times D}$=0.002; Fig. 3.1), and the lack of a significant interaction ($P_{W \times N}$=0.23) indicated their effects were additive (a summary of all ANOVA P-values for 2008 is provided in Table 3.1). Aboveground productivity in both winter and year-round warmed plots was significantly higher than in ambient plots but there was no significant difference between the two warming treatments (Tukey's HSD test). The aboveground productivity of *B. inermis* also increased significantly in response to both warming and nitrogen addition ($P_{W \times D}$=0.046 and $P_{N \times D}$<0.001; Fig. 3.2), and there was no significant difference between winter and year-round warming (Tukey's HSD test). The aboveground productivity of *P. pratensis* increased significantly in response to nitrogen addition (P_N=0.028; Fig. 3.3) but not warming. Percent cover of *C. arvense* was significantly higher in ambient and winter-warmed plots than in year-round warmed plots (P_W=0.027; Fig. 3.4A) and the opposite trend was marginally significant for *L. corniculatus* (P_W=0.056; Fig. 3.4B) (Table 3.2). Root mass (all species) in 2008 was

significantly higher in winter and year-round warmed plots than in ambient plots

(P_W=0.045) in both April (warmed, 62 ± 7 g m^{-2}; ambient, 46 ± 3 g m^{-2}) and July

(warmed, 70 ± 3 g m^{-2}; ambient, 55 ± 3 g m^{-2})
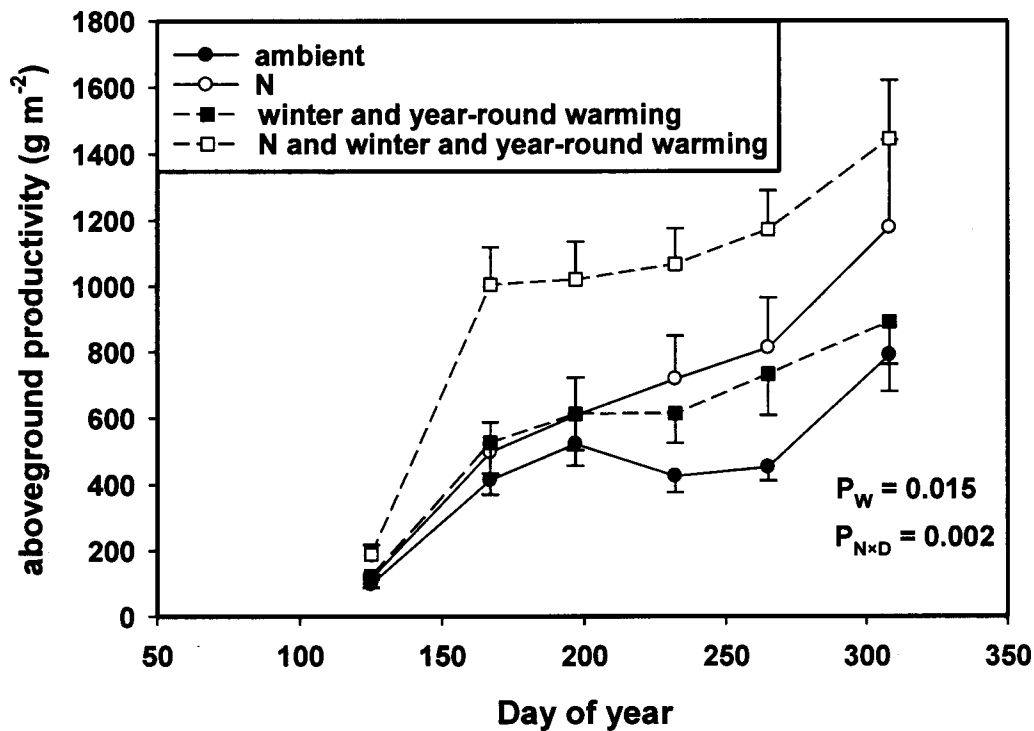
Figure 3.1 Total aboveground productivity over the 2008 growing season for ambient

temperature plots (n=10), nitrogen addition plots (n=10), both warming treatments pooled

(n=20) and nitrogen additions with both warming treatments pooled (n=20). Error bars

denote standard errors. Associated significance tests are shown in Table 3.1.

Table 3.1. Summary of ANOVA P-values for effects of treatment and date on plant productivity estimates.

Effect	2007				2008			
	Aboveground productivity			Root mass	Aboveground productivity			Root mass
	Total	*P. pratensis*	*B. inermis*	(all species)	Total	*P. pratensis*	*B. inermis*	(all species)
W	0.722	0.564	0.688	0.872	0.015*	0.444	0.014*	0.045*
N	0.913	0.647	0.955	0.742	0.001**	0.028*	0.005**	0.615
D	0.003**	<0.001***	0.055	-	<0.001***	<0.001***	<0.001***	<0.001***
W×N	0.767	0.307	0.825	0.096	0.231	0.695	0.258	0.328
W×D	0.934	0.873	0.951	-	0.060	0.323	0.046*	0.991
N×D	0.736	0.614	0.965	-	0.002**	0.301	<0.001***	0.883
W×N×D	0.493	0.120	0.228	-	0.209	0.414	0.274	0.687

W - warming; N - Nitrogen; D - Date. Asterisks denote significance (*0.05-0.01,**0.01-0.001,***<0.001).

Figure 3.2 Aboveground productivity of *Bromus inermis* over the 2008 growing season

for ambient temperature plots (n=10), nitrogen addition plots (n=10), both warming

treatments pooled (n=20) and nitrogen additions with both warming treatments pooled

(n=20). Error bars denote standard errors. Associated significance tests are shown in

Table 3.1.
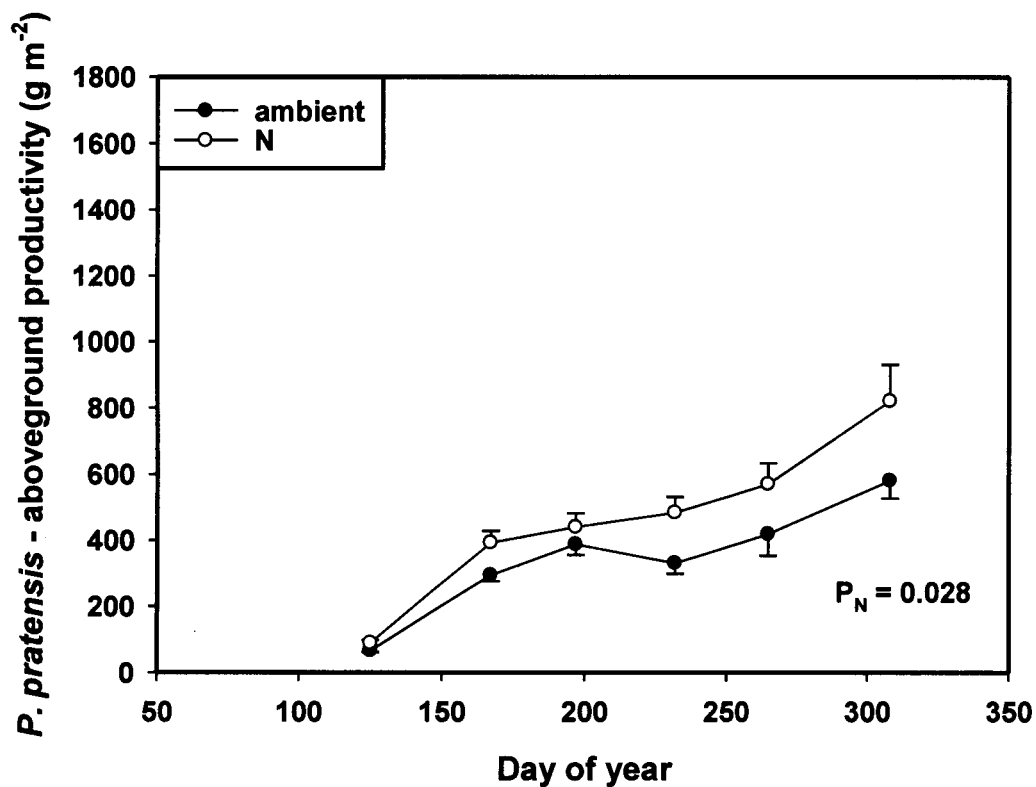
Figure 3.3 Aboveground productivity responses of *Poa pratensis* over the 2008 growing season for ambient nitrogen plots (n=30) and nitrogen addition plots (n=30), pooled over warming treatments. Error bars denote standard error. Associated significance tests are shown in Table 3.1.
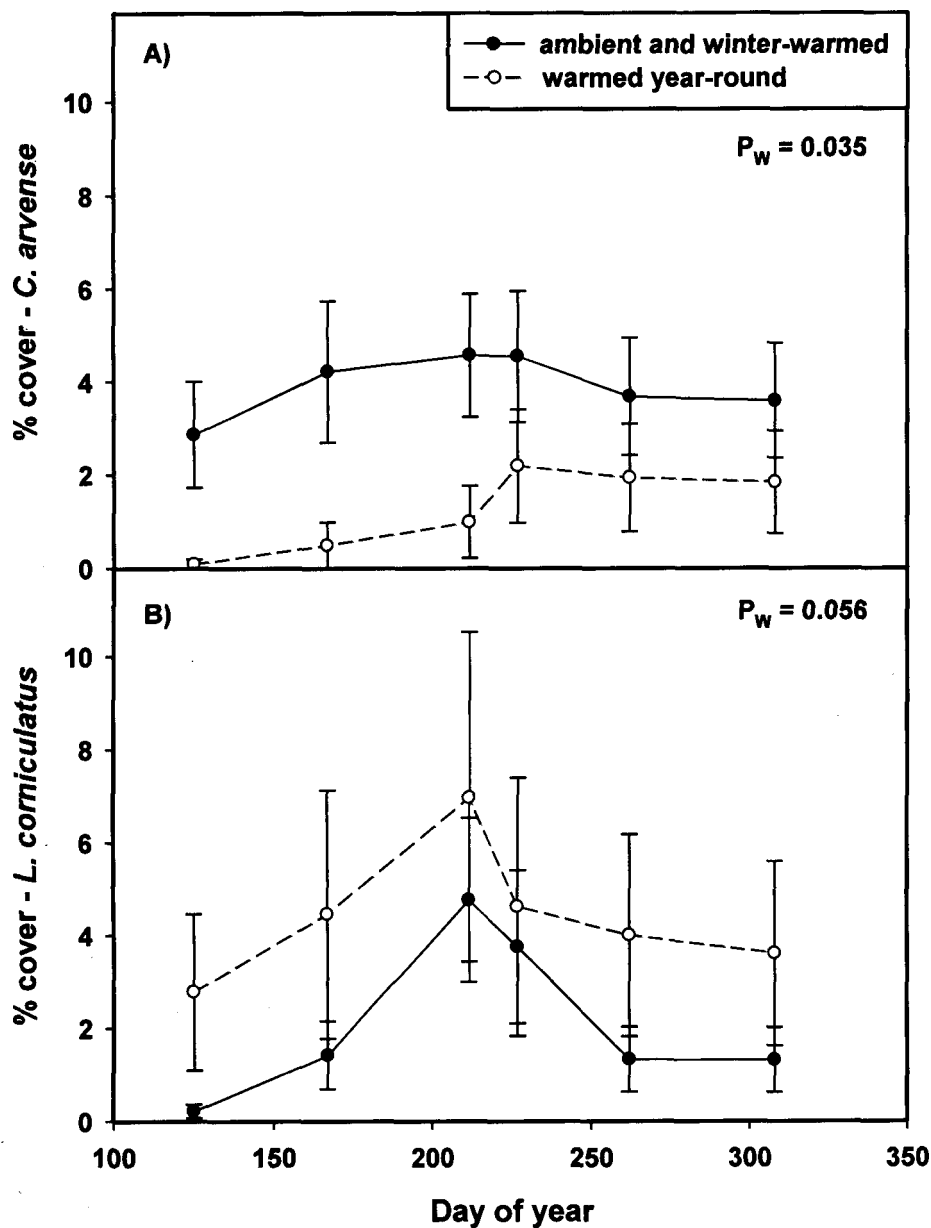
Figure 3.4 Percent cover of A) *Cirsium arvense* and B) *Lotus corniculatus* over the 2008

growing season for ambient and winter-warmed plots (n=40) compared to all-year

warming plots (n=20), pooled over nitrogen additions. Error bars denote standard errors.

Associated significance tests are shown in Table 3.2.

Table 3.2. Summary of ANOVA P-values for effects of treatment and date on plant cover.

Effect	*C. arvense*	*L. corniculatus*
W	0.035*	0.056
N	0.396	0.510
D	0.108	<0.001***
W×N	0.851	0.426
W×D	0.545	0.744
N×D	0.348	0.972
W×N×D	0.808	0.597

W - warming; N - Nitrogen; D - Date.

Asterisks denote significance (*0.05-0.01,**0.01-0.001,***<0.001).

3.2 NDVI (Normalized difference vegetation index)

In 2007, there were no significant treatment effects on NDVI at mid-summer when there was a peak in green biomass, although added nitrogen significantly increased NDVI relative to N control plots over the late-summer and fall sampling dates (P_N=0.038; Fig. 3.5; Table 3.3). In 2008, N addition significantly increased NDVI during the early season growth and peak green biomass phases (P_N=0.0138 and P_N=0.021, respectively), but not over the late-summer and fall sampling dates (Fig. 3.6; Table 3.3). Overall, increases in NDVI in response to N were proportionally smaller than increases in aboveground biomass (comparison of Figs. 3.1 and 3.5).
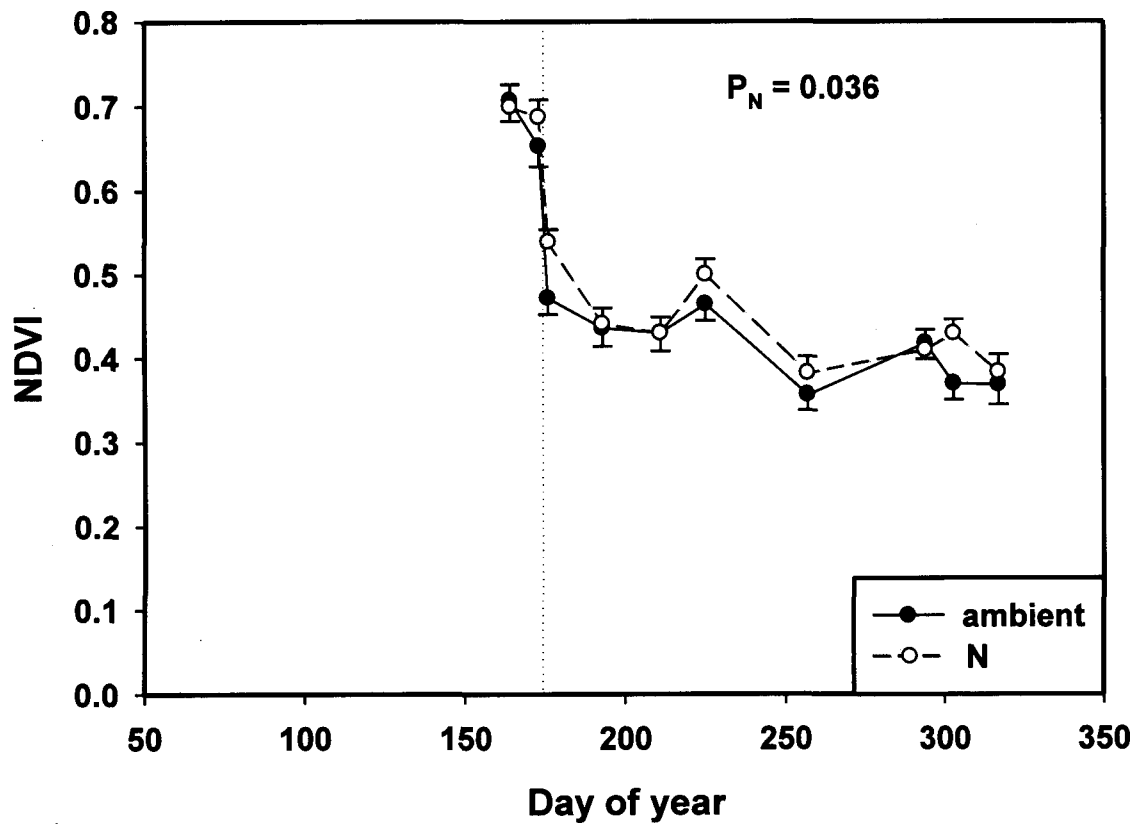
Figure 3.5 NDVI trends over the 2007 growing season in response to nitrogen pooled over warming treatments (n=30) compared with ambient plots (n=30). Error bars denote standard errors. Associated significance tests are shown in Table 3.3.

Table 3.3. Summary of ANOVA P-values for effects of treatment and date on NDVI.

	2007		2008		
Effect	13 Jun-22 Jun	25 Jun-13 Nov	3 Apr-12 May	25 May-25 Jun	4 Jul-4 Nov
W	0.906	0.696	0.726	0.199	0.288
N	0.509	0.036*	0.026*	0.042*	0.725
D	0.054	<0.001***	<0.001***	<0.001***	<0.001***
W×N	0.736	0.814	0.502	0.649	0.566
W×D	0.791	0.787	0.254	0.499	0.102
N×D	0.214	0.321	0.022*	0.959	0.758
W×N×D	0.636	0.853	0.367	0.515	0.894

W - warming; N - Nitrogen; D - Date. Asterisks denote significance (*0.05-0.01,**0.01-0.001,***<0.001).
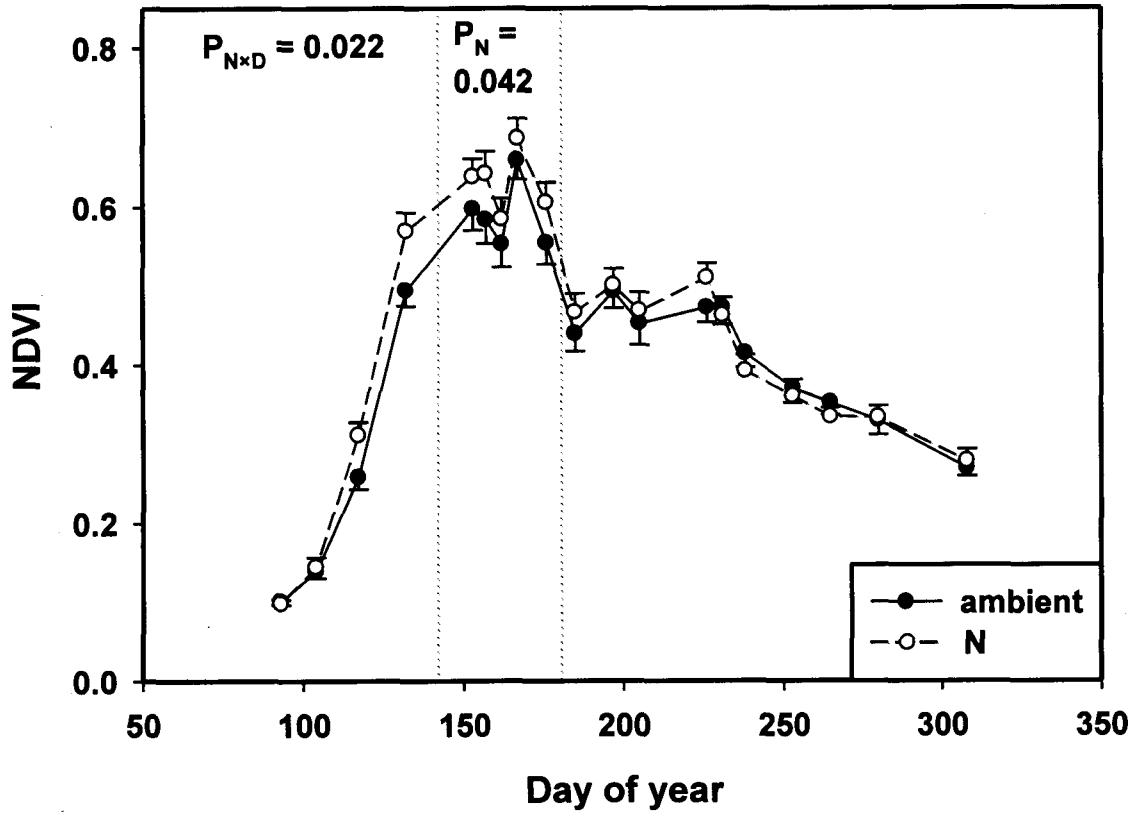
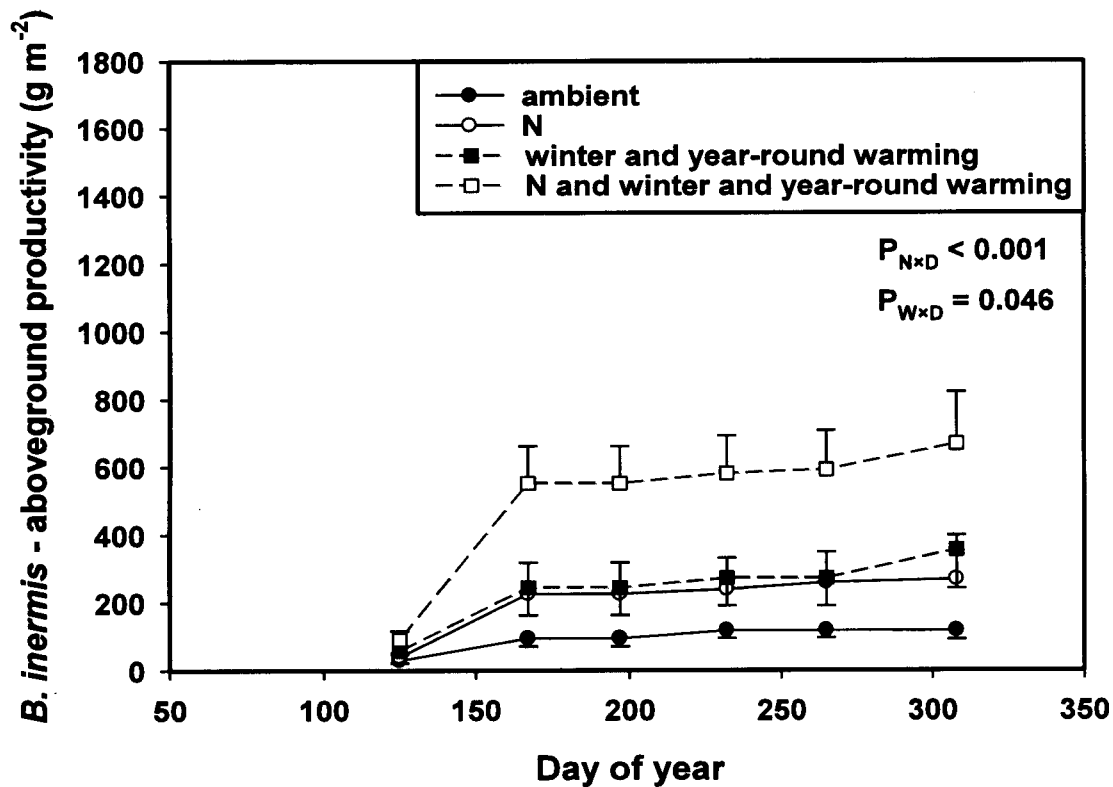**Figure 3.6** NDVI trends over the 2008 growing season in response to nitrogen pooled

over warming treatments (n=30) compared with ambient plots (n=30). Phases separate by

dotted lines 1. green-up and early-season growth, 2. peak green biomass, and 3.

senescence. Error bars denote standard errors. Associated significance tests are shown in

Table 3.3.

CHAPTER FOUR: DISCUSSION AND CONCLUSIONS

4.1 Interactive effects of warming and nitrogen on productivity

Overall, the differences in treatment effects on plant productivity between the

2007 and 2008 growing seasons, which differed substantially in water availability over

summer, demonstrated a large potential for interactions among climate warming, nitrogen

deposition and precipitation. Such large interannual variation in treatment effects is

consistent with the results observed in long-term global-change field experiments (e.g.

Dukes *et al.* 2005; Harte and Shaw 1995; Marion *et al.* 1997; Saleska *et al.* 1999). The

2007 growing season was not useful for exploring potential interactions among warming

and nitrogen addition since neither of these treatments had any significant effect on plant

growth over that summer. Although the effects of low precipitation on soil moisture can

be exacerbated by warming (Ciais *et al.* 2005), the effects of warming on soil moisture

were small relative to the seasonal variation in soil moisture in our system (Fig. 2.2).

Nevertheless, in 2008, when plant productivity increased substantially in response to both

warming and nitrogen addition, the lack of a significant interaction between these factors

indicated that, contrary to my prediction, the warming effect on primary productivity was

not diminished as a result of nitrogen losses over winter, as I had predicted. On the

contrary, the increase in biomass in response to winter-only warming was equal to that

for year-round warming, which indicates that the earlier start to the growing season

afforded by a warmer winter was primarily responsible for the overall warming effect.

The lack of an interactive effect between warming and nitrogen addition on

primary productivity is consistent with a nitrogen tracer study conducted simultaneously

in the experimental plots (Turner and Henry 2009). The latter study indicated that

nitrogen losses were not enhanced by warming over the previous winter, despite an

increase in the frequency of freeze-thaw cycles in response to warming. Furthermore, the

severity of soil freeze-thaw cycles did not increase substantially in response to warming

(minimum soil temperatures only reached -2 °C at 1 cm depth; Fig. 2.2), and laboratory

incubations of soils collected adjacent to the experimental plots revealed that soil

nitrogen is only released when these soils are frozen to -10 °C or more (Elliott and Henry

2009). Therefore, changes to soil freezing dynamics in response to warming do not

appear to increase soil nitrogen losses over winter in this system. This finding contrasts

with the results of studies that have shown strong freeze-thaw cycle effects on soil

nitrogen losses (Wang and Bettany 1994; Sulkava and Huhta 2003) but is consistent with

others that have shown no freeze-thaw cycle effects (Grogan *et al.* 2004; Sjursen *et al.*

2005). The main factor that appears to explain the variation in results among these studies

is the severity of freeze-thaw cycles that are administered, with a large freeze-thaw cycle

effect only reported in response to extreme freeze-thaw cycle amplitudes (Henry 2007).

While freeze-thaw cycles can reduce root growth over the following growing

season (Kreyling *et al.* 2008), I instead observed increased root biomass in response to

warming in 2008, which provides further evidence that soil freeze-thaw effects are mild

in this system. As with aboveground biomass, root biomass increased equally in response

to both winter-only and year-round warming, which indicates that an earlier start to the

growing season was responsible for increased root biomass over the summer. Although

root biomass did not increase in response to N addition, the large increase in aboveground

production in response to N addition decreased the overall root:shoot ratio, which is a

common plant response to N addition in N limited-systems (Agren and Ingestad 1987). Given that I did not examine root turnover, my root biomass measures could not provide an accurate estimate of root productivity (Stewart and Frank 2008). However, aboveground biomass was an order of magnitude greater than belowground biomass. Therefore, despite my root biomass measures providing an underestimate of root productivity, the latter appears to be a minor contributor to total primary productivity at the study site.

In contrast to the roots, my sampling design for aboveground biomass allowed me to account for turnover and estimate aboveground productivity. For *B. inermis*, the two clear growth phases, defined by senescence in both mid-summer and late fall, made it easy to account for losses of aboveground biomass to seed set and leaf senescence over the second half of the growing season. Although the same approach was used for *P. pratensis*, more continuous leaf turnover coupled with a very high density of small tillers made it more difficult to account for all leaf losses to senesence, which may explain the small drop in estimated productivity from the third to the fourth sampling dates. Likewise, herbivory by meadow voles and slugs on *P. pratensis* (Getz 1959; Lindroth and Batzli 1984), while not visibly obvious, may have contributed to biomass losses at this time. These losses would not bias the relative treatment effects on productivity, provided that herbivore pressure is not strongly affected by the treatments. I did not observe any differences among plants of the same species in different treatments, such as leaf morphology, fungal or microbial disease.

While changes in relative plant abundance may be difficult to assess over the time scale of two years in a system dominated by perennial species, my results suggest an

increased dominance by grasses in response to the combined effects of warming and nitrogen deposition, since none of the forb species increased in response to nitrogen, and the responses of forbs to warming were mixed. Community response to nutrient addition depends on the differential responses of grasses and legumes (Grunzweig and Korner 2003). Consistent with functional groups responding differently to nutrient addition, legume growth can be suppressed with increased nitrogen because of competition from grasses; however, forb response differed with some species being unresponsive to nutrient addition (Grunzweig and Korner 2003). Declines in *C. arvense* cover in response to warming contrasted with the trend of increasing *L. corniculatus* cover in these plots, which suggests that warming may have altered the competitive balance among these forbs. Over the longer term, increased grass biomass in response to the combined effects of warming and nitrogen deposition could delay the establishment and growth of tree and shrub seedlings at this old field site (Davis *et al.* 1998). Nutrient addition usually leads to the replacement of species that are fast growing with high nutrient losses (Aerts 1999).

4.2 Treatment effects on NDVI

Contrary to my hypothesis, treatment effects on NDVI did not correspond closely with effects on aboveground biomass, particularly in 2008, when the latter were pronounced. Although NDVI has correlated closely with vegetation biomass elsewhere (Running 1990; Myeni *et al.* 1997; Birky 2001), the results of the latter study were obtained from temperate deciduous forests at a larger spatial scale than in my study. At my site, the relatively uniform grass cover, coupled with the upright orientation of grass

shoots and leaves, may have largely decoupled grass biomass from overhead measures of NDVI (e.g. taller grasses may not look substantially greener than shorter grasses when viewed from above). In addition, NDVI values may have saturated at a relatively low aboveground biomass such that the large treatment effects on aboveground biomass by mid summer could not be discerned. N addition resulted in a small but significant increase in NDVI in both 2007 and 2008, which may have indicated increased leaf greenness with increased tissue nitrogen content. Richardson *et al.* (2002) concluded that spectral measures provide reliable estimates of leaf chlorophyll.

Despite any weakness of NDVI to capture treatment differences in aboveground biomass, it appears that this measure successfully captured leaf senescence over late summer and fall. Nevertheless, there were no effects of warming on late-season NDVI in either 2007 or 2008. This result contrasts with the result of studies that have demonstrated delayed fall senescence in response to warming (Wather *et al.* 2002; Parmesan and Yohe 2003; Sherry *et al.* 2006) and those where warming-induced reductions in soil moisture have resulted in the opposite effect (Dunne *et al.* 2003, Zavaleta *et al.* 2003). Increased late-summer NDVI indicated a potential delay in senescence in nitrogen-addition plots in 2007 but this effect was not significant in 2008. Nitrogen availability can decrease the rate of leaf senescence (Guitman *et al.* 1991) if nitrogen demand does not exceed the supply. However, studies on leaf lifespan have found contradicting results with an increase (Shaver and Chapin 1995), decrease (Aerts 2009), or no effect at all (Aerts 1989).

4.3 Potential limitations

One of the potential limitations of my productivity estimates throughout the growing season was the loss of biomass to herbivory by snails, slug, meadow voles, insects, nematodes and microorganisms. In addition to the effects of herbivory on aboveground production (Cargill and Jefferies 1984), detritivores may impact soil development and remove aboveground litter, increasing light penetration to the soil surface and promoting seedling growth. It was not clear to what extent the warming and nitrogen treatments may have attracted or repelled herbivores or detritivores from the plots, either directly or indirectly. Furthermore, not all plant species were represented evenly among plots, such that the effects of the treatments on the less common forbs at the site was difficult to assess due to a very limited flora in the areas.

Increased allocation to roots occurs when a lack of water and nutrients limit plant growth (Stulen and den Hertog, 1993). I measured root responses destructively only twice in one growing season, and more frequent harvests may be required to detect changes in belowground production because of the high turnover rate or roots (Garwood 1967). To measure root turnover and measure root length non-destructively and more accurately, mini-rhizotrons could have been used (Murphy *et al.* 1994).

NDVI has been used to describe phenological changes in vegetation at large scales (Birky 2001; Moody and Johnson 2001) using satellite-derived NDVI. My values seemed to reach a peak value, and increasing amounts of green vegetation made little difference in NDVI. Similarly, in a study conducted by Stellers (1987), canopy density reached a peak value ~ 0.7 regardless of any new green vegetation. The fertilized plots

in my study were greener than unfertilized plots, which may have been driven by changes in plant greenness at the leaf level, not an increase in plant biomass.

4.4 Directions for future research

Warming and nitrogen both have a positive effect on plant growth over the short-term; however, there have been studies where lag times in treatment effects on systems occurred (Chapin *et al.* 1995). In particular, in a system dominated by perennial plants it may take longer for large changes in species composition to occur. In a global change context, interspecific variation in competitive abilities and seed dispersal could result in substantial changes plant community composition at this site over the next decades or century, yet my experiment was restricted to testing a present day community in the context of future plant growth conditions. In particular, it would be valuable to explore the extent to which global change might facilitate the establishment and dominance of invasive species (Dukes and Mooney 1999). In addition, other important global-change factors such as increased atmospheric carbon dioxide concentrations may interact with climate warming and increased atmospheric nitrogen deposition (Shaw *et al.* 2002).

Cumulative changes in site conditions in response to experimental treatments could also affect the productivity response over time. For example, productivity responses to nitrogen often diminish over time when nitrogen saturation occurs (Agren and Bosatta 1988). The buildup of plant litter and soil carbon in response to increased plant productivity could also feed back on plant growth, although the decomposition of this organic matter would also be affected directly by the warming and nitrogen treatments (Rustad *et al.* 2001; Hobbie *et al.* 2002; Allison *et al.* 2009).

The generality of my experiment is also limited with respect to the levels of warming and nitrogen that were imposed. My data do not provide information on the linearity of productivity responses to warming, yet clearly more extreme warming could be detrimental for plant growth, particularly if it exacerbated water stress. Likewise, more extreme climate variability in the form of extreme heat waves, droughts and mid-winter melts is predicted by climate models (IPCC 2007), and their effects could differ considerably from those caused by a mean increase in temperatures.

4.5 Conclusions

Both nitrogen addition and an earlier start to the growing season caused by warming increased plant productivity and there were no interactive effects between warming and nitrogen addition on aboveground productivity. These results are consistent with the results of parallel studies at my site, which indicated that winter warming does not seem to increase soil nutrient losses or root damage in this system. In addition, although NDVI may be a valuable tool for monitoring plant growth in the early growing season and leaf senescence at the end of the growing season, it was not a useful tool for inferring treatment effects on aboveground productivity in our experiment.

CHAPTER FIVE: RESEARCH FINDINDINGS

5.1 Research findings

My study explored biomass production both above and below ground, as well as species composition, and how these were affected by warming and nitrogen deposition over the course of two growing seasons. There were no effects of either warming or nitrogen on plant productivity in 2007, likely due to low precipitation and low soil water content, which often limit growth responses of grasses (Chaves *et al.* 2002). Aboveground productivity increased the following year in response to both warming and nitrogen. Warming may have slightly decreased soil water content; nevertheless this was not significant enough to decrease productivity. Contrary to my hypothesis, productivity does not appear to be diminished by changes in soil freezing dynamics over winter in response to warming, nor are were there effects of warming on soil nitrogen dynamics over this season (Turner and Henry 2009). Likewise, although root-freezing damage in response to freeze-thaw cycles can reduce plant growth over the following growing season (Coursolle *et al.* 2002), there was no evidence for decreased root biomass in response to winter warming, which was likely due to the low severity of freeze-thaw cycles at this site. Overall, the increase in aboveground biomass in response to warming and nitrogen was particularly interesting since the effects of warming with nitrogen appear to be additive, which suggests a strong increase in the productivity of grasslands in this region over the next century. However, the increased biomass in response to both warming treatments suggests that an earlier start to the growing season was responsible

for this increase, rather than an increase in the mean air temperature over summer. To facilitate the estimation of aboveground biomass, I took weekly spectroradiometer reading from the subplots, yet there was no clear link between the treatments effects on aboveground productivity and NDVI, which responded only slightly to nitrogen addition.

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